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Ecosystem effects of expanding populations of *Avicennia germinans* in a southeastern Louisiana *Spartina alterniflora* saltmarsh

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ECOSYSTEM EFFECTS OF EXPANDING POPULATIONS OF *AVICENNIA GERMINANS*
IN A SOUTHEASTERN LOUISIANA *SPARTINA ALTERNIFLORA* SALTMARSH

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The Department of Oceanography and Coastal Sciences

by
Carey Lynn Perry
B.S., Eckerd College, 2005
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ABSTRACT

Although the Earth may be in the early stages of the projected trends of global warming, several ecological responses to recent warming are already evident. The timing of seasonal activities of plants and animals has begun to shift, and the advancement of species poleward is occurring in several regions of the world. One unique distributional shift is the movement of *Avicennia germinans* (black mangrove) northward into temperate salt marshes dominated by the marsh grass, *Spartina alterniflora*. In Louisiana, black mangroves were historically restricted to the southernmost barrier islands and beaches; however, in recent years a noticeable expansion of *Avicennia* northward into *Spartina* marshes has been observed. To date, no research documents the effects mangroves may have on ecosystem processes within salt marshes. The goal of this research was lessen this gap in scientific knowledge by examining the effects of expanding populations of *Avicennia* on the ecosystem processes of accretion, organic matter production and decomposition, and carbon assimilation.

Study results indicate that, to date, *Avicennia* expansion has had no major effects on essential ecosystem processes within the salt marsh. No differences were detected in accretion rates, using sediment trap, feldspar, or ^{137}Cs techniques, decomposition rates, belowground production, or carbon assimilation rates between *Avicennia* and *Spartina* areas. However, edaphic parameters such as elevation, redox potentials, bulk density, and soil ammonium were slightly higher, while soil moisture and porewater salinity were somewhat lower where *Avicennia* expanded into the surrounding *Spartina* salt marsh.

Also, differences were detected in the relative rates at which mangrove and salt marsh tissues decomposed. Decomposition of *Avicennia* leaves (0.63-1.0% loss d^{-1}) and roots (0.055-0.30% loss d^{-1}) was quicker than that of *Spartina* leaves (0.52-0.83 % loss d^{-1}) and roots

(0.074-0.25% loss d⁻¹). Moreover, root biomass belowground degraded quite slowly, with 50-60% of roots remaining after 384 days. In contrast to quick leaf degradation and the export of leaf litter, slow root degradation and retention within the soil suggest that roots have more potential to contribute organic matter to this Louisiana salt marsh, particularly *Spartina* roots which degraded even more slowly than *Avicennia* roots.

INTRODUCTION

Global climate change models have predicted increases in air temperature of 1.4-5.8 °C by 2100, and the Earth's temperature has already warmed by approximately 0.6 °C over the past 100 years (USGCRP 2002; IPCC 2007). Although the Earth may be in the early stages of the projected trends of global warming, several ecological responses to recent temperature change are already evident. The timing of seasonal activities of plants and animals has begun to shift in response to recent temperature increases. Spring activities are occurring earlier than in the past with earlier breeding in amphibians, birds, and butterflies (Roy and Sparks 2000; Brown et al. 1999; Crick and Sparks 1999; McCleery and Perrins 1998; Beebee 1995; Sparks and Carey 1995; MacInnes 1990), earlier arrival of migratory birds and insects (Sparks et al. 2005; Butler 2003; Sparks and Yates 1997), earlier appearances of spring wildflowers and leafing out of trees (Menzel and Estrella 2001; Fitter et al. 1995; Oglesby and Smith 1995; Sparks and Carey 1995), and earlier spawning of intertidal bivalves, copepods, diatoms, and dinoflagellates (Winder and Schindler 2004; Philippart et al. 2003; Edwards and Richardson 2004). In addition to altering seasonal activities of species, it is generally agreed that temperature regimes influence species' distributions (Hoffman and Parsons 1997; Woodward 1987). With general warming trends, species are expected to shift their distributions poleward (Walther et al. 2002).

The advancement of species poleward has been documented in terrestrial systems in several regions of the world. In Europe, New Zealand, and Sweden, warming has facilitated treeline advancement toward higher latitudes (Meshinev et. al 2000; Kullman 2001). In Alaska, arctic shrub vegetation has expanded into areas that were previously shrub-free (Sturm et al. 2001). Recent distributional shifts linked to warmer temperatures have also been documented for several species of birds in Great Britain (Thomas and Lennon 1999), butterflies in North

America and Europe (Parmesan 2006; Parmesan et al. 1999; Dennis 1993), and mammals in Canada (Hersteinsson and MacDonald 1992; Payette 1987).

Species in marine and coastal environments are also shifting their distributions in response to global warming. In the North Pacific, where distributions of Sockeye salmon have begun to shift, Welch et al. (1998) has suggested that with continued warming salmon will be squeezed out of the North Pacific completely and into the Bering Sea. In the western Mediterranean, the northward distributional range shift of several benthic and nekto-benthic marine species has been linked to recent temperature change (Bianchi and Morri 2000; Francour et al. 1994). Along California's coast and in the North Atlantic, warmer coastal ocean temperatures have facilitated the northward expansion of warm-water species of copepods, zooplankton, intertidal invertebrates, and fish (Beaugrand et al. 2002; Sagarin et al. 1999; Alheit and Hagen 1997; Holbrook et al. 1997; Southward et al. 1995). Unlike studies of marine animals, relatively little research emphasis has focused on the effects warming has had on the distribution of marine and coastal plant communities. A small body of research in seagrass ecosystems, however, suggests that warmer temperatures will likely alter distributions of these aquatic plants (de Cock 1981; McMillan 1982; Durako and Moffler 1987; Short et al. 1999).

One unique distributional shift presently occurring in coastal plant communities is the movement of the black mangrove, *Avicennia germinans* (hereafter referred to as *Avicennia*), a subtropical to tropical species, northward into temperate salt marshes dominated by the marsh grass, *Spartina alterniflora* (hereafter referred to as *Spartina*). These species grow sympatrically in Florida, Louisiana, and Texas, where *Avicennia* reaches its northern limit in the northern hemisphere. In the marshes of Louisiana, black mangroves were historically restricted to the southernmost barrier islands and beaches where they often occurred adjacent to mono-specific

stands of *Spartina*. However, in recent years a noticeable expansion of *Avicennia* northward into *Spartina* marshes has been observed (Figure 1), and mangroves now commonly grow in clumps among the salt marsh vegetation (I. Mendelssohn, K. McKee, personal observations). This northward expansion is likely to continue if increases in temperature occur as predicted by climate change models (IPCC 2007).

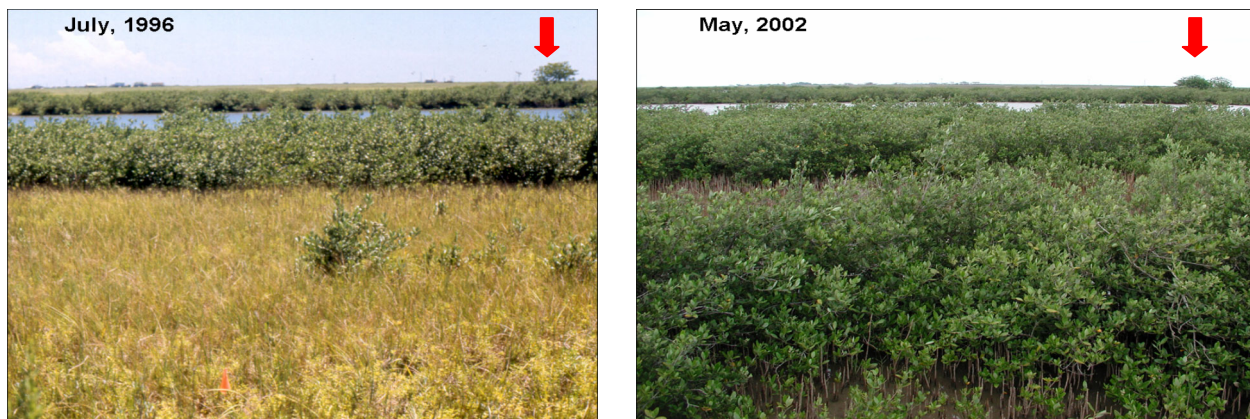


Figure 1. Expansion of *Avicennia* (black mangrove) into a mixed *Spartina* salt marsh following several years of mild winters in southeastern Louisiana. Arrows identify landmark common to both photographs (photos courtesy of B. Milan).

