



Review of elevated atmospheric CO₂ effects on agro-ecosystems: residue decomposition processes and soil C storage

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Abstract

A series of studies using major crops (cotton [*Gossypium hirsutum* L.], wheat [*Triticum aestivum* L.], grain sorghum [*Sorghum bicolor* (L.) Moench.] and soybean [*Glycine max* (L.) Merr.]) were reviewed to examine the impact of elevated atmospheric CO₂ on crop residue decomposition within agro-ecosystems. Experiments evaluated utilized plant and soil material collected from CO₂ study sites using Free Air CO₂ Enrichment (FACE) and open top chambers (OTC). A incubation study of FACE residue revealed that CO₂-induced changes in cotton residue composition could alter decomposition processes, with a decrease in N mineralization observed with FACE, which was dependent on plant organ and soil series. Incubation studies utilizing plant material grown in OTC considered CO₂-induced changes in relation to quantity and quality of crop residue for two species, soybean and grain sorghum. As with cotton, N mineralization was reduced with elevated CO₂ in both species, however, difference in both quantity and quality of residue impacted patterns of C mineralization. Over the short-term (14 d), little difference was observed for CO₂ treatments in soybean, but C mineralization was reduced with elevated CO₂ in grain sorghum. For longer incubation periods (60 d), a significant reduction in CO₂-C mineralized per g of residue added was observed with the elevated atmospheric CO₂ treatment in both crop species. Results from incubation studies agreed with those from the OTC field observations for both measurements of short-term CO₂ efflux following spring tillage and the cumulative effect of elevated CO₂ (> 2 years) in this study. Observations from field and laboratory studies indicate that with elevated atmospheric CO₂, the rate of plant residue decomposition may be limited by N and the release of N from decomposing plant material may be slowed. This indicates that understanding N cycling as affected by elevated CO₂ is fundamental to understanding the potential for soil C storage on a global scale.

Abbreviations: FACE – Free Air CO₂ Enrichment; OTC – open top chambers

Introduction

The rise of CO₂ in the atmosphere is well documented (Keeling et al., 1989); what has not been documented are the sinks for this C, with an estimated unknown sink of 1.4×10^{15} g C yr⁻¹ arising from the global C

balance (Schimel et al., 1995). Soil plays a major role in the global accounting of C not only due to the large amount of C stored in soil, with estimates ranging from 1395 to 1636×10^{15} g (Ajtay et al., 1979; Post et al., 1992; Schlesinger, 1984), but also since soil contribution to the annual flux of CO₂ to the atmosphere is 10 times that contributed by fossil fuel burning (Post et al., 1990). One hypothesis that has been forwarded is

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that C is being stored in terrestrial ecosystems (Fisher et al., 1994; Tans et al., 1990) as a result of higher plant productivity induced by elevated CO₂. Carbon fixed within biomass ultimately enters the soil where it may reside for hundreds of years (Parton et al., 1986; Wallace et al., 1990), therefore, understanding changes in soil C due to elevated atmospheric CO₂ is essential to understanding global C cycling.

Agro-ecosystems are important in the global context since it is estimated that 1.3×10^{15} g of gross CO₂ is removed from the atmosphere by crops each year (Jackson, 1992). Furthermore, soil C storage in agro-ecosystems could be altered since they are very sensitive to management practices (e.g. conservation practices, tillage systems and cropping systems) (Kern and Johnson, 1993). It has been estimated that the 'pioneer agriculture effect in the USA' released some 60×10^{15} g C to the atmosphere from 1860 to 1890 (Wilson, 1978). This is 1.5 times the amount of C emitted by all industrial sources (mainly fossil fuel usage) prior to 1950. All these factors combined make the understanding of the C cycling in soil of agro-ecosystems important.

The ability of soil to store C in a future CO₂-enriched world, however, is a highly debated scientific question. Changes in plant morphology (Prior et al., 1995; Thomas and Harvey, 1983), physiology (Amthor, 1991; Amthor et al., 1994; Rogers and Dahlman, 1991; Rogers et al., 1994) and phytochemistry (Lekkerkerk et al., 1990; Liljeroth et al., 1994) as a result of increasing levels of atmospheric CO₂ will likely have dramatic impacts on plant-microbe interactions and, thus, on C cycling and the potential for C storage in soil. Schlesinger (1986, 1990) found little evidence for soil C storage, and Lamborg et al. (1984) have argued that increased soil microbial activity would prevent accumulation of soil organic C. Alternatively, Goudriaan and De Reiter (1983) proposed that increased soluble, easily decomposed C inputs (as a consequence of CO₂ enrichment) would accentuate substrate preferences among soil microbes. They further speculated that preference for easily decomposable substrates would retard the decomposition of recalcitrant plant debris and native soil organic matter. The end result would be an accumulation of soil organic matter. Experimental evidence put forth by Lekkerkerk et al. (1990) has supported the contentions of Goudriaan and De Reiter (1983) with wheat grown under CO₂-enriched conditions in a short-term growth chamber experiment.

Understanding how crop residues are changed in quantity and quality by growth under elevated atmospheric CO₂ are both key to understanding changes in soil C cycling. For example, the effect of elevated CO₂ on the amount of crop residues left in the field may depend on the differences of elevated CO₂ effect on the crop species utilized in agro-ecosystems. Because of the differences in how CO₂ is utilized in photosynthesis, crop species with C3 photosynthesis pathways have been shown to have a greater yield response compared to crop species with C4 photosynthesis pathways (Rogers et al., 1997). Also, changes in residue quality such as an increase in C:N ratios of plants with elevated CO₂ has led to the hypothesis that decomposition rates in an elevated CO₂ environment will be slower (Bazzaz, 1990) and will limit plant response to CO₂ enrichment and long-term C storage (Strain and Cure, 1985). The increase in C:N ratio with elevated CO₂ is well documented in agricultural plants (Cotrufo et al., 1998; Rogers et al., 1994). However, Lamborg et al. (1984) have argued that increased soil microbial activity resulting from greater biomass C inputs in an elevated CO₂ world could lead to increased soil organic matter decomposition (i.e. 'the priming effect') and, therefore, atmospheric CO₂ enrichment would not result in accumulation of soil organic C.

To address some of the above issues, several recently published studies have investigated different aspects of soil C cycling as affected by crop growth under elevated atmospheric CO₂ conditions. The objective of this study was to review the results of these separate investigations to determine the effect of elevated atmospheric CO₂ on residue decomposition processes on soil C storage in agro-ecosystems representing four major crop species: cotton, wheat, grain sorghum and soybean.

Materials and methods

Data presented in this publication were collected from a series of experiments conducted within field studies examining the impact of elevated atmospheric CO₂ in agro-ecosystems (i.e. cotton [*Gossypium hirsutum* L.], wheat [*Triticum aestivum* L.], grain sorghum [*Sorghum bicolor* (L.) Moench.] and soybean [*Glycine max* (L.) Merr.]). The field sites were located at Maricopa Agricultural Center for Resources and Extension of the University of Arizona at Maricopa, AZ, and the USDA-ARS National Soil Dynamics Laboratory at Auburn, AL. Presented here is a general description of

the materials and methods used in these studies; more detailed descriptions are provided in the manuscripts cited here.

Field studies

At Maricopa, experiments were conducted using a free-air CO₂ enrichment (FACE) system (Hendrey et al., 1993). Cotton and wheat were grown on a Trix clay loam [fine, loamy, mixed (calcareous), hyperthermic Typic Torrifluvents (USDA classification)] under two atmospheric CO₂ levels (370 μmol mol⁻¹=ambient and 550 μmol mol⁻¹=FACE) (Prior et al., 1997b). At Auburn, open top field chambers, 3-m in diameter and 2.4-m high, (Rogers et al., 1983) were used in an outdoor soil bin, 2-m deep, 7-m wide and 76-m long, uniformly filled with the surface soil of a Blanton loamy sand [loamy, siliceous, thermic Grossarenic Paleudult (USDA classification)] that had been continuously fallow for more than 25 years prior to study initiation. In this study, soybean and grain sorghum were grown under two CO₂ concentrations (≈375 and 705 μmol mol⁻¹ CO₂) (Torbert et al., 1996).

