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Carbon monoxide consumption and production by wetland peats

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Abstract

Wetland peats were analyzed for their potential to consume and produce carbon monoxide (CO) under aerobic and anaerobic conditions. Kinetic and functional characteristics of anaerobic CO consumption were compared with those of methanogenesis. Inhibitors of methanogenesis and sulfate reduction decreased the rate of CO consumption by 30 and 20%, respectively, suggesting that methanogens and sulfate reducers played secondary roles in CO uptake. Low concentrations of nitrate (0.2 mM) stimulated CO uptake, while high concentrations (20 mM) were partially inhibitory. Sulfate (20 mM), ferric iron (60 μmol cm^{-3}), and acetate (10 mM) had no effect on CO consumption. Formate and glucose (10 mM) temporarily stimulated net CO and H_2 production. Aerobic incubations of previously anaerobic peat stimulated transient CO production. Kinetic analysis of anaerobic CO consumption by two sediment types (organic peat and mineral silt) showed that maximum potential uptake velocities (V_{maxp}) in each sediment were similar, 1–2 nmol CO cm^{-3} sediment h^{-1}, with apparent half saturation constants (K_{app}) ranging from 5 to 37 nM CO. Anaerobic CO consumption may limit CO accumulation in wetland peats and sediments, thereby affecting CO emissions. Understanding the role and characteristics of wetland CO consumption may help explain current and future patterns in wetland CO dynamics.

Keywords: Anaerobic carbon monoxide consumption; Wetland peat; Carbon monoxide; Methane; Hydrogen; Methanogen; Sulfidogen

1. Introduction

Carbon monoxide (CO) concentrations are supersaturated relative to the atmosphere in anoxic environments such as wetlands [1,2]. The extent of CO emissions from these systems may be determined in part by anaerobic CO consumers and producers [1,3–5]. However, the specific characteristics of microbial CO production and consumption in wetlands have not been previously reported.

Though distinct from aerobic CO-oxidizing bacteria (i.e., the carboxydotrophs), methanogens, acetogens, sulfate reducers, and certain phototrophs, e.g., *Rhodopseudomonas* sp., also oxidize CO via carbon monoxide dehydrogenase [6]. This enzyme catalyzes the reversible reaction: $CO+H_2O \rightarrow CO_2+H_2$. CO oxidation can generate energy, while CO_2 and CO are exchanged during acetyl-CoA synthesis or cleavage [7,8]. Since CO is an intermediate and not a major end product of respiration, net CO production is limited [9–11]. Transient pulses of CO form in anaerobic sludge digesters after organic carbon loading (i.e., glucose, formate, or acetate; 25–100 mM), but subsequent consumption keeps levels low [12,13].

Since methanogenic, acetogenic, and sulfate-reduc-

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ing bacteria consume and produce CO in culture [9,14–17], Conrad [5] suggested that these organisms were responsible for controlling CO levels in situ. However, the microbial characteristics and controls of anoxic CO consumption and production remain unknown [18]. Therefore, the objective of this study was to characterize anaerobic CO consumption and production by wetland peats in vitro. Aerobic CO production was addressed as well.

2. Methods

2.1. Sampling description

Peat samples were obtained from a freshwater wetland dominated by *Typha latifolia* (cat-tail); for a description see [19]. Cores were obtained using sharpened 6.4-cm (ID; 7.0 cm OD) acrylic tubes 30 cm in length and transported intact to the laboratory. Cores collected on 24 November 1996 were stored (<3 months) at 10°C. Samples for kinetic analyses were obtained on 7 April 1997 from a submerged stream bank dominated by *T. latifolia* and characterized by two distinct layers: a brown organic peat (0–10 cm) and a gray mineral silt (10–18 cm); estimated bulk densities were 0.14 ± 0.00 and 0.73 ± 0.02 g dry wt cm^{-3}, respectively ($n = 3$); pH for all peat and sediment ranges between approximately 3.8 and 4.2.

2.2. Slurry preparation

Peats were homogenized and diluted in sealed flasks with deionized, deoxygenated H_2O in a disposable glove bag flushed with nitrogen (<10 ppm oxygen). Subsamples of slurry were transferred using techniques for handling anaerobes to bottles which were subsequently sealed with teflon-faced butyl (The West, CA) or neoprene stoppers and flushed with nitrogen as above. Slurries were assayed for CO consumption and methane production or stored at 10°C until use (=16 days).

