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Soil-atmosphere exchange of CH_4, CO_2, NO_x, and N_2O in the Colorado shortgrass steppe under elevated CO_2

A.R. Mosier[1,4], J.A. Morgan[1], J.Y. King[1], D. LeCain[1] & D.G. Milchunas[2,3]
[1]*USDA/ARS, Fort Collins, CO;* [2]*NREL, Colo. St. Univ.;* [3]*Rangeland Ecosystem Science Department, Colo. St. University, USA;* [4]*Corresponding author**

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Abstract

In late March 1997, an open-top-chamber (OTC) CO_2 enrichment study was begun in the Colorado shortgrass steppe. The main objectives of the study were to determine the effect of elevated CO_2 ($\sim$720 μmol mol^{-1}) on plant production, photosynthesis, and water use of this mixed C_3/C_4 plant community, soil nitrogen (N) and carbon (C) cycling and the impact of changes induced by CO_2 on trace gas exchange. From this study, we report here our weekly measurements of CO_2, CH_4, NO_x and N_2O fluxes within control (unchambered), ambient CO_2 and elevated CO_2 OTCs. Soil water and temperature were measured at each flux measurement time from early April 1997, year round, through October 2000. Even though both C_3 and C_4 plant biomass increased under elevated CO_2 and soil moisture content was typically higher than under ambient CO_2 conditions, none of the trace gas fluxes were significantly altered by CO_2 enrichment. Over the 43 month period of observation NO_x and N_2O flux averaged 4.3 and 1.7 in ambient and 4.1 and 1.7 μg N m^{-2} hr^{-1} in elevated CO_2 OTCs, respectively. NO_x flux was negatively correlated to plant biomass production. Methane oxidation rates averaged -31 and -34 μg C m^{-2} hr^{-1} and ecosystem respiration averaged 43 and 44 mg C m^{-2} hr^{-1} under ambient and elevated CO_2, respectively, over the same time period.

Introduction

During the past few decades, the atmospheric concentration of CO_2 has increased at historically unprecedented rates (IPCC, 1995), as have N_2O (CMDL, 2000) and CH_4 (IPCC, 1995). Increasing CO_2 concentrations will have a direct effect on plant production and plant communities and indirectly feed back into a number of soil biotic systems that influence long term ecosystem viability (Hungate et al., 1997a,b,c; Owensby et al., 1993a). The impact of elevated CO_2 on the shortgrass steppe, which is used extensively for grazing and is similar to regions which occupy about 8% of the US and about 11% of global land area (Bailey, 1979) has not been previously addressed. These interactive feedbacks on the soil C and N cycles and their influence on trace gas fluxes have potentially important impacts on the global atmospheric budgets of the gases and the long term sustainability of the grassland. Earlier studies within the shortgrass steppe have demonstrated that such grasslands play an important role in global atmospheric N_2O and CH_4 concentrations; as a consumer of atmospheric CH_4, and producer of N_2O (Mosier et al., 1991, 1996, 1997). The impact of elevated CO_2 on the production and consumption of other trace gases (NO_x, N_2O and CH_4) is not well understood and had not been assessed in semiarid grasslands. The few measurements of NO_x, N_2O, $CH_4$and CO_2 in CO_2 enrichment studies give contradictory results, and long term measurements have not been made within any ecosystem.

Ineson et al. (1998) measured the soil-atmosphere exchange of N_2O, CH_4 and CO_2 semicontinuously within a free-atmosphere CO_2-enrichment (FACE)

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* FAX No: 1970-490-8213.
E-mail: amosier@lamar.colostate.edu

study in Switzerland for 11 d immediately after a grass (*Lolium perenne*) harvest. During the measurement period, plots were irrigated and N-fertilized with 14 g N m^{-2} of ammonium nitrate. They observed that, during the brief measurement period, N_2O emissions were ~27% higher under elevated (600 $\mu l\ l^{-1}$) CO_2 while the rate of uptake of atmospheric CH_4 was approximately three times greater in ambient CO_2 soils. Dark respiration was ~10% higher in ambient CO_2 plots than from elevated CO_2 plots, suggesting that more C may be stored in this grassland under elevated CO_2.

In another study, Arnone and Bohlen (1998) moved soil-vegetation monoliths from a perennial grassland in northwestern Switzerland into greenhouses where the atmospheres were maintained at either ambient or 600 μmol mol^{-1} CO_2 concentration. The monoliths were maintained in the greenhouse for two years before the gas sampling was conducted. N_2O and CO_2 (net ecosystem dark respiration) fluxes were measured once immediately before harvesting the above ground vegetation and again one month later. N_2O fluxes under elevated CO_2 were double those observed under ambient CO_2. Ecosystem respiration was also about double under elevated CO_2 compared to ambient CO_2 monoliths. The higher N_2O and CO_2 fluxes under elevated CO_2 were attributed to improved soil moisture and increases in C supplies to soil organisms that are responsible for mineralization, nitrification and denitrification.

