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ARTICLE

Salt Marsh Carbon Pool Distribution in a Mid-Atlantic Lagoon, USA: Sea Level Rise Implications

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Abstract The distribution of carbon (C) within a salt marsh may vary among vegetation zones depending on production and decomposition dynamics and organic and mineral depositional history. We examined spatial and temporal variation of plant and soil C pools within a salt marsh fringing a coastal lagoon along the mid-Atlantic coast of the U.S. The total plant C pool increased from high marsh shrub to low marsh grass dominated areas. Much of the spatial variation in plant C pool was due to fine roots and small organic matter (dlm) that could not be identified by species, which averaged 2398 gC m^{-2} in *Spartina patens*-dominated, 2215 gC m^{-2} in *Spartina alterniflora*-dominated, and 676 gC m^{-2} in *Juncus roemerianus*-dominated areas. Belowground C pool loss was 36% less for *S. patens* than *S. alterniflora* and was similar between *S. alterniflora* and *J. roemerianus*. Accretion and C accumulation rates were greater in the *S. alterniflora*-dominated stand than in the *J. roemerianus*-dominated stand. Our results suggest that landward migration onto terrestrial soils can lead to an estimated 80% increase in belowground plant C composed primarily of fine roots and dlm and 36–70% increase in soil carbon between 15 and 30 cm depths.

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Introduction

Salt marshes have some of the highest rates of carbon (C) storage of any ecosystem. Globally, the average C accumulation rate in salt marsh soils is 210 g CO_2 m^{-2} yr^{-1} (Chmura et al. 2003). The production and decomposition of fixed C of wetland macrophytes largely influences C-cycling in salt marshes. Fixed C may be released as CO_2 by microorganisms during decomposition or stored belowground where anaerobic decomposition occurs slowly and recalcitrant C may remain for millennia (Orson et al. 1987, van de Plassche et al. 2001). Because the majority of the fixed carbon belowground originates primarily from *in situ* macrophyte production (Gallagher 1974; Valiela et al. 1976), salt marsh plants play an important role in the flux of greenhouse gases such as CO_2 and the storage of C in wetland soils.

Species that occupy different marsh zones may differ in their C pool dynamics associated with differences in the seasonal quantity and allocation of biomass, turnover rates, and loss through decomposition (Gallagher and Plumley 1979; Schubauer and Hopkinson 1984; Neves et al. 2007). The processes that determine the fate of aboveground and belowground production such as microbial decay, export, and burial influence carbon budgets at the ecosystem level. Because much of the aboveground litter remains in the wetland and is not exported to coastal waters (Dame and Stilwell 1984; Bouchard and Lefeuvre 2000), mechanical breakdown and decomposition *in situ* are important processes. Whereas the contribution of aboveground litter to soil organic matter pools has not been established, belowground produc-

tion of roots and rhizomes has been shown to be highly variable and differ significantly among species (Good et al. 1982; Roman and Daiber 1984; Connor and Chmura 2000).

Different rates of belowground organic production, decomposition, and burial among plant communities will influence the concentration and accumulation of soil C in wetlands. Increasingly, studies have focused on the processes that influence soil C accumulation (Connor et al. 2001; Chmura et al. 2003; Craft 2007) and species effects on soil carbon storage (Rothman and Bouchard 2007; Mahaney et al. 2008) and marsh accretion (Rooth et al. 2003). Primary production (Blum 1993) and decomposition (Craft 2007; Rothman and Bouchard 2007) have both been suggested to be the predominant biotic process regulating soil carbon content and accumulation. There is significant spatial variability in soil C accumulation in wetlands, which has been associated with differences in sediment deposition rate (Khan and Brush 1994; Chmura et al. 2003), but the nature of C burial is not fully understood.

Relative sea level rise may alter the distribution and quantity of carbon within coastal wetlands, altering the relative proportion of plant zones, causing species shifts and landward migration, and contributing to the direct loss of wetland area. Species shifts in response to relative sea level rise may cause lower marsh species to replace upper marsh species as the wetland moves landward (Kraft et al. 1992; Warren and Niering 1993; Donnelly and Bertness 2001). The consequences of species shifts on salt marsh C pools are poorly understood. A shift from a C_4-dominated community (e.g., *Spartina alterniflora* or *Spartina patens*) to a C_3-*Juncus roemerianus* dominated community in a Florida salt marsh was associated with a decline in belowground C sequestration (Choi et al. 2001), but the mechanisms resulting in this reduction are not clear.

The goal of this study was to examine some of the factors that may influence the distribution of plant and soil C among different salt marsh plant communities. We examined potential differences in C distribution among plant zones and plant processes (production and decomposition), along with an estimate of sediment accumulation to assess how species shifts and landward migration may influence the quantity and distribution of C pools as the relative sea level rises. Carbon pool was defined as the C inventory (mass per area). We measured the seasonal aboveground and belowground plant C pools and aboveground and belowground C pool loss through decomposition for four dominant plant species representing four vegetation zones from the seaward edge to the terrestrial border, seasonal soil properties (bulk density, % organic matter, and % organic C) within each zone, and the rates of organic and mineral matter accumulation and accretion in the low and high marsh plant communities.

Methods

Site Description

The study area was a natural marsh along the northern border of Little Assawoman Bay, a coastal lagoon, between Bethany Beach, Delaware and Ocean City, Maryland, USA (Fig. 1). Salt water from the Atlantic Ocean enters the bay through the Assawoman Canal, constructed in the 1890's,

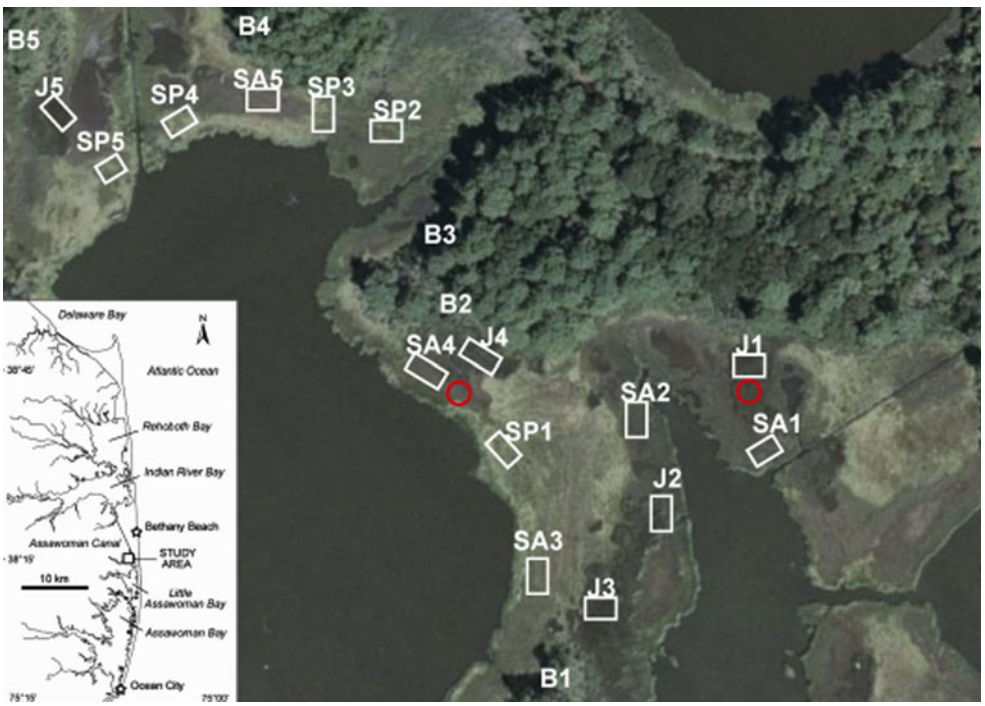

Fig. 1 The study area in a natural salt marsh fringing the northern border of Little Assawoman Bay, Delaware, USA (38°25′ N, 75°04′ W). Stands of *Baccharis halimifolia* ('B'), *Juncus roemerianus* ('J'), *Spartina patens* ('SP'), and *Spartina alterniflora* ('SA') are shown and the locations of two soil cores collected for radionuclide analysis are represented by circles

