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Carbon monoxide uptake by temperate forest soils: the effects of leaves and humus layers

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ABSTRACT

Carbon monoxide (CO) fluxes between soil and atmosphere were measured between October 1990 and December 1991 in a temperate, deciduous forest near Darmstadt, Germany. Flux measurements were made with an enclosed chamber technique before and after the removal of leaves and humus from the forest floor as well as from leaves and humus alone. CO depth profiles were obtained during the period July to December, 1991. A net uptake of CO was observed under all conditions with an average of -47.3 ± 24.0 ng CO m^{-2} s^{-1} for undisturbed forest soils, which increased significantly when the leaves or both leaves and humus were removed from the forest floor. The mean deposition velocity in undisturbed conditions was 0.027 ± 0.008 cm s^{-1}. Our results indicate that CO has a short lifetime within the soil and that the consumption of atmospheric CO occurs mainly in the top few centimeters of the humus layer (O horizon). We conclude that temperate forests are a significant net sink for atmospheric CO and that leaves and humus significantly affect CO fluxes. The global soil sink for atmospheric CO was estimated to be 115–230 Tg CO yr^{-1}.

1. Introduction

Carbon monoxide is known to determine many aspects of tropospheric photochemistry, especially through its influence on the concentrations of ozone (O_3) and hydroxyl radical (OH), the dominant oxidizing species in the troposphere (Crutzen, 1987). The interaction between the soil-vegetation system and the atmosphere significantly affects the atmospheric budget of CO (Prather et al., 1995; Sanhueza et al., 1995). Soils are generally recognized to consume atmospheric CO at rates between 190 and 580 Tg yr^{-1} (Conrad and Seiler, 1985). However, net production of CO has also been observed from dry soils in sub-tropical (Conrad and Seiler, 1982) and tropical ecosystems (Scharffe et al., 1990; Sanhueza et al., 1994b). Here we report the first published uptake rates for atmospheric CO by temperate, deciduous forest soils and the effects of leaves and humus layers upon those fluxes in a forest in Germany.

2. Experimental

CO fluxes were measured between October 1990 and December, 1991 in a deciduous forest near Darmstadt, Germany (49.86°N, 8.65°E). This forest contains mature beech and oak trees, has not been disturbed for more than 80 years, and has a density of about 600 trees per hectare; the soil is a cambisol. The forest floor's top layer

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consists of fresh and partly decomposed leaves of 1–2 cm depth, below which the O horizon ($\sim$5 cm depth) can be found, which, in this paper, we will refer to as humus layer. The texture of the third layer, the A horizon (mineral soil), is sand. The soil pH, the carbon, hydrogen and nitrogen contents, and bulk densities of the various soil layers are given in Dong et al. (1997). Flux measurements were first made from undisturbed soils (the forest floor as found at the site), after the removal of leaves (soil without leaves), and after removal of both the leaves and humus from the forest floor (mineral soil). Gas fluxes from leaves and humus were also measured separately.

An enclosed chamber technique was used, which employed acrylic chambers made of two parts, a box (without top and bottom) of $\sim$0.45 m^2 surface area and $\sim$70 liters of volume, which was inserted into the soil, and a cover, which was closed during and opened between experiments. Blank test did not show any significant flux of CO, indicating that neither the chamber nor the tubing material interfere with the measurements. Carbon monoxide mixing ratios were measured in situ by gas chromatography using a gas-reduction detector (Trace Analytical). An automated injection system was used (Scharffe et al., 1990), where gas samples were circulated between the chamber and the detector with a Teflon covered membrane pump (ASF) at a flow rate of 1 l min^{-1}. Each individual flux experiment lasted for about 30 min during which CO mixing ratios were measured every two minutes. Atmospheric levels were recorded before and after each experiment and calibrations were carried out using gravimetric standards (Deuste Steininger). Air temperatures outside and inside the chamber were continuously monitored and minimum temperatures between 0 and 5°C were recorded between December and February with maximum temperatures of about 25°C during the summer months. Rainfall statistics are reported in Dong et al. (1997).

