

## PHOTOSYNTHETIC GAS EXCHANGE AND WATER RELATION RESPONSES OF THREE TALLGRASS PRAIRIE SPECIES TO ELEVATED CARBON DIOXIDE AND MODERATE DROUGHT

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Undisturbed tallgrass prairie was exposed to ambient and elevated (twice-ambient) levels of atmospheric CO<sub>2</sub> and experimental dry periods. Seasonal and diurnal midday leaf water potential ( $\Psi_{\text{leaf}}$ ), net photosynthesis ( $A_{\text{net}}$ ), and stomatal conductance ( $g_s$ ) responses of three tallgrass prairie growth forms—a C<sub>4</sub> grass, *Andropogon gerardii*; a broad-leaved woody C<sub>3</sub> shrub, *Symphiocarpos orbiculatus*; and a C<sub>3</sub> perennial forb, *Salvia pitcheri*—were assessed.  $\Psi_{\text{leaf}}$  in *A. gerardii* and *S. orbiculatus* was higher under elevated CO<sub>2</sub>, regardless of soil moisture, while  $\Psi_{\text{leaf}}$  in *S. pitcheri* responded only to drought. Elevated CO<sub>2</sub> always stimulated  $A_{\text{net}}$  in the C<sub>3</sub> species, while *A. gerardii*  $A_{\text{net}}$  increased only under dry conditions. However,  $A_{\text{net}}$  under elevated CO<sub>2</sub> in the C<sub>3</sub> species declined with drought but not in the C<sub>4</sub> grass. Under wet conditions,  $g_s$  reduced in elevated CO<sub>2</sub> for all species. During dry periods,  $g_s$  at elevated CO<sub>2</sub> was sometimes higher than in ambient CO<sub>2</sub>. Our results support claims that elevated CO<sub>2</sub> will stimulate tallgrass prairie productivity during dry periods and possibly reduce temporal and spatial variability in productivity in these grasslands.

### Introduction

Increasing atmospheric CO<sub>2</sub> is expected to strongly stimulate the productivity of the humid temperate tallgrass prairie of central North America (Parton et al. 1994). This is in part due to improved seasonal water status accompanying lower stomatal conductances (Knapp et al. 1993b; Owensby et al. 1993b; Knapp et al. 1994a; Parton et al. 1994; Ham et al. 1995), reduced photoinhibition, and increased CO<sub>2</sub> fixation by ribulose-1,5-carboxylase/oxygenase (Long 1991). The latter could be important for C<sub>3</sub> plants growing in grasslands dominated by C<sub>4</sub> grasses. C<sub>3</sub> grassland species, though a small portion of total biomass, comprise most of the species diversity, spanning a wide range of growth forms possessing physiological, morphological, and phenological adaptations for persistence in a C<sub>4</sub> “sea of grass” (Fahnestock and Knapp 1994; Turner et al. 1995). This diversity of plant form and function could lead to shifts in grassland community structure, and subsequent function, in an elevated CO<sub>2</sub> world (Owensby et al. 1993b).

An ongoing 6-yr study on the impacts of elevated CO<sub>2</sub> on intact tallgrass prairie has shown that CO<sub>2</sub> enrichment stimulates biomass accumulation more in dry years compared with wet years, a result of improved water status and higher sustained photosynthetic rates in the C<sub>4</sub> dominant grass, *Andropogon gerardii* (Knapp et al. 1993b, 1994a, 1994b; Owensby et al. 1993b; Ham et al. 1995). Even in a wet year, elevated CO<sub>2</sub> reduced whole canopy evapotranspiration by 26% (Ham et al. 1995) and stem sap flow in *A. gerardii* by 18% (Bremer et al. 1996). In wet years, total biomass was similar between elevated and ambient CO<sub>2</sub>, but C<sub>3</sub> species biomass, especially herbaceous forbs and

woody perennials, increased markedly under elevated CO<sub>2</sub> (Owensby et al. 1993b). Several greenhouse and growth chamber studies implicate that C<sub>3</sub> grassland and grassland/steppe plants will replace C<sub>4</sub> species, though higher temperatures and water stress can result in stronger positive effects of elevated CO<sub>2</sub> on C<sub>4</sub> photosynthesis and productivity (Carter and Peterson 1984; Smith et al. 1987; Johnson et al. 1993; Morgan et al. 1994; Read and Morgan 1995; Hunt et al. 1996). However, the interaction of drought and elevated CO<sub>2</sub> on photosynthesis in native C<sub>3</sub> tallgrass prairie plants in an intact C<sub>4</sub> grassland is not well understood. Knapp et al. (1996) found that stomatal conductance and water relations responses to seasonal water stress under elevated CO<sub>2</sub> were species specific, even within certain growth forms. Early in the growing season, all species had lower stomatal conductances and higher water potentials under elevated CO<sub>2</sub>. In drier late-season conditions, only a C<sub>4</sub> grass and a C<sub>3</sub> forb maintained this pattern (Knapp et al. 1996). However, the degree to which this improved carbon uptake is not known.

Here, we present a study assessing the gas exchange and water relations responses of three important tallgrass prairie plant growth forms, a fibrous rooted C<sub>4</sub> grass (big bluestem, *Andropogon gerardii*), a deeply rooted C<sub>3</sub> perennial forb (pitcher sage, *Salvia pitcheri*), and a shallowly rooted C<sub>3</sub> broad-leaved woody shrub (buck brush, *Symphiocarpos orbiculatus*) to elevated CO<sub>2</sub> and experimental drought in intact tallgrass prairie. These species have distinct above- and below-ground physiognomies (Weaver 1954) and differ in photosynthetic capacity and seasonal water relations (Fahnestock and Knapp 1994; Turner et al. 1995; Knapp et al. 1996). We predicted that carbon enrichment would have greater benefits for the C<sub>3</sub> species in moist conditions, while, in drier conditions, we expected greater benefits for the C<sub>4</sub> dominant. These findings could be relevant to predicting shifts in species productivity patterns that could alter species composition, potentially impacting ecosystem processes in tallgrass prairie.