Robinson and Conroy (1999) conducted growth chamber studies with soil columns seeded with *Panicum coloratum* under ambient and 1000 μmol mol^{-1} CO_2 atmospheres. They measured soil nitrate concentrations and N isotopic composition of the nitrate during a 41-d growth period. In the presence of plants under elevated CO_2, they found that the delta ^{15}N of residual soil nitrate increased. This increase was attributed to enhanced N loss by denitrification under elevated CO_2, because of wetter soils and increased plant root oxygen consumption. They suggested that greater N_2O emissions are likely under elevated CO_2.

An open-top-chamber (OTC) study was conducted in California, USA in a mainly annual grassland (Hungate et al., 1997a,b,c). Microplots were fertilized with 20 g urea N m^{-2}. They simulated a first autumn rainfall event with the addition of 9-cm water to microplots contained within the OTCs. Immediately before and after water addition, gross mineralization, nitrification, ammonium and nitrate consumption and N_2O and NO fluxes were measured. Gas fluxes were measured for 9 days after wet up. Hungate et al. (1997 b,c) found that, during wet up, NO emissions were depressed by 55% in high nutrient conditions under elevated CO_2 (ambient + 360 μmol mol^{-1}) while there was no difference among treatments in N_2O emissions. Where no additional N was supplied, NO and N_2O fluxes were not different under ambient and elevated CO_2. In nutrient addition plots, elevated CO_2 stimulated N immobilization, decreased nitrification and decreased NO emission, thereby increasing N retention of added N during the early season wet up.

Growth chamber studies suggest that plant C/N ratios, nitrogen use efficiency and water use efficiency all increase under enhancedCO_2 (Drake et al., 1996; Morgan et al., 1994; Rogers et al., 1994). In the short term, resulting increases in soil moisture contents (Hungate et al., 1997a,b,c) may accelerate rates of C and N mineralization and N availability for plant uptake. Over the long term, however, decreased litter quality will increase N immobilization rates, likely reducing N availability for plant uptake. From these observations, we hypothesized that initially elevated CO_2 would induce increased soil moisture and increased N mineralization rates. As a result, CO_2, NO and N_2O emissions should increase on the short term under elevated CO_2, while CH4 uptake should decrease. Over the longer term, however, increased C/N ratios in plant litter and roots would result in longer term decreases in N mineralization rates, and decreased NO and N_2O fluxes would be observed. To test these responses, the soil-atmosphere exchange of CO_2, NO_x, N_2O and CH_4 were monitored weekly, year-round, April 1997 to November 2000 on unchambered control, ambient CO_2 and ~720 μmol mol^{-1} CO_2 experimental plots in the Colorado shortgrass steppe.

Materials and methods

The CO_2 enrichment studies are being conducted at the USDA/ARS Central Plains Experimental Range (CPER) on which is located the Shortgrass Steppe long-term-ecological-research (LTER) project, about 60 km NE of Fort Collins, near Nunn, CO (40° 50′ N, 104 42′ W). The semiarid grassland site is at 1650 m elevation and has a long term average annual precipitation of ~320 mm. Annual mineral nitrogen input is an estimated 0.5 g N m^{-2} mainly through wet and dry atmospheric deposition (Mosier et al., 1996).

Table 1. Selected soil properties[a] of the soil at the Open-Top-Chamber study site

Soil depth (cm)	Sand	Silt	Clay	pH	Total N	Total C	Bulk density
	————	%	————		————	% ————	g cm^{-3}
0–10	76	14	10	7.3	0.101	0.891	1.28
10–20	74	15	11	8.1	0.077	0.606	1.42
20–30	74	13	13	8.0	0.076	0.584	1.48

[a] Gravimetric soil water content for the 0–15 cm depth at water filled pore space of 0.2, 0.4 and 0.6 is 7.2, 14.4 and 21.6 kg kg^{-1}, respectively (Mosier et al., 1998).

Experimental site

In the fall of 1995, vegetation and soil surveys were conducted in native shortgrass steppe at the experimental site. The survey results enabled a selection of relatively similar experimental plots on the basis of soil and plant community information and documented plot differences before the treatments were implemented. The grassland community is comprised of over 25 species of forbs and grasses, but dominated by three grass species, *Bouteloua gracilis* (C_4, accounts for approximately 42% of total aboveground biomass), *Pascopyrum smithii* (C_3, 21% of total aboveground biomass) and *Stipa comata* (C_3, 26% of total aboveground biomass). Nine experimental plots of similar plant species composition were selected on the basis of this initial survey. The soil within the study site is a Remmit fine sandy loam (Ustollic camborthids) which holds 18% (gravimetric) water at field capacity, and 4% at the permanent wilting point (Table 1).

On six of the nine plots, open-top chambers (4.5 m diameter by 3 m height) of similar design to Owensby et al. (1993a,b) were installed in March 1997 (Morgan et al., 2001a). All chambers are equipped with blowers to exchange 1.5 air volumes per minute. Three of the chambers have precision valve outlets located in-line between the blowers and the chambers and attached to a compressed CO_2 source for elevating CO_2 to approximately 720 μmol mol^{-1}. An instrument trailer is located at the site, with data acquisition/control equipment. Carbon dioxide in the chambers is controlled only during the growing season, from approximately early April to late October. Chambers are removed in the winter. Daily precipitation is measured at a meteorological station located about 50 m from the OTCs.