The sequence of measurements made during each one-day campaign in the field was as follows: First, the lower part of chamber one was pressed about 5 cm deep into the forest floor, and after about 60 minutes it was closed and flux measurements from undisturbed soil were performed. After the experiment, this chamber was opened, the leaves were removed from the forest floor and placed inside a second chamber with a closed bottom to obtain flux measurements from leaves only. Chamber one was then closed again and flux measurements from the soil without leaves were performed. Finally, chamber one was opened and the soft, soil humus material (O horizon) was removed and placed in chamber number two for flux measurements from humus alone. Chamber one was closed again and measurements from the mineral soil were obtained. For every one-day experiment, a different plot was selected within the same area of the forest. Considering the large spatial variation observed in soil flux measurements (Sanhueza et al., 1990), this method of covering a larger area within the same forest gives us a larger scatter in data but also more confidence that our mean results are more representative for this forest in general.

Since the net soil-air flux of CO is determined by the coexistence of biogenic CO consumption, which is proportional to the atmospheric mixing ratio of CO, and CO production from chemical reactions in the soil, an exponential decrease of CO mixing ratios was observed during all chamber experiments. In most of the cases, an equilibrium mixing ratio was reached after a relatively short period (Fig. 1). Therefore, the net flux (F) was estimated from linear regression by using only the first few data points obtained during a particular run (linear portion of exponential curve). Some experiments showed a non-linear change in mixing ratios after the chamber was closed. In those cases, the slope, which represents the uptake rate, was still calculated from the first three points, which yielded a slight underestimation of those fluxes. The net flux F of CO between soil and atmosphere is defined as the difference of CO production P and CO uptake rate, which is a product of the

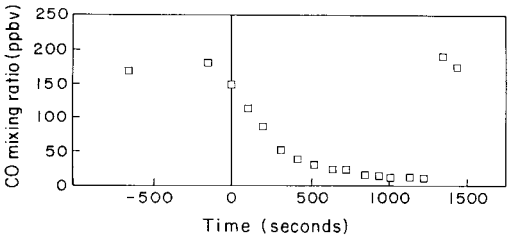

Fig. 1. Change of CO mixing ratios in the flux chamber during a typical experiment. At time = 0 the chamber was closed and re-opened at $\sim$1300 s. Mixing ratios before and after the experiment reflect ambient CO levels.

deposition velocity v_d and the atmospheric mixing ratio $[CO]_{atm}$

$$F = P - v_d\ [CO]_{atm}. \quad (1)$$

Once the equilibrium mixing ratio is reached inside the flux chamber, the net flux becomes zero and the following equation applies:

$$P - v_d\ [CO]_{eq} = 0. \quad (2)$$

Production rates and the deposition velocities were calculated using equations 1 and 2 with the experimentally determined net flux and the ambient and equilibrium mixing ratios during each experiment; $v_d = F/([CO]_{eq} - [CO]_{atm})$.

Depth profiles of CO mixing ratios were measured between 5 June and 30 October 1991. The samples were collected using 3.15 mm OD stainless steel probes equipped with a septum and gas-tight syringes. Probes were inserted at depths of 5, 10, 20, 30, and 50 cm into the soil and, after four hours, 10 ml samples were taken simultaneously from all depths. The CO was immediately analyzed in the field.

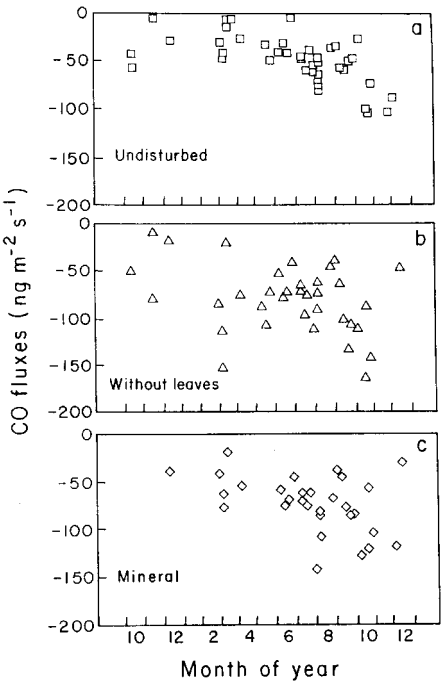

Fig. 2. CO fluxes from undisturbed and disturbed forest soils.

3. Results and discussion

The annual change of net CO fluxes from undisturbed soil, soil without leaves, and mineral soil are presented in Fig. 2. No measurements were made between 8 December, 1990 and 28 February, 1991, because of a frozen or snow-covered forest soil. Fluxes did not show any significant seasonal variation, thus, only annually averaged soil fluxes are reported in Table 1. Also, several 24-h experiments did not reveal any significant diurnal cycle and the results were combined with those from the regular dataset.

