Elevated Atmospheric Carbon Dioxide Effects on Soybean and Sorghum Gas Exchange in Conventional and No-Tillage Systems

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Increasing atmospheric CO_2 concentration has led to concerns about potential effects on production agriculture. In the fall of 1997, a study was initiated to compare the response of two crop management systems (conventional tillage and no-tillage) to elevated CO_2. The study used a split-plot design replicated three times with two management systems as main plots and two atmospheric CO_2 levels (ambient and twice ambient) as split plots using open-top chambers on a Decatur silt loam soil (clayey, kaolinitic, thermic Rhodic Paleudults). The conventional system was a grain sorghum [*Sorghum bicolor* (L.) Moench.] and soybean [*Glycine max* (L.) Merr.] rotation with winter fallow and spring tillage practices. In the no-tillage system, sorghum and soybean were rotated, and three cover crops were used [crimson clover (*Trifolium incarnatum* L.), sunn hemp (*Crotalaria juncea* L.), and wheat (*Triticum aestivum* L.)]. Over multiple growing seasons, the effect of management and CO_2 concentration on leaf-level gas exchange during row crop (soybean in 1999, 2001, and 2003; sorghum in 2000, 2002, and 2004) reproductive growth were evaluated. Treatment effects were fairly consistent across years. In general, higher photosynthetic rates were observed under CO_2 enrichment (more so with soybean) regardless of residue management practice. Elevated CO_2 led to decreases in stomatal conductance and transpiration, which resulted in increased water use efficiency. The effects of management system on gas exchange measurements were infrequently significant, as were interactions of CO_2 and management. These results suggest that better soil moisture conservation and high rates of photosynthesis can occur in both tillage systems in CO_2–enriched environments during reproductive growth.

For over 200 yr, intense row crop agriculture has been practiced in the southeastern United States. These practices (i.e., inversion tillage with fallow winter periods) have left the soil relatively infertile, highly eroded, and low in organic matter (Carreker et al., 1977). Crops in the southeast are often subjected to periods of water deficit during times of high demand, such as reproductive growth. The use of conservation practices that include less tillage and the use of cover crops can help counter the soil degradation caused by years of intense agriculture. These practices enhance soil C storage and improve soil physical properties that can reduce erosion and increase plant-available water (Phillips et al., 1980; Gebhardt et al., 1985; Kern and Johnson, 1993; Hunt et al., 1996; Diaz-Zorita et al., 2002; Triplett and Dick, 2008). Additional water can become available to plants in conservation systems when plant residue left on the soil surface serves as mulch and reduces evaporative losses (Reicosky et al., 1999). Within the last two decades, the adoption of conservation tillage systems has dramatically increased (CTIC, 2004).

In addition to alterations in management practices, the environment is also changing. Atmospheric CO_2 concentration is rising at an unprecedented rate caused by fossil fuel burning and land use change (Keeling and Whorf, 2001). Increasing atmospheric CO_2 concentration has led to concerns about its potential effects on production agriculture. Elevated CO_2 has the potential to enhance crop system processes such as photosynthesis and plant water use efficiency (WUE), leading to increased biomass production (Rogers et al., 1983b; Amthor, 1995; Kimball et al., 2002). As with conservation systems, elevated CO_2 can improve soil quality through the addition of organic residue above and below ground (Rogers et al., 1999; Torbert et al., 2000; Prior et al., 2003). This also has the ability to help mitigate global climate change by sequestering atmospheric CO_2 in plant and soil systems.

Long-term CO_2 studies evaluating C_3 and C_4 crops grown under the same experimental conditions are lacking. Although both of these photosynthetic types benefit from increased WUE, they are known to respond differently to elevated CO_2 with regard to carbon metabolism (Rogers et al., 1983b; Amthor, 1995). This difference

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Abbreviations: CT, conventional tillage; DOY, day of year; g_s, conductance; NT, no-till; P_n, photosynthesis; Tr, transpiration; WUE, water use efficiency.

in response could become important with regard to future management decisions. There have been no long-term studies comparing conventional tillage (CT) with conservation tillage or no-tillage (NT) systems under varying levels of atmospheric CO_2. The objective of the current study was to examine the interactive effects of management (CT and NT) and atmospheric CO_2 concentration (ambient and twice ambient) on leaf-level gas exchange during row crop (soybean, a N-fixing C_3 crop, and grain sorghum, a C_4 crop) reproductive growth over multiple seasons.

Materials and Methods

This study was conducted on an outdoor soil bin (7 m by 76 m) at the USDA–ARS National Soil Dynamics Laboratory in Auburn, Alabama (32.6° N, 85.5° W). The bin was filled with a Decatur silt loam soil (clayey, kaolinitic, thermic Rhodic Paleudults) (Batchelor, 1984). Open-top chambers, comprised of a structural aluminum frame (3 m in diameter by 2.4 m in height) covered with a 0.2-mm PVC film panel (Rogers et al., 1983a), were used for CO_2 exposure. 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 h d^{-1}) using a time-shared manifold with samples drawn through solenoids to an infrared CO_2 analyzer (Model 6252; LI-COR, Inc., Lincoln, NE). The target concentration for the elevated CO_2 treatment was twice ambient (~720 $\mu L\ L^{-1}$). The mean (± SE) daytime CO_2 concentrations across the six growing seasons of the study were 366.35 ± 0.07 and 691.80 ± 0.31 for the ambient and elevated CO_2 treatments, respectively ($n = 58230$). Plot locations were permanently delineated using an anchored structural aluminum ring (3 m in diameter) as a precaution to prevent lateral surface flow of water into or out of plots.

Two crop management systems (CT and NT) were established in the fall of 1997. In the CT system, grain sorghum [*Sorghum bicolor* (L.) Moench. 'Pioneer 8282'] and soybean [*Glycine max* (L.) Merr. 'Asgrow 6101'] were rotated each year with spring tillage after winter fallow. The NT system also used a grain sorghum and soybean rotation with three cover crops [crimson clover (*Trifolium incarnatum* L. 'AU Robin'), sunn hemp (*Crotalaria juncea* L. 'Tropic Sunn'), and wheat (*Triticum aestivum* L. 'Pioneer 2684')] grown using no-tillage practices. In both management systems, row crop seeds were sown (20 per meter of row) on 0.38-m row spacings. Planting dates for soybean were 19, 23, and 27 May for 1999, 2001, and 2003, respectively; dates for sorghum were 2, 6, and 12 May for 2000, 2002, and 2004, respectively. Extension recommendations were used in managing the crops; fertilizer rates were based on standard soil tests guidelines as recommended by the Auburn University Soil Testing Laboratory (Adams et al., 1994). Soybeans were grown with no nitrogen fertilization, but seeds were inoculated with commercial *Rhizobium* (Nitragin Co., Milwaukee, WI) before planting. For grain sorghum, fertilizer N (ammonium nitrate) was hand-broadcast at a rate of 34 kg N ha^{-1} shortly after planting, and an additional 101 kg N ha^{-1} was similarly applied 30 d after planting. Cover crops and sorghum (regrowth prevention) were terminated with glyphosate (N-[phosphonomethyl] glycine) 10 d before planting the following crop. All crops were harvested using standard procedures; yield and biomass were recorded as described in detail by Prior et al. (2005). Harvest dates for soybean were 25, 22, and 20 October for 1999, 2001, and 2003, respectively; dates for sorghum were 14, 14, and 17 August for 2000, 2002, and 2004, respectively. After harvest, all remaining residues were uniformly spread over their respective study plot. All operations described above were also conducted on nonexperimental areas to ensure uniform treatment of areas bordering the study plots.

During reproductive growth for 6 yr, leaf level measurements of photosynthesis (P_n), stomatal conductance (g_s), and transpiration (Tr) were made twice weekly using a LI-6400 Portable Photosynthesis System (LI-COR, Inc., Lincoln, NE) for soybean (C_3 photosynthesis) and grain sorghum (C_4 photosynthesis). Visual assessments of approximate growth stage were also conducted during this period for soybean (Ritchie et al., 1992) and sorghum (Vanderlip, 1979). Gas exchange measurements were taken at midday on leaves (fully expanded, sun-exposed leaves at the canopy top) from three randomly selected plants per plot and were initiated at the start of reproductive growth. Water use efficiency ($\mu mol\ CO_2\ mmol^{-1}\ H_2O$) was calculated by dividing P_n by Tr (i.e., $\mu mol\ CO_2\ m^{-2}\ s^{-1}/mmol\ H_2O\ m^{-2}\ s^{-1}$). Rainfall was recorded on site throughout each sampling period (Table 1).

The experiment was conducted using a split-plot design with three replicate blocks. Whole-plot treatments (tillage system) were randomly assigned to half of each block. Split-plot treatments (CO_2 levels) were randomly assigned to two chambers (3 m in diameter) within each whole plot. There were a total of 12 chamber plot locations; six were ambient CO_2 treatments (three for CT and three for NT), and six were elevated CO_2 treatments (three for CT and three for NT). Data from each chamber were averaged before statistical analysis. Statistical analyses of data were performed using the Mixed procedure of the Statistical Analysis System (Littell et al., 1996). A significance level of $P \leq 0.10$ was established a priori.

Results

Soybean

In 1999, elevated CO_2 significantly increased P_n on 17 of 21 sampling dates (Table 2; Fig. 1a). Days without a significant CO_2 effect tended to occur later in the growing season when

Table 1. Rainfall recorded on site during each sampling period (the growing season and sampling period for soybean is longer than for sorghum).

Species	Year	Rainfall	No. of events	No. >10 mm
		mm		
Soybean	1999	161.29	14	5
	2001	156.21	15	5
	2003	261.62	18	9
Sorghum	2000	88.90	9	3
	2002	67.31	7	3
	2004	184.15	9	5

Table 2. Statistics (Pr > *F*; italics represent significance) for carbon dioxide concentration, tillage system, and their interaction on soybean gas exchange variables for the various sampling dates in 1999.

