

Responses in stomatal conductance to elevated CO₂ in 12 grassland species that differ in growth form

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Abstract

Responses in stomatal conductance (g_{st}) and leaf xylem pressure potential (ψ_{leaf}) to elevated CO₂ (2x ambient) were compared among 12 tallgrass prairie species that differed in growth form and growth rate. Open-top chambers (OTCs, 4.5 m diameter, 4.0 m in height) were used to expose plants to ambient and elevated CO₂ concentrations from April through November in undisturbed tallgrass prairie in NE Kansas (USA). In June and August, ψ_{leaf} was usually higher in all species at elevated CO₂ and was lowest in adjacent field plots (without OTCs). During June, when water availability was high, elevated CO₂ resulted in decreased g_{st} in 10 of the 12 species measured. Greatest decreases in g_{st} (ca. 50%) occurred in growth forms with the highest potential growth rates (C₃ and C₄ grasses, and C₃ ruderals). In contrast, no significant decrease in g_{st} was measured in the two C₃ shrubs. During a dry period in September, reductions in g_{st} at elevated CO₂ were measured in only two species (a C₃ ruderal and a C₄ grass) whereas increased g_{st} at elevated CO₂ was measured in the shrubs and a C₃ forb. These increases in g_{st} were attributed to enhanced ψ_{leaf} in the elevated CO₂ plants resulting from increased soil water availability and/or greater root biomass. During a wet period in September, only reductions in g_{st} were measured in response to elevated CO₂. Thus, there was significant interspecific variability in stomatal responses to CO₂ that may be related to growth form or growth rate and plant water relations. The effect of growth in the OTCs, relative to field plants, was usually positive for g_{st} and was greatest (> 30%) when water availability was low, but only 6–12% when ψ_{leaf} was high.

The results of this study confirm the importance of considering interactions between indirect effects of high CO₂ of plant water relations and direct effects of elevated CO₂ on g_{st} , particularly in ecosystems such as grasslands where water availability often limits productivity. A product of this interaction is that the potential exists for either positive or negative responses in g_{st} to be measured at elevated levels of CO₂.

Introduction

When plants are exposed to levels of atmospheric CO₂ above ambient, stomatal conductance (g_{st}) is usually decreased (Cure & Acock 1986; Eamus & Jarvis 1989; Tyree & Alexander 1993). There is substantial variation in this response, however, often attributable to growth conditions (greenhouse vs. field, root restriction in pots, length of exposure; Thomas & Strain 1991; Retuerto & Woodward 1993); light, water or nutrient levels (Bunce 1992a; Samuelson & Seiler 1993; Tschaplinski et al. 1993) or interspecific differences

(Cure & Acock 1986; Tyree & Alexander 1993). An assessment of the degree of species-specific variability in responses to elevated CO₂ is especially important if community-level responses are to be evaluated (Bazzaz 1990).

Elevated CO₂ directly increases leaf-level net photosynthesis in many plant species (Dahlman 1993). Moreover, reductions in g_{st} may enhance plant water status and indirectly enhance CO₂ uptake and growth, even in those species such as C₄ grasses that show little direct response in photosynthesis to elevated CO₂ (Knapp et al. 1993, 1994). Indeed, the critical interac-

tive effects of plant water status and responses to elevated CO_2 have recently been explored in plants from a variety of ecosystems (Paez et al. 1983; Luo & Strain 1992; Masle 1992; Morison 1993; Morse et al. 1993; Samuelson & Seiler 1993). Under certain conditions, enhanced plant water status at elevated CO_2 may offset the effect on CO_2 -induced reductions in g_{st} , as determined by comparative studies with plants simultaneously exposed to ambient CO_2 (Eamus & Jarvis 1989). This is because improved plant water relations may increase g_{st} . Clearly, understanding how plant water status and elevated CO_2 interact to impact g_{st} under field conditions is critical to predicting gas exchange and growth responses in plants at high levels of atmospheric CO_2 .

Interpretation of this water relations-elevated CO_2 interaction is further complicated in field studies that use open-top chambers (OTC) to expose plants to elevated CO_2 (Leadley & Drake 1993). The presence of these chambers often alters the energy and water balance of the plants under study (Ham et al. 1995) such that plant and soil water relations may be enhanced relative to plants grown in field plots without chambers. This is particularly true in ecosystems such as grasslands with high solar radiation and windspeeds. In some cases, the "chamber effect" can increase plant production relative to unchambered field plots as much as production is increased in elevated CO_2 OTCs relative to ambient OTCs (Owensby et al. 1993).

The goal of this research was to evaluate responses in g_{st} to elevated CO_2 under field conditions (within OTCs) in a variety of different tallgrass prairie plant species. Although C_4 grasses dominate this grassland type in terms of biomass, a variety of different growth forms, with varying growth rates and above and below-ground architecture, comprise the tallgrass prairie plant community (Freeman & Hulbert 1985). From a biodiversity viewpoint, it is the sub-dominant growth forms that contribute most to the relatively high species diversity in this system (Turner et al. 1995). Yet little is known of the responses of these species to elevated CO_2 or other stresses. Specifically, we compared responses in g_{st} and xylem pressure potential (ψ_{leaf}) to elevated CO_2 in 12 species that were grouped as follows: C_3 shrubs, C_3 forbs, C_3 ruderals, and C_3 and C_4 grasses. All measurements were made on plants exposed to their respective CO_2 treatments for 2 years, thus the responses documented are representative of chronic, not short-term exposure to elevated CO_2 . Measurements were made early and late in the growing season to span the range of water availability and ψ_{leaf}

that species in this grassland ecosystem typically experience. Our objectives were to (1) assess the degree of interspecific variability in stomatal responses to long-term exposure CO_2 in these grassland species that differ in growth form and rate, and (2) determine how seasonal changes in water availability may affect these responses. In addition, we measured g_{st} and ψ_{leaf} concurrently in plants outside, but adjacent to, the OTCs to evaluate the effect that the OTC environment had on plant water status and stomatal responses.

