*Regular paper*

# The effect of $CO_2$ enrichment on leaf photosynthetic rates and instantaneous water use efficiency of *Andropogon gerardii* in the tallgrass prairie

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## Abstract

Open-top chambers were used to study the effects of $CO_2$ enrichment on leaf-level photosynthetic rates of the $C_4$ grass *Andropogon gerardii* in the native tallgrass prairie ecosystem near Manhattan, Kansas. Measurements were made during a year with abundant rainfall (1993) and a year with below-normal rainfall (1994). Treatments included: No chamber, ambient $CO_2$ (A); chamber with ambient $CO_2$ (CA); and chamber with twice-ambient $CO_2$ (CE). Measurements of photosynthesis were made at 2-hour intervals, or at midday, on cloudless days throughout the growing season using an open-flow gas-exchange system. No significant differences in midday rates of photosynthesis or in daily carbon accumulation as a result of $CO_2$ enrichment were found in the year with abundant precipitation. In the dry year, midday rates of photosynthesis were significantly higher in the CE treatment than in the CA or A treatments throughout the season. Estimates of daily carbon accumulation also indicated that $CO_2$ enrichment allowed plants to maximize carbon acquisition on a diurnal basis. The increased carbon accumulation was accounted for by greater rates of photosynthesis in the CE plots during midday. During the wet year, $CO_2$ enrichment decreased stomatal conductance, which allowed plants to decrease transpiration while still photosynthesizing at rates similar to plants in ambient conditions. During the dry year, $CO_2$ enrichment allowed plants to maintain photosynthetic rates even though stomatal conductance and transpiration had been reduced in all treatments due to stress. Estimates of instantaneous water-use efficiency were reduced under $CO_2$ enrichment for both years.

*Abbreviations:* A – ambient-no chamber; CA – chamber-ambient; CE – Chamber-enriched; DOY – day of year; $g_s$ – stomatal conductance; WUE – water-use efficiency (peak biomass/water used); $WUE_{CE}/WUE_{CA}$ – ratio of CE WUE to CA WUE; $WUE_E$ – percent contribution of transpiration to change in $WUE_{CE}/WUE_{CA}$; $WUE_i$ – instantaneous water use efficiency (photosynthesis/transpiration); $WUE_{PSN}$ – percent contribution of photosynthesis to change in $WUE_{CE}/WUE_{CA}$

## Introduction

Rangelands (total estimated potentially grazeable land) occupy 70% of the earths land area (Williams et al. 1968) and 61% of the United States (FAO 1992), so effects of elevated $CO_2$ on rangelands may have a significant impact on global climate. In 1989, a project was initiated to characterize the effects of increased atmospheric $CO_2$ levels on a tallgrass prairie ecosystem (Owensby et al. 1989).

One aspect of the tallgrass prairie project has been to determine the effects of elevated $CO_2$ on *Andropo-*

*gon gerardii* Vitman., a dominant $C_4$ species of the tallgrass prairie. Biomass production of *A. gerardii* has been greater under elevated $CO_2$ levels in years with substantial water stress (Owensby et al. 1993). The greater biomass production of *A. gerardii* under $CO_2$ enrichment was due to a more efficient use of water (Owensby et al. 1993). Stomates partially close in response to elevated $CO_2$ (Mott 1990), which reduces stomatal conductance (Morison and Gifford 1984; Knapp et al. 1994a) and transpiration, and increases leaf water potential (Knapp et al. 1993). In the water-limited tallgrass prairie (Knapp 1984), $C_4$ plants have shown responses to $CO_2$ enrichment. Bremer et al. (1996) showed that elevated $CO_2$ reduced sap flow in *A. gerardii* by 18% and whole-chamber evapotranspiration by 23–27%, resulting in consistently higher soil water content.

