

# Effects of elevated atmospheric CO<sub>2</sub> on root dynamics and productivity of sorghum grown under conventional and conservation agricultural management practices

Seth G. Pritchard<sup>a,\*</sup>, Stephen A. Prior<sup>b</sup>, Hugo H. Rogers<sup>b</sup>, Micheal A. Davis<sup>c</sup>,  
G. Brett Runion<sup>b</sup>, Thomas W. Popham<sup>d</sup>

<sup>a</sup>Department of Biology, College of Charleston, Science Center, 58 Coming Street, Charleston, SC 29401, USA

<sup>b</sup>USDA-ARS National Soil Dynamics Laboratory, 411 S. Donahue Drive, Auburn, AL 36832, USA

<sup>c</sup>Department of Biology, University of Southern Mississippi, Hattiesburg, MS 39406-5018, USA

<sup>d</sup>USDA-ARS Southern Plains Area, 1301N Western Road, Stillwater, OK 74075-2714, USA

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## Abstract

Although it is widely acknowledged that rising atmospheric CO<sub>2</sub> concentrations will increase crop root growth, no study has considered how this response could be influenced by agricultural management practices. Therefore, we examined the influence of elevated atmospheric CO<sub>2</sub> (ambient + 360 μmol mol<sup>-1</sup>) on root dynamics of sorghum (*Sorghum bicolor*) produced under conventional (tillage following winter fallow) and conservation (no-till following clover (*Trifolium repens*) winter cover crop) agricultural management practices. Crops were grown in an outdoor soil bin facility and CO<sub>2</sub> treatments were administered using open-top field chambers (OTC). Root dynamics were analyzed using minirhizotrons. In conventional tillage plots, CO<sub>2</sub>-enrichment increased sorghum seasonal root production and mortality by 58 and 59%, respectively. Root growth, however, was unaffected by [CO<sub>2</sub>] in conservation plots. Growth in CO<sub>2</sub>-enriched atmospheres increased residue production by 15 and 11% in conventional and conservation plots, respectively. Grain production was 6% greater in the conservation than conventional plots but was unaffected by atmospheric CO<sub>2</sub>. Neither carbon dioxide nor management practices had any impact on the proportion of roots that died by physiological maturity (i.e., root turnover). The fraction of roots that had died by physiological maturity decreased in a linear fashion from shallow to greater soil depths. Although management did not affect cumulative seasonal root production or mortality it did influence vertical root distribution; conservation management favored shallow root systems whereas conventional management favored deeper rooting. Data emphasize the importance of quantifying production and mortality as separate processes. This study suggests that conversion from conventional to conservation management practices might diminish stimulation of rooting by rising atmospheric CO<sub>2</sub>, at least in the C<sub>4</sub> crop sorghum.

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## 1. Introduction

Root growth of crop plants, almost without exception, is enhanced in CO<sub>2</sub>-enriched atmospheres (Pritchard and Amthor, 2005; Rogers et al., 1994). In fact roots are often stimulated to a greater extent than are leaves, stems, and

reproductive structures (Kimball et al., 2002; Norby et al., 1992). Roots become more numerous, longer, thicker, and faster growing in crops exposed to high CO<sub>2</sub> (Chaudhuri et al., 1990; Prior et al., 1994a,b, 1995). Root systems of CO<sub>2</sub>-enriched crops are often more highly branched, especially at shallower soil depths, compared to roots of crops grown in ambient air (*Sorghum bicolor*, Chaudhuri et al., 1986; *Triticum aestivum*, Chaudhuri et al., 1990, Fitter et al., 1996; *Carotonia siliqua*, Cruz et al., 1997; *Glycine*

\* Corresponding author. Tel.: +1 843 953 5995; fax: +1 843 953 5453.  
E-mail address: [pritchards@cofc.edu](mailto:pritchards@cofc.edu) (S.G. Pritchard).

max, Del Castillo et al., 1989; *Gossypium hirsutum*, Rogers et al., 1992). These effects indicate altered belowground plant function, and also suggest that higher level soil ecological processes may change as atmospheric CO<sub>2</sub> concentrations continue to rise (Pritchard and Rogers, 2000; Rogers et al., 1997, 1999).

