

ECOSYSTEM EFFECTS OF EXPANDING POPULATIONS OF *AVICENNIA GERMINANS* IN A LOUISIANA SALT MARSH

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Abstract: The advancement of species poleward, due to global warming, has recently been documented worldwide. In Louisiana, *Avicennia germinans* (black mangrove) is moving northward into *Spartina alterniflora* salt marshes. Mangroves were historically restricted to southernmost islands and beaches by winter freezes; however, recently a noticeable expansion has occurred. The influence that mangroves have on ecosystem processes within Louisiana salt marshes has not been documented. Thus, this research examined the effects of mangrove expansion on sediment accretion, organic matter production and decomposition, and carbon assimilation, as well as edaphic parameters. Our results indicate that presently mangrove expansion has had no major effects on the ecosystem processes measured. Sediment accretion, belowground production, decomposition, and carbon assimilation were similar between *Avicennia* and *Spartina*. Where mangroves expanded into the surrounding salt marsh, elevation, redox potential, bulk density, and soil ammonium were slightly higher, while soil moisture and porewater salinity were somewhat lower. Because the mangroves are small in stature and areal extent, significant effects on ecosystem processes may presently be somewhat muted. However, if stands continue to grow, noted effects may occur in the future. Our research provides a baseline from which future ecosystem responses may be evaluated as mangroves in Louisiana continue to develop.

Key Words: *Avicennia germinans*, salt marsh/mangrove ecotone, *Spartina alterniflora*

INTRODUCTION

Although the Earth may be in the early stages of the projected trends of global warming, ecological responses to recent warming are already evident. For instance, spring activities of numerous terrestrial and marine plants and animals are occurring earlier than in the past (Walther et al. 2002). In addition, the advancement of plants and animals northward, presumably due to global climate warming, has recently been documented in several regions of the world (Payette 1987, Hersteinsson and MacDonald 1992, Dennis 1993, Parmesan et al. 1999, Thomas and Lennon 1999, Meshinev et. al. 2000, Kullman 2001, Parmesan 2006).

One expected distribution shift occurring in intertidal plant communities along the northern Gulf of Mexico coast is the movement of the subtropical black mangrove, *Avicennia germinans* (hereafter referred to as *Avicennia*), northward into temperate salt marshes dominated by *Spartina alterniflora* (hereafter referred to as *Spartina*). This is the only intertidal plant association in North America that, to our knowledge, is presently experiencing a northward expansion. *Avicennia* and

Spartina grow sympatrically in Florida, Louisiana, and Texas, where *Avicennia* reaches its northern limit in the northern hemisphere. In Louisiana marshes, black mangroves were historically restricted to the southernmost barrier islands and beaches by winter freeze events. However, in recent years freeze-free winters have facilitated a noticeable expansion of *Avicennia* northward into *Spartina* marshes (Figure 1). This northward expansion is likely to continue if increases in temperature occur as predicted by climate change models (IPCC 2007).

While several studies have documented temperature-induced distributional shifts, few have addressed the ecological consequences of these shifts. However, alterations in the ecosystem processes of sediment accretion, organic matter decomposition, above and belowground production, and nutrient cycling, as well as other essential ecosystem functions and services, have recently been attributed to plant expansions in temperate coastal ecosystems (Cohen and Carlton 1998, Olenin and Leppakoski 1999, Nehring 2006). For example, the expansion of *Phragmites australis* into intertidal marshes has resulted in increased elevations of the marsh surface (Windham and Lathrop 1999), as well as increased

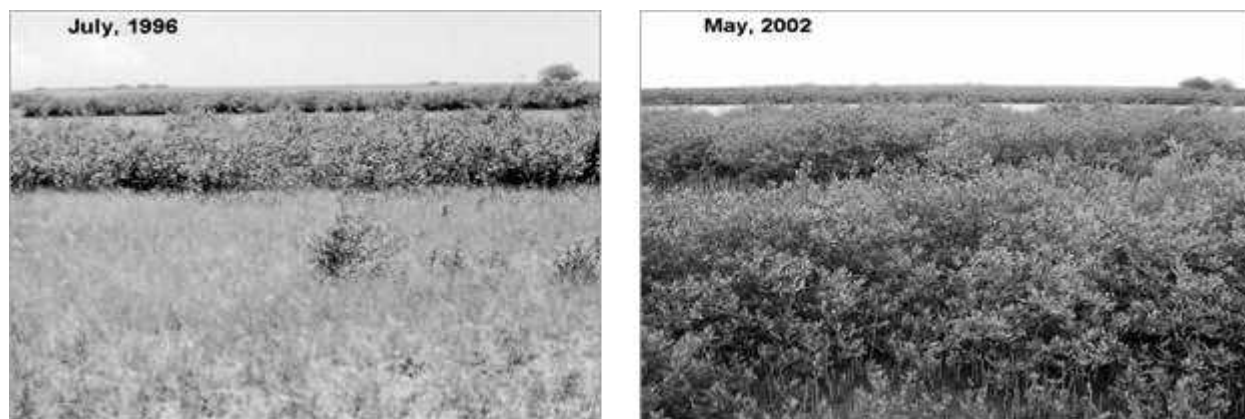


Figure 1. Expansion of *Avicennia germinans* (black mangrove) into a mixed *Spartina alterniflora* salt marsh following several years of mild winters in southeastern Louisiana. Both photographs are of the same view. (photos courtesy of B. J. Milan).

sedimentation due to reduced water flow by fallen plants (Weinstein and Balletto 1999). Similarly, plant expansions can have both direct and indirect effects on soil and porewater chemistry. For instance, newly established plants can alter soil chemistry by releasing oxygen from their roots into the surrounding soil and porewater and, in turn, the oxidation of soil and porewater can influence redox potential and affect plant productivity (Howes et al. 1986) and nutrient availability (Wigand et al. 1997).