While several studies, as mentioned above, have documented temperature-induced distributional shifts, few have addressed the ecological consequences of these shifts. However, expansions of current species' distributions could lead to multiple ecosystem effects such as alterations in system level resource availability, alterations in carbon flow between trophic levels, alterations in primary production, and alterations in organic matter decomposition (D'Antonio and Vitousek 1992; Occhipinti-Ambrogi 2007). Although some research has emphasized controls on *Avicennia* and *Spartina* zonation within a given wetland (Patterson et al. 1993; Patterson et al. 1997; Stevens et al. 2006), the effects that mangroves may have on ecosystem processes within salt marshes have not been investigated. The goal of this research was to lessen this substantial gap in scientific knowledge by examining the effects of expanding

populations of *Avicennia* on the essential ecosystem processes of 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?

It was initially hypothesized that as *Avicennia* moved northward into salt marsh there would be changes to three ecosystem processes: surface sediment accretion, belowground production, and organic matter decomposition. It was expected that surface sediment accretion would be greater in mangrove areas of the salt marsh, where aboveground aerial roots would trap more sediments than surrounding *Spartina* stems. Belowground productivity, and thus organic matter contribution, was also expected to be greater in mangrove areas. And lastly, it was hypothesized that mangrove tissues would be more resistant to degradation, as several studies have suggested (Twilley et al. 1986; Robertson 1988; McKee 1995). Together these processes would have a positive effect on elevation, and a greater potential for positive elevation change was expected in areas where *Avicennia* were growing.

With greater elevations, it was hypothesized that flooding would be less frequent. This reduction in hydroperiod would, in turn, ameliorate several soil conditions such that mangrove soils would become more oxidized, sulfide concentrations would be reduced, and several nutrients would become more readily available for mangrove growth. Under these favorable conditions, mangrove productivity, reproduction, as well as growth and survival of mangrove seedlings and saplings, would also be enhanced. As a result of heightened growth and survival, a positive feedback loop would allow for further and future expansions of *Avicennia*.

MATERIALS AND METHODS

Study Site Description

In Louisiana, *Avicennia* (black mangrove) has predominantly established in the southeastern part of the state. The most extensive black mangrove populations occur near Grand Isle and 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); however, a hard freeze over several days in December 1989 killed most black mangroves along the Louisiana coast. Since this time, nearly two decades of mild winters have allowed mangroves to recolonize and expand into areas of *Spartina* salt marsh.

The study site was located in a salt marsh adjacent to Bayou Lafourche near Leeville, Louisiana, USA (29.16289°N 90.24295°W to 29.21119°N 90.25082°W). A randomized block design with 10 blocks (sampling stations), each containing paired habitats: a black mangrove (*Avicennia*) habitat and a smooth cordgrass (*Spartina*) habitat was used (Figure 2). The sampling stations were located randomly on the east and west sides of a pipeline canal dredged in the 1950's 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. The study site is generally inundated throughout most of the summer when south winds move water from the adjacent canal onto the marsh, but water levels are low in the winter when north winds push water south into the Gulf of Mexico. Several biotic and abiotic variables were measured in the *Avicennia* habitat and compared to those in the *Spartina* habitat. 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. Data were collected over a 14-month study period, March 2006 to May 2007.

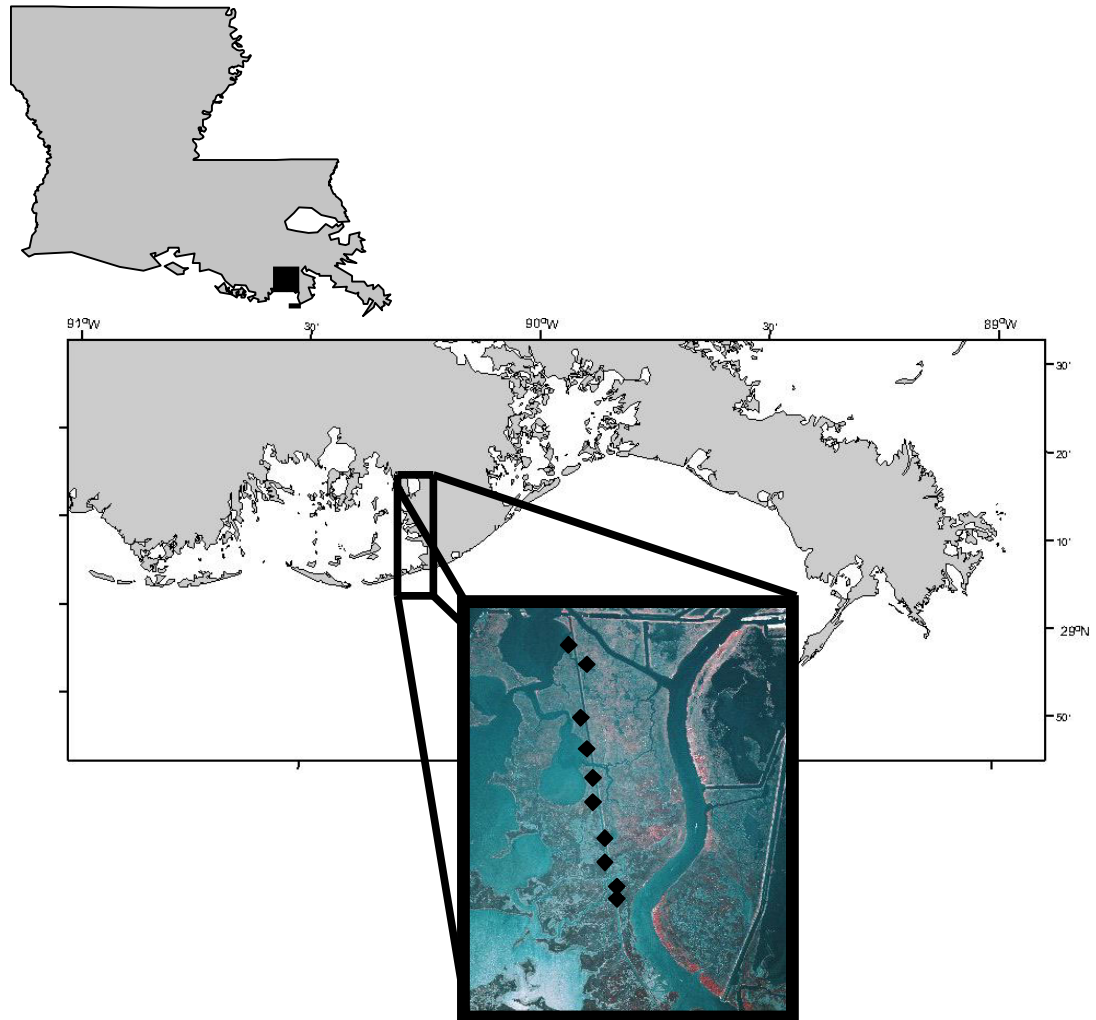


Figure 2. Sampling stations were located in a salt marsh adjacent to Bayou Lafourche near Leeville in southeastern Louisiana, USA. Diamonds on the map denote the 10 sampling stations.

Elevation

In August 2006, elevations of each habitat at all sampling stations were determined. Five elevation measurements were taken within each plot using a rotary laser. The rotary laser was used to obtain relative elevations for stations 1 through 6 and also stations 7 through 10. The

elevations for stations 1 through 6 were then coupled with elevations for stations 7 through 10 using a constant water level at slack high tide. This water level at slack high tide was then set to 0.00 cm, and mean elevations (cm) were expressed relative to this datum.

Sediment Accretion

Three approaches were used to examine sediment accretion: (1) Mini compact discs (sediment traps) to measure short-term (2-4 weeks) accretion. (2) Feldspar marker horizons to measure medium-term (several months) accretion. (3) ^{137}Cs to measure decadal accretion.

Short-term sediment accretion was examined throughout summer (July 2006, August 2006, September 2006, and October 2006) and winter (November 2006, December 2006, and January 2007) when active sedimentation is greatest in south Louisiana marshes due to summer storm events and winter cold front passages (Cahoon and Turner 1989). Mini compact discs (8 cm diameter) were pre-weighed and placed 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). In March 2006 0.25 m^2 plots of G200 feldspar were laid down in each habitat at all ten sampling stations. Sediment cores (~10 cm long) were taken seasonally (July 2006, November 2006, and March 2007) through the white feldspar marker horizon with a 3-cm diameter, narrow wall aluminum corer. The depth of sediment (mm) that had accreted above the marker horizon was measured at three locations around the core with calipers.

