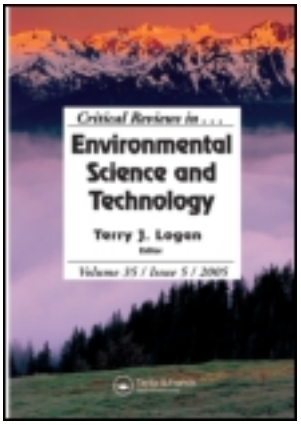

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Everglades Periphyton: A Biogeochemical Perspective

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Periphyton is an important component of the Everglades biogeochemical cycle but remains poorly understood. From a biogeochemical perspective, periphyton is a dense aggregation of diverse microorganisms (autotrophic and heterotrophic) and particles (mineral and detrital) imbedded within an extracellular matrix. The authors synthesize Everglades periphyton biogeochemistry and diversity at the ecosystem and community scales. The primary regulator of biogeochemical processes (material flux, transformation, and storage) is photosynthesis, which controls oxidation-reduction potentials and heterotrophic metabolism. Eutrophication and hydrologic alterations have resulted in fundamental periphyton biogeochemical differences. Elucidation of these processes is required to predict and interpret responses to ecosystem restoration.

KEYWORDS: Algae, phosphorus, primary production, diatoms, Cyanobacteria

INTRODUCTION

Comprising a consortium of algae, bacteria, fungi, and invertebrates imbedded within a matrix attached to a substrate, periphyton is a ubiquitous feature of the Everglades. *Periphyton*, however, is a general term that does not

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adequately convey the impressive structural and functional diversity present throughout the ecosystem. Well described are the spatial patterns in algal species composition, abundance, and appearance with water quality and hydrologic conditions and alterations (Browder et al., 1994; Gaiser et al., 2011; McCormick et al., 2002). Numerous ecosystem functions have been attributed to periphyton, but they are understood to a significantly lesser degree. Important functions include biogeochemical processes (e.g., dissolved oxygen production, nutrient uptake) and the suspected contribution to the food web (Browder et al., 1994; McCormick et al., 2002). Restoring and maintaining native periphyton structure and functionality is, therefore, a critical component of Everglades restoration. With the added value as a sensitive indicator of water quality and hydrologic conditions (McCormick and Stevenson, 1998), periphyton is a key target and evaluation metric for restoration (Gaiser, 2009).

Here we synthesize the broad topic of Everglades periphyton biogeochemistry. First, we describe the types of endemic periphyton and the biological (autotrophic, heterotrophic, and faunal) structure. As a framework (identifying the key drivers) and context (existing studies) for contrasting biogeochemical cycles, we present generalized conceptual biogeochemical models noting that cycles contain different elements depending on environmental conditions, scale, or periphyton type (i.e., not all elements need be present). We then synthesize periphyton biogeochemistry studies conducted at the ecosystem and community levels. We conclude with the restoration relevance of periphyton biogeochemistry.

THE STRUCTURE OF EVERGLADES PERIPHYTON

From a biogeochemical perspective, periphyton is a dense aggregation of biogeochemically diverse microorganisms (photoautotrophs, chemoautotrophs, and heterotrophs) and particles (mineral and detrital) intimately imbedded within an extracellular polymeric matrix (Kühl et al., 1994). Characterization of Everglades periphyton structure has centered on microscopic taxonomic identification of photoautotrophs, mainly algae and cyanobacteria. More recently, the lesser known, but biogeochemically important, microbes and fauna have been studied using alternative methods. Prime examples include photosynthetic pigments (Cleckner et al., 1998; Hagerthey et al., 2006; T. E. Smith, 2009), gene sequencing (Jasrotia and Ogram, 2008), and phospholipid fatty acids (PLFA; Bellinger, unpublished data, 2009). The use of fluorescent microscopy (Donar et al., 2004; Sharma et al., 2005) and scanning electron microscopy (Bellinger et al., 2010) have aided in visualizing the intimate spatial relationships among organisms within a periphyton complex.

Periphyton Types

Within the Everglades, there is a great diversity of periphyton types, commonly distinguished by the substrate on which they occur (Stevenson, 1996);

epiphyton, attached to plants; *epipelon*, or benthic periphyton, attached to soils; and *metaphyton*, which is not strictly associated with a substrate nor freely suspended. A more biogeochemically relevant descriptor is the algal-specific growth form, which consists of cyanobacteria-dominated cohesive, laminated calcitic mats (Figure 1A); thin sheet-like, desmid rich, communities loosely attached to substrates (Figure 1B); amorphous, gelatinous clouds of filamentous green algae (Figure 1C); or feathery filamentous cyanobacteria or green algae. The cohesive, laminated mats are synonymous with cyanobacterial mats and stromatolites common to marine and extreme environments (Whitton and Potts, 2000). The loosely attached assemblages are analogous to ombrotrophic temperate peatlands assemblages (Hagerthey et al., 2010). The cloud-like and feathery filamentous green algae (*Spirogyra* and *Mougeotia*) and cyanobacteria are typical of mesotrophic or eutrophic aquatic habitats.

Photoautotrophs

The major biological component of Everglades periphyton is comprised of oxygenic photosynthesizers. The flora is species rich and well studied (Gaiser et al., 2011), with more than 1700 taxa having been identified (Hagerthey, unpublished data, 2010), the majority belonging to the Cyanophyta (cyanobacteria), Bacillariophyta (diatoms), and Chlorophyta (green algae). Species relationships with environmental conditions are well described (Browder et al., 1994; Gaiser et al., 2011; McCormick et al., 2002). Anoxygenic photosythesizers have been found in some periphyton types. Bacteriochlorophyll *a*, an indicator of purple sulfur bacteria (PSB), is the most prevalent, occurring in periphyton from eutrophic habitats (Cleckner et al., 1998, 1999). Bacteriochlorophylls *c* and *d*, indicators of green sulfur bacteria (GSB), are occasionally found (Hagerthey, unpublished data, 2008). These photosynthetic bacteria do not produce oxygen (O_2) and utilize sulfide as the electron donor (Stal, 2000).

Chemoautotrophs

Chemoautotrophs are mostly bacteria that derive energy from the oxidation of inorganic compounds. Their distribution as a component of Everglades periphyton is poorly documented, but has been noted or suspected in some periphyton types. Cleckner et al. (1999) suggested sulfate-reducing bacteria (SRB) are present in green filamentous dominated and decomposing periphyton. SRB PFLA biomarkers (15:1ω6, 17:1ω7, and i17:1ω7) have been found in numerous periphyton types (Figure 2), suggesting a broad distribution. The presence of methanogens is inconclusive. Using gene sequencing, Jasrotia and Ogram (2008) found two proteobacteria in eutrophic periphyton related to type II methanotrophs and one proteobacteria in oligotrophic periphyton related to *Methylomonas*, a type I methanotroph, and methane production

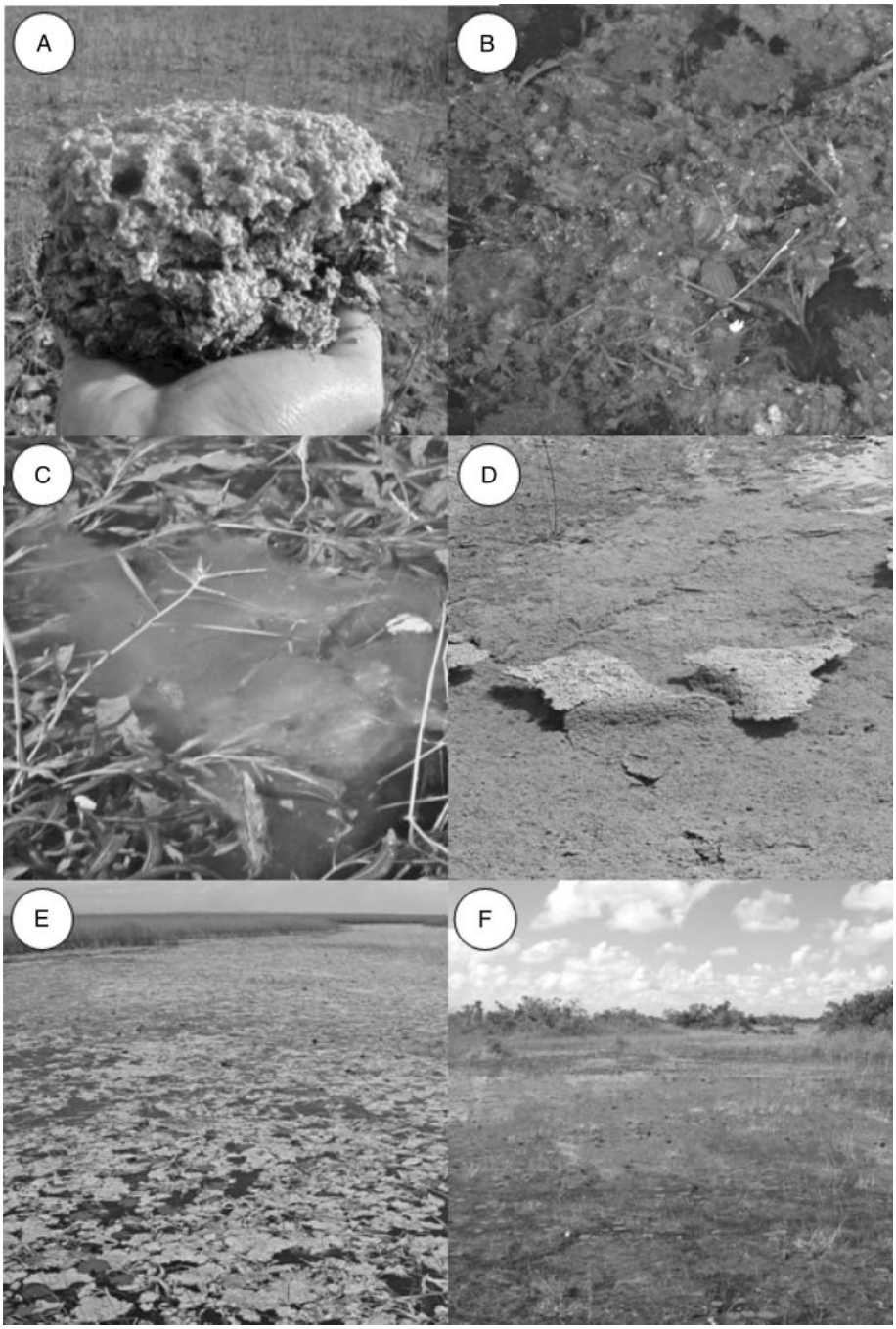

FIGURE 1. The forms of periphyton common to the greater Everglades ecosystem. (A) cohesive, laminated mats; (B) thin sheet-like, desmid rich, communities loosely attached to substrates; (C) amorphous, gelatinous cloud of filamentous green algae; (D) oligotrophic epipelic crusts; (E) oligotrophic-alkaline metaphyton; (F) ombrotrophic metaphyton. Photo credits: E. Gaiser (A) and S. Hagerthey (B–F).

