The effect of CO₂ 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 CO₂ enrichment on leaf-level photosynthetic rates of the C₄ 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 CO₂ (A); chamber with ambient CO₂ (CA); and chamber with twice-ambient CO₂ (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 CO₂ 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 CO₂ 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, CO₂ 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, CO₂ 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 CO₂ enrichment for both years.

Abbreviations: A = ambient-no chamber; CA = chamber-ambient; CE = chamber-enriched; DOY = day of year; gs = stomatal conductance; WUE = water-use efficiency (peak biomass/water used); WUEₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑ水肿

Introduction

Rangelands (total estimated potentially grazeable land) occupy 70% of the earth's land area (Williams et al. 1968) and 61% of the United States (FAO 1992). so effects of elevated CO₂ on rangelands may have a significant impact on global climate. In 1989, a project was initiated to characterize the effects of increased atmospheric CO₂ 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 CO₂ on Andropo-


gon gerardii Vitman, a dominant C4 species of the tallgrass prairie. Biomass production of A. gerardii has been greater under elevated CO2 levels in years with substantial water stress (Owensby et al. 1993). The greater biomass production of A. gerardii under CO2 enrichment was due to a more efficient use of water (Owensby et al. 1993). Stomates partially close in response to elevated CO2 (Mott 1990), which reduces stomatal conductance (Morrison 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), C4 plants have shown responses to CO2 enrichment. Bremer et al. (1996) showed that elevated CO2 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 C3 plants are enhanced under elevated CO2 (Accock and Allen 1985; Oechel and Strain 1985; Cure and Accock 1986), but C4 plants have shown little increase in photosynthetic capacity (Kramer 1981; Mooney et al. 1991). Also, lower stomatal conductance, such as is usually seen in CO2 enrichment, typically has little effect on photosynthesis of C4 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 CO2 on vegetation have been derived from short-term treatments (i.e. days to weeks) in controlled environments (Accock and Allen 1985; Cure and Accock 1986). These data show that species vary widely in rates of photosynthesis in response to CO2, and the response is coupled to environmental factors (Wong 1979; Cure and Accock 1986).

Little is known about the field effects or ecosystem processes resulting from long-term exposure of native plant communities to elevated CO2 (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 CO2 (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 CO2 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 CO2 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 CO2 enrichment; (2) plants under CO2 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 C4 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 Argustolls). 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 twice times, were ambient CO2, no chamber (A); ambient CO2, with chamber (CA); and enriched (twice-ambient) CO2, 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 CO2 – 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 (gs), 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$_2$O$^{-1}$). 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 LSMEANS (Littel et al. 1996b) 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, gs, 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).
Figure 1. Leaf-level measurements of photosynthetic rate (photosyn.), stomatal conductance ($g_\text{s}$), transpiration rate and instantaneous water use efficiency (WUE$_1$) 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$_1$ 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
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).
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 $\times$ time interaction.

Discussion

Photosynthesis rates of leaves (Figures 1 and 3) and daily photosynthetic 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
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\textsubscript{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\textsubscript{CE}/WUE\textsubscript{CA} values for both years. In studies summarized by Allen (1994), the C\textsubscript{4} plants respond to increased CO\textsubscript{2} mainly by increasing stomatal resistance and decreasing transpiration, whereas C\textsubscript{3} plants respond mainly by increasing photosynthesis. These results support that conclusion in the wet year (1993) in which WUE\textsubscript{E} was greater than WUE\textsubscript{PSN}. However, in the dry year WUE\textsubscript{PSN} was greater than WUE\textsubscript{E}, a response Allen (1994) has shown to occur in C\textsubscript{3} plants.

An exception to the pattern of higher photosynthetic rates and lower transpiration rates under CO\textsubscript{2} enrichment in the dry year occurred on DOY 227 (Figure 2). On this day, photosynthetic carbon accumulation in the CO\textsubscript{2} enriched atmosphere was almost double that in ambient conditions, yet the conductances and transpiration rates were similar. This indicates that the greater CO\textsubscript{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\textsubscript{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\textsubscript{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 CO₂ 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 CO₂ 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 C₄ perennial tallgrass plant *Andropogon gerardii* under CO₂ enrichment had similar rates of photosynthesis, but used less of the available soil moisture. In normal, low-rainfall conditions, however, the plants under CO₂ enrichment were able to maintain normal photosynthesis rates, whereas non-CO₂-enriched plants had reduced rates due to a lack of moisture, especially at midday. These responses allowed the enriched plants to have greater WUE'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 CO₂ enrichment photosynthesized at a higher rate due to the greater CO₂ gradient. Finally, reduced transpiration rates throughout the season under CO₂ 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 CO₂ atmosphere on C₄ grasses may be realized through its influence on water-use efficiency and water conservation.

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References


Ham JM, Owensby CE, Coyne PJ and Bremer DJ (1995) Field-scale fluxes of CO₂ and water vapour from a prairie ecosystem exposed to ambient and elevated CO₂ atmospheric CO₂. Agric For Meteorol 77: 73–93


Knapp AK, Cocke M, Hamerlynck EP and Owensby CE (1994a) Effect of elevated CO\textsubscript{2} on stomatal density and distribution in a C\textsubscript{3} grass and a C\textsubscript{4} forb under field conditions. Ann Bot 74: 595–599


Neffel A, Moor E, Oeschger H and Stauffer B (1985) Evidence from polar ice cores for the increase in atmospheric CO\textsubscript{2} in the past two centuries. Nature 315: 45–47


Rice CW, Garcia FO, Hampton CO and Owensby CE (1994) Soil microbial response in tallgrass prairie to elevated CO\textsubscript{2}. Plant Soil 165: 67–74


Tyree MT and Alexander JD (1993) Plant water relations and the effects of elevated CO\textsubscript{2}. A review and suggestions for future research. Vegetatio 104/105: 47–62

Vong NQ and Murata Y (1977) Studies on the physiological characteristics of C\textsubscript{3} and C\textsubscript{4} crop species. 1. The effects of air temperature on the apparent photosynthesis, dark respiration and nutrient absorption of some crops. Jpn J Crop Sci 46: 45–52


Wong SC (1979) Elevated atmospheric partial pressure of CO\textsubscript{2} and plant growth. 1. Interactions of nitrogen nutrition and photosynthetic capacity in C\textsubscript{3} and C\textsubscript{4} plants. Oecologia 44: 68–74


Ziska LH, Drake BG and Chamberlain S (1990) Long-term photosynthetic response in single leaves of a C\textsubscript{3} and C\textsubscript{4} salt marsh species grown at elevated atmospheric CO\textsubscript{2} in situ. Oecologia 83: 469–472