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# Integrated Carbon Budget Models for the Everglades Terrestrial-Coastal-Oceanic Gradient: Current Status and Needs for Inter-Site Comparisons

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# INTEGRATED CARBON BUDGET MODELS FOR THE EVERGLADES TERRESTRIAL- COASTAL-OCEANIC GRADIENT

Current Status and Needs  
for Inter-Site Comparisons

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Photo courtesy of  
Jessica Schedlbauer

**ABSTRACT.** Recent studies suggest that coastal ecosystems can bury significantly more C than tropical forests, indicating that continued coastal development and exposure to sea level rise and storms will have global biogeochemical consequences. The Florida Coastal Everglades Long Term Ecological Research (FCE LTER) site provides an excellent subtropical system for examining carbon (C) balance because of its exposure to historical changes in freshwater distribution and sea level rise and its history of significant long-term carbon-cycling studies. FCE LTER scientists used net ecosystem C balance and net ecosystem exchange data to estimate C budgets for riverine mangrove, freshwater marsh, and seagrass meadows, providing insights into the magnitude of C accumulation and lateral aquatic C transport. Rates of net C production in the riverine mangrove forest exceeded those reported for many tropical systems, including terrestrial forests, but there are considerable uncertainties around those estimates due to the high potential for gain and loss of C through aquatic fluxes. C production was approximately balanced between gain and loss in Everglades marshes; however, the contribution of periphyton increases uncertainty in these estimates. Moreover, while the approaches used for these initial estimates were informative, a resolved approach for addressing areas of uncertainty is critically needed for coastal wetland ecosystems. Once resolved, these C balance estimates, in conjunction with an understanding of drivers and key ecosystem feedbacks, can inform cross-system studies of ecosystem response to long-term changes in climate, hydrologic management, and other land use along coastlines.

## INTRODUCTION

The future of coastal wetland ecosystems is uncertain due to a combination of climate change impacts (sea level rise, changes in storm activity, altered freshwater availability) and human activities (population growth, changes in resource and land use). Consequences of coastal ecosystem loss are not limited to the regional services they provide (e.g., storm mitigation, aquifer recharge, fisheries) but rather extend globally through impacts on biodiversity, biogeochemical cycling, and atmospheric interactions. For instance, recent studies show that vegetated coastal systems store up to 50 times more carbon (C) than tropical forests (1,000 Mg organic C ha<sup>-1</sup>) due to high productivity and low C loss through respiration (Bouillon, 2011; Mcleod et al., 2011; Fourqurean et al., 2012b). Studies examining patterns and controls on

long-term spatial and temporal patterns in C gain and loss in coastal wetlands will reduce uncertainty about their persistence and the future of related ecosystem services from local to global scales.

The Florida Everglades contains wetlands that have been profoundly transformed through a history of large-scale land conversion and water diversion (Figure 1). These wetlands are now exceptionally exposed to added pressures of sea level rise, changes in storm frequency and severity, and extreme weather perturbations (i.e., drought or alterations in the timing of rain events; IPCC, 2007). The unprecedented landscape-scale restoration of the Everglades is expected to improve freshwater flow to coastal wetlands, but the degree to which restoration will mitigate the effects of sea level rise and storms, as well as how it will interact with activities of the

9 million residents in the watershed, is uncertain. Thus, the Everglades ecosystem is an exemplary model for the types of exposures threatening coastal wetlands globally. Long-term studies facilitated by the Florida Coastal Everglades Long Term Ecological Research (FCE LTER) project are providing uncommon and valuable insight into how changes in freshwater supply and climate variability interact to affect C gains, losses, and storage in the coastal wetlands. Such insights are critical to determining long-term C persistence in the face of change (DeLaune and White, 2012).

Until recently, little was known about C cycling, mechanisms controlling its variability in coastal ecosystems (Mcleod et al., 2011), or the relevance of coastal C cycling to global biogeochemical cycles (Donato et al., 2011). Initial C balance approaches applied in South Florida coastal ecosystems have shown that mangrove forests sequester globally relevant quantities of C at rates that are sensitive to climate change and disturbance (Twilley et al., 1992; Bouillon et al., 2008; Barr et al., 2012; Breithaupt et al., 2012; Malone et al., 2013). Because coastal wetlands are often characterized by tidal action or flowing water, their carbon budgets must also take into account exchange over the water-atmosphere interface and exchange of C due to lateral transport (i.e., aquatic C entering and exiting the ecosystem). In this paper, we present estimates of net ecosystem C balance (NECB), net ecosystem exchange (NEE), and aquatic C flux for Everglades freshwater marsh, mangrove forest, and seagrass ecosystems, where available, to make strides toward C budget estimates for these systems. We also identify areas of study that will reduce

uncertainty in these estimates and their drivers, and point out discoveries that can emerge from regional and global comparisons using consistent approaches and methodologies.

## FLORIDA COASTAL EVERGLADES STUDY AREA

The FCE LTER site is situated in Everglades National Park, which can be thought of as a series of linked habitats that include freshwater marshes, mangrove forests, and subtidal areas where seagrasses are the dominant producers. Freshwater marshes are characterized by flooding, with hydroperiods as short as 0–6 months or as long as 9–12 months of the year. They are dominated by sawgrass, spikerush, and expansive mats of periphyton (an assemblage of microorganisms including algae, bacteria, and fungi; Gaiser et al., 2012). Everglades periphyton assemblages form

mats that are dominated by calcium carbonate (30–50% of dry mass), and their residual C is primarily detrital (Donar et al., 2004), with autotrophic and heterotrophic microbes comprising the small remainder of biomass. These freshwater marshes grade into mangrove forests through an “oligohaline ecotone” that expresses marked variability in salinity and nutrient availability, depending on freshwater flows and marine exposure (Rivera-Monroy et al., 2011; Troxler et al., 2013). Mangrove forests vary from short to tall, and most are influenced by semi-diurnal tides (Chen and Twilley, 1999; Ewe et al., 2006). Shallow seagrass ecosystems (with associated macro- and microalgal assemblages) dominate the southwestern estuaries of Florida Bay. A mix of seagrass beds dominated by *Thalassia testudinum* and calcareous rhizophytic macroalgae of *Halimeda* and *Penicillus* spp. covers the Florida Bay subtidal marine

environments. Distribution of seagrass species and macroalgae assemblages responds to salinity and nutrient gradients (Zieman et al., 1989).

The FCE LTER study design employs a transect approach (Figure 1) to track water flow and ecosystem properties along the two main Everglades drainages, Taylor Slough/Panhandle (which has a short hydroperiod) and Shark River Slough (which has a long hydroperiod). Research sites along these two freshwater flowpaths allow study of the contrasting influences of freshwater inputs and seawater exposure, peat and marl soils, herbaceous and woody plant species, and phosphorus (P) status (Myers and Ewell, 1990).