2.3. Depth profile

Discrete layers in the peat were sliced and teased apart with a serrated knife. The layers were characterized by: fine plant tissue (0–2 cm), abundant roots and rhizomes (2–9 cm), occasional intact roots and rhizomes (9–15 cm), and primarily peat (15–20 cm); estimated densities (mean ± S.D.) were 0.04 ± 0.01, 0.08 ± 0.02, 0.10 ± 0.01, and 0.07 ± 0.02 g dry wt cm^{-3}, respectively ($n = 6$). Each layer was divided equally for use in aerobic and anaerobic CO consumption assays. Sub-sections were homogenized and diluted 1:4 (1 part peat to 4 parts H_2O), and CO was added to 20 cm^3 of slurry in 160-ml serum bottles for a final mixing ratio of 10 ppm. Slurries were incubated in the dark on a rotary shaker (150 rpm) at room temperature (approximately 22–25°C).

CO generally decreased exponentially with time in assays with initial values of 10 ppm CO. Therefore, a first order rate constant was determined using Kaleidagraph™ software for regression analysis. Methane production in anaerobic incubations was estimated by linear regression analysis.

2.4. Responses to exogenous substrates and inhibitors

Inhibitors, electron acceptors, and carbon sources were added in 2-ml aliquots from anaerobic stock solutions to 20 cm^3 of slurry (diluted 1:4) in 160-ml serum bottles prior to CO uptake assays. Controls run in parallel received only anaerobic deionized H_2O. Slurries were flushed with nitrogen prior to the addition of CO (diluted in nitrogen) to a final headspace mixing ratio of 10 ppm. Slurries were inverted and incubated in the dark on a rotary shaker (150 rpm) at room temperature during time course experiments.

Headspace samples were analyzed by gas chromatography at intervals after the treatments were initiated. CO consumption and methane production rates for all treatments were determined from regression analysis of three time points taken during the initial 24 h of incubation.

To test the effect of aerobic incubations on CO production, a freshly homogenized sediment core was analyzed for CO, CH_4, and H_2 evolution immediately after exposure to air. Slurries were prepared and subsampled in a glove bag flushed with nitrogen. Three replicate slurries were open to ambient laboratory air for approximately 1 min before sealing for the aerobic treatment. Controls were not open to air. Slurries were vigorously shaken by hand for 30 s and

the subsequent evolution of gas measured at intervals as the samples were shaken at 150 rpm on an orbital shaker at room temperature.

2.5. Kinetic analyses

A progress curve analysis was used to estimate the kinetics of anaerobic CO consumption by approximately 50 cm^3 of organic peat and mineral silt obtained 24 h prior to the assay and diluted 1:1 (100 cm^3 of slurry) in 1.2-l solution bottles. CO was added to the headspace (initial mixing ratio of approximately 20 ppm), and 4-cm^3 samples were collected over time. Bottles were incubated in the dark and vigorously shaken at 250 rpm on a rotary shaker at room temperature.

Kinetic constants were determined by fitting the data to the integrated form of the Michaelis-Menten kinetic equation using Kaleidagraph™ software: $t = (S_0 - S + K_{app}\ln(S_0/S)) \div V_{maxp}$; where t = time, S_0 = substrate concentration at time zero, S = instantaneous substrate concentration, V_{maxp} = maximum potential uptake velocity, and K_{app} = apparent half saturation constant [20].

2.6. Gas chromatography

Headspace samples (4 cm^3) were collected with disposable syringes fitted with removable GC needles (Hamilton™) and analyzed immediately (<5 s). An RGA3 (Trace Analytical) and a Shimadzu™ GC-14A as previously described [21] were used for CO and CH_4 analysis, respectively. The RGA3 was equipped with a mercury vapor detector operated at 265°C and fitted with a gas sampling valve and a 1-m Molecular Sieve 5A column operated at 105°C and an air carrier flow rate of 20 cm^3 min^{-1}. Its detection limit was <10 ppb CO; the instrument was standardized using a certified 91.9-ppb CO standard (NOAA), 10.8-ppm CO standard (Maine Oxy Supply), and laboratory dilutions (1–30 ppm) of certified 996-ppm CO (Maine Oxy Supply). The instrument response above about 2–5 ppm CO was non-linear, and the relationship between detector response and concentration was established by non-linear curve fitting. The GC-14A was standardized with certified 2.6- and 1011-ppm CH_4 standards. Hydrogen was also measured with CO samples using the RGA3, but not quantified by reference to a standard. Syringes and needles were flushed with nitrogen prior to removing each sample from anaerobic headspaces.