Rates of photosynthesis of $C_3$ plants are enhanced under elevated $CO_2$ (Acock and Allen 1985; Oechel and Strain 1985; Cure and Acock 1986), but $C_4$ plants have shown little increase in photosynthetic capacity (Kramer 1981; Mooney et al. 1991). Also, lower stomatal conductance, such as is usually seen in $CO_2$ enrichment, typically has little effect on photosynthesis of $C_4$ plants because diffusion rates into the leaf are not usually limited by stomatal aperture (Mooney et al. 1991). However, most of the available data on the effects of elevated $CO_2$ on vegetation have been derived from short-term treatments (i.e. days to weeks) in controlled environments (Acock and Allen 1985; Cure and Acock 1986). These data show that species vary widely in rates of photosynthesis in response to $CO_2$, and the response is coupled to environmental factors (Wong 1979; Cure and Acock 1986).

Little is known about the field effects or ecosystem processes resulting from long-term exposure of native plant communities to elevated $CO_2$ (Oechel and Strain 1985). Preliminary data for a dry year in the tallgrass prairie project at Kansas State University showed greater photosynthetic capacity of *A. gerardii* under elevated $CO_2$ (Knapp et al. 1993). Ham et al. (1995) found a slight increase in field-scale net carbon exchange in a wet year as a result of $CO_2$ enrichment and attributed that increase to delayed senescence, although this may also be interpreted as extending the leaf replacement process. Our objectives were: (1) to monitor the diurnal and seasonal responses of photosynthetic rate, stomatal conductance and rate of transpiration of *A. gerardii* leaves to $CO_2$ enrichment under field conditions; (2) to use these data to obtain an estimate of water-use efficiency; and (3) to observe how these parameters vary as a result of seasonal differences. We hypothesize that: (1) photosynthetic rate will be enhanced and that stomatal conductance and transpiration rate will be reduced under $CO_2$ enrichment; (2) plants under $CO_2$ enrichment will exhibit a greater water-use efficiency; and (3) the degree of change in these parameters will vary as a result of diurnal and seasonal influences.

## Materials and methods

The experimental site was in a tallgrass prairie north of Manhattan, KS (39.12° N, 96.35° W, 324 m above sea level). This is a native tallgrass prairie site dominated by $C_4$ perennial tallgrasses, mainly *Sorghastrum nutans* (L.) Nash and *Andropogon gerardii* Vitman. Soils in the area are transitional from Ustolls to Udolls (Tully Series: Fine, mixed, Mesic Montmorillonitic, Pachic Argiustolls). The 30-year average precipitation for the growing season (May through September) is 52.9 cm. Growing-season precipitation for 1993 and 1994 was 116.8 cm and 42.1 cm, respectively. The 30-year average annual precipitation is 85.9 cm. Total precipitation in 1993 and 1994 was 143.5 cm and 68.2 cm, respectively.

Treatments, replicated two times, were ambient $CO_2$, no chamber (A); ambient $CO_2$, with chamber (CA); and enriched (twice-ambient) $CO_2$, with chamber (CE). Chamber design, and chamber data acquisition and control, are as previously reported (Ham et al. 1995). The four chambers used were relocated (on the same experimental site) in the spring of 1993. For the ambient $CO_2$ – no chamber treatment, plants were selected from the surrounding area.

Midday leaf xylem pressure potentials in 1993 were above –1.2 MPa for most of the season for all treatments (Knapp et al. 1994b). In 1994, the leaf xylem pressure potentials were at or below –1.5 MPa after DOY 170 and decreased as the season progressed (Knapp et al. 1996). Volumetric soil water content was summarized in Owensby et al. (1999). Soil water content was near 40% for all treatments for most of the season in 1993, but decreased after DOY 180 in 1994 from 40%, 38% and 33% in the CE, CA and A plots. Contents were 30% or below in the CA and A plots after DOY 230 in 1994. For both leaf water potentials and soil moisture content, the CE treatment had higher values than the CA and A treatments in 1994.