DOY†	Gas exchange variable											
	P_n			g_s			Tr			WUE		
	CO_2	Till	C × T	CO_2	Till	C × T	CO_2	Till	C × T	CO_2	Till	C × T
196	*0.007*	0.578	0.482	0.507	0.688	0.611	0.331	0.910	0.486	*<0.001*	0.372	0.711
200	*0.002*	0.720	0.602	*0.007*	0.805	0.239	*0.015*	0.584	0.171	*<0.001*	0.761	*0.004*
202	*<0.001*	0.692	0.258	*0.007*	0.777	0.394	*0.021*	0.364	0.868	*<0.001*	0.440	0.874
207	*0.006*	0.880	0.494	0.356	0.441	0.990	0.270	0.612	0.951	*0.007*	0.514	0.976
210	*0.006*	0.168	0.606	0.633	0.192	0.820	0.861	0.170	0.974	*0.003*	0.511	0.287
214	*0.003*	0.158	0.310	0.430	0.202	0.386	0.426	0.192	0.157	*0.005*	0.142	*0.052*
218	*0.001*	0.353	*0.013*	0.781	0.120	*0.058*	0.958	0.372	*0.080*	*<0.001*	0.434	0.107
221	*0.009*	0.165	0.724	0.339	0.246	0.418	0.515	0.227	0.748	*0.002*	0.613	0.825
224	*0.022*	0.257	0.739	0.813	0.560	0.600	0.477	0.763	0.662	*0.004*	0.126	0.223
228	*0.012*	0.220	0.641	0.545	0.326	0.522	0.844	0.398	0.518	*<0.001*	0.737	0.958
231	0.163	0.242	0.506	0.420	0.950	0.498	0.604	0.607	0.728	*0.013*	0.258	0.185
238	*<0.001*	0.309	*0.025*	*0.098*	0.455	0.241	0.284	0.110	0.172	*0.001*	0.748	0.935
242	*<0.001*	0.156	0.102	*0.005*	0.117	*0.017*	*0.036*	0.312	*0.055*	*0.001*	0.785	0.956
246	*0.005*	0.367	0.625	*0.085*	0.657	0.610	*0.055*	0.653	0.517	*<0.001*	0.633	0.384
250	*0.015*	0.766	0.718	0.109	0.650	0.610	0.130	0.297	0.643	*0.003*	0.112	0.682
253	0.122	0.876	0.730	*0.050*	0.618	0.737	*0.013*	0.977	0.706	*<0.001*	0.794	0.976
257	*0.018*	0.324	*0.008*	*0.010*	0.634	*0.021*	*0.008*	0.899	*0.012*	*0.003*	0.702	0.883
260	*0.051*	0.283	0.728	0.213	0.466	0.948	0.257	0.280	0.926	*0.004*	0.710	0.929
264	0.406	0.837	0.206	*0.021*	0.119	0.126	*0.016*	0.306	*0.099*	*0.003*	0.530	0.545
267	*0.023*	0.854	0.660	0.412	0.699	0.536	0.448	0.706	0.683	*<0.001*	*0.081*	0.555
273	0.573	0.979	0.696	*0.006*	0.442	0.712	*0.008*	0.577	0.802	*<0.001*	0.184	0.422
Avg.	*<0.001*	0.324	0.620	*0.002*	0.649	0.474	*0.005*	0.861	0.400	*<0.001*	0.125	0.148

† C × T, interaction between carbon dioxide concentration and tillage system; CO_2, carbon dioxide concentration; DOY, day of year; g_s, conductance (mol H_2O m^{-2} s^{-1}); P_n, photosynthesis (μmol CO_2 m^{-2} s^{-1}); Till, tillage system; Tr, transpiration (mmol H_2O m^{-2} s^{-1}); WUE, water use efficiency (μmol CO_2 $mmol^{-1}$ H_2O).

plants were becoming senescent. There were no significant effects of tillage on P_n (Table 2). Significant interactions of CO_2 and tillage were noted only on three dates (Table 2). Early in the season (day of year [DOY] 218), CO_2 increased P_n under NT conditions. However, later in the season (DOY 238 and 257), this condition was reversed in that CO_2 increased P_n under CT.

The 2001 growing season was similar to 1999 in that elevated CO_2 significantly increased P_n on 17 of 22 sampling dates (Table 3; Fig. 2a). Again, days with no CO_2 effect tended to occur later in the growing season. Also similar to 1999, there tended to be no main effects of tillage on P_n, with the exception of DOY 262 (Table 3), when NT reduced P_n. Significant interactions of CO_2 and tillage were noted only on two dates (DOY 226 and 236; Table 3). These interactions were similar to that which occurred early in 1999 in that elevated CO_2 increased P_n under NT.

In 2003, elevated CO_2 significantly increased P_n on 17 of 19 sampling dates (Table 4; Fig. 3a). As in the prior two seasons, days with no CO_2 effects occurred late in the season. Again, tillage tended to have no significant effect on P_n; exceptions were noted on DOY 220, 234, 241, and 255 (Table 4). On the first two of these dates, NT increased P_n, whereas on the latter two dates, NT significantly reduced P_n. Interactions of CO_2 with tillage were noted on two dates (Table 4). As in 1999, on the early date (DOY 213), elevated CO_2 increased P_n under NT. However, later in the season (DOY 255), elevated CO_2 increased P_n under CT.

Elevated CO_2 significantly increased seasonal averages for P_n in each of the 3 yr (Tables 2–4; Fig. 1–3) and when averaged across all three seasons ($P < 0.001$). These seasonal and total averages reflected no main effect of tillage (total average $P = 0.794$) or interaction between CO_2 and tillage (total average $P = 0.903$).

In 1999, g_s was significantly lower in the elevated CO_2 treatment on 9 of 21 sampling dates (Table 2; Fig. 1b). There were no main effects of tillage on g_s (Table 2). Significant interactions of CO_2 and tillage were noted only on DOY 218, 242, and 257 (Table 2). On DOY 218 under ambient CO_2, g_s was significantly lower under NT compared with CT. On the latter two dates, elevated CO_2 significantly reduced g_s only in the NT treatment.

The effect of CO_2 on g_s in 2001 was similar to 1999 in that elevated CO_2 significantly reduced g_s on 10 of 22 sampling dates (Table 3; Fig. 2b). Also similar to 1999, there tended to be no main effects of tillage on g_s, with exceptions on DOY 198, 220, and 226 (Table 3). On the first date, g_s was significantly reduced under NT, whereas on the latter two dates, NT significantly increased g_s. Significant interactions of CO_2 and tillage were noted on DOY 215, 220, and 243 (Table 3). The first two dates were similar to that which occurred early in 1999 in that elevated CO_2 significantly reduced g_s in the NT treatment. However, on DOY 243, this condition was reversed in that elevated CO_2 significantly reduced g_s under CT.

In 2003, elevated CO_2 significantly reduced g_s on 10 of 19 sampling dates (Table 4; Fig. 3b). A tillage effect on g_s was noted only on DOY 241 and 255 (Table 4); in both cases, NT significantly reduced g_s. In 2003, there were no significant interactions between CO_2 and tillage on g_s (Table 4).

Elevated CO_2 significantly reduced seasonal averages of g_s in each of the 3 yr and when averaged across all three seasons ($P < 0.001$). These seasonal (Tables 2–4; Fig. 1–3) and total averages reflected no main effect of tillage (total average $P = 0.868$) or interaction between CO_2 and tillage (total average $P = 0.821$).

In 1999, elevated CO_2 significantly reduced Tr on 8 of 21 sampling dates (Table 2; Fig. 1c). There were no main effects of tillage on Tr (Table 2). Significant interactions of CO_2 and tillage were noted on DOY 218, 242, 257, and 264 (Table 2). On DOY 218 under ambient CO_2, Tr was significantly lower under NT compared with CT. On the remaining dates, elevated CO_2 significantly reduced Tr only in the NT treatment.

The effect of CO_2 on Tr in 2001 was similar to 1999 in that elevated CO_2 significantly reduced Tr on 9 of 22 sampling dates (Table 3; Fig. 2c). Also similar to 1999, there tended to be no main effects of tillage on Tr, with exceptions on DOY 198 and 220 (Table 3) when NT significantly reduced Tr on the first date but significantly increased Tr on the second. Significant interactions of CO_2 and tillage were noted on DOY 215 and 220 (Table 3); as in 1999, elevated CO_2 reduced Tr only in the NT treatment.

In 2003, elevated CO_2 significantly reduced Tr on 6 of 19 sampling dates (Table 4; Fig. 3c). Although tillage effects remained infrequent, significant effects were noted on DOY 234, 241, and 255 (Table 4). On the first date, NT increased Tr, whereas it was reduced in this treatment on the latter two dates. In 2003, a significant interaction between CO_2 and tillage was noted only on DOY 255 (Table 4); as in other years, elevated CO_2 reduced Tr only under NT.

Elevated CO_2 significantly reduced seasonal averages for Tr in each of the 3 yr (Tables 2–4; Fig. 1–3) and when averaged across all three seasons ($P < 0.001$). These seasonal and total averages reflected no main effect of tillage (total average $P = 0.692$) or interaction between CO_2 and tillage (total average $P = 0.611$).

