DIVISION S-10—WETLAND SOILS

Methane Production and Emissions from Four Reclaimed and Pristine Wetlands of Southeastern United States

Louis A. Schipper* and K. R. Reddy

ABSTRACT

Wetlands are significant contributors to global CH₄ emission. We measured CH₄ emissions at two pristine wetlands (Okefenokee swamp and the Everglades (Water Conservation Area 2A)) and two reclaimed wetlands (Sunny Hill Farm and Apopka Marsh) in Southeastern USA, and we attempted to relate emissions to CH₄ production rates of the soil and the soil's biological and chemical properties. Methane emissions through cattail [Typha sp.] and waterlily (Nymphaea odorata (L.)) ranged from 0.09 to 1.7 g CH₄ m⁻² d⁻¹ and exhibited high spatial and temporal variability. Diffusive flux of CH₄ was calculated using dissolved CH₄ profiles in the soil pore water and accounted for <5% of the plant-mediated emissions. Potential CH₄ production rates were measured as a function of depth using soil samples obtained at 2-cm increments. Methane production rates were the same order of magnitude at all sites (<1–70 ng CH₄-C g⁻¹ soil C d⁻¹) and were highest in the surface soils (0–6 cm) at three of the wetland sites, indicating that the predominant source of C available to methanogens was in the surface soils. Methane production rates in the top 2 cm ranged from 0.3 to 1.1 g CH₄ m⁻² d⁻¹ and annual C losses due to anaerobic decomposition accounted for between 0.68 and 3.7% of the total C in the surface 24-cm soil depth. Methane production was observed at sites with porewater SO₄ concentrations of up to 20 mg SO₄⁻² L⁻¹, suggesting that methanogenesis occurred in the same soil layer as SO₄ reduction, possibly in microsites where SO₄ concentration was depleted.

RECENT attention has focused on the importance of CH₄ as a greenhouse gas. Tropospheric CH₄ concentrations have increased during the last 10 yr at a rate >1% per year and wetlands are considered a major source of atmospheric CH₄ (Bole et al., 1986). Flooded soils, including rice paddies and natural wetlands, provide conditions where methanogenesis is favored, because they often have high C content due to the high productivity of wetland plant species and the slow rate of decomposition of plant matter under anaerobic conditions (Reddy and Patrick, 1984). In recent years, increased efforts have been made to quantify CH₄ emissions from various wetlands (summarized by Bartlett and Harriss, 1993), and many of these studies have reported a high degree of variability both within and between wetland sites. Some of the variability of CH₄ emissions from wetlands has been attributed to temperature (Crill et al., 1988; Lansdown et al., 1992), water depth (Sebacher et al., 1986; Harriss et al., 1988), soil salinity (Bartlett et al., 1987), CH₄ oxidation rate (King et al., 1990), and vegetation presence and productivity (Whiting et al., 1991). However, few studies have examined the importance of soil physico-chemical properties as regulators of CH₄ production and emissions (Bartlett et al., 1987; Bachoon and Jones, 1992; Bridgham and Richardson, 1992). Harriss and Sebacher (1981) suggested that CH₄ emissions were correlated to C inputs and cycling in cypress swamps.

Methanogenesis is often the terminal step of organic matter decomposition in freshwater wetlands. Methanogenic bacteria are able to use only a limited array of low molecular weight C compounds for energy production and are dependent on a consortium of hydrolytic and fermentative bacteria to break down higher molecular weight compounds into lower molecular weight compounds (Oremland, 1988). In surface soils, the presence of electron acceptors such as NO₃ and SO₄ may result in methanogens being outcompeted by other anaerobic bacteria (Oremland, 1988). At lower soil depths, remaining C is likely to have already undergone considerable decomposition, and bioavailability of C may limit CH₄ production. The importance of electron acceptors and organic matter quality on methanogenesis in wetland soil profiles has rarely been studied.

