

ECOSYSTEM DEVELOPMENT OF A SANDBAR EMERGENT TIDAL MARSH, ALTAMAHA RIVER ESTUARY, GEORGIA, USA

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Abstract: Vegetation structure and soil properties were measured on a sandbar, a three year old sandbar emergent marsh (SEM), and five mature *Spartina alterniflora* Loisel marshes located near the mouth of the Altamaha River (Georgia, USA) to determine how quickly tidal marsh vegetation and soils develop during primary succession. Those data were compared to published data collected from young (10–16 yr old) natural marshes in Virginia and young (1–28 yr old) constructed marshes in North Carolina to determine if the rate of ecosystem development is similar among tidal marshes of the southeastern US coast. Within three years of emergence, aboveground biomass of SEM was comparable to mature marshes in the area, although stem height and density were distinctly different as the SEM contained more stems that were of shorter height than mature marshes. Following colonization by vegetation, soil properties (0–30 cm) of SEM had begun to differentiate from sediments of the sandbar. Surface (0–10 cm) and subsurface (10–30 cm) soil bulk density was less, and organic carbon (C), nitrogen (N), and percent silt (0–10 cm) were greater in sediments of SEM than in the sandbar. Even so, soils of SEM contained less organic C, N, silt, and clay than mature marshes. However, accumulation rates of organic C ($260 \pm 40 \text{ g m}^{-2} \text{ yr}^{-1}$) and N ($11 \pm 3 \text{ g m}^{-2} \text{ yr}^{-1}$) in soils of SEM was 5 to 7 times greater than in mature marshes ($35 \pm 4 \text{ g C m}^{-2} \text{ yr}^{-1}$, $2 \pm 0.2 \text{ g N m}^{-2} \text{ yr}^{-1}$). Trajectories of development for soil organic C and N pools were similar for our SEM, young natural *S. alterniflora* marshes in Virginia, and young constructed *S. alterniflora* marshes in North Carolina suggesting that soil development proceeds at similar rates for tidal marshes along much of the southeast US coast.

Key Words: nitrogen, nutrient pools, organic carbon, phosphorus, primary succession, salt marsh, Sapelo Island, soils, *Spartina alterniflora*, vegetation

INTRODUCTION

Coastal salt marshes are communities of emergent halophytic vegetation in areas regularly inundated by tidal action. The development of a salt marsh occurs within the inter-tidal zone when sediment accumulates, increasing surface elevation and reducing the duration and velocity of tidal inundation, enabling pioneer vascular plants to colonize the site (Silvestri and Marani 2004). Once vegetation is established, detritus accumulates with sediments and soil organic matter and nutrient pools increase, leading to conditions suitable for further vegetation growth and development (Silvestri and Marani 2004).

Vegetation structure and soil properties evolve as the marsh develops over time. Soils of young natural marshes often contain mineral sediments (sand in particular) with less organic matter and nutrients, whereas mature marshes have finer-grained, organic rich soils with larger nutrient pools (Osgood and Zieman 1993). In addition, young marshes generally lack well-developed surface drainage and are lower in elevation compared to the mature marshes that

have a well-developed system of tidal creeks and higher overall elevation (Osgood and Zieman 1993). While published studies document differences in ecosystem structure and function among young and mature marshes, little is known about natural marsh ecosystem development or the rate at which salt marsh vegetation and soils change (Osgood and Zieman 1993, Osgood et al. 1995, Edwards and Proffitt 2003).

A sandbar formed in the Altamaha River (Georgia) in 2002 and was partially colonized by smooth cordgrass (*S. alterniflora*) in 2003, providing an opportunity to assess incipient tidal marsh ecosystem development. Vegetation structure (stem height, density, aboveground biomass) and soil properties (bulk density, nutrients (C, N, and P), particle size) were measured in the unvegetated sandbar, the recently vegetated sandbar emergent marsh (SEM), and five mature natural *S. alterniflora* marshes nearby and elsewhere on the Georgia coast to determine the rate of tidal marsh vegetation and soil development during primary succession. In addition, vegetation and soil properties of the Georgia marshes were compared with young natural

marshes in Virginia and constructed marshes in North Carolina to evaluate whether trajectories of ecosystem development are similar among tidal marshes of the southeast US coast.

METHODS

Site Descriptions

Georgia. The unvegetated sandbar, SEM, and mature marshes were located on the coast of Georgia (Figure 1A). The Altamaha River (Figure 1B) influenced all of the marshes. The sandbar, part of which was colonized by *S. alterniflora* (SEM), formed naturally in 2002 where the Altamaha River and Atlantic Ocean converge. Aerial photographs of the region reveal that the sandbar was not present in 1999 and by 2005, the sandbar was about 1.2 ha in size and about half of it was vegetated (GPS coordinates 31°19'00" north, 81°20'00" west). The site experiences diurnal tidal inundation of 2.3 m with salinities ranging from 14 to 19 ppt (2002–2003) and *S. alterniflora* dominated the vegetation (Table 1).

