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Carbon monoxide consumption in upland boreal forest soils

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Abstract

Biological consumption by aerobic soils is an important, but poorly understood sink for carbon monoxide, a chemically active atmospheric trace gas. We used laboratory experiments to characterize CO consumption in representative soils of the northern boreal forest. This ecozone may be important in atmospheric CO consumption because it occupies 13% of the world's landmass. Soils initially showing net CO consumption emitted CO following biocidal treatment (ethylene oxide or γ-irradiation), indicating that CO consumption was biologically mediated. The use of selective inhibitors (cycloheximide, streptomycin) suggested that both prokaryotes and eukaryotes were responsible. Soil profiles generally indicated net consumption of atmospheric CO to a depth of 15 cm (concentrations decreasing from ~150 to <20 nl l^{-1} with depth) and a dynamic equilibrium between CO production and consumption in deeper soils (concentrations nearly constant at <20 nl l^{-1}). Soils to a depth of 30 cm showed vigorous CO-consuming activity, suggesting that local CO production provided necessary substrate beneath the 15 cm surface zone of atmospheric influence. Radiotracer experiments demonstrated that only 5–7% of assimilated ^{14}CO was incorporated into biomass in 5 cm core sections taken to 30 cm and that <1% of assimilated ^{14}CO was incorporated into cellular material by a methanotroph isolated from this soil. Collectively, these data point to nonutilitarian oxidation of CO by a diverse microbial community. Carbon monoxide oxidation increased with increasing temperature over the range 4–34°C, with a Q_{10} of 1.8. Apparent half-saturation constants (8–36 (μl CO l^{-1}), and maximum rates of CO consumption (0.7–2.7 μg g dry soil^{-1} h^{-1}) were comparable to reports for diverse temperate soil environments, pointing to a fundamental similarity among CO-consuming microbial communities in aerobic soils. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Carbon monoxide oxidation; Boreal forest; Carboxydotrophs

1. Introduction

Carbon monoxide is a chemically active atmospheric trace gas that directly or indirectly affects concentrations of other chemically or radiatively important atmospheric trace gases, such as methane and ozone (Daniel and Solomon, 1998). Sources of atmospheric CO include technology (transport, industrial processes, incineration etc.), biomass burning, oxidation of methane and non-methane hydrocarbons, emission from oceans and degradation of plant material while primary sinks include reaction with the OH radical and consumption by soil microbes (Prather et al., 1995).

Knowledge of the atmospheric CO budget is characterized by uncertainty. In particular, estimates of the soil sink term range over a factor of 40, from 15 to 640 Tg CO y^{-1} (reviewed by King, 1999a). The most widely accepted range of 250–640 Tg CO y^{-1} is 9–36% of the estimated annual production of 1800–2700 Tg CO from all sources (Prather et al., 1995). Although CO consumption by soil microbes is clearly an important term in the atmospheric CO budget, the microbiology and environmental controls on CO consumption are poorly understood. Methanotrophs, ammonia oxidizers, carboxydobacteria, unknown oligotrophic bacteria as well as some fungi and algae have been demonstrated to aerobically oxidize CO (Chappelle, 1962; Inman and Ingersoll, 1971; Conrad and Seiler, 1982a; Bédard and Knowles, 1989; Conrad, 1996), but the relative importance of these groups in oxidizing atmospheric CO is unresolved (Conrad, 1995). Environmental controls on aerobic microbial CO consumption include soil temperature, moisture and organic content (Conrad and Seiler, 1980, 1985; Spratt and Hubbard, 1981; Duggin and Cataldo, 1985; Moxley and Smith, 1998a; Sanhueza et al., 1998; King, 1999a).

The northern boreal forest occupies 13% of the Earth's continental landmass (Schultz, 1995), indicating that soil-atmosphere exchange of radiatively or chemically active trace gases from this biome may significantly influence

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climate. Currently, the role of boreal forest soils in the atmospheric CO budget remains speculative (King, 1999a), while simulation models point to a generalized need for an improved understanding of the role of soils from remote regions in the atmospheric CO budget (Potter et al., 1996). Currently, extant data for the upland boreal forest are limited to field (static chambers) and laboratory (cores) measurements of CO flux and supporting environmental variables in two Canadian soils (Zepp et al., 1997; Kuhlbusch et al., 1998).

We conducted a detailed, process-level investigation to characterize aerobic CO consumption in representative upland boreal forest soils with the overall goal of comparing rates and environmental controls on CO oxidation in these soils with their more extensively studied lower latitude counterparts. We thereby expected to provide regional information necessary to improve our understanding of soil-atmosphere exchange of CO in present climates and to more accurately forecast future trends in the concentration of atmospheric CO. We used laboratory studies to evaluate the rates, depth distributions and temperature dependence of CO consumption as well as the functional microbial groups involved. Further, we assessed the kinetics of microbial CO consumption for these soils and the distribution of end products (biomass and CO_2) of ^{14}CO consumption by both an isolated methanotroph and the entire soil microbial community.

2. Methods

2.1. Site description

Research was conducted during the summers of 1992 and 1993 in the Bonanza Creek Experimental Forest (BCEF), near Fairbanks, Alaska (64°N, 148°W). Four sites typifying transitional stages in ecosystem development were chosen for study. Intermediate successional stages were represented by south-facing aspen (*Populus tremuloides*; site AS2) and north-facing birch (*Betula papyrifera*; site NB1) communities, while advanced successional stages were represented by north-facing black spruce (*Picea mariana*; site BS2) and south-facing white spruce (*Picea glauca*; site UP3A) stands. The deciduous sites are characterized by an extensive ground cover of leaf litter and an insignificant understory of shrubs and herbs. The coniferous sites both show a continuous ground cover of feather mosses, but BS2 is further invaded by shrubs (*Vaccinium* spp.) and lichens. Soils within BCEF are a well-drained, stone-free micaceous loess. Soil pH varies from 4.6 to 7.0, with lowest values found at the coniferous sites. Percent organic content in the 0–5 cm horizon is lower at deciduous sites (35–50%) than at coniferous sites (80–98%) and decreases steadily with increasing depth at all sites to values of 1.5–5% at 50 cm. Detailed descriptions of the vegetation and soil physicochemical properties of the study site are given in Whalen et al. (1992).