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## Material and methods

### STUDY SITE AND DRY DOWN REGIME

Research was conducted in native tallgrass prairie in the Flint Hills of northeast Kansas near Manhattan, Kansas (lat. 39.12°N, long. 96.35°W, 385 m above sea level). This portion of undisturbed tallgrass prairie had been exposed to ambient (350–360  $\mu\text{L L}^{-1}$ ) and twice-ambient (700  $\mu\text{L L}^{-1}$ ) CO<sub>2</sub> in four large (4.5-m diameter, 4.0-m height) open-top chambers (OTCs) for 4 yr at the time of this study. OTCs were subjected to three drying/wetting cycles early (DOY [day of year] 161–193), mid (DOY 198–221), and late (DOY 198–221) in the 1995 growing season. Drying cycles were initiated by shutting off an irrigation system normally used to return precipitation intercepted by the OTC roof into the chamber. A high-speed fan used to maintain OTC atmospheric pressure also reduced precipitation input into the chambers as well. Subsurface shielding (aluminum flashing) buried to 0.9 m blocked subsurface water infiltration, a problem in previous experiments (Nie et al. 1992). This protocol reduced precipitation by 98%–99% in the OTCs (J. M. Ham, unpublished data). After a minimum dry period of 14 d, plots were monitored for visible signs of plant stress (e.g., leaf curling), then irrigated for 2 d. There were two waterings, one on July 13–14 (9.7 cm) and the other on August 10–11 (7.2 cm). The chambers were left undisturbed for two additional days, and another drying cycle was initiated.

### LEAF-LEVEL MEASUREMENTS

**GAS EXCHANGE.** Seasonal and diurnal leaf-level photosynthetic gas exchange measurements were made on a C<sub>4</sub> grass (big bluestem, *Andropogon gerardii* Vit.), a perennial C<sub>3</sub> forb (blue pitcher sage, *Salvia pitcheri* Torr.), and a C<sub>3</sub> woody shrub (buckbrush, *Symphoricarpos orbiculatus* Moench.). These species were selected as representative growth forms in tallgrass prairie and occurred frequently enough in the OTCs for replicate sampling. Photosynthesis ( $A_{\text{net}}$ ) and stomatal conductance ( $g_s$ ) were estimated in the field with a closed-system portable IRGA (LiCOR Li-6200) using the equations of von Caemmerer and Farquhar (1981). Leaf temperature was measured with a fine-wire type-T (copper/constantan) thermocouple pressed to the abaxial side of the leaf. Photosynthetic photon flux density (PPFD in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was measured with a silicon photodiode attached to the outside of a 0.25-L cuvette. Leaves were maintained as close to natural orientation as possible. The enclosed leaf was held in the cuvette for a 10-s sampling period, which usually resulted in a 2–5- $\mu\text{L L}^{-1}$  drawdown of CO<sub>2</sub>. Only samples with <2% change in cuvette RH were analyzed to ensure accuracy of  $g_s$  estimations. Four plants of each species in each CO<sub>2</sub> treatment-chamber and from adjacent field control plots were sampled for seasonal and diurnal courses of gas exchange. Seasonal gas exchange dynamics were compiled from midday measurements made ca. every 3 d from June 9 to September 12, 1995, in ambient light conditions. Diurnal gas exchange curves were made early and late (DOY 165 and DOY 193) in the early-season drying cycle.

**WATER RELATIONS.** Seasonal midday (ca. 1130 to 1400 Central Daylight Time [CDT]) and diurnal leaf water potential ( $\Psi_{\text{leaf}}$ ) was measured from *A. gerardii* in the same chambers and field plots sampled for gas exchange measurements. Seven mature leaves were harvested, placed into sealable plastic bags, and transported to the lab for determination of

$\Psi_{\text{leaf}}$  with a Scholander-type pressure bomb (PMS Model 1000, Corvallis, Oreg.). This sampling protocol allowed for rapid processing of a large number of samples gathered in the field across a short period (ca. 10–15 min) and avoided diurnal effects (Fahnestock and Knapp 1994).  $\Psi_{\text{leaf}}$  was estimated ca. every 3 d through the season. Diurnal  $\Psi_{\text{leaf}}$  was tracked early (DOY 158, 2 d before starting) and late (DOY 193, +33 d into) the early-season drying cycle. There were not enough individuals of the other two species to measure seasonal  $\Psi_{\text{leaf}}$ ; only measurements pooled from the start and end of the early- and midseason drying cycles were made for *S. pitcheri* and *S. orbiculatus*. Four leaves of each two species in each chamber these species were collected, giving a total sample size of eight.

### STATISTICAL ANALYSIS

A repeated-measures, split-plot, two-way ANOVA (General ANOVA/ANCOVA, Statistix v4.1, Analytical Software, St. Paul, Minn.) was used to detect combined drought/CO<sub>2</sub> treatment effects within each species. Data were pooled from three sampling days at the start (wet treatment) and 3 d at the end (dry treatment) of each of the three drying cycles (early-, mid-, and late-season), giving a whole-plot treatment structure of wet/elevated, wet/ambient, dry/elevated, dry/ambient, and field control, with drying cycle and the cycle  $\times$  treatment interaction as subplot factors for ANOVA. Since the same plots were measured for each sampling date, this is a repeated-measures design with four and seven replications for gas exchange and  $\Psi_{\text{leaf}}$  measurements, respectively. Also, drying cycles reflected seasonal changes in plant performance. The whole-plot error term for  $F$ -tests was the replication  $\times$  treatment interaction, with the subplot-error term being the date  $\times$  treatment  $\times$  replication interaction. A probability level of 0.05 was considered significant, with means separation by LSD. Since no rainout shelters were constructed to provide a balanced factorial 3  $\times$  2 treatment structure, CO<sub>2</sub> treatment main effects were tested by post hoc generalized contrasts with Scheffe's  $F$ -test using the whole-plot error term (Statistix v4.1).