About 30% of the total surface area of Florida is wetlands (Dahl, 1990). In spite of these vast areas of wetlands, few field measurements of CH₄ emissions have been made in southern Florida, and those were predominantly made in the Everglades (Sebacher et al., 1985; Harriss et al., 1988; Whiting et al., 1991). There is a growing interest in Florida and elsewhere to reclaim previously drained wetlands, which up until recently, were used for intensive agriculture (Lowe et al., 1989). Under drained conditions, these sites have had substantial losses of surface organic matter due to accelerated decomposition. These reclaimed wetlands have been re-flooded and established with wetland plant species. Previous studies have not measured CH₄ emissions from reclaimed wetlands, and additional measurements are required to obtain more reliable estimates of their contribution to global CH₄ flux.

In this study, we compared the production and emissions of CH₄ from selected reclaimed and pristine wetlands in Florida and Georgia. Our objectives were to determine (i) the diffusive and plant-mediated CH₄ emissions; (ii) the CH₄ potential production in the soil profile; and (iii) the relationship between electron acceptor availability and potential CH₄ production.

MATERIALS AND METHODS

Site Descriptions

Four wetland sites were selected for measurements of CH₄ emission and production. Selected soil characteristics are


shown in Table 1. Soils could be broadly classified as Histosols; these wetlands have not been mapped, however, and further soil classification was not possible under the current classification system. The C and N content was measured using a Carlo- Erba CNS analyzer (Sturmentazione, Italy) and organic matter content was determined by weight loss following ignition at 550°C in a muffle furnace (Hesse, 1971).

Okefenokee Swamp. Okefenokee Swamp is located at the border of Florida and Georgia on the lower Atlantic Coastal Plain and covers an area of approximately 1770 km². Within the Okefenokee swamp, a sample location was selected in Grand Prairie (30°40'N, 82°13'W). This area was an open classification was not possible under the current classification these wetlands have not been mapped, however, and further soil measurements of CH\textsubscript{4} emissions were made in a waterlily slough. Measure-

Area 2 unimpacted from agricultural runoff (Koch and Reddy, 1992 Site S, 26°40'N 80°26'W). Vegetation at this site was predominantly sawgrass (Cladium sp.) and waterlily. Measurements of CH\textsubscript{4} emissions were made in a waterlily slough.

Sunny Hill Farm. Sunny Hill Farm was originally a large wetland system (29°00'N 81°48'W) surrounding the Oklawaha River that was subsequently drained, fertilized, and used for growing crops and dairy production. Because this agricultural land was located near an environmentally sensitive aquatic system, the St John's River Water Management District (Pat-

Apopka Marsh. Apopka Marsh is a cattail-dominated marsh (28°41'N 81°41'W) adjacent to Lake Apopka. Prior to 1991, this marsh was a 4 km² muck farmland. Lake Apopka is a hypereutrophic lake, and currently lake water is being pumped through the Apopka Marsh in an attempt to filter particulate N and P prior to discharge of water back into the lake (Lowe et al., 1989). Two sites were chosen in the marsh with the first site located 100 m from the inflow of lake water and the second site 3000 m from the inflow.

In Situ Methane Emissions

In situ emissions of CH\textsubscript{4} were measured using a closed chamber technique. Six 30 by 30 cm clear Plexiglas bases were installed at sites 10 d prior to measuring CH\textsubscript{4} emissions to minimize soil and plant disturbance prior to sampling. Bases were 30 cm high and open topped with a small trough running around the top edge. Immediately prior to measuring CH\textsubscript{4} emissions, a second Plexiglas box (30 by 30 cm) was placed on top of the base unit and a gas-tight seal was achieved by filling the trough with water. Gas samples were taken through a stopcock and needle installed through a rubber stopper in the top of the lid. Temperature was monitored using a thermometer passed through a second stopper. An end of Tygon tubing was passed through the third stopper, the other end kept underwater during the sampling period to act as a pressure equilibrator. A small battery-operated fan had been installed into the side of the top chamber to facilitate headspace gas mixing. Where plants were taller than 60 cm, another Plexiglas unit of the same design as the base unit was added to increase the height of the chamber. During the sampling period, chambers were covered with shade cloth to minimize temperature increases within the chamber, and changes in temperature were generally <5°C.