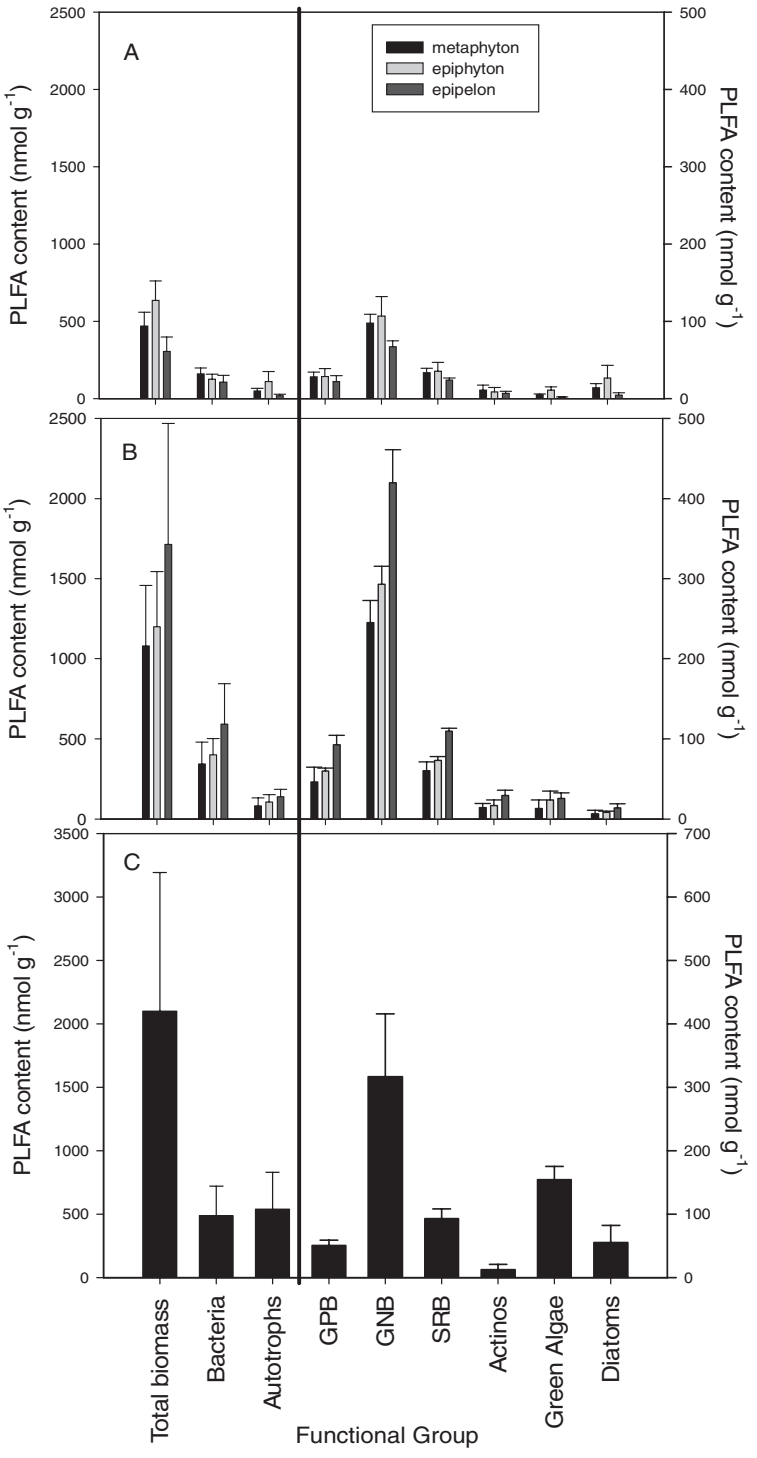

FIGURE 2. Total, bacterial, and autotrophic PLFA abundance (nmol PLFA g^{-1}) and functional microbial group abundances for periphyton from the (A) oligotrophic WCA-2A, (B) eutrophic WCA-2A, and (C) ombrotrophic WCA-1.

has been detected in cohesive epipelon (Write Wright and Reddy, 2008). Although methanogens have PLFA biomarkers (16:ω8 and 18:1ω8), detection is difficult with current methods. Gene sequencing used to characterize the denitrifying, sulfate-reducing, and methanogenic bacterial diversity in Everglades soils (Castro et al., 2005; Chauhan and Ogram, 2006; J. M. Smith and Ogram, 2008) has the potential to elucidate further the chemoautotrophic structure of periphyton.

Heterotrophs: Bacteria and Fungi

Bacteria and fungi that derive energy from organic carbon (C) are a poorly characterized component of Everglades periphyton. Periphyton bacteria abundances, estimated using the DNA specific stain SYBR green, range between 1.3×10^9 and 8.1×10^9 cells cm^{-2} (Thomas et al., 2006). Actively respiring bacterial numbers, estimated using 5-cyano-2,3-ditolyl tetrazolium chloride (CTC), range from 2.5×10^8 to 1.2×10^9 cells g^{-1} (Wheeler, unpublished data, 2009). Wright and Reddy (2008), using chloroform fumigation, estimated microbial biomass to be 16.9 g C kg^{-1}. Recently, bacterial functional groups have been investigated using PFLA biomarkers (Figure 2). Gram-negative bacteria (GNB), gram-positive bacteria (GPB), and actinomycetes are found in many periphyton types (Figure 2). However, GPB and actinomycetes best characterized the heterotrophic assemblage since some autotrophs (e.g., cyanobacteria, PSB, and GSB) are GNB. Actinomycete abundances are low (Figure 2) and indicate an anaerobic environment may persist in some periphyton types. The arbuscular mycrorrhizal fungi (AMF) biomarker 16:1ω5 abundances are also low. The biomarker for ectomycorrhizal fungi (EMF), 18:2ω6, cannot be used because it also occurs in cyanobacteria.

Heterotrophs: Fauna

A truly detailed quantitative study of perifauna (protozoans and animals) has yet to be undertaken. Van Meter Kasanof (1973) noted several protozoa in periphyton, including flagellated (Mastigophora), amoeboid (Lobsa), and ciliated forms (Ciliatea). Cladocerans, copepods, amphipods (Crustacea), gastropods (Gastropoda and Bivalvia), hydrozoans (Hydrozoa), nematodes (Secernentea), and rotifers (Monogononta) are also noted. Liston and Trexler (2005) provided the first quantitative study of periphyton macroinvertebrates. Total densities range between 50 and 150 individuals g^{-1} AFDM with 26 taxa identified with compositional differences between periphyton types and with time. Chironomids, the midge *Dasyhelea*, and nematodes dominated epiphyton and *Dasyhelea*, the amphipod *Hyalella azteca*, cladocerans, and the

freshwater snail *Physella* dominated metaphyton. Although the taxa identified thus far span the major functional groups (herbivore, omnivore, carnivore, and parasites), it is unclear what role invertebrates have in biogeochemical cycling.

CONCEPTUAL MODELS

Figure 3 depicts two conceptual models that provide a contextual framework to discuss periphyton biogeochemistry. The first illustrates the factors and processes that operate at the ecosystem level (Figure 3A), whereas the second focuses on the dynamics within a periphyton matrix (Figure 3B). Clearly the factors and processes differ among periphyton types and environmental conditions. It becomes readily apparent that there is a great disparity in the knowledge between the models. At the ecosystem level, periphyton is treated as a *black box*, affecting biogeochemistry through material flux, transformations, and storage. The majority of studies fall within this type. In contrast, investigations inside the black box are limited but studies are beginning to reveal the biogeochemical cycling intricacies and complexities within the matrix.

As photoautotrophs dominate periphyton biomass, oxygenic photosynthesis has the strongest influence on biogeochemistry by regulating (a) O_2 produced by the oxidation of water catalyzed by photosystem II during the light-dependent reactions that covert light energy to the energy-storage molecules ATP and NADPH and (b) light-independent reduction of carbon dioxide (CO_2) via the Calvin cycle to carbohydrates (Falkowski and Raven, 1997, Kirk, 1994). O_2 production sustains aerobic metabolism of organic matter and affects nutrient cycling by controlling oxidation-reduction reactions. The sugars produced by C-fixation provide the chemical energy required to synthesize other biological compounds (e.g., amino acids, proteins) and influence the uptake, transformation, and availability of other essential elements (e.g., phosphorus [P] and nitrogen [N]). The organic matter fuels heterotrophic microbial and animal metabolism. Microbial heterotrophic metabolism may result in O_2 depletion, thereby favoring anaerobic microbial processes such as denitrification, sulfate reduction, and methanogensis. In addition, photosynthesis can induce precipitation and dissolution of calcium carbonate ($CaCO_3$).