2.2. Gas analysis

Carbon monoxide concentrations were measured using a Trace Analytical (Menlo Park, CA) Model RGA3 Reduction Gas Analyzer fitted with a 0.5-ml sample loop. Gases were separated on sequential stainless steel columns (77 cm length × 0.3 cm dia) packed with Unibeads 1S (60/80) and molecular sieve 5A (60/80). The carrier gas was ultra-high purity N_2 (20 cm^3 min^{-1}) and column and detector temperatures were 105 and 265°C, respectively. The instrument was calibrated with commercial CO-air blends (Scott-Marrin Inc., Riverside, CA; Scott Specialty Gases, Plumsteadville, PA) that are relatable to National Institute of Standards and Technology standards. The precision of analysis expressed as a coefficient of variation for 10 replicate injections of an 870 nl CO l^{-1} standard was 0.5% and the detection limit was 5 nl CO l^{-1}. The instrument response was nonlinear at CO concentrations above about 1.5 μl l^{-1}. Samples were diluted in He-filled serum vials capped with a silicon stopper (Sigma-Aldrich, Milwaukee, WI) as necessary prior to CO determination to ensure linearity between the detector response and CO concentration. Measured CO concentrations were corrected for dilution.

2.3. Field sampling

Cores were collected to a depth of either 20 cm (AS2, NB1 and UP3A) or 30 cm (BS2) with a 15 cm dia stainless steel coring apparatus and were cut horizontally into 5 cm sections. The center of each core was then subcored with a 6.7-cm ID plastic tube. All core sections were extruded intact into ~1 l borosilicate preserving jars. In some cases, bulk samples collected from the 0–10 cm zone with a garden trowel were homogenized, sieved (4-mm), and placed in a foil-covered polyethylene tub. All soils were stored at 4°C. Experiments were usually initiated within 1 day of sample collection, but were sometimes stored for up to 3 weeks with no loss of CO-oxidizing activity.

Soil gas samples were obtained at 5-cm intervals from the soil surface to the maximum depth of core collection with a 30-ml polyethylene syringe attached to a stainless steel tube (1-mm ID × 0.5-m length). A 20-ml serum vial prefilled with He and capped with a silicon stopper was evacuated in the field with a hand-operated vacuum pump (Nalgene, Rochester, NY) and immediately filled with the soil gas sample. The vial was then re-evacuated and slightly overpressured by again filling with a gas sample. Carbon monoxide concentrations remained unchanged to at least 24 h for samples stored in this manner.

2.4. Experimental

2.4.1. General procedures

Experiments involving ^{14}CO addition to soils were conducted on homogenized 40–60 g field-moist samples in ~250 ml borosilicate preserving jars. Experiments assessing rates of ^{14}CO consumption by a culture or rates of

unlabeled CO consumption by homogenized composites (75–100 g field-moist soil) or core sections were performed in 1 l borosilicate preserving jars. Incubation vessels were equipped with an o-seal fitting to allow syringe sampling of the headspace gas. Photochemical production of CO can occur simultaneously with microbial CO consumption at the soil surface (Zepp et al., 1997). Consequently, incubations of surface soils were conducted in the ambient light environment of the laboratory, while soils from all other depths were incubated in the dark. However, borosilicate glass is known to filter part of UV-B (280–315 nm) radiation (Zepp et al., 1997). Most experiments involved the addition of CO to soil in jars and time-course measurement (3–15 min intervals) of the headspace CO concentration in static 20–300 min incubations at room temperature. Headspace gas samples (3 ml) from preserving jars and stoppered serum vials were obtained with 5-ml glass syringes. Gases were immediately replaced with an equal volume of ultra-high purity N_2. Dilution was taken into account in all calculations. Carbon monoxide analysis was completed within 2 h of collection for samples from preserving jars and within 12 h for soil gases stored in serum vials. Tests showed no change in CO concentration in storage. Exceptions to the above experimental procedures are noted where appropriate.

Carbon monoxide can be simultaneously produced and oxidized in soils. In some cases, soils equilibrated with a free-air atmosphere (~150 nl CO l^{-1}) were sealed in jars and the headspace CO concentration was assessed at 24 h to test for net production or consumption of CO and to determine the equilibrium concentration (production equals consumption) of CO. Headspaces of core sections showing net CO consumption were adjusted to about 400 nl CO l^{-1} and time courses for change in headspace CO concentration were then used to calculate first order rate constants for net (k_n) or gross (k_g) CO consumption (h^{-1}).

Experiments evaluating community response to multiple treatments for a manipulated variable by time course analysis of change in substrate concentration involve compromises regarding sample frequency and replication. This is particularly true when rates cannot be determined from time-linear observations, as in the determination of rate constants for CO oxidation here. In many experimental manipulation, we directed our efforts toward firmly establishing the rate constant for a single sample at each treatment by making multiple observations of headspace CO concentration closely spaced in time for each time course experiment used for rate determinations. Values for r^2 in regression equations used to determine rate constants for CO oxidation always exceeded 0.95. We minimized the potential influence of sample-to-sample differences in soil properties and size of the microbial community by using relatively large (40–100 g) homogenized soil samples for each treatment. In cases where the rate constant for CO oxidation was determined for replicate samples here and in other experiments assessing CO consumption, coefficients of variation averaged 7.4%. High r^2 values for regression equations used in rate constant determinations and low coefficients of variation for rate constants involving replicate samples suggest that a single rate determination provided an accurate measure of the response of CO oxidation to the manipulated variable in homogenized soils. In some instances, an assessment of spatial variability was an experimental goal. Accordingly, replicate samples from the same site or depth were experimentally manipulated and variability is reported.

