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THE PACE OF ECOSYSTEM DEVELOPMENT OF CONSTRUCTED *SPARTINA ALTERNIFLORA* MARSHES

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Abstract. Ecological attributes were measured along a chronosequence of 1- to 28-yr-old, constructed *Spartina alterniflora* marshes to identify trajectories and rates of ecosystem development of wetland structure and function. Attributes related to biological productivity and diversity (*Spartina*, epiphytic and sediment algae, benthic invertebrates), soil development (sediment deposition, organic C, N, P, organic matter quality), and microbial processes (C mineralization) were compared among eight constructed marshes and eight paired natural reference marshes. Most ecological attributes developed in a predictable manner over time, and most achieved equivalence to natural marshes 5–15 yr after marsh construction. An exception was soil organic C and N pools (0–30 cm) that, after 28 yr, were significantly lower in constructed marshes. Development of habitat structure (*Spartina* stem height and density) and biodiversity (algae and invertebrates) developed concurrently with functional characteristics such as biomass, chlorophyll *a*, and invertebrate density. Processes related to hydrology, sediment deposition and soil C and N accumulation, developed almost instantaneously with the establishment of *Spartina*, and young (1- to 3-yr-old), constructed marshes trapped sediment and sequestered N at higher rates than comparable reference marshes. Development of heterotrophic activity (C mineralization, invertebrate density) was strongly linked to surface (0–10 cm) soil organic C content. Ecosystem development of constructed (and natural) salt marshes depended on a minimum of 100 g N/m^2 (0.05–0.1% N) to support emergent vegetation and 1000 g C/m^2 (0.5–1% C) to sustain the heterotrophic community.

Key words: chronosequence; ecosystem development; North Carolina; reference wetland; restoration and rehabilitation; salt marshes; Spartina alterniflora; *wetland creation.*

Introduction

Wetlands frequently are constructed to mitigate for the loss of ecosystem services caused when human activities, such as surface mining, oil and natural gas extraction, highway and pipeline construction, and urban–suburban development, lead to the destruction or degradation of natural wetlands (Kusler and Kentula 1989, National Research Council 1992, Thayer 1992, Zedler 1996*b*, 2001, Zedler et al. 2001). Wetland construction typically involves recreating wetland hydrology and establishing hydrophytic vegetation by planting, seeding, or adding donor wetland soil or seed bank (Kusler and Kentula 1989). However, many wetland construction projects fail to monitor the development of wetland dependent ecosystem services following construction (National Research Council 1992). When post-construction monitoring is undertaken, it usually is limited to the first few years following creation/restoration, and only a few ecological attributes related to vegetation (e.g., percent cover, biomass) are monitored (Zedler 2000).

Post-construction evaluation of created and restored wetlands is limited by the paucity of long-term data sets that describe the development of wetland-dependent ecosystem services (Streever 2000). One study has monitored a suite of ecosystem services, but the monitoring period (3 yr) was too short to assess whether the constructed wetland provided the same level of functionality as natural wetlands (Mitsch et al. 1998). Other studies have tracked the development of wetland-dependent ecological attributes for a longer time (5–25 yr), but the suite of ecosystem services measured was limited in number (Zedler 1996*b*, 2000, 2001, Craft et al. 1999, 2002).

Long-term post-construction monitoring of constructed wetlands suggest that there is an initial lag before these ecosystems provide the same level of ecosystem services as natural wetlands that they were designed to replace (Craft et al. 1988, Sacco et al. 1994, Levin et al. 1996, Scatolini and Zedler 1996, Zedler

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TABLE 1. Characteristics of constructed and natural reference *Spartina alterniflora* salt marsh study sites.

Marsh	Size (ha)†	Age (yr)‡	Tidal range (m)†	Salinity (ppt)†	Geomorphic position†	Soil classification§
1) DOT	0.9	1	1.0	20–30	back barrier flats	typic psammaquent
2) Consultant	1.0	3	1.0	17–32	back barrier flats	typic hydraquent
3) Port	1.0	8	1.0	18–30	back barrier flats	typic psammaquent
4) Swansboro	1.2	11	1.1	20–30	riverine	typic psammaquent
5) Dill's Creek	0.3	13	1.0	14–33	submerged upland	typic hydraquent
6) Pine Knoll	0.3	24	1.0	20–30	back barrier fringe	typic psammaquent
7) Marine lab	0.2	26	1.0	20–30	back barrier flats	typic hydraquent
8) Snow's Cut	0.8	28	1.2	5–20	riverine	typic medisaprist

Note: Marshes were constructed for shoreline stabilization (marsh number 6), dredge spoil stabilization (7, 8), research (3, 4), mitigation on dredge spoil (1, 2), and mitigation on graded upland soil (5).

† Constructed and natural reference marshes. Salinity, in ppt, is grams of salt per kilogram of water.

‡ Constructed marshes only.

§ Natural reference marshes only. All constructed marsh soils are classified as typic psammaquents except Dill's Creek, which was classified as a typic hydraquent (USDA 1975).

2000). In some instances, certain ecosystem services that were lost when natural wetlands are degraded or destroyed required considerable time to develop (Craft et al. 1999, 2002) or never were adequately replaced (Zedler 1993). If wetland creation and restoration is to be successful at replacing wetland loss, it is important to know (1) how much time is needed for these ecosystems to achieve equivalence to natural wetlands and, (2) once equivalence is achieved, whether these ecosystems persist and provide long-term ecological benefits.

METHODS

Site description

We used the chronosequence approach to assess ecosystem development of constructed *Spartina alterniflora* Loisel salt marshes. The chronosquence approach relies on selecting sites that have similar environmental conditions, but differ only with respect to their age. The obvious strength of this approach is that it ''compresses'' time, avoiding the need for long-term repeated measurements on a single site. A limitation of the approach is that, because of variable disturbance histories, differences among sites may be incorrectly attributed to ecosystem development rather than past disturbance events (Pickett 1989).

In this study, we measured a variety of ecological attributes in eight constructed marshes that possess similar tidal inundation, salinity, vegetation, and soils, but differed with respect to age (Table 1). Between 1970 and 1997, salt marsh wetlands were constructed along the North Carolina coast for a variety of purposes, including dredge spoil and shoreline stabilization, and mitigation of wetland loss (Figs. 1 and 2). Marshes were constructed by mechanically grading the planting substrate to intertidal elevation, then planting elevations between mean sea level and mean high water with cordgrass, *Spartina alterniflora* Loisel (Broome et al. 1988). Because the marshes are relatively young ($<$30 yr), we are aware of construction practices and the disturbance history of the eight sites.

Although the constructed marshes were similar in most respects, they differed in their geomorphic or landscape position. Most marshes were located on extensive flats behind barrier islands (back barrier flats). Two marshes were located along intertidal rivers (riverine). The remaining two marshes consisted of a narrow fringe marsh and a submerged upland marsh (Table 1). Differences in geomorphic position might lead to differences in the rate of ecosystem development among the constructed marshes. To reduce this variability, each constructed marsh was paired with a nearby natural marsh of the same geomorphic position, salinity, and vegetation (*S. alterniflora*) to serve as a reference against which to measure ecosystem development of individual constructed marshes. Reference wetlands were used to set performance goals for created and restored wetlands (Aronson et al. 1993*a*, *b*, 1995, Brinson and Rheinhardt 1996, Rheinhardt et al. 1999, Whigham 1999). There was some concern, however, that using one or two references site does not capture the dynamic spatial variability among ecosystems of the same type (Pickett and Parker 1994). But, by pairing each constructed marsh with a reference marsh, we captured much of the dynamic spatial variability of the natural marshes that using one or two reference marshes does not capture.

Paired reference marshes were located adjacent to each corresponding constructed marsh so that marsh pairs had similar geomorphic position, tidal inundation, salinity, and vegetation, but often had different soil types (Table 1). In each natural marsh, the area sampled was comparable in size to the size of the constructed marsh (Table 1). Ecological attributes of reference marshes were statistically tested to determine whether references marshes could be ''pooled'' to create a single reference mean (see *Statistical analysis*). For all attributes, statistically significant differences among natural marshes precluded pooling sites so individual constructed marshes were compared with their respective reference marsh pair.

