Role of Microorganisms in the Consumption and Production of Atmospheric Carbon Monoxide by Soil

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Consumption and production of atmospheric CO was measured under field conditions in three different types of soil. CO was consumed by an apparent first-order reaction and produced by an apparent zero-order reaction, resulting in a dynamic equilibrium with the consumption of atmospheric CO as the net reaction. CO consumption was higher in summer than in winter. Laboratory experiments on five different soil types showed that CO consumption was strongly inhibited by the presence of streptomycin or cycloheximide (Actidione), or both. Thus, eucaryotic as well as procaryotic microorganisms were apparently responsible for the observed CO consumption. The aerobic carboxydobacterium *Pseudomonas carboxydovorans* added to sterile soil was able to utilize the low amounts (ca. 0.7 ppmv) of CO present in laboratory air. CO was consumed by soil under aerobic as well as anaerobic conditions. Anaerobic preincubation of the soil stimulated the anaerobic CO consumption and reduced the aerobic CO consumption. In contrast to CO consumption, CO production was stimulated by autoclaving, by ultraviolet-irradiation, by fumigation with NH₃ or CHCl₃, by treatment with streptomycin or cycloheximide or both, by addition of NaCN, NaN₃, or Na₂HAsO₄ (or all three) in the presence of glucose under an atmosphere of pure oxygen, or by a drying and rewetting procedure. The consumption of atmospheric CO by soil is a microbial process, but the production of CO is apparently not a metabolic process.

Soil is one of the major sinks for atmospheric carbon monoxide (CO). The most recent reports indicate a global CO consumption of 500 Tg year⁻¹ by soil, which is approximately 40% of the total sink strength (30). The consumption of CO by soil is assumed to be a biological process because of its temperature optimum at 30°C and its loss upon heating or upon treatment with antibiotics. The CO consumption activity of autoclaved soil is found to recover when the soil is inoculated with fresh, nonsterile soil (16, 18, 24, 30).

Pure-culture studies have shown that CO can be utilized by fungi (17), algae (5), anaerobic bacteria (8, 9, 12-14, 23, 36, 41), and aerobic bacteria (2, 20-22, 26, 27, 42). The CO consumption process may be due to the catabolic oxidation of CO by autotrophic microorganisms to serve as an electron, energy, or carbon source or to the cometabolism of CO by heterotrophic microorganisms to serve as an additional electron donor or as a carbon source. Therefore, the atmospheric CO can either be incorporated into cell material and metabolic products or be oxidized to CO₂. The latter process seems to be dominant in soil (2). It is not known whether fungal or bacterial CO oxidation is more important with respect to the amount of CO oxidized.

Reports on CO consumption under anaerobic conditions are contradictory. Inman et al. (18) found no CO uptake under anaerobic conditions, although the soil had been incubated for 5 days under pure nitrogen. Bartholomew and Alexander (2), on the other hand, found a conversion of ¹⁴CO to ¹⁴CO₂ under anaerobic conditions and explained the discrepancy as possibly being due to equal consumption and production rates, such that no net change of the CO concentration occurs. The formation of CO at anaerobic sites within the soil was proposed by Zavarzin and Nozhevnikova (42) and is consistent with depth profiles of CO mixing ratios in soil air (23, 24). These profiles show a decrease in the CO mixing ratios from approximately 0.2 to 0.3 ppmv in air above the soil surface to values below 0.02 ppmv in the upper soil layers, indicating consumption of atmospheric CO. However, the CO mixing ratios increase again in anaerobic soils above the groundwater level and reach values of more than 6 ppmv.

Further reports on the production of CO by soil are scarce. Seiler (30) demonstrated that soil produces small but significant amounts of CO, resulting in an equilibrium between CO consumption and CO production. CO production by soil is apparently stimulated by heating to tem-

peratures above 40°C (16, 18, 24, 30). The nature of the CO production processes is unknown so far.

We report on field and laboratory measurements of CO consumption and production by soil. A very sensitive method for measuring CO (31) allowed the application of CO mixing ratios in the ppbv/ppmv range, which is typical for the ambient atmosphere and for the soil air. Our results show that CO consumption and production processes occur simultaneously in soil. Eucaryotic as well as procaryotic microorganisms are responsible for CO consumption, whereas the main CO production processes are apparently not due to metabolism.