Our understanding of crop root responses to elevated CO<sub>2</sub> is far from complete. It is, in fact, based almost entirely on data from isolated destructive root harvests, often from container grown plants (Norby, 1994). While this approach may provide useful information about root and whole plant function at a single moment in time, it does little to further our understanding of how more dynamic aspects of root structure and function may be affected. For example, our understanding of the effects of rising atmospheric CO<sub>2</sub> levels on C allocation belowground is primarily based on static measures of R:S (root:shoot ratio). This measure not only ignores C lost through respiration, exuded into soil, diverted to symbionts, and grazed by soil fauna, but it also discounts C lost through the process of root mortality (turnover). This is a significant omission since root turnover may represent one of the greatest belowground energy expenditures to plants (Caldwell, 1977; Canadell et al., 1996). By quantifying root production and mortality separately, much can be learned about how rising CO<sub>2</sub> might affect seasonal C allocation to roots. It will also provide important information about how root longevity may respond to rising CO<sub>2</sub>. Furthermore, quantifying seasonal root production, in conjunction with measures of soil organic C content, will provide much needed data on the potential for agricultural soils to sequester C (Pritchard and Rogers, 2000).

Some form of conservation tillage is expected to be adopted on 60–80% of agricultural land in the USA by the year 2010 (Lee et al., 1993). Tillage and residue management practices affect soil characteristics such as water holding capacity, soil physical properties, temperature, and microbial activity. In turn, these changes influence root growth dynamics (Turman et al., 1995). For example, roots growing under no-till conditions are often distributed more densely in shallow soil layers whereas tilled soil promotes root growth at greater soil depths (Cheng et al., 1990; Rasse and Smucker, 1998; Whiteley and Dexter, 1982). But, as is the case with CO<sub>2</sub>-enrichment, the effects of agricultural management practices on temporal root growth patterns are not well understood (Swinnen et al., 1995; Van Noordwijk et al., 1994). No data are available concerning the influence of atmospheric [CO<sub>2</sub>] on root dynamics of any crop grown under different agricultural management practices. Our first objective, therefore, was to evaluate the influence of CO<sub>2</sub>-enrichment on root production and mortality of a sorghum crop grown with conventional and conservation management practices.

Prior et al. (2005) recently reported for this experiment on the effects of management and [CO<sub>2</sub>] on aboveground biomass production with an emphasis on changes in soil C storage. They found a substantial increase in soil C

concentration at the 0–5 cm depth increment in the conservation system compared to the conventional system, and in the CO<sub>2</sub>-enriched compared to ambient plots, after two cropping cycles (4 years). Our second objective, therefore, was to identify a mechanism to explain these effects (Prior et al., 2005).

## 2. Materials and methods

### 2.1. Crop management

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 soil bin contained a Decatur silt loam soil (clayey, kaolinitic, thermic Rhodic Paleudults; FAO classification Haplic Acrisols) supported on a tile and gravel drainage basin in an experimentally constructed soil profile of field proportions (Batchelor, 1984). This provides a consistent rooting bed and allows an assessment of plant response both above and below the ground.

This study compared sorghum response to elevated atmospheric CO<sub>2</sub> under two cropping systems — “conventional” and “conservation.” In the conventional system, the plots were left fallow over the winter and then were tilled before planting sorghum (‘Savanna 5’). In the conservation plots, clover was planted as a winter cover crop and its residue remained on the soil surface. The conservation plots were not tilled before planting.

Sorghum was planted 4–7 May, 1998 at a density of 20 plants per meter in rows 38 cm apart on the entire soil bin. To ensure plant establishment, fertilizer N was applied at a rate of 34 kg N ha<sup>-1</sup> shortly after planting. An additional 101 kg N ha<sup>-1</sup> was applied 30 days later. All other nutrients were applied according to standard soil test recommendations. All plots received ambient rainfall and were irrigated only when necessary to prevent drought-induced mortality; a surface drip irrigation system was used to uniformly distribute water throughout the bin. The total amount of water received (rainfall + irrigation) was 379 mm over the course of the growing season. Prior to planting, weeds were controlled, and clover was terminated, by applying glyphosate<sup>1</sup> (N-[phosphonomethyl] glycine) at a rate of 1.0 kg ha<sup>-1</sup>. During the season, weeds were removed by hand.

Open top field chambers were used to administer two levels of atmospheric CO<sub>2</sub> concentrations: ambient (365 μmol mol<sup>-1</sup>) and twice-ambient (720 μmol mol<sup>-1</sup>). 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 (polyvinyl chloride) film panel (0.2 mm thickness) similar to that described by Rogers et al. (1983). Carbon dioxide was supplied from a 12.7 Mg liquid CO<sub>2</sub>

<sup>1</sup> Use of trade names is provided for information only and does not constitute endorsement by the USDA over similar products.

receiver through a high volume dispensing manifold and the atmospheric CO<sub>2</sub> concentration was elevated by continuous injection of CO<sub>2</sub> into plenum boxes (for a more complete explanation of the controls over CO<sub>2</sub> levels, refer to Mitchell et al., 1995). Briefly, 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 h day<sup>-1</sup> for both ambient and elevated chambers) using a time-shared manifold with samples drawn through solenoids to an infrared CO<sub>2</sub> analyzer (Model 6252, LI-COR Inc., Lincoln, NE). Values were continuously recorded every 15–30 min for each chamber, depending upon whether or not an additional CO<sub>2</sub> study was on line.