Photosynthesis coupled biogeochemical processes are regulated by environmental factors, principally light and temperature (Figures 3C, 3D, and 3E). With respect to light, photosynthesis rates are controlled by photoautotrophic light utilization efficiency and incident irradiation quantity and quality. Efficiency is determined by a complex and highly variable set of physiological and environmental factors involved in photochemical reactions (Falkowski and Raven, 1997). The relationship between photosynthesis and

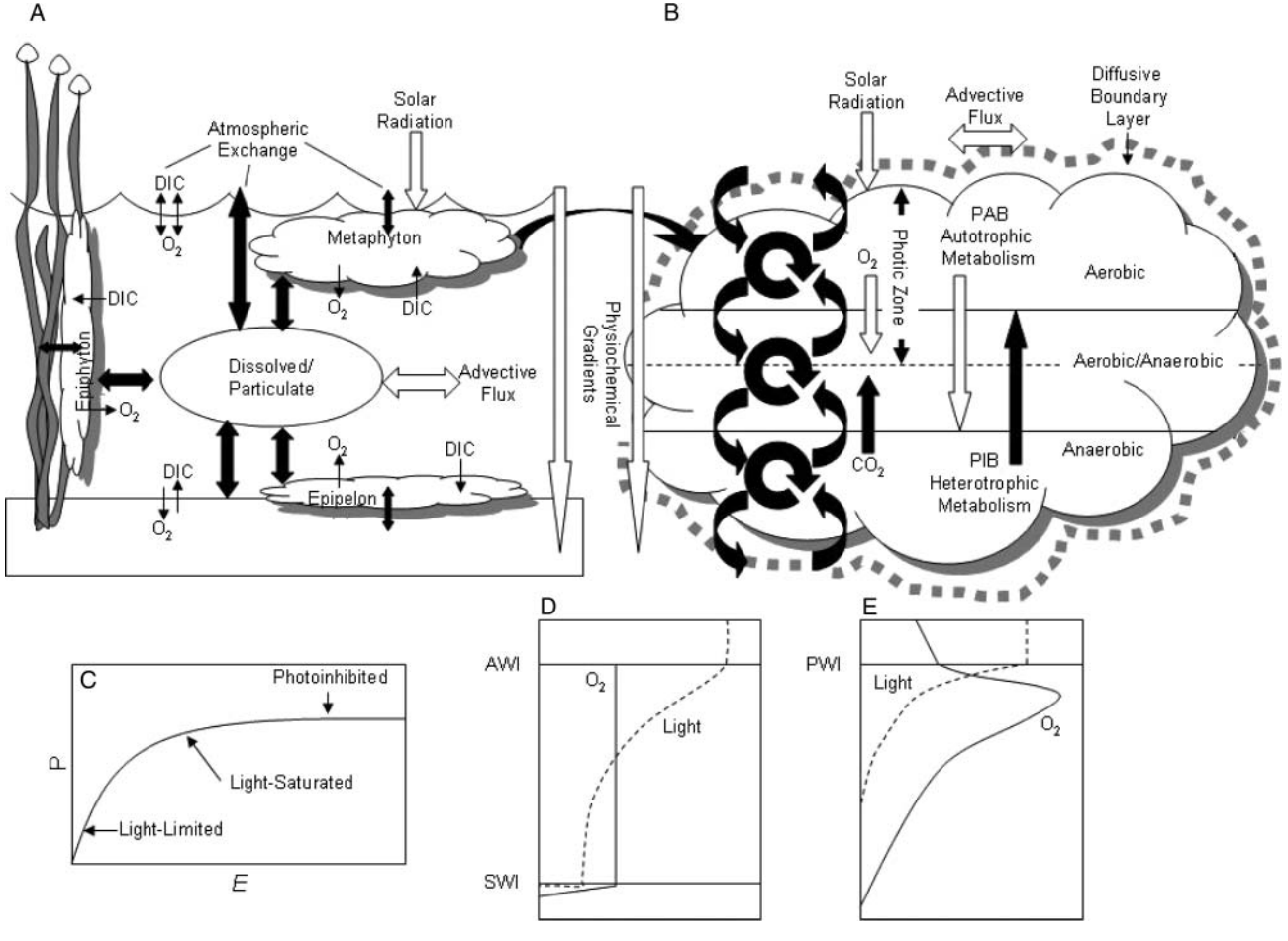

FIGURE 3. Conceptual model of biogeochemical processes and fluxes occurring (A) at the ecosystem scale and (B) community (i.e., within the periphyton mat). Light-driven biogeochemical processes are a function of photosynthetic capacity of periphyton, which can be modeled with P-E curves (C). Physiochemical gradients (e.g., light and O_2) are common features at both scales (D and E). AWI = Air-water interface; SWI = sediment-water interface; PWI = periphyton-water interface.

irradiance is a curve (i.e., P-E curve) that increases linearly (light-limited region), then increases nonlinearly to a maximum (light-saturated region), followed by a possible reduction (photoinhibited region; Figure 3C; Falkowski and Raven, 1997). Pertinent to Everglades photosynthesis is the recognition that (a) emergent macrophytes and the optical properties of the water column (e.g., dissolved organic carbon [DOC]) and periphyton rapidly attenuate irradiance and (b) ambient irradiance levels (>2000 μmoles m^{-2} sec^{-1}) can substantially exceed the photosynthesis maximum (P_{max}). Thus, photoinhibition, photoadaptation, and photoacclimation are relevant to the study of periphyton. Temperature affects the enzyme-catalyzed reactions associated with C-fixation and electron transport in the light-dependent reaction (Falkowski and Raven, 1997). Temperature and photosynthesis are positively related until temperatures exceed 30–35°C.

Photosynthesis provides the chemical energy needed to synthesize biological compounds that are regulated, in part, by the availability of essential elements (e.g., P and N). Thus, photoautotrophic demand and uptake mediates external concentrations. More importantly, periphyton biotically and abiotically transform elements by the uptake and conversion of inorganic elements, the enzymatic hydrolysis of organic matter, photoautotrophic mediation of oxidation-reduction reactions, adsorption to metal or inorganic complexes, and chemical precipitation-dissolution reactions. Material flux between periphyton and the adjacent substratum (air, water, macrophyte, or soil) is controlled by the diffusive boundary layer and the substratum physiochemical properties (Boudreau and Jørgensen, 2001; Figure 3).

Ecosystem Level Periphyton Biogeochemistry

Periphyton biomass, elemental content, productivity, and biogeochemistry vary considerably throughout the Everglades (Tables 1 and 2). However, it is important to recognize that biogeochemical interpretations are dependent on whether parameters are expressed as content (mass $mass^{-1}$) or concentration (mass $volume^{-1}$ or mass $area^{-1}$; Pametta and Gelinas, 2009; Tolhurst et al., 2005). In the Everglades literature, rates expressed using content and concentration are referred to as biomass-specific and areal, respectively, and often yield contradictory, sometimes paradoxical, interpretations.

Primary Production

Periphyton is a prolific component of the Everglades ecosystem. Biomass ranges between 3 and 6235 g ash free dry weight (AFDW) m^{-2} (Table 2), generally exceeding values for other wetlands (Goldsborough and Robinson, 1996). Paradoxically, biomass is greater in the open-water, oligotrophic marsh than the eutrophic marsh due to emergent macrophytes limiting light

TABLE 1. Nutrient content ($M \pm SD$) of various Everglades periphyton types

Region	Nutrient status	Periphyton type	TC (g kg^{-1})	TOC (g kg^{-1})	TP (mg kg^{-1})	TN (g kg^{-1})	TCa (g kg^{-1})	TS (g kg^{-1})
WCA-1	Oligotrophic	Metaphyton	404 ± 194	399 ± 19	453 ± 97	26 ± 3	16 ± 20	4.9 ± 0.3
		Epipelon	438 ± 265	431 ± 22	405 ± 136	38 ± 3	8 ± 2	
	Eutrophic	Metaphyton	369 ± 59	293 ± 64	954 ± 403	27 ± 7	115 ± 76	
WCA-2A	Oligotrophic	Metaphyton	230 ± 19	165 ± 22	175 ± 71	11 ± 3	216 ± 33	
		Epiphyton	250 ± 166	185 ± 27	205 ± 107	12 ± 3	188 ± 36	7.2 ± 0.5
		Epipelon	262 ± 26	203 ± 27	310 ± 83	18 ± 3	191 ± 32	9.1 ± 0.1
	Eutrophic	Metaphyton	312 ± 59	261 ± 79	1312 ± 996	24 ± 11	183 ± 122	4.6 ± 0.7
WCA-3A	Oligotrophic	Metaphyton	355 ± 25		306 ± 57	21 ± 5	70 ± 24	
		Epiphyton	345 ± 39		282 ± 265	17 ± 3	111 ± 50	
		Epipelon	445 ± 14		509 ± 78	43 ± 3	20 ± 2	
	Eutrophic	Metaphyton	368 ± 157		4686 ± 691	32 ± 16	150 ± 46	
WCA-3B	Oligotrophic	Metaphyton	220 ± 29	142 ± 47	134 ± 51	8 ± 3	222 ± 41	
		Epiphyton	260 ± 42	193 ± 54	191 ± 84	13 ± 4	192 ± 59	
		Epipelon	317 ± 75	239 ± 81	330 ± 139	22 ± 9	150 ± 61	
SRS	Oligotrophic	Metaphyton	240 ± 375	174 ± 56	125 ± 64	11 ± 4	202 ± 57	
		Epiphyton	273 ± 47	207 ± 62	131 ± 77	13 ± 4	178 ± 62	4.1 ± 0.1
		Epipelon	260 ± 74	185 ± 82	205 ± 114	16 ± 8	195 ± 73	4.3 ± 0.4
TS	Oligotrophic	Metaphyton	230 ± 31	149 ± 46	96 ± 52	10 ± 3	238 ± 42	
		Epiphyton	238 ± 40	165 ± 50	84 ± 46	9 ± 3	229 ± 42	
		Epipelon	228 ± 53	198 ± 60	127 ± 115	11 ± 6	241 ± 57	

Note. TC = total carbon; TOC = total organic carbon; TP = total phosphorus; TN = total nitrogen; TCa = total calcium; TS = total sulfur; WCA = Water Conservation Area; SRS = Shark River Slough; TS = Taylor Slough. Data were collected as part of long-term monitoring programs maintained by the Everglades Division of the South Florida Water Management District and TS data was provided by Bellinger (unpublished data, 2009).