Chemical analysis

In general, the following methods were used for plant and soil sampling in all of the experiments. Soil samples were dried (60 °C) and ground to pass a 0.15 mm sieve and analyzed for total N (Fison NA1500 CN Analyzer; Fison Instruments Incorp., Beverly, MA). Soil organic C was determined with a LECO CR12 Carbon Determinator (LECO Corp., Augusta, GA; Chichester and Chaison, 1992). Total C and N contents of plant samples were determined using a Fison NA1500 CN Analyzer (Fison Instruments, Inc., Beverly, MA). Sieved soil samples (2 mm sieve) were used for soil inorganic N (NO₂-N + NO₃-N and NH₄-N) analyzed by extracting with 2 M KCl and measuring with standard colorimetric procedures on a Technicon Autoanalyzer (Technicon Industrial Corp., Tarrytown, NY).

Incubation procedures

Laboratory incubation studies were conducted to examine the impact of elevated atmospheric CO₂ on soil C and N cycling (Prior et al., 1997b; Wood et al., 1994). Also, the effect of elevated atmospheric CO₂ on plant matter decomposition was measured in incubation studies independent of the changes to soil (Henning et al., 1996; Torbert et al., 1995, 1998b).

The incubation studies were conducted using either a Falcon filter unit (Model no. 7102, Beckon Dickinson Labware, Franklin Lakes, NJ) technique (Nadelhoffer, 1990) or a Mason jar technique (Torbert et al., 1998b).

In both techniques, sieved soil samples (2 mm sieve) were weighed (25 g dry weight basis) and then deionized water was added to adjust soil water content (soil water content equivalent to -20 kPa at a bulk density of 1.3 Mg m⁻³). Containers were incubated in the dark at 25 °C for various lengths of time up to 60 d. C turnover was calculated by using potential C mineralization divided by total organic C of soil. To identify effects of the plant matter independent of soil, blanks were used in the incubation studies. Blanks consisted of using identical procedures on soil samples without plant additions.

Field measurements

Measurements in the field were also reported for the Auburn experimental field site for soil CO₂ flux (Prior et al., 1997a), surface residue decomposition via litter bag (Prior et al., 1996), nitrate leaching below the rooting zone (Torbert et al., 1996) and stable C isotope (δ¹³C) measurements of soil C storage (Torbert et al., 1997a).

Soil CO₂ efflux and temperature measurements were made with LI-COR 6200 gas exchange system equipped with a soil respiration chamber (Model 6000-09, LI-COR, Inc., Lincoln, NE) (Prior et al., 1997a). Over-winter decomposition of plant surface residue was measured through mass losses in litter bags (Prior et al., 1996); Nylon litter bags (15 × 20 cm with a 1 mm mesh) were filled with 10 g of either leaf or stem residue. Soil solution samplers (porous cup suction lysimeters # 1900L4, Soil Moisture Corp. Santa Barbara CA.) installed at the 90-cm soil depth were used to measure nitrate leaching.

Soil samples were collected at the end of the second growing season for δ¹³C measurements of total soil C and soil C fractions (MinC) (Torbert et al., 1997a). Soil samples were analyzed for soil carbon fractions using the procedures of Cambardella and Elliot (1992). Air, plant and soil samples were measured for δ¹³C content on a SIRA Series II isotope ratio mass spectrometer (VG ISOGAS, Middlewich, UK) after combustion in an elemental analyzer. Isotopic ratios of C, with δ¹³C defined as:

$$\delta^{13}\text{C} = \left[\frac{{}^{13}\text{C}/{}^{12}\text{C}_{\text{sample}} - {}^{13}\text{C}/{}^{12}\text{C}_{\text{standard}}}{{}^{13}\text{C}/{}^{12}\text{C}_{\text{standard}}} \right] \times 1000$$

Table 1. Chemical characteristics of cotton plant residue utilized in this study^a

	P	N	C	Cell content ^b	Cellulose	Hemicellulose	Lignin	Mineral	C:N ratio
	$\mu\text{g g}^{-1}$				g kg^{-1}				
Leaves									
Ambient	14.2 a	3.6 a	37.1 a	46.9 a	23.6 a	15.3 a	13.0 a	25.5 a	10.4 a
FACE ^c	12.8 b	3.0 b	36.7 b	53.1 b	21.2 a	13.6 a	11.2 a	25.6 a	12.2 b
Stems									
Ambient	4.4 a	1.0 b	42.5 a	22.6 a	41.7 a	13.1 a	22.6 a	9.7 a	44.2 a
FACE ^c	4.4 a	0.8 a	42.6 a	24.0 a	40.1 a	13.3 a	22.6 a	7.4 a	54.8 b
Roots									
Ambient	3.1 a	0.6 a	44.1 a	13.7 a	41.7 a	14.8 a	26.7 a	2.6 a	80.2 a
FACE ^c	2.5 b	0.5 b	44.1 a	18.5 a	44.6 a	15.0 a	24.7 b	2.3 a	84.1 a

^aValues represent means of four replicates. Values within a row followed by the same letter do not differ significantly (0.05 level).

^bCellular content includes compounds such as proteins, starch, sugars, organic acids and pectin.

^cFACE – free air CO₂ enrichment.

(with a standard of Pee Dee belemnite) were used as a natural tracer of atmospheric CO₂ into the soil system (Boutton, 1991).

The $\delta^{13}\text{C}$ content of root tissue was sufficiently different from the initial soil SOMC and MinC $\delta^{13}\text{C}$ content to allow tracking of new C originating from the crops into the soil. Isotopic mass balance methods (Balesdent et al., 1988; Leavitt et al., 1994) and the following equation were utilized:

$$\delta^{13}\text{C}_{\text{soil}} = f_{\text{input}}(\delta^{13}\text{C}_{\text{input}}) + f_{\text{soil original}}(\delta^{13}\text{C}_{\text{soil original}})$$

where $\delta^{13}\text{C}_{\text{soil}}$ is the $\delta^{13}\text{C}$ content of the soil C samples, $\delta^{13}\text{C}_{\text{input}}$ is the $\delta^{13}\text{C}$ content of new plant biomass input, $\delta^{13}\text{C}_{\text{soil original}}$ is the original $\delta^{13}\text{C}$ content of soil C measured initially, f_{input} is the fraction of soil C originating from the new crop production, and $f_{\text{soil original}}$ is the fraction of soil C originally in the soil before initiation of the study. The average $\delta^{13}\text{C}$ content from both years of root material from each plot was used for the new plant biomass input value.

Results and discussion

Incubation studies were conducted on soil samples collected from the FACE cotton experiment after three years of CO₂ exposure (Wood et al., 1994). In this study, it appeared that soil C and N cycling patterns were altered under the FACE compared to ambient CO₂. Measurements of increased soil CO₂-C mineralization and increased soil C turnover during this

soil incubation did not correspond well to the concentration of organic C found in the soil or to biomass production, suggesting that factors in addition to residue quantity (i.e. residue quality) contributed to the C cycling processes. Likewise, in a similar incubation study with wheat after two years of FACE (Prior et al., 1997b), difference in soil C and N cycling between CO₂ treatments occurred, but with somewhat different results noted between the interaction of FACE and the soil moisture conditions relative to cotton. In the case of cotton, decreased C turnover was observed under conditions where moisture was not limiting, whereas with wheat, no difference was observed for potential C turnover for different soil moisture conditions. In both the cotton and wheat studies, data indicated that increased C storage could result under elevated CO₂ conditions, but the potential changes in long-term C storage from alterations in residue quality and quantity were not clear, since evidence to support several contradictory hypotheses were found in these data.

The results of these FACE incubation studies established the importance of examining the impact of residue decomposition as affected by elevated CO₂ independent of the cumulative impact to the soil. Thus, experiments were undertaken to examine the soil decomposition processes as it was affected by additions of plant material, grown under elevated CO₂ conditions, to soil that had no previous history of elevated CO₂ conditions (Henning et al., 1996; Torbert et al., 1995, 1998b).