Water use efficiency was the most consistent variable measured in 1999; this measure was significantly increased by elevated CO_2 on all dates (Table 2; Fig. 1d). A main effect of tillage on WUE was noted on DOY 267 (Table 2) when WUE was increased

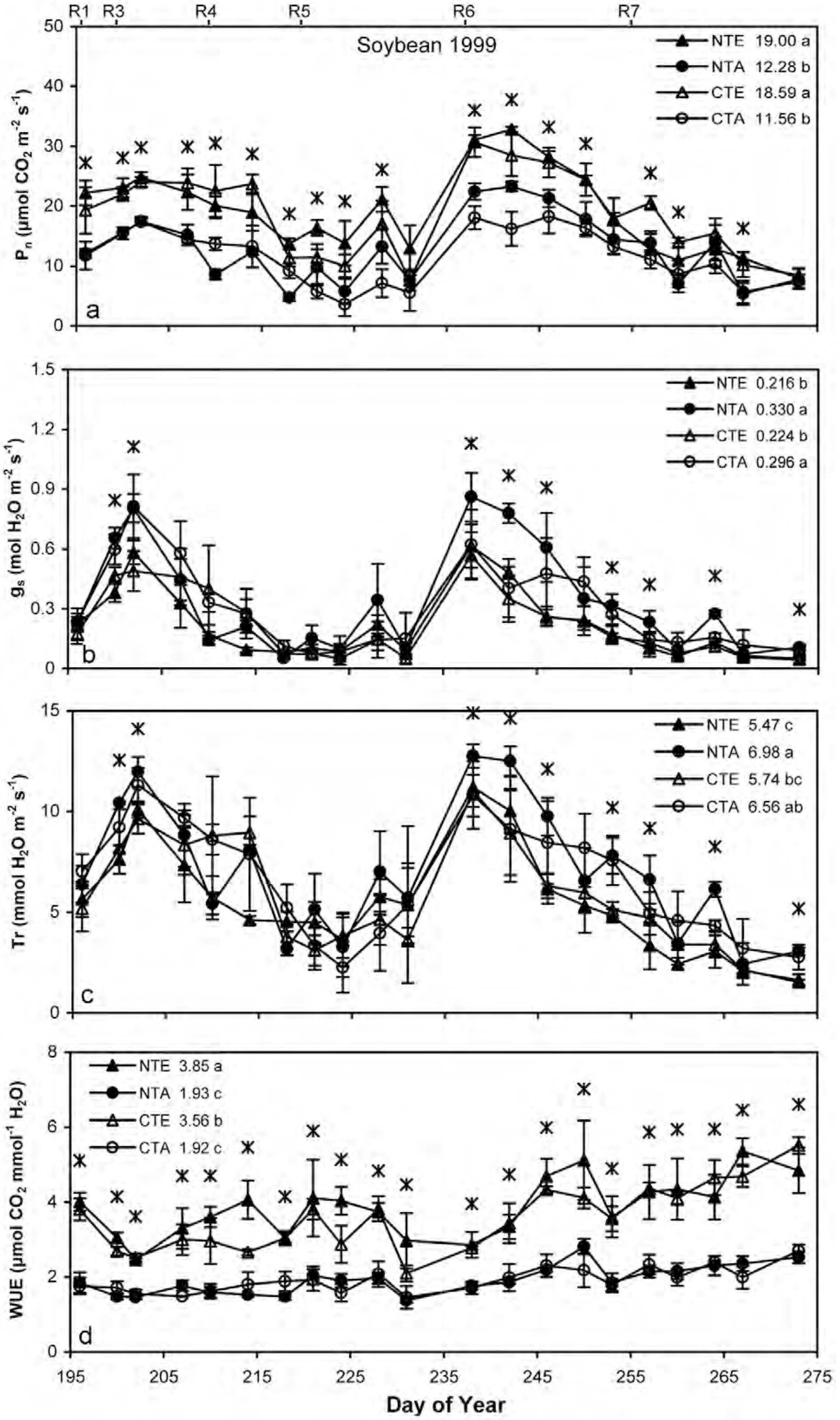

Fig. 1. Soybean gas exchange measures taken during reproductive growth in 1999: (a) Photosynthesis (P_n), (b) Stomatal conductance (g_s), (c) Transpiration (Tr), and (d) Water use efficiency (WUE). Soybean was grown under conventional tillage (CT) or no-tillage (NT) and exposed to ambient (A) or elevated (E) atmospheric CO_2. Asterisks indicate dates with a significant CO_2 effect ($P \leq 0.10$). Values within graphs are seasonal averages; averages followed by different letters were significantly different (LSMeans procedure, Proc Mixed, SAS; $P \leq 0.10$; $n = 3$). Growth stages are noted at the top of the figure: R1 (beginning bloom), R3 (beginning pod), R4 (full pod), R5 (beginning seed), R6 (full seed), and R7 (beginning maturity).

Table 3. Statistics (Pr > *F*; italics represent significance) for carbon dioxide concentration, tillage system, and their interaction on soybean gas exchange variables for the various sampling dates in 2001.

DOY†	Gas exchange variable											
	P_n			g_s			Tr			WUE		
	CO_2	Till	C × T	CO_2	Till	C × T	CO_2	Till	C × T	CO_2	Till	C × T
198	*0.092*	0.222	0.765	0.231	*0.091*	0.884	0.169	*0.066*	0.784	*<0.001*	0.119	0.335
200	*0.008*	0.386	0.397	0.383	0.355	0.412	0.348	0.429	0.145	*0.002*	0.567	0.334
205	*<0.001*	0.920	0.867	*0.001*	0.595	0.654	*0.002*	0.993	0.787	*0.005*	0.993	0.918
208	*<0.001*	0.248	0.105	*0.089*	0.674	0.682	0.280	0.480	0.632	*<0.001*	*0.060*	0.284
212	*<0.001*	0.605	0.944	0.312	0.678	0.890	0.551	0.702	0.941	*<0.001*	0.813	0.541
215	0.130	0.757	0.129	0.107	0.944	*0.042*	*0.022*	0.680	*0.029*	*0.008*	0.325	0.353
220	*0.003*	0.146	0.320	*0.012*	*0.012*	*0.007*	0.139	*0.061*	*0.051*	*0.006*	0.738	0.256
222	*0.094*	0.533	0.724	*0.024*	0.353	0.386	*0.018*	0.326	0.402	*<0.001*	0.256	0.563
226	*<0.001*	0.231	*0.002*	*<0.001*	*0.003*	0.630	*0.001*	0.195	0.421	*<0.001*	0.535	0.233
229	*0.008*	0.664	0.929	*0.002*	0.390	0.468	*0.024*	0.818	0.567	*<0.001*	0.727	0.288
233	*0.006*	0.985	0.365	0.615	0.853	0.445	0.871	0.844	0.526	*0.009*	0.520	0.386
236	*0.002*	0.349	*0.009*	0.916	0.718	0.186	0.711	0.597	0.206	*0.001*	0.830	*0.088*
240	0.177	0.249	0.103	*<0.001*	0.902	0.127	*<0.001*	0.484	0.255	*<0.001*	0.636	0.652
243	*0.041*	0.943	0.636	0.607	0.644	*0.044*	0.575	0.601	0.114	*0.003*	*0.092*	*0.035*
247	*0.018*	0.468	0.270	*0.001*	0.529	0.236	*0.003*	0.366	0.237	*<0.001*	0.338	0.466
249	*0.012*	0.944	0.111	0.538	0.324	0.161	0.748	0.529	0.196	*0.001*	0.505	0.940
255	*0.015*	0.583	0.627	*0.035*	0.598	0.712	*0.023*	0.385	0.924	*<0.001*	0.746	0.987
257	*0.013*	0.412	0.519	0.757	0.240	0.761	0.752	0.454	0.458	*0.001*	0.423	0.707
262	0.835	*0.048*	0.859	*0.080*	0.116	0.675	*0.078*	0.105	0.957	*0.002*	0.540	0.124
264	*0.031*	0.640	0.451	0.683	0.669	0.469	0.798	0.626	0.481	*<0.001*	0.611	0.218
268	0.254	0.945	0.458	0.192	0.750	0.449	0.217	0.813	0.525	*0.002*	0.931	0.654
270	0.638	0.601	0.136	0.682	0.419	0.234	0.703	0.348	0.258	*<0.001*	0.157	*0.006*
Avg.	*<0.001*	0.849	0.797	*<0.001*	0.613	0.987	*0.002*	0.959	0.981	*<0.001*	0.555	*0.081*

† C × T, interaction between carbon dioxide concentration and tillage system; CO_2, carbon dioxide concentration; DOY, day of year; g_s, conductance (mol H_2O m^{-2} s^{-1}); P_n, photosynthesis (μmol CO_2 m^{-2} s^{-1}); Till, tillage system; Tr, transpiration (mmol H_2O m^{-2} s^{-1}); WUE, water use efficiency (μmol CO_2 $mmol^{-1}$ H_2O).

under NT. Significant interactions of CO_2 and tillage occurred on DOY 200 and 214 (Table 2). On the first date, elevated CO_2 increased WUE in both tillage treatments, with the magnitude being greater under NT. On the latter date, elevated CO_2 increased WUE only under NT.

In 2001, WUE was similar to 1999 in that elevated CO_2 significantly increased WUE on all dates (Table 3; Fig. 2d). Main effects of tillage on WUE were observed on DOY 208 and 243 (Table 3) when WUE under NT was increased on the first date and reduced on the second. Significant interactions of CO_2 and tillage were noted on DOY 236, 243, and 270 (Table 3). On the first date, elevated CO_2 increased WUE in both tillage treatments with a greater magnitude of response under NT. On the second date, elevated CO_2 increased WUE only under CT. On the third date, elevated CO_2 increased WUE only under NT.

In 2003, elevated CO_2 significantly increased WUE on all dates (Table 4; Fig. 3d). There was a main effect of tillage only on DOY 259 (Table 4), when NT increased WUE. Significant interactions of CO_2 and tillage occurred on DOY 225, 232, and 259 (Table 4); in all cases, elevated CO_2 significantly increased WUE in both tillage treatments, with a greater magnitude of response under NT.

Elevated CO_2 significantly increased seasonal averages for WUE in each of the 3 yr (Tables 2–4; Fig. 1–3) and when averaged across all three seasons ($P < 0.001$). These seasonal and total averages reflected no main effect of tillage (total average $P = 0.263$). Interactions of CO_2 and tillage occurred in 2001 (Table 3), in 2003 (Table 4), and when averaged across all three seasons ($P = 0.003$); elevated CO_2 increased WUE in both tillage treatments, with a greater magnitude of response under NT.