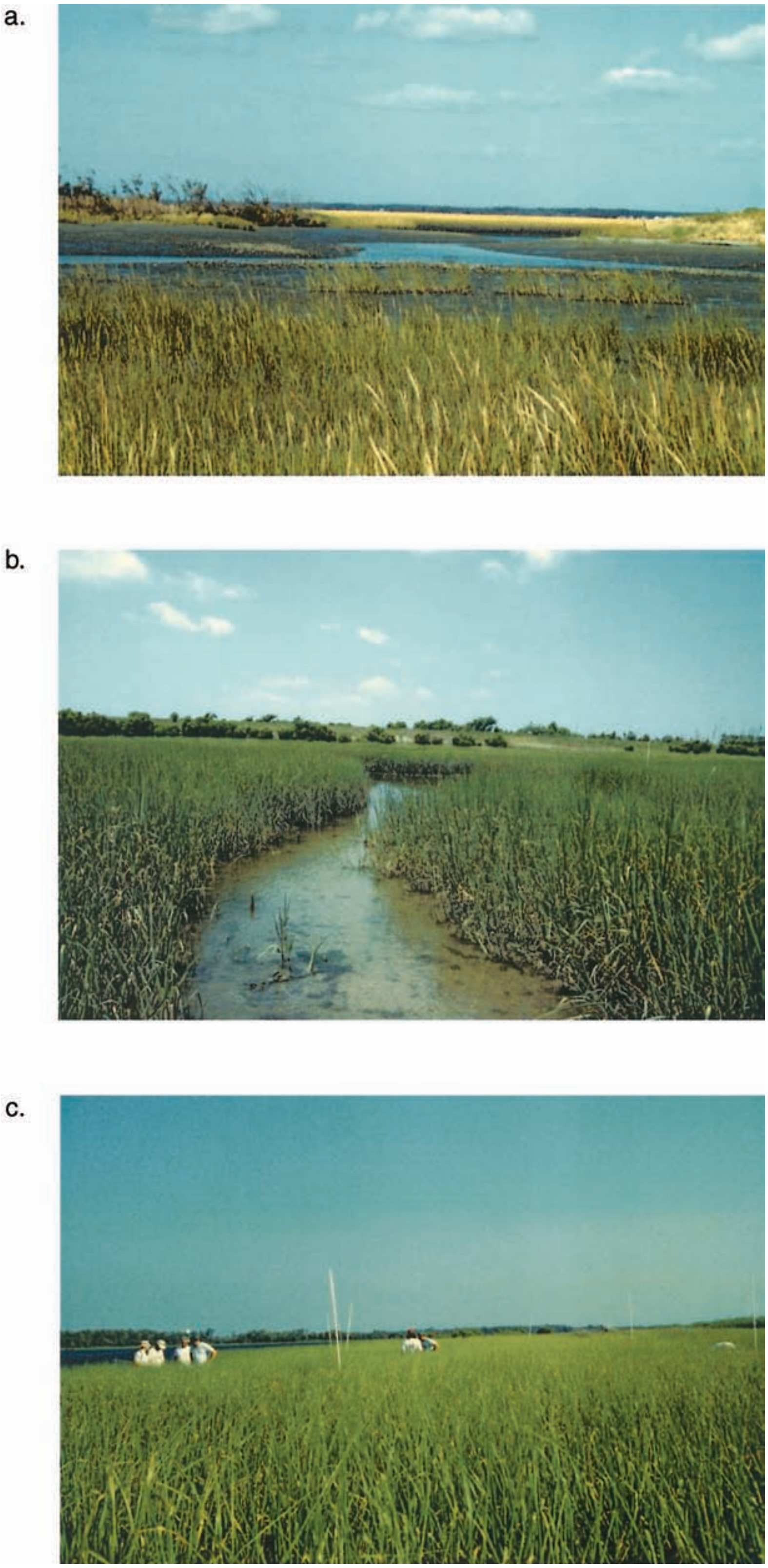


FIG. 1. Photographs of the (a) 3-yr-old (Consultant Marsh), (b) 8-yr-old (Port Marsh), and (c) 28-yr-old (Snow's Cut) constructed marshes. The photographs were taken in June (Consultant Marsh, Port Marsh) and October (Snow's Cut) 1998. Photographs by Christopher Craft.

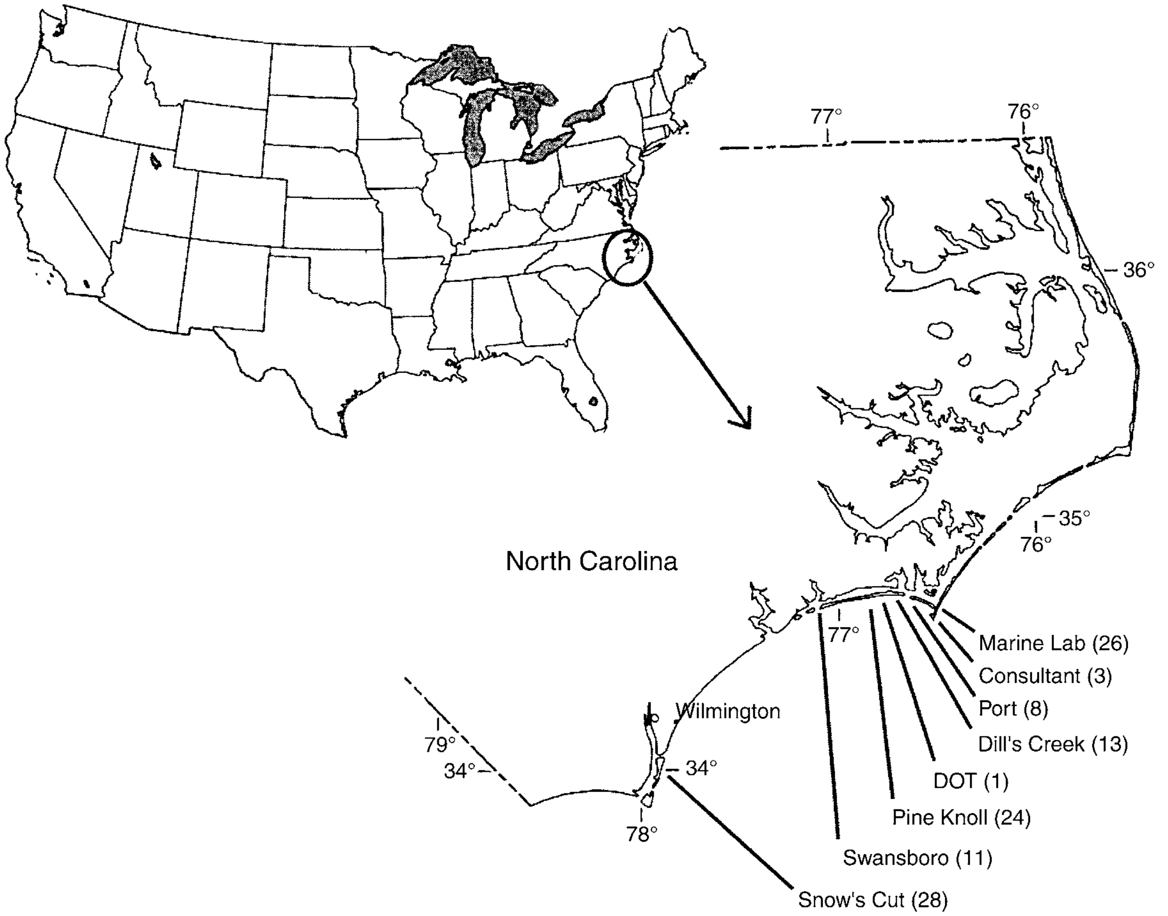


FIG. 2. Map showing the location of constructed *Spartina alterniflora* marshes along the North Carolina coast. Ages of constructed marshes in years are in parentheses.

Sample collection and analysis

We measured ecological attributes related to producers, consumers, and soil/microbial processes. Most attributes described community structure (Zedler and Lindig-Cisneros 2000), but indices of ecosystem function (e.g., biomass) also were measured. Direct measures of ecosystem function included sedimentation, soil organic C, N and P accumulation, and soil organic carbon mineralization. Within each marsh, sampling was stratified with half of the samples randomly collected along the streamside (levee) zone and the other half randomly collected from the marsh interior (marsh plain). Because of the small number of vegetation samples ($n = 5$) collected from each zone, streamside and interior marsh samples were combined for statistical analyses.

Primary production was estimated by measurements of *Spartina* biomass and algae chlorophyll *a*. Aboveground biomass and macro-organic matter (MOM) of *Spartina* ($n = 10$ vegetation and MOM samples per marsh) were collected in October 1998 and processed as described in Craft et al. (1999). Stem density and height of the five tallest stems were also measured. Epiphytic and sediment algae samples ($n = 8$ and 16 per marsh, respectively) were collected in 1998 and analyzed as described by L. Zheng, R. J. Stevenson, and C. B. Craft (*unpublished manuscript*). Secondary production was estimated by measuring the density of benthic invertebrates. Invertebrate samples ($n = 25$ per marsh, 0–5 cm depth) were sampled, processed, and identified as described in Craft et al. (1999).

Soil processes consisted of measurements of sediment deposition and accumulation and storage of soil organic C, N, and P. Sediment deposition was measured two ways: (1) feldspar marker layers and (2) fine particles (silt plus clay) in surface soil. Feldspar was added to two 0.25-m^2 plots in each marsh in October 1998. Five months later (March 1999), five cores per plot were collected, and sediment deposition was measured as described by Cahoon (1994). Ten soil cores (8.5 cm diameter by 30 cm deep) per marsh were collected in June 1998 for particle size analysis. Silt plus clay was measured in surface 0–10 cm subsamples using the hydrometer method (Gee and Bauder 1986). The same soil cores (0–10 cm, 10–30 cm) were analyzed for bulk density, organic C, and total N and P as described in

Craft et al. (1999) to quantify organic C and nutrient pools. In constructed marshes, accumulation of soil organic C, N, and P was calculated as [(0–30 cm organic C, N, P pool) − (10–30 cm organic C, N, P pool) × 1.5))/marsh age] (Craft et al. 1988). Accumulation rates were based on the assumption that, at time 0, organic C was uniformly distributed throughout the 0–30 cm depth. Thus, organic C enrichment of the 0–10 cm depth (relative to the 10–30 cm depth) represents organic C that accumulated since time 0. All of our constructed marshes were mechanically graded such that the planting substrate consisted of the ‘‘C’’ horizon containing essentially no soil organic matter. Thus, our assumption of uniform soil organic C (and N) content in the upper 30 cm of constructed marshes is valid, because we are evaluating ecosystem development during primary, rather than secondary succession.