Craft (2007) compared soil properties and accumulation in nine mature tidal marshes in and around Sapelo Island, Georgia, including the Altamaha River. Using that data, we selected five marshes based on similarities in salinity, vegetation, and tidal inundation to represent the successional endpoint of marsh ecosystem development for SEM (Figure 1B, Table 1). We used data collected from natural levee locations for comparisons with SEM because of similar inundation regimes (twice daily to an average depth of 30 cm in the mature marshes and about 45 cm in the SEM, personal observations).

Virginia. Data for Virginia marshes were obtained from two published studies. Osgood and Zieman (1993) studied two young (10–13 yrs old) and two mature (40+ years) natural *S. alterniflora* marshes located on the sound side of barrier islands on the eastern shore of Virginia (Figure 1C). Osgood et al. (1995) compared one of the young marshes (now 14–16 yrs old) from the 1993 study and a sandflat that was formed after extensive over wash occurred during a coastal storm in late October 1991 (Figure 1C). Salinity ranged from 30–35 ppt (Table 1). Virginia and Georgia marshes differ in that Virginia sites were located on sediment starved barrier islands and Georgia sites were located in sediment-rich areas of the Altamaha River delta. However, similar vegetation, age, and tidal inundation make them reasonable sites to compare ecosystem development.

North Carolina. Craft et al. (2003) studied constructed marshes in North Carolina created by mechanically grading the substrate to inter-tidal elevation, then planting *S. alterniflora* between mean sea level and mean high water (Figure 1D). These marshes had a variety of geomorphic positions ranging from back barrier flat to submerged upland to riverine locations. Salinities ranged from 5–33 ppt (Table 1). These sites had comparable vegetation, tidal inundation, and age compared to the SEM in Georgia, but the salinity range was more variable due to the range of geomorphic locations.

Data Collection in Georgia

Aboveground vegetation of SEM was collected from five randomly selected 0.25 m² quadrats in vegetated areas at the end of the growing season (October) of 2005. As a result, our measurements of aboveground biomass serve as a conservative surrogate for net primary production (NPP). Vegetation was clipped, bagged, and returned to the laboratory where the number and height of stems in each quadrat were measured. The plant material was then dried at 70°C and weighed.

Ten randomly selected soil cores, five from SEM and five from the sandbar, were collected with minimal compaction using an 8.5 cm diameter by 30 cm deep stainless steel corer. Cores were divided into 0–10 and 10–30 cm depths, dried at 70°C, weighed, ground, and sieved through a 2 mm mesh screen (Craft et al. 2003). Bulk density was calculated from the dry weight per unit volume for each depth increment (Blake and Hartge 1986) after correcting for moisture content of an oven-dried sub-sample (105°C).

Sub-samples of soil were analyzed for total organic C, total N, total P, and particle size. Organic C and N were determined using a Perkin Elmer 2400 CHN analyzer; analysis of an internal marsh standard yielded a recovery rate of 98%. Total P was determined by nitric-perchloric digestion followed by colorimetric analysis (Sommers and Nelson 1972); analysis of NIST standard (# 1646a) estuarine sediment yielded a recovery rate of 94% for P. Particle size of surface soils (0–10 cm) was determined using the hydrometer method (Gee and Or 2002).

Nutrient pools for each core (0–30 cm) were calculated using depth weighted (0–10, 10–30 cm) bulk density, N, P, and organic concentrations as follows:

$$\text{Nutrient Pool (g m}^{-2}\text{)} = \text{bulk density (g cm}^{-3}\text{)} \cdot$$

$$\text{C, N, or P (g/g)} \cdot 10,000 \text{ cm}^3 \text{ m}^{-2} \cdot 30 \text{ cm depth}$$

Accumulation rates of organic C, N, and P were calculated by:

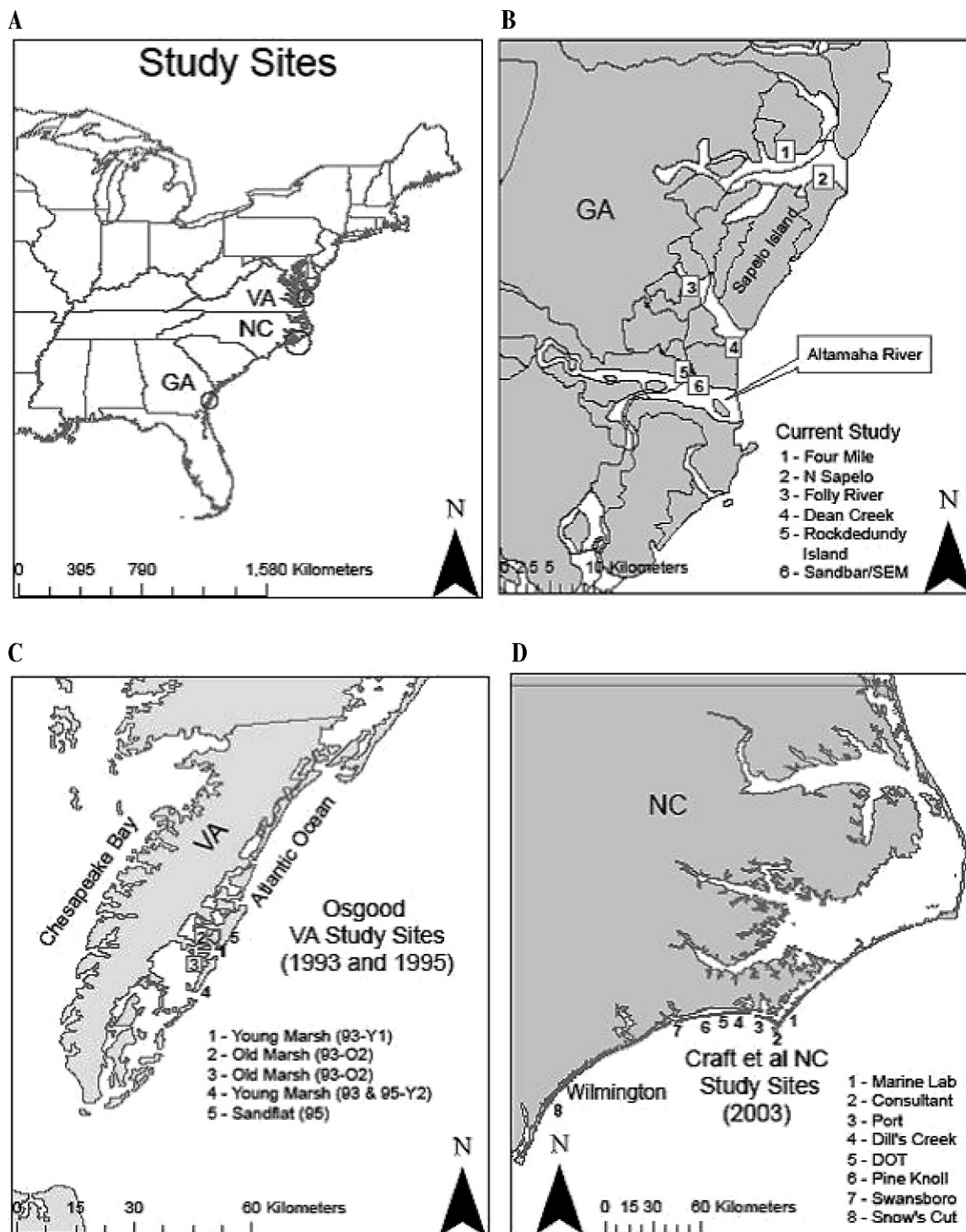


Figure 1. A) Map of southeastern US coast, B) our study areas on the coast of Georgia, USA, C) Virginia studies (Osgood and Zieman 1993, Osgood et al. 1995) and D) the North Carolina study (Craft et al. 2003).

$$\text{Accumulation Rate} = (A - B)/T$$

where A = soil organic C, N, or P pool (0–30 cm depth), B = soil organic C, N, or P pool (10–30 cm depth) · 1.5, and T = age of the marsh (Craft et al.

1988). Our accumulation rates assumed that surface (0–10 cm) enrichment of soils with organic C, N, and P was the result of colonization of the site with emergent vegetation and subsequent additions of plant detritus and sediment. The uniform organic C,

Table 1. Characteristics of young (natural, constructed) and mature (natural) *Spartina alterniflora* salt marsh study sites.

State	Origin	Age (yrs)	Tidal Range (m)	Salinity ¹ (ppt)	Geomorphic Position
Georgia					
Sandbar	Natural	1	2.3	14–19	Riverine
Sandbar Emergent Marsh (SEM)	Natural	3	2.3	14–19	Riverine
Mature Marshes					
Four Mile (1)	Natural	> 200	2.3	25–29	Estuarine
N Sapelo (2)	Natural	> 200	2.3	28–32	Estuarine
Folly River (3)	Natural	> 200	2.3	22–25	Estuarine
Dean Creek (4)	Natural	> 200	2.3	25–29	Estuarine
Rockdedundy Island (5)	Natural	> 200	2.3	14–19	Riverine
Virginia					
Sandbar	Natural	1		33–35	Back barrier flats
Young Marsh 1	Natural	10–12		30–38	Back barrier fringe
Young Marsh 2	Natural	11–13		30–38	Back barrier fringe
Young Marsh 3	Natural	14–16		30–33	Back barrier fringe
Mature Marsh	Natural	> 200		34–41	Back barrier flats
Mature Marsh	Natural	> 200		34–41	Back barrier flats
North Carolina					
DOT	Constructed	1	1.0	20–30	Back barrier flats
Consultant	Constructed	3	1.0	17–32	Back barrier flats
Port	Constructed	8	1.0	18–30	Back barrier flats
Swansboro	Constructed	11	1.1	20–30	Riverine
Dill's Creek	Constructed	13	1.0	14–33	Submerged upland
Pine Knoll	Constructed	24	1.0	20–30	Back barrier fringe
Marine Lab	Constructed	26	1.0	20–30	Back barrier flats
Snow's Cut	Constructed	28	1.2	5–20	Riverine
Mature Marsh 1	Natural	> 200	1.0	20–30	Back barrier flats
Mature Marsh 2	Natural	> 200	1.0	17–32	Back barrier flats
Mature Marsh 3	Natural	> 200	1.0	18–30	Back barrier flats
Mature Marsh 4	Natural	> 200	1.1	20–30	Riverine
Mature Marsh 5	Natural	> 200	1.0	14–33	Submerged upland
Mature Marsh 6	Natural	> 200	1.0	20–30	Back barrier fringe
Mature Marsh 7	Natural	> 200	1.0	20–30	Back barrier flats
Mature Marsh 8	Natural	> 200	1.2	5–20	Riverine