Materials and methods

Research sites were located in native tallgrass prairie near Manhattan Kansas (United States). Sites were selected that were representative of the region (dominated by *Andropogon gerardii* Vitman. and *Sorghastrum nutans* Nash.) and with levels of aboveground primary production ca. $425 \text{ g m}^{-2} \text{ yr}^{-2}$ (8–10% of this total from C_3 forbs; Owensby et al., 1993). Plants studied were located in open-top chambers (OTCs) that were 4.5 m in diameter and 4.0 m in height with a cone-top baffle that reduced the top opening to a 1.5 m diameter circle. Rainfall intercepted by this top was captured via guttering, then pumped to a central sprinkler head located 1 m above the ground within each chamber. The aluminum structural frame was covered with 1.5 mm, UV resistant polyethylene film. Chambers were maintained in the same location for the year of this study (1994) and the previous year. Two chambers were used to expose plants to elevated (double ambient) CO_2 concentrations from late April until October and two chambers were used as ambient controls. Measured ambient CO_2 at 1 m in the ambient chambers was ca. $330 \mu\text{l l}^{-2}$ during the day but was $> 400 \mu\text{l l}^{-2}$ at night. CO_2 concentrations in the elevated chambers tracked the target concentration of $2 \times$ ambient CO_2 within $\pm 2\%$. Windspeeds in the chambers ranged from 0.4 m s^{-2} to 1.2 m s^{-2} and were less variable than windspeeds outside the chambers (Owensby et al., 1993). Incident photosynthetic photon flux was reduced by ca. 10% relative to outside the chambers. Additional information about the experimental design and the microclimatic characteristics of the chambers can be found in Owensby et al. (1993) and Ham et al. (1995).

To characterize plant water status throughout the growing season (May - September), midday (ca. 1300 hrs Central Daylight Time) estimates of leaf xylem pressure potential (ψ_{leaf}) were made weekly for *A. gerardii*, the dominant C_4 tallgrass prairie grass. Upper

canopy leaves (5–7) were collected and stored in plastic bags for less than 10 minutes before ψ_{leaf} could be estimated with a Scholander-type pressure chamber (PMS model 1000, Plant Moisture Stress, Inc., Corvallis, OR). Volumetric soil water content in elevated CO₂ and ambient OTCs and adjacent field plots was also measured at ca. weekly intervals using a dual-probe gamma attenuation system (Troxler Laboratories, Research Triangle Park, NC) to characterize water availability. Measurements were made to 0.3 m below the soil surface and gamma attenuation was recorded for 30 s intervals to estimate water content (Reginato & Van Bavel 1964).

Early in June, the chambers were surveyed for plant species that (1) encompassed a variety of growth forms, and (2) were present in sufficient numbers to allow for destructive sampling for water status measurements as well as replicate measurements of stomatal conductance to water vapor (g_{st}). Ten species were identified as having at least six individual plants in ambient and elevated OTCs. These were the C₃ shrubs *Symphoricarpos orbiculatus* Moench. and *Amorpha canescens* Pursh.; the C₃ forbs *Baptisia australis* (L.) R. Br. var *minor* (Lehn.), *Vernonia baldwini* Torr., *Salvia pitcheri* Torr. and *Artemisia ludoviciana* Nutt.; the C₃ ruderals *Eupatorium altissimum* L. and *Ambrosia psilostachyia* DC.; and the C₄ grasses *A. gerardii* and *Sorghastrum nutans* (L.) Nash (*Nomenclature*: follows Freeman and Hulbert 1985). All of these species were also found in abundance in undisturbed sites adjacent to the OTCs. Two C₃ grasses, *Bromus inermis* Leyss. and *Elymus canadensis* L. could only be found in the elevated CO₂ chambers and in the adjacent field plots, but were sampled nonetheless.

Twice during the growing season, 27 June and 22 August, ψ_{leaf} was determined on 5–7 upper canopy leaves from all 12 species. Leaves were collected (each leaf from a separate plant) at midday from the four OTCs and two adjacent field plots. More frequent estimates of ψ_{leaf} were not possible due to the limited number of plants available and the destructive nature of the sampling. In June, stomatal conductance (g_{st}) was measured separately on adaxial and abaxial leaf surfaces from at least six individuals from each of the three treatments (three individuals from each OTC/field plot when possible). Late season estimates of g_{st} were delayed until September until plant water status of *A. gerardii* had decreased to relatively low values. At this time of year, the C₃ grasses had senesced and no green leaves were available for measurement. In early September, plants were sampled after late season

rain (79 mm in late August) and during a relatively dry period. For each of the three sampling periods, measurements of g_{st} required several days, but care was taken to sample plants under similar environmental conditions during the midday/afternoon hours (photosynthetic photon flux (PPF) > 1400 $\mu\text{mol m}^{-2} \text{s}^{-1}$; air temperature 29–34 C; vapor pressure deficits of 2.8–3.4 kPa in June, and 2.8–3.1 and 2.1–2.4 kPa during the wet and dry periods, respectively, in September). A null-balance porometer (LICOR 1600, LICOR Inc., Lincoln, NE) was used to estimate g_{st} (adaxial, abaxial and total) on leaves oriented in their natural position in the OTCs/field. The porometer was calibrated in the field at ca. 0.5 hr intervals and the desiccant was changed daily. Care was taken to avoid shading the measurement plants at all times except during the ca. 30–60 sec period of measurement with the porometer.

