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The Role of the Everglades Mangrove Ecotone Region (EMER) in Regulating Nutrient Cycling and Wetland Productivity in South Florida

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The authors summarize the main findings of the Florida Coastal Everglades Long-Term Ecological Research (FCE-LTER) program in the EMER, within the context of the Comprehensive Everglades Restoration Plan (CERP), to understand how regional processes, mediated by water flow, control population and ecosystem dynamics across the EMER landscape. Tree canopies with maximum height <3 m cover 49% of the EMER, particularly in the SE region. These scrub/dwarf mangroves are the result of a combination of low soil phosphorus (P < 59 μg P g dw^{-1}) in the calcareous marl substrate and long hydroperiod. Phosphorus limits the EMER and its freshwater watersheds due to the lack of terrigenous sediment input and the phosphorus-limited nature of the freshwater Everglades. Reduced freshwater delivery over the past 50 years, combined with Everglades compartmentalization and a 10 cm rise in coastal sea level, has led to the landward transgression (~1.5 km in 54 years) of the mangrove ecotone. Seasonal variation in freshwater input strongly controls the temporal variation of nitrogen and P exports (99%) from the Everglades to Florida Bay. Rapid changes in nutrient availability and vegetation distribution during the last 50 years show that future ecosystem restoration actions and land use decisions can exert a major influence, similar to sea level rise over the short term, on nutrient cycling and wetland productivity in the EMER.

KEYWORDS: mangrove, phosphorus, nitrogen, carbon, Florida Bay, soil biogeochemistry, water quality

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INTRODUCTION

Along with the Pantanal project in Brazil (e.g., Harris et al., 2005) and the Ciénaga Grande de Santa Marta rehabilitation project in Colombia (Rivera-Monroy et al., 2004; Rivera-Monroy et al., 2006; Twilley et al., 1998), the Comprehensive Everglades Restoration Plan (CERP) is among the largest and most ambitious ecosystem restoration projects in subtropical and tropical regions. The goal of CERP is to restore the quantity, quality, timing, and distribution of water flow throughout the Everglades ecosystem watershed (~7,300 km^2) that encompasses a unique network of subtropical freshwater and coastal wetlands. These wetlands have been negatively impacted by major hydrological changes in the region during the last 100 years (e.g., Light and Dineen, 1994). The underlying approach of the plan is to capture and store fresh water—that is presently discharged east to the Atlantic Ocean—during the dry season, using 80% of the captured water for the natural system, and 20% for agricultural and urban needs (Carter, 2001). As

initially formulated in 2001, CERP includes the removal of 240 miles of levees and canals and construction of a network of reservoirs, underground storage wells, and pumping stations to capture and then redistribute water to restore a more natural flow. CERP is expected to be implemented in a step-wise fashion within the next 30 years with an estimated price tag of ~$8 billion plus annual operation and maintenance cost estimated at $182 million (NRC, 2005). These high costs partially reflect the magnitude of the ecological goods and services that wetlands provide to coastal regions (Ewel et al., 1998).

The Everglades mangrove ecotone region (EMER) lies at the interface of land (i.e., freshwater marsh) and sea (Florida Bay or Gulf of Mexico). As a result, it has been one of the areas most impacted by changes in flows through the Everglades over the last 100 years (Ross et al., 2000). This zone is critical in regulating the transport of organic matter and nutrients into coastal waters (Chen and Twilley, 1999b; Davis et al., 2004; Sutula et al., 2003). The EMER represents a combination of different mangrove ecotypes (sensu Lugo and Snedaker, 1974) distributed across, and sensitive to, gradients in resources, regulators, and hydroperiod (Chen and Twilley, 1999a; Twilley, 1998; Twilley and Rivera-Monroy, 2005). Although the EMER represents a significant fraction of mangrove cover (roughly 1445 km^2) in the state of Florida and continental United States (Simard et al., 2006), information gaps on factors regulating distribution and productivity of these wetland forests exist. This lack of information (e.g., hydroperiod, soil sulfide and salt concentration, soil accretion and elevation, primary productivity, denitrification and nitrogen fixation) is significant when trying to establish restoration performance measures (PMs; Zedler, 2001).

A challenge in restoration assessment is deciding which attributes of ecosystems to monitor, and which of the observed changes represent significant departures from expected natural variability (Twilley and Rivera-Monroy, 2005). Several efforts have attempted to define and quantify mangrove PMs in the context of CERP (Davis et al., 2005); however, specific measures and targets are limited due to the lack of an integrative understanding of biogeochemistry and productivity patterns of mangrove forests in South Florida. In addition, restoration programs need to spatially differentiate among functional properties of mangroves throughout the Everglades to operationally define PMs that help determine if regional restoration actions are effective. The Taylor and Shark River Sloughs of the Everglades (Figure 1) exhibit major hydrogeomorphological differences, and the EMER at the terminus of these distinct flow paths should be considered separately as they respond to restoration efforts. In an attempt to understand the ecological response of the EMER, particularly the Taylor and Shark River Sloughs, to restoration, the Florida Coastal Everglades Long-Term Ecological Research (FCE-LTER; initiated in 2000) program established transects from the freshwater Everglades to coastal waters in both the western and southeastern region

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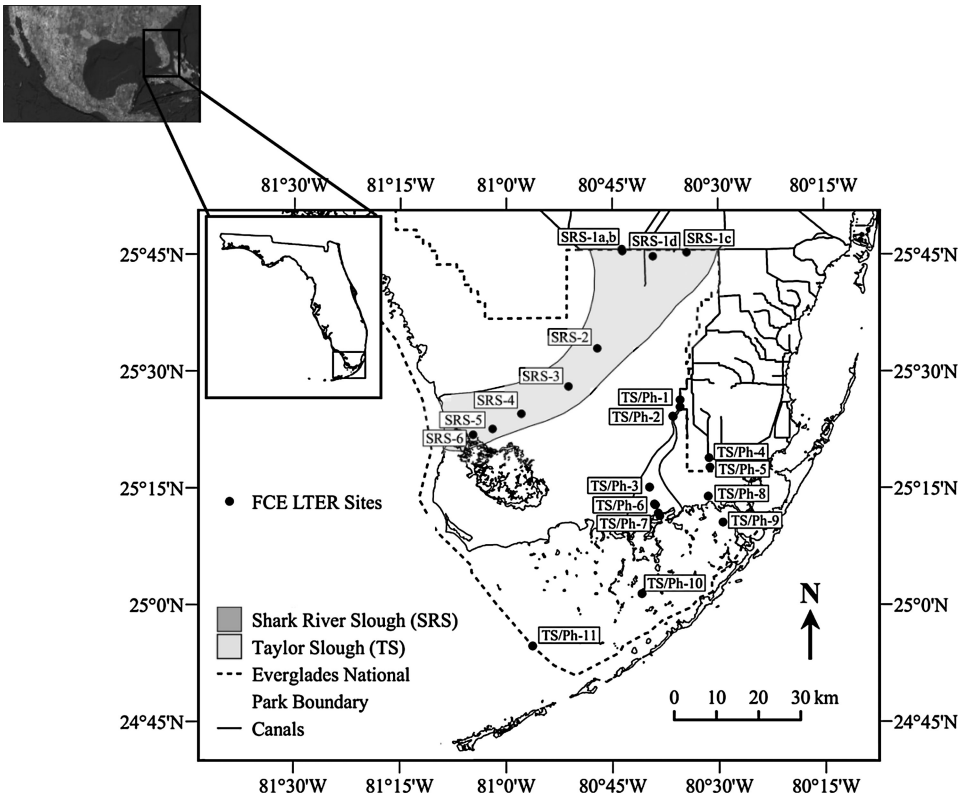

FIGURE 1. Map of South Florida showing the 17 FCE LTER sites. SRS-1 through -6 are along the Shark River Slough transect; TS/Ph-1, -2, -3, -6, and -7 are in Taylor Slough; TS/Ph-4, -5, and -8 in the C-111 basin/ENP panhandle; and TS/Ph-9, -10, and -11 are in Florida Bay. Mangrove sites in the Mangrove Ecotone Region are SRS-4, SRS-5, SRS-6, TS/Ph-6, TS/Ph-7 and TS/Ph-8.

of Everglades National Park (ENP; Figure 1; Childers, 2006). A major goal of the FCE-LTER program has been to understand how regional processes, mediated by water flow, control the EMER's population and ecosystem level dynamics and how these dynamics vary across the coastal Everglades landscape (Childers, 2006; Trexler et al., 2006).

In this paper, we summarize the main findings of the FCE-LTER research in the EMER within the context of the CERP. We accomplish this first by characterizing the hydrological and vegetation differences between EMER flow paths and along FCE-LTER transects, then by analyzing soil properties to determine the interaction between soil fertility and hydroperiod affecting mangrove productivity. Given the importance of both phosphorus (P) and nitrogen (N) availability for mangrove productivity in this region (Chen and Twilley, 1999b; Koch and Snedaker, 1997), we assess the ecological importance of dissolved organic matter in controlling internal nutrient cycling and discuss the significance of carbon (C) export to adjacent coastal waters.

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Next, we analyze the effect of natural disturbances and the potential interactions with human disturbances at different spatial scales, including climate change and sea level rise. Finally, we frame this synthesis in the context of present and future research related to Everglades restoration goals and the importance of developing realistic and ecologically-based performance measures.

