Elevated atmospheric CO_2 alters stomatal responses to variable sunlight in a C_4 grass

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ABSTRACT

Native tallgrass prairie in NE Kansas was exposed to elevated (twice ambient) or ambient atmospheric CO_2 levels in open-top chambers. Within chambers or in adjacent unchambered plots, the dominant C_4 grass, *Andropogon gerardii*, was subjected to fluctuations in sunlight similar to that produced by clouds or within canopy shading (full sun > 1500 μmol m^{-2} s^{-1} versus 350 μmol m^{-2} s^{-1} shade) and responses in gas exchange were measured. These field experiments demonstrated that stomatal conductance in *A. gerardii* achieved new steady state levels more rapidly after abrupt changes in sunlight at elevated CO_2 when compared to plants at ambient CO_2. This was due primarily to the 50% reduction in stomatal conductance at elevated CO_2, but was also a result of more rapid stomatal responses. Time constants describing stomatal responses were significantly reduced (29–33%) at elevated CO_2. As a result, water loss was decreased by as much as 57% (6·5% due to more rapid stomatal responses). Concurrent increases in leaf xylem pressure potential during periods of sunlight variability provided additional evidence that more rapid stomatal responses at elevated CO_2 enhanced plant water status. CO_2-induced alterations in the kinetics of stomatal responses to variable sunlight will likely enhance direct effects of elevated CO_2 on plant water relations in all ecosystems.

Key-words: Andropogon gerardii; Poaceae; big bluestem; elevated CO_2; stomatal conductance; photosynthesis; plant water status.

INTRODUCTION

Exposure of plants to elevated levels of atmospheric CO_2 can alter rates of photosynthesis and respiration, plant water relations, individual plant growth, community productivity, and competitive interactions among species (Carter & Peterson 1983; Bazzaz & Carlson 1984; Strain & Cure 1985; Bunce 1990; Miao, Wayne & Bazzaz 1992). In contrast to plants with the C_3 photosynthetic pathway, leaf-level photosynthesis in C_4 plants is generally not increased at elevated CO_2, primarily because a high concentration of CO_2 occurs in bundle sheath cells of C_4

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plants at ambient CO_2 levels (Rogers, Thomas & Bingham 1983; Ziska, Drake & Chamberlain 1990; 1991; Mooney *et al.* 1991). Productivity in C_4 dominated plant communities may still be enhanced at elevated levels of CO_2, but the mechanism for this production response may be improved water status. Plant water status in C_4 plants may be enhanced due to reductions in stomatal conductance, rather than direct effects on CO_2 uptake (Morison 1985; Cure & Acock 1986; Eamus 1991; Idso 1991, Owensby *et al.* 1993).

Plants in most ecosystems must cope with extended periods of variability in incident sunlight due to clouds and within-canopy shading (Knapp & Smith 1987, 1990; Chazdon 1988; Pearcy 1990). As atmospheric CO_2 increases in the future, greater canopy leaf area and a concurrent increase in inter-plant shading will result in an even greater proportion of each day that leaves are exposed to fluctuations between sunlight and shade (cast by clouds or surrounding plants). During periods of variable sunlight, responses in stomatal conductance to rapid changes in sunlight are slower than photosynthetic responses, particularly when transitions from sun to shade occur. Water use efficiency (carbon gain per unit water loss) may be significantly reduced because CO_2 uptake is decreased almost instantaneously in shade, but stomatal closure and reductions in transpiration occur more slowly (Knapp & Smith 1990).

Increasing the rate of change in stomatal conductance as sunlight varies, or reducing the period of time that stomata are in transition from one steady-state level to another, will conserve water and enhance carbon gain (Knapp & Smith, 1990). For example, recent studies indicate that inherently smaller differences between sun and shade levels of stomatal conductance in C_4 versus C_3 plants enables C_4 species to be significantly more water use efficient during periods of variable sunlight (Knapp 1993). The objective of this research was to compare gas exchange responses in a C_4 grass, *Andropogon gerardii*, exposed to fluctuations in sunlight at elevated and ambient levels of CO_2. Because elevated CO_2 reduces stomatal conductance in this, and virtually all plant species, we hypothesized that transitions in stomatal conductance from sun to shade light levels would occur more rapidly at elevated CO_2. As a consequence, water loss would be reduced during periods of sunlight variability.