Data were analyzed by species with single factor ANOVA and LSD tests to compare means among treatments (Statistix, Version 4.1, Analytical Software, St. Paul, MN.). For the C₃ grasses, only two treatment comparisons could be made since these species were absent from the ambient CO₂ chambers. Regression analysis was used to evaluate the relationship between changes in ψ_{leaf} and g_{st} . Arcsine transformation of data was completed prior to analysis when data were expressed as proportional differences among treatments. Adaxial, abaxial, total g_{st} (sum of adaxial and abaxial) and ratios of these values were all compared among treatments. No patterns were detected when adaxial and abaxial values or ratios were considered separately, thus only analyses for total g_{st} are presented.

Results

Precipitation during the 1994 growing season (May – September, 420.6 mm) was below the 30 year mean for the site (532.4 mm; Kansas State University Weather Data Library) with the driest period occurring from mid-August through September. Total precipitation by month from May through September was: May = 81.8 mm, June = 143.7 mm, July = 103.4 mm, August = 80.8 mm and September = 10.9 mm. Seasonal patterns in soil water content and midday ψ_{leaf} in *A. gerardii* reflected this precipitation pattern with lowest values measured late in the summer (Figures 1 and 2).

In general, soil water content was greater ($P < 0.05$) in the elevated CO₂ OTCs and lowest in the field plots (Figure 1). Differences among treatments were great-

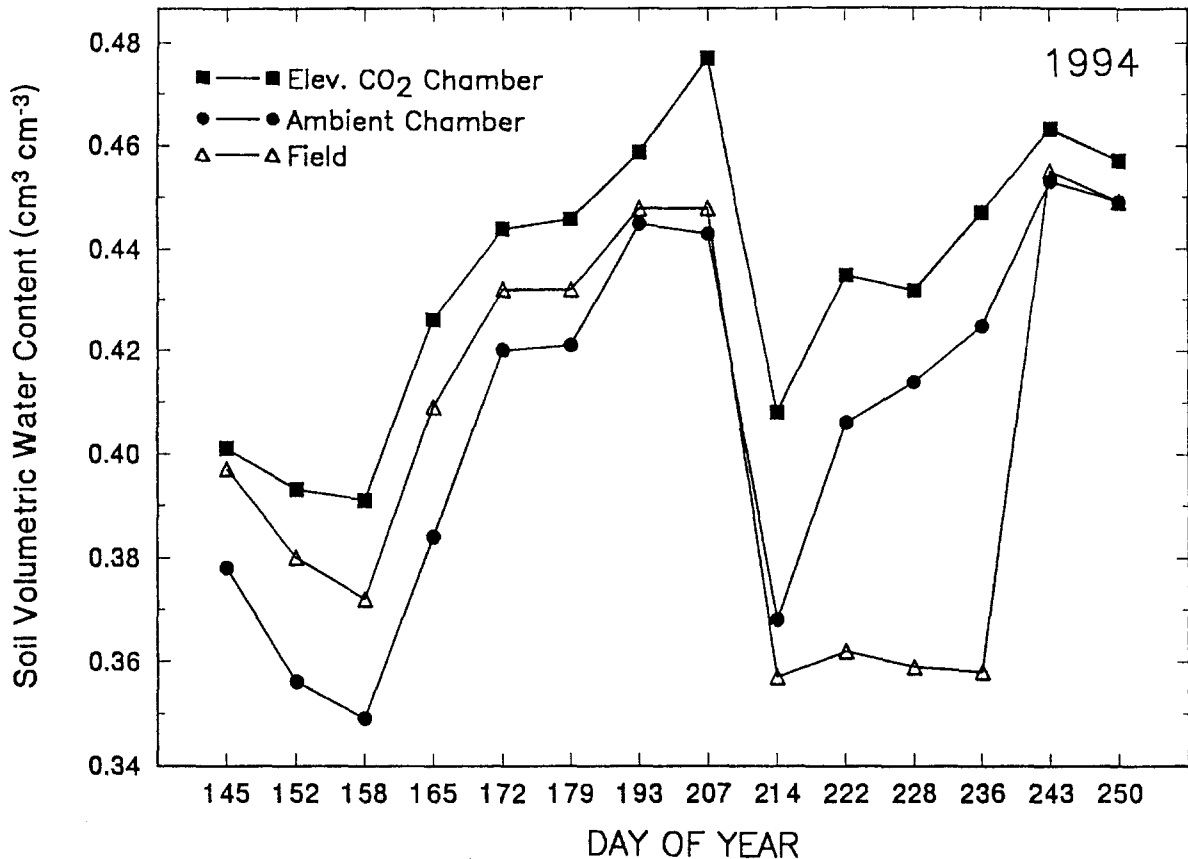


Figure 1. Seasonal (1994) course of volumetric soil water content in open top chambers with elevated levels (2x ambient) of CO₂, ambient CO₂ and in adjacent field plots in undisturbed tallgrass prairie. Each point is the mean of measurements from two chambers or plots. Error bars are smaller than the symbols.

est in late summer (DOY 210–235) when soils were driest. Similar patterns occurred in plant water status in *A. gerardii*, with highest ψ_{leaf} measured in plants growing in the elevated CO₂ OTCs and lowest ψ_{leaf} in plants in the field (Figure 2). Both seasonal means and minimum ψ_{leaf} were significantly different among the treatments ($P < 0.05$). For all 12 species sampled in June and August, a similar pattern among treatments was evident (Figure 3), although for individual species, differences were not always statistically significant, particularly between ambient OTC and field plots.