At final harvest, all plants were removed and total fresh weights recorded. The stalks were cut into approximately 15 cm lengths using hedge clippers. A subsample of the non-yield material (residue) was taken and its fresh weight recorded; the subsample was dried (55 °C) and total residue was determined by calculation using the fresh weight to dry weight ratio for each plot. Fresh weights and moisture of threshed grain (Almaco Thresher, Model SVPT, Allan Machine Co., Nevada, IA) were determined; total yields were determined following correction for moisture (Model SL95 Moisture Meter, The Steinlite Corp., Atchison, KS). After threshing, sorghum chaff was added back to the appropriate study plots. All harvest operations described above were conducted on all non-experimental areas to insure uniform treatment of areas bordering the study plots.

## 2.2. Minirhizotron analysis of root dynamics

A total of 24 minirhizotrons (two per chamber) were installed 1 June 1998. Minirhizotrons are clear plastic tubes (o.d. = 56 mm) that allow repeated, non-invasive measurement of root growth. These clear tubes were installed at an angle of 45° from vertical to a vertical depth of 31 cm. Tubes were installed equidistant between, and parallel to, sorghum rows oriented towards the door so that repeated measures could be made with minimal disturbance to experimental plots. The portion of the minirhizotron tube extending above the ground was covered with a closed-cell polyethylene sleeve, and the end was sealed with a rubber cap to exclude light and minimize heat exchange between the air and the tube. A PVC cap was then installed over the end to protect the rubber cap from UV damage, and to further protect and insulate the tube. To prevent minirhizotron tubes from moving, aluminum brackets were clamped to tubes and anchored into the ground with 40 cm stainless steel rods.

A BTC-100× microvideo camera (Bartz Technologies, Santa Barbara, California) was inserted into minirhizotrons 41, 59, 80, and 94 days after planting and images of roots growing along the top surface of tubes were recorded. The

camera was equipped with an indexing handle allowing very precise and consistent camera placement over time (Johnson and Meyer, 1998). Video frames were replayed in the laboratory, still images were manually digitized, and root data were extracted using the image analysis program RooTracker (Dave Tremmel, Duke University). A total of 16 frames representing depths from 0 to 31 cm were analyzed from all 24 tubes at each date for a total of 1534 images (16 depths × 24 tubes × 4 dates). Each frame represents a one-dimensional area of soil equivalent to 144 mm<sup>2</sup>.

Several variables were recorded for each minirhizotron frame at each date including the number of live roots, number of dead roots, length of live roots, length of dead roots, and root diameters. Roots were considered dead when they either disappeared from view, or when their structural integrity began to deteriorate (e.g., upon root fragmentation). Therefore, mortality includes all roots lost to grazing by soil herbivores. In some cases, roots may indeed have been dead and nonfunctional, but since they were still visible in minirhizotron video frames, they were still considered live. From these basic data, root production per day, root mortality per day, and average diameter per root was calculated and the data presented. Seasonal root production (in root length, not mass) was calculated by summing the new root lengths that had appeared between each sampling interval. Unfortunately, we were unable to convert root length to mass (and total carbon) because specific root lengths were not measured.

## 2.3. Statistical analyses

The experiment was implemented using a split-plot design with three blocks (i.e., three replications). One-half of each block was managed as a conventional system and the other half as a conservation system. Split-plot treatments (CO<sub>2</sub> level) were randomly assigned within blocks. Each experimental plot contained two subsample minirhizotron tubes. The minirhizotron frames (16 per tube) were grouped into eight depth classes to determine treatment effects on vertical root distribution (depth 1 = 0–3.8 cm, depth 2 = 3.9–7.6 cm, depth 3 = 7.7–11.4, depth 4 = 11.5–15.2 cm, depth 5 = 15.3–19.0 cm, depth 6 = 19.1–22.8 cm, depth 7 = 22.9–26.6, depth 8 = 26.7–30.4 [numbers were separated by tenths to correspond exactly to minirhizotron frame depth]). The sub-unit factor depth is a split block because depths were not randomly assigned within the minirhizotron frames (Steele et al., 1997). Data were analyzed as a repeated measures design (repeated measure being time) using the mixed model procedure (PROC MIXED) of the Statistical Analysis System (Littell et al., 1996). Because date was not a factor for the variables cumulative seasonal root length production and mortality, these data were analyzed using ANOVA with the PROC MIXED procedure. Data were considered significantly different when probability levels were <0.05. Statistical trends were considered at 0.05 < *P* < 0.15.