## Results

### SEASONAL DYNAMICS

**GAS EXCHANGE.** Net photosynthetic rates ( $A_{\text{net}}$ ) under elevated CO<sub>2</sub> were similar between wet and dry periods in *Andropogon gerardii*, while  $A_{\text{net}}$  in ambient CO<sub>2</sub> OTC plants declined significantly by 23% (fig. 1; table 1). In elevated CO<sub>2</sub>,  $A_{\text{net}}$  in OTC *Symphoricarpos orbiculatus* declined by 25% in response to experimental drought, while *Salvia pitcheri* showed a 20% decrease in assimilation rates (fig. 1; table 1). Drought-induced declines in  $A_{\text{net}}$  were most pronounced in ambient OTC *S. orbiculatus*, reducing by 61%. Stimulation of  $A_{\text{net}}$  by elevated CO<sub>2</sub> was greatest in *S. orbiculatus* in dry conditions, which increased by 192%, compared with a 50% stimulation under moist conditions. Drought widened the difference in  $A_{\text{net}}$  between elevated and ambient *A. gerardii*, increasing from 6% to 40% higher photosynthetic rates going from wet to dry periods (fig. 1).  $A_{\text{net}}$  in elevated CO<sub>2</sub> *S. pitcheri* increased only slightly over rates expressed in ambient CO<sub>2</sub>, with a 28% in wet and a 33% stimulation in dry conditions, respectively. There were unexpected increases in  $A_{\text{net}}$  in *A. gerardii* and *S. pitcheri*

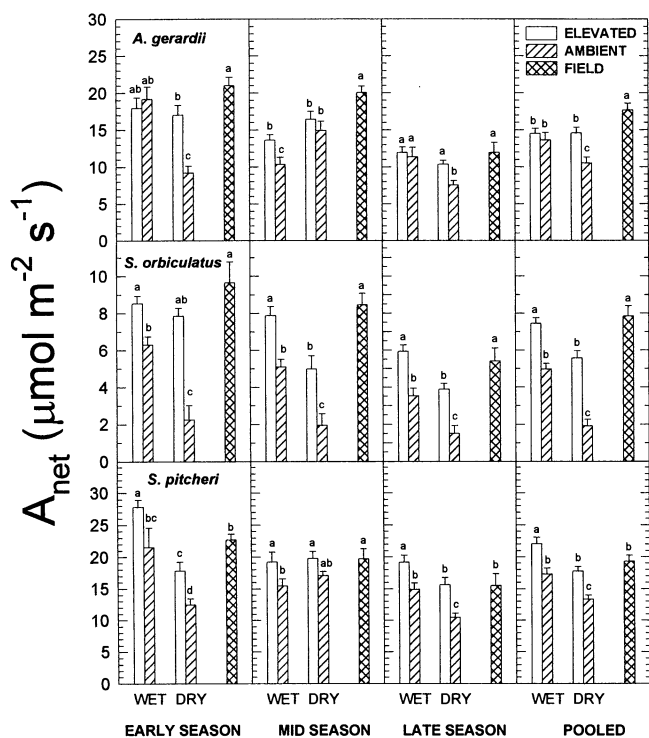


Fig. 1 Leaf-level net photosynthetic gas exchange ( $A_{net}$ ) of *Andropogon gerardii*, a  $C_4$  grass, *Symphiocarpus orbiculatus*, a  $C_3$  shrub, and *Salvia picheri*, a  $C_3$  forb, in elevated and ambient  $\text{CO}_2$  open-top (OTC) chambers subjected to drying cycles. Bars indicate  $\pm 1$  SE ( $n = 12$ ), letters differ significantly within each panel at  $P < 0.05$  (LSD).

during the dry portion at the end of the midseason cycle, especially in ambient OTC *A. gerardii* (fig. 1), which led to significant treatment  $\times$  season interactions in  $A_{net}$  for these species (table 1). Only in *S. orbiculatus* did  $\text{CO}_2$ /moisture treatment effects on  $A_{net}$  remain constant through the growing season (fig. 1; table 1). Pooled across treatment combinations and the season, photosynthetic rates were higher in elevated than ambient  $\text{CO}_2$  OTC plants for all three species (table 2).  $A_{net}$  was usually highest in field plants, with the exception of *S. picheri*, in which  $A_{net}$  was similar between elevated  $\text{CO}_2$  OTC and field controls (table 2).

There were significant treatment  $\times$  season interactions on stomatal conductances ( $g_s$ ) in all three growth forms (fig. 2; table 1). For *A. gerardii* and *S. picheri*,  $g_s$  remained constant between wet and dry conditions but reduced significantly in ambient OTC plants under drought conditions. However, at the end of the midseason drying cycle,  $g_s$  in these species was markedly higher than  $g_s$  shortly after watering, especially in *S. picheri* (fig. 2). Drought reduced *S. orbiculatus*  $g_s$  in the early-season and midseason drying cycles but did not at midseason (fig. 2). Pooled across the season, drought did not reduce  $g_s$  in either  $\text{CO}_2$  treatment in *A. gerardii* but did narrow the reduction between elevated and ambient  $\text{CO}_2$  treatments, from 48% lower in elevated  $\text{CO}_2$  in wet conditions to a -27% difference in dry (fig. 2). Drought reduced  $g_s$  most in am-

Table 1

ANALYSIS OF SEASONAL PHOTOSYNTHETIC GAS EXCHANGE AND WATER RELATIONS RESPONSES OF THREE TALLGRASS PRAIRIE SPECIES TO COMBINED  $\text{CO}_2$  AND DROUGHT TREATMENTS