Despite the clear effects that plant expansions can have on coastal ecosystem processes in temperate wetlands, little research has focused on the effects subtropical to tropical species may have as they move northward replacing temperate vegetation, as in the salt marsh/mangrove ecotone of Louisiana and Florida. A small body of research has emphasized controls on *Avicennia* and *Spartina* zonation within Gulf coast wetlands (Patterson and Mendelssohn 1991, Patterson et al. 1993, Patterson et al. 1997, Stevens et al. 2006, McKee and Rooth, in press); however, the effects that black mangroves have on ecosystem processes as they expand into *Spartina* salt marsh are still understudied. The goal of this research was to fill this substantial gap in knowledge by examining the effects that expanding populations of *Avicennia* have on the essential ecosystem processes of surface sediment accretion, organic matter production, organic matter decomposition, and carbon assimilation.

This research addressed the following questions: Does the expansion of *Avicennia* into salt marsh 1) Increase the potential for positive elevation change? 2) Accelerate rates of organic matter production and/or decomposition? 3) Increase carbon assimilation? 4) Alter soil and porewater physicochemical characteristics? We predicted that mangroves with their extensive above- and belowground structure,

and high rates of primary production, would better promote the potential for positive elevation change compared to *Spartina*, even though soil organic matter decomposition might be higher in mangrove habitats due to greater soil aeration.

METHODS

Study Site

Louisiana's coastal salt marshes have been, and are still, dominated by the salt marsh grass *S. alterniflora*. Historically, black mangroves have been present as only small populations within salt marshes in the southeastern part of the state. Presently, the most extensive black mangrove populations occur near Grand Isle and south of Leeville (Lester et al. 2005). Black mangrove presence along this part of the coast was documented as early as the 1940's (O'Neil 1949).

Prior to the initiation of our research, aerial photographs (1956, 1957, 1978, 1983, 1985, 1989, 1990, 1995, 1998, 2000, and 2005) were examined to determine an approximate date when black mangroves first established within our particular study site. Based on this historical photo analysis, we determined that black mangroves at the study site were not present in aerial photographs until 1995, although mangroves along the coastal area south of the study site were visible in imagery prior to 1995. Since their establishment in 1995, nearly 15 years of mild winters have allowed existing, and additional, black mangroves to colonize and expand into areas of *Spartina* salt marsh.

The study site was located in a *Spartina* salt marsh adjacent to Bayou Lafourche near Leeville, Louisiana, USA, approximately 8 km from the Gulf of Mexico coast (29.16289°N 90.24295°W to

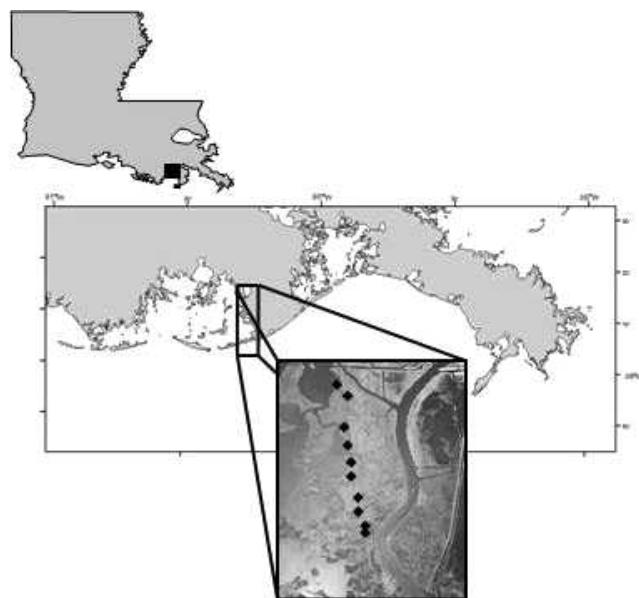


Figure 2. Sampling stations were located in a salt marsh adjacent to Bayou Lafourche near Leeville in southeastern Louisiana, USA. Diamonds on the map denote the 10 sampling stations.

29.21119°N 90.25082°W) (Figure 2). We used a randomized block design with 10 blocks (sampling stations), each containing paired habitats, a black mangrove (*Avicennia*) habitat and a smooth cordgrass (*Spartina*) habitat. Sampling stations were located randomly along a 4 km transect on the east and west sides of a canal dredged in the early 1950s and were characterized by healthy *Avicennia* growing directly adjacent to healthy *Spartina* at equal distances from the canal edge. *Avicennia* and *Spartina* were the dominant plant species, with some *Batis maritima*, *Distichlis spicata*, and *Salicornia* sp. sparsely distributed near most sampling stations. Generally, the stations were no more than 0.5 km from one another, with the exception of stations 9 and 10, which were approximately 2.0–2.5 km north of site 7. The study site was generally inundated throughout most of the summer when south winds moved water onto the marsh, but water levels were often low in the winter when north winds pushed water south into the Gulf of Mexico. Sampling plots were located haphazardly within each habitat at all sampling stations. Each sampling plot consisted of a 3–4 m radius around a central marker. We collected data over a 14-month study period, March 2006 to May 2007.

Sampling

At the initiation of the study, we determined elevations of each habitat at all sampling stations.