Sorghum

In 2000, elevated CO_2 significantly increased P_n on 6 of 13 sampling dates (Table 5; Fig. 4a). Main effects of tillage were noted on five dates (Table 5). No-till increased P_n on DOY 217 but reduced it on DOY 189, 193, 201, and 220. There was a significant interaction of CO_2 and tillage on DOY 209 (Table 5) when elevated CO_2 increased P_n only under CT.

The 2002 growing season was similar to 2000 in that elevated CO_2 significantly increased P_n only on three of nine sampling dates (Table 6; Fig. 5a). There were no main effects of tillage on P_n (Table 6). A significant interaction of CO_2 with tillage occurred on DOY 210 (Table 6); under elevated CO_2, P_n was significantly higher under NT compared with CT.

In contrast to the previous two seasons, elevated CO_2 significantly increased P_n on 8 of 10 sampling dates in 2004 (Table 7; Fig. 6a). No-till significantly reduced P_n on DOY 212 and 217 (Table 7). Significant interactions of CO_2 with tillage occurred on the final two sampling dates (DOY 224 and 226) (Table 7); elevated CO_2 significantly increased P_n only under NT.

Elevated CO_2 significantly increased seasonal averages for P_n in each of the 3 yr (Tables 5–7; Fig. 4–6) and when averaged across all three seasons ($P < 0.001$). No-till significantly reduced P_n in 2000 (Table 5) and when averaged across all seasons ($P = 0.054$). There were no significant interactions between CO_2

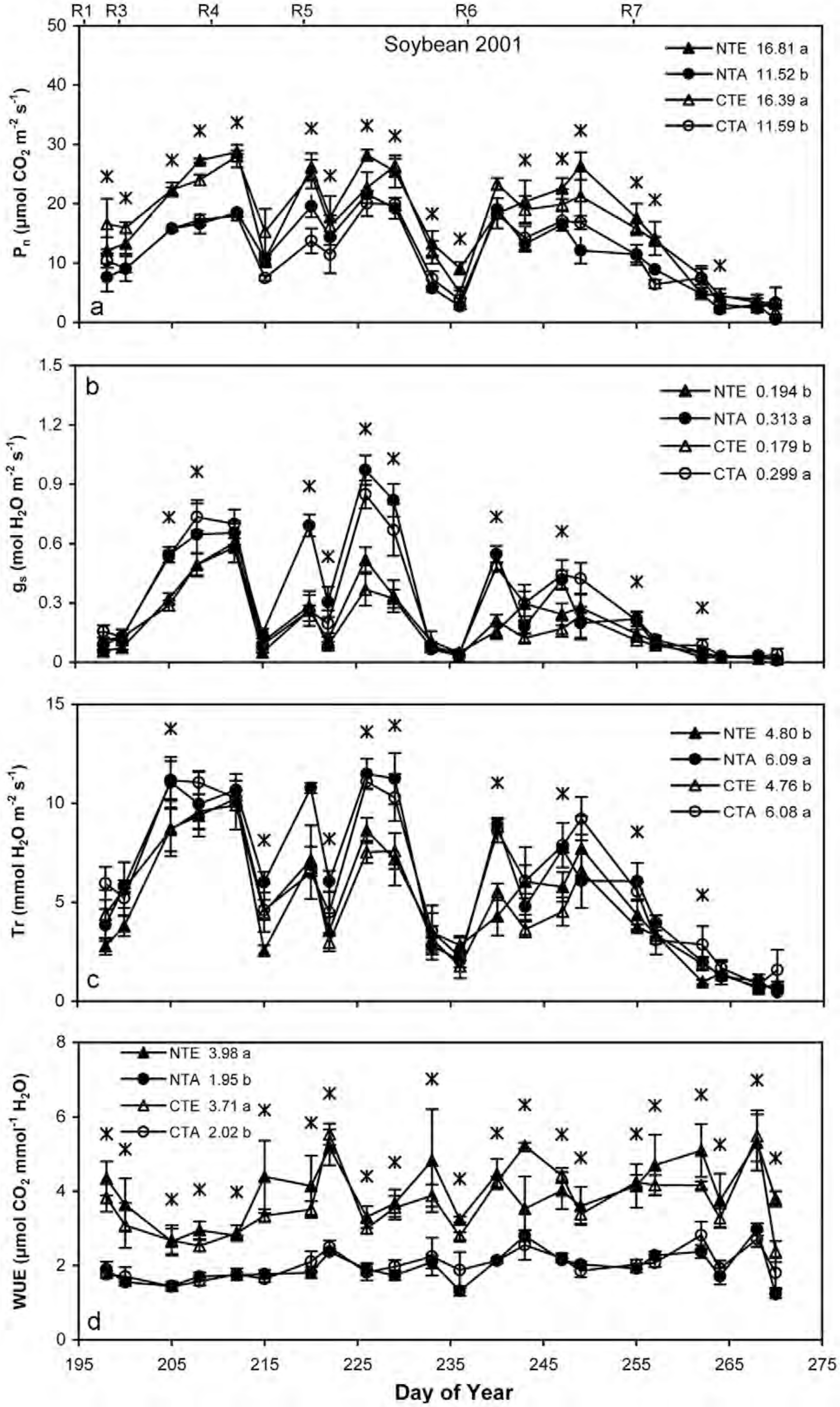

Fig. 2. Soybean gas exchange measures taken during reproductive growth in 2001: (a) Photosynthesis (P_n), (b) Stomatal conductance (g_s), (c) Transpiration (Tr), and (d) Water use efficiency (WUE). Soybean was grown under conventional tillage (CT) or no-tillage (NT) and exposed to ambient (A) or elevated (E) atmospheric $\mathrm{CO_2}$. Asterisks indicate dates with a significant $\mathrm{CO_2}$ effect ($P \leq 0.10$). Values within graphs are seasonal averages; averages followed by different letters were significantly different (LSMeans procedure, Proc Mixed, SAS; $P \leq 0.10$; $n = 3$). Growth stages are noted at the top of the figure: R1 (beginning bloom), R3 (beginning pod), R4 (full pod), R5 (beginning seed), R6 (full seed), and R7 (beginning maturity).

and tillage on seasonally averaged P_n (total average $P = 0.785$) (Tables 5–7).

In 2000, elevated $\mathrm{CO_2}$ significantly reduced g_s on 5 of 13 sampling dates (Table 5; Fig. 4b). No-till reduced g_s only on DOY 193 (Table 5). No significant interaction of $\mathrm{CO_2}$ and tillage was observed (Table 5).

In 2002, elevated $\mathrm{CO_2}$ significantly reduced g_s on seven of nine sampling dates (Table 6; Fig. 5b). Similar to 2000, NT reduced g_s only on one date (DOY 199) (Table 6), and no significant interactions of $\mathrm{CO_2}$ and tillage were observed (Table 6).

In 2004, elevated $\mathrm{CO_2}$ significantly reduced g_s on the final 6 of the 10 sampling dates (Table 7; Fig. 6b). No-till significantly reduced g_s on only DOY 217 (Table 7). Significant interactions of $\mathrm{CO_2}$ with tillage occurred on two dates (Table 7). On DOY 212, elevated $\mathrm{CO_2}$ reduced g_s only under CT. On DOY 226, elevated $\mathrm{CO_2}$ reduced g_s in both tillage treatments, with the magnitude of response being greater in the CT system.

Elevated $\mathrm{CO_2}$ significantly reduced seasonal averages for g_s in each of the 3 yr (Tables 5–7; Fig. 4–6) and when averaged across all three seasons ($P < 0.001$). These seasonal and total averages reflected no main effect of tillage (total average $P = 0.207$). A significant interaction between $\mathrm{CO_2}$ and tillage occurred in 2004 (Table 7) when elevated $\mathrm{CO_2}$ reduced the seasonal average for g_s in both tillage treatments, with the magnitude of response being greater in CT. The interaction between $\mathrm{CO_2}$ and tillage did not affect g_s when averaged across the three seasons ($P = 0.245$).

In 2000, elevated $\mathrm{CO_2}$ significantly reduced Tr on only 3 of 13 sampling dates (Table 5; Fig. 4c). No-till significantly reduced Tr only on DOY 193 (Table 5). A single significant interaction of $\mathrm{CO_2}$ and tillage was noted on DOY 196 (Table 5). Elevated $\mathrm{CO_2}$ reduced Tr under NT; unexpectedly, elevated $\mathrm{CO_2}$ increased Tr under CT.

Elevated $\mathrm{CO_2}$ significantly reduced Tr on 6 of 9 sampling dates in 2002 (Table 6; Fig. 5c). There were no significant main effects of tillage or interactions of $\mathrm{CO_2}$ with tillage on Tr (Table 6).

Table 4. Statistics (Pr > *F*; italics represent significance) for carbon dioxide concentration, tillage system, and their interaction on soybean gas exchange variables for the various sampling dates in 2003.

