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Catabolic diversity of periphyton and detritus microbial communities in a subtropical wetland

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Abstract The catabolic diversity of wetland microbial communities may be a sensitive indicator of nutrient loading or changes in environmental conditions. The objectives of this study were to assess the response of periphyton and microbial communities in water conservation area-2a (WCA-2a) of the Everglades to additions of C-substrates and inorganic nutrients. Carbon dioxide and CH_4 production rates were measured using 14 days incubation for periphyton, which typifies oligotrophic areas, and detritus, which is prevalent at P-impacted areas of WCA-2a. The wetland was characterized by decreasing P levels from peripheral to interior, oligotrophic areas. Microbial biomass and N mineralization rates were higher for oligotrophic periphyton than detritus. Methane production rates were also higher for unamended periphyton (80 mg CH_4-C kg^{-1} d^{-1}) than detritus (22 mg CH_4-C kg^{-1} d^{-1}), even though the organic matter content was higher for detritus (80%) than periphyton (69%). Carbon dioxide production for unamended periphyton (222 mg CO_2-C kg^{-1} d^{-1}) was significantly greater than unamended detritus (84 mg CO_2-C kg^{-1} d^{-1}). The response of the heterotrophic microbial community to added C-substrates was related to the nutrient status of the wetland, as substrate-induced respiration (SIR) was higher for detritus than periphyton. Amides and polysaccharides stimulated SIR more than other C-substrates, and methanogenesis was greater contributor to SIR for periphyton than detritus. Inorganic P addition stimulated CO_2 and CH_4 production for periphyton but not detritus, indicating a P limitation in the interior areas of WCA-2a. Continued nutrient loading into oligotrophic areas of WCA-2a or enhanced internal nutrient cycling may stimulate organic matter decomposition and further contribute to undesirable changes to the Everglades ecosystem caused by nutrient enrichment.

Keywords Catabolic diversity · Everglades · Nutrient enrichment · Periphyton · Substrate-induced respiration

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Introduction

The Florida Everglades was historically a P-limited wetland, but as a result of drainage, altered hydrologic conditions, and nutrient runoff from agricultural soils, the ecosystem has significantly changed in past decades. The Everglades has been divided into several distinct hydrologic units and water conservation

areas, with water conservation area-2a (WCA-2a) being the most studied due to the presence of distinct gradients in total P concentrations from sites of water inflow extending into its interior. Nutrient loading into WCA-2A, in addition to altered hydrologic conditions, has been implicated in causing shifts in vegetation community structure from the indigenous *Cladium* slough areas in the wetland interior to dense stands of *Typha* in P-impacted peripheral areas (Miao and Sklar 1998; Childers et al. 2003). In addition to contributing to changes in vegetation patterns in the Everglades, nutrient loading has altered soil microbial processes (Newman et al. 2001; Wright and Reddy 2001b; Corstanje et al. 2007).

Surface soils from P-impacted and oligotrophic areas of WCA-2a have different composition (McCormick et al. 1996; DeBusk and Reddy 1998), microbial properties, and physiology (Castro et al. 2002). Detritus in the eutrophic areas in the periphery of WCA-2a were comprised of remnants of decaying *Typha*, while the oligotrophic interior of the wetland contained *Cladium* residues overlain by calcareous periphyton (Miao and Sklar 1998; McCormick and O'Dell 1996). Periphyton in WCA-2a consists of assemblages of calcite-precipitating cyanobacteria, diatoms, eukaryotic algae, heterotrophic bacteria, and decomposing *Cladium* residues on submerged surfaces (McCormick and O'Dell 1996; Scinto and Reddy 2003). While detritus in P-impacted areas is dominated by heterotrophic microorganisms, periphyton in oligotrophic areas contains more autotrophic algal and microbial populations (Drake et al. 1996; Castro et al. 2002; Gaiser et al. 2006). Thus, these different areas may exhibit variable responses to nutrient loading or eutrophication, and the microbial activity at these sites may be used as indicators of changes in the trophic status of wetlands or changes in environmental conditions (McCormick et al. 1996; Corstanje et al. 2007).