Precipitation falling on the chamber tops is collected and delivered to reservoirs where pumps re-apply the water back onto the experimental plots through an automated irrigation system. Water meters in the irrigation system record amounts of water applied back to plots, and additional irrigation water is added as needed to correct for occasional unequal collection among the chambers.

Trace gas flux measurements

We measured fluxes of NO_x, N_2O, CH_4 and CO_2, weekly, from two 20 cm diameter locations within each OTC and control (unchambered) plot from April 1997 through October 2000. Gas flux sampling locations were established by driving flux chamber anchors (20 cm diameter, 10 cm high PVC cylinder) 8- cm into the soil, about a year before flux measurements were begun. Midmorning of each sampling day, N_2O, CH_4 and CO_2 fluxes were measured using a vented closed chamber method (Hutchinson and Mosier, 1981; Mosier et al., 1991) where the changes in concentration of N_2O, CO_2 and CH_4 within the chamber were measured by withdrawing samples from the chamber by syringe at three time periods and analyzing the gas concentrations by gas chromatography (Mosier et al., 1996, 1997, 1998). Nitric oxide flux was monitored from the same chamber anchors on the same day using a flow-through chamber system (Martin et al., 1998) and a Thermo Environmental Instruments model 42C chemiluminescence NO-NO_2-NO_x analyzer that is housed in the instrument trailer (Mosier et al., 1998). NO_x emissions from the soil are typically $>$ 90% NO, so fluxes will generally be discussed in terms of NO only (Martin et al. 1998; Mosier et al., 1998). Soil water content was monitored weekly to a depth of 1 m by neutron probe and time domain reflectrometry (TDR) for 0–15 cm surface soils.

Statistical analyses

Gas flux measurements, soil moisture and soil temperatures within each treatment replicate (OTC or unchambered location) were averaged (n=3) for each observation time. Over each specific time interval, e.g. season, year, 4 years, data were averaged and single factor analysis of variance was performed (Microsoft Excel). Individual CO_2 treatments were compared for a designated time interval using a paired *t*-test. Significance levels of 0.05 were used unless specifically noted.

Results

Trace gas fluxes and soil temperature and water content over the 43 month observation period

Growth of both C_3 and C_4 plants was enhanced under elevated CO_2. Both mid-season and seasonal aboveground production increased by 26% in 1997 and 47% in 1998, respectively, at elevated CO_2 with no differences in response of C_3/C_4 grasses or forbs being observed (Morgan et al., 2001a,b). Soil water content was generally higher under elevated CO_2 than within the ambient chambers and was generally similar to the unchambered control (Morgan et al., 2001a). In 1999 and 2000, a similar response of plant growth to elevated CO_2 was observed (unpublished data).

Monthly precipitation at the site varied between zero and almost 160 mm with highest amounts of precipitation typically occurring during the summer months and lowest during the winter (Figure 1a). Annual precipitation, with approximately 80% falling between April and October each year, was 387, 565, 402, 557 and 299 mm during 1996, 1997, 1998, 1999, and 2000. Year 2000 was particularly dry with little winter and early spring precipitation. Approximately one third of the annual precipitation fell during a single half-hour long rain event on the 16th August. Soil volumetric water content ranged between 2 and 23% and was much greater in the unchambered control soils during the 1997 growing season than within ambient or elevated CO_2 chambers (Figures 1b and 2f). These early differences in water distribution are attributed to problems with the chamber water collection and distribution system which were partly corrected in 1997 and finally resolved in early 1998. Also, canopy air temperature in the OTCs averaged 2.6 °C warmer than over the unchambered control plots, resulting in more desiccating environments inside the OTCs (Morgan et al., 2001a). Throughout the sampling period, growing season soil water content in control soils was generally higher than in elevated CO_2 soils. Soil water content was significantly lower ($P<0.05$) in ambient chamber soils compared to both control and elevated CO_2 soils (Figures 1b, c and 2f; Table 2). Soil temperature (T), measured at 5 cm depth, was generally 1–2 °C higher in chambered soils than in the control plots at the time of gas flux measurements. Soil T did not differ significantly between ambient and elevated chambers (Figure 2e, Table 2).

Over the 43-month measurement period, CO_2, CH_4 and N_2O fluxes were not significantly different ($P>0.1$) in control, ambient or elevated CO_2 locations (Table 2). Ecosystem respiration (CO_2 flux) followed the anticipated seasonal trends with winter fluxes declining to near zero during the coldest periods and increasing with increased plant growth during the growing seasons (Figure 2d). Although uptake of atmospheric CH_4 into the soil was not statistically significantly influenced by CO_2 enrichment, CH_4 consumption under elevated CO_2 tended to be greater than in control and ambient CO_2 soils. CH_4 uptake rates were typically highest during the summer and lower during the winter, but seasonal differences in uptake rates were small (Figure 2b; Table 2). There was no detected CO_2 treatment effect on N_2O emissions (Table 2). Nitrous oxide flux was low annually and differed little seasonally (Figure 2c; Table 2). N_2O emissions generally increase following precipitation events and were observed over only a relatively narrow flux range of -1 to less than 10 μg N m^{-2} hr^{-1}.