MATERIALS AND METHODS

Andropogon gerardii Vitman is the dominant tallgrass prairie species in North America and its field ecophysiology at ambient CO_2 is well-known (Knapp 1985; Svejcar & Browning 1988). We used a well-defined experimental procedure to measure stomatal and photosynthetic responses to variations in sunlight in *A. gerardii* (Knapp & Smith 1989; 1990). Plants studied had been exposed to elevated (double ambient) CO_2 concentrations continuously from the beginning of the 1992 growing season in large, open-top chambers. Responses in plants exposed to elevated CO_2 were compared to plants in identical chambers at ambient CO_2 and to nearby plants outside the chambers. Open-top chambers were 4·5 m in diameter and 4·0 m in height with a cone-top baffle that reduced the top opening to 3 m. The aluminum structural frame was covered with 1·5 mm, UV-resistant polyethylene film. Precipitation intercepted by the baffle was estimated to be 54%, and within 24 h of rainfall, an equivalent amount was added to each chambered plot. Plants were measured in two chambers with ambient CO_2 levels, two chambers with elevated CO_2 and two unchambered plots. Additional details about the experimental design and microclimate characteristics within the chambers can be found in Owensby *et al.* (1993).

Gas exchange measurements were made on cloud free days in late June and July 1992. We subjected plants growing in undisturbed grassland within the chambers/plots to experimental light manipulations designed to mimic a sunlight regime typically produced by intermittent cloud cover or inter-plant shading (Knapp & Smith 1987; Smith, Knapp & Reiners 1989). Plants ($n = 6$ per treatment) were exposed to alternating 8 ± 1-min periods of full sunlight ($> 1500\ \mu$mol m^{-2} s^{-1} photon flux density [PFD], 0·4–0·7 μm) and 5 ± 1-min periods of shade ($350 \pm 30\ \mu$mol m^{-2} s^{-1}). Net photosynthesis and stomatal conductance in three to four leaves placed in a 0·25 dm^3 cuvette were measured at ca. 1-min intervals with a closed gas exchange system (Li-Cor 6200, Li-Cor Inc., Lincoln, NE, USA). Individual leaves were from separate tillers and were always measured under constant conditions of full sunlight for several minutes prior to light manipulations to insure that gas exchange was not affected by repeated opening and closing of the cuvette. Three sets of leaves from plants in each of the two chambers/plots per treatment were measured. Steady-state gas exchange responses to PFD were also measured for all treatments. Maximum A and g in ambient and elevated CO_2 plants were compared with a two sample t-test ($P < 0.05$). Light was manipulated with neutral density screens measuring 80×80 cm. The gas exchange system was calibrated for CO_2 and water vapour by the manufacturer prior to this study and calibrations were checked weekly with certified standards (2% accuracy verified with a calibrated infrared gas analyser; Matheson Gas Products, Newark, NJ, USA). The humidity sensor was checked with a ventilated psychrometer.

More detailed measurements of gas exchange responses

to changes in PFD were made by abruptly changing PFD from sun to shade (or *vice versa*) and measuring gas exchange responses until a new steady state was achieved ($n = 5$–10 sets of leaves). The response time of the gas exchange system was 17.50 ± 0.96 s to equilibrate at a new CO_2/H_2O concentration and data presented are corrected for this system lag time. Flow rate and system volume was held constant for all treatments, thus system response times were also constant. To quantify response dynamics of stomatal conductance (g), we used a first-order exponential model:

$$g = g_{(max,\ min)} \times [1 - \exp(-t/\tau)],$$

where $g_{(max,\ min)}$ is the maximum or minimum steady state level of stomatal conductance at sun or shade light levels, t is the time since an abrupt change in light, and τ is a time constant signifying when 63% of the response has occurred (Knapp, 1993). Nonlinear, least-squares regression software was used to fit the pooled data to this model (FitAll, Standard Edition, version 4·01, MTR Software, Toronto, Canada). We also used simple, linear regression models, where appropriate, to describe initial changes in g during the first 2 min after an abrupt change in PFD. Data were pooled within treatments from plants measured in both chambers/plots.