(Mixing ratios, given as ppmv = microliters per liter or ppbv = nanoliters per liter, are pressure and temperature independent. Therefore, the term mixing ratio is preferred to the term concentration [e.g., micrograms per liter] in this paper.)

MATERIALS AND METHODS

Field measurements were carried out at three field stations near Mainz, West Germany. The soil types were eolian sand, loess, and loess loam. The soil surface was covered with grass and small plants. The measurements were carried out by covering the soil surface with a glass box and determining the decrease in CO with time inside the glass box (7, 30, 32). The results were not influenced by the plants, as shown by control measurements after removal of the vegetation.

Laboratory experiments were carried out with soil (top 10 cm) samples taken from different locations near Mainz with soil types eolian sand, loess loam, chernozem, vertisol, and grey-brown podzolic soil. The physical properties of the soils have already been described (32). The soils were passed through a 4-mm mesh screen and stored in polyethylene bottles at 4°C. The CO consumption activity of the soils did not change significantly during a period of several months. The soil water content was determined by weight after drying at 104°C for 24 h. Soil samples (100 g, fresh weight) were put into glass flasks (1 liter) and gassed for 15 min with synthetic air or nitrogen (Air Liquide, Essen, Germany) purified from traces of CO by passing the gas stream through molecular sieve 5 Å (E. Merck AG, Darmstadt, West Germany) and Hopkalite (Drägerwerke, Lübeck, West Germany). The air pressure inside the flasks was adjusted to 1.3 bars (1.3×10^5 Pa). CO contained in air or nitrogen was injected into the flasks to give the required CO mixing ratio. The flasks were incubated at 22 to 25°C in the dark. The CO mixing ratio inside the flasks was determined in small air samples (1 to 10 ml), which were taken with gas-tight syringes (Glenco, Houston, Tex.), and analyzed in a CO analyzer based on the HgO-to-Hg vapor conversion (31). The lower detection limit for CO was 0.002 ppmv. The principles of the CO analysis have already been described in detail (30).

Soil was treated with antibiotics by mixing 0.2 g of streptomycin or cycloheximide or both in 95 g (fresh

weight) of soil and then adding 5 ml of water. CO consumption and production rates were determined 4 days later. Treatment with NaCN, NaN₃ (both 0.1 g), or Na₂HAsO₄ (0.5 g) was done by mixing the compounds in 95 g (fresh weight) of soil and then adding 5 ml of water. CO production rates were determined 1 day later. Fumigation was done as follows. The flasks with soil samples (100 g, fresh weight) were evacuated and then refilled with air which had been saturated with NH₃ or CHCl₃. The flasks were flushed for 10 min and subsequently incubated under this vapor for 1 h. Then the flasks were evacuated again and flushed with laboratory air until the typical odor of the fumigation vapor was no longer detectable. Ultraviolet irradiation was done by exposing 20 g (fresh weight) of soil to the radiation of a Pen-Ray lamp (Ultraviolet Products, San Gabriel, Calif.). The soil was slowly stirred by a magnetic bar during irradiation for 1 h.

A suspension of actively growing *Pseudomonas carboxydovorans* strain OM5 (DSM 1227) was kindly provided by O. Meyer, Göttingen, West Germany. The cells were grown under CO-autotrophic conditions in fluted 2-liter Erlenmeyer flasks as described elsewhere (26), harvested during the exponential growth phase at a dry weight of 0.65 mg ml⁻¹, and resuspended in mineral medium. Eolian sand was autoclaved at 120°C for 30 min and then dried in laboratory air under aseptic conditions for 22 days. A 90-g portion of dried soil was put into a glass flask, and the cell suspension was added together with water to give a final soil water content of 10% (wt/wt). A 10-ml amount of water without bacteria was added to a control flask. The flasks were gassed with laboratory air containing approximately 0.7 ppmv of CO by means of a metal bellows pump (Metal Bellows Corp., Sharon, Mass.). The pressure inside the flasks was adjusted to 1.3 bars. Gas sampling was started immediately.

