Implications of Elevated CO_2-Induced Changes in Agroecosystem Productivity

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SUMMARY. Since CO_2 is a primary input for crop growth, there is interest in how increasing atmospheric CO_2 will affect crop productivity and alter cropping system management. Effects of elevated CO_2 on grain and residue production will be influenced by crop selection. This field study evaluated soybean [C_3; *Glycine max* (L.) Merr.] and grain sorghum [C_4; *Sorghum bicolor* (L.) Moench.] cropping systems managed under conservation tillage practices and two atmospheric CO_2 concentrations

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(ambient and twice ambient) for three growing seasons. Elevated CO_2 increased soybean and sorghum yield by 53% and 17% increase, respectively; reductions in whole plant water use were also greater for soybean than sorghum. These findings suggest that increasing CO_2 could improve future food security, especially in soybean production systems. Elevated CO_2 increased aboveground residue production by > 35% for both crops; such shifts could complement conservation management by increasing soil surface cover, thereby reducing soil erosion. However, increased residue could negatively impact crop stand establishment and implement effectiveness during tillage operations. Elevated CO_2 increased total belowground dry weight for both crops; increased root proliferation may alter soil structural characteristics (e.g., due to increased number and extent of root channels) which could lead to increases in porosity, infiltration rates, and subsequent soil water storage. Nitrate leaching was reduced during the growing season (due to increased N capture by high CO_2-grown crops), and also during the fallow period (likely a result of altered decomposition patterns due to increased C:N ratios of the high CO_2-grown material). Enhanced crop growth (both above- and belowground) under elevated CO_2 suggests greater delivery of C to soil, more soil surface residue, and greater percent ground coverage which could reduce soil C losses, increase soil C storage, and help ameliorate the rise in atmospheric CO_2. Results from this study suggests that the biodegradability of crop residues and soil C storage may not only be affected by the environment they were produced in but may also be species dependent. To more fully elucidate the relationships between crop productivity, nutrient cycling, and decomposition of plant materials produced in elevated CO_2 environments, future studies must address species effects (including use of genetically modified crops) and must also consider other factors such as cover crops, crop rotations, soil series, tillage practices, weed management, and regional climatic differences. *[Article copies available for a fee from The Haworth Document Delivery Service: 1-800-HAWORTH. E-mail address: <docdelivery@haworthpress.com> Website: <http://www.HaworthPress.com>]*

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INTRODUCTION

The global environment is changing with the rise in atmospheric CO_2 concentration (Keeling and Whorf, 1994) and the process is expected to continue into the future (Bolin et al., 1986). This rise can be attributed mainly to fossil

fuel burning and land use change associated with industrial and/or population expansion (Houghton, Jenkins, and Ephraums, 1990). The most discussed consequence of the rise in atmospheric CO_2, along with other greenhouse trace gases, is a predicted shift in the Earth's climate. Aside from this debate, vegetation will be directly affected by the increase in atmospheric CO_2, the essential substrate of photosynthesis.

Since CO_2 is a primary input for crop growth, there is interest in how the rise in atmospheric CO_2 concentration will affect highly managed agricultural systems. Research has shown major plant responses, including increased growth and yield, increased water use efficiency (Rogers and Dahlman, 1993; Amthor, 1995), increased photosynthetic capacity (Huber, Rogers, and Israel, 1984; Radin et al., 1987; Bowes, 1991; Lawlor and Mitchell, 1991; Long and Drake, 1992), decreased respiration (Bunce, 1990; Amthor, Koch, and Bloom, 1992; Mousseau, 1993; Wullschleger, Ziska, and Bunce, 1994), and changes in plant structure (Pritchard et al., 1999). Relative to aboveground processes, CO_2 effects on crop root systems have received less attention despite their importance in attaining essential soil resources (i.e., water and nutrients) (Rogers, Runion, and Krupa, 1994). Crops have often shown increases in root dry weight under CO_2-enriched conditions (Chaudhuri et al., 1986; Del Castillo et al., 1989; Chaudhuri, Kirkham, and Kanemasu, 1990; Rogers et al., 1992) and in many cases, the largest proportion of the extra biomass produced as a result of elevated CO_2 is found belowground (Bazzaz, 1990; Rogers, Runion, and Krupa, 1994; Wittwer, 1995; Rogers et al., 1996). Findings suggest that whole plant nutrient uptake and nutrient utilization efficiency are increased while nutrient tissue concentration and nutrient uptake efficiency decline under elevated CO_2 (Rogers, Runion, and Krupa, 1994). However, most CO_2 studies have been conducted with containerized plants (i.e., confined rooting volume) in controlled environments which may obscure responses (above- and belowground) that would occur in the field (Sionit et al., 1984; Arp, 1991; Thomas and Strain, 1991).

Improved predictions on how changes in the global environment will impact agroecosystems will depend on obtaining realistic field data. Consequently, many current efforts focus on in-ground CO_2 studies utilizing open top chambers (OTC) and free-air CO_2 enrichment (FACE) (Allen et al., 1992). Recent field work has shown that elevated CO_2 can increase above- and belowground biomass (Mauney et al., 1994; Prior et al., 1994b; Kimball et al., 1995), alter root morphology (Prior et al., 1995) and the root system's capacity to explore soil volume through shifts in fine root distribution patterns (Prior et al., 1994a, 1994b; Weschsung et al., 1995, 1999), and induce changes in residue quality which alter soil carbon (C) and nitrogen (N) dynamics (Torbert, Prior, and Rogers, 1995; Henning et al., 1996; Torbert et al., 1996; Prior et al., 1997c). However, the extent of these CO_2-induced changes can be highly spe-

cies dependent. The quantity and quality of crop residues produced under elevated CO_2 are important factors influencing soil C storage patterns (Torbert et al., 1997; Torbert et al., 2000). Furthermore, soil C storage in agroecosystems can be altered since they are very sensitive to management practices (e.g., conservation practices, tillage systems, and cropping systems) (Kern and Johnson, 1993; Potter et al., 1997, 1998; Torbert, Prior, and Reeves, 1999). The capability of soil to act as a sink for C storage in CO_2-enriched agroecosystems is a highly relevant issue since the potential for C storage in agricultural soils is of special interest in the current climate change policy debate. This has resulted from the possibility of developing CO_2 sequestration credits for land use changes to meet the CO_2 emission limits proposed by the Kyoto Protocol.

