

ECOSYSTEM GAS EXCHANGE ACROSS A CREATED SALT MARSH CHRONOSEQUENCE

Jeff A. Cornell¹, Christopher Craft², and Patrick Megonigal³

¹George Mason University
4400 University Drive
Fairfax, Virginia, USA 22030

²School of Public and Environmental Affairs,
Indiana University
Bloomington, Indiana, USA 47405

³Smithsonian Environmental Research Center
P.O. Box 28, 647 Contees Wharf Road
Edgewater, Maryland, USA 21037-0028
E-mail: megonigalp@si.edu

Abstract: Salt marshes created on dredge spoil were compared to natural marshes to evaluate the capacity of created marshes to perform carbon cycle functions. Several carbon cycle attributes were measured in eight created *Spartina alterniflora* Loisel salt marshes that ranged from one to 28 years, each paired with a nearby mature natural reference marsh. The attributes measured included gross primary production, respiration, net ecosystem exchange, potential microbial respiration (CH₄ and CO₂), and aboveground biomass. *In situ* exchange rates of CO₂ and plant biomass in created marshes met or exceeded those of reference marshes in three to four years. There was some evidence that ecosystem gas exchange in created marshes developed slightly faster than aboveground biomass production. Soil carbon mineralization per gram carbon was generally higher in the created marshes than reference marshes, suggesting higher carbon quality and/or nutrient availability in the created marshes. However, carbon mineralization rates per gram soil were relatively low in the created marshes due to lower soil organic matter content. With proper construction, we suggest most major carbon fluxes can be established in created salt marshes in less than five years.

Key Words: carbon cycle, created marsh, gas exchange, *Spartina alterniflora*, succession

INTRODUCTION

Wetland creation in the U.S. is a common strategy to mitigate wetland losses due to draining and filling (LaSalle et al. 1991, Noon 1996, Shafer and Streever 2000) or to stabilize sediments (Seneca et al. 1985, Broome et al. 1988). Numerous salt marshes have been created on sandy, low organic matter substrates dredged from North Carolina's Intercoastal Waterway since about 1971 (Craft et al. 1999). These projects involved the creation of large dredge spoil-islands that were later graded and planted with appropriate marsh plant species, such as *Spartina alterniflora* Loisel and *S. patens* (Aiton) Muhl (Radford et al. 1968), which stabilize the dredge material. It is often assumed that a young salt marsh created on dredge spoil substrate is functionally equivalent to a natural salt marsh of a comparable age, and that created marshes have the potential to replace the functions of mature natural salt marshes given enough time (Langis et al. 1991, Craft 1997,

Craft et al. 1999). However, few studies have been conducted to test these assumptions (Poach and Faulkner 1998).

Carbon is arguably the most fundamental element to quantify when assessing the pace of ecosystem development. Most wetland services are influenced directly or indirectly by the capacity of the ecosystem to produce, process, and store organic carbon (Craft et al. 1988a, Craft et al. 2003). Gross primary production (GPP) largely establishes the upper limit of heterotrophic activity in the system, including the secondary productivity of consumers. Microbial respiration (R) and decomposition of organic matter either releases or sequesters nitrogen (and other nutrients), depending on the chemical characteristics of the detritus. Labile carbon availability influences rates of microbial redox transformations such as denitrification. The capacity of an ecosystem to sequester atmospheric CO₂ in biomass or soil organic matter represents an imbalance

Table 1. Characteristics of created marshes, including their age when the study was completed in 1999.

Marsh Name	Site	Age (yr)	Substrate	County (NC)	Year Planted	Salinity (ppt)	Tidal Range (m)
DOT	Y1	1–2	Dredge Spoils	Carteret	1997	20–30	1.0
Consultant	Y3	3–4	Dredge Spoils	Carteret	1996	17–32	1.0
Port	Y8	8–9	Dredge Spoils	Carteret	1990	18–30	1.0
Swansboro	Y11	11–12	Dredge Spoils	Onslow	1987	20–30	1.1
Dill's Creek	Y13	13–14	Graded-Upland	Carteret	1985	14–33	1.0
Pine Knoll	Y24	24–25	Dredge Spoils	Carteret	1974	20–30	1.0
Marine Lab	Y26	26–27	Dredge Spoils	Carteret	1972	20–30	1.0
Snow's Cut	Y28	28–29	Dredge Spoils	New Hanover	1970	5–20	1.2

between GPP and R (i.e., net ecosystem production, NEP), and the net exchange of particulate and dissolved organic carbon with adjacent ecosystems.

Most previous studies of created wetlands have focused on changes in the size of key carbon pools such as soil organic matter (Craft *et al.* 1988a, b, Craft *et al.* 1989, Dayton *et al.* 1996, Padgett and Brown 1999, Streever 2000), organically bound soil nutrients (Langis *et al.* 1991, Craft 1997), and plant biomass (Broome *et al.* 1986, Craft *et al.* 1999). Based largely on changes in pool sizes and pool accumulation rates, Craft *et al.* (2003) proposed a conceptual model consisting of three distinct trajectories of ecosystem development in a chronosequence of created *S. alterniflora* marshes ranging from one to 28 years old. The ecological attributes that developed most rapidly, such as sediment and particulate carbon accumulation, were linked directly to the successful establishment of hydrology. Biological attributes such as plant biomass required five to 15 years to converge on the range expected for natural salt marshes, and more than 28 years was required for pools of soil organic matter to reach natural marsh levels. Similar patterns have been observed in other studies of soil carbon pools (Craft 1988b, Langis *et al.* 1991, Craft 1997, Craft 1999).

Although some previous studies of created wetlands evaluated aspects of carbon cycling, none focused on the full suite of processes that constitute the ecosystem carbon cycle. In particular, the key processes of GPP, R, and net ecosystem exchange (NEE) of carbon dioxide have been overlooked. Immature marshes with low biomass can be expected to have relatively low GPP and R compared to mature marshes with high-biomass. As created marshes age, GPP, R, and NEE should increase to levels that meet or exceed those characteristic of mature ecosystems (Odum 1969). We evaluated development of these relatively dynamic features of the carbon cycle in a chronosequence of created *S. alterniflora* marshes. Our goal

was to determine the amount of time required for carbon pools and gas exchange rates in created salt marshes to reach parity with natural marshes. In particular, we tested the hypothesis that GPP, R, and NEE would be lower in newly created marshes than in nearby natural marshes, but the performance of created marshes would increase to meet or exceed the natural marshes.