In June, g_{st} was significantly reduced in elevated vs. ambient OTCs in 10 of the 12 species studied (Figure 4). An average reduction in g_{st} of about 40% was measured in elevated vs. ambient CO₂ chambers, and the degree of reduction in g_{st} appeared to be related to the growth form. For example, the growth forms with the presumed highest growth and photosynthetic rates (the grasses and the ruderals) were the most respon-

sive to CO₂ whereas g_{st} was not significantly reduced in the shrubs (Figure 4). Although there was a trend for the decrease in g_{st} at elevated CO₂ to be correlated with increased ψ_{leaf} in these species, there was no statistical significance to this relationship.

In September, there were fewer significant reductions in g_{st} at elevated CO₂, but the trend towards greater reductions in g_{st} in the grasses and ruderals continued (Fig. 5). However, during the September dry period when overall g_{st} for all species was markedly reduced, g_{st} was actually significantly increased at elevated CO₂ in both shrubs and the forb *B. australis*. Conversely, there were still significant CO₂-induced reductions in g_{st} in two of the faster growing species (Fig. 5). Summed over all species, g_{st} was relatively unresponsive (a 6.4% increase) to increased CO₂ during this dry period. During a wet period in September, g_{st} was greater in all species and when stomatal responses to elevated vs. ambient CO₂ were compared,

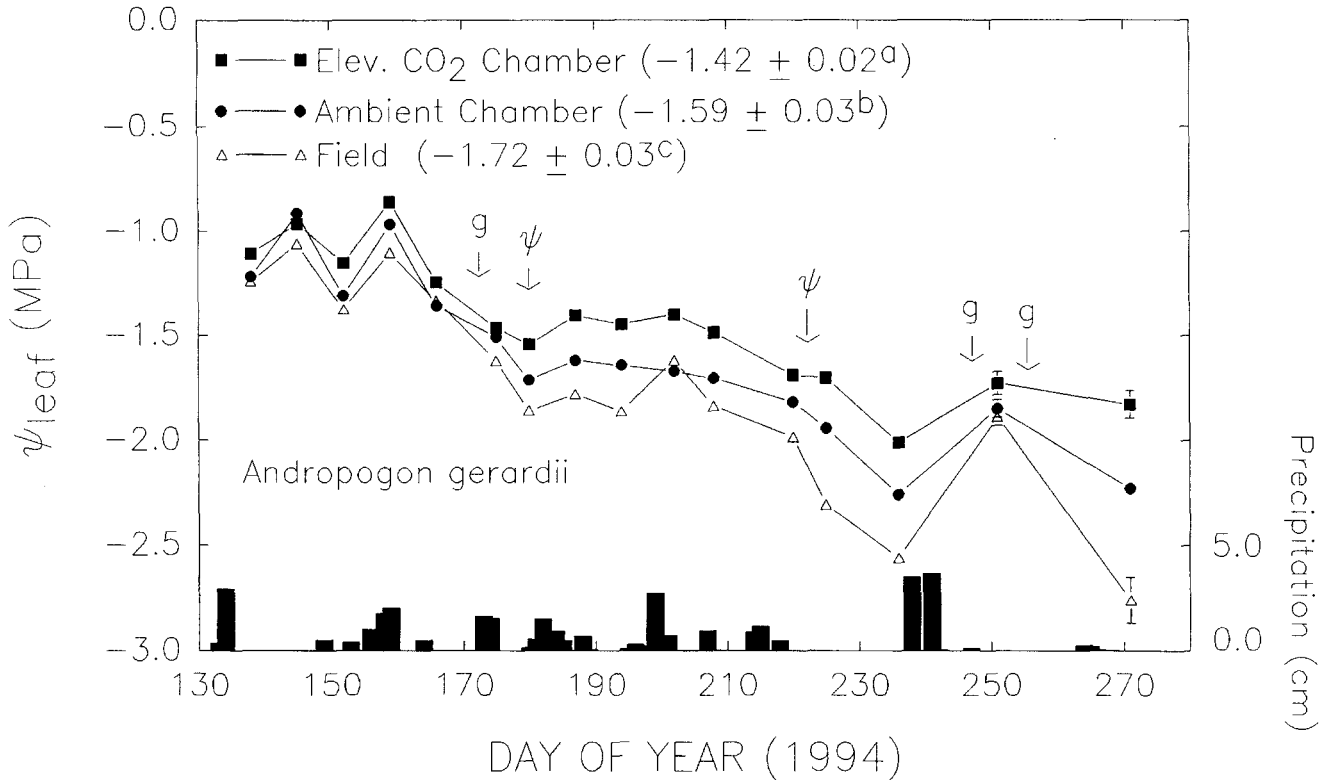


Figure 2. Seasonal (1994) course of midday leaf xylem pressure potential (ψ_{leaf}) in *Andropogon gerardii* in open top chambers with elevated levels (2x ambient) of CO₂, ambient CO₂ and in adjacent field plots in undisturbed tallgrass prairie. Values in () are seasonal means for each treatment (+ 1 standard error of the mean) and different letters indicate significant differences (ANOVA, $P > 0.05$). Vertical bars indicate + 1 SE for individual dates. In most cases bars are smaller than the symbols. Arrows labeled either g or ψ indicate the approximate times of the season when intensive measurements of stomatal conductance (g) or xylem pressure potential were measured in 11 additional tallgrass prairie species.

only significant reductions in g_{st} occurred in response to 2x CO₂ (Figure 5). Moreover, the average proportional reduction in g_{st} at high CO₂ for all species (32.3%) was similar in magnitude to that measured in June (Figure 4).

The effect that the growth environment in OTCs (the "chamber effect") had on g_{st} was assessed by comparing responses in plants in the ambient CO₂ OTCs with plants in adjacent field plots. In June, although g_{st} in a few individual species was significantly increased by growth in the OTCs, the overall chamber effect was small (6%; Figure 6). In contrast, the chamber effect was much greater during the dry period in September (30%) with g_{st} in some species increased dramatically. During the wet period in September, the chamber effect decreased to 12% when averaged for all species. There was no apparent relationship between the magnitude of the chamber effect and growth form.