2.4.2. Kinetics of CO oxidation

The substrate dependence of CO consumption was assessed in initial velocity experiments (Whalen et al., 1990) where one core from each site was exposed to 12–15 different initial headspace concentrations ranging to 700 μl CO l^{-1}.

2.4.3. Effect of selective biological inhibitors, sterilization or CH_4 on CO oxidation and production

Several experiments involving homogenized soil composites (0–10 cm zone) were intended to provide insight into functional groups responsible for CO consumption or the relationship between CO consumption and abiotic CO production. In one experiment, soil was sterilized with 25 kGy of γ-irradiation (Powlson and Jenkinson, 1976) from a ^{137}Cs source (Model 68, Shepherd and Associates, Glendale, CA) at a dose rate 18 kGy h^{-1}. The time course for change in CO concentration was then determined. Soils were then incubated overnight at 60°C, cooled, and time course determinations were repeated. In a second experiment, soil was sterilized with 20% ethylene oxide (by weight) for 12 h and the time course for change in headspace CO concentration was assessed. A third experiment involved treatment of soils with streptomycin or cycloheximide or both. The experimental procedure used followed Conrad and Seiler (1980), except that time courses for CO consumption were determined 1 day rather than 4 days after antibiotic addition. In all of these experiments, headspaces were flushed with synthetic air and adjusted to 600–1200 nl CO l^{-1} prior to time course determinations. In both the ^{137}Cs and ethylene oxide (CH_2CH_2O) experiments, headspaces of all jars were also adjusted to about 10 μl CH_4 l^{-1} and the change in headspace CH_4 concentration was used to further assess the effectiveness of treatments intended to eliminate microbial activity. Soils at all sites oxidize CH_4 at all depths, although rates were highest in the 10–20 cm zone (Whalen et al., 1992). In a final experiment, the influence of CH_4 on CO consumption was determined by adjusting the headspace of two samples to 200 μl CO l^{-1} and the headspace of an additional sample to 200 μl l^{-1} of both CO and CH_4. Midway through the time course, CH_4 was added to one of the samples initially amended only with CO to give a headspace concentration of 200 CH_4 μl l^{-1}. First order rate constants for net CO consumption (k_n) were determined for aliquots of the homogenized soil dispensed into

incubation vessels prior to treatment in all experiments and were re-evaluated in response to the intended treatment.

2.4.4. Depth and temperature dependence of ^{14}CO oxidation in soils

Experiments involving the addition of ^{14}CO (specific activity 1.96 GBq mmol^{-1}; Amersham International, Amersham, UK) were used to further assess the ecology and microbiology of CO consumption. Depth distributions for the end products of ^{14}CO consumption were determined for homogenized soils from each 5 cm depth interval while the temperature dependence of ^{14}CO consumption was determined for homogenized soil samples acclimated overnight to temperatures ranging from 4 to 34°C. All soils amended with ^{14}CO were incubated in the dark to avoid photosynthetic uptake of respired radiocarbon. Experiments were 1 h (temperature dependence) or 2 h (depth profiles) in duration and involved a single endpoint for samples amended with 3.9 kBq ^{14}CO plus unlabeled CO (final headspace concentration of about 850 nl CO l^{-1}). Experiments were terminated by addition of 2 ml C_2H_2 (Bédard and Knowles, 1989) and immediate freezing. Unreacted ^{14}CO and respired $^{14}CO_2$ were recovered in a stripping/oxidation line, while ^{14}C-biomass was assayed by combustion of freeze-dried samples in a Harvey Biological Material Oxidizer (R.J. Harvey Instrument Corp., Hillsdale, NJ).

2.4.5. ^{14}CO oxidation by an isolated soil methanotroph

The ability of methanotrophs in these soils to utilize CO was assessed with a methanotrophic bacterium isolated from the 10 to 20 cm depth interval at BS2 following procedures of Whalen et al. (1990). The pure culture was grown to the exponential phase and the headspace (~850 ml) was amended with 1.08 MBq ^{14}CO to give gas and aqueous phase ^{14}CO concentrations of about 15 μl l^{-1} and 12 nM (based on Bunsen solubility coefficients of Cargill, 1990), respectively. The culture was shaken by hand for ~2 min to equilibrate ^{14}CO between the aqueous and gas phases and was placed on a rotary shaker (200 rev min^{-1}). Headspace samples (10 ml) were periodically withdrawn to 24 h and introduced into the stripping/oxidation line. On sampling, headspaces were immediately injected with 10 ml of ultra-high purity N_2. Dilution was taken into account in all calculations. At the termination of the experiment, residual ^{14}CO and $^{14}CO_2$ were stripped from the aqueous medium and jar headspace. Samples of the culture were filtered (0.2μ Gelman PTFE; >99% cell retention) and the filter and filtrate were retained. Cells in a subsample of the culture were enumerated with an electronic particle counter (Coulter Corp., Hialeah, FL). Radioactivity in CO, CO_2, particulate matter (cells) and dissolved organic carbon was determined with a Model LS3801 liquid scintillation counter (Beckman Instruments, Fullerton, CA). Details of recovery of radiolabeled compounds in all experiments as well as methanotroph isolation and culture are given previously (Whalen et al., 1990, 1992). Mass balances showed full recovery (98 ± 7%; $\bar{x} \pm$ SD) of label in all experiments involving ^{14}CO addition.

2.5. Statistics and calculations

First order rate constants for net (k_n) or gross (k_g) CO consumption (h^{-1}) were calculated according to Conrad and Seiler (1980). Values of k_n were compared by Analysis of Covariance (ANCOVA) to ensure that rates of net CO consumption were not significantly different among samples prior to experimental manipulation. The subsequent effect of treatment on k_n was also frequently analyzed by ANCOVA. The apparent half-saturation constant for gross CO consumption (K_m) and the maximum rate of CO consumption (V_{max}) in initial velocity experiments were estimated by directly fitting the data for CO consumption rate (calculated according to Conrad and Seiler, 1980) vs. CO concentration to the Michaelis–Menten model. A nonlinear curve fitting routine (SYSTAT; SPSS Inc., Chicago, IL) was used. Rates of CO production in irradiated samples and rates of ^{14}CO oxidation in temperature dependence experiments were determined by linear regression of data for headspace ^{12}CO concentrations or $^{14}CO_2$ activity vs. time, respectively. A significance level of $\alpha = 0.05$ was used for all statistical tests.