The chemicals were obtained from the following sources. Streptomycin sulfate (723 U mg⁻¹) and cycloheximide (Actidione, pure) were from Serva, Heidelberg, West Germany; Na₂HAsO₄·7H₂O was from Sigma Chemical Co., St. Louis, Mo.; NaCN was from Riedel de Haën, Hannover, West Germany; and the other chemicals were from E. Merck AG.

RESULTS

Dynamic equilibrium between CO consumption and CO production. Field measurements of the change in the CO mixing ratio, m , inside a glass box covering the soil surface demonstrated that CO was consumed until a certain equilibrium value, m_e , was reached. Then the CO mixing ratio within the glass box remained constant. The same equilibrium value was reached when the glass box was flushed with CO-free air, demonstrating that CO was simultaneously produced and consumed by soil. Whereas the CO consumption was an apparent first-order reaction, with k_c as the rate constant

$$-\frac{dm}{dt} = k_c m \quad (1)$$

the CO production was an apparent zero-order reaction:

$$\frac{dm}{dt} = k_p \quad (2)$$

Since CO consumption and production occur simultaneously, the following equation is derived:

$$\frac{dm}{dt} = k_p - k_c m \quad (3)$$

or in its integrated form with the boundary conditions $t = 0, m = m_0$, and $t = \infty, m = m_e$

$$k_c = \frac{1}{t} \ln \frac{m_0 - m_e}{m - m_e} [\text{min}^{-1}] \quad (4)$$

Equation 4 was used to calculate the CO consumption rate, C , from the temporal decrease of the CO mixing ratio inside the glass box

$$C = k_c m_a \frac{V}{A} [\text{nl cm}^{-2} \text{ min}^{-1}] \quad (5)$$

where $m_a = 0.2 \text{ ppmv}$ or 0.2 nl ml^{-1} CO mixing ratio as representative for continental air (33), V = volume of the glass box (cubic centimeters), and A = exposed soil surface (square centimeters). The CO production rate, P , was calculated by using the equilibrium condition

$$k_p = k_c m_e \quad (6)$$

or

$$P = C = k_c m_e \frac{V}{A} [\text{nl cm}^{-2} \text{ min}^{-1}] \quad (7)$$

Extended field measurements were carried out during 1978 and 1979 on undisturbed, natural

soil at three field stations with different types of soil. The observed CO production and consumption rates are summarized in Fig. 1. The individual data points fitted equation 4 and therefore demonstrate that the consumption of atmospheric CO by soil is indeed a dynamic process between CO consumption and production. During all measurements a net CO consumption by soil was observed. The CO consumption rates varied between 0.13 and $1.03 \text{ nl cm}^{-2} \text{ min}^{-1}$ based on a CO mixing ratio of 0.2 ppmv as representative for continental air at a latitude of 50°N (33). The CO production rates varied between 0.01 and $0.26 \text{ nl cm}^{-2} \text{ min}^{-1}$. The consumption as well as the production rates were apparently higher during summer than during winter.

Influence of antibiotics on CO consumption and production. Results obtained after treatment of different types of soil with antibiotics are shown in Fig. 2a and b. CO was always consumed by untreated soils following an apparent first-order reaction. CO production could only be observed when CO-free air ($\leq 0.02 \text{ ppmv}$ of CO) was used. The rates of CO increase were almost undetectable ($< 1 \text{ nl min}^{-1}$). The CO consumption and production rates observed on untreated soils changed considerably when the soils had been treated with streptomycin, cycloheximide, or both. The influence of the antibiotics was observed immediately after their addition, but it increased after an incubation period of 3 to 4 days. As a rule, the consumption of CO by soil was inhibited by the antibiotics (Fig. 2). Cycloheximide had a greater effect than streptomycin in eolian sand, but streptomycin had a greater effect in loess loam, chernozem, and vertisol. Treatment with both antibodies had a

FIG. 1. Consumption (open symbols) and production (closed symbols) of CO by soil in situ at three different field stations near Mainz, West Germany. Symbols: Loess soil at Max-Planck-Institut, Mainz (○, ●); loess loam in Finthen near Mainz (△, ▲); and eolian sand in Waldthausen near Mainz (□, ■).