### 3. Results

Greatest root length production was observed between 4 and 15 cm soil depths (Fig. 1, Table 1). By physiological maturity, the highest root mortality was observed at these same depths (Fig. 1). By physiological maturity, a larger percentage of total root length had died at shallow soil depths compared to deeper depths; for example, 87% of roots produced at the shallowest soil depth died before harvest compared to 48% at the greatest depth. In fact, there was a significant linear negative relationship between percent mortality and soil depth (Fig. 1;  $P < 0.0004$ ,  $R^2 = 0.89$ ). There was no effect of management, CO<sub>2</sub> treatment, or significant interactive effects of these treatments with depth on the percentage of roots to die by physiological maturity indicating that root longevity was

unchanged (data not shown). None of the treatments (depth, tillage, CO<sub>2</sub>, or date) had any effect on root diameters observed against minirhizotron tubes (data not shown). Diameters of roots that died during the course of the experiment did not differ from diameters of roots that remained alive.

Root length production per day, mortality per day, and live root length were all affected by date ( $P < 0.003$ ; Table 1). Daily production of new roots occurred primarily in the early part of the growing season (Fig. 2). Daily mortality of roots increased steadily over the growing season in a linear fashion ( $R^2 = 0.99$ ; Fig. 2). The maximum amount of live fine roots, which represents the balance between production and mortality, was observed 59 days after planting (DAP). Maximum RLD occurred when mortality and production rates were nearly equivalent (Fig. 2).

Table 1

Results of the repeated measures mixed model analysis (PROC MIXED; SAS, 1999) and mean values for main effects of agricultural management (Manage), [CO<sub>2</sub>], depth, and date

Treatments	Variables <sup>a</sup>				
	Seasonal production	Seasonal mortality	Mortality/day	Production/day	Root length
Manage	NS	NS	NS	NS	NS
CO <sub>2</sub>	0.07	NS	NS	0.06	0.08
Depth	0.005	<0.0001	<0.0001	<0.0001	0.02
Date	–	–	0.003	<0.0001	<0.0001
Manage × CO <sub>2</sub>	0.10	0.14	0.14	0.11	NS
Manage × depth	0.05	0.02	0.02	0.006	NS
CO <sub>2</sub> × depth	0.11	0.13	0.13	NS	0.12
Manage × CO <sub>2</sub> × depth	NS	NS	NS	NS	NS
Manage × date	–	–	NS	NS	NS
CO <sub>2</sub> × date	–	–	NS	NS	NS
Depth × date	–	–	NS	<0.0001	NS
Manage × CO <sub>2</sub> × date	–	–	NS	NS	NS
Manage × depth × date	–	–	NS	<0.0001	NS
CO <sub>2</sub> × depth × date	–	–	NS	0.03	NS
Manage × CO <sub>2</sub> × depth × date	–	–	NS	NS	NS
CO <sub>2</sub> level					
Elevated	13.9	6.14	0.119 <sup>b</sup>	0.111	10.0
Ambient	10.8	4.98	0.095	0.084	7.75
Tillage					
Conventional	12.7	5.54	0.111	0.101	9.23
Conservation	12.0	5.58	0.103	0.093	8.57
Depth (cm)					
0.3–8	6.56	4.59	0.082	0.070	3.26
3.9–7.6	16.2	10.4	0.197	0.162	8.30
7.7–11.4	16.5	10.1	0.190	0.137	7.75
11.5–15.2	15.9	6.93	0.132	0.120	6.81
15.3–19.0	11.0	4.38	0.088	0.083	6.83
19.1–22.8	9.80	2.23	0.043	0.064	6.22
22.9–26.6	11.4	3.01	0.061	0.071	11.2
26.7–30.4	11.4	2.79	0.062	0.073	11.7
Date					
41 DAP	–	–	–	0.230	9.46
59 DAP	–	–	0.074	0.140	10.6
80 DAP	–	–	0.106	0.015	8.71
94 DAP	–	–	0.141	0.004	6.79

<sup>a</sup> All values are in units of mm frame<sup>-1</sup>.

<sup>b</sup> In some cases values for mortality per day exceed production per day because production numbers are averages of four dates (four sampling intervals) whereas mortality numbers represent only three dates (three sampling intervals).