After the chamber had been sealed, gas samples (8 mL) were taken by syringe at 0, 20, and 40 min and injected into 7-mL Vacutainers (Becton Dickinson, Rutherford, NJ). Methane was detected in newly purchased Vacutainers. Therefore, the day prior to sampling, Vacutainer stoppers were removed and the Vacutainer was allowed to equilibrate with the atmosphere. The stopper was then replaced and the air removed using a vacuum pump. After the final gas sample was taken, the top box was removed and the plants were exposed for 40 min. This sampling routine was repeated up to five times on a single day at each site. At the end of the measurements, the aboveground plant biomass was harvested, air dried, and weighed.

Methane concentration in Vacutainers was determined using a gas chromatograph (Hewlett Packard 5840A, Avondale, PA) equipped with a flame ionization detector. The injector temperature, oven temperature, and detector temperature were 100, 50, and 200°C, respectively. The carrier gas was N\textsubscript{2} (20 mL min\textsuperscript{-1}), and the flame gases were H\textsubscript{2} (20 mL min\textsuperscript{-1}) and compressed air (150 mL min\textsuperscript{-1}). Gas standards were made by diluting 100% CH\textsubscript{4} in serum bottles containing N\textsubscript{2}. The rate of CH\textsubscript{4} emission was calculated by fitting a linear regression to the increase in CH\textsubscript{4} concentrations and adjusting for the volume of the chamber.

Dissolved Methane and Sulfate in Soil Pore Water

Pore water equilibrators (Hesse, 1976) were used to determine dissolved CH\textsubscript{4} and SO\textsubscript{4} in soil pore water. Equilibrators were constructed from Plexiglas sheets with cells (8 cm\textsuperscript{2}) at 1-cm intervals. Cells were filled with distilled water and covered with a 0.2-μm membrane filter (Supor-200 Gelman Sciences, Ann Arbor, MI) and a support netting. Equilibrators were then purged overnight with N\textsubscript{2} to strip dissolved O\textsubscript{2}. Equilibrators were installed at all wetland sites and allowed to equilibrate for 10 d. After equilibration in the field, pore water equilibrators were removed from the soil. To determine pore water CH\textsubscript{4} concentration, 2-mL water samples were taken from each of the cells by syringe and transferred into 3-mL Vacutainers, which contained 1.5 mL of N\textsubscript{2}. Addition of N\textsubscript{2} to the Vacutainer ensured a slight positive pressure following

<table>
<thead>
<tr>
<th>Site</th>
<th>Pore water pH</th>
<th>Bulk density</th>
<th>Organic matter</th>
<th>C kg kg\textsuperscript{-1}</th>
<th>N kg kg\textsuperscript{-1}</th>
<th>Porosity cm\textsuperscript{3} cm\textsuperscript{-3}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Okefenokee Swamp</td>
<td>4.2-5.2</td>
<td>0.074</td>
<td>920-960</td>
<td>0.53</td>
<td>0.03</td>
<td>0.88</td>
</tr>
<tr>
<td>Sunny Hill Farm</td>
<td>6.0-7.0</td>
<td>0.46</td>
<td>80-200</td>
<td>0.04-0.25</td>
<td>0.003-0.02</td>
<td>0.79</td>
</tr>
<tr>
<td>Apopka Marsh</td>
<td>6.7-7.1</td>
<td>0.39</td>
<td>610</td>
<td>0.35-0.38</td>
<td>0.02-0.03</td>
<td>0.78</td>
</tr>
<tr>
<td>Site 1</td>
<td>5.5-7.5</td>
<td>0.27</td>
<td>810-450</td>
<td>0.46-0.51</td>
<td>0.03</td>
<td>0.90</td>
</tr>
<tr>
<td>Site 2</td>
<td>7.0-7.7</td>
<td>0.09</td>
<td>720-910</td>
<td>0.44-0.52</td>
<td>0.03-0.04</td>
<td>0.88</td>
</tr>
</tbody>
</table>

Table 1. Soil properties from field study sites. Ranges are given where parameter varied with depth. Bulk density and soil porosity were measured in the region where the CH\textsubscript{4} gradients were observed.