FIG. 2. Influence of antibiotics on the consumption and production of CO by soil. Measurements were carried out 3 to 4 days after treatment of loess loam and eolian sand (a) and chernozem and vertisol (b), using CO mixing ratios of 0.5 to 0.7 ppmv (upper curves) and ≤ 0.02 ppmv (lower curves). The soil water content was 14 to 16% (wt/wt). Symbols: +, control; O, with streptomycin; Δ , with cycloheximide; $\bullet$, with streptomycin plus cycloheximide.

synergistic effect and even resulted in a CO increase to mixing ratios >1 ppmv of CO. The CO production by soil, on the other hand, was apparently not inhibited by the antibiotics. The experiments carried out under a CO-free atmosphere showed high rates of CO increase when the soils had been treated with antibiotics (Fig. 2). This CO increase is probably due to unmasking the CO production by inhibiting the CO consumption, rather than by stimulating the CO production.

CO consumption by *P. carboxydovorans*. To test the ability of aerobic carboxydobacteria to consume atmospheric CO, autoclaved soil was amended with cell suspensions of CO autotrophically grown *P. carboxydovorans*. Figure 3

shows that sterile eolian sand did not consume the CO of laboratory air. In contrast, a significant CO production by soil which had been autoclaved 22 days before was observed. However, as soon as cells of *P. carboxydovorans* were added, atmospheric CO was consumed by an apparent first-order reaction. The CO consumption rates increased with the amount of bacteria added. The CO of laboratory air was also consumed by the cell suspension alone without soil.

Anaerobic CO consumption. To test whether CO can also be consumed by anaerobic processes, chernozem was incubated under an atmosphere of nitrogen containing 0.7 ppmv of CO. Figure 4 shows that CO was indeed con-

FIG. 2b.

sumed under anaerobic conditions, although the rate was about four times less anaerobically ($k_c = 0.016 \text{ min}^{-1}$) than aerobically ($k_c = 0.072 \text{ min}^{-1}$). When the soil was preincubated anaerobically, the anaerobic consumption rate constant increased to 0.019 min^{-1} after 1 day, whereas the aerobic consumption rate constant decreased to 0.042 min^{-1} . Compared with aerobic conditions, the anaerobic CO equilibrium value was higher, reflecting the dynamic equilibrium between the lower CO consumption rate and the constant CO production.

Stimulation of CO production by different treatments. To determine whether CO production by soil is due to microbial metabolism, eolian sand was autoclaved, irradiated with ultraviolet light, fumigated with NH_3 and CHCl_3 , or incubated in the presence of 0.1% (wt/wt) NaCN , 0.1% NaN_3 , or 0.5% Na_2HAsO_4 . CO production was then measured, using synthetic air

with 0.01 ppmv of CO. The above-mentioned treatments, which are known to destroy or inhibit the microbial activity, resulted in a significant increase of the CO production rate from $<1 \text{ nl min}^{-1}$ in the control to 17 to 54 nl min^{-1} in the treated samples. Treatment with arsenate plus azide had an additive effect. The rate of CO production also increased when 1% (wt/wt) glucose was mixed into the soil. CO production increased further when NaCN , NaN_3 , or NaHAsO_4 was added in addition to glucose. Similar results were obtained when chernozem or loess loam was tested. Stimulation of CO production was also observed when soil was dried in laboratory air and then rewetted (Fig. 5). The CO production after rewetting was maximal at a soil water content of 3% (wt/wt). The CO production was higher after longer drying periods. A test atmosphere of pure oxygen instead of air greatly stimulated the CO production.

FIG. 3. Consumption of atmospheric CO by *P. carboxydovorans* on eolian sand. The soil had been autoclaved before different volumes (1, 3, and 6 ml) of cell suspension ($0.65 \text{ mg [dry weight] mL}^{-1}$) were added.

FIG. 5. Influence of drying and rewetting on CO production by soil. Eolian sand was dried in laboratory air for periods of 6 (○), 42 (●), or 60 (△) days. A 100-g amount of dried soil was added to glass flasks (1 liter), and increasing amounts of water were added to give the required soil water content. The flasks were gassed with CO-free synthetic air (○, △) or with pure oxygen (●) to a final gas pressure of 1.3 bars. The sampling was started immediately thereafter.