## APPROACHES FOR ESTIMATING C UPTAKE, STORAGE, AND TRANSPORT ACROSS THE LAND-WATER CONTINUUM

Two main approaches are available for determining NECB: (1) summing the change in C for all pools (i.e., net above- and belowground production and soil storage), and (2) using eddy covariance-based NEE measurements combined with estimates of aquatic C flux (the C entering and leaving the system in dissolved and particulate form through aquatic transport). Ideally, NECB estimates would be independently estimated by each approach and compared. However, if aquatic flux is not known, it can be estimated by combining NECB determined from the sum of the changes in C pools with NEE. Important insights into the magnitude of ecosystem C accumulation and C flux (both vertical and lateral aquatic transport) can be achieved when applied along coastal ecosystem gradients from freshwater to mangrove forests (Engel et al., 2011; Rivera-Monroy et al., in press).

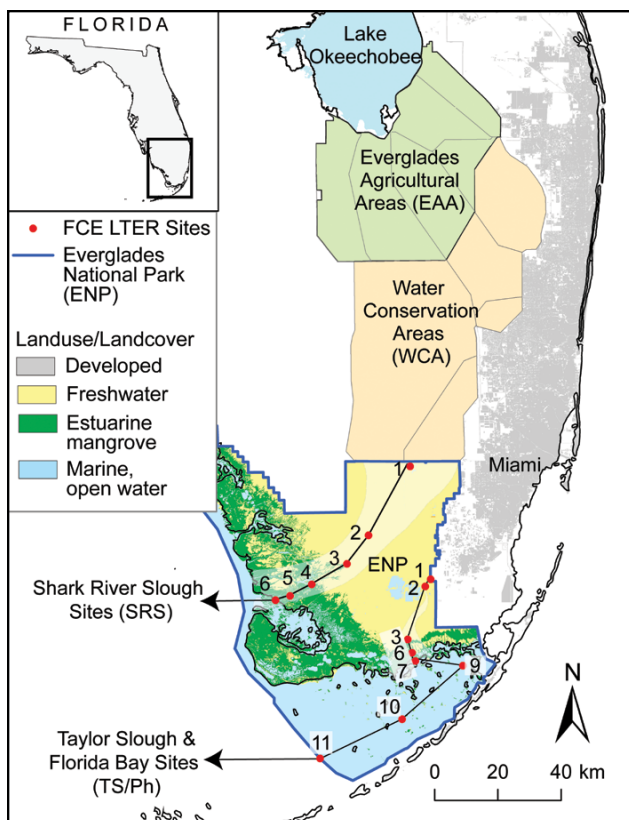


Figure 1. Florida Coastal Everglades Long Term Ecological Research (FCE LTER) site map, including locations of 14 biophysical research sites (red dots) along transects through Shark River Slough and Taylor Slough into to Florida Bay within Everglades National Park (ENP). Cross-cutting research will extend beyond these into the South Florida Urban Gradient to examine socio-hydrological underpinnings of current, past, and future conditions in the oligohaline ecotone. Map created by M. Ruggie

Net Ecosystem C Balance as the Change in Ecosystem C Pools  
NECB can be approximated following Lovett et al. (2006) as the change in organic C pools per year:

$$\text{NECB} = \Delta\text{AGB} + \Delta\text{BGB} + \Delta\text{S} + \Delta\text{CWD} + \Delta\text{Litter}, \quad (1)$$

where NECB (for both mangrove and sawgrass marsh) equals the sum of the change in C in aboveground ( $\Delta\text{AGB}$ ) and belowground biomass stock ( $\Delta\text{BGB}$ ), soil ( $\Delta\text{S}$ ), coarse woody debris stock ( $\Delta\text{CWD}$ ), and litter stock ( $\Delta\text{Litter}$ ). Assuming that the change in C stocks of CWD and litter are small relative to  $\Delta\text{AGB}$ ,  $\Delta\text{BGB}$ , and  $\Delta\text{S}$ ,  $\text{NECB} = \Delta\text{AGB} + \Delta\text{BGB} + \Delta\text{S}$ . The net change in soil C, approximated as soil C accumulation, integrates litter and root inputs, heterotrophic respiration, and leaching/export. Soil C accumulation can be constrained by estimating these parameters, but soil C accumulation estimated by other means (i.e., radiocarbon dating) provides a first-order approximation toward estimation of NECB.

## NECB and NEE

Following the Chapin et al. (2006) approach, the amount of C accumulating in the ecosystem (NECB; in mass of C  $\text{area}^{-1} \text{time}^{-1}$ ) equals the net ecosystem exchange of  $\text{CO}_2$  ( $-\text{NEE}$ ), with the negative sign accounting for uptake from the atmosphere, plus the net flux ( $F_{\text{TOT}}$ ) of all other forms of C through the system (dissolved inorganic C, dissolved organic C, particulate organic C, carbon monoxide, methane, and volatile organic C; Chapin et al., 2006):

$$\text{NECB} = -\text{NEE} + F_{\text{TOT}} \quad (2)$$

The aquatic C flux as organic C in particulate and dissolved form and dissolved inorganic C complicate estimation of NECB because wetlands can be both a source and a sink for these forms of laterally transported C. In the Everglades, all three forms of C are transported through freshwater marsh ridges and sloughs downslope along a gentle topographic gradient that develops a hydrologic and salinity gradient from freshwater marshes upstream to mangrove wetlands along the coast. For

a particular Everglades wetland landscape (i.e., marsh or wetland forest), as in Figure 2, particulate organic, dissolved organic, and dissolved inorganic C also enter from upstream ecosystems, with C potentially derived from marshes, tree islands, and managed flows in canals, or seepage from associated levees. Carbon exiting the system serves as input to downstream ecosystems that include mixed marsh and scrub mangroves, mangrove forests, and seagrass meadows.

## CARBON BUDGETS FOR EVERGLADES ECOSYSTEMS

### Methods for Estimation of NEE and NECB Parameters

To develop estimates of NEE for Everglades coastal ecosystems, a combination of eddy covariance studies from FCE LTER sites were aggregated for a mangrove site in Shark River Slough (Barr et al., 2010) and marsh sites in Everglades Shark River and Taylor Sloughs (Jimenez et al., 2012; recent work of author Malone and colleagues). Ewe et al. (2006) summarize methods for obtaining input parameters to estimate

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NECB in marshes and mangroves.

Iwaniec et al. (2006) describe methods for determining periphyton accumulation rates and gross primary production and ecosystem respiration, and, by difference, net ecosystem production. Periphyton estimates were considered separately and not included in NECB estimates for sawgrass marsh. Soil C accumulation was estimated using radiometric analyses of soil ( $^{210}\text{Pb}$  and  $^{137}\text{Cs}$ ) and accelerated mass spectrometry  $^{14}\text{C}$  dating of fossilized plant material as described in Saunders et al. (2007) and Smoak et al., (2013).

