

Spatial and temporal patterns of aboveground net primary productivity (ANPP) along two freshwater-estuarine transects in the Florida Coastal Everglades

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Abstract

We present here a 4-year dataset (2001–2004) on the spatial and temporal patterns of aboveground net primary production (ANPP) by dominant primary producers (sawgrass, periphyton, mangroves, and seagrasses) along two transects in the oligotrophic Florida Everglades coastal landscape. The 17 sites of the Florida Coastal Everglades Long Term Ecological Research (FCE LTER) program are located along fresh-estuarine gradients in Shark River Slough (SRS) and Taylor River/C-111/Florida Bay (TS/Ph) basins that drain the western and southern Everglades, respectively. Within the SRS basin, sawgrass and periphyton ANPP did not differ significantly among sites but mangrove ANPP was highest at the site nearest the Gulf of Mexico. In the southern Everglades transect, there was a productivity peak in sawgrass and periphyton at the upper estuarine ecotone within Taylor River but no trends were observed in the C-111 Basin for either primary producer. Over the 4 years, average sawgrass ANPP in both basins ranged from 255 to 606 g m⁻² year⁻¹. Average periphyton productivity at SRS and TS/Ph was 17–68 g C m⁻² year⁻¹ and 342–10371 g C m⁻² year⁻¹, respectively. Mangrove productivity ranged from 340 g m⁻² year⁻¹ at Taylor River to 2208 g m⁻² year⁻¹ at the lower estuarine Shark River site. Average *Thalassia testudinum* productivity ranged from 91 to 396 g m⁻² year⁻¹ and was 4-fold greater at the site nearest the Gulf of Mexico than in eastern Florida Bay. There were no differences in periphyton productivity at Florida Bay. Interannual comparisons revealed no significant differences within each primary producer at either SRS or TS/Ph with the exception of sawgrass at SRS and the C-111 Basin. Future research will address difficulties in assessing and comparing ANPP of different primary producers along gradients as well as the significance of belowground production to the total productivity of this ecosystem.

Introduction

One excellent assessment of ecosystem function is via aboveground net primary productivity (ANPP). Aboveground NPP, the measure of net

rate of photosynthetic carbon sequestration by plants into aboveground components, is often used to provide insight into key ecological processes (e.g. Clark et al., 2001). For example, ANPP can be compared across landscapes to

identify the primary ecosystem drivers and delineate the sources and relative importance of these drivers (Graumlich et al., 1989; Raich et al., 1997; Hansen et al., 2000; Schuur & Matson, 2001; Childers et al., 2006a). In terrestrial ecosystems, drivers of spatial and temporal landscape productivity patterns include factors such as precipitation, temperature, humidity, soil moisture, and topography (Sala et al., 1988; Chen & Twilley, 1999; Hansen et al., 2000). In coastal ecosystems such as the Everglades, overall productivity of key producers is influenced by hydrology, nutrient supply and availability, as well as salinity (Fourqurean et al., 1992; Fourqurean & Zieman, 2002; Childers et al., 2006a).

The Everglades is an oligotrophic (Noe et al., 2001) phosphorus (P) limited (Koch & Reddy, 1992; Davis, 1994) wetland system largely driven by rainfall-derived seasonal sheetflow. This system encompasses a broad range of habitats, from sawgrass (*Cladium jamaicense*) dominated marshes in the freshwater wetlands to mangrove forests in estuarine ecotones, and shallow subtidal seagrass beds in Florida Bay. In most subtropical estuaries worldwide, productivity tends to be nitrogen (N) limited (Vitousek & Howarth, 1991; Chen et al., 2000), with the limiting nutrient being supplied by the upstream watershed. In estuaries of the Everglades however, P is primarily supplied by the Gulf of Mexico and not the oligotrophic upstream areas (Childers et al., 2006b). The low levels of P ($\approx 0.25 \mu\text{M l}^{-1}$) in most of the Everglades limit production and control the dominant biotic processes within this ecosystem (Fourqurean et al., 1992; Chen & Twilley, 1999; Noe et al., 2001; Fourqurean & Zieman, 2002; Gaiser et al., 2006). Over the last 100 years however, agriculturally derived P inputs have increased (Davis, 1994; McCormick et al., 1996; Smith & McCormick, 2001). Phosphorus enrichment has altered species composition, standing biomass and nutrient turnover within primary producer communities (Noe et al., 2001; Sklar et al., 2001), potentially affecting food web relationships within the ecosystem.

The Florida Coastal Everglades Long Term Ecological Research program (FCE LTER) presents a unique opportunity to determine trends in ANPP at a landscape scale. The purpose of the FCE LTER is to investigate how freshwater flows control estuarine dynamics over spatial (i.e.

landscape-level) and temporal (i.e. multi-decadal) scales, taking into account key drivers, such as hydrologic restoration and sea level rise (Childers et al., 2006a). We are interested in understanding how patterns and the magnitude of primary productivity are controlled by nutrient source and availability. We originally hypothesized a productivity peak in the low salinity ecotone region of the western Everglades but not in the southern Everglades. This productivity peak was hypothesized to be a result of the mixing of freshwater that was low in P and higher in N with marine water that was higher in P and lower in N (Rudnick et al., 1999; Childers et al., 2006b). Due to lower hydrologic exchanges between eastern Florida Bay and the Gulf of Mexico, marine waters intruding inland at the southeastern Everglades were not expected to be a significant contributor of P to the estuarine ecotone of this area (Nuttle et al., 2000; Childers et al., 2006b).

Gradients of hydrology, salinity and nutrient availability have been well documented in this region (Fourqurean et al., 1992; Boyer et al., 1999; Fourqurean & Robblee, 1999; Rudnick et al., 1999; Childers et al., 2006b). Relationships between ANPP and the quantity and timing of water inputs to the freshwater Everglades freshwater wetlands have been documented by previous researchers (e.g. Childers et al., 2006a; Iwaniec et al., 2006). The relationship between nutrient inputs and ANPP of key producers has also been examined in the freshwater Everglades (e.g. Craft et al., 1995; Chiang et al., 2000; Daoust and Childers, 2004, Iwaniec et al., 2006) and Florida Bay (e.g. Frankovich and Fourqurean, 1997; Armitage et al., 2005). Although ANPP has been examined in individual producers across sites within habitats, landscape scale spatial and temporal patterns of ANPP from the freshwater-marine gradient in the Everglades have never been contrasted.