† WCA = water conservation area.
introduction of the pore water sample. The headspace (gas space) of the Vacutainers was analyzed for CH₄ using a thermal conductivity detector installed on the gas chromatograph. Injector temperature, oven temperature, and detector temperature were 120, 60, and 250°C, respectively. The carrier gas was He at 20 mL min⁻¹. Methane dissolved in the pore water aqueous phase was calculated using Henry's law. A second sample of pore water was taken by syringe and analyzed for NO₃ and SO₄ concentrations using an ion chromatography (Dionex Series 450i, Smyrna, GA); the eluent was 3.6 mmol Na₂CO₃ L⁻¹ and 3.4 mmol NaHCO₃ L⁻¹. The regenerator was 12.5 mmol H₂SO₄ L⁻¹.

**Methane Production Potential of Soils**

Methane production potential of soils were measured as a function of depth at all sites except Apopka Marsh Site 1. Triplicate soil cores were obtained from each site by driving plastic cores (6.3-cm diam.) to a depth of ≈28 cm. Cores were sealed with butyl rubber stoppers and returned to the laboratory where they were extruded and sectioned at 2-cm intervals. A known amount of each section was quickly transferred into serum bottles (160 mL) to minimize contact with air. Serum bottles were immediately sealed with butyl rubber stoppers and aluminum crimp (Belloco Glass Inc., Vineland, NJ). A needle with an attached stopcock valve was passed through the stopper for headspace gas sampling. The headspace was flushed with N₂ for 4 min to remove O₂. Bottles were statically incubated at 30°C in a temperature-controlled incubator for 4 wk. Weekly, a gas sample (3 mL) was removed from the headspace, transferred to a Vacutainer (2.7 mL), and stored until analyzed for CH₄ and CO₂ concentration using the thermal conductivity detector described above. Prior to sampling, the headspace pressure was measured using a pressure transducer (Cole Palmer, Niles, IL). Methane and CO₂ measured was adjusted for pressure and volume of gas previously removed. Methane and CO₂ production was linear (generally r² > 0.9) for the first 4 wk of incubation, and the rate of gas production was determined by linear regression of gas production with time.

At the end of the incubation, stoppers were removed, bottles were filled with water, and the headspace volume was determined gravimetrically. Bottles were then placed in a 105°C oven to determine the soil dry weight. Soil was ground to a powder in a ball mill and analyzed for C, N, and organic matter separately collected soil cores of a known volume, and soil porosity was calculated with the assumption that the soil was water saturated.

**RESULTS AND DISCUSSION**

Plant-mediated CH₄ emissions varied both with sampling site and time (Table 2), ranging between 0.09 and 0.9 g m⁻² d⁻¹ at the pristine wetland sites and from 0.15 to 1.7 g m⁻² d⁻¹ at the reclaimed sites. We did not observe significant trends with time in the measured CH₄ emissions during the day. Others have also observed a high degree of temporal and spatial variability of CH₄ emissions (Wilson et al., 1989; Bartlett et al., 1987; Sebacher et al., 1986; Crill et al., 1991). The CH₄ emission rates observed at the pristine sites fell within the ranges previously measured at Okefenokee (Bartlett and Harriss, 1993) and the Everglades Water Conservation Area-2A (Harriss et al., 1988). Previous measurements at reclaimed wetlands have not been made, and the emissions were generally higher than, but within the range of, CH₄ emissions measured in temperate and subtropical wetlands (Bartlett and Harriss, 1993). As a result of being reclaimed as wetlands, Sunny Hill Farm and Apopka Marsh have undergone rapid invasion and growth of vegetation. It has previously been shown that CH₄ emissions from wetlands may be related to plant productivity (Whiting et al., 1991), and the high rates from these reclaimed sites may have been due to the initially high productivity of re-establishing aquatic vegetation at the reclaimed sites.