The effect of elevated CO_2 on grain yield and the amount of crop residue left in the field may depend on the differential effect of CO_2 on crop species utilized in agroecosystems. There have been few CO_2 studies with C_3 and C_4 crops grown concurrently under the same field conditions; these two photosynthetic types are known to respond differently to elevated CO_2 both with regard to C metabolism and water use (Rogers et al., 1983; Rogers, Thomas, and Bingham, 1983; Amthor, 1995). Due to differences in CO_2 utilization during photosynthesis, plants with a C_3 photosynthetic pathway often exhibit greater growth response relative to those with a C_4 pathway (Bowes, 1993; Poorter, 1993; Amthor, 1995; Amthor and Loomis, 1996; Rogers et al., 1997). For C_4 species, the CO_2-concentrating mechanism at the site of ribisco often limits their response to elevated CO_2. However, both C_3 and C_4 species do exhibit improved plant water relations under CO_2 enrichment due to decreased stomatal conductance and increased water use efficiency (Eamus and Jarvis, 1989; Rogers et al., 1983; Rogers, Thomas, and Bingham, 1983). For C_3 crops, the greater increase in biomass production coupled with improved plant water relations may impart a more competitive advantage over C_4 crops in a future CO_2-enriched world. This difference in response could become important with regard to future management decisions. In the current study, soybean [*Glycine max* (L.) Merr.] (a N-fixing C_3 crop) and grain sorghum [*Sorghum bicolor* (L.) Moench.] (a C_4 crop) were grown in a large outdoor soil bin under two atmospheric CO_2 concentrations; ambient and twice-ambient CO_2 levels were selected since atmospheric CO_2 may increase to 700 $\mu L\ L^{-1}$ within the next 100 years (Houghton, Callander, and Varney, 1992). The study design offered the opportunity to make a direct statistical comparison of C_3 and C_4 crop species under field conditions over a multi-year period. Our goal was to evaluate the effects of changing CO_2 level on biomass production for soybean and grain sorghum and the implications of these findings as they relate to food security issues, residue management, and belowground processes.

MATERIALS AND METHODS

Soybean ('Stonewall') and grain sorghum ('Savanna 5') were chosen as test crops to represent legume and non-legume crop species, respectively. Plants were grown from seed to maturity in open top field chambers at two atmospheric CO_2 concentrations (ambient and twice-ambient) for three growing seasons (1992-1994). The experimental site was an outdoor soil bin (2-m deep, 6-m wide, and 76-m long) located at the USDA-ARS National Soil Dynamics Laboratory, Auburn, AL, USA (32.6 °N, 85.5°W). The bin contained a Blanton loamy sand (loamy, siliceous, thermic Grossarenic Paleudult) that had been fallow for over 25 years prior to 1992 (Batchelor, 1984). Initial levels of phosphorus (8 kg ha^{-1}) and potassium (14 kg ha^{-1}) were in the 'very low' range. Cation exchange capacity averaged 2.45 $cmol_c$ kg^{-1}, and soil pH averaged 4.7. The initial level of organic matter averaged 5.0 g kg^{-1} and total N was 0.06 g kg^{-1}. A detailed description of the soil status prior to initiation of the study, fertilizer and lime amendments, and soil analysis results have been reported previously (Reeves et al., 1994).

The open top field chambers were constructed of a structural aluminum frame (3-m in diameter by 2.4-m in height) covered with a PVC film panel (0.2 mm thickness) similar to that described by Rogers, Heck, and Heagle (1983). Carbon dioxide was supplied from a 12.7 Mg liquid CO_2 receiver through a high volume dispensing manifold and the atmospheric CO_2 concentration was elevated by continuous injection of CO_2 into plenum boxes. Air was introduced into each chamber through the bottom half of each chamber cover which was double-walled; the inside wall was perforated with 2.5-cm diameter holes to serve as ducts to distribute air uniformly into the chamber. Three chamber volumes were exchanged every minute. Carbon dioxide concentrations were continually monitored (24 hr day^{-1}) using a time-shared manifold with samples drawn through solenoids to an infrared CO_2 analyzer (Model 6252, LI-COR, Inc., Lincoln, NE). Values were continuously recorded every 15-30 minutes for each chamber, depending upon whether or not an additional CO_2 study was on line. In 1992, the mean seasonal daytime CO_2 concentrations were 357.4 ± 0.1 (SE) and 705.0 ± 0.3 $\mu L\ L^{-1}$ for ambient and enriched plots, respectively. In 1993, the mean CO_2 concentrations were 364.0 ± 0.2 and 731.7 ± 0.4 $\mu L\ L^{-1}$. In 1994, the mean CO_2 concentrations were 359.0 ± 0.1 and 706.9 ± 0.4 $\mu L\ L^{-1}$.

Seeds were sown in 6-m rows oriented across the width of the soil bin on 2 June, 5 May, and 6 May in 1992, 1993, and 1994, respectively. In 1994, sorghum plots were replanted in mid June because the first crop failed owing to root rot caused by moist cool soil. Soybean seeds were inoculated with commercial *Rhizobium* (Lipha Tech, Inc., Milwaukee, WI[1]) prior to planting. Plants were thinned for uniformity to a final density of 30 plants m^{-2} for soy-

bean and 26 plants m^{-2} for sorghum. To ensure adequate plant establishment, fertilizer N was broadcast at a rate of 34 kg N ha^{-1} to both the grain sorghum and the soybean shortly after planting. In the grain sorghum, an additional 67 kg N ha^{-1} was applied 30 days after planting. All plots received ambient rainfall and were irrigated only when necessary to prevent drought-induced mortality; a drip irrigation system was used to uniformly distribute water throughout the bin. Total amounts of water received (rainfall + irrigation) were 623, 724, and 1001 mm for 1992, 1993, and 1994, respectively. Weeds were controlled manually. In the off season, weed control was both manually and by glyphosate (N-[phosphonomethyl] glycine) at a rate of 1.0 kg ai ha^{-1}. For three seasons, plants were grown as described above and managed using no-till practices.

The experiment used a split-plot design with three replications. Whole-plot treatments (plant species) were randomly assigned to half of each replication. Subplot treatments (CO_2 levels) were randomly assigned to two open top chambers (3 m diameter) within each whole-plot. Statistical analyses of data were performed using the mixed procedure of the Statistical Analysis System (Littell et al., 1996). A significance level of $P < 0.10$ was established *a priori*. Significant year effects were often observed for the measurements discussed due to the influence of different planting dates coupled with year-to-year weather variability, thus data were reported separately by year.

Plant material was collected at physiological maturity in all years. At each harvest, 12 and 16 plants were collected per chamber in 1992 and 1993/94. Leaf area was determined photometrically and dry weights of organ parts were determined after drying to constant weight at 55°C. In addition, estimates of root system biomass were calculated based on soil core (Prior and Rogers, 1992) and root extraction techniques (Bohm, 1979). Twelve root-soil cores (2.4 cm diameter, 30 cm length) were collected from each chamber. Roots were separated from soil with a hydropneumatic elutriation system (Gillison's Variety Fabrication, Inc., Benzonia, MI; Smucker, McBurney, and Srivastava, 1982). Organic debris was removed with tweezers and spring-loaded suction pipettes and root length was measured with a Comair Root Length Scanner (Hawker de Havilland, Victoria, Australia). Root weight was determined after drying samples at 55°C. The root extraction technique used a manual winch (Model 527, Fulton, Milwaukee, WI) mounted onto a portable metal tripod with a cable gripping tool (Model 72285K8, Klein Tools, Chicago, IL) attached to the plant stalk to break the roots from the soil; a scale (Model 8920, Hanson, Northbrook, IL) measured the peak force (load-kg $plant^{-1}$) required to uproot the plant (Prior et al., 1995). Root samples were collected from 12 and 16 plants per chamber in 1992 and 1993/94, respectively. Plants adjacent to uprooted plants were not sampled in subsequent measurements. After soaking in water, root samples were washed free of soil using a soft bristle brush, dried at 55°C, and weighed. Root dry weights from each root sampling method were

expressed on an area basis and combined for an estimate of total belowground dry weight. Remaining plant stalks within each chamber were cut into 15 cm pieces using hedge clippers; aboveground non-yield residue, including 10% (by weight) of the seed yield, was added back to study plots to simulate normal farm operations (Prior et al., 1997b). Chambers were then removed during the fallow period, but their locations remained fixed and delineated by a permanent 3-m aluminum rings. Bird netting (1.6 cm by 1.9 cm openings; Dalen Products, Inc., Knoxville, TN) was placed over the entire soil bin to prevent movement of aboveground residue into or out of plots.

