Plant and Soil **202:** 167–174, 1998.

Elevated CO_2, rhizosphere processes, and soil organic matter decomposition

Weixin Cheng[1,3] and Dale W. Johnson[1,2]
[1]*Biological Sciences Center, Desert Research Institute, P.O. Box 60220, Reno, NV 89506, USA*;* [2]*Environmental and Resource Sciences, University of Nevada, Reno, NV 89512, USA;* [3]*Present address: Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA*

Received 23 July 1997. Accepted in revised form 8 April 1998

Key words: ^{13}C, ^{14}C, decomposition, elevated CO_2, respiration, rhizosphere, soil carbon

Abstract

The rhizosphere is one of the key fine-scale components of C cycles. This study was undertaken to improve understanding of the potential effects of atmospheric CO_2 increase on rhizosphere processes. Using C isotope techniques, we found that elevated atmospheric CO_2 significantly increased wheat plant growth, dry mass accumulation, rhizosphere respiration, and soluble C concentrations in the rhizosphere. When plants were grown under elevated CO_2 concentration, soluble C concentration in the rhizosphere increased by approximately 60%. The degree of elevated CO_2 enhancement on rhizosphere respiration was much higher than on root biomass. Averaged between the two nitrogen treatments and compared with the ambient CO_2 treatment, wheat rhizosphere respiration rate increased 60% and root biomass only increased 26% under the elevated CO_2 treatment. These results indicated that elevated atmospheric CO_2 in a wheat-soil system significantly increased substrate input to the rhizosphere due to both increased root growth and increased root activities per unit of roots. Nitrogen treatments changed the effect of elevated CO_2 on soil organic matter decomposition. Elevated CO_2 increased soil organic matter decomposition (22%) in the nitrogen-added treatment but decreased soil organic matter decomposition (18%) without nitrogen addition. Soil nitrogen status was therefore found to be important in determining the directions of the effect of elevated CO_2 on soil organic matter decomposition.

Introduction

The physiological response of plants to elevated atmospheric CO_2 has received considerable attention because CO_2 is a substrate for photosynthesis, and its atmospheric concentration is predicted to double in the next century if the current trend continues (Keeling et al., 1989). Although some attention has been given to belowground response to CO_2 increase (Schimel, 1995), predicting changes in belowground C storage in response to CO_2 increase remains to be one of the greatest challenges in closing the global C budget (Mooney, 1991).

Effects of elevated CO_2 such as increased plant photosynthesis, altered litter quality (C/N ratio), and changes in soil moisture have been extensively studied (Anderson, 1992; Nie et al., 1992; Peterjohn et al., 1993; Post et al., 1992). However, the effect of elevated CO_2 concentration on original soil organic matter (SOM) decomposition via plant roots has rarely been investigated. This process has the potential to link increased CO_2 concentration with soil C sequestration/loss and soil nutrient cycling.

Rhizosphere processes play an important role in C sequestration and nutrient cycling in terrestrial ecosystems (Helal and Sauerbeck, 1989; Van Veen et al., 1991). The rhizosphere has been identified as one of the key fine-scale components in the overall global C cycle (Coleman et al., 1992). Plants (C_3) grown under elevated CO_2 conditions often exhibit increased growth, a more than proportional increase in C allocation to roots (Norby et al., 1986; Pregitzer et al.,

* FAX No: 702 673 7485. E-mail:wcheng@dri.edu

1995), and increases in other rhizosphere processes such as total rhizosphere respiration and rhizodeposition (Billés et al., 1993; Gorissen, 1996; Hungate et al., 1997; Ineson et al., 1996; Kuikman et al., 1990; Lekkerkerk et al., 1990; Whipps, 1985). The fate of this increased C input into the belowground system and its subsequent influence on soil C storage bears important implications for global carbon cycles.

Our main research objectives were to investigate C input to belowground systems when wheat plants are grown under elevated CO_2 concentrations and to understand the subsequent influence of the C input on rhizosphere processes. The specific research questions addressed in this study were: (1) Is there an increase of rhizospheric C input, such as root exudates and rhizosphere microbial respiration, when wheat plants are grown in an elevated CO_2 atmosphere? and (2) Will nitrogen fertilization alter rhizosphere respiration and SOM decomposition when plant-soil systems are maintained in an elevated CO_2 atmosphere?

