

Water use of two Mojave Desert shrubs under elevated CO₂

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Abstract

Plant responses to elevated atmospheric CO₂ have been characterized generally by stomatal closure and enhanced growth rates. These responses are being increasingly incorporated into global climate models that quantify interactions between the biosphere and atmosphere, altering climate predictions from simpler physically based models. However, current information on CO₂ responses has been gathered primarily from studies of crop and temperate forest species. In order to apply responses of vegetation to global predictions, CO₂ responses in other commonly occurring biomes must be studied. A Free Air CO₂ Enrichment (FACE) study is currently underway to examine plant responses to high CO₂ in a natural, undisturbed Mojave Desert ecosystem in Nevada, USA. Here we present findings from this study, and its companion glasshouse experiment, demonstrating that field-grown *Ephedra nevadensis* and glasshouse-grown *Larrea tridentata* responded to high CO₂ with reductions in the ratio of transpirational surface area to sapwood area (LSR) of 33% and 60%, respectively. Thus, leaf-specific hydraulic conductivity increased and stomatal conductance remained constant or was increased under elevated CO₂. Field-grown *Larrea* did not show a reduced LSR under high CO₂, and stomatal conductance was reduced in the high CO₂ treatment, although the effect was apparent only under conditions of unusually high soil moisture. Both findings suggest that the common paradigm of 20–50% reductions in stomatal conductance under high CO₂ may not be applicable to arid ecosystems under most conditions.

Keywords: conductance, desert plants, elevated CO₂, *Ephedra nevadensis*, *Larrea tridentata*, sap flux

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Introduction

Responses of the terrestrial biosphere to future concentrations of atmospheric CO₂ are increasingly being incorporated into global climate change models (Henderson-Sellers *et al.* 1995; Sellers *et al.* 1996). These responses generally take the form of increases in carbon assimilation and sequestration as a result of CO₂ fertilization, with concurrent reductions in water vapour fluxes due to stomatal closure (Sellers *et al.* 1996). Both responses have been frequently reported in growth chamber, glasshouse, and field Free Air CO₂ Enrich-

ment (FACE) studies (e.g. Ceulemans & Mousseau 1994; Amthor 1995; Saxe *et al.* 1998). However, these studies have been conducted predominantly on temperate forest or crop species. In order to incorporate direct effects of CO₂ on vegetation in global models, CO₂ trials must be conducted on other important components of the biosphere. Because arid and semiarid lands occupy the greatest terrestrial surface area of any vegetation cover type (Dregne 1991), a FACE site was constructed in the Mojave Desert, North America's most arid region, to evaluate CO₂ effects in a severely water-limited ecosystem.

Desert plants may show vastly different responses to elevated CO₂ from crop or forest species due to the

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evolutionary pressures of strong water limitation (Smith *et al.* 1997). Many desert species are adapted to brief periods of available water followed by periods of greatly reduced physiological activity, and CO₂ responses may be confined to periods following rainfall events. This phenomenon has already been observed in the photosynthetic down-regulation response of the desert shrub *Larrea tridentata* under high CO₂, whereby the magnitude of down-regulation was greatest under moist conditions (Huxman *et al.* 1998).

Responses are likely to vary by functional group, as has been noted recently by Saxe *et al.* (1998), who described a trend in the stomatal response to elevated CO₂ of herbaceous > woody deciduous > woody coniferous species. In this study, we assessed the effects of elevated CO₂ on sap flux and stomatal conductance of two desert shrubs, *Larrea tridentata* (DC.) Cov. (creosote bush, a microphyllus evergreen) and *Ephedra nevadensis* S. Wats. (Mormon tea, a leafless, stem photosynthesizing evergreen) at the Nevada Desert FACE Facility (NDDFF). We hypothesized that CO₂-induced reductions in water use would be small in comparison to typical responses of herbaceous species, and more comparable to responses of evergreen trees. In addition, due to the severe water limitations in this ecosystem, we hypothesized that responses would be observed only under relatively moist conditions. The unusually wet spring and early summer in the Mojave Desert in the 1998 El Niño year provided ideal conditions in which to test this hypothesis.

