Sediment and Nutrient Deposition Associated with Hurricane Wilma in Mangroves of the Florida Coastal Everglades

Edward Castañeda-Moya · Robert R. Twilley · Victor H. Rivera-Monroy · Keqi Zhang · Stephen E. Davis III · Michael Ross

Received: 27 March 2009 / Revised: 6 November 2009 / Accepted: 10 November 2009 / Published online: 22 December 2009 © Coastal and Estuarine Research Federation 2009

Abstract The distribution of mangrove biomass and forest structure along Shark River estuary in the Florida Coastal Everglades (FCE) has been correlated with elevated total phosphorus concentration in soils thought to be associated with storm events. The passage of Hurricane Wilma across Shark River estuary in 2005 allowed us to quantify sediment deposition and nutrient inputs in FCE mangrove forests associated with this storm event and to evaluate whether these pulsing events are sufficient to regulate nutrient biogeochemistry in mangrove forests of south Florida. We sampled the spatial pattern of sediment deposits and their chemical properties in mangrove forests along FCE sites in December 2005 and October 2006. The thickness (0.5 to 4.5 cm) of hurricane sediment deposits decreased with distance inland at each site. Bulk density, organic matter content, total nitrogen (N) and phosphorus (P) concentrations, and inorganic and

organic P pools of hurricane sediment deposits differed from surface (0-10 cm) mangrove soils at each site. Vertical accretion resulting from this hurricane event was eight to 17 times greater than the annual accretion rate $(0.30\pm$ 0.03 cm year⁻¹) averaged over the last 50 years. Total P inputs from storm-derived sediments were equivalent to twice the average surface soil nutrient P density (0.19 mg cm⁻³). In contrast, total N inputs contributed 0.8 times the average soil nutrient N density (2.8 mg cm⁻³). Allochthonous mineral inputs from Hurricane Wilma represent a significant source of sediment to soil vertical accretion rates and nutrient resources in mangroves of southwestern Everglades. The gradient in total P deposition to mangrove soils from west to east direction across the FCE associated with this storm event is particularly significant to forest development due to the P-limited condition of this carbonate ecosystem. This source of P may be an important adaptation of mangrove forests in the Caribbean region to projected impacts of sea-level rise.

E. Castañeda-Moya (⋈) · R. R. Twilley · V. H. Rivera-Monroy Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, LA 70803, USA e-mail: ecasta1@tigers.lsu.edu

K. Zhang

Department of Environmental Studies & International Hurricane Research Center, Florida International University, Miami, FL 33199, USA

S. E. Davis III Department of Wildlife & Fisheries Sciences, Texas A&M University, 2258 TAMU, College Station, TX 77843-2258, USA

M. Ross

Department of Environmental Studies & Southeast Environmental Research Center, Florida International University, Miami, FL 33199, USA **Keywords** Hurricane Wilma · Sediment deposition · Mangroves · Accretion · Nutrient biogeochemistry · Florida Everglades

Introduction

Hurricanes are large-scale pulsing events that shape community structure and function of tropical and subtropical forest ecosystems (Michener et al. 1997; Lugo 2000, 2008). Hurricane effects often include widespread changes in the physical environment of the forest, vegetation structure, species composition, succession, nutrient cycling, and animal population dynamics (Lodge and McDowell



1991; Lugo 2008). Mangrove forests are particularly more susceptible to physical changes in forest structure because of their position in the intertidal zone, usually experiencing the brunt of tropical storms (Sherman et al. 2001; Piou et al. 2006). Hurricane effects on mangrove forests depend on several factors such as the position of the forest relative to hurricane track, physical characteristics of a storm (i.e., intensity, radius to maximum wind speed, velocity), and the degree of protection offered by topographic features (Krauss et al. 2005; Piou et al. 2006; Zhang et al. 2008).

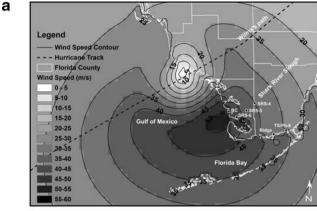
Despite their low floristic complexity relative to tropical rainforests, Neotropical mangrove forests are highly resilient to natural disturbances such as tropical storms or hurricanes. These forested wetlands have developed key life history traits that allow trajectories in ecosystem structure and function at decadal time scales depending on the frequency and intensity of hurricane disturbances (Smith et al. 1994; Alongi 2008). Such resilient traits include large nutrient reserves (belowground biomass, soil and litter), rapid nutrient turnover rates (litter immobilization, efficient microbial-plant interactions), high rates of water-use and nutrient-use efficiency, and a unique and simple tree architecture that, for some mangrove species, includes resprouting from epicormic shoots (Alongi 2008). Hurricane events also trigger processes that help to maintain soil vertical accretion through large-scale sediment deposition and redistribution by storm surge (Cahoon 2006; Day et al. 2007; Turner et al. 2007). Yet, few studies have documented the positive role of hurricane deposition in controlling soil vertical accretion in coastal wetlands (Cahoon et al. 1995; Nyman et al. 1995; Turner et al. 2007; Whelan et al. 2009) or have focused on the potential influence of these disturbance processes in maintaining mangrove soil elevation relative to sea level.

Hurricanes can also play an important role in the nutrient biogeochemistry of mangroves in zones of high disturbance frequency, which influences patterns in vegetation structure and community composition. Allochthonous mineral input has been recognized as a key process in controlling soil formation in mangrove wetlands (Chen and Twilley 1999a). Mineral inputs (i.e., Ca-bound P) during storm events to the mouth of Shark River estuary from the Gulf of Mexico, rather than upland inputs of nutrients, are hypothesized to control patterns of mangrove forest structure and productivity in the southwestern Everglades (Chen and Twilley 1999a, b). These allochthonous mineral inputs enhance P concentrations and lower N/P ratios in mangroves at the mouth of Shark River estuary, where soil properties are strongly associated with higher biomass (150-200 Mg ha⁻¹) and tree height (18–20 m) in contrast to upstream sites of this estuary and other regions of southeastern Florida (biomass <50 Mg ha⁻¹; tree height <5 m; Ewe et al. 2006; Simard et al. 2006). Simulation models of soil organic matter content and bulk density along Shark River estuary demonstrated that field observations could only be calibrated by varying allochthonous inputs of mineral matter during storm events at the mouth of the estuary (Chen and Twilley 1999a). There was some documentation of this phenomenon from Hurricane Irene (1999) when sediment deposits were measured as sources of carbonate-bound P to the Taylor River mangrove ecotone of south Florida (Davis et al. 2004).

South Florida is characterized by a high recurrence of tropical storms and hurricanes as other mangrove areas in the Caribbean-Gulf of Mexico region, and thus it is an excellent region to test storm effects on the structure and function of mangrove forests (Duever et al. 1994; Smith et al. 1994; Krauss et al. 2005). It is estimated that south Florida has been struck by 40 hurricanes between 1871 and 2003, with an average frequency of about once per 3 years (Lodge 2005). Moreover, the frequency of direct hits by major storms (categories 3-5) in south Florida is approximately once every 20 years (Gentry 1974). Hurricane Wilma, a Category 3 storm, made landfall on the southwestern coast of Florida between Everglades City and Cape Romano on October 24, 2005 (Fig. 1a; Zhang et al. 2008). Maximum sustained winds over the Florida Coastal Everglades (FCE) were estimated to be near 105 km h⁻¹ when it made landfall (Pasch et al. 2006). The eye of the hurricane had a diameter of 89-105 km and a wind speed of 43 and 46 m s⁻¹ at Broad Creek and Shark River, respectively (Fig. 1a; Zhang et al. 2008). For a time, hurricane Wilma was the strongest Atlantic tropical storm on record with a minimum central pressure at the time of peak intensity of 882 mb (Pasch et al. 2006). The large-scale physical damage to mangrove forest structure included defoliation, tree snapping, and uprooting, depending on the distance from and compass position relative to the eye wall.