FCE-LTER EMER TRANSECTS

The FCE-LTER study sites are located along the path of water flow through the southwest Florida landscape and coastal Everglades and out to the Gulf of Mexico (Childers, 2006). The first site along the Shark River Slough (SRS-1) transect is located at the S-12C structure (Figure 1). Farther downstream, the SRS-3 and SRS-4 sites delineate the boundary between freshwater and estuarine ecotones, respectively. Sites SRS-4 through SRS-6 span the mangrove ecotone in the southwestern region where some mangrove canopies as tall as 18 m (Simard et al., 2006; Smith and Whelan, 2006). In contrast, the Taylor Slough/Panhandle (TS/Ph) transect spans two flow paths—one starting at the L-31W canal and adjacent water detention areas and flowing through Taylor Slough to east-central Florida Bay, and the other starting at the C-111 canal and flowing through shorter hydroperiod marshes in ENP's eastern panhandle to eastern Florida Bay (Childers et al., 2006). Surface water presently enters Taylor Slough (TS/Ph-1, -2, -3, -6, and -7) from both adjacent ENP wetlands to the north and west and as seepage and occasional overflow from a managed detention area to the east. The mangrove ecotone along TS/Ph is narrow and extends from TS/Ph-6 to TS/Ph-7. For further details about the sites, see Childers et al. (2006) and the FCE-LTER website (http://fcelter.fiu.edu/research/index.htm).

HYDROLOGY

Subtropical wetland environments dominate South Florida, where hydrological conditions (in terms of water volume, source, and residence time) plays a major role in controlling ecosystem structure and function (Light and Dineen, 1994). The region experiences dry (November through May) and wet seasons (June through October), which typically coincide with the frontal and the hurricane seasons, respectively. South Florida normally experiences at least one tropical storm and several winter frontal passages each year (e.g., Wanless et al., 1994a). The recurrence interval of these events alone suggests their importance in shaping the coastal Everglades (e.g., Lorenz et al., 2001). The wet season delivers approximately 75% of annual precipitation (~1,500 mm; Chen and Gerber, 1990), and overland sheet flow is driven

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by freshwater inputs from the upstream wetlands, resulting in a pronounced surface flooding that ranges from six to seven months in the Taylor Slough. Although the dry season starts at the end of October, a significant dry-down of the EMER does not occur until late January or early February. Throughout the dry season, decreased freshwater inputs and high evaporative losses often result in the wind-driven advection of Florida Bay water into the ecotone (Sutula et al., 2001).

Hydrological conditions in EMER are distinctly different between Shark River Slough and Taylor Slough. Shark River Slough is far larger in area and discharge more freshwater than Taylor Slough. Water inputs to the northern boundary of each slough are largely controlled by water management structures, but inputs to Shark River Slough are directly from Water Conservation Area (WCA) 3A, whereas inputs of WCA water to Taylor Slough are via canals and detention areas. Shark River Slough flows and water levels beyond its northern region are influenced by local rainfall, evaporation, and water management, similarly to Taylor Slough and the ENP panhandle, where water levels are partially regulated by seepage losses toward the C-111 canal to the east (Childers et al., 2006; Ross et al., 2006a, Swain and James, 2008; Figure 1). Tides in the Shark River mangrove region are semidiurnal, with a mean tidal range of 1 m. Tides in the coastal boundary of Taylor Slough are significantly less than 0.5 m with little subdaily variation, as the tidal prism is strongly attenuated throughout Florida Bay, particularly in the northeastern region. Krauss et al. (2006) and Rivera-Monroy et al. (2007) showed that flood duration in the Shark River region, averaged across 2 years (2002–2003), ranged from 2542 to 4622 h/year, with surface flooding in the wet season more common than flooding in the dry season. The duration of inundation decreased upstream in Shark River, underscoring the higher tidal influence in SRS-6 and its attenuation upstream at SRS-4. Indeed, lower groundwater levels at SRS-4 reflect the interaction between groundwater and freshwater inundation as indicated by lower salinities throughout most of the year (i.e., 4.0 ± 1.2 ppt). In contrast, due to lack of tidal signature, the period of inundation is longer in the mangrove Taylor Slough sites where seasonal flooding, strongly influenced by winds, is correlated with rainfall and water management upstream. A long-term analysis of freshwater discharge in Taylor River, one of the main channels discharging into Florida Bay (Michot et al., in review), shows the strong influence of regional precipitation on water level in mangrove wetlands (Figure 2A) and on discharge values to Florida Bay at the mouth of Taylor River (Figure 2B).

Because of the controlling effect of precipitation on water levels and discharge in the EMER, this area is very susceptible to major changes in climate. Davis et al. (2004) and Childers et al. (2006) showed how tropical storms and hurricanes could produce significant changes in surface water dynamics and exchange of materials with Florida Bay. Similarly, Childers

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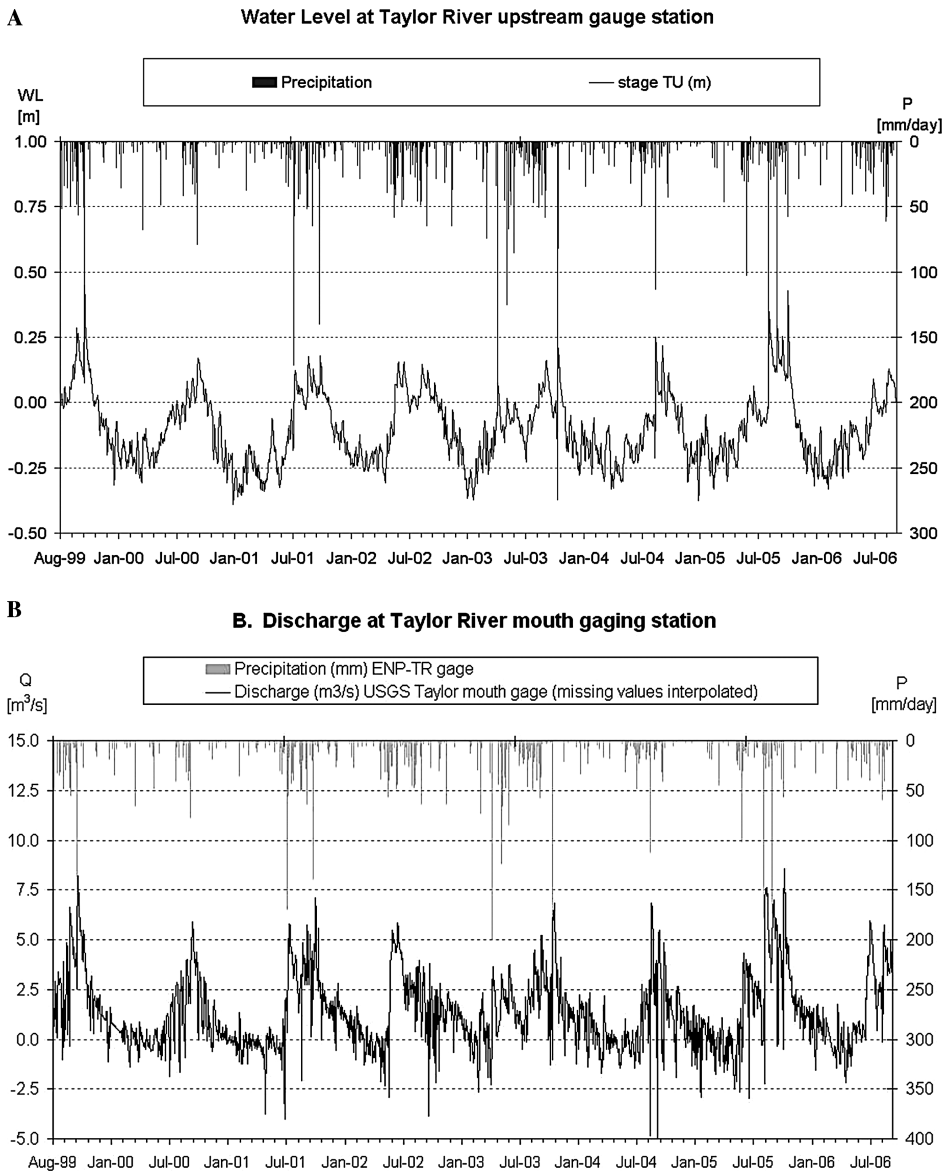

FIGURE 2. Time series (1999–2006) of stage, discharge, and precipitation in Taylor River. (A) Upstream Taylor River (Latitude: 251241 Longitude: −803853). (B) Mouth of Taylor River (Latitude: 251127 Longitude: −803821. Data from USGS and ENP monitoring stations (http://sofia.usgs.gov/exchange/zucker_woods_patino/index.html, http://everdata.dnsalias.org/wordpress/wp-content/themes/rjfsandbox/ever-dfelogin.php).

et al. (2006) demonstrated how El Niño Southern Oscillation (ENSO) events tend to disrupt the seasonality of rainfall without altering cumulative annual precipitation. The ENSO index was positively correlated with both annual rainfall and the ratio of dry season to wet season precipitation. This ENSO-driven disruption in seasonal rainfall affected salinity patterns and tended

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to reduce marine inputs of phosphorous (P) to Everglades estuaries. ENSO events also decreased dry season residence times, reducing the importance of estuarine nutrient processing (Childers et al., 2006). Recently, Kelble et al. (2007; Williams et al., and Briceno and Boyer, 2010) also showed how hurricanes and ENSO dramatically affect salinity and nutrient transport patterns of Florida Bay on interannual time scales, noting the relationship between a northward expansion of the mangrove ecotone and the effect of reduced freshwater flow on increased porewater salinities.

The interaction of P limitation and hydroperiod (mediated by winter and summer storms) needs to be considered in developing conceptual mangrove models and PMs to evaluate the effect of hydrological modifications as a result of the CERP (Twilley and Rivera-Monroy, 2009). Although disturbance events, relative sea level, and water management practices are clearly identified as major forcing functions controlling mangrove function (Davis et al., 2005), further analyses are necessary to evaluate the degree of control by each forcing variable (Williams et al., 2008). It is expected that the structurally diverse mangrove forests of the EMER may respond differently to hydrological modifications (i.e., increased freshwater flow and duration).