Species and effect	MS	F	df	Significance
AG:				
$A_{net}$ :				
Treat .....	23.9	36.5	4, 15	*
Cycle.....	619.3	40.1	2, 150	*
T $\times$ C .....	108.6	6.7	8, 150	*
$g_s$ :				
Treat .....	$1.1 \times 10^5$	13.5	4, 15	*
Cycle.....	$6.9 \times 10^3$	9.3	2, 150	*
T $\times$ C .....	$3.4 \times 10^3$	4.6	8, 150	*
$\Psi_{leaf}$ :				
Treat .....	7.15	94.6	4, 65	*
Cycle.....	17.0	145.8	2, 550	*
T $\times$ C .....	0.4	3.4	8, 550	*
SO:				
$A_{net}$ :				
Treat .....	202.1	43.0	4, 15	*
Cycle.....	123.3	21.5	2, 150	*
T $\times$ C .....	7.6	4.7	8, 150	ns
$g_s$ :				
Treat .....	$2.2 \times 10^5$	5.5	4, 15	*
Cycle.....	$3.3 \times 10^3$	3.3	2, 150	*
T $\times$ C .....	$3.5 \times 10^3$	1.7	8, 150	*
SP:				
$A_{net}$ :				
Treat .....	364.6	43.0	4, 15	*
Cycle.....	431.3	21.5	2, 150	*
T $\times$ C .....	93.9	4.7	8, 150	*
$g_s$ :				
Treat .....	$4.0 \times 10^5$	5.5	4, 15	*
Cycle.....	$2.2 \times 10^6$	3.3	2, 150	*
T $\times$ C .....	$4.6 \times 10^6$	6.7	8, 150	*

Note. AG = *Andropogon gerardii* ( $C_4$  grass), SO = *Symphiocarpus orbiculatus* ( $C_3$  shrub), and SP = *Salvia picheri* ( $C_3$  forb). An asterisk indicates significance at  $P < 0.05$ . Means comparisons for each parameter can be found in figures 1, 2, and 3.

bient OTC *S. orbiculatus* (ca. -35%), while  $g_s$  did not change under elevated  $\text{CO}_2$ . Comparing  $g_s$  between elevated and ambient  $\text{CO}_2$  *S. orbiculatus*, we found that  $g_s$  was 2% higher in ambient  $\text{CO}_2$  plants, while in wet conditions,  $g_s$  was 20% lower. In *S. picheri*,  $g_s$  was significantly lower (48%) under elevated  $\text{CO}_2$  compared with ambient  $\text{CO}_2$  during favorable moisture conditions but was not under drought (fig. 2). Overall,  $g_s$  was significantly lower under elevated  $\text{CO}_2$  than ambient  $\text{CO}_2$  OTC or field controls only in *A. gerardii*. Elevated and ambient OTC *S. orbiculatus* had similar  $g_s$ , which were both lower than field controls, while in *S. picheri*, only elevated  $\text{CO}_2$  OTC plants had  $g_s$  significantly lower than those in field conditions (table 2).

**WATER RELATIONS.** Leaf water potentials ( $\Psi_{leaf}$ ) reduced less in response to drying in *A. gerardii* in elevated (-19%) than in ambient  $\text{CO}_2$  (-27%) OTC pooled across the season (fig. 3; table 1).  $\Psi_{leaf}$  in OTCs were higher than field controls after watering, but only ambient OTC plants had  $\Psi_{leaf}$  consistently lower than

Table 2

GENERAL CONTRASTS OF MAIN EFFECTS OF ELEVATED CO<sub>2</sub>OTC (E), AMBIENT CO<sub>2</sub>OTC (A), AND FIELD CONTROL (F) PLANTS ON GAS EXCHANGE OF THREE TALLGRASS PRAIRIE SPECIES

Species and contrast	SS	F	Significance	Outcome
AG:				
<i>A<sub>net</sub></i> :				
E vs. A .....	220.4	7.4	*	E > A
E vs. F .....	231.4	7.8	*	F > E
A vs. F .....	747.2	25.2	*	F > A
<i>g<sub>s</sub></i> :				
E vs. A .....	2.8 × 10 <sup>5</sup>	8.8	*	E < A
E vs. F .....	2.8 × 10 <sup>5</sup>	8.7	*	E < F
A vs. F .....	9.1 × 10 <sup>3</sup>	0.3	ns	A = F
SO:				
<i>A<sub>net</sub></i> :				
E vs. A .....	339.1	36.1	*	E > A
E vs. F .....	42.6	4.5	*	E < F
A vs. F .....	465.2	49.5	*	A < F
<i>g<sub>s</sub></i> :				
E vs. A .....	2.0 × 10 <sup>4</sup>	0.9	ns	E = A
E vs. F .....	7.3 × 10 <sup>5</sup>	31.2	*	E < F
A vs. F .....	5.5 × 10 <sup>5</sup>	23.3	*	A < F
SP:				
<i>A<sub>net</sub></i> :				
E vs. A .....	769.0	22.4	*	E > A
E vs. F .....	8.7	0.3	ns	E = F
A vs. F .....	382.2	11.3	*	A < F
<i>g<sub>s</sub></i> :				
E vs. A .....	6.1 × 10 <sup>6</sup>	2.1	ns	E = A
E vs. F .....	1.4 × 10 <sup>7</sup>	4.9	*	E < F
A vs. F .....	3.1 × 10 <sup>6</sup>	1.1	ns	A = F

Note. AG = *Andropogon gerardii* (C<sub>4</sub> grass), *Symphiocarpus orbiculatus* (C<sub>3</sub> shrub), and SP = *Salvia pitcheri* (C<sub>3</sub> forb). An asterisk indicates significance at *P* < 0.05.

field controls in dry periods (fig. 3), which led to a significant treatment × season interaction (table 1). Compared with ambient CO<sub>2</sub> OTC,  $\Psi_{leaf}$  in *A. gerardii* were ca. 11% higher, regardless of drought treatment (fig. 3). Water potentials for *S. orbiculatus* and *S. pitcheri* declined significantly from wet to dry conditions, reduced by ca. 26% in the former and 37% in the latter, regardless of CO<sub>2</sub> treatment (table 3). For both of these species,  $\Psi_{leaf}$  was higher under elevated CO<sub>2</sub> conditions (ca. 17% in *S. orbiculatus*, 6% for *S. pitcheri*) than ambient CO<sub>2</sub> OTC, though this difference was significant only for *S. orbiculatus* (table 3).