Finally, we subjected large groups of individual *A. gerardii* plants to alternating sun and shade periods under a variety of environmental conditions. Neutral density screens were used to cast 10-min periods of shade that alternated with equivalent periods of full sunlight incident on > 50 tillers of *A. gerardii* in chambers and the unchambered plots. At ca. 1 min intervals, individual leaves were collected and leaf ψ was measured immediately in a Scholander-type pressure chamber (PMS model 1000, Plant Moisture Stress, Corvallis, OR, USA). Sun/shade measurements of plant water status were replicated five times for a total of 100 measurements per treatment. Measurements were made from 1000 to 1300 h (CDT) from 15 July to 28 July, 1992 [a period of unusually abundant rainfall (> 15 cm)]. Experiments were conducted on clear days when air temperatures were similar to those that leaves experienced during gas exchange measurements (25–33 °C). Ambient CO_2 plants and those in adjacent plots did not differ significantly in ψ; thus, data were pooled for statistical comparison with elevated CO_2 plants (t-test, $P < 0.05$).

RESULTS

Steady-state responses in net photosynthesis and stomatal conductance to elevated CO_2 (Fig. 1) indicate that little direct photosynthetic enhancement occurred in *A. gerardii* at any light level. However, exposure to elevated CO_2 led to reductions in stomatal conductance of 51% at full sunlight and 47% at typical shade light levels (350 μmol m^{-2} s^{-1}). Photosynthetic responses measured in the field under
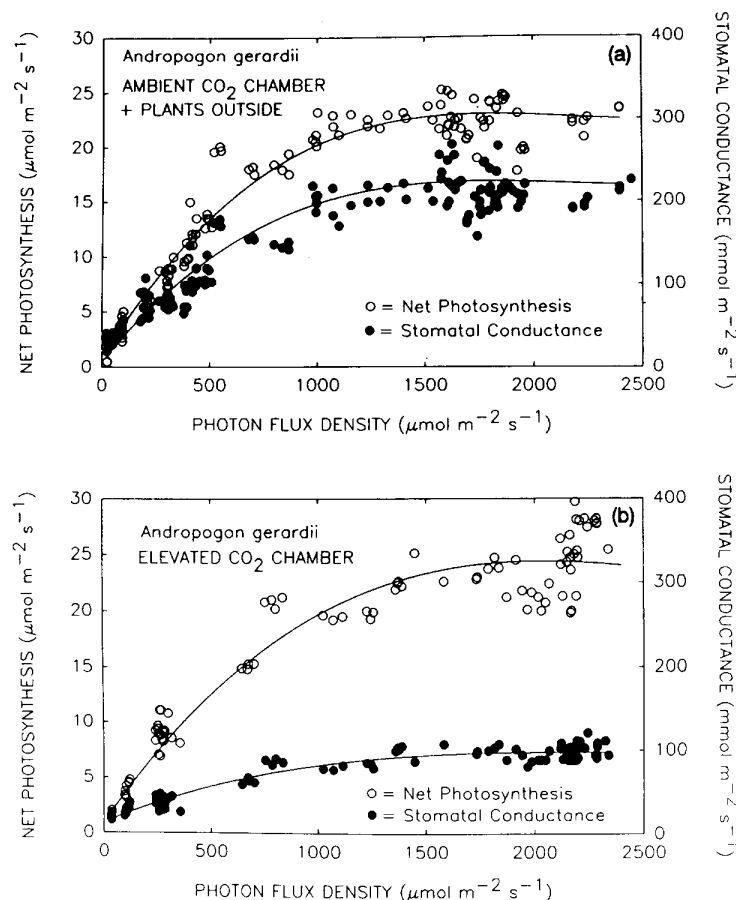
Figure 1. The relationship between net photosynthetic CO_2 uptake and photon flux density in *Andropogon gerardii* grown in open-top chambers with (a) ambient CO_2 concentrations and (b) elevated (double ambient) CO_2. Data are also shown for plants grown outside the chambers. Values are steady-state measurements made after a set of leaves had equilibrated to a new light level within a gas exchange cuvette. Each curve includes data from > 12 plants. Maximum, light-saturated photosynthetic rates were not significantly different between plants exposed to ambient versus elevated CO_2 but stomatal conductance was significantly reduced at elevated CO_2.

