Substrate-Induced Respiration for Phosphorus-Enriched and Oligotrophic Peat Soils in an Everglades Wetland

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The Florida Everglades ecosystem developed as relatively nutrient poor and supported vegetation adapted to these conditions. In the past century, the Everglades was drained and separated into hydrologic units where water movement and storage were controlled. Nutrient runoff from agricultural soils and altered hydrologic conditions have changed the Everglades ecosystem by increasing soil nutrient levels, particularly P, which promoted vegetation intrusions by cattail (Typha domingensis Pers.) into areas previously dominated by the indigenous sawgrass (Cladium jamaicense Crantz) (Davis, 1991; Childers et al., 2003).

In addition to contributing to changes in vegetation patterns in the Everglades, nutrient loading has altered soil biogeochemical properties (Newman et al., 2001; Wright and Reddy, 2001a, 2001b; Corstanje et al., 2007). The addition of limiting nutrients to ecosystems can alter the structure and function of the vegetation and soil microbial communities. The response of the microbial community, however, may be quicker and more sensitive to elevated nutrient levels than vegetation. Changes in vegetation patterns due to nutrient loading may take years to be observed (Chiang et al., 2000; Noe et al., 2002), while microbial processes may be altered after only a short exposure (McCormick and O’Dell, 1996; Corstanje et al., 2007). Thus, microbial processes and patterns may be suitable as sensitive early indicators of nutrient enrichment or changes in environmental conditions.

Organic matter decomposition and HMA in wetland soils depends on many factors, including available nutrients, organic substrates, and environmental factors such as temperature, pHi, and redox potential (D’Angelo and Reddy, 1999). Available C may limit microbial activity in Everglades soils even though total C levels may be high (Amador and Jones, 1995; Wright and Reddy, 2001a). Carbon in wetland soils is present as lignocellulose, lignin, or other fractions with varying degrees of recalcitrance (DeBusk and Reddy, 1998). Organic matter in wetland soils often undergoes a short-term rapid breakdown of labile portions of the dissolved organic C pool followed by a longer term degradation of more recalcitrant fractions (Chrost, 1991). Decomposition of lignin, lignocellulose, and other plant residues produces polysaccharides and amino acids, which are 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 charac-

Nutrient enrichment may alter patterns of heterotrophic microbial activity (HMA) in wetland soils and influence organic matter decomposition dynamics. The response of the heterotrophic microbial community to C substrates (alcohols, amides, amino acids, aromatics, plant residues, and polysaccharides) was measured as CO2 and CH4 production in detritus and soil (0–10 cm) collected from P-enriched and oligotrophic areas of Water Conservation Area 2a (WCA-2a) of the Everglades. The wetland was characterized by decreasing P levels from peripheral to interior, oligotrophic areas. Denitrification and SO4 reduction appeared to be the primary metabolic pathways at the P-enriched site, whereas the contribution of methanogenesis to organic matter decomposition was greater in the oligotrophic interior of the wetland. Methane production averaged 38 and 48% of the total CO2 + CH4 production for P-enriched and oligotrophic detritus, respectively. Basal CO2 production of detritus was 36% higher at the P-enriched than the oligotrophic site, but CH4 production was 43% greater at the oligotrophic site. All C substrates enhanced CO2 and CH4 production, indicating that labile organic C may be limiting in this wetland, and the types of C substrates used by the heterotrophic microbial community varied between P-enriched and oligotrophic sites. Substrate-induced respiration was 71 and 48% greater at the P-enriched than the oligotrophic site for detritus and soil, respectively. Nutrient loading, particularly P, promoted the development of a N-limited system near the periphery of the wetland, while the oligotrophic interior was characterized by P-limited conditions. Continued nutrient loading into oligotrophic areas of WCA-2a may enhance HMA and stimulate organic matter decomposition and nutrient regeneration, and further contribute to undesirable changes to the Everglades ecosystem.

Abbreviations: HMA, heterotrophic microbial activity; SIR, substrate-induced respiration; WCA-2a, Water Conservation Area 2a.
terization of microbial ecophysiology using measurements of their short-term response to C-substrate addition (Degens and Harris, 1997; Degens, 1999). Substrate-induced respiration is often used as a measure of microbial ecophysiology, as the response of HMA to added C substrates may indicate the catabolic diversity of soil heterotrophs (Degens and Harris, 1997).

