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Soil Development in a Coastal Louisiana Wetland during a Climate-Induced Vegetation Shift from Salt Marsh to Mangrove

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Kelly M. Henry* and Robert R. Twilley

Department of Oceanography and Coastal Sciences
School of the Coast and Environment
Louisiana State University
Baton Rouge, LA 70803, U.S.A.
khenry4@ucmerced.edu

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ABSTRACT

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Mild winter temperatures are facilitating the expansion of black mangrove (*Avicennia germinans*) into smooth cordgrass (*Spartina alterniflora*) marshes along the northern Gulf of Mexico. These expansions have the potential to alter soil development because of differences in productivity and tissue chemistry between *Spartina* and *Avicennia*. Here, we examined changes in soil-nutrient chemistry at 2-cm intervals in 30-cm soil cores collected from *Spartina* and *Avicennia* habitats at two different sites in Fourchon, Louisiana. Beginning in 1959 and continuing through 2009, our chronology shows that the species shift had no effect on bulk density (mean ± standard error [SE]: 0.68 ± 0.02 g cm^{-3}), organic matter (mean ± SE: 8.36 ± 0.29 %), or nitrogen content (mean ± SE: 1.15 ± 0.03 mg cm^{-3}). Phosphorus densities were significantly greater in *Avicennia* habitats (mean ± SE: 0.32 ± 0.01 mg cm^{-3}) than they were in *Spartina* habitats (mean ± SE: 0.28 ± 0.01 mg cm^{-3}), which we attributed to *Avicennia* occurring at higher elevations in more oxidizing soils. We observed significant variability with depth (proxy for time) and between sites in all soil properties measured. This variability can be attributed to the dominance of allochthonous sediment deposition from natural and anthropogenic disturbances compared with the lesser influence of vegetation on autochthonous soil development. In the highly disturbed region of Fourchon, Louisiana, the shift from *Spartina* marshes to scrub *Avicennia* stands does not appear to affect the chemistry of soil development.

ADDITIONAL INDEX WORDS: Avicennia germinans, *black mangrove, carbon, climate change, Mississippi River Delta, nitrogen, organic matter, phosphorus, smooth cordgrass,* Spartina alterniflora.

INTRODUCTION

Located at the northernmost extent of mangroves in the Gulf of Mexico, coastal Louisiana provides an excellent opportunity to study the effects of a climate-induced vegetation shift on soil development within a wetland ecosystem. Low-energy coastlines throughout temperate latitudes are dominated by salt marshes, whereas mangrove forests occupy a similar niche in the coastal tropics. In Louisiana, recent evidence suggests that temperatures have increased (Ning *et al.,* 2003), and the frequency of extreme freezes has decreased (Figure 1). Warmer temperatures and milder winters are not specific to Louisiana but are occurring in many regions worldwide (IPCC, 2007; Twilley *et al.,* 2001). In the northern Gulf of Mexico, these changes are facilitating expansions of the tropical black mangrove (*Avicennia germinans*) into smooth cordgrass (*Spartina alterniflora*) marshes of Florida, Louisiana, and Texas (Perry and Mendelssohn, 2009; Sherrod and McMillan, 1985; Stevens, Fox, and Montague, 2006).

The survival of mangroves and their replacement of salt marsh are directly related to freeze frequency (Chen and Twilley, 1998). The occurrence of more than one freeze every eight years inhibits the survival of mangroves, whereas a freeze frequency of 12 years allows mangroves to replace salt marsh (Chen and Twilley, 1998; Day *et al.,* 2005). The last frost-induced dieback of Louisiana *Avicennia* occurred in 1989, more than 20 years ago. Since then, the northward expansion of *Avicennia* into *Spartina* marshes has not been restricted by sustained periods of below freezing winter temperatures, which is a normal constraint at this latitude. Louisiana *Avicennia* are typically found in scrub form (<2.5 m high) because of the occasional frost and reduced number of degree days (Chen and Twilley, 1998; Lugo and Zucca, 1977).

Previous research in the Louisiana salt marsh–mangrove ecotone has examined controls on plant zonation (Patterson, McKee, and Mendelssohn, 1997; Patterson, Mendelssohn, and Swenson, 1993) as well as differences in soil physicochemical variables (Patterson and Mendelssohn, 1991) and ecosystem function (Perry and Mendelssohn, 2009) between the two

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* *Present address: Kelly M. Henry, School of Natural Sciences, University of California, 5200 North Lake Road, Merced, CA 95343, U.S.A.*
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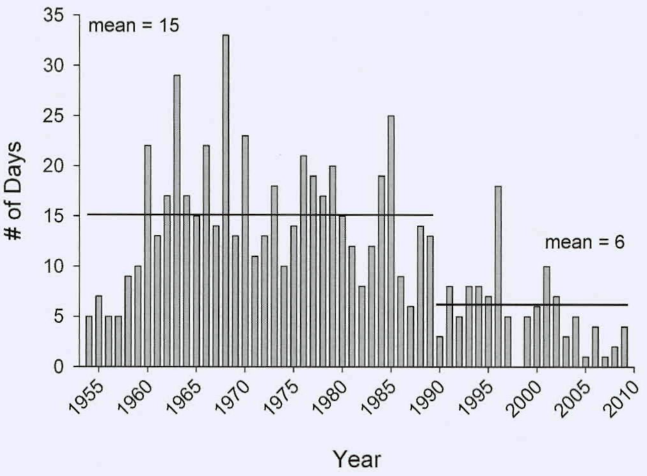

Figure 1. Number of days *per* year with a mean temperature below freezing (0 °C) in New Orleans, Louisiana (National Climatic Data Center, 2011). Horizontal black lines represent mean number of days before and after 1989, which marks the most recent frost-induced *Avicennia* dieback in southern Louisiana.

habitats. The results pertinent to soil organic matter and nutrient content are highly variable. Bulk density (dry mass *per* cubic volume), elevation, and oxidation–reduction potential are frequently greater in soils containing *Avicennia* (Patterson and Mendelssohn, 1991; Perry and Mendelssohn, 2009), whereas soils in *Spartina* habitats are more reducing, with higher concentrations of porewater sulfides, ammonium, and phosphate (Patterson and Mendelssohn, 1991). In contrast to these disparities, no significant differences have been detected in sediment accretion, belowground production, decomposition, and carbon assimilation (Perry and Mendelssohn, 2009).