which connects Little Assawoman Bay to Indian River Bay, approximately 6 km to the north. Drainage occurs through a narrow strait into Assawoman Bay to the south. The back bays have limited drainage and are subject to high water levels during prolonged periods of onshore flow. They have an average low-water depth of about 1 to 3 m (Horsley & Witten 1998). Wetlands along Little Assawoman Bay eroded at a rate of approximately 0.8 m yr^{-1} from 1929 to 1977 (Kraft et al. 1992).

The wetland area over the study period (2005–2006) was characterized by open water, tidal creeks, mosquito ditches, and hummocks covered by pine trees and fringed by high marsh shrubs. The plant community was a mosaic, which consisted of patches of medium-form *Spartina alterniflora* and *Spartina patens* along the shoreline, short-form *S. alterniflora* in the low marsh, a mixed community of *S. patens* and *Distichlis spicata* in the mid-marsh, and patches of *J. roemerianus* in the mid-to-high marsh just seaward of the shrub community, which was dominated by *Iva frutescens* and *Baccharis halimifolia*. We chose to examine the C pools of four of the dominant species from each zone, *B. halimifolia*, *J. roemerianus*, *S. patens*, and *S. alterniflora*, as well as soil C pools in areas dominated by the four species.

The four species differ in morphology. *Baccharis halimifolia* is a deciduous multi-stemmed shrub that ranges in height from 1.5 to 4.5 m and width from 1.5 to 2.1 m with alternate simple coarsely serrated leaves, 2.5 to 7.5 cm length (Silberhorn 1982). *Juncus roemerianus* is a perennial rush growing in dense stands of nearly uniform height of 0.6–1.5 m. The stems (cylindrical leaf blades) are stiff, coarse and outwardly simple with the tip ending in a sharp point (Silberhorn 1982). *Spartina patens* is a perennial fine wiry grass species that appears collectively as a densely matted patch of meadow. It stands from 0.4 to 1.5 m tall with the long tapering leaves rolled inward and appearing round. The longest leaves are one and a half to two-thirds the length of the stem. The base of the stem is weak and tends to bend (Silberhorn 1982). Short-form *Spartina alterniflora* grows 0.3−0.6 m in height with smooth leaves and culms which are 0.63−1.3 cm wide and 20−30 cm long (Silberhorn 1982). Means of reproduction for the herbaceous species is predominantly vegetative through rhizomes.

Estimation of *Baccharis halimifolia* Biomass

The biomass of *B. halimifolia* in the marsh was estimated using the relationship between easily measured parameters and the biomass of harvested shrubs. Shrub biomass can be estimated using an allometric equation that relates properties such as height and crown area to aboveground biomass (Rittenhouse and Sneva 1977; Thomson et al. 1998; Sah et al. 2004). We measured maximum canopy height, canopy area (elliptical crown area), and the number of primary and secondary stems that originated between the base and a 1-m height for five shrubs that were subsequently harvested and dried for biomass determination. The elliptical crown area (*ECA*) was calculated from the canopy width along its widest dimension (*W*) and canopy width perpendicular to the widest dimension (*P*):

$$ECA = \frac{\pi(W)(P)}{4} \quad (1)$$

(Peek 1970; Rittenhouse and Sneva 1977). Five shrubs located in an accessible area at the University of Delaware Research Park in Lewes, Delaware were measured and extracted from the ground in July 2006 using a backhoe. To minimize the loss of roots, the soil around the base and roots was gently removed. Shrubs were washed and sorted into categories of leaves, green stems, wood, large roots, and fine roots. Plant parts were dried at 60°C to a constant weight. The resulting allometric equation was applied to estimate the biomass of the shrubs in the marsh.

Field Sampling

In August and November 2005 and March and June 2006, five similarly-sized *B. halimifolia* shrubs occurring in different stands were sampled for green leaves, new stems, 3-year old stems, and large and fine roots. Three-year old stems, identified based on both branching pattern and subsequent growth ring analysis, were collected to quantify carbon contained in the older woody growth. Leaf and stem litterfall was collected by placing three litter traps, each with a 27-cm diameter, under the canopy of one shrub from each of the five stands from October to February. The litter traps were constructed of 5-gallon (18.1 liter) plastic buckets with holes in the bottom for drainage and a mesh screen to contain fallen litter. The traps were attached to a wooden frame and elevated off the ground to avoid water-logging and soil contamination. Approximately 30% of the canopy area of each shrub was underlain by litter traps. The area of the litter traps was standardized to one meter for analyses. Soil samples were collected under each shrub using a 3.5-cm diameter×45-cm long coring device constructed from a chrome-plated brass sink trap pipe. A moveable plunger was inserted into the pipe to create a vacuum, minimizing compaction and to extrude the core. The bottom edge was sharpened to further reduce compaction.

Percent cover of each species was measured seasonally in 1.0 m^2 plots within five stands dominated by each, short-form *S. alterniflora*, *S. patens*, and *J. roemerianus* (Fig. 1). For each species present in the plots, we used percent cover categories using a modification of the Daubenmire method (Brower et al. 1998). Aboveground and belowground biomass was collected from each of the five stands in August and November 2005 and March and June 2006.

Aboveground biomass and litter were collected from the center of the 1 m^2 plot within 0.1 m^2 quadrats for *J. roemerianus* and *S. alterniflora* and within a 0.025 m^2 quadrat for *S. patens*. Aboveground biomass was harvested by clipping vegetation at the soil surface. Belowground plant material was collected from each of the five clipped plots for each species using a PVC corer with a diameter of 15 cm and a length of 30 cm. Larger cores were collected from the herbaceous species rather than from under the shrubs because in the former we were quantifying belowground biomass in addition to collecting soil samples, while we were collecting only soils under the shrubs. Soil samples were collected from the side of each core section (0–15 and 15–30) of the larger biomass cores at 7.5 and 22.5 cm using a 1.5-cm diameter×10-cm long stainless steel soil corer.

Plant and Soil Processing

Biomass and soil samples were stored at 5°C until processed. Aboveground material of *J. roemerianus*, *S. patens*, and *S. alterniflora* was washed and separated into green leaves, green stems, attached dead (brown leaves and brown stems attached to the roots), unattached dead (dead leaves and stems that were among the standing plant material that had not yet become a part of the litter on the marsh surface), and litter (dead leaves and stems on the marsh surface). Based on the decrease in the live root and rhizome density near the 15-cm depth, the belowground cores were sectioned into two depth segments, 0–15 and 15–30 cm. Core sections were washed over a 1-mm mesh sieve and the biomass was separated into the following categories: live rhizomes, live large roots (≥1 mm), fine roots, dead big macroorganic matter retained on a 2 mm-mesh sieve (dbm), and dead little macroorganic matter finer than 2 mm and retained on a 1 mm mesh-sieve (dlm).