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SOIL FERTILITY

Soil chemical and physical properties have been suggested as significant constraints on mangrove structure and productivity and can be analyzed as the integrated outcome of processes occurring over extended time scales—much in the same way that climate is a description of aggregate weather conditions for a region (Chambers and Pederson, 2006; Chen and Twilley, 1999b). Soil formation has also been considered an important process contributing to biogenic carbon sinks in tropical coastal regions (Parkinson et al., 1994; Twilley et al., 1992). Soil formation is the combination of several ecological processes including organic matter production (above- and belowground components), export, decomposition, and burial; as well as sedimentation of allochthonous inorganic matter (Chen and Twilley, 1999a). Organic matter dynamics are tightly coupled to the biogeochemical cycles of N and P in mangrove soils by the processes of decomposition, mineralization, and plant uptake (Twilley and Rivera-Monroy, 2009). Chen and Twilley (1999b) and Chambers and Pederson (2006) characterized the spatial variation of soil properties along the FCE-LTER transects and have shown systematic variation in soil bulk density, organic content, pools of P, inorganic sulfur, and extractable iron. Spatial differences are consistent with observed differences in mangrove productivity, which is known to be limited by P availability (total P averaged 200 μg g dw^{-1} in soils from the eastern Taylor Slough/Panhandle

and was on average three times higher in soils from the western Shark River Slough; Chambers and Pederson, 2006).

Soil nutrient concentrations in FCE-LTER Shark River and Taylor River sites are listed in Table 1. These values show a distinct spatial gradients, from upstream to downstream, particularly in the case of soil total [P]. Both total [C] and [N] in the top 40 cm of mangrove soils increased with distance from the mouth (Gulf of Mexico) of Shark River estuary; soil [P] showed an inverse relationship (SRS-4: 0.07; SRS-5: 0.13; SRS-6: 0.21 mg cm^{-3}; Chen and Twilley, 1999b; Figure 1). A similar study also found the same gradient where TP values varied from 0.07 to 0.18 mg cm^{-3} (Mancera-Pineda et al., 2009). Soil [N] differences along the EMER SRS transect were lower than for [P] (Table 1). Soil N:C ratios ($\times$1000) varied from 12 to 53, while N:P ratios were 114 in the upper mangrove zone (SRS-4) and 30 for two sites downstream Shark River (SRS-5, SRS-6). Dissolved inorganic nitrogen (DIN) in porewater shows larger variations with no clear spatial patterns. Chen and Twilley (1999b) measured [DIN] in the period from 1995 to 1996 in mangrove forests along the Shark River and found that [NO_2] and [NO_3] were <1 μM and <0.5 μM, respectively, and mean soluble reactive phosphorus (SRP) was <5.0 μM. Mancera-Pineda et al. (2009) also found that porewater [DIN] was similar along Shark River FCE-LTER sites ranging from 0.6 to 8.0 μM. However, average SRP increased significantly from 0.27 μM in the upper mangrove zone (SRS-4) to 2.24 μM close to the mouth (SRS-6; Mancera-Pineda et al., 2009; Table 1).

As in the case of Shark River, average mangrove soil [P] (in mg cm^{-3}) along the EMER gradient of Taylor River Slough increased from 0.04 upstream to 0.16 close to the Gulf of Mexico (Florida Bay; Table 1). In contrast soil [N] was similar along this P gradient (2.42–2.46 mg cm^{-3}). Soil N:C ($\times$1000) ratios varied from 40.8 to 50, and there was a seaward gradient in soil N:P ratios from 120 to 72 to 43. Mean porewater [DIN] varied from 4.3 to 46.2 μM in the Taylor River sites. Porewater [NH_4^+] ranged from 0.5–32 μM with an annual average of 5.8 μM; [PO_4^{3}] varied from 0.13 to 8.8 μM with an annual average of 0.9 μM (Castañeda-Moya, 2010). Collectively, low P concentrations contribute to the oligothrophic conditions of the lower Taylor Slough.

Soil N and P are closely related to patterns of forest development in Shark River, with higher soil fertility at the mouth of the estuary as indicated by higher concentrations of soil TP and available P (Chen and Twilley, 1999b). The more fertile sites of the lower estuary (SRS-6) are dominated by *L. racemosa*, whereas the less fertile sites in the intermediate (SRS-5) and upper (SRS-4) estuaries are dominated by *R. mangle*. Relative N mineralization per unit of total N is higher in the lower estuary and is positively related to concentrations of available P, indicating the importance of turnover rates and nutrient interactions to soil fertility (Chen and Twilley, 1999b). The concentrations of Ca-bound P per volume of soil from SRS-6 is 40-fold higher

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TABLE 1. Porewater and soil characteristics of six mangrove sites (SRS-4, SRS-5, SRS-6, TS/Ph-6, TS/Ph-7, TS/Ph-8) in Florida Everglades National Park

Variable	Sites	Koch (1997)	Chen and Twilley (1999a)	Chambers (2007)
Salinity (g kg^{-1})	SRS-4		4.0	
	SRS-5	60	15.0	
	SRS-6	27*	17.0	
	TS/Ph-6			
	TS/Ph-7			
	TS/Ph-8			
$NO_3^- + NO_2^-$ (μM)	SRS-4		0.7–1.1	
	SRS-5		0.5–1.1	
	SRS-6		0.4–0.8	
	TS/Ph-6			
	TS/Ph-7			
	TS/Ph-8			
NH_4^+ (μM)	SRS-4		1.1–4.5	
	SRS-5		0.6–12.5	
	SRS-6		0.5–7.0	
	TS/Ph-6			
	TS/Ph-7			
	TS/Ph-8			
DIN (μM) ($NO_3^- + NH_4^+$)	SRS-4			
	SRS-5			
	SRS-6			
	TS/Ph-6			
	TS/Ph-7			
	TS/Ph-8			
Soluble Reactive Phosphorus (μM)	SRS-4		0.1–0.5	
	SRS-5		0.5–1.5	
	SRS-6		0.5–5.0	
	TS/Ph-6			
	TS/Ph-7			
	TS/Ph-8			

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Redox (mv)	SRS-4				6
	SRS-5	1017			-1
	SRS-6	214*			3
	TS/Ph-6				-6
	TS/Ph-7				-8
	TS/Ph-8				-9
Bulk Density (g cm^{-3})	SRS-4		0.14	019	0
	SRS-5	015	0.15	025	0
	SRS-6	023*	0.21	055	0
	TS/Ph-6			076	0
	TS/Ph-7			047	0
	TS/Ph-8			035	0
TC (mg cm^{-3})	SRS-4		50.30		4
	SRS-5	590	46.10		5
	SRS-6	476*	39.30		4
	TS/Ph-6				0
	TS/Ph-7				4
	TS/Ph-8				5
TN (mg cm^{-3})	SRS-4		2.70		2
	SRS-5	210	2.19		2
	SRS-6	26*	2.03		2
	TS/Ph-6				2
	TS/Ph-7				2
	TS/Ph-8				2
TP (mg cm^{-3})	SRS-4		0.07	017	0
	SRS-5	012	0.13	020	0
	SRS-6	033*	0.21	030	0
	TS/Ph-6			005	0
	TS/Ph-7			017	0
	TS/Ph-8			016	0

* = mangrove site is located 4 km downstream from SRS-6.
** = range mean values for dry and rainy seasons in the period 2001–2002.
***range mean values for dry and rainy seasons in the period 2001–2005.
& = range mean values for dry and rainy seasons in the period 2001–2003.
Note. Values are means over each study period. Bulk density and nutrient concentrations in mangrove soils are integrated over the top 10 cm (Chambers and Pederson, 2006), 30 cm (Koch, 1997), and 40 cm (Chen and Twilley, 1999a, b; Poret et al., 2007).

than in SRS-4 and along with an increase in residual P in the upper estuary, indicate a shift from mineral to organic P along the estuarine gradient. Mineral inputs to the mouth of Shark River estuary from the Gulf of Mexico, in contrast to upstream inputs, seems to control patterns of mangrove structure and productivity (Castañeda-Moya, 2010; Chen and Twilley, 1999b). It has been assumed that marine sediment inputs as represented by 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 (Castañeda-Moya, 2010; Chen and Twilley 1999a, 1999b; Simard et al., 2006).

The pool of available nutrients in mangrove soils is a product of several processes that proceed on different time scales: above- and belowground plant production, decomposition of leaf litter, mineralization of organic matter, nutrient inputs from rainfall and groundwater, sedimentation by tides and upstream runoff, and uptake by plants (Alongi and McKinnon, 2005; Alongi et al., 2004; Clough, 1992; Twilley et al., 1997; Twilley and Rivera-Monroy, 2009). In South Florida, information is lacking on how N transformation rates (e.g., denitrification, nitrogen fixation, nitrification, mineralization, microbial assimilation, plant uptake) are modified via hydrologic changes across Taylor Slough and Shark River Slough and how these changes affect the exchange of N at the mangrove ecotone—bay interface (Sutula et al., 2001). Because hydroperiod in the Taylor and Shark Rivers and in adjacent wetlands is driven by seasonal events such as precipitation and wind, it is highly likely to observe low litter fall turnover and greater immobilization of N during litter decomposition. Additionally, immobilization may occur as result of less litter loss from the system due to limited tidal export, compared to other coastal tropical and subtropical ecosystems (e.g., Twilley, 1995). Indirect evidence of this is seen in high litter accumulation in scrub mangroves next to Taylor River and tree islands (>3 kg m^{-2}; Rivera-Monroy, personal observation). High organic matter accumulation is one of the features that make these ecosystem components candidates for biogeochemical hot spots in the Everglades (McClain et al., 2003). Organic matter in wetland sediments accumulates on decadal time scales (Cahoon, 2006), and N immobilization in soils can eventually contribute to the burial of N, reducing its availability to the Everglades.

