



Photosynthetic responses of *Larrea tridentata* to a step-increase in atmospheric CO₂ at the Nevada Desert FACE Facility

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Of all terrestrial ecosystems, the productivity of deserts has been suggested to be the most responsive to increasing atmospheric CO₂. The extent to which this prediction holds will depend in part on plant responses to elevated CO₂ under the highly variable conditions characteristic of arid regions. The photosynthetic responses of *Larrea tridentata*, an evergreen shrub, to a step-increase in atmospheric CO₂ (to 550 μmol mol⁻¹) were examined in the field using Free-Air CO₂ Enrichment (FACE) under seasonally varying moisture conditions. Elevated CO₂ substantially increased net assimilation rate (A_{net}) in *Larrea* during both moist and dry periods of the potential growing season, while stomatal conductance (g_s) did not differ between elevated and ambient CO₂ treatments. Seasonal and diurnal gas exchange dynamics in elevated CO₂ mirrored patterns in ambient CO₂, indicating that elevated CO₂ did not extend photosynthetic activity longer into the dry season or during more stressful times of the day. Net assimilation *vs.* internal CO₂ (A/C_i) responses showed no evidence of photosynthetic down-regulation during the dry season. In contrast, after significant autumn rains, A_{max} (the CO₂ saturated rate of photosynthesis) and CE (carboxylation efficiency) were lower in *Larrea* under elevated CO₂. *In situ* chlorophyll fluorescence estimation of *Larrea* Photosystem II

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efficiency (F_v/F_m) responded more to water limitation than to elevated CO_2 . These findings suggest that predictions regarding desert plant responses to elevated CO_2 should account for seasonal patterns of photosynthetic regulatory responses, which may vary across species and plant functional types.

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Introduction

Water-limited arid and semi-arid systems are expected to show potentially dramatic responses to increased levels of atmospheric CO_2 and associated climate change (Smith *et al.*, 1997). Simulations have shown that elevated CO_2 can stimulate productivity to a greater extent under water-limited conditions than in more mesic ecosystems (Melillo *et al.*, 1993; Parton *et al.*, 1994). This is primarily a result of elevated CO_2 minimizing stomatal limitations on photosynthesis, although non-stomatal limitations could be reduced as well (Hunt *et al.*, 1996; Knapp *et al.*, 1996). Thus, for aridland species active during seasonal dry periods, elevated CO_2 may result in greater relative increases in photosynthesis than during wet periods, and possibly contribute a greater proportion to total annual primary production. This is the case in tallgrass prairie, where elevated CO_2 increases the proportional productivity of warm-season grasses during dry years, a direct result of improved water status and enhanced photosynthetic rates (Knapp *et al.*, 1993; Owensby *et al.*, 1993; Hamerlynck *et al.*, 1997). A similar response also appears to occur in annual grasslands of California (Jackson *et al.*, 1994; Field *et al.*, 1997).

Elevated CO_2 can directly stimulate photosynthesis by overcoming diffusional limitations and decreasing the oxygenase activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), the primary carbon-fixation enzyme (Sage & Sharkey, 1987; Long, 1991). However, a wide variety of plants show reduced CO_2 -saturated rates of photosynthesis (A_{max}) and carboxylation efficiency (CE) following exposure to elevated CO_2 (Sage *et al.*, 1989; Sage, 1994; Jacob *et al.*, 1995). This down-regulation of photosynthesis would be ecologically important if it balances resource acquisition and utilization by plants (Stitt, 1991). Down-regulation is thought to be a function of the relative strengths of source/sink relationships (Thomas & Strain 1991; Stirling *et al.*, 1997) that eventually affect photosynthetic gene and protein expression (Griffin & Seemann, 1996). Down-regulation is known to be sensitive to water and nutrient availability (Huxman *et al.*, 1998a; Sims *et al.*, 1998), temperature (Lewis *et al.*, 1996; Stirling *et al.*, 1997) and species-specific growth patterns (Stirling *et al.*, 1997). Also, under conditions of high light, high temperature, and low stomatal conductance, elevated CO_2 may ameliorate photoinhibition (Long, 1991; Huxman *et al.*, 1998b). However, some studies show that down-regulated plants have reduced the capacity for dissipation of excess light energy (Roden & Ball, 1996). Therefore, for highly variable and stress-prone systems like deserts, the potential for down-regulation needs to be assessed under contrasting environmental conditions to develop predictions regarding future productivity at elevated CO_2 .

Larrea tridentata Cav. (Zygophyllaceae), commonly known as creosotebush, is the dominant perennial shrub of North American warm desert ecosystems. As an evergreen, it is physiologically active during all times of the year (Bamberg *et al.*, 1975; Smith *et al.*, 1997), and both water and nitrogen availability strongly limit its productivity under field conditions (Lajtha & Whitford, 1989). *Larrea* is thus a model organism to study how desert plants may respond to elevated CO_2 under the contrasting wet/dry and nutrient availability conditions that typify desert systems. Here we present a study using Free Air

CO₂ Enrichment (FACE; Hendrey & Kimball, 1994) that assessed the field responses of mature *Larrea* shrubs to elevated CO₂ under naturally varying soil moisture and temperature regimes.