Decadal-scale sediment accretion was determined once (November 2006) with ^{137}Cs dating (DeLaune et al. 1978). Cesium-137, which does not occur naturally, is a product of

nuclear weapons testing. Atmospheric deposition of ^{137}Cs began in the early 1950's, with peak quantities detected in 1963 (Pennington et al. 1973). Thus, the profile of ^{137}Cs activity with sediment depth shows maximum activity at a depth corresponding to 1963 and is used as the marker layer above which vertical accretion can be estimated. Sediment cores were collected to a depth of 50 cm with 12-cm diameter stainless steel tubes. Cores were transported and stored upright, kept cold until analysis, and any sediment compaction that may have occurred was quantified. The cores were sectioned into 2-cm depth intervals, dried to a constant weight at 65 °C, and ground using a mortar and pestle. Once ground, approximately 2 g of sediment were packed into 10-mm diameter vials to a standard height of 33 mm, sealed with epoxy, and ^{137}Cs activity counted with a lithium drifted germanium detector. Accretion (cm 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 (DeLaune et al. 1978).

Belowground Primary Production

The in-growth core method of Gallagher et al. (1984) for estimating belowground biomass production in salt marshes was used. In April 2006, four in-growth cores per habitat were created by removing a 7.5 cm x 30 cm soil volume, which was replaced with root and rhizome-free sediment collected from the adjacent pipeline canal. In-growth cores were removed seasonally (July 2006, October 2006, February 2007, and April 2007) during a one-year period, washed over a 1 mm² sieve, and live roots, live rhizomes, and all dead material were sorted, dried to a constant weight at 65 °C, and weighed. Total belowground production ($\text{g m}^{-2} \text{yr}^{-1}$) was estimated by summing all live and dead biomass produced during the one year study period.

Decomposition Rates

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 cellulolytic activity. Seasonally, (July 2006, October 2006, February 2007, and April 2007) canvas strips (10 cm wide x 30 cm long) were inserted lengthwise into the soil using a flat-edged hand tool. A horizontal cut was made on each strip at the marsh surface to mark its location. 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: $CTSL (\%d^{-1}) = [(1-N/C)/D] \times 100$, where N is strength of the substrip (Newtons), C is mean strength of the reference substrips, and D is days in the marsh.

The litter bag technique (Hackney and de la Cruz 1980) was used 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. Live roots were distinguished by color, turgidity, and structural integrity; rhizomes were not used. Mesh bags (8 x 30 cm) were 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 in April 2006. Leaves were also collected near the study site, air-dried to a constant mass (8 g), placed in mesh bags (8 x 30 cm), and anchored to

the marsh surface in February 2007. Root bags were retrieved after 195 and 384 days (October 2006 and April 2007). Leaf bags were retrieved after 69 days (April 2007).

After collection, litter material in the leaf and root bags was cleaned with deionized water, and extraneous material was removed. New roots often grew into root bags, but immediate processing allowed separation of ingrown from original root material. All material was then dried to a constant mass at 65 °C. Percentage loss day^{-1} was calculated for each species. Total percentage remaining (X) for leaves and roots was calculated from the weight at the end of the study (X_t) and the initial biomass (X_o) as: $X = 100 * (X_t/X_o)$.

Photosynthetic Rates

On a cloudless day in February 2007, photosynthetic rates were determined as instantaneous net CO_2 assimilation using a LI-6400 portable photosynthesis system outfitted with a 2 cm x 3 cm leaf chamber containing a red and a blue light source and an internal CO_2 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 CO_2 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 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$.

Leaf area index (LAI) was measured 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. In May 2007, replicate measurements above the vegetation canopy and four measurements below the vegetation were taken. Whole canopy photosynthesis (P_s) was then calculated:

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

Soil and Porewater Physicochemical Analyses

Soil cores (5 cm diameter x 10 cm long) were collected seasonally (May 2006, September 2006, and January 2007) 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, NH_4 , S, and Zn. All elemental concentrations were determined with inductively coupled argon plasma (ICP) emission spectrometry (Spectro Ciros CCE, Spectro Analytical Instruments, Germany).

In addition to porewater nutrients, extractable soil elemental concentrations (Ca, Cu, Fe, Mg, Mn, $\text{NH}_4\text{-N}$, P, K, Na, and Zn), bulk density, and percentage moisture were determined on the soil collected for interstitial water. Ammonium ($\text{NH}_4\text{-N}$) 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, $\text{NH}_4\text{-N}$ 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 nutrient concentrations were determined with inductively coupled argon plasma (ICP) emission spectrometry (Spectro Ciros CCE, Spectro Analytical Instruments, Germany).

Additional soil cores were collected once in October 2006, and percentage organic matter and particle size distribution (texture) were determined. 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).

Soil redox potentials were measured seasonally (May 2006, September 2006, and January 2007) at 7.5 cm below the soil surface using a calomel reference electrode, brightened 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 (> 300 mV), moderately reduced (100 to 300 mV), reduced (-100 to 100 mV), or strongly reduced (< -100 mV) (Patrick et al. 1996).

Statistical Analysis

All statistics were calculated and all tests of significance were made using the Statistical Analysis System (SAS, Version 9.0, SAS Institute, Inc). A one-way analysis of variance (ANOVA) was used 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 was used to test for significant habitat, sampling period, and interaction effects on accretion, bulk density, % moisture, and cotton strip and leaf decomposition. A three-way ANOVA was used to test for significant habitat, species, and sampling period effects on root decomposition. A MANOVA was used to test for significant habitat, sampling period, and interaction effects on soil and porewater physicochemical variables. Subsequent two-way

ANOVAs were used to determine how individual soil and porewater variables differed with habitat and sampling period.

All model residuals were tested for normality (Shapiro-Wilk test) and homogeneity of variance (plot of residuals). Where necessary, transformations were used to improve normality and homogeneity of variance. Differences between habitats, species, sampling periods, and all interactions were tested with post-hoc, Tukey Multiple Comparison tests. All significant differences are at a probability level ≤ 0.05 .

RESULTS AND DISCUSSION

Elevation

Avicennia occurred in areas of higher elevation (2.95 ± 0.67 cm) than *Spartina* (-3.50 ± 0.29 cm) ($P = 0.0024$). Similar elevation patterns have been previously documented in southeastern Louisiana where mangroves dominated higher elevation sites such as creek banks, bay shores, and barrier islands, and *Spartina* occurred at lower elevation sites that experience greater depth and duration of tidal flooding (Patterson et al. 1991; McKee 2004).

Sediment Accretion

Short-term Accretion. Short-term sediment accretion did not differ between habitats, where it ranged from 0.0037 to 1.29 $\text{g m}^{-2} \text{d}^{-1}$ on mini compact discs in the *Avicennia* habitat and from 0.0074 to 1.16 $\text{g m}^{-2} \text{d}^{-1}$ in the *Spartina* habitat. Sediment accumulation was generally greater in summer and early fall (significant main effects of sampling period, $P < 0.0001$) compared to other times of the year (Figure 4).