SURFACE WATER CARBON AND NUTRIENT CONCENTRATIONS AND FLUXES

One of the major concerns with the CERP implementation is the effect of the reintroduction of freshwater on downstream water quality. It is generally acknowledged that differences in water quality criteria may differ depending

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on the location at the landscape level, thus "what is acceptable for some upstream purpose is often entirely unacceptable for introduction into pristine, highly oligotrophic subtropical coastal waters" (National Research Council, 2008). Therefore, assessing how CERP freshwater diversions affect Florida oligotrophic estuaries is paramount to water management regimes in the future.

Carbon

Studies have documented strong temporal and spatial variability in carbon and nutrient concentrations in coastal waters of South Florida. In a comprehensive water quality analysis, Boyer (2006) found three major water quality parameter groupings described as "organic" (alkaline phosphatase activity [APA]—a proxy for microbial activity driven by phosphorus availability—TN, and total organic carbon [TOC]), "dissolved inorganic nitrogen" (NO_3^-, NO_2^-, NH_4^+), and "phytoplankton" (TP—a limiting factor of algal production—chlorophyll *a*, and turbidity). All 47 stations aggregated into six classes with similar water quality patterns including: Mangrove Rivers, Whitewater Bay, Gulf Islands, Coot Bay, Blackwater River, and Inland Waterway (Figure 3). Another major finding was a strong south to north gradient in

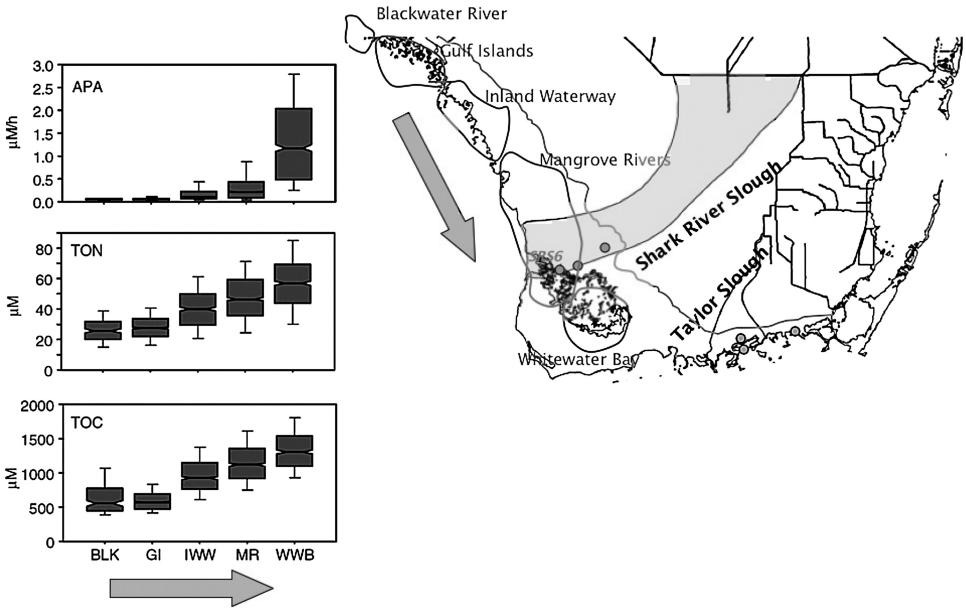

FIGURE 3. Spatial differences in alkaline phosphatase activity (APA), total organic nitrogen (TON), and total organic carbon (TOC) along the western coast of the mangrove ecotone from North to South. BLK = Blackwater River; GI = Gulf Islands; IWW = Inland Waterway; MR = Mangrove Rivers; WWB = Whitewater Bay (modified from Boyer, 2006).

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P availability as evidenced by APA values (relative to N) along the southwestern coast of the EMER, as a result of marked differences in land use, freshwater input, geomorphology, and sediment characteristics up the coast. Along this gradient, much of the N and P was in an organic form and TOC concentrations were as high as 1900 μM (Figure 3). Boyer (2006) suggested that the output of TON and TOC in the southern estuaries (particularly the Shark River) was enhanced by high mangrove production. Indeed, mangrove annual net primary productivity in this area ranges from 1173 ($\pm$65) to 2066 ($\pm$48) g C m^{-2} yr^{-1} and is 6 times higher than productivity in the Taylor Slough region (340 $\pm$ 30; Ewe et al., 2006) where mangroves are <5 m in height. A close association between high [TOC] in Florida coastal waters and mangrove productivity (see subsequent paragraphs) provides strong support for the role of mangrove vegetation in the carbon cycle of this coastal region.

In a recent study, Maie et al. (2008) showed how DOC (mainly tannins) derived from mangrove litter in Shark River influences dissolved organic nitrogen (DON) cycling. Using excitation–emission matrix fluorescence spectra, they determined that a large portion of tannins could be physically eliminated from aquatic environments by precipitation as tannin-protein complexes in saline water and also by binding to sediments. Although tannins are not detected at a significant level in most natural waters, they can play an important ecological role by preserving N and buffering its cycling in estuarine ecosystems through the prevention of rapid DON export/loss from mangrove fringe areas or from rapid microbial mineralization (Maie et al., 2008).

There are no estimates of net carbon flux available to evaluate the functional role of the EMER as a sink or source of carbon as has been proposed for other mangrove-dominated ecosystems (Bouillon et al., 2003; Kristensen et al., 2008). Globally, >50% of the carbon fixed by mangrove vegetation is still unaccounted for (Bouillon et al., 2008). Further work is needed to estimate flux at the boundary between the EMER and the Gulf of Mexico as well as the boundary between the forest and atmosphere. The present work using the eddy diffusion method may help develop carbon budgets and establish carbon sequestration rates under future scenarios of climate change and sea level rise (Barr et al., 2008).

While there are no net TOC and DOC flux estimates between the mangrove ecotone and coastal waters, there is information on the net exchange of DOC between the mangrove forest at SRS-6 and Shark River (Romigh et al., 2006). A multiseason study found that DOC concentrations were highest during the dry season (11 mg l^{-1}; May) followed by the wet (8 mg l^{-1}; October) and cold front (6 mg l^{-1}; December) seasons in 2003. This pattern was explained as a combination of litter production and inundation patterns of the mangrove wetland. Net DOC export was measured in October and December (i.e., the mangrove forest was a source of DOC to the river). Net annual export of DOC from the mangrove to the tidal creek was 56 g C m^{-2}

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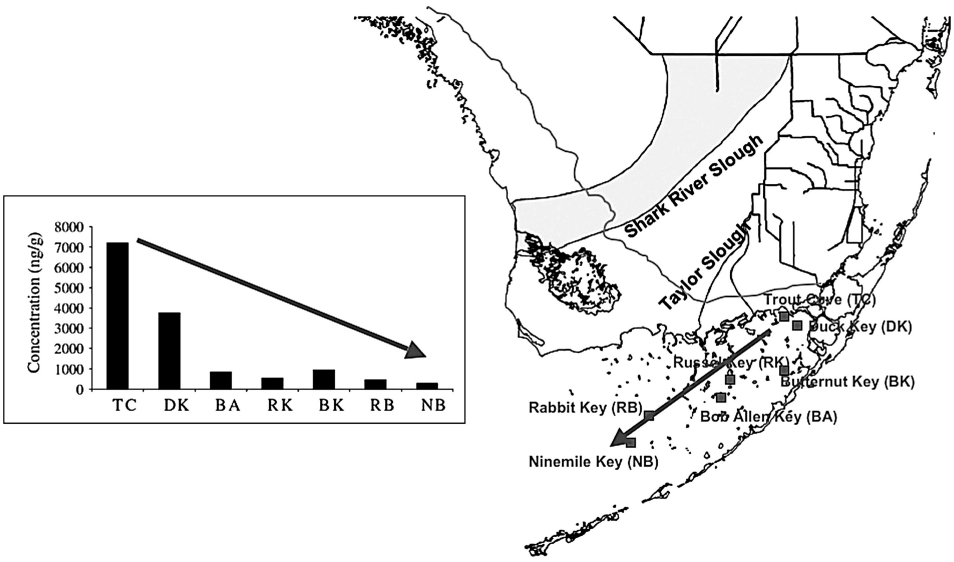

FIGURE 4. Spatial distribution of taraxerol concentration in surface sediments of Florida Bay (modified from Xu et al., 2006). TC = Trout Cove; DK = Duck Key; BK = Butternut Key; RK = Russell Key; BA = Bob Allen Key Bank; RK = Rabbit Key; NB = Ninemile Key.

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y^{-1}. Seasonal flux patterns indicate that DOC flux was controlled by both river discharge and tidal range. This seasonal export coincides with other studies showing the relative importance of leaf leaching as a source of DOC to the surface water (Davis and Childers, 2007). Despite the strong spatial gradient and high [TOC] in Florida coastal waters adjacent to tall riverine mangrove forests (Boyer, 2006), TOC export from the TS/Ph mangrove ecotone is much less. Mangroves form a narrow band of vegetation ~5 km wide that borders the coast and is clearly delimited by a coastal limestone rock ridge. This physical barrier and negligible tidal influence limits direct water exchange with Florida Bay, particularly in the dry season.

The location and size of carbon export has been indirectly assessed by measuring taraxerol, a biomarker for mangroves in sediments (Figure 4). Pentacyclic 3-oxytriterpenoid with the carbon skeleton of taraxerol are derived from higher plants (Xu et al., 2006). Analyses show that mangroves leaves contain high levels of taraxerol (1.4 mg g^{-1}; Versteegh et al., 2004), and sedimentary levels decreased from 7200 ng g^{-1} in nearshore NE Florida Bay (i.e., Trout Cove and Duck Key) to 284 ng g^{-1} in the SW section of Florida Bay (Ninemile Key). These two end members suggest that >60% of sedimentary organic matter is derived from terrestrial (i.e., mangrove) contributions at the edge of the northeastern bay compared to ~12% in the central and southwest. Further, these results suggested that mangrove islands scattered across the bay may play a more important role in providing organic matter

accumulated in sediments of the central and SW bay, in addition to contributions from particulate transport processes from coastal fringe mangroves (Xu et al., 2006).