3. Results

3.1. Effect of selective biological inhibitors, sterilization or CH_4 on CO oxidation and production

3.1.1. Sterilization with ^{137}Cs

Carbon monoxide can be simultaneously produced and oxidized in soils (Conrad and Seiler, 1980). Consequently, unless CO consumption is fully inhibited, time courses for change in headspace CO represent the net effect of CO consumption and production. Samples exposed to ^{137}Cs clearly showed altered time courses for change in headspace CO and CH_4 concentrations relative to unirradiated controls. Duplicate soil samples from NB1 and BS2 exhibited net CO consumption prior to γ-irradiation and within-site values of k_n did not differ significantly. The randomly selected sample from BS2 that was then subjected to ^{137}Cs showed an increase in headspace CO, while the sample from NB1 showed no change in headspace CO concentration (Fig. 1(A)). Headspace CH_4 concentrations decreased by 1.3 (NB1) and 2.4 (BS2) μl l^{-1} in unkilled controls but remained unchanged in irradiated samples (data not shown), providing additional evidence that treatment totally eliminated biological CO-oxidizing activity. Carbon monoxide production was 1.8 ng g_{dw}^{-1} h^{-1} (dw = dry soil mass) in the irradiated sample from BS2. All soils produced CO (Fig. 1(B)) but did not oxidize CH_4 (data not shown) after an overnight incubation at 60°C. The rate of CO production was similar at 0.8 ng g^{-1} h^{-1} for irradiated and control soils at NB1. Higher rates were obtained for BS2 soils. Carbon monoxide production rates

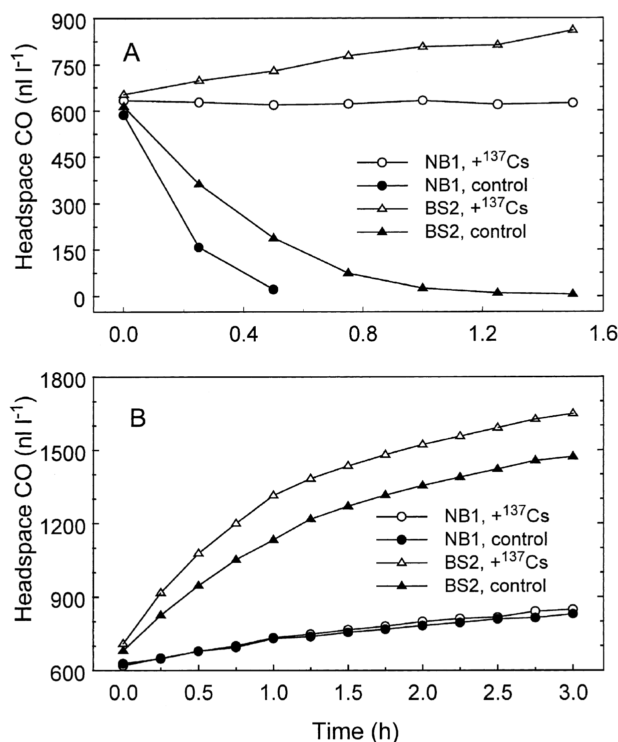

Fig. 1. Time courses for change in headspace CO concentration for homogenized boreal forest soils. (A) One sample each from sites NB1 and BS2 was irradiated with ^{137}Cs to terminate biological activity, while an additional non-irradiated sample served as a control. (B) These same samples were then incubated overnight at 60°C and time courses for change in headspace CO were reassessed.

were 4.0 ng g^{-1} h^{-1} for the control sample and 4.5 ng g^{-1} h^{-1} for the irradiated sample. The latter rate of CO production exceeded that of the irradiated sample prior to heat exposure by a factor of 2.5.

3.1.2. Sterilization with ethylene oxide

Ethylene oxide treatment gave results similar to irradiation experiments (data not shown). Duplicate soil samples from AS2 and BS2 showed net CO consumption prior to the addition of CH_2CH_2O and within-site values of k_n were not significantly different. A randomly selected sample from each site that was then exposed to CH_2CH_2O produced CO the next day, while the unkilled control continued to oxidize CO. Concurrently, headspace CH_4 concentrations decreased by 3.0 (AS2) and 4.5 (BS2) μl l^{-1} in unkilled controls but remained unchanged in CH_2CH_2O-amended samples. Rates of CO production in CH_2CH_2O-amended samples from AS2 and BS2 were 3.2 and 6.7 ng g_{dw}^{-1} h^{-1}.

3.1.3. Selective inhibition with antibiotics

The addition of antibiotics clearly inhibited CO consumption (Fig. 2). Quadruplicate soil samples from UP3A showed net CO consumption prior to treatment with antibiotics, with k_n values that did not differ significantly. A randomly selected sample amended with a combination of cycloheximide and streptomycin in deionized water showed no change in headspace CO concentration with time. In contrast, a control soil amended with deionized water continued to oxidize CO with $k_n = 1.53\ h^{-1}$. This was significantly higher than the values for samples amended individually with streptomycin ($k_n = 1.11\ h^{-1}$) or cycloheximide ($k_n = 1.23\ h^{-1}$), which did not differ significantly from one another.