Photosynthetic rates of *A. gerardii* were measured during the 1993 and 1994 growing seasons on leaves

of vegetative (i.e. nonreproductive) tillers in the upper part of the canopy that were receiving nearly full sunlight. The uppermost, fully-expanded leaf from each of five plants in each chamber and each open area was selected, and five estimates of photosynthetic rates were made on the middle segment of each leaf lamina with an open-flow gas-exchange system (LCA-3, Analytical Development Company, Inc., UK). The system was calibrated for $CO_2$ throughout each sampling day with known span gases. The humidity sensors were calibrated on each sampling day using a dewpoint generator (Li-Cor 610, Li-Cor Inc., Lincoln, Nebraska, USA). The measurement regime included monthly diurnal measurements (2-h intervals from 8:00 to 18:00), and midday (from 12:00 to 14:00) measurements at 2 week intervals. Stomatal conductance in *A. gerardii* responds rapidly to variations in sunlight (Knapp et al. 1994a), and so a clear day is necessary for consistent photosynthetic measurements through time. Consequently, the precise date for each measurement was determined by prevailing atmospheric conditions.

Parameters measured by the gas-exchange system were leaf photosynthetic rate, stomatal conductance ($g_s$), leaf transpiration rate, leaf temperature ($T_L$), air temperature ($T_a$), and photosynthetically active radiation (PAR). Instantaneous water use efficiency ($WUE_i$) was calculated by dividing leaf photosynthetic rate by leaf transpiration (resulting units were $\mu$mol $CO_2$ mmol $H_2O^{-1}$). Ratios of CE–CA and CE–A WUE values were calculated, and the percent contributions of photosynthesis ($WUE_{PSN}$) and of transpiration ($WUE_E$) to the change in the ratio due to $CO_2$ enrichment were also determined according to the method of Allen (1994). The CE–CA ratios ($WUE_{CE}/WUE_{CA}$) were chosen as being representative of the overall response to $CO_2$ enrichment. The data were analyzed as repeated measures in a completely randomized design using PROC Mixed LS-MEANS (Littel et al. 1996) with the $\alpha$-level set at 0.1.

Trend lines of seasonal leaf photosynthesis values were constructed by graphing treatment means from the midday sampling time for each consecutive sampling day within each year (Figure 1). Diurnal responses of photosynthesis, $g_s$, transpiration and $WUE_i$ on each sampling day were integrated, and the area under the response curve determined to give an indication of daily totals of these parameters (Figure 2). Based on these determinations,one diurnal from each year was chosen for analysis and discussion (Figure 3). These diurnals were representative of their respective

year and fell on similar days of the year (i.e. DOY 208 in 1993 and DOY 203 in 1994). They were also characterized by cloudless skies and similar temperatures (approx. 40 °C at midday).

## Results

### Midday trends

No differences in midday rates of photosynthesis were observed during 1993 (Figure 1), with the exception of DOY 254, when a 50% increase ($P < 0.2$) was observed in the CE plots. Midday stomatal conductance and transpiration were lower in the CE plots than in the CA and A plots on most dates in 1993. Midday $WUE_i$ in the CE plots was significantly higher ($P < 0.1$) than in the non-enriched treatments throughout the 1993 season. No significant trends were found in $WUE_{CE}/WUE_{CA}$ (Figure 4). $WUE_E$ had a stronger effect on $WUE_{CE}/WUE_{CA}$ than $WUE_{PSN}$ did.

During 1994, midday rates of photosynthesis (Figure 1) in the CE plots were significantly higher than in the CA and A plots ($P < 0.05$), while the two non-enriched treatments were similar throughout the season. Leaf stomatal conductance and transpiration were similar for all three treatments for most measurement days in 1994, except for DOY 203 when stomatal conductance and transpiration in the A plots were significantly higher than in the CE ($P < 0.05$) and CA ($P < 0.1$) plots. Midday $WUE_i$ in $CO_2$ enrichment were double those in the two non-enriched treatments throughout the 1994 season. As in 1993, no significant trends in $WUE_{CE}/WUE_{CA}$ were observed for 1994 (Figure 4). However, $WUE_{PSN}$ had a stronger effect than $WUE_E$ in 1994. The effect of $WUE_{PSN}$ on $WUE_{CE}/WUE_{CA}$ was significantly greater ($P < 0.001$) in 1994 than in 1993. No significant day-to-day variation in either $WUE_{PSN}$ or $WUE_{CE}/WUE_{CA}$ was observed.