DIURNAL DYNAMICS

GAS EXCHANGE. *A<sub>net</sub>* in *A. gerardii* was generally slightly higher (in elevated than in ambient CO<sub>2</sub> during wet conditions; fig. 4), reaching midday highs (ca. 16.0–20.0 μmol m<sup>-2</sup> s<sup>-1</sup>) between 1200 and 1400 CDT. *A<sub>net</sub>* in elevated CO<sub>2</sub> on a dry day was considerably higher (25%–100%) through the day compared with ambient CO<sub>2</sub> (fig. 4). *A<sub>net</sub>* in ambient CO<sub>2</sub> OTC varied little throughout the day, rarely reaching above 8.0 μmol m<sup>-2</sup> s<sup>-1</sup>. Stomatal conductances in *A. gerardii* (fig. 5) showed the greatest reductions in *g<sub>s</sub>* between elevated and ambient CO<sub>2</sub> treatments occurring in wet soil conditions. In dry conditions, *g<sub>s</sub>* in elevated

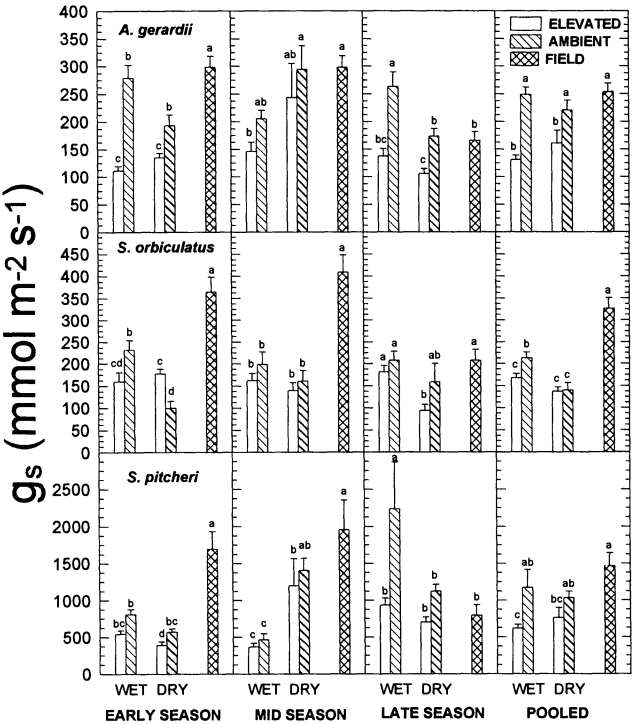


Fig. 2 Seasonal midday leaf stomatal conductance to water vapor (*g<sub>s</sub>*) in *Andropogon gerardii*, *Symphiocarpus orbiculatus*, and *Salvia pitcheri* in elevated and ambient CO<sub>2</sub> OTC exposed to drying cycles. Bars indicate ± 1 SE (*n* = 12); letters within each panel differ significantly at *P* < 0.05 (LSD).

CO<sub>2</sub> was similar to those in wet soils, but in ambient CO<sub>2</sub>, *g<sub>s</sub>* was reduced to levels closer to those in elevated CO<sub>2</sub>.

*Symphiocarpus orbiculatus* *A<sub>net</sub>* was consistently higher in elevated than in ambient CO<sub>2</sub> during wet conditions, with the latter similar to *A<sub>net</sub>* in elevated CO<sub>2</sub> in drought (fig. 4). During dry periods, *A<sub>net</sub>* was 300%–1200% higher through the day compared with ambient CO<sub>2</sub> (fig. 4), which was near zero through much of the day (fig. 4). This decline was accompa-

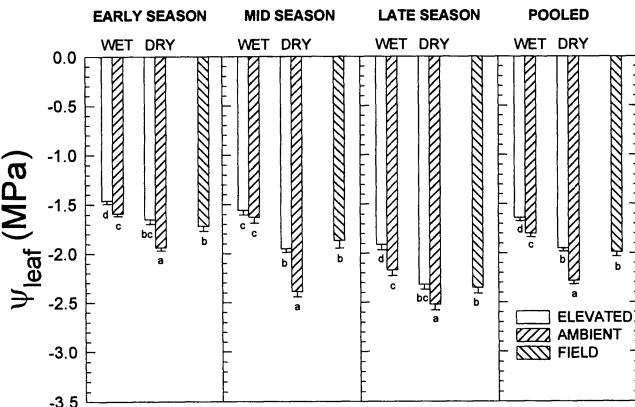


Fig. 3 Seasonal midday water potential ( $\Psi_{leaf}$ ) of *Andropogon gerardii* in elevated and ambient OTCs exposed to drying cycles. Bars indicate ± 1 SE of the mean (*n* = 14); letters within each panel differ significantly at *P* < 0.05 (LSD).

**Table 3**

POOLED MIDDAY WATER POTENTIAL MEASUREMENTS ( $\psi_{\text{leaf}}$  in MPa) OF TWO TALLGRASS PRAIRIE SPECIES EXPOSED TO ELEVATED AND AMBIENT  $\text{CO}_2$  CONCENTRATIONS AND MILD WATER STRESS