Dissolved organic carbon seems to be closely coupled to the immobilization of P, particularly when water residence time is short. Labile organic C may be depleted in the water column in scrub mangrove forest in Taylor Slough when water residence times are long, thus resulting in low microbial densities, and higher P availability in this region (Davis and Childers, 2007). The potential regulatory role of DOC on P availability is underlined by the significant release of TOC, 40–50 mmoles gdw^{-1}) by *R. mangle* leaves compared with other wetland species (e.g., *Cladium jamaicense, Spartina alterniflora, Eleocharis* spp; Davis et al., 2006). This organic C may contribute to higher waterborne [DOC] observed in the mangrove ecotone region, particularly at the beginning of the rainy season. Understanding the mechanisms that regulate leaching of fresh plant litter at the landscape level should help to determine the relative role of this material as an autochthonous source of nutrients and carbon across the salinity gradients of the mangrove ecotone region—especially when freshwater flow is increased as result of CERP.

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Nitrogen and Phosphorus

It has been estimated that Everglades freshwater contributes <12% of all N input to Florida Bay (Rudnick et al., 1999). Total P levels are set to <10 ppb as a restoration goal to maintain oligotrophic conditions across the Everglades, but levels of inorganic and organic N needed to maintain oligotrophic conditions are unknown. This uncertainty is confounded by the lack of information on the spatial variation of nutrient cycling rates and the factors that regulate their magnitude. Mangrove forests that border Florida Bay influence the net exchange of material between these systems. For example, a mass balance study at the boundary between Florida Bay and creeks draining Taylor Slough showed that hydrologic import to Taylor Slough was within the range of estimated sediment P burial, while N sediment burial exceeded the amount estimated hydrologic N import (Sutula et al., 2001). These N flux discrepancies were attributed to different amounts of N fixation and denitrification. However, rates of these processes were assumed and other N transformations have not been quantified, especially relative to shifts in vegetation communities associated with increased freshwater delivery and upstream N fluxes (for further details about N fluxes, see Inglet et al., 2011).

Shark River Slough and the Gulf of Mexico

Overall, information on historical nutrient concentration and fluxes in the EMER is limited. Rivera-Monroy et al. (2007) found that [NO_2^- + NO_3^-] ranged from 0–3.5 μM, and [NH_4^+] from 0 to 4.8 μM in a small tidal creek near

SRS-6. Mean [TN] ranged from 12 μM in May to 39 μM in December 2003, while [TP] ranged from 0.2 to 2.9 μM and [SRP] from 0 to 0.8 μM. Brand (2002) showed that concentrations of inorganic nitrogen varied from 2–4 μM at the mouth of Shark River to 0–2 μM in the Gulf of Mexico. Childers et al. (2006) showed that DIN was approximately 8% of TN in the mangrove zone, split evenly between NH4 + and [NO_2^- + NO_3^-], whereas about 15% of TP was SRP. TN:TP ratios vary dramatically through the Shark River Slough system, ranging from about 310 (in the upper slough), increasing to 730 (about 5 km down the Slough) and then steadily decreasing to a low of about 40 near the mouth of the slough (Rudnick et al., 1999). Most studies indicate that surface water [P] in the Shark River increases down-estuary, while TN concentrations follow the opposite pattern (Childers et al., 2006; Chen and Twilley, 1999b). In one study, [TP] decreased from a range of 0.6 to 0.8 μM at the mouth of the Shark River to a range of 0.4–0.6 in the coastal waters of the Gulf of Mexico (GOM), and from 0 to 0.4 μM farther from the coast (Brand, 2002). In the GOM (about 10 km offshore from the river mouth), [TP] was higher than in freshwater wetlands but much lower than in the mangrove zone (0.4 μM; Rudnick et al., 1999). Further, [TP] in the mangrove zone were higher than expected based on conservative mixing of Shark River and GOM waters indicating a potential net P source within the EMER (Rudnick et al., 1999).

Taylor Slough Through Florida Bay

South Florida coastal waters are generally P-limited because, in this shallow carbonate environment, calcium carbonate chemically scavenges phosphate from the water. Ratios of TN:TP and DIN:SRP are well above the Redfield ratio of 16 throughout Florida Bay (Boyer et al., 1997; Fourqurean et al., 1993). In the saline mangrove zone of the Taylor Slough and in coastal Florida Bay waters, [TP] is higher than in the upstream wetlands (Rudnick et al., 1999). High [TP] in the mangrove zone is hypothesized to originate from the bay when water flows north through the Taylor creek during some dry seasons (Rudnick et al., 1999). Childers et al. (2006) found that [TN] and [TP] in the mangrove zone were also higher than Florida Bay sites, indicating nutrient regeneration or retention in the mangrove zone.

In the mangrove zone of Taylor Slough, 11% of TN was DIN, which was mostly NH_4^+, and 10% of TP was SRP (Childers et al., 2006). Davis et al. (2004) showed that Florida Bay is a source of dissolved inorganic nutrients into the mangrove areas of the lower Taylor River. TN and TP are imported by the scrub mangrove wetlands 87 $\pm$ 10% and 48 $\pm$ 17% of the year, respectively (Davis et al., 2003a, 2003b). In a study along the lower Taylor River, [SRP] was typically less than 0.1 μM and often below the detection limit, but in May 1998 (i.e., end of dry season), [SRP] was significantly higher (0.13–0.24 μM; Davis et al., 2001b). Overall, SRP was 5–25% of TP, which varied from 0.18–0.67 μM. In the same study, N concentrations ranged from

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0.2 to 5.75 μM (N+N), from 0.1 to 6.3 μM (NH_4), and from 41 to 89 μM (TN). In Florida Bay, [TP] was <0.4 μM in the east region and increased to >0.8 μM in the NW bay (Brand, 2002). Inorganic nitrogen concentrations varied from >8 μM in the eastern bay to <2 μM in SW Florida Bay (Brand, 2002). In general, P and N concentrations are lower in Florida Bay than in EMER.

Groundwater discharge represents a potentially important driver of wetland productivity in the EMER, particularly in Taylor Slough. Price et al. (2006) characterized this as a source of brackish water discharged into coastal wetlands along the EMER and suggested its importance as a source of phosphorus to the mangrove ecotone. Ewe et al. (2007) tracked the uptake of this water by vegetation and documented seasonal shifts between uptake from shallow soils and deeper groundwater sources. For example, *Rhizophora mangle* (the dominant species in the lower EMER of Taylor Slough) uses deep roots to extract groundwater during the dry season, probably as a strategy that not only reduces excess uptake of salt but also potentially allows the plant to access groundwater P sources (Ewe et al., 2007).

Discerning the role of mangroves as sinks, sources, or transformers of nutrients is a challenge given that few studies are available from different geomorphological settings (Lugo and Snedaker, 1974; Twilley, 1995). Denitrification does not necessarily measure net N loss because this process must be balanced with measures of N fixation. Presently there are no N fixation rates reported for Taylor River. A study along lower Shark River showed that N fixation could supply 7% of the N required for mangrove growth, contributing ~8.3 mg N m^{-2} d^{-1} to the forest floor (Pelegri et al., 1997). This study concluded that N fixation could supply 2.6 times the N eliminated by denitrification. Sutula et al. (2001) presented N and P budgets for Taylor River and concluded that atmospheric deposition was the dominant source of TP for the P limited wetlands, whereas surface water was the major TN source during the wet season but was equal to the atmospheric N deposition on annual basis. However, the lack of published rates of N fixation and denitrification created uncertainties in mass balance calculations (Sutula et al., 2001).

MANGROVE ISOTOPIC SIGNATURE

Stable isotopes provide a powerful method to trace sources and transfers of organic matter through food webs and can be used to detect environmental stress on plant metabolism (Fry and Smith, 2002; Montoya and McCarthy, 1995; Peterson and Fry, 1987). Studies have demonstrated that environmental stress derived from drought, nutrient limitation, and hypersalinity can change the δ ^{13}C and δ ^{15}N signatures of mangrove leaf tissue (Farquhar et al., 1982; Fry et al., 2000; Lin and Sternberg, 1992a, 1992b; Mancera et al., 2009; McKee

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et al., 2002; Medina and Francisco, 1997; Naidoo, 1985). Strong P limitation across the EMER combined with regional variation in productivity and growth form of the dominant mangrove species (*R. mangle*) has led to studies using stable isotopes to understand the effect of environmental stressors on plant development and growth (Fry et al., 2000; Lin and Sternberg 1992a, 1992b; McKee et al., 2002). Carbon isotopic composition of leaves changes proportionally along salinity gradients in the intertidal region (Lin and Sternberg 1992a; McKee et al., 2003). Tall fringe mangroves have lower $\delta\ ^{13}C$ values (−29 to −28‰) than scrub mangroves (−26.5 to −25.5‰) suggesting that scrub trees have lower stomatal conductance (and more conservative use of water) resulting in lower internal [CO_2] and lower $\delta\ ^{13}C$ discrimination due to higher salinity stress.