Materials and methods

Study site

The NDDFF, which has been operating since April 1997, consists of nine 23-m-diameter plots located in an undisturbed *Larrea tridentata*–*Ambrosia dumosa*–*Lycium* spp. community at the Nevada Test Site (NTS) (Jordan *et al.* 1999). Six plots are surrounded by a plenum pipe from which 32 vertical PVC pipes release air. Three of these six plots are fumigated with ambient air, three are treated with CO₂-enriched air to maintain a target concentration of 550 µmol mol⁻¹, and three plots are nonblower controls. The design utilizes FACE technology developed by the Brookhaven National Laboratory (Hendrey *et al.* 1992; Hendrey & Kimball 1994). In order to minimize soil compaction and disturbance of the biological crust of lichens, fungi, and cyanobacteria, which covers 35–63% of the soil surface area of each plot, plants are accessed by an aerial walkway that rotates around the radius of each plot. A moveable sled is suspended from each walkway so that all portions of the plots are accessible.

Sap flow measurements

In May 1998, 5–10-mm-diameter whole-branch sap flow sensors (Dynamax, Inc., Houston, TX, USA) were installed on two *Larrea tridentata* and two *Ephedra nevadensis* individuals in each blower plot, for a total of 24 gauges. Sap flow gauges operated on the Stem Heat Balance principle after van Bavel & van Bavel (1990) and Baker & van Bavel (1987). Gauges were placed on smooth, branchless sections of stems and shielded with aluminium foil after Gutierrez *et al.* (1994). Large temperature differences above and below heater in the absence of a supplied voltage (exceeding ± 0.5 °C), which may be an issue in large and/or unshielded and poorly insulated stems (Gutierrez *et al.* 1994; Grime & Sinclair 1999), were not observed during the test period just prior to the study. Both inner and outer canopy branches were chosen so that mean values would be representative of mean whole plant fluxes. Initially 4.5 V was applied to the gauges, but this was reduced to 3.5 V by the end of study to maintain sap temperature increases of 2–5 °C as flow rates declined during the drought period. Such adjustments to the supplied voltage have been found to minimize measurement errors (Grime & Sinclair 1999). At the initiation of the study, the gauges were heated at full power for several 24-h periods in order to determine the appropriate time-period to obtain sheath conductance (K_{sh}) values. K_{sh} appeared to stabilize at high values (zero sap flux) in the two hours before dawn. For the remainder of the study, the voltage was stepped down to 1.5 V from 20.00 to 04.00 hours to avoid stem damage, and reset at 04.00 hours to obtain daily K_{sh} values from 04.00 to 06.00 hours. As sap flux calculations are subject to error during transitional periods of rapid temperature change and low flow rates at dawn and dusk (van Bavel & van Bavel 1990), these values were eliminated from the analyses.

A temperature and relative humidity sensor (HMP 35C probe, Vaisala, Helsinki, Finland) was placed at mid-canopy (c. 0.5 m aboveground) level. Sap flow and atmospheric data were collected half-hourly using data loggers (Campbell Scientific, Inc., Logan, UT, USA) from 16 June until the end of July. Sap flow data were corroborated monthly with leaf-level gas exchange measurements of stomatal conductance (g_s) taken diurnally (LI-COR 6400, LI-COR, Inc., Lincoln, NE, USA), with cuvette conditions matching the ambient conditions in the plots being sampled. For these measurements, one shoot on the external edge of the canopy was chosen in each ring and marked, so that the same shoot could be utilized during the diurnal period. Instantaneous measurements were made over 30-s periods after the coefficient of variation was reduced below 1. Shoots were measured at six intervals during

each day, after which time the shoot was harvested to determine leaf area.

Allometric relationships

Sap flow measurements were expressed both per unit cross-sectional stem area as sap flux (J_s , $\text{g m}^{-2} \text{s}^{-1}$) and on a transpirational surface-area basis. For the purposes of this study, the entire cross-section was assumed to be conductive sapwood. (During off-plot harvests, no heartwood formation was observed in branches of similar sizes.) The transpirational surface-area of each measured branch was estimated allometrically: for *Larrea* leaf area was measured destructively off-plot with a digital leaf area meter (Delta T Devices Ltd, Cambridge, UK) and related to leaf number (leaf area in $\text{cm}^2 = 0.65 \times \text{leaf no}$, $P = 0.0001$, $r^2 = 0.99$). Allometric relationships were compared with physical samples removed periodically from all plots to ensure minimal variation due to phenological or CO_2 effects. The leaves of measured branches were then counted to predict leaf area. For *Ephedra*, which transpires through photosynthetic stems, surface area was calculated from measurements of lengths and diameters of whorls of green stems produced from large, basal, nonphotosynthetic stems on which sap flow gauges were placed, and diameters measured. The ratio of leaf area to cross-sectional sapwood area was calculated for each species within treatments (LSR, $\text{m}^2 \text{cm}^{-2}$).