Characterization of the metabolic activities of the heterotrophic microbial communities has been successfully utilized in understanding C flow in ecosystems (Degens, 1999; Corstanje et al., 2007). Eutrophication of Everglades wetlands has increased enzyme activity and C metabolism (Wright and Reddy, 2001b; Corstanje and Reddy, 2004), and altered organic matter decomposition dynamics (DeBusk and Reddy, 2003). Wetland soils at different trophic states may exhibit variable HMA, which ultimately influences organic matter dynamics by altering the metabolic pathways of decomposition. The objectives of this study were to determine the response of heterotrophic microbial communities to added C substrates and inorganic nutrients for P-enriched and oligotrophic detritus and soil in WCA-2a of the Everglades.

**MATERIALS AND METHODS**

**Site Description and Sampling**

The study was conducted in WCA-2a (44,700 ha) of the northeastern Florida Everglades. This wetland was historically P limited and vegetated by *Cladium*, periphyton, and open-water sloughs (Davis, 1991; Childers et al., 2003). 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 structures extending into the interior of the wetland (DeBusk et al., 1994; Childers et al., 2003). Nutrient loading has been implicated as a factor in causing ecosystem shifts including changes in vegetation patterns from indigenous *Cladium* to *Typha*-dominated ecosystems, resulting in changes in organic matter accumulation rates, water quality, and biogeochemical processes (Reddy et al., 1993; DeBusk and Reddy, 2003).

Detritus and soil samples (0–10 cm) were collected in March 1999 at two sites along a nutrient-enrichment gradient 2.3 (P-enriched) and 10.2 km (oligotrophic) south of the S10-C water inflow structure of WCA-2a. Detritus consisted of recently deposited plant material while peat consisted of consolidated and decomposed organic matter. Sampling sites encompassed a range of soil P concentrations and vegetative zones, from *Typha* at the P-enriched site to *Cladium*-periphyton-dominated areas in the oligotrophic interior of the wetland. A total of nine soil cores (15-cm diameter) were taken at each site, with triplicate cores composited to yield three replicate samples per site. Detritus was collected from above the cored soil, and all samples were stored at 4°C until analysis.

**Soil Characterization**

Loss-on-ignition was determined as the mass loss of soil after ashing for 4 h at 550°C. Extractable organic C was measured by extraction with 0.5 mol L⁻¹ K₂SO₄ followed by analysis with a Dohrmann total organic C analyzer (Teledyne Tekmar, Mason, OH). Microbial biomass C was measured by fumigation-extraction (Vanca et al., 1987) with an extraction efficiency factor of 0.37 for biomass C (Sparling et al., 1990). Microbial biomass P was calculated as the difference between the total P of 0.5 mol L⁻¹ NaHCO₃ extracts of chloroform-fumigated and unfumigated samples (Ivanoff et al., 1998). Soil total P was determined by ashing at 550°C (Anderson, 1976) and NaHCO₃-P by extraction with 0.5 mol L⁻¹ NaHCO₃ (Corstanje et al., 2007), followed by colorimetric analysis (USEPA, 1993, Method 365.4).

**Basal and Substrate-Induced Respiration**

Amendments (C substrates, plant residues, and inorganic N and P) were added to the soil and the response of heterotrophic microbial communities measured as CO₂ and CH₄ production. The C substrates were selected based on their common presence in soil and prior utilization for measurement of catabolic diversity of soil microbial communities (Degens and Harris, 1997; Degens, 1998). The classes of substrates tested were alcohols (glycerol and mannitol), amides (glucuronamide), amino acids (alanine, cysteine, aspartate, and glutamine), aromatics (inosine), and polysaccharides (glucose and maltose). The C substrates were added in excess of microbial requirements to prevent limitation to growth. All C substrates were dissolved in distilled water, adjusted to the pH of the soil (pH = 7), and applied on a C-equivalent basis (25 g C kg⁻¹ soil), followed by thorough mixing into the soil. In addition, standing dead *Typha* and *Cladium* tissue was collected from respective sites, ground past a 0.5-mm sieve, and applied on a C-equivalent basis. Inorganic N and P were utilized to assess the response of the heterotrophic microbial community to nutrient loading. Inorganic N was applied at 1.0 mmol L⁻¹ as NH₄Cl and inorganic P at 0.1 mmol L⁻¹ as NaH₂PO₄ solutions buffered to pH 7.