Despite the establishment of plots in relatively monospecific stands of the target species, there was overlap among species both aboveground and belowground. Leaves, stems, rhizomes, large roots, and dbm from sub-dominant species were processed for biomass determination for three of the four sampling dates (November, March, and June). The fine roots and dlm could not be distinguished to species and therefore could not be assumed to be that of the dominant species.

Soil samples were weighed, dried at 60°C, and re-weighed for bulk density (g dry weight cm^{-3}). Loss on ignition (LOI) or percent organic matter was determined by the percent of mass lost following 8 hours in a muffle furnace at 460°C. Samples were finely ground, fumed with 12 M HCl, and analyzed for organic C. Plant and soil samples were dried at 60°C to a constant weight and finely ground through a 40-mesh screen using a Wiley Mill. Carbon and nitrogen concentrations were determined using a Costech Elemental Combustion System 4010 (Costech Analytical Technologies, Inc.).

Carbon Pool Loss

To assess C pool loss from tissues during decomposition, we conducted a litterbag study and measured microbial respiration rates on litter after the marsh incubation period. Senescence and litterfall of *B. halimifolia* in southern Delaware occurs within a short timeframe in the winter. To determine the decomposition rate of litter on the marsh surface, we measured the percentage of mass loss from January to July (182 days). Litterbags (20×10 cm, 2-mm mesh) containing leaves were placed under adult *B. halimifolia* shrubs both above and below the grass (*S. patens*) cover because litter has been observed in both locations. Newly dead leaves, stems, dead roots, and rhizomes (dbm) of herbaceous species, were collected from five stands in the study area in May and July and were used to measure seasonal decomposition. We used larger litterbags (50×10 cm) for the taller stems of *J. roemerianus*. Approximately 10 g of fresh aboveground and 50 g of fresh belowground material were each placed into separate bags. Aboveground litterbags were placed on the marsh surface from May to July (54 days) and July to October (73 days), and belowground litterbags were buried approximately 10-cm below the marsh surface during the warm (May to October, 155 days) and cool seasons (October to May, 219 days) in five stands of the respective species. Four fresh subsamples of each litter type were dried at 60°C to a constant weight to determine an initial dry weight/fresh weight ratio, ground, and analyzed for initial C concentration. The plant material collected from the litterbags was rinsed, dried, ground, and analyzed for final C concentration.

Decomposition rates are typically calculated by fitting mass loss to the single negative exponential model, $e^{-kt}=x_t/x_o$, where k is the decay constant, x_t/x_o is the proportion of original mass remaining at time t, and t is the time elapsed in years (Jenny et al. 1949; Olson 1963). This calculation requires the deployment of many litterbags that are successively retrieved for each species, plant part, and time period and was beyond the scope of the present study. Although there may be limitations to our method, we were primarily interested in comparing decomposition rates among species and plant parts over different seasons.

Microbial respiration rates were measured on three subsamples from each litterbag, which were weighed, placed in BOD bottles, and filled with creek water collected from the field site. Respiration rates were measured on leaf litter of *B. halimifolia* in July when water temperature was 28°C and salinity was 24 psu. Aboveground litter of the herbaceous species was incubated in July and October when water temperatures were 26 and 18°C, respectively, and water salinity was 24 and 20 psu, respectively. Belowground organic matter was tested in October and May at 18°C and 20 psu and 19.3°C and 17 psu,

respectively. Respiration rate was calculated on a dry weight basis from changes in dissolved oxygen that were measured with a digital oxygen meter (YSI Model 58) using the methods described in Gallagher and Pfeiffer (1977).

Radionuclide Measurements and Rates of Accretion and Mass Accumulation

We collected two cores (10-cm diameter×80-cm depth) in 2008, one from the low marsh short-form *S. alterniflora* zone and one from the high marsh *J. roemerianus* zone to determine rates of marsh accretion and organic matter and mineral accumulation. Soil cores were collected using a 10-cm diameter×1.5-m long piston-driven PVC pipe attached to a tripod winch by a cable (Church et al. 2006). Both the sharpened bottom edge of the PVC pipe and the piston, which countered friction between the soil core and the pipe, minimized compaction. We measured compaction by determining the difference in the marsh surface in and out of the core barrel, which was <2 mm. Cores were sectioned into 2-cm depth increments, dried to a constant weight at 120°C, ground, and analyzed for ^{210}Pb and ^{137}Cs activity by gamma spectroscopy following methods described in Cutshall et al. (1983). Samples were counted at constant geometry for 24 h on a Canberra Instruments Model 2020 low-energy Germanium detector (LEGe). The depth of peak ^{137}Cs activity in the core was used to calculate a marsh accretion rate (mm yr^{-1}) relative to ca. 1963, the year of maximum fallout from the atmosphere (Ritchie and McHenry 1990). The downcore profile of excess ^{210}Pb activity was used to calculate an accretion rate following the constant initial concentration model (Robbins 1978). When the specific activity of ^{210}Pb (Bq kg^{-1} sediment) and accretion rate have remained constant through time, the activity-depth profile is described by:

$$A = A_0 \exp(-\lambda z/S) \quad (2)$$

where A is the specific activity of excess ^{210}Pb at sediment depth z, A_o is the initial activity of ^{210}Pb at the marsh surface, λ is the decay constant for ^{210}Pb (0.0311 y^{-1}), and S is the accretion rate (cm yr^{-1}). At steady state a profile of excess ^{210}Pb activity will decrease monotonically with depth when plotted semi-logarithmically, and the slope of a regression line fit to the data is proportional to the accretion rate.

Organic and mineral matter accumulation rates (g m^{-2} y^{-1}) were determined from the method-average accretion rate, % LOI, and dry-bulk density of each core section. The % organic C of each core section was calculated from % LOI based upon the quadratic relationship developed for salt marsh soils by Craft et al. (1991):

$$\%\text{organic C} = (0.40)\text{LOI} + (0.0025)\text{LOI}^2. \quad (3)$$

The fraction of bulk density comprised of carbon was calculated as the product of the % organic C and the bulk density and C accumulation rate was computed as the product of the C density and marsh accretion rate.

Statistical Analyses

To determine the allometric equation that best related measured parameters to the biomass of *B. halimifolia*, correlation coefficients were determined and forward selection regression was used to derive predictive equations (SAS 2003). Each model was tested for normality using normal probability plots of residuals and the Shapiro-Wilk statistic, *W* (SAS Institute, Inc. 2003). We selected the regression model based on the highest R^2 and the lowest standard error of estimate with a significant fit ($p<0.05$). The total aboveground dry weight in grams ('*y*') of *B. halimifolia* was best estimated using *ECA* (m^2) and the number of secondary stems that grew between the base of the shrub and 1-m high (*SS*). The allometric equation developed was:

$$y = -1511 + 1705(ECA) + 585(SS), \quad (4)$$

which had an associated R^2 of 0.9730 ($p=0.0270$).