The proximity of Wilma's landfall relative to our longterm mangrove study sites in FCE provided an excellent opportunity to evaluate the role of these pulsing events on soil nutrient biogeochemistry, forest community structure, and net primary productivity. In this study, we report on the quantity of sediment deposition and changes in soil nutrient pools in our mangrove sites to evaluate whether pulsing events such as Hurricane Wilma are significant to soil nutrient inventories and vertical accretion by addressing the following questions: (1) What are the sediment characteristics and distribution and thickness of the sediments deposited by Hurricane Wilma in FCE mangrove sites? (2) What are relative inputs of total N and P from hurricane deposits to the nutrient pools accumulated in mangrove soils? (3) What are the fractions of inorganic and organic P in storm deposits, and how do these pools differ from those already present in mangrove soils? (4) What is the role of





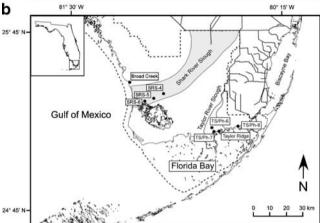


Fig. 1 a Hurricane Wilma's track and wind fields during its passage across south Florida, USA. The wind field was created using observations at 10:30 UTC on October 24, 2005. The wind speed represents maximum 1-min sustained surface wind 10 m above the ground/ocean surface. The wind field and track data were obtained from the Hurricane Research Division and the National Hurricane Center of the US National Oceanic and Atmospheric Administration, respectively. **b** Location of the study sites in the Everglades National Park, south Florida, USA. *SRS-4*, *SRS-5*, and *SRS-6* along Shark River Slough; *TS/Ph-6*, *TS/Ph-7* along Taylor River Slough and *TS/Ph-8* in Joe Bay are part of the Florida Coastal Everglades Long-Term Ecological Research program. The Taylor Ridge site was located ~1 km east of the Taylor River mouth. The *inset* shows the location of ENP in southern Florida, USA

hurricane sediment deposition in maintaining landscape patterns of soil fertility and vertical accretion of mangroves in FCE? We report on the short-term effect of a hurricane disturbance on spatial patterns of sediment deposition and surface nutrient pools to understand how these processes may influence longer term mangrove forest dynamics as has been hypothesized for FCE.

Study Sites

This study was conducted in mangrove forests of Everglades National Park (ENP), which occupy an estimated total area of 144,447 ha (Fig. 1b; Simard et al. 2006). This

area represents approximately two thirds of all mangrove cover in south Florida and is the largest mangrove area in the continental USA (Lodge 2005). Mangrove forests form a continuous band that extends along a freshwater–estuarine gradient from the southernmost freshwater marshes of the Everglades and Big Cypress Swamp to the open waters of Florida Bay and the Gulf of Mexico (Wanless et al. 1994).

Mangrove forests in south Florida are distributed along the coastal margin where the limestone platform is covered with a thick layer (0.5-6.5 m) of wetland peat deposits (Wanless et al. 1994; Ewe et al. 2006). In 2000, mangrove sites were established along the Shark River and Taylor River estuaries as part of the FCE Long-Term Ecological Research (LTER) program (Childers 2006; http://fcelter.fiu. edu/). Mangrove forests along Shark River are characterized as riverine mangroves consisting of Rhizophora mangle (L.), Avicennia germinans (L.), and Laguncularia racemosa (Gaertn). Conocarpus erectus L. is restricted to upstream locations (SRS-4) of Shark River. Shark River sites are located approximately 4.1 km (SRS-6), 9.9 km (SRS-5), and 18.2 km (SRS-4) from the mouth of Shark River estuary (Fig. 1b). Lower Shark River sites (SRS-5 and SRS-6) are tide dominated, while SRS-4 is influenced by runoff, although a tidal influence is observed, particularly in the dry season (Chen and Twilley 1999b). A similar riverine mangrove site was established 2 km upstream from the mouth of Broad Creek (BC), approximately 11 km northwest of Shark River (Fig. 1b; Zhang et al. 2008). Tides in the Everglades are semidiurnal with mean tidal amplitude of 1.1 m in the southwestern region and from negligible to 0.5 m in the southeastern region and Florida Bay (Wanless et al. 1994).

Along the southeastern edge of the Florida peninsula along Florida Bay, mangrove zones are dominated by R. mangle scrub forest (tree heights ≤1.5 m) with clusters of C. erectus. A 1-km wide depositional berm (Buttonwood Ridge; ~0.5 m in height) that stretches roughly 60 km across the southern tip of Florida isolates these scrub forests (e.g., TS/Ph-6 and TS/Ph-7) from the direct influence of Florida Bay (Davis et al. 2004). Forests on the Buttonwood Ridge are dominated by C. erectus and A. germinans, while R. mangle borders it. Taylor River is one of several small mangrove channels that cut through the Buttonwood Ridge and serves as a surface water link between the southern Everglades and Florida Bay (see description in Davis et al. 2001). The study site in the Buttonwood Ridge was established approximately 1 km east of the Taylor River mouth site (TS/Ph-7; Fig. 1b). Another site, TS/Ph-8, was located near Snook Creek, a tributary of Joe Bay (Fig. 1b), which is not bounded by Buttonwood Ridge. This site supports a mixed community of sawgrass (Cladium jamaicense) and mangroves, with mangrove tree heights



of about 3–4 m. *R. mangle* dominates the fringe areas and tidal creeks, whereas *C. erectus* is found in the interior parts (Ewe et al. 2006). Mangrove waterways of this southeastern Everglades region are nontidal systems in contrast to Shark River and Broad Creek, and water flow is determined by the interactions of seasonal precipitation, upland runoff, and wind (Sutula 1999; Davis et al. 2001).

We compared storm deposits in all six of the long-term FCE mangrove plots and those along new transects established for this post-hurricane study. Comparisons among mangrove transect and plots of southwest (Shark River and Broad Creek) and southeast (Taylor River, Taylor Ridge, and Joe Bay) Florida allow us to test if there are gradients in storm-related nutrient inputs to the mangroves of FCE. In addition, two of the FCE mangrove plots (TS/ Ph-6 and TS/Ph-7) along Taylor River are isolated from Florida Bay by the Buttonwood Ridge, compared to Joe Bay (TS/Ph-8) that is hydrologically coupled to Florida Bay. It has been suggested that this ridge prevents storm deposits from fertilizing mangroves and thus limiting mangrove structure. Finally, location of plots inland from the mouths of Shark and Taylor Rivers allow us to test how far inland storm deposits can impact the nutrient inventory of mangrove soils. These results are specific to the conditions of Hurricane Wilma but present one observation to test these ideas as to how nutrient redistribution during storm events may impact mangrove patterns in this oligotrophic coastal ecosystem (Childers 2006).

Materials and Methods

Hydrology and Storm Surge

Water levels were measured in some of the FCE-LTER mangrove locations affected by Hurricane Wilma (SRS-4, SRS-5, and SRS-6 as well as TS/Ph-8). Ultrasonic water level recorders (model 220, Infinities USA, Inc., Port Orange, FL) were installed in the interior of each mangrove site about 50–80 m from shore. Water level recorders were placed on top of a PVC pipe (1.5 m above the soil surface) that was placed approximately 1 m below the soil surface. Water levels relative to soil surface were recorded at 1 h intervals.

Sediment Core Collection and Analyses

We measured the physico-chemical properties, distribution, and thickness of storm sediments from duplicate sediment cores collected at sampling points along transects at Broad Creek (December 2005), at SRS-6 (December 2005), and Taylor Ridge (October 2006). All soil-sediment cores were collected with a piston corer (2.5 cm diameter×15 cm

length) and sectioned into two layers, storm deposits (of variable depths) and surface mangrove soils (top 10 cm), and the depth of each layer was registered. The storm layer was easily distinguished from the mangrove soil layer because of its gray color, fine sand texture, and organic-free deposits. Samples were temporarily stored in plastic bags at 4°C and brought to the laboratory for further analyses.

Transects were positioned perpendicular from the mangrove shoreline (i.e., 0 m from water) to the interior of the mangrove forest at each site, and transect lengths varied depending on soil elevation and mangrove cover at each site. The SRS-6 transect is across an island (700 m wide) surrounded by numerous channels as part of original classification of vegetation. For the purposes of this study, we divided the transect into two sections, SRS-6E (250 m in length) and SRS-6W (350 m in length) to characterize storm sediment deposition with distance inland from shoreline on both sides of the island. The Buttonwood Ridge transect was 150 m in length and established from the shoreline with Florida Bay to the interior of Taylor Ridge. Soil-sediment cores were also collected from two permanent vegetation plots at SRS-6 (n=8) in December 2005 and at TS/Ph-8 (n=4) in October 2006. Vegetation plots were located 50 m (SRS-6) and 30 m (TS/Ph-8) from the shorelines of Shark River estuary and Joe Bay, respectively. The plots of SRS-6 were located approximately 100 m north of the 700-m long transect (east-west direction).