a controlled, alternating sun/shade light regime were similar among the three treatments (Fig. 2). In contrast, stomatal conductance in plants exposed to elevated CO_2 appeared to achieve new steady-state levels (during sun or shade) more rapidly than plants exposed to ambient CO_2.

More detailed measurements of stomatal conductance made after abrupt changes in light (Fig. 3) indicated that stomatal closure was more rapid than opening in all treatments and that time constants for leaves exposed to elevated CO_2 were reduced by 29–33% relative to ambient CO_2 plants. Absolute rates of change in stomatal conductance during the initial 2 min after a reduction in light (fit with a linear model; m = slope) were not significantly different between elevated and ambient CO_2 plants [$m_{ambient} = -23.7 \pm 2.77$ (SD) ($r^2 = 0.76$) versus $m_{elevated} = -19.7 \pm 1.67$ ($r^2 = 0.85$); intercepts did not differ significantly from 0]. However, the ca. 50 mmol m^{-2} s^{-1} reduction in stomatal conductance that occurred during this period represented 84% of the total reduction required

to attain a new steady state in elevated CO_2 plants. In contrast, 50 mmol m^{-2} s^{-1} was only 37% of the reduction in stomatal conductance required to achieve a new steady state in plants grown in ambient CO_2. Increases in stomatal conductance were faster ($P<0.05$) in ambient CO_2 plants during this initial 2-min period [$m_{ambient} = 33.6 \pm 3.91$ ($r^2 = 0.71$) versus $m_{elevated} = 19.7 \pm 1.67$ ($r^2 = 0.91$)]. Overall though, reduced differences between sun versus shade stomatal conductance in plants exposed to elevated CO_2 led to the more rapid attainment of new steady state levels. For example, the time required to achieve 90% of steady state conductance after a change in light was reduced by almost 2.0 min in plants exposed to elevated versus ambient CO_2 during both sun and shade periods.

Leaf ψ in full sunlight was significantly higher in elevated versus ambient CO_2 plants (0.31 MPa). Moreover, during shade periods, ψ initially increased at a rate of 0.13 MPa/min in elevated CO_2 plants vs 0.08 MPa min^{-1} in ambient CO_2 plants ($P<0.05$, t-test, simple linear regres-