Glasshouse experiment

Sap flux data were collected during a period of soil drying when volumetric soil water content at 0–50 cm declined from 8.1% to 5.6%. The shoot-level data for *Larrea* showed a reduction in stomatal conductance under high CO_2 in May when soil moisture was unusually high due to heavy spring rains (Fig. 3); however, sap flux data were not available for this period. Therefore, in order to test whether CO_2 effects would be apparent in *Larrea* under higher soil moisture regimes, we conducted an experiment on *Larrea* seedlings at a glasshouse facility located at the University of Nevada, Las Vegas, which operates in conjunction with the NDFF.

In this facility, soil moisture levels could be controlled such that J_s could be measured during a period of moist conditions followed by imposed drought. The glasshouse contained two chambers fumigated with CO_2 to maintain a target concentration of $700 \mu\text{mol mol}^{-1}$, as well as a chamber flushed with ambient air. All rooms were illuminated with ambient light (maximum photosynthetic photon flux density = $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$), and temperature and humidity were controlled to track the ambient room within 3%. Three-month-old *Larrea* seed-

lings were transplanted into the glasshouse in spring 1996 and grown in 1-m-tall \times 0.15-m-diameter pots filled with an 80:20 mixture of commercial sand and silt, to approximate the native soil found at the NDFF. Seedlings were watered twice each week with 400 mL of 10% strength Hoagland's solution until the initiation of the experiment. Eight seedlings in each treatment were fitted with 5-mm sap flow gauges (Dynamax, Inc.) in October 1998 and monitored during a period in which water was withheld. On three days during the experiment, diurnal g_s measurements were made (LI-COR 6400, LI-COR, Inc.) on five seedlings in each treatment as described above, in addition to predawn leaf water potential measurements (Soil Moisture Equipment Corp., Goleta, CA). Soil moisture content was measured with Time Domain Reflectometry. Ten-cm-long stainless steel rods were placed horizontally into five pots in each treatment at 20 cm and 70 cm from the top of the pot. Soil water content was measured from the rods with a cable tester (1502B, Tektronix, Beaverton, OR, USA). After the cessation of sap flux and gas exchange measurements, seedlings were provided with 600 and 200 mL of water in two waterings, and soil water content continued to be monitored. In order to disrupt the boundary layer so that sap flux-derived conductance (see below) and g_s could be compared directly, fans blew adjacent to the seedlings for the duration of the study.

Following the experiment, seedlings were harvested, and the shoot on which g_s measurements were made was separated from each sample. The leaf area of this shoot was determined using a digital scanner (Hewlett Packard Co., Palo Alto, CA, USA) using software based on NIH Image, National Institute of Health (Scion Corp., Frederick, MD, USA). These subsamples were then dried for at least 48 h at 85°C and weighed to calculate the mean specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$) for each treatment. As there was no treatment effect on SLA (t -test, $P > 0.05$, Table 1), one mean was used across treatments. Mean SLA was multiplied by the dry weight of the total biomass of each seedling to estimate the leaf area for each treatment. LSR was then calculated for each treatment with leaf area and cross-sectional area.

Canopy stomatal conductance

Sap flux is equivalent to transpiration on timescales particular to the plant size of interest, as size-dependent time lags between sap flux at the stem and water loss at the leaves occur as a result of water storage capacity. Although capacitance in large trees may cause time-lags exceeding the 30-min averaging period used in this study, the effect has been found to be negligible in small plants (Carlson & Lynn 1991; Phillips *et al.* 1997); thus sap flux was assumed to be equivalent to transpiration in

Table 1 Biomass, specific leaf area (SLA), leaf area, and sapwood area of glasshouse seedlings grown under ambient and 700 $\mu\text{mol mol}^{-1}$ CO_2 for three years. Values are shown \pm SE. Asterisks indicate a significant difference between treatments by Student's *t*-test, or heteroscedastic *t*-test when necessary, $\alpha = 0.05$.

	Ambient	700 $\mu\text{mol mol}^{-1}$
Biomass (g)		
Total	4.86* \pm 0.64	2.69 \pm 0.15
Leaf	1.59* \pm 0.36	0.63 \pm 0.10
Branch	3.27* \pm 0.35	2.06 \pm 0.10
SLA ($\text{cm}^2 \text{g}^{-1}$)	67.4 \pm 12.0	66.0 \pm 9.1
Leaf area (m^2)	0.02* \pm 0.004	0.008 \pm 0.001
Sapwood area (cm^2)	0.111 \pm 0.010	0.100 \pm 0.004

order to calculate the average stomatal conductance of the canopy (in this case, a single branch), or canopy stomatal conductance (G_s):