MATERIALS AND METHODS

Study Sites

We studied eight created marshes in coastal North Carolina that ranged in age from two to 29 years as of November 1999 (Table 1). Each created marsh was paired with a nearby natural marsh to allow comparisons between created and natural marshes of similar hydrology, salinity, temperature, and other location-specific parameters (e.g., Conn and Day 1997, Craft 1997). Natural marshes were assumed to represent created marshes in a late stage of development. Each marsh experiences high tides twice daily with tidal ranges of approximately 1 m.

The created marshes were generally established on sandy dredge spoil islands, with the sole exception of Dill's Creek marsh, which was created on graded, upland soil. All of the created marshes were originally planted with *S. alterniflora*, which still dominated the plant community at the time of the study. Sampling took place within the *S. alterniflora* community along 30 m-long transects oriented parallel to the closest shoreline or tidal creek, approximately 10 m inland where practical.

Net Ecosystem Exchange

NEE of CO₂ was measured using static chambers. The frames for two static chambers were constructed from 2.5-cm-wide angle aluminum. The base dimensions were 0.5 m × 0.5 m, and the heights were either 0.9 m or 1.5 m to accommodate different

vegetation heights. Closed-cell foam was attached to the bases to insure an airtight seal between the chamber bottom and collars, which were permanently installed in the soil to a depth of 5 cm. Chamber walls were constructed of Tefzel (DuPont, Inc., Circleville, Ohio), which is a clear sheeting that is impermeable to gases. Air temperature changes in the chamber were less than 1°C during incubations.

One month prior to our first sampling campaign, five aluminum collars were randomly placed along a 30-m transect at each marsh. The minimum distance between collars was 3 m. Chambers were clamped to the collars to maintain an airtight seal.

A LI-COR 6200 Portable Infrared Gas Analyzer (herein IRGA) was connected with Bev-a-Line tubing (Thermoplastic Processes, Inc., Stirling, New Jersey) to the chambers for CO₂ measurement. The IRGA was run in closed mode so that chamber air was replaced after sampling. Tubing inside the chamber was oriented to avoid re-sampling. Brushless electric fans were positioned near the chamber base and top to circulate chamber air.

CO₂ fluxes were measured quarterly five times over 13 months beginning in July 1998. Respiration was measured in July and October 1998, as well as January, March, and July 1999. NEE and GPP were measured in July 1998 and July 1999. Incubation time was generally less than 180 s. NEE was measured in full sunlight, which was generally greater than 1,000 μmol m⁻² s⁻¹ and stable during the incubation. Using the same incubation procedure as described above, respiration rates were determined by placing an opaque cover over the chamber. GPP rates were calculated as:

$$\text{GPP} = \text{NEE} + \text{R} \quad (1)$$

Note that both GPP and R are reported as positive values with the understanding that the actual carbon fluxes are in opposite directions relative to the atmosphere.

In July 1999, light response curves were generated by measuring NEE at five different light levels. Light levels were manipulated by placing layers of nylon window screening over the chamber. Two light curves were generated at each marsh.

To obtain a more robust estimate of NEE over a typical summer day (July 1999), we modeled daily NEE using empirical relationships between photosynthetically active radiation (PAR) and temperature (Morris and Whiting 1986, Neubauer et al. 2000). The model was driven by PAR and temperature data measured at the Institute of Marine Sciences in Morehead City, North Carolina (IMS 1999), which was within 140 km of all sites and within 10 km of most sites.

GPP was modeled as a hyperbolic function of light on an hourly time step:

$$\text{GPP} = [(a * I)/(b + I)] \quad (2)$$

where I is average hourly photon flux and a and b are empirically derived constants with units of μmol C m⁻² h⁻¹ and μE m⁻² h⁻¹, respectively (Neubauer 2000). Hourly temperature data was used to calculate R rates (n = 2) as:

$$\text{R}_t = \text{R}_0 \times \text{Q}_{10}^{[(T_t - T_0)/10]} \quad (3)$$

where R_t is the calculated respiration rate (μmol C m⁻² h⁻¹), R₀ is the initial ecosystem respiration rate, Q₁₀ is the temperature coefficient, T₀ is the initial air temperature (°C), and T_t is the air temperature at one of the hourly time steps. Hourly GPP and R rates were summed to obtain daily rates (Neubauer 2000). Q₁₀ was calculated as:

$$\begin{aligned} \log \text{Q}_{10} &= \log(k_2/k_1) \\ &= (E_a/2.3R) \times 10/(T_2 \times T_1) \end{aligned} \quad (4)$$

where E_a is the activation energy, R is the gas constant, k₁ and k₂ are reaction rates, T₁ and T₂ are air temperatures (ideally a 10°K temperature difference, °K), and the term E_a/2.3R was determined from the slope of an Arrhenius plot of log(k) versus 1/temperature (Segel 1976).

Live and standing-dead stem and leaf material was removed from inside the aluminum collars in November 1999. Plant material was returned to the laboratory and dried at 70°C to constant weight. Biomass data from these marshes was previously reported by Craft et al. (2003). However, the Craft et al. (2003) data were collected in October 1998 from locations several meters away from our gas flux plots. The biomass data reported in the present study were collected from the field CO₂ exchange plots, which allowed us to correlate biomass with CO₂ exchange on a per plot basis.

Microbial Respiration

We previously reported rates of potential CO₂ production (per gram dry weight soil) in a synthesis paper (Craft et al. 2003). These data are also reported in the present paper in order to contrast them with potential CO₂ production expressed on a per gram ash-free dry weight basis, and to make comparisons with potential CH₄ production. In July 1999, samples of the top 10 cm of soil were randomly collected from each created and natural marsh along two 30-m transects; one was the same transect used for the CO₂ exchange measurements, and the other was about 10 meters further inland.