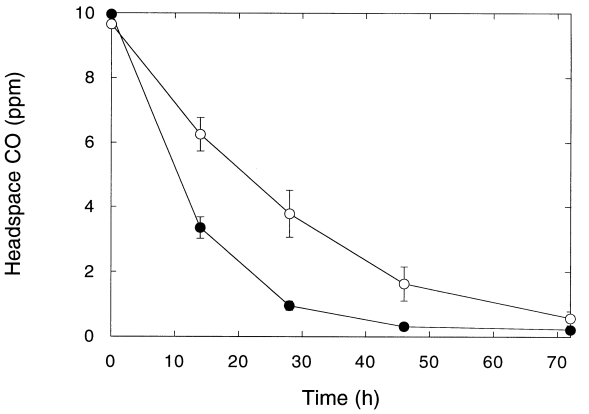

Fig. 1. CO consumption by wetland peats incubated under aerobic (●) and anaerobic (○) conditions. A peat core was sub-sectioned, homogenized and diluted before initiating assays of slurries incubated on a rotary shaker at room temperature. Data are means ± 1 S.E. ($n = 3$).

3. Results

3.1. Depth profile

CO was actively consumed by wetland sediment under anaerobic and aerobic conditions (Fig. 1; Table 1). Rates of aerobic and anaerobic CO consumption and CH_4 production varied similarly with

Table 1
Potential rates of CO consumption and CH_4 production by depth[a]

Peat depth (cm)	CO consumption[b]		CH_4 production
	Aerobic	Anaerobic	
0–2	0.8 ± 0.0	0.3 ± 0.1	21 ± 6
2–9	1.3 ± 0.1	0.5 ± 0.2	29 ± 7
9–15	1.1 ± 0.1	0.4 ± 0.0	9 ± 0
15–20	0.4 ± 0.0	0.2 ± 0.1	1 ± 1

[a]Data are means ± S.D. ($n = 3$); rates are in nmol CO or methane cm^{-3} peat h^{-1}.

[b]Rates were calculated by multiplying the first order rate constant, k h^{-1}, by a headspace CO concentration of 10 ppm normalizing for headspace and peat volume (approximately 140 and 4 cm^3, respectively).