### Estimates for NEE and NECB in Everglades Coastal Wetlands

In deriving estimates for each of the coastal Everglades ecosystems—riverine mangrove forest, freshwater marsh in Shark River and Taylor Sloughs, and seagrass—we combined Equations 1 and 2 to determine

$$\Delta\text{AGB} + \Delta\text{BGB} + \Delta\text{S} = -\text{NEE} + \text{F}_{\text{TOT}}$$

Mangrove forests were sinks for  $\text{CO}_2$  ( $-\text{NEE} = 1,170 \text{ g C m}^{-2} \text{ yr}^{-1}$ ;  $\text{NECB} = 1,038 \text{ g C m}^{-2} \text{ yr}^{-1}$ ). This range approximated and exceeded rates of NEE found for tropical and temperate systems in large part due to low respiration rates (Barr et al., 2010). Annual net aboveground primary production ( $\Delta\text{AGB}$ ) of litterfall and wood was  $14.51 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ . Overall, litterfall production had the highest contribution to annual net aboveground primary production, accounting for approximately 70% of the total. Total net aboveground ( $\Delta\text{AGB}$ ) and belowground ( $\Delta\text{BGB}$ ) primary production was  $19.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ , with the total over two times higher at the Shark River riverine mangrove site as compared to an average value for Taylor River mangrove sites ( $8.3 \pm 0.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ). Annual net belowground primary production ( $\Delta\text{BGB}$ ) made a significant

contribution to this total (Castañeda-Moya et al., 2011, in press). Soil C accumulation, estimated from radiometric analyses (Smoak et al., 2013) was  $194 \text{ g C m}^{-2} \text{ yr}^{-1}$ . Thus, employing the equation above, total aquatic C flux ( $\text{F}_{\text{TOT}}$ ) is  $-131 \pm 155 \text{ g C m}^{-2} \text{ yr}^{-1}$  (Table 1). An upper-bound estimate of  $\text{F}_{\text{TOT}}$  could also be derived by assuming that over the longer term (decades to centuries), the C accumulation in live biomass is negligible when considered on an annual basis ( $191 \text{ g C m}^{-2} \text{ yr}^{-1}$ , assuming wood burial is estimated as 60% of standing dead wood; Robertson and Daniel, 1989; Krauss et al., 2005) or an estimate of aquatic export of  $784 \text{ g C m}^{-2} \text{ yr}^{-1}$ . This upper-bound value is nearly a third larger than the estimated aquatic C flux using approximations derived from studies and model estimates of dissolved organic, inorganic, and particulate organic C flux ( $\sim 500 \text{ g C m}^{-2} \text{ yr}^{-1}$ ; Twilley,

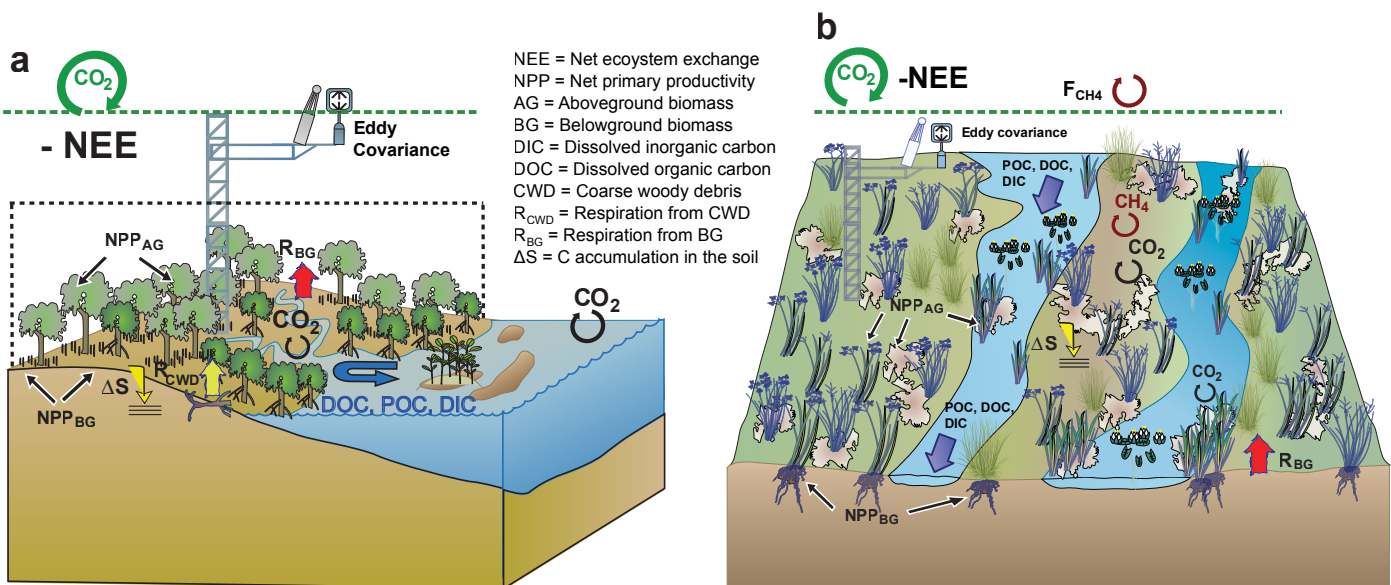


Figure 2. Balancing coastal Everglades ecosystem C budgets. Schematics showing  $\text{CO}_2$  uptake, transport, and storage (S) components and land-water-atmospheric fluxes that will be used to balance the FCE LTER site C budget. Existing eddy covariance towers in the Shark River Slough (SRS) riverine mangroves (A) and SRS and Taylor Slough/Panhandle (TS/Ph) marsh (B) will be supplemented by new towers in the TS/Ph dwarf mangroves and Florida Bay. Aboveground and belowground net primary production and ecosystem R are measured at all sites, and C flux research is being expanded to quantify lateral transport of DIC, DOC, and POC in Taylor and Shark Rivers. Storage is estimated using sediment elevation tables and dated sediment cores. By quantifying these parameters across a spatio-temporally variable template of fresh and marine water delivery, we can create dynamic C budgets to determine how changes in water supply influence the balance of C uptake, storage, and transport. Figure created by J. Barr

1985; Romigh et al., 2006, as summarized in Barr et al., 2010) but does not consider aquatic export, sediment-water or groundwater-surface water exchange, or C transformations. These large uncertainties identify the need for estimating  $F_{TOT}$  via measurements of dissolved organic, inorganic, and particulate organic C through tidal creeks and larger rivers, as long as drainage for these creeks and C flux approximations are further verified with process-based studies. On an annual basis, the NECB validation provides important insights into aquatic C export, although major sources of uncertainty remain.