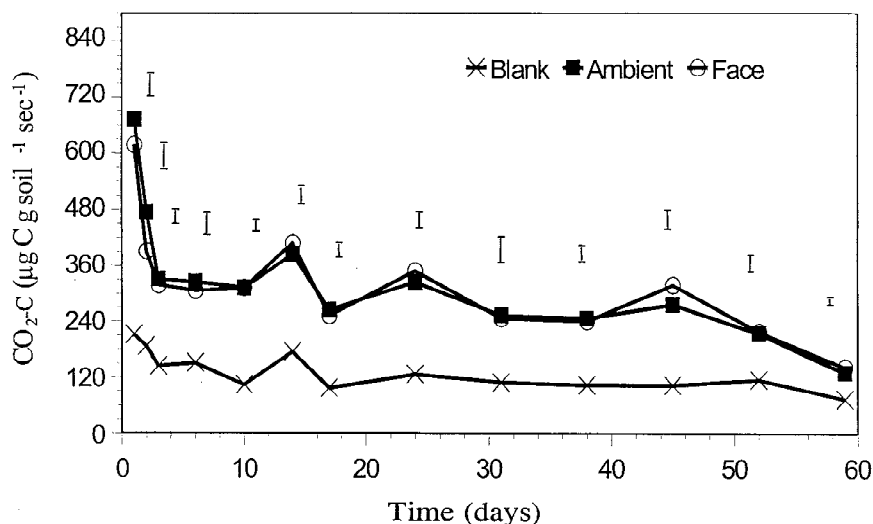


Figure 1. Soil respiration rates during incubation of free air CO₂ enrichment (FACE) and ambient cotton plant residue amended soils, averaged across soil series and plant residue type. Treatment LSD bars are for $\alpha=0.05$ level.

Cotton material grown under the FACE experimental conditions was utilized in an incubation study to examine the impact of elevated CO₂ on plant decomposition in soil (Torbert et al., 1995). Individual plant parts (leaf, stem and root) (Table 1) were examined separately by adding the material to three different soil series (sandy loam, silt loam and clay loam) that had not been previously exposed to elevated CO₂ conditions. This work indicated that, contrary to the effect commonly hypothesized, decomposition rates of crop residue grown under elevated CO₂ though having higher C:N ratios (Cotrufo et al., 1998; Rogers et al., 1994) may not decompose at slower rates (Figure 1). Results indicate that increased levels of easily decomposable components (Table 1) compensated for higher C:N ratios resulting in similar decomposition rates among residues from different CO₂ treatments. Although soil C mineralization rates of residue amended soils were similar for ambient compared to FACE, increased storage of C in soil could still occur under elevated atmospheric CO₂ conditions because of increased biomass production under CO₂-enriched conditions.

While soil C mineralization showed little effect due to amendments to soil with residues grown under FACE, the net N immobilization/mineralization rates of amended soils were impacted. With all the plant parts, the release of inorganic N into the soil solution was slower with FACE compared to the ambient CO₂ resulting in an increase in the net N immobilization with FACE (Figure 2). As noted by Strain and

Cure (1985), plant response to CO₂ fertilization may be limited by N immobilization in an elevated CO₂ world. These data indicate that changes to the plant material produced under elevated CO₂ conditions may impact the availability of N in the plant/soil system. Likewise, results from this study also indicated that differences in soil series could exert an important control on decomposition rates of plant residue produced under elevated CO₂ (Figure 3). The rate of decomposition seemed to be controlled by the ability of the soil to supply nutrients (especially N), as indicated by change in the relative order of C emission when corrected for C content of the soil. This suggests that changes in nutrient cycling due to soil series may be an important factor controlling the impact of elevated CO₂ on soil C storage.

Additional studies were conducted utilizing grain sorghum and soybean material grown in CO₂-enriched conditions using OTC at the Auburn experiment (Henning et al., 1996). Individual plant parts were examined separately by adding the material to soil which had not been previously exposed to elevated CO₂ conditions. In this study, while differences were observed between plant parts and species, no significant difference was observed for C mineralization due to elevated CO₂ conditions taken at physiological maturity (Table 2). This study, however, did not consider changes due to the potential 'priming effect' as defined by Lamborg et al. (1984).

To address this point further, a study was undertaken to examine the impact of elevated CO₂ on the

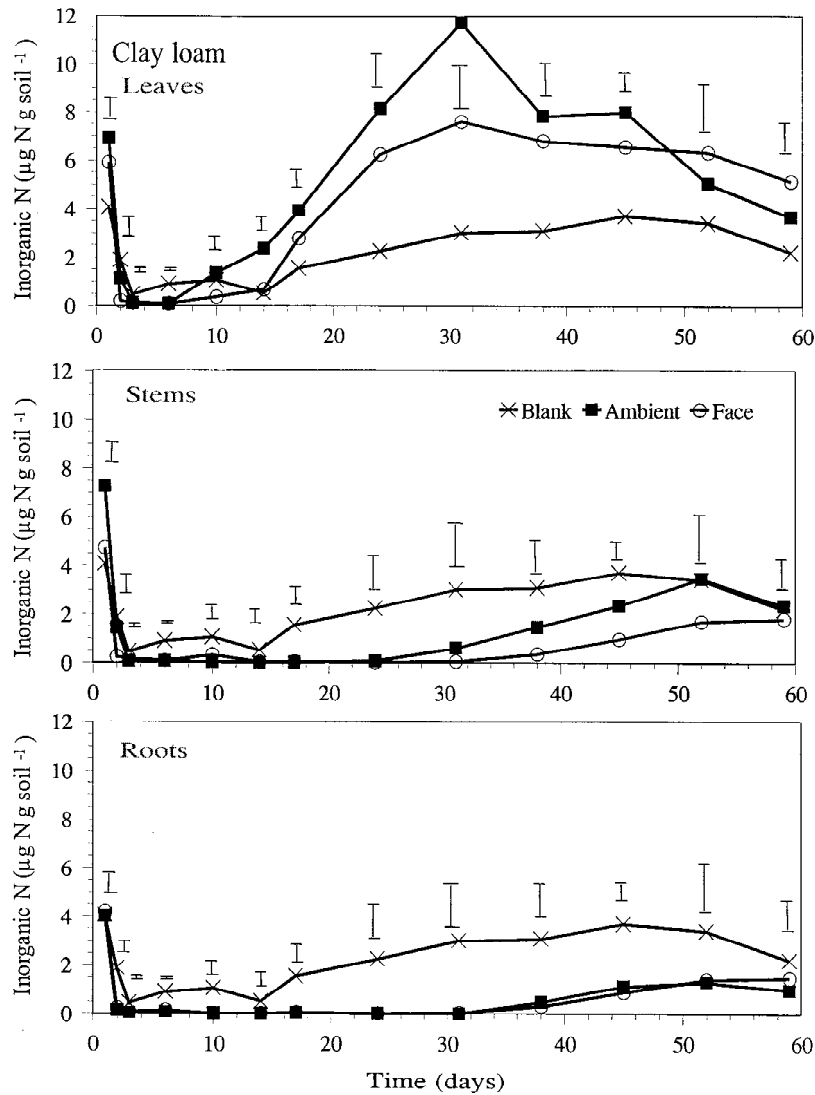


Figure 2. Inorganic N concentration in leachate during a clay loam soil incubation following additions of leaf, stem, root or no (blank) cotton plant residue from FACE and ambient growing conditions. Treatment LSD bars are for $\alpha=0.05$ level.

decomposition of crop residues: grain sorghum and soybean (Torbert et al., 1998b). But in this case, crop residues from the Auburn OTC experiment were utilized to compare not only the difference between ambient and elevated CO_2 residue (i.e. tissue composition), but also the difference in plant residue additions at rates proportional to the amount produced in the field experiment (Table 3). In addition, because differences were observed between N mineralization/immobilization (as well as trends for the elevated CO_2 effect) between the different plant parts when studied separately (Henning et al., 1996), this study utilized the crop residue (a mixture of senesced plant

parts) sampled from each plot at final harvest. During the first 14 d of the incubation, an interaction was observed between crop species and CO_2 treatments for C mineralization (Table 4). With grain sorghum, C mineralization was either not changed (day 3) or reduced (day 14) with residue from elevated CO_2 added at uniform and at proportional weights compared to the respective ambient CO_2 treatment. In the case of the N rich soybean residue, only the elevated CO_2 at the proportionally higher weight treatment resulted in higher C mineralization compared to ambient CO_2 (Table 4). After 14 d, C mineralization with the ambient CO_2 treatment was higher than that of elevated CO_2 (same