Heterotrophic microbial activity in wetland soils depends on many factors including nutrients and organic substrate bioavailability, temperature, pH, and redox potential (D'Angelo and Reddy 1999). Bioavailable organic C may limit microbial activity in Everglades soils even though total C levels may be high (Wright and Reddy 2001a). Organic C in wetland soils is present as ligno-cellulose, lignin, or other fractions with varying degrees of recalcitrance (DeBusk and Reddy 1998). Decomposition of particulate organic matter proceeds from the action of fungi and bacteria on plant residues and floc, resulting in production of smaller molecules contributing to the dissolved organic matter pool (Chrost 1991). Labile dissolved organic matter in wetland soils rapidly degrades while more recalcitrant fractions take longer (Chrost 1991). Decomposition of lignin, ligno-cellulose, and other plant residues produces polysaccharides and amino acids utilized in microbial respiratory pathways (Chrost 1991). Decomposition of these compounds by fermentative microorganisms produces alcohols, carboxylic acids, and inorganic nutrients. The exposure of the soil heterotrophic microbial community to broad classes of substrates enables characterization of microbial ecophysiology using measurements of their short-term response to C-substrate addition (Degens and Harris 1997; Degens 1999). Substrate-induced respiration (SIR) is often used as a measure of microbial ecophysiology or metabolic pathways, as the response to added C-substrates may indicate the catabolic diversity of heterotrophs (Degens and Harris 1997). The objectives of this study were to assess the catabolic diversity of the microbial community of P-impacted detritus and oligotrophic periphyton for a subtropical wetland in the Florida Everglades and determine their response to nutrient enrichment.

Materials and methods

Site description and sampling

The study site was located in WCA-2a (44,700 ha) of the Northern Florida Everglades. External nutrient loading increased P concentrations in the soil and water column and contributed to the development of distinct gradients in soil P from primary water inflow points extending into the interior of the wetland (DeBusk et al. 1994; Childers et al. 2003). Sampling sites encompassed a range of P concentrations and vegetative zones, from cattail (*Typha* sp.) at the P-impacted site to sawgrass (*Cladium jamaicense*) and periphyton dominated areas in the interior of the wetland. Delineation of sites was based on trophic state, as the eutrophic site experienced significant external nutrient loading and elevated nutrient levels. The site in the interior of WCA-2a was deemed oligotrophic due to its low nutrient levels, even though

this site may be exposed to low-level nutrient loading. Samples (0–10 cm depth) were collected in June 2001 at two sites along a nutrient enrichment gradient 1.8 km (P-impacted) and 10.8 km (oligotrophic) south of the S10-C water inflow structure. Triplicate cores (15 cm diameter) collected at the P-impacted site were comprised of decomposed *Typha* detritus. Triplicate cores taken in a slough at the oligotrophic site were comprised of calcareous periphyton. All samples were stored at 4°C until analysis.

Analysis of biogeochemical properties

Bulk density was determined on a dry-weight basis after drying at 70°C. Loss on ignition was determined as the mass loss of soil after ashing for 4 h at 550°C. Total C and N were measured after drying (70°C) with a Carlo-Erba NA 1500 CNS Analyzer (Haak-Buchler Instruments, Saddlebrook, NJ). Extractable organic C was measured by extraction with 0.5 M K_2SO_4 (White and Reddy 2000) and analysis with a Dohrmann total organic C analyzer (Rosemount Analytical, Santa Clara, CA). Total P was determined using the ashing method (Anderson 1976) followed by colorimetric analysis (Kuo 1996). Total inorganic P was measured after extraction with 1 M HCl for 3 h, and the $NaHCO_3$-Pi fraction by extraction with 0.5 M $NaHCO_3$, followed by colorimetric analysis (Corstanje et al. 2007). Microbial biomass C and N were measured by chloroform fumigation-extraction (Vance et al. 1987) with an extraction efficiency factor of 0.37 for biomass C and 0.54 for biomass N (Sparling et al. 1990). Microbial biomass P was calculated as the difference between the total P of 0.5 M $NaHCO_3$ extracts of chloroform-fumigated and unfumigated samples (Ivanoff et al. 1998). Mineralizable N and P for periphyton and detritus were measured following incubation for 10 days under N_2 in the dark, followed by extraction with 0.5 M K_2SO_4 (for N) and 1.0 M HCl (for P) and subtraction of initial N and P concentrations (Corstanje et al. 2007).