Based on previous observations, we tested several hypotheses. First, elevated CO₂ should stimulate net photosynthesis in *Larrea* during times of the year when environmental conditions are conducive to positive net CO₂ assimilation (hypothesis 1). Second, due to the purported water-saving benefits of plant growth at elevated CO₂, the evergreen *Larrea* should show enhanced gas exchange activity extended into the summer dry season (hypothesis 2). Third, photosynthetic down-regulation will be less pronounced in this desert shrub during dry conditions (hypothesis 3). In dryland environments, drought has been shown to diminish photosynthetic down-regulation and sometimes promotes up-regulation in elevated CO₂-grown plants (Oechel *et al.*, 1995; Huxman *et al.*, 1998a). And fourth, reductions in the photochemical efficiency of Photosystem II function (as a measure of photoinhibition) will be less pronounced during drought in *Larrea* under elevated CO₂ compared to ambient atmospheric levels (hypothesis 4) (Roden & Ball 1996; Huxman *et al.*, 1998b).

Materials and methods

FACE site description

Fumigation of an intact Mojave Desert ecosystem commenced on 28 April 1997 on the Nevada Test Site, a National Environmental Research Park, using Free Air CO₂ Enrichment (FACE) technology (Hendrey & Kimball, 1994). Nine 25-m diameter circular plots were established, three at elevated CO₂ (set point of 550 $\mu\text{mol mol}^{-1}$; 'elevated ring'), three ambient rings, and three non-ring controls (Jordan *et al.*, 1999). Ambient CO₂ averaged 360 $\mu\text{mol mol}^{-1}$, both day and night, at this remote desert site. All plots were similar in overall species composition, density, and cover. Fumigation occurs continuously, except when wind speeds exceed 8 m s⁻¹ over a 5 min period (*ca.* < 5% of the time). A computer-controlled algorithm opens and closes valves on 32 2.0-m high PVC risers connected to a circular above-ground plenum that surrounds the plot. CO₂ is injected into an ambient air stream created by a large circulating fan attached to the plenum. Under calm conditions (< 0.1 m s⁻¹) every other valve is opened, while at greater wind speeds, upwind valves are opened so that CO₂ moves with the airstream across the plot, and downwind valves are closed. This protocol maintains CO₂ concentrations within $\pm 5\%$ of the targeted set point over a 5 min averaging period. Plants were accessed from a suspended, moveable platform attached to a pivoting 22-m long rotating aluminum catwalk supported 2.2 m above ground level. In order to avoid microclimate effects created by air exiting the risers, plants located less than 1 m from the risers were not sampled. A comprehensive description of this facility, its operations, and site characteristics can be found in Jordan *et al.* (1999), and at the NDFE web site: http://www.unlv.edu/Colleges/Sciences/Biology/Climate_Change_Research/

Seasonal and diurnal gas exchange and water potentials

Following a 24 mm rain storm on 12 June 1997 (prior to 12 June, the Mojave Desert experienced a pronounced climatic drought), mid-morning (08 00–11 00 h) net CO₂ assimilation and stomatal conductance to water vapour were measured weekly through the summer for *Larrea tridentata* using a Li-COR 6400 (Li-COR Inc., Lincoln, NE, U.S.A.) open-flow portable photosynthesis system. Ambient humidity and temperature conditions were maintained in the cuvette by entering values measured after shading the

open cuvette for 5 min into the control software. Cuvette CO₂ was set to that of the treatment plot being sampled (550 μmol mol⁻¹ for elevated blowers, 360 μmol mol⁻¹ for ambient blowers and non-blower controls) by mixing ambient air with CO₂ from an internal CO₂ injection system. Two plants were sampled and values pooled for a ring mean ($n = 3$ rings) used in statistical analysis.

Diurnal gas exchange in *Larrea* was measured on 19 June and 16 July, one week and one month after a 24-mm rainfall event, respectively. Measurements were made on two *Larrea* plants per plot, starting shortly after sunrise and passing once through each treatment combination (9 rings) four times during the day, from 05 30 h to 20 00 h.

Midday plant water potential (ψ) was determined using a Scholander-type pressure chamber (Soil Moisture Stress Inc., Santa Barbara, CA, U.S.A.). Two shoots from different *Larrea* in each ring were harvested and immediately measured, with the subsequent ψ values pooled to give a plot mean.

Photosynthetic responses

Response curves of net photosynthesis to internal CO₂ concentration (A/C_i) were made on *Larrea* in the field between April and October 1997. Measurements were made in late spring during a protracted dry season, with less than 8 mm of rain received from February to May, as well as during the summer/early autumn monsoon season after separate rain events of 24, 25 and 20 mm. One plant per treatment plot ($n = 3$ per treatment) was sampled repeatedly throughout this period.