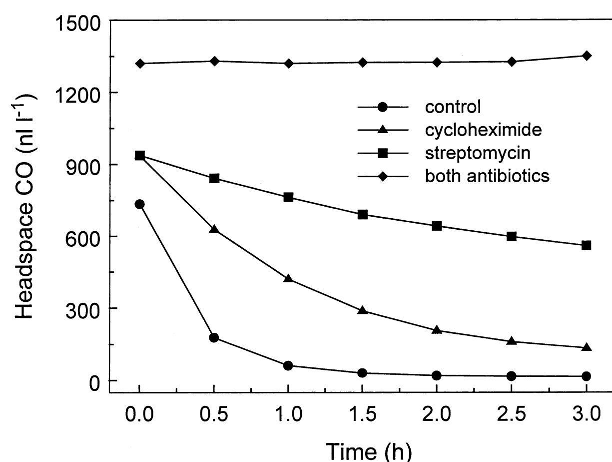

Fig. 2. Time courses for change in headspace CO concentration for homogenized boreal forest soils from site UP3A. Soils had been previously amended with cycloheximide, streptomycin, cycloheximide plus streptomycin or deionized water (control).

3.1.4. Methane addition experiments

High CH_4 concentrations had no influence on net CO consumption (data not shown). Triplicate soil samples from UP3A all showed net CO consumption and statistically similar k_n values prior to treatment. Samples subsequently amended with CO alone or additionally amended with CH_4 at zero time or after 2 h showed values of k_n that still did not differ significantly and ranged from 1.65 to 1.73 h^{-1}.

3.2. CO oxidation by an isolated soil methanotroph

Tracer experiments indicated that methanotrophs from this boreal forest soil were capable of consuming CO. Radiolabeled CO_2 accumulated and ^{14}CO simultaneously decreased in the jar headspace when a methanotroph isolated from BS2 was exposed to ^{14}CO (Fig. 3). However, little ^{14}CO was incorporated into biomass. The distribution of end products of ^{14}CO consumption at the termination of the experiment was 99% $^{14}CO_2$ and less than 1% ^{14}C-biomass, with an insignificant fraction as dissolved organic-^{14}C. This culture oxidized ^{14}CO at a rate of 1.13 fg $cell^{-1}$ d^{-1}.

3.3. Depth profiles for CO concentration and CO oxidation

In most cases, soil concentrations of CO were near atmospheric (~150 nl l^{-1}) at 1 cm below the surface and decreased with increasing depth to about 15 cm (Fig. 4(A)). Occasionally, however, surface soils (<10 cm depth) showed elevated concentrations of CO relative to the atmospheric level,

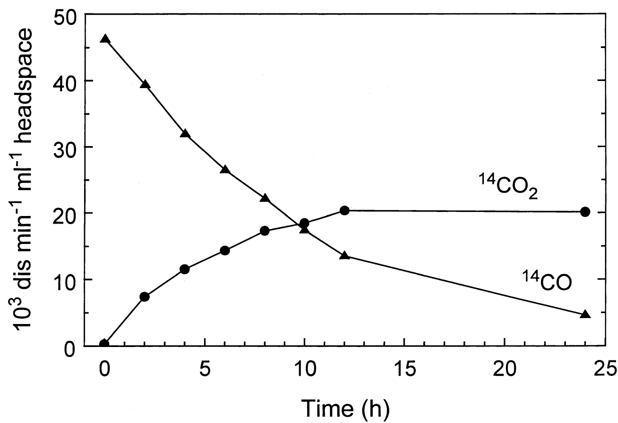

Fig. 3. Time course for change in headspace $^{14}CO_2$ and ^{14}CO in a culture of a methanotroph isolated from site BS2 and exposed to ^{14}CO.

indicating a zone of net CO production (Fig. 4(B)). Carbon monoxide concentrations remained essentially constant at <5–20 nl l^{-1} in all profiles for soils $\geqq 15$ cm, indicating that consumption of atmospheric CO was limited to soils above this depth.

Time courses for change in CO concentration in amended atmosphere experiments involving 5 cm core sections from the four sites gave variable results for surface soils. The 0–5 cm zone showed net CO consumption in five instances (e.g. Fig. 5(A)), net CO production in one core from UP3A (Fig. 5(B)) and BS2 (data not shown) and no net change in CO concentration in the other core from BS2. In contrast, core sections at >5 cm below the soil surface consistently showed net CO consumption, in accord with most soil CO profiles (Fig. 4(A)). First order rate constants for gross CO consumption were generally highest in the 0–5 cm core sections and diminished somewhat with increasing depth (Table 1). Notably, soils beyond the zone of atmospheric influence were capable of rapidly oxidizing CO.

The depth distribution of end products of ^{14}CO consumption was assessed in a single core from each site (data not

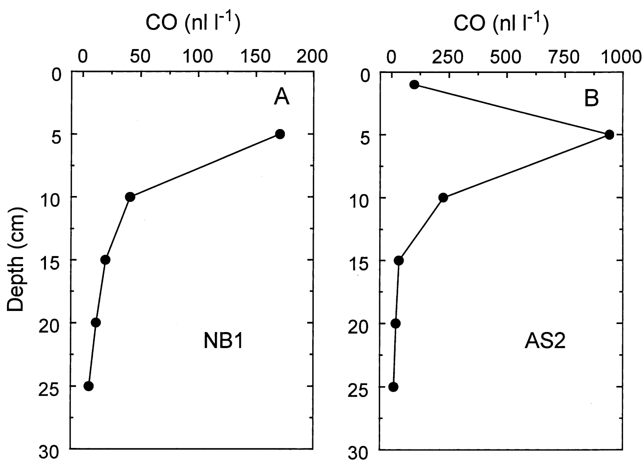

Fig. 4. Representative depth distributions for CO in boreal forest soils. Sampling sites are (A) NB1 and (B) AS2.