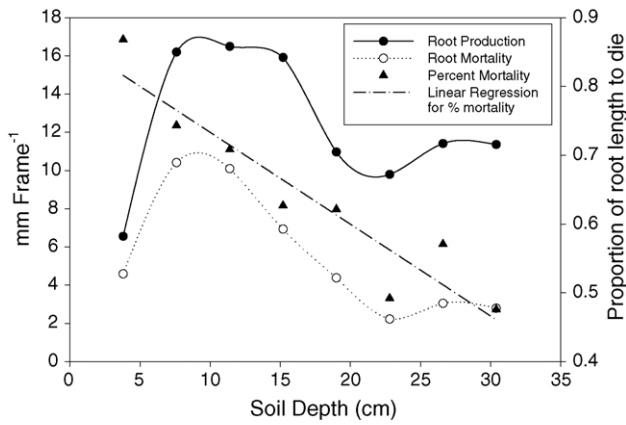


Fig. 1. Root production and mortality for sorghum grown in soil in open top chambers. Circles indicate seasonal root production and mortality to a depth of 31 cm (axis Y1 in units of mm frame<sup>-1</sup>). Triangles represent the relationship between soil depth and the proportion of roots to die by physiological maturity (axes Y2) (the equation for the line:  $y = 0.87 - 0.05x$ ;  $R^2 = 0.89$ ).

There was no main effect of management on any root variable (Table 1). There were, however, trends indicating a main effect of the CO<sub>2</sub> treatment for several variables. There was also a trend suggesting a management × CO<sub>2</sub> interaction for all variables with the exception of standing root length. CO<sub>2</sub>-enrichment enhanced cumulative seasonal root length production (+58%) and mortality (+59%) within conventionally managed sorghum, but had no effect within conservation system plots (Fig. 3). CO<sub>2</sub>-enrichment enhanced shoot biomass production by 14% but did not influence grain production (Fig. 4). Although management had no effect on residue production, grain production was 6% higher in conservation compared to conventional plots ( $P = 0.008$ ; Fig. 4).

Complex three way interactions were observed for root length production per day (management × depth × date and

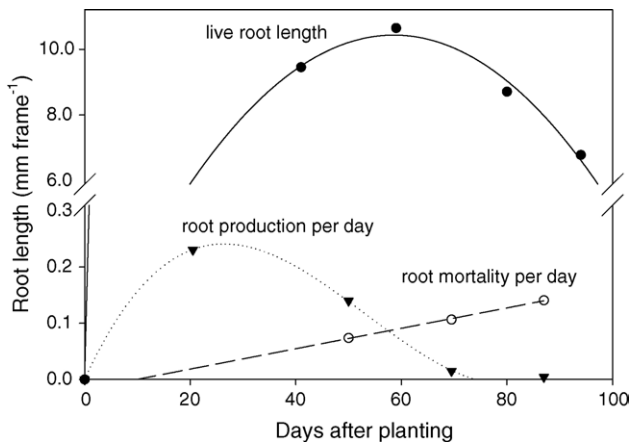


Fig. 2. Changes in standing live root crop, root production per day, and mortality per day throughout the growing season for sorghum measured with minirhizotrons. Values are averaged across all treatments. Equations for standing live root crop,  $y = 0.011 + 0.356(x) - 0.003(x^2)$ ; root production per day,  $y = -0.00024 + 0.020x - 0.00052(x^2) + 0.0000032x^3$ ; and root mortality per day,  $y = -0.0179 + 0.0018x$ .

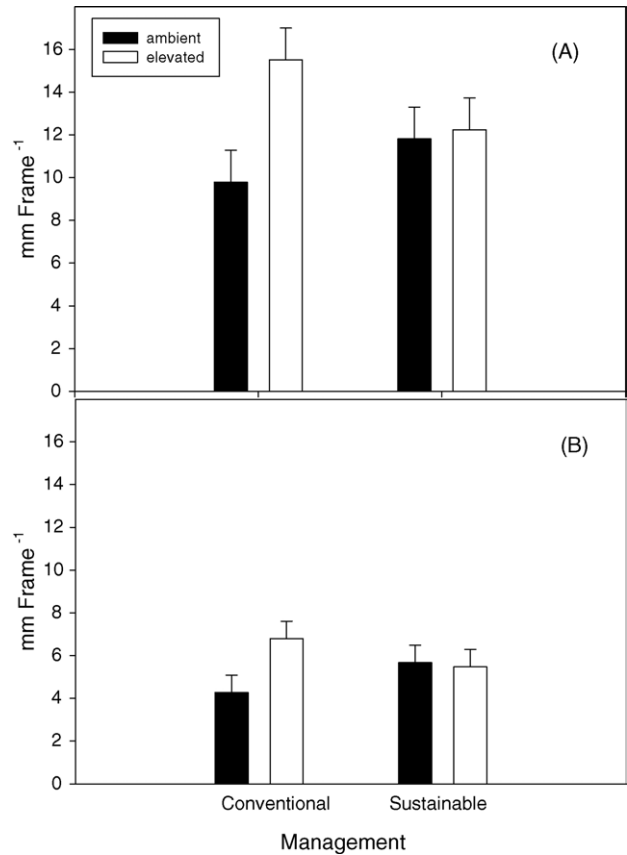


Fig. 3. Interaction between atmospheric CO<sub>2</sub> and management treatments on seasonal root production (A) and mortality (B) of sorghum grown in open top chambers. Bars represent pooled S.E.'s derived from the PROC MIXED procedure of SAS.