A/C_i curves were made using a Li-COR 6400 programmable, open-flow gas exchange system. Cuvette temperature was held at 25°C at relative humidities of 15 to 25%. This resulted in leaf temperatures of 25 to 29°C in spring and fall, and 29 to 34°C in summer, with corresponding leaf-to-air vapour pressure deficits of 2.8–3.2 kPa and 3.1–3.8 kPa, respectively. All measurements were made under saturating photosynthetic photon flux densities (PPFD) using ambient light (800 to 1800 μmol m⁻² s⁻¹ PPFD) or an external high intensity LED red light source (1500 μmol m⁻² s⁻¹ PPFD). Side-by-side comparisons of these light sources showed no differences in A/C_i responses of *Larrea* in a glasshouse (T. Huxman, unpublished data). Measurements were made from 08 00 to 12 00 h to avoid diurnal changes in photosynthetic activity and stomatal closure. Cuvette CO₂ concentrations (C_a) were set by mixing CO₂ from an internal source and ambient air. Shoots were exposed to 5 min of 200 μmol mol⁻¹ CO₂ to stimulate stomatal opening. C_a was reduced to 75 μmol mol⁻¹, then raised incrementally to 2000 μmol mol⁻¹. C_i at each C_a was calculated using the equations of von Caemmerer & Farquhar (1981). Nonlinear least-squares regression (Sigmaplot version 4.0, Jandel Scientific, San Rafael, CA, U.S.A.) using an exponential model from Jacob *et al.* (1995) was applied to estimate CO₂-saturated photosynthetic rate (A_{\max}) and mesophyll carboxylation efficiency (CE).

Rubisco assays

Leaf samples for Rubisco analysis were taken concurrent with $A-C_i$ measurements for *Larrea* from shoots adjacent to gas exchange measurements, and immediately preserved in liquid N₂. Tissue was harvested on 20 May and 29 September 1997, *ca.* 3.5 months and 1 month following rain. Stems and dead leaves were removed prior to grinding in a mortar. About 0.15 g of leaves were ground in 1.5 ml buffer containing 100 mM Bicine pH 7.8, 5 mM MgCl₂, 1 mM EDTA, 5 mM DTT, 0.1% (v/v) Triton X-100, 25 mM KCl and 20% (w/w) polyvinylpyrrolidone. Extracts were filtered through Miracloth and centrifuged for 1 min at 10,000 g. Rubisco catalytic sites were determined by immunoprecipitation, as described by Evans & Seemann (1984).

Chlorophyll a fluorescence

In situ chlorophyll fluorescence (F_v/F_m) was used to assess the efficiency of excitation energy transfer within Photosystem II in *Larrea*. F_v/F_m was measured in May (3.5 months without rain), July and October of 1997 (each *ca.* 1 month after a major rain event). Three plants per plot were dark-adapted for 1 hour by wrapping the terminal shoot in aluminum foil. F_v/F_m was determined using a pulse-amplitude-modulated (PAM) fluorimeter (Model MFMS/2S, Hansatech Instruments Ltd., Kings Lynn, U.K.) under PC control (Minirec version 2.1, Hansatech Instruments Ltd., U.K.). F_o was established with a low light source (583 nm light at $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD), with a demodulator gain of 80 and a response time of 0.1 s. Saturating light (0.5 s pulses at a PPFD of $8500 \mu\text{mol m}^{-2} \text{s}^{-1}$) at 1 Hz frequency was supplied by a fiber optic cable carrying light from a Hansatech FLS1 light source and was used to determine maximal fluorescence (F_m). F_v/F_m was calculated as:

$$(\text{maximal } F_m \text{ achieved} - F_o \text{ averaged over 30 s after beam on})/F_m.$$

Statistical analyses

Two-way (for A/C_i summer season gas exchange, and chlorophyll fluorescence data) and three-way (for diurnal data) split-plot repeated measures ANOVA models were used to test for significance of CO₂ concentration and time (General ANOVA/ANCOVA, Statistix version 4.0, Analytical Software, St. Paul, MN, U.S.A.). A/C_i data for *Larrea* were pooled by spring, summer, and fall samples, respectively.

In all analyses, CO₂ treatment was the whole-plot factor, with data pooled from each treatment ring to give three replicate measures for the whole-plot CO₂ factor. The CO₂ treatment \times ring replicate was the whole-plot *F*-test denominator, while time (either sampling date, or season), and time \times treatment interactions were the sub-plot factors, using the three-way interaction (CO₂ treatment \times time \times replicate) as the sub-plot *F*-test denominator. Of specific interest were the treatment \times time interactions, which would indicate treatment-specific changes in plant function through time. F_v/F_m data were arcsine transformed to meet ANOVA data distribution assumptions (Zar, 1974). An α of 0.05 was considered significant, with *post hoc* General Linear Contrasts (Scheffe's *F*) made using the appropriate error terms as the *F*-test denominator.

A student's *t*-test was used to test for significant means differences between elevated and ambient CO₂ blower treatments on *Larrea* fresh weight Rubisco content. Comparisons were made for the two sampling dates (20 May and 29 October).

Results and discussion

During the summer growth season elevated CO₂ significantly stimulated net photosynthetic rate (A_{net}) in *Larrea tridentata* ($MS = 163.9$; $F = 22.7$; 2, 6 df.). An approximate doubling of A_{net} (13.2 vs. $6.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ at elevated and ambient CO₂, respectively) was observed immediately following major rainfall events in early June and September. During the summer dry season (July and August; Fig. 1), A_{net} in *Larrea* was *ca.* 80% higher at elevated CO₂ than at ambient CO₂ (7.0 vs. $3.9 \mu\text{mol m}^{-2} \text{s}^{-1}$). Since the plants in the current study had been exposed only to a short-term step increase in CO₂, as well as to an extended winter–spring drought, this 80–100% increase in A_{net} can probably be viewed as an upper range of photosynthetic stimulation in this system. Therefore, the data clearly support hypothesis 1, that elevated CO₂ stimulates net photosynthesis during times of the year when environmental conditions are conducive to positive net CO₂ assimilation. However, we anticipate this response