3.1. *Net flux, production and uptake*

Net fluxes from undisturbed soils (Fig. 2a) were always negative, representing a ubiquitous uptake by these soils at all times with a mean of -47.3 ± 24.0 ng CO m^{-2} s^{-1}. Uptake rates found between September and December, 1991, were larger than normal and probably caused by high ambient CO mixing ratios (0.3 to 1 ppmv compared to an average of ~ 0.2 ppmv for the rest of the year).

The production (P) of CO and the deposition velocities (v_d) obtained in each individual chamber experiment are given in Figs. 3 and 4 as a function of the temperature and the water filled pore space (WFPS), respectively. The data did not show any significant statistical correlation between production and either air temperature or soil moisture. This contrasts with results obtained in subtropical (Conrad and Seiler, 1985) and tropical soils (Scharffe et al., 1990), where a significant increase of production rates was observed for changes in soil temperature between about 20°C and 40°C. Furthermore, the dry deposition velocity did not show any significant dependence on soil moisture, which changed between 18% and 56% WFPS during the measurement period. This does not agree with data from dry savannah soils, where v_d values were reported to be very sensitive to changes in soil moisture (Conrad and Seiler, 1985). However, under warm and dry conditions in tropical and sub-tropical savannah soils, no significant correlation was observed between v_d and temperature (Conrad and Seiler, 1985; Scharffe et al., 1990). In our case, it is possible that temperature and soil moisture effects mask each other, but we

Table 1. *Net fluxes, production rates, and dry deposition velocities v_d of CO in undisturbed and disturbed soils in the Darmstadt forest, and net fluxes from leaves only and humus only*

Type of experiment		Net flux (ng CO m^{-2} s^{-1})	Production (ng CO m^{-2} s^{-1})	v_d (cm s^{-1})
undisturbed soil	avg.	−47.3	21.7	0.027
	std.	24.0	8.1	0.008
	med.	−45.6	19.9	0.026
	N	43	29	29
soil without leaves	avg.	−83.7	20.0	0.038
	std.	49.0	20.3	0.013
	med.	−76.0	12.4	0.035
	N	45	32	32
mineral soil	avg.	−70.9	10.1	0.035
	std.	29.2	4.6	0.012
	med.	−67.9	9.5	0.032
	N	30	24	24
leaves only	avg.	6.2		
	std.	25.2		
	med.	1.7		
	N	43		
humus only	avg.	−54.3		
	std.	17.6		
	med.	−54.6		
	N	14		

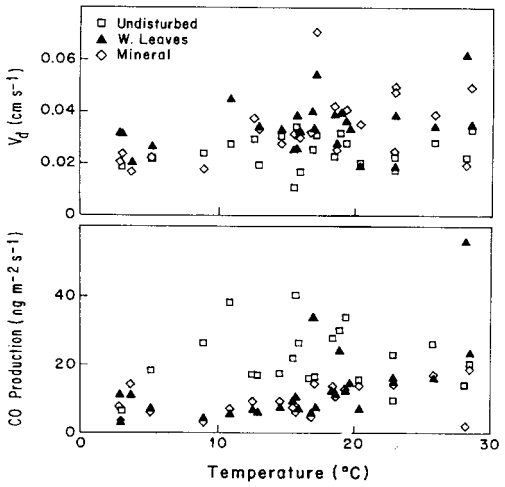

Fig. 3. CO production and v_d values for undisturbed and disturbed soil conditions as a function of temperature. W. Leaves: soil without leaves; Mineral: mineral soil, no leaves or humus.