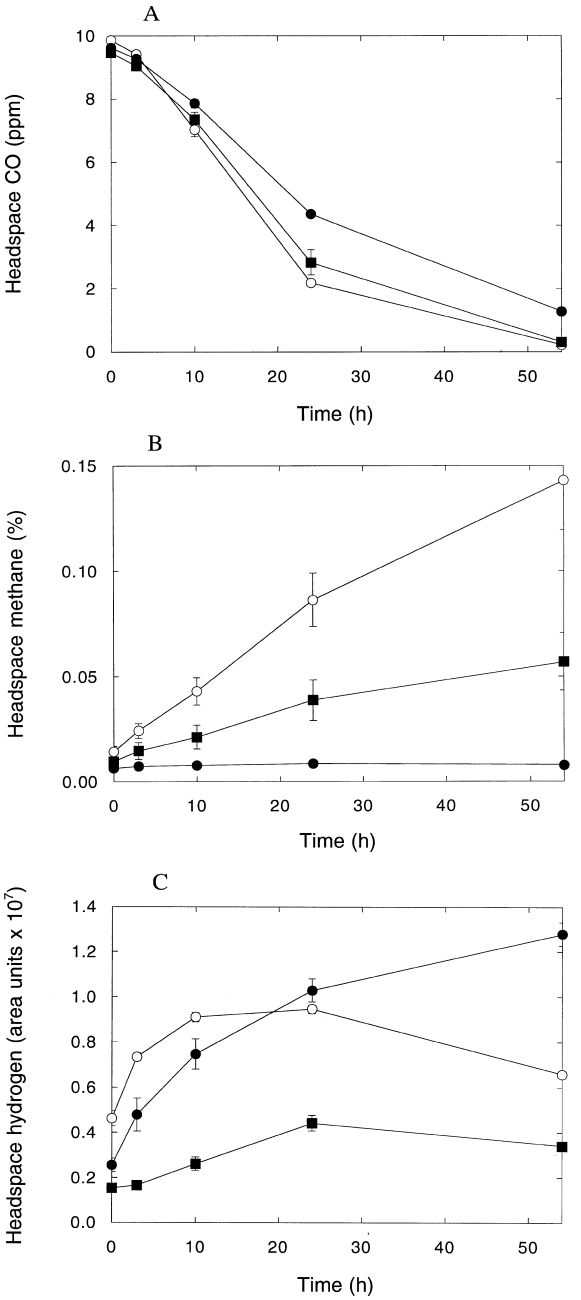

Fig. 2. Anaerobic (A) CO consumption and (B) methane and (C) hydrogen accumulation in the presence of 100 mM BES (●), 20 mM sulfate (■), and the control (○). Time course assays were initiated 3 h after substrate (inhibitors and electron acceptors) additions. Data are means ± 1 S.E. ($n = 3$).

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depth; the highest values were observed for samples from the rooting zone (2–9 cm) and the least at 15–20 cm depth. Anaerobic CO oxidation was between approximately 38–50% of the aerobic rate over the 0–20-cm interval (Table 1).

3.2. Responses to exogenous substrates and inhibitors

Specific inhibitors for methanogenesis (bromoethanesulfonic acid, BES) and sulfate reduction (sodium molybdate) decreased the rate of CO consumption by approximately 30 and 20%, respectively, relative to the control (Table 2; Fig. 2). Bromoethanesulfonic acid completely inhibited CH_4 production while sodium molybdate had no effect on methanogenesis. BES and sodium molybdate had little effect on hydrogen accumulation (Fig. 2C; data not shown).

Low concentrations of nitrate significantly stimulated the rate of CO consumption (Table 2). However, high concentrations (20 mM) partially inhibited it; 0.2 and 20 mM nitrate dramatically inhibited CH_4 production by 90 and 100%, respectively. The inhibition of methanogenesis by 0.2 mM nitrate was temporary as production resumed (similar to the control) between 1 and 3 days after nitrate addition (data not shown). In samples amended with 20 mM

Table 2
Responses of anaerobic CO consumption and CH_4 production to exogenous inhibitors and electron donors and acceptors

Treatment	(mM)[b]	Rate (% of control)[a]	
		CO	CH_4
BES	100	70 ± 0	0 ± 0
Sodium molybdate	20	80 ± 10	100 ± 30
Nitrate	0.2	240 ± 30	10 ± 0
Nitrate	20	50 ± 30	0 ± 0
Sulfate	20	90 ± 10	40 ± 20
Iron(III)[c]	60	100 ± 10	60 ± 0
Formate	10	40 ± 0	300 ± 20
Glucose	10	70 ± 10	260 ± 40
Acetate	10	100 ± 0	40 ± 10
Syringic acid	0.1	130 ± 60	190 ± 30
Autoclaved	–	0 ± 0	0 ± 0

[a]Data are means ± S.D. ($n = 3$).
[b]Final concentration 2–3 h prior to assay.
[c]Iron(III) was added as a suspension consisting of amorphic oxyhydroxide synthesized according to Lovley and Phillips [22].
BES = Bromoethanesulfonic acid.