Additional studies from *Spartina* marshes and neotropical scrub mangrove stands draw attention to potential differences between these species in productivity and tissue chemistry. Salt marsh productivity exhibits a latitudinal gradient, with the most productive salt marshes in North America occurring along the Gulf of Mexico (Turner, 1976). Published rates of aboveground primary productivity (APP) in *Spartina* marshes throughout Louisiana range from 700 to 3570 g m^{-2} y^{-1} (Darby and Turner, 2008; Edwards and Mills, 2005; Kaswadji, Gosselink, and Turner, 1990; Kirby and Gosselink, 1976). *Spartina* belowground primary productivity (BPP) appears more variable, with rates between 1670 and 11,680 g m^{-2} y^{-1} (Darby and Turner, 2008; Edwards and Mills, 2005; Perry and Mendelssohn, 2009). Rates of mangrove productivity also show a distinct trend with latitude; however, the most productive systems are located near the equator (Saenger and Snedaker, 1993; Twilley, Chen, and Hargis, 1992). Studies measuring the APP of scrub mangrove stands throughout the Neotropics found rates to vary from 170 to 490 g m^{-2} y^{-1} (Castañeda-Moya, 2010; Day *et al.,* 1996; Ewe *et al.,* 2006; Twilley, Lugo, and Patterson-Zucca, 1986), whereas published rates of BPP in this same region are between 20 and 1630 g m^{-2} y^{-1} (Castañeda-Moya *et al.,* 2011; McKee and Faulkner, 2000; McKee, Cahoon, and Feller, 2007; Perry and Mendelssohn, 2009). These studies suggest that the APP and BPP of coastal Louisiana *Avicennia* is only one-half the APP and BPP of *Spartina*, which may ultimately affect the quantity of organic matter deposited in coastal wetland soils.

The difference in foliar carbon (C) and nitrogen (N) content between *Spartina* and *Avicennia* may also affect soil development, more specifically the soil C : N ratio. Reported molar C : N ratios in the green leaves of *Spartina* and *Avicennia* range from 23 to 37 and 26 to 29, respectively (Lawton-Thomas, 1997; Osgood and Zieman, 1993; Twilley, Lugo, and Patterson-Zucca, 1986). When the comparison is made between green *vs.* senescent leaves, it is clear that both species retranslocate nitrogen before shedding leaves. *Spartina* retranslocates nitrogen to underground rhizomes and roots, whereas nitrogen from mangroves leaves is stored in aboveground stems. Although, it appears as though *Spartina* retranslocates more nitrogen when shedding leaves, resulting in a higher C : N ratio in *Spartina* litter (65 to 92) than found in *Avicennia* litter (47 to 55) (Breteler *et al.,* 1981; Lawton-Thomas, 1997; Twilley, Lugo, and Patterson-Zucca, 1986). As *Spartina* marshes change to *Avicennia* stands, the lower C : N ratio in the litter of *Avicennia* may increase the nitrogen content of the soil.

To better understand how the shift from *Spartina* marshes to *Avicennia* scrub mangrove stands affects nutrient chemistry during wetland soil development, we measured changes in soil bulk density as well as organic matter; nitrogen, and phosphorus content within the salt marsh–mangrove ecotone of Fourchon, Louisiana. Soils in low-energy coastal systems preserve historical conditions of plant community dynamics and maintain a record of natural and anthropogenic disturbances. Soil stratigraphy is frequently used as a tool in ecological studies to reconstruct past ecosystem dynamics and to elucidate patterns, causes, and rates of change (Willard and Cronin, 2007). Rates of sediment, nutrient, and heavy metal accumulation (DeLaune, Reddy, and Patrick, 1981; Reddy *et al.,* 1993), the timing and frequency of episodic events (*e.g.*, fires and hurricanes) (Liu and Fearn, 2000; Liu, Lu, and Shen, 2008), and shifts in hydrology and vegetation (Brenner, Schelske, and Keenan, 2001; Kim and Rejmánková, 2002) can all be determined from soil records.

In this study, shallow soil stratigraphy from *Spartina* and *Avicennia* habitats were compared to evaluate whether expanding populations of *Avicennia* will affect organic matter and nutrient accumulation during soil development. To place our stratigraphy in the appropriate historical context, we used previously published accretion rates for Fourchon (Perry and Mendelssohn, 2009) and a time series of aerial photographs and satellite images. Remote sensing is another tool often used in ecology to reconstruct previous ecosystem conditions and to characterize historical variability (Morgan, Gergel, and Coops, 2010). Studies in mangrove forests have incorporated both aerial photography and satellite imagery to determine community structure (*e.g.*, species, genera, and typology) (Dahdouh-Guebas *et al.,* 2000; Verheyden *et al.,* 2002), to analyze temporal dynamics (Kovacs, Wang, and Blanco-Correa, 2001; Rodriguez and Feller, 2004), and, more specifically, to document the expansion of *Avicennia* into *Spartina* marshes (Stevens, Fox, and Montague, 2006).