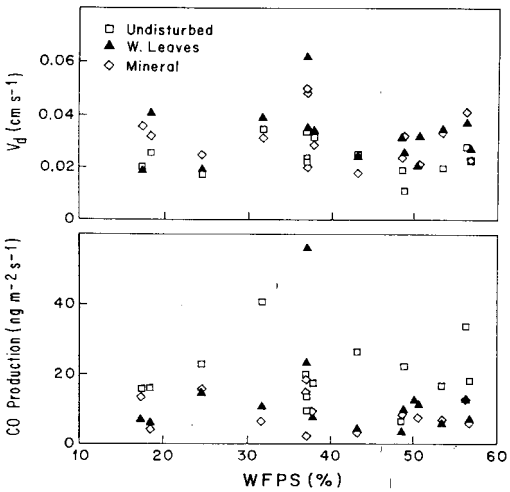

Fig. 4. CO production and v_d values for undisturbed and disturbed soil conditions as a function of soil moisture. WFPS was calculated after Saxton et al. (1986). W. Leaves: soil without leaves; Mineral: mineral soil, no leaves or humus.

do not have enough evidence to deduce significant differences. Also, it is important to mention that the WFPS was always below 56%, and that soil aeration becomes a limiting factor only above 60% WFPS (Williams et al., 1992).

The range of v_d values obtained for undisturbed conditions in the temperate forest in Darmstadt of 0.027 ± 0.008 cm s^{-1} agrees well with those reported for other ecosystems (Table 2). It appears

Table 2. *Dry deposition velocities of CO for various locations*

Site	Vegetation	v_d (cm s^{-1})	Soil temp. (°C)	Ref.
Mainz, Germany	grass/small plants	0.03	not reported	Conrad and Seiler, 1980, 1985
Andalusia, Spain	unplanted field	0.01–0.04	20–40	Conrad and Seiler, 1985
Transvaal, S. Africa	savannah	0.05	22-40	Conrad and Seiler, 1985
Guri, Venezuela	grassland savannah	0.02–0.03	22–40	Scharffe et al., 1990
Darmstadt, Germany	deciduous forest	0.027 ± 0.008	3–17	This work

that similar CO dry deposition velocities can be found in a variety of very different ecosystems, with a best estimate of 0.03 cm s^{-1}. From the dataset of global vegetation given in Melillo et al. (1993), we infer a total area of 100×10^{12} m^2 for global terrestrial ecosystems, which could possibly consume atmospheric CO. Assuming that the best-estimate deposition velocity of 0.03 cm s^{-1} is representative for this mixture of ecosystems, and assuming that 10% of the continental area has boundary CO mixing ratios between 40 and 60 ppbv (mainly southern hemisphere; Khalil and Rasmussen, 1994; Novelli et al., 1994), 30% are at 60–120 ppbv (mostly tropics, Gregory et al., 1986; Kirchhoff and Marinho, 1990; Donoso et al., 1996), 40% are at 100–200 ppbv (rural regions of the northern hemisphere, Chin et al., 1994; Klemm et al., 1996), and that 20% of the total area has mixing ratios of 200–400 ppb (polluted areas such as suburban and tropical biomass burning regions, Crutzen et al., 1985; Kirchhoff and Rasmussen, 1990; Klemm et al., 1996), we estimate that the global gross uptake of CO ranges from 115 to 230 Tg CO yr^{-1}.

This estimate is lower than that reported by Conrad and Seiler (1985) of 190–580 Tg CO yr^{-1}, which is based on the same approach used here, but it is significantly higher than that of Potter et al. (1996) of 16–50 Tg CO yr^{-1}, estimated using a modified version of Fick's first law based on computations for diffusivity in aggregated media, together with a soil water balance model. Our estimate uses practically the same deposition velocities as were used previously by Conrad and Seiler (1985), hence the lower global estimates are probably due to differently distributed CO mixing ratios and different areas for the various active ecosystems. The gross CO uptake given above is independent of the global CO production by soils, which was estimated at about 30 Tg CO yr^{-1} (Conrad and Seiler, 1985), and will decrease our uptake to a net amount of 85–200 Tg CO yr^{-1}. This amount is about 4–8% of the total, global CO sink strength, which is dominated by reaction with OH radicals (Prather et al., 1995; Sanhueza et al., 1995).

3.2. *CO depth profiles*

Depth profiles of the CO mixing ratio in soil air indicate a very rapid uptake of CO within the first 5 cm of the soil (Fig. 5). Mixing ratios of CO below 10 cm depth remain about constant and are close to zero. Liebl and Seiler (1976) and Seiler et al. (1977) also found negligible amounts of CO at soil depths below 1 cm in unforested, temperate soils. This is in good agreement with the idea that CO has a very short lifetime within the soil (Sanhueza et al., 1994a), and that both production and consumption processes occur mainly in the top few centimeters of the soil. As we will see below, the overlying humus layer consumes CO very actively at the Darmstadt forest site. The fact that similar depth profiles were observed after large changes in soil moisture (7% to 22%, which correspond to 18% and 56% WFPS, Fig. 5) also supports the idea that CO consumption occurs within the top layer of the forest soil, as any process located deeper in the soil would require