At each site, sixteen soil cores were collected, eight from the front transect and eight from the back transect. Adjacent cores in each transect were paired and bulked to create four replicates per transect or eight per site. Soils were kept on ice until they were sieved (5.6-mm mesh) in a cold room within an N₂ atmosphere to remove large roots and shells. Forty-g wet-weight sediment samples were placed in 473-ml glass jars and sealed. Because anaerobic conditions dominate tidal marsh soils, the jars were filled with saline water (30 ppt salinity), leaving a 273-ml headspace, and maintained in an anaerobic atmosphere. Periodically, 10 ml of headspace gas was removed from each jar and replaced with industrial-grade N₂ to reduce concentrations of potentially toxic gases.

Jars were incubated in a temperature-controlled room at 25°C. CO₂ flux was measured on five dates over the course of a 76-day incubation and averaged. Soil respiration sampling, which began 14 days after collection, was measured as CO₂ accumulation in the jar headspace using a LI-COR 6200 Portable Infrared Gas Analyzer that was connected with Bev-a-Line tubing and operated in closed loop mode. The jar headspace was flushed with N₂ prior to sampling, and three separate flux measurements were made per jar. We used the minimum flux measurement of the three for our analysis to avoid artifacts that may have been introduced by connecting the IRGA. Periodically during the incubations, 50 ml of soil water was removed and replaced with new saline water to restore salinity and reduce the concentration of potential toxic substances.

Methane in the jar headspace was sampled through rubber septa 4–7 times over a period of 13 days, beginning 25 days after soil collection. The vast majority of the jars were sampled four times while a small number were incubated up to five days longer to improve the regression fit for the flux measurements. Ten ml of gas was removed with syringes and replaced with industrial-grade N₂. Methane concentration was determined using a Hewlett Packard 5890 gas chromatograph fitted with a flame ionization detector and Porapak Q column. Gas samples that were not immediately analyzed were refrigerated for a maximum of two days. Previous studies showed CH₄ concentrations decreased by less than 10% during storage using the same methods (Megonigal and Schlesinger 2002). Two days after collection, soils were dried at 105°C to constant weight, then combusted at 400°C for 16 hours to quantify soil organic matter (SOM) measured as % loss-on-ignition (LOI). The loss of carbon during the incubation was a negligible fraction of the SOM pool.

Statistical Analysis

A balanced design for within-marsh replication was used for field and lab experiments. The significance level was set at $\alpha = 0.05$ for all statistical tests. Statistical differences between created marsh and natural marsh pairs were assessed using the Wilcoxon exact test (Sokal and Rohlf 1981). Ordinary least squares regressions and correlations were performed to assess relationships among carbon cycle attributes and created marsh age. SAS statistical software was used to generate descriptive statistics and perform statistical tests (SAS 1990).

RESULTS

Plant Biomass

Two created marshes, Y1 and Y11, had significantly less aboveground biomass than their natural reference sites ($p < 0.04$), while two older created marshes, Y13 and Y28, had significantly more aboveground biomass ($p < 0.04$, Figure 1a). There were no significant differences in biomass on the remaining sites, which ranged in age from four to 27 years. These results generally agreed with data reported by Craft *et al.* (2003) for the same sites one year earlier, with two exceptions. They found that the 3-year-old created marsh had significantly less biomass than its paired natural marsh, whereas we found no significant difference between the two marshes a year later when the created marsh was 4 years old. In addition, they found no difference in aboveground biomass between the created 28-year-old site (Y28) and its natural marsh reference.

Field CO₂ Exchange

GPP was generally comparable in even the youngest of the created and natural marsh pairs (Figure 2a). The only exception was the Y11 site, which significantly under-performed its natural reference marsh in the first year (July 1998, $p = 0.02$). At 3 years of age, site Y3 had significantly lower GPP than its reference marsh (July 1998, $p = 0.02$), but at 4 years of age there was no significant difference between the sites (July 1999, $p = 0.84$). Natural marsh GPP was correlated with created marsh age (July 1999, $r^2 = 0.59$, $p = 0.03$, Figure 2b).

Marsh R was significantly greater in created marshes than natural marshes in several instances (Y8 and Y28 in October 1998; Y28 in January 1999; Y8 in July 1999; $p < 0.02$). R was significantly lower in the created marsh Y11 than its natural marsh in

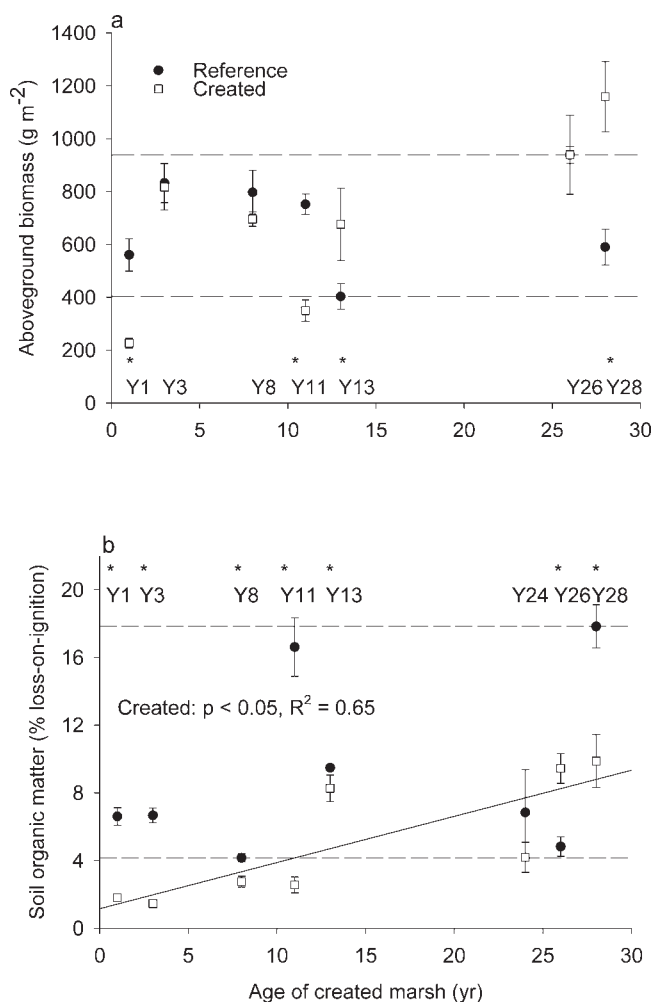


Figure 1. a) Marsh aboveground biomass and b) soil organic matter. Asterisks indicate that the created and paired reference marshes were significantly different ($p < 0.05$) based on Wilcoxon exact tests. Horizontal dashed lines represent the range of values measured in the reference marshes. Regression line illustrates the relationship between created marsh SOM and marsh age. All data are expressed as mean \pm 1 SE.