DOY†	Gas exchange variable											
	P_n			g_s			Tr			WUE		
	CO_2	Till	C × T	CO_2	Till	C × T	CO_2	Till	C × T	CO_2	Till	C × T
206	*<0.001*	0.873	0.784	0.533	0.388	0.791	0.410	0.258	0.453	*0.005*	0.235	0.287
210	*0.004*	0.782	0.434	0.194	0.714	0.365	0.194	0.577	0.227	*0.056*	0.347	0.157
213	*<0.001*	0.663	*0.069*	0.157	0.641	0.105	0.411	0.711	0.198	*<0.001*	0.811	0.680
216	*0.001*	0.764	0.325	*0.004*	0.920	0.626	*0.072*	0.875	0.431	*<0.001*	0.838	0.695
220	*<0.001*	*0.028*	0.607	*0.006*	0.521	0.258	*0.022*	0.447	0.350	*0.002*	0.614	0.879
225	*<0.001*	0.227	0.984	*0.002*	0.205	0.198	*0.036*	0.131	0.425	*<0.001*	0.186	*0.068*
227	*0.007*	0.638	0.251	*0.081*	0.454	0.323	0.222	0.692	0.415	*0.010*	0.824	0.818
232	*<0.001*	0.183	0.400	*0.047*	0.534	0.913	0.182	0.677	0.419	*<0.001*	0.576	*0.014*
234	*<0.001*	*0.068*	0.955	*0.024*	0.565	0.937	*0.004*	*0.013*	0.335	*<0.001*	0.853	0.530
238	*0.001*	0.539	0.546	*0.015*	0.782	0.294	*0.064*	0.517	0.945	*0.001*	0.781	0.453
241	*<0.001*	*0.025*	0.154	*0.021*	*0.010*	0.140	0.215	*0.024*	0.966	*0.001*	0.223	0.151
245	*0.006*	0.354	0.892	0.218	0.515	0.991	0.487	0.619	0.717	*0.002*	0.825	0.602
248	*0.039*	0.738	0.325	0.151	0.727	0.694	0.122	0.675	0.647	*<0.001*	0.489	0.673
252	*0.045*	0.971	0.578	*0.039*	0.860	0.252	0.101	0.988	0.417	*<0.001*	0.561	0.493
255	*0.001*	*0.016*	*0.087*	0.305	*0.013*	0.150	0.171	*0.040*	*0.099*	*0.001*	0.944	0.130
259	*0.037*	0.158	0.581	0.316	0.105	0.846	0.519	0.114	0.423	*<0.001*	*0.098*	*0.002*
262	0.347	0.439	0.834	0.215	0.302	0.568	0.215	0.276	0.921	*0.013*	0.542	0.138
267	0.125	0.883	0.525	*0.024*	0.884	0.857	*0.006*	0.784	0.921	*0.009*	0.667	0.353
269	*0.025*	0.125	0.979	0.430	0.229	0.341	0.498	0.114	0.816	*0.008*	0.980	0.321
Avg.	*<0.001*	0.410	0.604	*<0.001*	0.259	0.322	*0.012*	0.250	0.995	*<0.001*	0.171	*0.027*

† C × T, interaction between carbon dioxide concentration and tillage system; CO_2, carbon dioxide concentration; DOY, day of year; g_s, conductance (mol H_2O m^{-2} s^{-1}); P_n, photosynthesis (μmol CO_2 m^{-2} s^{-1}); Till, tillage system; Tr, transpiration (mmol H_2O m^{-2} s^{-1}); WUE, water use efficiency (μmol CO_2 $mmol^{-1}$ H_2O).

Table 5. Statistics (Pr > *F*; italics represent significance) for carbon dioxide concentration, tillage system, and their interaction on sorghum gas exchange variables for the various sampling dates in 2000.

DOY†	Gas exchange variable											
	P_n			g_s			Tr			WUE		
	CO_2	Till	C × T	CO_2	Till	C × T	CO_2	Till	C × T	CO_2	Till	C × T
182	0.171	0.449	0.532	0.191	0.823	0.247	0.236	0.800	0.486	*0.009*	0.428	0.801
187	*0.079*	0.967	0.893	0.130	0.753	0.902	0.175	0.804	0.915	*<0.001*	0.103	*0.093*
189	0.933	*0.098*	0.871	0.238	0.232	0.952	0.397	0.335	0.931	*0.004*	0.534	0.262
193	0.404	*0.016*	0.511	*0.093*	*0.021*	0.597	0.110	*0.022*	0.974	*0.001*	0.848	0.675
196	*0.034*	0.434	0.114	0.702	0.991	0.286	0.534	0.992	*0.003*	*0.012*	0.631	0.425
201	*0.075*	*0.088*	0.474	0.191	0.275	0.617	0.362	0.217	0.732	*0.014*	0.928	0.628
203	*0.018*	0.333	0.466	0.742	0.511	0.453	0.857	0.613	0.466	*0.022*	0.619	0.518
207	0.899	0.912	0.378	*<0.001*	0.480	0.719	*0.002*	0.644	0.421	*<0.001*	0.120	0.328
209	*0.082*	0.435	*0.090*	0.122	0.844	0.150	0.137	0.680	0.212	*0.024*	0.756	0.417
214	0.575	0.439	0.223	*0.060*	0.239	0.147	*0.073*	0.328	0.223	*0.004*	0.796	0.484
217	0.794	*0.096*	0.195	*0.035*	0.395	0.502	*0.015*	0.174	0.549	*0.002*	0.525	0.582
220	0.334	*0.061*	0.985	*0.055*	0.286	0.952	0.121	0.341	0.996	0.120	0.444	0.773
222	*0.034*	0.322	0.878	0.395	0.407	0.611	0.590	0.443	0.729	*0.043*	0.669	0.539
Avg.	*0.003*	*0.025*	0.550	*<0.001*	0.197	0.916	*<0.001*	0.283	0.794	*<0.001*	0.996	0.309

† C × T, interaction between carbon dioxide concentration and tillage system; CO_2, carbon dioxide concentration; DOY, day of year; g_s, conductance (mol H_2O m^{-2} s^{-1}); P_n, photosynthesis (μmol CO_2 m^{-2} s^{-1}); Till, tillage system; Tr, transpiration (mmol H_2O m^{-2} s^{-1}); WUE, water use efficiency (μmol CO_2 $mmol^{-1}$ H_2O).

The effect of CO_2 on Tr in 2004 was similar to 2002 in that elevated CO_2 significantly reduced Tr on 7 of 10 sampling dates (Table 7; Fig. 6c). Also similar to 2002, there were no main effects of tillage on Tr (Table 7). However, significant interactions of CO_2 and tillage were noted on two dates (Table 7). On DOY 212, elevated CO_2 reduced Tr only under CT. On DOY 224, elevated CO_2 significantly reduced Tr in both systems, with the magnitude of response being greater under CT.

Elevated CO_2 significantly reduced seasonal averages for Tr in each of the 3 yr (Tables 5–7; Fig. 4–6) and when averaged across all three seasons ($P < 0.001$). These seasonal and total averages reflected no main effect of tillage (total average $P = 0.323$) or interaction between CO_2 and tillage (total average $P = 0.868$).

As with soybean, WUE was the most consistent variable measured in sorghum. In 2000, elevated CO_2 significantly increased WUE on all but one date (Table 5; Fig. 4d). There were no main effects of tillage on WUE (Table 5). A signifi-

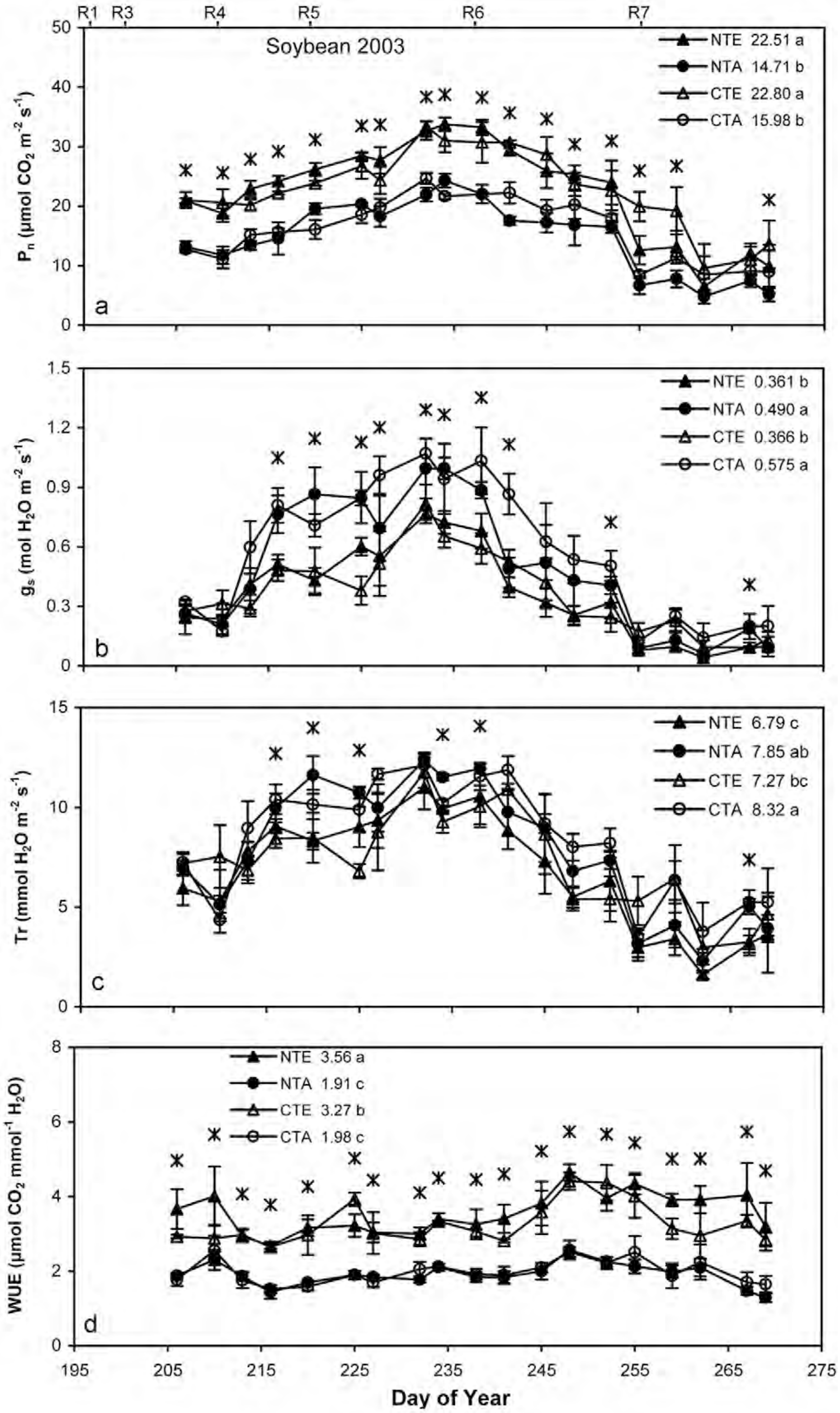

Fig. 3. Soybean gas exchange measures taken during reproductive growth in 2003: (a) Photosynthesis (P_n), (b) Stomatal conductance (g_s), (c) Transpiration (Tr), and (d) Water use efficiency (WUE). Soybean was grown under conventional tillage (CT) or no-tillage (NT) and exposed to ambient (A) or elevated (E) atmospheric CO_2. Asterisks indicate dates with a significant CO_2 effect ($P \leq 0.10$). Values within graphs are seasonal averages; averages followed by different letters were significantly different (LSMeans procedure, Proc Mixed, SAS; $P \leq 0.10$; $n = 3$). Growth stages are noted at the top of the figure: R1 (beginning bloom), R3 (beginning pod), R4 (full pod), R5 (beginning seed), R6 (full seed), and R7 (beginning maturity).

cant interaction of CO_2 with tillage was observed on DOY 187 (Table 5); elevated CO_2 increased WUE in both systems, with the magnitude of response being slightly greater under NT conditions.