Shade cloth was used to minimize increases in internal chamber temperature; however, temperature increased by as much as 5°C on some of the hotter days. This increase in internal temperature might lead to increased ventilation by both cattail and waterlily, which are considered to transport gases by active thermally driven ventilation systems (Chanton and Dacey, 1991; Sebacher et al., 1985). Chanton et al. (1992) showed that CH₄ emissions could be successfully measured using simple chamber techniques on plants where molecular diffusion is the mechanism for gas transport. A number of studies have used simple chambers to measure CH₄ emissions through plants in which gas transport is thermally driven (Sebacher et al., 1986; Crill et al., 1991). The CH₄ emissions measured at the reclaimed sites fall within the range of, but are generally lower than, those measured at pristine wetlands.

![Table 2](attachment:table2.png)

**Table 2.** Plant mediated CH₄ emissions (determined by chamber method) and diffusive flux of CH₄ (determined from pore water gradients). Okefenokee Swamp and the Everglades site are pristine wetlands, whereas Sunny Hill Farm and Apopka Marsh are reclaimed wetlands. Numbers in parentheses denote number of samples taken.

<table>
<thead>
<tr>
<th>Site</th>
<th>Date sampled</th>
<th>Vegetation</th>
<th>Water depth (cm)</th>
<th>Temperature °C</th>
<th>CH₄ chamber flux g m⁻² d⁻¹</th>
<th>CH₄ diffusive flux Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Okefenokee Swamp</td>
<td>23 June 1992</td>
<td>waterlily (Nymphaea odorata)</td>
<td>30</td>
<td>29-34</td>
<td>0.86 (28) 0.42 0.017 (2) 0.022</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>9 Sept. 1992</td>
<td></td>
<td>nd</td>
<td>29</td>
<td>0.013 (3) 0.006</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1 Mar. 1993</td>
<td></td>
<td>46</td>
<td>15-20</td>
<td>0.10 (15) 0.20 0.008 (3) 0.002</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sunny Hill Farm</td>
<td>10 July 1992</td>
<td>cattail (Typha sp.)</td>
<td>46</td>
<td>30-36</td>
<td>1.4 (30) 0.91 0.012 (2) 0.008</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>22 Jan. 1993</td>
<td></td>
<td>58</td>
<td>24-28</td>
<td>0.29 (15) 0.25 0.013 (2) 0.009</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Everglades</td>
<td>22 July 1992</td>
<td>waterlily</td>
<td>78</td>
<td>27-28</td>
<td>0.09 (4) 0.044 0.009 (2) 0.002</td>
<td></td>
<td></td>
</tr>
<tr>
<td>WCAt-2</td>
<td></td>
<td></td>
<td>nd</td>
<td>24-28</td>
<td>nd nd nd nd</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apopka Marsh</td>
<td>(i) Site 1</td>
<td>cattail</td>
<td>74</td>
<td>24-27</td>
<td>1.7 (18) 2.0 nd nd</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(ii) Site 2</td>
<td>cattail</td>
<td>38</td>
<td>19-21</td>
<td>0.16 (17) 0.077 0.042 (3) 0.011</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

† SD = standard deviation; nd = not determined; WCA = water conservation area.
acher et al., 1985; Bartlett et al., 1987), but it is not clear how increases in chamber temperature might influence CH₄ emissions from these plants. Knapp and Yavitt (1992) observed changes in stomatal conductance and large increases in temperature (>9°C) following placement of plastic bags around cattail leaves, which affected CH₄ emissions.

Dissolved CH₄ profiles in the soil pore water exhibited distinct gradients, and the diffusive flux of CH₄ was determined using Fick's law:

\[ J = -\frac{dC}{dx}D_o \theta \]