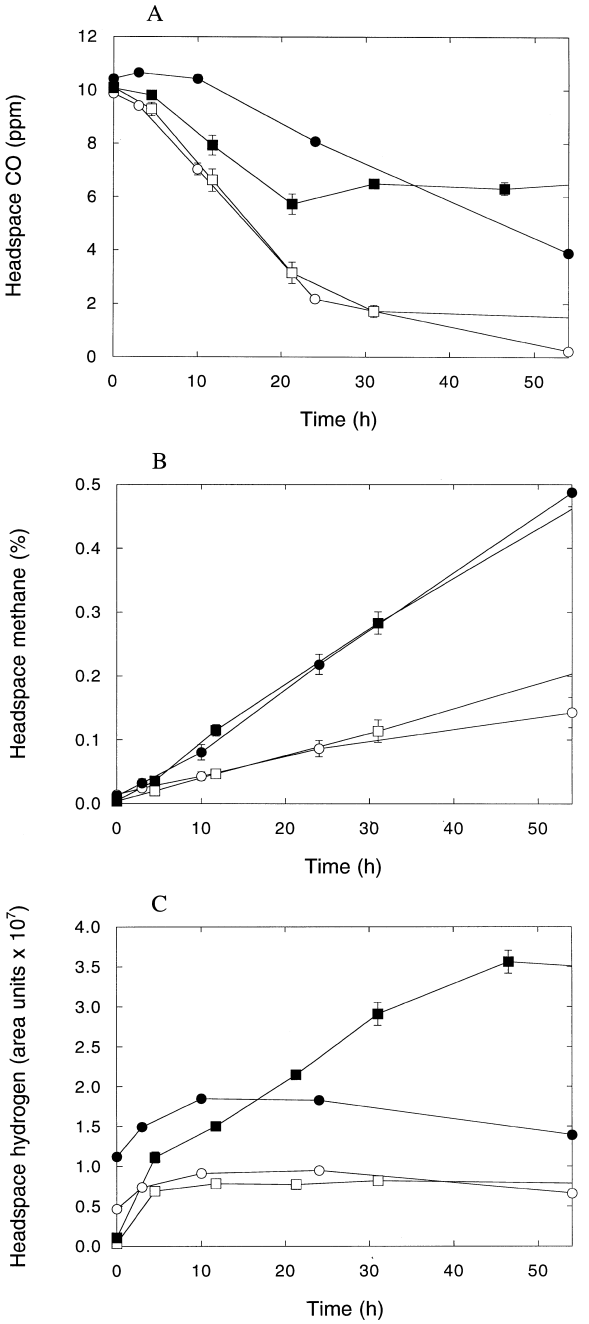

Fig. 3. (A) CO, (B) methane, and (C) hydrogen dynamics in the presence of 10 mM formate (●) and glucose (■) and corresponding controls (○,□). Substrates were added approximately 3 h before assays. Data are means ± 1 S.E. ($n = 3$).

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nitrate, pH_2 remained low, but the effect of 0.2 mM nitrate on pH_2 was minimal (data not shown).

Sulfate addition did not affect CO consumption, while it reduced CH_4 production by approximately 60% and significantly decreased pH_2 (Fig. 2C and Table 2). Iron(III) did not affect either CO consumption or pH_2, but decreased the rate of CH_4 production by 40%. Formate and glucose decreased the rate of CO consumption, and stimulated CH_4 production (Table 2). However, acetate (10 mM) affected neither CO consumption nor pH_2, but resulted in an approximately 60% lower accumulation of CH_4. Low concentrations of syringic acid (0.1 mM) had no effect on CO consumption, while stimulating CH_4 production.

Net anaerobic CO production occurred upon the addition of formate and for 24 h after glucose addition (Fig. 3A). Glucose and formate stimulated CH_4 production similarly (Fig. 3B) but affected H_2 generation differently (Fig. 3C). During incubation with formate, rapid hydrogen formation occurred with maximum levels in the first 2–10 h of the assay as for CO production (Fig. 3A and C). In the presence of glucose, abundant hydrogen formation was delayed and net CO production also occurred later (Fig. 3A and C). Hydrogen levels were greatest after 45 h in the presence of glucose, at which point CO production was enhanced; CO increased to 9 ppm after 7 days while only 0.3 ppm CO was present in the control (data not shown).

3.3. Aerobic CO production

Aerobic incubations stimulated a rapid 3 ppm CO increase compared to the control (Fig. 4A). Net CO production in the aerobic treatment ceased after 30 min, when CO oxidation became the dominant process. The aerobic rate of CO production between 0–12 min was 133 ± 26 pmol CO cm^{-3} peat min^{-1}. The increase in CO was due to production and not to degassing since during this interval only 4 ± 4 pmol CO cm^{-3} peat min^{-1} was produced in the control. As expected, methane and hydrogen were higher in the controls, but their production ceased and CO formation was stimulated during the assay (Fig. 4).