### Daily accumulation

Estimates of carbon accumulated on a daily basis indicated no treatment effect in 1993 (Figure 2). In 1994, daily accumulation in the CE plots was greater than in the CA or A plots. Stomatal conductance and transpiration were decreased in the CE plots in 1993 and 1994 compared to the CA or the A plots. An increased daily average WUE was observed in the CE treatment, compared to the CA or A treatments, for every measurement day in both years (Figure 2).
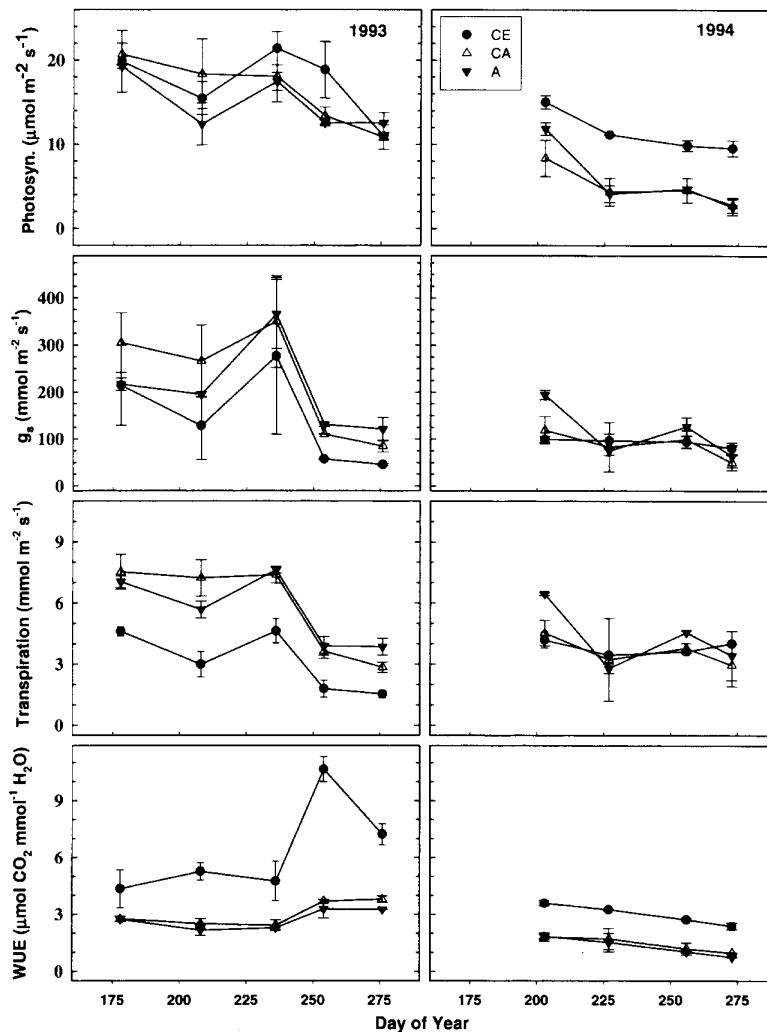
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*Figure 1.* Leaf-level measurements of photosynthetic rate (photosyn.), stomatal conductance ($g_s$), transpiration rate and instantaneous water use efficiency ($WUE_i$) of *Andropogon gerardii* taken at midday throughout the growing season in the tallgrass prairie for a wet year (1993) and a dry year (1994). $WUE_i$ is calculated as photosyn./transpiration. Treatments are: CE, $CO_2$-enriched, with chamber; CA, ambient $CO_2$, with chamber; A, ambient $CO_2$, no chamber.