Basal and substrate-induced CO_2 and CH_4 production

Amendments (C-substrates, plant residues, and inorganic N and P) were added to samples and the response of the heterotrophic microbial community measured as CO_2 and CH_4 production. All incubations were carried out in triplicate and in the dark to minimize autotrophic CO_2 consumption and production. The C-substrates were selected based on their common presence in soil and prior utilization for measurement of catabolic diversity of microbial communities (Degens and Harris 1997; Degens 1998). The classes of substrates tested were alcohols (glycerol, mannitol), amides (glucuronamide), amino acids (alanine, cysteine), aromatics (inosine), carboxylic acids (acetate, formate, oxalate), polysaccharides (glucose, maltose), and plant residues (*Typha*, *Cladium*). The C-substrates were added in excess of microbial requirements to prevent limitation to growth, with the proper application rates determined by prior experimentation (Wright and Reddy 2001a). All C-substrates were dissolved in water, adjusted to the pH of the sample (pH 7), and applied on a C-equivalent basis (25 mg C g^{-1} dry matter) to field-wet samples. In addition, *Typha* and *Cladium* (standing dead tissue) were collected from their respective locations along the nutrient gradient, ground past a 0.5 mm sieve, and added to samples at the same rate as other C-substrates. Inorganic N (as NH_4Cl) was mixed into detritus and periphyton at 1.0 mM and inorganic P (as NaH_2PO_4) at 0.1 mM in solutions buffered to pH 7.

To measure CO_2 production, 10 g of sample were incubated in the dark with amendments under N_2 in 120-ml glass bottles with vials containing 3 ml of 0.5 M NaOH at 30°C. Vials containing NaOH were removed and capped at 2-day intervals until 14 days. For analysis, 1.0 ml of 3 M HCl was added to enclosed vials and resulting headspace CO_2 quantified by gas chromatography (Shimadzu GC-8A, thermal conductivity detector at 25°C, Porapak N column at 20°C). SIR was calculated as the slope of the regression of cumulative CO_2 production over the 14-day incubation period.

To measure CH_4 production, 10 g of sample were incubated in the dark with amendments in 60-ml glass serum bottles under N_2 at 30°C. Aliquots of headspace were taken at 2-day intervals and analyzed for CH_4 using a Shimadzu GC-8A fitted with a flame ionization detector (160°C) and a Carboxen 1000 column (Supelco Inc., Bellefonte, PA) at 110°C. Methane production rates were calculated as the slope of the regression of cumulative CH_4 production during 14 days.

Incubations were also carried out in the absence of C-substrates and nutrients to determine basal

CO_2 and CH_4 production rates. All 14-day incubations were carried out after a 3-day pre-incubation period.

Data analysis

A completely randomized experimental design was utilized with factors being amendment and sampling site along the nutrient gradient. Both CO_2 and CH_4 production rates were linear over the 14-day incubation period, and production rates were calculated as the slope of the regression. Data were analyzed using a two-way ANOVA model to determine significant main effects of amendment and sampling site using Fisher's LSD at $P < 0.05$ (CoStat Statistics Software 2005). Individual amendment comparisons for each site were made using a one-way ANOVA model with the LSD at $P < 0.05$. Cumulative CO_2 and CH_4 production were calculated for each class of C-substrates and for inorganic nutrients (Figs. 1, 2). A one-way ANOVA was used to differentiate main effects of C-substrate class for each site.