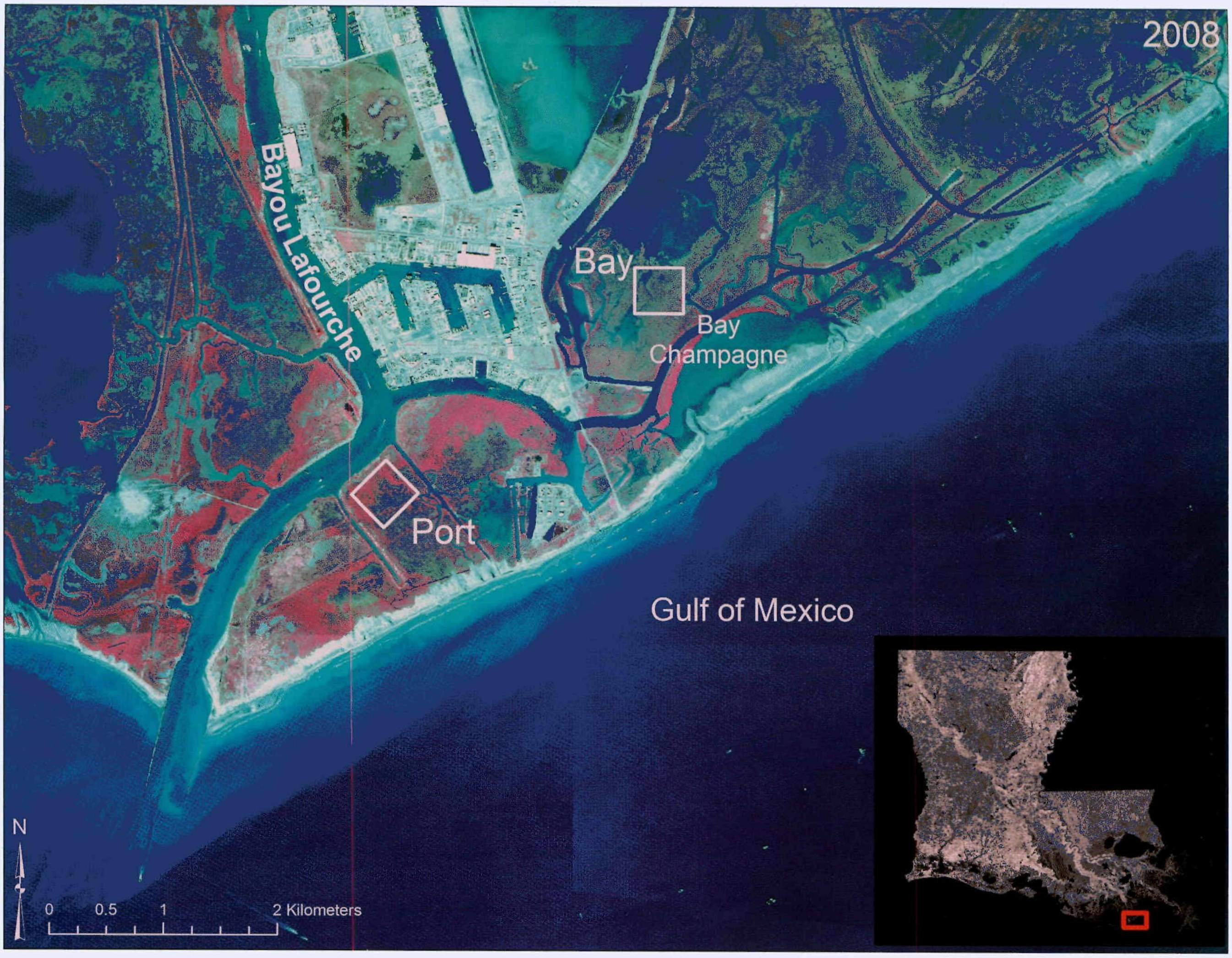

Figure 2. Sampling locations in Fourchon, Louisiana. Image courtesy of the Louisiana Department of Natural Resources. Wetlands in gray-brown were dominated by *Spartina*; wetlands in bright pink were dominated by *Avicennia*. White areas were nonvegetated sediment.

Here, we specifically sought to answer the following questions: (1) Does the shift from *Spartina* to *Avicennia* influence the chemistry of soil development? (2) Does the proximity and exposure of the salt marsh–mangrove ecotone to storm events from the Gulf of Mexico alter the soil response to this species shift? In Louisiana's coastal wetlands, mineral sediment input during episodic storm events can account for a significant portion of vertical marsh accretion (Turner *et al.*, 2006, 2007). Thus, we anticipated that increased exposure to the Gulf of Mexico and high mineral sediment input during storm events would mask any differences in soil development between these species. However, in regions more protected from the Gulf of Mexico, we anticipated that wetland soils would exhibit a decrease in carbon content and a subtle increase in nitrogen content as they shifted from *Spartina* marshes to *Avicennia* scrub mangrove stands.

MATERIALS AND METHODS

Study Area and Sampling Locations

The study area was located in salt marsh–mangrove ecotone of Fourchon, Louisiana, just east of Bayou Lafourche, less than 2 km from the Gulf of Mexico (Figure 2). The Fourchon region is located in the Barataria basin system of the Mississippi River Delta plain and was formed as part of the Lafourche lobe 2500 to 800 YBP (Coleman, Roberts, and Stone, 1998; Roberts, 1997). Before the completion of the Donaldsonville dam in 1904, Bayou Lafourche served as an outlet for the Mississippi River. A pumping station constructed in 1955 now allows approximately 6 m^3 s^{-1} of Mississippi River flow into the Bayou Lafourche (CWPPRA, 2011). Hydroperiod in the region is predominately controlled by diurnal microtides averaging 0.3 m in range, with strong meteorological influences during winter cold fronts and summer tropical storms and hurricanes (Zetler and Hansen, 1972). Precipitation (160 cm y^{-1}) comprises most freshwater inputs to the bayou, and, as a result, salinities are comparable to the Gulf of Mexico (~30‰) (Louisiana Department of Natural Resources, 2011). The climate of southern Louisiana is humid subtropical (Peel, Finlayson, and McMahon, 2007), with mean monthly temperatures between 6 and 30 °C (National Climatic Data Center, 2011). The Port of Fourchon serves as a major support center for petroleum exploration and production in the central Gulf of Mexico and is considered a highly industrialized area.

We established two sites in Fourchon (Figure 2). The Bay site (29°07′14″ N, 90°10′54″ W) was located less than 0.5 km NW of Bay Champagne, in a wetland that is highly exposed to winds and waves from the Gulf of Mexico. The Port site (29°06′21″ N, 90°12′30″ W) was located S of Port Fourchon and E of Bayou Lafourche. A levee prevents direct overbank flooding from Bayou Lafourche into the port site, and approximately 1 km of wetland and barrier beach protect this site from the Gulf of Mexico. Each site contained monospecific habitats of *Spartina* and *Avicennia*. When selecting sites, an effort was made to select sites near natural creeks and to avoid sites adjacent to dredged canals and their associated spoil banks. These particular sites were chosen because of their accessibility and the close proximity of *Spartina* habitats to well-developed stands of *Avicennia*.

Elevation Survey and Water Level Measurements

In July 2009, a 0.01-km^2 grid of approximately 35 sampling points and a permanent benchmark were established at the Bay and Port sites. This size grid provided ample space to collect soil cores and ensured hydrologic connectivity between *Spartina* and *Avicennia* habitats. Elevation of each sampling point relative to the benchmark was measured with a Sokkia LP30A Class 1 laser level, and the habitat type (*Avicennia* or *Spartina*) was recorded. The benchmark elevations were corrected to North American Vertical Datum of 1988 (NAVD88) using a Trimble R8 Global Navigation Satellite System (GNSS) dual-frequency receiver and elevation control points within the Continuously Operating Reference Stations (CORS) of the Louisiana State University (LSU) GULFNet real-time network (error: ±2 cm; Center for GeoInformatics, 2011).