Organic C, N, and P accumulation in reference marshes was determined using ^{137}Cs and ^{210}Pb along with measurements of soil bulk density and organic C concentrations at 0–10 cm depth (Craft and Casey 2000). One core, 8.5 cm diameter by 30 cm deep, was collected from each natural marsh and sectioned into 2-cm depth increments. ^{137}Cs and ^{210}Pb of depth increments was measured by gamma analysis of the 661.62-keV (kiloelectronvolt) and 46.5-keV photopeaks, respectively. ^{137}Cs- and ^{210}Pb-based vertical accretions were calculated as described in Craft and Casey (2000). Only soil cores containing interpretable ^{137}Cs and ^{210}Pb profiles, such as the ones in Fig. 3, were used to calculate C, N, and P accumulation.

Quality of accumulating MOM (n = 10 per marsh) was determined gravimetrically by sequential extraction in 0.5 mol/L H_2SO_4 and cetyltrimethylammonium bromide to remove water-soluble extractives, followed by extraction with concentrated H_2SO_4 to remove cellulose (Ryan et al. 1990). The material remaining after extraction was combusted at 450°C for 8 h. Lignin was calculated based on the mass lost during combustion (Ryan et al. 1990).

Microbial processes consisted of measurements of potential soil organic C mineralization. Carbon mineralization was measured by laboratory incubations under anaerobic conditions. Eight samples (0–10 cm) per marsh, ~40 g wet mass, were collected in July 1999. Soils were sieved to remove roots, placed in 473-mL capacity glass canning jars and flooded with saline water (30 ppt [grams of salt per kilogram of water]), leaving a 250-mL headspace. The jars were sealed and incubated at 25°C under N_2 atmosphere. CO_2 fluxes were measured roughly every 2 wk over 76 d beginning on day 14. On each date, three 1-min measurements of CO_2 efflux measurements were made per jar by replacing the lid with a modified LI-COR 6400 infrared gas analyzer (LI-COR, Lincoln, Nebraska, USA). The efflux rate was calculated by regression of the CO_2 concentration vs. time, and the average rate of CO_2 evolution was calculated for each marsh for the 76-d period. Periodically, 50 mL of soil water was removed and replaced with fresh saline water (30 ppt) to maintain salinity and reduce the concentration of potential toxic substances.

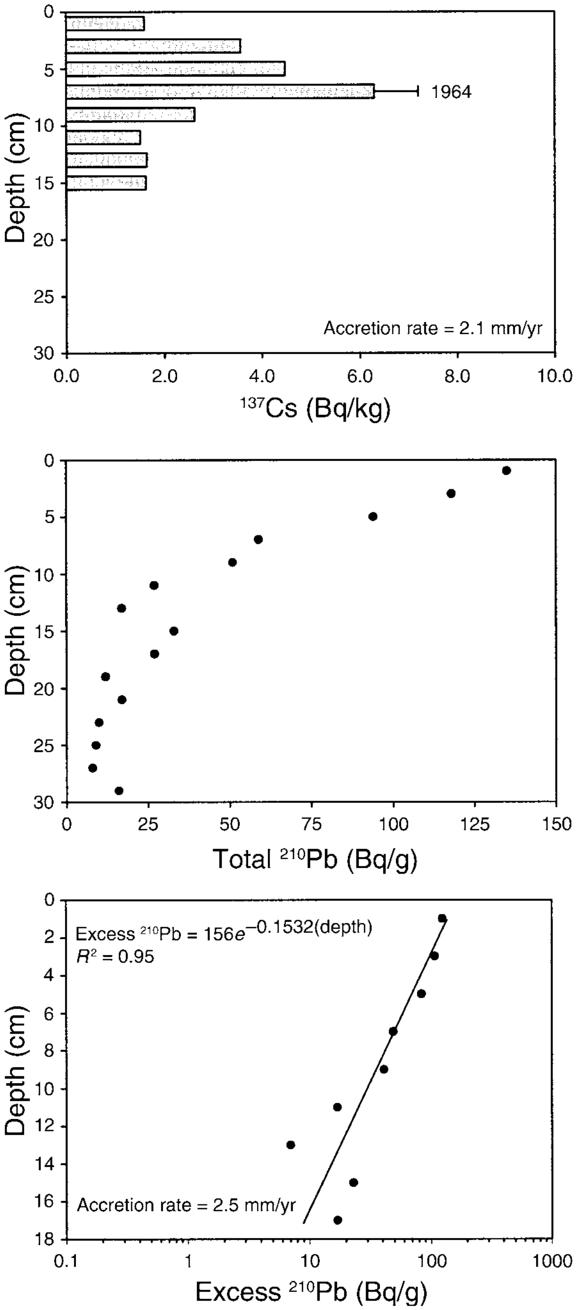


FIG. 3. Depth distribution of ^{137}Cs, total ^{210}Pb, and excess ^{210}Pb in a soil core collected from the natural DOT Marsh. Only profiles like these, that are interpretable, were used to calculate soil organic C, N, and P accumulation of natural marshes. The error bar for 1964 in the top panel is the counting error of the gamma spectrometer.

Measurements of aerobic C mineralization were not made even though it is likely that, in young constructed

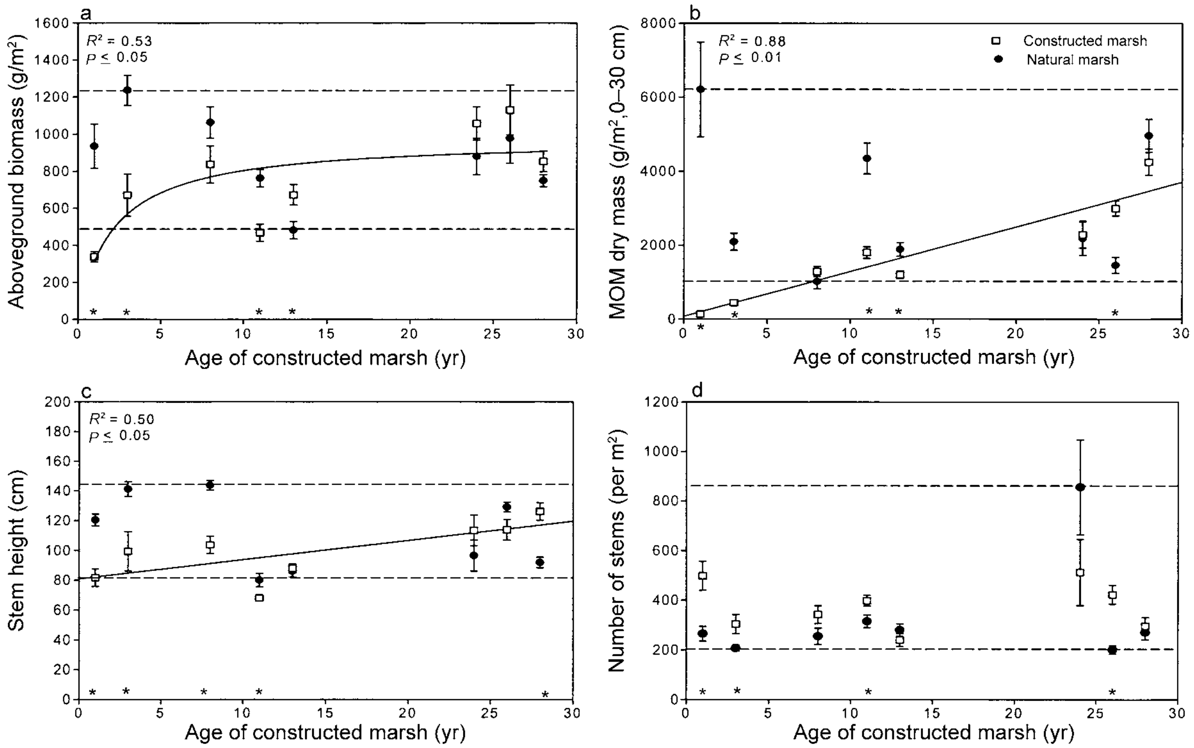


FIG. 4. (a) Aboveground biomass, (b) macro-organic matter, (c) stem height, and (d) stem density of *Spartina alterniflora* along a chronosequence of constructed salt marshes and natural reference marshes. Asterisks (*) indicate that the constructed and paired reference marshes are significantly different ($P \leq 0.05$) according to Student's *t* test. Dashed lines represent the range of values measured in the natural marshes.

marshes, aerobic decomposition may be more important than anaerobic decomposition as a result of coarser (sandy) soil texture and higher redox potential (Eh). As constructed marshes age, accumulation of fine sediments and organic matter may lead to decreased soil Eh with anaerobic processes becoming more important to decomposition and C mineralization.

Statistical analysis

Analysis of variance (ANOVA) was used to test for differences in ecological attributes among natural marshes to determine whether natural marshes could be pooled to calculate a single overall reference mean. ANOVA followed by the Ryan-Einot-Gabriel-Welsch multiple range test (SAS 1996) revealed significant differences ($P \leq 0.05$) among natural marshes that were sometimes, but not always, related to differences in geomorphic position. For this reason, pairwise *t* tests were used to test for differences in ecological attributes between constructed and natural marsh pairs (SAS 1996). Where appropriate, tests were based on the assumption of unequal variances. All tests of significance were made at $P = 0.05$. Regression analysis was used to describe relationships between the measured attributes and constructed marsh age.