Surface soil and storm layers of cores were oven-dried at 60°C to a constant weight and weighed to determine bulk density. Core samples were ground with a Wiley Mill to pass through a 250-µm-mesh screen. Organic matter content is defined as percent of ash-free dry weight, determined by combusting samples in a furnace for 2 h at 550°C (Davies 1974). Data were expressed on a volume basis (mg cm⁻³) using bulk density values. Total nitrogen (N) was determined on two analytical replicates of each core sample with an ECS 4010 elemental analyzer (Costech Analytical Technologies, Inc., Valencia, CA). Total phosphorus (P) was extracted on duplicate core samples with 1 N HCL after combustion in a furnace at 550°C (Aspila et al. 1976) and determined by colorimetric analysis using a segmented flow analysis Flow Solution IV autoanalyzer (OI Analytical, College Station, TX).

We used a sequential fractionation scheme (Hedley et al. 1982) to determine inorganic and organic pools of P in soil and sediment core samples. First, labile inorganic P (labile P_i) that is directly exchangeable with soil solution was measured with anion-exchange resin strips (2×6 cm) in bicarbonate form and subsequently extracted with 0.5 M HCL (Lajtha et al. 1999). Second, labile and plant-available P sorbed onto soil surfaces (labile sorbed- P_i) was extracted with 0.5 M NaHCO₃. Next, an extraction



with NaOH 0.1 M released Fe and Al-bound inorganic P (Fe/Al-bound P_i). Then, occluded Fe and Al-bound inorganic P were extracted by ultrasonification (for 20 min in a bath sonicator) with fresh NaOH 0.1 M. Finally, Ca-bound inorganic P (Ca-bound P_i) was extracted with 1 M HCL. All extractions were equilibrated for a period of 18 h by continuous shaking on a mechanical shaker at 180 rpm. Subsamples of the NaHCO3 and NaOH extracts were digested using an alkaline persulfate digestion procedure to determine total P in the extract. Organic P in each extract was calculated as total P less inorganic P in the extract (Laitha et al. 1999). Residual P was determined as the difference between total P extracted with the Aspila et al. (1976) method and the sum of all extracted forms of P. After each step, extracts were centrifuged, and the supernatants were analyzed colorimetrically for soluble reactive phosphate (assumed to be inorganic PO₄⁻³) using a segmented flow analysis Flow Solution IV autoanalyzer.

Statistical Analyses

All statistical analyses were performed with PROC MIXED (SAS Institute, Cary, NC, USA). Data collected within the plots of SRS-6 and TS/Ph-8 were analyzed separately with a two-way analysis of variance (ANOVA) to test for differences in organic matter content, bulk density, and nutrient concentrations (total N and P) among sites and layers. For the transect data, we used a randomized block ANOVA design to test for differences in deposition depth, bulk density, organic matter content, and total N and P among sites, distance along transects, and layer (soil vs. sediment). Differences among inorganic and organic pools of P were tested independently within each layer using the same randomized block ANOVA design. All effects were considered fixed. Distance was nested within each site and was treated as a block. Prior to analysis, the actual sampling distance along each transect was normalized on a scale of 0 to 1 to facilitate further ANOVA comparisons among main effects. The ANOVA design was unbalanced for each variable due to differences in the number of sampling points and total number of observations recorded along each transect. The Kenward-Roger procedure was used to adjust the degrees of freedom of the F test statistics when an unequal variance model was significant (SAS Institute, Cary, NC, USA; Kenward and Roger 1997). Interaction effects were considered for all analyses. Pairwise comparisons were performed with Tukey's honestly significant difference (HSD) test when significant differences (p < 0.05) were observed within a main effect or interaction. The assumption of normality was tested using normal probability plots and ANOVA residuals. The assumption of homocedasticity was tested using the "null model" likelihood ratio test of the residual errors with a chi-square distribution. All variables were log-transformed (ln (x+1)) prior to analysis to meet the ANOVA assumptions, except total N, total P, bulk density, and deposition depth. Unless otherwise stated, data presented are means (± 1 SE) of untransformed data.

Results

Hydrology and Storm Surge

Water levels from Shark River estuary responded to a distinct storm surge on October 24, 2005 (Fig. 2). Storm surge within the forest (relative to soil surface) was higher at the mouth of Shark River (SRS-6 and SRS-5) and decreased upstream (SRS-4, 18.2 km from the mouth). The estimated water level in SRS-6 was approximately 3-4 m above soil level, based on field observations (see dotted line in Fig. 2). The water level recorder is positioned 1.5 m above the soil surface, preventing any actual measurements above that depth. Water marks on tree trunks of mangroves and hurricane sediment deposition observed in equipment positioned on platforms above soil level (~3-4 m) in the interior part of the forest (100 m inland) suggest the estimated maximum water level reached during the storm surge. Water levels in SRS-5 and SRS-4 peaked at 1.04 and 0.46 m above the soil surface, respectively. In Shark River, water levels peaked at the downstream sites in the morning compared to late afternoon at upstream site. At TS/Ph-8, peak water level was about 0.86 m above the soil surface in the morning. Overall, the storm surge in our mangrove sites lasted approximately 7-8 h, based on data recorded by the instruments (Fig. 2).

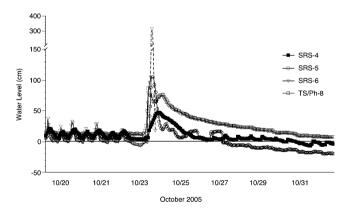


Fig. 2 Water levels in mangrove forests of the Florida Coastal Everglades Long-Term Ecological Research program during the passage of Hurricane Wilma on October 24, 2005. The *zero mark* is relative to the soil surface in each site. All water level data are not referenced to the North American Vertical Datum of 1988 (NAVD88). The *dotted line* indicates the maximum water level observed in SRS-6 based on field observations



Soil and Sediment Properties

There was a different pattern of sediment deposition among the long-term mangrove plots compared to transects established to measure post-hurricane effects (Table 1). The most inland plot of Shark River Slough, SRS-4 (18.2 km from the mouth of Shark River), had no observed sediment deposits, compared to a slight film of deposits in SRS-5 that was not measurable using our coring technique (<0.5 cm). This is in contrast to significant deposits measured in both plots and transects of SRS-6 and along the transect of Broad Creek, both in close proximity to the Gulf of Mexico. In southeastern FCE, the inland plots of Taylor River, TS/Ph-6 and TS/Ph-7, had no observable storm deposits, compared to measurable deposits in TS/Ph-8 plots and the Taylor Ridge transect near Taylor River (Table 1).

There was a significant decrease in thickness of storm sediment with distance inland from shore along each of four transects (Table 2; Fig. 3). Sediment deposition averaged 2.5 cm within the first 250 m from shore at Broad Creek transect and decreased to 1.0 cm from 450 to 700 m inland. In SRS-6E, deposition averaged 2.5 cm within the first 100 m and decreased to 1.0 cm at 250 m inland. At SRS-6W, sediment deposition decreased from 1.3 to 0.5 cm along the 350-m transect. Along the Taylor Ridge transect, deposition was highly variable and averaged 2.2 cm during the first 40 m from shore and decreased to 1.0 cm at the end

of the transect (Fig. 3). In TS/Ph-8, deposition on the permanent plots was 4.5 ± 0.5 cm (n=4), while in the SRS-6 plots deposition averaged 2.3 ± 0.1 cm (n=8).

Bulk density was significantly different between sediment and soil layers (Tables 1 and 2), with higher bulk density in the storm sediment layer (650.4±30.9 mg cm⁻³) compared to surface soil layer (top 10 cm of soil=366.2±11.8 mg cm⁻³). There was a significant interaction between sites and layers (Tables 1 and 2). All sites had higher bulk densities in the storm sediments (range from 489.9±46.9 to 716.5±108.6 mg cm⁻³) than in surface soils (range from 153.1±10.3 to 180.5 ± 17.5 mg cm⁻³), except on Taylor Ridge, where both storm sediments and surface soils had high bulk density values (Table 1). In plots of TS/Ph-8 and SRS-6, bulk density of storm sediment deposits was two and three times that of mangrove soils, respectively (interaction site × layer, F_{1-20} =26.8, p<0.001; Table 1).