The flux of NO_x differed only between the control plots and the chambered plots and there was no discernable CO_2 effect (Table 2). NO_x emissions were much greater from the control plots during the 1997 growing season and were also significantly higher than from chambered plots during the 1998 and 1999 growing seasons, but by much smaller amounts. We attribute the treatment difference in 1997 to the timing and greater amount of rainfall that reached the control plots relative to the chambered plots that year. During the much drier 2000 growing season, NO_x fluxes did not differ among treatments (Table 2), although higher emission from ambient plots compared to elevated CO_2 chambers was observed the day after the large rain event in August (Figure 2a).

Seasonal trace gas fluxes and soil temperature and water content

Chambered period (April–October)

During the time when the OTCs were operating, no differences in whole system respiration (dark chamber CO_2 flux measurements), CH_4 uptake or N_2O emissions were observed when fluxes were averaged over the whole period (4-period mean; Table 2). NO_x

Table 2. Seasonal and mean trace gas flux rates and soil temperature and water content for April 1997 through October 2000 within the shortgrass steppe open-top-chamber CO_2 enrichment study

CO_2 treatment	CO_2 mg C m^{-2} hr^{-1}	CH_4 μg C m^{-2} hr^{-1}	NO_x	N_2O	Soil T °C	Volumetric Soil H_2O m^3 m^{-3}
			μg N m^{-2} hr^{-1}			
Mean Flux Rates April 1997–November 2000						
Control	56a	−29a	11a	1.6a	11.4b	11.5a
Ambient	43a	−31a	4.3b	1.7a	12.5a	7.7b
Elevated	44a	−34a	4.1b	1.7a	12.3a	10.1a
Chambered Period (April–November)-4-Period Mean						
Control	74a	−31a	15a	1.7a	15.9b	11.4a
Ambient	56a	−31a	6.4b	1.8a	17.1a	7.1c
Elevated	58a	−35a	5.0b	1.8a	17.0a	9.5b
Chambered Period (April–November) For each Year						
1997						
Control	94a	−31a	37a	1.8a	17.1b	10.5a
Ambient	87a	−36a	11.9b	1.7a	18.6a	5.8c
Elevated	70a	−36a	11.1b	1.1b	18.1a	7.1b
1998						
Control	86a	−30a	15a	1.7a	14.3b	13.8a
Ambient	62a	−30a	5.5b	1.6a	15.2a	8.7c
Elevated	77a	−36a	4.9b	1.9a	14.8a	11.0b
1999						
Control	72a	−33a	9.0a	1.8a	14.4b	12.4a
Ambient	47a	−33a	5.5b	1.6a	15.6a	8.1c
Elevated	45a	−36a	3.6b	1.5a	15.6a	11.3b
2000						
Control	45a	−30a	0.1a	1.2a	15.9b	11.4a
Ambient	34a	−27ab	2.2a	2.3a	17.1a	7.1b
Elevated	42a	−34a	0.4a	1.9a	17.0a	9.5a
Unchambered Period (November through March)-3-Period Mean						
Control	11.2a	−24a	−0.5a	1.5a	1.2a	11.2a
Ambient	11.4a	−29a	−0.9a	1.6a	1.7a	8.1b
Elevated	11.7a	−31a	−0.9a	1.5a	1.6a	10.6a
Unchambered Period (November through March)						
1997–1998						
Control	11.6a	−23a	−1.0a	1.5a	0.99a	11.6a
Ambient	11.1a	−29a	−1.7a	1.3a	0.99a	10.2b
Elevated	11.4a	−27a	−1.9a	1.58a	0.95a	11.4a
1998–1999						
Control	11.4a	−21b	−0.39a	2.0a	0.67a	13.6a
Ambient	12a	−28a	−0.87a	1.9a	1.05a	12.3b
Elevated	11.9a	−30a	−0.79a	1.5a	1.05a	13.2a
1999–2000						
Control	10.9a	−31b	−0.2a	1.5a	1.2a	11.3a
Ambient	10.6a	−35ab	0.1a	2.0a	1.7a	8.7b
Elevated	11.1a	−39a	0.1a	1.9a	1.6a	11.2a

*Numbers in each column followed by the same letter are not significantly different ($P > 0.05$) for each group of three.