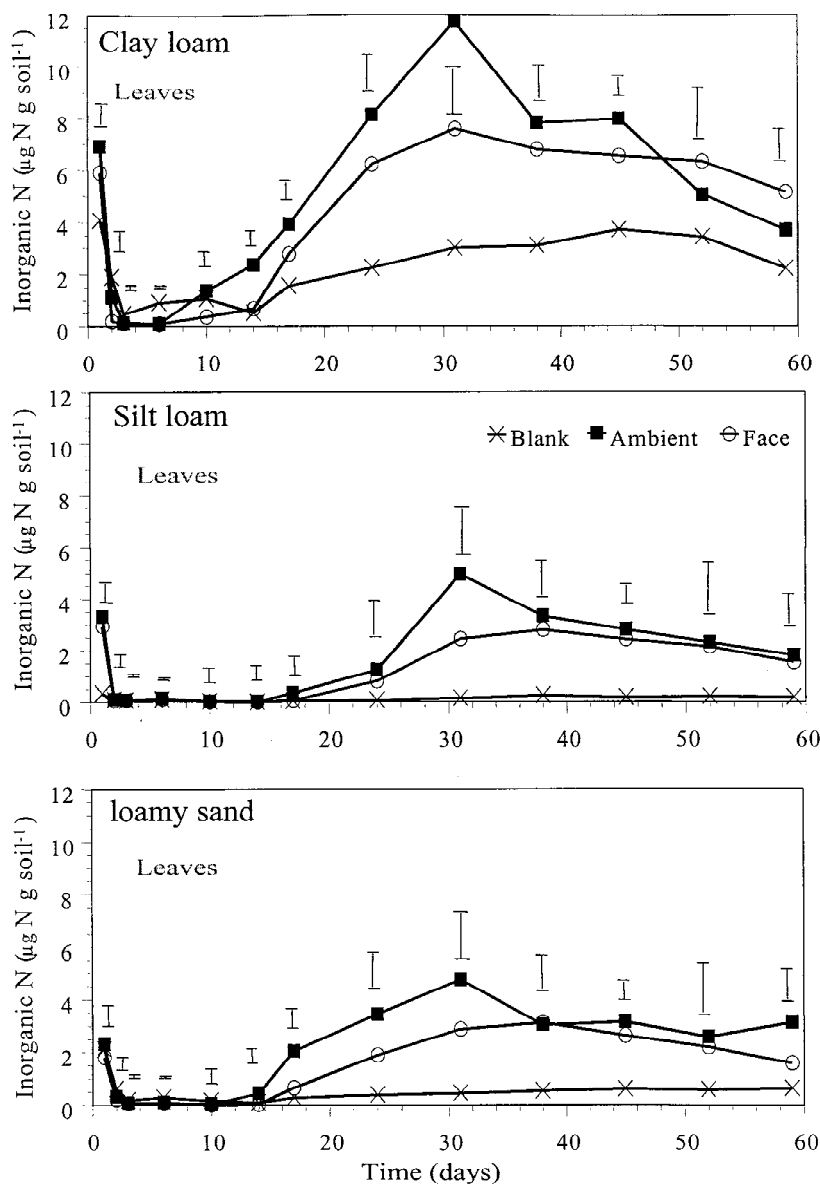


Figure 3. Inorganic N concentration in leachate during a clay loam, silt loam and loamy sand soil incubation following additions of cotton leaf plant residue from FACE and ambient growing conditions. Treatment LSD bars are for $\alpha=0.05$ level.

weight) in both plant species (Table 5). This indicated that decreases in residue quality (due to elevated CO_2 during plant growth) may slow residue decomposition. However, the effect of residue quality (due to elevated CO_2) on C mineralization was reduced when the difference between biomass production was included in the comparison (Table 5). But even at the end of 60 d, under ideal conditions for microbial decomposition, there was no significant difference (with means being lower) in the level of C mineralization with the

higher levels of biomass additions in the elevated CO_2 treatment.

The differences observed between the elevated CO_2 and the ambient CO_2 at proportionally higher weight treatment indicated that a priming effect may occur in soil due to the increase in biomass additions, as predicted by Lamborg et al. (1984). But, the impact of residue quality (due to CO_2 treatment) may have an overriding impact on the level of residue decomposition. Furthermore, residue decomposition

Table 2. Carbon turnover, relative N mineralization, C:N mineralized and cumulative C and N mineralization during laboratory incubation from soil amended with plant residues grown under ambient or elevated atmospheric CO₂

Tissue	Treatment	C	Relative N	C:N	Cumulative	Cumulative N
		Turnover	mineralized	mineralized	C mineralized	mineralized
		$\mu\text{g g}^{-1} (\mu\text{g g}^{-1})^{-1}$			$\mu\text{g g}^{-1}$	
Soybean						
Leaf	Elevated	0.157	0.047	21.6	734	33.5
	Ambient	0.101	0.041	16.0	473	29.6
	Mean	0.129	0.044	18.8	604	31.6
Stem	Elevated	0.177	0.026	50.6	912	18.2
	Ambient	0.190	0.026	54.4	977	18.6
	Mean	0.184	0.026	52.5	944	18.4
Sorghum						
Leaf	Elevated	0.102	0.023	29.3	473	15.9
	Ambient	0.108	0.025	29.7	500	16.9
	Mean	0.105	0.024	29.5	486	16.4
Stem	Elevated	0.144	0.016	66.2	728	11.1
	Ambient	0.099	0.013	57.2	508	8.8
	Mean	0.122	0.015	61.7	618	10.0
Control	–	0.082	0.028	18.5	337	18.6
Analyses of variance ($P > F$)						
Soybean						
Leaf	E vs. A ^{ab}	0.275	0.463	0.167	0.275	0.478
	E vs. C ^{ac}	0.040	<0.001	0.748	0.031	<0.001
	A vs. C ^c	0.572	<0.001	0.790	0.432	<0.001
Stem	E vs. A	0.816	0.832	0.818	0.815	0.794
	E vs. C	0.012	0.531	0.004	0.004	0.836
	A vs. C	0.006	0.624	0.002	0.002	0.975
Sorghum						
Leaf	E vs. A	0.793	0.409	0.944	0.790	0.407
	E vs. C	0.561	0.165	0.268	0.431	0.215
	A vs. C	0.454	0.348	0.251	0.347	0.431
Stem	E vs. A	0.089	0.221	0.272	0.075	0.228
	E vs. C	0.085	0.002	<0.001	0.030	0.003
	A vs. C	0.611	<0.001	0.001	0.325	0.003

^aE, elevated CO₂; A, ambient CO₂; C, control (no residue).

^bE vs. A comparisons were made using a split plot model.

^cE vs. C, and A vs. C comparisons made using a model with a 2 × 2 × 2 factorial design.

Table 3. Total dry weight and C:N ratio of crop residue grown under ambient or elevated atmospheric CO₂ concentrations^a

Crop	Total Dry Weight			C:N		
	Ambient	Elevated	Contrast	Ambient	Elevated	Contrast
—Mg ha ⁻¹ —						
Grain Sorghum	515	666	<0.01	74.9	87.4	0.01
Soybean	290	517	<0.01	27.3	28.5	0.71

^aValues represent means of three replicates.

with the elevated CO₂ treatment was the same or lower than that observed with the ambient CO₂ after 60 d, regardless of the increased biomass input.

The impact of residue quality on C cycling in soil was also demonstrated from the analysis of CO₂-C evolved per g of residue added to the soil (Table 6). A significant reduction in CO₂-C mineralized per g of residue added was observed with the elevated CO₂ treatment compared to the ambient treatment at all but the first sampling period. When ambient residue was compared to the elevated CO₂ residue added at proportional levels, there was a significant reduction at all sampling dates. While there was an increase in the level of CO₂-C evolved when more residue was added, it was small compared to the increase in residue added.

Data from this study also indicated that low soil N availability limited microbial decomposition in both grain sorghum and soybean, with net N immobilization conditions persisting throughout most of the 60 d incubation. Also, as was observed with the cotton plant decomposition, the release of inorganic N into the soil solution with soybean was slower in the elevated CO₂ compared to the ambient CO₂ treatment. The limitations on inorganic N meant that, in general, N availability was imposing an important controlling effect on the residue decomposition processes in soil, but the level of this control was plant species dependent (Torbert et al., 1998b).