Materials and methods

A laboratory experiment was carried out using environmentally controlled plant growth chambers and C isotope methods. A split-plot experimental design was used with three replicate growth chambers at ambient CO_2 (360 μL L^{-1}) and three at an elevated CO_2 level (700 μL L^{-1}). The chambers were naturally lit and equipped with full controls on air CO_2 concentrations and air temperature. Typical sunny day photon flux density was approximately 1600 μmol m^{-2} s^{-1}. Air temperature inside the chambers were controlled at 12 °C during night time and at 22 °C during day time. The day length was approximately 14 h on average during the period of this experiment. Treatments consisted of two CO_2 concentrations (350 and 700 μL L^{-1}) and two nitrogen additions (0 and 51.7 mg N kg^{-1} of soil, an equivalent of 100 kg N ha^{-1}). Each chamber contained all levels of the nitrogen treatment randomly distributed within the plant growing area. We used spring wheat (*Triticum aestivum* L., Andy), a species commonly used in rhizosphere research.

Plastic containers (5 cm dia., 20 cm long, 393 cm^3 vol.) were used to grow plants and instrumented for measuring soil respiration by attaching Tygon tubing to the top and the bottom of the containers and fitting with needle valves for recovery of soil CO_2 (Cheng, 1996).

Surface layer soil (0–20 cm) was obtained from a Tallgrass prairie field at the Konza Prairie Long-Term Ecological Research site, Kansas, USA. Vegetation at this site has been dominated by C4 grasses for possibly thousands of years. The $\delta^{13}C$ signature of the soil C reflects that of C4 plants, which is very different from C3 plants such as wheat. By growing wheat (C3) plants in these soils with C4 signature, we could use natural ^{13}C abundance as a tracer to separately monitor plant-derived C (i.e., wheat) and soil-derived C (Cheng, 1996). The soil was sieved (<2 mm), homogenized, and air-dried before use. Konza Prairie soil was mixed 1:1 with C-free sea sand for ease of handling and diluting the soil nutrient release due to disturbance (Johnson et al., 1995).

Plants were grown in the plastic containers under controlled growth chamber conditions. Soils (380 g dry wt) were packed into each container to a predetermined bulk density of 1.3 g cm^{-3}. Germinated wheat seeds were planted approximately 2 cm deep into each container. Three seedlings were kept in each container by thinning out additional ones immediately after emergence. Water content in each container was monitored daily by weighing and was maintained at approximately 80% field water holding capacity by adding deionized water according to the weight loss. Two weeks post-germination, all containers were sealed at the base of the plant with low melting point paraffin (m.p. 42 °C) to separate the aboveground atmosphere from the belowground. The integrity of the seal was verified by submerging the plastic container in water and checking for gas leaks. This paraffin seal did not damage the plant seedlings and was strong enough for carrying out the gas exchange measurements (Cheng, 1996).

Belowground respiration for each treatment was determined using a continuous flow-through system (Cheng, 1996). CO_2 free air was pulled through the soil column by vacuum, and exiting air was trapped in an alkaline trapping solution (0.5 *M* NaOH). An aliquot of NaOH solution was analyzed for total C using a Shimadzu TOC Analyzer. The remainder of the trapping solution was mixed with excess $SrCl_2$, and the $\delta^{13}C$ value of the precipitate ($SrCO_3$) was analyzed by mass spectrometry (Harris et al., 1997). The principle of the ^{13}C natural tracer method was based on the difference in ^{13}C:^{12}C ratio (reported in $\delta^{13}C$ values) between plants with the C3 versus the C4 photosynthesis pathways. C3 plants such as wheat were depleted in ^{13}C, while C4 soil C used in this experiment had a mean $\delta^{13}C$ of –15‰. The C entering the soil via roots

of the C3 plants had a different δ^{13}C value than the δ^{13}C value of the soil. Based on Cerri et al. (1985), we used the following equation to partition soil-derived C4 C from plant-derived C3 C:

$$C3 = Ct(\delta_t - \delta_4)/(\delta_3 - \delta_4) \quad (1)$$

where Ct = C3+C4, is the total C from belowground CO_2; C3 is the amount of C derived from C3 plants; C4 is the amount of C derived from C4 soil; δ_t is the δ^{13}C value of the Ct C; δ_3 is the δ^{13}C value of the C3 plant C (the δ^{13}C value of wheat roots in this study); δ_4 is the δ^{13}C value of the C4 soil C (the δ^{13}C value of CO_2 from the soil-only treatment in this study).