TABLE 2. Literature values of biogeochemical processes measured for Everglades periphyton

Attribute	Region	Nutrient Status	Periphyton Type	Range	Units	Reference
GPP	WCA-1	Oligotrophic		2–15	g O_2 m^{-2} day^{-1}	McCormick et al., 1997
	WCA-2A	Eutrophic	Periphyton	0–2	g O_2 m^{-2} day^{-1}	McCormick et al., 1997
				1–7	g C fixed m^{-2} day^{-1}	McCormick et al., 1998
				25–45	mg O_2 g $AFDW^{-1}$ mol photons^{-1} m^{-2}	McCormick et al., 1998
		Oligotrophic	Periphyton	0.3–7.1	g C fixed m^{-2} day^{-1}	McCormick et al., 1998
				1–20	g O_2 m^{-2} day^{-1}	McCormick et al., 1997
				9–12	mg O_2 g $AFDW^{-1}$ mol photons^{-1} m^{-2}	McCormick et al., 1998
	WCA-3A	Oligotrophic	Periphyton	5–13	g O_2 m^{-2} day^{-1}	McCormick et al., 1998
	SRS	Oligotrophic	Epipelon	17–68	g C m^{-2} yr^{-1}	Ewe et al., 2006
	C-111 Basin	Oligotrophic	Epipelon	1293–10371	g C m^{-2} yr^{-1}	Ewe et al., 2006
				0.2–1.3	mg C $AFDW^{-1}$ h^{-1} *(NP)	Iwaniec et al., 2006
				0.1–0.5	mg C $AFDW^{-1}$ h^{-1} **(R)	
	TS	Oligotrophic	Epipelon	342–1797	g C m^{-2} $yr^{-}1$	Ewe et al., 2006
				0.4–1.5	mg C $AFDW^{-1}$ h^{-1} *(NP)	Iwaniec et al., 2006
				0.4–0.5	mg C $AFDW^{-1}$ h^{-1} **(R)	
Biomass	WCA-1	Oligotrophic	Metaphyton	40–225	g AFDW m^{-2}	McCormick et al., 1998
	WCA-2A	Eutrophic	Metaphyton	3–53	g AFDW m^{-2}	McCormick et al., 1998
		Oligotrophic	Periphyton	570–996	g AFDW m^{-2}	McCormick et al., 1998
				≤ 251	g AFDW m^{-2}	Turner et al., 1999
	WCA-3A	Oligotrophic	Periphyton	≤ 24	g AFDW m^{-2}	Turner et al., 1999
	SRS	Oligotrophic (LH)	Epipelon	286–1000	g AFDW m^{-2}	Gottlieb et al., 2006
		Oligotrophic (SH)		2000–3665	g AFDW m^{-2}	Gottlieb et al., 2006
	C-111 Basin	Oligotrophic	Periphyton	326–6253	g AFDW m^{-2}	Iwaniec et al., 2006
	TS	Oligotrophic	Periphyton	178–2578	g AFDW m^{-2}	Iwaniec et al., 2006

(Continued on next page)

TABLE 2. Literature values of biogeochemical processes measured for Everglades periphyton *(Continued)*

Attribute	Region	Nutrient Status	Periphyton Type	Range	Units	Reference
P-uptake	WCA-2A	Oligotrophic	Metaphyton	0.50 ± 0.06	μmol P g^{-1} DW min^{-1}	Scinto and Reddy 2003
			Epiphyton	0.74 ± 0.06		
			Epipelon	0.24 ± 0.04		
		Eutrophic	Periphyton	–10–300	μg SRP hr^{-1} g^{-1} AFDM	McCormick et al., 2008
		Oligotrophic	Periphyton	10–150	μg SRP hr^{-1} g^{-1} AFDM	Mccormick et al., 2008
	STA-1W	Eutrophic	Metaphyton (cyano)	80–164	μg P g^{-1} AFDM h^{-1}	McCormick et al., 2006
			Metaphyton (chloro)	33–61	μg P g^{-1} AFDM h^{-1}	
N-fixation	WCA-2A	Eutrophic	Metaphyton	90–116	nmol g^{-1} h^{-1}	Inglett et al., 2004
		Oligotrophic	Metaphyton	65–70	nmol g^{-1} h^{-1}	Inglett et al., 2004
THg	System			0.07–0.8	kg	Liu et al., 2008a
				2.4–92	ng g^{-1}	Liu et al., 2008b
TMeHg	System			3.5–37	g	Liu et al., 2008a
				0.04–9.4	ng g^{-1}	Liu et al., 2008b
SRR	WCA-2A	Eutrophic	Metaphyton	500 ± 200	μmol g^{-1}	Cleckner et al., 1999
		Oligotrophic	Periphyton	200 ± 20	μmol g^{-1}	Cleckner et al., 1999
	WCA-3A	Oligotrophic	Periphyton	2 ± 4	μmol g^{-1}	Cleckner et al., 1999
Hg methylation	WCA-2A	Eutrophic	Metaphyton	0.09–3	Fraction d^{-1}	Cleckner et al., 1999
		Oligotrophic	Periphyton	0–0.01	Fraction d^{-1}	Cleckner et al., 1999
	WCA-3A	Oligotrophic	Periphyton	0–0.01	Fraction d^{-1}	Cleckner et al., 1999

Note. Values are ranges or $M \pm SD$. Where periphyton type was not identified, the general term *periphyton* is used. NP = net productivity; R = respiration; LH = long hydroperiod; SH = short hydroperiod.

(Table 2; Grimshaw et al., 1997). Direct measures of C-fixation are lacking, but are typically estimated measuring O_2 and subsequently converted to C assuming a C:O_2 molar ratio of 0.375 and a photosynthetic quotient of 1.2 (Iwaniec et al., 2006; McCormick et al., 1998). Biomass-specific productivity is standardized to light (mg C g^{-1} AFDM mol^{-1} photons m^{-2}; McCormick et al., 1998; Thomas et al., 2006) or reported as mg C g^{-1} AFDW hr^{-1} (Iwaniec et al., 2006). Biomass-specific productivity varies greatly among and within periphyton types and is positively associated with P (Table 2); however, expressed on an areal basis (mg C m^{-2} d^{-1}), productivity is negatively related to P (McCormick et al., 1998). C-fixation rates for the Everglades (Table 2) eclipse values reported for other wetlands (Goldsborough and Robinson, 1996).

Heterotrophy

Catabolism is poorly understood for Everglades periphyton. Bulk respiration (R) rates vary greatly, from 0.14 to 6.7 g O_2 m^{-2} d^{-1} (Belanger and Platko, 1986) and from 2.4 to 12 g C m^{-2} d^{-1} (Iwaniec et al., 2006). Alternatively, anaerobic catabolism can occur in periphyton with methane (CH_4) and CO_2 production equaling 80 and 222 mg C kg^{-1} d^{-1}, respectively, and are 2.6–4 times greater than for detritus (Wright and Reddy, 2008). Methanogenesis likely dominates anaerobic catabolism in periphyton when nitrate (NO_3) and sulfate (SO_4) concentrations are limiting, whereas denitrification and sulfate reduction may dominate when concentrations are elevated.

Oxygen

Periphyton productivity has a profound effect on the O_2 dynamics, and therefore biogeochemistry, of Everglades surface waters (Belanger and Platko, 1986; Hagerthey et al., 2010; McCormick et al., 1997; McCormick and Laing, 2003). Since periphyton gross primary production (GPP) consistently exceeds R (GPP:R range 1.8–7.8; Belanger et al., 1989; Iwaniec et al., 2006), O_2 readily diffuses from periphyton into the water column. Periphyton's contribution to the O_2 budget is photosynthesis dependent, which varies with environmental conditions (e.g., light availability and temperature) and biomass, which varies in space and time. The high areal productivity of oligotrophic periphyton results in the oxygenation of the water column with characteristic diurnal patterns (Figures 4A and 4B) whereas the lower areal productivity associated with eutrophication does not (Figure 4C). Despite the high productivity of periphyton, water column net heterotrophy (R > GPP) persists because of high sediment R (Hagerthey et al., 2010). The highest rates of aquatic GPP occur in short hydroperiod marl prairies and the marsh-mangrove ecotone where the standing stock of emergent macrophytes is low and periphyton

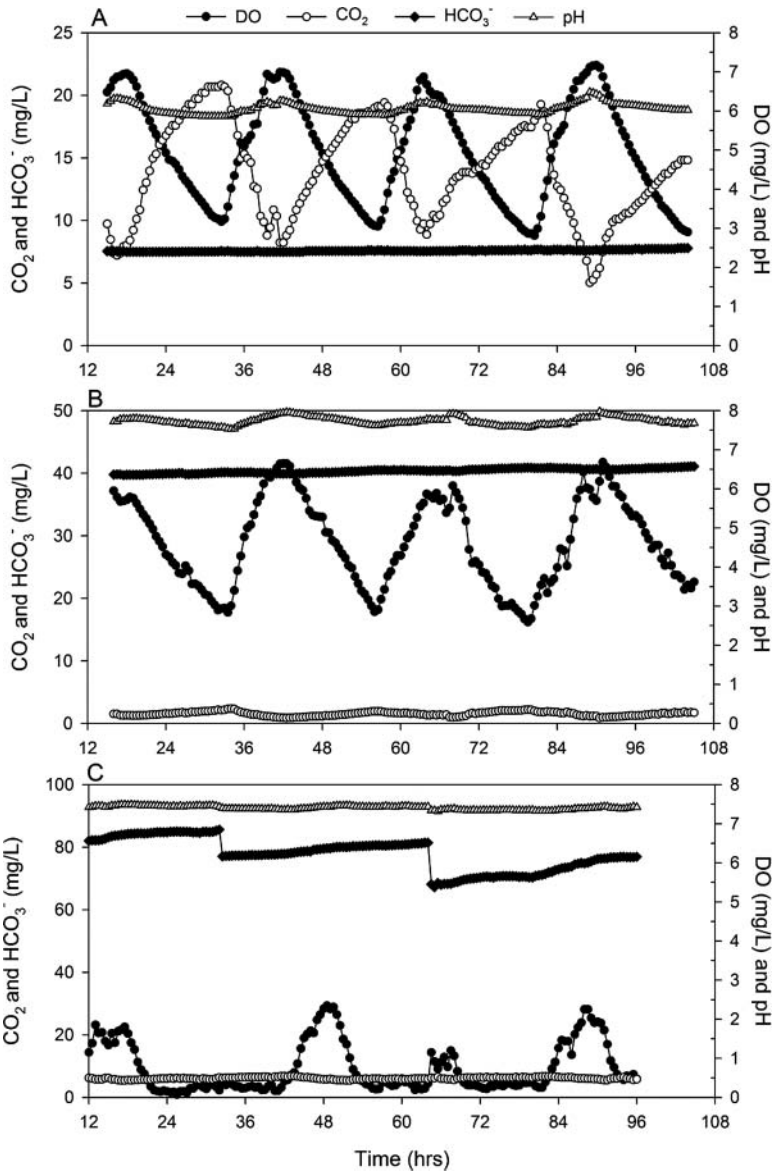

FIGURE 4. Periphyton affects on diurnal dissolved oxygen, inorganic carbon, and pH patterns in the aquatic environments of (A) the ombrotrophic marsh, (B) oligotrophic marsh, and (C) eutrophic marsh.

is high (Hagerthey et al., 2010). The regulation of surface water O_2 concentrations by periphyton has important biogeochemical and ecological ramifications. O_2 regimes determine ecosystem aerobic and anaerobic metabolism rates (Hagerthey et al., 2010; McCormick et al., 1998), influence fish (Belanger et al., 1989) and invertebrate distributions (McCormick et al., 2004; Rader and

Richardson, 1994), and promote nutrient and metal fluxes from wetland soils (Reddy et al., 1999).