For measurement of CO₂ production, 10 g of soil was incubated with amendments under N₂ in 120-mL glass bottles with 20-mL vials containing 3 mL of 0.5 mol L⁻¹ NaOH at 30°C. Vials containing NaOH were removed and capped at 2-d intervals for 14 d. For analysis, 1.0 mL of 3 mol L⁻¹ HCl was added to enclosed vials and resulting headspace CO₂ quantified by gas chromatography (S Haupt GC-8A thermal conductivity detector at 25°C, Shimadzu Corp., Kyoto, Japan; Poropak N column at 20°C). Substrate-induced respiration was calculated as the slope of the regression of cumulative CO₂ production during the 14-d period.

For measurement of CH₄ production, 10 g of soil was incubated with amendments in 60-mL glass serum bottles under N₂ at 30°C. Every 2 d, aliquots of headspace were analyzed for CH₄ using a Shimadzu GC-8A fitted with a flame ionization detector (160°C) and a Carbosyn 1000 column (Supelco, Bellefonte, PA) at 110°C. Methane production rates were calculated as the slope of the regression of cumulative CH₄ production during 14 d. Incubations were also performed in the absence of C substrates and nutrients to determine basal respiration rates.

**Data Analysis**

No significant differences in the response of C substrates within groups were observed, so C substrates were grouped into alcohols, amides, amino acids, aromatics, plant residues, and polysaccharides for analyses and presentation. A completely randomized experimental design was used, with factors being amendment, sampling site, and soil depth. Data were analyzed using a three-way ANOVA model to determine significant main effects of amendment, sampling site, and depth using Fisher’s LSD at P < 0.05 (CoHort Software, 2005). Individual treatment comparisons for each site and depth were made using a one-way ANOVA with the LSD at P < 0.05.

**RESULTS**

**Biogeochemical Parameters**

Soil moisture content averaged 94% and bulk density 0.09 g cm⁻³, and neither was affected by P enrichment (data...
The aromatic and plant residue amendments promoted higher CO2 production for P-enriched and oligotrophic detritus, and all soil for most treatments. The majority of C substrates stimulated site. For detritus, relatively few C substrates caused higher CH4 proportion of CO2 + CH4 production to 10-cm soil, in addition to a greater contributed a greater proportion of total 10-cm soil, respectively. Methanogenesis production for the detritus and the 0- to 10-cm soil, however, basal CH4 production was lower than all C-substrates treatments. Basal CO2 production and SIR were higher in detritus than soil for most treatments. The majority of C substrates stimulated CO2 production for P-enriched and oligotrophic detritus, and all C substrates enhanced CO2 production for the 0- to 10-cm soil relative to basal respiration. For both P-enriched and oligotrophic detritus, polysaccharides provoked a significantly greater response in CO2 production than other C substrates, while plant residues provoked the least response. Alcohol treatments generally had the lowest CO2 production, while few differences between other C substrates were observed. Averaged across C substrates, the P-enriched site had 71% and 48% greater CO2 production in detritus and soil, respectively, than the oligotrophic site.

Detritus CH4 production exhibited a mixed response to P loading (Table 3). Basal CH4 production did not differ between sites, but SIR for alcohol and polysaccharide amendments was greater for oligotrophic than P-enriched detritus, while CH4 production for amide, aromatic, and plant residue treatments was greater for P-enriched than oligotrophic sites. In the soil, basal CH4 production did not differ between sites. The aromatic and plant residue amendments promoted higher soil CH4 production at the P-enriched than the oligotrophic site. For detritus, relatively few C substrates caused higher CH4 production than the unamended treatment. For the 0- to 10-cm soil, however, basal CH4 production was lower than all C-substrate treatments.

Basal and substrate-induced CH4 production was higher in detritus than the 0- to 10-cm soil for both sites. Basal CO2 production was 60% higher than CH4 production for P-enriched detritus, but CH4 production was 22% higher than CO2 production at the oligotrophic site. Averaged across C substrates, CO2 production was 17% and 145% greater than CH4 production for the detritus and the 0- to 10-cm soil, respectively. Methanogenesis contributed a greater proportion of total SIR for detritus than the underlying 0- to 10-cm soil, in addition to a greater proportion of CO2 + CH4 production at the oligotrophic than the P-enriched site (Fig. 1).