Carbon-14 pulse-labeling and isotopic trapping (Cheng et al., 1993, 1994) were used to separate root and rhizo-microbial respiration and to measure root exudate concentration in the rhizosphere. Briefly, isotopic trapping is achieved through substrate competition. When the ^{14}C of low weight molecules is exuded by roots after a pulse labelling of the shoot and simultaneously taken up by the rhizosphere microorganisms, adding glucose to the rhizosphere will reduce the microbial uptake of ^{14}C exudates. This occurs because the microorganisms will use both the added glucose and the exudates instead of solely relying on the root exudates. Therefore, rhizo-microbial respiration ($^{14}CO_2$ evolved from microbial utilization of exudates) must be inversely proportional to the glucose-^{12}C concentration in the rhizosphere; whereas root respiration is independent of the glucose-^{12}C concentration in the rhizosphere. The following equation can be written for each glucose concentration, and a family of two equations can be established for two glucose concentrations in the same experiment:

$$(Z_G - R)/(Z_W - fR) = C_S/(C_S + C_G) \quad (2)$$

where Z_G is the $^{14}CO_2$ evolution rate from the glucose-treated container; Z_W is the $^{14}CO_2$ evolution rate from the container of water addition control; R is the $^{14}CO_2$ evolution rate due to root respiration; C_S is soluble C concentration in the rhizosphere (g C L^{-1}); and C_G is the added glucose-C concentration (g C L^{-1}). The two unknown variables in the equation are the $^{14}CO_2$ evolution rate that is due solely to root respiration (R) and the soluble C concentration in the rhizosphere (C_S). By simultaneously solving two equations in a family, the values of the two variables can be determined.

Following isotopic trapping, aboveground vegetation was collected and roots were separated from the soil by hand. Roots, shoots (or stems and needles), and soils were oven-dried at 60 °C, weighed, pulverized in a ball mill, and combusted in a Biological Oxidizer. Radioactivity was measured by liquid scintillation counting. Shoot, roots, and soil were also analyzed for δ^{13}C using mass spectrometry.

Results

CO_2 concentration at 700 μL L^{-1} significantly increased wheat plant primary production and the increase was enhanced by nitrogen addition (Table 1). With nitrogen fertilizer addition, elevated CO_2 caused shoot mass, root mass, total plant mass, and total belowground respiration to increase by approximately 60%, 37%, 49%, and 34%, respectively (Figure1). Without nitrogen addition, elevated CO_2 caused shoot mass, root mass, total plant mass, and total belowground respiration to increase by approximately 28%, 14%, 21%, and 7%, respectively. The root:shoot ratio decreased under elevated CO_2 in both nitrogen treatments, even though not statistically significant.

Using ^{13}C as a natural tracer, we were able to separate total belowground respiration into: (1) total rhizosphere respiration (source of C from current plants including root respiration and rhizosphere microbial respiration) and (2) native soil respiration (source of C from the soil). The δ^{13}C values shown in Table 1 and Equation (1) were used in the calculation. Elevated atmospheric CO_2 significantly increased total rhizosphere respiration by approximately 55% in the nitrogen-added treatment and 66% without nitrogen addition (Table 1, Figure 1). Specific rhizosphere respiration (i.e. rhizosphere respiration per unit of root biomass) also increased when wheat plants were grown under elevated CO_2. The specific rhizosphere respiration increase was 18% with nitrogen addition and 44% without nitrogen addition.

Using the ^{14}C isotope trapping technique, we measured current photosynthate allocation to root respiration, rhizo-microbial respiration, and soluble C concentrations in the rhizosphere (Table 2). There was approximately a 60% increase in soluble C concentration in the rhizosphere when plants were grown under elevated CO_2 concentration. Total carbon allocation to root respiration and rhizo-microbial respiration increased slightly under elevated CO_2. However, percent C allocation to root respiration and rhizo-microbial respiration did not change under elevated CO_2. This indicated that the relative C allocation pattern was not altered by higher CO_2 concentrations.