For Everglades freshwater sawgrass marsh sites, NEE estimates show that Shark River Slough is a small source of  $CO_2$ , and Taylor Slough is a small sink (Table 1). Along the Shark River Slough transect, sawgrass aboveground net primary production is about 400–700 g dw  $m^{-2} yr^{-1}$  and is higher than that in the Taylor Slough transect, which is 250–400 g dw  $m^{-2} yr^{-1}$ . In Taylor Slough, plants are smaller, but culm (stem) density is higher. Also, because Taylor Slough freshwater marsh sites dry more frequently and for a longer time, these sites are dominated by marl, a calcitic mineral soil, rather than peat soil. Annual belowground sawgrass productivity averaged 450 g dw  $m^{-2} yr^{-1}$ , with approximately two-thirds occurring in the top 10 cm of soil (Juszli, 2006). These root-production estimates are generally consistent with rates measured in other freshwater marshes (Birch and Cooley, 1982; Symbula and Day, 1988) but lower than those reported for salt marshes (Valiela et al., 1976; Schubauer and Hopkinson, 1984). Given the higher sawgrass aboveground primary production,  $\Delta AGB$  was higher in Shark River Slough than in Taylor Slough and  $\Delta BGB$

values were approximately equivalent (Table 1; Juszli, 2006). Soil C accumulation was estimated as 90 g C  $m^{-2} yr^{-1}$  (Saunders et al., 2007). The low values for NEE relative to aboveground and belowground net primary production, and equivalent rate of soil C accumulation, suggest that exported C mass and C accumulated in living biomass are equivalent (Table 1). This is in good agreement with rates of leaf turnover for sawgrass plants estimated to occur three to four times within a year (Childers et al., 2006). Furthermore, these low NEE values also suggest that water-table variation has a significant effect (Schedlbauer et al., 2010) and that periphyton may contribute to  $CO_2$  uptake. Field tests, however, suggest that periphyton does not contribute significantly to NEE (Schedlbauer et al., 2012), although this result assumes that aquatic C import is negligible, and it neglects the role of flocculent material production and deposition, also reported to be important in Everglades freshwater marsh C cycling (Troxler and Richards, 2009, and references therein).

Periphyton biomass is high compared to algal biomass in other wetland ecosystems, averaging over 100 g C  $m^{-2}$  and attaining up to 10,000 g AFDM  $m^{-2}$  (AFDM = ash-free dry mass) at some localities (Ewe et al., 2006; Iwaniec et al., 2006; Gaiser, 2009; Gaiser et al., 2011)

vs. 10–50 g  $m^{-2} yr^{-1}$  from other wetland types (Vymazal and Richardson, 1995). Determining the influence of periphyton on NEE is complicated by difficult-to-capture metabolic pulses that occur during drying or wetting events (Thomas et al., 2006) and by exchanges of organic C among the mat, sediment, and water column that are not measured in standard approaches. Schedlbauer et al. (2012) attempted to evaluate the influence of periphyton on net ecosystem  $CO_2$  exchange at the short-hydroperiod Taylor Slough marsh and found that periphyton did not significantly contribute to  $CO_2$  fluxes. While it is clear that periphyton can regulate water-column oxygen concentrations (McCormick et al., 1997; McCormick and Laing, 2003) and aquatic production and respiration (Hagerthey et al., 2011), these whole-system studies suggest that heterotrophic processes in the mat and of mat-produced C in the floc and water column may, in fact, balance gross primary production (Schedlbauer et al., 2012). This is supported by the C balance estimates we determined for the freshwater sawgrass marsh in Taylor Slough. However, periphyton also likely plays a major role in the cycling of inorganic C between dissolved and particulate forms.

Carbon from primary production of seagrasses, estimated for Florida Bay at

Table 1. Values for annual net ecosystem C balance (NECB), net ecosystem exchange (NEE), and derived aquatic carbon (Aq C) export.

Ecosystem	Site	g C $m^{-2} yr^{-1}$		Soil	AG	BG	Aq C Export
		NECB	-NEE				
Marsh	SRS	621 ± 59	-45 ± 16	90	291 ± 35	240 ± 48	666 ± 61
	TS	457 ± 61	50 ± 15	90	122 ± 12	245 ± 60	407 ± 63
Mangrove <sup>ψ</sup>	SRS	1,038 ± 88	1,170 ± 127	194	638 ± 36	206 ± 80	-131 ± 155
Seagrass	FL Bay				75 ± 40		

<sup>ψ</sup> Mangrove root production estimates for size classes < 2 mm to 20 mm in diameter (to a depth of 90 cm). AG = aboveground. BG = belowground. SRS = Shark River Slough. TS = Taylor Slough.

a rate of 31–182 g C<sub>org</sub> m<sup>-2</sup> yr<sup>-1</sup> (Zieman et al., 1989) with ~ 37% of net aboveground primary production, is channelled into belowground biomass (Herbert and Fourqurean, 2009) and, eventually, the sediment (Orem et al., 1999). New results suggest that C storage in seagrass sediment rivals that of tropical forests, and that Florida Bay sediment is C-rich compared to seagrass systems worldwide (Fourqurean et al., 2012a,b). This high capacity for storing C results from high primary production of seagrass meadows, their capacity to filter out particles from the water column, and their subsequent storage in soils (Fourqurean et al., 2012b). Low decomposition rates in the oxygen-poor seagrass soils allow accumulation over millennia and yield high stability of seagrass C<sub>org</sub> storage.

### Aquatic C Export

Although aquatic C flux can only be derived by combining estimates for NEE and NECB, FCE LTER research

conducted in the Everglades illustrates some important patterns, linkages, and insights into important C processes and transformations, and it provides preliminary estimates of C flux. Figure 3 shows the main biogeochemical processes involved in organic matter (OM) source, transport, and fate for the freshwater marsh, the estuarine ecotone, and the marine end-member for the Everglades. Differences in OM between Shark River and Taylor Sloughs are derived from biomass and thus are related to vegetation cover and primary productivity and, consequently, to aquatic C exchange. In Everglades marshes, the source materials for particulate OM production, deposition, and accumulation are mainly derived from periphyton and freshwater macrophytes. Although oligotrophy limits the presence of free-floating plankton as a potential source for particulate organic C, this C pool is mainly represented in the form of flocculent material and is spatially controlled by

local vegetation patterns and periphyton production (Neto et al., 2006; Pisani et al., in press). In the estuarine ecotone, mangrove-derived OM likely dominates the particulate organic C source, either in the form of detritus or of resuspended sediment mobilized through tidal action (Mead, 2003; Ding He, Florida International University, *pers. comm.*, 2013). Lastly, particulate organic C in the marine end-members is, to a large extent, a mixture of terrestrial particulate organic C export and marine-derived OM sources such as phytoplankton and seagrass detritus (Jaffé et al., 2001; Hernandez et al., 2001; Xu et al., 2006, 2007; Xu and Jaffé, 2007).