Table 1
Depth profiles for soil organic content and first order rate constants for gross CO consumption, k_g (± 1 SEM), for duplicate core sections in boreal forest soils

Site	Depth interval (cm)	Organic content (%)	k_g (h^{-1})
AS2	0–5	35.9	19.9 (0.4)
	5–10	6.6	12.4 (8.6)
	10–15	7.7	10.6 (2.9)
	15–20	2.3	6.6 (3.6)
NB1	0–5	47.3	13.2 (3.0)
	5–10	7.4	13.8 (0.9)
	10–15	4.6	11.0 (2.3)
	15–20	3.6	11.5 (3.1)
UP3A	0–5	78.7	15.1[a]
	5–10	43.9	14.9 (4.7)
	10–15	4.8	13.0 (1.7)
	15–20	4.4	8.0 (4.0)
BS2	0–5	96.3	[b]
	5–10	97.8	16.3 (0.8)
	10–15	90.7	5.8 (1.8)
	15–20	48.9	8.9 (1.2)
	20–25	14.6	6.9 (2.4)
	25–30	5.4	4.5 (1.6)

[a] Value for single core section; companion section showed net CO production.
[b] One core section showed net CO production and the other showed no net change in CO.

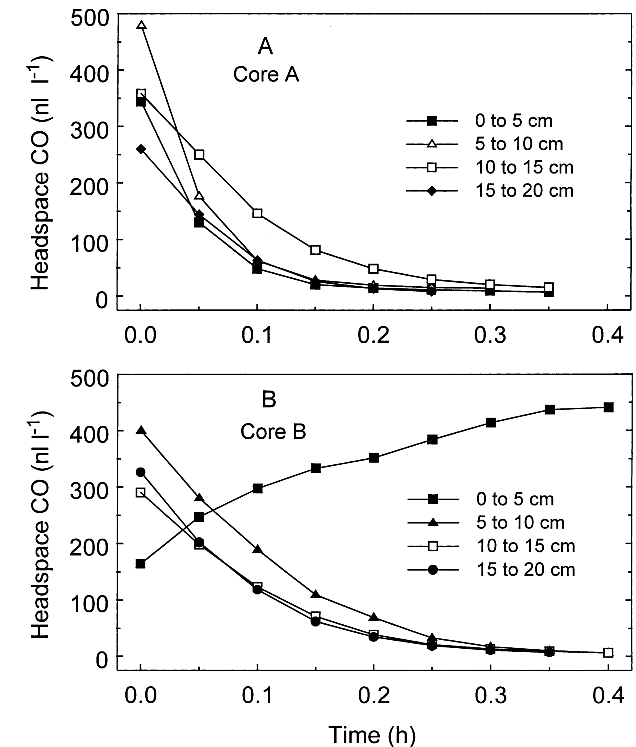

Fig. 5. Representative time courses for change in headspace CO concentration in amended atmosphere experiments involving 5 cm sections of duplicate cores (A and B). Sampling locations were separated by <1 m at site UP3A.

Table 2
Kinetics of net CO consumption by homogenized boreal forest soils

	μl CO l^{-1}		μg CO g_{dw}^{-1} h^{-1}	
Site	K_m	95% CI[a]	V_{max}	95% CI
AS2	8	6–10	0.87	0.84–0.89
NB1	19	16–22	2.72	2.63–2.80
UP3A	36	25–47	0.78	0.70–0.87
BS2	21	16–26	0.67	0.63–0.73

[a] 95% confidence interval.

shown). Carbon monoxide consumption was essentially constant with depth at UP3A and AS2 but decreased with increasing depth at BS2 and NB1. The fraction of assimilated ^{14}CO that was incorporated into biomass was somewhat higher in the 0–5 cm depth (8–10%) interval than in deeper soils (3–7%) at all sites. Depth-integrated incorporation of assimilated ^{14}CO into biomass was remarkably similar among sites, 5–7%.

3.4. Kinetics of CO oxidation

Kinetic experiments for gross CO consumption by homogenized boreal forest soils gave values for K_m that ranged over a factor of less than 5, from 8 to 36 μl CO l^{-1} (Table 2). Values for V_{max} showed similar variability, ranging from 0.67 to 2.72 μg CO g_{dw} $^{-1}$ h^{-1}. Based on overlap of 95% confidence intervals, K_m for AS2 appeared to be lower than values for other sites, while V_{max} for NB1 was clearly higher than values for other sites.

3.5. Temperature dependence of CO oxidation

The single experiment evaluating the temperature dependence of CO oxidation showed a linear increase in $^{14}CO_2$ over the temperature range 4–34°C (Fig. 6). The regression equation ($r^2 = 0.93$) describing the relationship between $^{14}CO_2$ accumulation and temperature gave a slope of 1.46 and *y*-intercept of 3.34, from which we calculate a temperature coefficient (Q_{10}) of about 1.8 for CO oxidation in this soil.

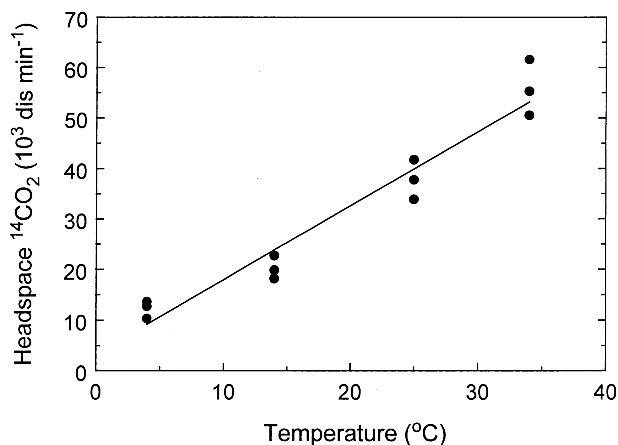

Fig. 6. Temperature dependence of ^{14}CO oxidation to $^{14}CO_2$ in homogenized soil samples from site UP3A.