Organic matter content was significantly lower in storm sediments (84.5±7.2 mg cm⁻³) compared to surface soils (top 10 cm=118.3±7.3 mg cm⁻³; Tables 1 and 2). There was a significant interaction between sites and layers (Tables 1 and 2). All sites had higher organic matter content in soil surface (top 10 cm) compared to storm sediment deposits, except in Taylor Ridge, where organic matter content was not significantly different between the two layers (Table 1). In general, organic matter content in surface soils ranged from 61.6±0.5 mg cm⁻³ (TS/Ph-8) to 147.3±8.5 mg cm⁻³ (Taylor Ridge), and from 60.0±

Table 1 Bulk density and organic matter content of storm sediments and surface soils (top 10 cm) measured in transects and plots of mangrove forests in the Florida Coastal Everglades after the passage of Hurricane Wilma

Site	Bulk density (mg cm ⁻³)		Organic matter (mg cm	-3)
	Storm sediments	Surface soils	Storm sediments	Surface soils
Transects				
Broad Creek	489.9 (46.9) a, B	180.5 (17.5) b, B	60.0 (1.9) b, B	104.1 (6.9) a, B
SRS-6E	642.9 (112.2) a, AB	156.9 (15.1) b, B	68.9 (9.6) b, B	109.9 (8.1) a. AB
SRS-6W	716.5 (108.6) a, AB	153.1 (10.3) b, B	77.6 (12.7) b, B	111.7 (6.0) a. AB
Taylor Ridge	748.8 (44.1) b, A	974.1 (28.7) a, A	131.8 (4.9) a, A	147.3 (8.5) a, A
Plots ^a				
SRS-4 ^b				
SRS-5 ^c				
SRS-6	686.5 (33.3) a, A	203.7 (7.0) b, A	69.0 (3.7) b, A	123.8 (6.8) a, A
TS/Ph-6 ^b				
TS/Ph-7 ^b				
TS/Ph-8	371.5 (45.9) a, B	194.1 (15.2) b, A	80.7 (11.7) a, A	62.4 (8.9) a, B

Means (± 1 SE) followed by different small letters within each row are significantly different for each variable (Tukey HSD post hoc test, p < 0.05). Means (± 1 SE) followed by different capital letters within each column are significantly different (Tukey HSD post hoc test, p < 0.05)

^c Storm sediments not sufficient amount (<0.5 cm) to sample



^a Statistical results using only plot data

^b Storm sediments were not observed in these plots, and therefore sampling was not performed

Table 2 Statistical results of physico-chemical properties measured in storm sediments and surface soils (top 10 cm) along transects in mangrove forests of the Florida Coastal Everglades after the passage of Hurricane Wilma

	Site			Distance (site)		Layer (se	diment vs	s. soil)	Site × la	yer	
Variables	df	F	p	df	F	p	df	F	p	df	F	p
Deposition depth (cm)	3, 20	12.5	***	23, 20	10.3	***	_	_	_	_	_	_
Bulk density (mg cm ⁻³)	3, 21.6	125.9	***	25, 18.2	1.1	ns	1, 22.4	73.2	***	3, 21.6	43.8	***
Organic matter (mg cm ⁻³)	3, 72	31.6	***	25, 72	1.0	ns	1, 72	38.7	***	3, 72	4.1	**
Total N (mg cm ⁻³)	3, 72	12.3	***	25, 72	1.9	*	1, 72	20.3	***	3, 72	2.2	ns
Total P (mg cm ⁻³)	3, 72	17.6	***	25, 72	1.5	ns	1, 72	30.9	***	3, 72	21.1	***

The degrees of freedom (df) of the denominator were adjusted with the Kenward-Roger method when required, SAS Proc Mixed ns not significant, – not determined

 1.9 mg cm^{-3} (BC) to $131.8\pm4.9 \text{ mg cm}^{-3}$ (Taylor Ridge) in storm sediment deposits (Table 2).

Total N concentrations were significantly lower in storm sediments $(2.7\pm0.1~{\rm mg~cm}^{-3})$ than in the soil surface $(3.2\pm0.2~{\rm mg~cm}^{-3})$; Table 2), and there was no significant interaction between sites and layers (Table 2; Fig. 4a). In general, N concentrations in the storm deposits ranged from $1.9\pm0.3~({\rm BC})$ to $3.2\pm0.1~{\rm mg~cm}^{-3}$ (Taylor Ridge) compared to $2.8\pm0.1~({\rm SRS-6W})$ to $3.4\pm0.2~{\rm mg~cm}^{-3}$ (Taylor Ridge) in the soil surface layer (Fig. 4a). Results in the plots of SRS-6 and TS/Ph-8 were different, with higher total N in storm deposits of TS/Ph-8 ($2.4\pm0.4~{\rm mg~cm}^{-3}$) compared to soil surface ($1.9\pm0.3~{\rm mg~cm}^{-3}$), although this difference was not significant; whereas SRS-6 followed the same pattern as results for the transects in the southwest, with lower total N in sediment deposits compared to soils (interaction site×layer, $F_{1.20}=14.0, p=0.0013$; Fig. 4a).

Mean total P concentrations were significantly different among sites and layers (Table 2, Fig. 4b). In contrast to N, total P was significantly higher in storm deposits (0.36± 0.02 mg cm^{-3}) compared to the soil surface $(0.22\pm$ 0.02 mg cm⁻³). There was a significant interaction between sites and layers (Table 1; Fig. 4b). Sites SRS-6W, SRS-6E, and BC had significantly higher P concentrations in storm deposit sediments (range from 0.38 to 0.51 mg cm⁻³) compared to soil surface (range from 0.16 to 0.29 mg cm⁻³; Fig. 4b). The same trend was observed for the plots of SRS-6 with a higher total P density in storm sediments compared to soils, whereas TS/Ph-8 had significantly lower total P density in sediment deposits, similar to that of soil surface (interaction site \times layer: $F_{1, 20}$ =6.4, p=0.0196; Fig. 4b). Total P density in SRS-6 sediment deposits was significantly seven times higher than in TS/Ph-8 (Fig. 4b). In contrast, an opposite trend was observed in Taylor Ridge with lower values in storm sediments $(0.10\pm0.01 \text{ mg cm}^{-3})$; Fig. 4b) than in soil surface $(0.22\pm0.02 \text{ mg cm}^{-3})$.

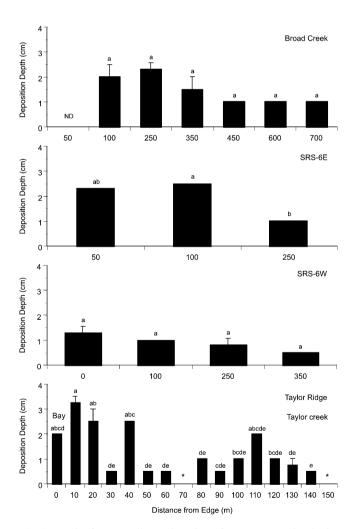


Fig. 3 Depth of storm sediment deposits at four mangrove sites in the Florida Coastal Everglades after the passage of Hurricane Wilma on October 24, 2005. Different letters indicate significant differences (p<0.05) among sampling points along each transect. ND indicates samples were not collected. Asterisks indicate no storm deposition



^{*}p<0.05; **p<0.01; ***p<0.001; indicate significant levels

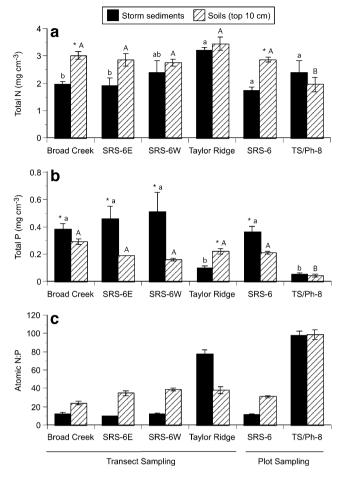
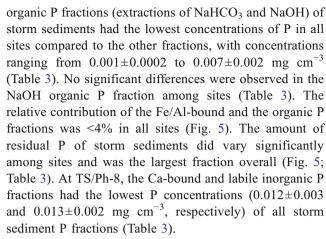