¹ Annual (2003 and 2002) salinity of the Georgia marshes was calculated from daily measurements in the water column of the adjacent estuary.

N, and P concentrations (and bulk density) in the sandbar supported this assumption.

These methods were the same as those used to sample and analyze vegetation and soil samples from Georgia mature marshes (soils from Craft 2007; vegetation from Steve Pennings, University of Houston, unpublished data), and similar to those used in Virginia natural marshes (Osgood and Zieman 1993, Osgood et al. 1995) and North Carolina constructed marshes (Craft et al. 2003).

Statistical Analysis

Student's T-test was used to test for differences in vegetation structure and function between SEM and mature marshes. T-tests also were used to compare stem density of individual height classes (20 cm

increments). Differences in soil properties among sites (sandbar, SEM, and mature marshes) and between sampling depths (0–10, 10–30 cm) were compared using analysis of variance followed by post-hoc comparisons using the Ryan-Einot-Gabriel-Welsch Multiple Range Test (REGWQ) (SAS/STAT 1996). Regression analysis was used to relate nutrient pools (C and N) and age for southeastern US (GA, VA, NC) marshes (SigmaPlot, Systat Software Corporation 2006). Mature marshes for a given region (Georgia and North Carolina) were combined into single data points (mean \pm standard error) for this analysis. The constructed marshes (in NC) were presented separately because their varying ages (1–30 years-old) and degree of ecosystem development contribute to differences in soil C and N pools. All tests of significance were made at $\alpha = 0.05$.

RESULTS

Vegetation

The mean length of *S. alterniflora* stems was shorter (93 ± 4 cm vs. 138 ± 8 cm) and mean stem density was greater (282 ± 47 m⁻² vs. 91 ± 5 m⁻²) in SEM compared to the mature marshes (Figure 2A). The SEM contained about twice as many stems (44%) that were shorter than 40 cm compared to the mature marshes (19%) (Figure 2B). Despite differences in canopy architecture, mean aboveground *S. alterniflora* biomass of SEM (1160 ± 300 g m⁻²) was comparable to levels found in the mature marshes (1440 ± 120 g m⁻²) (Figure 2A).

Soils

In 2005, SEM soil properties were different from those of the unvegetated sandbar. Mean bulk density (0–10 and 10–30 cm) was less (Figure 3A) and organic C and N concentrations were greater (Figure 3B) in SEM. Mean particle size (upper 10 cm) differed as well (Figure 4A) with SEM soils containing less sand ($85 \pm 1\%$) and more silt ($10 \pm 1\%$) and organic matter ($2.8 \pm 0.2\%$) than the sandbar ($96 \pm 1\%$ sand, $2 \pm 0.4\%$ silt, and $0.4 \pm 0.2\%$ organic matter). There was no difference in clay content or P concentrations (Figure 4B) between SEM and sandbar.

Although soils of SEM differed from the sandbar, they had not achieved equivalence to soils of mature marshes in the region. Mature marsh soils (0–10 cm and 10–30 cm) had lower bulk density (Figure 3A) and more organic C and N (Figure 3B) compared to SEM. The mature marshes also contained less sand and more silt, clay, and organic matter than the SEM (Figure 4A). Phosphorus concentrations also were significantly lower in mature marshes (Figure 4B).

Surface (0–10 cm) soil properties of SEM had started to differentiate from subsurface (10–30 cm) soils. Bulk density was less and organic C and N were greater in 0–10 cm depth than 10–30 cm depth of SEM (Figures 3a and 3b). Soil properties of the sandbar and mature marshes did not differ between surface and subsurface layers.