RESULTS AND DISCUSSION

In the context of future economic and environmental concerns, it is important to assess the response of crops managed under field conditions to reliably predict how agroecosystems will be altered in a future CO_2-enriched world. Most elevated CO_2 research has focused on crop plants, but the majority of these efforts have not been in-ground field studies (see reviews: Kimball, 1983; Rogers and Dahlman, 1993; Rogers, Runion, and Krupa, 1994; Strain and Cure, 1994). Increased C uptake and assimilation generally results in increased crop growth under CO_2-enriched conditions. Plants with a C_3 photosynthetic pathway often exhibit greater growth response relative to those with a C_4 pathway (Bowes, 1993; Poorter, 1993; Amthor, 1995; Amthor and Loomis, 1996; Rogers et al., 1997). The CO_2-concentrating mechanism utilized by C_4 species limits the response to CO_2 enrichment. For C_3 plants, positive responses are mainly attributed to competitive inhibition of photorespiration by CO_2 and the internal CO_2 concentrations of C_3 leaves (at current CO_2 levels) being less than the Michaelis-Menton constant of ribulose bisphosphate carboxylase/oxygenase (Amthor and Loomis, 1996). Furthermore, C_3 species exhibit improved plant water relations by reductions in stomatal apertures and leaf-level conductance under elevated CO_2 (Eamus and Jarvis, 1989; Rogers et al., 1983; Rogers, Thomas, and Bingham, 1983; Prior et al., 1991); C_4 plants also exhibit growth stimulation due to lowered conductance and increased water use efficiency (Rogers et al., 1983; Rogers, Thomas, and Bingham, 1983). A previous report from our field study demonstrated that elevated CO_2 decreased whole plant water use for both C_4 sorghum and C_3 soybean, but this reduction was greater for soybean (Dugas, Prior, and Rogers, 1997). Thus, part of the larger increase in water use efficiency for C_3 vs. C_4 plants with elevated CO_2 (Morrison, 1993) may be attributed to a greater decrease in whole plant water use and a greater increase in biomass production for C_3 crops.

In our study, differences between species were observed for most measured variables (Tables 1 and 2). Both crops exhibited increases in node number,

TABLE 1. Aboveground growth variables for sorghum (SG) and soybean (SB) grown under ambient (A) and CO_2-enriched (E) conditions in 1992, 1993, and 1994. Means and probabilities are shown.

Treatment	Height (cm)	Node Number	Stem Diameter (mm)	Leaf Area (cm^2)	Seed Number	Seed Mass $Seed^{-1}$ (g)
1992						
A-SG	131.9	8.5	9.83	988.4	683.2	0.0273
E-SG	155.4	9.5	10.46	1468.4	756.1	0.0279
A-SB	81.5	13.1	5.57	1360.6	61.8	0.0758
E-SB	95.3	13.5	6.78	1637.0	86.7	0.0819
SPP[a]	0.0001	0.0002	0.0001	0.0279	0.0001	0.0009
CO_2	0.0006	0.0598	0.0166	0.0056	0.1681	0.0054
SPPxCO_2	0.1380	0.4342	0.3765	0.3426	0.4789	0.0103
1993						
A-SG	126.2	8.8	10.74	1333.1	1030.1	0.0233
E-SG	157.3	10.8	12.27	1850.5	1106.0	0.0241
A-SB	84.5	13.8	6.13	1660.7	70.2	0.0517
E-SB	95.2	15.0	7.09	1947.7	91.4	0.0612
SPP	0.0001	0.0001	0.0013	0.0364	0.0001	0.0020
CO_2	0.0003	0.0067	0.0002	0.0001	0.5024	0.0248
SPPxCO_2	0.0052	0.3446	0.0404	0.0132	0.7022	0.0417
1994						
A-SG	105.6	9.8	6.98	647.3	323.3	0.0302
E-SG	128.9	10.2	7.67	784.5	398.2	0.0290
A-SB	95.4	13.5	6.37	1636.4	61.3	0.0965
E-SB	106.8	14.1	7.08	1775.1	79.7	0.1166
SPP	0.0003	0.0001	0.0239	0.0001	0.0010	0.0001
CO_2	0.0002	0.0047	0.0001	0.0012	0.1442	0.0190
SPPxCO_2	0.0526	0.5494	0.8581	0.9771	0.3647	0.0126

[a] Values are Pr > F from mixed model analysis; SPP = main effect of species, CO_2 = main effect of CO_2 level, SPPxCO_2 = interaction.

basal diameter, and height under elevated CO_2 (Table 1). In general, elevated CO_2 increased sorghum and soybean stem biomass by > 45% (averaged across years) (Table 2). Leaf area and leaf dry weight were usually higher for soybean versus sorghum and CO_2-induced increases in these measures were due to larger leaves rather than a change in leaf number (data not shown). Elevated

TABLE 2. Above- and belowground dry weights (g m^{-2}) for sorghum (SG) and soybean (SB) grown under ambient (A) and CO_2-enriched (E) conditions in 1992, 1993, and 1994. Means and probabilities are shown.

Treatment	Stem	Leaf	Hull or Head[a]	Residue[b]	Seed	Belowground[c]
1992						
A-SG	253.5	110.3	89.2	453.0	472.5	130.6
E-SG	351.5	155.9	105.0	612.4	543.0	179.1
A-SB	244.1	148.7	127.5	409.8	142.9	199.9
E-SB	371.8	187.0	178.8	552.7	213.2	285.3
SPP[d]	0.7760	0.0077	0.0006	0.7817	0.0001	0.0001
CO_2	0.0003	0.0032	0.0070	0.0270	0.0105	0.0002
SPPxCO_2	0.4413	0.6938	0.0831	0.8611	0.9985	0.1211
1993						
A-SG	360.2	178.7	147.3	686.2	584.5	226.7
E-SG	540.4	250.6	161.8	952.8	672.5	271.7
A-SB	412.2	224.4	130.7	767.3	108.5	156.2
E-SB	663.1	304.9	193.4	1161.8	168.5	228.7
SPP	0.0074	0.0003	0.5012	0.0074	0.0001	0.0457
CO_2	0.0001	0.0001	0.0075	0.0001	0.0139	0.0054
SPPxCO_2	0.0506	0.5400	0.0569	0.0362	0.5707	0.2688
1994						
A-SG	171.9	76.8	63.0	311.8	245.5	120.7
E-SG	239.9	99.2	75.7	414.8	299.9	188.1
A-SB	480.1	235.2	131.7	847.0	177.8	196.7
E-SB	649.4	264.0	175.0	1088.5	273.2	280.8
SPP	0.0001	0.0001	0.0003	0.0001	0.1877	0.0591
CO_2	0.0001	0.0001	0.0083	0.0001	0.0040	0.0048
SPPxCO_2	0.0038	0.2653	0.0570	0.0015	0.1787	0.5848

[a] Soybean pod hull weight or sorghum head weight, minus seed.
[b] Sum of all aboveground non-yield components.
[c] Total root dry weight including nodules for soybean.
[d] Values are Pr > F from mixed model analysis; SPP = main effect of species, CO_2 = main effect of CO_2 level, SPPxCO_2 = interaction.