July 1998 and January and March 1999 ($p < 0.04$). R in created marshes was related to marsh age in July 1998 and 1999 ($p < 0.04$, $r^2 = 0.54$ and 0.57 , respectively, Figures 2c,d). However, R in natural marshes was also related to created marsh age in July 1999 ($r^2 = 0.61$, $p = 0.02$, Figure 2d). R in created marshes was correlated with SOM content in January 1999 only ($r = 0.78$, $p = 0.04$).

Although the overall significance of differences between created and natural marshes was not tested because of the chronosequence design, mean created marsh NEE was greater than natural reference marsh NEE in 79% of the cases (Figures 2e,f). This suggested a tendency for the carbon sequestration potential of created marshes to equal or exceed that

of the natural marshes. However, there was no relationship between instantaneous NEE and created marsh age (Figures 2e,f). Created sites Y11 and Y28 had significantly greater NEE than their natural marsh reference in July 1998, and site Y13 had significantly greater NEE in July 1999 ($p < 0.04$).

Daily Integrated NEE

Q_{10} values were 1.6 at natural marsh Y26 and 1.4 at natural marsh Y28 during July 1999 sampling. We used the average of these values to model hourly and daily R. Although instantaneous CO_2 exchange was based on three to five plots (usually five) per site, daily CO_2 exchange could only be modeled for two plots per site. Therefore, comparing instantaneous and modeled gas exchange data directly between marsh pairs would be inappropriate. However, modeled GPP and R followed the same patterns as the instantaneous results when all marsh pairs were considered. Due to the variability in NEE and small sample sizes, there was no clear relationship between modeled and instantaneous NEE across all marsh pairs.

Daily integrated natural marsh GPP and R, which were measured and modeled independently, were significantly related ($p < 0.01$, adj. $r^2 = 0.81$). Old created marshes generally had higher daily R and GPP rates than the young created marshes, but the statistical differences could not be tested due to sample size limitations. There were no consistent patterns in NEE in comparisons of young (< 5 years) versus intermediate-aged (9–14 years) created marshes or intermediate versus old created marshes.

Microbial Respiration

On a soil dry weight basis, potential microbial respiration (CO_2 and CH_4) determined in lab incubations was significantly lower in created sites Y1, Y3, and Y11 than in the natural reference sites ($p < 0.01$; Figures 3a,b). Created marsh Y28 had lower potential CO_2 production than its reference marsh, a difference that was marginally significant ($p = 0.049$, Wilcoxon test, Figure 3a). Although it is a minor issue with respect to our data interpretation, Craft et al. (2003) analyzed the same data set using a paired t-test and found no significant difference between the Y28 marshes. Created site Y26 was the only marsh with significantly higher potential microbial CO_2 respiration than its natural reference site ($p < 0.01$). Potential microbial respiration from created marsh soils was significantly related to marsh age ($p < 0.05$). Methane production repre-