In Louisiana, a number of studies (Baumann et al. 1984; Cahoon and Turner 1989; Reed 1989; Boumans and Day 1994) have concluded that winter cold fronts are responsible for the majority of sediment deposition in coastal marshes. However, this study documented lowest rates of short-term sediment accumulation in winter and highest rates in summer and early fall. While these findings are contrary to the majority of published results, the seasonal pattern observed is similar to that observed by Cahoon and Reed (1995) for a Terrebonne basin salt marsh. In their study, sedimentation was greatest in summer when daily flooding of the marsh is tidally

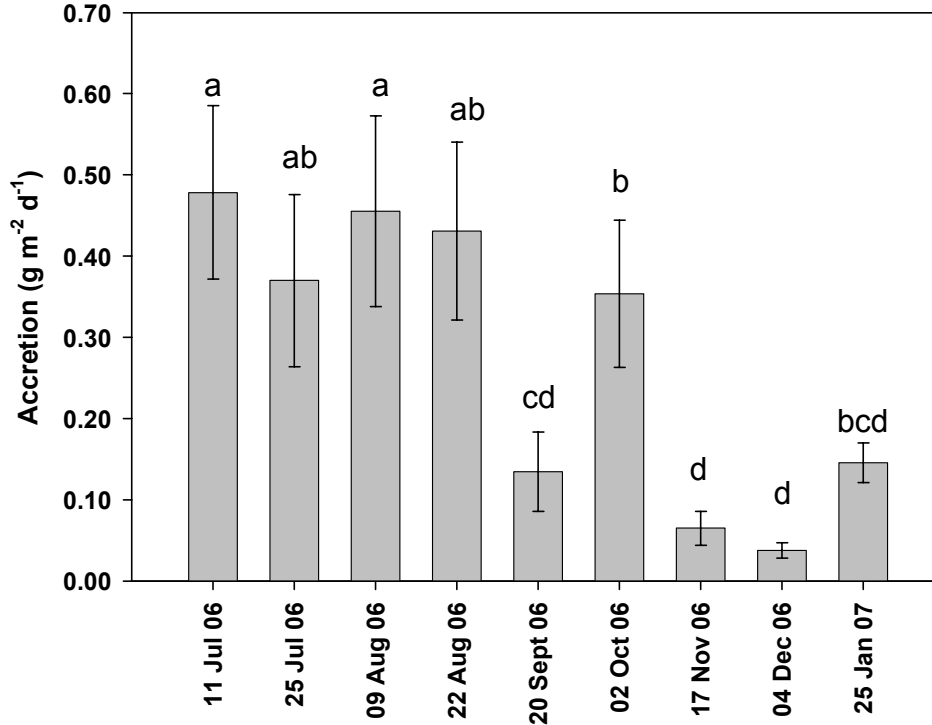


Figure 4. Short-term sediment accretion on mini-compact discs during each sampling period. Data are means \pm 1 SE ($n = 20$) of *Avicennia* and *Spartina* habitats combined. Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, $P < 0.05$).

dominated and least in winter when hydroperiod is shortened by winter storms and strong northerly winds, which lower water levels. With lower than average tides, the study site does not flood (personal observation). The low sedimentation rates during winter are probably due to restricted tidal flooding at the study site.

Medium-term Accretion. Similar to short-term estimates, medium-term sediment accretion, which ranged from 0.0 to 17.7 mm yr⁻¹ (mean = 6.6 ± 0.58 mm yr⁻¹) above feldspar horizons in the *Avicennia* habitat and from 0.0 to 23.5 mm yr⁻¹ (mean = 5.9 ± 0.69 mm yr⁻¹) in the *Spartina* habitat, was not different between habitats. Although vertical accretion, using feldspar marker horizons, displayed strong variability, mean rates are similar to published values in other microtidal salt marshes: 6.6 mm yr⁻¹ in a *Spartina patens* marsh in coastal Louisiana

(DeLaune et al. 1983), 6.0 mm yr⁻¹ at canal-edge sites to 9.9 mm yr⁻¹ at natural streamside levee sites in *Spartina* marshes in Lafourche Parish, Louisiana (Cahoon and Turner 1989), 4.4 mm to 27.8 mm yr⁻¹ in *Spartina* and *Spartina patens* marshes receiving Mississippi River water from three diversions in Louisiana (Lane et al. 2006), and 6.7 mm yr⁻¹ in a *Spartina* marsh in Massachusetts (Roman et al. 1997).

Likewise, mangrove forests from a variety of geographical areas worldwide have similar accretion rates. For example, Krauss et al. (2003) reported accretion rates of 7.2 mm yr⁻¹ using feldspar marker horizons in pneumatophore areas of a Micronesian mangrove forest. Following the dieback of interior portions of mangrove forests in Homebush Bay, Australia, Rogers et al. (2005) documented accretion rates ranging from 2.6 mm yr⁻¹ in the most impacted forests to 7.1 mm yr⁻¹ in control forests. In Rookery Bay, Florida, Cahoon and Lynch (1997) estimated an accretion rate of 6.0 mm yr⁻¹ for basin sites dominated by a mixture of *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*.

Decadal-scale Accretion. Although only one core from each habitat was processed, ¹³⁷Cs accretion values support the preceding short-term and medium-term accretion results demonstrating no differences between habitats. Decadal-scale accretion rates for *Avicennia* and *Spartina* habitats (0.53 and 0.58 cm yr⁻¹, respectively) were similar (Figure 5). Estimates of accretion in *Spartina* habitats using ¹³⁷Cs as a soil marker are in agreement with others in Lafourche Parish, Louisiana (0.47 to 0.68 cm yr⁻¹, DeLaune et al. 1989). For *Avicennia* habitats, accretion rates are higher than those documented for mangrove forests in Florida (0.29 cm yr⁻¹, Lynch et al. 1989), but fall within the range reported for mangrove forests in Boca Chiga and Estero Pargo, Mexico (0.12 to 0.71 cm yr⁻¹, Lynch et al. 1989). It is important to note that the

mangroves studied are relatively young (15-20 years old) and that estimates of decadal-scale accretion using ^{137}Cs are likely quantifying both a *Spartina* and early *Avicennia* growth period.

Nevertheless, with increased *Avicennia* presence, it becomes essential to accurately estimate the potential for soil accretion and elevation gain in mangrove areas of Louisiana's salt marshes. Unlike Rogers et al. (2006) who documented greater accretion rates in mangrove zones than in salt marsh zones within a wetland in southeast Australia (0.65 to 9.49 mm yr⁻¹ for mangrove and 0.33 to 5.93 mm yr⁻¹ for salt marsh using feldspar horizons), *Avicennia* and *Spartina* accretion rates were similar using sediment trap, feldspar, or ^{137}Cs techniques.

The main sources of sediment for the study site are likely 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 nor from the Mississippi River via Bayou Lafourche. 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) and from offshore input from hurricanes (Turner et al. 2006). The studied *Avicennia* and *Spartina* habitats are at similar distances from these sediment sources. The two habitats should also experience similar frequency and duration of flooding because they are located adjacent to each other with only a 6-cm average difference in elevation. The observed similarities in sediment accretion are likely attributable to the similar elevations and the similar sediment sources of the two habitats.

Decomposition Rates

Cellulytic Activity. Cellulytic degradation did not differ between habitats, except for in October 2006 when degradation was significantly higher in the *Avicennia* habitat (significant habitat x sampling period interaction, $P = 0.0021$) (Figure 6). In both habitats, decomposition was greatest in summer and fall and lowest in winter and early spring (Figure 6). The temporal

differences in cotton strip decomposition are probably most reflective of temporal variation in soil temperature, with more decomposition occurring in summer and fall when temperatures are at their highest at the study site. Depth had no significant effect on cotton strip decomposition possibly because both habitats occurred in streamside locations where soil water drainage is maximum (Mendelsohn and Seneca 1980).

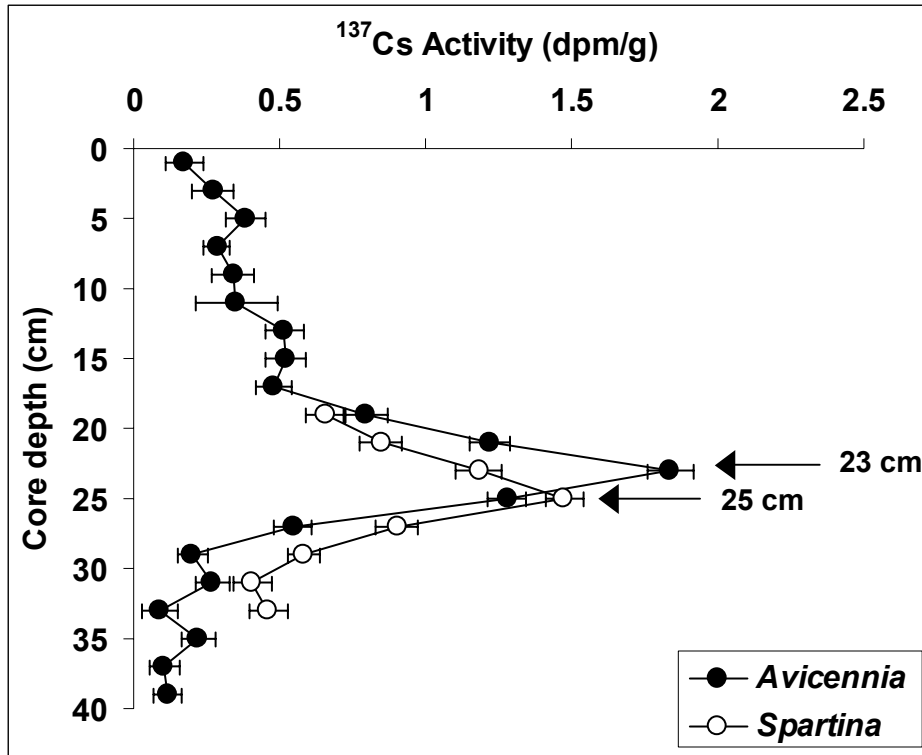


Figure 5. ¹³⁷Cs profiles from one *Avicennia* and one *Spartina* core. ¹³⁷Cs activity peaks at a depth of 23 cm in the *Avicennia* core and at 25 cm in the *Spartina* core.