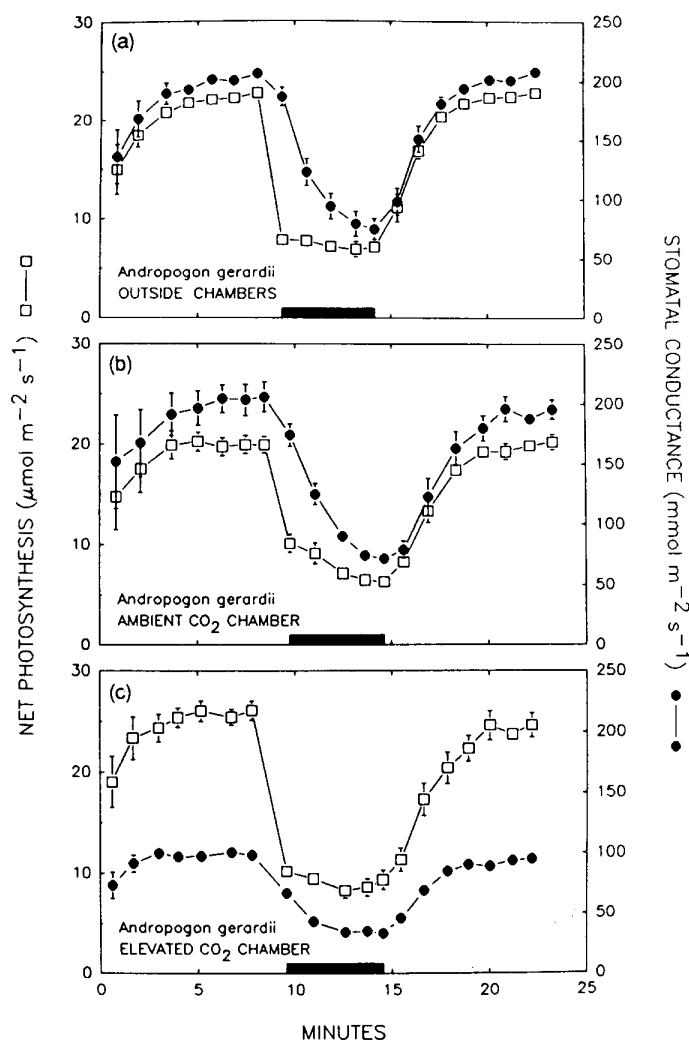**Figure 2.** Responses in net photosynthesis and stomatal conductance in *Andropogon gerardii* to a 5-min period of shade (350 μmol m^{-2} s^{-1} denoted by the dark bar along the x-axis) preceded and followed by full sunlight. Plants were measured in the field (a) in adjacent grassland outside the chambers and in open-top chambers at (b) ambient and (c) elevated CO_2. Responses shown are the mean of at least four sets of leaves subjected to three consecutive sun/shade cycles. Thus, A and g data used to plot these sun-shade-sun responses represent the means of at least 12 measurements. Data were combined for 1–1·5-min intervals and are plotted as means along the x-axis as well. Vertical bars represent ± 1 SEM for A and g (error bars for time were smaller than the symbols on the figure).

sion for the initial 3 min). As a result, the maximum difference between ψ in elevated versus ambient CO_2 plants occurred during shade periods. After 10 min of shade, leaf ψ averaged 0·45 ± 0·06 MPa for all treatments, an increase of 0·35–0·66 MPa from full sun levels. Reductions in ψ in sun periods occurred at similar rates in both ambient and elevated CO_2 plants.

DISCUSSION

Maximum photosynthetic rates in *A. gerardii* were not affected by elevated CO_2 levels, but stomatal conductance was decreased by ca. 50% (Fig. 1). These data are consistent with previous studies (Kirkham *et al.* 1991). More