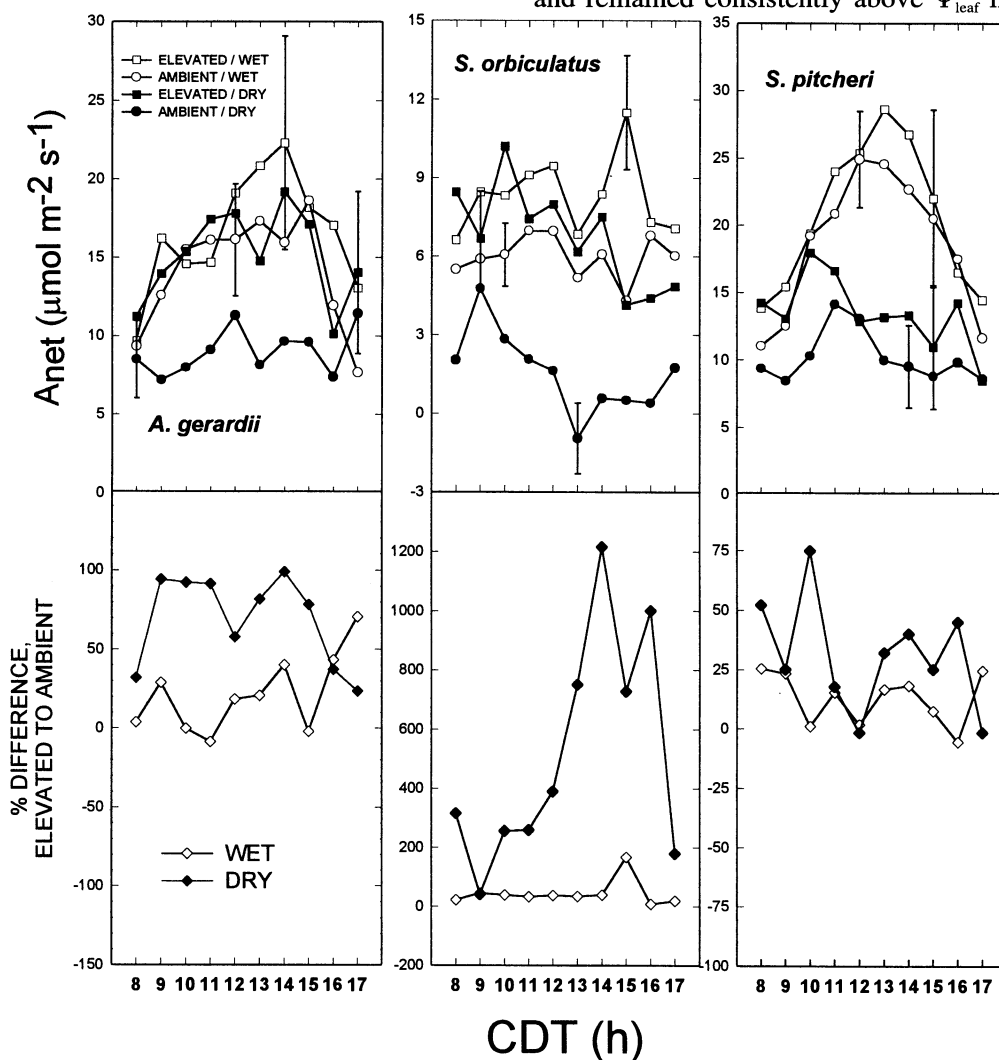
$\text{CO}_2$ treatment	<i>Symphiocarpus orbiculatus</i>		<i>Salvia pitcheri</i>	
	Wet	Dry	Wet	Dry
Elevated ...	-1.69 (0.14) <sup>a</sup>	-2.15 (0.11) <sup>b</sup>	-1.09 (0.08) <sup>a</sup>	-1.46 (0.06) <sup>b</sup>
Ambient ...	-2.07 (0.08) <sup>b</sup>	-2.56 (0.16) <sup>c</sup>	-1.14 (0.08) <sup>a</sup>	-1.59 (0.08) <sup>b</sup>

Note. Each value is the mean of four measurements, pooled across two repeated measures. Letters differ significantly within each species at  $P = 0.05$ ; SE of the mean is in parentheses.

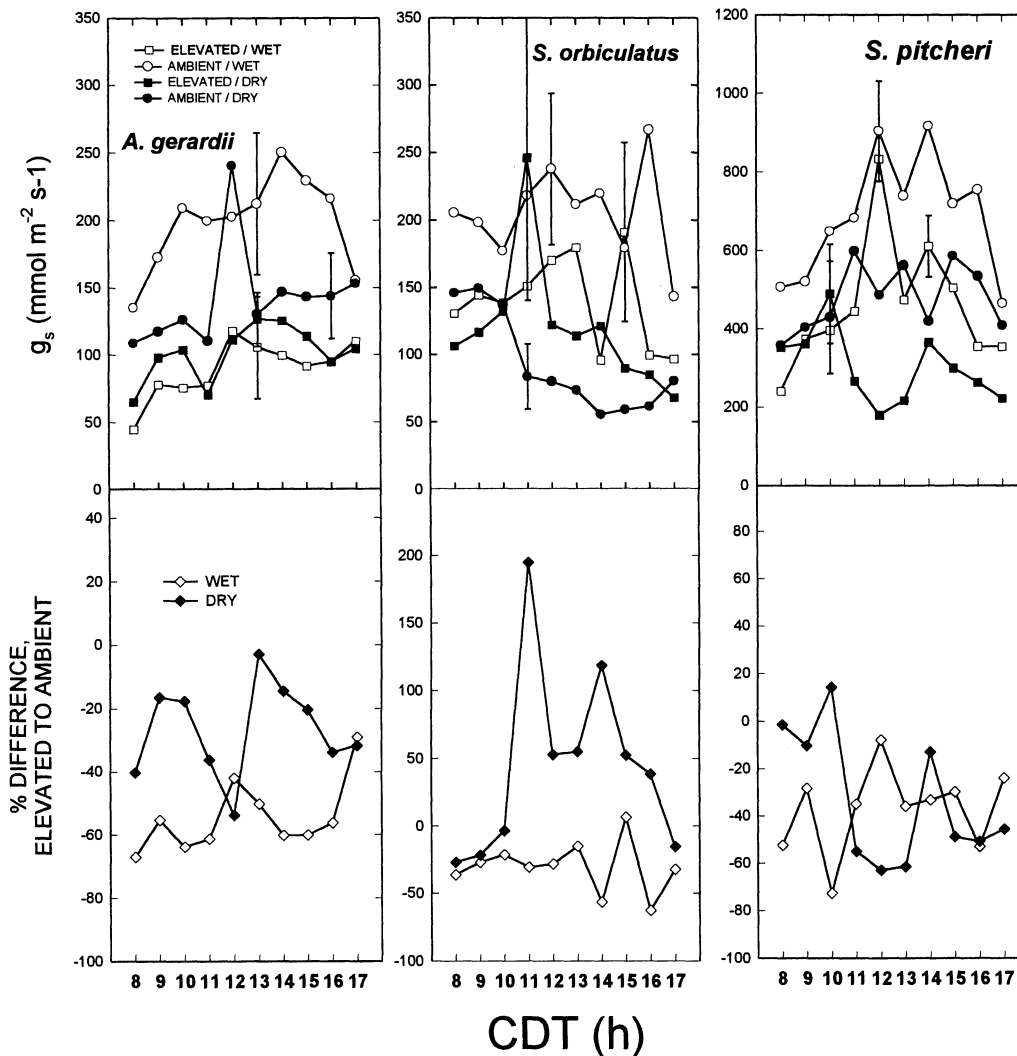
nied by marked reductions in  $g_s$  (fig. 5). The difference in  $g_s$  between elevated and ambient  $\text{CO}_2$  was more pronounced in dry conditions, with  $g_s$  in ambient  $\text{CO}_2$  often lower than in elevated  $\text{CO}_2$ .