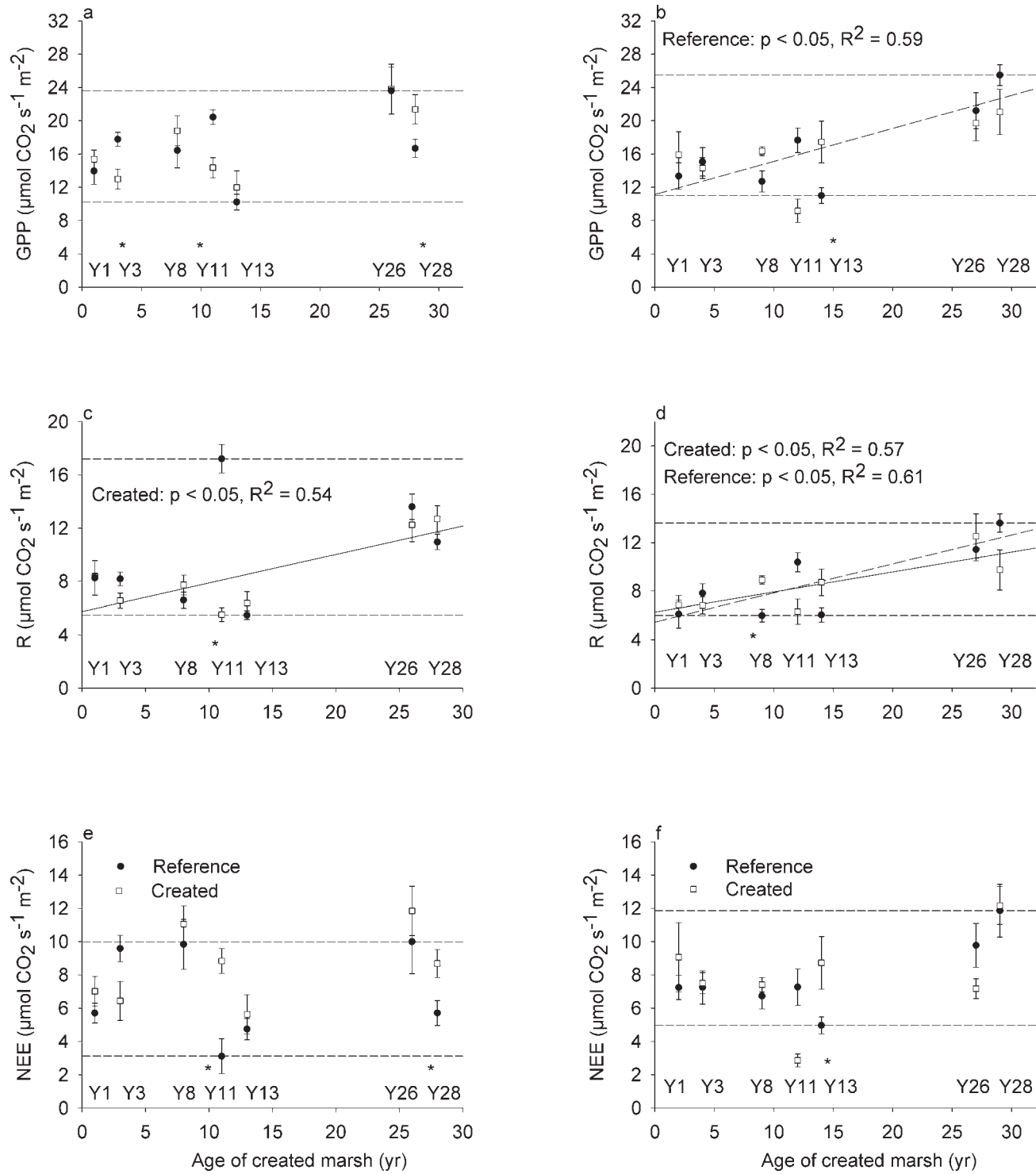


Figure 2. Gross primary productivity (a-1998, b-1999), respiration (c-1998, d-1999) and net ecosystem exchange (e-1998, f-1999) in July 1998 and 1999 versus created marsh age. Asterisks indicate that the created and paired reference marshes were significantly different ($p < 0.05$) based on Wilcoxon exact tests. Horizontal dashed lines represent the range of values measured in the natural marshes. Regression lines (created-solid, reference-dashed) indicate a significant relationship between the marsh component and created marsh age. Note that summer 1999 was hotter and drier than summer 1998. All data are expressed as mean \pm 1 SE.

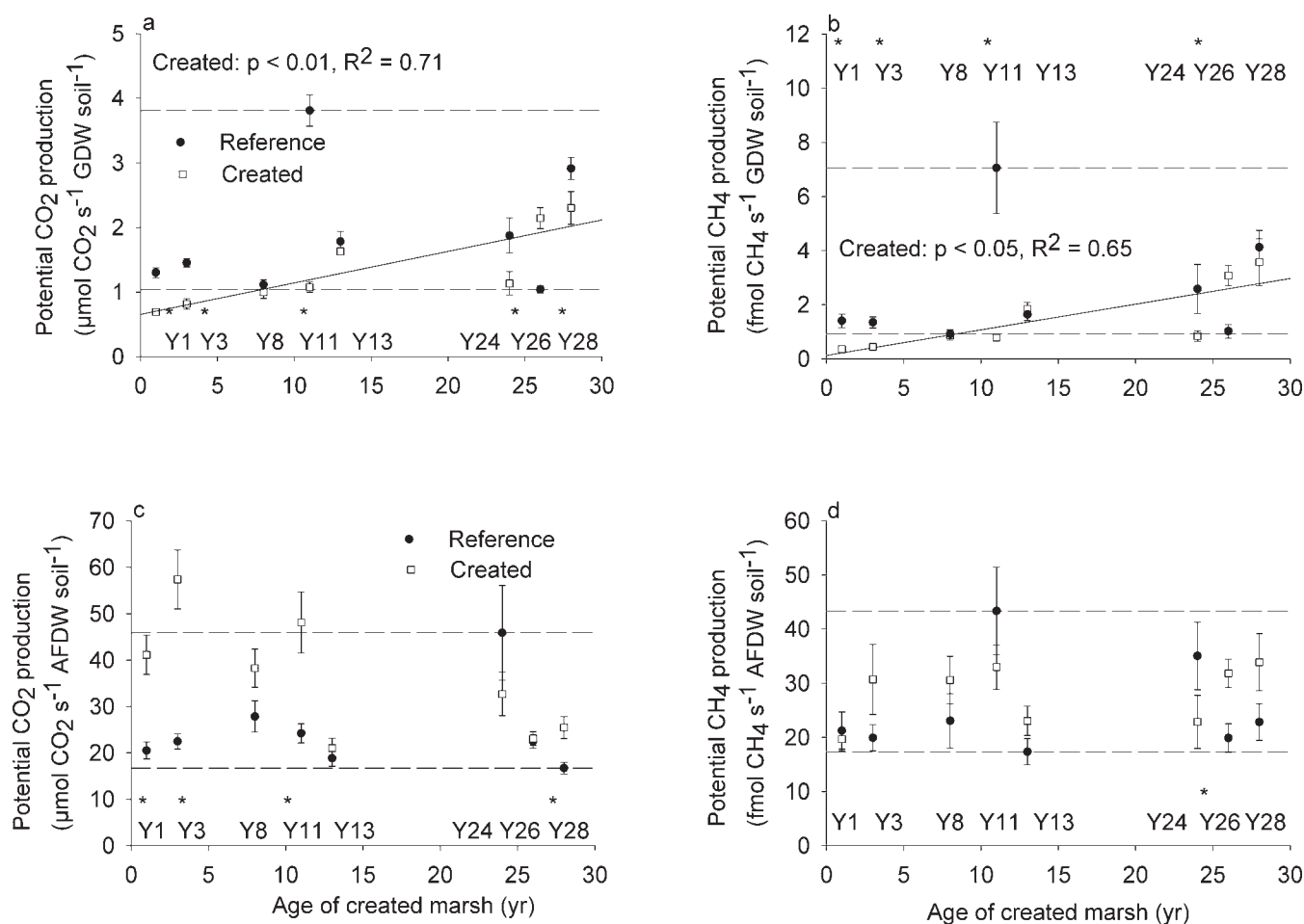


Figure 3. Potential CO₂ production (a-per GDW, c-per AFDW) and potential CH₄ production (b-per GDW, d-per AFDW). Asterisks indicate that the created and natural reference marshes were significantly different ($p < 0.05$) based on Wilcoxon exact tests. Horizontal dashed lines indicate the range of values measured in the reference marshes. Regression lines indicate a significant relationship between the created marsh component and created marsh age. Panel a is reprinted with permission from Craft et al. (2003). All data are expressed as mean \pm 1 SE.

sented less than 1% of total microbial respiration in created and natural marshes as expected given high concentrations of sulfate in the incubation water. Microbial respiration was correlated with above-ground biomass and *in situ* R in July 1999 ($p < 0.05$, $r > 0.76$).