The resulting allometric equation was then used to estimate the total aboveground dry weight of each of the sampled *B. halimifolia* shrubs (Table 1). Shrubs used to develop the allometric equation had a crown area range of 0.55–3.4 m^{-2} and two to five secondary stems; this equation may not be applicable to shrubs outside of this size range (Table 1). Belowground dry weight was estimated from the root-to-shoot ratio of the harvested shrubs. Biomass (g m^{-2}) was calculated by dividing the total dry weight by the crown area. The allometric equation was then applied to each shrub sampled seasonally for carbon concentration to estimate biomass.

Seasonal differences in the C pools and fluxes among the four species were determined using a two-way analysis of variance followed by Least Square Means Tukey test for multiple comparisons of significant interactions. Carbon pool (g m^{-2}) data were log-transformed and percent data was converted to proportions and arcsine square root transformed, where appropriate, to meet assumptions of ANOVA. The software JMP SAS 5.01 and SAS 8.0 (SAS Institute Inc. 2003) were used for data analyses.

Results

Species richness declined from the high marsh *J. roemerianus*-dominated areas to the low marsh *S. alterniflora*-dominated areas (Table 2). Plant community shifts were evident from the accumulation of large quantities of dead big organic matter

Table 1 Parameters measured for two *Baccharis halimifolia* populations in southern Delaware. The Harvested Lewes population was used to derive an allometric equation to relate measured parameters to above— and belowground dry weight

Parameter	*Baccharis halimifolia* population	
	Harvested Lewes n=5, mean ± s.e.	Assawoman n=20, mean ± s.e.
Height (m)	1.85±0.13	1.99±0.04
Crown area ($m^{2)}$	1.55±0.51	2.55±0.28
Number of primary stems	1.20±0.20	2.00±0.27
Number of secondary stems	3.20±0.58	5.15±0.47
Total aboveground dry weight (g)	3006±1177	5854±644[a]
Total belowground dry weight (g)	1004±393	1955±215[b]

[a] Estimated using: Aboveground dry weight=−1511+1705(crown area) + 585(# of secondary stems)

[b] Estimated using: Belowground dry weight = aboveground dry wt*0.334

(dbm) in areas with little or no live biomass. In the *J. roemerianus*-dominated areas, *J. roemerianus* comprised over 95% of the aboveground biomass and over 90% of the live belowground biomass. Biomass originating from other species comprised a small portion of the live material but a much larger percentage of the dead material, which averaged 36% percent in the upper 0–15 cm and 28% in the lower 15–30 cm (Table 2). *Spartina patens*-dominated areas represented a mixed community with *D. spicata* as the sub-dominant species (Table 2). Despite the limited amount of live *S. alterniflora* biomass in *S. patens*-dominated areas, over one third of the dbm originated from *S. alterniflora*. *Spartina alterniflora* comprised 82% of the aboveground biomass and over 95% of the live belowground biomass in *S. alterniflora*-dominated areas. Dead material of higher marsh species made up 15% of the dead biomass in the upper 15-cm and 63% in the lower 15–30 cm.

Dominant Plant Carbon Pools

The aboveground C pool of *B. halimifolia* averaged 1140 g m^{-2}, which was significantly greater than that of the other species ($F_{3,74}$=101.6, p<0.0001). Only 19.4 gC m^{-2} of leaf litter and 3.6 gC m^{-2} of stem litter of the potential≈ 340 gC m^{-2} of green leaves and stems fell directly below the shrub and comprised a minor C pool per unit area. The C pool loss from *B. halimifolia* leaves over 182 days was surprisingly small, averaging 28%, which was similar above and below the grass understory (Table 3a).

Juncus roemerianus had 817 gC m^{-2} aboveground, almost two times greater than *S. patens*, and over four times greater than *S. alterniflora* (Fig. 2). *Juncus roemerianus* and *S. patens* had larger dead C pools aboveground (368 and 328 gC m^{-2}, respectively) than *S. alterniflora* (144 gC m^{-2}); however, the magnitude of this difference depended on stage of decay and season ($F_{12,143}$=8.1, p<0.0001) (Fig. 3).

The leaf litter of *S. alterniflora* had a considerably higher rate of C loss than that of *S. patens* from May to July, however, from July to October, C loss was similar among species (Season*Species: $F_{1,16}$=5.9, p=0.0271) (Table 3a). Microbial respiration rates measured on dead leaves from litterbags were similar between the two grasses. The C pool loss from dead stems of *S. alterniflora* averaged over the two seasons (55%) was greater than that of either *J. roemerianus* (23%) or *S. patens* (17%) ($F_{2,27}$=28.4, p<0.0001) potentially related to lower initial C/N ratios (Table 3a).

Belowground C pools were generally greater in July than in the other months (Fig. 2). The belowground live C pool was similar among *B. halimifolia*, *S. alterniflora*, and *S. patens* (Fig. 2). The live root and rhizome C pool of *J. roemerianus* (591 gC m^{-2}) was greater than that of *S. patens* (366 gC m^{-2}) (p=0.0037) and similar to that of *S. alterniflora* and *B. halimifolia*. When large dead material (dbm) was included, the C pool of both *Spartina patens* and *S. alterniflora* was greater than that of *J. roemerianus* ($F_{2,57}$=13.8, p<0.0001) (Fig. 2). The fine root and dlm C pool of the *S. patens*-dominated zone (2398 gC m^{-2}) and the *S. alterniflora*-dominated zone (2215 gC m^{-2}) was significantly greater than that of the *J. roemerianus*-dominated zone (676 gC m^{-2}) ($F_{2,57}$=77.0, p<0.0001). *Juncus roemerianus*-dominated areas had organic matter originating from *J. roemerianus* and other marsh species to a depth of approximately 15-cm, below which was a substrate high in sand content, indicative of more recent marsh development.

Carbon pool loss belowground (dbm) was greater in the warmer part of the year than the colder ($F_{1,22}$=14.6, p=0.0009) (Table 3b). *Spartina patens* had a greater percentage of dbm C pool remaining after litterbag incubation than *S. alterniflora* ($F_{2,25}$=10.4, p=0.0005). Despite similar C pool loss rates of dbm between *S. alterniflora* and *J. roemerianus*, the microbial respiration rate was higher on dbm of *S. alterniflora* than *J. roemerianus* after both time intervals in the marsh ($F_{2,27}$=4.7, p=0.0168) (Table 3b).