Fig. 4 Mean (± 1 SE) total nitrogen (a) and total phosphorus (b) concentrations, and atomic N/P ratios (c) in storm sediments and surface soils (top 10 cm) at sites sampled in transects and long-term plots in the Florida Coastal Everglades after the passage of Hurricane Wilma on October 24, 2005. *Asterisks* indicate significant differences (p<0.05) within each site. *Different small letters* indicate significant differences (p<0.05) among sites in the storm sediment layer for each sampling technique (transects vs. plots). *Different capital letters* indicate significant differences (p<0.05) among sites in the surface soil layer for each sampling technique (transects vs. plots)

Ca-bound P_i was significantly the largest bioavailable fraction of P in storm deposits at all sites ranging from 0.029 ± 0.003 (Taylor Ridge) to 0.130 ± 0.03 mg cm⁻³ (SRS-6W; Table 3), and accounted for up to 25-29% of total P (Fig. 5). The amount of labile P_i fraction was the second largest fraction of storm sediment deposits in all sites, with the highest concentrations in SRS-6E (0.050 ± 0.01 mg cm⁻³) and lowest in Taylor Ridge (0.027 ± 0.003 mg cm⁻³; Table 3); the contribution of this fraction comprised 11-23% of total P (Fig. 5). Concentrations of the Fe/Al-bound P_i fraction of storm deposits were also significantly different among sites, with BC, SRS-6E, and SRS-6W showing the highest concentrations of P relative to Taylor Ridge. Mean P concentrations of this fraction ranged from 0.002 ± 0.0002 to 0.011 ± 0.001 mg cm⁻³. The



The P fractions in mangrove soils showed a similar trend among sites as storm deposits, although concentrations and relative contributions (<15% of total P) were lower (Table 3; Fig. 5). In general, the Ca-bound P_i and labile P_i concentrations were significantly higher in soils at all sites; however, the amount of the NaOH organic P fraction in SRS-6E, SRS-6W, and BC was also a significant pool of total P (Table 3). The Ca-bound P fraction had the highest concentration in Taylor Ridge soils (0.040±0.01 mg cm⁻³) and the lowest in SRS-6W $(0.009\pm0.003~{\rm mg~cm}^{-3})$. There were no significant differences in the labile inorganic fraction among sites, with values ranging from 0.014 to 0.018 mg cm⁻³ (Table 3). The Fe/Al-bound P_i and NaHCO₃ Po fractions represented the smallest soil pools at all sites ranging from 0.001 to 0.010 mg cm⁻³ (Table 3). The amount of residual P in soils did not vary significantly among sites and was consistently the largest soil P fraction (Fig. 5, Table 3). In TS/Ph-8, the Ca-bound and labile inorganic P fractions had the lowest P concentrations $(0.007\pm0.001 \text{ and } 0.009\pm0.001 \text{ mg cm}^{-3}, \text{ respectively}) \text{ of }$ all soil P fractions (Table 3).

Discussion

Storm Surge and Soil Vertical Accretion

The passage of Hurricane Wilma through FCE had significant effects on local hydrology, sediment deposition, and nutrient biogeochemistry of mangrove soils. The storm surge within mangroves was ~3 m at the mouth of Shark River estuary and decreased to 0.50 m at the upper mangrove sites about 18 km from the mouth of the estuary. This pattern is consistent with water levels >4 m in mangrove sites adjacent to the Gulf of Mexico coast compared to water levels of about 0.5–1.0 m in upstream locations during the passage of Hurricanes Andrew and Wilma across several locations on southwestern ENP (Risi et al. 1995; Smith et al. 2009). Similarly, in the Florida Bay



Table 3 Phosphorus (P) fractions in storm sediments and surface soils (top 10 cm) in mangrove forests of the Florida Coastal Everglades after the passage of Hurricane Wilma

Site	Soil P fractions (mg cm ⁻³)	3)				
	Ca-bound P _i	Labile P _i	Fe/Al-bound P _i	NaHCO ₃ P _o	NaOH P _o	Residual P
Storm sediments						
Broad Creek	0.105 (0.015) a, A	0.042 (0.003) b, AB	0.011 (0.001) c, A	0.007 (0.002) cd, A	0.007 (0.005) ce, A	0.211 (0.044) a, A
SRS-6E	0.129 (0.015) a, A	0.050 (0.008) b, A	0.008 (0.001) ce, A	0.003 (0.000) de, AB	0.001 (0.001) be, A	0.261 (0.072) a, A
SRS-6W	0.130 (0.026) a, A	0.056 (0.011) b, AB	0.007 (0.001) c, A	0.003 (0.001) d, B	0.003 (0.001) de, A	0.310 (0.105) a, A
Taylor Ridge	0.029 (0.003) a, B	0.027 (0.003) a, B	0.002 (0.0002) b, B	0.003 (0.001) bc, B	0.004 (0.001) bd, A	0.051 (0.016) a, B
$TS/Ph-8^a$	0.012 (0.003)	0.013 (0.002)	0.002 (0.0002)	0.001 (0.0002)	0.002 (0.0004)	0.017 (0.001)
Surface soils						
Broad Creek	0.025 (0.006) b, AB	0.018 (0.003) bc, A	0.010 (0.0016) cd, A	0.002 (0.0008) e, B	0.016 (0.0036) bd, A	0.220 (0.013) a, A
SRS-6E	0.014 (0.007) b, BC	0.014 (0.001) bc, A	0.005 (0.0003) e, AB	0.001 (0.0002) f, B	0.017 (0.0013) bd, A	0.135 (0.010) a, A
SRS-6W	0.009 (0.003) b, C	0.014(0.002) bc, A	0.004 (0.0007) e, B	0.001 (0.0001) f, B	0.013 (0.0019) d, A	0.123 (0.008) a, A
Taylor Ridge	0.040 (0.006) b, A	0.017 (0.004) c, A	0.002 (0.0003) df, C	0.006 (0.0018) e, A	0.002 (0.0006) bf, B	0.156 (0.021) a, A
$TS/Ph-8^a$	0.007 (0.001)	0.009 (0.001)	0.003 (0.0006)	0.002 (0.0006)	0.001 (0.0002)	0.026 (0.008)
ANOVA source ^b :	Storm sediments		Surface soils			
Site	$F_{3, 5.2}=21.7**$		$F_{3, 172}=22.9***$			
Distance (site)	$F_{18, 61.2}=2.2*$		$F_{18, 172}$ =4.1***			
P Fraction	$F_{5, 12.6} = 321.0***$		$F_{5, 172} = 401.0***$			
Site × P Fraction	$F_{15, 24.6}=6.6**$		$F_{15, 172}=20.9***$			

Means (±1 SE) followed by different small letters across each row are significantly different (Tukey HSD post hoc test). Means (±1 SE) followed by different capital letters within each column are significantly different (Tukey HSD post hoc test)

ns not significant

*p<0.05; **p<0.01; ***p<0.001, indicate ANOVA source with significance

^a Not included in any of the statistical analysis

^b Degrees of freedom (df) of the denominator for each effect were adjusted with the Kenward-Roger method when required, SAS Proc Mixed



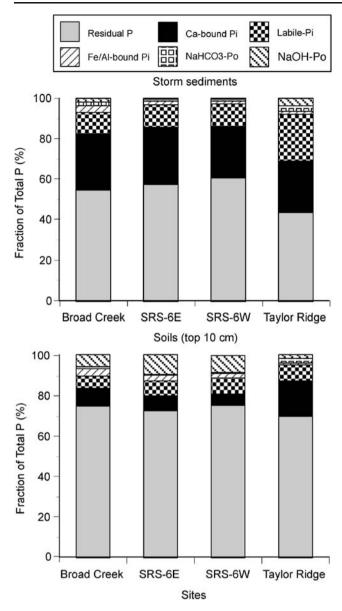


Fig. 5 Contribution of P fractions to the total P pool in storm sediments and surface soils (top 10 cm) at four mangrove sites in the Florida Coastal Everglades after the passage of Hurricane Wilma on October 24, 2005

area, Davis et al. (2004) documented a flood surge depth from about 0.2 to 0.5 m across the Taylor Ridge area, east of Taylor River from Hurricane Irene in 1999.