where \( J \) is the diffusive flux (µg cm⁻² s⁻¹), \( D_o \) is the diffusivity coefficient of the species (cm² s⁻¹), and \( \theta \) is soil porosity (cm³ cm⁻³) determined for the region where the CH₄ gradient was observed (Table 1). The gradient \( dC/dX \) was determined by linear regression where \( C \) is the dissolved CH₄ concentration (µg cm⁻³) at depth \( X \). The diffusivity coefficient used for CH₄ was \( 2.15 \times 10^{-5} \) cm² s⁻¹ (Klump and Martens, 1981). Diffusive flux of CH₄ was similar at all sites and generally <5% of the chamber-measured emissions (Fig. 1, Table 2; similar to findings by Whiting and Chanton, 1992). As dissolved CH₄ diffuses through the soil surface layers, up to 90% can be oxidized to CO₂ by methane-oxidizing bacteria (King et al., 1990), and thus only a small fraction of the CH₄ is directly released from the soil to the atmosphere. The wetlands we studied were all vegetated and diffusive losses of CH₄ through the soil were likely to be of little importance relative to CH₄ emissions through plants.

The method used to measure potential CH₄ production did not include amendments that might stimulate or inhibit microbial activity. Both CH₄ and CO₂ production rates were linear (data not shown), supporting the suggestion that substantial change in microbial population had not occurred during incubation.

Maximum potential rates of methanogenesis in soil profiles were in the same order of magnitude at all sites despite differences in soil characteristics, such as pore water pH, C, N, and organic matter content (Fig. 2, Table 1). This suggested that the methanogenic populations are adapted to the environmental conditions found at different sites. Potential CH₄ and CO₂ production rates expressed on the soil C basis (Fig. 2a) indicated that the C that
was most available to methanogens was in the surface soils, but at lower depths, C was presumably more recalcitrant. Previous studies have also found a maximum of CH₄ production in the top few centimeters (Sass et al., 1990; Bachoon and Jones, 1992).

Methanogen activity is known to be inhibited by the presence of electron acceptors including O₂, NO₃, and SO₄ (Oremland, 1988). The soils at all sites were flooded, and O₂ concentrations in the surface layers would be low due to slow O₂ diffusion and rapid consumption. Whereas NO₃ was not detected at any of the sites, relatively high dissolved SO₄ concentrations were observed up to 15 cm below the soil surface at both the Everglades and Apopka Marsh sites (Fig. 3). The soil pore water and floodwater at Okfhenokee and Sunny Hill Farm contained <0.2 mg SO₄ L⁻¹. Sulfate-reducers and methanogenic bacteria have a number of C substrates in common, and in the presence of SO₄, methanogens can be outcompeted for energy sources by sulfate-reducers (Capone and Kiene, 1988). At the Everglades site, CH₄ concentration increased in the pore water once SO₄ concentration was reduced (Fig. 1 and 3). This suggested that CH₄ production occurred at lower depths at this site than at the other wetlands studied. However, at both the Everglades and Apopka Marsh sites, potential rates of CH₄ production were high in the surface soils even where SO₄ was not depleted. Because growth of methanogenic population was not thought to have occurred during serum bottle incubations, high potential CH₄ production suggested that a significant methanogenic population existed in the surface soils where SO₄ concentration was also high. Methanogenic bacteria may be active in the center of microsites (such as soil aggregates and organic particles) where SO₄ is depleted. Methane may be oxidized as it diffuses out from the center of these microsites either aerobically or anaerobically and not be detected in the pore water. Crill and Martens (1983) showed in a study of marine sediments that the CH₄ production peak lay below SO₄ reduction peak. They suggested that in saltwater systems, the activity of SO₄ reducers outcompeted methanogens for C supply, suppressing the development of a methanogenic population in the surface sediments. In these marine sediments, SO₄ concentrations were more than two orders of magnitude higher than those found at the Everglades and Apopka sites. Lovely and Klug (1983) showed that SO₄ reducers can outcompete methanogens for C sources at low SO₄ concentrations; however, results presented here suggest that both these groups of microorganisms were active in the same soil layer. This is contrary to the conceptual model of layered regions of anaerobic respiratory activity where the activity of anaerobic microorganisms is driven top down by the decreasing concentrations of electron acceptors. Support for the activity of different anaerobic respiratory pathways occurring in the same soil layer has also been found in other studies (Kerner, 1993; Westermann and Ahring, 1987). It may be more appropriate to apply the layered model at the soil aggregate or particle scale, in a similar manner to the concepts used to explain denitrification in aerobic soils (Tiedje et al., 1984). This may be especially true when concentrations of electron acceptors in pore water are low and removed at the outer surface of soil particles or aggregates. However, the layered model may be appropriate at higher concentrations of electron acceptors, such as SO₄ in marine sediments (Crill and Martens, 1983) or NO₃ in wetlands enriched with wastewater.