Inorganic Carbon

The effect of periphyton photosynthesis on dissolved inorganic carbon (DIC) is dependent on antecedent CO_2, bicarbonate (HCO_3^-), and carbonate (CO_3^{2-}) concentrations. CO_2 concentrations are greater for ombrotrophic (acidic) waters and photosynthesis causes strong CO_2 diurnal patterns out of phase with O_2 (Figure 4A). HCO_3^- dominates minerotrophic (alkaline) waters and the greater buffering capacity does not result in photosynthesis induced diurnal patterns (Figures 4B and 4C).

It is well established that C-acquisition mechanisms differ among algal species (Badger and Price, 1992; Spijkerman et al., 2005). Algae require an active mechanism (e.g., H^+-ATPase, carbonic anhydrase) to acquire HCO_3^-, whereas CO_2 is acquired passively or actively. Thus, Hagerthey et al. (2010) hypothesized that the antecedent DIC complex is likely an important determinant of alagal species patterns in the Everglades if C acquisition mechanisms differ among taxa.

Organic Carbon

The total organic carbon (TOC) content of Everglades periphyton varies threefold, from 142 to 431g kg^{-1} for cohesive cyanobacteria mats and thin, sheet-like desmid communities, respectively (Table 1). These values correspond to 65% and 99% of the total carbon (TC) for these periphyton types, respectively. TOC comprises carbohydrates produced by the light-independent reactions and used to synthesize biomolecules (e.g., lipids), storage products (e.g., starch, chrysolaminaran; Bertocchi et al., 1990), and extracellular polymeric substances (EPS) (Decho, 1990; Sutherland, 1999).

The hydrocarbons (e.g., lipids, sterols, alkanes) of Everglades periphyton are poorly characterized. Algae produce long and short-chain hydrocarbons of varying degrees of desaturation, branching, and aromaticity. Short-chain hydrocarbons are also products of catabolism and natural degradation (e.g., photodegradation). Periphyton-derived hydrocarbons are in Everglades' surface water dissolved organic matter (DOM) in various quantities and qualities (Lu et al., 2003; Maie et al., 2005, 2006), which are regulated by physical (e.g., hydrology) and microbial processes (Maie et al., 2006). Periphyton leachate is mostly *O*-alkyl C (>63%) and alkyl C (>14%) and with low overall aromaticity (3%). The most abundant phenolic compounds are 1,4-dimethoxybenzene and 1,2,4-triomethoxybenze. Some hydrocarbons are unique to algae and are used as biomarkers for DOM transport (Jaffé et al., 2006), deciphering peat formation (Hajje and Jaffé, 2006), and paleoecological studies (Xu et al., 2007). Gao et al. (2007) recently described a

diverse class of periphyton hydrocarbons, botryococcenes, whose function is unknown but thought to have a role in structuring periphyton.

EPS comprise heteropolymers (glucose, galactose, arabinose, xylose, fucose, rhamnose, mannose, and uronic acids), lipids, proteins, and DNA (Bertocchi et al., 1990; Hoagland et al., 1993). EPS production may result from nutrient limitation (Hoagland et al., 1993), photosynthetic overflow (Stal, 2000), or cell motility (Consalvey et al., 2004). EPS serves as a C-substrate for bacterial metabolism after polysaccharide hydrolysis to simple saccharides (Colombo et al., 2004), protection against desiccation (Gaiser et al., 2011), and protection from high irradiances (Garcia-Pichel and Castenholz, 1991). Since polymers differ in hydrophobicity, hydrophilicity, and polymerization, EPS have several structural roles (Bhaskar and Bhosle, 2005; Decho, 1990). EPS can mediate $CaCO_3$ deposition (Merz, 1992; Pentecost and Riding, 1986), nutrient and metal binding and sequestration (Decho, 1990; Freire-Nordi et al., 2005), attachment of exoenzymes (e.g., alkaline phosphatase) to cell surfaces (Sharma et al., 2005; Spijkerman and Coesel, 1998), and regulation of polymer adhesion–cohesion with polymers, cells, or substrates (Domozych et al., 2007; Hoagland et al., 1993).

Everglades periphyton EPS range between 2 and 20 mg g^{-1} (Bellinger et al., 2010) and rivals or exceeds values for lakes (0.01–0.3 mg g^{-1}; Hirst et al., 2003), rivers (2–6 mg g^{-1}; Spears et al., 2008), and estuaries (<1–20 mg g^{-1}; Hanlon et al., 2006). However, EPS composition differs among periphyton types, with ombrotrophic desmid periphyton having more glucose, galactose, and arabinose and less xylose, fucose, and rhamnose than cohesive-cyanobacterial mats (Bellinger et al., 2010). The EPS compositions are characteristic of desmids (Kiemle et al., 2007) and cyanobacterial mats (Bertocchi et al., 1990). Saccharides are leached from periphyton and are a component of Everglades DOM (Maie et al., 2005). The saccharides xylose, rhamnose, and fucose are refractory (Giroldo et al., 2003) and known to accumulate in temperate peats (Macko et al., 1990) and induce flocculation (Zhou et al., 1998). Their presence in periphyton EPS may, therefore, be important in the formation of Everglades floc and peat.

Phosphorus

Periphyton total P (TP) content varies from 8 to 4686 mg kg^{-1} (Table 1). Periphyton has a major role in Everglades P cycling through biotic and, to a lesser extent, abiotic processes. Uptake is determined by periphyton type, composition, biomass, metabolic activity, advective transport, and form of P (Dodds, 2003; McCormick et al., 2006; Scinto and Reddy, 2003). Concordant with productivity, biomass-specific P uptake (μg g^{-1} hr^{-1}) is higher for eutrophic periphyton (McCormick et al., 1998) but areal uptake (μg m^{-2} d^{-1}) is greater for oligotrophic periphyton (McCormick et al., 1998; Newman et al., 2003). Periphyton growth is dependent on inorganic P availability;

however, in the oligotrophic Everglades inorganic P is scarce. To combat this problem, periphyton induce phosphatase enzymes to utilize organic P (Newman et al., 2003; Noe et al., 2003; Scinto and Reddy, 2003; Sharma et al., 2005; Thomas et al., 2006) at rates equivalent to inorganic P (Scinto and Reddy, 2003).

Everglades periphyton maintain low TP concentrations (<10 μg L^{-1}). Michaelis-Menton kinetic experiments suggest that ambient TP concentrations are below periphyton K_m values, indicating that uptake for periphyton are well below V_{max} (Scinto and Reddy, 2003). Thus, available P is quickly sequestered and thereby maintains low ambient TP (Thomas et al., 2006). For periphyton with a high calcium (Ca) content, abiotic adsorption of inorganic P to $CaCO_3$ is also a mechanism (Noe et al., 2003; Scinto and Reddy, 2003). The intramatrix microbiota utilize Ca-P as an inorganic P source. The variety of abiotic and biotic mechanisms combined with the intimacy between photoautotrophs and heterotrophs enables periphyton to efficiently recycle and retain P (Dodds, 2003; McCormick and Scinto, 1999).

Periphyton are fundamentally more important in the short-term, rather than long-term, storage of P. Nonetheless, periphyton mediates long-term P retention through the storage of cellular organic P, metal-phosphate deposition, Ca and Mg coprecipitation, and adsorption to inorganic complexes such as $CaCO_3$ (Dodds, 2003; Scinto and Reddy, 2003). Thus, periphyton has been investigated as means to remove P (DeBusk et al., 2004; McCormick et al., 2006; Thomas et al., 2002) but the effectiveness is inconclusive. Coprecipitation with Ca is often a P sink (Rejmánková and Komárkova, 2005), but is likely a minor mechanism in the Everglades (Noe et al., 2003; Scinto and Reddy, 2003; Vymazal et al., 1994; Vymazal and Richardson, 1995;). Alternatively, decomposing and the rewetting of desiccated of periphyton can be P sources (Gottlieb et al., 2005; McCormick et al., 2006; Thomas et al., 2006).

Nitrogen

The total N (TN) content of Everglades periphyton ranges from 8 to 43 g kg^{-1} (Table 1). Although an essential element, little is known about N cycling in the Everglades periphyton. Periphyton rapidly assimilate inorganic N from the water column; verified through pulse-chase tracer studies utilizing ^{15}N labeled $Ca(NO_3)_2$ (Wozniak et al., 2008) and NH_4Cl (Hagerthey et al., unpublished data, 2008). Most inorganic N is likely converted to organic N (e.g., amino acids, amines, nucleotides); however, although nitrification and denitrification has not been directly measured, they cannot be easily discounted because anoxia does occur in periphyton (Cleckner et al., 1999) and denitrifying enzyme activity (DEA) has been measured (White and Reddy, 1999). White and Reddy (2003) reported the denitrification potential for Everglades

soils and Smith and Ogram (2008) characterized the diversity of bacterial denitrifies using two nitrate reductase genes (*nirK* and *nirS*).