Discussion

Previous studies in this tallgrass prairie have documented consistent increases in ψ_{leaf} for *A. gerardii* in elevated CO₂ OTCs vs. ambient OTCs, as well as higher leaf water status in ambient OTCs vs. the field (Owensby et al. 1993; Knapp et al. 1993). Data from this study confirm that relationship (Figure 2) and extend it to several other species (Figure 3) although our data on these additional species are limited to two sampling dates. Nonetheless, when statistically significant differences were detected, highest ψ_{leaf} was always measured in plants in the elevated CO₂ OTCs and lowest ψ_{leaf} in the field. Such consistency in response among species has important implications for predicting community-level responses to elevated CO₂.

The proportional reductions in g_{st} at elevated CO₂ for the 12 tallgrass prairie species selected were within the range of values reported in other studies (Cure & Acock 1986; Eamus & Jarvis 1989). Moreover, the

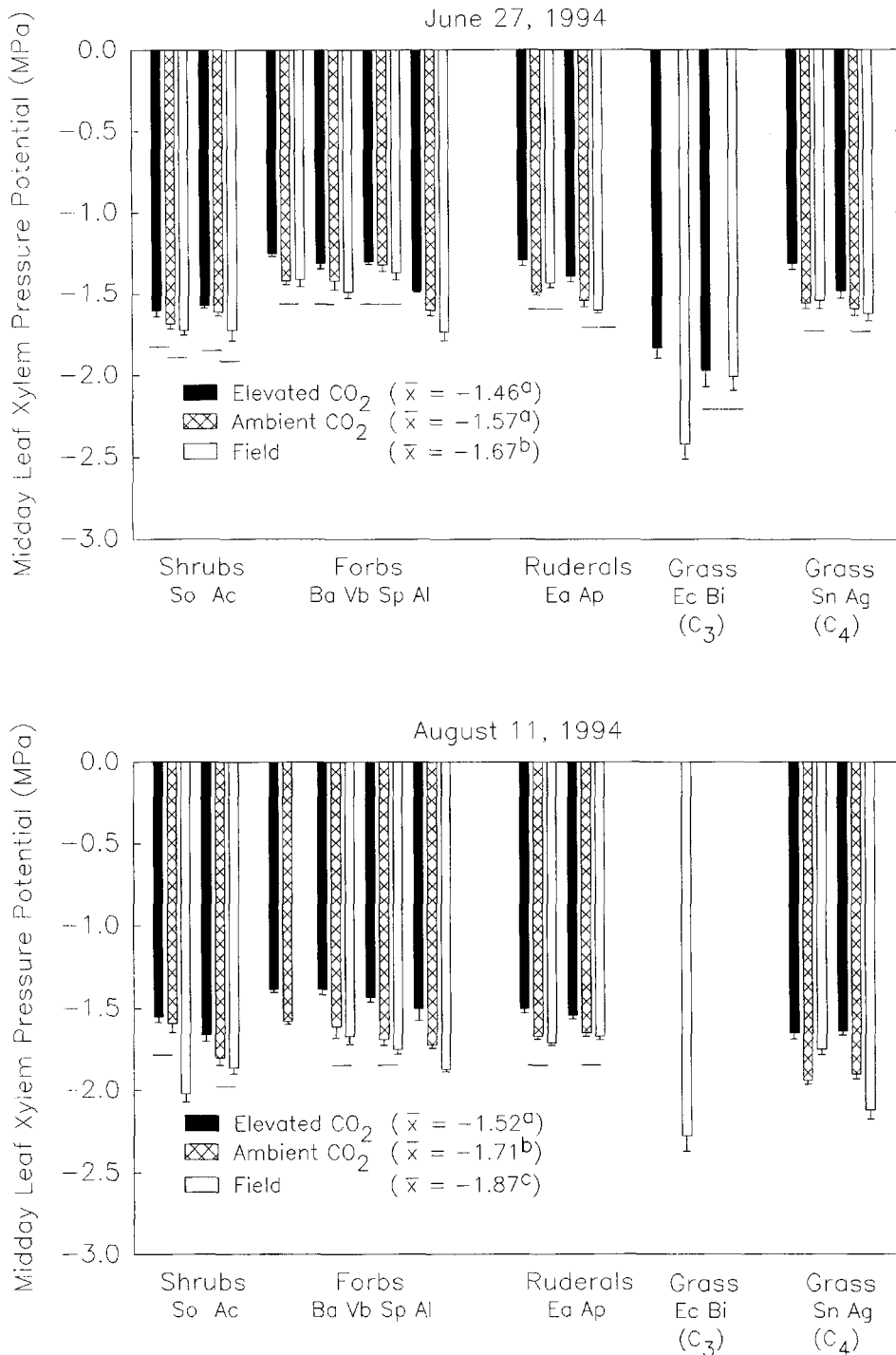


Figure 3. Midday leaf xylem pressure potential measured in June and August (1994) in 12 tallgrass prairie species growing in open top chambers with elevated levels (2x ambient) of CO₂, ambient CO₂ and in adjacent field plots in undisturbed tallgrass prairie. Horizontal lines that connect bars within a species indicate that mean ψ_{leaf} were not significantly different. One standard error of the mean is also indicated on each bar. Also shown are mean levels of ψ_{leaf} for all species combined. Different letters following means + SE indicate that values are significantly different. Two C₃ species were not found in ambient CO₂ chambers in June and only one C₃ grass species was found in abundance in the field in August. So = *Symphoricarpos orbiculatus*, Ac = *Amorpha canescens*, Ba = *Baptisia australis*, Vb = *Vernonia baldwini*, Sp = *Salvia pitcheri*, Al = *Artemisia ludoviciana*, Ea = *Eupatorium altissimum*, Ap = *Ambrosia psilostachya*, Ec = *Elymus canadensis*, Bi = *Bromus inermis*, Sn = *Sorghastrum nutans*, Ag = *Andropogon gerardii*.