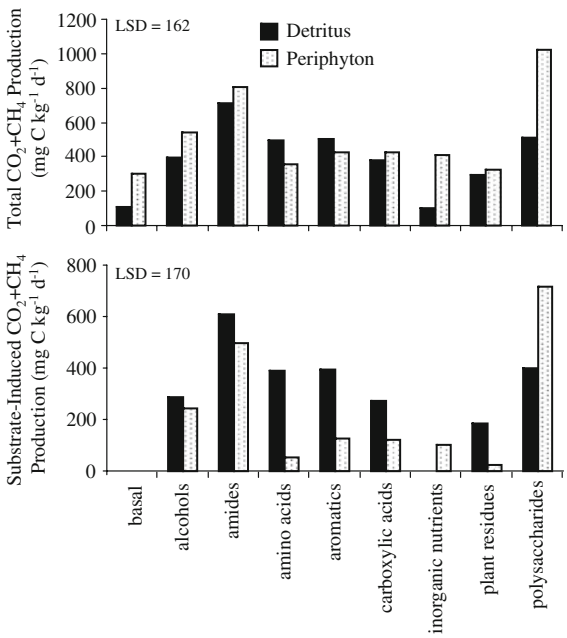

Fig. 1 The total $CO_2 + CH_4$ production rates for detritus and periphyton amended with C-substrates and nutrients. The second graph shows $CO_2 + CH_4$ production after subtracting rates for unamended detritus and periphyton. Data were grouped into the different classes of C-substrates

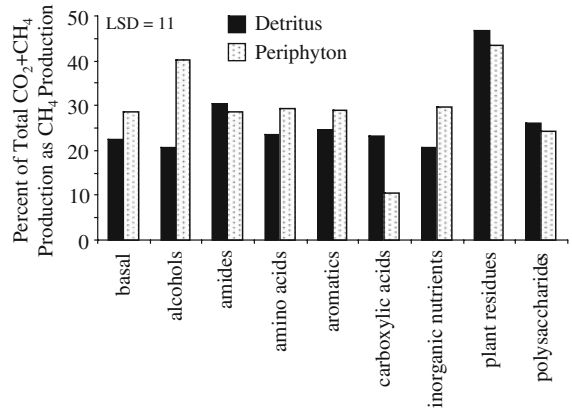

Fig. 2 The percentage of the $CO_2 + CH_4$ production rates as CH_4 production for detritus and periphyton of water conservation area-2a

Results

Biogeochemical properties of detritus and periphyton

Samples from the two sites averaged 90% moisture by weight which is typical for this wetland (Table 1). Bulk density was significantly higher for detritus than periphyton. The primary difference in chemical properties between the two sites was evident by the P status. Total P and inorganic P were 156% and 94% greater for detritus than periphyton. The differences between detritus and periphyton were best illustrated by labile P, which decreased from 77 mg P kg^{-1} at the P-impacted site to 2 mg P kg^{-1} at the interior site.

Extractable NH_4 concentrations were higher in periphyton than detritus (Table 1). Total C levels and LOI were higher in detritus resulting from nutrient-driven increases in plant production and turnover deposition. The inorganic component of the periphyton was greater for periphyton than detritus due to the presence of $CaCO_3$ associated with periphyton communities, thus the lower LOI and organic C concentration at this site.

Even though P levels and organic matter content were higher for detritus than periphyton, microbial biomass C, N, and P were higher for periphyton (Table 1). Patterns of N and P mineralization were similar to those of available inorganic N and P, as mineralizable N was significantly higher for periphyton and mineralizable P tended to be higher for detritus.