rapid stomatal responses to sunlight variability at high CO_2 have two potential consequences: (1) water loss during shade periods may be reduced more rapidly, and hence, plant water status may increase more rapidly; and (2) more rapid stomatal opening during sun periods could potentially increase carbon uptake. Only minor differences were apparent in the time course of the post-shade recovery in net photosynthesis between ambient and elevated CO_2 plants (Fig. 2), and regression analysis did not identify significant differences in the slope of photosynthesis versus time during sun periods. This suggests that non-stomatal limitations to photosynthesis may be more important during these periods (Pearcy & Seeman 1990; Pons, Pearcy & Seeman 1992). Slower stomatal responses after
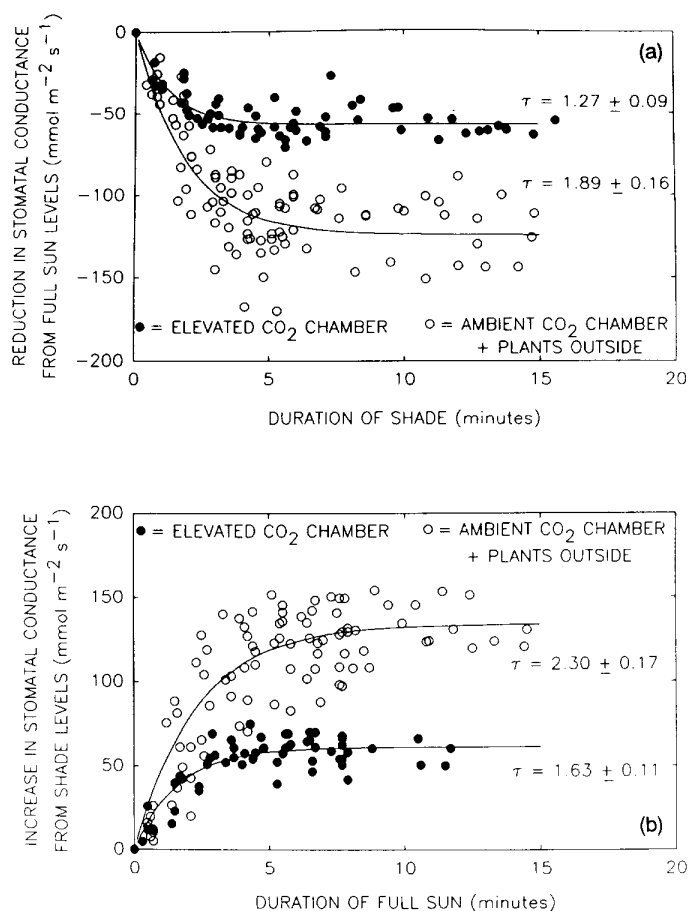
Figure 3. Effects of atmospheric CO_2 concentration on the time course of (a) the decrease or (b) the increase in stomatal conductance in *Andropogon gerardii* after abrupt changes in light from sun to shade or *vice versa*. Plants were measured in open-top chambers at ambient and elevated CO_2, as well as outside of the chambers at ambient CO_2. Data shown are pooled from at least 15 plants measured under a variety of environmental conditions. Time constants (τ) are from a first-order exponential model fit to the data ($\pm$ 1 SEM). For reductions in stomatal conductance (g) during shade, the best model fit was g = -57.5 [1-exp($-t/1.27$)] at elevated CO_2 and g = -124.8 [1-exp($-t/1.89$)] at ambient CO_2. For increases in stomatal conductance during sun: g = 61.5 [1-exp($-t/1.63$)] at elevated CO_2 and g = 134.1 [1-exp($-t/2.30$)] at ambient CO_2, where t = the time since an abrupt change in light level.

abrupt changes to sun would conserve water, but a 'cost' in CO_2 uptake may result because stomatal limitations to photosynthesis would increase concurrently (Knapp & Smith 1990).

Given that > 50 'shade' events of >2 min are common on days with intermittent cloud cover, and that the frequency of shade events increases within plant canopies due to inter-plant shading (Knapp & Smith 1987; Chazdon 1988; Knapp 1993), the accumulative effect of these differences in stomatal response on gas exchange can be substantial. To quantify the carbon and water relations consequences of differences in stomatal responses between ambient and elevated CO_2 plants, we used a two-state, statistically based simulation model (Knapp 1992, 1993). With this model we estimated carbon gain, transpiration, and water use efficiency (WUE) in plants exposed to identical environmental conditions (alternating sun/shade peri-

