Elevated Atmospheric Carbon Dioxide Effects on Cotton Plant Residue Decomposition

H. A. Torbert,* S. A. Prior, and H. H. Rogers

ABSTRACT

Assessing the impact of elevated atmospheric CO_2 concentration on the global environment is hampered due to a lack of understanding of global C cycling. Carbon fixed within plant biomass ultimately enters the soil via plant residues, but the effects of elevated-CO_2-grown plant material on decomposition rates and long-term soil C storage are unknown. The objective of this study was to determine the decomposition rate of plant residues grown under an elevated CO_2 environment as affected by soil type. Cotton (*Gossypium hirsutum* L. 'Delta Pine 77') samples were collected from a free-air CO_2 enrichment (550 $\mu L\ L^{-1}$) experiment. The plant residues were incubated under ambient CO_2 conditions to determine decomposition rates of leaves, stems, and roots and potential N and P mineralization–immobilization in three soil series: a Blanton loamy sand (loamy siliceous, thermic Grossarenic Paleudult), a Decatur silt loam (clayey, kaolinitic, thermic Rhodic Paleudult), and a Houston clay loam (very fine, montmorillonitic Typic Chromudert). No significant difference was observed between plant residue grown under CO_2 enrichment vs. ambient CO_2 conditions for soil respiration or P mineralization–immobilization. Significantly greater net N immobilization was observed during the incubation in all soil types for plant residue grown at elevated CO_2. These results indicate that while decomposition of plant residue may not be reduced by CO_2 enrichment, N dynamics may be markedly changed.

There is no doubt that the combined impact of population increases, industrial expansion, and deforestation has resulted in changes to the global environment. One important aspect of these changes is an increased atmospheric CO_2 concentration (Holland, 1978; Smil, 1985; Warneck, 1988), which is projected to double in the next century (Bolin, 1986). However, estimates of the probable influences of elevated CO_2 are hampered by a lack of understanding of global C cycling.

A central problem in understanding global C cycling is the inability of scientists to account for the flow of C. While sources of atmospheric CO_2 are well documented, sinks for C are not, with an unknown sink of 2.2×10^{15} g C yr^{-1} (Houghton et al., 1990; Schlesinger, 1991). Tans et al. (1990) hypothesized that the surplus C is being stored in terrestrial ecosystems as a result of higher plant productivity caused by elevated atmospheric CO_2 levels (Kimball, 1983; Allen, 1990; Lekkerkerk et al., 1990). Carbon fixed within plant biomass ultimately enters the soil via plant residues, where it may reside for hundreds of years (Parton et al., 1986). Ultimately, the rate and extent of turnover of organic C produced in an elevated CO_2 environment will control C storage in terrestrial ecosystems (Van Veen et al., 1991).

The decomposition of plant residue is dependent on several plant, soil, and climatic conditions. Factors (controlled by climate and soil conditions) include soil water content, soil temperature, soil pH, soil aeration, and available nutrients, while factors controlled by plants include age, size, lignin content, and the C/N ratio of plant residue (Parr and Papendick, 1978; Ghidey and Alberts, 1993).

Carbon dioxide–induced changes in soil N dynamics could also affect decomposition by reducing N availability via alterations in the composition of plant residue and soil C/N ratios. However, while the C/N ratio of a plant residue grown under elevated CO_2 conditions is usually higher, lower lignin/N and lignin/P ratios of the plant residue will probably increase the decomposition rate (Conroy, 1992). The decomposition rate of plant residue assimilated under elevated CO_2 conditions thus will probably depend on the specific chemistry of the residue and on the supply of nutrients from exogenous sources (Polglase and Wang, 1992). Therefore, the impact of soil type on decomposition rates of plant materials may have substantial importance on global-scale evaluations of C cycling.

Few studies have attempted to measure the effects of CO_2 enrichment of C cycling in terrestrial ecosystems. In a growth chamber study, Lekkerkerk et al. (1990) found that increased photosynthetic fixation with elevated CO_2 resulted in a proportional increase in the distribution of C to plant and soil compartments; thus, elevated CO_2 levels resulted in increased C input into soil. In a review by Bazzaz (1990), it was suggested that decomposition rates of plant residue from high-CO_2 environments would be slower. However, no experimental evidence for this hypothesis was given. Lekkerkerk et al. (1990) found that elevated CO_2 levels led to a faster input of easily decomposable root-derived C compounds to soil. Their data indicated a net increase in soil organic matter when wheat (*Triticum aestivum L.*) was exposed to 700 $\mu L\ L^{-1}$.

Increased cotton biomass production under elevated CO_2 concentration with FACE at the Maricopa, AZ, location has been observed (Prior et al., 1994), including residue components (leaves, stems, roots) that will be returned to the field. One study has suggested that these increases have led to a small increase in the organic C content of the soil but no difference in the organic N content (Wood et al., 1994). Measures of the potential C and N mineralization of the soil, however, indicated that factors other than total biomass input were affecting C cycling within the experimental FACE plots (Wood et al., 1994).

The objective of this study was to determine the role of soil type in controlling the decomposition rate of plant residue grown under an elevated CO_2 environment. Plant residue decomposition was evaluated by measuring microbial respiration and potential N and P mineralization–immobilization in three soil types following amendment with plant material. Leaf, stem, and root samples from

H.A. Torbert, USDA-ARS Blackland, Soil and Water Research Lab., 808 East Blackland Rd., Temple, TX 76502; and S.A. Prior and H.H. Rogers, USDA-ARS National Soil Dynamics Lab., Box 3439, Auburn, AL 36831-3439. Received 28 July 1994. *Corresponding author (torbert @brcsun0.tamu.edu).