After completing the elevation survey, an Onset HOBO U20 titanium water-level logger was installed at the lowest point in each site. Each water-level recorder was suspended inside a well casing and placed approximately 1.5 m below the soil surface. Water levels relative to the soil surface were recorded hourly from August 2009 to August 2010.

Soil Core Collection and Analysis

In July 2009, six cores (15 cm internal diameter by 30 cm long) were collected from the Bay site, three cores each from the *Spartina* and *Avicennia* habitats. Soil cores were collected using a polyvinyl chloride (PVC) suction-coring device (Meriwether *et al.,* 1996). We were only able to retrieve five cores from the Port site, two from the *Spartina* habitat and three from the *Avicennia* habitat. Soil cores, including any roots, rhizomes, and organisms, were extruded and sectioned into 2-cm intervals. Each soil section was oven-dried at 60 °C to a constant weight and then ground to 250 μm with a Wiley Mill. Before grinding, bulk density was calculated for each section as the total dry weight divided by the section volume. Total organic matter was determined by loss on ignition at 550 °C for 2 hours (Davies, 1974). Total carbon and nitrogen concentrations were determined with an ECS 4010 elemental analyzer (Costech Analytical Technologies, Inc., Valencia, California). Total phosphorus was extracted from the soil with 1 M HCl after combustion in a furnace for 2 hours at 550 °C (Aspila, Agemian, and Chau, 1976) and was determined by colorimetric analysis using a Flow Solution IV autoanalyzer (OI Analytical, College Station, Texas). Soil nutrient data are expressed on a volume basis using bulk densities.

Statistical Analysis

Elevation data were analyzed with a two-way analysis of variance (ANOVA) to test for differences between sites (Bay and Port) and habitat types (*Spartina* and *Avicennia*). A three-way ANOVA with repeated measures was used to determine whether statistical differences existed between sites or habitat types with depth for all soil variables (bulk density, organic matter content, nitrogen density, phosphorus density, molar C : N ratio, and nitrogen to phosphorus ratio [N : P]). The three-way ANOVA was run twice; the first run incorporated each individual section (0–2 to 28–30 cm) and will be referred to as the *section analysis*. In the second run, the mean of 0–10 cm was compared with the mean of 20–30 cm and will be referred to as the *mean analysis*. Interaction effects were considered for all analyses, and pairwise comparisons among treatments were described with a Tukey's honestly significant difference (HSD) test. All statistical analyses were performed with SAS PROC Mixed software, and significance was assessed at the 0.05 level (SAS Institute, 2011).

Interpretation of Aerial Photographs and Satellite Images

A time series of aerial photographs (resolution: 1 to 3 m) and satellite images (Landsat, path 22/row 40; resolution: 30 to 60 m) was obtained from the Louisiana State University Maps Library (1952 and 1957), the U.S. Geological Survey (1972, 1983, and 1991), and the Louisiana Department of Natural Resources (2008). Habitat type was primarily determined by variation in tone, color, texture, and shadow (Morgan, Gergel, and Coops, 2010). In the 1952 and 1957 aerial photographs, wetlands dominated by *Spartina* appeared gray, wetlands dominated by *Avicennia* appeared black, and nonvegetated sediment (*e.g.*, beach sand or dredge spoil) appeared white. In the 1972, 1983, 1991, and 2008 aerial photographs and satellite images, wetlands dominated by *Spartina* appeared gray–brown, wetlands dominated by *Avicennia* appeared bright pink, and nonvegetated sediment again appeared white. In addition to determining the presence or absence of *Avicennia* in our study sites, photographs and images were analyzed for changes in wetland geomorphology, such as coastal erosion and canal construction.

RESULTS

On average, elevation at the Bay site was (mean ± SE) 13.3 ± 1.2 cm significantly greater than it was at the Port site (Table 1). Within both sites, *Spartina* occurred at significantly lower

Table 1. *Elevation and hydroperiod data for* Spartina *and* Avicennia *habitats in the Bay and Port sites of Fourchon, Louisiana.*

	Bay		Port	
	Spartina	*Avicennia*	*Spartina*	*Avicennia*
Elevation (cm)[a,b]	28.1 ± 0.9, b	38.7 ± 1.1, a	18.2 ± 0.3, d	21.4 ± 0.4, c
(n)	(16)	(16)	(15)	(21)
Hydroperiod				
Duration (h y^{-1})[c]	3707		5780	
Duration (%)	42		66	
Frequency (events y^{-1})[d]	246		183	

[a] Mean ± 1 SE presented for elevation data.
[b] Within row, means followed by the same letter are not significantly different according to Tukey's HSD ($p > 0.01$).
[c] Duration = number of hours water level exceeded zero.
[d] Frequency = number of times water level changed from <0 to ≥0.

elevations than did *Avicennia*. Hydroperiod varied between the two sites (Table 1). The Bay site was flooded 42% of the year and experienced 246 flood-events y^{-1}, whereas the Port site was flooded 66% of the year, but only experienced 183 flood-events y^{-1}. It appears as though the lower-elevation Port site does not drain as frequently, and as a result, a longer flood at the Port site registers as two or more flood events at the higher-elevation Bay site.

The complete depth profile for all variables from the Bay site showed marked variability in the top 0 to 10 cm relative to the lower 20 to 30 cm, with a transition zone from 10 to 20 cm (Table 2, Figure 3). Soils in the top 10 cm from the Bay site exhibited a mineral-rich signature, with high bulk density and phosphorus density and low organic matter content and nitrogen density. Below 20 cm, soil bulk density and phosphorus density decreased, whereas organic matter content and nitrogen density increased. The profiles for all soil variables from the five Port cores strongly contrasted with those from the Bay cores, exhibiting the opposite trends with depth (Table 2, Figure 3). Soils in the top 10 cm from the Port site were enriched in organic matter, with low bulk density and phosphorus density. From 20 to 30 cm, soil bulk density and phosphorus density increased, whereas organic matter content and nitrogen density decreased. There were no notable differences between the *Spartina* and *Avicennia* profiles from either the Bay or the Port site (Figure 3).