CO_2 increased soybean pod hull weight by ~ 40% (averaged across years), but had little effect on sorghum head weight (Table 2). Total non-yield residue production (i.e., stover) for both crops was increased by > 35% (averaged across years) due to elevated CO_2. Differences in seed number were observed between sorghum and soybean, but were not affected by CO_2 level. However,

weight per seed increased for soybean under elevated CO_2 and soybean seed biomass was increased by 53% (averaged across years) compared to a 17% increase for sorghum (Table 2).

In the context of food security, the reported yield responses for these important crops is significant. The observed increase in soybean yield may have implications for major soybean production regions (FAO, 1996) located in the United States, South America (e.g., Brazil and Argentina), and Asia (e.g., China and India). Sustainability of sorghum production is also critical since it historically represents one of five major cereal crops used for food and is also important for animal consumption (Doggett, 1988; Bennett, Tucker, and Maunder, 1990). Major regions of sorghum production (FAO, 1996) are located in the United States, Mexico, Asia (e.g., China and India) and throughout Africa. Since sorghum is a major food staple for many developing countries (FAO, 1996), especially in semiarid regions (Doggett, 1988; Bennett, Tucker, and Maunder, 1990), it is essential to evaluate changes in the global environment that will affect productivity. Although reported increases in sorghum yield were substantially less than for soybean (Table 2), small yield shifts may be significant, particularly for semiarid regions of the world where reduced whole plant water use (Dugas, Prior, and Rogers, 1997) could help ameliorate periods of drought stress. Special emphasis should also be given to the reported positive shifts in non-yield biomass production in terms of future residue management considerations in these regions. For example, selecting planting and seed zone preparation implements that minimize disturbance of residue and underlying soil can lead to soil water conservation (Reicosky et al., 1999; Prior et al., 2000) which could be critical to successful seedling establishment in these semiarid regions. In order to improve food security and to alleviate poverty on the African continent, the African Conservation Tillage Network (ACT) has recently been established to promote the adoption of conservation tillage practices to ensure more sustainable use of the soil resources and to combat desertification (ACT, 2000). Findings from the current study suggest that CO_2-induced shifts in grain yield and crop water use could improve food security while increases in non-yield residue could complement conservation management efforts by ensuring greater soil surface coverage thereby promoting more soil water storage while preventing soil erosion losses. However, it is important to note that our work was conducted in a temperate region and more CO_2 research in this and other areas (e.g., semiarid and tropical regions) which evaluate regional crop management systems are needed before firm conclusions can be made.

Positive increases in non-yield residue inputs (Table 2) returned to the soil surface may impact implement effectiveness during tillage operations. In conventional tillage systems, the degree of residue cutting/burial (e.g., disc, chisel plow operations) may be altered by increased residue inputs resulting from

CO_2 enrichment. Such occurrences may require increasing tillage depth which could increase future field operational expenses (e.g., energy/fuel cost and tractor/equipment wear). However, current debate highlights the importance of modifying traditional tillage practices to promote sequestration of soil C in agroecosystems; management decisions that reduce tillage activities in favor of maintaining more soil surface residue and greater percent ground cover could reduce soil C losses, increase soil C storage, and help ameliorate the rise in atmospheric CO_2 (Follett, 1993; Lal et al., 1998a, 1998b). Adoption of such practices would also reduce water losses, erosion processes, and possibly improve overall soil quality (Reeves, 1997). In this context, land managers could realize some benefits by continuing to follow current operational schemes and accept less residue cutting/burial in conventional tillage systems.

In conservation tillage systems, these same CO_2-related advantages would exist, but to a greater extent due to lack of tillage and a higher accumulation of non-yield residue (Table 2). Previous work from our study showed a significant increase in percent ground cover under CO_2-enrichment (Figure 1; Prior et al., 1997b), but no significant effect on percent residue biomass recovery in litter bags was noted (Figure 2; Torbert et al., 2000). Measurement of mass losses from leaves and stems indicated a species effect which varied by tissue type; decomposition of soybean leaf tissue proceeded more rapidly than sor-

FIGURE 1. The average percent ground cover following an over-winter fallow period for sorghum and soybean (A) and for ambient and enriched CO_2 treatments (B). Main effect means are shown. Adapted from Prior et al. (1997b).