Published in Soil Sci. Soc. Am. J. 59:1321–1328 (1995).

Abbreviations: FACE, free-air CO_2 enrichment; ET, evapotranspiration; ANOVA, analysis of variance; LSD, least significant difference.

plants exposed to two CO_2 levels (ambient, 360 μL L^{-1}, enriched, 550 μL L^{-1}) were compared.

MATERIALS AND METHODS

Study Site

Cotton 'Delta Pine 77' was grown at a field site located at the Maricopa Agriculture Center of the Univ. of Arizona at Maricopa, AZ (33°10′N, 112°0′W). Soil at the site is a Trix clay loam (fine, loamy, mixed [calcareous], hyperthermic Typic Torrifluvent). A FACE application system (Hendrey et al., 1993) was used to achieve CO_2 exposure at the 550 μL L^{-1} level under field conditions. Cotton was grown under ambient CO_2 conditions (360 μL L^{-1}) also. Cotton was planted on 23 Apr. 1990 with a 1-m row spacing and a final plant population of 100 000 ha^{-1}. Following chisel plowing, cotton was planted into raised beds under dry soil conditions, then irrigated with a subsurface drip irrigation system to a water content approximating field capacity (−0.03 MPa).

Following the initial water application, irrigation was applied biweekly, with the application rate based on a target of returning 100% of ET based on pan evaporation measurements. Fertilizer N was applied through the irrigation system at a rate of 5.6 kg N ha^{-1} wk^{-1} for a total of 39.2 kg N ha^{-1} yr^{-1}. Other cultural practices used were according to recommended farming practices for the area. Plant material used in the incubation was collected on 17 Sept. 1990 as described by Prior et al. (1994).

Sample Preparation and Incubation

Potential C, N, and P mineralization–immobilization were quantified using techniques described by Nadelhoffer (1990). Briefly, a modified 150-mL Falcon filter unit (Model no. 7102 or 7103, Becton Dickinson Labware, Franklin Lakes, NJ) was used as an incubation chamber. The filter units were modified to allow both measurement of leaching of N and gas sampling of CO_2 evolved during soil respiration. The upper chamber of the filter units held the soil sample, while the lower chamber (separated by a nondegradable glass fiber filter 5.5 cm in diam. and 0.26 mm thick) collected leachate during leaching procedures.

Twenty-gram (dry-weight basis) soil samples were weighed into the microlysimeters along with 0.105 g of plant residues that were mixed into the soil samples. In addition, microlysimeters containing only soil samples with no plant residue amendments were included. Microlysimeters containing no soil or plant residue were included for background correction during incubation measurements.

Three soil series, a Blanton loamy sand, a Decatur silt loam, and a Houston clay loam were used in the study. Soil samples were taken from the National Soil Dynamics Lab. engineering soil bins (large soil containment facilities used for equipment evaluation) where these soils had been continuously fallow since 1966 (Bachelor, 1984). The soils were all formed under humid climatic conditions and were chosen on the basis of wide differences in physical and chemical characteristics (Table 1) but had been maintained with long-term fallow conditions to limit the impact of previous plant residue additions.

Plant samples of leaves, stems, and roots, collected from the FACE experiment as described by Prior et al. (1994), were dried at 55°C (until weight loss was complete) and ground to pass a 2-mm screen. Lint and seed were not included because these plant parts typically are not returned to the field.

After soil and plant residue amendments, microlysimeters were immediately preleached, evacuated with 0.06 MPa vacuum, and incubated in the dark at 25°C under ambient CO_2 conditions. Air ports of the microlysimeters were open during incubation to ensure aerobic conditions, and lids remained in place to minimize soil water loss. Microlysimeters were leached with 40 mL of 0.01 *M* $CaCl_2$ solution for determination of N and P; the $CaCl_2$ solution was added to the microlysimeters, allowed to equilibrate for ≈ 1 h, and evacuated with 0.06 MPa vacuum.

To measure CO_2 evolution, microlysimeters were evacuated with CO_2-free air, sealed, and allowed to incubate at 25°C for ≈ 1 hr. The CO_2 concentration of air samples collected from the head space of microlysimeters was determined with an ADC-225-MK3 CO_2 analyzer (Analytical Development Co., Ltd., Hoddesdon, England). Measurement of CO_2 evolution and leaching was performed 13 times at 1, 2, 3, 6, 10, 14, 17, 24, 31, 38, 45, 52, and 59 d after initiation of the experiment.

In the analysis reported in Table 1, pH was determined with a glass electrode (soil/water ratio, 1:1), organic and inorganic C were determined with a Leco CR12 Carbon Determinator[1] (Leco Corp., Augusta, GA; Chichester and Chaison, 1992), total N and total P were determined colorimetrically on a Technicon Autoanalyzer, following digestion of soil by a salicylic acid modification of a semimicro-Kjeldahl procedure (Technicon Industrial Systems, 1976). Chemical attributes of the plant residue are given in Table 2. Carbon and N were determined with a Leco CHN-600 analyzer (Leco Corp.). Plant concentrations of lignin, cellulose, hemicellulose, minerals, and cell content were determined by the methods of Goering and Van Soest (1970). Leachate was colorimetrically analyzed for NO_2–N + NO_3–N, NH_4–N, and P concentration using a Technicon Autoanalyzer (Technicon Industrial Systems, 1973).