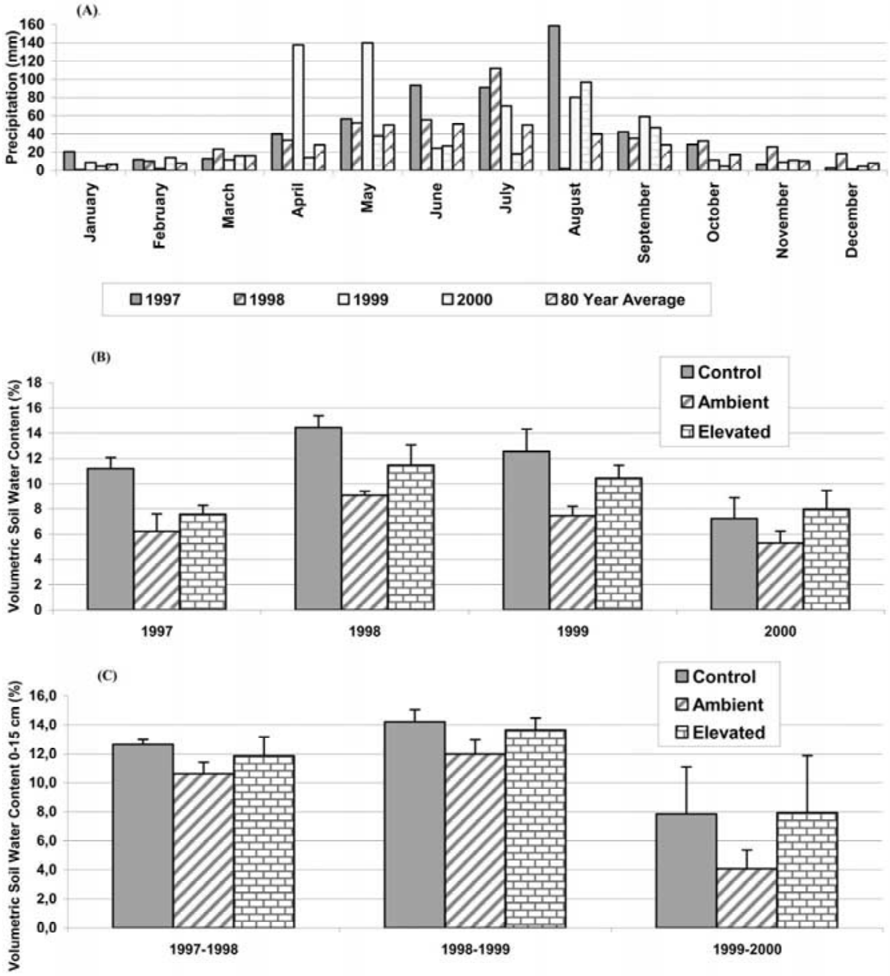

Figure 1. a) OTC site monthly precipitation for 1997–2000 and 80 year average; (b) volumetric soil water content, 0–15 cm depth, for the 1997–2000 growing seasons; and (c) volumetric soil water content, 0–15 cm depth, for the winter (OTC unchambered periods) during 1997–2000. Soil water measurements were made at the time of gas flux measurements, weekly from April, 1997 through October 2000.

emissions were significantly higher from the control plots. Soil temperature was generally lower in control plots compared to chambered plots. Soil water content was, in order of decreasing amount, control>high chamber>ambient chamber over the 4 years. During 1997, the main differences appear in soil water content and NO_x flux. Soil water content was much lower in ambient chambers than in high chambers, which was much lower than in the control plots. NO_x flux averaged more than three times higher from the control plots than from the chambered plots. During 1998 and 1999, the same trends are evident but the differences are not as large. CO_2 emissions averaged approximately 4% higher, but not significantly ($P>0.05$) from the elevated CO_2 plots and CH_4 uptake tended to be higher, but not significantly ($P>0.05$) under elevated CO_2. Soil temperatures were not significantly ($P>0.05$) higher in ambient OTC soils compared to elevated CO_2 OTC soils, while both ambient and elevated CO_2 OTC soil T averaged 0.5–1.2 °C higher than control soils during the times of each year when OTCs were in place (Table 2).

Unchambered period (November–March)

During the time when the OTCs were removed from the CO_2 enrichment plots (winter), soil water content tended to equilibrate and soil T was not different. Nitrous oxide emissions were not different among treatments and averaged about the same during the winter as during the chambered periods. Soils were net sinks for NO_x during the winter and did not differ with CO_2 treatment (Figure 2a). Methane uptake ten-