Table 1 Chemical and microbial properties of P-impacted detritus and oligotrophic periphyton from water conservation area-2a

Indicator	Detritus	Periphyton	$P < 0.05$
Moisture content (%)	89	91	NS
Bulk density (g cm^{-3})	0.10	0.07	*
Total P (mg P kg^{-1})	1,090	426	*
Total inorganic P (mg P kg^{-1})	388	200	*
$NaHCO_3$-Pi (mg P kg^{-1})	77	2	*
Extractable NH_4(mg N kg^{-1})	50	136	*
Total N (g N kg^{-1})	26	31	NS
Total C (g C kg^{-1})	409	343	*
Loss on ignition (%)	80	69	*
Extractable organic C (mg C kg^{-1})	2800	2,370	*
Microbial biomass C (mg C kg^{-1})	4040	16,900	*
Microbial biomass N (mg N kg^{-1})	721	2,919	*
Microbial biomass P (mg P kg^{-1})	105	134	NS
N mineralized at 10 days (mg N kg^{-1} d^{-1})	22	84	*
P mineralized at 10 days (mg P kg^{-1} d^{-1})	6	3	NS

*Statistical differences ($P < 0.05$) between detritus and periphyton are denoted by significant; NS: not significant

Basal and substrate-induced CO_2 and CH_4 production

Methane production rates were significantly higher for unamended periphyton (80 mg CH_4-C kg^{-1} d^{-1}) than unamended detritus (22 mg CH_4-C kg^{-1} d^{-1}) because of the higher microbial biomass for periphyton even though the organic matter content was higher for detritus. Calculation of SIR involved subtraction of basal CO_2 and CH_4 production rates of unamended samples to assess the response to added C-substrates. Utilization rates of various C-substrates and nutrients varied between detritus and periphyton (Table 2). The greatest stimulation of detritus CH_4 production occurred when samples were amended with glucuronamide, *Typha* residue, and alanine, while periphyton CH_4 production was stimulated the most by mannitol, glucuronamide, and glucose. For periphyton, addition of carboxylic acids did not enhance CH_4 production, and in fact decreased production to rates lower than without amendment. Accounting for basal CH_4 production rates, utilization of C-substrates was significantly greater for detritus than periphyton for most C-substrates except glucose and mannitol.

Similar to CH_4 production, CO_2 production for unamended periphyton (222 mg CO_2-C kg^{-1} d^{-1}) was significantly greater than unamended detritus (84 mg CO_2-C kg^{-1} d^{-1}), illustrating the contribution of periphyton to CO_2 production at the oligotrophic site. However, the response of the detritus heterotrophic microbial community to C-substrate addition was greater than periphyton as demonstrated by higher respiration for the P-impacted site (Table 2).

The greatest enhancement of CO_2 production occurred for detritus amended with glucuronamide, maltose, and alanine, and for periphyton amended with maltose and glucose (Table 2). Utilization rates of polysaccharides by periphyton were greater than other C-substrates. Glucuronamide was readily utilized by both detritus and periphyton as evidenced by high CH_4 and CO_2 production. However, other N-containing C-substrates did not enhance SIR relative to substrates providing only organic C. Most C-substrates, with the exception of maltose and glucose, enhanced CO_2 production for detritus more than periphyton. Similar to CH_4 production, periphyton utilized polysaccharides to a greater degree than detritus. Utilization of plant residues was greater for detritus than periphyton, and residues also enhanced CH_4 production relative to CO_2 production for periphyton.

Total $CO_2 + CH_4$ production for the various types of C-substrates and nutrients is depicted in Fig. 1. The amides and polysaccharides enhanced SIR more than other C-substrates. Some treatments had greater total $CO_2 + CH_4$ production for periphyton than detritus, but when basal respiration was accounted for, the response to C-substrates was greater for detritus than periphyton for all C-substrates except polysaccharides. The proportion of the total $CO_2 + CH_4$ production as CH_4 production averaged 23% and 29% for detritus and periphyton, respectively. The contribution of CH_4 production was often greater for periphyton than detritus, especially when amended with alcohols (Fig. 2). Somewhat surprising was that plant residue-amended periphyton and detritus had the largest proportion of CH_4 production to total $CO_2 + CH_4$ production, averaging 45%. Apparently, heterotrophic microorganisms in periphyton were capable of the rapid breakdown and utilization of particulate

Table 2 CO_2 and CH_4 production rates for detritus and periphyton amended with C-substrates and inorganic nutrients