C:N:P ratios varied among the sandbar, SEM, and mature marshes (Table 2). Soil C:N (upper 10 cm) ratios were significantly higher in SEM (15 ± 1) and mature marshes (18 ± 1) than in the sandbar (9 ± 2). In subsurface soils, C:N ratios increased in the following order: sandbar < SEM < mature marshes (Table 2). N:P ratios did not differ between sandbar and SEM soils, but were significantly lower compared to mature marsh soils (Table 2). Within 3

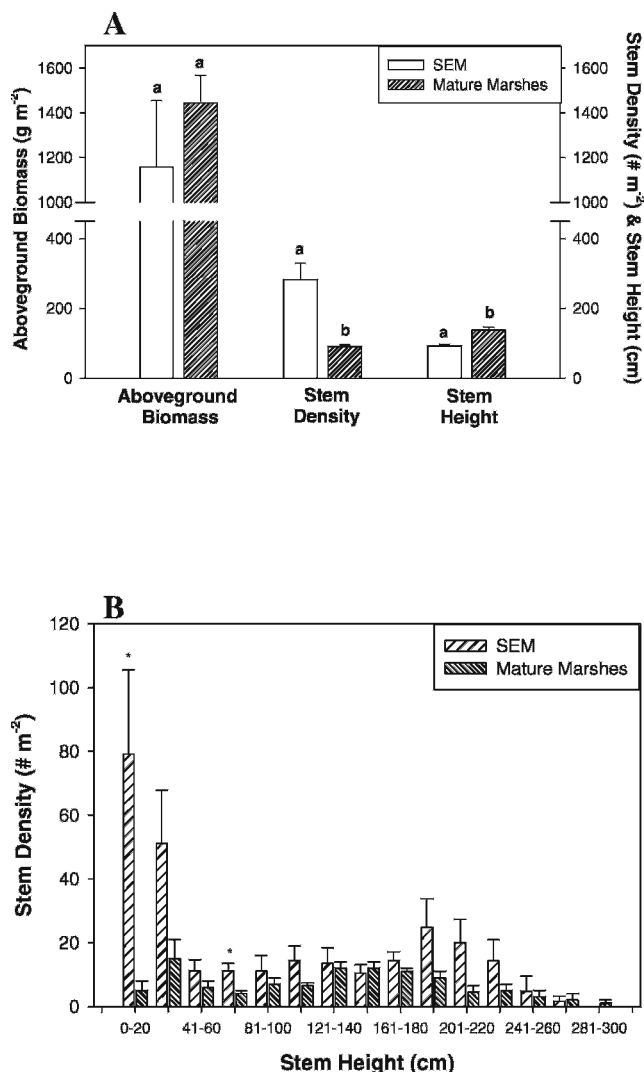


Figure 2. A) Mean aboveground biomass, stem density and stem height (± 1 SE) of the SEM and five mature marshes. Means labeled by the same letter are not significantly different according to the Ryan-Einot-Gabriel-Welsch multiple range test ($p > 0.05$). B) Mean stem density by height classes (± 1 SE) among sandbar emergent and five mature marshes. Asterisks (*) denotes that, for a given height class, the SEM contains significantly ($p \leq 0.05$) more stems than the five mature marshes according to Student's t-test.

years, the SEM had developed significantly greater organic C pools when compared to the sandbar (Table 3A). Even so, SEM soils contained only 27% of the organic C and 41% of the N found in mature marsh soils. However, accumulation of soil N and organic C was five to seven time greater, respectively, in the SEM than in the mature marshes (Table 3B).

Trajectories of tidal marsh ecosystem development, represented by soil organic C and N pools, were developed using data from this study, from a