In this paper we have synthesized ANPP of dominant ecosystem components from two freshwater-marine transects, collected by various researchers, from 2001 to 2004. These data do not attempt to represent total ecosystem productivity nor do they include primary production by all autotrophs. Instead, we present measures of ANPP by the dominant primary producers in each ecosystem type studied. Spatial and temporal

patterns in these ANPP data provide a broad-stroke picture of productivity patterns across the coastal Everglades landscape. Specifically, we compare and contrast the spatial and temporal patterns of ANPP of sawgrass, periphyton, mangroves, and seagrasses across the landscape. We also address limitations of the existing data and suggest refinements for future data collection.

Methods

Study sites

Seventeen study sites were established in two major drainage basins of Everglades National Park (ENP), Florida, USA (Fig. 1). Both transects extend from the freshwater marshes to the estuarine

and subtidal marine environments. The large Shark River Slough (SRS) basin discharge is channeled via Shark River (Fig. 1). The Taylor River/C-111/Florida Bay Basin (TS/Ph) drains southeast Everglades National Park and is a much smaller basin that drains into a considerably larger estuarine and subtidal area (Fig. 1). This system contributes to the upper Florida Bay ecosystem and has been the focus of much ecological research and restoration (e.g. Rudnick et al., 1999).

Six sites are located along the SRS transect. The three upstream sites (SRS 1–3) are representative of freshwater marshes with vegetation dominated by sawgrass (*Cladium jamaicense*) interspersed with wet prairie, open sloughs, and tree islands (Fig. 1, Table 1). Although other emergent species (e.g. *Eleocharis* spp., *Nelumbo nucifera*, *Panicum hemitomon*, etc.) and submergent aquatics (e.g. *Utricu-*

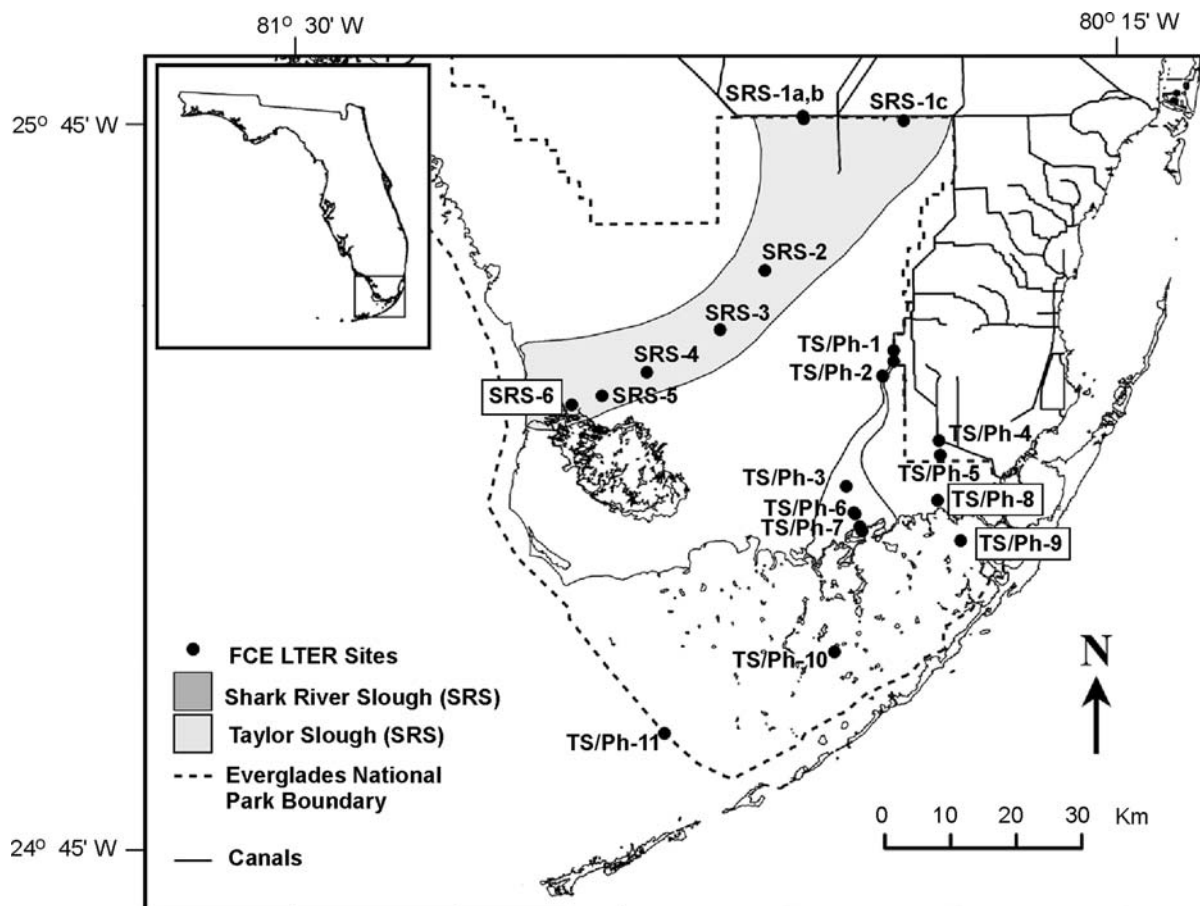


Figure 1. Map of Everglades National Park indicating the locations of the Shark River Slough (SRS) and Taylor River/Florida Bay (TS/Ph) study sites along the two transects (dotted red lines).