The total plant C pools of *S. patens* in the mid-marsh averaged 1962 gC m^{-2}, excluding the fine roots and small organic matter (dlm), which could not be identified by species (2398 gC m^{-2}). This was similar to the 1983 gC m^{-2} pool of *S. alterniflora* (fine roots and dlm averaged 2215 gC m^{-2}). *Juncus roemerianus* had a C pool of 1798 gC m^{-2} (fine roots and dlm averaged 676 gC m^{-2}), and the shrub *Baccharis halimifolia* had a total C pool of 1490 gC m^{-2}. When C pools were calculated for all species within each vegetation zone, the *J. roemerianus*-dominated area had approximately 980 gC m^{-2} above-

Table 2 Percent cover in 1.0 m^2 plots and aboveground and belowground biomass (g ash-free dry weight m^{-2}) of species in three vegetation zones in a salt marsh along Little Assawoman Bay, averaged across November, March, and June (n=15, ± s.e.). Belowground biomass was from two depth sections of 0–15 cm and 15–30 cm and does not include fine roots and dead little macroorganic matter, which could not be determined to species

Species	Percent cover	Aboveground biomass (g m^{-2})	Belowground biomass (g m^{-2}) (0–15 cm)		Belowground biomass (g m^{-2}) (15–30 cm)	
		live + dead	live	dead	live	dead
High marsh *Juncus roemerianus* zone						
Juncus roemerianus	70±4	1375±125	1285±137	589±72	2±2	177±30
Spartina alterniflora	2±1	41±15	69±30	213±142	4±4	78±41
Spartina patens	2±2	<1	28±28	27±25	3±3	90±76
Distichlis spicata	<1	9±4	7±5	254±90	0	15±10
Aster tenuifolius	<1	0	0	0	0	0
Schoenoplectus robustus	<1	15±10	0	15±10	0	0
Total	76	1399	1389	1098	9	360
Mid-marsh *Spartina patens* zone						
Spartina patens	79±3	550±66	527±68	1146±155	14±6	929±126
Distichlis spicata	14±3	273±73	418±80	532±110	0	156±43
Spartina alterniflora	5±2	30±19	124±53	742±152	20±10	421±88
Juncus roemerianus	0	0	0	0	0	12±8
Aster tenuifolius	<1	0	0	0	0	0
Total	98	853	1069	2420	34	1518
Low marsh *Spartina alterniflora* zone						
Spartina alterniflora	73±6	217±26	915±91	1900±115	60±15	543±63
Spartina patens	13±7	24±18	41±20	296±85	0	517±130
Distichlis spicata	3±1	16±15	9±9	73±44	0	351±181
Juncus roemerianus	0	0	0	0	0	60±38
Total	89	257	965	2269	60	1471

ground and 2067 gC m^{-2} to a 30-cm depth belowground. The *S. patens*-dominated area had 500 gC m^{-2} aboveground and 5119 gC m^{-2} belowground. The *S. alterniflora*-dominated areas had 250 gC m^{-2} aboveground and 4694 gC m^{-2} belowground.

Soil Properties

Soil properties were similar over the seasons at both depths in the four vegetation zones. Soil bulk density, percent organic matter, and soil organic C in *S. alterniflora*— and *S. patens*-dominated areas were similar at both 7.5 and 22.5 cm depths (Table 4). The *J. roemerianus*-dominated areas had higher bulk density and lower soil C at 22.5 cm than at 7.5 cm depth (p=0.0196). Soil under *B. halimifolia* shrubs had higher bulk density and lower organic matter and soil C than soil under the grass species at both depths.

Total belowground plant pools measured in this study represented 25–36% of the organic soil C in the *S. alterniflora* and *S. patens*-dominated areas. Biomass C pool in cores from *J. roemerianus*-dominated areas were 18% of soil C in the upper 0–15 cm and 8% in the lower 15–30 cm.

Total Organic C Pool

Total organic C pool (soil+aboveground) was approximately 8637 gC m^{-2} for *B. halimifolia*-dominated areas, 11984 gC m^{-2} for *J. roemerianus*-dominated areas, 16645 gC m^{-2} for *S. patens*-dominated areas, and 15635 gC m^{-2} for *S. alterniflora*-dominated areas.

Marsh Accretion

Accretion rate, averaged between the ^{137}Cs and ^{210}Pb dating methods, was higher in the *S. alterniflora*-dominated stand (2.5 mm yr^{-1}) than the *J. roemerianus*-dominated stand (1.9 mm yr^{-1}) (Fig. 4). The soil under the high marsh *J. roemerianus* had approximately 68% organic matter in the upper 8-cm, declining to <10% below 25-cm and remaining low at depth (Fig. 5). Bulk density remained less than 0.3 g cm^{-3} to approximately 18-cm depth below which it increased in a relatively linear fashion corresponding to a stratigraphic change from marsh to terrestrial soil. This trend was spatially consistent in *J. roemerianus* stands throughout the marsh, as our 20 biomass cores all had the

Table 3 Percent dry mass and carbon (C) pool remaining of aboveground litter on the surface (a) and dead big organic matter (dbm) 10-cm below the surface (b) of species after two time intervals in a salt marsh in southern Delaware (n=5). Respiration rates of decomposers on the litter were measured at the end of the time period. Values are means±1 standard error

Species	Part	Time interval	% dry mass remaining	% C pool remaining	Initial C/N ratio	Final C/N ratio	Respiration rate (mg C g^{-1} DW d^{-1})
a							
Baccharis halimifolia	leaves	Jan–Jul (182 d)	82.3±3.2	72.1±3.7	33	22±1	0.72±0.06
Juncus roemerianus	stems	May–Jul (54 d)	89.0±3.6	82.0±2.8	62	63±5	1.16±0.20
		Jul–Oct (73 d)	80.7±2.6	70.6±2.8	77	66±9	0.74±0.08
Spartina patens	leaves	May–Jul (54 d)	88.7±5.4	100.0±6.5	46	32±1	1.20±0.15
		Jul–Oct (73 d)	62.6±11.8	57.5±10.3	30	42±3	1.25±0.14
	stems	May–Jul (54 d)	84.5±5.1	85.8±5.2	52	47±1	0.90±0.10
		Jul–Oct (73 d)	89.0±5.5	80.5±4.5	49	55±6	0.90±0.06
Spartina alterniflora	leaves	May–Jul (54 d)	60.8±7.5	60.5±7.3	59	54±5	1.61±0.35
		Jul–Oct (73 d)	44.7±1.9	41.9±1.8	45	66±13	1.76±0.18
	stems	May–Jul (54 d)	64.3±5.9	62.4±6.1	35	45±4	1.40±0.25
		Jul–Oct (73 d)	25.8±4.6	23.3±3.9	43	46±4	1.85±0.20
b							
Juncus roemerianus		May–Oct (115 d)	82.7±0.6	71.0±0.8	53	136±33	0.24±0.03
		Oct–May (219 d)	72.5±2.9	71.7±2.8	63	103±23	0.37±0.04
Spartina patens		May–Oct (115 d)	90.0±4.1	77.3±4.0	58	97±20	0.71±0.07
		Oct–May (219 d)	80.7±5.3	78.4±5.1	71	82±25	0.34±0.04
Spartina alterniflora		May–Oct (115 d)	71.5±2.6	65.6±1.9	61	74±13	0.86±0.08
		Oct–May (219 d)	70.1±2.9	64.5±3.8	73	56±5	0.52±0.06

distinct sandy soil originating approximately 15-cm below the surface. The low marsh colonized by *S. alterniflora*, on the other hand, had higher soil organic matter and lower soil bulk density values with depth (Fig. 5).

The average rate of organic matter accumulation after 1963 was greater in the low marsh *S. alterniflora* stand (289 g m^{-2} yr^{-1}) than in the high marsh *J. roemerianus* stand (213 g m^{-2} yr^{-1}) (t_{10}=70.5, p<0.0001). Similarly, the rate of organic C accumulation in the *S. alterniflora* stand was 159 g m^{-2} yr^{-1}, which was greater than the 119 g m^{-2} yr^{-1} measured in the *J. roemerianus* stand (t_{10}=29.3, p=0.0003). The average soil C density was greater in the *J. roemerianus* stand (0.063 g cm^{-3}) than in the *S. alterniflora* stand (0.054 g cm^{-3}) (t_{10}= 11.6, p=0.0067). Mineral matter accumulation under *S. alterniflora* was twice that of *J. roemerianus*, averaging 236 and 121 g m^{-2} yr^{-1}, respectively (t_{10}=25.0, p=0.0005).