Mancera-Pineda et al. (2009) showed a negative correlation between foliar $\delta\ ^{13}C$ abundance and P (including plant P, soil P, and SRP) for all mangrove species along the EMER. The difference in ^{13}C discrimination among species associated with low soil [P] suggested a connection between P availability and water use efficiency. P deficiency may contribute to drought stress in plants that are inundated with water by reducing root hydraulic conductivity (Radin and Boyer, 1982). Therefore, mangroves across the landscape are stressed by resource (i.e., P) and regulator (i.e., sulfide) gradients. Less negative $\delta\ ^{13}C$ leaf values at Taylor Slough (Ts/Ph-6 and Ts/Ph-7), where hydroperiod is longer than at Shark River (SRS-5 and SRS-6), suggest that hydroperiod is an important factor determining carbon isotope fractionation between these two mangrove landscapes (Figure 5). Sulfide concentrations also showed a positive correlation with $\delta\ ^{13}C$ values for all mangrove species combined, indicating that mangroves are more water use efficient with increasing sulfide; $\delta\ ^{15}N$ patterns of mangrove species observed along the Shark and Taylor Rivers (Mancera-Pineda et al., 2009) supported the model proposed by Fry et al. (2000), hypothesizing that lower mangrove $\delta\ ^{15}N$ values are explained by the isotopic fractionation during N uptake in a high $\delta\ ^{15}N$ ratio environment. Because plants were ^{15}N-depleted in reference to soils, microbial fractionation was not likely an important process in the N cycle of the EMERM; ^{15}N discrimination reflected site N status and its range in mangrove species (from −0.1 to 7.7‰; e.g., *R. mangle*) is another response of mangrove vegetation to environmental stress (Figure 5; Mancera-Pineda et al., 2009).

An increase of P availability may increase N demand in these mangrove wetlands, thus reducing ^{15}N discrimination. For example, in a transect survey traversing the upstream margin of *Rhizophora* migration in the Taylor Slough, foliar nitrogen concentrations decreased significantly with distance (0–1200 m) from a canal inflow point (by approximately 10%; $r^2 = .99$; $p = .0002$), after which N concentration increased between 1500 and 2400 m downstream from the point of canal inflow (Troxler, unpublished data). This inflection point suggests the possible influence of variation in P availability, influencing N acquisition and storage. The high variability of mangrove $\delta\ ^{13}C$ and δ

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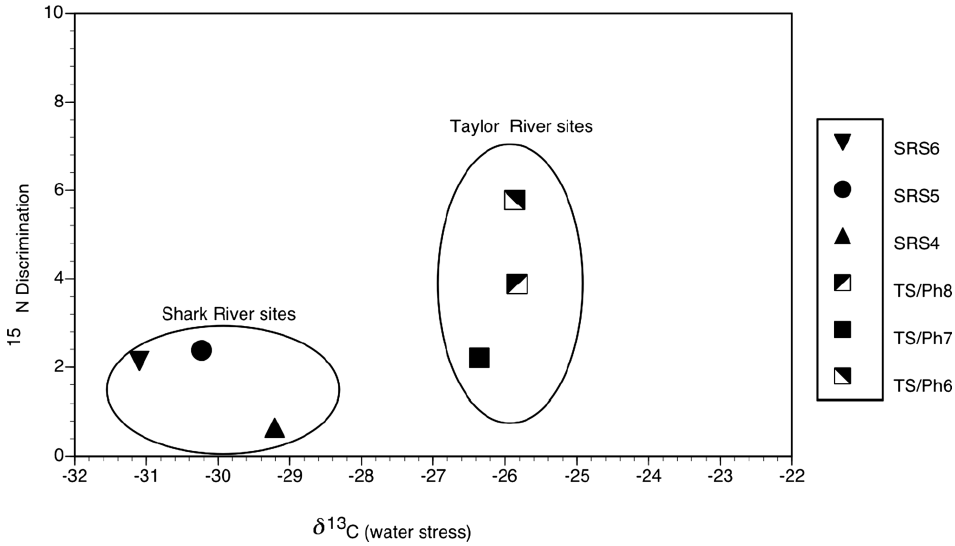

FIGURE 5. Nitrogen discrimination and carbon isotopic fractionation (‰) in *Rhizophora mangle* across an environmental stress gradient in the Everglades Mangrove Ecotone Region (EMER; from Mancera-Pineda et al., 2009).

^{15}N across these resource and regulator gradients could be a confounding factor obscuring the linkages between mangrove wetlands and estuarine food webs. These results support the hypothesis that landscape factors may control mangrove structure and function, so that nutrient biogeochemistry and mangrove-based food webs studies in adjacent estuaries should account for watershed-specific inputs (Mancera-Pineda et al., 2009). However, more isotopic studies are needed to determine the fate and role of organic matter from the mangrove ecotone region in supporting higher trophic levels in adjacent estuarine and coastal habitats in South Florida.

BIOMASS, PRODUCTIVITY, AND HURRICANES

Plant Community Structure

Three mangrove species occur in the EMER: the red mangrove, *Rhizophora mangle*, the black mangrove, *Avicennia germinans*, and the white mangrove, *Laguncularia racemosa*. A fourth species, buttonwood, *Conocarpus erectus*, is not a true mangrove, but it has a wide spatial distribution in the transition zone of the inland edge of mangrove ecosystems (Coronado-Molina et al., 2003; Odum et al., 1982; Tomlinson, 1995). A recent effort documenting the history of ENP vegetation changes during the past several decades (Welch et al., 1999) produced an extensive spatial delineation of Everglades vegetation patterns at the community and subcommunity level (Doren et al., 1999).

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TABLE 2. Mangrove categories and species in South Florida (Everglades National Park; Doren et al., 1999, Welch et al., 1999)

1) Forest—High-density stands of trees with heights >5 meters.	
EM	Mangrove Forest
FMa	Black (*Avicennia germinans*) Mangrove
FM1	White (*Laguncularia racemosa*) Mangrove
FMIb	White Mangrove or Buttonwood Forest—This class signifies that it is uncertain whether vegetation is white mangrove (*Laguncularia racemosa*) or buttonwood forest (*Conocarpus erectus*), since signatures on the aerial photographs are very similar. Field checking is required to correctly identify the species.
FMr	Red (*Rhizophora mangle*) Mangrove
FMx	Mixed mangrove—Specific mixtures of mangrove species, when identified, will be distinguished its subgroups.
FB	Buttonwood (*Conocarpus erectus*) Forest—*Conocarpus erectus* with variable mixtures of subtropical hardwoods.
2) Scrub—Low-density areas of trees and shrubs with heights under 5 meters.	
SM	Mangrove Scrub—The vegetation matrix in which the scrub occurs should be noted, e.g., within Eleocharis marsh.
SMr	Red (*Rhizophora mangle*)
SMa	Black (*Avicennia germinans*)
SM1	White (*Laguncularia racemosa*)
SM1b	White Mangrove or Buttonwood Scrub—This class signifies that it is uncertain whether vegetation is scub white mangrove (*Laguncularia racemosa*) or buttonwood scrub (*Conocarpus erectus*), since signatures on the aerial photographs are very similar. Field checking is required to correctly identify the species.
SMx	Mixed scrub—Sparse and high-density subgroups/modifiers can be distinguished.
SC	Buttonwood (*Conocarpus erectus*) Scrub

For mangrove communities, there was a clear distinction between vegetation height with two main categories: forest >5 m and scrub <5 m (Table 2). These categories reflect significant differences in hydrology (hydroperiod) and soil nutrient concentrations, which determine the dominance of each category and associated dominant plant communities (Chen and Twilley, 1999a; Coronado-Molina et al., 2003; Ross et al., 2001).

Biomass and Productivity

The conspicuous biomass gradient from scrub to fringing mangroves in the EMER is the result of environmental constraints that control mangrove forest structure and function (Figure 6). The relative effects and interactions of regulator gradients (e.g., salinity, sulfide), resource gradients (e.g., nutrients), and hydroperiod define a constraint envelope for determining the structure and productivity of mangrove wetlands (Berger et al., 2008; Twilley and Rivera-Monroy, 2005). Conceptual ecological models of the EMER indicate the importance of mangrove forest production, soil accretion, and water flow and flushing in slowing down the transgression of mangrove vegetation (Ross

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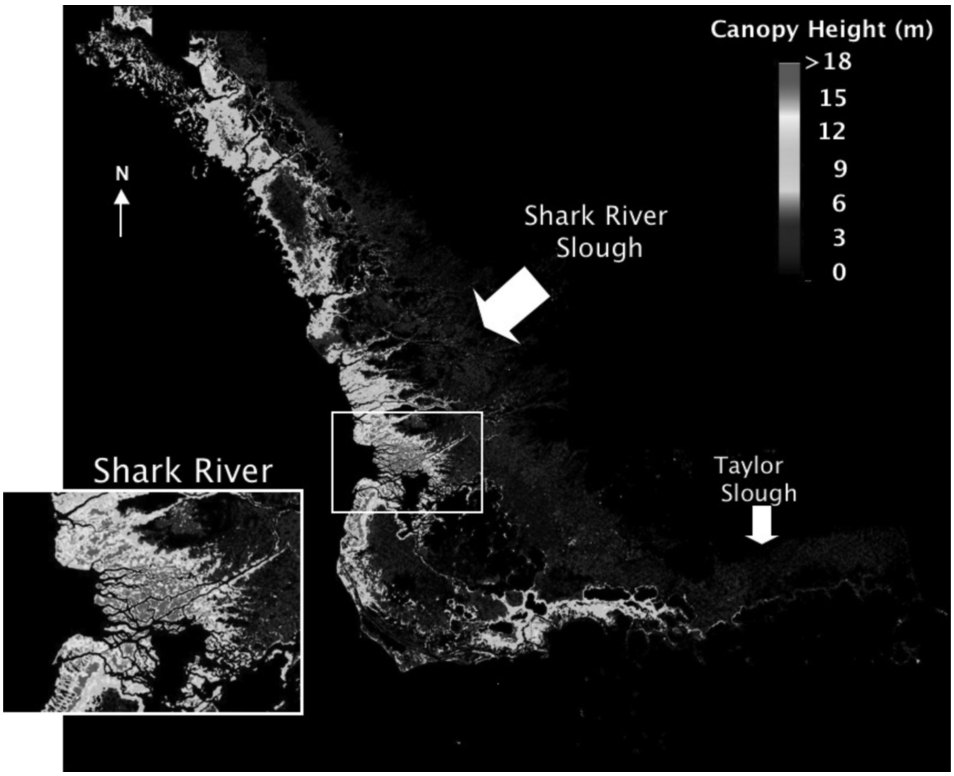

FIGURE 6. Map of mangrove mean tree height for the Everglades National Park, South Florida. This map shows that most of tall mangroves are found along the west coast along several tidal creeks, particularly around the mouth of the Shark River (Latitude 25° 21′N and Longitude 81° 7′ W; from Simard et al., 2006).