Table 1. Descriptions of the communities and physical attributes of each study site

Site	Productivity	Habitat	Hydrology	Soil	Dominant producers	Methods
SRS 1-3	Marsh and slough	Short and long hydroperiod marsh interspersed with permanently flooded slough.	Peat (0.3-1.5 m)	Sawgrass (<i>Cladium jamaicense</i> ; 0.5-1.5 m tall)	3 plots (1×1 m ²) sampled 6×/year non-destructively (Childers & Daoust, 1998). Biomass gain/site integrated annually to obtain ANPP (Childers et al., 2006a).	
SRS 4	Mangrove and <i>C. erectus</i>	Fresh (wet season) and brackish water (dry season) inputs.	Peat (1.5-2 m)	Mat periphyton (0.1-3 cm thick)	Biological oxygen demand (BOD) measured ($n=3$) when water depth >1 cm, and converted to carbon production (Iwaniec et al., 2006). After BOD sampling, all periphyton within a known area harvested for ash-free dry mass (AFDM). Daily productivity converted to ANPP by averaging and scaling up to annual basis.	
SRS 5	Mangrove	Seasonal fresh water and tidal oceanic inputs.	Peat, 2-3 m	<i>R. mangle</i> , <i>L. racemosa</i> , <i>C. erectus</i> (5-7 m tall)	Litter collected (10, 0.25 m ² traps) monthly from 2, 20×20 m plots. Tree height and dbh measured annually in plots. Annual ANPP = total litterfall + wood growth (Chen & Twilley (1999), Cintron & Novelli (1984), and Day et al. (1987)). Same as SRS 4.	
SRS 6	Mangrove	Seasonal fresh water and tidal oceanic inputs.	Peat, 4-6.5 m	Same as SRS 5 (15-20 m tall)	Same as SRS 4.	
TS/Ph 1-5	Marsh and slough	Same as SRS 1-3.	Peat-marl mix (≈1 m)	<i>C. jamaicense</i> Mat periphyton (0.1-3 cm thick)	Same as SRS 1-3. Same as SRS 1-3 except ANPP determined by integrating area below the curve for multiple measures.	

Ts/Ph 6	Estuarine ecotone (mangrove and marsh)	Seasonal freshwater and wind-driven estuarine inputs	Peat (<0.5 m) overlying marl	<i>Rhizophora mangle</i> (1–2 m) <i>C. jamaicensis</i>	Leaf turnover (losses and gains) counted twice year. Same as TS/Ph 1–5.
Ts/Ph 7	Estuarine ecotone	Seasonal fresh water and wind-driven estuarine inputs.	Peat (>1 m)	<i>R. mangle</i> (1–3 m tall)	Same as TS/Ph 6.
Ts/Ph 8	Mangrove forest	Seasonal fresh water and wind-driven estuarine inputs.	Marl (≈1 m)	<i>Laguncularia racemosa</i> , <i>C. erectus</i> (3–4 m tall)	Same as SRS 4 except litter traps are deployed only in 1 20×20 m plot.
Ts/Ph 9–11	Subtidal estuarine	Shallow (3–6 m deep) lagoon.	Marl depth: 9: <0.25 m; 10: <1 m; 11: >1 m	<i>T. testudinum</i> (0.1–0.5 m tall)	Quarterly, six 10×20-cm quadrats were haphazardly placed in a 10×10 m plot. Aboveground NPP of <i>T. testudinum</i> was measured using the modified leaf marking technique (Zieman, 1974). Biomass gain/area was calculated and scaled up to obtain annual ANPP.
				Periphyton (loose aggregate)	Glass slides ($n = 15$) deployed onto sediment surface between 15 and 30 days (Gaiser et al., 2005) bi-monthly. Accumulated AFDM/area/time was determined. Annual ANPP calculated as integral of multiple samplings during year.

Methods used to measure ANPP of the dominant species are shown.

laria purpurea) are found in areas of differing hydroperiods, sawgrass remains the dominant vegetation type in the freshwater marshes. Calcareous periphyton dominates in short hydroperiod Everglades marshes and are a significant component in long hydroperiod marsh communities (Gottlieb, 2003). In the saline brackish areas, mangroves dominate the landscape (Table 1). At SRS 4, *Rhizophora mangle* and *Laguncularia racemosa* are found with the mangrove associate, *Conocarpus erectus*. The two downstream sites, SRS 5 and 6, are dominated by a mix of *R. mangle*, *Avicennia germinans* and *L. racemosa*. There is a gradient in canopy height and soil depth, with the shortest canopy (5–7 m) trees and shallowest soil depth (≈ 2 m) found at SRS 4 and the tallest trees (≈ 20 m) with the deepest soils (> 4 m) encountered in SRS 6 (Table 1).

The TS/Ph transect is Y-shaped and consists of 11 sites (Fig. 1). Sites TS/Ph 1–3 are freshwater marsh communities while the ecotonal communities of TS/Ph 6 and 7 consist of a combination of freshwater *C. jamaicense-Eleocharis* sp. and scrub *R. mangle-C. erectus* (< 2 m) that dot the small tree islands (Table 1). TS/Ph 4 and 5 are freshwater marshes dominated by *C. jamaicense*, located on the south side of the C-111 canal that is a main drainage avenue for the south-eastern Everglades. TS/Ph 8 is also an ecotonal sawgrass-mangrove (3–4 m) forest where sawgrass and *C. erectus* dominate the interior areas and *R. mangle* fringe the channels. The three (TS/Ph 9–11) shallow (< 5 m) subtidal Florida Bay sites, although not located along major water flow paths, are key indicators of ecological processes within Florida Bay as they are influenced by differing amounts of Gulf of Mexico inputs (Fourqurean et al., 1992). The two eastern-most Florida Bay sites (TS/Ph 9 and 10) are less influenced by the Gulf of Mexico relative to TS/Ph 11. All three sites are dominated by the seagrass *Thalassia testudinum* with local patches of *Halodule wrightii* and *Ruppia maritima*.

Productivity

Aboveground NPP was measured using standardized methods that have been documented in other studies (Table 1). Attempts were made to use the same methods to measure ANPP across the ecosystem but differences in community structure often necessitated different methodologies. For

example, at TS/Ph 1–6, periphyton is primarily attached to the limestone or marl soil while in Florida Bay (TS/Ph 9–11) the periphyton forms a loose, unconsolidated mat. Therefore at TS/Ph 9–11, periphyton ANPP was measured as the rate of biomass accumulation on glass plates deployed onto the sediment surface (i.e. periphytometer method, Gaiser et al., 2005) while at the other sites, ANPP was measured using oxygen flux methods on periphyton mat cores (Iwaniec et al., 2006). In the mangrove forests of SRS 4–6 and TS/Ph 8, litter traps and tree height and diameter-at-breast-height (dbh) increment were used to estimate ANPP but in the scrub forests of TS/Ph 6 and 7, the low stature of the canopy precluded litter trap deployment and dbh measurement. Instead, we measured leaf turnover twice a year (Table 1).