These studies also indicate that canal inputs (Lu et al., 2003; Yamashita et al., 2010), leachates of soils, and plant exudates (Lu et al., 2003; Scully et al., 2004; Davis et al., 2006; Maie et al., 2006; Yamashita et al., 2010) are quantitatively important inputs of dissolved organic C to the estuarine ecotone (Cawley

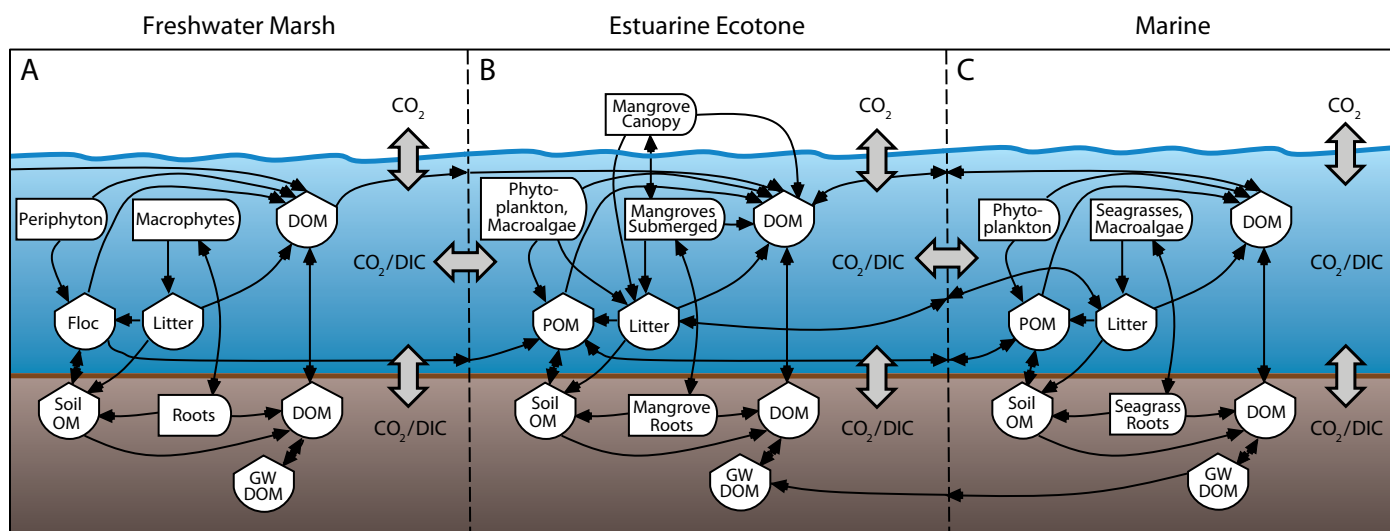


Figure 3. Conceptual model of organic matter (OM) compartments and fluxes, based on research conducted by the FCE. The lower diagram refers to drivers of ecosystem structure and exchange. Figure 2 summarizes the flows connecting environments and the drivers affecting the exchange of OM (timing, quality, quantity). Both particulate organic matter (POM, as floc) and dissolved organic matter (DOM, derived from freshwater plant production) are delivered to the estuarine ecotone from upstream. Seagrass-derived litter, POM, and DOM are delivered to the ecotone from downstream. Hydrology and biogeochemical processing control the degradation and residence times of these C pools, and are not fully understood. Thus, whether these allochthonous sources of OM help to fuel the estuarine productivity peak remains to be determined. Although we have made great strides in understanding OM dynamics in the FCE, there are still many OM pools and pathways to investigate in the context of a dynamic south Florida hydroscape. Figure created by R. Chambers, R. Jaffe, and V. Rivera-Monroy

et al., in press). In addition, there are sources from the fringe mangrove forests (Jaffé et al., 2004; Cawley et al., in press) as well as potential exchange with groundwater (Chen et al., 2010, 2013). Mangroves were found to contribute up to 30% of the dissolved organic carbon that is transported by the Shark River.

## UNCERTAINTIES AND AREAS FOR FURTHER WORK


Key areas of uncertainty that will be better constrained by resolving input parameters and synthesizing process-based studies are estimates of net soil C change, aquatic C flux, and, specifically, the contribution of water table variation and periphyton to NEE. Soil C process-based studies can be used to constrain these values of net soil C change and, in some cases, to validate these estimates (e.g., Chambers, 2012). While the approaches we employed were useful in constraining aquatic flux estimates, further uncertainties remain with regard to C form and porewater exchange of dissolved inorganic C in mangroves, recently illustrated to exceed dissolved organic C flux (Alongi et al., 2012). Comparing these fluxes and stock changes, which can represent different temporal scales, is also a challenge that requires a unified approach beyond what is considered here (Chapin et al., 2006), especially for cross-system studies. Integrating process-based studies with estimates of NECB and aquatic flux estimates will further improve this work (e.g., Cawley et al., in press). Another source of uncertainty that would be common in estimates of NEE in wetlands is that imposed by water-table variation. A proportion of the ecosystem-atmosphere CO<sub>2</sub> exchange that would occur in wetlands with low or no water-table inundation would be reduced

significantly in wetlands where plants were inundated and that fraction would likely be exported through lateral flux.

Synthesis of NEE data sets of longer time series will also improve integration of NEE and NECB. Although seagrass metabolism may be the easiest to infer from whole-system measurements, more work is needed to understand how C cycling within and among ecosystem components contributes to estimates of NECB in these ecosystems. In Everglades freshwater marshes, methane could have a substantial impact on ecosystem C balance. While ecosystem-scale measures of CH<sub>4</sub> concentration are not yet available, data from small-scale experiments could be considered in order to reduce uncertainty around its potential contribution. Other areas of anticipated work include development of modeled scenarios of regional climate and hydrologic models (e.g., Fitz and Sklar, 1999) and continued mechanistic advances in microbial pathways and rates of change in fluxes (Chambers, 2012). Moreover, while the approaches we used for these initial estimates were informative, a resolved approach for addressing areas of uncertainty is critically needed for coastal wetland ecosystems. The intensive C budget studies summarized here and the approach of the Chapin et al. (2006) framework in Equations 1 and 2 can be combined to provide a strong basis for coastal LTER inter-site C research. Synthesis efforts such as these that draw on long-term, integrated data sets for multiple sites broaden the ecological, geographical, and social contexts necessary to understand drivers and effects of their interactions, reduce uncertainties, and predict change. These efforts can increase understanding of coastal ecosystem drivers and the patterns and processes

with which critical global policy issues, including land use change in the coastal zone, can be addressed.

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## REFERENCES

- Alongi, D.L., N.A. de Carvalho, A.L. Amaral, A. Da Costa, L. Trott, and F. Tierni. 2012. Uncoupled surface and below-ground soil respiration in mangroves: Implications for estimates of dissolved inorganic carbon export. *Biogeochemistry* 109:151–162, <http://dx.doi.org/10.1007/s10533-011-9616-9>.
- Barr, J.G., V.C. Engel, J.D. Fuentes, J.C. Zieman, T.L. O'Halloran, T.J. Smith III, and G.H. Anderson. 2010. Controls on mangrove forest-atmosphere carbon dioxide exchanges in western Everglades National Park. *Journal of Geophysical Research* 115, G02020, <http://dx.doi.org/10.1029/2009JG001186>.
- Barr, J.G., V. Engel, T.J. Smith, and J.D. Fuentes. 2012. Hurricane disturbance and recovery of energy balance, CO<sub>2</sub> fluxes and canopy structure in a mangrove forest of the Florida Everglades. *Agricultural and Forest Meteorology* 153:54–66, <http://dx.doi.org/10.1016/j.agrformet.2011.07.022>.