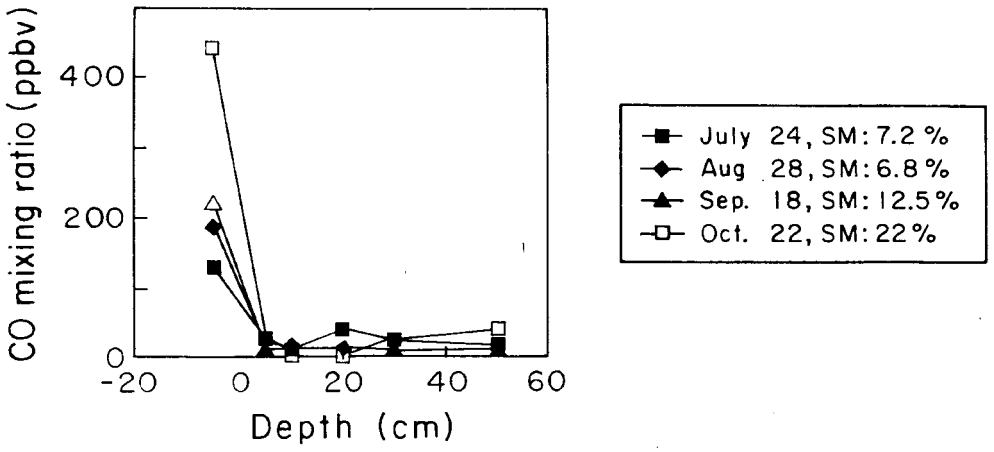

Fig. 5. Concentration depth profiles of CO. Gravimetric soil moisture for the 2–7 cm soil layer is given in the legend (SM).

considerable transport, which, at high soil moisture, is restricted.

3.3. *Effects of leaves and humus on CO fluxes*

Table 1 summarizes the net fluxes obtained under undisturbed and disturbed soil conditions as well as the average fluxes from the experiments with leaves only and humus only. As expected, the manipulation of the soil produced some disturbances (e.g., aeration, decompaction) and the combined fluxes obtained on separated layers do not add up to the fluxes from undisturbed soil.

Compared to the uptake rates recorded in undisturbed conditions (Fig. 2a), a substantial increase in the consumption of CO occurred after the removal of leaves (Fig. 2b), and uptake rates between those of the previous conditions were found when the humus layer was removed, too (Fig. 2c). The ratios of uptake rates from disturbed/undisturbed soils for the individual experiments are shown in Fig. 6. The median for the ratio F(without leaves)/F(undisturbed) is 1.85 and that of F(mineral)/F(undisturbed) is 1.51, indicating an increase in CO uptake of $\sim$80% after the removal of the leaves and $\sim$50% when both leaves and humus were removed.

Even though a CO uptake was recorded during some of the experiments with leaves only, their average flux was positive, representing a small production of CO on the order of 6.2 ng CO m^{-2} s^{-1} (Table 1). Uptake of CO,

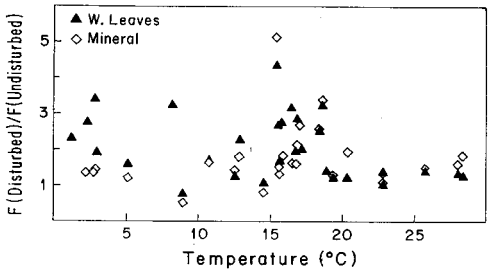

Fig. 6. Ratios of fluxes from disturbed to undisturbed conditions as a function of temperature. Triangle: F(soil without leaves)/F(undisturbed soil); Diamonds: F(mineral soil)/F(undisturbed soil).

which we occasionally encountered with leaves only, was probably caused by the presence of humus material on the surface of the leaves. This might explain some of the significant scatter in our data, and makes it likely that our value for the production of CO from leaves is somewhat underestimated.

The stronger net uptake of CO after the removal of leaves may be explained both by production by the leaves and enhanced uptake of CO due to an increased contact between atmospheric CO and the biologically active humus layer, which consumes CO. Both processes are needed to explain the observations, because the CO production by leaves can explain the difference in production rates of undisturbed soil and soil without leaves, but cannot account for the differences in net fluxes.