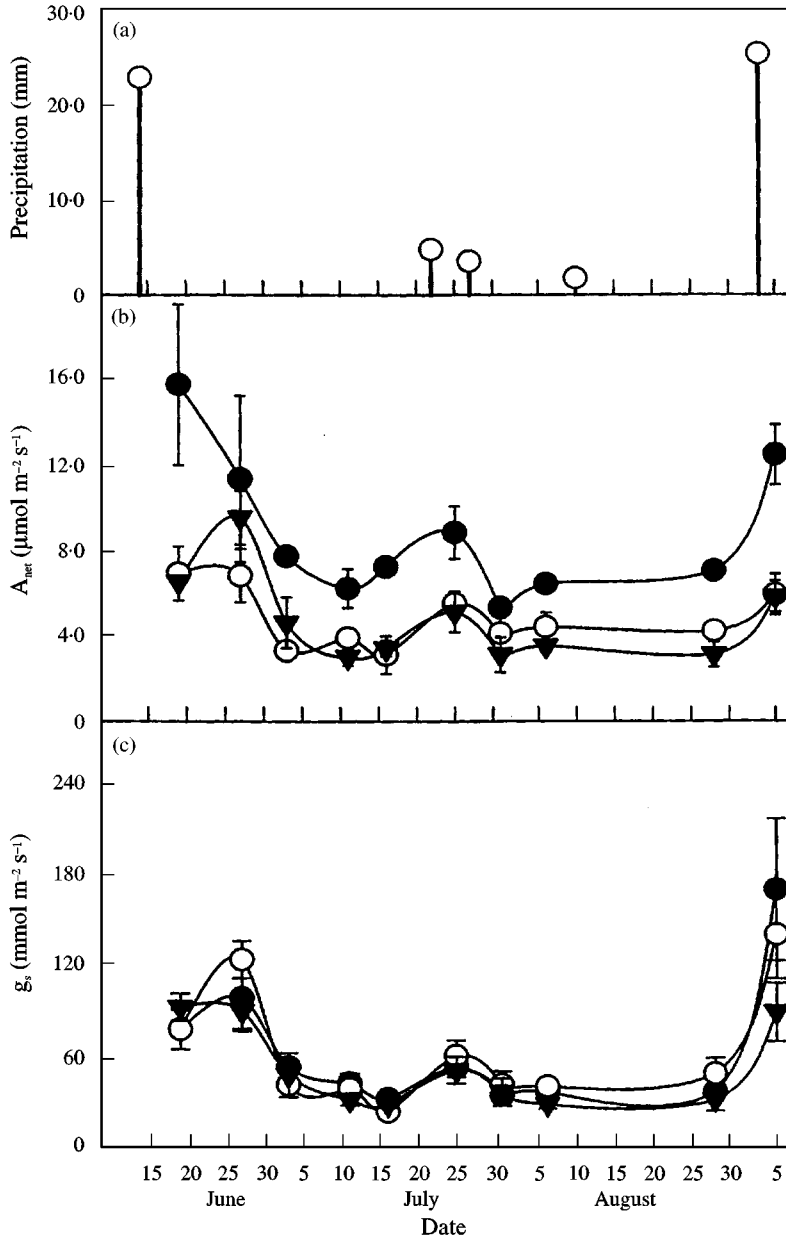


Figure 1. Seasonal patterns in precipitation (a), net photosynthesis (A_{net} ; (b)) and stomatal conductance (g_s ; (c)) of *Larrea tridentata* under elevated CO_2 ($550 \mu\text{mol mol}^{-1}$; closed symbols) and ambient CO_2 ($360 \mu\text{mol mol}^{-1}$; open symbols). Ambient CO_2 treatments include ambient FACE rings (circles) and non-ring controls (triangles). Each data point is the mean of three measurements; bars indicate \pm one SE of the mean.

to become less pronounced as plants are exposed to elevated CO_2 over longer time periods.

There was no apparent time \times treatment interaction, as A_{net} under elevated CO_2 mirrored the temporal patterns in ambient CO_2 plants in *Larrea* (Fig. 1). Elevated CO_2

did not extend productivity into the more stressful periods of the growing season (i.e. seasonal declines in A_{net} after the early June rain event were similar between ambient and elevated CO₂-grown plants), a hypothesized benefit of elevated CO₂ in arid and semi-arid systems (Melillo *et al.*, 1993; Parton *et al.*, 1994; Oechel *et al.*, 1995). Therefore, hypothesis 2 was not supported by the data. This response in a desert shrub contrasts with observed patterns from semi-arid grasslands and chaparral, where seasonal drying and higher temperatures have been found to amplify the difference between ambient and elevated-CO₂-grown plants (Knapp *et al.*, 1993, 1996; Oechel *et al.*, 1995; Hunt *et al.*, 1996; Hamerlynck *et al.*, 1997).