Moderate drought reduced the marked diurnal response of  $A_{\text{net}}$  in *S. pitcheri* in wet soil (fig. 4), though in both conditions,  $A_{\text{net}}$  in elevated and ambient  $\text{CO}_2$  OTC were quite similar.  $A_{\text{net}}$  enhancement in elevated  $\text{CO}_2$  was highest (25%–50%) during dry conditions (fig. 4). Stomatal conductances were lower in elevated and ambient  $\text{CO}_2$  during drought, with more pronounced midday stomatal closure in elevated  $\text{CO}_2$  treatments (fig. 5). Unlike the other  $\text{C}_3$  species, drought did not increase the difference between elevated and ambient  $\text{CO}_2$   $g_s$  (fig. 5).

**WATER RELATIONS.** During wet periods, *A. gerardii*  $\Psi_{\text{leaf}}$  changed less on a diurnal basis in elevated  $\text{CO}_2$  and remained consistently above  $\Psi_{\text{leaf}}$  in ambient  $\text{CO}_2$



**Fig. 4** Top row, Diurnal responses of net photosynthesis ( $A_{\text{net}}$ ) of *Andropogon gerardii* ( $\text{C}_4$  grass), *Symphiocarpus orbiculatus* ( $\text{C}_3$  shrub), and *Salvia pitcheri* ( $\text{C}_3$  forb) in elevated (squares) and ambient (circles)  $\text{CO}_2$  OTC at the start (wet; empty symbols) and end (dry; filled symbols) of a drying cycle. Each point is the mean of four measurements; bars indicate maximum SE of the mean. Bottom row, Percentage change of  $A_{\text{net}}$  in elevated  $\text{CO}_2$  compared with ambient  $\text{CO}_2$  OTC plants in wet (empty symbols) and dry (filled symbols) soil moisture conditions.



**Fig. 5** Top row, Diurnal responses of stomatal conductance ( $g_s$ ) of *Andropogon gerardii* ( $C_4$  grass), *Symphiocarpus orbiculatus* ( $C_3$  shrub), and *Salvia pitcheri* ( $C_3$  forb) in elevated (squares) and ambient (circles) CO<sub>2</sub> OTC at the start (wet; empty symbols) and end (dry; filled symbols) of a drying cycle. Each point is the mean of four measurements; bars indicate maximum SE of the mean. Bottom row, Percentage change of  $g_s$  in elevated CO<sub>2</sub> compared with ambient CO<sub>2</sub> OTC plants in wet (empty symbols) and dry (filled symbols) soil moisture conditions.

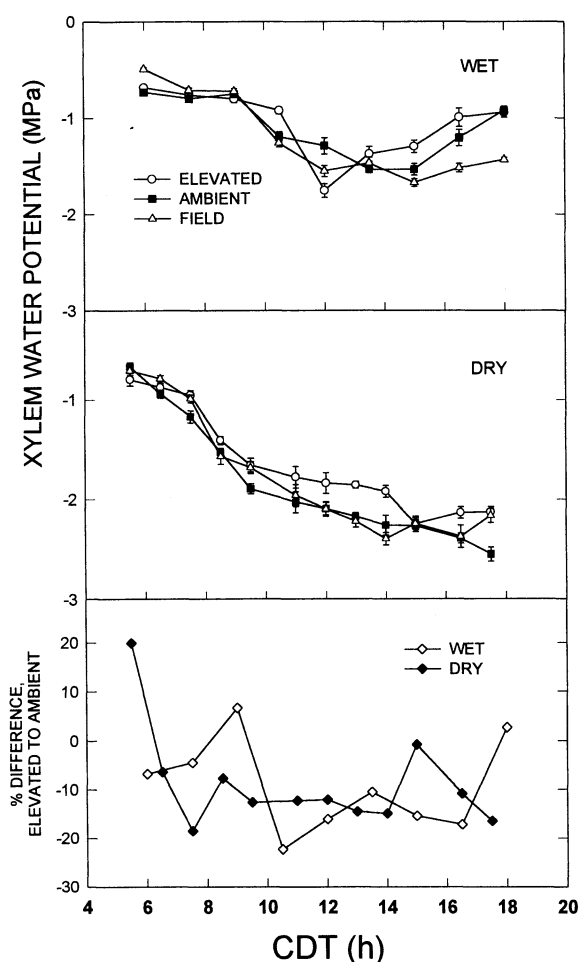
chambers (fig. 6). Both chambered treatments showed markedly lower  $\Psi_{\text{leaf}}$  later in the afternoon compared with field water potentials. On a dry day, after 1000 CDT,  $\Psi_{\text{leaf}}$  in elevated CO<sub>2</sub> remained at about  $-1.8$  MPa throughout most of the day, while  $\Psi_{\text{leaf}}$  in ambient CO<sub>2</sub> OTC was reduced from  $-2.0$  to  $-2.5$  MPa (fig. 6). Overall, elevated CO<sub>2</sub> resulted in a 10%–20% increase in  $\Psi_{\text{leaf}}$ , regardless of soil water status (fig. 6).