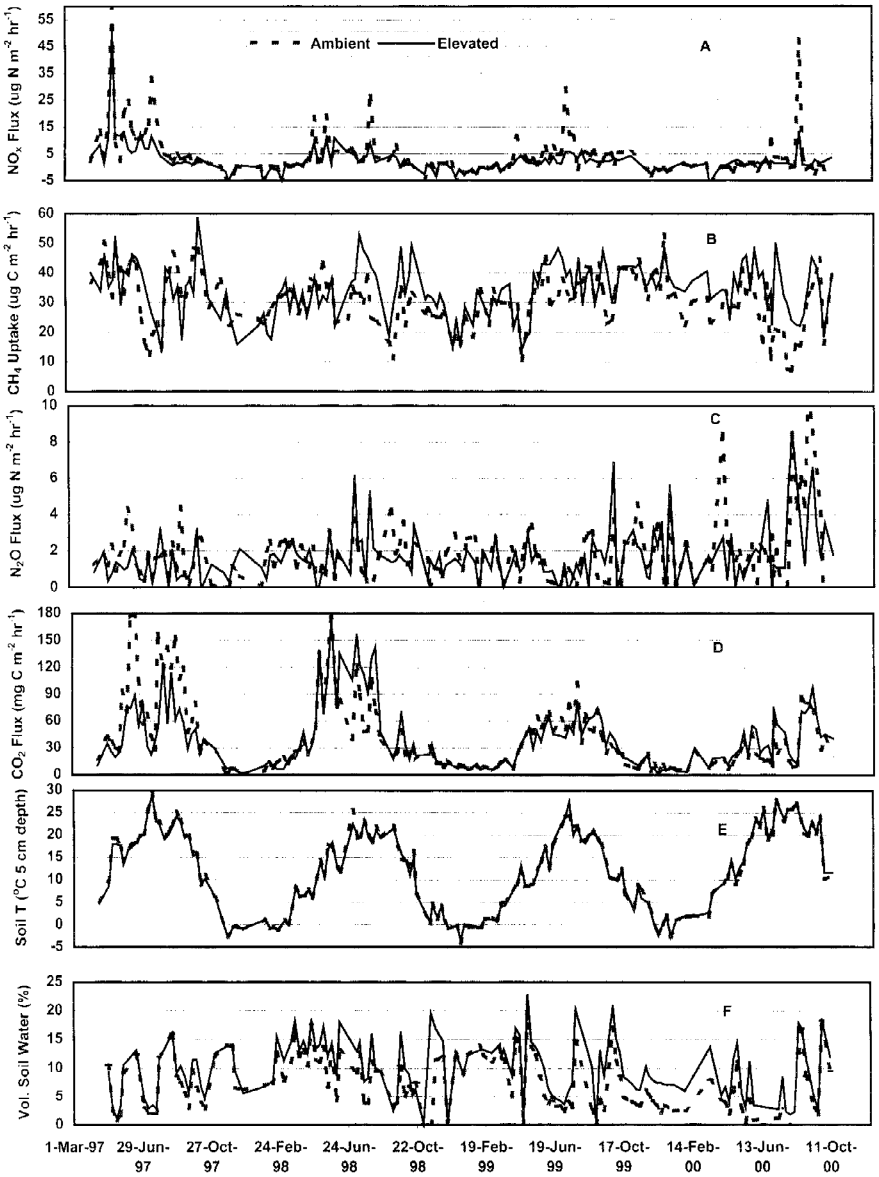

Figure 2. Trace gas flux, soil temperature and soil water content in ambient and elevated CO_2 chambers: (a) NO_x flux; (b) uptake of atmospheric CH_4 by soil micro-organisms; (c) N_2O flux; (d) dark chamber CO_2 flux; (e) 5 cm depth soil temperature; and (f) volumetric soil water content, 0–15 cm depth. Gas flux measurements for CO_2, CH_4 and N_2O were taken weekly using a closed chamber technique (Mosier et al., 1991, 1996) and NO_x flux measurements were made using a continuous flow system at the same sampling locations (Martin et al., 1998; Mosier et al., 1998) Soil water and temperature measurements were made at the time of gas flux measurements. Measurements were made weekly from April 1997 through October 2000.

ded to be higher (P>0.1) in the previously OTC plots than in the control. CO_2 flux was not different among treatments during the winter months (Table 2).

Discussion

Trace gas fluxes

Studies at the shortgrass steppe, along with data from other research, indicate that rates of N gas loss are similar to rates of atmospheric N inputs. This suggests that exports of N in gaseous form may well be the principal control on long-term grassland N balance and productivity (Groffman et al., 1993; Martin et al., 1998; Mosier et al., 1991). One of the dominant pathways of ecosystem N loss at the CPER and other grasslands appears to be efflux of NO (Martin et al., 1998; Mosier et al., 1998; Williams and Fehsenfeld, 1991). Emissions of NO, N_2O and N_2 from soils represents loss of end products, by products, and intermediates of several interacting biotic and abiotic processes.

The responses of grasslands to increased atmospheric CO_2 will ultimately depend on a complicated interaction of plant and microbial responses that are linked through the N cycle. Elevated CO_2 enhances water use efficiency in grasslands (Morgan et al., 2001b), which can increase soil water content, thereby enhancing the supply of mineral N. At the same time, however, CO_2-induced plant production increase will increase the demand for soil N. In the tallgrass prairie Williams et al. (2001) found that soil microbes out competed the plants for available N supply. Microbial biomass control of plant N uptake in the N-limited tallgrass prairie was implicated. For the shortgrass steppe, the result may be that mineral N pools will be smaller than the typically low levels for the tallgrass prairie, as suggested by the data of Morgan et al. (1994). Enhanced production and higher C/N ratios under elevated CO_2, and transfer of that C below ground can result in immobilization of N, further limiting soil mineral N. In a California annual grassland, Hungate et al. (1997b) observed that increased N mineralization under elevated CO_2 was balanced by decreased microbial production of NO, N_2O and N_2. In another report, Hungate et al. (1997c) found increased N mineralization due to increased soil water content under elevated CO_2, which should increase NO and N_2O emissions. This overall result would be a more rapid depletion of soil mineral N. Studies conducted in more humid grasslands indicate that NO_x and N_2O emissions may be enhanced under elevated CO_2 (Arnone and Bohlen, 1998; Ineson et al., 1998; Robinson and Conroy, 1999). In contrast, Hungate et al. (1997b) observed a decrease in nitrification and NO_x emissions in an N-fertilized annual grassland under elevated CO_2. In the semi-arid shortgrass steppe we observed no general CO_2-induced effect on NO_x and N_2O flux.