Elevated CO₂ did not reduce stomatal conductance (g_s) in *Larrea*, even following significant rain (Fig. 1). Such low g_s — the highest reported here being lower than any reported in other field CO₂ studies — suggests desert shrubs with low g_s may not reduce stomatal conductance under elevated CO₂ as do plants growing in more favourable habitats (Jackson *et al.*, 1994; Jacob *et al.*, 1995; Knapp *et al.*, 1996; Hamerlynck *et al.*, 1997). However, even in plants with markedly higher g_s than reported here for *Larrea*, elevated CO₂ does not always induce lower g_s (Stirling *et al.*, 1997; Pataki *et al.*, 1998). The findings reported here suggest that stomatal acclimation to elevated CO₂ under field conditions may depend on the initial degree of stomatal opening, or might follow slower time-courses than those observed in controlled environment studies (Santrucek & Sage, 1996). Stomatal conductance in *Larrea* may have been relatively unresponsive to elevated CO₂ because of the high vapour pressure deficits that typify the Mojave Desert environment in summer, and also because summer rains are not as effective in recharging soil moisture as are winter rains (Smith *et al.*, 1997). Controlled-environment studies with *Larrea* have shown that plant hydraulic conductivity is not responsive to growth in elevated CO₂ (Huxman *et al.*, 1999). Since there were no differences in leaf temperature between CO₂ treatments in the microphyllous *Larrea* (data not shown), and therefore VPD would not be different, g_s is directly related to transpiration in this species. Because hydraulic conductivity and VPD were both similar at each CO₂ treatment, resulting in no differences in transpiration (at the leaf level), then g_s should also be similar. Furthermore, since g_s was not different between CO₂ treatments, plant water-use efficiency (WUE) mirrored increases in A_{net} (i.e. WUE was 80–100% greater at elevated CO₂).

A_{net} in *Larrea* was significantly higher on a diurnal basis under elevated CO₂ throughout the day (MS = 116.5; F = 24.3; 2, 6 df.), either shortly after a large rainfall event or over a month without precipitation (Fig. 2), without any significant date \times treatment interaction. Stomatal conductance did not differ between CO₂ treatments, but changed in response to time of day (MS = 16.244; F = 132.3; 1, 42 df.) and date (MS = 18.209; F = 148.3; 1, 42 df.). There were significant interactions in g_s between CO₂ treatment and date (MS = 450.8; F = 3.7; 2, 42 df.), and time of day with date (MS = 2.343; F = 19.1; 3, 42 df.). Diurnal gas exchange data followed trends seen in seasonal measurements (Fig. 1). Elevated CO₂ did not extend photosynthetic activity longer into the day, even when soil moisture conditions might have been more conducive to prolonging activity. This result was probably due to g_s , and hence transpiration, being the same between treatments. When g_s is reduced under elevated CO₂, there is usually an increase in soil water reserves and improved plant water status brought about by lower transpiration (Field *et al.*, 1995; Knapp *et al.*, 1996). However, there was no increase in soil moisture content at either 0–15 cm or 15–30 cm depths in the elevated CO₂ rings in this first year of CO₂ enrichment at the Nevada Desert FACE site (data not shown).

The results from this study support hypothesis 3, that photosynthetic down-regulation in a desert shrub grown under elevated CO₂ depends on plant water status. For the evergreen *Larrea*, CO₂-saturated photosynthetic rate (A_{max}) and carboxylation efficiency (CE) were significantly lower under elevated CO₂ at higher plant water potentials (i.e. moist conditions). At more negative ψ values during drought conditions in the

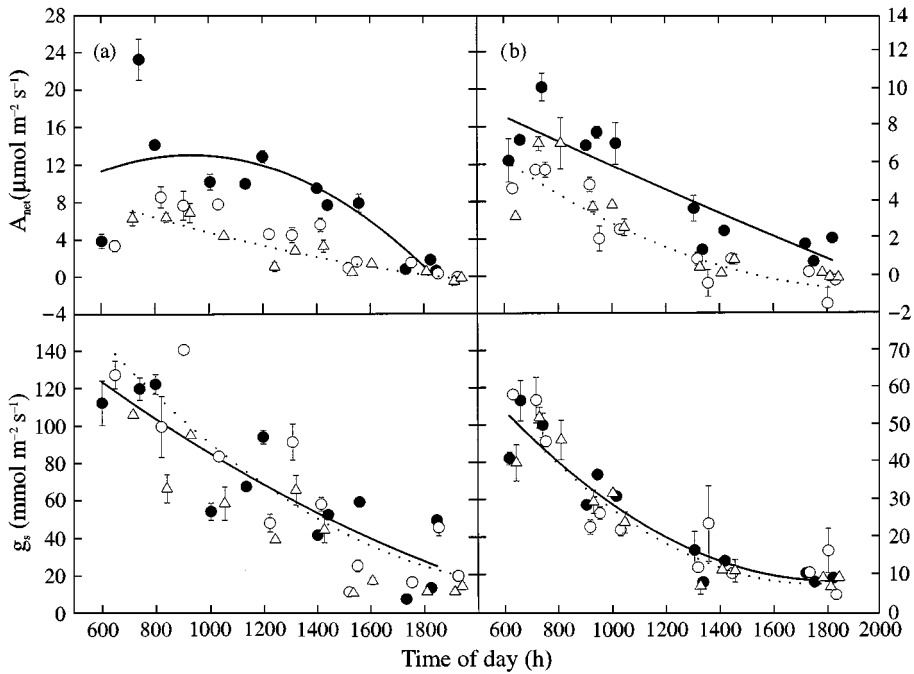


Figure 2. Diurnal course of net photosynthesis (A_{net} ; top) and stomatal conductance (g_s ; bottom) of *Larrea tridentata* under elevated CO_2 ($550 \mu\text{mol mol}^{-1}$; solid symbols, solid line) and ambient CO_2 (open symbols, dotted line) shortly after (June; (a)) and one month after (July; (b)) a major rain. Each data point is the mean of three measurements; bars indicate \pm one SE of the mean. Note different ordinate scales. ● Elevated ring; ○ Ambient ring; △ Non-ring control.