These laboratory incubation studies indicate that the impact of elevated atmospheric CO₂ concentration on N cycling in soil may be as important as the impact on plant residue quantity in determining C cycling in soil. Therefore, the potential effect of elevated atmospheric CO₂ concentration on C storage in agro-ecosystems will be dependent on the crop species grown. Nitrogen cycling within the plant/soil system will likely be the controlling factor for C storage in these systems.

Field studies

Results from the laboratory incubation studies can be utilized to explain field observation for different aspects of soil C and N cycling as impacted by elevated atmospheric CO₂. Several efforts have been undertaken to examine the impact of elevated CO₂ on grain sorghum and soybean within the Auburn OTC field study. The interpretations of these field observations are more discernable when examined as a whole, with

the time differential considered and compared with the results from the incubation studies.

Studies at the Auburn location examined the impact of spring tillage on the short-term CO₂ efflux from the field plots prior to planting (Prior et al., 1997a). The results from these CO₂ efflux measurements were consistent with the measured CO₂ evolution from the crop residue decomposition in soil (Table 5). The CO₂ efflux from the field plots increased in the elevated CO₂ plots that had been previously cropped with soybean but decreased from the elevated CO₂ plots previously cropped with grain sorghum compared to the ambient plots. In this study, CO₂ efflux measured over an 8 d period was 1.01 and 1.22 mol m⁻² from soybean plots and 0.92 and 0.88 mol m⁻² from grain sorghum plots for both ambient and elevated atmospheric CO₂ concentrations, respectively (Prior et al., 1997a).

The results from the CO₂ flux measurements in the field corresponded to the results observed with the first 14 d of the grain sorghum and soybean incubation study (Table 5). Despite higher biomass inputs for grain sorghum with elevated CO₂ in both field and incubation studies, there was no effect on CO₂ efflux rates. However, the CO₂ induced increase in biomass production in combination with the much lower C:N ratio of soybean tissue compared to sorghum tissue (Table 3) resulted in greater N availability to microbes and led to higher CO₂ flux in both field and incubation studies.

Intermediate length studies were undertaken to examine the impact of elevated CO₂ on plant decomposition processes over the winter fallow period using a litter bag technique (Prior et al., 1996). Measurement of mass losses from leaves and stems of grain sorghum and soybean indicated that there was a species effect which varied based on tissue type for the percent residue biomass recovery. While there was a significant increase in percent ground cover measured under elevated CO₂-enriched conditions, there was no significant effect on percent biomass recovery due to elevated CO₂ in the litter bags (Figure 4). The decomposition of soybean leaf tissue proceed more rapidly compared to the grain sorghum, as would be expected with a lower C:N ratio, however, the opposite pattern was observed with stem tissue. This was consistent with the finding from the two incubations studies using individual plant parts (Figure 1 and Table 2) which found differences between the individual plant parts, but no elevated CO₂ effect. Even though CO₂ concentration did not affect percent biomass recov-

Table 4. The effect of plant species and atmospheric CO₂ concentration during plant growth on cumulative soil carbon mineralization on days 3 and 14 of the incubation^a

Time (days)	Grain Sorghum			Soybean			Blank
	Ambient	Elevated	Elevated-PRO	Ambient	Elevated	Elevated-PRO	
	—μg CO ₂ -C g ⁻¹ soil—						
0–3	169	159	171	166	176	220	134
0–14	464	343	390	482	443	580	147
Contrast		0–3 day	0–14 day				
Soybean vs. Sorghum		0.132	0.013				
Amb. vs. Elv. (sorghum)		NS	0.039				
Amb. vs. Elv.-PRO (sorghum)		NS	0.175				
Elv. vs. Elv.-PRO (sorghum)		NS	0.1421				
Amb. vs. Elv. (soybean)		NS	NS				
Amb. vs. Elv.-PRO (soybean)		0.028	0.080				
Elv. vs. Elv.-PRO (soybean)		0.021	0.001				

^a Values represent means of three replicates.

Table 5. The effect of atmospheric CO₂ concentration during plant growth on incubated soil cumulative carbon mineralization^a

Time (days)	0–3	0–14	0–30	0–60
	—μg CO ₂ -C g ⁻¹ soil—			
Ambient	168	473	640	708
Elevated	167	393	505	568
Elevated-PRO	191	485	555	662
Blank	134	147	156	255
Contrast				
Amb. vs. Elv.	NS	0.052	0.007	0.006
Amb. vs. Elv.-PRO	0.071	NS	0.044	NS
Elv. vs. Elv.-PRO	0.0918	0.006	NS	NS

^a Values represent means of three replicates.

ery, greater production under elevated CO₂ resulted in more biomass remaining after the over-winter fallow period.

Studies of soil C storage after the cumulative effect of 2 years of elevated CO₂ conditions using δ¹³C techniques were also conducted (Torbert et al., 1997a). Results from this study also agree with the findings of the incubation studies and help explain the observed results from cumulative effect of elevated atmospheric CO₂ conditions in this system.

With grain sorghum, MinC and the calculated new C in MinC suggested increased soil C storage (Tables 7 and 8). Since most of the soil C was found in this C pool, this would indicate that increased soil storage of C may occur over the long-term. With the grain

sorghum residue in the incubation study, there was no evidence from observations of C mineralization of a priming effect from the increased biomass addition due to elevated CO₂ (Table 4). Likewise, after 2 years of elevated CO₂ in the field, grain sorghum resulted in more new C with elevated CO₂ for both total soil C and MinC (Tables 7 and 8).

With soybean, the calculated new C in elevated CO₂ was decreased, compared to ambient CO₂ in both total soil C and MinC (Tables 7 and 8). This indicated a priming effect with soybean in elevated CO₂ treatment, as was observed with the initial levels of CO₂ evolution with soybean residue in the incubation study (Table 4). However, elevated CO₂ had no significant effect on total soil C in soybeans, with means being higher with the elevated CO₂ treatment. Thus, the increase in new C decomposition with elevated CO₂ was apparently accompanied by a reduction

Table 6. The effect of atmospheric CO₂ concentration during plant growth on the cumulative mg of CO₂ evolved per g of residue added^a

Time (days)	0–3	0–14	0–30	0–60
	—μg CO ₂ -C g ⁻¹ soil—			
Ambient	138 a	389 a	526 a	581 a
Elevated	137 a	322 b	413 b	428 b
Elevated-PRO	105 b	257 c	300 c	355 b

^a Values represent means of three replicates. Values within a column followed by the same letter do not differ significantly (0.10 level).

Table 7. The effect of plant species and atmospheric CO₂ on total soil organic carbon content and soil new carbon content (isotopically determined)^a

Crop	Total			New		
	Ambient	Elevated	Mean	Ambient	Elevated	Mean
	g m ⁻²					
Grain Sorghum	1224	1193	1208 a	28.8	161.9	67.9 a
Soybean	1172	1204	1208 a	291.4	120.0	221.8 b
Mean	1198 a	1198 a		160.1 a	140.9 b	
Contrast						
A vs. E sorghum		NS			0.001	
A vs. E soybean		NS			0.003	

^aValues represent means of three replicates. Values within a row or within a column followed by the same letter do not differ significantly (0.10 level).

Table 8. The effect of plant species and atmospheric CO₂ on total soil mineral associated organic matter carbon content and soil new soil mineral associated organic matter carbon content (isotopically determined)^a

Crop	Total			New		
	Ambient	Elevated	Mean	Ambient	Elevated	Mean
	g m ⁻²					
Grain Sorghum	935	962	950 a	26.3	65.8	43.1 a
Soybean	873	948	922 b	70.7	58.8	70.7 a
Mean	904 a	955 b		48.5 a	62.3 a	
Contrast						
A vs. E sorghum		0.03			NS	
A vs. E soybean		NS			0.07	

^aValues represent means of three replicates. Values within a row or within a column followed by the same letter do not differ significantly (0.10 level).

in original soil organic matter decomposition. This was consistent with the incubation study of soybean residue decomposition which indicated that while the initial level of CO₂ evolution was greater for soybean, the total cumulative level of CO₂ evolution was not greatly impacted due to elevated atmospheric CO₂ concentration (Table 5). The observed levels of soil C with soybeans is consistent with the hypotheses of Goudriaan and De Ruiter (1983) which proposed that increased soluble, easily decomposed C inputs as a consequence of higher atmospheric CO₂ could accentuate the substrate preferences of soil microbes, and a preference for easily decomposable substrates would retard the decomposition of plant debris and native soil organic matter. This hypothesis is also consistent with data reported by Lekkerkerk et al. (1990) using ¹⁴C techniques, who found that the input of easily decomposable root-derived material in the soil of wheat plants was increased but, due to microbial preference

for these materials, turnover of more resistant soil organic matter was reduced under elevated CO₂.