CONSTRUCTED MARSH ECOSYSTEM DEVELOPMENT

Structure and function of producers and consumers

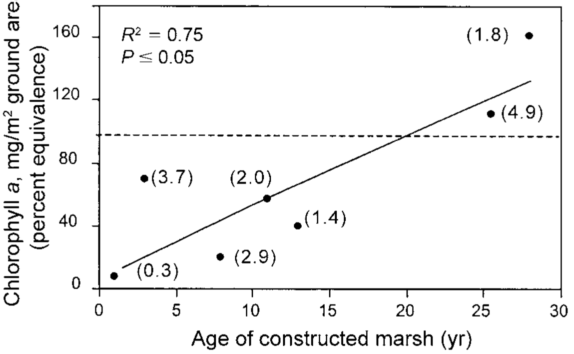
Primary producers.—Aboveground biomass of *Spartina* was significantly related to constructed marsh age ($R^2 = 0.53$), but considerable time elapsed before end-of-season aboveground biomass developed to levels found in natural marshes (Fig. 4a). The 1-, 3-, and 11-yr-old constructed marshes contained significantly less aboveground biomass than comparable natural marshes. Aboveground biomass in the 13-yr-old constructed marsh, however, was significantly greater than the reference marsh. The relationship between aboveground biomass vs. marsh age improved dramatically when the 11-yr-old marsh was excluded from the analysis ($R^2 = 0.87$).

Macro-organic matter (MOM), the living and dead root and rhizome mat, also increased with constructed marsh age ($R^2 = 0.88$), but it required longer to develop than aboveground biomass. Although MOM in the 8-yr-old constructed marsh and paired reference marsh were similar, MOM did not consistently achieve equivalence to the natural marshes for 15 yr (Fig. 4b).

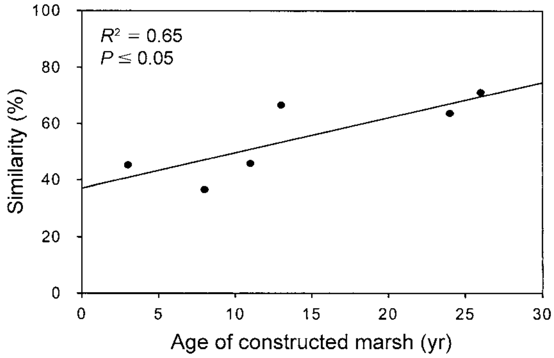
Like biomass, *Spartina* stem height increased with constructed marsh age ($R^2 = 0.50$, and $R^2 = 0.70$ excluding the 11-yr-old marsh), achieving equivalence to the natural marshes after ~12 yr (Fig. 4c). Stem height was strongly correlated with aboveground biomass ($r = 0.82$), suggesting that height is a useful surrogate for aboveground biomass and *Spartina* production. There was no relationship, however, between stem density and constructed marsh age (Fig. 4d), although constructed marshes generally had more stems per square meter than reference marshes. In constructed marshes, *Spartina* produced more stems that were shorter as compared to *Spartina* stems of natural marshes (Fig. 4c, d). Relatively short *Spartina* canopies have been observed in constructed *S. foliosa* marshes in southern California (Zedler 1993), and yearly N additions were needed to consistently produce taller stems that were characteristic of natural marshes in the area (Boyer and Zedler 1998).

In contrast to *Spartina*, algal biomass as measured by chlorophyll *a* was unrelated to constructed marsh age. But, when the data were plotted as ratio of constructed marsh to reference marsh, chlorophyll *a* of epiphytic algae increased with constructed marsh age (Fig. 5a). Chlorophyll *a* of epiphytic algae approached equivalence to natural marshes after 15 yr, roughly the time required for the *Spartina* canopy (stem height and density) to develop, although we found no correlation between the chlorophyll *a* of epiphytic algae and *Spartina* aboveground biomass ($r = 0.12$), stem height ($r = -0.01$), or stem density ($r = 0.04$). There was no relationship between percent equivalence of chlorophyll *a* in surface sediments and constructed marsh age (data not shown). When averaged across all marshes, sediments (4.4 ± 0.5 mg/m^2 [mean ± 1 SE]) and epiphytes (4.2 ± 1.1 mg/m^2) contained similar amounts of chlorophyll *a*, illustrating the importance of both epiphytic and sediment algae to marsh primary production. Percent similarity of diatom species between constructed and reference marshes also increased along the chronosequence (Fig. 5b, c). Minimum similarity index (Gauch 1982) of epiphytic diatoms was 35–46% in constructed marshes younger than 12 yr, increasing to 64–71% in marshes 13 yr old and older (Fig. 5b). The sediment diatom community was slower to develop than epiphytic diatoms. After 25–30 yr, percent similarity of sediment diatoms in constructed marshes was ~50% relative to natural marshes (Fig. 5c). A total of 362 taxa, mostly diatoms (342), filamentous green algae, and blue-green algae (cyanobacteria), were identified in constructed and natural marshes (L. Zheng, R. J. Stevenson, and C. B. Craft, *unpublished manuscript*). More taxa (292) were associated with sediments than with epiphytes (225). The most common soft algae genera included the green algae, *Enteromorpha* and *Rhizoclonium*, and the cyanobacteria, *Ocillatoria* and *Schizothrix*.

a) Epiphytic algae



b) Epiphytic diatoms



c) Sediment diatoms

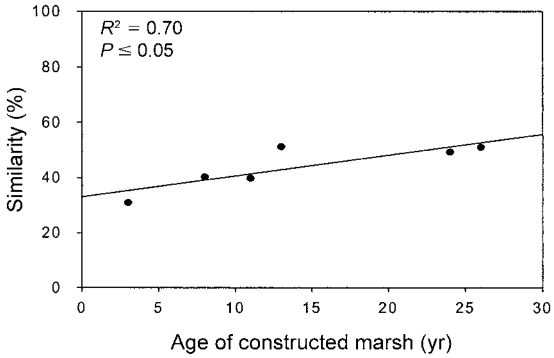


FIG. 5. Percentage equivalence of (a) epiphytic algae chlorophyll *a* along a chronosequence of constructed salt marshes relative to natural reference marshes. Values in parentheses are chlorophyll *a* of the constructed marshes in summer 1998. Percent similarity of (b) epiphytic and (c) sediment diatom communities along a chronosequence of constructed salt marshes and natural reference marshes in spring 1998.

Benthic invertebrates.—Density of benthic invertebrates was significantly lower in the 1- and 3-yr-old constructed marshes as compared to natural marshes (Fig. 6a). Constructed marshes >5 yr old supported invertebrate populations comparable to their natural marsh counterparts. Our findings suggest relatively rapid development of the invertebrate community that contrasts with previous studies of older (up to 16 yr) constructed marshes (Sacco et al. 1994). Invertebrate density was significantly related to constructed marsh age ($R^2 = 0.89$, $P < 0.001$). Young constructed marshes also contained fewer invertebrate taxa than comparable

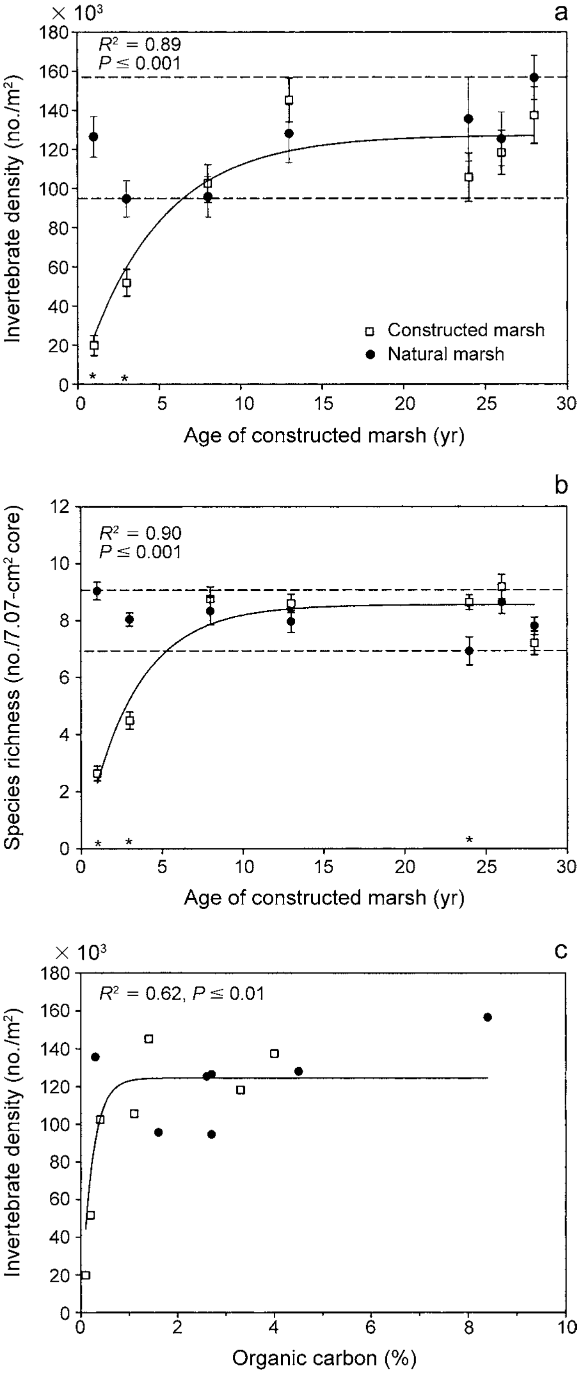


FIG. 6. (a) Density (in thousands per m²) and (b) taxa richness (number of taxa per 7.07-cm² core) of benthic invertebrates along a chronosequence of constructed salt marshes and natural reference marshes. Asterisks (*) indicate that the constructed and paired reference marshes are significantly different ($P \leq 0.05$) according to Student's *t* test. Dashed lines represent the range of values measured in the natural marshes. (c) Regression of benthic invertebrate density vs. percent soil organic C (0–10 cm depth) of constructed and natural marshes.

reference marshes. Species richness was significantly lower in the 1- and 3-yr-old constructed marshes as compared to natural marshes whereas constructed marshes >5 yr old had similar number of taxa as natural marshes (Fig. 6b). Like density, invertebrate taxa richness was strongly related to constructed marsh age ($R^2 = 0.90$, $P < 0.001$).