Large amounts of sediment from the coastal shelf were redistributed and deposited across mangrove forests of FCE associated with the storm surge. We observed maximal deposition in mangrove areas adjacent to the mouth of Shark River and found no storm deposits from Wilma in areas 18.2 km (SRS-4) from the Gulf of Mexico. Patterns in sediment deposited by Hurricane Wilma were relatively similar to those observed following Hurricane Andrew, ranging from 1–10 to 0–20 cm in mangrove forests between

Lostman's River (~12 km northwest of Broad Creek) and Shark River (Smith et al. 1994; Risi et al. 1995). Sediment deposition during Andrew extended up to 10-15 km inland across mangrove wetlands, becoming thinner with distance from the Gulf of Mexico, with no deposition in the upstream bays such as the Tarpon Bay area (near our SRS-4 site). A separate survey following Wilma measured maximal sediment deposition (<10 cm) in mangrove areas adjacent to the coast (2-5 km) between Lostman's River and areas south of Shark River (Smith et al. 2009). Deposits gradually decreased upstream of tidal rivers, with no deposition in mangrove forests located approximately 15.5 km from the Gulf of Mexico. All of these studies, including our survey, found that sediment deposition varied spatially within each mangrove site, with higher deposition in areas adjacent to the shore in the fringe mangrove zone and lower deposition in the interior forest.

In the Florida Bay area, Davis et al. (2004) also found a similar pattern of sediment deposition (5 cm) in the Taylor Ridge area as a result of Hurricane Irene in October 1999. Yet, the deposition associated with this relatively weak category 1 storm was confined to a 60-m zone in the center of Taylor Ridge, while our results show that deposition from Wilma was maximal in the shore fringe of Taylor Ridge (Fig. 3). The overall variability in sediment deposition along Taylor Ridge could be attributed to the geomorphology of the coast, the local microtopography, the accumulation of sediments in depressions as the surge receded, and the direction and strength of the storm surge as it struck the area (Davis et al. 2004).

Sediment deposited by Hurricane Wilma represents a significant adjustment in soil elevation of mangroves compared to vertical accretion rates estimated with radioisotope methods. This impact of hurricane Wilma on mangrove forests within FCE is localized within 10 km upstream of the Gulf of Mexico in areas that do not have geomorphic features that act as barriers to storm surge effects. This allochthonous sediment input along with autochthonous processes (belowground root growth) occurring in the soil profile result in vertical accretion (Cahoon and Lynch 1997). Accretion is often measured using techniques such as soil marker horizons (feldspar; Cahoon et al. 1996) or radionuclides (137Cs, 210Pb; Callaway et al. 1996) that integrate accretion and erosion processes on longer time scales than single depositional events. Sediment deposition estimated in SRS-6 and TS/ Ph-8 plots resulting from Hurricane Wilma was eight and 17 times greater than the annual vertical accretion rate $(0.30\pm0.03 \text{ and } 0.27\pm0.03 \text{ cm year}^{-1}, \text{ respectively})$ based on ¹³⁷Cs data (Castañeda-Moya, unpublished data). If compared to higher estimates of vertical accretion based on ²¹⁰Pb (Chen and Twilley 1999a; 0.89 cm year⁻¹), sediment deposition is three times the long-term accretion



rate. The lower accretion rates are similar to those reported for fringe and riverine mangrove forests in the Gulf of Mexico region (0.16–0.24 cm year⁻¹) using ¹³⁷Cs and ²¹⁰Pb radionuclides (Lynch et al. 1989) and also comparable with those reported for other coastal wetlands after hurricane events (Cahoon et al. 1995; Nyman et al. 1995; Turner et al. 2007). For instance, storm-associated sediments from Hurricane Andrew were four to 11 times greater than the long-term (30 years; ¹³⁷Cs techniques) annual rate in Louisiana coastal marshes (Cahoon et al. 1995; Nyman et al. 1995), generating about 2–6 cm of deposition from this hurricane event. It is evident that in both mangroves and salt marshes, hurricanes can deliver significant short-term changes to elevation of coastal wetlands.

Storm surge sediments are particularly important in the carbonate environmental setting of south Florida where the terrestrial sediment supply is low or absent, resulting in root production as one of the primary soil-building mechanisms in mangrove wetlands (Parkinson et al. 1994; Chen and Twilley 1999a). Although our results showed a relative gain in soil elevation of FCE mangrove forests after the passage of Hurricane Wilma, other soil processes linked to hydrological conditions in this region, including sediment erosion and compaction (Cahoon et al. 2003), soil shrinking and swelling (Whelan et al. 2005), and shallow subsidence (Cahoon et al. 1995; Cahoon and Lynch 1997), need to be considered as potential factors controlling soil elevation changes in mangroves. For instance, Wilma increased soil elevation 4.3 cm in SRS-6, and within 1 year after the storm there was a decrease in elevation to 3.3 cm due to erosion (0.9 cm) and compaction from shallow subsidence (0.1 cm; Whelan et al. 2009). Thus, long-term effects of hurricane sediment deposits due to sediment volume changes may be limited compared to other factors (e.g., groundwater).

Soil Nutrient Inputs

Sediment deposition from Hurricane Wilma made significant contributions to the nutrient pools of mangrove soils at specific locations along FCE. Bulk sediment inputs from Broad Creek to Taylor Ridge ranged from 500 to 700 mg cm⁻³, compared to <400 mg cm⁻³ in Joe Bay on the eastern edge of FCE. Wilma approached into south Florida from the west southwest and had a greater impact from Shark River to Taylor Ridge compared to the eastern edge of FCE. Over the study area, maximum sustained wind speeds for Hurricane Wilma reached 45–50 m s⁻¹ in the Shark River and Broad Creek areas at landfall compared to weaker winds (30–35 m s⁻¹) in the Joe Bay area (Fig. 1a). These conditions determined the magnitude of storm-surge-related sediment deposition patterns between

the western and eastern Everglades. Inputs of organic matter and total N followed these patterns of bulk density gradients, with the exception of higher nitrogen input to Joe Bay mangroves relative to sediment deposition. Total N concentrations of sediment deposited during this hurricane event accounted for 7% (SRS-6W), 8% (SRS-6E), 9% (BC), 12% (Taylor Ridge), and 14% (SRS-6) of the total N pool in the top 10 cm of mangrove soils, except in TS/Ph-8 where the contribution was 56%. In contrast, the contribution of total P from this hurricane event was significantly higher, ranging from 20% (BC), 23% (SRS-6W), 30% (SRS-6E), 39% (SRS-6) to 54% (TS/Ph-8), with the exception of Taylor Ridge that only had 7% of the soil total P deposited during this single event.

The gradient in total P input across mangrove zones located near shore from west (Broad Creek, 0.81± $0.09 \text{ mg } Pg^{-1} \text{ dry mass})$ to east (TS/Ph-8, $0.14\pm$ 0.03 mg Pg⁻¹ dry mass) direction across FCE is proportionally higher than the magnitude of sediment deposition. This is also evident when comparing the N/P ratios of sediment input across this west to east gradient (Fig. 4c). To the west near Broad Creek and mouth of Shark River, N/P ratios of sediment input range from 9.6 to 12.3, indicating an enrichment of total P in the bulk sediments deposited (Fig. 4c). Along Taylor Ridge, the N/P ratio dramatically increases to 77, and at TS/Ph-8 the ratio is near 98, similar to the ratio of soils in mangroves of that area (Fig. 4c). This gradient of lower P deposition in mangroves along the eastern region of Florida Bay is similar to that found in seagrass communities across this coastal landscape (Fourqurean et al. 1992). There is a strong gradient in P content and corresponding shift in N/P ratios in seagrass communities from west to east of Florida Bay. Foliar P concentrations of *Thalassia testudinum*, used as a proxy for P availability, decreases from northwest $(2.0 \text{ mg Pg}^{-1} \text{ dry mass})$ to the east $(0.5 \text{ mg Pg}^{-1} \text{ dry mass})$ of the bay, while foliar N/P ratios increase from 20 to 80 along the same gradient (Fourqurean et al. 1992). This P gradient has been suggested to control productivity and species composition of seagrass communities in this region (Herbert and Fourgurean 2009). Our survey suggests that this P gradient from west to east may also result in a gradient of P input associated with sediment deposition during storm events in this region, contributing to gradients in mangrove productivity (Ewe et al. 2006).