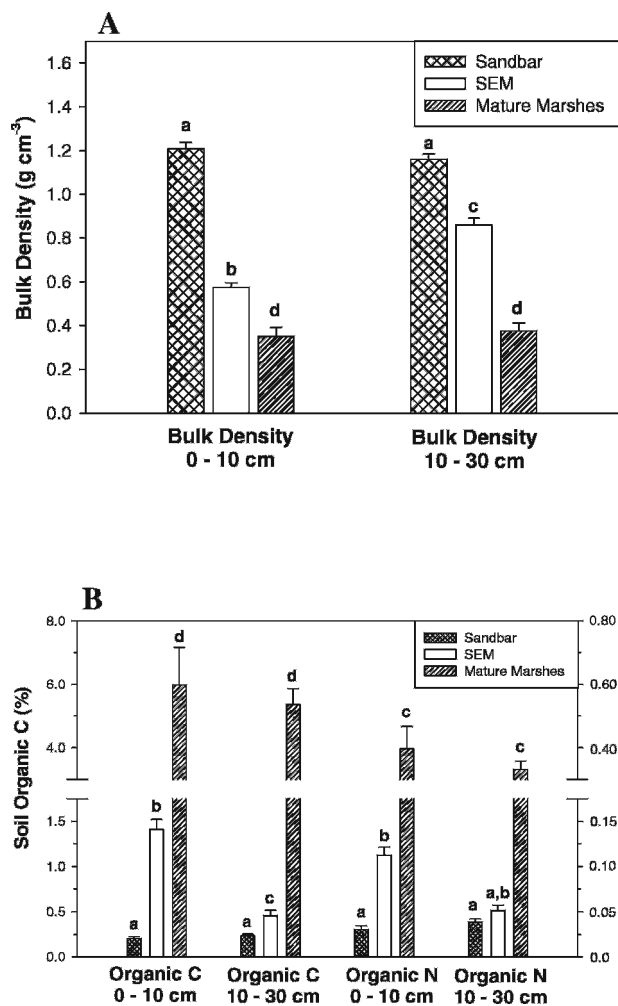


Figure 3. A) Bulk density and B) organic carbon and nitrogen (means \pm 1 SE) of the sandbar, SEM and five mature marshes. Means labeled by the same letter are not significantly different according to the Ryan-Einot-Gabriel-Welsch multiple range test ($p > 0.05$).

sandbar and young and mature *S. alterniflora* back barrier marshes in Virginia (Osgood and Zieman 1993, Osgood et al. 1995), and from young constructed marshes and mature natural *S. alterniflora* marshes in North Carolina (Craft et al. 2003) (Figures 5A and 5B). An asymptotic line described the increase in organic C ($r^2 = 0.90$) and N ($r^2 = 0.70$) with age for marshes from all three regions.

DISCUSSION

Vegetation

Our finding of fewer but taller stems in the mature marshes compared to the SEM is consistent with studies of *S. alterniflora* marshes in North Carolina and *S. foliosa* marshes in southern California, which found young constructed (1 to 3 years) marshes were

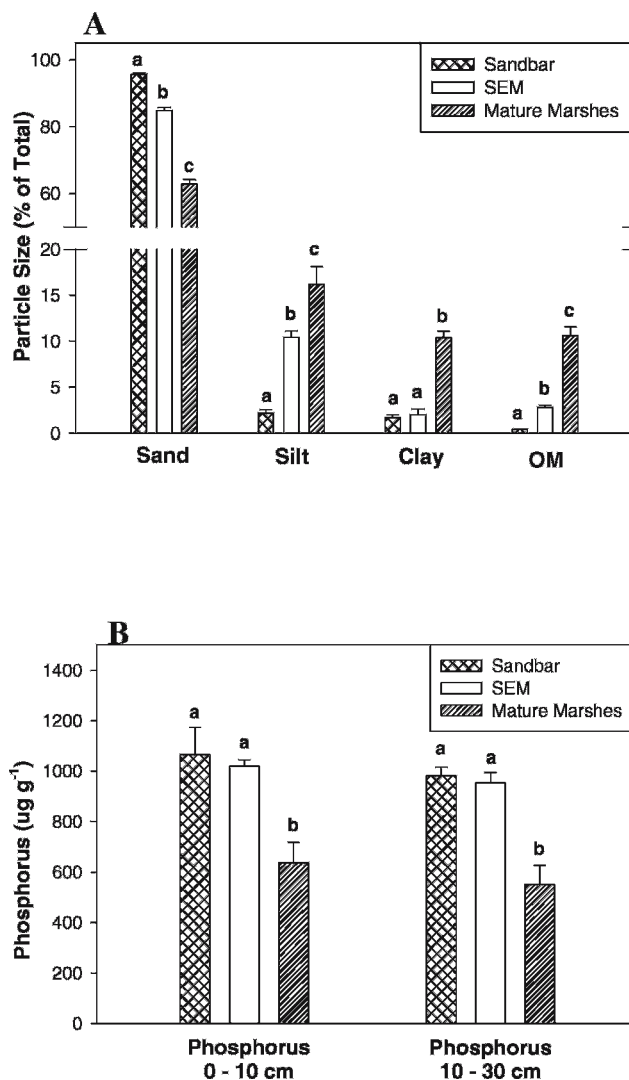


Figure 4. A) Mean percent sand, silt, clay, and organic matter in the upper 10 cm (\pm 1 SE) of the sandbar, SEM and five mature marshes. B) Mean soil phosphorus concentration (\pm 1 SE) of sandbar, SEM and five mature marshes. Means labeled by the same letter are not significantly different according to the Ryan-Einot-Gabriel-Welsch multiple range test ($p > 0.05$).

composed of numerous, short stems whereas mature marshes contain taller but fewer stems (Zedler 1993, Craft et al. 2003). In contrast, Osgood and Zieman (1993) did not observe a difference in stem height between young (10–13 yr old) and mature Virginia marshes; the young marshes in that study were older than our SEM, which could explain the lack of differences. In our study, we observed no difference in biomass between SEM and mature marshes. Craft et al. (2003), however, reported that 1 and 3 yr old constructed marshes in North Carolina contained significantly less biomass than comparable mature natural marshes, which could be attributed to the planting of those marshes with *S. alterniflora*

Table 2. Mean soil C:N and N:P ratios (± 1 standard error) for the sandbar, sandbar emergent marsh and five mature marshes. Means within the same column followed by the same letter are not significantly different according to the Ryan-Einot-Gabriel-Welsch multiple range test ($p > 0.05$).