Invertebrate density was strongly related to percent soil organic C (0–10 cm depth) across all marshes ($R^2 = 0.62$, $P < 0.01$; Fig. 6c). The relationship between invertebrate density and organic C was even stronger when only constructed marshes were analyzed ($R^2 = 0.90$, $P < 0.001$). However, it appears that a critical or "threshold" concentration of ~0.5% to 1% soil organic C is needed to support the high density of benthic invertebrates found in natural marshes (Fig. 6c). Above this threshold concentration, invertebrate densities are relatively uniform across the range from 1% to 8% organic C (Fig. 6c).

Structure and function of wetland soils

Sediment deposition.—Constructed marshes and natural marshes were sinks for suspended sediment although sediment deposition was significantly greater in the 1- and 11-yr-old constructed marshes than in comparable natural marshes (Fig. 7a). There was no difference in sediment deposition between older (24- to 28-yr-old) constructed marshes and comparable reference marshes. Similar to this study, higher rates of sedimentation were measured in young (1- to 3-yr-old) constructed *S. alterniflora* marshes (21–36 $kg \cdot m^{-2} \cdot yr^{-1}$) than in natural reference marshes (<2 $kg \cdot m^{-2} \cdot yr^{-1}$) (Craft 1997). As *Spartina* becomes established, increasing stem density reduces velocity of tidal water and facilitates deposition of suspended particles (Gleason et al. 1979, Knutson 1988). Over time, sedimentation increased the proportion of fine particles in constructed marsh surface soils. Percentage of silt plus clay (0–10 cm depth) increased along the chronosequence of constructed salt marshes ($R^2 = 0.53$; Fig. 7b). Young constructed marsh soils were dominated by sand particles (>90%), whereas natural marshes and the oldest constructed marshes contained less sand (50–70%) and more silt and clay.

Element sequestration.—Soil organic C and N pools were slow to develop in constructed marshes so that, after 28 yr, constructed marshes still contained significantly less soil organic C and N than natural marshes (Fig. 8a, b). Only the 24-yr-old constructed marsh contained soil C and N similar to its paired reference marsh. In constructed marshes, soil N and organic C pools were significantly related to marsh age ($R^2 = 0.69$–0.80). In contrast to C and N, soil P pools generally were larger in the constructed marshes (Fig. 8c). Large amounts of P in constructed marshes probably reflect greater P sorption and precipitation with Fe, Al, and Ca in the low organic matter, high mineral content soils (Craft 1997). Carbon, N, and P stored as macro-

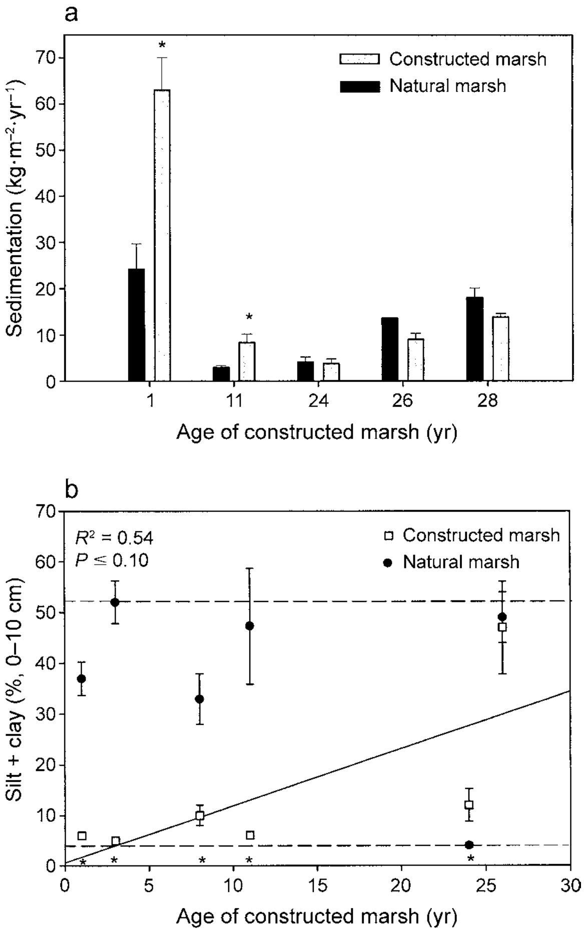


FIG. 7. (a) Sediment deposition and (b) soil silt plus clay (0–10 cm depth) along a chronosequence of constructed salt marshes and natural reference marshes. Asterisks (*) indicate that the constructed and paired reference marshes are significantly different ($P \leq 0.05$) according to Student's *t* test. Dashed lines in (b) represent the range of values measured in the natural marshes. The 13-yr-old constructed marsh (Dill's Creek) was excluded from the analysis because of its terrestrial origin (submerged upland) and, hence, high initial clay content.

organic matter also increased in a predictable manner over time in constructed marshes ($R^2 = 0.86$–0.92, data not shown). However, C, N, and P stored in MOM was an order of magnitude less as compared to C, N, and P in soil.

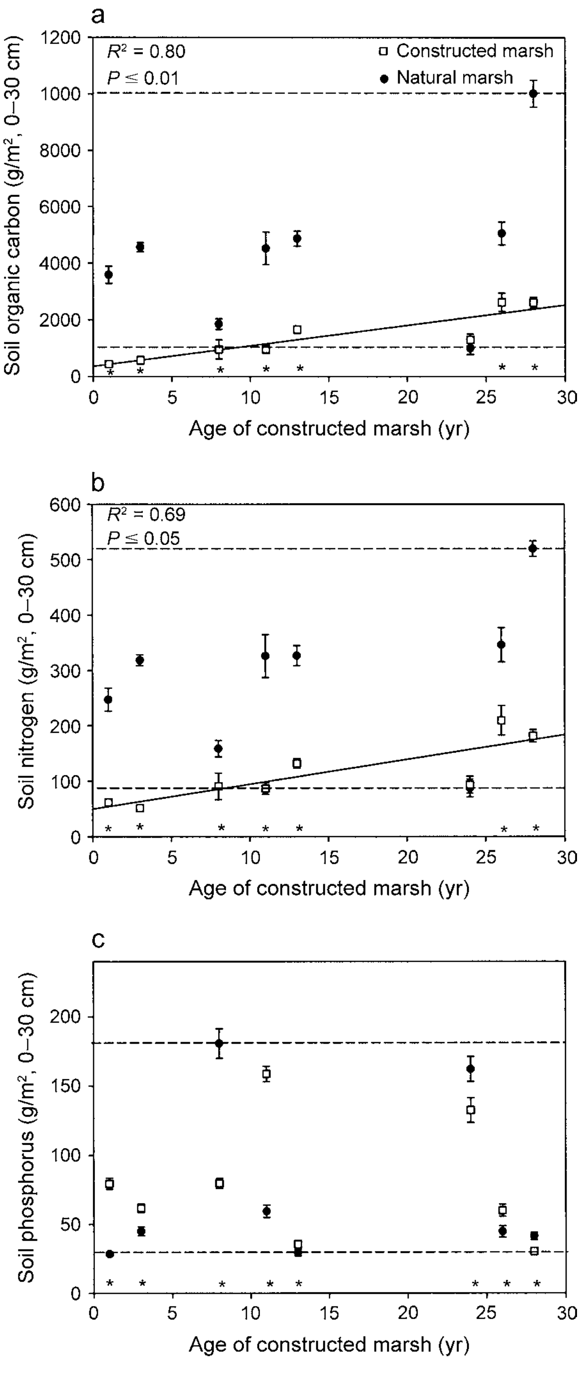


FIG. 8. Soil (a) organic carbon, (b) nitrogen, and (c) phosphorus pools (0–30 cm depth) along a chronosequence of constructed salt marshes and natural reference marshes. Asterisks (*) indicate that the constructed and paired reference marshes are significantly different ($P \leq 0.05$) according to Student's *t* test. Dashed lines represent the range of values measured in the natural marshes.

In spite of smaller soil organic C pools, constructed marshes sequestered C at rates comparable to C accumulation in natural marshes. Organic C accumulation ranged from 18 to 99 g C·m^{-2}·yr^{-1} in constructed marshes (mean = 42 g C·m^{-2}·yr^{-1}) as compared to 0–115 g C·m^{-2}·yr^{-1} (mean = 43 g C·m^{-2}·yr^{-1} based on ^{137}Cs, and 40 g C·m^{-2}·yr^{-1} based on ^{210}Pb) in natural marshes (Table 2). The percentage of above- and belowground net primary production (NPP) buried annually also was similar in constructed (9%) and natural marshes (6%) (Table 2). Percent NPP buried annually in the 1-yr-old constructed marsh (35%) was eight times greater as compared to its paired reference marsh (4%). Among the natural marshes, riverine marshes (Snow's Cut, Swansboro) sequestered proportionally

TABLE 2. Soil organic carbon, nitrogen, and phosphorus accumulation along a chronosequence of constructed salt marshes and natural reference marshes.