Increases in inorganic N or P concentration in the leachate of plant-amended soils compared with nonamended soils were considered to have potential net N or P mineralization, while decreases in inorganic N or P concentration in the leachate of plant-amended soils compared with nonamended soils was considered to have potential net N or P immobilization.

The experimental design was a completely random arrangement with four replications. Treatments were three soil types, two CO_2 levels, and three plant tissue types. Data were analyzed using ANOVA procedures, and means were separated using

[1] Trade names and products are mentioned solely for information. No endorsement by the USDA is implied.

Table 1. Chemical and physical characteristics of soils in this study.

Soil		Surface			Total	Organic	Total				
Series	Subgroup	texture†	pH	CEC‡	N	C	P	$CaCO_3$	Sand	Silt	Clay
				$cmol_c$ kg^{-1}	g kg^{-1}				%		
Blanton	Grossarenic Paleudults	ls	5.4	2	0.03	0.38	0.02	0.03	82.9	12.6	4.5
Decatur	Rhodic Paleudults	sil	5.9	9	0.05	0.49	0.05	0.06	18.8	54.9	26.3
Houston	Typic Chromuderts	cl	7.2	44	0.18	2.18	0.07	0.106	5.1	32.4	62.5

† ls = loamy sand; sil = silt loam; cl = clay loam.
‡ CEC = cation-exchange capacity.

Table 2. Chemical characteristics of cotton plant residue utilized in this study.†

	P	N	C	Cell content‡	Cellulose	Hemicellulose	Lignin	Mineral	C/N ratio
	g kg^{-1}	g 100 g^{-1}							
					Leaves				
Ambient	5.7 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§	5.1 a	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	1.8 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	1.8 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	1.3 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	1.0 a	0.5 b	44.1 a	18.5 a	44.6 a	15.0 a	24.7 b	2.3 a	84.1 a

† Values represent means of four replicates. Values within a row followed by the same letter do not differ significantly (0.05 probability level).
‡ Cellular content includes compounds such as proteins, starch, sugars, organic acids, and pectin.
§ FACE = free-air CO_2 enrichment.

a protected LSD method at a 0.05 probability level (SAS Institute, 1982).

RESULTS

Results from chemical analyses of plant components indicated that growth under elevated CO_2 levels affected the tissue composition of cotton (Table 2). While the C content of the plant parts was not affected by elevated CO_2, the concentration of N in leaves, stems, and roots was reduced under FACE relative to plants grown under ambient CO_2 conditions. Other studies have also noted reduced plant N concentrations in plants grown under elevated CO_2 (Larigauderie et al., 1988; Conroy, 1992; Coleman et al., 1993). This effect occurs regardless of soil available N (Conroy, 1992). Lower tissue N concentrations resulted in higher C/N ratios of both the leaves and stems of cotton grown under elevated CO_2 (Table 2).

Atmospheric CO_2 levels did not affect cell wall components (cellulose, hemicellulose, and lignin) of shoots and roots but did affect the lignin content of roots (Table 2). Lignin content was significantly higher in roots of ambient CO_2-grown plants than in plants grown under FACE treatment. A significantly higher concentration of cellular content compounds were found in FACE treatment plants compared with the ambient CO_2 treatment for leaves, with a similar trend ($P \leq 0.13$) for roots.

Soil Respiration

No significant main effect or interaction effect for CO_2 concentration treatment was observed for soil respiration. Soil respiration was significantly affected by both plant part and soil type, with a significant interaction between plant part and soil type also observed. In general, soil respiration rates were greatest during the first 6 d of the incubation (Fig. 1). After this period, soil respiration slowly declined until it approached levels of nonamended soils. Short-duration increases in soil respiration were also observed during several periods of the incubation (i.e., day of incubation 14, 24, and 45).

Soil type influenced the degree to which soil respiration rates changed during the incubation. In the clay loam soil, soil respiration rates remained relatively high throughout the incubation from amended and nonamended soils, ranging from 2.5 to 24.1 mg C kg^{-1} soil min^{-1} (Fig. 1a). During the first 17 d of incubation, the leaf-residue-amended soils maintained higher soil respiration rates than either stem- or root-amended soils, with an average soil respiration rate during this period of 15.6, 10.0, and 7.9 mg C kg^{-1} soil min^{-1} for leaf, stem, and root amendments, respectively. After 24 d, stem-amended soils had higher respiration rates (11.8 mg C kg^{-1} soil min^{-1}), and by Day 52, root amendments produced the highest respiration rates (7.5 mg C kg^{-1} soil min^{-1}). In the clay loam soil, short-duration increases