Plant Litter Decomposition. Leaves degraded quickly on the marsh surface, with only $47 \pm 1.61\%$ of *Avicennia* and $54 \pm 1.38\%$ of *Spartina* biomass remaining after 69 days. The habitat into which leaves were placed did not significantly affect degradation rates. In contrast, *Avicennia* leaves ($0.63\text{-}1.0\%$ loss d^{-1}) degraded faster than *Spartina* leaves ($0.52\text{-}0.83\%$ loss d^{-1}) ($P < 0.0001$), 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).

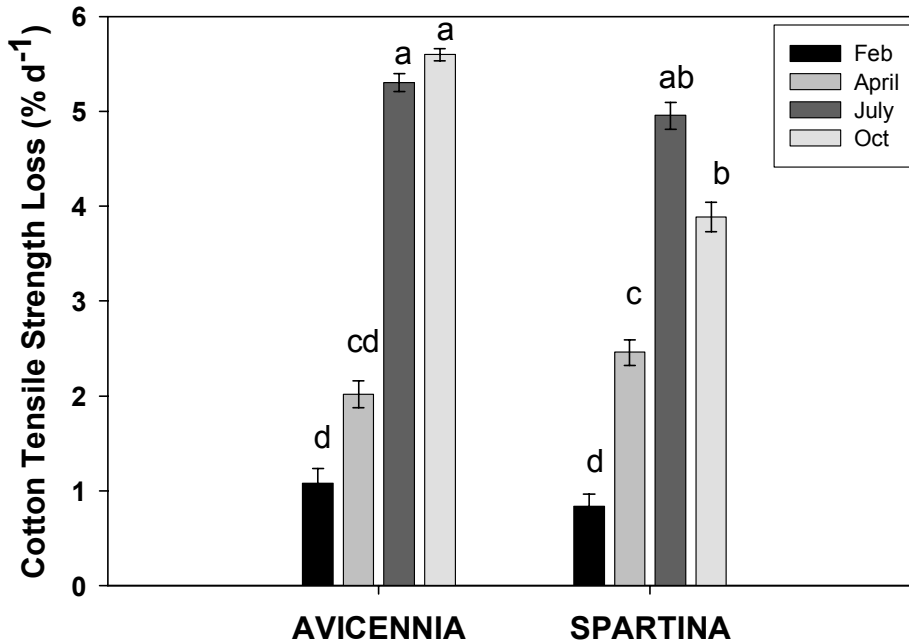


Figure 6. Cotton tensile strength loss for each sampling period in *Avicennia* and *Spartina* habitats. Data are means \pm 1 SE (n = 10). Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, $P < 0.05$).

Leaf degradation rates reported in this study are slightly higher than the range of values reported for similar mangrove and salt marsh species (0.20-0.67% loss d^{-1} [White et al. 1978 in Louisiana, Woodroffe 1982 in New Zealand, van der Valk and Attiwill 1984 in Australia, Twilley et al. 1986 in Florida, Robertson 1988 in Australia, Twilley et al. 1997 in Ecuador, Middleton and McKee 2001 in Belize]). The somewhat higher leaf degradation rates documented in this study may be attributable to frequent flooding of the marsh surface in the non-winter months and Louisiana's warm temperatures, which together promote leaching of dissolved organic carbon from leaves and maintenance of the moisture and temperature needed for optimal microbial decay (Reice et al. 1984; Middleton and McKee 2001).

Belowground degradation of root tissue (0.055-0.30% loss d^{-1} and 0.074-0.25% loss d^{-1} for *Avicennia* and *Spartina*, respectively) was much slower than that of leaf tissue on the marsh

surface. Nevertheless, regardless of habitat, *Avicennia* roots degraded quicker than *Spartina* roots after 195 and 384 days (Figure 7) ($P < 0.0001$). Moreover, root degradation rates were similar to those documented in other studies (0.10-0.39% loss d^{-1} ; Albright 1976; van der Valk and Attiwill 1984; Benner et al. 1991; Robertson et al. 1992; Middleton and McKee 2001; Poret et al. 2007). These decomposition results support those of other researchers, suggesting that degradation of plant material is slower belowground than on the marsh surface (Hackney and de la Cruz 1980; Hackney 1987; McKee and Faulkner 2000; Middleton and McKee 2001); however, a direct comparison of the same plant tissue above- and belowground was not made.

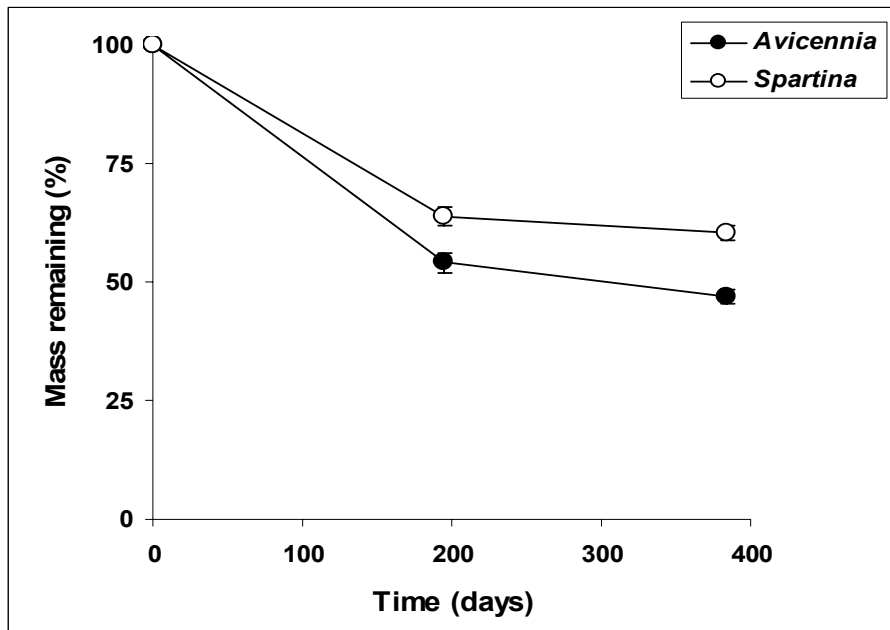


Figure 7. Percentage of *Avicennia* and *Spartina* roots remaining in litter bags after 195 and 384 days. Data are means \pm 1 SE ($n = 10$).

Belowground Primary Productivity

Belowground biomass in the ingrowth cores increased overtime and was significantly greater after 12 months than after 3 months ($P = 0.0051$) (Figure 8). After one year, total belowground productivity did not differ significantly between *Avicennia* ($1628 \pm 148.5 \text{ g m}^{-2} \text{ yr}^{-1}$) and *Spartina* ($1667 \pm 180.2 \text{ g m}^{-2} \text{ yr}^{-1}$). Estimates of *Avicennia*

belowground production are higher than those previously recorded in other mangrove forests: 0-656 g m⁻² yr⁻¹ in fringe and basin mangrove forests of Honduras (Cahoon et al. 2003), 18.3 to 1146 g m⁻² yr⁻¹ in basin forests of Florida (McKee and Faulkner 2000), 489 g m⁻² yr⁻¹ in monospecific stands of *Avicennia* in Florida (Giraldo-Sanchez 2005), but *Spartina* belowground production at the site was within the range reported for other *Spartina* marshes along the Atlantic and Gulf of Mexico coasts: 99 and 1253 g m⁻² yr⁻¹ in a Virginia creekside marsh for two growing seasons, respectively (Blum 1993), 1460 g m⁻² yr⁻¹ in Georgia (Gallagher et al. 1984), 1900 g m⁻² yr⁻¹ in southwest Louisiana (Edwards and Mills 2005), 2520 g m⁻² yr⁻¹ in a high marsh in Massachusetts (Valiela et al. 1976).