Discussion

C Pool Dynamics

In the study area the total plant C pool generally increased from high to low marsh with the majority of the C pool of the dominant species shifting from aboveground to belowground. Soil carbon pool was greatest in mid and low marsh areas dominated by *S. patens* and *S. alterniflora*, respectively. Carbon accumulation rate was also estimated to be higher in the *S. alterniflora*-dominated area where C burial by mineral sediments is a significant process. The difference in C pools among the vegetation zones was related to species morphology, environmental conditions of the habitat, and colonization history.

The aboveground C pool of the high marsh shrub species, *B. halimifolia*, was greater than that of the other species with 56% allocated to stem and trunk wood. Based on the low quantity of litterfall under the shrub canopy (6.8% of the potential), annual leaf and non-woody stem production would not contribute significantly to soil organic carbon in the immediate vicinity despite a relatively slow decomposition rate. Wind and winter storms were the most likely vectors dispersing senescent leaves, with the remaining C pool on the ground under the shrub 6 to 16 times less than that of the other species. In contrast, the herbaceous species provided a large, almost continuous supply of detrital C throughout the year feeding microbial communities and contributing to soil organic carbon.

The relatively large constant aboveground C pool of *J. roemerianus* contributes to the seasonal C dynamics through uptake, maintenance, death, and decomposition

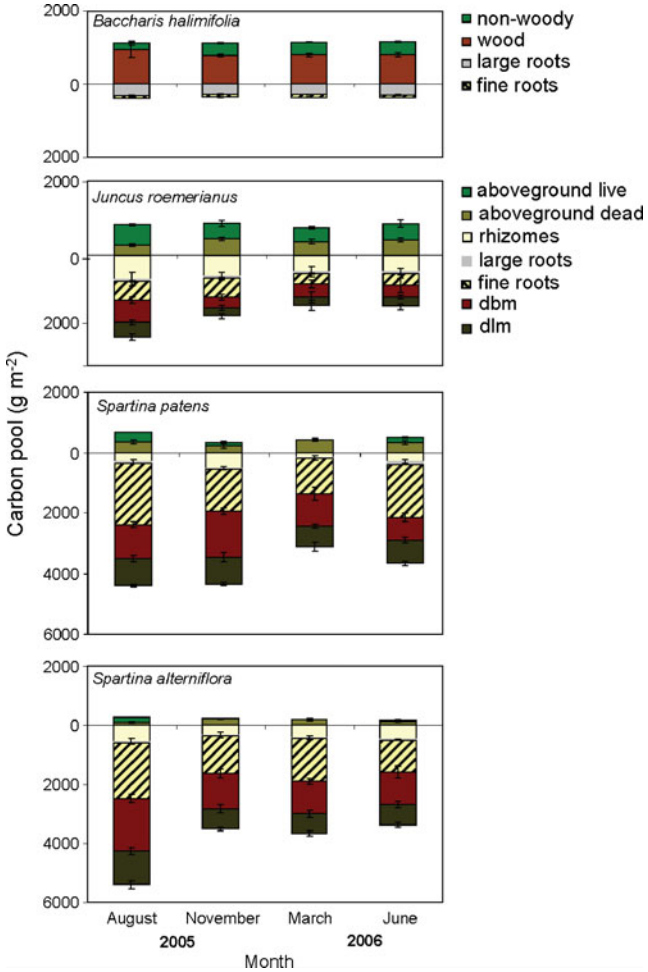

Fig. 2 Carbon pools of four salt marsh species at four times of the year in Little Assawoman Bay, South Bethany, Delaware (n=5). Values are means±1 standard error for the carbon pool of each part. The zero along the y-axis represents the marsh surface, dividing aboveground from belowground pools. Fine root and dlm pools represent the total found in the core and could not be distinguished by species. The graphs of the four species were plotted on equivalent y-axes

and potentially longer-term soil C pools through burial. The live-stem biomass was relatively constant throughout the seasons, whereas seasonal changes in the amount of dead stems suggested a large turnover of aboveground material. Similar to results found by Williams and Murdoch (1972) in North Carolina and Gallagher et al. (1980) in Georgia, we found *J. roemerianus* in Delaware to be productive aboveground with an increase in growth occurring in the spring despite relatively constant total pools. The C pool of dead aboveground *J. roemerianus* was 61% larger than that of *S. alterniflora* and aboveground decomposition was over 58% slower. Therefore, the potential for aboveground litter to contribute to soil organic carbon may be greater for *J. roemerianus* than for *S. alterniflora*.

Seasonal fluctuations in dominant plant C pools increased among species from high to low marsh. *Baccharis halimifolia* and *J. roemerianus* had more constant C pools over the year than the grass species. The total C pool of *S. patens* was retained for a longer period of time over the year compared to that of *S. alterniflora*. Similar findings for *S. patens* and *S. alterniflora* were documented in marshes of Louisiana (White et al. 1978) and along the Bay of Fundy (Connor and Chmura 2000). For *S. patens* the maintenance of C pools in our study was associated with low decomposition rates aboveground and belowground. The majority of the plant C pool in the areas dominated by the grass species was fine roots. We observed a large fluctuation in the fine root C pool in the grass species zones throughout the year with a 36% loss in *S. patens*-dominated

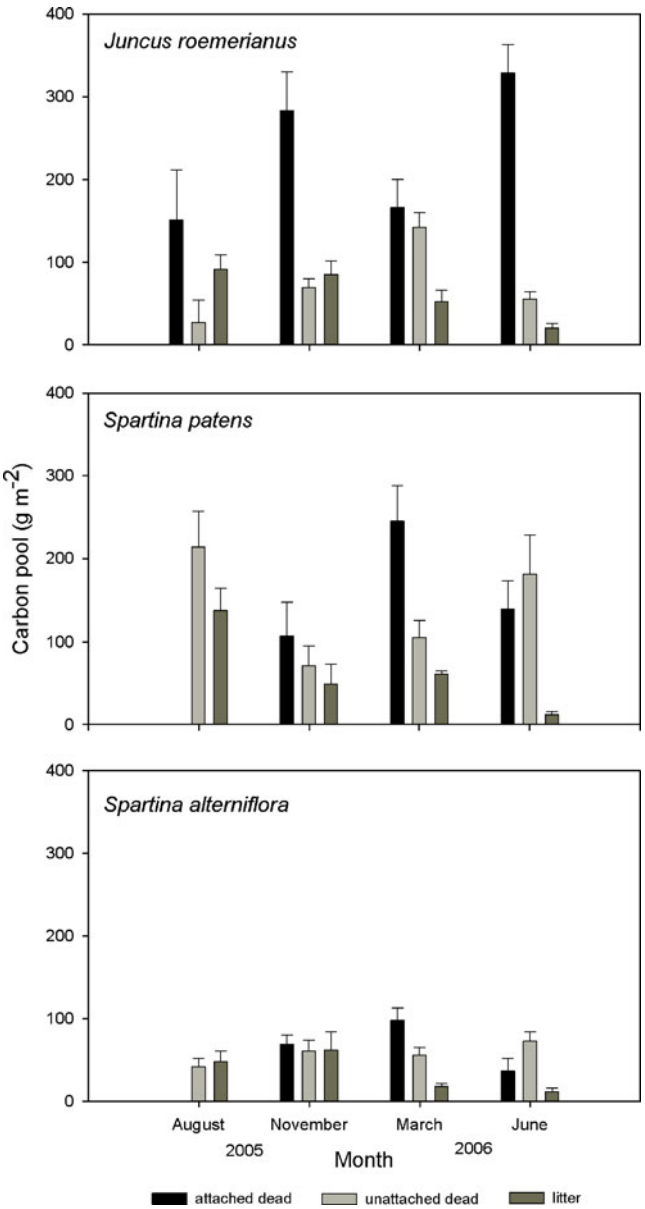

Fig. 3 Carbon pool in aboveground parts in different stages of decay of three herbaceous salt marsh species at four times of the year (n=5). Values are means±1 standard error