The mineral soil consumes significant amounts of CO in our experiments. However, because the mean, net flux of -54.3 ng CO m^{-2} s^{-1} obtained from experiments with the humus layer alone is about the same as the one obtained from the mineral soil, and the fact that the net uptake in the experiments without leaves are larger than that observed after both leaves and humus were removed (Table 1), it is likely that the net uptake from undisturbed soils is mainly due to the consumption of CO in the humus layer. This notion is also supported by our depth profiles that show a 95% decrease in CO mixing ratios within the first 5 cm, which is about the depth of the humus layer. Finally, the results suggest that the diffusion of atmospheric CO through the layer of leaves is an important factor in controlling the uptake rate of CO in these forest soils, because the soil without leaves showed a significantly larger uptake rate compared to undisturbed soils.

CO production and v_d values obtained during individual experiments in disturbed soil are given in Figs. 3 and 4. As in the case with undisturbed soil, both P and v_d in disturbed soil do not show any significant dependence with temperature (Fig. 3) or WFPS (Fig. 4). The data indicate that, with only a few exceptions, the v_d measured under disturbed conditions were higher than those observed in undisturbed soil. It is interesting to note that even though the removal of leaves and humus increases aeration and therefore the production of CO in the mineral soil, the production from this layer (9.5 ng CO m^{-2} s^{-1}) was lower than that observed from the soil without leaves (12.8 ng CO m^{-2} s^{-1}), indicating that most of the production of CO measured in the undisturbed soil (19.9 ng CO m^{-2} s^{-1}) occurs in the leaves and humus layers. This is in agreement with results from Conrad and Seiler (1980; 1985) which show that the production of CO seems to occur predominantly in the active topsoil.

Taken together, these results show that forest soils both produce and destroy atmospheric CO simultaneously, hence, are likely to act as a buffer. As either atmospheric CO concentrations or the accumulation rates of leaves and humus change, temperate, deciduous forest soils are likely to exhibit a change in the uptake rate for atmospheric CO.

4. Conclusions

This study suggests that temperate forest soils are a minor, but significant sink for atmospheric CO. Our results show that the most active region for the uptake of CO within the soil is the top humus layer and they indicate that both the leaves and humus layers are important factors in controlling CO uptake by deciduous forest soils. Changes in the depth of the leaf and the humus layers affect the uptake rates of atmospheric CO by temperate forest soils.

REFERENCES

Chin, M., Jacob, D. J., Munger, W., Parrish, D. D. and Doddridge, B. G. 1994. Relationship of ozone and carbon monoxide over North America. *J. Geophys. Res.* **99D**, 14 565–14 573.

Conrad, R. and Seiler, W. 1980. Role of microorganism in the consumption and production of atmospheric carbon monoxide. *Appl. Environ. Microbiol.* **40**, 437–445.

Conrad, R. and Seiler, W. 1982. Arid soils as a source of atmospheric carbon monoxide. *Geophys. Res. Lett.* **9**, 1353–1356.

Conrad, R. and Seiler, W. 1985. Influence of temperature, moisture, and organic carbon on the flux of H_2 and CO between soil and atmosphere: field studies in subtropical regions. *J. Geophys. Res.* **90**, 5699–5709.

Crutzen, P. J. 1987. Rôle of the tropics in atmospheric chemistry. In: *The geophysiology of Amazonia, vegetation, climate interactions,* pp. 109–131. Dickinson R. E. (ed.). J. Wiley, Chichester, UK.

Crutzen, P. J., Delany, A. C., Geenberg, J., Haageson, P., Heidt, L., Lueb, R., Pollock, W., Seiler, W., Wartburg, A. and Zimmerman, P. 1985. Tropospheric chemical composition measurements in Brazil during the dry season. *J. Atmos. Chem.* **2**, 233–256.

Dong, Y., Scharffe, D., Lobert, J. M., Crutzen, P. J. and Sanhueza, E. 1997. Fluxes of CO_2, CH_4, and N_2O from a temperate forest soil: The effects of leaves and humus layers. *Tellus*, submitted.

Donoso, L., Romero, R., Rondón, A., Fernandez, E., Oyola, P. and Sanhueza, E. 1996. Natural and anthropogenic C_2 to C_6 hydrocarbons in the central-eastern Venezuelan atmosphere during the rainy season. *J. Atmos. Chem.* **25**, 201–214.