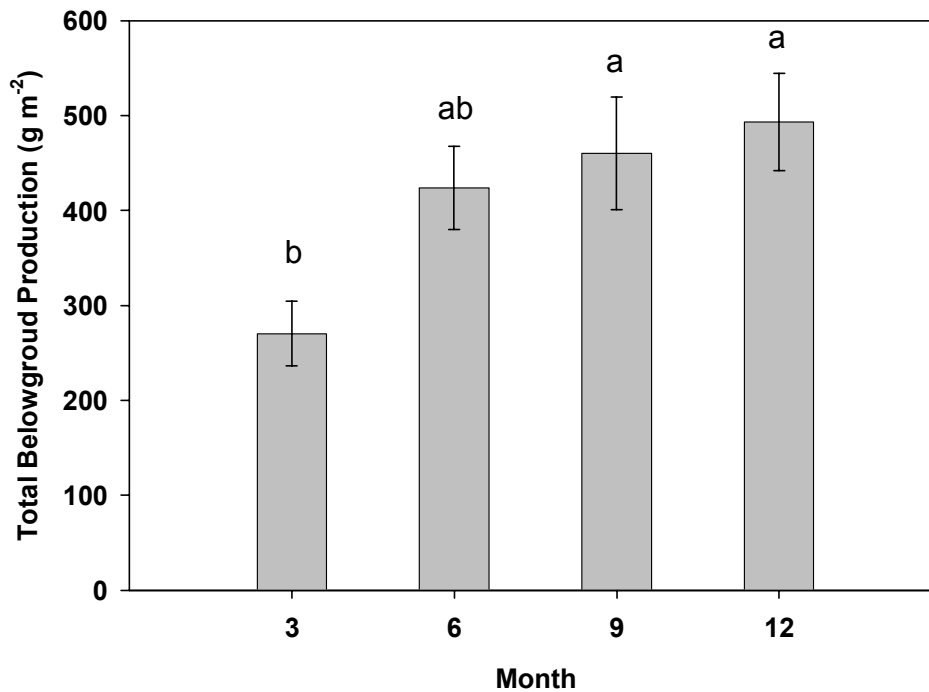


Figure 8. Total belowground productivity after each sampling period. Data are means \pm 1 SE ($n = 20$) of *Avicennia* and *Spartina* habitats combined. Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, $P < 0.05$).

Mangrove primary productivity is affected by soil conditions such as soil texture, salinity, flooding, and nutrient availability (McKee and Faulkner 2000). The high rate of production documented for *Avicennia* may partly be due to the streamside location of the sampled mangroves. The streamside environment provides adequate moisture and tidal flushing, high macro- and micronutrient input, relatively aerated soils, moderate salinities, and little to no non-resource stressors (i.e., low sulfide concentrations, near neutral pH, low metal concentrations).

Photosynthetic Rates and Leaf Area Index

Plant species had a significant effect on both P_n and LAI, individually. Even though leaf specific photosynthesis (P_n) was nearly twice as great for *Spartina* ($P = 0.0003$), there was significantly more *Avicennia* leaf area per unit area of marsh (LAI) ($P = 0.0025$) (Table 1). Thus, when photosynthetic rates were weighted by LAI, whole canopy carbon fixation was similar for the two species (Table 1). This suggests that regardless of the plant that is present, the amount of carbon fixed per unit area of salt marsh is nearly equal at this stage of mangrove and salt marsh development.

Estimates of P_n agree with values reported for similar mangrove species worldwide: 7-10 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Avicennia* in northern Florida (Lovelock and Feller 2003), 6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Rhizophora apiculata* in the Matang Mangrove Forest Reserve of Malaysia (Jin-Eong et al. 1995), 0-20 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Rhizophora apiculata* in peninsular Malaysia (Clough et al. 1997), 6.13 and 8.27 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Ceriops australis* and *Bruguiera gymnorrhiza* mangroves in Australia (Clough 1998), 10.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Rhizophora mangle* in Panama (Lovelock et al. 2004). P_n estimates for *Spartina* are also within the range reported by others: 7.81 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Pezeshki 1997), 7.2-19.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and 7.0-17.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for tall and short forms in winter and summer, respectively (Dai and Wiegert 1996). Similarly,

LAI values agree with values reported for similar salt marsh and mangrove species worldwide (Dai and Wiegert 1996; Clough et al. 1997; Clough 1998; Kovacs et al. 2005; Neves et al. 2007).

Table 1. Photosynthetic rates (P_n and whole canopy) and leaf area index (LAI) for each species. 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 ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$)	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

Soil and Porewater Variables

The combined response of all soil and porewater variables was analyzed with a factorial MANOVA, which demonstrated a significant habitat and sampling period interaction ($P = 0.0008$). Univariate ANOVAs were then used to determine treatment effects on individual variables of interest.

Bulk density was significantly higher ($P = 0.0245$) in the *Avicennia* habitat, where values ranged from 0.43 to 0.96 g cm^{-3} , than in the *Spartina* habitat where values ranged from 0.36 to 0.89 g cm^{-3} (Table 2). Soil percentage moisture was greater in the *Spartina* habitat ($P = 0.0195$) (Table 2). The slightly higher elevation in the *Avicennia* habitat likely promotes better soil drainage, thus explaining the lower percentage moisture.

Relative percentages of organic matter, sand, silt, and clay did not differ between habitats (Table 2). These results are very similar to those of Patterson and Mendelsohn (1991), who also documented no differences in soil texture between *Avicennia* and *Spartina* areas of the marsh, but higher bulk density and lower percentage moisture in *Avicennia* areas. However, unlike

Patterson and Mendelsohn (1991) who documented significantly greater amounts of organic matter in *Avicennia* areas of a Louisiana salt marsh, values in this study were not significantly different between habitats. Nevertheless, slightly higher organic matter was documented in *Spartina* soils. Leaves and roots are important contributors to organic matter in wetlands (Robertson and Daniel 1989; McKee and Faulkner 2000; Middleton and McKee 2001). The slight differences in organic matter between *Avicennia* and *Spartina* habitats may be attributable to the relative rates at which *Avicennia* and *Spartina* leaves and roots degrade, with *Spartina* tissues degrading more slowly and contributing slightly more organic matter to the soil.

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 x sampling period interaction, $P = 0.0277$) (Figure 9). 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.

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). Better soil drainage in the *Avicennia* habitat allows soils to be more oxidized than soils of the *Spartina* habitat and explains the generally higher Eh values of the *Avicennia* habitat. In addition, several studies have demonstrated that the oxidation-reduction status of marsh and mangrove soils is strongly influenced by the presence of roots (Mendelsohn and Postek 1982; Thibodeau and Nickerson 1986; McKee et al. 1988; McKee 1993). The somewhat higher Eh values I recorded in the *Avicennia* habitat are likely reflective

of the presence of the aerial roots, or pneumatophores, of the black mangrove (Scholander et al. 1955) in conjunction with higher elevation and presumably better soil drainage in this habitat.

Table 2. Soil texture and physical variables. Data are means \pm 1 SE in parentheses (n = 10). Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, $P < 0.05$).

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

Extractable soil Mg, Mn, and Na did not differ significantly between habitats or sampling periods (Table 3). Soil NH₄-N was twice as great in the *Avicennia* habitat than in the *Spartina* habitat ($P = 0.0104$), and soil Fe was lower in the *Spartina* habitat in January 2007 than on any other sampling occasion (Table 3). Time had a significant effect on soil Ca, Cu, K, P, and Zn ($P = 0.279$, $P < 0.0001$, $P < 0.0001$, $P < 0.0001$, and $P < 0.0001$, respectively), with lowest Ca, Cu, K, and P in January 2007 and lowest Zn in May and September 2006 (Table 3).

The mean values of NH₄-N are within the range reported in Louisiana salt marsh soils by Brupbacher et al. (1973) and Buresh et al. (1980). Plant utilization of NH₄-N is a substantial 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 NH₄-N by *Spartina* plants.