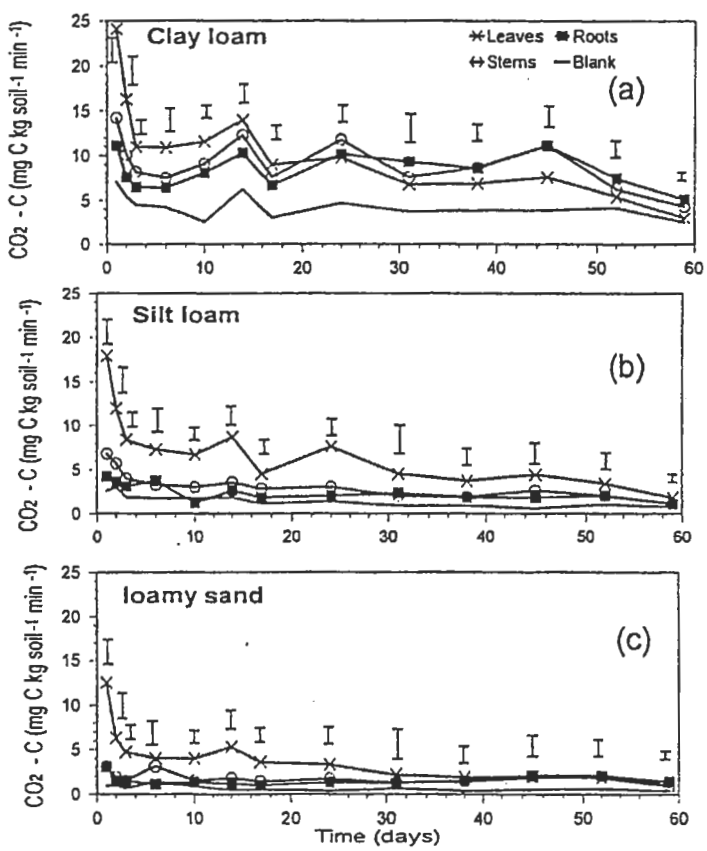

Fig. 1. Soil respiration during incubation of a clay loam, a silt loam, and a loamy sand soil following addition of leaf, stem, root, or no cotton plant residues (blank), averaged across CO_2 treatments. Treatment LSD bars are for $\alpha = 0.05$ level.

in soil respiration were observed at Days 14, 24, and 45 for all plant parts.

In the silt loam soil, CO_2 evolution rate was significantly different for the plant parts during the first 7 d of incubation (Fig. 1b). During this period, the highest rates of soil respiration were from leaf-amended soils, followed by stem-, root-, and nonamended soils, with soil respiration rates averaging 11.4, 5.0, 3.7, and 3.2 mg C kg^{-1} soil min^{-1} for leaf-, stem-, root- and nonamended soils, respectively. After this period, leaf-amended soils sustained a higher soil respiration rate until Day 59. Beyond the first week of incubation, only small differences distinguished stem- from root-amended soils (between 1.2 and 3 mg C kg^{-1} soil min^{-1}), and at Day 59, little difference between soil respiration rates of plant-residue-amended soils and nonamended soils were detectable $\approx$ 1.4 mg C kg^{-1} soil min^{-1}). Short-duration increases in soil respiration were observed on Days 14 and 24 for the leaf-residue-amended soils only.

After an initial pulse, the loamy sand soil respiration rate fell to a level much lower than the other soil types and did not vary throughout the remainder of the incubation (Fig. 1c). Leaf amendments had the highest initial soil respiration rates of 12.5 mg C kg^{-1} soil min^{-1}, compared with stem amendments of 3.1 mg C kg^{-1} soil min^{-1} and root amendments of 3.0 mg C kg^{-1} soil min^{-1}. Little difference was observed between root and stem during most of the incubation (between 1.0 and 3.0 mg C kg^{-1} soil min^{-1}), with these samples maintaining levels only slightly above that of the nonamended soils. After 38 d of incubation in the loamy sand soil, all plant material produced the same rates of soil respiration ($\approx$2.0 mg C kg^{-1} soil min^{-1}). In this soil, the short-duration increases in soil respiration were observed for the leaf-amended soil on Day 14 only.

Overall, soil respiration of leaf-amended soils exceeded that of root- or stem-amended and was least for root-amended soils (Fig. 1). This generally is consistent with the expected rate of decomposition based on C/N ratios, with the lowest C/N ratio for leaf residue and the highest for roots (Table 2). When averaged across sampling dates, however, no significant difference in soil respiration was observed between plant residues grown at elevated and ambient CO_2 concentrations (Fig. 2).

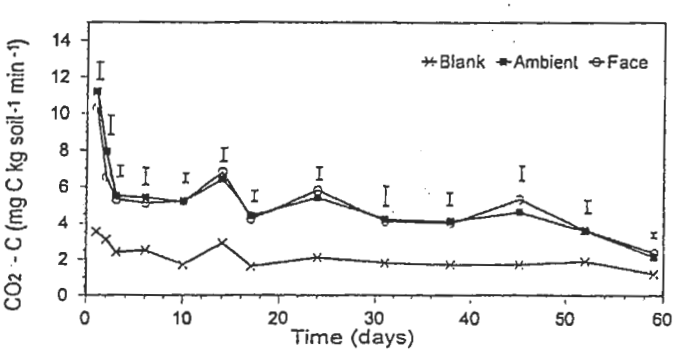

Fig. 2. Soil respiration rates during incubation of free air CO_2 enrichment (FACE) and ambient cotton plant residue amended soils, averaged across soil type and plant residue type. Treatment LSD bars are for α = 0.05 level.

This finding contradicts predictions of decomposition rates based on C/N ratios alone (Table 2). Evidently, the quality of the residue grown under FACE (as evidenced by a higher concentration of easily decomposable compounds, Table 2) was sufficient to negate the impact of higher C/N ratios of the plant residue. This is consistent with the findings of Wood et al. (1994), which indicated that factors such as quality of plant residue produced under FACE conditions affected C cycling.

The response of plant residue decomposition was not simply a function of the organic C content of the soils. When CO_2 emission rates were calculated based on the C content of the soil rather than on a soil dry-weight basis, significant differences between soil types for soil respiration were observed. However, the order for soil respiration rates between treatments changed, with silt loam > loamy sand > clay loam soil for CO_2 emission. Average soil respiration rates of 787, 569, and 376 mg CO_2–C kg^{-1} organic C min^{-1} were observed for silt loam, loamy sand, and clay loam, respectively. These data indicate that most of the microbial activity occurred in the new plant residue and that the nutrient-supplying power of the soil may be very important to the decomposition rate of plant residue.