However, this effect of microbial preference was only observed with soybean and not with grain sorghum. The differences observed between species (soybean and grain sorghum) for plant decomposition mechanisms could likely be driven by N availability in the residues of the two species. Green et al. (1995) reported that additions of NO₃ following corn production promoted corn residue decomposition but suppressed C mineralization from native soil organic matter. Difference in N availability (as was observed in the incubation studies) between the two plant species could result in the same type of preferential decomposition observed in the corn field study.

An investigation was also conducted to monitor the level of NO₃ movement below the rooting zone in both grain sorghum and soybean in the Auburn study (Torbert et al., 1996). Results indicate that both crop species and atmospheric CO₂ concentration will affect

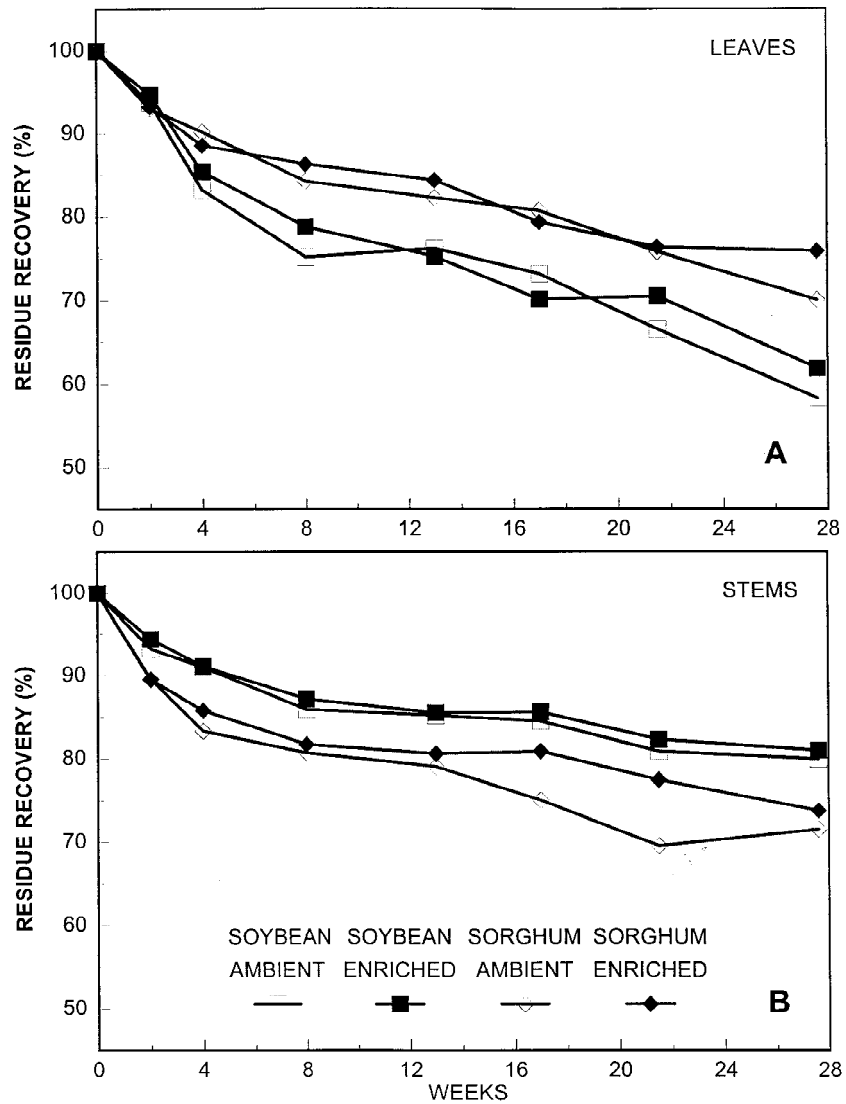


Figure 4. Recovery (%) of ambient and elevated CO_2 grown soybean and grain sorghum leaf (A) and stem (B) residue during an over winter fallow period. Values represent means of three replicates, differences between CO_2 were non significant at the $\alpha=0.05$ level.

$\text{NO}_3\text{-N}$ levels moving to groundwater (Figures 5 and 6). The $\text{NO}_3\text{-N}$ concentrations below the rooting zone of soybean were generally higher compared to grain sorghum, most likely the result of higher N input into the soil system due to soybean symbiotic N_2 fixation and the lower C:N ratio of the soybean plant residue compared to grain sorghum. The observed reduction in $\text{NO}_3\text{-N}$ concentrations below the root zone under CO_2 -enriched conditions during the growing season could have been caused by an increase in root proliferation with elevated CO_2 (Prior et al., 1994), resulting in increased N interception for plant growth. During

the winter fallow period, reduction $\text{NO}_3\text{-N}$ concentrations under CO_2 -enriched conditions could be due to either a reduction in plant biomass decomposition or by a reduction in N released from decomposing plant biomass produced under elevated atmospheric CO_2 conditions. However, the observations of both the grain sorghum and the soybean correspond to the responses of the inorganic N in soil solution observed in the incubation studies, indicating that changes in the N release from the plant material was responsible for most of the observed effect. In this case, the reduction in N released may not only impact residue decompos-

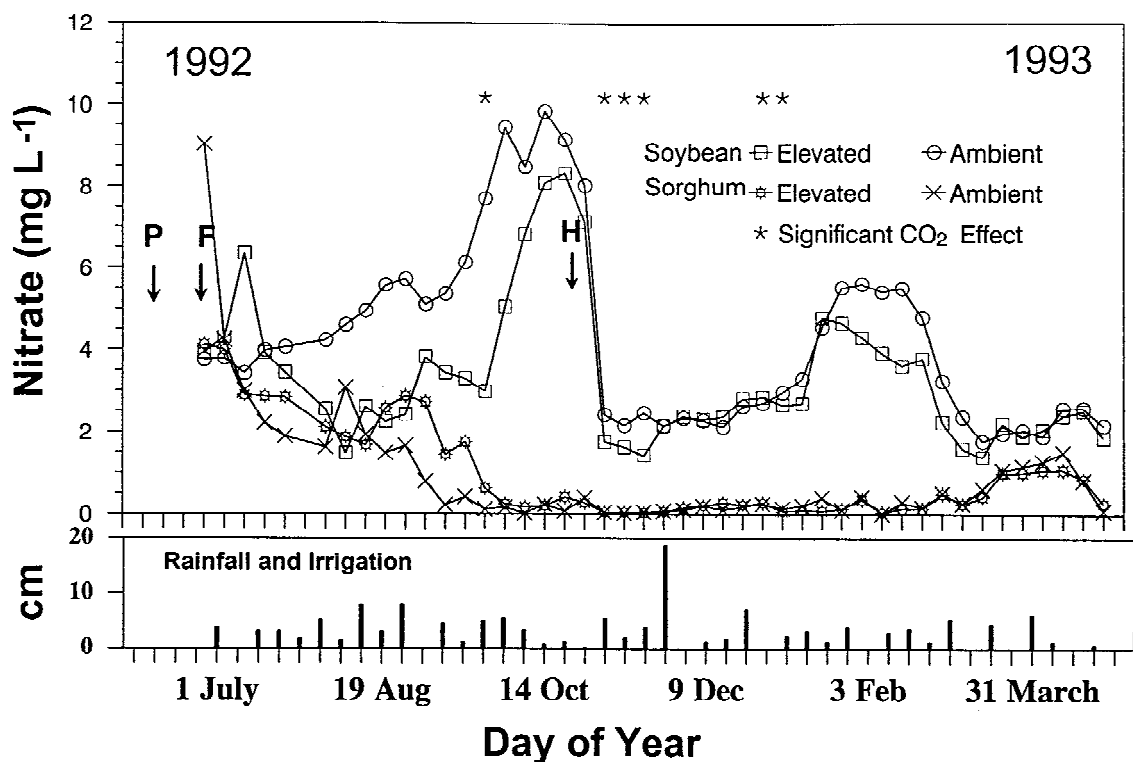


Figure 5. Soil solution $\text{NO}_3\text{-N}$ sampled from a 90-cm depth for grain sorghum and soybean plants grown under ambient or elevated atmospheric CO_2 concentrations from 1 July 1992 to 5 May 1993. Means are for three replications and an asterisk denotes dates with significant CO_2 effects at the $\alpha=0.1$ level. Planting date (P), fertilizer application date (F) and final harvest date (H) are noted.

ition processes, but since elevated atmospheric CO_2 concentrations reduced the $\text{NO}_3\text{-N}$ levels leaching below the rooting zone, a reduction in the degradation of groundwater quality beneath agro-ecosystems could be expected.