On a carbon mass (i.e., ash-free dry weight) basis, all created marshes but Y24 and Y26 had higher potential CO₂ production than their natural reference marsh. CO₂ production in created marshes was significantly greater than in reference marshes for sites Y1, Y3, Y11, and Y28 (Figure 3c). Created site Y26 had a significantly higher potential CH₄ production rate than its natural reference marsh. SOM content (AFDW) explained a significant amount of the variation in potential CH₄ production in the created and natural marshes (adj. $r^2 = 0.85$, $p < 0.001$, adj. $r^2 = 0.59$, $p = 0.02$, respectively). There was no relationship between potential microbial

CO₂ production and SOM content in either the created or natural marshes.

DISCUSSION

A conceptual model proposed by Craft et al. (2003) identified three distinct trajectories of ecosystem development in created salt marshes. In this model, plant biomass quickly reached parity with natural marshes, but other carbon pools, such as SOM, developed much more slowly (e.g., Seneca et al. 1985, Broome et al. 1986, Craft et al. 1999). Our process-level investigations suggest that key carbon fluxes develop rapidly in created salt marshes, essentially at a pace that matched, or perhaps exceeded, that of plant biomass.

Generally, created marsh aboveground biomass either matched or exceeded reference marsh aboveground biomass. The only exceptions were the

youngest site (1 year) and the consistently underperforming Y11 marsh. In comparison to a study that occurred one year earlier in these same marshes, two of the created marshes showed significant improvement relative to the biomass of their reference marshes. Craft *et al.* (2003) determined that there was no difference between created and natural marsh aboveground biomass in Y28 (28 years old) and significantly less biomass in Y3 (3 years old). One year later, we found that Y28 had significantly more biomass than its reference marsh, and there was no significant difference in Y3. Assuming that the Y11 marsh was an outlier (see discussion following), we suggest that a minimum of three years is required before aboveground plant biomass will meet or exceed levels in natural marshes. Several previous studies have reported comparable rates of plant biomass development in created tidal marshes (Broome *et al.* 1982, Broome *et al.* 1988, Craft *et al.* 1999), while others suggested a somewhat longer time frame of between 5 and 15 years (Seneca *et al.* 1985, Broome *et al.* 1986, Langis *et al.* 1991, Craft *et al.* 2003). A relevant question is whether a minimum period of 3–5 years to reach reference levels of plant biomass is a constraint on the pace of CO₂ gas exchange development in created wetlands. In other words, how closely does ecosystem gas exchange track shoot biomass in developing tidal marshes?

Although the pace of development for both gas exchange and shoot biomass was rapid, there were differences in the trajectories of these attributes that suggest gas exchange may not strictly track shoot biomass. In fact, created marsh plant biomass did not correlate with GPP, R, or NEE (p-values ranged from 0.07 to 0.21). The youngest site (Y1) had significantly less shoot biomass than the natural reference site in 1998 (Craft *et al.* 2003) and 1999 (present study), yet there were no significant differences in GPP, R, or NEE. Some disparity can be expected between the gas exchange and shoot biomass data in these studies because they were measured at different times of year (July and October, respectively), and each represents different levels of temporal integration (instantaneous versus cumulative, respectively). Nonetheless, the present data suggest that it is possible for a created marsh to meet or exceed reference marsh gas exchange rates 1–2 years before shoot biomass becomes comparable. This could occur if plants at young sites (< 3 years old) have higher leaf-level photosynthetic rates than in the natural marshes. Rather than allocating photosynthate to shoot production, plants in the Y1 marsh may have allocated energy to root production to mine N, P, or other nutrients

from the nutrient-poor sandy substrate. We do not have sufficient data to evaluate this hypothesis, but it is notable that Y1 had significantly higher leaf N levels (1.23%, mean of 10 observations, unpublished analysis) than the other created sites in this study (range 0.68% to 0.99%). Leaf N content is generally positively correlated with leaf-level photosynthetic rates because Rubisco and chlorophyll, key biochemicals in the photosynthetic apparatus, are N enriched. Soil nutrient status might be an important regulator of this response because GPP tracked biomass more closely at site Y3 where leaf N levels were comparable to its paired natural site (0.80% and 0.71%, respectively). Testing this hypothesis would require closely following changes in plant physiology in the first few years following marsh creation, and perhaps simultaneously manipulating soil N availability.

The positive correlation between created marsh R and created marsh age would seem to suggest that the oldest created marshes were at an intermediate phase of succession nearly 30 years after marsh creation. However, because reference marsh GPP and R were also related to created marsh age, marsh location and marsh age might be confounded variables for these carbon cycle attributes. We cannot explain why location may have affected gas exchange rates, but possibilities include local nutrient sources and differences in solar exposure. There were no similar correlations between created marsh age and reference marsh plant biomass or soil organic matter. Thus, the appropriate comparisons for assessing change in gas exchange rates over time were between created and reference marsh pairs, and these data suggest that either gas exchange attributes develop very rapidly (*i.e.*, < 3 years) or the model proposed by Odum (1969) does not apply to created marshes. To assess early and intermediate successional patterns in field CO₂ exchange as described by Odum (1969), future research should focus on following young (1–5 years old) created marshes with frequent sampling.

Site Y11 was a consistent exception to the general pattern of rapid convergence of natural and created marsh carbon cycling. The created Y11 site had significantly lower aboveground biomass, SOM, GPP (July 1998), R (July 1998), and potential CH₄ and CO₂ production than its natural reference marsh. We attribute the site's poor performance primarily to flaws in design and construction. Unlike natural marshes that grade smoothly into upland, created marsh Y11 was bordered by a large sand berm that was upwards of 3 m higher than the adjacent marsh. It appeared that sand transport off the berm onto the marsh surface was stressing plants

through burial and thereby limiting overall carbon cycling. Our supposition is in agreement with Craft et al. (2003) who observed significantly higher sedimentation rates in created Y11 than its natural reference marsh. Site Y11 emphasizes the importance of considering the adjacent upland system when designing created tidal marshes.