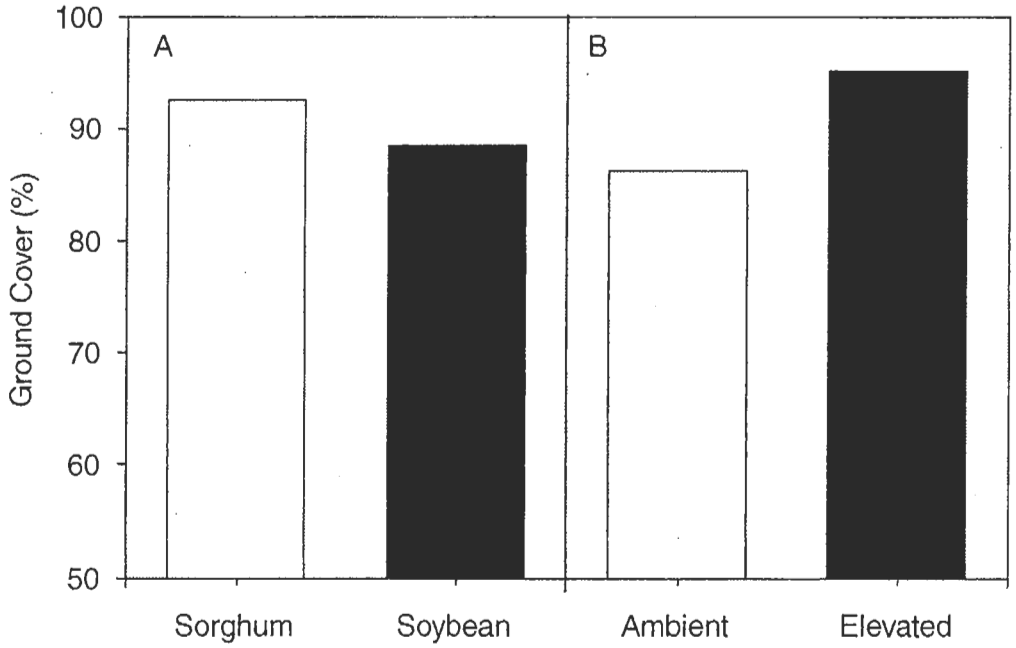
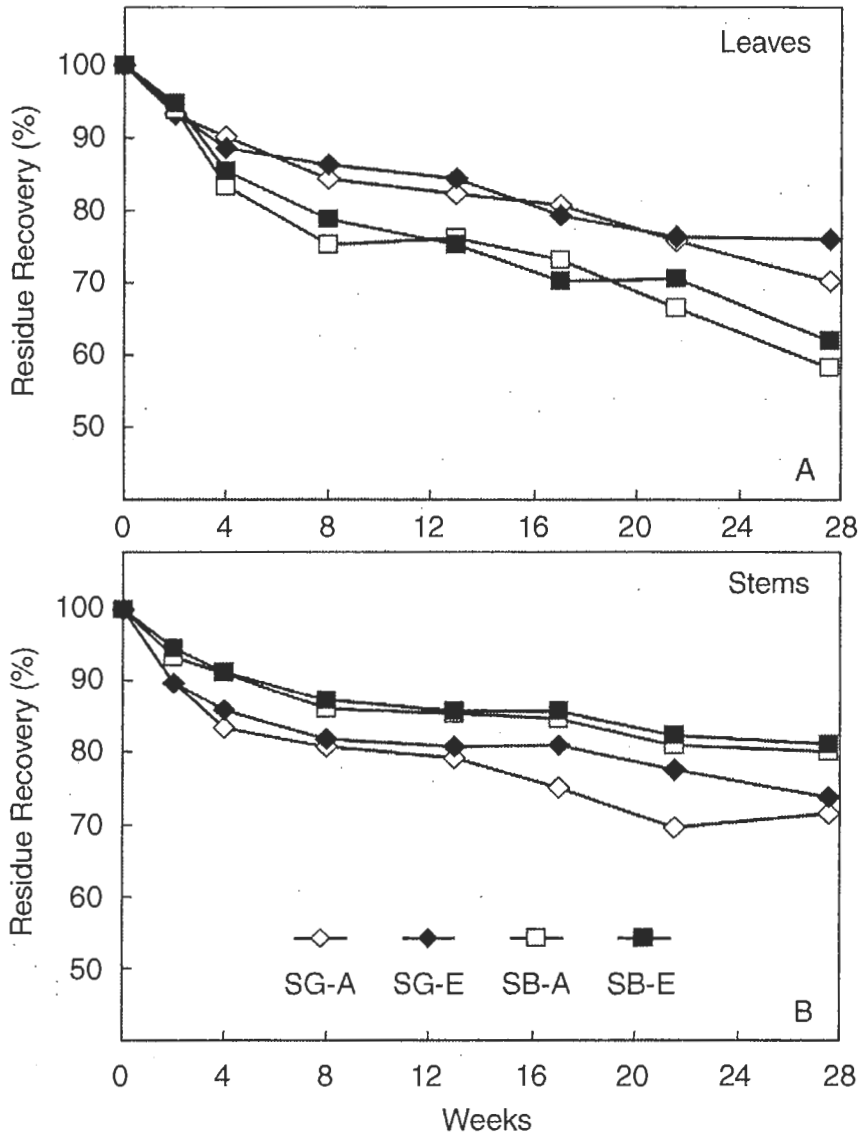


FIGURE 2. Recovery (%) of ambient and elevated CO_2-produced sorghum and soybean leaf (A) and stem (B) residue during an over-winter fallow period. Adapted from Torbert et al. (2000).



ghum, as would be expected with a lower C:N ratio; however, the opposite pattern was observed with stem tissue. Even though CO_2 level did not affect percent biomass recovery, greater production under elevated CO_2 resulted in more biomass remaining after the over-winter fallow period.

Some disadvantages associated with greater residue accumulation could occur in relation to crop stand establishment. Planter designs used in current conservation systems often have problems handling high amounts of residue during seed bed preparation/planting (e.g., clogged planters) resulting in poor

stands (Phillips, 1984; Throckmorton, 1986). Precluding significant improvements in planter design, CO_2-induced increases in residue production could exacerbate this problem, especially in systems with additional residues from cover crops. Increased residue coverage of the soil surface can also reduce soil temperatures below optimum for seed germination, thereby delaying stand development (Erbach et al., 1986; Unger, 1986; Potter, Morrison, and Torbert, 1996). Higher production of non-yield residue in a CO_2-enriched world may require land managers to select conservation tillage methods such as strip tillage as opposed to no-tillage during planting to overcome such problems.

Relative to aboveground responses, CO_2 effects on root systems have received less attention despite their importance in attaining essential soil resources and their residue contributions to soil organic matter. In the current study, total belowground dry weight was increased by 44 and 38% (averaged across years) for soybean and sorghum, respectively (Table 2). CO_2-induced increases in soybean and sorghum root biomass have been previously reported (Chaudhuri et al., 1986; Chaudhuri, Kirkham, and Kanemasu, 1990; Del Castillo et al., 1989; Rogers et al., 1992) and in many instances the largest proportion of the extra phytomass produced as a result of elevated CO_2 is found belowground (Bazzaz, 1990; Rogers, Runion, and Krupa, 1994; Wittwer, 1995). Fine root density patterns (both length and dry weight) were also assessed in the current study and the extent of CO_2-induced changes were found to be species dependent; elevated CO_2 had a much greater positive affect on soybean compared to sorghum (Figures 3 and 4).

Other field studies using FACE have shown that high CO_2 can increase belowground production (Prior et al., 1994b), alter plant root morphology (Prior et al., 1995), and increase the root system's capacity to explore soil volume through shifts in fine root distribution patterns (Prior et al., 1994a; Weschsung et al., 1999). Such CO_2-induced changes in rooting patterns may influence whole-plant nutrient dynamics, thus influencing crop performance when demand for nutrients and water is high. In general, whole plant nutrient uptake and nutrient utilization efficiency are increased under elevated CO_2, while nutrient tissue concentration and nutrient uptake efficiency are lowered (Rogers, Runion, and Krupa, 1994; Prior et al., 1998). Nutrient management decisions may also be impacted by CO_2-induced shifts in root distribution patterns which could alter nutrient stratification within the soil profile. This would be more likely in reduced-tillage systems compared to conventional tillage systems which exhibit a more homogeneous plow layer due to mixing of soil with residues and amendments (e.g., fertilizers and lime).

The quality of water moving in the hydrological cycle is critically important in agroecosystems. Positive CO_2-induced shifts in crop root systems may enhance the ability of plants to capture a greater proportion of available nutrients, thus reducing the leaching of nutrients, such as nitrates, into groundwater. The

FIGURE 3. The effect of CO_2 concentration (A = ambient; E = elevated) on sorghum (SG) and soybean (SB) root length density (RLD) in 1992, 1993, and 1994.