- Birch, J.B., and J.L. Cooley. 1982. Production and standing crop patterns of giant cutgrass (*Zizaniopsis miliacea*) in a freshwater tidal marsh. *Oecologia* 52:230–235, <http://dx.doi.org/10.1007/BF00363842>.
- Bouillon, S., A. Borges, E. Castañeda-Moya, K. Diele, T. Dittmar, N.C. Duke, E. Kristensen, S.Y. Lee, C. Marchand, J.J. Middelburg, and others. 2008. Mangrove production and carbon sinks: A revision of global budget estimates. *Global Biogeochemical Cycles* 22, GB2013, <http://dx.doi.org/10.1029/2007GB003052>.
- Bouillon, S. 2011. Carbon cycle: Storage beneath mangroves. *Nature Geoscience* 4:282–283, <http://dx.doi.org/10.1038/ngeo1130>.
- Breithaupt, J.L., J.M. Smoak, T.J. Smith, C.J. Sanders, and A. Hoare. 2012. Organic carbon burial rates in mangrove sediments: Strengthening the global budget. *Global Biogeochemical Cycles* 26, GB3011, <http://dx.doi.org/10.1029/2012GB004375>.
- Castañeda-Moya, E., R.R. Twilley, V.H. Rivera-Monroy, B. Marx, C. Coronado-Molina, and S.E. Ewe. 2011. Patterns of root dynamics in mangrove forests along environmental gradients in the Florida Coastal Everglades, USA. *Ecosystems* 14:1,178–1,195, <http://dx.doi.org/10.1007/s10021-011-9473-3>.
- Castañeda-Moya, E., R.R. Twilley, and V.H. Rivera-Monroy. In Press. Allocation of biomass and net primary productivity of mangrove forests along environmental gradients in the Florida Coastal Everglades, USA. *Forest Ecology and Management*.
- Cawley, K., Y. Yamashita, N. Maie, and R. Jaffé. In press. Using optical properties to quantify fringe mangrove inputs to the dissolved organic matter (DOM) pool in a subtropical estuary. *Estuaries and Coasts*.
- Chambers, L.G. 2012. Biogeochemical effects of simulated sea level rise on coastal wetland soil carbon. PhD dissertation, University of Florida, Gainesville.
- Chapin, F.S., G.M. Woodwell, J.T. Randerson, E.B. Rastetter, G.M. Lovett, D.D. Baldocchi, D.A. Clark, M.E. Harmon, D.S. Schimel, R. Valentini, and others. 2006. Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems* 9:1,041–1,050, <http://dx.doi.org/10.1007/s10021-005-0105-7>.
- Chen, M., N. Maie, K. Parish, and R. Jaffé. 2013. Spatial and temporal variability of dissolved organic matter in an oligotrophic subtropical coastal wetland. *Biogeochemistry*, <http://dx.doi.org/10.1007/s10533-013-9826-4>.
- Chen, M., R.M. Price, Y. Yamashita, and R. Jaffé. 2010. Comparative study of dissolved organic matter from groundwater and surface water in the Florida coastal Everglades using multi-dimensional spectrofluorometry combined with multivariate statistics. *Applied Geochemistry* 25:872–880, <http://dx.doi.org/10.1016/j.apgeochem.2010.03.005>.
- Chen, R., and R.R. Twilley. 1999. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida. *Estuaries* 22:955–970, <http://dx.doi.org/10.2307/1353075>.
- Childers, D.L., D. Iwaniec, D. Rondeau, G.A. Rubio, E. Verdon, and C.J. Madden. 2006. Responses of sawgrass and spikerush to variation in hydrologic drivers and salinity in southern Everglades marshes. *Hydrobiologia* 569:273–292, <http://dx.doi.org/10.1007/s10750-006-0137-9>.
- Davis, S.E., D.L. Childers, and G.B. Noe. 2006. The contribution of leaching to the rapid release of nutrients and carbon in the early decay of wetland vegetation. *Hydrobiologia* 569:87–97, <http://dx.doi.org/10.1007/s10750-006-0124-1>.
- DeLaune, R.D., and J.R. White. 2012. Will coastal wetlands continue to sequester carbon in response to an increase in global sea level? A case study of the rapidly subsiding Mississippi river deltaic plain. *Climatic Change* 110:297–314, <http://dx.doi.org/10.1007/s10584-011-0089-6>.
- Donar, C., K. Condon, M. Gantar, and E. Gaiser. 2004. A new technique for examining the physical structure of Everglades floating periphyton mat. *Nova Hedwigia* 78:107–119, <http://dx.doi.org/10.1127/0029-5035/2004/0078-0107>.
- Donato, D.C., J.B. Kauffman, D. Murdiyarso, S. Kurnianto, M. Stidham, and M. Kanninen. 2011. Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience* 4:293–297, <http://dx.doi.org/10.1038/ngeo1123>.
- Engel, V., J.G. Barr, J.D. Fuentes, V. Rivera-Monroy, E. Castañeda-Moya, T. Troxler, D.T. Ho, S. Ferron-Smith, J. Smoak, T.J. Smith III, and R.R. Twilley. 2011. Paper presented at Ameriflux/NACP meeting, New Orleans, LA, 2011.