The potential impact of elevated CO_2 on soils in agro-ecosystems may be important for the future management and productivity of these systems. The implications of the studies reviewed here (especially differences observed between short-term and long-term observations) demonstrate the need for long-term field studies to fully understand the potential changes to soil in agro-ecosystems. For example, small improvements in soil organic C can have important positive influences on soil physical properties such as soil hydraulic conductivity, soil bulk density, soil porosity, soil aggregate stability, soil water retention and rainfall infiltration. These positive effects to the soil physical conditions could also lead to a positive feedback to crop productivity. Likewise, increased residue production (as measured by Prior et al., 1996) could lead to reduced soil erosional losses, prevent surface

sealing and reduce evaporative water losses from the soil surface due to the mulching effect, which could also have a positive effects over the long-term for the productivity of agro-ecosystems. On the other hand, the direct effect of elevated CO_2 on plant productivity may result in an increase in the competitiveness of some weed species in agro-ecosystems. Also, increased residue levels could lead to increased weed and disease pressure on crop production. These potential changes could have important implications for the productivity and future management decisions of these systems for such things as fertilizer and weed control management.

Long-term studies are also needed that include the potential impact of management decision, such as the cropping sequence and the tillage operations utilized. Agro-ecosystems are very dynamic in time, with choices of crop species and tillage operations being made on at least an annual basis. The choice of crop sequence and the type and amount of soil tillage utilized will have a great impact on the amount of soil organic C found in soil (Potter et al., 1997;

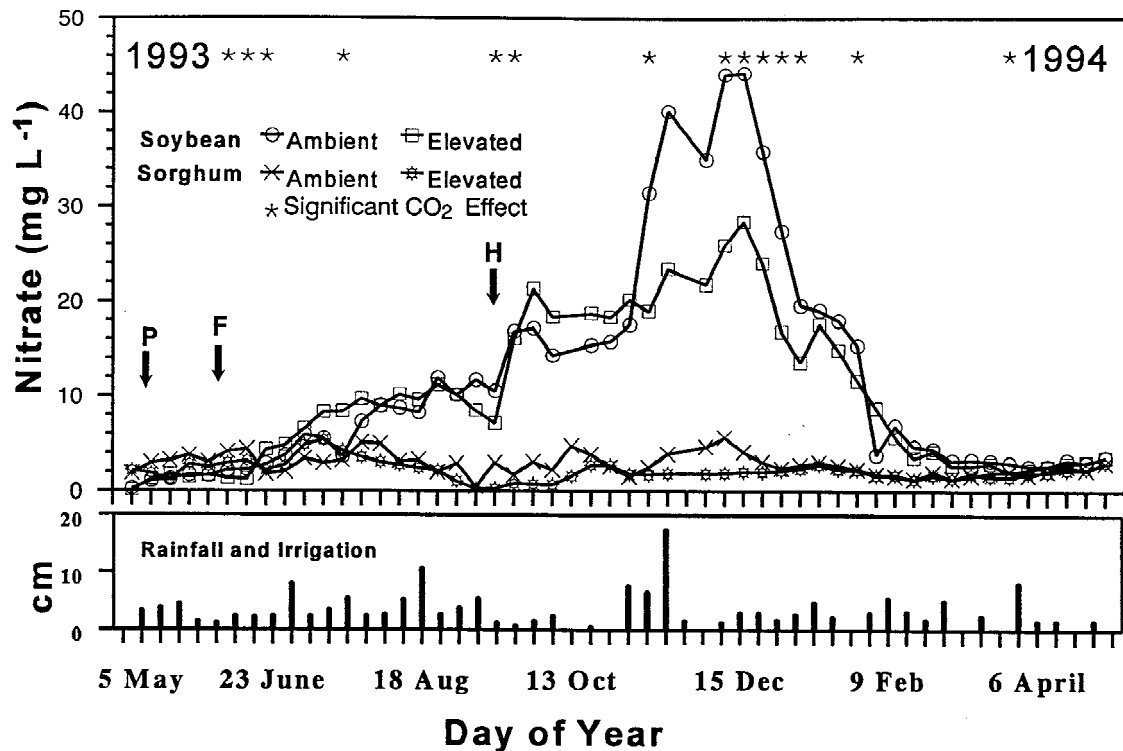


Figure 6. Soil solution $\text{NO}_3\text{-N}$ sampled from a 90-cm depth for grain sorghum and soybean plants grown under ambient or elevated atmospheric CO_2 concentrations from 5 May 1993 to 28 April 1994. Means are for three replications and an asterisk denotes dates with significant CO_2 effects at the $\alpha=0.1$ level. Planting date (P), fertilizer application date (F) and final harvest date (H) are noted.

Reicosky et al., 1997; Torbert et al., 1997b, 1998a). The interaction between elevated atmospheric CO_2 and crop production management can only be analyzed with long-term studies in the field and the use of process driven models to explore different agro-ecosystem management scenarios. Understanding this interaction will be essential for the assessment of the potential C sequestration in agro-ecosystem soils.

References

- Ajtay G L, Ketner P and Duvigneaud P 1979 Terrestrial primary production and phytomass. *In* The Global Carbon Cycle. Eds B Bolin, ET Degens, S Kempe and P Ketner. pp 129–181. John Wiley & Sons, New York.
- Amthor J S 1991 Respiration in a future, higher- CO_2 world. *Plant Cell Envir.* 14, 13–20.
- Amthor J S, Mitchell R J, Runion G B, Rogers H H, Prior S A and Wood C W 1994 Energy content and construction costs of plants grown in elevated CO_2 . *New Phytol.* 128, 443–450.
- Balesdent J, Wagner G H and Mariotti A 1988 Soil organic matter turnover in long-term field experiments as revealed by carbon-13 natural abundance. *Soil Sci. Soc. Am. J.* 52, 118–124.
- Bazzaz F A 1990 The response of natural ecosystems to the rising global CO_2 levels. *Annu. Rev. Ecol. Syst.* 21, 167–196.
- Boutton T W 1991 Stable carbon isotope ratios of natural materials: I. sample preparation and mass spectrometric analysis. *In* Carbon Isotope Techniques. Eds DC Coleman and B Fry. Academic Press, Inc. San Diego, California.
- Cambardella C A and Elliott E T 1992 Particulate soil organic-matter changes across a grassland cultivation sequence. *Soil Sci. Soc. of Am. J.* 56, 777–783.
- Chichester F W and Chaison R F Jr. 1992 Analysis of carbon in calcareous soils using a two temperature dry combustion infrared instrumental procedure. *Soil Sci.* 153, 237–241.
- Cotrufo M F, Ineson P and Scott A 1998 Elevated CO_2 reduces the nitrogen concentration of plant tissues. *Global Change Biol.* 4, 43–54.
- Fisher M J, Rao R M, Ayarza M A, Lascano C E, Sanz J I, Thomas R J and Vera R R 1994 Carbon storage by introduced deep-rooted grasses in the South American savannas. *Nature* 371, 236–238.
- Goudriaan J and De Ruiter H E 1983 Plant growth in response to CO_2 enrichment at two levels of nitrogen and phosphorus supply. 1. Dry matter, leaf area and development. *Neth. J. Agric. Sci.* 31, 157–169.
- Green C J, Blackmer A M, Horton R 1995 Nitrogen effects on conservation of carbon during corn residue decomposition in soil. *Soil Sci. Soc. Am. J.* 59, 453–459.
- Hendrey G R, Lewin K F and Nagy J 1993 Free-air carbon dioxide enrichment: development, process, results. *Vegetatio* 104/105, 17–31.
- Henning F P, Wood C W, Rogers H H, Runion G B and Prior S A 1996 Composition and decomposition of soybean and sorghum