In 2002, elevated CO_2 significantly increased WUE on all dates (Table 6; Fig. 5d). As in 2000, there were no main effects of tillage on WUE, and there was only one significant interaction (DOY 206) (Table 6) when elevated CO_2 increased WUE in both systems, with the magnitude of response being greater under NT.

As in 2002, elevated CO_2 significantly increased WUE on all dates in 2004 (Table 7; Fig. 6d). No-till significantly reduced WUE on DOY 210 (Table 7). As in the previous 2 yr, a single significant interaction of CO_2 and tillage occurred (Table 7); on DOY 212, elevated CO_2 increased WUE only under CT.

Elevated CO_2 significantly increased seasonal averages for WUE in each of the 3 yr (Tables 5–7; Fig. 4–6) and when averaged across all three seasons ($P < 0.001$). These seasonal and total averages reflected no main effect of tillage (total average $P = 0.913$) or interaction between CO_2 and tillage (total average $P = 0.310$).

Discussion

Conservation agricultural practices can be beneficial in terms of reduced erosion and increased water infiltration and soil C storage, leading to better nutrient and water retention (Phillips et al., 1980; Gebhardt et al., 1985; Kern and Johnson, 1993; Hunt et al., 1996; Diaz-Zorita et al., 2002; Triplett and Dick, 2008). Residues left on the soil surface in NT systems act as a mulch that enhances water infiltration, reduces evaporation, and aids in water conservation (Unger, 1984; Norwood, 1994; Reicosky et al., 1999). It is expected that these benefits would result in increased crop growth and yield, which has led to widespread adoption of NT systems in the last two decades (CTIC, 2004). However, the effects of conservation practices on crop yield have been inconsistent, with increases, decreases, or no effect being reported (Edwards et al., 1988; Torbert et al., 2001; 2009; Izumi et al., 2004; Balkcom et al., 2006). For example, sorghum yields from this study showed a significant increase (10.9%) in 2000, a nonsignificant increase (4.5%) in 2003, and a nonsignificant decrease (−3.2%) in 2004 under NT compared with CT (data not shown). Tillage treatment had no statistically significant impact on soybean yields in all 3 yr; however, the yield was 6.2% higher under NT in 1999 but was 4.4 and 5.5% lower under NT in 2001 and 2003, respectively (data not shown).

Studies that might explain this variability by examining the effects of conservation practices on crop physiology (i.e., photosynthesis and gas exchange) are lacking. Given the inconsistent yield responses alluded to above, one would expect that gas exchange measures would also vary. Tennakoon and Hulugalle (2006) reported no difference in WUE and Tr between minimum tilled and conventionally tilled cotton. Data from the current study support this finding. Significant effects of tillage on gas exchange measures were infrequent and varied as to whether NT resulted in an increase or a decrease. For example, tillage significantly affected P_n on only five sampling dates across the 3 yr of study in soybean and on only eight dates in sorghum; P_n was lower under NT on three dates in soybean and on seven dates in sorghum (Tables 2–7). Other gas exchange measures followed a similar pattern. These data are supported by the fact that the effects of tillage on plant biomass (a cumulative measure of season-long photosynthate production) were also small and variable (Prior et al., 2005).

Available soil water is necessary to maintain adequate rates of P_n during crop development, and water deficit is known to decrease P_n and Tr (Boyer, 1982). Therefore, when plant-available water is adequate, NT may have little effect on crop gas exchange. However, given the beneficial effects of NT on soil water, P_n rates can be sustained at least into early drought stages. Arriaga et al. (2009) found that tillage had little effect on cotton gas exchange measurements when rainfall was frequent. Under drought conditions, NT plots conserved soil water and maintained higher

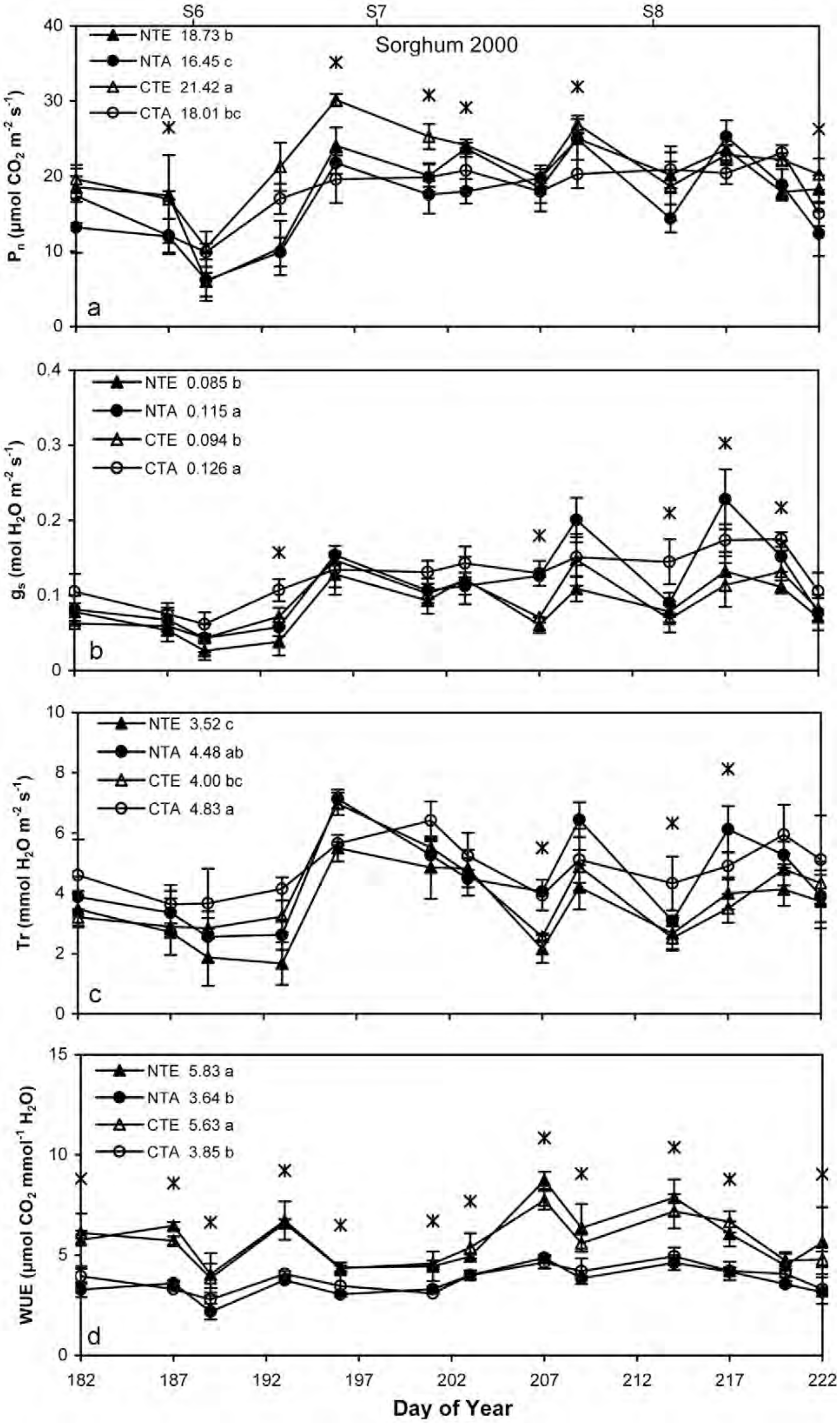

Fig. 4. Sorghum gas exchange measures taken during reproductive growth in 2000: (a) Photosynthesis (P_n), (b) Stomatal conductance (g_s), (c) Transpiration (Tr), and (d) Water use efficiency (WUE). Sorghum was grown under conventional tillage (CT) or no-tillage (NT) and exposed to ambient (A) or elevated (E) atmospheric CO$_2$. Asterisks indicate dates with a significant CO$_2$ effect ($P \leq 0.10$). Values within graphs are seasonal averages; averages followed by different letters were significantly different (LSMeans procedure, Proc Mixed, SAS; $P \leq 0.10$; $n = 3$). Growth stages are noted at the top of the figure: S6 (half bloom), S7 (soft dough), and S8 (hard dough).

Table 6. Statistics (Pr > *F*; italics represent significance) for carbon dioxide concentration, tillage system, and their interaction on sorghum gas exchange variables for the various sampling dates in 2002.