- Ewe, S.M.L., E.E. Gaiser, D.L. Childers, V.H. Rivera-Monroy, D.L. Iwaniec, J. Fourqurean, and R.R. Twilley. 2006. Spatial and temporal patterns of aboveground net primary productivity (ANPP) in the Florida Coastal Everglades LTER (2001–2004). *Hydrobiologia* 569:459–474, <http://dx.doi.org/10.1007/s10750-006-0149-5>.
- Fitz, H.C., and F.H. Sklar. 1999. Ecosystem analysis of phosphorus impacts and altered hydrology in the Everglades: A landscape modeling approach. Pp. 585–620 in *Phosphorus Biogeochemistry in Subtropical Ecosystems*. K.R. Reddy, G.A. O'Connor, and C.L. Schelske, eds, Lewis Publishers, Boca Raton, FL.
- Fourqurean, J.W., G.A. Kendrick, L.S. Collins, and M.A. Vanderklift. 2012a. Carbon and nutrient storage in subtropical seagrass meadows: Examples from Florida Bay and Shark Bay. *Marine and Freshwater Research* 63:967–983, <http://dx.doi.org/10.1071/MF12101>.
- Fourqurean, J.W., C.M. Duarte, H. Kennedy, N. Marbà, M. Holmer, M.A. Mateo, E.T. Apostolaki, G.A. Kendrick, D. Krause-Jensen, K.J. McGlathery, and O. Serrano. 2012b. Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience* 5:505–509, <http://dx.doi.org/10.1038/NCEO1477>.
- Gaiser, E.E. 2009. Periphyton as an indicator of restoration in the Everglades. *Ecological Indicators* 9(6):S37–S45, <http://dx.doi.org/10.1016/j.ecolind.2008.08.004>.
- Gaiser, E.E., P. McCormick, and S.E. Hagerthey. 2011. Landscape patterns of periphyton in the Florida Everglades. *Critical Reviews in Environmental Science and Technology* 41(S1):92–120, <http://dx.doi.org/10.1080/10643389.2010.531192>.
- Gaiser, E., J. Trexler, and P. Wetzel. 2012. The Everglades. Pp. 231–252 in *Wetland Habitats of North America: Ecology and Conservation Concerns*. D. Batzer and A. Baldwin, eds, University of California Press, Berkeley.
- Hagerthey, S.E., B.J. Bellinger, K. Wheeler, M. Gantar, and E. Gaiser. 2011. Everglades periphyton: A biogeochemical perspective. *Critical Reviews in Environmental Science and Technology* 41(S1):309–343, <http://dx.doi.org/10.1080/10643389.2010.531218>.
- 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, <http://dx.doi.org/10.1007/s12237-008-9116-x>.
- Hernandez, M.E., R. Mead, M.C. Peralba, and R. Jaffé. 2001. Origin and transport of *n*-alkane-2-ones in a sub-tropical estuary: Potential biomarkers for seagrass-derived organic matter. *Organic Geochemistry* 32:21–32, [http://dx.doi.org/10.1016/S0146-6380\(00\)00157-1](http://dx.doi.org/10.1016/S0146-6380(00)00157-1).
- IPCC, 2007. *Climate Change 2007: The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller, eds, Cambridge University Press, Cambridge, UK, and New York, NY, USA.
- Iwaniec, D., D.L. Childers, D. Rondeau, C.J. Madden, and C.J. Saunders. 2006. Effects of hydrologic and water quality drivers on periphyton dynamics in the southern Everglades. *Hydrobiologia* 569(1):223–235, <http://dx.doi.org/10.1007/s10750-006-0134-z>.
- Jaffé, R., M.E. Hernandez, R. Mead, M.C. Peralba, and O.A. DiGuida. 2001. Origin and transport of sedimentary organic matter in two subtropical estuaries: A comparative, biomarker-based study. *Organic Geochemistry* 32:507–526, [http://dx.doi.org/10.1016/S0146-6380\(00\)00192-3](http://dx.doi.org/10.1016/S0146-6380(00)00192-3).
- Jaffé, R., J.N. Boyer, X. Lu, N. Maie, C. Yang, N. Scully, and S. Mock. 2004. Source characterization of dissolved organic matter in a mangrove-dominated estuary by fluorescence analysis. *Marine Chemistry* 84:195–210, <http://dx.doi.org/10.1016/j.marchem.2003.08.001>.
- Jimenez, K.L., G. Starr, C.L. Staudhammer, J.L. Schedlbauer, H.W. Loescher, S.L. Malone, and S.F. Oberbauer. 2012. Carbon dioxide exchange rates from short- and long-hydroperiod Everglades freshwater marsh. *Journal of Geophysical Research* 117, G04009, <http://dx.doi.org/10.1029/2012JG002117>.
- Juszli, G.M. 2006. Patterns in belowground primary productivity and belowground biomass in marshes of the Everglades' oligohaline ecotone. Master's thesis, Florida International University, Miami.
- Krauss, K.W., T.W. Doyle, R.R. Twilley, T.J. Smith III, K.R.T. Whelan, and J.K. Sullivan. 2005. Woody debris in mangrove forests of south Florida. *Biotropica* 37:9–15, <http://dx.doi.org/10.1111/j.1744-7429.2005.03058.x>.