Considered to be a mechanism to deal with N-limitation, N_2 fixation occurs in Everglades periphyton (Inglett et al., 2004, 2009; Table 2). Biomass-specific nitrogenase activity is greater for eutrophic, N-limited periphyton (Table 2), but areal estimates are greater for oligotrophic periphyton (>9 g N m^{-2} yr^{-1}) and rivals other wetlands (Inglett et al., 2004). Since O_2 prohibits N_2 fixation, specialized cells (heterocysts), or anoxia are required. While N_2 fixation is attributed to heterocystic filamentous cyanobacteria, the presence of the *nifH* gene in nonheterocystic cyanobacteria and bacteria suggests a greater diversity in N_2 fixation potential, especially for cohesive mats (Jasorotia and Ogram, 2008).

Calcium

Algal requirements for Ca are highly variable (Vymazal, 1995) and uncertain for the Everglades taxa. However, periphyton $CaCO_3$ precipitation is an important ecosystem function. $CaCO_3$ precipitation occurs in oligotrophic, alkaline cohesive periphyton mats constructed of filamentous cyanobacteria, mainly *Schizothrix calcicola* and *Scytonema hofmanni* (Browder et al., 1994); thus, Ca content ranges from 8 to 241 g kg^{-1} (Table 1). Gleason and Spackman (1974) found cyanobacterial filaments encrusted in $CaCO_3$ (Figure 5) and suggested that precipitation was regulated by the degree of $CaCO_3$ saturation. Models of cyanobacterial induced $CaCO_3$ precipitation have been proposed (Dittrich and Obst, 2004) and provide the rationale for impregnation of cyanobacterial sheaths with $CaCO_3$ (Merz, 1992). Active cell membrane pumps exchange intracellular Ca for protons (H^+) during uptake of HCO_3, increasing extracellular Ca and pH. Concomitantly, extracellular CO_3^{2-} increases as extracellular CO_2 reacts with water. The steep microgradient between extra- and intracellular pH and CO_2 partial pressure forms a region with a lower saturating $CaCO_3$ concentration that increases the likelihood of precipitation. The $CaCO_3$ nucleation sites are likely uronic acid moieties that create the template for crystal growth (Dittrich and Obst, 2004; Merz, 1992; Pentecost and Riding, 1986).

With eutrophication, the calcareous cohesive periphyton mats and their important ecosystem functions disappear (Dong et al., 2002; Gaiser et al., 2006; McCormick et al., 1996). Mechanistically it is unclear why but hypotheses abound. As P supply increases, uptake rates for oligotrophic periphyton likely approach V_{max} (Scinto and Reddy, 2003), fundamentally changing biochemical processes and species interactions that results in the assimilation capacity for P to increase and eventually be exceeded (Dong et al., 2002; Gaiser et al., 2004). P assimilation capacity for calcareous periphyton is coincident with a TP content of 110 μg g^{-1} (Gaiser et al., 2004) and 450 μg g^{-1} for periphyton with a high organic content (Table 2). Gaiser et al. (2011)

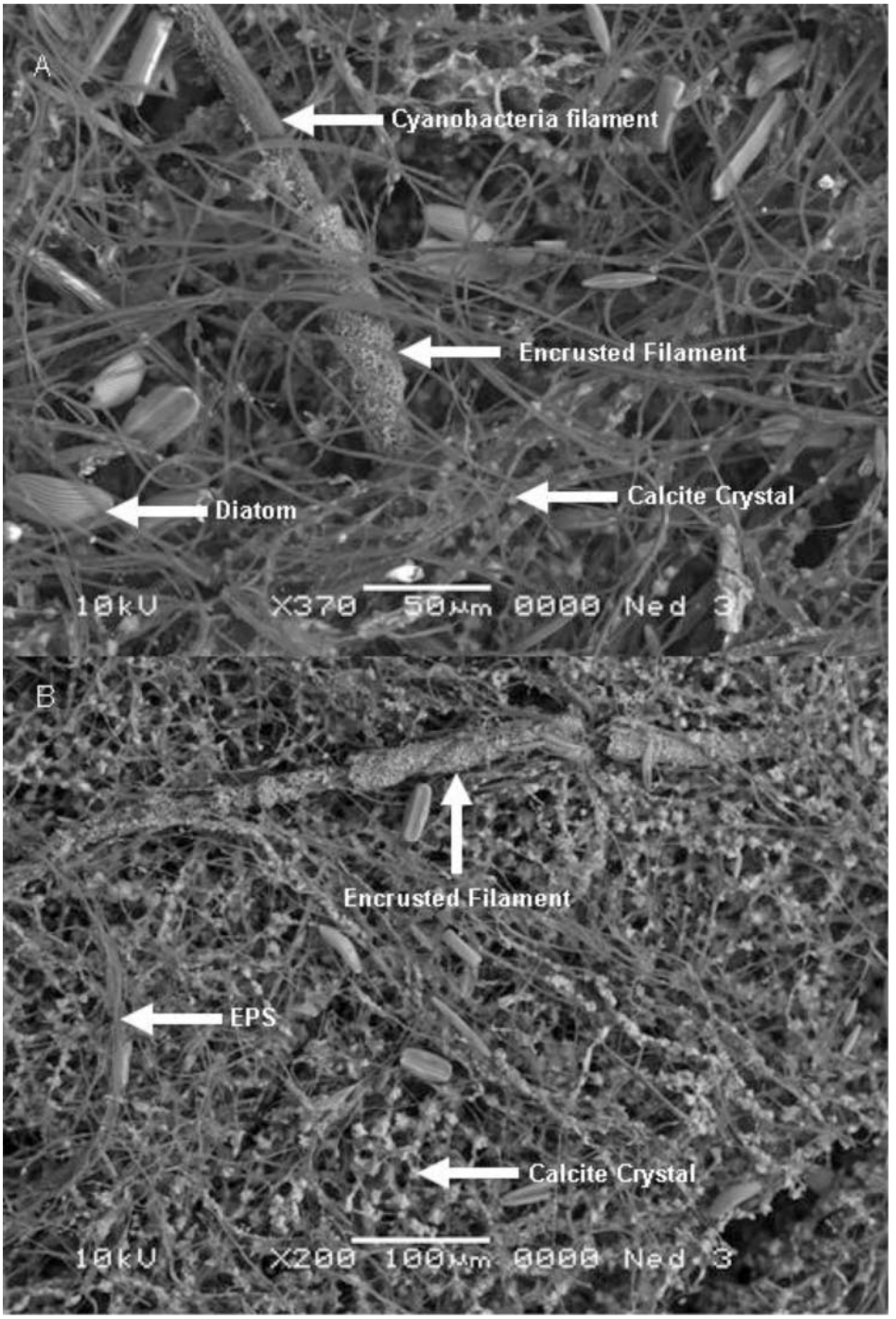

FIGURE 5. Variable pressure scanning electron microscopy pictures of periphyton collected from the interior of WCA-2A. Images show the $CaCO_3$ encrustation of filamentous cyanobacteria and EPS.

postulated that with P enrichment, increased heterotrophic metabolism of the EPS matrix increases CO_2 production and $CaCO_3$ dissolution, along with competitive displacement by green algae. Alternatively, with enrichment, the structural rigidity of the EPS matrix of P limited cohesive periphyton may be reduced by a reduction in EPS production and excess P out-competing carboxyl groups for Ca (Bellinger, unpublished data, 2009).

Sulfur

Sulfur (S) is an essential element required for metabolism (Hell et al., 2008) and suspected to be important in Everglades periphyton biogeochemistry (Bates et al., 1998). Given the broad spatial and temporal variability in SO_4 throughout the ecosystem (0.4 to >100 mg L^{-1}), S content varies among periphyton types (Table 1). Total S ranges from 4.1 to 9.1 g kg^{-1} (Bellinger, unpublished data, 2009) and an organic content of 0.59% has been reported (Bates et al., 1998).

The S cycle is linked to photosynthetic microbes that include hydrogen sulfide (H_2S) oxidation by PSB and dissimilatory sulfate-reduction by SRB (Hell et al., 2008). PSB have been found in Everglades periphyton (Cleckner et al., 1999; Hagerthey, unpublished data, 2008) but, while undocumented, cyanobacteria capable of H_2S-dependent anoxygenic photosynthesis and colorless aerobic S bacteria may be important (Stal, 2000). Whereas distinct SRB assemblages have been identified for eutrophic and oligotrophic soils (Castro et al., 2002), characterization of periphyton SRB are lacking but similar distinctions are expected since SO_4 reduction has been measured in loosely bound filamentous green algae (*Spirogyra* and *Mougeotia*) common to P enriched regions, heavily decomposed, black periphyton from low P environments, and oligotrophic cohesive mats (Table 2; Cleckner et al., 1999). SRB metabolic activity is closely linked with mercury (Hg) methylation (Cleckner et al., 1998, 1999), to EPS, specifically glycolate, production (Stal, 2000), and to $CaCO_3$ deposition during degradation of EPS (Dupraz et al., 2004).

Mercury

The transformation of inorganic mercury (Hg) to methylmercury (MeHg) occurs in Everglades periphyton with SRB (Cleckner et al., 1998, 1999). Although periphyton account for 0.2–0.7% of the total MeHg in the Everglades (Liu et al., 2008a), it is an important vector for Hg biomagnification (Cleckner et al., 1999; Liu et al., 2008b). Methylation rates can be 100 times greater for eutrophic than oligotrophic periphyton due to greater O_2 availability in the latter, causing demethylation or differences in SRB composition between eutrophic and oligotrophic periphyton (Cleckner et al., 1999). Periphyton, by facilitating the photochemical sorption–desporption of Hg, also influence diurnal Hg patterns in surface waters (Krabbenhoft et al., 1998).

Other Elements

The cycling of many other elements is affected by the nutritional requirements of algae (Vyzmazal, 1995). Potassium, magnesium, sodium, silicon, iron, manganese, chloride, zinc, copper, and selenium are important in many enzyme mediated and biochemical reactions. While Everglades algal species patterns are strongly correlated with surface water ion chemistry (McCormick et al., 2002; Swift and Nicholas, 1987), including rapid responses to mineral-rich canal water intrusions (Slate and Stevenson, 2000; Hagerthey et al., submitted), detailed studies are lacking.