	C:N (mole:mole)		N:P (mole:mole)	
	0–10 cm	10–30 cm	0–10 cm	10–30 cm
Sandbar	9 \pm 2.0 a	7 \pm 0.3 a	0.7 \pm 0.2 a	0.9 \pm 0.1 a
Sandbar Emergent Marsh	15 \pm 1.0 b	10 \pm 0.5 b	2.4 \pm 0.2 a	1.2 \pm 0.2 a
Mature Marsh	18 \pm 1.0 b	19 \pm 1.0 c	14.5 \pm 2.9 b	14.4 \pm 2.4 b

compared to the natural development of the Georgia marsh.

Soils

Soils of SEM contained more organic C, N, organic matter, and silt, and less sand compared to bare sandbar. Osgood et al. (1995) also found that young Virginia marshes contained more organic C and N than sandbars, and Poach and Faulkner (1998) observed that percent sand decreased with marsh age and organic C, clay, and silt increased with age in naturally colonizing marshes of Louisiana. Similarly, soils of young, constructed marshes in North Carolina contained mostly sand whereas regional natural marshes contained proportionally less sand and more silt and clay (Craft et al. 2003). In Virginia, Osgood et al. (1995) observed no difference in particle size between sandbar and the 14–16 year old marsh that may be attributed to the sediment-starved back-barrier marshes of the Virginia coast as compared to the marshes of the sediment-rich Altamaha River estuary.

Although soils of SEM have begun to differentiate from the sandbar, they have not reached

equivalence with the mature marshes. Consistent with our results, Craft et al. (2003) and Edwards and Proffitt (2003) observed that mature marshes have lower bulk density than young constructed marshes in North Carolina and Louisiana. Craft et al. (2003) and Osgood et al. (1995) also reported higher organic C and N content in mature marshes, relative to young constructed and natural marshes in North Carolina and Virginia. Several studies also found that mature marshes have less sand and more silt, clay, and organic matter compared to younger marshes (Osgood and Zieman 1993, Poach and Faulkner 1998, Craft et al. 2003, Edwards and Proffitt 2003). Contrary to the results of this study, Poach and Faulkner (1998) observed increasing P with age of natural marshes in the Atchafalaya River, Louisiana, an area rich in sediment and P (Poach and Faulkner 1998).

Differences in soil properties of the SEM can be attributed to both ecological succession and differences in elevation among the sandbar, SEM, and mature marshes. Production and decomposition of *S. alterniflora* roots add organic matter to the soil that leads to a reduction in bulk density and an increase in organic C (Craft 2007). Accumulation of

Table 3. A) Mean pools (± 1 SE) and B) accumulation of soil organic carbon, nitrogen, and phosphorus in a sandbar, sandbar emergent marsh, and five mature marshes. Means within the same column followed by the same letter are not significantly different according to the Ryan-Einot-Gabriel-Welsch multiple range test ($p > 0.05$).

A.			
	Pools		
	Carbon (g m ⁻²)	Nitrogen (g m ⁻²)	Phosphorus (g m ⁻²)
Sandbar	790 \pm 35 a	125 \pm 7 a	360 \pm 20 a
Sandbar Emergent Marsh	1580 \pm 110 b	150 \pm 10 a	220 \pm 12 b
Mature Marsh	5830 \pm 250 c	370 \pm 20 b	65 \pm 12 c
B.			
	Accumulation		
	Carbon (g m ⁻²)	Nitrogen (g m ⁻²)	
Sandbar Emergent Marsh	263 \pm 37.0 a	10.8 \pm 3.1 a	
Mature Marsh	35.2 \pm 3.7 b	2.1 \pm 0.2 b	