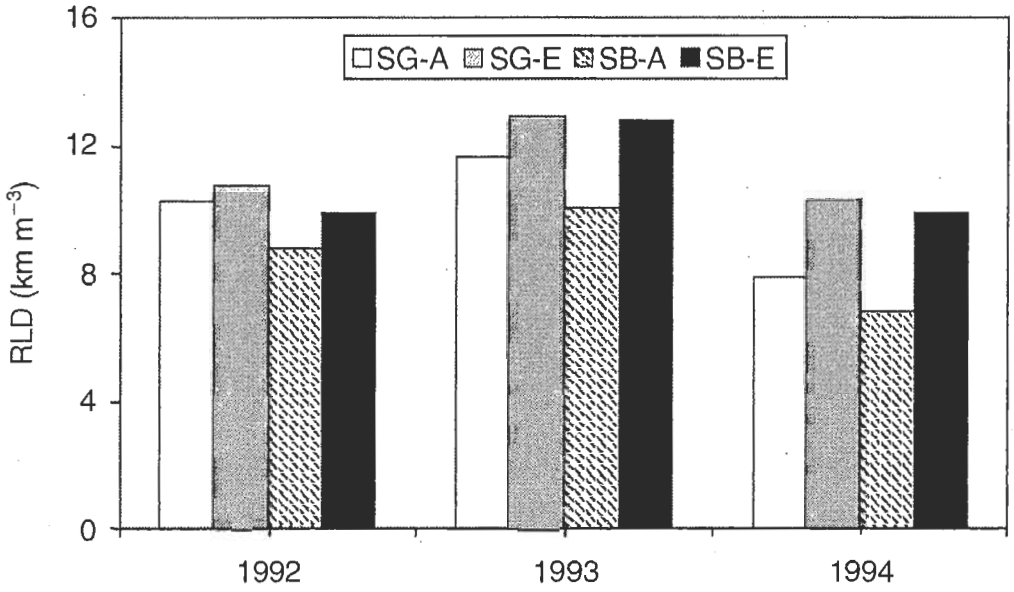
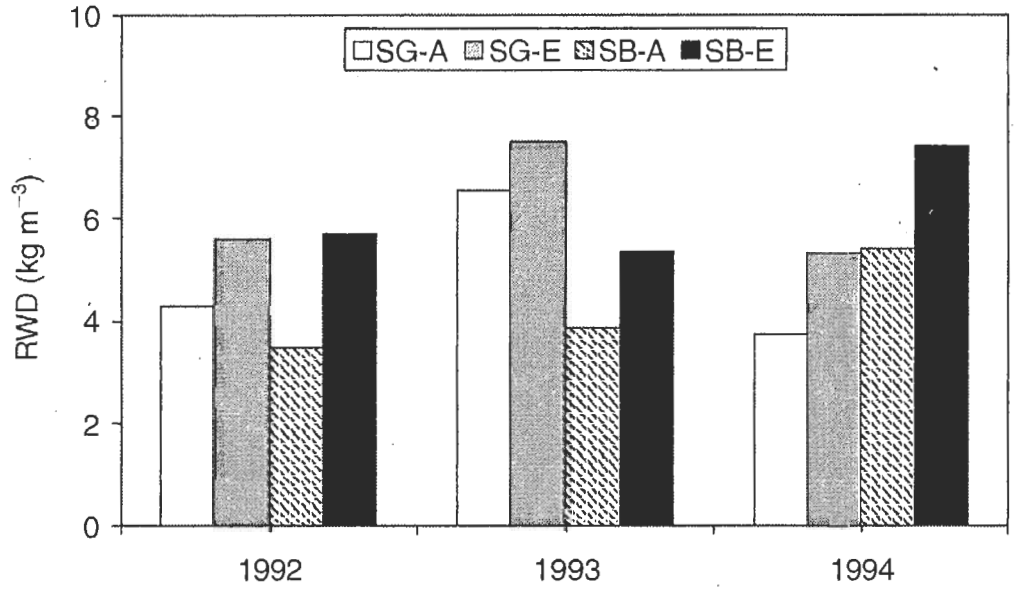


FIGURE 4. The effect of CO_2 concentration (A = ambient; E = elevated) on sorghum (SG) and soybean (SB) root dry weight density (RWD) in 1992, 1993, and 1994.



fate of N is a growing concern since nitrate contamination of groundwater is associated with potential health risks. Belowground N content is a balance of N in biomass, N loss processes such as nitrate leaching and denitrification, and N inputs through fertilizers, atmospheric deposition, and N_2 fixation by certain plant species. Nitrate leaching is dependent on the amount of nitrate in the edaphic environment and on the amount of water percolating through the soil profile. These factors may be altered by changes in atmospheric CO_2. Our study has previously demonstrated that elevated CO_2 will change both the C:N ratio of residue inputs to the soil (affecting the soil nitrate content; Torbert et al., 1996) and plant water relations (affecting water movement through the soil profile; Dugas, Prior, and Rogers, 1997). Results from two years of CO_2 enrichment in our study showed that nitrate leaching was reduced during the growing season because more N was captured by high CO_2-grown crops (Torbert et al., 1996). Furthermore, leaching was also reduced during the fallow period, which may be related to altered decomposition patterns resulting from the increased C:N ratio of residue. Nitrate leaching was generally higher for soybean compared to sorghum most likely due to higher N inputs to the soil from symbiotic N_2 fixation and lower residue C:N ratio. Furthermore, analysis of nitrate solution for ^{15}N content indicated that most of the N measured below the root zone originated from native N pools rather than from N-fertilizer application in both cropping systems. It is important to note that results from our study are indicative of leaching patterns associated with areas cropped with soybean and sorghum on a loamy sand soil under a no-till management system. Leaching patterns will likely vary with soil series and tillage practice. The impact of leaching on groundwater quality may be even more critical during disturbance events (e.g., plowing) which occur in conventional tillage systems.

Knowledge of changes in soil C due to elevated atmospheric CO_2 is essential to understanding global C cycling. Enhanced crop growth (both above- and belowground) under elevated CO_2 as reported in Table 2 suggests greater delivery of C to soil; extra C from elevated atmospheric CO_2 can enter the rhizosphere via residue decomposition, root growth, turnover, and exudation (Norby et al., 1987; Lekkerkerk, Van de Geijn, and Van Veen, 1990; Zak et al., 1993). Despite the well documented rise in atmospheric CO_2 concentration (Keeling and Whorf, 1994), not all C sinks are well defined, i.e., an estimated unknown sink of 1.4×10^{15} g C year^{-1} arises from the global C balance (Schimel et al., 1995). Crucial considerations in balancing the global C budget are that biospheric uncertainties are very large, that anthropogenic CO_2 is small relative to the natural exchange and abundance of C (Sundquist, 1993), and that description of the C cycle is incomplete (Bolin, 1981; Whipps, 1990). Although its specific identity has eluded detection, the sink is probably somewhere in the world's terrestrial plants and soils (Sundquist, 1993; Schimel, 1995). Soil plays a major role in the global accounting of C not only due to the