Table 4 Soil properties in plant communities dominated by different species at two depths ($n=20, \pm$s.e.). The high marsh, *Baccharis halimifolia* and *Juncus roemerianus*-dominated communities overlay terrestrial or sandy soil, the mid-marsh, *Spartina patens*-dominated community contains organic matter from a variety of species including *Spartina alterniflora*, and the low marsh was dominated by *S. alterniflora* organic matter at 7.5 cm but a greater quantity of *S. patens* and *Distichlis spicata* at 22.5 cm. Soil properties with the same letter indicate no significant difference among species and soil depth

Dominant species	Depth (cm)	Bulk density (g cm^{-3})	Organic matter content (%)	Soil organic C (%)	Soil C (g m^{-2})
Baccharis halimifolia	7.5	1.14 ± 0.16^{B}	11 ± 3^{BC}	4.5 ± 1.3^{C}	5081 ± 529^{B}
	22.5	1.63 ± 0.07^{B}	6 ± 4^{C}	1.0 ± 0.2^{D}	2416 ± 657^{C}
Juncus roemerianus	7.5	0.27 ± 0.08^{A}	34 ± 9^{AB}	17.5 ± 2.6^{B}	6391 ± 1847^{AB}
	22.5	1.47 ± 0.27^{B}	15 ± 9^{BC}	3.5 ± 0.6^{CD}	4848 ± 1521^{B}
Spartina patens	7.5	0.19 ± 0.01^{A}	58 ± 11^{A}	30.1 ± 0.9^{A}	8582 ± 791^{A}
	22.5	0.17 ± 0.01^{A}	63 ± 3^{A}	28.4 ± 0.9^{A}	7580 ± 775^{A}
Spartina alterniflora	7.5	0.22 ± 0.03^{A}	58 ± 5^{A}	27.4 ± 1.2^{A}	7602 ± 536^{A}
	22.5	0.17 ± 0.02^{A}	53 ± 5^{A}	27.8 ± 1.6^{A}	7822 ± 601^{A}

areas and a 43% loss for *S. alterniflora*-dominated areas over the winter and spring. The majority of the fine roots appeared to be dead, and thus decomposition, growth, and turnover of fine roots are important processes that affect the size of the C pool belowground. Although fine root C pools fluctuate seasonally and play an integral role in the seasonal dynamics of the plant C pools, fine roots comprise over a third of the total belowground biomass and thus make an important contribution to the storage of C in marsh soils. Despite a relatively large seasonal flux in belowground plant C pools, particularly for *S. alterniflora*, there was no apparent seasonal change in soil C.

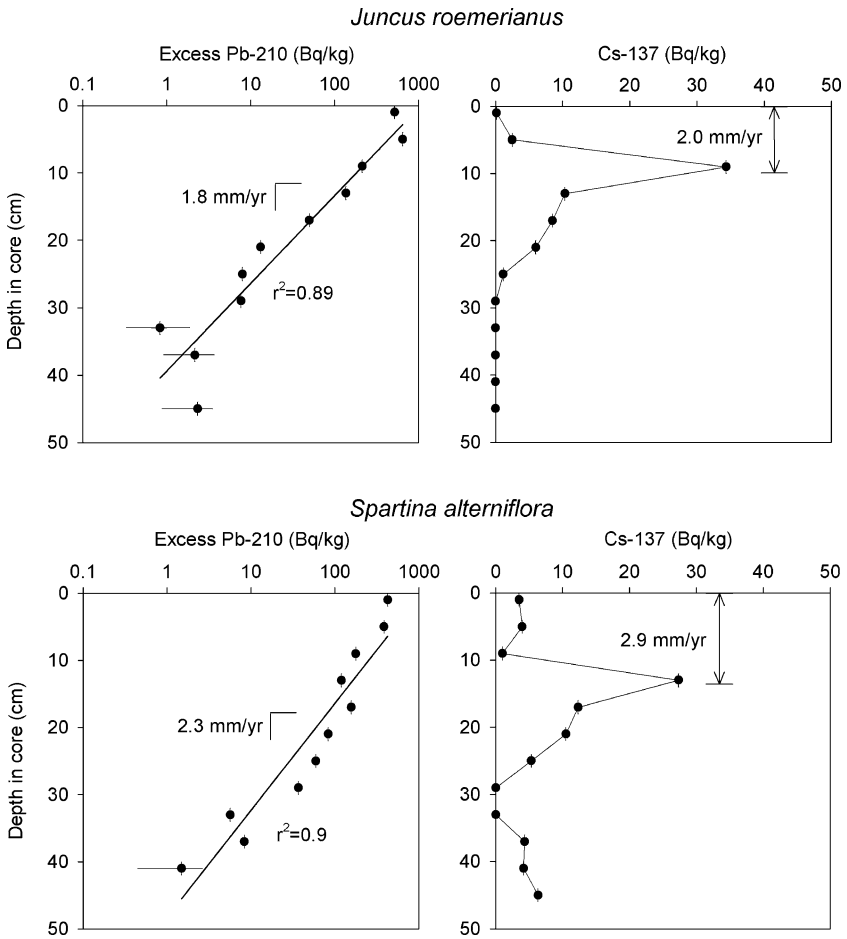

Fig. 4 Radionuclide activity-depth profiles for the *Juncus roemerianus* and *Spartina alterniflora* sites. Sediment accretion rates computed from the slope of the ^{210}Pb decay profile and from depth of ^{137}Cs activity peak (relative to 1964) are shown. ^{137}Cs activity extending below 30 cm in the *Spartina* core indicates downward mixing by bioturbation or chemical diffusion. See Fig. 1 for coring locations