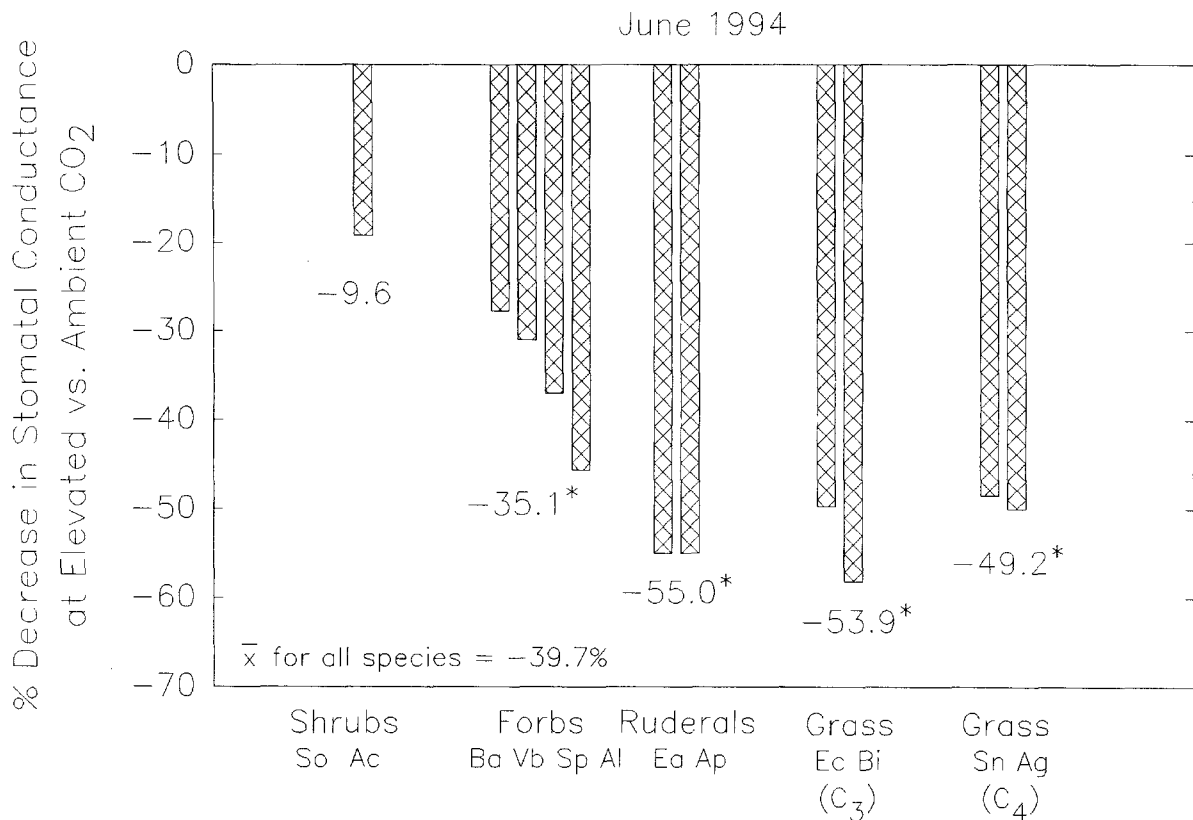


Figure 4. The proportional decrease in stomatal conductance (g_{st}) in 12 tallgrass prairie species in June (1994) growing in open top chambers at elevated CO₂ (2x ambient) vs. ambient CO₂. The average % decrease for each growth form (shrubs, forbs, etc.) is also shown. "*" indicates that g_{st} was significantly reduced ($P < 0.05$) for all species within a growth form when absolute values were compared. Species abbreviations and mean values of g_{st} (adaxial + adaxial, + maximum SE in $\text{mmol m}^{-2} \text{s}^{-1}$) were: So = *Symphoricarpos orbiculatus*, 219.8 + 58.7; Ac = *Amorpha canescens*, 490.7 + 47.7; Ba = *Baptisia australis*, 651.6 + 11.2; Vb = *Vernonia baldwini*, 429.8 + 30.8; Sp = *Salvia pitcheri*, 566.0 + 24.8; Al = *Artemisia ludoviciana*, 423.9 + 26.9; Ea = *Eupatorium altissimum*, 631.3 + 19.0; Ap = *Ambrosia psilostachya*, 898.5 + 46.0; Ec = *Elymus canadensis*, 455.5 + 28.2; Bi = *Bromus inermis*, 573.5 + 29.8; Sn = *Sorghastrum nutans*, 292.7 + 17.9; Ag = *Andropogon gerardii*, 261.8 + 24.4. The % decrease for the C₃ grasses was calculated from comparisons with field values (shown above) since neither of these two species were found in sufficient abundance in the ambient open top chambers.

relatively smaller responses to elevated CO₂ in the two shrub species are consistent with some reports that woody plant stomata respond less to elevated CO₂ than herbaceous species (Bunce 1992b; Ceulemans & Mousseau 1994). Whether reduced stomatal responsiveness to CO₂ in these woody species is related to growth form *per se* (Knapp & Smith 1989; Gunderson & Wullschleger 1994) or rates of gas exchange (Mansfield et al. 1990; Knapp 1992) is yet to be determined. Although net photosynthesis was not measured concurrently with water relations responses to CO₂, there are sufficient data to suggest that the ordering of species along the x-axis in Figures 3, 4 and 5 represents a gradient from low to high growth and photosynthetic rates (Svejar & Browning 1988; Knapp 1993; Knapp et al. 1994; Fahnestock & Knapp 1994; Turner et al. 1995,

Knapp unpubl. data). Mansfield et al. (1990) presented data from a variety of sources that suggested that g_{st} was less responsive to increased CO₂ in plants with low g_{st} compared to plants with high g_{st} . The data in Figure 4 are consistent with this relationship. Similarly, Hunt et al. (1991) concluded from comparative studies of the response of 27 herbs to CO₂ enrichment that the 'competitive' species were the most responsive to elevated CO₂.