Resource gradients in P density also exist in mangrove soils from shoreline to more inland locations that regulate mangrove productivity (Chen and Twilley 1999b). For example, mangroves along Shark River estuary have concentrations of Ca-bound P (top 20 cm of mangrove soils) that are 40-fold higher at the mouth of Shark River than in SRS-4, 18.2 km from the mouth. It has been assumed that marine sediment inputs as represented by this



Ca-bound P fraction from the Gulf of Mexico during hurricane events are the source of P that controls and supports optimum mangrove forest development near the mouth of Shark River estuary (Chen and Twilley 1999a, b). Our results reveal that the Ca-bound P portion of storm deposits was the most significant fraction contributing 25–29% to the total P pool. Moreover, the lower residual P (44–46%) of storm deposits compared to surface soils (70–75%; Fig. 5) reflects the contribution of mineral sediments during this hurricane event. These patterns of Ca-bound portion of TP in storm sediment deposits associated with the passage of Wilma, along with the significant total load of P compared to soil nutrient inventories, support this assumption.

In addition, mangrove forests along Taylor River inland of the Buttonwood Ridge are isolated from P deposited during these storm events (Davis et al. 2004). It has been hypothesized that this reduction in P loading during hurricanes due to this geomorphic feature results in P-limited scrub mangrove forests in this region of FCE (Koch 1997; Ewe et al. 2006). This geomorphic feature, along with the gradient in reduced P concentration to the east of Florida Bay, resulted in less P loading to mangroves in this region of FCE during Hurricane Wilma. Each hurricane that hits the region has a different direction, angle of approach, strength, size etc. and therefore has a unique effect on storm surge-related sediment deposition and nutrient input to mangrove soils. Yet, it is apparent from this hurricane and evidence from previous storm events that these loadings and concentration gradients of P in the region of Buttonwood Ridge have a profound effect on sediment and nutrient distribution in mangrove soils.

Allochthonous mineral inputs through sedimentation can significantly contribute to the long-term P storage and soil fertility condition in wetlands (Reddy and DeLaune 2008). Input of nutrients from Hurricane Wilma-in a single pulsing event—is an important contribution to soil fertility of mangrove forests in near-shore mangroves in western regions of FCE. In areas that do not receive this pulse of P including more inland regions of the western FCE, mangroves inland of Buttonwood Ridge and those farther east of Florida Bay have lower accumulation of total P in soils. These features of the landscape control storm surge distribution (distance inland and geomorphic features) and nutrient gradients (west to east gradients of Florida Bay) and therefore establish the oligotrophic condition of this ecosystem (Noe et al. 2001). The contrasting landscape scale patterns of P-limited conditions from west to east and from shore to inland locations associated with mangrove biomass (Simard et al. 2006) and productivity (Ewe et al. 2006) are evidently influenced by hurricane events that distribute sediment and nutrients. This additional input of nutrients with storm deposits can explain why total P is three times higher in western Shark River estuary than in Taylor River Slough (Chambers and Pederson 2006).

Landscape vegetation patterns of mangrove forests in the FCE represent the interplay of gradients in resources, regulators, and hydroperiods (Twilley and Rivera-Monroy 2005). Hurricane disturbances not only play an important role in inducing changes to vegetation but also by distributing nutrients at fine spatial and temporal scales that can influence mangrove forest regeneration (Lugo 2008). This is particularly true in a carbonate-based coastal setting where patterns of P accumulation in mangrove soils result in strong gradients in mangrove forest structure and productivity in the Everglades. In addition, hurricane deposits are relatively more stable and consolidated than organic peat deposits, further contributing to soil volume and hence elevation. Allochthonous mineral inputs during hurricane events have also been associated with the long-term vertical accretion and stability of mangrove forests of the Everglades landscape (Chen and Twilley 1999a). For both salt marshes and mangroves, such pulsed events may be particularly important to how coastal wetlands have adapted to the impact of sea-level rise (Gilman et al. 2007; McKee et al. 2007) and increased frequency and intensity of hurricanes over the past half century (Webster et al. 2005). This feedback of hurricane disturbance on sediment deposition, accretion and nutrient deposition in this P-limited carbonate ecosystem may have important implications as to how soil formation and accretion serve as adaptations of mangroves to future impacts of sea-level rise.

Acknowledgments This research was conducted as part of the Florida Coastal Everglades Long-Term Ecological Research (FCE-LTER) program funded by the National Science Foundation (Grants #DBI-0620409 and #DEB-9910514). We would like to thank Jennifer Overton, Matthew Heels, Leander J. Lavergne, and Peter Lenaker for laboratory assistance. Special thanks to the Florida Bay Interagency Science Center-Everglades National Park for logistic support during the study. The authors thank John W. Day Jr., John R. White, Brian Marx, Charles Johnson, and two anonymous reviewers for constructive comments on earlier versions of this manuscript.

References

Alongi, D.M. 2008. Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. *Estuarine, Coastal and Shelf Science* 76: 1–13.

Aspila, K.I., H. Agemian, and S.Y. Chau. 1976. A semi-automated method for the determination of inorganic, organic and total phosphate in sediments. *Analyst* 101: 187–197.

Cahoon, D.R. 2006. A review of major storm impacts on coastal wetland elevations. *Estuaries and Coasts* 29: 889–898.

Cahoon, D.R., and J.C. Lynch. 1997. Vertical accretion and shallow subsidence in a mangrove forest of southwestern Florida, U.S.A. Mangroves and Salt Marshes 1: 173–186.



- Cahoon, D.R., D.J. Reed, J.W.J. Day, G.D. Steyer, R.M. Boumans, J.C. Lynch, D. McNally, and N. Latif. 1995. The influence of Hurricane Andrew on sediment distribution in Louisiana coastal marshes. *Journal of Coastal Research* 21: 280–294.
- Cahoon, D.R., J.C. Lynch, and R.M. Knaus. 1996. Improved cryogenic coring device for sampling wetland soils. *Journal of Sedimentary Research* 66: 1025–1027.
- Cahoon, D.R., P. Hensel, J. Rybczyk, K.L. McKee, E. Proffitt, and B. C. Perez. 2003. Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. *Journal of Ecology* 91: 1093–1105.
- Callaway, J.C., J.A. Nyman, and R.D. DeLaune. 1996. Sediment accretion in coastal wetlands: A review and simulation model of processes. Current Topics in Wetland Biogeochemistry 2: 2– 23.
- Chambers, R.M., and K.A. Pederson. 2006. Variation in soil phosphorus, sulfur, and iron pools among south Florida wetlands. *Hydrobiologia* 569: 63–70.
- Chen, R., and R.R. Twilley. 1999a. A simulation model of organic matter and nutrient accumulation in mangrove wetland soils. *Biogeochemistry* 44: 93–118.
- Chen, R., and R.R. Twilley. 1999b. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida. *Estuaries* 22: 955–970.
- Childers, D.L. 2006. A synthesis of long-term research by the Florida Coastal Everglades LTER Program. *Hydrobiologia* 569: 531– 544
- Davies, B.E. 1974. Loss-on-ignition as an estimate of soil organic matter. Soil Science Society of American Proceedings 38: 150– 151.
- Davis, S.E., D.L. Childers, J.W. Day Jr., D.T. Rudnick, and F. Sklar. 2001. Nutrient dynamics in vegetated and unvegetated areas of a southern Everglades mangrove creek. *Estuarine, Coastal and Shelf Science* 52: 753–765.
- Davis, S.E.I., J.E. Cable, D.L. Childers, C. Coronado-Molina, J.W.J. Day, C.D. Huttle, C.J. Madden, E. Reyes, D. Rudnick, and F. Sklar. 2004. Importance of storm events in controlling ecosystem structure and function in a Florida Gulf coast estuary. *Journal of Coastal Research* 20: 1198–1208.
- Day, J.W.J., D.F. Boesch, E.J. Clairain, G.P. Kemp, S.B. Laska, W.J. Mitsch, K. Orth, H. Mashriqui, D.J. Reed, L. Shabman, C.A. Simenstad, B.J. Streever, R.R. Twilley, C.C. Watson, J.T. Wells, and D.F. Whigham. 2007. Restoration of the Mississippi Delta: Lessons from Hurricanes Katrina and Rita. Science 315: 1679–1684.
- Duever, M.J., J.F. Meeder, L.C. Meeder, and J.M. McCollom. 1994. The climate of South Florida and its role in shaping the Everglades ecosystem. In *Everglades: The ecosystem and its* restoration, ed. S.M. Davis, and J.C. Ogden, 225–248. Delray Beach: St. Lucie.
- Ewe, S.M.L., E.E. Gaiser, D.L. Childers, D. Iwaniec, V. Rivera-Monroy, and R.R. Twilley. 2006. Spatial and temporal patterns of aboveground net primary productivity (ANPP) along tow freshwater-estuarine transects in the Florida Coastal Everglades. *Hydrobiologia* 569: 459–474.
- Fourqurean, J.W., J.C. Zieman, and G.V.N. Powell. 1992. Phosphorus limitation of primary production in Florida Bay: Evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography* 37: 162–171.
- Gentry, R.C. 1974. Hurricanes in South Florida. I. In *Environments of South Florida: Present and past*, ed. P.J. Gleason. Miami: Miami Geologic Society.
- Gilman, E., J. Ellison, and R. Coleman. 2007. Assessment of mangrove response to projected relative sea-level rise and recent historical reconstruction of shoreline position. *Environmental Monitoring and Assessment* 124: 105–130.