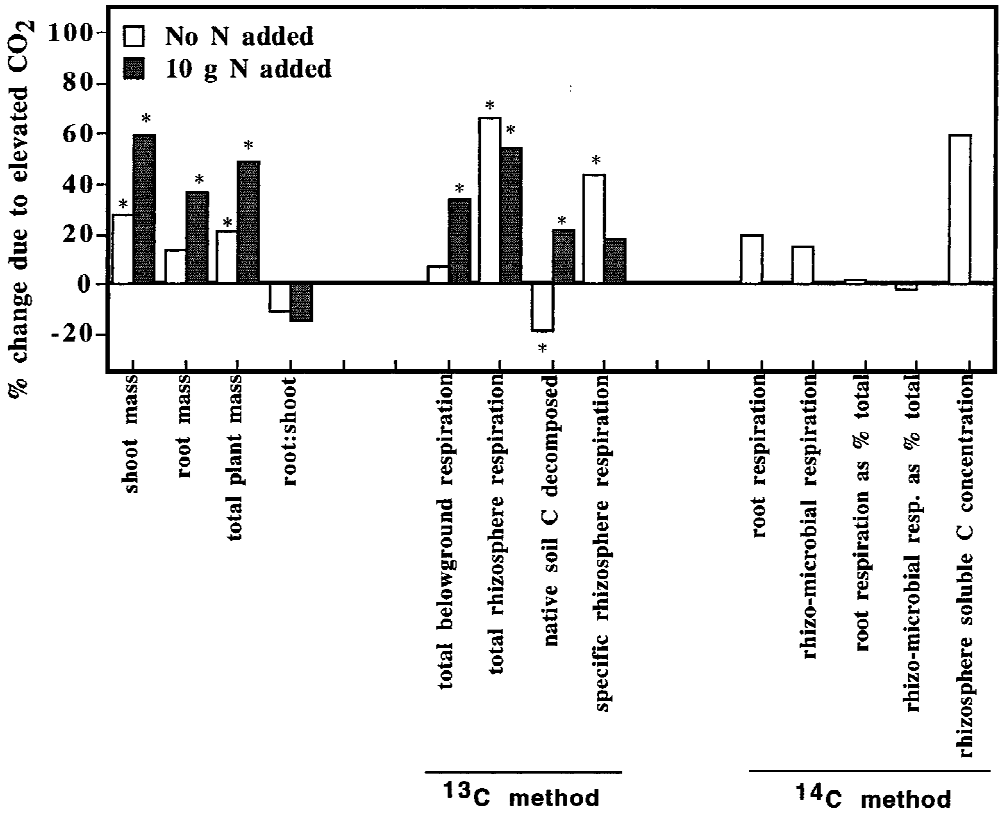

Figure 1. The effects of elevated CO_2 on wheat plant growth, root respiration, belowground respiration, rhizosphere respiration, and soluble carbon concentrations in the rhizosphere. * Statistically significant ($P < 0.05$).

Table 1. Mean comparisons between ambient and elevated CO_2 treatments with and without nitrogen addition. Numbers in each row with the same letter are not significantly ($P < 0.05$) different by Fisher's LSD test

		Ambient CO_2		700 μL L^{-1} CO_2		Soil only
Measurement	Unit	No added N	+N	No added N	+N	
Shoots mass	gram container^{-1}	0.406a	0.453a	0.521b	0.724c	
Roots mass	gram container^{-1}	0.397a	0.421a	0.452a	0.578b	
Total biomass	gram container^{-1}	0.803a	0.875a	0.973b	1.302c	
Root:shoot		0.972a	0.943ab	0.868ab	0.806b	
Total CO_2 belowground	mg C container^{-1} d^{-1}	18.07a	19.53a	19.39a	26.12b	8.78c
Rhizosphere respiration (RR)	mg C container^{-1} d^{-1}	5.46a	7.09b	9.09c	10.96d	
CO_2 from soil	mg C container^{-1} d^{-1}	12.62a	12.44a	10.30b	15.16c	
Specific RR	mg C g^{-1} root d^{-1}	14.68a	17.58ab	21.07b	20.28b	
$\delta^{13}C$ of roots	‰	–31.0a	-31.8a	–43.5a	–44.9a	
$\delta^{13}C$ of shoots	‰	–32.2a	–33.2a	–44.7b	–46.1b	
$\delta^{13}C$ of total CO_2	‰	–21.3a	–22.6a	–29.6b	–28.8b	–17.2c

Table 2. Cumulative $^{14}CO_2$ evolved (0.5–4.5 h) in root-soil columns; calculated root respiration, rhizo-microbial respiration, and concentration of soluble C in the rhizosphere of 30-day old wheat. Mean glucose concentration was calculated based on the amount of glucose added and the uptake rate of 8.68 mg glucose container^{-1} h^{-1} obtained from a separate study under the same soil and plant conditions. Numbers with the same letter are not significantly ($P < 0.05$) different between the two CO_2 treatments

Mean glucose concentration	700 μL L^{-1}	Ambient
(g C L^{-1} soil water)		
glucose-I	1.19	1.19
glucose-II	6.78	6.78
$^{14}CO_2$ evolved (KBq container^{-1}) (mean $\pm$ 1 SE)		
water only	21.9a	18.7b
glucose-I	16.0a	12.6b
glucose-II	12.7a	10.3b
Root respiration		
(KBq container^{-1})	11.5	9.6
(% water addition)	52.3	51.3
Rhizo-microbial respiration		
(KBq container^{-1})	10.5	9.1
(% water addition)	47.7	48.7
Water soluble-C		
(mg C L^{-1} soil water)	927	581