Data analysis

Annual ANPP for sawgrass, mangroves, and seagrasses were converted from grams biomass ($\text{g m}^{-2} \text{ year}^{-1}$) to grams carbon ($\text{g C m}^{-2} \text{ year}^{-1}$) based on plant carbon content prior to analysis. Sawgrass dry weight biomass was 48% C (Childers, data at <http://www.fcelter.fiu.edu>), mangroves 44% C (Ewe, unpublished data), and the seagrass *Thalassia testudinum* was approximately 39% C (Fourqurean, data at <http://www.fcelter.fiu.edu>). The data were checked for normality using the Shapiro-Wilks test; non-normal data (i.e. periphyton in SRS and Taylor River) were log transformed prior to analysis.

A repeated measures analysis-of-variance (ANOVA) was used to compare sawgrass annual ANPP within each basin using plots within a site as replicates. Aboveground NPP for periphyton, mangroves, and seagrasses were analyzed with single-factor ANOVAs to determine differences between sites and years. Spatial and temporal variability in sampling between and across sites and among years and/or differences in replication at sampling precluded using repeated-measures comparison for those three primary producers. For each single-factor ANOVA, the annual ANPP of each primary producer was used. The significance level of each analysis was then Bonferroni-corrected ($p < 0.025$ ($=0.05/2$)) for the number of analyses (time, site) conducted on each producer.

All data were analyzed using SPSS 13.0 (SPSS Inc., Chicago, IL).

Results

Along the SRS transect, sawgrass ANPP did not differ significantly among the three sites (Table 2). Sawgrass ANPP ranged from approximately $80 \text{ g C m}^{-2} \text{ year}^{-1}$ (SRS 1 in 2003) to $384 \text{ g C m}^{-2} \text{ year}^{-1}$ at SRS 2 in 2004 (Fig. 2, Table 2). There was also a significant site \times year interaction (Table 2). Periphyton productivity at SRS also did not differ significantly among sites or years (Table 2). Although the 4-year average periphyton ANPP at SRS 1 was only $17.2 \text{ g C m}^{-2} \text{ year}^{-1}$ compared to the $67.9 \text{ g C m}^{-2} \text{ year}^{-1}$ observed at SRS 3 (Table 3), these differences were not statistically significant due to high interannual variability (Fig. 2). Spatial differences were however observed in the estuarine ecotone mangroves (Table 2). Four-year average productivity ranged from $1173 \text{ g biomass m}^{-2} \text{ year}^{-1}$ at SRS 5 to $2208 \text{ g biomass m}^{-2} \text{ year}^{-1}$ at SRS 6 (Table 3) with the lowest ANPP consistently observed at SRS 5 (Fig. 2). No interannual differences were observed in mangrove ANPP (Table 2).

At Taylor River, both sawgrass and periphyton ANPP differed among sites (Table 2). Sawgrass ANPP ranged from 205 to $523 \text{ g biomass m}^{-2} \text{ year}^{-1}$ in southern Everglades, with highest average 4-year productivity observed at TS/Ph 3 (Table 3). Although sawgrass ANPP increased from TS/Ph 1–3, productivity declined at TS/Ph 6. At the C-111 Basin, sawgrass ANPP did not differ among sites but differed significantly among years

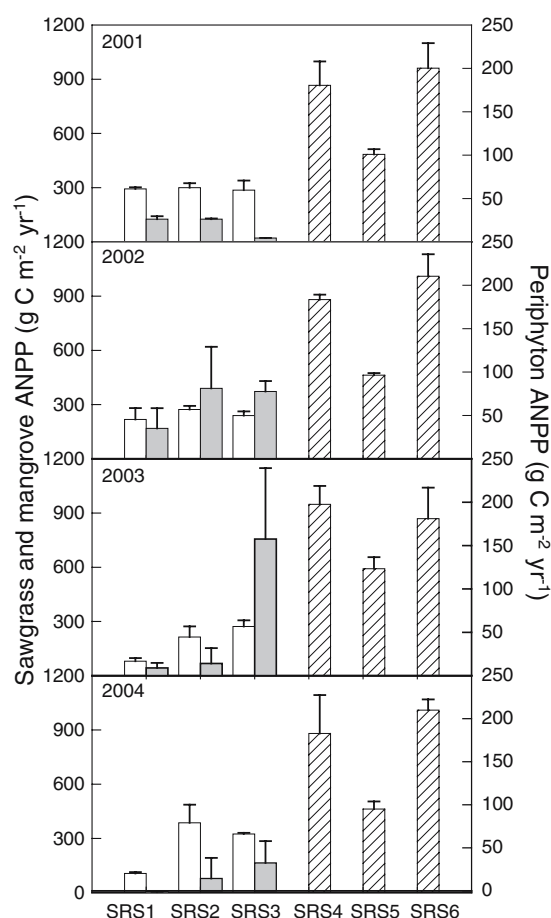


Figure 2. Annual net primary productivity (ANPP) for sawgrass (\square), periphyton (\blacksquare), and mangroves (▨) at the Shark River Slough sites.

and for the interaction term as well (Table 2). Productivity was lowest in 2003 and but annual trends changed between sites depending on year

Table 2. Comparison of site and annual differences in ANPP for each producer within the different basins

Basin	Sawgrass			Periphyton			Mangrove			Seagrass		
	Site	Year	Site \times Year	Site	Year	Site \times Year	Site	Year	Site \times Year	Site	Year	Site \times Year
Shark River Slough	n.s.	**	**	n.s.	n.s.		***	n.s.				
Taylor River	**	n.s.	n.s.	*	n.s.							
C-111 Basin	n.s.	*	*	n.s.	n.s.							
Florida Bay				n.s.	n.s.					***	n.s.	

Sawgrass data was analyzed with a repeated measures ANOVA using plot ANPP as replicates. Single-factor ANOVAs were used to analyze the periphyton, mangrove, and seagrass data for mean annual differences among sites and years separately. The data from these three primary producers were not amenable to repeated-measures analyses because of differences in sampling frequency, and replication within and among sites and years.