*Diurnal patterns*

No significant differences in photosynthesis rates due to treatment were found on DOY 208 in 1993, although rates in the CA plots tended to be slightly higher than in the other two treatments throughout the day (Figure 3). On DOY 203 in 1994, rates in the CE plots increased and rates in the CA and A plots decreased after 8:00 (Figure 3). By 14:00, rates in the CE plots were double ($P = 0.0001$) those in the non-enriched plots. Photosynthesis rates before 16:00 in

the CE plots were higher in 1994 in the CE plots than in 1993.

Stomatal conductance in the non-enriched plots was 100-250% greater than in the CE plots on DOY 208 in 1993 (Figure 3). Differences were significant at 8:00, 10:00 and 14:00 ($P < 0.20$). On DOY 203 in 1994, conductance in the CE plots was approximately 50% lower than in the non-enriched plots at 8:00, 10:00 and 16:00 ($P < 0.1$). Stomatal conductance in the CA plots was higher in 1993 than in 1994, while conductance in the A plots was higher in the latter part
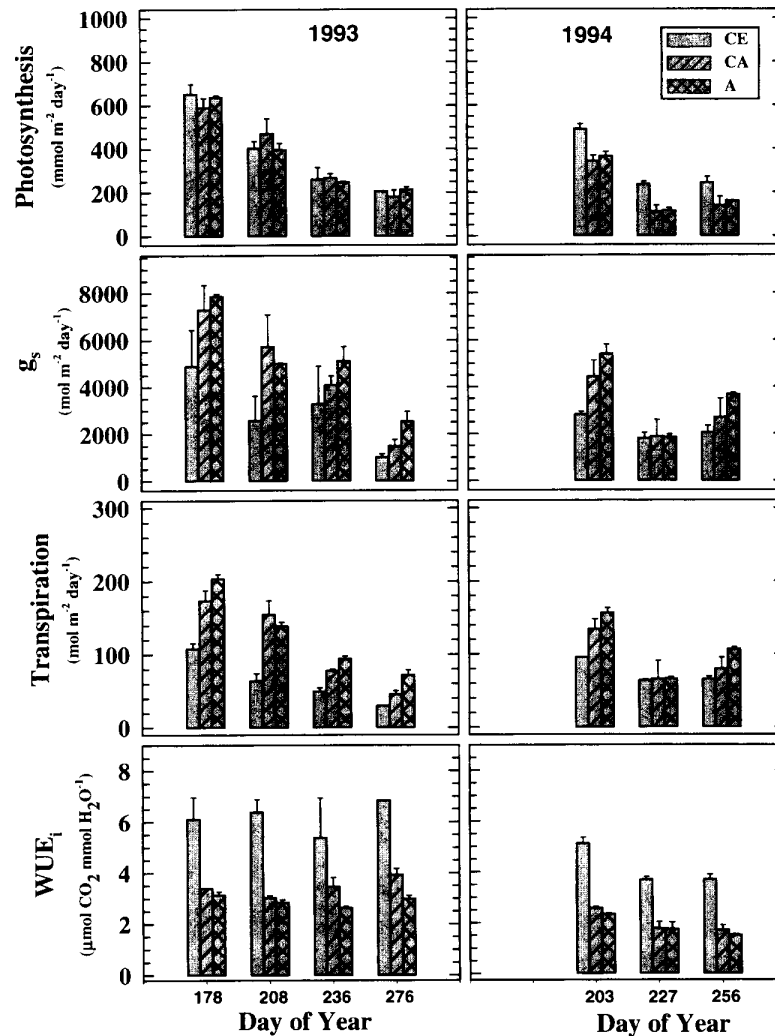
*Figure 2.* Total area under the curve of the diurnal response of leaf photosynthesis (photosyn.), stomatal conductance ($g_s$), transpiration and instantaneous water use efficiency ($WUE_i$) of *Andropogon gerardii* in the tallgrass prairie for each diurnal measuring day of the season for a wet year (1993) and a dry year (1994). $WUE_i$ is calculated as photosyn./ transpiration. Treatments are: CE, $CO_2$-enriched, with chamber; CA, ambient $CO_2$, with chamber; A, ambient $CO_2$, no chamber.

of the day in 1993 than in the latter part of the day in 1994. Stomatal conductance in the CE plots was similar both years.