CO<sub>2</sub> × depth × date; Table 1, Fig. 5). In general, CO<sub>2</sub>-enriched sorghum produced more roots at shallow soil depths compared to ambient plots and much of this additional root production occurred early in the growing season. Conventionally managed sorghum produced less root length in the top few centimeter of soil compared to conservation plots. Daily root length production shifted to deeper soil in conventionally managed sorghum exposed to elevated CO<sub>2</sub> compared to sorghum grown with CO<sub>2</sub>-enrichment in conservation plots.

Management × depth interactions were observed for most variables (Table 1). All variables followed a similar pattern as root length production per day (Fig. 5). For example, seasonal root length mortality and production were higher at the shallowest soil depth in the conservation plots than in the conventional plots.

#### 4. Discussion

##### 4.1. Temporal and spatial differences in root production and mortality

Most sorghum root production occurred early in the growing season and had ceased by 70 DAP. Mortality also



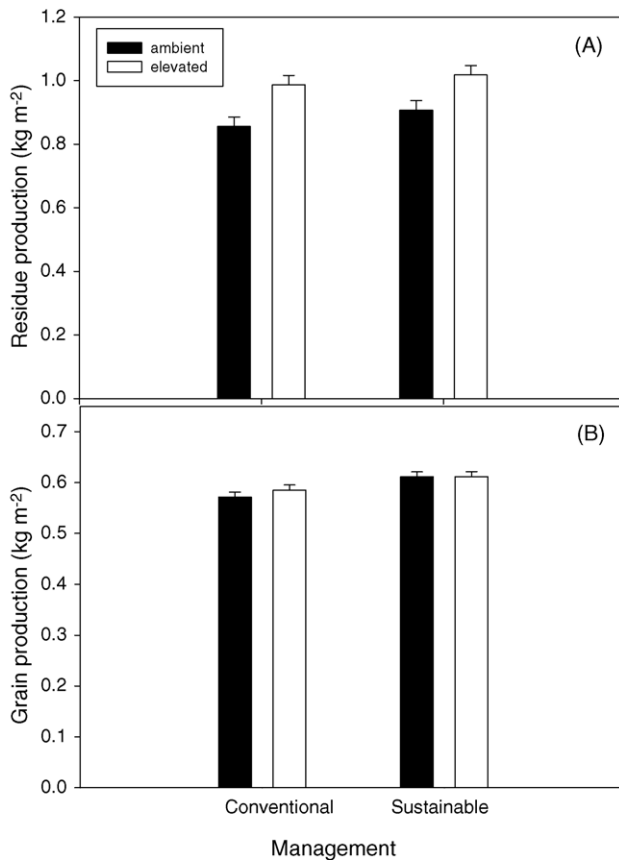


Fig. 4. Aboveground residue biomass production (A) and grain biomass production (B) of sorghum grown in open top chambers. Bars represent pooled S.E.'s derived from the PROC MIXED procedure of SAS.

began very early in the growing season, but increased linearly through physiological maturity ( $R^2 = 0.99$ ). Interestingly, the relationship between root production, root mortality, and standing live root crop, observed here for sorghum (Fig. 2), is nearly identical to the theoretical pattern suggested by Huck et al. (1987) (see also Pritchard and Rogers, 2000). Similar rooting habits have been reported previously for sorghum (Cheng et al., 1990), soybean (Hoogenboom et al., 1987; Huck et al., 1987), and cotton (Klepper et al., 1973). In these species, root production and mortality are overlapping processes with live root length at any given time representing the balance of these two processes. This temporal pattern of root deployment is consistent with the finding that carbon allocation to roots is highest during early vegetative growth and then decreases as plants mature and switch to reproductive growth (Swinen et al., 1994).

These data illustrate how isolated measures of root length used as a surrogate for “production” can be misleading. In this case, instantaneous (standing) root length would lead one to believe that most sorghum roots were produced at the 23–31 cm depth (last column of Table 1). However, seasonal root production values based on analysis of sequential minirhizotron images clearly indicates that most sorghum

root production actually occurred at the 4–15 cm depth (first column of Table 1). This apparent inconsistency regarding production is easily explained by examining patterns of root mortality at different soil depths.