Table 2. *Vertical distribution of nitrogen and phosphorus density for each site in the salt marsh–mangrove ecotone of Fourchon, Louisiana.*

	Nitrogen Density (mg cm^{-3})		Phosphorus Density (mg cm^{-3})	
Depth (cm)	Bay[a] $\bar{X}$ ± SE	Port[b] $\bar{X}$ ± SE	Bay[a] $\bar{X}$ ± SE	Port[b] $\bar{X}$ ± SE
0–2	0.54 ± 0.13	0.79 ± 0.05	0.40 ± 0.05	0.17 ± 0.01
2–4	0.52 ± 0.33	1.11 ± 0.09	0.53 ± 0.03	0.27 ± 0.03
4–6	0.47 ± 0.30	1.61 ± 0.18	0.47 ± 0.02	0.21 ± 0.02
6–8	1.27 ± 0.27	1.39 ± 0.12	0.45 ± 0.02	0.19 ± 0.01
8–10	1.13 ± 0.24	1.39 ± 0.10	0.40 ± 0.03	0.21 ± 0.02
10–12	1.38 ± 0.09	1.55 ± 0.09	0.30 ± 0.02	0.24 ± 0.01
12–14	1.32 ± 0.13	1.41 ± 0.07	0.30 ± 0.03	0.27 ± 0.02
14–16	1.30 ± 0.12	1.34 ± 0.09	0.25 ± 0.03	0.31 ± 0.02
16–18	1.38 ± 0.09	1.22 ± 0.07	0.22 ± 0.02	0.35 ± 0.02
18–20	1.33 ± 0.04	1.11 ± 0.12	0.22 ± 0.03	0.36 ± 0.01
20–22	1.42 ± 0.08	0.79 ± 0.04	0.19 ± 0.01	0.35 ± 0.01
22–24	1.39 ± 0.03	0.82 ± 0.03	0.20 ± 0.01	0.40 ± 0.01
24–26	1.48 ± 0.09	0.78 ± 0.05	0.19 ± 0.01	0.39 ± 0.02
26–28	1.42 ± 0.07	0.77 ± 0.04	0.20 ± 0.01	0.41 ± 0.01
28–30	1.35 ± 0.05	0.79 ± 0.03	0.22 ± 0.01	0.39 ± 0.02

[a] Bay site: $n = 6$; Port site: $n = 5$.
[b] Mean ± 1 SE presented for all data.

The section analysis demonstrated a significant effect of depth and a significant interaction between site and depth for all soil variables, except C : N (Table 3). The only significant difference between habitat types was in total phosphorus density, with lower phosphorus content in *Spartina* soils (mean ± SE: 0.28 ± 0.01 mg cm^{-3}) than found in *Avicennia* soils (mean ± SE: 0.32 ± 0.01 mg cm^{-3}) (Table 3). The mean values for each soil variable from 0–10 cm and from 20–30 cm further supported the results of the section analysis (Figure 4). There was a significant interaction between site and depth for all variables measured, except C : N, and the only significant difference between habitat types was in phosphorus density (Table 3).

DISCUSSION

A Note on the Chronosequence Analyzed in this Study

Extensive documentation exists of daily (sediment traps), annual (feldspar marker horizons), and decadal-scale (^{137}Cs and ^{210}Pb) accretion rates throughout coastal Louisiana wetlands (Cahoon and Turner, 1989; DeLaune *et al.*, 1989; Perry and Mendelssohn, 2009; Reed, 1989; among others). Most accretion estimates for the region are between 0.6 and 1.5 cm y^{-1}, with higher rates of deposition occurring along natural creeks and during episodic events, such as winter cold fronts and summer storms (Baumann, Day, and Miller, 1984; Childers and Day, 1990; Hatton, DeLaune, and Patrick, 1983; Reed, 1989). In 2006, Perry and Mendelssohn (2009) measured accretion rates in the salt marsh–mangrove ecotone of Fourchon and observed constancy between daily, annual, and decadal-scale rates. Furthermore, their results showed no significant difference in accretion between *Spartina* and *Avicennia* habitats. To facilitate interpretation of our data, we divided soil profiles from the Bay and Port sites into two periods: recent soil development (0–10 cm) and early soil development (20–30 cm), with a transitional period in between. We assumed similar accretion rates between the habitats of *Spartina* and *Avicennia*. Based on the previously published decadal-scale accretion rate (0.6 cm y^{-1}) for the Fourchon region (Perry and Mendelssohn 2009), early soil development likely covers 1959 to 1976, whereas recent soil development spans 1992 to 2009.

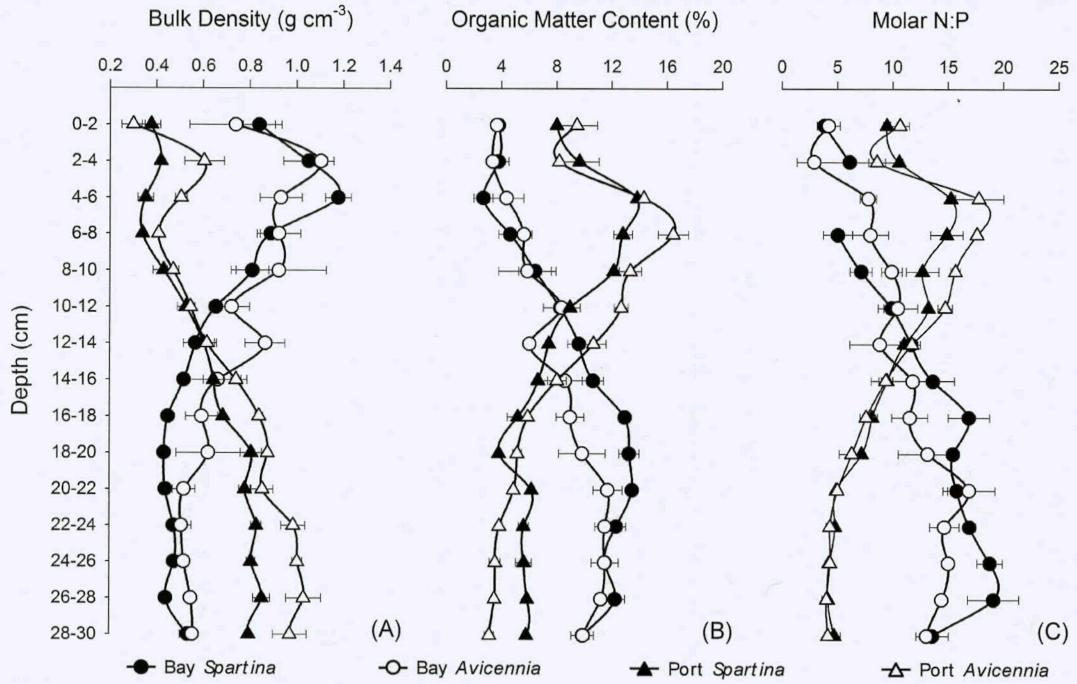

Figure 3. (A) Bulk density, (B) organic matter content, and (C) molar N : P profiles for *Spartina* and *Avicennia* soils in Bay and Port sites. Each data point is mean ($\pm$1 SE) of three cores, except *Spartina* at the Port site, which is the mean of two cores.