Potential microbial respiration rates were generally higher in created marshes than reference marshes when expressed as CO₂ production per gram of soil organic matter (Figure 3c). This suggests that heterotrophic microbes in the created marshes mineralized organic carbon more efficiently than those in the natural marshes. Because the incubation conditions were the same for all sites, differences in mineralization efficiency were due to soil properties such as nutrient availability or soil organic carbon quality. A difference in soil carbon quality is consistent with the fact that the lignin content of soil macro-organic matter, consisting largely of live and dead root material, was significantly higher in reference sites than created sites Y1, Y3, Y8, and Y13 (Craft et al. 2003). The influence of this age-related decline in soil carbon respiration efficiency (i.e., respiration per gram carbon) was offset by the increase in the size of the soil carbon pool because the overall soil organic matter mineralization rate (i.e., per gram soil) increased with age and soil organic carbon content (Figures 1b, 3a–d). Although it can take two decades to establish natural levels of soil carbon in created salt marshes, we show that most of the major carbon fluxes are established in less than five years.

Microbial respiration appeared to contribute less than root respiration to total CO₂ emissions from these created marsh soils. Despite the increase in soil organic matter mineralization rate (see previous paragraph), *in situ* summer R (i.e., microbial + root respiration) did not increase with age when compared to the reference marshes (Figures 2c,d). Only in January 1999, when plant respiration was minimal, was *in situ* R in the created marshes significantly related to SOM content (adj. $r^2 = 0.52$, $p = 0.04$). In addition, daily integrated rates of marsh R and GPP in the natural marshes were highly related ($p < 0.01$, adj. $r^2 = 0.81$) suggesting that labile plant compounds were the largest source of CO₂ measured in soil respiration. Most respiration of labile carbon would be expected to occur directly in the roots rather than by microbial respiration of rhizodeposits. The observation that SOM content (AFDW) explained a significant amount of the variation in potential CH₄ suggests that methanogens were carbon limited as expected in wetland soils (Meronigal et al. 2004).

In contrast to the 2–3 year time frame for aboveground biomass restoration, Craft et al. (2003) reported that more than 28 years was required before created marsh SOM content reached levels that met or exceeded the natural marshes on the same chronosequence. Several processes have contributed to the linear increase in SOM with marsh age that they reported. Initially, plant biomass increases, which injects root carbon into the soil profile and deposits shoot carbon on the soil surface. Increasing shoot biomass favors deposition of fine suspended sediments (Darke and Meronigal 2003) and associated particulate carbon. As soil elevation increases due to sediment deposition on the soil surface, flooding frequency and associated sediment inputs decline (Morris et al. 2002, Darke and Meronigal 2003), resulting in less dilution of carbon inputs by sediment. We did not evaluate whether the created marshes were accumulating soil organic carbon at the same rate as natural marshes because surface accretion rates were not measured and radionuclide dating was not possible on created sites. However, we speculate that accretion was more rapid at the young created sites because of their relative low elevations compared with natural or old created sites (e.g., Ward et al. 2003). Craft et al. (2003) reported that sedimentation rates were significantly higher in the created Y1 and Y11 marshes than their paired natural marshes, but there were no corresponding significant differences for created marshes aged 24–28 years (rates were not measured at Y3, Y8, or Y13). Thus, the capacity of created and natural marshes to sequester carbon may be similar at ages less than 30 years despite lower soil carbon concentrations at the created sites.

As with all space-for-time substitution studies, we assumed that differences caused by age would be greater than differences caused by other sources of variability. This assumption held in some instances (e.g., potential CO₂ mineralization, Figures 3a,b) where the response variable was significantly related to created-site age across the created sites, but not the natural sites. In other cases, this assumption did not hold (e.g., July 1999 R, Figures 2d), and interpretation depended on comparisons between a pair of created and natural plots at the same location. The paired-site-comparison approach presumably accounted for variation among sites caused by location-specific environmental factors such as salinity (Table 1). However, there could also be stochastic influences on ecosystem development related to initial conditions that are marsh-specific (Haltner et al. 1997, Boyer et al. 2000, Zedler and Callaway 2000), which a paired-site approach would not capture. All of these issues can be avoided by

tracking ecosystem development on replicate sites in real time, an approach that is feasible for these low-stature ecosystems (e.g., Craft *et al.* 1999).

In conclusion, aboveground biomass in created and natural salt marshes in North Carolina reached parity within 2 to 3 years unless the site was improperly constructed. Plant productivity at one site (Y11) seemed to be under stress due to constant burial from an upland source of sand. GPP, R, and NEE developed at a pace similar to plant biomass development. The possibility that GPP, R, and NEE may develop more rapidly than plant biomass deserves attention from ecophysiologicalists because it suggests there are feedbacks between changes in plant physiology and ecosystem processes that have been overlooked in created marsh research. Further studies of soil elevation change with age are required to understand feedbacks between elevation, sedimentation, and carbon cycle development.

ACKNOWLEDGMENTS

We acknowledge the kind support of Donald Kelso and capable assistance from Joanna Cornell, Milena Arciszewski, Kristin Fitzgerald, Andy May, Carrie deJaco, Cheryl Vann, Bill Kornicker, Shamus Goss, and Katherine Connors. This research was supported by a grant from the U.S. Environmental Protection Agency's Science To Achieve Results (STAR) program through grant #826111-01-0. Although the research described in the article has been funded wholly or in part by the U.S. Environmental Protection Agency's STAR program through grant #826111-01-0, it has not been subjected to EPA review and therefore does not necessarily reflect the views of the Agency, and no official endorsement should be inferred.