large amount of C stored in soil (estimates of 1395 to 1636 $\times 10^{15}$ g) (Ajtay, Ketner, and Duvigneaud, 1979; Post, Emanuel, and King, 1992; Schlesinger, 1984), but also since annual soil flux of CO_2 to the atmosphere is 10 times that contributed by fossil fuel burning (Post et al., 1990). Enting and Pearman (1986) suggested that although in the past the biosphere has been a net C source, it is currently acting as a C sink. This is supported by estimates that the "pioneer agriculture effect in the USA" released some 60 $\times 10^{15}$ g C to the atmosphere from 1860 to 1890 (Wilson, 1978) which is 1.5 times the amount released by all industrial sources (mainly fossil fuel usage) prior to 1950. A portion of the terrestrial sink is likely the result of converting agricultural land back to natural or perennial vegetation (Post and Kwon, 2000). However, if the terrestrial biosphere has changed from a CO_2 source to a CO_2 sink, then agriculture, which accounts for fully 10% of all land on earth (Schlesinger, 1990), may play a pivotal role in global C sequestration (Cole et al., 1993; Kern and Johnson, 1993; Paustian et al., 1997; Lal et al., 1998a, 1998b). In a global context, agroecosystems are significant since approximately 1.3 $\times 10^{15}$ g of gross atmospheric CO_2 is removed by crops each year (Jackson, 1992) and soil C storage patterns in these systems are very sensitive to management practices (e.g., conservation practices, tillage systems, and cropping systems) (Kern and Johnson, 1993). All these factors combine to make the understanding of C cycling in soils of agroecosystems important, especially in the context of rising atmospheric CO_2.

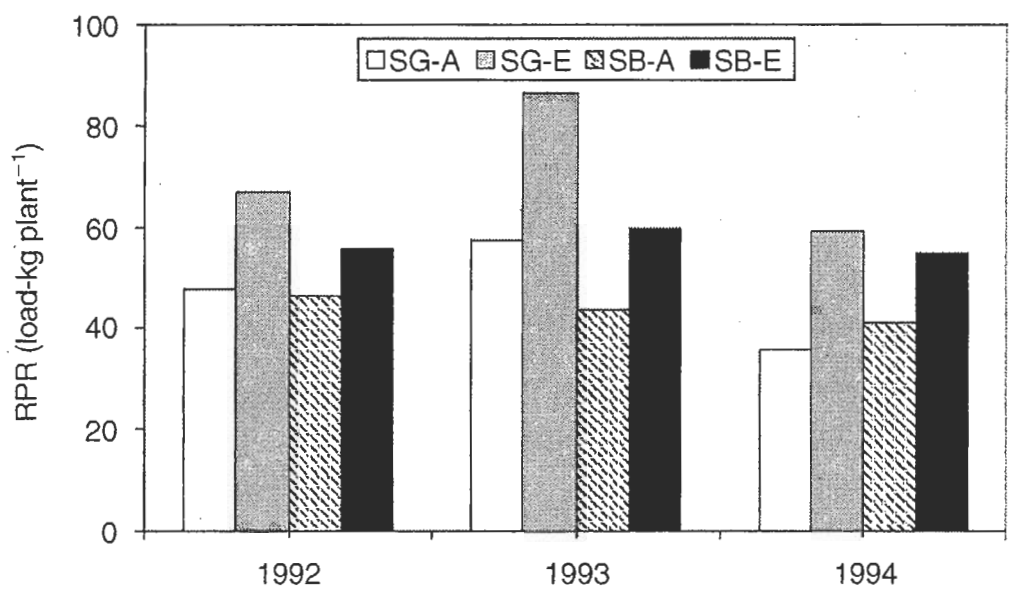
The ability of terrestrial ecosystems to sequester additional C in soil from increasing levels of CO_2 in the atmosphere is highly debated. Schlesinger (1986, 1990) found little evidence for soil C storage and Lamborg, Hardy, and Paul (1984) have argued that increased soil microbial activity due to greater biomass C inputs in an elevated CO_2 environment (i.e., "the priming effect") would prevent accumulation of soil organic C. Alternatively, Goudriaan and de Ruiter (1983) proposed that increased soluble, easily decomposable C inputs (due to CO_2 enrichment) would accentuate soil microbial substrate preference mechanisms; that is preference for easily decomposable substrates would retard the decomposition of recalcitrant, structural plant debris and native soil organic matter resulting in an accumulation of soil organic matter. Experimental evidence with wheat (*Triticum aestivum* L.) grown under elevated CO_2 in a short-term growth chamber experiment (Lekkerkerk, Van de Geijn, and Van Veen, 1990) has supported the contentions of Goudriaan and De Ruiter (1983). Long-term field studies (at our laboratory and others) indicate that agroecosystems have the potential to sequester C from the atmosphere into the soil (Wood et al., 1994; Leavitt et al., 1994; Torbert, Prior, and Rogers, 1995; Henning et al., 1996; Prior et al., 1997c; Torbert et al., 1997). A 3-year study with cotton (*Gossypium hirsutum* L.) has suggested that soil C storage is more likely under non-limiting soil water conditions when CO_2 concentration is

raised (Wood et al., 1994). Their findings indicated that factors other than total biomass input may affect soil C and N cycling; a possible explanation may be related to a differential effect of CO_2 and irrigation treatment on residue structure/composition which has altered decomposition patterns. In a similar study, an evaluation of soils after 2 years of wheat residue inputs indicated that more C storage may occur under elevated CO_2 for both irrigated and non-irrigated farm systems (Prior et al., 1997c). In our study, we observed that short-term CO_2 fluxes were greater for soybean under tillage or elevated CO_2; flux rates in the sorghum crop were affected by tillage, but they were not impacted by CO_2 level (Prior et al., 1997b). It is important to note that these short-term results were based on characterizing C losses associated with a simulated spring tillage event on microplots, thus, results should be viewed with caution when predicting long-term C turnover in agroecosystems. However, working in the same study using stable isotope techniques, Torbert et al. (1996) also noted differences in C storage patterns for sorghum and soybean after 2 years of CO_2 treatment. The high C:N ratio of sorghum residue slowed microbial decomposition resulting in increased new soil C, but CO_2-induced C storage occurred in the mineral fraction only. In comparison, the low C:N ratio of soybean residue promoted decomposition of new C inputs which reduced the decomposition of old C thereby increasing soil C storage. For a more thorough discussion on elevated CO_2 effects on residue decomposition as it relates to soil C and soil N interactions see Torbert et al. (2000). Collectively, the results suggest that the biodegradability of crop residue may not only be affected by the environment they were produced under but may also be species dependent, thereby accounting for differences in soil C storage patterns. To more fully elucidate the relationships between nutrient cycling and decomposition of plant materials produced in an elevated CO_2 environment, future studies must be concerned with crop species effects and must also consider the influence of other factors such as cover crops, crop rotations, soil series, tillage practices, and regional climatic differences.