- Hedley, M.J., J.W.B. Stewart, and B.S. Chauhan. 1982. Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations. *Soil Science Society of America Journal* 46: 970–976.
- Herbert, D.A., and J.W. Fourqurean. 2009. Phosphorus availability and salinity control productivity and demography of the seagrass *Thalassia testudinum* in Florida Bay. *Estuaries and Coasts* 32: 188–201.
- Kenward, M., and Roger, J. 1997. Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* 53: 983– 997
- Koch, M.S. 1997. Rhizophora mangle L. seedling development into sapling stage across resource and stress gradients in subtropical Florida. Biotropica 29: 427–439.
- Krauss, K.W., T.W. Doyle, R.R. Twilley, and T.J.I. Smith. 2005. Woody debris in the mangrove forests of south Florida. *Biotropica* 37: 9–15.
- Lajtha, K., C.T. Driscoll, W.M. Jarrel, and E.T. Elliot. 1999. Soil phosphorus characterization and total element analysis. In *Standard soil methods for long-term ecological research*, ed. G. P. Robertson, D.C. Coleman, C.S. Bledsoe, and P. Sollins, 115–142. New York: Oxford University Press.
- Lodge, T.E. 2005. The everglades handbook: Understanding the ecosystem, 2nd ed. Boca Raton: CRC.
- Lodge, D.J., and W.H. McDowell. 1991. Summary of ecosystem-level effects of Caribbean hurricanes. *Biotropica* 23: 373–378.
- Lugo, A.E. 2000. Effects and outcomes of Caribbean hurricanes in a climatic change scenario. Science of the Total Environment 262: 243–251.
- Lugo, A.E. 2008. Visible and invisible effects of hurricanes on forest ecosystems: An international review. *Austral Ecology* 33: 368– 308
- Lynch, J.C., J.R. Meriwether, B.A. McKee, F. Vera-Herrera, and R.R. Twilley. 1989. Recent accretion in mangrove ecosystems based on ¹³⁷Cs and ²¹⁰Pb. *Estuaries* 12: 284–299.
- McKee, K.L., D.R. Cahoon, and I.C. Feller. 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography* 16: 545–556.
- Michener, W.K., E.R. Blood, K.L. Bildstein, M.M. Brinson, and L.R. Gardner. 1997. Climatic change, hurricanes and tropical storms, and rising sea level in coastal wetlands. *Ecological Applications* 7: 770–801.
- Noe, G.B., D.L. Childers, and R.D. Jones. 2001. Phosphorus biogeochemistry and the impact of phosphorus enrichment: Why is the Everglades so unique? *Ecosystems* 4: 603–624.
- Nyman, J.A., C.R. Crozier, and R.D. DeLaune. 1995. Roles and patterns of hurricane sedimentation in an estuarine marsh landscape. Estuarine, Coastal and Shelf Science 40: 665– 679
- Parkinson, R.W., R.D. DeLaune, and J.R. White. 1994. Holocene sealevel rise and the fate of mangrove forests in the Wider Caribbean region. *Journal of Coastal Research* 10: 1077–1086.
- Pasch, R.J., E.S. Blake, H.D. Cobb, and D.P. Roberts. 2006. Tropical cyclone report Hurricane Wilma. National Weather Service. National Hurricane Center, http://www.nhc.noaa.gov., Miami, Florida.
- Piou, C., I.C. Feller, U. Berger, and F. Chi. 2006. Zonation patterns of Belizean offshore mangrove forests 41 years after a catastrophic hurricane. *Biotropica* 38: 365–374.
- Reddy, K.R., and R.D. DeLaune. 2008. *Biogeochemistry of wetlands: Science and applications*. Boca Raton: CRC.
- Risi, J.A., H.R. Wanless, L.P. Tedesco, and S. Gelsanliter. 1995. Catastrophic sedimentation from Hurricane Andrew along the southwest Florida coast. *Journal of Coastal Research* 21: 83– 102.



- Sherman, R.E., T.J. Fahey, and P. Martinez. 2001. Hurricane impacts on a mangrove forest in the Dominican Republic: Damage patterns and early recovery. *Biotropica* 33: 393–408.
- Simard, M., K. Zhang, V. Rivera-Monroy, M.S. Ross, P.L. Ruiz, E. Castañeda-Moya, R.R. Twilley, and E. Rodriguez. 2006. Mapping height and biomass of mangrove forests in Everglades National Park with SRTM elevation data. *Photogrammetric Engineering and Remote Sensing* 72: 299–311.
- Smith, T.J.I., M.B. Robblee, H.R. Wanless, and T.W. Doyle. 1994. Mangroves, hurricanes, and lightning strikes. *BioScience* 44: 256–262.
- Smith, T.J.I., G.H. Anderson, K. Balentine, G. Tiling, G.A. Ward, and K.R.T. Whelan. 2009. Cumulative impacts of hurricanes on Florida mangrove ecosystems: Sediment deposition, storm surges and vegetation. Wetlands 29: 24–34.
- Sutula, M. 1999. Processes controlling nutrient transport in the southeastern Everglades wetlands. Ph.D. Dissertation. Louisiana State University, Baton Rouge.
- Turner, R.E., E.M. Swenson, C.S. Milan, and J.M. Lee. 2007. Hurricane signals in salt marsh sediments: Inorganic sources and soil volume. *Limnology and Oceanography* 52: 1231– 1238.

- Twilley, R.R., and V. Rivera-Monroy. 2005. Developing performance measures of mangrove wetlands using simulation models of hydrology, nutrient biogeochemistry, and community dynamics. *Journal of Coastal Research* 40: 79–93.
- Wanless, H.R., R.W. Parkinson, and L.P. Tedesco. 1994. Sea level control on stability of Everglades wetlands. In *Everglades. The* ecosystem and its restoration, ed. S.M. Davis, and J.C. Ogden, 199–223. Delray Beach: St. Lucie.
- Webster, P.J., G.J. Holland, J.A. Curry, and H.R. Chang. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* 309: 1844–1846.
- Whelan, K.R.T., T.J.I. Smith, D.R. Cahoon, J.C. Lynch, and G.H. Anderson. 2005. Groundwater control of mangrove surface elevation: Shrink and swell varies with soil depth. *Estuaries* 28: 833–843.
- Whelan, K.R.T., T.J.I. Smith, G.H. Anderson, and M.L. Ouellette. 2009. Hurricane Wilma's impact on overall soil elevation and zones within the soil profile in a mangrove forest. *Wetlands* 29: 16–23.
- Zhang, K., M. Simard, M.S. Ross, V. Rivera-Monroy, P. Houle, P.L. Ruiz, R.R. Twilley, and K.R.T. Whelan. 2008. Airborne laser scanning quantification of disturbances from hurricanes and lightning strikes to mangrove forests in Everglades National Park, USA. Sensors 8: 2262–2292.