Toxins and Biologically Active Compounds

Many algae, especially cyanobacteria, chrysophytes, and cryptophytes, produce toxins and biologically active compounds with varying degrees of ecological significance. Recent studies suggest that these compounds are common to Everglades periphyton. Bellinger and Hagerthey (2010) screened several periphyton types for saxitoxin, microcystin, domoic acid, anatoxin-a, debromoaplysiatoxin, and lyngbyatoxin-a. Low levels of toxins (<1000 ng g^{-1}) were detected and toxin composition varied among types. In a survey of south and central Florida freshwaters, 17% of 122 tested cyanobacteria strains produced compounds with developmental toxicity (Berry et al., 2007). For cyanobacteria isolated from the Everglades, the ecological effects are wide-ranging. Some produce allelochemicals that inhibit or stimulate the growth of other cyanobacteria and green algae (Berry et al., 2008; Gantar et al., 2008). One strain of cyanobacterium, *Lyngbya* sp. 15–2, inhibits the growth of bacteria (*Bacillus*), yeast (*Saccharomyces*), green algae, cyanobacteria, a number of cancer cell lines, and zebrafish embryos (Berry et al., 2004, 2007). Two active cytotoxic cyclic peptides, pahayokolide A and B, have been isolated from this strain (An et al., 2007). *Pseudanabaena* sp. 21–9-3, *Synechococcus* sp. 36–8, and *Lyngbya* sp. strain 15–2 exhibit anti-larval activity as evident by 100% mortality of mosquito larvae, *Aedes aegypti* (Berry et al., 2008). Thus, the low standing stocks of Everglades invertebrates and fish (Turner et al., 1999) may be attributed, in part, to toxins or biologically active compounds.

COMMUNITY LEVEL PERIPHYTON BIOGEOCHEMISTRY

Within the periphyton matrix (Figure 3B), biological processes induce strong internal environmental and chemical gradients that span relatively short distances (μm to cm) and regulate material flux, transformation, and storage (Figure 3E). However, sophisticated techniques are not necessary to validate the inherent biogeochemical complexity of periphyton but can be inferred

TABLE 3. Visual and textural attributes of Everglades periphyton indicative of taxonomic or biogeochemical characteristics

	Indicator
Color Attributes	
Golden brown	Diatoms
Blue-green	Cyanobacteria
Olive green	Cyanobacteria
Bright green	Filamentous green algae like *Spirogyra* or *Mougeotia*
Rusty reddish hue	Iron oxides or the photoprotective pigment scytonemin
White	Precipitated calcium carbonate
Black	Hydrogen sulfide
Textural Attributes	
Sliminess	Extracellular polysaccharides (EPS)
Grittiness	Mineral precipitates

from observations of color and texture (Table 3). The distinctly colored laminations characteristic of cohesive mats reflect microbiota or chemical reaction end products (Figure 6; Table 3) and the sliminess felt when picking up a gelatinous mat of *Spirogyra* or *Mougeotia* is EPS (Mitova et al., 1999). With limited data for the Everglades, we present preliminary high-resolution data

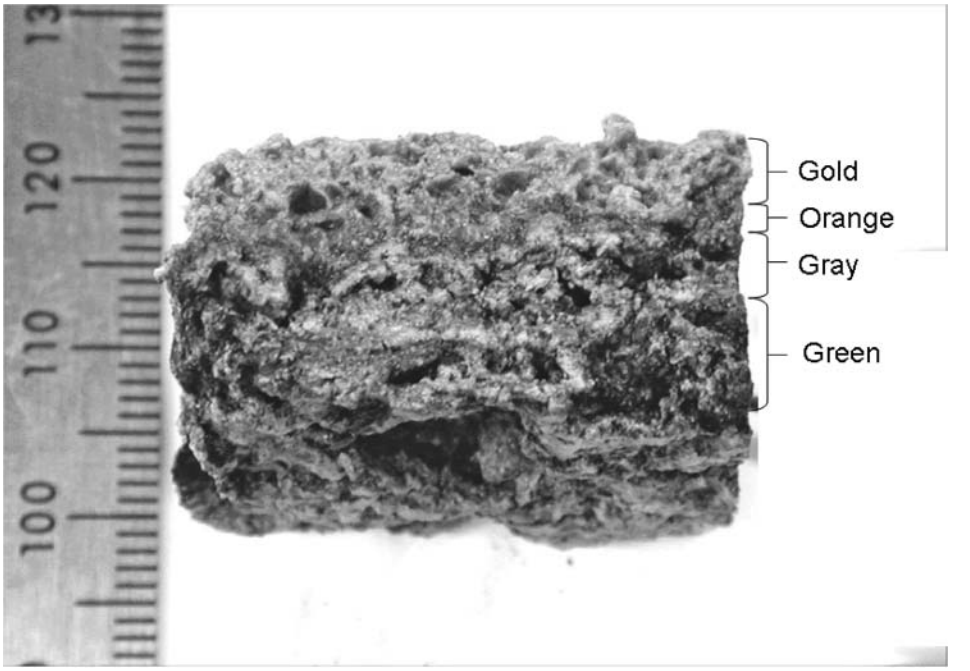

FIGURE 6. Vertical profile of cohesive epipelon encrusted with $CaCO_3$ with distinct laminations. The laminations have distinct colors reflecting strong oxidation-reduction gradients and unique microbial communities. Photo by L. Scinto.

obtained using techniques common to the study of microbial mats. We do so not to make any conclusions but to stimulate and provide focus for future studies.

Internal Structure

Fine-scale studies of the microbial and physiochemical distributions within Everglades periphyton are not especially common. Thomas et al. (2006) reported differences in the biomass, nutrient content, and metabolism between the top 1–2 mm (grey/brown layer) and 13 mm (tan bottom layer) of a cohesive mat. Sharma et al. (2005) coupled vertical thin-sectioning techniques with enzyme-labeled fluorescence phosphatase substrate (ELF-P) to determine that activity is localized to bacterial, rather than algal, surfaces in the middle and lower sections of the mat indicating that P hydrolysis is species-specific and there is a cooperative interaction between algae and bacteria. Donar et al. (2004) utilized a thin-sectioning technique and fluorescent microscopy to enumerate the vertical distribution of algae in a cohesive mat. Techniques such as variable pressure (VPSEM) and low-temperature (LTSEM) scanning electron microscopy that maintain structural integrity are helpful for visualizing internal structures (Figure 5).

Nondestructive collection (Wiltshire et al., 1997), high-resolution horizontal sectioning methods (Kelly et al., 2001; Köster et al., 2008), and stable isotope enrichment experiments (Middleburg et al., 2000) common to estuarine sediment studies offer an approach for studying Everglades periphyton. These methods preserve ultrastructure and yield biochemical information at spatial resolutions comparable to microprobe measurements, thereby enabling coupling of the microbiology with physiochemical properties (e.g., Köster et al., 2008). Methods are available to generate high-resolution profiles of algal pigments, algal abundances, prokaryotic abundances, bulk density, organic carbon, EPS, and enzyme activity (Kelly et al., 2001; Köster et al., 2008). High-resolution studies, however, must take into account the inherent transient dynamics and diurnal patterns. One factor not examined in the Everglades yet is the migratory behavior of microorganism, a phenomenon common to many biofilms (Consalvey et al., 2004; Garcia-Pichel et al., 1994).

Internal Processes

Periphyton photosynthesis is regulated, in part, by optical properties, the density and arrangement of organisms and particles, which vary greatly among periphyton types (Figures 1 and 5). The inherent scattering and absorption mechanisms (arrangement of pigment-containing organisms, EPS, and minerals) determine light attenuation and penetration (i.e., photic depth). With the advent of fiber-optic microprobes, downwelling and scalar