Early Soil Development, 1959 to 1976

Bay Site

At the Bay site, soil development from 1959 to 1976 (20–30 cm) exhibited a signature characteristic of a coastal Louisiana wetland, with low bulk density and high organic matter content (Figures 3 and 4). Both bulk density and organic matter content in these soils were within the range of values previously published for salt marshes (DeLaune, Reddy, and Patrick, 1981; DeLaune *et al.,* 1989; Patterson and Mendelssohn, 1991; Perry and Mendelssohn, 2009). Although few studies specific to the region have measured nitrogen and phosphorus content, our values are on the same order of magnitude as those reported by DeLaune, Reddy, and Patrick (1981) (mean $\pm$ SE N: 2.8 $\pm$ 0.075 mg g^{-1}, mean $\pm$ SE P: 0.4 $\pm$ 0.003 mg g^{-1}). The relatively high bulk density and low organic matter and nitrogen content in these soils in comparison to

Table 3. *ANOVA results from section analysis and mean analysis testing for effects of site (S), habitat (H), and depth (D) on soil properties in the salt marsh–mangrove ecotone of Fourchon, Louisiana. ANOVA p values from SAS PROC Mixed, ns = not significant (p > 0.05).*

	Bulk Density (g cm^{-3})	Organic Matter (%)	Nitrogen (mg cm^{-3})	Phosphorus (mg cm^{-3})	Molar C : N[b]	Molar N : P[b]
Section analysis[a]						
Site	NS	NS	NS	NS	NS	0.04
Habitat	NS	NS	NS	0.05	NS	NS
Site × habitat	NS	NS	NS	NS	NS	NS
Depth	<0.0001	<0.0001	<0.0001	<0.0001	0.05	<0.0001
Site × depth	<0.0001	<0.0001	<0.0001	<0.0001	NS	<0.0001
Habitat × depth	NS	0.0003	0.01	NS	NS	0.02
S × H × D[c]	NS	<0.0001	NS	NS	NS	NS
Mean analysis[d]						
Site	NS	NS	NS	0.02	NS	NS
Habitat	NS	NS	NS	0.02	NS	NS
Site × habitat	NS	NS	NS	NS	NS	NS
Depth	NS	NS	NS	0.004	NS	NS
Site × depth	<0.0001	<0.0001	0.0005	<0.0001	NS	<0.0001
Habitat × depth	NS	0.03	NS	NS	NS	0.04
S × H × D[c]	NS	NS	NS	NS	NS	NS

[a] Section analysis incorporated each individual depth section from 0 to 30 cm for a total of 15 depths.
[b] Molar carbon to nitrogen ratio (C : N), molar nitrogen to phosphorus ratio (N : P).
[c] S × H × D = three-way interaction effect between site, habitat, and depth.
[d] Mean analysis compared the mean of 0 to 10 cm values to the mean of 20 to 30 cm values.

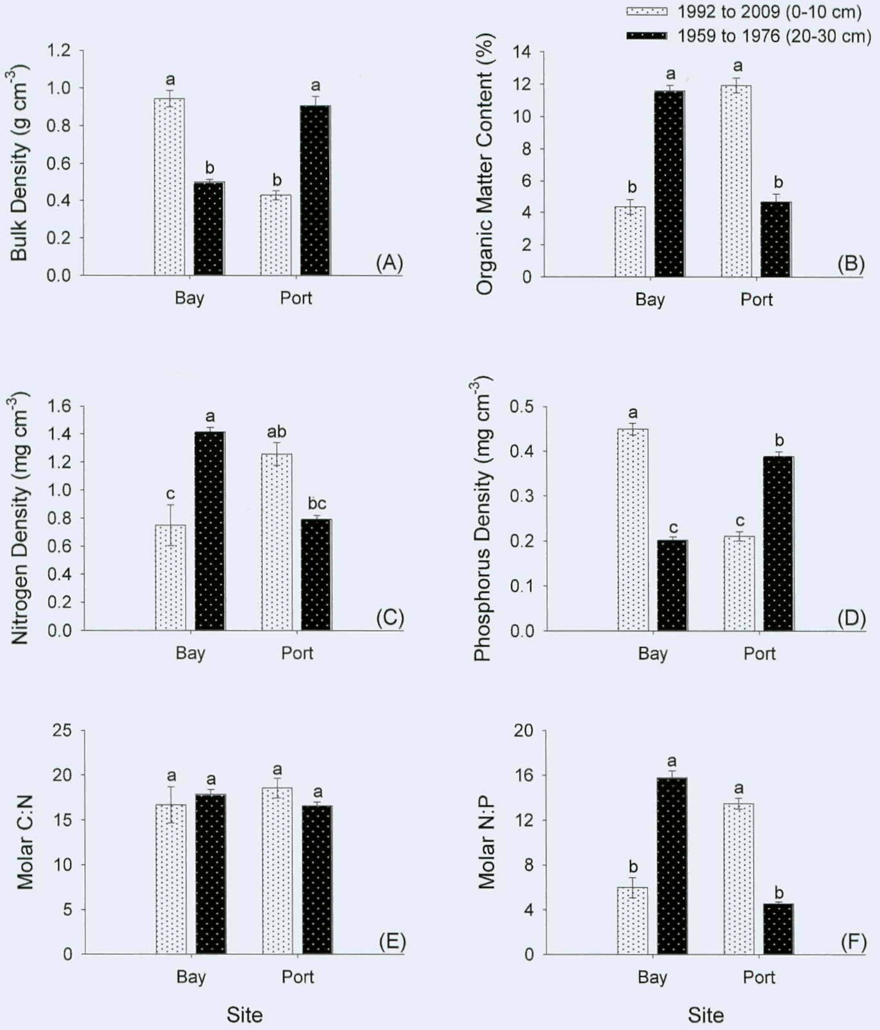

Figure 4. Mean (±1 SE) (A) bulk density, (B) organic matter content, (C) nitrogen density, (D) phosphorus density, (E) molar C : N, and (F) molar N : P in top 10 cm (1992 to 2009) and 20 to 30 cm (1959 to 1976) of Bay and Port sites. Lowercase letters correspond to ANOVA results from SAS PROC Mixed. Within figures, means (Bay $n = 6$; Port $n = 5$) followed by the same letter are not significantly different according to Tukey's HSD ($p > 0.05$).

previous studies may be attributed to the close proximity of the Bay site to the Gulf of Mexico and a disproportionate contribution of marine sediment to the site (Hatton, DeLaune, and Patrick, 1983).