FIG. 4. Consumption and production of CO under aerobic and anaerobic conditions. A 95-g (fresh weight) portion of chernozem together with 5 ml of water was added to glass flasks (1 liter) to give a final soil water content of 15% (wt/wt). The soil was incubated under an atmosphere of pure nitrogen or laboratory air for 1 day. Then the flasks were gassed with either nitrogen (●) or CO-free synthetic air (○). The gas pressure was adjusted to 1.3 bars, and the sampling was immediately started (lower curves). Otherwise, the experiment was started by injecting CO-containing nitrogen or synthetic air to give an initial CO mixing ratio of 0.7 ppmv (upper curves).

DISCUSSION

Our field measurements have shown that soil is a sink for atmospheric CO. Our results confirm and extend previous observations (24, 30, 32). The CO consumption rates obtained at three locations near Mainz with different soil types did not show significant systematic differences. The individual rates varied in total by a factor of 3 to 4. This seems to be dependent on weather conditions, which influence the soil temperature and the soil water status and therefore presumably the microbial activities as well. The CO consumption rates in December to February varied between 0.13 and 0.39 nl cm⁻² min⁻¹, but in the other months the rates varied between 0.25 and 1.03 nl cm⁻² min⁻¹. This pattern reflects a seasonal variation of CO consumption, with low rates during the winter months when the microbial population is relatively small or the microbial activity is relatively low.

Our results clearly show that the observed CO consumption is the result of a dynamic equilibrium between consumption and production of CO by soil. Net CO consumption is observed at CO mixing ratios higher than the equilibrium value; net CO production is observed at CO mixing ratios lower than the equilibrium value. At atmospheric CO mixing ratios identical to the equilibrium value, the net CO flux between soil and atmosphere is zero, although the CO turnover or the gross fluxes might be high. Therefore, the use of CO mixing ratios representative of ambient air is imperative for determining whether soil acts as a source or a sink for atmospheric CO.

The assumption that CO consumption is accomplished by microbial metabolism (see above) is confirmed by the observation that CO consumption is severely inhibited by streptomycin and cycloheximide. The inhibition was observed immediately after addition of the antibiotics, although it increased further with time for a certain incubation period. As the antibiotics inhibit only the protein synthesis of the microorganisms and not their catabolism, the CO consumption must be strictly controlled by the anabolic activity. This indicates that CO is mainly consumed by growing microorganisms, but is not consumed when turnover and biosynthesis of protein are blocked.

Streptomycin and cycloheximide have been used to quantify the bacterial and fungal contributions to soil respiration (1). The basis for these experiments is the specific inhibition of protein synthesis on procaryotic ribosomes by streptomycin (19) and on eucaryotic ribosomes by cycloheximide (28). Our results indicate that the contribution of procaryotic and eucaryotic microorganisms to CO consumption by soil de-

pends on the soil type. Whereas eucaryotes, e.g., fungi, were more important in eolian sand and in grey-brown podzolic soil (data not shown), procaryotes were more important in loess loam, chernozem, and vertisol. Treatment with streptomycin plus cycloheximide, inactivated the CO consumption activity almost completely. Any residual CO consumption was masked by the strong simultaneous CO production. Therefore, the residual activity could only be estimated to a value of approximately <10% of the control. Grey-brown podzolic soil was less susceptible to inhibition by antibiotics. Treatment with streptomycin plus cycloheximide inactivated CO consumption activity by 66% (data not shown). Either the transport of the antibiotics to the sites of the CO-consuming microorganisms was impeded by the particular soil texture or the microorganisms of that particular soil were more resistant to the antibiotics (15, 38).