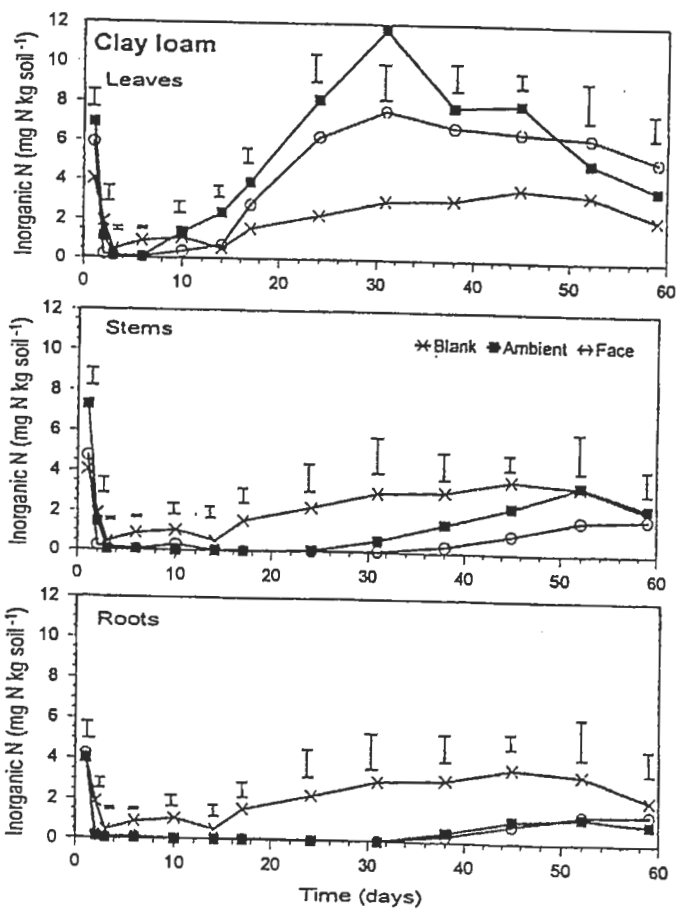

Fig. 3. Inorganic N concentration in leachate during soil incubation of a clay loam soil following addition of leaf, stem, root, or no cotton plant residue (blank). Treatment LSD bars are for α = 0.05 level (FACE = free-air CO_2 enrichment).

Net Nitrogen and Phosphorus Mineralization–Immobilization

The release of soluble P into soil solution (as measured by P concentration in leachate) was very small and ranged from 0 to 0.36 mg P kg^{-1} soil (data not shown). No significant difference in the P concentration between CO_2 treatment or soil types was observed. The average P concentration in leachate was 0.1, 0.06, and 0.08 mg P kg^{-1} soil for clay loam, silt loam, and loamy sand, respectively.

Net N mineralization–immobilization was measured as the amount of inorganic N released into soil solution by combining NO_3–N and NH_4–N in leachate samples. However, most of the inorganic N in leachate was in the NO_3–N form. The NH_4–N fraction of leachate was on average ≈ 15% of total inorganic N and was significantly affected by plant parts only (data not shown).

Net N mineralization–immobilization, as observed with C mineralization, was significantly affected by soil type and plant part; a significant soil type × plant part interaction was also observed. However, unlike C mineralization, net N mineralization–immobilization was also significantly affected by the CO_2 level at which plants were grown. There were significant CO_2 × plant part and CO_2 × soil type interactions with total inorganic N concentration. Such treatment effects were also observed for several individual sampling periods.

In general, the highest net N mineralization rates occurred in clay soils amended with plant residue. In all soil types, leaf tissue amendments led to the highest associated solution N contents (Fig. 3–5). After initial leaching, net N immobilization occurred, with the concentration of inorganic N in the leachate dropping to a level near or below the nonamended soil level in all soil types and for all plant residue amendments. For stem and root amendments, net N immobilization continued for the duration of the incubation, with the concentration of inorganic N remaining below the level of nonamended soil. However, after 10 to 15 d of incubation, net N mineralization was observed in all three soils receiving leaf residue. Only after 31 d in the clay loam soil did the inorganic N concentration of soils amended with stem and root residue begin to rise, until little difference between plant-residue-amended soil and nonamended soil was observed. With the clay loam soil, the decomposition of even high C/N ratio plant residue occurred at a rate fast enough to release N by the end of the incubation period (52 d).

This rate of net N mineralization–immobilization would be expected with the C/N ratios of the plant