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Table 3. Average ANPP (\pm standard error) for each producer type over the sample period (2001–2004)

Site	Sawgrass	Periphyton	Mangrove	Seagrass
Shark River Slough				
SRS 1	361 \pm 103	17.2 \pm 8.2		
SRS 2	606 \pm 74	65.8 \pm 29.1		
SRS 3	580 \pm 36	67.9 \pm 33.4		
SRS 4			2066 \pm 48 ^a	
SRS 5			1173 \pm 65 ^b	
SRS 6			2208 \pm 88 ^a	
Taylor River				
TS/Ph 1	255 \pm 26 ^a	1276 \pm 502 ^{ab}		
TS/Ph 2	304 \pm 19 ^a	342 \pm 392 ^a		
TS/Ph 3	441 \pm 40 ^b	1797 \pm 324 ^b		
TS/Ph 6	308 \pm 35 ^a			
TS/Ph 7				
C-111 Basin				
TS/Ph 4	291 \pm 17	10371 \pm 3812		
TS/Ph 5	358 \pm 47	1293 \pm 455		
TS/Ph 8			340 \pm 30	
Florida Bay				
TS/Ph 9		4.7 \pm 0.8		91.1 \pm 8.2 ^c
TS/Ph 10		7.7 \pm 1.2		92.0 \pm 10.0 ^c
TS/Ph 11		8.2 \pm 0.8		396 \pm 114 ^d

With the exception of periphyton ($\text{g C m}^{-2} \text{ year}^{-1}$), ANPP for the all other producers are expressed in grams biomass $\text{m}^{-2} \text{ year}^{-1}$. Values for each primary producer followed by the same letter do not differ significantly among/between sites within each basin.

(Fig. 3) Periphyton ANPP was highly variable along the TS/Ph transect (Fig. 3). Productivity ranged from -148 to $20,599 \text{ g C m}^{-2} \text{ year}^{-1}$ (Fig. 3) but no periphyton was found in TS/Ph 2 the first 2 years of sampling or at TS/Ph 6. Average productivity over the 4 years was highest along Taylor River at TS/Ph 3, approximately 70% greater than TS/Ph 1 (Table 3). The most productive periphyton along the TS/Ph transect was at TS/Ph 4 ($1551\text{--}20,599 \text{ g C m}^{-2} \text{ year}^{-1}$) in the C-111 Basin (Fig. 3, Table 3). Although periphyton productivity was almost 8-fold greater in TS/Ph 4 relative to TS/Ph 5, there were no significant differences between these two populations due to large variances (Tables 2 and 3). There were also no interannual differences in periphyton ANPP between sites in either basin (Table 2, Fig. 3).

In Florida Bay, the 4-year average for periphyton ANPP ranged from $4.7 \pm 0.8 \text{ g C m}^{-2} \text{ year}^{-1}$ at TS/Ph 9 to $8.2 \pm 0.8 \text{ g C m}^{-2} \text{ year}^{-1}$ at TS/Ph 11 (Table 3) although there was no significant difference

among sites ($p=0.06$) due to large variability in productivity. *Thalassia testudinum* productivity was however significantly different among sites (Table 2). Productivity in this seagrass in Florida Bay ranged from 30 to $324 \text{ g biomass m}^{-2} \text{ year}^{-1}$, with highest ANPP observed at TS/Ph 11 (Fig. 3, Table 3). Average ANPP at TS/Ph 11 was over 4-fold greater than at TS/Ph 9 or 10 (Table 3).

Although the data were not explicitly collected for landscape level comparisons, some general comparisons and observations can nonetheless be made. Aboveground NPP for sawgrass over the study period were similar among basins (Table 3). Sawgrass ANPP at the TS/Ph 1–6 were similar to the SRS sites and comparable to mangrove productivity at TS/Ph 8. Mangrove productivity was also higher at SRS 4–6 compared to TS/Ph 8 (Table 3). However, when comparing periphyton between SRS 1–3 versus TS/Ph 1–5 (measured using same methods), ANPP was on average significantly higher at the TS/Ph sites relative to SRS (Table 3).