Although it is apparent that microorganisms are responsible for the destruction of atmospheric CO by soil, it was unclear whether CO at these low mixing ratios could be utilized by carboxydobacteria (42). Strains of this group of bacteria have been isolated under conditions in which high CO mixing ratio (>10%) allowed the chemolithotrophic growth on CO as a source for energy, electrons, and carbon (26, 42). Recently it has been shown that the ability to utilize a gas for growth does not necessarily prove that this gas is also used when it is supplied as a trace constituent of air. Hydrogen bacteria, for example, are able to grow autotrophically with H₂ as a source of energy and electrons, but they are unable to utilize the low amounts of H₂ in ambient air (6). Therefore, it is interesting that the aerobic carboxydobacterium *P. carboxydovorans* is able to utilize the CO present in laboratory air (0.7 ppmv of CO). This result shows that *P. carboxydovorans* is a genuine oligocarbophilic microorganism. Its ecological niche in nature may well be the utilization of the CO present in the atmosphere.

CO can be consumed anaerobically as well as aerobically, but the consumption rate under anaerobic conditions was lower. Anaerobic CO consumption was observed in fresh soil, which had not yet been incubated under anaerobic conditions. Therefore, microorganisms able to consume CO anaerobically as well as aerobically must be present in the soil or the soil must contain anaerobic sites where a particular microbial flora uses CO anaerobically. One-day preincubation of the soil under anaerobic conditions enhanced the anaerobic CO consumption by 15% and simultaneously reduced the aerobic CO consumption by 40%. This result indicates that either induction and repression processes or changes of the microbial population occurred

during the preincubation period. The observation of anaerobic CO consumption agrees with the conversion of ^{14}CO to $^{14}\text{CO}_2$ under anaerobic conditions, as found by Bartholomew and Alexander (2). The ability of soil to consume CO anaerobically suggests that anaerobic microorganisms are also of significance in the consumption of atmospheric CO observed in the field.

The important role of microorganisms in consumption of CO by soil has extensive experimental support. However, whether the CO production by soil is due to microbial metabolism is questionable. CO production has previously been observed during the catabolism of heme and cobalamine compounds by bacteria (10, 11) and of flavonoids by *Aspergillus flavus* and other fungi (37). Trace amounts of CO were also produced during growth of yeasts and bacteria on glucose (29). Furthermore, there are a number of reports on light-dependent CO production by algae, cyanobacteria, and phototrophic bacteria (3, 25, 34, 35). However, the CO production which we observed in soil was apparently not related to the metabolic activity of microorganisms. Strong CO production was observed by the inhibition of microbial anabolism or catabolism. Strong CO production was also observed after the application of sterilizing conditions to the soil (e.g., heat, ultraviolet light, fumigation), or after the application of a drying and rewetting procedure. These observations suggest that the CO production by soil is a chemical rather than a metabolic process. The CO is probably formed during the lysis of microorganisms, during the oxidation of dead microbial material, or during unspecified chemical or biochemical reactions with soil organic matter. The stimulation of CO production under a pure oxygen atmosphere also suggests a chemical oxidation process. CO production by chemical processes was reported for CO evolution from heat-sterilized culture broths (4), and photooxidative CO production by phototrophic microorganisms (3) and seawater (39) has been reported. We thus contend that non-metabolic oxidation processes are responsible for the CO production from the soil surface observed during the field measurements: in particular, drying and rewetting of the soil surface may initiate CO production processes. The origin of CO observed in soil air above the groundwater level (24, 32) remains unexplained. We do not exclude that metabolic reactions may play a significant role during anaerobic CO production, especially in permanently anaerobic soil. In this respect it is still unclear whether CO is a methanogenic substrate of ecological significance (40).

ACKNOWLEDGMENTS

We thank W. Geins and J. Steffen for technical assistance and A. M. Cook, Zürich, Switzerland, and O. Meyer, Göttingen,

West Germany, for valuable discussion and critical reading of the manuscript.

This work was financially supported by the Deutsche Forschungsgemeinschaft (SFB 73).