LITERATURE CITED

- Boyer, K. E., J. C. Callaway, and J. B. Zedler. 2000. Evaluating the progress of restored cordgrass (*Spartina foliosa*) marshes: belowground biomass and tissue nitrogen. *Estuaries* 23(5): 711–21.
- Broome, S. W., E. D. Seneca, and W. W. Woodhouse Jr. 1982. Establishing brackish marshes on graded upland sites in North Carolina. *Wetlands* 2:152–78.
- Broome, S. W., E. D. Seneca, and W. W. Woodhouse Jr. 1986. Long-term growth and development of transplants of the salt-marsh grass *Spartina alterniflora*. *Estuaries* 9:63–74.
- Broome, S. W., E. D. Seneca, and W. W. Woodhouse Jr. 1988. Tidal salt marsh restoration. *Aquatic Botany* 32:1–22.
- Conn, C. E. and F. P. Day Jr. 1997. Root decomposition across a barrier island chronosequence: litter quality and environmental controls. *Plant and Soil* 195:351–64.
- Craft, C. B. 1997. Dynamics of nitrogen and phosphorous retention during wetland ecosystem succession. *Wetlands Ecology and Management* 4:177–87.
- Craft, C. B., S. W. Broome, and E. D. Seneca. 1988a. Nitrogen, phosphorous, and organic carbon pools in natural and transplanted marsh soils. *Estuaries* 11:272–80.
- Craft, C. B., S. W. Broome, E. D. Seneca, and W. J. Showers. 1988b. Estimating sources of soil organic matter in natural and transplanted estuarine marshes using stable isotopes of carbon and nitrogen. *Estuarine, Coastal and Shelf Science* 26:633–41.
- Craft, C. B., S. W. Broome, and E. D. Seneca. 1989. Exchange of nitrogen, phosphorous, and organic carbon between transplanted marshes and estuarine waters. *Journal of Environmental Quality* 18:206–11.
- Craft, C., J. Reader, J. N. Sacco, and S. W. Broome. 1999. Twenty-five years of ecosystem development of constructed *Spartina alterniflora* (Loisel) marshes. *Ecological Applications* 9:1405–19.
- Craft, C., P. Megonigal, S. Broome, J. Stevenson, R. Freese, J. Cornell, L. Zheng, and J. Sacco. 2003. The pace of ecosystem development of constructed *Spartina alterniflora* marshes. *Ecological Applications* 13:1417–32.
- Darke, A. K. and J. P. Megonigal. 2003. Control of sediment deposition rates in two mid-Atlantic coast tidal freshwater wetlands. *Estuarine and Coastal Shelf Science* 57:255–68.
- Dayton, P. K., L. A. Levin, T. S. Talley, A. McCray, and A. R. Bustamante. 1996. Early successional measurements in a restored tidal marsh. p. 197–202. *Scripps Institution Oceanography, University of California, San Diego, CA, USA.*
- Haltiner, J., J. B. Zedler, K. E. Boyer, G. D. Williams, and J. C. Callaway. 1997. Influence of physical processes on the design, functioning and evolution of restored tidal wetlands in California (USA). *Wetlands Ecology and Management* 4:273–91.
- Langis, R., M. Zalejko, and J. B. Zedler. 1991. Nitrogen assessments in a constructed and a natural salt marsh of San Diego Bay. *Ecological Applications* 1:40–51.
- LaSalle, M. W., M. C. Landin, and J. G. Sims. 1991. Evaluation of the flora and fauna of a *Spartina alterniflora* marsh established on dredged material in Winyah Bay, South Carolina. *Wetlands* 11:191–208.
- Megonigal, J. P. and W. H. Schlesinger. 2002. Methane-limited methanotrophy in tidal freshwater swamps. *Global Biogeochemical Cycles* 16:1062.
- Morris, J. T., P. V. Sundareshwar, C. T. Nietch, B. Kjerfve, and D. R. Cahoon. 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83:2869–77.
- Neubauer, S. C., W. D. Miller, and I. C. Anderson. 2000. Carbon cycling in a tidal freshwater marsh ecosystem: a carbon gas flux study. *Marine Ecology Progress Series* 199:13–30.
- Noon, K. F. 1996. A model of created wetland primary succession. *Landscape and Urban Planning* 34:97–123.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* 164:262–70.
- Padgett, D. E. and J. L. Brown. 1999. Effects of drainage and soil organic content on growth of *Spartina alterniflora* (Poaceae) in an artificial salt marsh mesocosm. *American Journal of Botany* 86:697–702.
- Poach, M. E. and S. P. Faulkner. 1998. Soil phosphorous characteristics of created and natural wetlands in the Atchafalaya Delta, LA. *Estuarine, Coastal and Shelf Sciences* 46:195–203.
- Radford, A. E., H. E. Ahles, and C. R. Bell. 1968. *Manual of the vascular flora of the Carolinas.* The University of North Carolina Press, Chapel Hill, NC, USA.
- SAS. 1990. *SAS/STAT User's Guide, version 6.* SAS Institute, Cary, NC, USA.
- Segel, I. H. 1976. *Biochemical Calculations: How to Solve Mathematical Problems in General Biochemistry.* John Wiley & Sons, Inc., New York, NY, USA.
- Seneca, E. D., S. W. Broome, and W. W. Woodhouse Jr. 1985. Comparison of *Spartina alterniflora* Loisel. transplants from different locations in a man-initiated marsh in North Carolina. *Wetlands* 5:181–90.
- Shafer, D. J. and W. J. Streever. 2000. A comparison of 28 natural and dredged material salt marshes in Texas with an emphasis on geomorphological variables. *Wetlands Ecology and Management* 8:353–66.

- Sokal, R. R. and F. J. Rohlf. 1981. Biometry, second edition. W. H. Freeman and Company, San Francisco, CA, USA.
- Streever, W. J. 2000. *Spartina alterniflora* marshes on dredged material: a critical review of the ongoing debate over success. Wetlands Ecology and Management 8:295–316.
- Ward, K. M., J. C. Callaway, and J. B. Zedler. 2003. Episodic colonization of an intertidal mudflat by native cordgrass (*Spartina foliosa*) at Tijuana Estuary. Estuaries 26(1):116–30.
- White, D. S. and B. L. Howes. 1994. Nitrogen incorporation into decomposing litter of *Spartina alterniflora*. Limnology and Oceanography 39:133–40.
- Zedler, J. B. and J. C. Callaway. 2000. Evaluating the progress of engineered tidal wetlands. Ecological Engineering 15(3–4):211–25.
- Manuscript received 6 March 2006; revision received 27 November 2006; accepted 23 January 2007.