- tissue grown under elevated atmospheric carbon dioxide. *J. Environ. Qual.* 25, 822–827.
- Jackson R B IV 1992 On estimating agriculture's net contribution to atmospheric carbon. *Wat. Air Soil Poll.* 64, 121–137.
- 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 CO₂ transport based on observed winds: observational data and preliminary analysis. *In Aspects of Climate Variability in the Pacific and the Western Americas.* Ed. DH Peterson. pp 165–235. Geophysical Monograph.
- Kern J S and Johnson M G 1993 Conservation tillage impacts on national soil and atmospheric carbon levels. *Soil Sci. Soc. Am. J.* 57, 200–210.
- Lamborg M R, Hardy W F and Paul E A 1984 Microbial effects. *In CO₂ and Plants: The Response of Plants to Rising Levels of Atmospheric CO₂.* Ed. ER Lemon. pp 131–176. Am. Assoc. Adv. Sci. Selected Symp., Washington, D.C.
- Leavitt S W, Paul E A, Kimball B A, Hendrey G R, Mauney J R, Rauschkolb R, Rogers H H, Lewin K F, Nagy J, Pinter P J Jr. and Johnson H B 1994 Carbon isotope dynamics of free-air CO₂-enriched cotton and soils. *Agric. For. Meteorol.* 70, 87–101.
- Lekkerkerk L J A, Van de Geijn S C and Van Veen J A 1990 Effects of elevated atmospheric CO₂ 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, New York.
- Liljeroth E, Kuikman P and Van Veen J A 1994 Carbon translocation to the rhizosphere of maize and wheat and influence on turnover of the native soil organic matter at different soil N levels. *Plant Soil* 161, 233–240.
- Nadelhoffer K J 1990 Microlysimeter for measuring nitrogen mineralization and microbial respiration in aerobic soil incubations. *Soil Sci. Soc. Am. J.* 54, 411–415.
- Parton W J, Schimel D S, Cole C V and Ojima D S 1986 Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Sci. Soc. Am. J.* 51, 1173–1179.
- Post W M, Emanuel W R and King A W 1992 Soil organic matter dynamics and the global carbon cycle. *In World Inventory of Soil Emission Potentials.* Eds NH Batjes and EM Bridges. International Soil Reference Information Center, Wageningen, The Netherlands.
- Post W M, Peng T H, Emanuel W R, King A W, Dale V H and DeAngelis D L 1990 The global carbon cycle. *Am. Sci.* 78, 310–326.
- Potter K N, Jones O R, Torbert H A and Unger P W 1997 Crop rotation and tillage effects on organic carbon sequestration in the semi-arid southern high plains. *Soil Sci.* 162, 140–147.
- Prior S A, Rogers H H, Runion G B and Hendrey G R 1994 Free-air CO₂ enrichment of cotton: vertical and lateral root distribution patterns. *Plant Soil* 165, 33–44.
- Prior S A, Rogers H H, Runion G B, Kimball B A, Mauney J R, Lewin K F, Nagy J and Hendrey G R 1995 Free-air CO₂ enrichment of cotton: Root morphological characteristics. *J. Environ. Qual.* 24, 678–683.
- Prior S A, Rogers H H, Runion G B, Torbert H A and Reicosky D C 1997a Carbon dioxide-enriched agroecosystems: influence of tillage on short-term soil carbon dioxide efflux. *J. Environ. Qual.* 26, 244–252.
- Prior S A, Torbert H A, Rogers H H and Runion G B 1996 Decomposition of soybean and sorghum residue produced under CO₂ enrichment. *Agron. Abstracts, ASA, Madison, WI.* 12 p.
- Prior S A, Torbert H A, Runion G B, Rogers H H, Wood C W, Kimball B A, Lamorte R L, Pinter P J and Wall G W 1997b Free-Air CO₂ enrichment of wheat: soil carbon and nitrogen dynamics. *J. Environ. Qual.* 26, 1161–1166.
- Reicosky D C, Dugas W A and Torbert H A 1997 Tillage-induced carbon dioxide loss from different cropping systems. *Soil Till. Res.* 41, 105–118.
- Rogers H H and Dahlman R C 1991 Crop responses to CO₂ enrichment. *Vegetatio* 104/105, 117–131.
- Rogers H H, Heck W W and Heagle A S 1983 A field technique for the study of plant responses to elevated carbon dioxide concentrations. *Air Poll. Cont. Assoc. J.* 33, 42–44.
- Rogers H H, Runion G B and Krupa S V 1994 Plant responses to atmospheric CO₂ enrichment with emphasis on roots and the rhizosphere. *Environ. Pollut.* 83, 155–189.
- Rogers H H, Runion G B, Krupa S V and Prior S A 1994 Plant responses to atmospheric CO₂ enrichment: implications in root-soil-microbe interactions. *In Advances in Carbon Dioxide Effects Research.* Eds LH Allen Jr, MB Kirkham and DM Olszyk et al. pp 1–34. ASA, Special Publication no. 61. Madison, Wisconsin.
- Schimel D, Enting I G, Heimann M, Wigley T M L, Raynaud D, Alves D and Siegenthaler U 1995 CO₂ and the carbon cycle. *In Climate Change 1994.* Eds JT Houghton, LG Meira Filho and J Bruce et al. pp 35–71. Cambridge University Press, Cambridge.
- Schlesinger W H 1984 Soil organic matter: a source of atmospheric CO₂. *In The Role of Terrestrial Vegetation in the Global Carbon Cycle.* Ed. GM Woodwell. pp 111–127. John Wiley, New York.
- Schlesinger W H 1986 Changes in soil carbon storage and associated properties with disturbance and recovery. *In The Changing Carbon Cycle: A Global Analysis.* Eds JR Trabalka and DE Reichle. pp 194–220. Springer-Verlag, New York.
- Schlesinger W H 1990 Evidence from chronosequence studies for a low carbon-storage potential of soils. *Nature* 348, 232–234.
- Strain B R and Cure D J (Ed.) 1985 Direct effects of increasing carbon dioxide on vegetation. DOE/ER-0238. Office of Energy Research, U. S. Dept. of Energy, Washington, D.C.
- Tans P P, Fung I Y and Takahashi T 1990 Observational constraints on the global atmospheric CO₂ budget. *Sci.* 247, 1431–1438.
- Thomas J F and Harvey C N 1983 Leaf anatomy of four species grown under continuous CO₂ enrichment. *Bot. Gaz.* 144, 303–309.
- Torbert H A, Rogers H H, Prior S A and Schlesinger W H 1997a Elevated atmospheric CO₂ in agro-ecosystems effects on soil carbon storage. *Global Change Biol.* 3, 513–521.
- Torbert H A, Potter K N and Morrison J E Jr 1997b Tillage intensity and fertility level effects on nitrogen and carbon cycling in a vertisol. *Commun. Soil Sci. Plant Anal.* 28, 699–710.
- Torbert, H A, Potter K N and Morrison J E Jr 1998a. Tillage intensity and crop residue effects on nitrogen and carbon cycling in a vertisol. *Commun. Soil Sci. Plant Anal.* 29, 717–727.
- Torbert H A, Prior S A, Rogers H H, Schlesinger W H and Mullins G L and Runion R G 1996 Elevated atmospheric CO₂ in agro-ecosystems affects groundwater quality. *J. Environ. Qual.* 25, 720–726.
- Torbert H A, Prior S A and Rogers H H 1995 Elevated atmospheric CO₂ effects on cotton plant residue decomposition. *Soil Sci. Soc. Am. J.* 59, 1321–1328.
- Torbert H A, Prior S A, Rogers H H and Runion G B 1998b Crop residue decomposition as affected by growth under elevated atmospheric CO₂. *Soil Sci.* 163, 412–419.
- Wallace A, Wallace G A and Cha J W 1990 Soil organic matter and the global carbon cycle. *J. Plant Nutr.* 13, 459–466.
- Wilson A T 1978 Pioneer agriculture explosion and CO₂ levels in the atmosphere. *Nature* 273, 40–41.
- Wood C W, Torbert H A, Rogers H H, Runion G B and Prior S A 1994 Free-air CO₂ enrichment effects on soil C and N. *Agric. For. Meteorol.* 70, 103–116.