LITERATURE CITED

- Anderson, J. P. E., and K. H. Domsch. 1973. Quantification of bacterial and fungal contributions to soil respiration. *Arch. Mikrobiol.* **93**:113-127.
- Bartholomew, G. W., and M. Alexander. 1979. Microbial metabolism of carbon monoxide in culture and in soil. *Appl. Environ. Microbiol.* **37**:932-937.
- Bauer, K., R. Conrad, and W. Seiler. 1980. Photooxidative production of carbon monoxide by phototrophic microorganisms. *Biochim. Biophys. Acta* **589**:46-55.
- Bouley, G., J. Godin, A. Roussel, and F. Girard. 1971. Mise en évidence d'une production importante de monoxyde de carbone par des milieux de culture bactériologiques stériles. *C.R. Acad. Sci. Ser. D* **272**:1459-1461.
- Chappelle, E. W. 1962. Carbon monoxide oxidation by algae. *Biochim. Biophys. Acta* **62**:45-62.
- Conrad, R., and W. Seiler. 1979. The role of hydrogen bacteria during the decomposition of hydrogen by soil. *FEMS Microbiol. Lett.* **6**:143-145.
- Conrad, R., and W. Seiler. 1979. Field measurements of hydrogen evolution by nitrogen-fixing legumes. *Soil Biol. Biochem.* **11**:689-690.
- Daniels, L., G. Fuchs, R. K. Thauer, and J. G. Zeikus. 1977. Carbon monoxide oxidation by methanogenic bacteria. *J. Bacteriol.* **132**:118-126.
- Diekert, G. B., and R. K. Thauer. 1978. Carbon monoxide oxidation by *Clostridium thermoaceticum* and *Clostridium formicoaceticum*. *J. Bacteriol.* **136**:597-606.
- Engel, R. R., J. M. Matsen, S. S. Chapman, and S. Schwartz. 1972. Carbon monoxide production from heme compounds by bacteria. *J. Bacteriol.* **112**:1310-1315.
- Engel, R. R., S. Modler, J. M. Matsen, and Z. J. Petryka. 1973. Carbon monoxide production from hydroxocobalamin by bacteria. *Biochim. Biophys. Acta* **313**:150-155.
- Fischer, F., R. Lieske, and K. Winzer. 1931. Biologische Gasreaktionen. I. Mitteilung: Die Umsetzung des Kohlenoxyds. *Biochem. Z.* **236**:247-267.
- Fischer, F., R. Lieske, and K. Winzer. 1932. Über die Bildung von Essigsäure bei der biologischen Umsetzung von Kohlenoxyd und Kohlensäure mit Wasserstoff zu Methan. *Biochem. Z.* **245**:2-12.
- Fuchs, G., U. Schnitker, and R. K. Thauer. 1974. Carbon monoxide oxidation by growing cultures of *Clostridium pasteurianum*. *Eur. J. Biochem.* **49**:111-115.
- Harris, P. J., and M. Woodbine. 1967. Antibiotic resistance of soil bacteria. I. Antibiotic resistance of bacteria from rhizosphere and non-rhizosphere soils. *Plant Soil* **27**:167-171.
- Ingersoll, R. B., R. E. Inman, and W. R. Fisher. 1974. Soil's potential as a sink for atmospheric carbon monoxide. *Tellus* **26**:151-159.
- Inman, R. E., and R. B. Ingersoll. 1971. Note on the uptake of carbon monoxide by soil fungi. *J. Air Pollut. Control Assoc.* **21**:646-647.
- Inman, R. E., R. B. Ingersoll, and E. A. Levy. 1971. Soil: a natural sink for carbon monoxide. *Science* **172**:1229-1231.
- Jacoby, G. A., and L. Gorini. 1967. The effect of streptomycin and other aminoglycoside antibiotics on protein synthesis, p. 726-747. In D. Gottlieb and P. D. Shaw (ed.), *Antibiotics*, vol. 1. Mechanism of action. Springer-Verlag, Berlin.
- Kirkconnell, S., and G. D. Hegeman. 1978. Mechanism of oxidation of carbon monoxide by bacteria. *Biochem. Biophys. Res. Commun.* **83**:1584-1587.
- Kistner, A. 1953. On a bacterium oxidizing carbon mon-