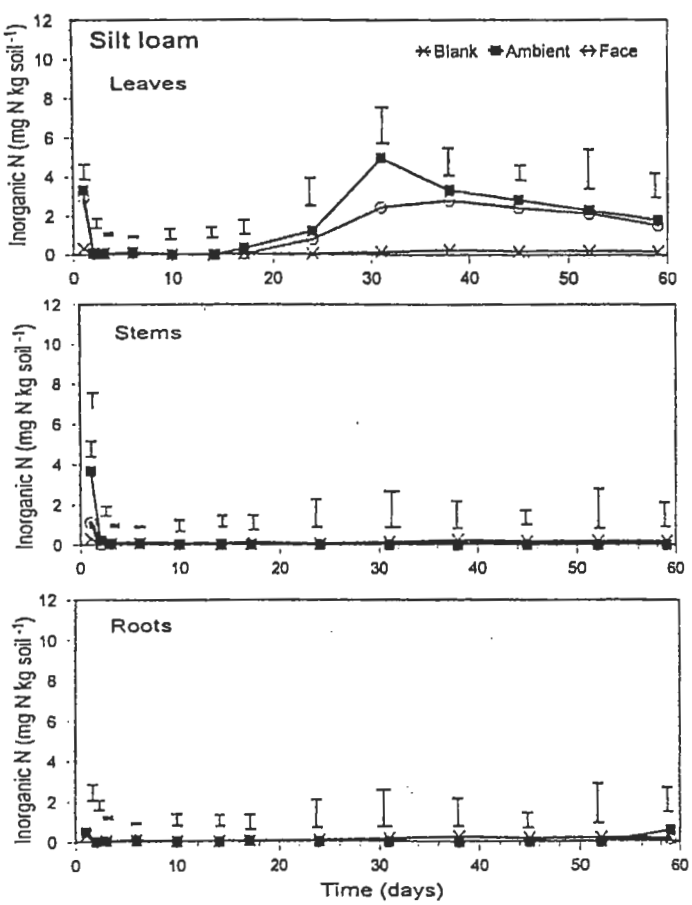

Fig. 4. Inorganic N concentration in leachate during soil incubation of a silt loam soil following addition of leaf, stem, root, or no cotton plant residue (blank). Treatment LSD bars are for α = 0.05 level (FACE = free-air CO_2 enrichment).

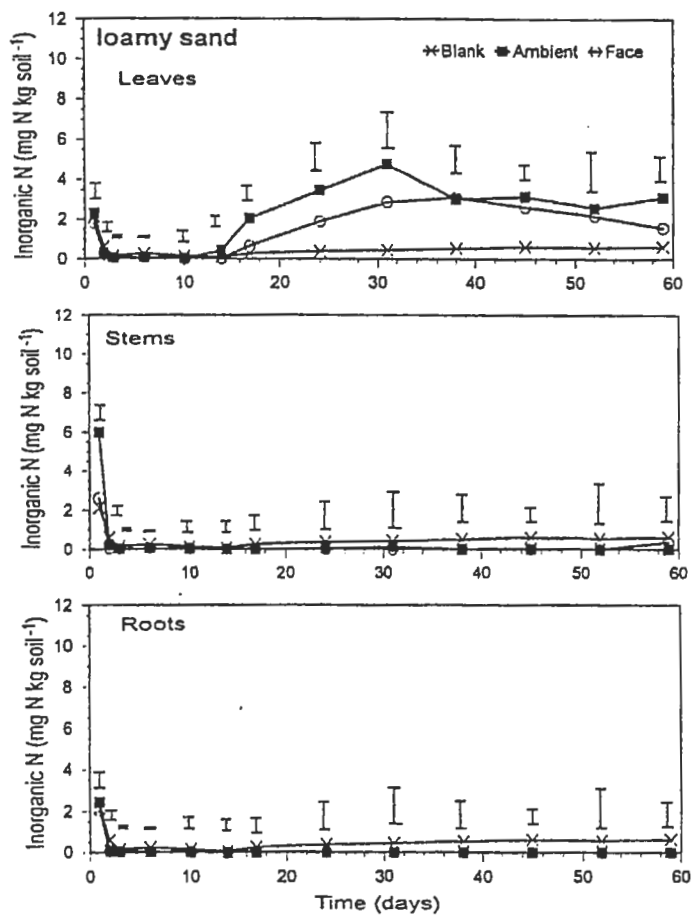

Fig. 5. Inorganic N concentration in leachate during soil incubation of a loamy sand soil following addition of leaf, stem, root, or no cotton plant residue (blank). Treatment LSD bars are for α = 0.05 level (FACE = free-air CO_2 enrichment).

residue. In general, N mineralization can be expected from plant residue with C/N ratios below 20:1 and immobilization with plant residue of C/N ratios of 33:1 or greater. The highest rate of net N mineralization occurred in the clay loam soil, and the lowest rate was observed in the loamy sand soil. Initiation of net N mineralization with leaf residue amendments was also controlled by soil type. Mineralization occurred after 10, 14, and 17 d of incubation for clay loam, silt loam, and loamy sand soils, respectively.

The source of plant residue (FACE or ambient) also significantly affected the net N mineralization–immobilization. The total amount of inorganic N released during the incubation for all plant residue types was significantly greater for the ambient-grown plant residue compared with the FACE-grown residue in all three soils (Table 3). In addition, significantly higher rates of net N mineralization were observed for ambient plant-residue-amended soils at several of the individual sampling periods during the incubation (Fig. 3–5). For example, after 10 d of incubation of the clay loam soil, ambient leaf-residue-amended soil began N mineralization (Fig. 3), while N mineralization in the FACE leaf-residue-amended soil did not begin until after 17 d and remained lower compared with the ambient leaf-residue-amended soil throughout the 52 d of incubation. Likewise, net N mineralization with ambient leaf-residue-amended silt loam and loamy sand soils was initiated sooner and was maintained at levels generally above that of FACE leaf-residue-amended soil for the duration of the incubation (Fig. 4 and 5).

In general, the net N mineralization–immobilization rates followed the same pattern as C mineralization. As with soil respiration, the highest rate of net N mineralization was observed in clay loam soil amended with leaf tissue (Fig. 1 and 3). This indicated that the rate of soil respiration may be controlled by the available N content both in the soil and in the decomposing plant residue. This is consistent with findings of Wood et al. (1994), which indicated that during the first 30 d of FACE soil incubation, N limitation to microbes due to N immobilization may have limited C mineralization.