As soil water content and ψ_{leaf} decreased late in the season (Figures 1, 2), reductions in g_{st} due to elevated CO₂ also decreased (Figure 5). This has been documented in other species (Jackson et al. 1994). Perhaps more surprising was the tendency for g_{st} in some species to be equal to or even higher at elevated CO₂ than at ambient CO₂ at this time of year (Figure 5).

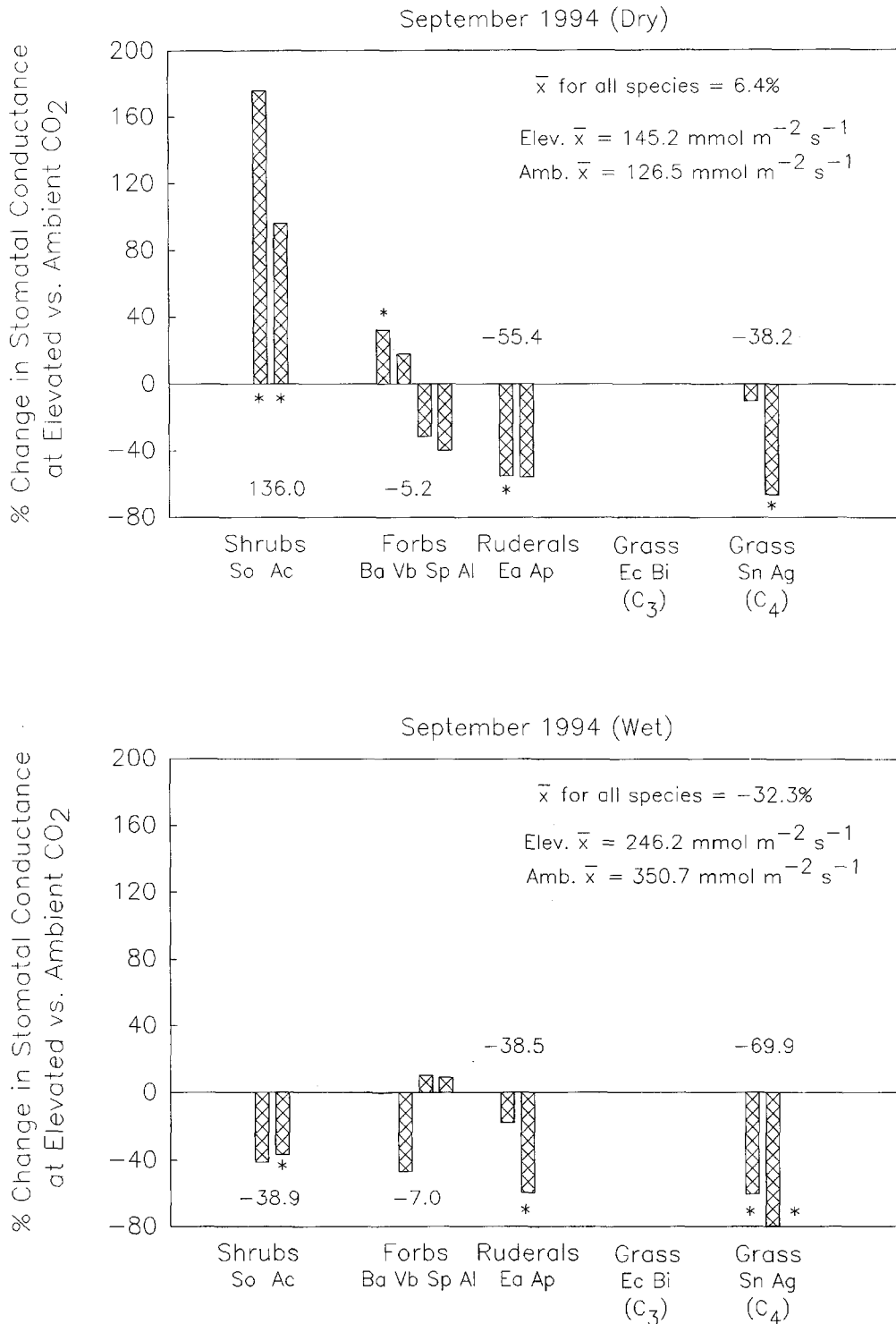


Figure 5. The proportional change in stomatal conductance (g_{st}) during dry and wet periods in September (1994) in 10 tallgrass prairie species growing in open top chambers at elevated CO₂ (2x ambient) vs. ambient CO₂. The average % decrease for each growth form (shrubs, forbs, etc.) is also shown. “*” indicates that g_{st} was significantly different ($P < 0.05$) for a species when absolute values were compared. Also shown are the average values of g_{st} for all plants in elevated vs. ambient CO₂ open top chambers. No data were available for the C₃ grasses in September due to plant senescence. Species names abbreviations are as in Fig. 4.