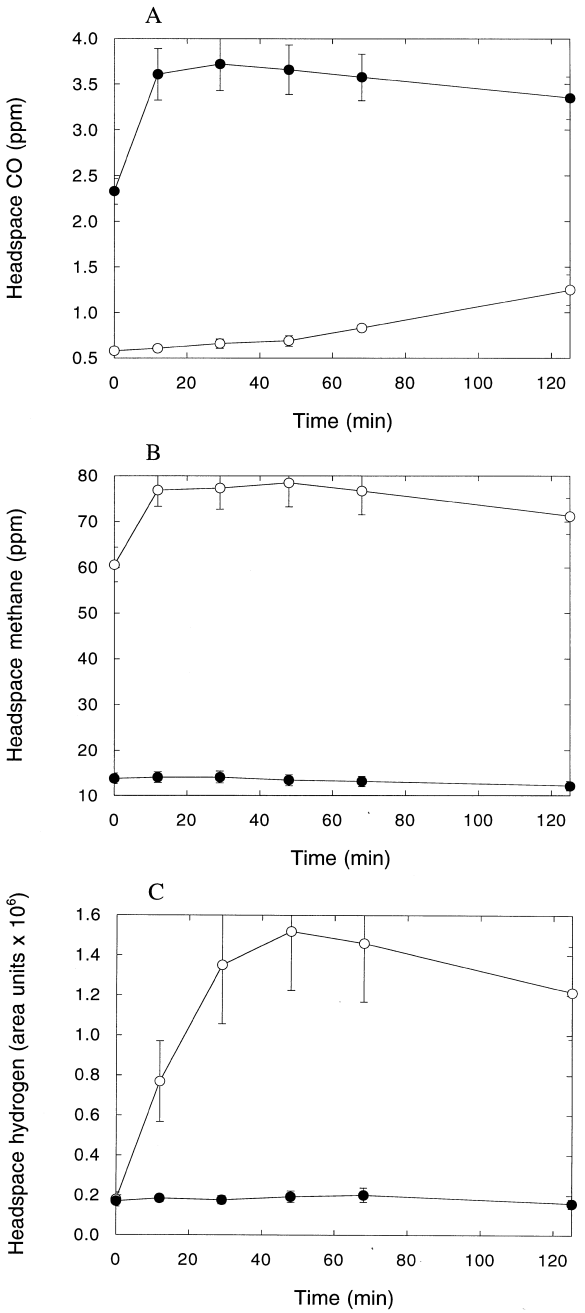

Fig. 4. (A) CO, (B) methane, and (C) hydrogen evolution from peats incubated aerobically (●) and the control (○). Fresh slurries were exposed to ambient laboratory air, vigorously shaken by hand, and gases immediately measured at various intervals; controls were not exposed to air. Data are means ± 1 S.E. ($n = 3$). ←

3.4. Kinetic analyses

Data from a progress curve analysis of anaerobic CO consumption were fitted to a non-linear version of the Michaelis-Menten equation. CO uptake was simulated using the calculated kinetic parameters and the Michaelis-Menten equation [$r = (V_{maxp}S/(K_{app}+S)$]. The model closely predicted observed rates of CO consumption (Fig. 5A). Maximum potential uptake velocities (V_{maxp}) for peat and silt were similar, though apparent half saturation constants (K_{app}) were higher in the organic rich peat (Table 3). Despite similar CO uptake, potential CH_4 pro-

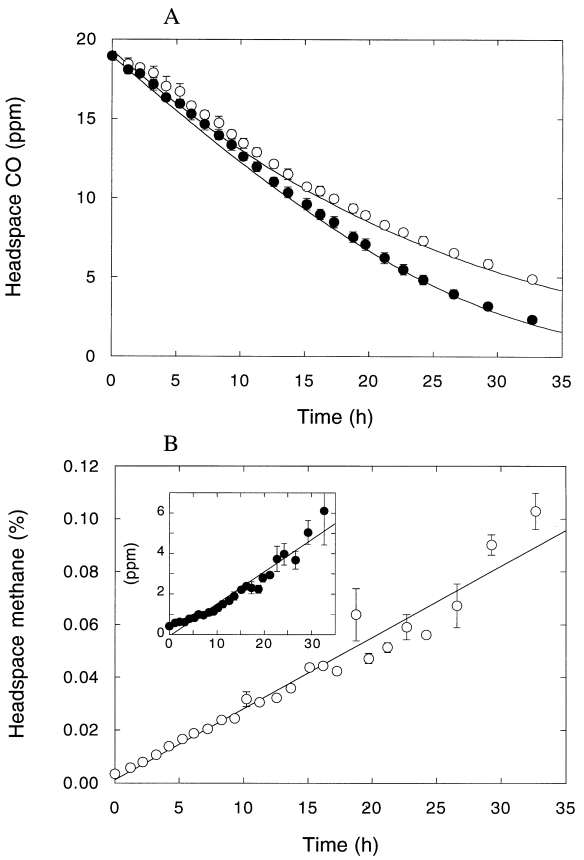

Fig. 5. Progress curve analysis of anaerobic (A) CO consumption and corresponding (B) methane production by organic peat (○) and mineral silt (●). CO data are fit by a simulation of the Michaelis-Menten equation using appropriate constants. Note the different scales for methane accumulation (inset). Data are means ± 1 S.E. ($n = 3$).