NO_x and N_2O

The lower NO_x emissions from both ambient and elevated CO_2 chamber soils compared to control may be related to N demand by the plants. Aboveground biomass production was higher in ambient chambers than control plots, and significantly higher under elevated CO_2 (Morgan et al., 2001a,b). A good relationship was observed between above ground biomass production and NO_x emissions for the 1997, 1998 and 1999 growing seasons (Figure 3). Even though N content of above ground biomass, in October of each year, tended to follow the pattern of elevated CO_2<ambient CO_2<control, the total N transferred from the soil into above ground biomass was greatest under elevated CO_2 (unpublished data).

This slight trend in decrease of NO_x and N_2O emissions under elevated CO_2 supports the concept of increased N uptake by plants grown under elevated CO_2 and decreased availability of mineral N to soil microbes (Hungate et al., 1997c; Hu et al., 2001). NO_x fluxes were much higher ($P<0.01$) from the control soils (15 μg N m^{-2} h^{-1}) than either the ambient OTC (6.4 μg N m^{-2} h^{-1}) or elevated CO_2 OTC (5.2 μg N m^{-2} h^{-1}). The control soils were generally wetter with less plant production than in chambered soils, likely resulting in higher N availability to soil microbes. Although soil water content was greater under elevated CO_2 than in the ambient OTC, the surface 15 cm soil on average was drier than control soil through the whole growing season within the OTCs, regardless of CO_2 enrichment.

The NO_x fluxes from the control plots were about 10 times greater than were N_2O fluxes, the NO_x emissions represent a significant loss of ecosystem N. During the first year of CO_2 enrichment, 1997, NO_x emissions totaled approximately 0.16 g N m^{-2} (calculated by summing daily fluxes obtained from linear interpolations of weekly observations) from the control plots compared to approximately 0.05 g N m^{-2} from both ambient and elevated CO_2 chambered plots. Growing season NO_x emissions from control plots continued to be higher than from chambered plots through 1998 and 1999 though by a smaller amount than in 1997 (Table 2). This probably occurred because the unchambered soils tended to be wetter than the chambered soils (Martin et al., 1998).

CO_2 and CH_4 fluxes

Ecosystem respiration, measured as dark chamber CO_2 flux, was not affected by elevated CO_2 over the

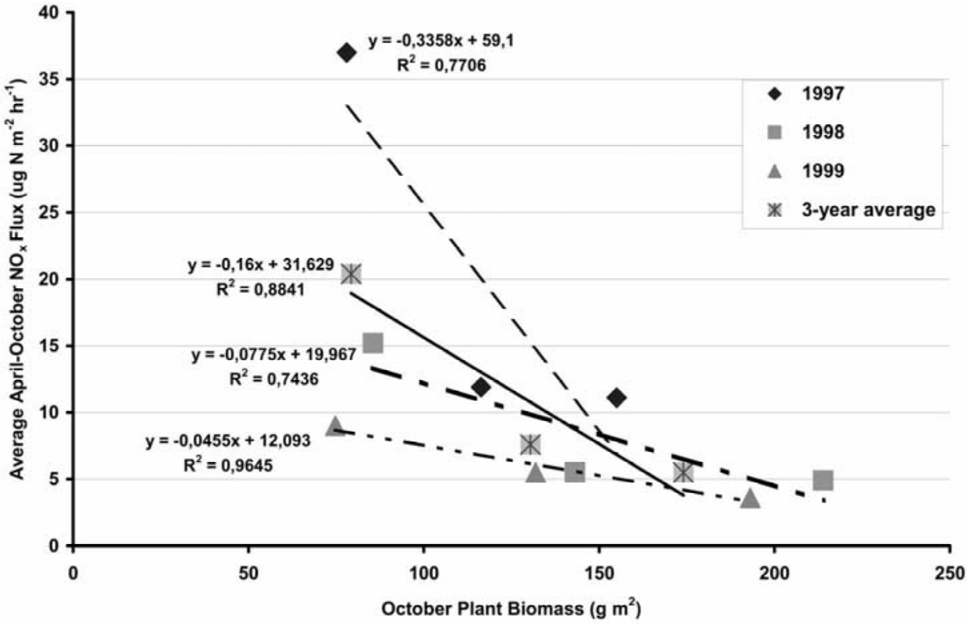

Figure 3. The relationship between above ground plant biomass production (October harvest data) in unchambered control, ambient and elevated OTC CO_2 treatments and NO_x fluxes during the 1997, 1998, and 1999 growing seasons.

43-month measurement period. During the growing seasons, when CO_2 flux included aboveground plant respiration, plant root respiration, and respiration of soil organisms, CO_2 emissions were not significantly different ($P>0.3$) in control, ambient or elevated CO_2 treatments. CO_2 emissions tended to be higher from the control soils ($P>0.2$) (Table 2), probably in response to higher soil moisture content. During the very dry 2000 spring and early summer, soils were wetter under elevated CO_2 than ambient chambers (Figure 2f) and occasionally higher CO_2 flux was observed from the elevated CO_2 ecosystem than from the ambient chambers (Figure 2d). During the winter, when maintenance root respiration and soil respiration were the main sources of emitted CO_2, we found no trends or differences among the three treatments. These observations suggest that, because of the increased above ground biomass production, the system should accrue carbon under elevated CO_2. We should be able to substantiate this supposition by the end of our 5-year study by measuring changes in soil C under ambient and elevated CO_2. The apparent imbalance between production and loss suggests that either plant respiration rates were lower under elevated CO_2 (Amthor, 1997) or that soil processes (including root respiration) were slower.