We then used three approaches to examine sediment accretion: 1) Sediment traps to measure short-term accretion; 2) Feldspar marker horizons to measure medium-term accretion; and 3) ^{137}Cs to measure decadal accretion. Short-term sediment accretion was examined throughout summer and winter when active sedimentation is greatest in south Louisiana marshes due to summer storm events and winter cold front passages (Cahoon and Turner 1989). Sediment traps were constructed by placing pre-weighed mini compact discs (8 cm diameter) on inverted 9 cm diameter Petri dishes, which were pushed into the marsh so that the discs were flush with the marsh surface (modified from Reed 1992). Sediment deposited on the mini discs was then quantified bi-weekly ($\text{g m}^{-2} \text{d}^{-1}$). Recent accretion rates were estimated for one year by measuring sediment accretion over a feldspar marker horizon (Cahoon and Turner 1989). Decadal-scale sediment accretion was determined with ^{137}Cs dating (DeLaune et al. 1978). One sediment core from each habitat was collected to a depth of 50 cm. Each core was sectioned into 2-cm depth intervals, dried to a constant weight at 65°C, ground, and ^{137}Cs activity counted with a lithium drifted germanium detector. Accretion (mm yr^{-1}) since 1963 was estimated from the depth of the soil layer containing the most ^{137}Cs and the number of years between core collection (2006) and 1963.

We used the in-growth core method of Gallagher et al. (1984) to estimate belowground biomass production. Four in-growth cores per habitat were created by removing a 7.5×30 cm soil volume, which was replaced with root and rhizome-free sediment collected from an adjacent canal. In-growth cores were removed seasonally, and live roots, live rhizomes, and all dead material were sorted and dried to a constant weight. Total belowground production ($\text{g m}^{-2} \text{yr}^{-1}$) was estimated by summing the total amount of live and dead biomass produced at the end of the one year study period.

Decomposition of organic matter was determined with 1) cellulose cotton strips (Maltby 1988) and 2) the litter bag technique (Hackney and de la Cruz 1980). Decomposition of cellulose in heavy artist canvas (12-ounce duck, very close construction, unprimed, raw, 100% cotton, un-dyed, style number 548) (Tara Materials, Inc., Lawrenceville, GA) was utilized as a proxy to examine cellulytic activity. Seasonally, canvas strips were inserted lengthwise into the soil. Strips were retrieved after 12–14 days in the marsh. Reference strips, used to quantify the tensile strength of non-decomposed material, were inserted into the soil and immediately retrieved and

thereafter handled the same as sample strips. All strips were rinsed in water to remove adhering soil, followed by a deionized water rinse, air-dried, and cut into 2-cm sections with a rotary blade. Tensile strength loss per day (CTSL) was then determined with a Dillon Quantrol snapshot tension compression motorized test stand tensometer connected to a Dillon Quantrol advanced force gauge: CTSL ($\%d^{-1}$) = $[(1-N/C)/D] \times 100$, where N is strength of the substrip (Newtons), C is mean strength of the reference substrips, and D is days in the marsh.

We used the litter bag technique (Hackney and de la Cruz 1980) to investigate *in situ* decomposition of roots and leaves. Live, belowground roots of each species were collected by excavation from monospecific stands near the study site and allowed to air dry for 1 week. Mesh bags (8 × 30 cm, 0.4 mm mesh) were then filled with air-dried root material (5 g) and inserted vertically into the soil so the midpoint of root material was 15 cm below the marsh surface. Root bags were retrieved after 195 and 384 days. Leaves were also collected near the study site, air-dried to a constant mass (8 g), placed in mesh bags (8 × 30 cm, 0.4 mm mesh), and anchored to the marsh surface. Leaf bags were retrieved after 69 days. Subsamples of air-dried litter from each species were oven-dried to a constant mass at 65°C to calculate a dry weight conversion factor (air-dry mass:oven-dry mass). The dry-weight conversion factor was then multiplied by the air-dry mass to determine the initial oven-dry mass of each sample. Upon retrieval, litter was again dried to a constant mass and total percentage remaining (X) for leaves and roots was calculated from the mass at the end of the study (X_t) and the initial mass (X_o) as: $X = 100 * (X_t/X_o)$.

We determined photosynthetic rates as instantaneous net CO₂ assimilation using a LI-6400 portable photosynthesis system outfitted with a 2 × 3 cm leaf chamber containing a red and a blue light source and an internal CO₂ controller (LI-COR Inc. Lincoln, Nebraska, USA). The leaf chamber conditions were set to light-saturating conditions of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR and an ambient CO₂ level of 370 ppm. Five measurements were conducted on the youngest fully expanded leaves of three representative *Spartina* plants and the second fully opened leaf on a terminal branch of *Avicennia* plants. Photosynthetic rate (P_n) was expressed as $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$.

We measured leaf area index (LAI) to quantify leaf area per unit ground area so that photosynthetic rates could be expressed m^{-2} of marsh surface. A LAI-2000 Plant Canopy Analyzer (LI-COR Inc. Lincoln, Nebraska, USA) was used to determine the *in situ* LAI. Whole canopy photosynthesis (P_s) was

then calculated: $P_s (\mu\text{mol CO}_2 \text{ m}^{-2} \text{ ground area s}^{-1}) = \text{LAI} \times P_n$, where LAI is leaf area index and P_n is mean rate of photosynthesis per leaf area.