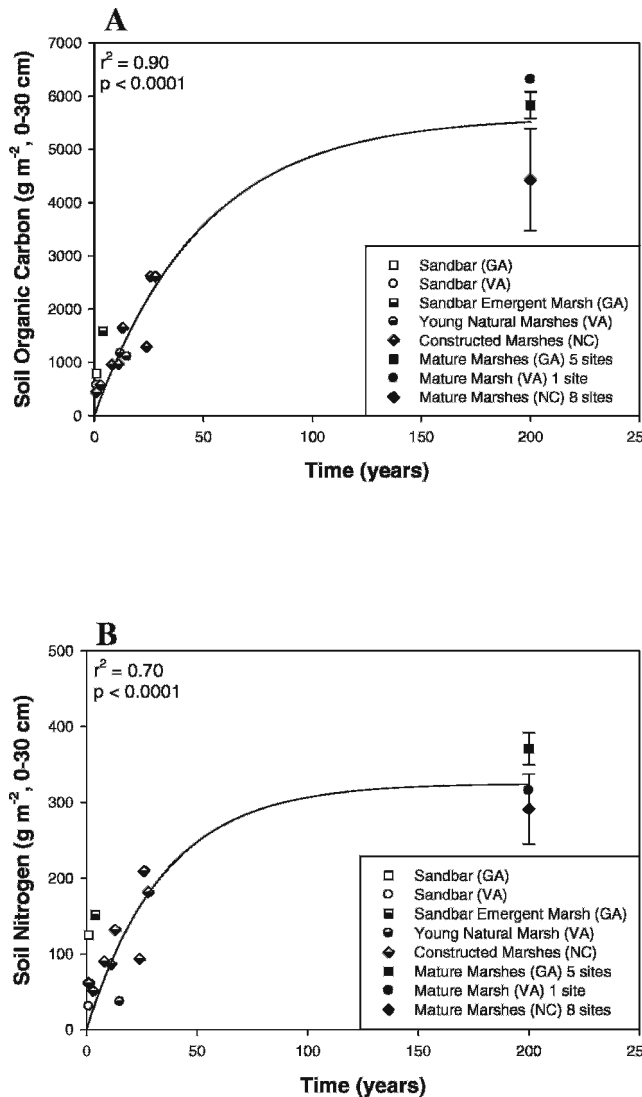


Figure 5. A) organic carbon and B) nitrogen pools of soils (0–30 cm) in Southeastern US *Spartina alterniflora* marshes. Data acquired from natural marshes in Georgia (this study) and Virginia (Osgood and Zieman 1993, Osgood et al 1995), and constructed marshes in North Carolina (Craft et al 2003). Error bars represent one standard error of each regional (e.g., Georgia) mean value.

soil organic matter also increases soil total N since 95% of N in tidal marsh soils exists as organic N (Craft et al. 1991). *Spartina alterniflora* also modifies soil texture as the stems dampen wave energy that allows silt- and clay-size particles to settle (Redfield 1972, Craft et al. 2003). This is evident in the increase in silt-size particles in the SEM relative to the sandbar and in greater silt- and clay-size particles in mature marshes relative to SEM.

Differences in elevation among the sandbar, SEM, and mature marshes also may contribute to differences in soil texture. The mature marshes, and

increasingly the SEM, exist at higher elevations relative to the sandbar (personal observation). During tidal inundation, silt- and clay-size particles are transported onto the marsh surface and deposited in the low(er) energy environment of the vegetated marsh.

Nitrogen:P ratios of the sandbar, SEM, and mature marsh soils were less than 15, indicating N limitation of vegetation according to the Redfield ratio (Redfield 1958) and N:P of 35 of wetland vegetation and soils (Bedford et al. 1999). Soil N:P (0–10 cm, 10–30 cm) increased with marsh age, which was attributed to both increasing N and decreasing P concentration with age.

As soils develop during primary succession, organic matter and nutrients increase as the ecosystem matures until a steady state is reached, at which the rate of nutrient accumulation in soils achieve a low but constant rate of accumulation driven by vertical accretion in response to rising sea level (Silvestri and Marani 2004). In our study, the mature marshes are accumulating C and N in low amounts relative to SEM, suggesting that the mature marshes have reached a steady state. The SEM is in the early stages of ecosystem development as accumulation rates of organic matter and N are considerably greater than in the mature marshes.

Organic C and N pools were larger in the SEM compared to the sandbar but the SEM contained only 27% of the C and 41% of the N found in the mature marshes. Osgood and Zieman (1993) and Craft et al. (2003) also report smaller pools of soil organic C and N in young versus mature marshes. The successional endpoints for natural and constructed *S. alterniflora* marshes along the southeast (GA, NC, VA) coast of the US are similar, about 4500–6500 g C m⁻² and 300–370 g N m⁻², although the rate of development varies as soil properties of salt marshes in river-dominated estuaries may develop faster than back barrier or lagoonal salt marshes in Virginia and North Carolina. Based on our trajectories, we estimate that, after 75 years, soil organic C and N pools of the newly emerging marsh will develop to about 78% to 88%, respectively, of the pools found in mature *S. alterniflora* marshes in the southeastern US coast.

In conclusion, ecosystem development of SEM has proceeded quickly during primary succession. Within three years following colonization by *S. alterniflora*, aboveground biomass was equivalent to mature marshes in the area. Surface soils of SEM had differentiated from the sandbar as organic C, N, and percent silt increased and bulk density and percent sand decreased. Even so, the SEM has not

achieved equivalence to mature marshes as *S. alterniflora* stem height, soil organic C and N pools were less and *S. alterniflora* stem density and soil bulk density were greater in the SEM compared to the mature marshes. Particle size composition also differed with SEM having more sand and less silt, clay, and organic matter than the mature marshes. Comparison of soil organic C and N pools of young natural and constructed tidal marshes of the southeastern US coast suggest that a single trajectory describes the rate of development for these limiting nutrients.

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