A larger proportion of roots produced in shallow soil had died by physiological maturity compared to roots located deeper (i.e., shallow roots had shorter lifespan than deeper roots). In fact, a negative linear relationship between soil depth and the proportion of roots that died was observed. A similar observation was made in a minirhizotron study on alfalfa roots (Goins and Russelle, 1996; Watson et al., 2000) and sugar beet (Van Noordwijk et al., 1994). Changes in nutrient availability, temperature, and moisture with depth provide one possible explanation for these observations (Watson et al., 2000). Generally, the top 10 cm of soil is subject to large diurnal fluctuations in soil temperature and water content compared to deeper soil which is buffered from such rapid changes.

If variation in temperature and moisture extremes did indeed control the proportion of roots that had died by physiological maturity (longevity), then differences in lifespan of roots should also have occurred between conservation and conventional plots, since the influence of tillage on soil moisture, temperature, soil strength, and distribution of mineral nutrients is well documented (Anderson et al., 1987; Chassot et al., 2001; Kladvik, 2001; Turman et al., 1995). Contrary to our expectations, management did not influence the proportion of roots to die by harvest. Vertical differences in rooting between conventional and conservation plots were observed, however, suggesting differences in soil conditions; root length at the 0–10 cm depth was greatest in conservation plots, but from 15 to 25 cm, root length was higher in the conventional plots. Unfortunately, we can only speculate about what caused different spatial rooting patterns because soil conditions were not characterized.

#### 4.2. Effects of CO<sub>2</sub>-enrichment and management on root dynamics

In the current study, neither elevated CO<sub>2</sub> nor agricultural management practices had any effect on the proportion of roots that died by physiological maturity (i.e., increases in root mortality in high CO<sub>2</sub> plots were proportional to production increases). These data suggest that [CO<sub>2</sub>] and tillage had no effect on root longevity. Root turnover was also unaffected in wheat grown in CO<sub>2</sub>-enriched environments (Fitter et al., 1996); although it is well known that few, if any, wheat roots die until the crop is well into reproductive growth (Gibbs and Reid, 1992; Pritchard and Rogers, 2000).

Understanding how global environmental changes will impact root longevity is currently of great interest (Norby and Jackson, 2000), and several hypothesis regarding the potential influence of elevated CO<sub>2</sub> on root longevity have been advanced. Eissenstat et al. (2000), for example, using an efficiency model, hypothesized that rising CO<sub>2</sub> will likely