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et al., 2000) as result of landscape level changes in hydrological conditions upstream and increasing sea level (Davis et al., 2005).

Recent efforts to map mangrove tree height (as a proxy for primary productivity) have produced the first map of structural properties in the EMER (Simard et al., 2006). The map is based on Shuttle Radar Topography Mission C-band elevation (SRTM) data in combination with Light Detection and Ranging (LIDAR) data. By relating tree height to available ground estimates of mangrove forest biomass at local scales, this information can be used to determine the capacity of mangrove forest as carbon sinks (Figures 6 and 7). This approach is based on reports that mangrove tree height is a good indicator of forest biomass (Bouillon et al., 2008; Cintron and Schaeffer-Novelli, 1984; Cintron-Molero and Schaeffer-Novelli, 1992; Soares and Schaeffer-Novelli, 2005).

Combining tree height and biomass information at different spatial scales may improve understanding of the role of tropical coastal wetlands in the

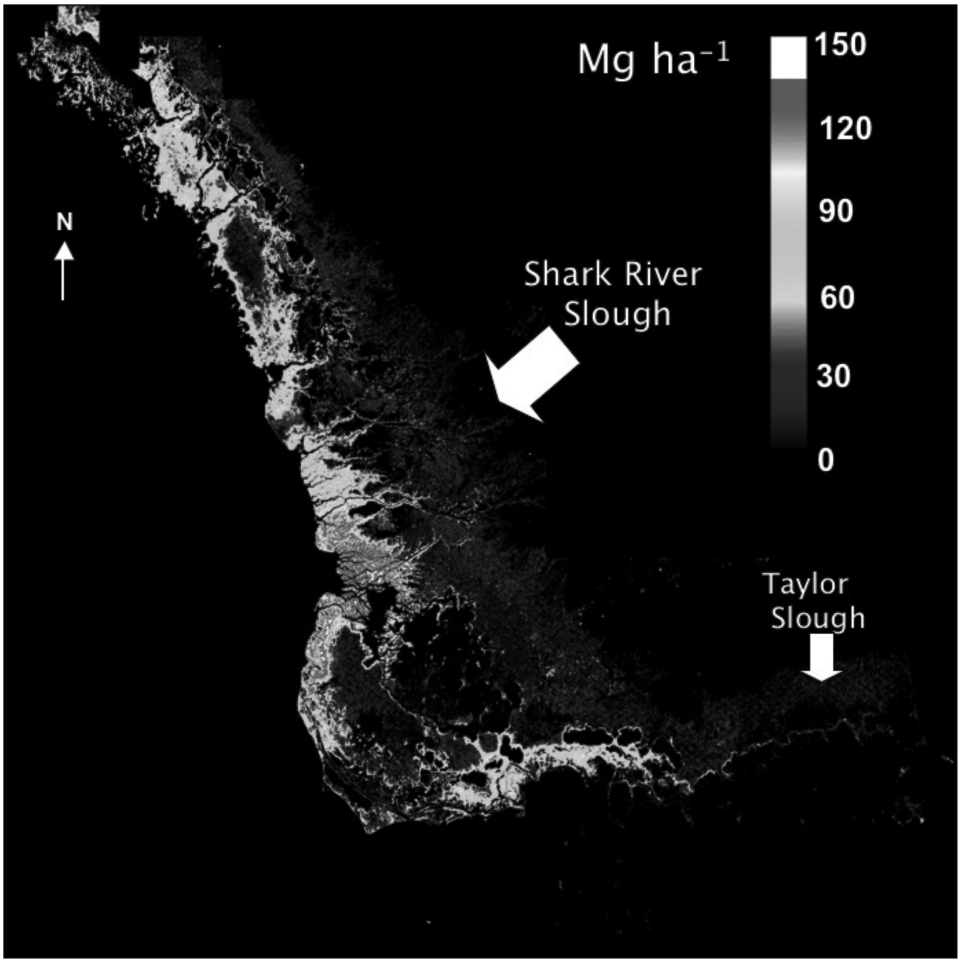

FIGURE 7. Map of mangrove standing biomass distribution in the Everglades National Park, South Florida. This map was computed using the mean tree height derived from SRTM elevation data (Simard et al., 2006) and a linear regression for the biomass versus mean height (Smith and Whelan, 2006).

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global carbon budget. Using vegetation polygons, Simard et al. (2006) estimated the mean ($\pm SD$) height of scrub mangrove in ENP at 3.2 ± 1.3 m and determined that most of the Park was occupied by this vegetation part. As discussed above, the low stature of these communities is associated with P limitation. Using tree height estimates based on RADAR and LIDAR measurements (Simard et al., 2006) and allometric equations relating crown-weighted mean canopy height (m) and biomass (Smith and Whelan, 2006), we estimated first-order biomass values across the EMER of 5 to 120 Mg ha^{-1}. The highest values were located close to the mouth of Shark River and other SW Florida estuaries (e.g., Harney Creek and Broad Creek; Figure 7) and

correlates with high water column [TOC] adjacent to the Shark River mouth (Figure 3; Boyer, 2006).

In contrast to riverine and fringe mangroves of the western region, scrub mangrove forests of the eastern region are less productive (340 g C m^2 y^{-1}; Ewe et al., 2006), partially as result of phosphorus-poor water from the freshwater Everglades (Childers et al., 2006; Davis et al., 2003a, 2003b; Davis et al., 2001a, 2001b). The lack of a strong tidal signature and pronounced seasonal flooding (wet vs. dry; with extensive periods of sediment air exposure on dry years) has a major influence on nutrient concentrations and fluxes in the region. As a result of hurricanes, large sediment inputs into the region have been documented, but the effect on mangrove productivity is not clear. Davis et al. (2004) analyzed the effect of Hurricane Irene on sediment deposition and found that as much as 5 cm of carbonate sediment was deposited in a nearby mangrove vegetated ridge (lower Taylor River), although much of the deposition was confined to a 60 m meter zone in the center of the ridge. Hurricane Wilma (in 2005) resulted in significant sediment deposition in lower Shark River—exceeding the normal annual accretion rate (5–15 mm) by 10 times (Castañeda-Moya, 2010). Davis et al. (2004) noted that hurricanes may serve as periodic sources of carbonate sediment (and carbonate-bound P) to the P-limited EMER contributing to the maintenance of the mangrove productivity and position relative to sea level.

Hurricanes and Gap Dynamics

Coastal ecosystems are influenced by pulsed events that operate across a range of spatial and temporal scales (Day et al., 2007; Lugo, 2000; Lugo et al., 2000). Global-scale events such as ENSO operate over long time scales, affecting annual hydrologic and productivity patterns (Childers et al., 2006). In contrast, short-term events such as hurricanes may last from hours to days, influence hundreds to thousands of kilometers, and have both acute and lasting effects on ecosystem processes (Davis et al., 2004; Doyle et al., 2009; Doyle et al., 1995). Mangrove forests are altered by hurricanes, frost, lightning, and even insects (Duke, 2001; Feller and McKee, 1999; Smith et al., 1994a). These disturbances reset the mangrove forest development clock, altering structure by damaging and killing trees, followed by recruitment and competition.

Smith et al. (1994) and Doyle et al. (2009) described the effects of Hurricane Andrew on vegetation structure and mortality. This work reported large physical changes to the forest and tree mortalities ranging from 25 to 75% in ENP (from Chatham River to Shark Point). However, there are no published maps showing the aerial coverage and recovery of such areas from the coastline to 20 km inland. Recently Krauss et al. (2005) performed a follow-up study in these areas after 9–10 years and presented information on woody debris as result of Hurricane Andrew impact. It is not clear what percentages

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of these areas have fully recovered or if mangrove coverage increased in the western region of the Everglades National Park (Figure 1). However, in a study tracking changes in forest structure of stands affected by Hurricane Andrew, Ward et al. (2006) showed that much of the forest has already returned to a closed canopy state based on regional allometric patterns and trends in biomass. These results suggest a shift from a regenerative state to an aging stand after a ~13-year period.

At the landscape level, mangrove forests exposed to frequent disturbance show characteristic patches in various stages of development. Lugo and Snedaker (1974) suggested that the maximum biomass and structural dimension that mangrove forests can develop in a hurricane zone is limited by storm activity, because mangrove forests usually reach maturity in 20–25 years, a period coincident with the frequency of hurricanes in the neo-tropics. The influence of this cyclic replacement process on nutrient and carbon cycling remains an open question, particularly given the profound effects of major disturbances on nutrient residence times and fluxes. Despite the high incidence of hurricanes in South Florida (e.g., Zhang et al., 2008) little quantitative information exists concerning hurricane impacts on mangrove forest structure, succession, species composition, and dynamics of mangrove dependent fauna or on rates of ecosystem recovery (Smith et al., 1994). Ward et al. (2006) showed how initial differences in stand structure and sapling establishment rates controlled development trends following disturbance. Light availability limited mangrove recruitment to the sapling stage and turnover in plots affected by Hurricane Andrew (1992) followed a classic large-gap phase dynamic. Ross et al. (2006b) found that the species composition of mangrove stands developing after Hurricane Andrew was affected by site productivity, with rapid canopy closure associated with the most productive sites favoring *R. mangle* over *L. racemosa*.