Amendment	CH_4 production (mg C kg^{-1} d^{-1})			CO_2 production (mg C kg^{-1} d^{-1})		
	Detritus	Periphyton	$P < 0.05$	Detritus	Periphyton	$P < 0.05$
Acetate	73	0	*	200	0	*
Formate	26	0	*	171	257	NS
Oxalate	108	0	*	248	276	NS
Alanine	143	86	*	306	0	*
Cysteine	43	0	*	293	85	*
Typha	148	58	*	112	0	*
Cladium	82	64	NS	31	0	NS
Maltose	128	122	NS	349	702	*
Glucose	93	150	*	233	463	*
Glucuronamide	198	147	NS	410	353	NS
Inosine	102	38	*	295	87	*
Glycerol	47	84	NS	238	0	*
Mannitol	74	183	*	220	228	NS
NH_4	8	0	NS	12	20	NS
P	0	170	*	0	0	NS
NH_4 + P	1	0	NS	1	204	*
LSD	79	58		168	214	

Rates for unamended detritus and periphyton were subtracted from the total CO_2 and CH_4 produced for amended samples

*Denotes significant differences between detritus and periphyton at $P < 0.05$; NS designates no significant differences

organic matter, likely as a result of the high microbial biomass.

Response of the heterotrophic microbial community to inorganic N and P

Inorganic N and P addition resulted in equivalent CO_2 and CH_4 production rates as unamended detritus and periphyton (Table 2). For detritus, nutrient addition did not enhance CO_2 or CH_4 production. However, P addition stimulated periphyton CH_4 production to rates exceeding that of detritus. Nitrogen + P addition also enhanced periphyton CO_2 production to levels greater than for detritus. Nitrogen addition failed to enhance SIR for periphyton because this site likely had non-limiting extractable NH_4 concentrations (Table 1).

Discussion

Nutrient loading in this wetland alleviated some nutrient limitations and altered the microbial ecophysiology and catabolic diversity of the microbial community, which may influence organic matter accumulation and decomposition dynamics (McCormick et al. 1996; Gaiser et al. 2005; Corstanje et al. 2007). Even though WCA-2a was historically P-limited, nutrient loading has removed the P limitation which may have induced a N limitation (White and Reddy 2003). Thus, available N was likely readily sequestered by biota at the P-impacted site which decreased soil and water NH_4 concentrations compared to the oligotrophic interior.

Differences in the P status between sites was most evident in total and labile P, which represented the cumulative effect of long-term external nutrient loading into this wetland primarily resulting from runoff and drainage of agricultural fields during the past century (Childers et al. 2003; Gaiser et al. 2006). The $NaHCO_3$-Pi fraction represents the most labile P form having the greatest potential for enhancing microbial activity and changing the wetland ecosystem. The ecosystem at the oligotrophic site is characterized by P-limited conditions where historic P inputs including deposition by rainfall and periodic overflow from Lake Okeechobee (Davis 1991; DeBusk et al. 1994). Thus, the vegetation and microbial communities developed under P-limited conditions. Changes to vegetation patterns induced in part by nutrient loading altered the catabolic diversity of the microbial communities and the wetland substrate from the indigenous periphyton to a detritus-based system, the composition of which changed from an autotrophic to

a more heterotrophic system. This resulted in the establishment of microbial communities with greater potential for organic matter decomposition, and ultimately increased rates of various other microbial processes.

Phosphorus mineralized by organic matter decomposition at the oligotrophic site is often rapidly sequestered by periphyton and the microbial community (McCormick et al. 1996), resulting in low levels of labile P (Noe et al. 2003). Likewise, lower NH_4 concentrations at the P-impacted site were an indication of N sequestration by the heterotrophic microbial community and removal of the P limitation. Similar results were observed in other studies, which indicated a N limitation in P-impacted areas of Everglades wetlands (White and Reddy 2003). Nutrient enrichment increased organic matter decomposition rates in Everglades wetlands (Amador and Jones 1995; Qualls and Richardson 2000; Newman et al. 2001). Higher organic matter mineralization rates in WCA-2a are evidenced by accumulation of inorganic N and P in soil, hence the close relationship between organic N and P mineralization rates and NH_4 and P accumulation.