Table 3. Total inorganic N content of leachate sampled during incubation.

	Blank	Leaves	Stems	Roots
	g kg^{-1}			
	Houston†			
Ambient	28.0	60.2	19.1	8.2
FACE‡		48.7	10.5	8.9
	Decatur†			
Ambient	1.7	20.4	2.5	4.2
FACE‡		15.4	1.4	1.4
	Blanton†			
Ambient	6.9	25.4	2.7	6.6
FACE‡		17.1	2.3	5.6
LSD (any two means)	3.97			

† Houston is a clay loam, Decature is a silt loam, and Blanton is a loamy sand.
‡ FACE = free-air CO_2 enrichment.

DISCUSSION

Several contradictory hypotheses addressing the potential for C storage in terrestrial ecosystems have been forwarded. The well-documented increase in C/N ratio with elevated CO_2 has led to the hypothesis that decomposition rates in an elevated CO_2 environment will be slower (Bazzaz, 1990) and will limit plant response to CO_2 enrichment and long-term C storage (Strain and Cure, 1985). Lamborg et al. (1984) have argued that increased soil microbial activity due to greater biomass C inputs in an elevated-CO_2 world could lead to increased soil organic matter decomposition (i.e., the "priming effect"), and therefore, atmospheric CO_2 enrichment would not result in accumulation of soil organic C. Alternatively, Goudriaan and de Ruiter (1983) proposed that increased soluble, easily decomposed C inputs as a consequence of higher atmospheric CO_2 could accentuate soil microbial substrate preference mechanisms. They further speculated that preference for easily decomposable substrates would retard the decomposition of plant debris and native soil organic matter. The end result of their scenario would be an accumulation of soil organic matter. To date, none of these hypotheses has been proven.

Results from this study indicate that differences in soil type will exert an important control on decomposition rates of plant residue when plants are produced at elevated CO_2. The rate of decomposition seems to be controlled by the ability of the soil to supply nutrients (especially N), as indicated by the change in the relative order of C emission when corrected for C content of the soil. The capacity of the soil to supply nutrients not only increased the rate of soil respiration but also increased the amount of perturbations in soil respiration. This was observed in the number of short-duration increases of CO_2 emissions measured in the plant residue with higher N content (leaf) and with the soil type with highest N content (clay loam).

This work further indicates that, contrary to the effect commonly hypothesized, decomposition rates of plant residue grown under elevated CO_2, though having higher C/N ratios, may not decompose at slower rates. Increased levels of easily decomposable components (Table 2) compensated for higher C/N ratios, resulting in similar decomposition rates among residue from different CO_2 treatments. The slower decomposition rates predicted by higher C/N ratio alone assume a constant distribution of C to different plant and cellular components. Under ambient CO_2 conditions, when an increase in C/N ratio occurs, a corresponding increase in microbially resistant plant constituents also occurs. However, with the cotton plant residue grown under elevated CO_2, the C/N ratios increased but the proportion of plant residue resistant to microbial decomposition tended to decrease or was not changed. Likewise, plant components not resistant to decomposition, such as sugars and proteins, either increased or were not changed with the FACE CO_2 treatment compared with the ambient CO_2 treatment (Table 2).

While the C/N ratio made a difference in the rate of soil respiration between soils amended with different

plant residues, for soil respiration within a given plant residue, the C/N ratio had no effect. This was most likely because within plant residues, the supply of N was not changed in proportion to the amount of N needed for the amount of C energy supplied. With the plant residue from the ambient CO_2 treatment, N content was in excess of that needed for microbial decomposition as measured through soil respiration. Therefore, as decomposition progressed, this excess N was released. With the FACE plant residue, N content was present at a level sufficient for microbial needs in proportion to the C energy available in the plant residue, therefore less N was released.

While soil respiration rates of residue-amended soils were essentially the same for ambient compared with FACE, it can be speculated that increased storage of C in soil may occur at elevated atmospheric CO_2 concentration. Since decomposition of plant residue proceeded at similar rates, increased storage is likely with increased production. These speculations, however, do not consider the potential of a "priming effect" as did Lamborg et al. (1984).

While soil respiration was not impacted by amendment of soils with residue grown under different CO_2 concentrations, the net N immobilization–mineralization rates of amended soils were impacted. As pointed out by Strain and Cure (1985), plant response to CO_2 fertilization may be limited by N immobilization in an elevated-CO_2 world. The N mineralization data from this study indicate that N cycling in the terrestrial ecosystem may very well determine increased soil C storage. This, in turn, indicates that any effort to model soil C storage on a global scale should also consider N cycling dynamics. However, C cycling models predicting more storage based on the higher C/N ratio of plant residues alone are not correct. Fundamental changes in plant structure and cellular composition under elevated CO_2 must also be considered as well.

These data indicate that potential N limitations in the decomposition of residues resulting from an elevated CO_2 level may be greatest in soils with low soil N availability and slow rates of N mineralization. Since the results of this study demonstrate differences in plant part decomposition, the management of plant residues following harvests in future elevated-CO_2 environments deserves further consideration. For example, if significant increases in N immobilization occur in a future elevated-CO_2 environment, then increased N fertilization rate (or other management techniques) may be necessary to maintain crop production.

ACKNOWLEDGMENTS

The authors are indebted to Barry G. Dorman and Robert Chaison for technical assistance. Support from the Carbon Dioxide Research Program of the Environmental Science Div., USDOE, is gratefully acknowledged.

REFERENCES

Allen, L.H., Jr. 1990. Plant responses to rising carbon dioxide and potential interactions with air pollutants. J. Environ. Qual. 19: 15–34.