Recent gap dynamic studies, using LIDAR measurements and field surveys in the Shark River region identified 400–500 lightning gaps km^{-2} (Zhang, 2008; Zhang et al., 2008). The distribution of gap sizes followed an exponential pattern and the area of gaps larger than 100 m^2 accounted for 55–61% of the total area of gaps. The area of gaps in this region was about 4–5% of the total forest area and the average gap formation rate is about 0.3% of the total area per year (Zhang, 2008). A similar study using the same methodological approach quantified the impact of hurricanes and lightning strikes before and after Hurricanes Katrina and Wilma in 2005 (Zhang et al., 2008). These storms created numerous canopy gaps, and the spatial density of gaps increased from about 400-500 m^2 to 4000 m^2 after Katrina and Wilma. The percentage of gaps in the forest increased from about 4–5% of the total forest to 12%. On an areal basis, it therefore appears that the relative contribution of hurricanes to mangrove forest disturbance in ENP is at least twice than that from resulting lightning strikes. These studies suggest that gap size in mangrove forests may have a critical role in defining the daily and seasonal

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light regime for the establishment of *L. racemosa*, a species characterized as early successional (e.g., Delgado et al., 2001).

Despite these unique impacts, hurricanes and lightning strikes disturb the mangrove forest in a similar fashion. Most seedlings in lightning gaps typically survive hurricane impact due to the protection of trees surrounding the gaps, and therefore provide an important resource for forest recovery after hurricane. Observations of the relative vulnerability of large trees to hurricanes are paralleled by others that show that scrub mangrove forest is less prone to full defoliation and tree mortality in contrast to taller mangroves (>10 m; Ross et al., 2006b; Smith et al., 1994). Thus, it is expected that mangrove succession and nutrient cycling might differ significantly between these two regions of the EMER (Figure 6). Further modeling (e.g., Berger et al., 2008; Chen and Twilley, 1999; Teh et al., 2008) is needed to forecast productivity trajectories with changing climate and hurricane frequency (Emanuel, 2005; Greening et al., 2006).

FUTURE EFFECTS OF CLIMATE CHANGES ON THE EMER

Process interactions and feedbacks in coastal wetlands (e.g., tidal flooding patterns, sedimentation, plant productivity, soil elevation) allow wetland elevation to self-adjust to changes in sea level (Cahoon, 2006; Day et al., 2008). Yet, impacts of sea level rise on coastal settings are better assessed using regional values instead of global averages (Church et al., 2004; White et al., 2005). Most intertidal wetlands in South Florida and the Caribbean can keep up with the present regional rates of sea level rise that ranges from 1.2 to 2.3 mm yr^{-1}, although localized areas of lower elevation are subject to shoreline transgression and landward migration of mangroves may continue at the local level where rates of peat or marl elevation do not keep up with rates of sea level rise (Davis et al., 2005). Saline intrusion into freshwater wetlands growing on peat substrate may cause wetland "collapse" and transformation to open saline ponds and estuaries (Wanless et al., 1994b, Davis et al., 2005). A good example of transgression as a result of sea level rise and historical water management in South Florida is the "white zone" along the NE region of Florida Bay and southern Biscayne Bay. The white zone is a region of the EMER where surface sediments are composed of marl, fresh storm deposits, and in some places periphyton; productivity is low, with short vegetation (<1 m) and sparse (<50%) cover. Over the past 50 years, the interior boundary of the white zone has encroached inland 1.5 km (Ross et al., 2000; Ross et al., 2002). Because of its conspicuous presence in the supratidal region of the coast (and easily identified in satellite images), shifts in the location of this zone has been proposed as a performance measure to monitor past and present changes in freshwater delivery as a result of CERP.

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CERP AND MANAGEMENT OF THE EMER

We recommend that the selection of reference conditions for EMER management be based on regional productivity and structural differences observed across this region. For example, the present inland expansion of mangroves in the Taylor Slough region could be a criterion to define the success of restoration. Thus an actual reduction of mangrove area could be considered a success, whereas in the west region (i.e., Shark River Slough) any loss of area could be considered a failure. This last point is based on the assumption that the present mangrove distribution within EMER reflects historical spatial distribution patterns influenced by human impacts and sea level rise. Further information on historical changes on mangrove spatial distribution is needed to establish reference criteria to adequately evaluate the effect of the CERP on mangrove productivity under present conditions of land use and climate change as indicated by recent CERP reviews (NRC, 2008).

Once reference conditions are defined, PMs need to be selected. Twilley and Rivera-Monroy (2005) proposed a series of PMs for mangrove forests to link specific objectives of restoration projects and modeling (Table 3). These PMs are based on two important characteristics: (a) the significance of the measures to tracking community structure and ecosystem function of mangrove wetlands to evaluate restoration effectiveness and (b) the relevance of PMs to improve model parameterization and validation. PMs were originally grouped into three categories used by the hydrogeomorphic (HGM) approach to classifying wetland functions including hydrology, biogeochemistry, and community ecology attributes (Brinson, 1993). Each of these categories includes a set of PMs for both wetland and estuary systems of a project area. Many wetland restoration monitoring programs only include PMs for mangrove wetlands, but as discussed in the previous sections, several measures of the estuary (e.g., salinity, sediments) are necessary to improve evaluation of mangrove wetlands (e.g., Twilley and Rivera-Monroy, 2005, 2009). In addition, each measure needs to be rated as high, medium, or low in priority relative to cost-effective decisions made in restoration monitoring programs. As budget and resources allow, a mangrove-monitoring program should first include all the high-rated PMs (e.g., mangrove cover, soil regulators, topography, hydroperiod, soil accretion/elevation, sediment deposition), and then include as many of the medium-rated indicators as possible (e.g., nutrient accumulation; see Twilley and Rivera-Monroy, 2005). This priority system may be amended depending on specific goals of a restoration plan because those measures associated with water quality have lower rankings than those that focus on recovery of vegetation (Bosire et al., 2008). Because the CERP goals include water quality and vegetation components, careful selection of PMs is paramount to evaluate mangrove dynamics in two different coastal settings (i.e., Taylor Slough vs. Shark River Slough) regarding long-term alterations

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TABLE 3. List of performance measures for mangrove ecosystems based on conceptual and simulations models of biogeochemistry and ecological attributes for both the Everglades mangrove ecotone region wetlands and Florida Bay (modified from Twilley and Rivera-Monroy, 2005)

Category of Performance Measure	Wetland Variables	Estuary Variables
1) Environmental Setting	• Total Mangrove cover • Meteorological measurements • Disturbance regime	• Mangrove to water ratio
2) Hydrology	• Soil Regulators (Salinity, H_2S, Redox) • Mangrove topography • Hydroperiod	• Salinity of tidal exchange • Tidal amplitude • Fresh water discharge
3) Biogeochemistry	• Soil Resources (OM, TN, TP, BD) • Soil accretion/elevation • Root biomass • Sediment deposition and accumulation • Carbon storage • N fixation and denitrification	• Water quality • Water residence time in estuary • Nutrient exchange with wetland • Nutrient removal in estuary • Plankton bloom potential
4) Ecology	• Forest dimension analysis-transects • Forest dimension analysis-plots • Sapling recruitment • Leaf area index • Net ecosystem production • Faunal relationships • Invasion of exotic species	• Growth rate of key species • Habitat suitability analysis • Isotope ratios of Indicator species • Production of commercial species • Census of bird populations • Submersed habitats

OM = Organic Matter; TN = Total Nitrogen, TP = Total Phosphorus; BD = Bulk Density.

in hydrology and nutrient inputs as result of implementing the Everglades Restoration plan.

CONCLUSION

Although we have focused only on the EMER in this work, EMER must be placed in the context of the hydrological connectivity along the Shark River and Taylor Sloughs and into Florida Bay and the GOM. Reduced freshwater delivery over the past 50 years combined with Everglades compartmentalization and a 10 cm rise in coastal sea level has led to the landward transgression (~1.5 km in 54 years) of the mangrove ecotone. Recent studies have shown a significant variation in N flux within dwarf and fringe mangrove areas of Taylor and Shark Rivers, while other studies have quantified N fluxes through this mangrove ecotone utilizing a hydrologic modeling approach. Despite these estimated N fluxes, it is still unclear how N and P

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cycles interact in controlling wetland productivity across hydrological gradients. Approximately 49% of the EMER is covered by tree canopies with maximum height of <3 m, particularly in the SE region. These scrub/coastal mangroves are the result of a combination of low soil P (<59 μg P g dw^{-1}) in the calcareous marl substrate and long hydroperiod. In contrast to other subtropical and tropical coastal ecosystems where the estuarine region is N-limited and the upstream areas are P-limited, both the EMER and its freshwater watersheds are limited by P due to the lack of terrigenous sediment input and the biogeochemistry of the Everglades. Thus, the primary source of P to this wetland ecosystem is the GOM instead of the upstream watershed. This P supply from the GOM is provided in pulses by tropical storms and hurricanes, which can deposit up to 6–56% of the TP already stored in the soil (735 μg g dw^{-1}) in a single event, supporting high mangrove net primary productivity (1100 g C m^{-2} yr^{-1}). Seasonal variation in freshwater input strongly controls the temporal variation of N and P exports (99%) to Florida Bay. Present estimates of annual N (0.46 g N m^{-2}) and P (0.007 g P m^{-2}) export from the mangrove ecotone (Taylor Slough) to adjacent coastal waters indicates the effect of land and water use upstream, which can drive major alterations in productivity and spatial distribution of wetland vegetation in EMER. Rapid changes in nutrient availability and vegetation distribution during the last 50 years show that restoration efforts and future land use decisions may exert, on the short term, a major influence at a scale similar to sea level rise, in regulating nutrient cycling and wetland productivity in the EMER.

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