The rate of transpiration in the A plots was similar in 1993 and 1994 (Figure 3). Transpiration in the CE plots was 45 to 65% lower than in the A plots throughout the day in 1993 and until midday in 1994 ($P <$ 0.05). After midday in 1994, transpiration in the CE plots was similar to that in the A plots. Transpiration in the CE plots was similar for the 2 years except for an increase around midday in 1994. In 1993, rates in the

CA plots were equal to or slightly higher than those in the A plots throughout the day. However, in 1994 CA transpiration rates were lower than A transpiration rates through midday, and equal thereafter.

Instantaneous WUE's for both diurnals was 111–137% greater ($P <$ 0.05) in the CE plots than in the other two treatments throughout each day (Figure 3). $WUE_i$ was essentially equal in the CA and A treatments. Diurnal trends of $WUE_{CE}/WUE_{CA}$ were similar for 1993 and 1994, and values of for both years were relatively constant throughout the day (Figure 4).
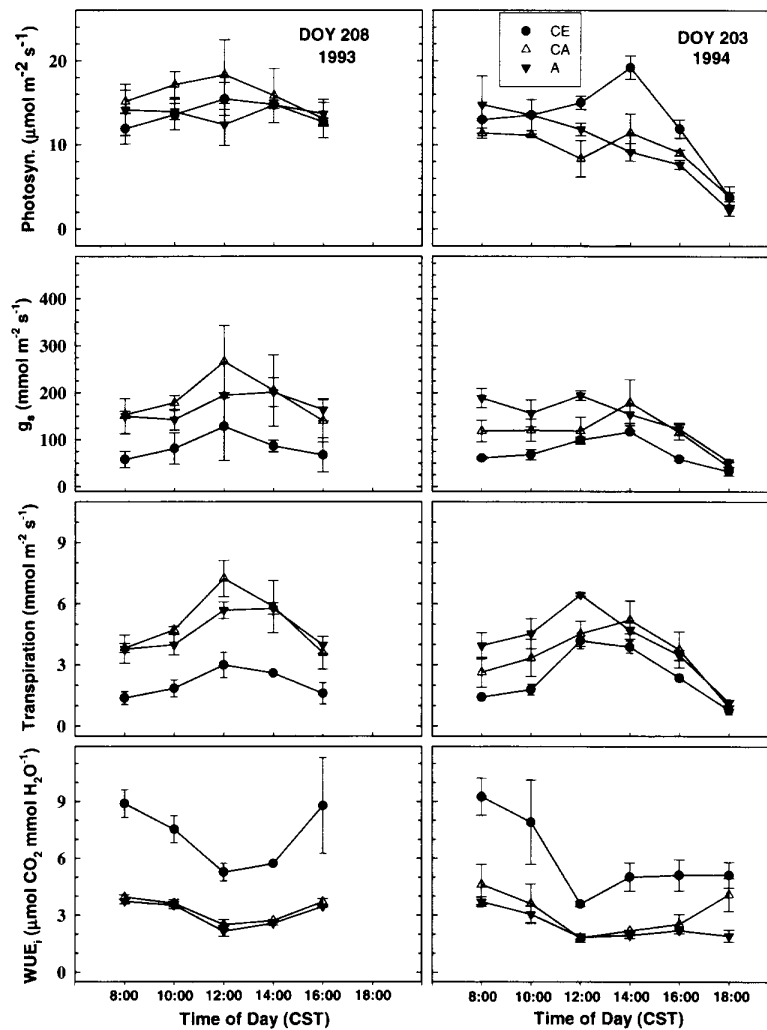
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*Figure 3.* Diurnal response of leaf photosynthetic rate (photosyn.), stomatal conductance ($g_s$), transpiration rate and instantaneous water use efficiency ($WUE_i$) of *Andropogon gerardii* in the tallgrass prairie for day of year 208 in a wet year (1993) and day of year 203 in a dry year (1994). $WUE_i$ is calculated as photosyn./ transpiration. Treatments are: CE, $CO_2$-enriched, with chamber; CA, ambient $CO_2$, with chamber; A, ambient $CO_2$, no chamber.