Discussion

Several studies have suggested that more carbon was fixed due to a large increase of leaf-level or canopy-level photosynthesis in systems exposed to elevated CO_2 than could subsequently be accounted for in the plant biomass or soils. This phenomenon has been called 'the locally missing carbon' as a separate reference from the missing carbon at the global scale. In an alpine grassland, a 41% increase in CO_2 uptake was reported during three years of CO_2 enrichment, but no aboveground biomass increase was observed and only a slight increase in belowground biomass was detected (Körner et al., 1996). In another study of yellow poplar (*Liriodendron tulipifera* L.) with continuous exposure to ambient and elevated concentrations of atmospheric CO_2 for three growing seasons, Norby et al. (1992) reported that there was no significant effect of CO_2 concentration on dry mass production, despite the sustained increase in photosynthesis and reduced foliar respiration. The causes of the so-called 'locally missing carbon' was hypothesized to be partly due to the increases of carbon allocation to some not-measured belowground components such as root turnover, root respiration, and root exudation. The results of this study supported this hypothesis since elevated CO_2 substantially increased C input to belowground components due to the enhancement of root exudation and rhizosphere respiration. This large amount of C input to the rhizosphere was not accounted for in the C budgets mentioned above.

There are two ways that this increased C in the rhizosphere is processed in the soil, which may have important implications for carbon cycling (Canadell et al., 1996). First, this C source is utilized by microorganisms and partially converted into SOM, thereby increasing soil C storage. Second, this readily available C source alters soil microbial processes by providing needed substrates, thereby either stimulating SOM decomposition due to the so-called 'priming effect' (stimulation of SOM decomposition caused by the addition of labile substrates, Dalenberg and Jager, 1989) (Billés et al., 1993; Zak et al., 1993) or suppressing SOM decomposition due to microbial immobilization (Díaz et al., 1993).

The results from this study suggested that the degree of CO_2 enhancement on rhizosphere respiration was much higher than on root biomass. Averaged between the two nitrogen treatments and compared with the ambient CO_2 treatment, wheat rhizosphere respiration rate increased 60% and root biomass only increased 26% under the elevated CO_2 treatment. Similar results were also reported by other studies. In a continuous ^{14}C-labelling study using wheat, Lekkerkerk et al. (1990) reported that the wheat plants grown under the elevated CO_2 treatment produced 74% more rhizosphere-respired C and only 17% more root biomass compared to the ambient treatment. Hungate et al. (1997), in a microcosm experiment with mixed grasses, reported that elevated CO_2 enhanced total rhizosphere deposition by 56% and root biomass by less than 15%. Two mechanisms could be posed as the potential causes of these results. First, roots grown under elevated CO_2 exuded more and had higher turnover rates than roots grown under the ambient treatment, resulting in a more than proportional increase in total rhizosphere respiration under elevated CO_2. Second, rhizosphere microbial associations were more enhanced under elevated CO_2 than under am-

bient CO_2, resulting in higher rhizosphere microbial activities per unit of root growth under elevated CO_2.

Some evidence supported the first hypothesis. Using the isotopic trapping method (Cheng et al., 1993, 1994), we found approximately a 60% increase in soluble C concentration in the rhizosphere when plants were grown under elevated CO_2 compared to ambient CO_2, indicating that roots grown under elevated CO_2 exuded more soluble C. Pregitzer et al. (1995) found that root turnover rates were higher for plants grown under elevated CO_2 than under ambient. However, the amount of extra C input to the rhizosphere due to the enhanced root turnover under elevated CO_2 was expected to be low in most tracer studies of short duration (i.e., this study; Hungate et al., 1997; Lekkerkerk et al., 1990) since the life span of the roots was probably longer than the duration of the experiment (Eissenstat and Yanai, 1997). Enhanced root exudation was probably the major component of this extra C input to the rhizosphere in these short experiments. The second hypothesis was widely supported by indirect evidence reported in the literature. Elevated CO_2 increased both percent infection of vescular-arbuscular mycorrhizae (Monz et al., 1994) and percent infection of ectomycorrhizae (Delucia et al., 1997; Ineichen et al., 1995; Norby et al., 1987; O'Neill, 1994; Rygiewicz et al., 1997). Elevated CO_2 also increased symbiotic N_2-fixation across several types of associations (Arnone and Gordan, 1990; Hibbs et al., 1995; Masterson and Sherwood, 1978; Norby, 1987; Philips et al., 1976; Thomas et al., 1991; Tissue et al., 1991). However, direct evidence of higher rhizosphere symbiotic activities per unit of root growth under elevated CO_2 is still lacking.