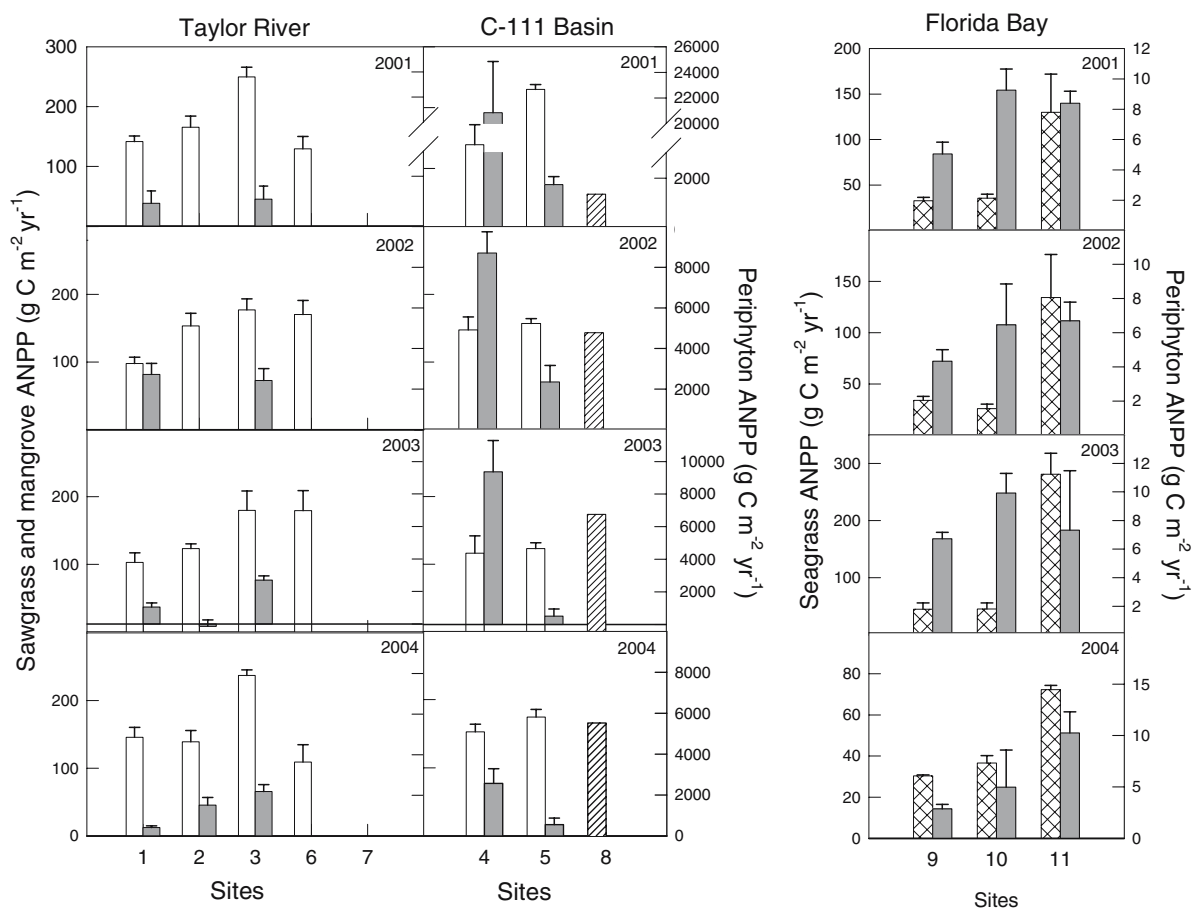


Figure 3. Annual net primary productivity (ANPP) for sawgrass (\square), periphyton (\square), mangroves (▨), and seagrass (⊠) at the Taylor River/Panhandle/Florida Bay sites.

Discussion

Although ANPP estimates have been published for various primary producers in the Everglades (e.g. Childers et al., 2006a) and Florida Bay (Fourqurean et al., 1992; Fourqurean & Zieman, 2002), this work is the first synthesis of landscape-level data examining the spatial and temporal trends of productivity along gradients of hydrology, salinity and nutrient availability. Inter-site differences were observed for several of the key producers but interannual differences were only found in sawgrass productivity.

Shark River Slough

Within the freshwater wetlands, sawgrass and periphyton ANPP data did not support our ori-

ginal hypothesis of a productivity peak at the estuarine ecotone as there was no increase in productivity at the upper estuarine ecotone (SRS 3). In the mangroves, there were differences in productivity with higher ANPP observed at SRS 4 and 6 relative to SRS 5. Chen & Twilley (1999) have indicated that P inputs to the Shark River estuary from the Gulf of Mexico control the spatial patterns of mangrove productivity while Childers et al. (2006b) have shown that from 2001 to 2003, mean water total phosphorus (TP) concentrations increased towards the Gulf of Mexico, with highest overall TP values observed at SRS 6. Findings from these studies support our observation of high productivity at SRS 6, closest to the Gulf of Mexico. At SRS 4, Childers et al. (2006b) also observed a wide range in mean monthly TP concentrations (from $\sim 0.2 \mu\text{mol l}^{-1}$

to $>1 \mu\text{mol l}^{-1}$); at times, mean TP concentrations at SRS 4 exceeded values at SRS 6. It is possible that these seasonal spikes in TP could have potentially contributed to high ANPP observed at SRS 4. Lower mangrove ANPP at SRS 5 relative to the other two sites appear to be unrelated to the landscape level P-concentrations and might be a function of interacting biotic and physical processes.

Taylor River/C-111 Basin/ Florida Bay

In Taylor River, where a productivity peak was not expected, sawgrass and periphyton productivity were significantly higher at the upper estuarine ecotone (TS/Ph 3) relative to the upstream sites (Table 3). Originally, we hypothesized no productivity peak in the estuarine ecotone region. One possibility for this increase in productivity is potentially from subsurface P inputs. Price et al. (2006) measured subsurface P-rich brackish water inputs into the upper estuarine ecotone during the dry season. Higher P availability has the potential to influence both spatial and temporal patterns of

ANPP in this estuarine ecotone (Fig. 4) and research currently being planned for the future (Childers et al., 2006a) will explicitly address the role of subsurface inputs into this area. In the lower estuarine ecotone (TS/Ph 6) salinity reduced sawgrass productivity (Childers et al., 2006a) and could have contributed to the absence of measurable periphyton productivity (Iwaniec, personal communication).

No spatial trends were observed in the C-111 Basin although temporal trends were observed in sawgrass ANPP. Sawgrass ANPP was lowest in 2003 and potentially related to water depth (Childers et al., 2006a). Deeper water levels in the freshwater marsh (data from <http://www.fcclter.fiu.edu>) were a consequence of the 2002–2003 El Nino (Childers et al., 2006b).

Primary producers

Sawgrass is the dominant macrophyte within the Everglades freshwater marsh, encompassing 65–70% of the freshwater marsh landscape (Loveless, 1959). Productivity of this species is not only

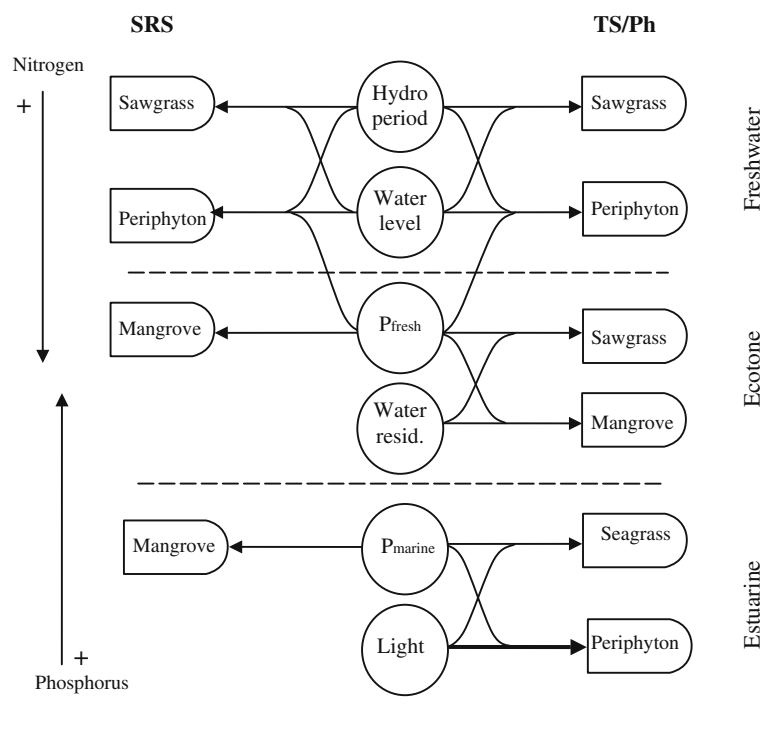


Figure 4. Conceptual model of ecosystem drivers of ANPP from fresh to marine habitats.