Areal rates of CH₄ production were calculated by summation of the potential rate of CH₄ production by depth using bulk density measurements at each depth increment (Table 3). These rates were the same order of magnitude as the emissions of CH₄ observed in chamber measurements (Table 2) and suggested that rates of CH₄ oxidation in the rhizosphere ranged widely (between 0 and 90%) depending on sampling date. Such a wide range of CH₄ oxidation has previously been reported by a number of studies (Sass et al., 1990; Schutz et al., 1989; Holzapfel-Pschorn et al., 1986) all of which also measured CH₄ oxidation in the root zone by indirect measures based on either differences observed between emission and CH₄ production or on soil incubations where CH₄ disappearance was observed. Factors that control the extent of CH₄ oxidation may mask the effect of soil biological and chemical factors that regulate CH₄ production.

Potential CO₂ production rates were similar in pattern to CH₄ production rates (Fig. 2b). The higher C content in the top 24 cm (Table 3) at the reclaimed wetland sites was due to higher bulk densities (Table 1) that probably developed as a result of previous agricultural management practices, which compacted the soil. The annual C loss in the top 24 cm of soil was calculated from the CH₄ and CO₂ production rates and varied between 0.68

---

Table 3. Potential CH₄ production rates (three replicates each) from study sites that were calculated using bulk density of soils in 2-cm increments. Annual C loss was calculated from summation of CH₄ and CO₂ potential production.

<table>
<thead>
<tr>
<th>Site</th>
<th>Potential CH₄ production</th>
<th>C in top 24 cm (g cm⁻³)</th>
<th>Annual C lost (g m⁻² d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Okefenokee Swamp</td>
<td>0.84</td>
<td>2.8</td>
<td>0.31</td>
</tr>
<tr>
<td>Sunny Hill Farm</td>
<td>1.1</td>
<td>2.8</td>
<td>0.24</td>
</tr>
<tr>
<td>Everglades WCA-1</td>
<td>0.34</td>
<td>0.9</td>
<td>1.10</td>
</tr>
<tr>
<td>Apopka Marsh Site 1</td>
<td>0.44</td>
<td>1.9</td>
<td>0.51</td>
</tr>
<tr>
<td>Apopka Marsh Site 2</td>
<td>0.44</td>
<td>1.9</td>
<td>0.51</td>
</tr>
</tbody>
</table>

† SD = standard deviation; WCA = water conservation area.
and 3.7\% (Table 3) of total C. Methane production accounted for \( \approx 70\% \) of the C losses at all sites.

As former agricultural land is restored to its prior wetland state, a concomitant increase in CH\(_4\) emissions can be expected and, at least initially, CH\(_4\) emissions from these sites may be high relative to pristine wetland areas. Further assessment of the area of reclaimed wetlands and the emission rate of CH\(_4\) is required to assess the importance of these areas in the global CH\(_4\) budget. Methane production was highest in the top 6 cm of the wetland soil, indicating the importance of available C as a regulator of methanogenesis. Electron acceptors were not a dominant regulator of the locus of methanogenesis in the soil profile primarily due to their low concentrations. At relatively low concentrations of SO\(_4\), it appeared that methanogenesis occurred at the same soil layer as SO\(_4\) reduction.

ACKNOWLEDGMENTS

We thank John Niaouris, Matt Fisher, and Bill DeBusk for their technical assistance. We are thankful for helpful reviews by Dr. Paula Gale, Dr. David Hubbel, and anonymous reviewers. The St John's River Water Management District, South Florida Water Management District, and the Okefenokee National Wildlife Refuge are thanked for access to field sites. This study was funded by a grant through Tulane University from the National Institute for Global Environmental Change, US Department of Energy.

REFERENCES