In 1993, the influence of $WUE_E$ was consistently greater than $WUE_{PSN}$ throughout the day. However, in 1994 $WUE_E$ on $WUE_{CE}/WUE_{CA}$ was greater than that of $WUE_{PSN}$ early in the day, but at midday and for part of the afternoon, the effect of $WUE_{PSN}$ was similar to or greater than the effect of $WUE_E$. The overall 1994 diurnal values for $WUE_{PSN}$ were significantly greater ($P < 0.05$) than the 1993 diurnal values for $WUE_{PSN}$, but there was no significant year × time interaction.

## Discussion

Photosynthesis rates of leaves (Figures 1 and 3) and daily photosynthate accumulation (Figure 2) were greater under $CO_2$ enrichment (as compared to ambient $CO_2$ concentrations) in a dry year (1994), but not in a wet year (1993). The greater daily photosynthetic accumulation in the CE plots than in the CA and A plots in 1994 suggests that the photosynthetic rates in the CA and A plots were reduced as a result of the greater water stress experienced by the plants in those
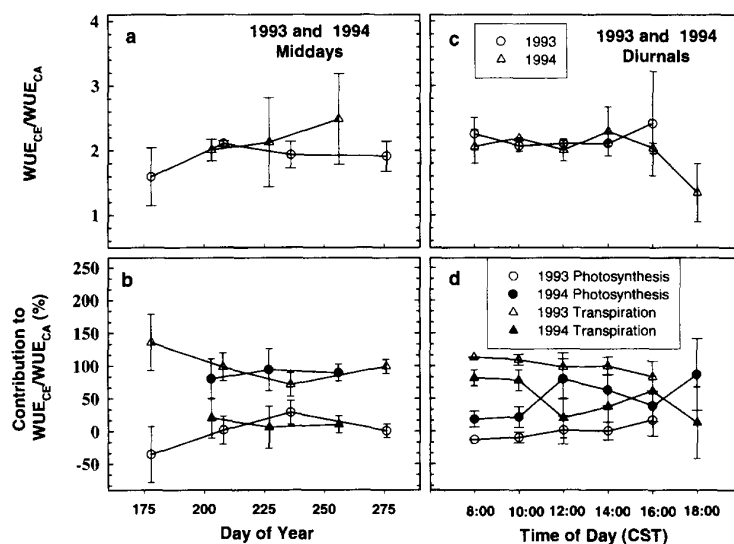
*Figure 4.* Seasonal/midday responses of (a) $WUE_{CE}/WUE_{CA}$ and (b) $WUE_{PSN}$ and $WUE_E$, and diurnal responses of (c) $WUE_{CE}/WUE_{CA}$ and (d) $WUE_{PSN}$ and $WUE_E$ for 1993 and 1994. Abbreviations are: $WUE_{CE}/WUE_{CA}$ – ratio of chamber-enriched WUE to chamber-ambient WUE; $WUE_{PSN}$ – percent contribution of photosynthesis to $WUE_{CE}/WUE_{CA}$; and $WUE_E$ – percent contribution of tranpiration to $WUE_{CE}/WUE_{CA}$.

treatments in 1994 (see Knapp et al. 1996). The reason for the greater values in the CE treatment can be seen in the diurnal responses (Figure 3), in which the CE plots were able to maintain or even increase photosynthesis rates at midday, while plants in the CA and A plots decreased throughout the day.