We collected soil cores seasonally to obtain porewater. In the field, cores were stored in 500 ml centrifuge bottles containing air-tight septa, purged with nitrogen gas for two minutes to create an anoxic environment, and stored in a cooler for transport to the laboratory. Once in the lab, the bottles were centrifuged for 30 minutes at 2817 g to extract porewater. Total sulfide concentration (Lazar Model IS-146 sulfide electrode), pH (Cole-Parmer Digi-Sense portable pH meter and electrode), and electrical conductivity (Cole-Parmer conductivity meter) were then measured on the supernatant. Additional aliquots of water were filtered and analyzed for Al, B, Ca, Cu, Fe, Mg, Mn, P, K, Na, NH₄, S, and Zn. All elemental concentrations were determined with inductively coupled argon plasma (ICP) emission spectrometry (Spectro Ciros CCE, Spectro Analytical Instruments, Germany).

We determined extractable soil elemental concentrations (Ca, Cu, Fe, Mg, Mn, NH₄-N, P, K, Na, and Zn), bulk density, and percentage moisture on the soil collected for interstitial water. Ammonium (NH₄-N) was extracted from soil with 2 M KCl (Bremner and Kenney 1996), P with Bray-2 (Byrnside and Sturgis 1958), Fe, Mn, Cu, and Zn with DPTA (Lindsay and Norvell 1978), and Ca, Mg, K, and Na with ammonium acetate (Thomas 1982). Once extracted, NH₄-N samples were filtered with a 45 μm syringe filter and analyzed with a segmented flow autoanalyzer (Flow Solution IV AutoAnalyzer, O-I Analytical, USA). All other elemental concentrations were determined with inductively coupled argon plasma (ICP) emission spectrometry (Spectro Ciros CCE, Spectro Analytical Instruments, Germany).

We collected additional soil cores to determine percentage organic matter and particle size distribution (texture). To determine organic matter content, 2–3 g of dry soil were treated with 1N HCl until all carbonates were volatilized. Organic matter in the soil was then measured as loss on ignition at 500°C (Nelson and Sommers 1996). Particle size distribution was determined using the pipette method (Soil Survey Investigations Manual 2004).

We also measured soil redox potential seasonally at 7.5 cm below the soil surface using a calomel reference electrode, bright platinum electrodes ($n = 3$), and a portable Cole-Parmer digital pH-mV meter. The known potential of a calomel reference electrode (+244 mV) was added to each mV reading to calculate Eh. Soils were classified as aerated

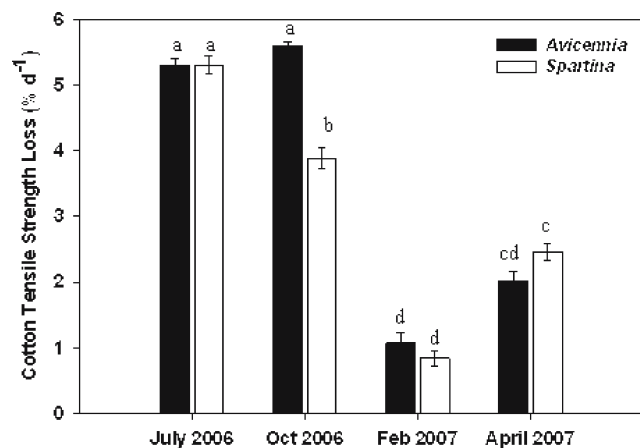


Figure 3. Cotton tensile strength loss for each sampling period in *Avicennia germinans* and *Spartina alterniflora* habitats. Data are means \pm 1 SE ($n = 10$). Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, $p < 0.05$).

(> 300 mV), moderately reduced (100 to 300 mV), reduced (−100 to 100 mV), or strongly reduced (< −100 mV) (Patrick et al. 1996).

Statistical Analysis

We calculated all statistics using the Statistical Analysis System (SAS, Version 9.0, SAS Institute, Inc). We used a one-way analysis of variance (ANOVA) with blocking to test for significant habitat effects on elevation, P_n , LAI, whole canopy carbon assimilation, belowground productivity, % OM, % sand, % silt, and % clay, a two-way ANOVA with blocking to test for significant habitat, sampling period, and interaction effects on accretion, bulk density, % moisture, and cotton strip and leaf decomposition, and a three-way ANOVA with blocking to test for significant habitat, species, and sampling period effects on root decomposition. We used a MANOVA to test for significant habitat, sampling period, and interaction effects on soil and porewater physicochemical variables and subsequent two-way ANOVAs to determine how individual soil and porewater variables differed with habitat and sampling period. We tested all model residuals for normality (Shapiro-Wilk test) and homogeneity of variance (plot of residuals). Where necessary, we used transformations to improve normality and homogeneity of variance. We tested differences between habitats, species, sampling periods, and all interactions with post-hoc, Tukey Multiple Comparison tests and report significant differences at a probability level ≤ 0.05 .

Based on published literature on belowground production, sedimentation rates, and many of the

other variables measured in this research, a sample size of 10 should be sufficient to detect ecologically and statistically significant differences, if they should exist, between *Avicennia* and *Spartina* habitats (Gallagher et al. 1984, Cahoon and Turner 1989, Reed 1989, Blum 1993, Windham and Lathrop 1999, Windham 2001). The same conclusion was apparent from retrospective power analyses of selected variables. For example, we calculated a power of 0.94 for detecting a difference in feldspar accretion of $0.08 \text{ g cm}^{-2} \text{ d}^{-1}$ at an alpha level of 0.05. Also, variables that were significantly different between habitats had higher coefficients of variation (*Avicennia*: 0.08 to 1.99, *Spartina*: 0.08 to 2.62) than non-significant variables (*Avicennia*: 0.23 to 1.45, *Spartina*: 0.09 to 1.09), suggesting that the inability to detect significant differences for some variables was not due to relatively higher variation in the data.