Gregory et al. 1986. Air chemistry over the tropical forest of Guyana. *J. Geophys. Res.* **91D**, 8603–8612.

Khalil, M. A. K. and Rasmussen, R. A. 1994. Global decrease of atmospheric carbon monoxide. *Nature* **370**, 639–641.

Kirchhoff, V. W. J. H. and Rasmussen, R. A. 1990. Time variations of CO and O_3 concentrations in a region subject to biomass burning. *J. Geophys. Res.* **95D**, 7521–7532.

Kirchhoff, V. W. J. H. and Marinho, E. V. A. 1990. Surface carbon monoxide measurements in Amazonia, *J. Geophys. Res.* **95D**, 16 933–16 943.

Klemm, O., Hahn, M. K. and Giehl, H. 1996. Airborne, continuous measurement of carbon monoxide in the lower troposphere. *Environ. Sci. Technol.* **30**, 115–120.

Liebl, K. H. and Seiler, W. 1976. CO and H_2 destruction at the soil surface. In: *Production and utilization of gases (H_2, CH_4, CO)*, (eds. Schlegel, H. G., Gottschslk G., and Pfenning N.), Goltze, Göttingen, Germany, 215–229.

Melillo, J. M., McGuire, A. D., Kicklighter, D. W., More III, B., Vorosmarty, C. J. and Schloss, A. L. 1993, Global climate change and terrestrial net primary production. *Nature* **363**, 234–240.

Novelli, P. C., Masarie, K. A., Tans, P. P. and Lang, P. M. 1994. Recent changes in atmospheric carbon monoxide. *Science, 263*, 1587–1590.

Prather, M., Derwent, R., Ehhalt, D., Fraser, P., Sanhueza, E. and Zhou, X. 1995. Other trace gases and atmospheric chemistry. In: *Climate Change 1994. Radiative forcing of climate change.* Hougthon, J. T., Meira Filho, L G., Bruce, J. Lee, H., Callander, B. A., Haites, E., Harris, N., and Maswell, K. (eds). Cambridge Univ. Press, Cambridge, 73–126.

Potter, C. S., Klooster, S. A. and Chatfield, R. B. 1996. Consumption and production of carbon monoxide in soils: a global model analysis of spatial and seasonal variation. *Chemosphere* **33**, 1175–1193.

Sanhueza, E., Hao, W. M., Scharffe, D., Donoso, L. and Crutzen, P. J. 1990. N_2O and NO emissions from soils of the northern part of the Guayana shield, Venezuela. *J. Geophys. Res.* **95D**, 22 481–22 488.

Sanhueza, E., Cardenas, L., Donoso, L. and Santana, M. 1994a. Effect of plowing on CO_2, CO, CH_4, N_2O, and NO fluxes from tropical savannah soils. *J. Geophys. Res.* **99D**, 16 429–16 434.

Sanhueza, E., Donoso, L., Scharffe, D. and Crutzen, P. J. 1994b. Carbon monoxide fluxes from natural, managed, or cultivated savannah grasslands. *J. Geophys. Res.* **99**, 16421–16427.

Sanhueza, E., Fraser, P. and Zander, R. 1995. Source Gases: Trends and Budgets. In: *Scientific assessment of ozone depletion: 1994*. WMO/UNEP. WMO report No. 37, 2.1–2.38.

Saxton, K. E., Rawls, W. J., Romenberg, J. S. and Papendick, R. I. 1986. Estimating generalized soil-water characteristics from texture. *Soil Sci. Soc. Am. J.* **50**, 1031–1036.

Scharffe, D., Hao, W. M., Donoso, L., Crutzen, P. J. and Sanhueza, E. 1990. Soil fluxes and atmospheric concentration of CO and CH_4 in the northern part of the Guayana shield, Venezuela. *J. Geophys. Res.* **95**, 22 475–22 480.

Seiler, W., Liebl, K. H., Stöhr, W. T. and Zakosek, H. 1977. CO- un H_2- Abbau in Böden. *Z. Pflanzenernähr. Bodenkde.* **140**, 257–272.

Williams, E. J., Hutchinson, G. L. and Fehsenfeld, F. C. 1992. NO_x and N_2O emissions from soils. *Global Biogeochem. Cycles* **6**, 351–388.