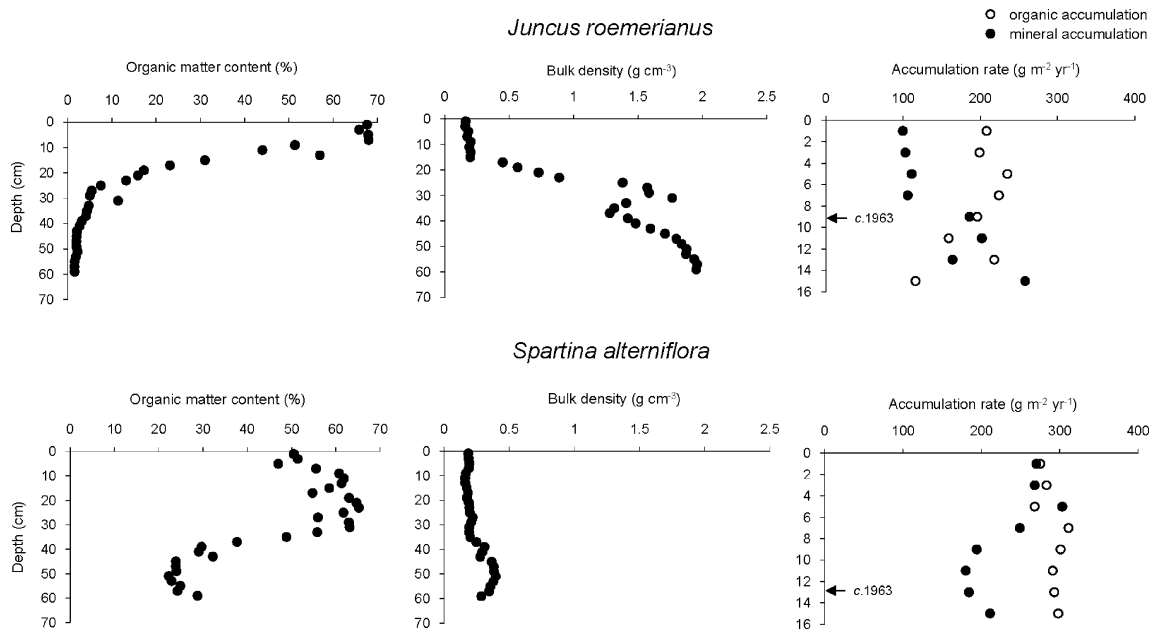

Fig. 5 Soil organic matter content (% loss on ignition), bulk density, and organic and mineral accumulation rates with depth from cores collected from the high marsh dominated by *Juncus roemerianus* and the low marsh dominated by *Spartina alterniflora* in a salt marsh fringing a coastal lagoon in southern Delaware. The change in soil properties with depth underlying *J. roemerianus* is indicative of a change in substrate from organic to sandy. The *S. alterniflora* stand overlays organic matter derived primarily from higher marsh species

When total belowground plant C pools and soil C within each of the plant zones were calculated by volume, we found that the measured biomass represented between 7 and 36% of the organic soil C pool. Potential sources of organic C include allochthonous contributions from upland plants, marsh macrophytes, and phytoplankton. In a Georgia salt marsh, 75% of the soil organic C was estimated to be derived from phytoplankton, based on C/N and $\delta^{13}C_{org}$ values (Gebrehiwet et al. 2008). In our study biomass and other sources of organic C smaller than the 1 mm mesh size comprised 64–93% of soil C.

Estimation of C Accumulation Rate

Accretion and carbon accumulation rates, based on two cores, were higher in the low marsh than in the high marsh. In the high marsh *J. roemerianus*-dominated stand, the stratigraphic sequence was that of a young developing marsh characterized by increased organic matter content towards the surface and high bulk density at depth. The low marsh stand appeared to be undergoing a transition from organic to mineral accumulation based on the decreased organic matter and increased mineral accumulation toward the marsh surface. This stratigraphic sequence was indicative of either a mineral matter-enriched or submerging marsh (e.g., Ward et al. 1998). A decline in organic matter toward the soil surface under the stand of *S. alterniflora* also corresponded to a shift from *S. patens* and *D. spicata* derived organic matter to *S. alterniflora* organic material. This may be due to a larger quantity of mineral sediment diluting the organic matter pool with the shift to *S. alterniflora*, which generally experiences a longer hydroperiod than *S. patens*. There also may be enhanced accumulation of *S. patens* organic matter due to slower decomposition than *S. alterniflora*. Both higher organic and mineral sediment accumulation in the low marsh stand resulted in a higher accretion rate than in the high marsh stand. It is unclear whether the low rate of accumulation in the high marsh will allow the encroachment of the more rapidly accumulating lower marsh, or whether organic matter accumulation in the high marsh will increase with continued marsh development.

The C sequestration rates in stands of *S. alterniflora* and *J. roemerianus* (154 and 119 gC m^{-2} yr^{-1}) in our study were approximately 65% of the global average for salt marshes (210 gC m^{-2} yr^{-1}), but are within the range found in marshes along the Atlantic coast (Chmura et al. 2003). For *S. alterniflora* marshes, C accumulation is predicted to increase with sea-level until the rate of sea-level rise precludes plant survival (Mudd et al. 2009). In addition, in mineral-poor marshes a reduction in sediment supply increases organic C storage, provided the rate of sea-level rise does not outpace marsh accretion (Mudd et al. 2009). Based on our soil profiles, organic accumulation may be more important in determining accretion rates in the high marsh, where there is less sediment accumulation, than in the low marsh. Based on

our plant C pool and C pool loss data, we might predict organic accumulation to be greater in the high marsh, *J. roemerianus* zone. However, due to the supply of mineral sediment and the rate of burial of organic C in the low marsh, C sequestration may ultimately be greater under *S. alterniflora*, regardless of the biomass dynamics.

Plant Community Shifts and Landward Migration

Plant community shifts were evident through changes in the dominant source of live and dead belowground biomass with depth. The low marsh *S. alterniflora* overlies large quantities of dead *S. patens* below 15-cm depth and thus may be moving landward replacing mid-marsh vegetation. However, the mid- and high marsh species overlie an accumulation of dead organic matter from lower marsh species indicating non-unidirectional species shifts in this salt marsh system. The accretion rate at the high marsh site was lower than the rate of relative sea level rise along coastal Delaware, 2–3 mm yr^{-1}, and the rate at the low marsh site was on the low end of the range of local relative sea level rise (Zervas 2001; CCSP 2009). Replacement of high marsh species with lower marsh species in response to an increase in the rate of sea level rise has been documented in New England marshes (Warren and Niering 1993; Donnelly and Bertness 2001). Based on the plant C pool dynamics in this marsh system, replacement of *S. patens* by *S. alterniflora* would result in an increase in the seasonal fluctuation of plant C pools and an increased loss of CO_2 through microbial respiration both aboveground and belowground. *Spartina patens* had a dead aboveground C pool that was over two times larger and a C loss rate that was slower than that of *S. alterniflora*, and therefore has the potential to contribute more to soil C through the burial of aboveground litter than *S. alterniflora*.

Along Little Assawoman Bay, there was little soil organic matter under the shrub community with approximately 1% soil carbon at the 22 cm depth. Belowground biomass of *J. roemerianus* at depth can be significant, as has been shown in Georgia (1340 gC m^{-2}) (Gallagher and Plumley 1979) and Mississippi marshes (9700–12,400 g DW m^{-2}) (de la Cruz and Hackney 1977). Likewise, soil organic matter content under *J. roemerianus*-dominated stands may also be high with up to 51% in North Carolina marshes (Woerner and Hackney 1997). The recent development of the *J. roemerianus*-dominated community was the factor influencing the low soil C at depth at our study site. With low marsh species migrating inland, our results suggest a 36–70% increase in soil carbon at depth at the marsh-upland border with continued marsh development. This scenario may be representative of soil carbon accumulation in sandy terrestrial areas that transition to wetlands as relative sea level increases.

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