RESULTS

Elevation and Sediment Accretion

On average, *Avicennia* occurred in areas of higher elevation ($2.95 \pm 0.67 \text{ cm}$) than *Spartina* ($-3.50 \pm 0.29 \text{ cm}$) ($p = 0.0024$). Even so, short-term ($0.22 \pm 0.03 \text{ g m}^{-2} \text{ d}^{-1}$ and $0.30 \pm 0.03 \text{ g m}^{-2} \text{ d}^{-1}$), medium-term ($6.6 \pm 0.58 \text{ mm yr}^{-1}$ and $5.9 \pm 0.69 \text{ mm yr}^{-1}$), and decadal-scale accretion (5.3 and 5.8 mm yr^{-1}) were similar between *Avicennia* and *Spartina* areas of the marsh, which suggests mangroves may have initially established at higher elevation sites within the marsh. It is important to note that only one core was processed for cesium dating per habitat and also that the mangroves we studied were relatively young (13–15 years old) so that accretion estimates using ^{137}Cs were likely quantifying both a *Spartina* and early *Avicennia* growth period. Nevertheless, ^{137}Cs accretion values do support short-term and medium-term accretion results.

Decomposition Rates

Cellulytic degradation did not differ between habitats, except in October 2006 when degradation was significantly higher in the *Avicennia* habitat (significant habitat \times sampling period interaction, $p = 0.0021$) (Figure 3). In both habitats, cellulose decomposition was greatest in summer and fall and lowest in winter and early spring (Figure 3). Depth had no significant effect on cotton strip decomposition.

Leaves degraded quickly on the marsh surface, with only $47 \pm 1.61\%$ of *Avicennia* and $54 \pm 1.38\%$

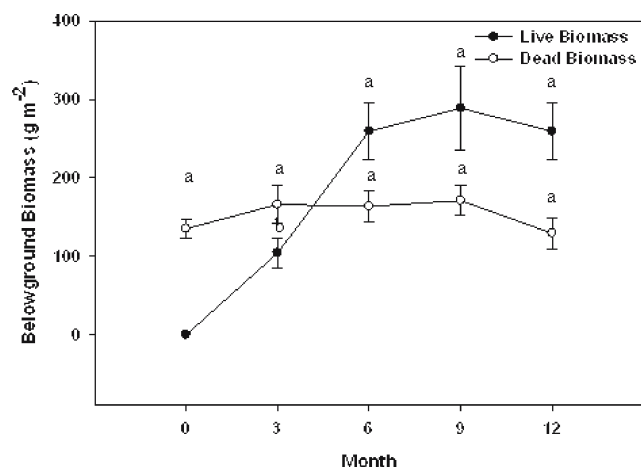


Figure 4. Dead and live belowground biomass after each sampling period. Data are means \pm 1 SE ($n = 20$) of *Avicennia germinans* and *Spartina alterniflora* combined. At time zero, there was no initial live biomass. For this reason, time zero biomass estimates were not included in the statistical analysis. Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, $p < 0.05$).

of *Spartina* biomass remaining after 69 days. The habitat into which leaves were placed did not significantly affect degradation rates. However, *Avicennia* leaves ($0.63\text{--}1.0\%$ loss d^{-1}) degraded faster than *Spartina* leaves ($0.52\text{--}0.83\%$ loss d^{-1}) ($p < 0.0001$). Likewise, regardless of habitat, *Avicennia* roots ($0.055\text{--}0.30\%$ loss d^{-1}) degraded quicker than *Spartina* roots ($0.074\text{--}0.25\%$ loss d^{-1}) ($p < 0.0001$).

Belowground Biomass and Productivity

The amount of dead and live belowground biomass in in-growth cores remained similar between *Avicennia* and *Spartina* throughout the entire study. Regardless of species, the amount of dead biomass did not differ with time; however, live biomass increased over time (Figure 4). The amount of live biomass present after nine months was significantly greater than the live biomass after three months ($p = 0.0044$) (Figure 4). After one year, total belowground productivity did not differ significantly

between *Avicennia* ($346.4 \pm 63.1 \text{ g m}^{-2} \text{ yr}^{-1}$) and *Spartina* ($436.2 \pm 53.9 \text{ g m}^{-2} \text{ yr}^{-1}$).

Photosynthetic Rates and Leaf Area Index

Plant species had a significant effect on both P_n and LAI, individually. Leaf specific photosynthesis (P_n) was nearly twice as great for *Spartina* than for *Avicennia* ($p = 0.0003$), while *Avicennia* leaf area per unit area of marsh (LAI) was significantly greater than for *Spartina* ($p = 0.0025$) (Table 1). Thus, when photosynthetic rates were weighted by LAI, whole canopy carbon fixation was similar for the two species (Table 1).

Soil and Porewater Variables

We analyzed the combined response of all soil and porewater variables with a factorial MANOVA, which demonstrated a significant habitat \times sampling period interaction ($p = 0.0008$). We then used univariate ANOVAs to determine treatment effects on individual variables of interest.