DOY†	Gas exchange variable											
	P_n			g_s			Tr			WUE		
	CO_2	Till	C × T	CO_2	Till	C × T	CO_2	Till	C × T	CO_2	Till	C × T
191	0.213	0.857	0.126	*0.081*	0.448	0.445	0.162	0.656	0.926	*0.071*	0.807	0.506
196	0.695	0.310	0.958	*0.008*	0.240	0.350	*0.055*	0.335	0.277	*0.063*	0.644	0.310
199	*0.004*	0.253	0.270	0.792	*0.006*	0.655	0.851	0.134	0.787	*0.028*	0.224	0.267
203	*0.064*	0.313	0.619	*0.008*	0.434	0.221	*0.011*	0.417	0.523	*<0.001*	0.773	0.656
206	0.646	0.542	0.478	*<0.001*	0.388	0.302	*<0.001*	0.491	0.152	*<0.001*	0.419	*0.073*
210	0.803	0.264	*0.059*	*0.014*	0.956	0.606	*0.044*	0.810	0.848	*0.023*	0.836	0.620
213	0.947	0.356	0.824	*0.031*	0.679	0.940	*0.015*	0.325	0.453	*0.002*	0.850	0.170
217	0.261	0.624	0.325	*0.039*	0.800	0.988	*0.045*	0.818	0.882	*0.016*	0.642	0.524
220	*0.004*	0.862	0.716	0.360	0.898	0.530	0.541	0.872	0.609	*0.001*	0.724	0.418
Avg.	*0.007*	0.944	0.418	*<0.001*	0.874	0.589	*<0.001*	0.999	0.931	*<0.001*	0.813	0.556

† C × T, interaction between carbon dioxide concentration and tillage system; CO_2, carbon dioxide concentration; DOY, day of year; g_s, conductance (mol H_2O m^{-2} s^{-1}); P_n, photosynthesis (μmol CO_2 m^{-2} s^{-1}); Till, tillage system; Tr, transpiration (mmol H_2O m^{-2} s^{-1}); WUE, water use efficiency (μmol CO_2 $mmol^{-1}$ H_2O).

Table 7. Statistics (Pr > *F*; italics represent significance) for carbon dioxide concentration, tillage system, and their interaction on sorghum gas exchange variables for the various sampling dates in 2004.

DOY†	Gas exchange variable											
	P_n			g_s			Tr			WUE		
	CO_2	Till	C × T	CO_2	Till	C × T	CO_2	Till	C × T	CO_2	Till	C × T
196	*0.035*	0.991	0.678	0.942	0.690	0.580	0.516	0.720	0.211	*0.040*	0.528	0.336
198	*<0.001*	0.315	0.608	0.229	0.786	0.361	*0.093*	0.433	0.490	*<0.001*	0.854	0.706
202	*0.003*	0.725	0.636	0.851	0.473	0.725	0.764	0.394	0.747	*0.002*	0.563	0.159
205	*0.042*	0.839	0.332	0.477	0.638	0.220	0.875	0.672	0.628	*0.001*	0.212	0.110
210	*0.021*	0.818	0.389	*0.002*	0.328	0.145	*0.001*	0.123	0.552	*<0.001*	*0.032*	0.368
212	0.979	*0.034*	0.191	*0.032*	0.278	*0.047*	*0.025*	0.516	*0.049*	*0.010*	0.472	*0.088*
217	0.202	*0.036*	0.198	*<0.001*	*0.011*	0.915	*0.008*	0.256	0.685	*0.002*	0.529	0.437
219	*0.021*	0.627	0.308	*0.057*	0.651	0.858	*0.001*	0.354	0.608	*0.001*	0.210	0.141
224	*0.031*	0.372	*0.045*	*0.001*	0.134	0.129	*0.002*	0.557	*0.030*	*<0.001*	0.498	0.118
226	*0.002*	0.513	*0.018*	*<0.001*	0.719	*0.006*	*0.002*	0.974	0.239	*0.006*	0.774	0.455
Avg.	*<0.001*	0.463	0.424	*<0.001*	0.467	*0.094*	*0.001*	0.523	0.424	*<0.001*	0.929	0.836

† C × T, interaction between carbon dioxide concentration and tillage system; CO_2, carbon dioxide concentration; DOY, day of year; g_s, conductance (mol H_2O m^{-2} s^{-1}); P_n, photosynthesis (μmol CO_2 m^{-2} s^{-1}); Till, tillage system; Tr, transpiration (mmol H_2O m^{-2} s^{-1}); WUE, water use efficiency (μmol CO_2 $mmol^{-1}$ H_2O).

rates of P_n; however, even this result was sporadically observed. The ability of NT to maintain P_n rates depends on the duration of drought; eventually soil water is depleted, and P_n subsequently declines. In addition to effects on soil water, NT can affect plant rooting. Due to the potential for higher mechanical impedance in NT soils, root penetration can be restricted to shallower soil depths (Izumi et al., 2004; Iijima et al., 2007). Furthermore, the mulching effect of additional unincorporated residues (including cover crop and nonyield residue from the previous row crop) in conservation systems (Prior et al., 2005) may also favor a shallower root system. This was observed with sorghum in our system, where NT favored shallow root systems, whereas CT favored deeper rooting (Pritchard et al., 2006). Having more roots in the upper soil profile may lead to more rapid depletion of soil water in this zone during drought. It is possible that rainfall was frequent enough in the present study to dampen the beneficial effects of NT on soil water conservation, resulting in little effect on crop gas exchange. The fact that CT tended to have higher P_n rates (on the few dates when a significant effect of tillage was observed) may be a result of deeper rooting in this system.

As with the effects of tillage systems, interactions between tillage and CO_2 were rarely observed (Tables 2–7) and varied as to whether a CO_2 response was observed in NT, CT, or both (with a difference in magnitude or direction). This was somewhat unexpected given the increased residue inputs and concomitant rise in soil C seen under elevated CO_2 and in the NT system (Prior et al., 2005). However, given the rarity and variability in tillage effects on gas exchange variables, perhaps this should not have been surprising. It is possible that some of these infrequent interactions were merely due to biotic or instrumental noise.

In contrast to the paucity of data on the effects of tillage on crop gas exchange, the impact of elevated CO_2 on these measures has been intensively examined. The best documented and repeatable response to atmospheric CO_2 enrichment is a significant increase in photosynthesis of C_3 plants (Rogers et al., 1983b; Long and Drake, 1992; Woodward, 1992; Amthor, 1995). This increased C uptake and assimilation generally results in increased crop growth under CO_2–enriched conditions. For C_3 plants, positive responses to elevated CO_2 are mainly attributed to competitive inhibition of photo-respiration 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). However, the CO_2–concentrating mechanism used by C_4 species limits the response to CO_2 enrich-

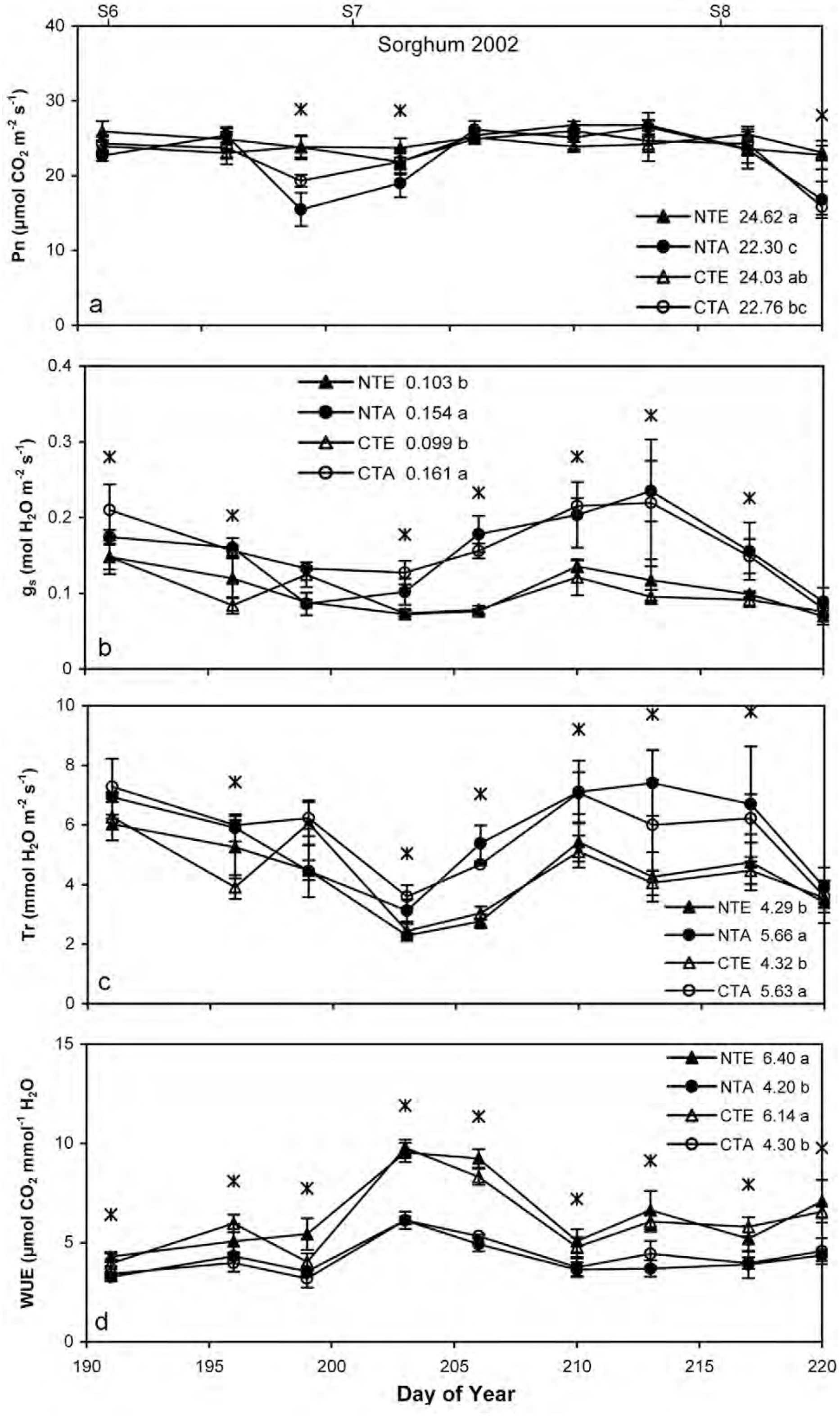

Fig. 5. Sorghum gas exchange measures taken during reproductive growth in 2002: (a) Photosynthesis (P_n), (b) Stomatal conductance (g_s), (c) Transpiration (Tr), and (d) Water use efficiency (WUE). Sorghum was grown under conventional tillage (CT) or no-tillage (NT) and exposed to ambient (A) or elevated (E) atmospheric CO_2. Asterisks indicate dates with a significant CO_2 effect ($P \leq 0.10$). Values within graphs are seasonal averages; averages followed by different letters were significantly different (LSMeans procedure, Proc Mixed, SAS; $P \leq 0.10$; $n = 3$). Growth stages are noted at the top of the figure: S6 (half bloom), S7 (soft dough), and S8 (hard dough).

ment (Amthor and Loomis, 1996). These differences in CO_2 utilization during photosynthesis result in the fact that 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). Summaries have consistently shown that biomass response to atmospheric CO_2 enrichment varies between plants with a C_3 (33–40% increase) vs. a C_4 (10–15% increase) photosynthetic pathway (Kimball, 1983; Prior et al., 2003).