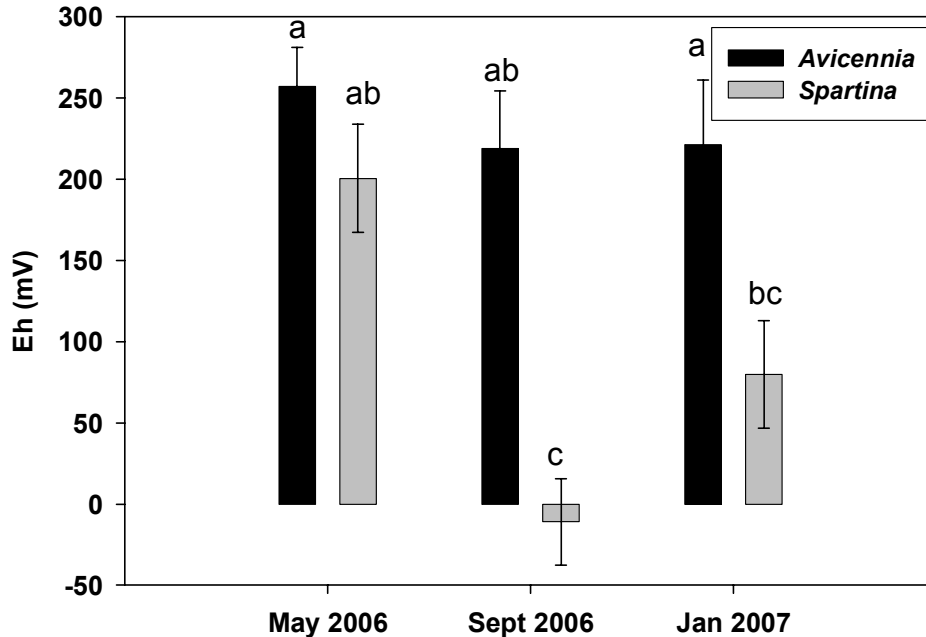


Figure 9. Soil Eh for each sampling period in *Avicennia* and *Spartina* habitats. Data are means \pm 1 SE (n = 10). Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, $P < 0.05$).

The *Avicennia* habitat had a higher pH than the *Spartina* habitat, but only in January 2007 (habitat x sampling period interaction, $P = 0.0060$) (Figure 10). Likewise, the *Avicennia* habitat had a higher salinity (26.7 ± 0.46 ppt) in May 2006 than the *Spartina* habitat (18.7 ± 0.32 ppt) in September 2006 (habitat x sampling period interaction, $P = 0.0020$). The only detectable sulfides were in the *Spartina* habitat, with a mean concentration of 0.018 ± 0.014 mM in May 2006 and 0.008 ± 0.005 mM in January 2007. Although significant, the differences in pH, salinity, and sulfides between habitats were minor and likely have no ecological effect.

Porewater Zn did not differ significantly between habitats or sampling periods. 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 (Table 4).

Local patterns of hydrology affect the chemical and physical characteristics of soils in wetlands. Both habitats are characterized by frequent tidal inundation and soil flushing. The degree of spatial and temporal variability in porewater nutrient concentrations is likely reflective of the signature of the water that was flooding the marsh during sampling. Fewer spatial and temporal differences in soil physicochemical characteristics may reflect a more stable environment, with little movement of soil into or out of the marsh with each tidal exchange.

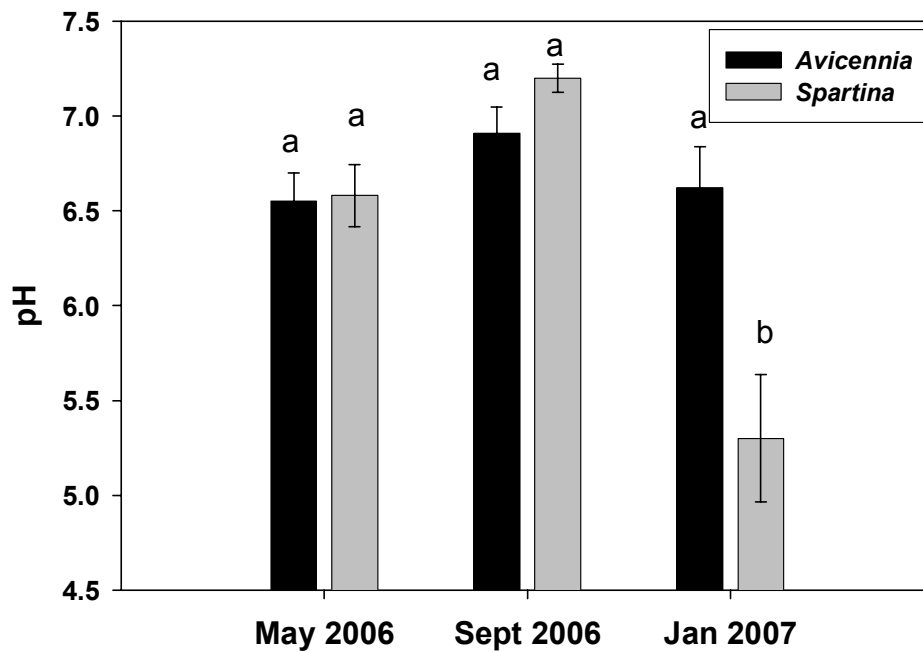


Figure 10. Porewater pH in *Avicennia* and *Spartina* habitats for each sampling period. Data are means \pm 1 SE (n = 10). Shared letters indicate no statistical differences between means (Tukey Multiple Comparison test, P < 0.05).

Table 3. Extractable soil elemental concentrations. Soil NH₄-N was the only nutrient that differed between habitats but not sampling periods. All other nutrient concentrations are presented with habitats pooled. A significant interaction between habitat and sampling date occurred for Fe. Data are means ± 1 SE in parentheses (n = 30 for NH₄-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	Ca	Mg	P	K	Na	NH ₄ -N
<i>Avicennia</i>							
<i>Spartina</i>							
	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	0.14 (0.02) ^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	0.07 (0.01) ^b
	Jan 2007	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	Fe	Mn	Cu	Zn		
<i>Avicennia</i>							
	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 2007		0.07 (0.02) ^a	0.00 (0.001) ^b	0.07 (0.007) ^a		
<i>Spartina</i>							
	May 2006	1.34 (0.23) ^b					
	Sept 2006	1.81 (0.27) ^b					
	Jan 2007	1.43 (0.27) ^b					
	May 2006	1.61 (0.25) ^b					
	Sept 2006	1.55 (0.18) ^b					
	Jan 2007	3.53 (0.49) ^a					

Table 4. Porewater elemental concentrations. Porewater Al, B, Mn, and NH₄ differed between sampling periods only 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, NH₄; 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 nutrient 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 2007	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) ^c
<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 2007	218 (25) ^{bc}	0.001 (0.0002) ^c	0.40 (0.19) ^c	710 (81) ^b	271 (31) ^b	0.53 (0.17) ^{ab}	4586 (52) ^d
Habitat	Date	Porewater nutrient concentrations (ppm)				NH ₄		
		Al	B	Mn				
	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 2007	0.034 (0.002) ^b	1.28 (0.18) ^b	0.42 (0.13) ^b	0.29 (0.06) ^a			

ECOLOGICAL IMPLICATIONS OF *AVICENNIA* EXPANSION

Alterations in the ecosystem processes of sediment accretion, organic matter decomposition, above and belowground production, and nutrient cycling, as well as essential ecosystem functions and services, have recently been attributed to plant expansions in coastal ecosystems (Cohen and Carlton 1998; Olenin and Leppakoski 1999; Nehring 2006). Nearly two decades of warm winter temperatures in coastal Louisiana have facilitated the northward expansion of *Avicennia* into *Spartina* salt marsh. With this expansion, several alterations to the essential ecosystem processes of the salt marsh were expected. The following discussion summarizes some of the alterations that have been documented in other coastal studies and whether mangrove expansion into *Spartina*-dominated salt marshes has caused similar effects.

Sediment Accretion

The expansion of plant species into coastal ecosystems can lead to distinct changes in sediment accretion rates and patterns (Windham 2001; Windham and Lathrop 1999; Rooth and Stevenson 2000). However, contrary to initial expectations and research in other coastal wetlands where larger diameter stems have been shown to reduce tidal flow and thus increase inorganic and organic sediment accumulation (Wienstein and Balleto 1999; Windham and Lathrop 1999; Angradi et al. 2001), *Avicennia* stems (trunks) and pneumatophores did not trap more sediment on the marsh surface than *Spartina* stems. Furthermore, the expansion of *Avicennia* into *Spartina* salt marshes in Louisiana does not seem to be influencing medium-term or decadal-scale surface accretion.