Vegetation surveys as early as 1932 document the presence of *Avicennia* in Louisiana *Spartina* marshes; however, these populations were sparse in their occurrence and primarily restricted to the southernmost portion of the state and the barrier islands (Penfound and Hathaway, 1938). After analyzing aerial photographs and satellite images of Lafourche Parish from 1957 and 1972, *Avicennia* did not appear to be present in the Bay site during that period (Figures 5 and 6). In the absence of *Avicennia*, the dominant vegetation type in both the *Spartina* and *Avicennia* habitats was likely *Spartina*. The absence of *Avicennia* from the Bay site may explain the similarities in soil development between the two habitat types from 1959 to 1976.

Port Site

Soil development from 1959 to 1976 (20–30 cm) in the Port site contrasts dramatically with that of the Bay site discussed above (Figures 3 and 4). The Port soil profile from this period was enriched in mineral sediment, exhibiting a signature more typical of dredge spoil or storm-surge deposits. Although the composition of storm deposits (and dredge spoil) can vary depending on sediment origin, they are typically dominated by mineral material with high bulk densities (>0.8 g cm^{-3}) and low organic matter content (<10%) (Cahoon *et al.,* 1995; Ford, Cahoon, and Lynch, 1999; Nyman, Crozier, and DeLaune, 1995; Turner *et al.,* 2006).

The Port site is located just south of Bayou Lafourche, which is a major transportation channel for vessels servicing the Gulf of Mexico petroleum industry from the Port of Fourchon. Frequent hydraulic dredging from the Flotation Canal to Belle Pass maintains these lower reaches at 24 to 30 feet; and up

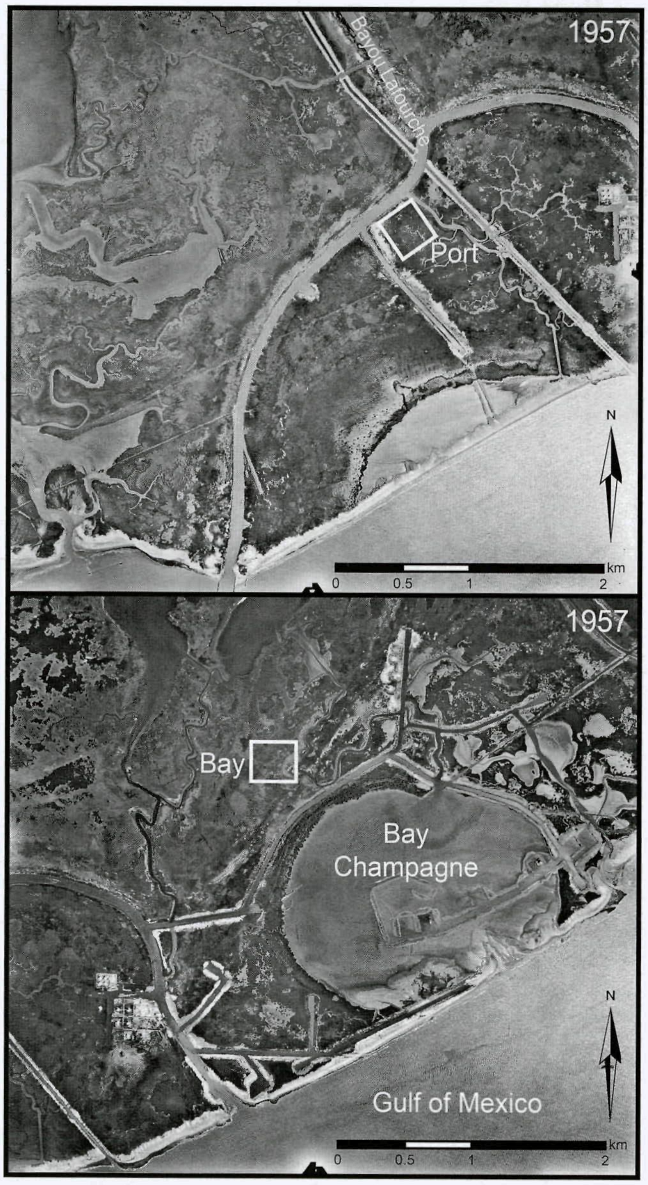

Figure 5. Sampling locations in 1957. Image courtesy of the Louisiana State University Map Library. Wetlands in gray were dominated by *Spartina*; wetlands in black were dominated by *Avicennia*. White areas were nonvegetated sediment.

until the late 1990s, the spoil was pumped into disposal areas along the channel banks (Ted M. Falgout, *personal communication*). Aerial photographs of the Port site from 1952 (not shown) and 1957 (Figure 5) show the construction of at least two additional canals with distinct spoil banks less than 0.5 km from the Port site. The natural creeks bisected by these canals may have facilitated transport and redistribution of dredge spoil into the Port site. The 1972 satellite image provides further evidence of dredge spoils in the wetlands neighboring the Port site during this period (Figure 6). Although a conscious effort was made to avoid locating our sites on visible levees and

Figure 6. Sampling locations in 1972. Image courtesy of the U.S. Geological Survey. Wetlands in gray–brown were dominated by *Spartina*; wetlands in bright pink were dominated by *Avicennia*. White areas were nonvegetated sediment.

spoil banks, it appears as though the Port cores were sampled on remnant dredge spoil. A few sparse populations of *Avicennia* may have been present in the Port site during this period. However, the high input of mineral sediment seems to have concealed any potential differences between *Spartina* and *Avicenna* soil development from 1959 to 1976.