affected by hydroperiod but also water depth (Childers et al., 2006a) (Fig. 4). It is tolerant of oligotrophic conditions in the Everglades and can be extremely productive. Daoust & Childers (1998) have reported sawgrass ANPP of $2991 \pm 891 \text{ g m}^{-2} \text{ year}^{-1}$ while Davis (1989) observed ANPP between 802 and $3035 \text{ g m}^{-2} \text{ year}^{-1}$. The average ANPP values presented here from both the TS/Ph and SRS transects range from 255 to $606 \text{ g m}^{-2} \text{ year}^{-1}$. These values are lower than those of Daoust & Childers (1998) but our data are in closer agreement with Davis (1989) and Browder et al. (1982) from the Everglades (Table 4). Our data also fall within the estimates from Vymazal (1995) and are comparable to boreal non-forested freshwater wetlands (ANPP: $390\text{--}757 \text{ g m}^{-2} \text{ year}^{-1}$) (Thormann & Bayley, 1997; Burrows et al., 2003) as well as temperate tallgrass prairies (Knapp et al., 2001). Given the widespread distribution and role of sawgrass as the dominant primary producer in the freshwater marshes of SRS, changes in ANPP of this macrophyte will potentially have a cascading

impact on the trophic structure of the Everglades.

Periphyton productivity was significantly lower at SRS 1–3 relative to TS/Ph 1–5. Differences in periphyton ANPP between SRS and TS/Ph may be explained by the differences in hydrology and substrate type. Periphyton production in calcareous freshwater wetlands is influenced by hydrology, light, and P availability (Fig. 4) (Gaiser et al., 2004). Hydrology controls substrate availability for periphyton colonization; semi-permanent to permanently flooded sloughs contain an abundance of submersed macrophytes (mainly *U. purpurea*) that form the backbone of floating metaphytic mats while short-hydroperiod settings are devoid of submersed plants and periphyton grows directly attached to the marl or limestone surface (Gottlieb et al., 2005). Substrate differences cause these two types of periphyton mats to function differently, especially with respect to seasonal dynamics. Production in metaphytic mats is linked to growth patterns of *U. purpurea*, which is most prolific during the late wet season

Table 4. Comparison of average ANPP from this study with findings from other tropical and subtropical research

Primary producers	Habitat	Geographic location	Reference
Emergents (g biomass $\text{m}^{-2} \text{ year}^{-1}$)			
255–620	Freshwater marsh (<i>C. jamaicense</i>)	Everglades, FL	This study
419–1744	Freshwater macrophytes	Everglades, FL	Browder et al. (1982)
802–2028	Freshwater marsh (<i>C. jamaicense</i>)	Everglades, FL	Davis (1989)
12–10,000	Range of freshwater marshes	Summary of 132 studies	Vymazal (1995)
Periphyton (g C $\text{m}^{-2} \text{ year}^{-1}$)			
17–10371	Freshwater marsh	Everglades, FL	This study
112–119*	Freshwater marsh	Southern Everglades	Browder et al. (1982)
5–714	Edaphic algae productivity	Average of 31 marshes	Vymazal (1995)
292–1095**	Freshwater wetlands	Belize	Rejmankova & Komarkova (2000)
Mangroves (g biomass $\text{m}^{-2} \text{ year}^{-1}$)			
340–2208	Estuarine forests	Everglades, FL	This study
468–2700	Range of mangrove forests	Florida to Puerto Rico	Lugo & Snedaker (1974)
320–2460	Dwarf to fringe forests	Mexico	Day et al. (1987)
860–2900	Dwarf to fringe forest	Biscayne National Park, FL	Ross et al. (2001)
1560–2500	Riverine to estuarine forests	Dominican Republic	Sherman et al. (2003)
Seagrass (g biomass $\text{m}^{-2} \text{ year}^{-1}$)			
91–396 ⁺	Shallow subtidal lagoons	Florida Bay, FL	This study
602–835	Shallow lagoon	Bahamas	Koch & Madden (2001)
360	Subtidal banks	Bahamas	Dierssen et al. (2003)
1423–1788 ⁺⁺	Coastal lagoon	Tobago	Juman (2005)

*scaled from $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$; **scaled from $\mu\text{g C cm}^{-2} \text{ h}^{-1}$; ⁺ scaled from $\text{g C m}^{-2} \text{ day}^{-1}$; ⁺⁺ scaled from $\text{g m}^{-2} \text{ day}^{-1}$.

(September–November). During this time of the year, new pinnae of *U. purpurea* persist 2–3 weeks before decaying, representing the maximum colonization period for periphyton (Childers et al., 2001). The SRS freshwater sites have this type of metaphyton community, which produce at a much slower rate than short-hydroperiod prairie counterparts. In contrast, production on bedrock or marl in prairie marshes is confined mostly to the flooded season. Colonization and community development is continuous throughout that period, encouraging thick (3–10 cm) and often laminated periphyton mats to form (Gottlieb et al., 2005). This mat is prolific throughout the Taylor River/C-111 Basin and may explain the extremely high levels of productivity there compared to SRS metaphyton.

The values of ANPP reported for periphyton in this Everglades study are some of the highest and most variable encountered in the world (Table 4). Water level and residence times (Fig. 4) may explain some of the differences in periphyton productivity among sites. Thomas et al. (2006) found that high periphyton production typically follows flooding at the onset of the wet season and that the occurrence of these pulsed events can drive production throughout the wet season. High production values for periphyton from marsh sites at TS/Ph 4 in 2001 may have resulted from such a pulsed event. That year was characterized by a prolonged summer drought followed by tropical-storm rains and sudden flooding during the wet season. Release of nutrients trapped during the prolonged desiccation likely promoted a community shift to high productivity green algae after flooding (Iwaniec, personal observation). The highly productive algal-dominated periphyton community was also observed in the early wet season at this site in 2002 and 2003. Water level is believed to contribute to the absence of periphyton from TS/Ph 2 in 2001 and 2002. Deeper than normal water levels for most of the growing season most likely precluded periphyton mat growth and formation (Iwaniec et al., 2006). Through their high productivity, periphyton in the southern Everglades have the capacity to regulate other ecosystem attributes including soil formation, water quality, and carbon fixation for the rest of the food web.