Bulk density was significantly greater in the *Avicennia* habitat ($p = 0.0245$) (Table 2), while soil moisture was greater in the *Spartina* habitat ($p = 0.0195$) (Table 2). Eh in this study ranged from +400 to -32 mV in the *Avicennia* habitat and from +341 to -142 mV in the *Spartina* habitat across sampling periods and are typical of wetland soils (+300 to -250 mV) (Patrick et al. 1996). Eh's were greater in the *Avicennia* habitat than in the *Spartina* habitat in September 2006 and January 2007, but were not significantly different in May 2006 (habitat \times sampling period interaction, $p = 0.0277$) (Figure 5). Soils were classified as moderately reduced in both habitats in May 2006 and in the *Avicennia* habitat in September 2006 and January 2007; soils were reduced in the *Spartina* habitat in September 2006 and January 2007 (Patrick et al. 1996). No distinct seasonal trend was evident.

Although statistically significant, the differences in pH ($p = 0.0400$), salinity ($p < 0.0001$), and sulfides ($p = 0.0400$) between habitats were minor and likely have no ecological effect (Table 3).

Table 1. Photosynthetic rates (P_n and whole canopy) and leaf area index (LAI) for *Avicennia germinans* and *Spartina alterniflora*. Data are means \pm 1 SE in parentheses ($n = 10$). Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, $p < 0.05$).

Species	P_n ($\mu\text{mol m}^{-2} \text{ leaf s}^{-1}$)	LAI (unitless)	Whole Canopy Photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ ground area s}^{-1}$)
<i>Avicennia</i>	6.99(0.51) ^b	3.74(0.24) ^a	25.52(1.86) ^a
<i>Spartina</i>	11.96(0.97) ^a	2.62(0.18) ^b	31.71(3.70) ^a

Table 2. Soil texture and physical variables. Data are means \pm 1 SE in parentheses ($n = 10$ for % sand, silt, clay, and organic matter; $n = 30$ for % moisture and bulk density). Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, $p < 0.05$).

Variable	<i>Avicennia</i>	<i>Spartina</i>
% sand	24.69(3.49) ^a	30.25(3.58) ^a
% silt	41.03(2.31) ^a	40.09(2.59) ^a
% clay	34.28(2.75) ^a	29.66(1.51) ^a
% organic matter	11.46(1.09) ^a	12.81(1.74) ^a
% moisture	52.14(1.37) ^b	58.59(1.15) ^a
Bulk density	0.70(0.03) ^a	0.57(0.02) ^b

However, soil $\text{NH}_4\text{-N}$ was twice as great in the *Avicennia* habitat than in the *Spartina* habitat ($p = 0.0104$) (Table 4). Extractable soil Mg, Mn, and Na did not differ significantly between habitats or sampling periods, while Fe was higher in the *Spartina* habitat in January 2007 than on any other sampling occasion ($p < 0.0001$) (Table 4). Time had a significant effect on soil Ca, Cu, K, P, and Zn ($p = 0.0290$, $p < 0.0001$, $p < 0.0001$, $p < 0.0001$, and $p < 0.0001$, respectively), with lowest Ca, Cu, K, and P in January 2007 and lowest Zn in May and September 2006 (Table 4). Porewater Zn did not differ significantly between habitats or sampling periods (Table 5). However, time had a significant effect on porewater Al, B, Mn, and NH_4 ($p < 0.0001$, $p = 0.0026$, $p = 0.0002$, and $p = 0.0033$, respectively) (Table 4). The interaction between habitat and sampling period had a significant effect on porewater Ca, Cu, Fe, K, Mg, P, and Na concentrations ($p = 0.0336$, $p = 0.0056$, $p = 0.0058$,

Table 3. Porewater pH, salinity, and sulfides. Data are means \pm 1 SE in parentheses ($n = 30$ for pH, salinity, and sulfides; $n = 3$ for salinity). Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, $p < 0.05$).

Variable	<i>Avicennia</i>	<i>Spartina</i>
pH	6.7(0.09) ^a	6.4(0.19) ^b
Salinity (ppt)	24.5(0.79) ^a	19.7(0.33) ^b
Sulfides (mM)	0.00(0.00) ^b	0.013(0.003) ^a

$p = 0.0110$, $p = 0.0287$, $p = 0.0457$, $p = 0.0352$, respectively) (Table 5).

DISCUSSION

Nearly two decades of warm winter temperatures in coastal Louisiana have facilitated the northward expansion of *Avicennia* into *Spartina* salt marshes. With this expansion, we expected several alterations to the essential ecosystem processes of the salt marsh. However, contrary to initial expectations, more sediment did not accumulate in the mangrove habitat than in the *Spartina* habitat. There are several possibilities that explain the similar rates of sediment accretion we observed between habitats. The main sources of sediment for the study site are Bayou Lafourche to the east and Timbalier Bay to the west. The study site no longer receives sediment from overbank flooding of the Mississippi River, which has been leveed, nor from the Mississippi River via Bayou Lafourche, which is now virtually isolated from the Mississippi River. Hence, sediment accretion in these marshes primarily occurs from the reworking of nearby bay bottom sediments during storms and cold fronts (Cahoon and Turner 1989; Reed 1989) and from offshore input from hurricanes (Turner et al. 2006). *Avicennia* and *Spartina* study habitats were at similar distances from these sediment sources. Likewise, the two habitats should experience a somewhat similar frequency and duration of flooding because they are located adjacent to each other with a mean difference in elevation of only 6 cm.