### Discussion

The drying treatments in this study resulted in moderate water stress, with midday water potentials in *Andropogon gerardii* similar to past seasonal drying trends and much higher than those experienced during severe drought (Knapp 1985; Knapp et al. 1993a). Photosynthetic gas exchange and water relations responses to elevated CO<sub>2</sub> and this moderate drought treatment were strongly influenced by growth form

specific seasonal dynamics. For the  $C_4$  grass, *A. gerardii*, elevated CO<sub>2</sub> almost completely counteracted drought stress, which resulted in markedly higher  $A_{\text{net}}$  and  $\Psi_{\text{leaf}}$  and lower  $g_s$  in elevated CO<sub>2</sub> compared with plant performance in ambient CO<sub>2</sub>. This supports findings showing that elevated CO<sub>2</sub> can stimulate photosynthesis in  $C_4$  grasses, especially in water-limited conditions (Reichers and Strain 1987; Wray and Strain 1987; Knapp et al. 1993b, 1994b; Cheng et al. 1994; Morgan et al. 1994).

Our findings also support claims that elevated CO<sub>2</sub> will stimulate tallgrass prairie productivity in dry years (Knapp et al. 1993b; Owensby et al. 1993a) or prolong the growing season by alleviating late-season water stress (Knapp et al. 1996). Elevated CO<sub>2</sub> could reduce intra-annual variability of productivity in tallgrass prairie by stimulating productivity in chronically water-limited areas of tallgrass prairie such as annually



**Fig. 6** Top row, Diurnal responses of leaf xylem water potential of *Andropogon gerardii* (a  $C_4$  grass) in elevated (squares) and ambient (circles)  $CO_2$  OTC at the start (wet; empty symbols) and end (dry; filled symbols) of a drying cycle. Each point is the mean of 14 measurements; bars indicate  $\pm 1$  SE of the mean. Bottom row, Percentage change in  $\Psi_{leaf}$  in elevated  $CO_2$  compared with ambient  $CO_2$  OTC plants in wet (empty symbols) and dry (filled symbols) soil moisture conditions.

burned prairie or exposed uplands, features that strongly influence productivity response to seasonal precipitation in these grasslands (Knapp and Seastedt 1986; Knapp et al. 1993a; Briggs and Knapp 1995). Also, the marked midseason increase in *A. gerardii*  $g_s$ , which could be accompanied by altered canopy transpiration (Ham et al. 1995), suggest that modeling efforts attempting to predict changes in primary productivity in grassland systems should take into account the seasonal patterns of water use and transpiration of canopy dominants as they are affected by elevated  $CO_2$  (Parton et al. 1994).

$CO_2$  enrichment directly benefited the  $C_3$  shrub species, *Symphycarpos orbiculatus*, the most in drought conditions compared with ambient  $CO_2$ . Drought at ambient  $CO_2$  often resulted in stomatal closure before midday, negative  $A_{net}$ , and leaf temperatures 4–5°C above air temperature. Elevated  $CO_2$  eliminated these limitations, even at similar leaf temperatures. Gas ex-

change and  $\Psi_{leaf}$  measurements indicate that this shrub was most responsive to rewatering. Thus, elevated  $CO_2$  may most benefit water status of shallowly rooted, broad-leaved  $C_3$  species (Knapp et al. 1996).

Elevated  $CO_2$  offset drought effects to a lesser extent in *Salvia pitcheri*, a  $C_3$  species of considerably greater photosynthetic capacity than *S. orbiculatus* (Turner et al. 1995). The late-season increases in  $g_s$  later may coincide with flowering or be due to leaf age-specific increases in photosynthetic capacity (Harper 1989). Our results also suggest that *S. pitcheri* has access to deeper water reserves than *S. orbiculatus*. Midday water potentials were markedly higher in *S. pitcheri* compared with the shrub, *S. orbiculatus*, and did not respond to elevated  $CO_2$ , while mild drought produced a relatively small, albeit significant, reduction in  $\Psi_{leaf}$ . Thus, elevated  $CO_2$  may not as strongly affect plant water status, and subsequent gas exchange performance, in this deep-rooted, drought-resistant, long-lived perennial  $C_3$  forb (Owensby et al. 1993b; Fahnestock and Knapp 1994; Turner et al. 1995; Knapp et al. 1996).

We found limited evidence that direct physiological effects of elevated  $CO_2$  will lead to rapid changes in the structure of this  $C_3/C_4$  system. Our results indicate that  $C_4$  tallgrass prairie grasses receive consistent benefits from atmospheric carbon enrichment, mainly through improved water status, and could continue dominating these systems. Elevated  $CO_2$  did alleviate drought effects compared with ambient  $CO_2$  in the  $C_3$  plants studied, especially for the woody shrub, *S. orbiculatus*. Biomass data has repeatedly shown increases in  $C_3$  biomass in tallgrass prairie exposed to elevated  $CO_2$  (Owensby et al. 1993b; J. M. Ham, unpublished data), but it is not known which growth forms constitute this increase. Our data suggest that broad-leaved woody  $C_3$  species might have the greatest potential for increased productivity compared with herbaceous forbs. However, both  $C_3$  species showed significant declines in  $A_{net}$  at elevated  $CO_2$  during dry periods, while the  $C_4$  grass did not. Elevated  $CO_2$  also resulted in consistently higher midday  $\Psi_{leaf}$  in *A. gerardii*, while results for the  $C_3$  species were mixed. This stands in contrast to other mixed  $C_3/C_4$  communities, which showed marked improvement in  $C_3$  plant performance that resulted in rapid increases in  $C_3$  species (Curtis et al. 1989; Ziska et al. 1990; Drake and Leadley 1991; Arp et al. 1993). However, the balance between  $C_3$  and  $C_4$  vegetation in tallgrass prairie is the result of complex interactions between climate (Borchert 1950; Axelrod 1985), grazing (Vinton et al. 1993; Fahnestock and Knapp 1994), and fire (Towne and Owensby 1984; Hulbert 1988; Briggs and Knapp 1995), not simply differences in photosynthetic rate. Rather, it seems that longer-term, cumulative effects such as tissue nutrient ratios, allocation patterns, belowground processes, nutrient limitations, and potential changes in the variability in future climates could more strongly mediate changes in tallgrass prairie community structure in an elevated  $CO_2$  world (Ow-

ensby et al. 1993a, 1993b; Kemp et al. 1994; Monz et al. 1994; Owensby et al. 1994; Parton et al. 1994; Rice et al. 1994).

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