Increasing atmospheric CO_2 changes the effect of rhizosphere processes on SOM decomposition in several possible directions. An increased rate of SOM decomposition under elevated CO_2 has been assumed to be more likely (Billés et al., 1993; Körner and Arnone, 1992; Luxmoore, 1981; Zak et al., 1993). However, results from the studies completed to date are inconsistent. Stimulatory (Billés et al., 1993; Zak et al., 1993), suppressive (Kuikman et al., 1990; Rouhier et al., 1994), and neutral (Liljeroth et al., 1990; Lin et al., in press) results have all been reported. Results from this study showed the status of soil nitrogen (with or without N fertilization) was an important modifier which switched the direction of the elevated CO_2 effect on SOM decomposition. Elevated CO_2 increased SOM decomposition in the nitrogen-added treatment but decreased SOM decomposition without nitrogen addition. Hungate et al. (1997) also found that elevated CO_2 increased SOM decomposition only in the nitrogen-added treatment, and did not significantly affect SOM decomposition without nitrogen fertilization. On the other hand, Cardon (1996) reported that elevated CO_2 decreased SOM decomposition in the nitrogen-fertilized treatment. In a growth chamber study with spring wheat grown in well fertilized soils using a continuous ^{14}C-labelling technique, Kuikman et al. (1990) reported that elevated CO_2 decreased SOM decomposition at the last sampling (49 days) but not at the first sampling (22 days). In a microcosm study using yellow birth (*Betula alleghaniensis*), Berntson and Bazzaz (1997) found that elevated CO_2 increased SOM decomposition (as indirectly indicated by nitrogen mineralization) during the initial period, but decreased SOM decomposition during the later period, suggesting that temporal variation changed the direction of the process. The results described above were obtained under diverse experimental conditions. These diverse results indicated that the effect of elevated atmospheric CO_2 on SOM decomposition was conditional of different plant-soil systems and was not mono-directional. Among many potentially relevant factors, soil mineral nutrition (Cardon, 1996; Hungate et al., 1997; this paper), plant species (Hungate et al., 1996), and temporal variation (Berntson and Bazzaz, 1997; Kuikman et al., 1990), were the important determinants of the direction and possibly the magnitude of the effect of elevated atmospheric CO_2 on SOM decomposition.

Based on the studies of Liljeroth et al. (1990) and Merckx et al. (1987), Kuikman et al. (1990) and Lekkerkerk et al. (1990) have suggested a hypothesis to explain why soil nutrition determines the direction of the effect of elevated atmospheric CO_2 on SOM decomposition. The hypothesis states that given adequate mineral nutrient supply, soil microorganisms prefer labile root-derived C to soil-derived carbon, resulting in decreased SOM decomposition; whereas, if mineral nutrients are in short supply, soil microorganisms prefer nutrient-rich SOM to root-derived C, resulting in increased SOM decomposition. The results of Cardon (1996) and Kuikman et al. (1990) seem to support this hypothesis, which show that elevated CO_2 in the fertilized treatment reduced SOM decomposition. But this hypothesis is in conflict with the results of Hungate et al. (1997) and this study, which indicate that elevated CO_2 in the fertilized treatment stimulated SOM decomposition. More mechanistic studies are needed to further clarify this issue.

Acknowledgements

We thank John Blair for providing the special soil, Guanghui Lin for ^{13}C analysis, Wenxiong Liu, Anne Hoylman, Elizabeth Sotoodeh, and Aimin Yang for laboratory assistance. Research was supported by National Science Foundation grant DEB-9496350 and a grant from the Research Institute of Innovative Technology for the Earth.

References

Anderson J M 1992 Responses of soils to climate change. Adv. Ecol. Res. 22, 163–210.

Arnone J A III and Gordon J C 1990 Effect of nodulation, nitrogen fixation and CO_2 enrichment on the physiology, growth and dry mass allocation of seedlings of *Alnus rubra* Bong. New Phytol. 116, 55–66.

Berntson G M and Bazzaz F A 1997 Nitrogen cycling in microcosms of yellow birch exposed to elevated CO_2: Simultaneous positive and negative below-ground feedbacks. Global Change Biol. 3, 247–258.

Billés G, Rouhier H and Bottner P 1993 Modifications of the carbon and nitrogen allocations in the plant (*Triticum aestivum* L.) soil system in response to increased atmospheric CO_2concentration. Plant Soil 157, 215–225.

Canadell J G, Pitelka L F and Ingram J I 1996 The effects of elevated [CO_2] on plant-soil carbon below-ground: A summary and synthesis. Plant Soil 187, 391–400.

Cardon Z G 1996 Influence of rhizodeposition under elevated CO_2 on plant nutrition and soil organic matter. Plant Soil 187, 277–288.

Cerri C C, Feller C, Balesdent J, Victoria R and Plenecassagne A 1985 Application du tracage isotopique naturel en ^{13}C á létude de la Oynamique de la matiére organique dans les sols. 300, G.R. Acad. Sci., Paris 423–428.

Cheng W 1996 Measurement of rhizosphere respiration and organic matter decomposition using natural ^{13}C. Plant Soil 183, 263–268.

Cheng W, Coleman D C, Carroll C R and Hoffman C A 1993 *In situ* measurement of root respiration and soluble carbon concentrations in the rhizosphere. Soil Biol. Biochem. 25, 1189–1196.