spring, A_{max} was lower at elevated CO_2 and CE was similar at the two CO_2 concentrations (Table 1). A depression at elevated CO_2 in the photosynthetic capacity of *Larrea* under well-watered conditions (13% lower than at ambient CO_2) was concurrent with 19% lower leaf Rubisco content (Table 1; Student's $t = 9.1$, $p < 0.001$). These findings suggest that down-regulation in *Larrea* may be transient, occurring only under conditions of high resource availability (Huxman *et al.*, 1998a), much as seasonal temperature patterns mediate photosynthetic responses to elevated CO_2 in other evergreen species (Lewis *et al.*, 1996). Drought has been found to reduce down-regulation, and even promote up-regulation, in evergreen chaparral species (Oechel *et al.*, 1995). Oechel *et al.* (1995) hypothesized that stomatal limitations during drought might reduce carbohydrate accumulation, thereby weakening feedbacks that would induce down-regulation under well-watered conditions. Also, fine root growth, a major factor linked to down-regulation in pot studies (Thomas & Strain, 1991), apparently does not change in *Larrea* under elevated CO_2 (BassiriRad *et al.*, 1997), which would potentially contribute to photosynthetic down-regulation if root growth following summer rains was greater at elevated CO_2 . A primary project ongoing at the Nevada Desert FACE Facility is the seasonal quantification of fine root growth; these observations will allow an assessment to be made of how root growth may feed back to above-ground photosynthetic and growth processes.

Support of hypothesis 4 was more equivocal. F_v/F_m values at elevated CO_2 were *ca.* 7% higher ($p < 0.05$) under moist conditions and 4% higher (N.S.) under drought (Table 1). Therefore, hypothesis 4 was supported statistically under moist conditions, but it is doubtful that the magnitude difference (7 *vs.* 4%) is ecologically

Table 1. Effects of elevated CO₂ on CO₂-saturated photosynthetic rate (A_{\max} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), carboxylation efficiency (CE; $\text{mmol m}^{-2} \text{s}^{-1}$), Rubisco content ($\mu\text{g mg}^{-1} \text{FW}$), and F_v/F_m ratio in leaves of *Larrea tridentata* growing at the Nevada Desert FACE Facility at low and high moisture stress. Plants at low moisture stress had midday water potentials of -2 to -4 MPa; plants at high moisture stress had midday water potentials of -6 to -7 MPa. Percent reduction refers to a change imposed in the parameter by the onset of stress. Asterisks after each 'elevated CO₂' data point indicate a significant difference from the ambient CO₂ data point directly above it; asterisks after percent reductions indicate a significant reduction in that parameter at high stress at that CO₂ treatment ($p = 0.05$ in each case)

Parameter	CO ₂ treatment	Low stress	High stress	% Reduction
A_{\max}	Ambient	32.8	20.4	37.8*
	Elevated	28.6*	24.6	14.0*
CE	Ambient	0.111	0.100	9.9*
	Elevated	0.091*	0.090	1.1
Rubisco content	Ambient	112.5	62.1	44.8*
	Elevated	91.2*	57.1	37.4*
F_v/F_m ratio	Ambient	0.611	0.530	13.3*
	Elevated	0.656	0.550	16.2*

meaningful. Indeed, Hymus *et al.* (1999) found little stimulation of F_v/F_m under elevated CO₂ in loblolly pine during periods of low active growth. Probably of greatest importance is the fact that F_v/F_m values for *Larrea* during both drought and well-watered conditions were above values reported to accompany inhibition of photosynthesis at high temperatures (Giardi *et al.*, 1996; Loik & Harte, 1996; Roden & Ball, 1996; Huxman *et al.*, 1998b). F_v/F_m under droughted conditions were reduced 13–16% compared to well-watered conditions (Table 1; MS = 0.07; $F = 58.2$; 1, 6 df.), and are comparable to levels correlated with high photosynthetic capacity achieved under more controlled conditions (Bilger *et al.*, 1995; Loik & Harte, 1996). This suggests that *Larrea* is able to balance photochemical utilization of light with carbon acquisition processes under extreme stress conditions, yet it is able to rapidly respond to favourable conditions, an attribute that has long been associated with the functional ecology of *Larrea* (Oechel *et al.*, 1972; Smith *et al.*, 1997). Perhaps because of the extreme physiological 'plasticity' of *Larrea* in response to stress, its stress tolerance system is not particularly responsive to elevated CO₂ *per se*.