4. Discussion

4.1. Effect of sterilization on CO oxidation

In three of four cases, surface soils characterized by net CO consumption showed CO production when exposed to γ-radiation (Fig. 1(A)) and CH_2CH_2O. Inability of irradiated soils to oxidize CH_4 strongly suggests that all biological activity was terminated. Strong CO production by sterilized soils has been interpreted (Inman et al., 1971; Smith et al., 1973; Conrad and Seiler, 1980,1982b; Moxley and Smith, 1998b) to indicate the involvement of poorly defined abiological processes, as is likely the case here. Our rates of CO production following sterilization (0–6.7 ng g_{dw}^{-1} h^{-1}) compare favorably with the average of 3.3 ng g_{dw}^{-1} h^{-1} reported by Ingersoll et al. (1974) for autoclaved potting soil subsequently incubated at 20°C, but are generally lower than rates of about 5–55 ng g^{-1} h^{-1} that we infer from data given by Moxley and Smith (1998b) for irradiated or autoclaved fresh Scottish soils. The cause of high variability among reported rates is unclear. The conditions required to kill microbes also break down soil organic matter (Moxley and Smith, 1998b), such that different biocidal treatments may vary in their influence on rates of abiotic CO production. Supporting evidence here is the 2.5-fold increase in the rate of CO production in irradiated BS2 soil and the production of CO by inactive, irradiated NB1 soil when these samples were subsequently heat-treated (cf. Fig. 1(A) and (B)). Soil moisture content (Moxley and Smith, 1998b) and organic matter quality (Conrad and Seiler, 1985) also affect rates of CO production and likely influence rates of CO production following biocidal treatment.

4.2. Effect of selective inhibitors on CO oxidation

Inhibition experiments indicate that CO consumption in this soil was biologically mediated. Streptomycin and cycloheximide inhibit prokaryotic and eukaryotic protein synthesis, respectively (Conrad and Seiler, 1980). Each antibiotic significantly inhibited CO consumption relative to controls, qualitatively suggesting that the CO-oxidizing community contains both eukaryotes (e.g. fungi) and procaryotes (Fig. 2). However, non-target inhibition by cycloheximide has been reported (Velvis, 1997) and it cannot be discounted that prokaryotes alone are responsible for CO consumption in this soil. The lack of change in headspace CO in soil simultaneously treated with both antibiotics may result from equilibrium between production and a lowered rate of consumption of CO. Alternatively, this soil may not produce CO and the synergistic effect of both antibiotics totally eliminated CO consumption. The overall response of this soil is in general agreement with a more detailed study for several similarly treated temperate soils (Conrad and Seiler,

1980). Otherwise, Inman et al. (1971) reported total elimination of CO-oxidizing activity in potting soil alternatively air-dried and drenched with a mixture of cycloheximide, erythromycin and cycloheximide in 1.5% ethanol by volume.

4.3. ^{14}CO oxidation by an isolated soil methanotroph

The demonstrated ability of the methanotroph isolated from BS2 to oxidize ^{14}CO (Fig. 3) compares favorably with previous observations of CO consumption by pure cultures or cell-free extracts of these microbes (Ferenci, 1974; Stirling and Dalton, 1979). The CO consumption rate of 1.13 fg cell^{-1} d^{-1} for this isolate is more than 1000-fold lower than the V_{max} of about 1900–2350 fg cell^{-1} d^{-1} for CH_4 consumption by methanotrophs isolated from other high latitude soils (Whalen et al., 1996). Low fractional incorporation of assimilated ^{14}CO into biomass (<1%) by this isolate is consistent with the inability of CO to support growth of methanotrophs (Ferenci, 1974). In contrast, high latitude soil microbial communities show 40–58% incorporation of assimilated $^{14}CH_4$ into biomass (Whalen et al., 1996).

Although at least one methanotroph in this soil is capable of CO consumption, two lines of evidence suggest that this functional group plays a minor role in CO consumption here. First, using values of k_g (Table 1) and soil CO profiles (Fig. 4) we calculate that depth-integrated CO consumption rates varied from 48 to 123 mg m^{-2} h^{-1} for the five cores that showed net CO consumption in all soil zones. Assuming a population of 10^5 methanotrophs g_{dw}^{-1} soil (Bender and Conrad, 1994) throughout the soil profile and that the cellular CO consumption rate of this culture is representative of all methanotrophs in this soil, this microbial group was responsible for a maximum of only 1.7 ± 1.2% ($\bar{x} \pm$ SD) of depth-integrated gross CO consumption in these cores. Second, CO consumption rates remained unchanged relative to controls for samples additionally amended with CH_4. Our results corroborate well a similar study for a temperate forest soil (King, 1999b) where it was concluded that methanotrophs played an insignificant role in CO consumption, based partly on the inability of known inhibitors of CH_4 oxidation to permanently reduce ^{14}CO oxidation.

4.4. Depth profiles for CO concentration and CO oxidation

Most depth profiles pointed to net consumption of atmospheric and any locally produced CO in the upper 15 cm and a dynamic steady state between CO production and consumption in deeper soils (Fig. 4(A)). Similar profiles have been reported for cultivated (King, 1999b; Yonemura et al., 1999) and forest soils (Kuhlbusch et al., 1998; Sanhueza et al., 1998), although the zone of atmospheric influence extended only 5 cm below the soil surface. Low bulk density in these highly organic soils facilitates diffusion (Whalen et al., 1992) and likely results in a more extensive zone of atmospheric CO consumption. Less frequently, depth profiles indicated a surface zone of net CO production (Fig. 4(B)), which has also been reported for a temperate coniferous forest (King, 1999b).

Boreal forest soils below the depth of penetration of atmospheric CO were capable of rapid CO consumption (Fig. 5 and Table 1). This is consistent with a previous report for Canadian boreal forest soils that showed high CO deposition velocities at depths to 20 cm in some cases (Kuhlbusch et al., 1998). Studies in temperate regions have also demonstrated continued but reduced potential for CO consumption in mineral soils beneath the zone of atmospheric influence (Moxley and Smith, 1998a; King, 1999a). Local chemical CO production (Conrad and Seiler, 1985) in highly organic boreal forest soils may provide sufficient substrate to maintain a microbial community capable of rapid CO consumption well below the soil surface. The 5–7% efficiency of incorporation of assimilated ^{14}CO into microbial biomass in these boreal forest soils is similar than the 3–7% reported for roadside temperate soils (Spratt and Hubbard, 1981) and lower than the 17% observed in optimized fermenter cultures of carboxydobacteria (Meyer and Schlegel, 1978). The low efficiency of biomass production in our study is consistent with Conrad's (1988) conclusion that microbial CO consumption in upland soils is predominately nonutilitarian.