Table 3
Kinetic constants for anaerobic CO consumption by wetland sediment

Sediment type	CO consumption		CH_4 production
	V_{maxp}	K_{app}	
Peat	2.4 ± 0.4	36.7 ± 9.5	27.0 ± 2.5
Silt	1.0 ± 0.1	5.0 ± 0.7	0.2 ± 0.1

Data are means ± S.D. ($n = 3$); units for V_{maxp} and methane production are in nmol cm^{-3} sed h^{-1}, K_{app} is in nM CO calculated with a solubility coefficient of 0.018 cm^3 CO ml^{-1} H_2O atm^{-1} CO at 20°C [23].

duction was over 100-fold greater in the peat samples (Table 3; Fig. 5B). Thresholds for CO uptake were below atmospheric levels (approximately 0.2 nM CO). Though steady-state was not absolutely established after a 1-week incubation, the concentration of CO was beginning to stabilize at 0.02 ± 0.01 nM CO in the silt, while consumption was still apparent at 0.13 ± 0.00 nM CO in peat (data not shown).

4. Discussion

CO was actively consumed under anaerobic conditions by wetland peat, while methane and hydrogen were rapidly produced. Methanogenic, acetogenic, and sulfate-reducing bacteria are known to oxidize CO via a carbon monoxide dehydrogenase [6]. Several methanogenic strains consume CO during growth on H_2 and CO_2, but growth on CO is very limited [17,24]. *Desulfovibrio vulgaris* utilizes CO for energy and sulfate reduction, but concentrations $>4.5\%$ in the headspace are inhibitory [14]. A few acetogens grow well on CO as an energy source [25,26], while others rapidly oxidize CO during growth on organics [16] and have the potential for chemolithotrophic growth with CO [27,28].

Bromoethanesulfonic acid (BES) and sodium molybdate selectively inhibit methanogenesis and sulfate reduction, respectively [29,30]. Low concentrations of BES (1 mM) were not adequate for complete inhibition of methanogenesis in the peats used for the study reported here (data not shown); 100 mM BES completely inhibited methanogenesis while only decreasing CO consumption by 30% (Table 2). In addition, CO uptake was similar in two different sediment types (organic peat and mineral silt) that had drastically different methane production rates (Table 3). Both results suggest that methanogens were not responsible for CO consumption.

Sodium molybdate (10 mM) and exogenous sulfate (20 mM) also had a minimal effect on CO consumption (20% reduction and no change, respectively; Table 2), which suggested that sulfate reducers were not primarily responsible for CO consumption. Sodium molybdate also had no effect on methanogenesis or hydrogen partial pressure, indicating that sulfate reducers were not actively competing with methanogens for substrate. However, sulfate substantially reduced rates of methanogenesis and hydrogen partial pressures as has been observed in other analyses of freshwater sediments [30] suggesting that sulfidogens are present and oxidize organic matter in syntrophic associations.

Since methanogens and sulfate reducers do not appear to consume much CO in the peats analyzed here, acetogenic bacteria may be responsible for the majority of anaerobic CO consumption. Acetogens utilize CO more readily than do methanogens or sulfate reducers [14,24–26]. For example, CO oxidation is much more active in carbon monoxide dehydrogenase extracts from acetogens than from a methanogen [16,17,28]. In addition, Drake et al. [31] reported that CO was converted to acetate in a forest soil in stoichiometries similar to CO-dependent acetogenesis in culture. Neither methanogens nor sulfate reducers were active in the latter system. However, the role of acetogens in peat CO metabolism remains unclear.

High concentrations of nitrate (20 mM) partially inhibited CO consumption. This effect may be explained in part by inhibition of carbon monoxide dehydrogenase by nitrous oxide produced by denitrifying bacteria. Lu and Ragsdale [32] reported that carbon monoxide dehydrogenase efficiently reduced nitrous oxide to nitrogen and that the enzyme was reversibly inactivated by N_2O. Nitrate may also have inhibited CO consumption by blocking the utilization of C_1 compounds and the autotrophic pathway in acetogens [33].