There are several possibilities that explain these similar rates of sediment accretion. One possibility is that the *Avicennia* trees at the study site are too small or too young to exert a significant effect on sedimentation rates. The trees have only recently colonized and reached

maturity in the last 15 to 20 years. While well-established mangrove forests found elsewhere in the tropics have very complex, extensive root systems that trap sediments and also contribute substantial quantities of peat to the marsh, there has been minimal accumulation of peat beneath the *Avicennia* trees at this study site during the 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. Moreover, the study site is only one of a number of areas in southeast Louisiana that could have been chosen for this investigation. Hence, it is possible that other mangrove-salt marsh areas in different hydrogeomorphic settings may show different responses.

Above and Belowground Production

In contrast to initial hypotheses and several studies (Windham 2001; Farnsworth and Meyerson 2003; Ravit et al. 2003; Windham and Meyerson 2003; Ruesink et al. 2006) that have observed higher rates of productivity in plants that have expanded into coastal ecosystems, total belowground production did not differ between *Avicennia* and *Spartina* during the one year study period. Likewise, whole canopy photosynthesis did not differ between the two species. These results suggests that for the time rates of organic matter production and carbon fixation are similar for *Avicennia* and *Spartina*, and thus these species are carrying out similar basic ecological functions. This, of course, may change if mangrove stands increase in aerial extent and stature as the temperature warms.

Furthermore, 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 salt marsh ecosystems.

Organic Matter Decomposition

The timing and rate of decomposition within a coastal ecosystem can be drastically altered by the introduction of a new plant species (Cameron and Spencer 1989; Emery and Perry 1996; Grout et al. 1997; Windham 2001). Unexpectedly, in the Louisiana marsh studied, above and belowground litter of the relatively newly established black mangroves decayed more rapidly than litter of the well-established *Spartina*. However, degradation rates of each species were similar in *Avicennia* and *Spartina* areas of the marsh. Even though *Avicennia* tissues are degrading quicker than *Spartina* tissues, there does not presently appear to be any major alterations in the studied ecosystem processes. Moreover, based on the production and decomposition findings of this study, because *Spartina* plants decompose more slowly they may actually contribute more organic matter to the marsh overtime than *Avicennia* plants, a conclusion contrary to my initial hypothesis. Likewise, it appears as though the potential for positive elevation gain may be greater in *Spartina* areas of the marsh. In future studies, monitoring elevation changes overtime in the two habitats may help shed light on which species is better able to contribute to elevation gain.

It is important to point out that only the microbial aspect of litter decomposition was examined in this study. *Avicennia* and *Spartina* tissues are initially degraded by detritivores that shred or consume litter. It is likely that the distribution of detritivores may differ between

Avicennia and *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.

Soil and Porewater Characteristics

Plants can have both direct and indirect effects on soil and porewater chemistry. For instance, they 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, which can strongly affect plant productivity (Howes et al. 1986) and nutrient availability (Wigand et al. 1997). Moreover, soil is a major reservoir for carbon in wetland ecosystems. Generally, carbon found in wetland soils is derived almost exclusively from the plants growing within the area. Consequently, the introduction of a new plant species is likely to alter soil carbon by means of differential rates of organic matter production and accumulation (Cheng et al. 2006).

In contrast to what was hypothesized, 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 and are likely a direct effect of its aerial roots, or pneumatophores, oxidizing the surrounding soil more than *Spartina* roots as well as the somewhat higher elevation (~ 6 cm) of the *Avicennia* habitat. Likewise, the lower ammonium levels in the *Spartina* habitat are probably a result of greater uptake of available $\text{NH}_4\text{-N}$ by *Spartina* plants.

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, as discussed previously, mangroves may actually contribute less organic matter to the marsh overtime than *Spartina* plants. Porewater salinity and pH values, on the other hand, differed significantly between habitats, but only at certain times of the year. More frequent sampling may be necessary to determine if these differences between habitats are typical or simply a function of the time of sampling.

Habitat Availability and Quality

The effects of plant species range expansion go beyond those exerted on the plant-soil environment (Benoit and Askins 1999; Leslie and Spotila 2001). As mangroves move into intertidal salt marshes, faunal changes will likely occur (Odum et al. 1982). In Florida, for instance, the greater volume and structural complexity of mangroves often support additional fauna when compared to salt marsh (Odum et al. 1982).

In this study, habitat availability and quality were not examined. However, in a recent study, similar taxa and densities of fish and crustaceans were collected in both mangrove and *Spartina* habitats in a southeastern Louisiana marsh (Caudill 2005). Even though similar densities were collected, fishes, especially gulf killifish and sheepshead minnows, showed greater affinities for *Spartina* areas, while decapod crustaceans, like white and brown shrimp, were more associated with *Avicennia* (Caudill 2005). Because Caudill's (2005) was the first and only study of its kind in Louisiana salt marshes, it is important that future research further examines fish and decapod use of *Avicennia* and *Spartina* habitats, as well as differential use of these habitats by birds, micro-invertebrates, and meiofauna.

Overall Implications

In summary, data from this study do not support my initial hypotheses. *Avicennia* expansion does not appear to be altering the processes of sediment accretion, belowground production, organic matter decomposition, or carbon assimilation at the present time. It does not appear that existing mangrove trees will create an environment that facilitates the future expansion of additional trees. Nevertheless, if temperatures continue to increase as predicted and the additional effects of global climate change become more apparent in the future, re-examination of the ecosystem processes investigated in the research, as well as the supplementary processes mentioned, will become essential to understanding the possible effects *Avicennia* expansion may have in Louisiana salt marshes.

CONCLUSIONS

Research spanning the previous century and encompassing nearly every major taxa and ecosystem on Earth has provided empirical evidence of the linkages between global climate warming and changes in the phenology and distribution of species. However, studies examining the ecological consequences of recent changes in natural systems linked to warming are lagging far behind. Of the studies that have documented changes to ecosystems, most deal with alterations to ecosystem properties and less often with changes in ecosystem processes or function. This research illustrates the importance of examining a suite of ecosystem processes within a single ecosystem where the historical distribution of species is changing, likely as a result of warmer temperatures.

Study results indicate that, to date, this expansion has had no major effects on the essential ecosystem processes within the salt marsh. In areas where *Avicennia* has expanded, elevation, redox potentials, bulk density, and soil ammonium concentrations are slightly higher, while soil moisture and porewater salinity are lower than that of the surrounding *Spartina* salt marsh. Even so, no differences were detected in accretion rates between *Avicennia* and *Spartina* areas of the marsh, using sediment trap, feldspar, or ^{137}Cs techniques. Furthermore, leaf and root decomposition, belowground production, and carbon assimilation rates were not different in areas where *Avicennia* had expanded.

Differences were detected, however, in the relative rates at which mangrove and salt marsh tissues decomposed. Decomposition of *Avicennia* leaves ($0.63\text{-}1.0\%$ loss d^{-1}) and roots ($0.055\text{-}0.30\%$ loss d^{-1}) was quicker than that of *Spartina* leaves ($0.52\text{-}0.83\%$ loss d^{-1}) and roots ($0.074\text{-}0.25\%$ loss d^{-1}). Moreover, root biomass belowground degraded quite slowly, with 50-60% of roots still remaining after 384 days. Unlike the degradation of leaf material on the

surface which is subject to removal by tides, roots generally degrade in the same location in which they were produced, which allows for greater organic matter contributions to the soil. In contrast to quick leaf degradation and subsequent export of leaf litter, slow root degradation and retention within the soil suggest that roots have more potential to contribute organic matter to this Louisiana salt marsh, particularly *Spartina* roots which degraded even more slowly than *Avicennia* roots.

Often, changes in vegetation and associated ecosystem processes are slow. To gain a better understanding and interpretation of the current study results, long-term research needs to be conducted in Louisiana salt marshes where populations of *Avicennia* are expanding. At the present time, for the selected plant-soil processes examined, no differences were detected between habitats. It is likely that as mangrove populations develop into larger stands and forests, significant changes in ecosystem processes may occur. At this point in their development in Louisiana, however, no major changes have been documented.

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