Furthermore, at this stage in their development, *Avicennia* trees at our study site may be too small or too young to exert a significant effect on sedimentation rates as would be expected in more mature mangrove forests. The trees have only recently colonized and reached maturity in the last 15 to 20 years since the freeze of 1989 that killed virtually all mature mangroves in southeastern Louisiana. While the majority of mangrove forests in the tropics are well-established and have very complex, extensive root systems that trap sediments and also contribute

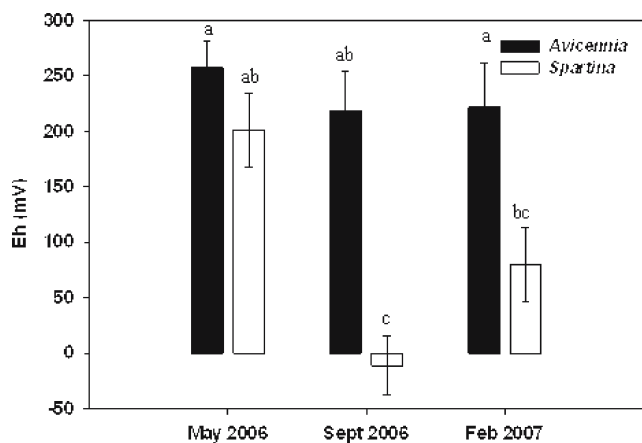


Figure 5. Soil Eh for each sampling period in *Avicennia germinans* and *Spartina alterniflora* habitats. Data are means \pm 1 SE ($n = 10$). Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, $p < 0.05$).

Table 4. Extractable soil elemental concentrations. Soil $\text{NH}_4\text{-N}$ differed between habitats, but not sampling periods. All other elemental concentrations are presented with habitats pooled. A significant interaction between habitat and sampling period occurred for Fe. Data are means \pm 1 SE in parentheses ($n = 30$ for $\text{NH}_4\text{-N}$; $n = 20$ for Ca, Mg, P, K, Na; $n = 10$ for Fe). Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, $p < 0.05$).

Habitat	Date	Extractable soil elemental concentrations ($\mu\text{mol cm}^{-3}$)					
		Ca	Mg	P	K	Na	$\text{NH}_4\text{-N}$
<i>Avicennia</i>							0.14(0.02) ^a
<i>Spartina</i>							0.07(0.01) ^b
	May 2006	16.33(0.67) ^a	46.80(2.32) ^a	0.90(0.06) ^a	20.61(0.59) ^a	275.25(16.07) ^a	
	Sept 2006	14.68(0.88) ^{ab}	44.89(3.26) ^a	0.73(0.05) ^b	20.38(1.07) ^a	261.39(21.10) ^a	
	Jan 2006	13.28(0.57) ^b	42.63(3.04) ^a	0.61(0.07) ^c	8.89(0.96) ^b	249.13(14.01) ^a	

Habitat	Date	Extractable soil elemental concentrations ($\mu\text{mol cm}^{-3}$)			
		Fe	Mn	Cu	Zn
	May 2006		0.07(0.02) ^a	0.03(0.003) ^a	0.04(0.003) ^b
	Sept 2006		0.10(0.03) ^a	0.02(0.003) ^a	0.04(0.003) ^b
	Jan 2006		0.07(0.02) ^a	0.00(0.001) ^b	0.07(0.007) ^a
<i>Avicennia</i>	May 2006	1.34(0.23) ^b			
	Sept 2006	1.18(0.27) ^b			
	Jan 2006	1.43(0.27) ^b			
<i>Spartina</i>	May 2006	1.61(0.25) ^b			
	Sept 2006	1.55(0.18) ^b			
	Jan 2006	3.53(0.49) ^a			

substantial quantities of peat to the marsh, there has been minimal accumulation of peat beneath the *Avicennia* trees at our Louisiana study site during the relatively short time they have been present nor has there been time for the trees to develop the same structural complexity of their root systems (personal observation). Also, the aerial extent of these mangrove stands, although representative of mangroves in Louisiana, was relatively small so that the

combined effects of hundreds of trees over a large area did not occur. In the future as mangrove trees develop into larger stands, it is possible that differences in sediment accumulation between *Avicennia* and *Spartina* habitats will become apparent.

The timing and rate of decomposition within a coastal ecosystem can be altered by the introduction of a new plant species (Cameron and Spencer 1989, Emery and Perry 1996, Grout et al. 1997, Windham

Table 5. Porewater elemental concentrations. Porewater Al, B, Mn, and NH_4 differed between sampling periods and are presented with habitats pooled. A significant interaction between habitat and sampling period occurred for Ca, Cu, Fe, K, Mg, P, and Na. Data are means \pm 1 SE in parentheses ($n = 20$ for Al, B, Mn, NH_4 ; $n = 10$ for Ca, Cu, Fe, K, Mg, P, Na). Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, $p < 0.05$).

Habitat	Date	Porewater elemental concentrations (ppm)						
		Ca	Cu	Fe	Mg	K	P	Na
<i>Avicennia</i>	May 2006	285(6.4) ^{ab}	0.001(0.0002) ^c	2.49(1.2) ^b	1084(24) ^{ab}	551(12) ^a	0.81(0.02) ^a	9779(104) ^c
	Sept 2006	336(39) ^a	0.003(0.0001) ^{ab}	2.47(1.4) ^b	1114(120) ^a	408(25) ^{ab}	0.16(0.09) ^b	14360(217) ^a
	Jan 2006	126(49) ^c	0.005(0.0001) ^a	0.12(0.1) ^c	407(159) ^c	186(71) ^c	0.18(0.01) ^b	2330(883) ^e
<i>Spartina</i>	May 2006	248(5.5) ^{ab}	0.001(0.0002) ^c	10.1(4.0) ^a	921(17) ^{ab}	408(9.6) ^{ab}	0.97(0.11) ^a	8267(80) ^c
	Sept 2006	311(6.3) ^{ab}	0.002(0.0007) ^b	1.37(0.98) ^b	1072(17) ^{ab}	383(9.2) ^{ab}	0.92(0.26) ^a	12082(199) ^b
	Jan 2006	218(25) ^{bc}	0.001(0.0002) ^c	0.40(0.19) ^c	710(81) ^b	271(31) ^b	0.53(0.17) ^b	4586(52) ^d