- oxide. Proc. K. Ned. Akad. Wet. Ser. C **56**:443-450.
22. Kistner, A. 1954. Conditions determining the oxidation of carbon monoxide by *Hydrogenomonas carboxydovorans*. Proc. K. Ned. Akad. Wet. Ser. C **57**:186-195.
 23. Kluyver, A. J., and C. G. Schnellen. 1947. On the fermentation of carbon monoxide by pure cultures of methane bacteria. Arch. Biochem. **14**:57-70.
 24. Liebl, K. H., and W. Seiler. 1976. CO and H₂ destruction at the soil surface, p. 215-229. In H. G. Schlegel, G. Gottschalk, and N. Pfennig (ed.), Microbial production and utilization of gases. E. Goltze KG, Göttingen.
 25. Loewus, M. W., and C. C. Delwiche. 1963. Carbon monoxide production by algae. Plant Physiol. **38**:371-374.
 26. Meyer, O., and H. G. Schlegel. 1978. Reisolation of the carbon monoxide utilizing hydrogen bacterium *Pseudomonas carboxydovorans* (Kistner) comb. nov. Arch. Microbiol. **118**:35-43.
 27. Meyer, O., and H. G. Schlegel. 1979. Oxidation of carbon monoxide in cell extracts of *Pseudomonas carboxydovorans*. J. Bacteriol. **137**:811-817.
 28. Obrig, T. G., W. J. Culp, W. L. McKeehan, and B. Hardesty. 1971. The mechanism by which cycloheximide and related glutarimide antibiotics inhibit peptide synthesis in reticulocyte ribosomes. J. Biol. Chem. **246**:174-181.
 29. Radler, F., K. D. Greese, R. Bock, and W. Seiler. 1974. Die Bildung von Spuren von Kohlenmonoxid durch *Saccharomyces cerevisiae* und andere Mikroorganismen. Arch. Microbiol. **100**:243-252.
 30. Seiler, W. 1978. The influence of the biosphere on the atmospheric CO and H₂ cycles, p. 773-810. In W. E. Krumbein (ed.), Environmental biogeochemistry and geomicrobiology, vol. 3, Methods, metals and assessment. Ann Arbor Scientific Publishers, Ann Arbor, Mich.
 31. Seiler, W., and C. Junge. 1970. Carbon monoxide in the atmosphere. J. Geophys. Res. **75**:2217-2225.
 32. Seiler, W., K. H. Liebl, W. T. Stöhr, and H. Zakosek. 1977. CO- und H₂-Abbau in Böden. Z. Pflanzenernaehr. Bodenkd. **140**:257-272.
 33. Seiler, W., and H. Zankl. 1976. Man's impact on the atmospheric carbon monoxide cycle, p. 25-37. In J. O. Nriagu (ed.), Environmental biogeochemistry, vol. 1, Carbon, nitrogen, phosphorous, sulfur and selenium cycles. Ann Arbor Scientific Publishers, Ann Arbor, Mich.
 34. Troxler, R. F. 1972. Synthesis of bile pigments in plants. Formation of carbon monoxide and phycocyanobilin in wild-type and mutant strains of the alga, *Cyanidium caldarium*. Biochemistry **11**:4235-4242.
 35. Troxler, R. F., and J. M. Dokos. 1973. Formation of carbon monoxide and bile pigment in red and blue-green algae. Plant Physiol. **51**:72-75.
 36. Uffen, R. L. 1976. Anaerobic growth of a *Rhodospseudomonas* species in the dark with carbon monoxide as sole carbon and energy source. Proc. Natl. Acad. Sci. U.S.A. **73**:3298-3302.
 37. Westlake, D. W. S., J. M. Roxburgh, and G. Talbot. 1961. Microbial production of carbon monoxide from flavonoids. Nature (London) **189**:510-511.
 38. Williams, S. T., and F. L. Davies. 1965. Use of antibiotics for selective isolation and enumeration of actinomycetes in soil. J. Gen. Microbiol. **38**:251-261.
 39. Wilson, D. F., J. W. Swinnerton, and R. A. Lamontagne. 1970. Production of carbon monoxide and gaseous hydrocarbons in seawater. Science **168**:1577-1579.
 40. Wolfe, R. S. 1979. Microbial biochemistry of methane—a study in contrasts. Part 1. Methanogenesis. Int. Rev. Biochem. **21**:267-300.
 41. Yagi, T. 1958. Enzymic oxidation of carbon monoxide. Biochim. Biophys. Acta **30**:194-195.
 42. Zavarzin, G. A., and A. N. Nozhevnikova. 1977. Aerobic carboxydobacteria. Microb. Ecol. **3**:305-326.