Shortgrass steppe plants grown under elevated CO_2 apparently do not release appreciable amounts of organic substances that stimulate microbial respiration, since little difference in system respiration was observed (Figure 2d; Table 2). This is different from the observations in the annual grassland where Hungate et al. (1996) observed stimulated microbial respiration under elevated CO_2. Ineson et al. (1998) observed a decrease in CO_2 emissions under elevated CO_2. They attributed this decrease to reduced root decomposition rates or lower soil respiration due to unspecified changes in soil physical conditions.

Rates of oxidation of atmospheric CH_4 were not affected by CO_2 enrichment in our study (Table 2). This contrasts with Ineson et al. (1998) who found that net CH_4 consumption was greater in control than in elevated CO_2 soils. It is not clear if elevated CO_2 inhibited CH_4 oxidation or if CH_4 diffusion was decreased because of the probably wetter soils under elevated CO_2. CH_4 oxidation rates in our study tended to be slightly higher under elevated CO_2 ($P>0.3$). Soil moisture content was significantly lower ($P<0.05$) in elevated CO_2 soils compared to controls and was much lower in ambient chamber soils. However, diffusion rates at higher soil water contents were likely counterbalanced by higher microbial activity under wetter conditions. The optimum soil moisture conditions for CH_4 oxidation in this soil texture is approximately 20% water filled pore space (Mosier et al., 1996).

Soil feed-backs on plant responses

The capability of plants to maintain continued CO_2-responsiveness, i.e., continued enhanced growth, depends on their ability to obtain additional water and essential nutrients (Sage, 1994), especially N (Stitt and Krapp, 1999), which in the shortgrass steppe are often in short supply (Lauenroth and Milchunas, 1991). Most studies of plant response indicate that CO_2 enrichment leads to enhanced productivity and lower tissue concentrations of N (Conroy, 1992; Owensby et al., 1993b), as is the case in our study (Morgan et al., 2001a). There is some evidence that reductions in tissue N concentrations are due, in part, to reduced soil N availability (Rice et al., 1993). In N-limited systems, these reductions may simply be the result of higher plant demand by larger plants under CO_2-enrichment, thus reducing the amount of soil available N. The possibility also exists that sequestration of more C belowground of higher C/N ratio tissues may lead to immobilization of soil N in plants/soils after long-term exposure to elevated CO_2 (Hunt et al., 1988; Morgan et al., 1994). Hu et al. (2001) suggest that soil microbial decomposition is slowed under elevated CO_2 because of N limitation. Loiseau and Soussana (2000) also observed that the soil N cycle appeared to be slowed under elevated CO_2. Conversely, Hungate et al. (1997c) found that higher soil water contents under elevated CO_2 in an annual grassland stimulated soil N mineralization and resulted in greater plant N uptake. Hungate et al. (1996) found that the direction and magnitude of CO_2-induced alteration in plant N pools and ammonium uptake were species dependent. It is possible that reduced plant tissue N under elevated CO_2 is not entirely driven by available soil N, but results, at least in part, from plant acclimation response to elevated CO_2 resulting in greater N use efficiency (Drake et al., 1996). The interactions of soil microbiology and plant physiology on CO_2-related alterations in soil available N are complex and may vary with time. In the shortgrass steppe where N input is exclusively from atmospheric deposition (Woodmansee 1978), the long-term impact on N availability requires an understanding of the relationships between CO_2 enrichment, water and N dynamics, represented by NO_x and N_2O fluxes, and their interactive effect on plant growth.

Summary

From weekly measurement of trace gas exchange in control, ambient CO_2 and elevated CO_2 OTCs we observed no statistically significant CO_2 enrichment effect on ecosystem respiration, oxidation of atmospheric CH_4, or emissions of NO_x or N_2O. Methane oxidation tended to be higher under elevated CO_2 while NO_x and N_2O tended to be lower, but not significantly in either case. Above ground biomass production was higher under elevated CO_2 (Morgan et al., 2001a), which utilized more soil N (unpublished data). Soils under elevated CO_2 were wetter than in ambient CO_2 OTCs, which should have enhanced soil N mineralization under elevated CO_2 (Hungate et al., 1997a,b,c). The two opposing processes apparently offset each other as NO_x and N_2O emissions, which reflect system N mineralization and nitrification, did not differ. Ecosystem respiration, which included soil respiration, was not generally higher under elevated CO_2. This suggests that readily mineralizable C exudates induced by elevated CO_2 are relatively small, or that enhanced C mineralization was either too small or too ephemeral to observe with weekly measurements. As CO_2 efflux was not greatly enhanced, the possibility of increased carbon storage from greater plant production under increasing CO_2 exists, if ecosystem productivity does not become N limited.

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