**Substrate-Induced Respiration**
Carbon dioxide production was higher at the P-enriched than the oligotrophic site for unamended detritus and for all C-substrate treatments (Table 2). Basal CO2 production for detritus was 36% higher at the P-enriched than the oligotrophic site. For the 0- to 10-cm soil, basal respiration rates did not vary between sites, and only for aromatic and polysaccharide amendments were differences in substrate-induced respiration (SIR) observed between sites. Basal CO2 production and SIR were higher in detritus than soil for most treatments. The majority of C substrates stimulated CO2 production for P-enriched and oligotrophic detritus, and all C substrates enhanced CO2 production for the 0- to 10-cm soil relative to basal respiration. For both P-enriched and oligotrophic detritus, polysaccharides provoked a significantly greater response in CO2 production than other C substrates, while plant residues provoked the least response. Alcohol treatments generally had the lowest CO2 production, while few differences between other C substrates were observed. Averaged across C substrates, the P-enriched site had 71% and 48% greater CO2 production in detritus and soil, respectively, than the oligotrophic site.

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**Response of Heterotrophic Microbial Community to Inorganic Nitrogen and Phosphorus**
Phosphorus addition stimulated CO2 production compared with basal respiration for both detritus and soil at the oligotrophic but not the P-enriched site (Table 2). In contrast, inorganic N addition stimulated CO2 production for P-enriched but not oligotrophic soil. Nitrogen-amended detritus and soil CO2 production were higher for the P-enriched than the oligotrophic site. The opposite occurred, however, for P-amended soil. Similar to CO2 production, inorganic P addition resulted in greater CH4 production at the oligotrophic than the P-enriched site (Table 3). Likewise, CH4 production in inorganic N-amended detritus tended to be greater at the P-enriched site.

**DISCUSSION**
Short-term incubations measure the ability of soil microorganisms to rapidly utilize C substrates and indicate the presence of enzyme systems capable of substrate utilization (Degens and Harris, 1997; Degens, 1998). This short-term utilization indicates a previous exposure to these C substrates and indicates the types of C substrates typically present in soil. All added C substrates enhanced SIR in the 14-d incubation for both detritus and soil, indicating that a wide range of substrates are typically produced during the decomposition of Typha and Cladium residues in this wetland. The ability of

<table>
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<th>Indicator</th>
<th>P-enriched</th>
<th>Oligotrophic</th>
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<tr>
<td>Detritus Total P, mg P kg(^{-1})</td>
<td>1890*</td>
<td>693</td>
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<tr>
<td>NaHCO(_3)-P, mg P kg(^{-1})</td>
<td>15*</td>
<td>0</td>
</tr>
<tr>
<td>Microbial biomass P, mg P kg(^{-1})</td>
<td>344*</td>
<td>151</td>
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<tr>
<td>Microbial biomass C, mg C kg(^{-1})</td>
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<td>4331</td>
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<tr>
<td>Extractable organic C, mg C kg(^{-1})</td>
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<td>3183</td>
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<td>Loss-on-ignition, %</td>
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<td>82</td>
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<tr>
<td>Soil Total P, mg P kg(^{-1})</td>
<td>796*</td>
<td>336</td>
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<tr>
<td>Microbial biomass C, mg C kg(^{-1})</td>
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<tr>
<td>Extractable organic C, mg C kg(^{-1})</td>
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<td>2290</td>
</tr>
<tr>
<td>Loss-on-ignition, %</td>
<td>89</td>
<td>85</td>
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*Significant difference between sites at \(P < 0.05\).

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<tr>
<td>Detritus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal</td>
<td>254 d</td>
<td>187 d</td>
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<tr>
<td>Alcohol</td>
<td>521 b</td>
<td>287 bc</td>
</tr>
<tr>
<td>Amides</td>
<td>519 b</td>
<td>311 ab</td>
</tr>
<tr>
<td>Amino acids</td>
<td>537 b</td>
<td>355 ab</td>
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<tr>
<td>Aromatics</td>
<td>530 b</td>
<td>293 b</td>
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<tr>
<td>Polysaccharides</td>
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<td>370 a</td>
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<tr>
<td>Plant residues</td>
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<td>202 cd</td>
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<tr>
<td>NH(_4)-N</td>
<td>208 de</td>
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</tr>
<tr>
<td>P</td>
<td>251 d</td>
<td>246 c</td>
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</table>

*Values in columns for each depth followed by the same letter were not significantly different at \(P < 0.05\).
the effects of nutrient loading on stimulation of microbial bio-

mass and elevated nutrient concentrations. Indeed, significant relationships between microbial biomass and microbial respiration were observed in other studies in the Everglades (DeBusk and Reddy, 1998; White and Reddy, 2000). Carbon dioxide and CH$_4$ production rates were higher in surface detritus than the underlying soil. Similar results were observed for other studies in the Everglades (Amador and Jones, 1995; Wright and Reddy, 2001a), as the most recently deposited material was more biologically active than the underlying soil.