Overall, the findings of this study show that elevated CO₂ could markedly increase productivity of Mojave Desert shrubs during periods of normally low photosynthetic activity in dry seasons (Fig. 1), and that desert shrubs have the capacity for regulatory responses to elevated CO₂. The coupling of regulatory responses with water status may be important in desert systems. South-western desert community structure and individual species performance are strongly influenced by spatially distinct patterns of soil horizon development that determine seasonal soil hydrology (McAuliffe, 1994; Smith *et al.*, 1995), which in turn may result in complex patterns of photosynthetic and productivity responses to elevated CO₂ across desert landscapes. Furthermore, if stomatal conductance is not responsive to elevated CO₂ during extended dry periods, then proposed enhancements in water balance due to reductions in plant transpiration at elevated CO₂ may not be realized in desert ecosystems that are dominated by extensive or unpredictable dry seasons. Knowledge of canopy and root dynamics, as well as continued monitoring of photosynthetic and stomatal responses over extended periods, will be needed across the full spectrum of plant life forms before conclusive statements

can be made about the actual impacts of elevated CO₂ on arid-land ecosystems. These studies are ongoing at the Nevada Desert FACE Facility.

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References

- Bamberg, S.A., Kleinkopf, G.E., Wallace, A. & Vollmer, A. (1975). Comparative photosynthetic production of Mojave Desert shrubs. *Ecology*, **56**: 732–736.
- BassiriRad, H., Reynolds, J.F., Virginia, R.A. & Brunelle, M.H. (1997). Growth and root NO₃⁻ and PO₄³⁻ uptake capacity of three desert species in response to atmospheric CO₂ enrichment. *Australian Journal of Plant Physiology*, **24**: 353–358.
- Bilger, W., Schreiber, B. & Bock, M. (1995). Determination of the quantum efficiency of photosystem II and of non-photochemical quenching of chlorophyll fluorescence in the field. *Oecologia*, **102**: 425–432.
- Evans, J.R. & Seemann, J.R. (1984). Differences between wheat genotypes in specific activity of RuBP carboxylase and the relationship to photosynthesis. *Plant Physiology*, **74**: 759–765.
- Field, C.B., Jackson, R.B. & Mooney, H.A. (1995). Stomatal responses to increased CO₂: Implications from the plant to the global scale. *Plant Cell and Environment*, **18**: 1214–1225.
- Field, C.B., Lund, C.R., Chiariello, N.R. & Mortimer, B.E. (1997). CO₂ effects on the water budget of grassland microcosm communities. *Global Change Biology*, **3**: 197–206.
- Giardi, M.T., Cona, A., Geiken, B., Kucera, T., Masojidek, J. & Mattoo, A.K. (1996). Long-term drought stress induced structural and functional reorganization of photosystem II. *Planta*, **199**: 118–125.
- Griffin, K.L. & Seemann, J.S. (1996). Plants, CO₂ and photosynthesis in the 21st century. *Chemistry and Biology*, **3**: 245–254.
- Hamerlynck, E.P., McAllister, C.A., Knapp, A.K., Ham, J.M. & Owensby, C.E. (1997). Photosynthetic gas exchange and water relations responses of three tallgrass prairie species to elevated CO₂ and moderate drought. *International Journal of Plant Sciences*, **158**: 608–616.
- Hendrey, G.R. & Kimball, B.A. (1994). The FACE program. *Agricultural and Forest Meteorology*, **70**: 3–14.
- Hunt, H.W., Elliot, D.T., Detling, J.K., Morgan, J.A. & Chen, D.-X. (1996). Responses of a C₃ and a C₄ perennial grass to elevated CO₂ and temperature under different water regimes. *Global Change Biology*, **2**: 35–47.
- Huxman, K.A., Smith, S.D. & Neuman, D.S. (1999). Root hydraulic conductivity of *Larrea tridentata* and *Helianthus annuus* under elevated CO₂. *Plant, Cell and Environment*, **22**: 325–330.
- Huxman, T.E., Hamerlynck, E.P., Moore, B.D., Smith, S.D., Jordan, D.N., Zitzer, S.F., Nowak, R.S., Coleman, J.S. & Seemann, J.R. (1998a). Photosynthetic down-regulation in *Larrea tridentata* exposed to elevated atmospheric CO₂: Interaction with drought under glasshouse and field (FACE) exposure. *Plant Cell and Environment*, **21**: 1153–1161.
- Huxman, T.E., Hamerlynck, E.P., Loik, M.E. & Smith, S.D. (1998b). Gas exchange and chlorophyll fluorescence responses of three southwestern *Yucca* species to elevated CO₂ and high temperature. *Plant Cell and Environment*, **21**: 1275–1284.
- Hymus, G.J., Ellsworth D.S., Baker, N.R. & Long, S.P. (1999). Does Free Air Carbon Dioxide Enrichment affect photochemical energy use by evergreen trees in different seasons? A chlorophyll fluorescence study of mature loblolly pine. *Plant Physiology*, **120**: 1183–1191.
- Jackson, R.B., Sala, O.E., Field, C.B. & Mooney, H.A. (1994). CO₂ alters water use, carbon gain, and yield in a natural grassland. *Oecologia*, **98**: 257–262.
- Jacob, J., Greitner, C. & Drake, B.G. (1995). Acclimation of photosynthesis in relation to Rubisco and non-structural carbohydrate contents and in situ carboxylase activity in *Scirpus olneyi* grown at elevated CO₂ in the field. *Plant Cell and Environment*, **18**: 875–884.