4.5. Kinetics of CO oxidation

Apparent K_m and V_{max} values for CO consumption by these boreal forest soils fall within the ranges reported for other soil systems (Table 3) and natural aquatic populations of unidentified oligotrophic microflora (~10 μl CO l^{-1}; Conrad and Seiler, 1982a). Comparison of apparent K_m's for CO consumption by natural soil samples and isolates from bacterial metabolic groups has been used to infer the composition of the soil CO oxidizing community. Apparent K_m values in Table 2 are one to two orders of magnitude lower than apparent K_m's for carboxydobacteria (465–1110 μl CO l^{-1}), leading to the suggestion (Conrad et al., 1981) that these microbes are not responsible for CO removal from ambient atmospheres. Apparent K_m's for CO oxidation by NH_4^+-oxidizing bacteria (Jones and Morita, 1983) and additional estimates for pure cultures of carboxydobacteria (Mörsdorf et al., 1992) approach (<200 μl CO l^{-1}) values for natural soils, indicating possible involvement of the former microbial group and a greater role for the latter. However, low rates of NH_4^+ oxidation in the soils studied here (Whalen, 2000) point to a minor role for nitrifiers and evidence given above excludes extensive CO consumption by methanotrophs. Similarly, based on studies involving specific metabolic inhibitors, King (1999b) discounted significant CO consumption by methanotrophs and nitrifiers in temperate forest soils, and instead argued for CO consumption by a diverse microbial community rather than a single, highly defined functional group. Two lines of evidence not only support this view, but also suggest a fundamental similarity among microbial communities

Table 3
Summary of kinetics constants for CO consumption in soils

Environment	K_m (μl CO l^{-1})	V_{max} (μg CO g^{-1} h^{-1})	Reference
Boreal forest	8–36	0.7–2.7	This study
Loess, sand, chernozem	5–8	0.3–1.3	Conrad et al. (1981)
Pine forest	17	11.1	King (1999b)
Hardwood forest, lawn	18–51	1.4–10.2	Duggin and Cataldo (1985)
Roadside soil	15	0.9	Spratt and Hubbard (1981)
Cropland soil	44	187	Bartholemew and Alexander (1981)

responsible for CO consumption across ecosystems. First, ranges of K_m and V_{max} for CO consumption (Table 3; exception: V_{max} for cropland soil) from a wide array of soil environments are remarkably narrow. Second, the limited published data for fractional incorporation of assimilated CO into cell material are in reasonable agreement.

4.6. Temperature dependence of CO oxidation

The increase in CO oxidation up to 34°C (Fig. 6) agrees with the generally modest increase reported elsewhere over a roughly similar temperature range (Inman et al., 1971; Liebl and Seiler, 1976; Kuhlbusch et al., 1998). Abiological CO production may show a stronger temperature response than biological CO consumption such that some tropical (Scharffe et al., 1990; Sanhueza et al., 1994) and temperate (King, 1999b) soils change from a sink to a source of CO above a critical temperature ranging from about 20 to 40°C. Accordingly, $^{14}CO + ^{12}CO$ and ^{12}CO were being simultaneously oxidized and produced, respectively, in our temperature dependence experiment. However, 10–20-fold higher rates of CO consumption relative to production in atmospheres initially adjusted to CO concentrations roughly similar to that of the temperature dependence experiment (Fig. 1(A)) ensures that the influence of simultaneous ^{12}CO production is small in this short duration (1 h) experiment. The data show a linear increase in CO oxidation with increasing soil temperature over the relevant range for the thaw season (>0–22°C; Whalen et al., 1991) and further suggest a continued linear response to the 4–6°C increase in regional summer air temperature predicted under future climates (Grissom et al., 2000). Although the optimum temperature for CO oxidation in our study is uncertain, it is undoubtedly higher than the 30°C reported by Ingersoll et al. (1974) for potting soil in an atmosphere adjusted to 100 μl CO l^{-1} and values (10–35°C) reported for lower latitude soils (Liebl and Seiler, 1976; Moxley and Smith, 1998a; King, 1999b), which frequently include the simultaneous influence of CO consumption and production. The Q_{10} of 1.8 for CO oxidation by this soil agrees with the single published average (±SD) of 1.5 ± 0.2 for several temperate forest, grassland and cropland soils (Bartholemew and Alexander, 1981) in amended atmosphere (3 μl CO l^{-1}) experiments.

5. Conclusions

Carbon monoxide consumption in boreal forest soils from intermediate and advanced successional stages was biologically mediated and probably involved both prokaryotic and eukaryotic organisms. However, CO consumption in these soils differed from the activity in their more well-studied temperate counterparts in two respects. First, the surface zone of atmospheric CO consumption was more extensive (to 15 cm depth vs. 5 cm). Second, boreal forest soil horizons at depths below the zone of atmospheric influence showed a high potential for CO consumption. These differences were attributed to firstly the low bulk density of surface horizons of boreal forest soils that facilitates diffusion and secondly the higher organic content at all depths. These two factors support both local CO production and a microbial community capable of CO consumption. However, in accord with reports from temperate regions, CO consumption in boreal forest soils was largely nonutilitarian. Only 5–7% of assimilated ^{14}CO by soil microbes was incorporated into biomass. Kinetic constants (K_m, V_{max}) between this soil and diverse lower latitude soils were similar, suggesting that soil CO oxidizing communities are not fundamentally different across ecosystems. Carbon monoxide oxidation showed a modest increase with increasing temperature over a range relevant for present and predicted future climates. Additional research on CO consumption in boreal forest soils should focus on the moisture response, as regional summer precipitation is expected to increase 5–60% above current in future climates (Grissom et al., 2000).

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