Habitat	Date	Porewater elemental concentrations (ppm)			
		Al	B	Mn	NH_4
	May 2006	0.018(0.006) ^c	1.86(0.07) ^a	1.96(0.23) ^a	0.18(0.02) ^{ab}
	Sept 2006	0.100(0.005) ^a	1.73(0.11) ^a	1.02(0.28) ^b	0.09(0.02) ^b
	Jan 2006	0.034(0.002) ^b	1.28(0.18) ^b	0.42(0.13) ^b	0.29(0.06) ^a

2001). Unexpectedly, in the Louisiana marsh we studied, above and belowground litter of the relatively newly established black mangroves decayed more rapidly than litter of the well-established *Spartina*, possibly due to higher nitrogen concentrations in the former (Twilley et al. 1986, Robertson 1988, McKee 1995) or lower amounts of more refractory lignin (Day 1982). Even though *Avicennia* tissues degraded quicker than *Spartina* tissues, major alterations to the studied ecosystem processes have not appeared at this time.

It is important to point out that only the microbial aspect of litter decomposition was examined in this study. *Avicennia* and *Spartina* tissues can be initially degraded by detritivores that shred or consume litter. It is likely that the distribution of detritivores may differ between newly established *Avicennia* and existing *Spartina* habitats, and thus detritivores may differentially affect decay rates within habitats even though microbial decomposition was similar. Future research that examines the role of both microbes and detritivores in litter decomposition will likely prove beneficial in assessing differences in ecosystem processes between *Avicennia* and *Spartina* areas of the salt marsh.

Several studies (Windham 2001, Farnsworth and Meyerson 2003, Ravit et al. 2003, Windham and Meyerson 2003, Ruesink et al. 2006) have observed higher rates of productivity in plants that have expanded into coastal ecosystems; however, total belowground production did not differ between *Avicennia* and *Spartina* during the one year study period. Our results suggest that belowground organic matter production is similar for *Avicennia* and *Spartina*, and, thus, these species are carrying out similar productivity functions. This, of course, may change if mangrove stands increase in aerial extent and stature as temperatures warm.

Photosynthesis results suggest that regardless of the plant that is present, the amount of carbon fixed per unit area of *Spartina* salt marsh is nearly equal at this stage of mangrove development. Despite similar rates of net photosynthesis between *Avicennia* and *Spartina* plants, the fate of the carbon fixed by the two species is likely quite different. Most of the aboveground production of *Avicennia* goes into wood, which persists throughout the year in the salt marsh; whereas, *Spartina* aboveground growth, or leaves, turns over each year and becomes available for food-web support or incorporation into the soil. In the future, studies that examine the fate of carbon fixed by *Avicennia* and *Spartina* plants will likely contribute to the current understanding of the effects black mangroves might have on trophic dynamics in salt marsh ecosystems.

Unlike other studies that have documented changes in wetland soil organic matter with species expansion (Templer et al. 1998, Cheng et al. 2006), there were no differences in the amount of organic matter between *Avicennia* and *Spartina* habitats. However, the more rapid degradation of mangrove versus *Spartina* tissues may actually lead to more soil organic matter accumulation overtime in *Spartina* areas of the marsh and a greater ability for these areas to keep pace with sea level rise in the future.

Relatively few differences were documented in soil and porewater variables between *Avicennia* and *Spartina* habitats. As predicted, somewhat higher Eh values were documented in the *Avicennia* habitat. Several studies have demonstrated that the oxidation-reduction status of marsh and mangrove soils is strongly influenced by the presence of roots (Mendelssohn and Postek 1982, Thibodeau and Nickerson 1986, McKee et al. 1988, McKee 1993). The somewhat higher Eh values we recorded in the *Avicennia* habitat are likely reflective of the presence of the aerial roots of the black mangrove (Scholander et al. 1955) in conjunction with higher elevation and presumably better soil drainage in this habitat. Plant utilization of $\text{NH}_4\text{-N}$ is an important factor regulating the concentration of extractable ammonium in salt marsh soils (Brannon 1973, Buresh et al. 1980). The lower ammonium levels in the *Spartina* habitat thus may reflect greater uptake of available $\text{NH}_4\text{-N}$ by *Spartina* plants, however, other factors, such as differential nitrogen mineralization rates, cannot be ruled out.

CONCLUSION

Given the present size and areal extent of black mangrove populations in Louisiana, *Avicennia* expansion does not appear to be altering the processes of sediment accretion, belowground production, or carbon assimilation in this historically, and presently still, *Spartina*-dominated ecosystem, despite the quicker decay of mangrove tissues. However, if black mangrove stands continue to grow in vertical and horizontal extent, effects on ecosystem processes may occur in the future. Furthermore, if temperatures continue to increase as predicted and black mangroves increase in stature and extent, re-examination of the ecosystem processes investigated in our research, as well as the supplementary processes we mention, will be essential to understanding the effects of *Avicennia* expansion into coastal salt marshes. Our research provides a baseline from which future ecosystem responses may be evaluated as mangrove popula-

tions in Louisiana, and the greater Gulf of Mexico region, continue to develop.

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