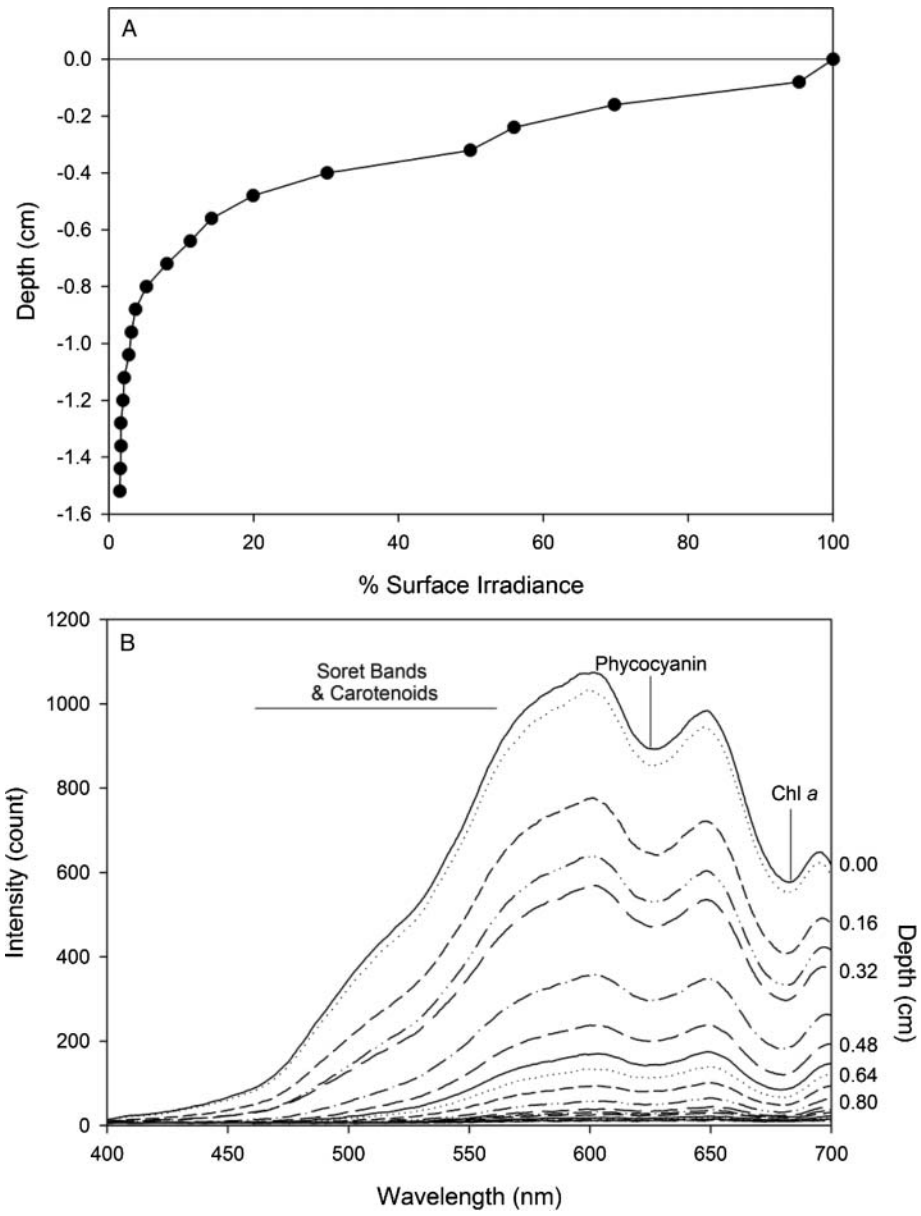

FIGURE 7. Irradiance depth profile (% surface irradiance) (A) and spectral depth profile (B) in an oligotrophic epipelic mat. Surface irradiance equaled 846 μmoles m^{-2} sec^{-1}. The photo zone, defined a 1% surface irradiance extends to a depth of 1.2 cm.

irradiance of microbial mats can be determined (Kühl et al., 1994). For example, downwelling irradiance within a cohesive mat declines exponentially to 1% surface values at 15 mm (Figure 7A), thus restricting photosynthesis to the upper 15 mm. Depth-specific spectral profiles can be used to deduce algal patterns and optical properties with depth (Kühl et al., 1994). The

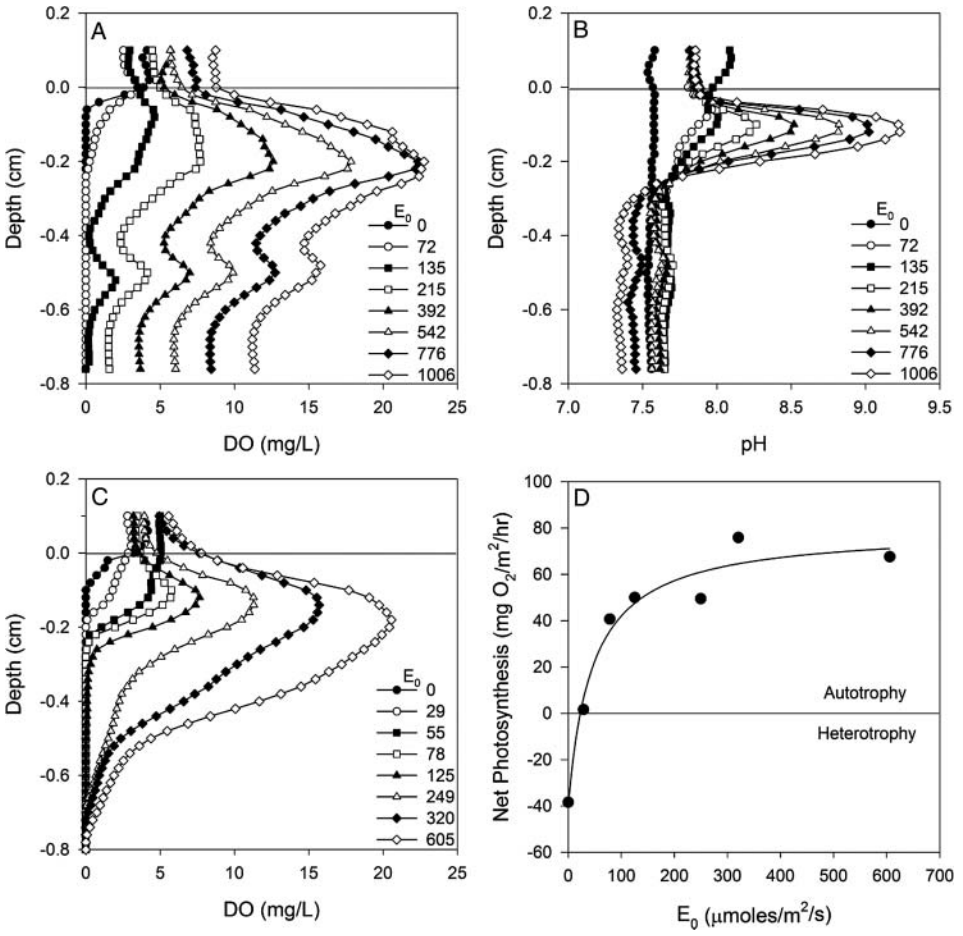

FIGURE 8. Depth profiles and transient dynamics of photosynthetic oxygen and pH for a cohesive metaphytic(A and B) and epipelic mat (C) with increasing irradiance. Oxygen profiles can be modeled to estimate photosynthesis and plotted against irradiance to develop a P-E curve (D).

cohesive mat profile shows the absorbance of the algal pigments phycocyanin and chlorophyll *a* at the appropriate wavelengths (Figure 7B).

Electrochemical and optical sensors are available that couple photosynthesis with biogeochemical measures (Kühl, 2005; Kühl and Polerecky, 2008). Strong vertical gradients develop and dissipate rapidly as a function of photosynthesis. This transient behavior is illustrated for two cohesive mats (Figure 8). Following 10 hr of dark adaptation (heterotrophic metabolism), both mats exhibit a classic clinograde O_2 profile with concentrations approaching 0 mg L^{-1} below 1 mm (Figures 8A and 8C). As irradiance increases to ~1000 μmoles m^{-2} sec^{-1}, positive heterograde O_2 curves quickly develop. Maximum O_2 exceeds 20 mg L^{-1} (>150% saturation) between 2 and 3 mm,

indicating that the highest photosynthesis rates do not occur at the surface, most likely an adaptation to curtail the deleterious effects of exposure to high irradiance. At the periphyton-water interface is the diffusive boundary layer, which regulates molecular diffusion of dissolved material (Boudreau and Jørgensen, 2001). Dynamics below the O_2 maximum differs between the two mats. For the metaphytic mat, higher irradiances increase the depth of O_2 penetration with a secondary maximum but for the epipelic mat a zone of anoxia persists. In the metaphytic mat, pH also exhibits transient behavior with increased irradiance (Figure 8B).

Net photosynthesis (NP), gross photosynthesis (GP), and R can be estimated from O_2 profiles, obtained nondestructively, by numerically solving a no-steady state diffusion-reaction model (Epping et al., 1999). For the epipelic mat (Figure 8C) this method yields NP estimates between −40 and 60 mg O_2 m^{-2} hr^{-1}, GP between 0 and 155 mg O_2 m^{-2} hr^{-1}, and R between 9 and 77 mg O_2 m^{-2} hr^{-1}. Metabolism increases nonlinearly with irradiance, as illustrated in the P-E curve (Figure 8D). With exposure to irradiance, balanced metabolism is rapidly established and net autotrophy sustained with P_{max} occurring between 200 and 400 μmol m^{-2} sec^{-1} and no evidence of photoinhibition (Figure 8D). These profiles illustrate that the oxidation-reduction potential that regulates other biogeochemical reactions (e.g., nitrate reduction, sulfate reduction, methanogenesis) vary dramatically over relatively small spatial (mm) and temporal (min–hr) scales.

RELEVANCE TO RESTORATION AND FUTURE DIRECTIONS

Here we have synthesized Everglades periphyton biogeochemistry in order to identify critical information gaps and needs relevant to restoration. Periphyton is clearly an important component of the Everglades landscape. The well-established relationship of periphyton structure with water quality and hydrology make for powerful metrics to establish Everglades restoration targets and evaluate trajectories (Gaiser, 2009). In contrast, the functional role of periphyton in Everglades biogeochemistry is not well established simply due to the complexity and diversity of the topic. With the possible exceptions of O_2 and P, our periphyton biogeochemistry understanding comes from an alarmingly small number of studies that are often limited in scope and/or spatiotemporal extent. For example, N_2-fixation and MeHg cycling in Everglades periphyton are described with just two published papers each. With limited information, it is difficult to scale up the biogeochemical responses to restoration to the ecosystem level with any degree of certainty. Research efforts should strive for a comprehensive biogeochemical understanding at the ecosystem and community level (Figure 3) that makes use of the wealth of biogeochemical knowledge that exists for other periphyton communities

and aquatic ecosystems (Hell et al., 2008; Paterson and Hagerthey, 2001; Whitton and Potts, 2000).

Among the many restoration uncertainties surrounding periphyton, two seem most worthy as research priorities. The first is to establish periphyton responses to water quality issues other than P. Of particular interest are the ecological consequences of shifting the mineral chemistry of source waters from ombrotrophic (i.e., precipitation) to more minerotrophic (reservoir and canal). One ecosystem consequence associated with mineral enrichment may be sediment stabilization caused by a regime shift (see Hagerthey et al., 2008) toward periphyton with greater inorganic C and EPS content. Such a shift was documented in WCA-2A by Slate and Stevenson (2000). Sediment stabilization by periphyton could alter the flow velocities and sediment transport needed to restore and maintain ridge and slough patterning (Larsen et al., 2011). The second priority is to verify the commonly held assumption that periphyton is the base of the Everglades food web. The conclusion is based on gut content analysis of invertebrates and fish (Browder et al., 1991; Hunt 1953; Rader, 1994); however, stable isotopes analyses (Wankel and Kendall et al., 2002; Kendall, 2001) and large-scale spatial studies of fish gut contents (Trexler, personal communication, 2007) suggests that detritus may be more important. Furthermore, biogeochemical factors such as high $CaCO_3$ content, the presence of toxins and biologically active compounds, and being carbon rich but nutrient poor (high C:P ratios) suggest that periphyton in the oligotrophic Everglades is a poor quality resource. Thus, wildlife restoration would benefit from a thorough investigation of the energetic pathways that connect organisms.

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