ods of equal length, air temperature 30 °C; relative humidity 40%) except for CO_2 concentration. We also used this model, to compare carbon and water relations in plants exposed to elevated CO_2 with hypothetical plants at high CO_2, but with stomatal response characteristics (τ values) of plants growing at ambient CO_2 levels. The model was parametrized with the relationships in Fig. 3 describing the time course of stomatal response after a change in light, and it calculated photosynthesis based on regression equations relating stomatal conductance to photosynthesis for ambient and elevated CO_2 plants (for full sunlight PFD, A = 2.77 + 0.092 g for ambient CO_2 plants; A = 2.36 + 0.218 g for elevated CO_2 plants; r^2 > 0.78). The model was run by inputting a typical time series of sun and shade periods (8-min periods of sunlight alternating with 5-min periods of shade) for both ambient and elevated CO_2 plants. Model output indicated that carbon gain during alternating
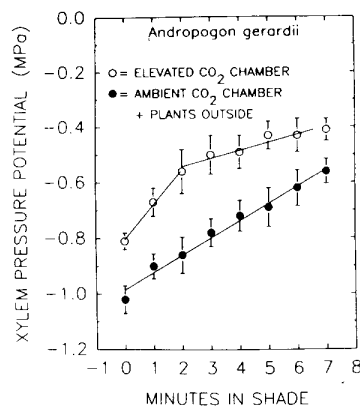
Figure 4. Effect of atmospheric CO_2 concentration on the time course of recovery in leaf xylem pressure potential (ψ) in *Andropogon gerardii* during periods of shade. Measurements were made in the field on plants exposed to ambient or elevated CO_2 and data shown are means ($\pm$ 1 SEM).

periods of sun and shade was not increased substantially at elevated levels of CO_2, consistent with field measurements (Fig. 2). But transpiration was reduced by 57% at elevated CO_2 and WUE increased by 138% during periods of sunlight variability. When time constants for stomatal responses of ambient plants were substituted for elevated CO_2 plants, instantaneous transpiration rates were increased by as much as 6·5% during shade. These results indicate that although more rapid rates of change in stomatal conductance to light contribute to reductions in transpiration, the greatest proportion of the increase in WUE at elevated CO_2 can be attributed to overall reductions in conductance at all light levels.

Grassland environments are characterized by seasonal periods of water stress, and the tallgrass prairies of North America are no exception (Weaver 1954; Knapp 1984; Walter 1985). Previous research has focused on gas exchange responses to elevated CO_2 under controlled, relatively constant environmental conditions. These studies have documented higher leaf xylem pressure potentials (ψ) in *A. gerardii* exposed to elevated CO_2, and this certainly contributes to enhanced productivity (Cure & Acock 1986; Kirkham *et al.* 1991; Owensby *et al.* 1993). Additional evidence that alterations in the kinetics of stomatal responses to variable light may enhance plant water status is provided by field measurements of leaf ψ. We measured not only higher leaf ψ in plants exposed to elevated CO_2, but also a consistently higher rate of increase in ψ in elevated versus ambient CO_2 plants immediately after a sun-to-shade transition occurred (Fig. 4). Thus, the greatest differences in ψ between elevated and ambient CO_2 plants were measured during periods of sunlight variability, not during constant sunlight. The relationship between leaf ψ and photosynthesis is nonlinear in *A. gerardii* (as in most plants) and absolute differences in ψ of 0·20–0·37 MPa can increase photosynthetic rates by as much as 45% (Knapp

et al. 1993). It is particularly important to note that maximum differences in water status between elevated and ambient CO_2 plants occurred after 2–3 min of shade; these durations of shade are commonly produced by both intermittent cloud cover and within-canopy shading (Chazdon 1988; Smith *et al.* 1989).

The importance of considering the effects of dynamic light regimes on productivity and fitness in plant systems is now well-documented (Knapp & Smith 1990; Pearcy 1990). We have presented evidence that response kinetics in leaf-level gas exchange will be altered as atmospheric CO_2 increases. In essence, stomata on plant leaves will require less time to achieve new steady state levels as light varies in a high CO_2 world. This will enhance plant water status, and consequently, carbon gain even in plants that show little direct effect of CO_2 on leaf-level photosynthesis (such as C_4 plants). These leaf and whole plant responses to fluctuations in sunlight at elevated CO_2 should be incorporated into mechanistic models of photosynthesis, and linked via trace gas fluxes into the appropriate biophysical elements of mesoscale climate models (Avissar & Pielke 1991; Dickinson *et al.* 1991). Although our data are specific to a C_4 grass in an ecosystem prone to water stress, alterations in gas exchange responses to variable sunlight at elevated CO_2 will probably enhance direct effects of elevated CO_2 on plant water relations in all ecosystems.

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