Periphyton is generally not exposed to the high levels of organic C inputs as the heterotrophic microbial community at the P-impacted site, primarily because of its nutrient-poor environment which limits plant production and decomposition (Miao and Sklar 1998). In fact, organic matter decomposition of periphyton at oligotrophic sites has been shown to be limited by inorganic P (Amador and Jones 1995). An advantage detritus has over periphyton for C utilization is the high levels of inorganic nutrients generated by higher organic matter decomposition rates (White and Reddy 2000; Corstanje et al. 2007).

The combination of changes in the litter source and nutrient concentrations has shifted both the quantity and quality of C inputs into the ecosystem (DeBusk and Reddy 1998). Heterotrophic bacteria dominated the P-impacted detritus (Wright and Reddy 2001a), and thus were more capable of rapidly utilizing added C-substrates and were more sensitive to nutrient and C inputs, or altered hydrologic conditions. Periphyton at the oligotrophic site contained higher proportions of algae, so the response to added C-substrates was lower. Even though basal CH_4 production was higher for periphyton than detritus, the response of the heterotrophic microbial community to C-substrates was greater for detritus than periphyton. Perhaps nutrient limitations to the microbial communities at the oligotrophic site limited SIR after exposure to high organic C inputs.

Methanogenesis was a dominant pathway of organic matter decomposition at the oligotrophic site, as aerobic respiration is curtailed by the presence of flooded conditions and the lack of O_2, and denitrification and SO_4 reduction were minimal due to low levels of NO_3 and SO_4 at this site (DeBusk et al. 1994; Wright and Reddy 2001a). In contrast, P-impacted areas typically have significantly higher NO_3 and SO_4 levels (DeBusk et al. 1994) which support higher rates of denitrification and SO_4 reduction than oligotrophic areas (Koch-Rose et al. 1994; Wright and Reddy 2001a). Thus, metabolic pathways having CO_2 as the primary endproduct dominated P-impacted areas while methanogenesis was more prevalent at oligotrophic areas. These findings have important implications since organic matter turnover rates are lower for methanogenesis than other metabolic pathways (Wright and Reddy 2001a). Increased nutrient loading to oligotrophic areas and the resulting increases in plant production and deposition of detritus may shift the heterotrophic microbial community away from methanogenesis and toward denitrification and SO_4 reduction, ultimately increasing organic matter turnover rates and nutrient regeneration, and potentially contributing to undesirable changes to the Everglades ecosystem which are currently observed in P-impacted areas.

Conclusions

Detritus and periphyton exhibited variable responses to addition of C-substrates and nutrients, indicating differences in the catabolic diversity of the heterotrophic microbial community resulting from nutrient enrichment. Nutrient loading changed the microbial community composition from a periphyton-dominated system in the oligotrophic interior of WCA-2a to a system dominated by heterotrophic microorganisms. The oligotrophic site was characterized by higher levels of microbial biomass which likely contributed to higher CO_2 and CH_4 production relative to P-impacted detritus. However, the heterotrophic microbial community for detritus was more sensitive to C-substrate addition by quickly utilizing more of

the substrates than periphyton. In contrast, the periphyton at the oligotrophic site was more sensitive and responded more readily to inputs of inorganic nutrients than detritus. These results indicate potential problems if future nutrient loading increases the extent of enrichment into the interior of WCA-2a. Continued nutrient loading or internal cycling from the periphery to the oligotrophic interior of the wetland may alter the catabolic diversity of the heterotrophic microbial community and stimulate organic matter decomposition. The resulting increase in nutrient availability may alter pathways of organic matter decomposition and stimulate denitrification and SO_4 reduction at the expense of methanogenesis. The resulting regeneration of N and P from organic matter decomposition to floodwater may further exacerbate the harmful effects of nutrient enrichment on the ecosystem which are currently observed in P-impacted areas.

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