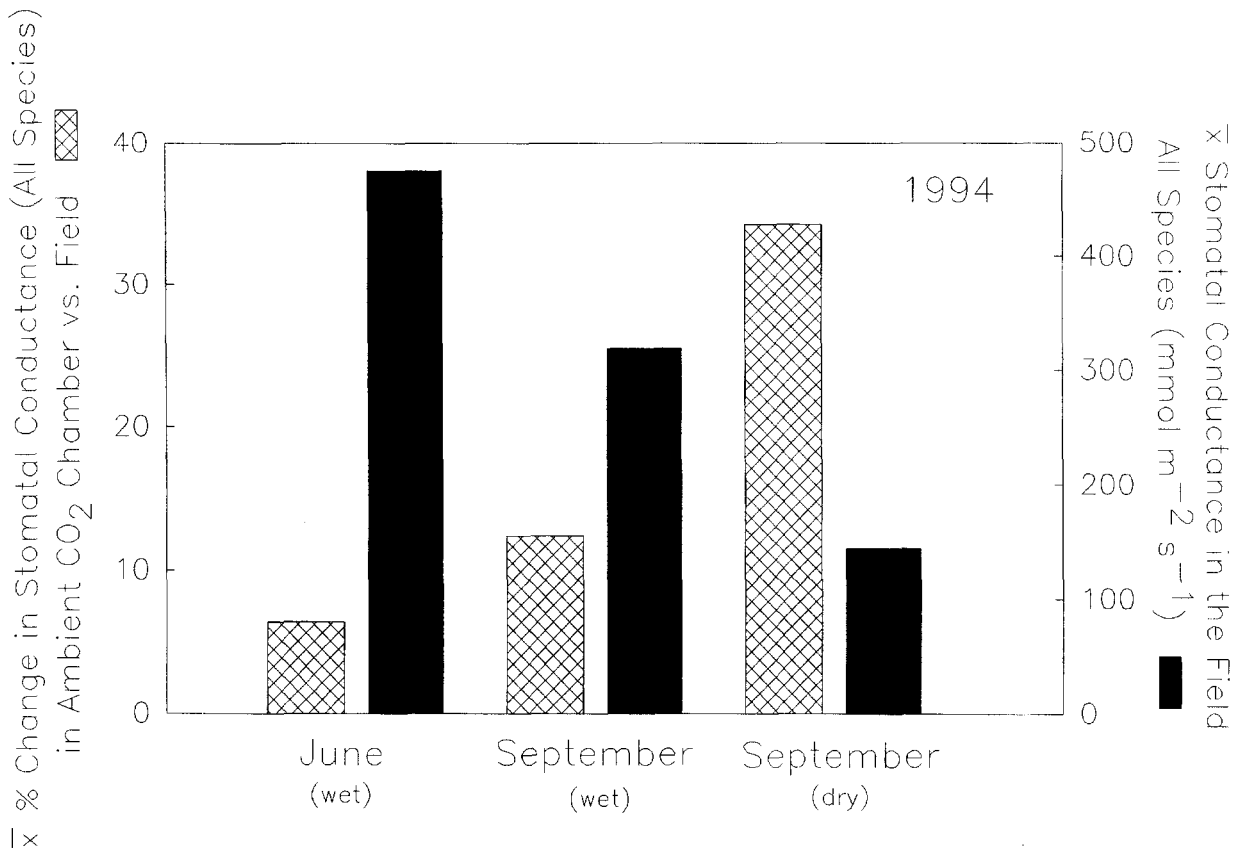


Figure 6. Comparison of the average % increase in stomatal conductance for all species combined when grown in the ambient CO₂ open top chamber vs. adjacent undisturbed tallgrass prairie. Three measurement periods are shown that differed in moisture availability. Also shown is the mean stomatal conductance for all species combined during these times of the 1994 season.

Although comparisons of means indicated that there were few statistically significant positive or negative effects of CO₂ during this dry period, the highest individual g_{st} values measured at this time were usually in plants at elevated CO₂, not ambient CO₂. Indeed, during this period, g_{st} was reduced by high CO₂ in only 2 of 10 species. These data suggest that increased ψ_{leaf} in elevated CO₂ OTCs may have more strongly influenced g_{st} than the direct effect of high CO₂ on g_{st} , particularly in those species that did not show large responses to CO₂ earlier in the season. Improved plant water status at elevated CO₂ at this time of year, with g_{st} equal to or higher than g_{st} in ambient plants, may be the result of significantly higher soil water availability (Figure 1) and/or reduced root resistance to water uptake. Root biomass is increased in this grassland, and in most other systems, at elevated CO₂ (Owensby et al. 1993; Rogers et al. 1994) and reductions in root resistance to water uptake could lead to higher ψ_{leaf}

even if soil water availability was identical in ambient and elevated CO₂ OTCs.

The impact of reductions in water availability later in the season on g_{st} is further illustrated by comparing the magnitude of the 'chamber effect' on g_{st} early in the season (high soil moisture) vs. late in the season when measurements were made during both wet and dry periods (Figure 6). This effect was much greater during the dry period in September than during periods of greater water availability in June and September. Because the relationship between ψ_{leaf} and g_{st} is non-linear in almost all species (Rogers et al. 1984), a likely explanation for the late season increase in the chamber effect is that as ψ_{leaf} decreased below a critical level in the field, differences between plants in ambient OTCs and the field in g_{st} were enhanced. However, there are several other important differences between the OTCs and the field, such as canopy stature, light penetration and windspeed that may increase the variance of the chamber effect among species.

Overall, these data, and those from previous studies (Eamus & Jarvis 1989; Luo & Strain 1992; Tyree & Alexander 1993), suggest that the interactive nature of the effects of elevated CO₂ on g_{st} and ψ_{leaf} and the feedback of ψ_{leaf} on g_{st} can result in species-specific stomatal responses to elevated CO₂ that can be either positive or negative. This may be particularly important in grasslands where different growth forms exploit different portions of the soil profile for water and nutrients.

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