- Jordan, D.N., Zitzer, S.F., Hendrey, G.R., Lewin, K.F., Nagy, J., Nowak, R.S., Smith, S.D., Coleman, J.S. & Seemann, J.R. (1999). Biotic, abiotic and performance aspects of the Nevada Desert Free-Air CO₂ Enrichment (FACE) Facility. *Global Change Biology*, **5**: 659–668.
- Knapp, A.K., Hamerlynck, E.P. & Owensby, C.E. (1993). Photosynthetic and water relations responses to elevated CO₂ in the C₄ grass *Andropogon gerardii*. *International Journal of Plant Sciences*, **154**: 459–466.
- Knapp, A.K., Hamerlynck, E.P., Ham, J.M. & Owensby, C.E. (1996). Responses in stomatal conductance to elevated CO₂ in 12 grassland species that differ in growth form. *Vegetatio*, **125**: 31–41.
- Lajtha, K. & Whitford, W.G. (1989). The effect of water and nitrogen amendments on photosynthesis, leaf demography, and resource-use efficiency in *Larrea tridentata*, a desert evergreen shrub. *Oecologia*, **80**: 341–348.
- Lewis, J.D., Tissue, D.T. & Strain, B.R. (1996). Seasonal response of photosynthesis to elevated CO₂ in loblolly pine (*Pinus taeda* L.) over two growing seasons. *Global Change Biology*, **2**: 103–114.
- Loik, M. & Harte, J. (1996). High-temperature tolerance of *Artemisia tridentata* and *Potentilla gracilis* under a climate change manipulation. *Oecologia*, **108**: 224–231.
- Long, S.P. (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: has its importance been underestimated? *Plant Cell and Environment*, **14**: 729–739.
- McAuliffe, J.R. (1994). Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. *Ecological Monographs*, **64**: 111–148.
- Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B. III, Vorosmarty, C.J. & Schloss, A.L. (1993). Global climate change and terrestrial net primary production. *Nature*, **363**: 234–240.
- Oechel, W.C., Strain, B.R. & Odening, W.R. (1972). Tissue water potential, photosynthesis, ¹⁴C-labeled photosynthate utilization, and growth in the desert shrub *Larrea divaricata* Cav. *Ecological Monographs*, **42**: 127–141.
- Oechel, W.C., Hastings, S.J., Vourlitis, G.L., Jenkins, M.A. & Hinkson, C.L. (1995). Direct effects of elevated CO₂ in chaparral and Mediterranean-type ecosystems. In: Moreno, J. & Oechel, W. (Eds), *Global Change and Mediterranean-Type Ecosystems, Ecological Studies* vol. 117, pp. 58–75. Berlin, Germany: Springer-Verlag, 527pp.
- Owensby, C.E., Coyne, P.I., Ham, J.M., Auen, L.M. & Knapp, A.K. (1993). Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated levels of CO₂. *Ecological Applications*, **3**: 644–653.
- Parton, W., Ojima, D. & Schimel, D. (1994). Environmental changes in grasslands: Assessment using models. *Climate Change*, **28**: 111–141.
- Pataki, D.E., Oren, R. & Tissue, D.T. (1998). Elevated carbon dioxide does not affect average canopy stomatal conductance of *Pinus taeda* L. *Oecologia*, **117**: 47–52.
- Roden, J.S. & Ball, M.C. (1996). The effect of elevated [CO₂] on growth and photosynthesis of two *Eucalyptus* species exposed to high temperatures and water deficits. *Plant Physiology*, **111**: 909–919.
- Sage, R.F. (1994). Acclimation of photosynthesis to increasing atmospheric CO₂: The gas exchange perspective. *Photosynthesis Research*, **39**: 351–368.
- Sage, R.F. & Sharkey, T.D. (1987). The effect of temperature on the occurrence of O₂- and CO₂-insensitive photosynthesis in field grown plants. *Plant Physiology*, **84**: 658–664.
- Sage, R.F., Sharkey, T.D. & Seemann, J.R. (1989). Acclimation of photosynthesis to elevated CO₂ in five C₃ species. *Plant Physiology*, **89**: 590–596.
- Santrucek, J. & Sage, R.F. (1996). Acclimation of stomatal conductance to a CO₂-enriched atmosphere and elevated temperature in *Chenopodium album*. *Australian Journal of Plant Physiology*, **23**: 467–478.
- Sims, D.A., Seeman, J.R. & Luo, Y. (1998). The significance of differences in the mechanisms of photosynthetic acclimation to light, nitrogen and CO₂ for return on investment in leaves. *Functional Ecology*, **12**: 185–194.
- Smith, S.D., Herr, C., Leary, K. & Piorkowski, J. (1995) Soil-plant water relations in a Mojave Desert mixed shrub community: a comparison of three geomorphic surfaces. *Journal of Arid Environments*, **29**: 339–351.
- Smith, S.D., Monson, R.K. & Anderson, J.E. (1997). *Physiological Ecology of North American Desert Plants*. Berlin: Springer-Verlag, 286 pp.

- Stirling, C.M., Davey, P.A., Williams, T.G. & Long, S.P. (1997). Acclimation of photosynthesis to elevated CO₂ and temperature in five British native species of contrasting functional type. *Global Change Biology*, **3**: 237–246.
- Stitt, M. (1991). Rising CO₂ levels and their potential significance for carbon flow in photosynthetic cells. *Plant Cell and Environment*, **14**: 741–762.
- Thomas, R.B. & Strain, B.R. (1991). Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon dioxide. *Plant Physiology*, **96**: 627–634.
- von Caemmerer, S. & Farquhar, G.D. (1981). Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta*, **153**: 376–387.
- Zar, J.H. (1974). *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall, 620pp.