Midday rates of stomatal conductance and transpiration, as well as those on a diurnal area basis, were consistently lower in the CE plots for both years (Figure 1). This was despite the greater water availability in the wet year, indicating that stomatal limitations were a direct effect of $CO_2$ on the stomates, or a sink limitation, rather than a water stress-induced effect. The lower transpiration rates in the wet year, and the higher photosynthesis rates in the dry year, resulted in a greater daily WUE (photosynthesis/transpiration) in the CE plots and similar $WUE_{CE}/WUE_{CA}$ values for both years. In studies summarized by Allen (1994), the $C_4$ plants respond to increased $CO_2$ mainly by increasing stomatal resistance and decreasing transpiration, whereas $C_3$ plants respond mainly by increasing photosynthesis. These results support that conclusion in the wet year (1993) in which $WUE_E$ was greater than $WUE_{PSN}$. However, in the dry year $WUE_{PSN}$ was greater than $WUE_E$, a response Allen (1994) has shown to occur in $C_3$ plants.

An exception to the pattern of higher photosynthetic rates and lower transpiration rates under $CO_2$ enrichment in the dry year occurred on DOY 227 (Figure 2). On this day, photosynthetic carbon accumulation in the $CO_2$ enriched atmosphere was almost double that in ambient conditions, yet the conductances and transpiration rates were similar. This indicates that the greater $CO_2$ gradient in the enriched plots allowed those plants to maintain higher photosynthesis rates than plants in the non-enriched plots. With the exception of the last sampling date in the wet year (DOY 276), seasonal trends indicate that midday rates of photosynthesis of plants in the CE plots late in the season (through DOY 254) were higher in both wet and dry years, but the difference was greater in a dry year (Figure 1).

These results support earlier work that reported increased biomass accumulation (Owensby et al. 1993) and photosynthetic capacity (Knapp et al. 1993) of *A. gerardii* in response to elevated $CO_2$ only in dry years. However, we show that plants in the CE plots were able to maintain higher levels of photosynthesis at midday in the latter part of the season, whether the season was wet or dry. This could be explained in one of two ways. First, the lower transpiration in $CO_2$-enriched conditions allowed conservation of soil moisture, thereby preventing the midday depression of

photosynthesis that is typically seen in tallgrass prairie plants. Second, it is possible that the greater $CO_2$ gradient in the enriched chambers allowed the plants to maintain constant photosynthesis rates, even when transpiration was reduced. These results are in agreement with those of Ham et al. (1995), who showed that in a wet year (1993), carbon assimilation on a canopy basis continued longer at the end of the season (through DOY 247) in the CE plots compared to the CA or A plots.

The greater canopy photosynthetic accumulation of *A. gerardii* demonstrated by Ham et al. (1995) was associated with reduced evapotranspiration under $CO_2$ enrichment in a wet year. This would result in greater WUE on a canopy basis. However, Owensby et al. (1993) indicated that greater WUE (calculated as biomass accumulated at time of peak biomass per unit of water used) in the CE plots resulted in the greater biomass production in these plots in dry years, but not in wet years (such as 1993). Possibly, if WUE were calculated using total biomass accumulated throughout the season (through October) instead of total biomass accumulated by the time of peak biomass production in early August (see Owensby et al. 1999), treatment differences in WUE (on a biomass basis) would be evident.

In conclusion, in wet conditions, the $C_4$ perennial tallgrass plant *Andropogon gerardii* under $CO_2$ enrichment had similar rates of photosynthesis, but used less of the available soil moisture. In normal, low-rainfall conditions, however, the plants under $CO_2$ enrichment were able to maintain normal photosynthesis rates, whereas non-$CO_2$-enriched plants had reduced rates due to a lack of moisture, especially at midday. These responses allowed the enriched plants to have greater $WUE_i$'s in both wet and dry conditions. In very dry conditions, when all the plants (enriched and non-enriched) had reduced stomatal conductance due to depleted soil moisture, the plants under $CO_2$ enrichment photosynthesized at a higher rate due to the greater $CO_2$ gradient. Finally, reduced transpiration rates throughout the season under $CO_2$ enrichment, resulting in increased soil moisture (see Owensby et al. 1999), allowed the plants to keep their leaves photosynthetically active, or to produce more leaves, later into the season. Therefore, based on the responses of *Andropogon gerardii* in this study, the main effect of a future, higher $CO_2$ atmosphere on $C_4$ grasses may be realized through its influence on water-use efficiency and water conservation.

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