Recent Soil Development, 1992 to 2009

Bay Site

From 1992 to 2009 (0–10 cm), mineral sediment deposition dominated the Bay site soil profile. Bulk density and phosphorus content were significantly higher, and organic matter and nitrogen content were significantly lower than soils deposited from 1959 to 1976 (Figures 3 and 4). All the soil variables measured were outside the range reported for Louisiana salt marsh soils and were more representative of dredge spoil or storm surge deposits (DeLaune, Reddy, and Patrick, 1981; Ford, Cahoon, and Lynch, 1999; Nyman, Crozier, and DeLaune, 1995; Perry and Mendelssohn, 2009; among others).

In the absence of fluvial inputs, episodic events, such as summer tropical storms and hurricanes and winter cold fronts, dominate allochthonous sediment deposition in the Mississippi River Delta (Turner *et al.,* 2006, 2007). From 1992 to 2009, approximately 18 tropical storms or hurricanes made landfall in coastal Louisiana; 14 of which occurred between 1999 and 2009 (National Hurricane Center, 2011). This represents a marked increase in storm activity compared with the period of early soil development (1959 to 1976) when only eight tropical storms or hurricanes made landfall in coastal Louisiana (National Hurricane Center, 2011). Significant sediment deposition in wetlands throughout the Delta plain was documented with the passage of Hurricane Andrew in 1992 (Cahoon *et al.,* 1995; Nyman, Crozier, and DeLaune, 1995).

Directly affecting the Fourchon region were hurricanes Lili (2002), Katrina and Rita (2005), and Gustav and Ike (2008) (Liu *et al.,* 2011). The storm surges during these events breached the sand barrier between Bay Champagne and the Gulf of Mexico, depositing prominent overwash fans behind the barrier beach (Liu *et al.,* 2011). A soil core collected from a wetland directly adjacent to the Bay site after the passage of Katrina and Rita showed approximately 5 cm of storm-derived sediment deposition (Edward Castañeda-Moya, unpublished data). More recently, the 2008 combination of Gustav and Ike completely inundated the coastal plain and caused extensive flooding in the Fourchon region (Liu *et al.,* 2011). These results support our hypothesis that the mineral-rich composition observed in soils at the Bay site from 1992 to 2009 corresponds to a period of enhanced storm activity in coastal Louisiana.

The distance today from the Bay site across Bay Champagne to the Gulf of Mexico is approximately one-half the distance that it was in 1957 (Figures 2 and 5). Furthermore, marsh deterioration during the past 10 years opened a direct path from Bay Champagne to the Bay site (Figures 2 and 7). The Bay site is situated to receive large amounts of reworked Bay Champagne and near-shore sediment during winter cold fronts and summer storm events because of its unprotected position. Despite the presence of a well-developed *Avicennia* stand in the Bay site, physical storm events appear to be the dominant signal from 1992 to 2009, obscuring any subtle differences in soil development between *Spartina* and *Avicennia*.

Port Site

From 1992 to 2009 (0–10 cm), soil development in the Port site exhibited a signature more typical of a Louisiana salt marsh. Bulk density and phosphorus content were significantly lower, and organic matter and nitrogen content were significantly higher than in soils deposited between 1959 and 1972 (Figures 3 and 4). The significantly lower contribution of mineral sediment from 1992 to 2009 in soil from the Port site (relative to the Bay site) during a period of high storm activity can be attributed to the more-protected location of this site from the Gulf of Mexico. Despite the loss of nearly 1 km of shoreline between 1957 and 2008, there is still >1 km of wetland between the Port site and the Gulf of Mexico (Figures 2 and 5). Thus, it appears as though the influence of storm events on soil development was not significant in the Port site as it was in the Bay site.

Several severe winters in the 1980s killed most of the *Avicennia* populations in the Fourchon region (Figure 7; Patterson and Mendelssohn, 1991; Perry and Mendelssohn, 2009). Since 1989, mild winters have allowed populations of *Avicennia* to expand back into areas of *Spartina* marsh. At the Port site, *Avicennia* likely began recolonizing the *Spartina* marshes in the early 1990s and was firmly established by 2008. However, even after nearly two decades of *Avicennia* presence at this site, we found no significant difference between soil stratigraphy from the *Spartina* and *Avicennia* habitats.

Throughout the entire study, the only significant differences observed between *Spartina* and *Avicennia* were in elevation and phosphorus density; *Avicennia* occurred at higher elevations in soils with greater phosphorus content. Previous research in the salt marsh–mangrove ecotone observed similar differences in elevation between *Avicennia* and *Spartina,* which coincided with significantly lower soil moisture and higher oxidation–reduction (redox) potential in *Avicennia* habitats (Patterson and Mendelssohn, 1991; Perry and Mendelssohn, 2009). Redox potential and the availability of sulfate and iron strongly influence the geochemical cycling of phosphorus in both salt marsh and mangrove wetlands (see Tobias and Neubauer [2009] and Twilley and Rivera-Monroy [2009] for comprehensive reviews). As redox potential increases and oxidizing conditions become more prominent, dissolved phosphate adsorbs onto iron oxyhydroxides, decreasing concentrations of soluble, reactive phosphate in the porewater and increasing total phosphorus in the soil. Therefore, the significantly greater phosphorus density observed in the *Avicennia* soils was likely caused by the more-oxidizing conditions in this habitat.

Figure 7. Sampling locations in 1991. Image courtesy of the U.S. Geological Survey. Wetlands in gray-brown were dominated by *Spartina*; wetlands in bright pink were dominated by *Avicennia*. White areas were nonvegetated sediment.

CONCLUSIONS

The shift from *Spartina* to *Avicennia* had no effect on soil bulk density, organic matter content, or nitrogen content. Our data did show significantly higher phosphorus densities in *Avicennia* habitats, which were likely caused by the occurrence of *Avicennia* at higher elevations in more oxidizing soils. The significant differences between the Bay and Port sites observed throughout the chronology can be attributed to a combination of autochthonous soil development and allochthonous deposition from both natural and anthropogenic disturbances. In conclusion, the initial expansion of *Avicennia* does not appear to be affecting soil development in the highly disturbed region of Fourchon. However, if the warming trend of the past several decades continues and populations of *Avicennia* increase in structural complexity (*e.g.*, basal area, tree height, and density) or areal coverage, there may be the potential for changes in wetland soil chemistry during soil development, provided a low occurrence of physical disturbance from storm events and human activities.

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