Cheng W, Coleman D C, Carroll C R and Hoffman C A 1994 Investigating short-term carbon flows in the rhizospheres of different plant species using isotopic trapping. Agron. J. 86, 782–791.

Coleman D C, Odum E P and Crossley D A 1992 Soil biology, soil ecology, and global change. Biol. Fertil. Soils 14, 104–111.

Dalenberg J W and Jager G 1989 Priming effect of some organic additions to ^{14}C-labelled soil. Soil Biol. Biochem. 21, 443–448.

Delucia E H, Callaway R M, Thomas E M and Schlesinger W H 1997 Mechanisms of phosphorus acquisition for ponderosa pine seedlings under high CO_2 and temperature. Ann. Bot. 79, 111–120.

Díaz S, Grime J P, Harris J and McPherson E 1993 Evidence of feedback mechanism limiting plant response to elevated carbon dioxide. Nature 364, 616–617.

Eissenstat D M and Yanai R D 1997 The ecology of root lifespan. Adv. Ecol. Res. 27, 1–60.

Gorissen A 1996 Elevated CO_2 evokes quantitative and qualitative changes in carbon dynamics in a plant/soil system: Mechanisms and implications. Plant Soil 187, 289–298.

Harris D, Porter L K and Paul E A 1997 Continuous flow isotope ratio mass spectrometry of carbon dioxide trapped as strontium carbonate. Commun. Soil Sci. Plant Anal. 28, 747–757.

Helal H M and Sauerbeck D R 1989 Carbon turnover in the rhizosphere. Z. Pflanzenernaehr. Bodenk. 152, 211–216.

Hibbs D E, Chan S S, Castellano M and Niu C H 1995 Response of red alder seedlings to CO_2 enrichment and water stress. New Phytol. 129, 569–577.

Hungate B A, Canadell J and Chapin F S, III 1996 Plant species mediate changes in soil microbial N in response to Elevated CO_2. Ecology 77, 2505–2515.

Hungate B A, Holland E A, Jackson R B, Chapin F S, III, Mooney H A and Field C B 1997 The fate of carbon in grasslands under carbon dioxide enrichment. Nature 388, 576–579.

Ineichen K. Wiemken V and Wiemkne A 1995 Shoots, roots and ectomycorrhiza formation of pine seedlings at elevated atmospheric carbon dioxide. Plant Cell Environ. 18, 703–707.

Ineson P, Cotrufo M F, Bol R, Harkness D D and Blum H 1996 Quantification of soil carbon inputs under elevated CO_2: C_3 plants in a C_4 soil. Plant Soil 187, 345–350.

Johnson D W, Walker R F and Ball J T 1995 Lessons from lysimeters: Soil N release from soil disturbance compromises controlled environment study. Ecol. Appl. 5, 395–400.

Keeling C D, Bacastow R B. Carter A F, Piper S C, Whorf T P, Heimann M, Mook W G and Roeloffzen H 1989 A three dimensional model of atmospheric CO_2 transport based on observed winds: 1. Analysis of observational data. *In* Aspects of Climate Variability in the Pacific and the Western Americas. Ed. D H Peterson. pp 165–236. Geophysical Monograph 55, Washington (USA).

Körner C and Arnone J A 1992 Responses to elevated carbon dioxide in artificial tropical ecosystems. Science 257, 1672–1675.

Körner C, Diemer M, Schäppi B and Zimmermann L 1996 The responses of alpine vegetation to elevated CO_2. *In* Carbon Dioxide and Terrestrial Ecosystems. Eds G W Koch and H A Mooney. pp 177-0196. Academic Press, San Diego, USA.

Kuikman P J, Lekkerkerk L J A and Van Veen J A 1990 Carbon dynamics of a soil planted with wheat under elevated CO_2 concentration. *In* Advances in Soil Organic Matter Research: The Impact on Agriculture and the Environment. Ed. W S Wilson. pp 267–274. The Royal Society of Chemistry, Special Publication 90, Cambridge, U.K.

Lekkerkerk L J A, Van De Geijn S C and van Veen J A 1990 Effects of elevated atmospheric CO_2-levels on the carbon economy of a soil planted with wheat. *In* Soils and the Greenhouse Effect. Ed. A F Bouwman. pp 423–429. John Wiley & Sons, New York.

Liljeroth J A, Van Veen J A and Miller H J 1990 Assimilate translocation to the rhizosphere of two wheat lines and subsequent utilization by rhizosphere microorganisms at two nitrogen concentrations. Soil Biol. Biochem. 22, 1015–1021.

Lin G, Ehleringer J R, Rygiewicz P T, Johnson M G and Tingey D T 1998 Elevated CO_2 and temperature impacts on different components of soil CO_2 efflux in Douglas-fir Terracosms. Global Change Biol. (*In press*).