- Lovett, G., J. Cole, and M. Pace. 2006. Is net ecosystem production equal to ecosystem carbon accumulation? *Ecosystems* 9:152–155, <http://dx.doi.org/10.1007/s10021-005-0036-3>.
- Lu, X.Q., N. Maie, J.V. Hanna, D. Childers, and R. Jaffé. 2003. Molecular characterization of dissolved organic matter in freshwater wetlands of the Florida Everglades. *Water Research* 37:2,599–2,606, [http://dx.doi.org/10.1016/S0043-1354\(03\)00081-2](http://dx.doi.org/10.1016/S0043-1354(03)00081-2).
- Maie, N., R. Jaffé, T. Miyoshi, and D.L. Childers. 2006. Quantitative and qualitative aspects of dissolved organic carbon leached from plants in an oligotrophic wetland. *Biogeochemistry* 78:285–314, <http://dx.doi.org/10.1007/s10533-005-4329-6>.
- Malone, S., G. Starr, C.L. Staudhammer, and M.G. Ryan. 2013. Effects of simulated drought on the greenhouse carbon balance of Everglades short-hydroperiod marsh ecosystems. *Global Change Biology* 19:2,511–2,523, <http://dx.doi.org/10.1111/gcb.12211>.
- McCormick, P.V., M.J. Chimney, and D.R. Swift. 1997. Diel oxygen profiles and water column community metabolism in the Florida Everglades, USA. *Archiv für Hydrobiologie* 40:117–129.
- McCormick, P.V., and J.A. Laing. 2003. Effects of increased phosphorus loading on dissolved oxygen in a subtropical wetland, the Florida Everglades. *Wetlands Ecology and Management* 11:199–216, <http://dx.doi.org/10.1023/A:1024259912402>.
- Mcloed, E., G.L. Chmura, S. Bouillon, R. Salm, M. Björk, C.M. Duarte, C.E. Lovelock, W.H. Schlesinger, and B.R. Silliman. 2011. A blueprint for blue carbon: Toward an improved understanding of vegetated coastal habitats in sequestering CO<sub>2</sub>. *Frontiers in Ecology and the Environment* 9:552–560, <http://dx.doi.org/10.1890/110004>.
- Mead, R.N. 2003. Organic matter dynamics in the Florida coastal Everglades: A molecular marker and isotopic approach. PhD dissertation, Florida International University.
- Myers, R., and J. Ewell, eds. 1990. *Ecosystems of Florida*. University of Central Florida Press, Orlando.
- Neto, R., R.N. Mead, W. Louda, and R. Jaffé. 2006. Organic biogeochemistry of detrital flocculent material (floc) in a subtropical, coastal wetland. *Biogeochemistry* 77:283–304, <http://dx.doi.org/10.1007/s10533-005-5042-1>.
- Orem, W.H., C.W. Holmes, C. Kendall, H.E. Lerch, A.L. Bates, S.R. Silva, A. Boylan, M. Corum, M. Marot, and C. Hedgeman. 1999. Geochemistry of Florida Bay sediments: Nutrient history at five sites in eastern and central Florida Bay. *Journal of Coastal Research* 15:1,055–1,071.
- Pisani, O., W. Louda, and R. Jaffé. In press. Biomarker assessment of spatial and temporal changes in the composition of flocculent material (floc) in the subtropical wetland of the Florida Coastal Everglades. *Environmental Chemistry*.
- Rivera-Monroy, V.H., E. Castaneda-Moya, J.G. Barr, V. Engel, J.D. Fuentes, T.G. Troxler, R. Twilley, S. Bouillon, T.J. Smith, and T.L. O'Halloran. In press. Current methods to evaluate net primary production and carbon budgets in mangrove forests. In *Methods in Biogeochemistry of Wetlands*. R.D. Delaune, K.R. Reddy, P. Megonigal, and C. Richardson, eds, Soil Science Society of America Book Series.
- Rivera-Monroy, V.H., R.R. Twilley, S.E. Davis, D.L. Childers, M. Simard, R. Chambers, R. Jaffé, J.N. Boyer, D.T. Rudnick, K. Zhang, and others. 2011. The role of the Everglades mangrove ecotone region (EMER) in regulating nutrient cycling and wetland productivity in South Florida. *Critical Reviews in Environmental Science and Technology* 41:633–669, <http://dx.doi.org/10.1080/10643389.2010.530907>.
- Robertson, A.I. and P.A. Daniel. 1989. The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. *Oecologia* 78:191–198, <http://dx.doi.org/10.1007/BF00377155>.
- Romigh, M.M., S.E. Davis, V.H. Rivera-Monroy, and R.R. Twilley. 2006. Flux of organic carbon in a riverine mangrove wetland in the Florida Coastal Everglades. *Hydrobiologia* 569:505–516, <http://dx.doi.org/10.1007/s10750-006-0152-x>.
- Saunders, C.J., D.L. Childers, W.T. Anderson, J. Lynch, and R. Jaffe. 2007. Understanding *Cladium jamaicense* dynamics over the last century in ENP using simulation modeling and paleoecological data: 24 month Report. Everglades National Park, National Park Service (#EVER-00278).
- Schedlbauer, J., S. Oberbauer, G. Starr, and K.L. Jimenez. 2010. Seasonal differences in the CO<sub>2</sub> exchange of a short-hydroperiod Florida Everglades marsh. *Agricultural and Forest Meteorology* 150:994–1,006, <http://dx.doi.org/10.1016/j.agrformet.2010.03.005>.
- Schedlbauer, J., J. Munyon, S. Oberbauer, E. Gaiser, and G. Starr. 2012. Controls on ecosystem carbon dioxide exchange in short- and long-hydroperiod Florida Everglades freshwater marshes. *Wetlands* 32:801–812, <http://dx.doi.org/10.1007/s13157-012-0311-y>.
- Schubauer, J.P., and C.S. Hopkinson. 1984. Above- and belowground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. *Limnology and Oceanography* 29:1,052–1,065.
- Scully, N.M., N. Maie, S. Dailey, J. Boyer, R.D. Jones, and R. Jaffé. 2004. Photochemical and microbial transformation of plant derived dissolved organic matter in the Florida Everglades. *Limnology and Oceanography* 49(5):1,667–1,678.
- Smoak, J.M., J.L. Breithaupt, T.J. Smith, and C.J. Sanders. 2013. Sediment accretion and organic carbon burial relative to sea-level rise and storm events in two mangrove forests in Everglades National Park. *Catena* 104:58–66, <http://dx.doi.org/10.1016/j.catena.2012.10.009>.
- Symbula, M., and F.P. Day. 1988. Evaluations of two methods for estimating belowground production in a freshwater swamp forest. *American Midland Naturalist* 120:405–415.
- Thomas, S., E.E. Gaiser, M. Gantar, and L.J. Scinto. 2006. Quantifying the responses of calcareous periphyton crusts to rehydration: A microcosm study (Florida Everglades). *Aquatic Botany* 84:317–323, <http://dx.doi.org/10.1016/j.aquabot.2005.12.003>.
- Troxler, T.G., and J.H. Richards. 2009.  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , carbon, nitrogen and phosphorus as indicators of plant ecophysiology and organic matter pathways in Everglades deep slough, Florida, USA. *Aquatic Botany* 91:157–165, <http://dx.doi.org/10.1016/j.aquabot.2009.04.003>.
- Troxler, T.G., D.L. Childers, and C.J. Madden. 2013. Drivers of decadal-scale change in southern Everglades wetland macrophyte communities of the coastal ecotone. *Wetlands*, <http://dx.doi.org/10.1007/s13157-013-0446-5>.
- Twilley, R.R. 1985. The exchange of organic carbon in basin mangrove forests in a Southwest Florida estuary. *Estuarine, Coastal and Shelf Science* 20:543–557, [http://dx.doi.org/10.1016/0272-7714\(85\)90106-4](http://dx.doi.org/10.1016/0272-7714(85)90106-4).
- Twilley, R.R., R.H. Chen, and T. Hargis. 1992. Carbon sinks in mangroves and their implications to carbon budget of tropical ecosystems. *Water, Air, and Soil Pollution* 64:265–288, <http://dx.doi.org/10.1007/BF00477106>.
- Xu, Y., C. Holmes, and R. Jaffé. 2007. Paleo-environmental assessment of recent environmental changes in Florida Bay, USA: A biomarker based study. *Estuarine, Coastal and Shelf Science* 73:201–210, <http://dx.doi.org/10.1016/j.ecss.2007.01.002>.
- Xu, Y., and R. Jaffé. 2007. Lipid biomarkers in suspended particulates from a subtropical estuary: Assessment of seasonal changes in sources and transport of organic matter. *Marine Environmental Research* 64:666–678, <http://dx.doi.org/10.1016/j.marenvres.2007.07.004>.
- Xu, Y., R.N. Mead, and R. Jaffé. 2006. A molecular marker-based assessment of sedimentary organic matter sources and distributions in Florida Bay. *Hydrobiologia* 569:179–192, <http://dx.doi.org/10.1007/s10750-006-0131-2>.
- Valiela, I., J.M. Teal, and N. Persson. 1976. Production dynamics of experimentally enriched salt marsh vegetation: Belowground biomass. *Limnology and Oceanography* 21:245–252.
- Vymazal, J., and C.J. Richardson. 1995. Species composition, biomass, and nutrient content of periphyton in the Florida Everglades. *Journal of Phycology* 31:343–354, <http://dx.doi.org/10.1111/j.0022-3646.1995.00343.x>.
- Yamashita, Y., L. Scinto, N. Maie, and R. Jaffé. 2010. Dissolved organic matter characteristics across a subtropical wetland's landscape: Application of optical properties in the assessment of environmental dynamics. *Ecosystems* 13:1,006–1,019, <http://dx.doi.org/10.1007/s10021-010-9370-1>.
- Zieman, J.C., J.W. Fourqurean, and R.L. Iverson. 1989. Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. *Bulletin of Marine Science* 44:292–311.