Heterotrophic microbial activity at the oligotrophic site appeared to be limited by inorganic P in addition to labile organic C. Addition of P did not increase HMA at the P-enriched site; however, both CO$_2$ and CH$_4$ production at the oligotrophic site increased with P addition, suggesting no P limitation. In other studies, P addition had no impact on microbial respiration for high-P soils in the Everglades (Amador and Jones, 1995). Addition of inorganic N to detritus and soil from the P-enriched site enhanced HMA in some cases, suggesting a possible N limitation in areas of WCA-2a having elevated P levels (White and Reddy, 2003). Water Conservation Area 2a was historically P limited, but external nutrient loading has resulted in significant increases in soil P in areas adjacent to water-inflow points (Childers et al., 2003). The removal of the P limitation by external nutrient loading probably induced a N limitation, as evidenced by stimulation of CO$_2$ and CH$_4$ production from inorganic N addition.

At both P-enriched and oligotrophic sites, CO$_2$ production was generally higher than CH$_4$ production. The plant residue amendments were expected to show the least enhancement of SIR of all C-substrate treatments due to their more complex nature compared with soluble C substrates. Decomposition of plant residues requires the presence of numerous extracellular enzymes needed for the breakdown of large particles into smaller molecules that can be taken up by microbial cells (Chrost, 1991). Methane production in treatments receiving plant residues was comparable to other treatments, however, especially at the oligotrophic site. In fact, CH$_4$ production often exceeded CO$_2$ production when plant residues were added (Tables 2 and 3), indicating the ability of the heterotrophic microbial community to rapidly utilize plant residues.

Increases in NO$_3$ and SO$_4$ concentrations have occurred near water-inflow points in WCA-2a concomitant with P enrichment (DeBusk et al., 1994). The contribution of CH$_4$ production to total CO$_2$ + CH$_4$ production was greater at oligotrophic sites (Fig. 1), probably because higher nutrient levels at P-enriched sites near water-inflow points supported denitrification and SO$_4$ reduction, resulting in high CO$_2$ production rates.
(DeBusk et al., 1994; Childers et al., 2003). In contrast, nutrient-poor conditions and lower NO$_3$ and SO$_4$$_2$ levels at the oligotrophic site (DeBusk et al., 1994) promoted methanogenesis and higher rates of CH$_4$ production relative to CO$_2$ production. Methanogens are often outcompeted for C substrates by NO$_3$$_2$- and SO$_4$$_2$-reducing microorganisms due to differences in potential thermodynamic energy yields (Achtnich et al., 1995; Drake et al., 1996), hence the greater proportion of CH$_4$ to total SIR in oligotrophic than P-enriched areas. Thus, the catabolic diversity of heterotrophic microbial communities varied with nutrient enrichment, from metabolic pathways with CO$_2$ as the end product at the eutrophic site to pathways producing CH$_4$ as the end product at the oligotrophic site.

CONCLUSIONS

Factors influencing HMA included C substrates and inorganic nutrients. The heterotrophic microbial community in WCA-2a possessed the ability to rapidly utilize a wide variety of C substrates, indicating that labile organic C was a limiting factor to HMA. Patterns of SIR varied between oligotrophic and P-enriched sites: CH$_4$ production had a greater contribution to total SIR in oligotrophic than P-enriched soils, indicating that external nutrient loading altered the metabolic pathways of organic matter decomposition. The diversity of heterotrophic microbial communities was also evident in that HMA was limited by inorganic N at the P-enriched site and by inorganic P at the oligotrophic site. Stimulation of the heterotrophic microbial community by inorganic nutrients, and the resulting increase in organic matter decomposition, has significant implications for management of the Everglades ecosystem. Continued external loading into WCA-2a and increased nutrient availability may alter pathways of organic matter decomposition and stimulate denitrification and SO$_4$$_2$ reduction at the expense of methanogenesis, decreasing total soil organic C storage in this wetland. The resulting regeneration of N and P from organic matter decomposition to floodwater may further exacerbate the harmful effects of nutrient enrichment on the Everglades ecosystem currently observed in P-enriched areas of WCA-2a.

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