Marsh	Age (yr)†	Organic C (g·m^{-2}·yr^{-1})‡ Constructed	Organic C (g·m^{-2}·yr^{-1})‡ Natural	Nitrogen (g·m^{-2}·yr^{-1}) Constructed	Nitrogen (g·m^{-2}·yr^{-1}) Natural	Phosphorus (g·m^{-2}·yr^{-1}) Constructed	Phosphorus (g·m^{-2}·yr^{-1}) Natural
DOT	1	99 (35%)	**30**–36 (4–5%)	12.5	**2.3**–2.8	5	**0.3**–0.3
Consultant	3	39 (7%)	35–**51** (3–5%)	5.5	2.6–**3.8**	0	0.5–**0.7**
Port	8	27 (4%)	**28**–32 (3–4%)	1.9	**2.1**–2.4	0.6	**1.7**–1.9
Swansboro	11	18 (5%)	105–**115** (13–18%)	1.3	6.2–**8.7**	0	0.5–**0.7**
Dill's Creek	13	62 (11%)	**0**–2 (0–<1%)	5.7	**0**–0.1	0.8	**0**–0.02
Pine Knoll Shores§	24	21 (2%)	···	1.9	···	0	···
Marine lab	26	34 (4%)	**0**–15 (0–2%)	2.7	**0**–15	0	**0**–0.02
Snow's Cut§	28	39 (5%)	77 (12%)	2.6	4.0	0.2	0.5
Mean (^{137}Cs)‖		42 ± 9 (9 ± 4%)	43 ± 16 (6 ± 3%)	4.3 ± 1.3	3.0 ± 1.1	0.8 ± 0.6	0.6 ± 0.2
Mean (^{210}Pb)			40 ± 11 (6 ± 2%)		2.8 ± 0.7		0.5 ± 0.2

Notes: Carbon, N, and P accumulation of natural marshes was calculated using ^{137}Cs (in bold) and ^{210}Pb. Carbon, N, and P accumulation of constructed marshes was calculated as described in Craft et al. (1988) (see *Methods* section for details).

† Constructed marshes only.

‡ Percentage of above- plus belowground net primary production (NPP) buried annually in each marsh is reported in parentheses. NPP (g C·m^{-2}·yr^{-1}) was measured as [end-of-season aboveground biomass + (1.1× belowground biomass) × 0.40] as described Craft et al. (1999).

§ No ^{137}Cs peak was discernable in the Snow's Cut marsh so only ^{210}Pb was used to calculate C, N, and P accumulation. Carbon, N, and P accumulation were not calculated for the Pine Knoll Shores Marsh because neither ^{137}Cs nor ^{210}Pb profiles were interpretable.

‖ Natural marshes only.

more NPP as soil organic matter (12–13%) than marshes located on other geomorphic positions (e.g., fringe, flat, submerged uplands; Table 2).

Constructed marsh soils also were sinks for N and, to a lesser extent, P (Table 2). Nitrogen accumulation in the 1- and 3-yr-old constructed marshes was 1.5 to four times greater (5.5–12.5 g·m^{-2}·yr^{-1}) as compared to reference marshes (2.3–3.8 g N·m^{-2}·yr^{-1}). The mean rate of N accumulation in constructed marshes was 4.3 g·m^{-2}·yr^{-1} as compared to 2.8 (^{210}Pb) to 3.0 g·m^{-2}·yr^{-1} (^{137}Cs) for reference marshes. Greater N accumulation in constructed marshes relative to natural marshes reflects strong N limitation and efficient retention of this element in these wetlands (Craft et al. 1999). With the exception of the 1-yr-old constructed marsh, which had the highest rate of P accumulation (5 gm^2/yr), P accumulation in constructed and natural marshes was <2 g·m^{-2}·yr^{-1}. Rates of N and P accumulation measured in our marshes are within the range reported for other natural, constructed, and restored salt marshes (Craft et al. 1999, Craft 2001).

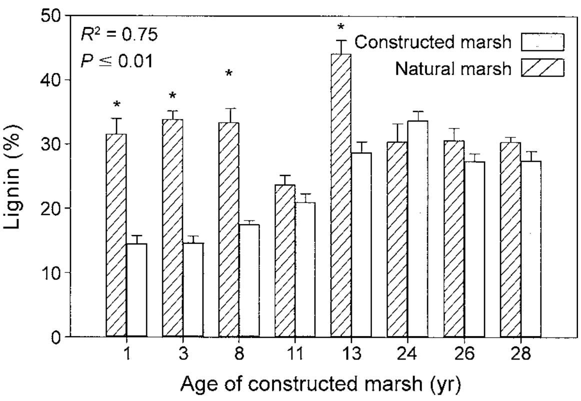


FIG. 9. (a) Lignin content of accumulating macro-organic matter (0–10 cm depth) along a chronosequence of constructed salt marshes and natural reference marshes. Asterisks (*) indicate that the constructed and paired reference marshes are significantly different ($P \leq 0.05$) according to Student's *t* test.

Not only did young constructed marshes sequester carbon at rates comparable to or exceeding that of natural marshes, but accumulating organic matter was of higher "quality" in these marshes as compared to older constructed marshes and natural marshes. In constructed marshes <20 yr old, accumulating macro-organic matter (MOM) contained more labile organic compounds (54–62% water-soluble extractives) and less recalcitrant material (14–34% lignin) than reference marshes (36–53% extractives and 24–44% lignin). Lignin content of MOM increased with constructed marsh age (R^2 = 0.75; Fig. 9), whereas water-soluble extractives decreased with marsh age (R^2 = 0.63, data not shown). Two frequently used indices of organic matter quality, lignin:N, and lignin:cellulose index (LCI; Melillo et al. 1982, Updegraff et al. 1995), also increased with constructed marsh age (lignin:N, $R^2 = 0.66$, $P \leq 0.05$; LCI, $R^2 = 0.63$, $P \leq 0.05$; data not shown). Lignin:N of young constructed marsh MOM was low (15–24) as compared to older constructed marshes (30–44) and natural marshes (29–46). Likewise, LCI was lower in young constructed marshes (0.24–0.39) than in older constructed marshes (0.45–0.63) and natural marshes (0.50–0.71).

In constructed marshes, the abundance of easily decomposable compounds in accumulating organic matter reflects the higher proportion of live roots in MOM as compared to natural marshes that contain more dead roots and decomposed organic matter. These data are consistent with our observation that a greater proportion of the soil organic matter pool is labile, based on carbon mineralization (see Fig. 10c), in constructed vs. natural marshes. There is a trade-off, however, between organic matter quality and C sequestration in soil such that young constructed marshes, with high quality, decomposable MOM, may be less effective in sequestering carbon over the long-term than natural marshes.

Microbial processes.—There was a significant relationship between anaerobic decomposition and percent soil organic C at the 0–10 cm depth (R^2 = 0.69 for all marshes, R^2 = 0.95 for constructed marshes only; Fig. 10a), underscoring the importance of accumulating soil organic carbon for sustaining heterotrophic microbial activity. Soil organic C mineralization increased with age of the constructed marshes (Fig. 10b). Anaerobic decomposition in the 1-, 3-, and 11-yr-old constructed marshes was significantly lower than in natural marshes. Except for the 26-yr-old constructed marsh, mineralization was highest in natural marshes with the highest soil organic C content. In constructed marshes, organic matter mineralization achieved equivalence to natural marshes after soil organic C accumulated to 0.5–1% (0–10 cm depth) or 1000 g/m^2 (0–30 cm depth).

When C mineralization data were expressed as CO_2 evolution per gram of soil organic carbon, CO_2 evolution was higher in the constructed marshes than in the corresponding natural marshes. For example, if constructed and natural marshes had similar CO_2 evolution per gram of soil organic C, the ratio of constructed marsh CO_2 to natural marsh CO_2 would fall along a 1:1 line (see Fig. 10c). Anaerobic incubations of marsh soils, however, revealed that the ratio of CO_2 evolution in young (<5 yr old) and intermediate (5–15 yr old) age constructed marshes vs. natural marshes lay mostly above the 1:1 line (Fig. 10c). These results indicate that, in young and intermediate age constructed marshes, decomposition of soil organic matter is more efficient than in older constructed marshes and natural marshes. Our results suggest that, in spite of low soil organic C and correspondingly low decomposition rate, young constructed marsh soils possess higher heterotrophic metabolism per unit of organic C than older natural marshes. Enhanced carbon metabolism in constructed marshes likely is due to higher quality accumulating macro-organic matter (see Fig. 9a), greater tidal flushing, and, possibly, better aeration of sandy constructed marsh soils as compared to fine-texture natural marsh soils (R. Freese, *unpublished data*).