Luxmoore R J 1981 CO_2 and phytomass. BioScience 31, 626.

Masterson C L and Sherwood M T 1978 Some effects of increased atmospheric carbon dioxide on white clover (*Trifolium repens*) and pea (*Pisum sativum*). Plant Soil 49, 421–426.

Merckx R A, Dijkstra A, den Hartog A and van Veen J A 1987 Production of root-derived materials and associated microbial growth in soil at different nutrient levels. Biol. Fert. 5, 126–132.

Monz C A, Hunt H W, Reeves F B and Elliott E T 1994 The response of mycorrhizal colonization to elevated CO_2 and climate change

in *Pascopyrum smithii* and *Bouteloua gracilis*. Plant Soil 165, 75–80.

Mooney H A 1991 Biological response to climate change: An agenda for research. Ecol. Appl. 1, 112–117.

Nie D, Kirkham M B, Ballou L K, Lawlor D J and Kanemasu E T 1992 Changes in prairie vegetation under elevated carbon dioxide levels and two soil moisture regimes. J. Veg. Sci. 3, 673–678.

Norby R J 1987 Nodulation and nitrogenase activity in nitrogen-fixing woody plants stimulated by CO_2 enrichment of the atmosphere. Physiol. Plant. 71, 77–82.

Norby R J, O'Neill E G and Luxmoore R J 1986 Effects of CO_2 enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. Plant Physiol. 82, 83–89.

Norby R J, O'Neill E G, Hood W G and Luxmoore R J 1987 Carbon allocation, root exudation, and mycorrhizal colonization of *Pinus echinata* seedlings grown under CO_2 enrichment. Tree Physiol. 3, 203–210.

Norby R J, Gunderson C A, Wullschleger S D, O'Neill E G and McCacken M K 1992 Productivity and compensatory responses of yellow-poplar trees in elevated CO_2. Nature 357, 322–324.

O'Neill E G 1994 Responses of soil biota to elevated atmospheric carbon dioxide. Plant Soil 165, 55–65.

Peterjohn W T, Melillo J M, Bowles F P and Steudle P A 1993 Soil warming and trace gas fluxes: Experimental design and preliminary flux results. Oecologia 93, 18–24.

Phillips D A, Newell K D, Hassell S A and Felling C E 1976 The effect of CO_2 enrichment on root nodule development and symbiotic N_2 fixation in *Pisum sativum* L. Am. J. Bot. 63, 356–362.

Post W M, Pastor J, King A W and Emanuel W R 1992 Aspects of the interaction between vegetation and soil under global change. Water Air Soil Pollut. 64, 345–363.

Pregitzer K S, Zak D R, Curtis P S, Kubiske M E, Teeri J A and Vogel C S 1995 Atmospheric CO_2, soil nitrogen and turnover of fine roots. New Phytol. 129, 579–585.

Rouhier H, Billés G, Elkohen A, Mousseau M and Bottner P 1994 Effect of elevated CO_2 on carbon and nitrogen distribution within a tree (*Castanea sativa* Mill) soil system. Plant Soil 162, 281–292.

Rygiewicz P T, Johnson M G, Ganio L M, Tingey D T and Storm M J 1997 Lifetime and temporal occurrence of ectomycorrhizae on ponderosa pine (*Pinus ponderosa* Laws.) seedlings grown under varied atmospheric CO_2 and nitrogen levels. Plant Soil 189, 275–287.

Schimel D S 1995 Terrestrial ecosystems and the carbon cycle. Global Change Biol. 1, 77–91.

Thomas R B, Richter D D, Ye H, Heine P R and Strain B R 1991 Nitrogen dynamics and growth of seedlings of an N-fixing tree (*Gliricidia sepium*) exposed to elevated atmospheric carbon dioxide. Oecologia 8, 415–421.

Tissue D T, Megonigal J P and Thomas R B 1997 Nitrogenase activity and N_2 fixation are stimulated by elevated CO_2 in a tropical N_2-fixing tree. Oecologia 109, 28–33.

Van Veen J A, Liljeroth E, Lekkerkerk L J A and Van de Geijn S C 1991 Carbon fluxes in plant-soil systems at elevated atmospheric CO_2 levels. Ecol. Appl. 1, 175–181.

Whipps J M 1985 Effect of CO_2-concentration on growth, carbon distribution and loss of carbon from the roots of maize. J. Exp. Bot. 36, 644–651.

Zak D R, Pregitzer K S, Curtis P S, Teeri J A, Fogel R and Randlett D L 1993 Elevated atmospheric CO_2 and feedback between carbon and nitrogen cycles. Plant Soil 151, 105–117.

Section editor: S Recous