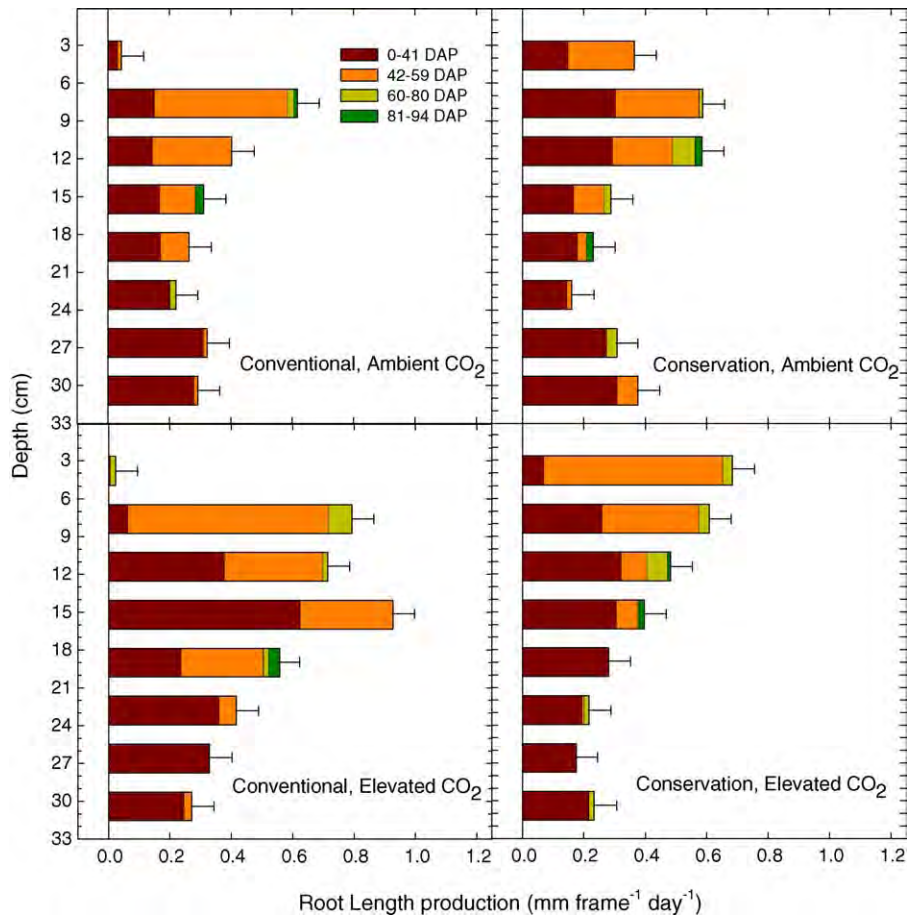


Fig. 5. Daily root length production for sorghum grown under ambient or elevated atmospheric  $\text{CO}_2$  conditions and either conventional or conservation agricultural management practices. Bars represent pooled S.E.'s derived from the PROC MIXED procedure of SAS.

increase average root lifespan. In contrast, other investigators have suggested that root lifespan are unlikely to change (Pritchard and Rogers, 2000; Van Noordwijk et al., 1998). It is very difficult to predict how root lifespan will be impacted by environmental changes because no consensus has yet been reached as to the causes or mechanisms of root death (Smit and Zuin, 1996). Our study provides evidence that root longevity of sorghum is not affected by tillage or atmospheric  $[\text{CO}_2]$ . Instead, longevity was apparently controlled by a roots position (i.e., depth) within the soil profile.

The observation that root turnover decreases with soil depth coupled with growing evidence that  $\text{CO}_2$ -enrichment stimulates root growth preferentially at shallow soil depths (Pritchard and Rogers, 2000) could have very important implications for understanding the role of agricultural soils in sequestering carbon. It could, for example, explain how exposure to high  $\text{CO}_2$  environments could increase root turnover without actually affecting the average lifespan of roots of a given order. In other words, rising  $\text{CO}_2$  could lead to greater root mortality (relative to live root length at a given time) simply because it stimulates production of shallow roots which are inherently shorter

lived. This idea deserves further experimentation. In a companion report on this same experiment, Prior et al. (2005) found that after 4 years of study,  $\text{CO}_2$ -enrichment resulted in a substantial increase in soil C sequestration at the 0–5 cm depth increment in the conservation plots under  $\text{CO}_2$ -enrichment compared to conservation plots exposed to ambient  $\text{CO}_2$ .

Significant interactions between agricultural management and  $\text{CO}_2$  availability were observed for several variables. In general,  $\text{CO}_2$ -enrichment stimulated rooting (i.e., cumulative seasonal production and mortality) more in conventional compared to conservation plots. This was probably caused by the effects of tillage on soil water content. Although not measured in this study, the presence of surface residues coupled with no-till management, has repeatedly been shown to enhance soil moisture absorption and retention compared to conventional tillage with no residue (Newell and Wilhelm, 1987). It is also well established that  $\text{CO}_2$ -enrichment stimulates productivity of  $\text{C}_4$  crops mainly by increasing water use efficiency (WUE) (Pritchard and Amthor, 2005). Thus, it is likely that water was not limiting in the conservation plots, and therefore plants were less responsive to  $\text{CO}_2$ -enrichment. On

the other hand, soil of conventional plots was drier and CO<sub>2</sub>-enrichment boosted productivity by improving WUE.

## 5. Conclusion

It was suggested that agricultural management practices will have a greater impact on root growth and soil carbon storage than rising atmospheric [CO<sub>2</sub>] (Canadell et al., 1996; Paustian et al., 1996). Using root length production as a metric of root biomass, our study does not support that contention (Table 1). Our data do suggest, however, that the stimulation in crop root growth anticipated from rising atmospheric [CO<sub>2</sub>] may be diminished by conversion from conventional to more conservation agricultural systems — at least in the C<sub>4</sub> crop sorghum. Our data also suggest that sorghum yield was higher under conservation compared to conventional management. Current estimates of crop responses to climate change may need modification to take into account interactive effects of agricultural management (Paustian et al., 1996; Tubiello et al., 2000).

The fraction of roots that had died by physiological maturity decreased in a linear fashion from shallow to greater soil depths. Although management did not affect cumulative seasonal root production or mortality it did influence vertical root distribution; conservation management favored shallow root systems whereas conventional management favored deeper rooting. Data emphasize the importance of quantifying production and mortality as separate processes. This study suggests that conversion from conventional to conservation management practices might diminish stimulation of rooting by rising atmospheric CO<sub>2</sub>, at least in the C<sub>4</sub> crop sorghum.

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