The effects of additional residue input from elevated CO_2 on soil physical properties and their impact on soil C storage, has not been well studied. A more extensive residue mat should promote more favorable soil surface characteristics such as prevention of soil crusting. Minimizing soil crusting could enhance seedling emergence, water infiltration, soil water retention, and reduced soil erosional processes. This study clearly demonstrated that elevated CO_2 increased non-yield residue returned to the soil surface (Table 2) and percent ground cover following an over-wintering period (Figure 1; Prior et al., 1997b). Stabilization of the soil matrix by larger root systems under elevated CO_2 can be inferred from an increase in vertical root-pulling resistance (Figure 5); this may suggest reduced wind and water erosion on cropping systems located on highly erodible lands. Vertical root-pulling resistance was increased by

30% (averaged across years) for soybean and by 53% for sorghum (Figure 5). This finding is in general agreement with results reported for cotton (Prior et al., 1995). Positive shifts in crop root systems (Table 2; Figures 3 and 4) may alter soil structural characteristics (e.g., due to increased number and extent of root channels) which could lead to increases in aggregate stability, porosity, infiltration rates, and subsequent soil water storage. Changes in soil structure could possibly lead to increased rates of soil genesis (Brinkman and Sombroek, 1996). However, most of these hypothesized changes have yet to be examined in detail. A preliminary evaluation of soil physical characteristics indicated that soil structure was altered by elevated CO_2 in the soybean system only (Prior and Amthor, unpublished). In this case, the soil had lower bulk density values, more water stable aggregates, and exhibited positive shifts in saturated hydraulic conductivity, thereby suggesting that soil porosity had been increased under elevated CO_2. Such changes in the soil may be due to soybean residue quality (lower C:N ratio) in combination with a greater positive affect of elevated CO_2 on soybean fine root density patterns (both length and dry weight) compared to sorghum (Figures 3 and 4). Detailed examination of residue input (quality and quantity) in relation to soil C and N dynamics indicates that N availability exerts a strong influence on belowground decomposition processes (see review; Torbert et al., 2000) which may alter soil physical and chemical properties. Such shifts, in conjunction with root turnover, root exu-

FIGURE 5. The effect of CO_2 concentration (A = ambient; E = elevated) on sorghum (SG) and soybean (SB) vertical root-pulling resistance (RPR) in 1992, 1993, and 1994.



dation, and other biological activity (increased populations of microbes and soil fauna and fungi), may influence soil aggregate formation and nutrient cycling. CO_2-induced changes in soil physicochemical characteristics may lead to improvements in overall soil quality; such changes, however, will likely be dependent on crop species and management.

The direct effect of elevated CO_2 noted for crop productivity may also impact weed control management in agroecosystems. Some weed species may have competitive advantages under high CO_2 due to differential effects of CO_2 on growth which favor C_3 over C_4 weeds (Patterson, 1993). The reported increases in non-yield residue for soybean and sorghum cropping systems may suppress weeds (mulch effect) in conservation management systems. Although, the introduction of genetically modified crops (e.g., glyphosate tolerant soybean) into production systems represents another means to combat weeds, it is unknown if they will show the same growth responses to CO_2 as current day varieties. Weed management may be further complicated by response of weed species to herbicides under high CO_2 conditions. Ziska, Teasdale, and Bunce (1999) studied two of the world's worst weeds, representing a C_3 species, common lambsquarters (*Chenopodium album* L.), and a C_4 species, redroot pigweed (*Amaranthus retroflexus* L.), to a widely used postemergence herbicide (glyphosate) under conditions of elevated CO_2. They reported that current application rates could control *A. retroflexus*, but the economic cost of controlling *C. album* may increase under elevated CO_2 as standard herbicides rates were inadequate. These differential responses coincided with changes in stomatal conductance; however, changes in foliar absorption (and uptake) were not documented. Some studies have shown that elevated CO_2 may increase epicuticular wax deposition (based on SEM micrographs; Thomas and Harvey, 1983), while others have reported a decrease in wax density (Graham and Noble, 1996; Prior et al., 1997a) and changes in wax morphology (Prior et al., 1997a). Thus, one other possible mechanism explaining this finding might be related to changes in epicuticular waxes (quantity, composition, or morphology) which could alter permeability to chemicals including herbicides (Martin and Juniper, 1970; Von Wetsein-Knowles, 1993). If increases in commercial application rates of herbicides are required to control some weeds under high CO_2, it is unknown if tolerance levels of genetically modified crops (e.g., glyphosate tolerant soybean and cotton) are adequate since no information exists on responses of these altered crops to elevated CO_2.

Another unknown aspect of genetically modified material is how the introduction of such material might alter decomposition processes and microbial populations in the soil environment. Ellis, Thompson, and Bailey (1995) demonstrated that introduction of genetically modified microorganisms (as a seed dressing) did not disrupt the natural succession of microbial communities in a

231-day sugar beet (*Beta vulgaris*) study. Saxena, Flores, and Stotzky (1999) found that an insecticidal toxin was released into the rhizosphere of *Bt*-modified corn through root exudates and that this toxin remained biologically active in soil for at least 234 days; the impacts of such genetically altered plants on rhizosphere and soil microbial populations are unknown. Microbes are important for maintaining plant health and productivity and elevated CO_2 has been shown to affect soil microbial community composition and activity (Zak et al., 1993; Rice et al., 1994; Runion et al., 1994). However, limited research precludes drawing firm conclusions regarding the effects of elevated CO_2 on interactions of microbes with plants and plant material in soil; adding use of genetically modified plants and microbes into this scenario makes it even more difficult to predict how crop productivity might be affected by future farming practices under increasing levels of atmospheric CO_2.

The atmospheric CO_2 concentration has risen by 30% since the onset of the Industrial Revolution in the late 18th century; this increase may be the most significant change taking place on the earth today. No sector has more to lose or gain, in regard to global environmental change, than agriculture. Growth and yield of most plant species, including economically important crops, have been shown to increase under elevated CO_2. We found that yield response to elevated CO_2 was greater for soybean than for sorghum; however, the response of non-yield residues (including roots) of these contrasting (C_3 vs. C_4) crops was similar. Our findings suggest that increasing levels of atmospheric CO_2 could improve food security, soil physical properties, and groundwater quality. Increases in the non-yield components could have implications for residue management including farming practices to increase soil C sequestration and protect soil resources. Research will be required to fully understand the relationships between biomass production, nutrient cycling, and decomposition of residue produced in elevated CO_2 environments. Effects of CO_2 on crops grown under conservation tillage systems require further investigation. Future studies should address not only species effects, but must also consider how other factors (cover crops, crop rotations, soil series, tillage practices, and regional climatic differences) influence the response of agroecosystems to rising levels of atmospheric CO_2. Such factors must be considered due to the wide diversity of farm management systems that exist over an international scale. Evaluation of farming systems representative of underdeveloped countries must also be included to accurately assess how these regions will be impacted by the rise in atmospheric CO_2. Understanding the whole biological chain of events starting with transfer of C from air to leaf, transformation within the plant for growth and yield, return of plant residue to the soil, decomposition, C storage within soils of agricultural systems, and finally impacts of other environmental factors (e.g., nutrients and water) on these processes is

necessary to optimize soil management for both agricultural production and C sequestration. Reducing uncertainty regarding the effects of rising atmospheric CO_2 is critical if the impacts of global change on agriculture and environmental quality are to be predicted.

NOTE

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

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