Conceptual Model of Salt Marsh Ecosystem Development

Ecological attributes describing constructed marsh ecosystem development exhibited three distinct trajectories. Processes linked to hydrology, such as sedimentation and organic C and N accumulation in soil,

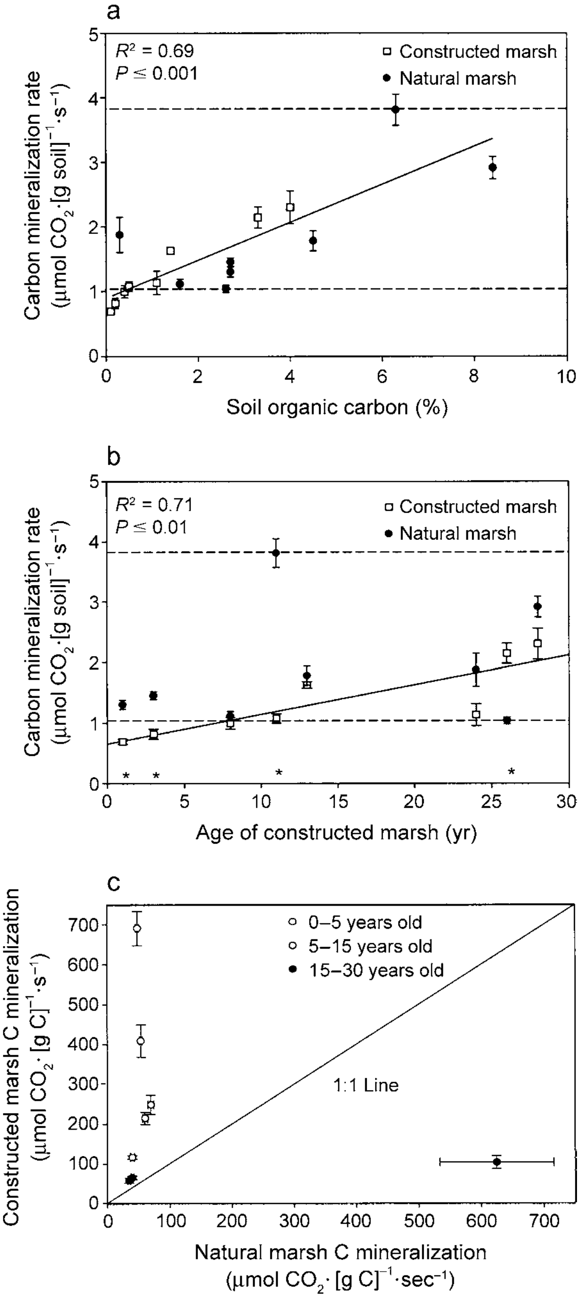


FIG. 10. (a) Regression of anaerobic carbon mineralization vs. percent soil organic C (0–10 cm depth) of constructed and natural marshes. (b) Decomposition of soil organic matter as measured by CO_2 evolution (µmol CO_2·[g soil]$^{-1}$·s^{-1}) during anaerobic lab incubations of constructed and natural marsh soils. Asterisks (*) indicate that the constructed and paired reference marshes are significantly different ($P \leq 0.05$) according to Student's *t* test. Dashed lines represent the range of values measured in the natural marshes. (c) CO_2 evolution (µmol CO_2·[g C]$^{-1}$·s^{-1}) of constructed vs. paired natural salt marsh soils (means ± 1 SE). If constructed and natural marshes possess similar rates of decomposition, the ratio of constructed marsh CO_2 to natural marsh CO_2 will fall along a 1:1 line.

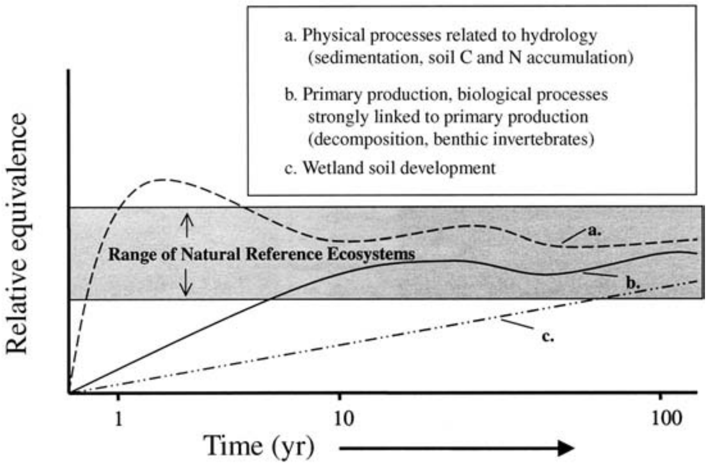


FIG. 11. Trajectories describing changes in functional and structural attributes during salt marsh ecosystem development. Trajectory ''a'' describes processes linked to hydrology (sedimentation, soil organic C and N accumulation) as well as organic matter quality and *Spartina* stem density. Trajectory ''b'' describes attributes of biological processes strongly linked to primary production (consumer and heterotrophic activity). Trajectory ''c'' describes wetland soil development (soil organic C and N pools) and diatom community similarity.

achieved or exceeded equivalence to natural marshes almost immediately following construction (Fig. 11, trajectory ''a''). Processes linked to hydrology are initially rapid because they are the direct result of grading the sites to elevations that are lower than natural marshes. This is especially true along the marsh–open water interface where constructed marshes lack the higher elevation streamside levee that is common to most natural marshes (R. Freese, *unpublished data*).

Biological processes such as primary production and heterotrophic activity increased gradually over time, converging to equivalence to natural marshes after 5–15 years (Fig. 11, trajectory ''b''). *Spartina* aboveground biomass and invertebrate density achieved equivalence within 8 to 13 years following construction. Macro-organic matter, stem height and density, and algal biomass developed somewhat slower, achieving equivalence to natural marshes after ~12–20 years. Biogeochemical processes dependent on soil organic C (e.g., decomposition) also exhibited this type of trajectory, converging to equivalence after 5–15 years.

Some ecological attributes did not achieve equivalence to natural marshes even after 28 years (Fig. 11, trajectory ''c''). Constructed marsh soils consistently contained less organic C and N in the top 30 cm depth than natural marshes regardless of age. This result may reflect differences in the quality of accumulating soil organic matter or physical properties that affect organic carbon protection. For example, greater hydraulic conductivity of the sandy-textured, constructed marsh soils may cause organic matter to decompose faster as compared to natural marsh soils that contain more silt and clay particles. Conversely, soil organic C and N pools (0–30 cm) may take longer to develop than the 28-yr period of record represented by our constructed marsh chronosequence.

Like soil C and N pools, similarity of constructed marsh epiphytic and sediment diatom communities also did not achieve 100% equivalence to natural marshes during the first 28 years. There was, however, a trend of increasing similarity over time as similarity index of epiphytic diatoms approached 70% after 28 years. But, in the case of sediment diatoms, similarity index was only 50% after 28 years following marsh construction. One would not expect 100% similarity of diatom communities between constructed and natural marshes or between two natural marshes for that matter. Natural freshwater wetlands with the same hydrology and vegetation exhibit diatom similarity on the order of 60–70% (J. Stevenson, *unpublished data*). These data suggest that, after ~15 years, our constructed marshes probably contain diatom assemblages that are comparable to natural salt marshes in the area.

From our study, it is apparent that trajectories exist to describe ecosystem development of certain ecological attributes following salt marsh construction. Trajectories describing development of *Spartina* biomass, soil organic matter (C, N), and benthic invertebrate density were previously reported for two of the constructed marshes (Pine Knoll Shores, Snow's Cut) based on periodic measurements of over a 25-year period (Craft et al. 1999). Similarly, trajectories describing development of macrophyte biomass (*Spartina cynosuroides*, *Juncus roemerianus*) and wetland soil characteristics over a 15-year period were reported for a constructed brackish-water estuarine marsh in North Carolina (Craft et al. 2002).

In contrast, ecological attributes of constructed estuarine marshes along the U.S. Pacific coast fail to exhibit directional trends with time or exhibit only weak trajectories following marsh construction (Simenstad and Thom 1996, Zedler and Callaway 1999). In two west coast marshes (southern California, Washington), soil organic matter and N exhibited a weak increase with marsh age, whereas attributes of the macrophyte and benthic invertebrate community were unrelated to marsh age, even 7–12 years after marsh construction (Simenstad and Thom 1996, Zedler and Callaway 1999). For some attributes such as benthic invertebrates and soils, the period of record (7–12 years) probably was too short to identify trajectories. Aboveground biomass and soils in the *Spartina patens* community in the brackish-water marsh in North Carolina also never achieved equivalence to the natural marsh because of infrequent tidal inundation (Craft et al. in 2002). For the constructed marshes, the lack of identifiable trajectories to describe the macrophyte community even after 7 to 15 years suggests that these marshes may never achieve full or complete equivalence to the natural marsh ''target'' (Zedler and Callaway 1999).

Since hydrologic forcing drives wetland ecosystem development, the slow rate of ecosystem development reported for some constructed marshes may result from infrequent and unpredictable delivery of freshwater, sediment, and nutrients. The west coast marshes are characterized by high interannual variability with respect to flood pulses (Zedler 2001) that results in high interannual variability of measurements (of biomass and stem height), making it difficult to identify trajectories (Zedler and Callaway 1999). Furthermore, seasonal (November–March) inputs of freshwater and hypersaline (>40 ppt) soil conditions (Zedler 2001) may slow the growth of *Spartina* and, hence, the rate of ecosystem development as compared to southeastern U.S. marshes where rainfall is greater and evenly distributed throughout the year. Comparison of west coast vs. east coast marshes revealed that constructed (192 g/m^2) and natural (453 g/m^2) marshes in southern California contained less *Spartina* biomass than marshes in North Carolina (constructed marsh = 713 g/m^2, natural marsh = 992 g/m^2) (Langis et al. 1991, Craft et al. 1999). In this study, our 3-yr-old constructed marsh contained three times more biomass (671 g/m^2) than a 4-yr-old *S. foliosa* marsh in southern California (192 g/m^2) (Langis et al. 1991).