Data from the current study support this response pattern. Across the entire study, elevated CO_2 significantly increased soybean (a C_3 crop) P_n by 48.5%. In comparison, sorghum (a C_4 crop) P_n was also significantly increased by elevated CO_2 but only by 15.5%; these numbers are analogous to those mentioned above. Across the entire study, elevated CO_2 increased soybean P_n on 83% of sampling dates (Tables 2–4; Fig. 1–3). Soybean P_n began to taper off toward the end of each season due to crop senescence, and days when soybean showed no significant CO_2 response tended to occur during these later periods. Significant increases in sorghum P_n tended to occur sporadically across the growing seasons (Tables 5–7; Fig. 4–6) and were observed less frequently (on 53% of sampling dates) than in soybean. The late-season tapering effect observed in soybean was not seen in the sorghum crops. This was logical in that sorghum is harvested at physiological maturity when plants are still green, whereas soybeans are harvested after plants defoliate and dry.

In addition to effects on P_n, elevated CO_2 is known to decrease g_s and Tr (Eamus and Jarvis, 1989; Rogers et al., 1983b; Prior et al., 1991). These reductions in g_s and Tr are due to the fact that elevated CO_2 induces the partial closure of stomates on leaf surfaces; this is true for C_3 and C_4 crops (Rogers and Dahlman, 1993; Allen and Amthor, 1995). In general, CO_2–induced growth stimulation in C_3 plants is primarily caused by increased P_n, whereas in C_4 plants it is mainly caused by reduced g_s and Tr.

In the present study, g_s and Tr generally decreased in both crops exposed to elevated CO_2. In soybean, these responses were less consistent than CO_2 effects on P_n, and significant effects of elevated CO_2 occurred on only 47 and 37% of sampling dates for g_s and Tr, respectively (Tables 2–4; Fig. 1–3). Elevated CO_2 reduced soybean g_s (33.3%) and Tr (17.0%), compared with the 48.5% increase seen in P_n. In sorghum, significant effects of CO_2 on g_s and Tr tended to occur sporadically across the growing seasons; significant reductions occurred on 53 and 59% of sampling dates (Tables 5–7; Fig. 4–6). These numbers are similar to the increases observed in P_n. Elevated CO_2 decreased sorghum g_s and Tr by 29.7 and 20.7% across all years, which was larger than the 15.5% increase in P_n.

Water use efficiency is a measure of the amount of carbon fixed per unit of water used. It is calculated by dividing P_n by Tr and therefore is influenced by a combination of these factors. Elevated atmospheric CO_2 generally results in increased WUE for plants with C_3 and C_4 photosynthetic pathways (Rogers et al., 1983b; Amthor, 1995). Data from the current study are no exception to this rule. In fact, increased WUE under elevated CO_2 was the most consistent response noted for both species with soybean (Tables 2–4; Fig. 1–3) showing ~70% greater increase in WUE than sorghum (Tables 5–7; Fig. 4–6). In C_3 plants, P_n generally plays a more important role in determining WUE, whereas in C_4 plants, Tr is usually the more dominant factor (Rogers and Dahlman, 1993). Soybean in our study was consistent with this pattern in that it showed a greater P_n than Tr response to elevated CO_2 (Tables 2–4); the response of Tr was slightly greater than P_n in sorghum (Tables 5–7).

In summary, tillage had infrequent and inconsistent effects on gas exchange in soybean and grain sorghum through a 6-yr field study. Increased photosynthesis, decreased stomatal conductance, and transpiration (leading to dramatically increased WUE) were consistently seen in both species when grown under elevated CO_2; these effects tended to be greater in soybean than in sorghum. Biomass production in this cropping system study followed similar response patterns to tillage

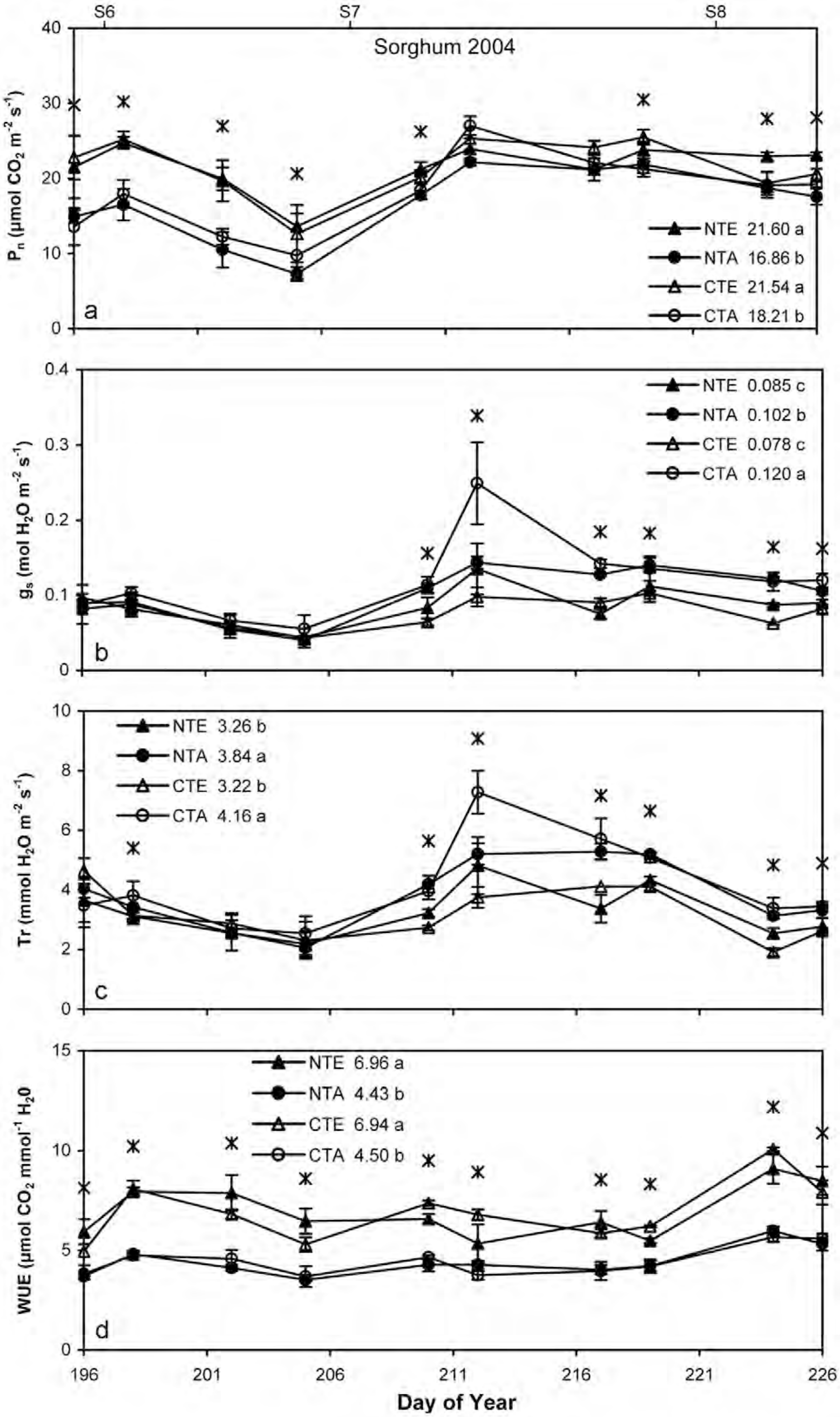

Fig. 6. Sorghum gas exchange measures taken during reproductive growth in 2004: (a) Photosynthesis (P_n), (b) Stomatal conductance (g_s), (c) Transpiration (Tr), and (d) Water use efficiency (WUE). Sorghum was grown under conventional tillage (CT) or no-tillage (NT) and exposed to ambient (A) or elevated (E) atmospheric CO_2. Asterisks indicate dates with a significant CO_2 effect ($P \leq 0.10$). Values within graphs are seasonal averages; averages followed by different letters were significantly different (LSMeans procedure, Proc Mixed, SAS; $P \leq 0.10$; $n = 3$). Growth stages are noted at the top of the figure: S6 (half bloom), S7 (soft dough), and S8 (hard dough).

and CO_2 (Prior et al., 2005). These results suggest that high rates of photosynthesis can occur in CO_2–enriched environments during reproductive growth in both tillage systems. When this increased photosynthesis is combined with more efficient use of water, greater productivity results from the rising concentration of atmospheric CO_2.

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