Batchelor, J.A., Jr. 1984. Properties of bin soils at the National Tillage Machinery Laboratory. Publ. 218. USDA-ARS Natl. Soil Dynamics Lab., Auburn, AL.

Bazzaz, F.A. 1990. The response of natural ecosystems to the rising global CO_2 levels. Annu. Rev. Ecol. Syst. 21:167–196.

Bolin, B. 1986. How much CO_2 will remain in the atmosphere? p. 93–155. *In* B. Bolin et al. (ed.) The greenhouse effect, climatic change, and ecosystems. John Wiley & Sons, New York.

Chichester, F.W., and R.F. Chaison, Jr. 1992. Analysis of carbon in calcareous soils using a two temperature dry combustion infrared instrumental procedure. Soil Sci. 153:237–241.

Coleman, J.S., K.D.M. McConnaughay, and F.A. Bazzaz. 1993. Elevated CO_2 and plant nitrogen-use: Is reduced tissue nitrogen concentration size-dependent? Oecologia 93:195–200.

Conroy, J.P. 1992. Influence of elevated atmospheric CO_2 concentration on plant nutrition. Aust. J. Bot. 40:445–456.

Ghidey, F., and E.E. Alberts. 1993. Residue type and placement effects on decomposition: Field study and model evaluation. Trans. ASAE 36:1611–1617.

Goering, H.K., and P.J. Van Soest. 1970. Forage fiber analyses (apparatus, reagents, procedures, and some applications). USDA-ARS Agric. Handb. 379. U.S. Gov. Print. Office, Washington, DC.

Goudriaan, J., and H.E. de Ruiter. 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.

Hendrey, G.R., K.F. Lewin, and J. Nagy. 1993. Free-air carbon dioxide enrichment: Development, process, results. Vegetatio 104/105:17–31.

Holland, H.D. 1978. The chemistry of the atmosphere and oceans. John Wiley & Sons, New York.

Houghton, J.T., G.J. Jenkins, and J.J. Ephraums (ed.). 1990. Climate change: The IPCC scientific assessment. Cambridge Univ. Press, Cambridge, England.

Kimball, B.A. 1983. Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. Agron. J. 75:779–788.

Lamborg, M.R., W.F. Hardy, and E.A. Paul. 1984. Microbial effects. p. 131–177. *In* E.R. Lemon (ed.) CO_2 and plants: The response of plants to rising levels of atmospheric CO_2. Am. Assoc. Adv. Sci. Selected Symp., Athens, GA. 23-28 May 1982. AAAS, Washington, DC.

Larigauderie, A., D.W. Hilbert, and W.C. Oechel. 1988. Effects of CO_2 enrichment and nitrogen availability on resource acquisition and resource allocation in a grass, *Bromus mollis*. Oecologia 77: 544–549.

Lekkerkerk, L.J.A., S.C. Van de Geijn, and J.A. Van Veen. 1990. Effects of elevated atmospheric CO_2-levels on the carbon economy of a soil planted with wheat. p. 423–429. *In* A.F. Bouwman (ed.) Soils and the greenhouse effect. John Wiley & Sons, NY.

Nadelhoffer, K.J. 1990. Microlysimeter for measuring nitrogen mineralization and microbial respiration in aerobic soil incubations. Soil Sci. Soc. Am. J. 54:411–415.

Parr, J.F., and R.I. Papendick. 1978. Factors affecting the decomposition of crop residues by microorganisms. p. 101–129. *In* W.R. Oschwald (ed.) Crop residue management systems. ASA Spec. Publ. 31. ASA, CSSA, and SSSA, Madison, WI.

Parton, W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima. 1986. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Sci. Soc. Am. J. 51:1173–1179.

Polglase, P.J., and Y.P. Wang. 1992. Potential CO_2-enhanced carbon storage by the terrestrial biosphere. Aust. J. Bot. 40:641–656.

Prior, S.A., H.H. Rogers, G.B. Runion, and J.R. Mauney. 1994. Effects of free-air CO_2 enrichment on cotton root growth. Agric. For. Meteorol. 70:69–86.

SAS Institute. 1982. SAS users guide: Statistics. SAS Inst., Cary, NC.

Schlesinger, W.H. 1991. Biogeochemistry: An analysis of global change. Academic Press, New York.

Smil, V. 1985. Carbon nitrogen sulfur: Human interference in grand biospheric cycles. Plenum Press, New York.

Strain, B.R., and J.D. Cure (ed.). 1985. Direct effects of increasing

carbon dioxide on vegetation. DOE/ER-0238. Office of Energy Research, U.S. Dep. of Energy, Washington, DC.

Tans, P.P., I.Y. Fung, and T. Takahashi. 1990. Observational constraints on the global atmospheric CO_2 budget. Science (Washington, DC) 247:1431–1438.

Technicon Industrial Systems. 1973. Nitrate and nitrite in water and waste water. Industrial method 100-70w. Technicon Industrial Syst., Tarrytown, NY.

Technicon Industrial Systems. 1976. Individual/simultaneous determination of nitrogen and/or phosphorus in BD acid digest. Industrial method 344-74a. Technicon Industrial Syst., Tarrytown, NY.

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

Warneck, P. 1988. Chemistry of the natural atmosphere. Academic Press, London.

Wood, C.W., H.A. Torbert, H.H. Rogers, G.B. Runion, and S.A. Prior. 1994. Free-air CO_2 enrichment effects on soil carbon and nitrogen. Agric. For. Meteorol. 70:103–116.