The mangrove ANPP values reported from the SRS sites are comparable to other estimates from

the Gulf of Mexico, which have the same species composition. For example Day et al. (1987) reported ANPP of 2458 and 1606 g m⁻² year⁻¹ in the tall mangrove forests of Boca Chica and Estero Pargo (Terminos Lagoon), Mexico, respectively. Sherman et al. (2003) reported ANPP of 1560–2500 g m⁻² year⁻¹ from the mangrove forests along a fresh–marine gradient in northwest Dominican Republic, comparable to the values obtained from SRS (Table 4).

Leaf and wood productivity in all three mangrove sites at Shark River was between 4 and 6 fold higher than ANPP of the scrub forest in TS/Ph 8. Low substrate organic content (TS/Ph 6 only), P inputs and long hydroperiods probably contribute significantly to the scrub stature and low mangrove productivity at TS/Ph 6–8. Based on the biannual sampling schedule at TS/Ph 6 and 7, it was not possible to estimate a productivity rate for each year (2001–2004) as in the case for the SRS sites, which were sampled monthly. Thus, we used the 4-year dataset and integrated the measurements to obtain an annual rate. Leaf productivity was estimated to be 258 and 303 g m⁻² year⁻¹ at TS/Ph 6 and 7, respectively. These scrub forest estimates are lower than the value observed for TS/Ph 8 (340 ± 30 g m⁻² year⁻¹) as they do not include wood production. As leaf production at TS/Ph 8 accounts for approximately 80% of total mangrove ANPP (data from <http://www.fcler.fiu.edu>), we estimate ANPP of the scrub mangroves to range from 322 to 378 g m⁻² year⁻¹ at TS/Ph 6 and 7. These estimates are comparable to ANPP at TS/Ph 8 but are only 15–30% of mangrove productivity at the three SRS sites. Although these rates are robust for comparing among sites, a more intensive sampling will be necessary in TS/Ph 6 and 7 to characterize the production of fruits, flowers, and wood.

In Florida Bay, periphyton growth on seagrasses is in part regulated by light and nutrient availability (Fig. 4). Frankovich & Zieman (2005) showed that light controls epiphyton thickness on seagrass in Florida Bay while nutrient availability structures diatom community composition (Frankovich et al., 2006). We did not find differences in periphyton productivity patterns across the landscape but this pattern is not surprising as periphyton productivity is less sensitive to moderate levels of nutrient availability (ambient Florida Bay

conditions) relative to seagrasses (Frankovich & Fourqurean, 1997).

Unlike the periphyton, we observed significant differences in *T. testudinum* ANPP among the three sites in Florida Bay. Aboveground NPP of this seagrass was consistently highest at TS/Ph 11 (Fig. 3). Many studies have shown that seagrass from western Florida Bay is not as P-limited as plants growing in the eastern bay (e.g. Fourqurean et al., 1992; Fourqurean & Zieman, 2002; Armitage et al., 2005) (Fig. 4), hence the observed gradient of increasing ANPP from east to west (Fig. 3). Increased P availability with increasing proximity to Gulf of Mexico P inputs is often enhanced by disturbances (currents and erosion; Armitage, personal communication). Nonetheless, *T. testudinum* ANPP at TS/Ph 11 was on average 4-fold greater than at TS/Ph 9 or 10.

Future research

This 4-year synthesis of ANPP across the landscape is a significant attempt at quantifying temporal and spatial variability in key primary producers within the Everglades. Based on the findings to date, we outline some refinements for future data collection that will provide a more robust dataset of baseline information on the patterns of productivity in key producers within the coastal Florida Everglades.

Scrub mangrove productivity

Measuring productivity at TS/Ph 6 and 7 presents a challenge as the forest defies conventional measures of dbh or litter trap deployment. A three-pronged approach combining more frequent sampling of the leaf turnover patterns (as opposed to twice/year), measuring wood biomass turnover, and quantifying prop root growth in *R. mangle* is currently being planned.

Capturing "pulse" vs. "press" events

Producers with high turnover such as periphyton respond quickly to environmental drivers (Fig. 4). Therefore sampling during events of high or low water flow may be critical in capturing the patterns of productivity within this system. More frequent and intensive sampling of periphyton during such events may refine our understanding of the responses of this community to seasonal and spatial

fluxes. Furthermore, establishing plots that allow for repeated sampling will also improve the robustness of the sampling methodology.

In long-lived macrophyte communities such as mangroves however, ANPP trends are the result of complex interacting responses of the abiotic and biotic environments. Plants respond not only to short-term nutrient and hydrologic inputs (Fig. 4) but also to longer term patterns of local and large-scale disturbances (e.g. lightning vs. hurricane), light spatial distribution within the forest canopy, dominant species previous to the disturbance, and seedling species-specific spatial distribution (e.g. McKee, 1993; Sousa et al., 2003; Twilley & Rivera-Monroy, 2005). For example, we expect Hurricane Wilma (24th October 2005), which caused more defoliation and stem damage at SRS 6 relative to SRS 4 (T. Grahl, personal communication) to significantly affect long-term mangrove productivity patterns across the landscape. Future work will incorporate measurements of disturbance on forest regeneration patterns and consequently, on ANPP of the mangroves.

Determining belowground allocation

Based on the theory of optimal allocation, plants tend to allocate more biomass belowground under nutrient limited conditions (Chapin, 1980; Chapin et al., 1990). Biomass allocation patterns can range from a root: shoot ratio of 0.5–2 (e.g. Ewe et al., unpublished data) and belowground allocation can represent significant biomass that can regulate aboveground and whole plant productivity. Work in progress examining belowground productivity in sawgrass and mangroves at the estuarine ecotone will contribute to our understanding of allocation patterns and allow for the estimation of total (above and belowground) primary productivity of key producers within this landscape.

Conclusion

It was originally hypothesized that a unimodal productivity peak would be observed at the estuarine ecotone in the SRS transect but not at the Taylor-River/C-111 basin (Childers et al., 2006a). Our data indicate that although spatial differences were observed in some primary producers, these

findings do not generally support the hypothesis. Interannual differences were only observed in sawgrass and not for periphyton, mangroves, or seagrasses.

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