In contrast, low nitrate concentrations (0.2 mM) significantly increased the rate of CO consumption, possibly as a result of coupled CO oxidation-nitrogenous oxide reduction. In our study, nitrate concentrations were presumably too low to inhibit carbon

monoxide dehydrogenase, but high enough to stimulate nitrate-linked CO oxidation. In support of this contention, Meyer et al. [34] reported that aerobic CO oxidizers (carboxydotrophs) reduced nitrate with CO as the electron donor. However, this reaction did not support growth [34].

CO production was observed in the presence of glucose and formate (Fig. 3). The amount of CO produced was small compared to methane. Similar trends in CO production were observed by Bae and McCarty [12] who added formate, glucose, and acetate to methanogenic sludge digesters. However, in contrast to Hickey et al. [13], who found that acetate (20 mM) stimulated CO production in sludge enrichments, acetate had no effect on CO dynamics in the peats used in our study. The difference in acetate effects may be due to the fact that Hickey et al. [13] enriched for acetate-utilizing methanogenic populations prior to the analysis, and acetate grown cells of *Methanosarcina barkeri* are extremely active CO producers in the presence of H_2 and CO_2 [10].

Data reported here indicate that CO production was linked to methanogenesis, but more closely associated with hydrogen generation (Fig. 3). Bae and McCarty [12] reported similar observations and Bott and Thauer [10] demonstrated that CO formation by methanogens was dependent on the presence of H_2 and CO_2. CO was not produced by *M. barkeri* cells during methane production from acetate, methanol, or methanol plus H_2 [10].

CO production was also stimulated by adding air to previously anaerobic sediments (Fig. 4). CO was produced during the initial stages of aerobic incubations only. Under aerobic conditions oxygen stimulates CO formation from porphyrin compounds [35,36], polyphenols [37], aromatic acids [38] and methionine precursors [39]. However, the mechanisms of production remain speculative, though the rapid nature of the reaction suggests that it is abiotic. Oxygen may stimulate peroxidation of fatty acids or destabilization of free radicals in humic substances, which can lead to CO formation [40,41].

Apparent half saturation constants (K_{app}) for sediments (5–37 nM CO) were in the same range as for aerobic soils, 4–41 nM CO [42–45]. This is surprising given the vastly different characteristics between systems. CO concentrations in aerobic soils range from <0.004 to 4 nM [46] while those in wetland pore waters are 12–136 nM (King, 1998, unpublished data). CO concentrations limit the rate of CO oxidation in aerobic soils, but concentrations are likely to be less limiting in anaerobic peats, since K_{app} for anaerobic consumption are at the lower range of pore water CO concentrations. Maximum potential uptake velocities (V_{maxp}) for sediments were 10–100 times lower than those reported for aerobic soils on a per volume basis [42–45]. This is not surprising given more suitable growth conditions in aerobic soils compared to anaerobic sediments with the former leading to higher growth yields of CO oxidizers.

CO concentrations were kept low (<0.4 nM CO) after extended anaerobic incubations with exogenous CO or at all times during anaerobic incubations without CO addition (data not shown). Anaerobic CO formation was limited, but production was observed during the initial stages of aerobic incubations. These data are inconsistent with CO concentrations found in pore waters and those reported by Conrad et al. [1] of >360 nM. This discrepancy shows that slurry steady-state concentrations may not be representative of those found in situ. Anaerobic slurry incubations may have eliminated CO production or stimulated CO consumption. However, trends in CH_4 and H_2 dynamics were as expected, suggesting that qualitative results from slurry incubations were at least partially representative of general trends in situ.

In conclusion, anaerobic bacteria in wetland peats had a high affinity for CO, but relatively low capacity for uptake. Methanogens and sulfate reducers were not likely responsible for the majority of anaerobic CO oxidation in wetland peats. Acetogens may be involved, but the organisms active in situ remain unidentified. Low levels of nitrate stimulated anaerobic CO consumption, perhaps coupled to denitrification. High concentrations of nitrate partially inhibited CO consumption perhaps by competitive inhibition from nitrogen oxides. Anaerobic CO production was insignificant, but coincident with high levels of hydrogen produced from formate and glucose (10 mM). Anaerobic CO consumers appear to substantially limit CO accumulation in wetland peats and sediments, and thus understanding their role and characteristics should help explain future patterns in wetland CO dynamics.

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