Human alteration of the surrounding landscape and watershed, as is the case in southern California, also may slow ecosystem development and potential for restoration (National Research Council 1992). Many marsh mitigation projects are located in urban environments where initial conditions, such as altered hydrology and invasive species, interfere with ecosystem development (Zedler and Callaway 1999). The coastal landscape of North Carolina is less degraded than that of southern California, so initial conditions probably are more favorable for ecosystem development to occur and for trajectories to be discerned.

INDICATORS OF STRUCTURAL AND FUNCTIONAL EQUIVALENCE

There is much interest in identifying indicators or performance criteria that can be used to assess functional and structural equivalence of wetland creation and restoration projects (Streever 2000, National Research Council 2001, Zedler 2001). The ideal indicator is one that accurately describes other attributes of ecosystem function and structure and, so, serves as an index for other ecological attributes. The ideal indicator also is predictable (i.e., it changes in a predictable manner over time), easy to measure, and inexpensive (Table 3). Based on these criteria, several soil- and *Spartina*-based indicators are useful for assessing full or complete restoration of created and restored salt marshes. Soil organic C, and to a lesser extent, MOM and N, were significantly correlated with heterotrophic activity (decomposition, benthic invertebrates) and wetland soil development (organic matter quality, silt plus clay) (Table 4), and ecological attributes were more highly correlated when soil organic C and N were expressed on an area basis (grams per square meter, 0–30 cm) rather than a mass basis (percentage, 0–10 cm) (Table 4). Characteristics of aboveground *Spartina* were not as strongly correlated with other ecological attributes as soil organic C and MOM (Table 4). Soil organic C is an excellent surrogate for heterotrophic activity, and it is much easier to measure than decomposition rate or benthic invertebrate community composition. It should be noted that, for benthic invertebrates, a threshold amount of organic C (0.5–1%) is needed to support densities comparable to natural marshes. Above this threshold, invertebrate numbers are relatively uniform up to 8% C, the highest C content reported for our natural marshes. Anaerobic C mineralization, on the other hand, increased linearly with soil organic C, suggesting that decomposition is not restricted by a threshold C concentration. Soil N is important because it represents ecosystem N capital, but, because most soil N is bound in organic C compounds in fairly fixed ratios, its abundance usually tracks that of organic C. Surprisingly, N was not correlated with measures of *Spartina* aboveground production (Table 4). Both C and N were predictable, relatively easy to use and inexpensive (Table 3). It is interesting to note that most ecological attributes required 5–15 years to achieve equivalence to natural marshes, the amount of time required to accumulate 1000 g organic C/m^2 and 100 g N/m^2 in the soil. Soil nutrient pools of 1000 g C/m^2 and 100 g N/m^2 also represent the lowest pools measured in our reference marsh soils (Fig. 8a, b). Bradshaw (1983) suggested that restoration of terrestrial ecosystems required a minimum of 100 g N/m^2 to support a productive, self-sustaining plant community.

In southern California, constructed *S. foliosa* marshes often fail to achieve equivalence because low N slows or arrests ecosystem development (Gibson et al. 1994, Zedler 1996*a*). Nitrogen additions stimulate growth of *Spartina foliosa*, but annual additions are needed to maintain tall stems and high levels of biomass (Boyer and Zedler 1998). Gibson et al. (1994) added 1500 g C/m^2 and up 107 g N/m^2 as alfalfa plus ammonium sulfate to accelerate ecosystem development of *S. foliosa* marshes. At the end of the experiment (20 mo), only 320 g C/m^2 and 36 g N/m^2 (0–8 cm depth) was recovered in the soil and less than 5% was

TABLE 3. Ecological attributes used to assess ecosystem development and structural/functional equivalence to natural marshes.

Ecological attribute	Time required to achieve equivalence (yr)	Indicator status: Predictable†	Easy to use	Inexpensive
Producers and consumers				
Spartina aboveground biomass	5–10	yes (0.53–0.87)	yes	yes
Spartina macro-organic matter (MOM)	15	yes (0.88)	no	yes
Spartina stem density	5–15	no	yes	yes
Spartina stem height	10–15	yes (0.50–0.70)	yes	yes
Algae chlorophyll *a* (epiphytic)‡	15	yes (0.81)	no	no
Algae chlorophyll *a* (sediment)‡	···	no	no	no
Diatom similarity (epiphytic)‡	>30	yes (0.66)	no	no
Diatom similarity (sediment)‡	>30	yes (0.71)	no	no
Benthic invertebrate density	5–10	yes (0.89)	no	no
Benthic invertebrate diversity	5–10	yes (0.90)	no	no
Wetland soils				
Sediment deposition§	instantaneous	···	no	no
Element sequestration				
Soil organic C pools (0–30 cm)	>30	yes (0.80)	yes	yes
Soil N pools (0–30 cm)	>30	yes (0.69)	yes	yes
Organic C and N accumulation§	instantaneous	···	no	no
Organic matter quality (lignin)§	5–15	yes (0.75)	no	no
Microbial processes				
Carbon mineralization	5–15	yes (0.71)	no	no

† Goodness of fit (R^2) of the regression between the ecological attribute and constructed marsh age.

‡ Ratio of constructed marsh to reference marsh.

§ Attributes that perform at a higher level in young constructed marshes as compared to older constructed marshes and natural marshes.

recovered in aboveground biomass (Gibson et al. 1994).

In southern California, reduced N sequestration in constructed marsh soils may be due to greater decomposition of soil organic matter as compared to marshes of the southeastern U.S. Natural marshes in southern California generally contain less soil organic matter (5–10%) than natural marshes elsewhere where soil or-

TABLE 4. Pearson correlation coefficients of ''candidate'' indicators of constructed salt marsh structural and functional equivalence.

	Aboveground biomass (g/m²)	MOM (g/m²)†	Stem height (cm)	Organic C (g/m²)†	Organic C (%)‡	Nitrogen (g/m²)†	Nitrogen (%)‡
Producers and consumers							
Aboveground biomass	···	···	···	···	···	···	···
Macro-organic matter (MOM)	0.64	···	···	···	···	···	···
Stem height	**0.82**	0.68	···	···	···	···	···
Stem density	0.04	−0.08	−0.07	−0.24	−0.21	−0.20	−0.19
Chlorophyll *a* (epiphytes)	0.12	−0.38	−0.01	−0.41	−0.48	−0.35	−0.47
Chlorophyll *a* (sediment)	−0.10	0.34	−0.20	0.22	0.16	0.25	0.11
Similarity (epiphytes)	0.55	0.62	0.35	**0.82**	**0.82**	0.74	0.73
Similarity (sediment)	0.56	0.71	0.29	**0.82**	**0.63**	0.77	0.63
Invertebrate density	0.64	0.71	0.55	**0.80**	0.68	**0.74**	0.61
Invertebrate richness	**0.82**	0.57	0.53	0.63	0.47	0.61	0.42
Wetland soils							
Silt + clay	0.54	0.58	0.37	**0.93**	**0.91**	**0.94**	**0.89**
Organic C (g/m²)	0.67	**0.89**	0.65	···	···	···	···
Organic C (%)	0.60	**0.91**	**0.70**	**0.97**	···	···	···
Nitrogen (g/m²)	0.63	**0.82**	0.58	**0.98**	**0.94**	···	···
Nitrogen (%)	0.57	**0.85**	0.65	**0.96**	**0.99**	**0.96**	···
Organic matter quality (lignin)	**0.72**	**0.70**	0.50	**0.70**	0.60	0.62	0.51
C mineralization	0.58	**0.87**	0.61	**0.99**	**0.98**	**0.97**	**0.96**

Notes: Coefficients were calculated from the mean values of the constructed marshes ($n = 8$, except for $n = 6$ [diatom similarity] and $n = 7$ [Chl *a*, silt + clay, invertebrates]). Coefficients in bold are significant at $P < 0.05$.

† 0–30 cm depth.

‡ 0–10 cm depth.

ganic matter may range from 10–40% (Craft et al. 1999, Callaway 2001). Mild temperatures throughout the year may accelerate decomposition, with resultant low soil organic matter and N pools (Callaway 2001). Another factor that may reduce soil organic matter stocks in southern California marshes is episodic sedimentation from winter storms that dilute surface soil organic matter pools with mineral sediment (Callaway 2001). Also, the amount of *Spartina* biomass produced in southern California marshes is less as compared to marshes of the southeastern U.S. (Langis et al. 1991, Craft et al. 1999) so that less detritus is added to the soil.

CONCLUSIONS

Most attributes of salt marsh structure and function developed in a predictable manner over time following marsh construction. Ecological attributes exhibited two general trajectories during ecosystem development: (1) Processes related to hydrology, such as sedimentation and soil organic C and N accumulation, developed almost instantaneously following marsh construction. (2) Attributes linked to heterotrophic processes tracked the development of soil organic C pools and gradually increased to convergence over time. Primary producers (*Spartina*, epiphytic algae) and heterotrophic activity (decomposition, benthic invertebrates) converged to equivalence within 5–15 years following marsh construction. Development of wetland soil organic C and N pools (0–30 cm depth) did not achieve equivalence to natural marshes within the first 28 years following marsh construction. Soil organic C is ideal for describing the development of salt marsh structure and function following marsh construction. It is predictable, easy to use, inexpensive, and accurately describes development of other ecological attributes. Most ecological attributes required 5–15 years to achieve equivalence to natural marshes, the time needed to accumulate 1000 g C/m^2 and 100 g N/m^2 in the soil. Once C and N accumulate to these levels, constructed marshes provided sustainable ecosystem services comparable to services provided by natural marshes.

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S. W. Broome was involved in design, construction, and monitoring of the six constructed marshes established during the period 1970 and 1990.

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