$$G_s = \frac{\gamma \lambda E_1}{\rho c_p \delta w}, \quad (1)$$

where γ is the psychrometric constant (kPa K^{-1}), λ is the latent heat of vaporization (J kg^{-1}), c_p is the heat capacity of air ($\text{J kg}^{-1} \text{K}^{-1}$), δw is the vapour pressure difference (kPa), and E_1 is transpiration ($\text{kg m}^{-2} \text{s}^{-1}$; Phillips & Oren 1998). When the canopy is well coupled to the atmosphere, and leaf and air temperatures are not different, the vapour pressure deficit (VPD) may be substituted for δw . If boundary layer conductance far exceeds the magnitude of stomatal conductance, as is often the case during conditions of high wind, over rough canopies, and where leaf dimensions are small, G_s will be equivalent to average true stomatal conductance, and reflect stomatal behaviour rather than physical processes governing the boundary layer (Whitehead & Jarvis 1981; Jones 1983).

Results

Field experiment

Sap flux was measured at the NDFP from 16 June – 3 August 1998. During this period, the average minimum and maximum temperatures were 11.4 and 37.0 °C, respectively. The dataset was chosen to fall within a period of drying soil with minimal precipitation. The recorded precipitation during the study was 21.8 mm, which fell on 23 and 24 July. Prior to the initiation of the study, precipitation of 236.5 mm had been recorded since January 1998, greatly exceeding the average annual precipitation in this area of the NTS of approximately 140 mm.

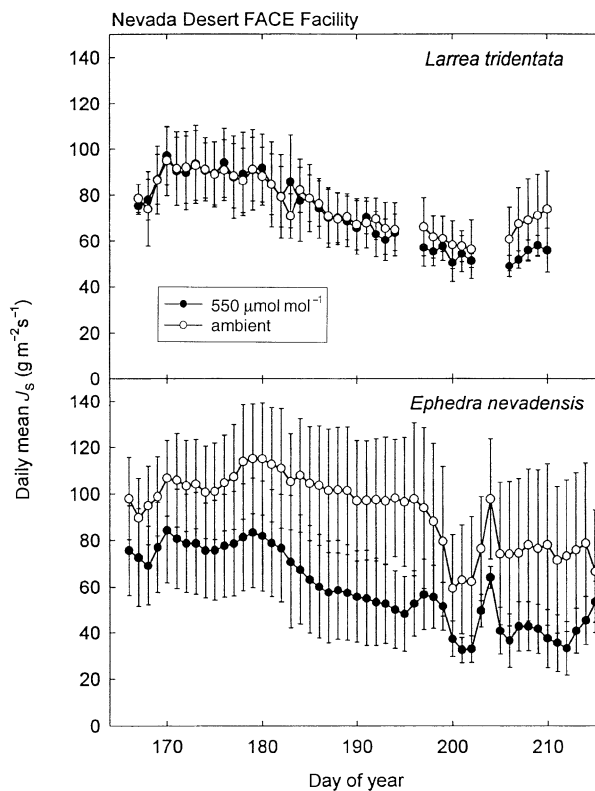


Fig. 1 Daily mean sap flux (J_s) of two desert shrub species in a Free Air CO_2 Enrichment (FACE) study from 16 June to 3 August 1998. Values are expressed on a cross-sectional stem area basis. Bars represent ± 1 SE, using true replication ($n = 3$).

The daily values of J_s from the experiment are shown in Fig. 1. Although no CO_2 effect was apparent in *Larrea* ($P > 0.05$, anova with each day treated as a repeated measure), *Ephedra* showed a trend toward lower flux per unit cross-sectional stem area under high CO_2 , consistent with a stomatal closure effect. However, variability in these data was high. In order to reduce this variability, J_s values were converted to G_s and expressed on a leaf-area basis according to (1). As a consequence of high flux rates, small leaf dimension, and wind speeds which generally exceeded 2 m s^{-1} , leaf and air temperature did not differ in *Larrea* ($P > 0.05$; Joradan and Nowak, unpubl. data), and thus VPD was substituted for δw in (1). As boundary layer conductance is likely to far exceed g_s as a result of these same conditions, G_s was assumed to largely represent stomatal behaviour.

Mean mid-morning G_s is shown in Fig. 2. Leaf-level gas exchange measurements indicated that peak conductance occurred mid-morning (Fig. 3), such that the largest treatment differences may be expected during this period. Because LSR values were not altered by the CO_2 treatment in *Larrea* ($P > 0.05$, *t*-test), this species still showed no CO_2 effect in morning conductance in either

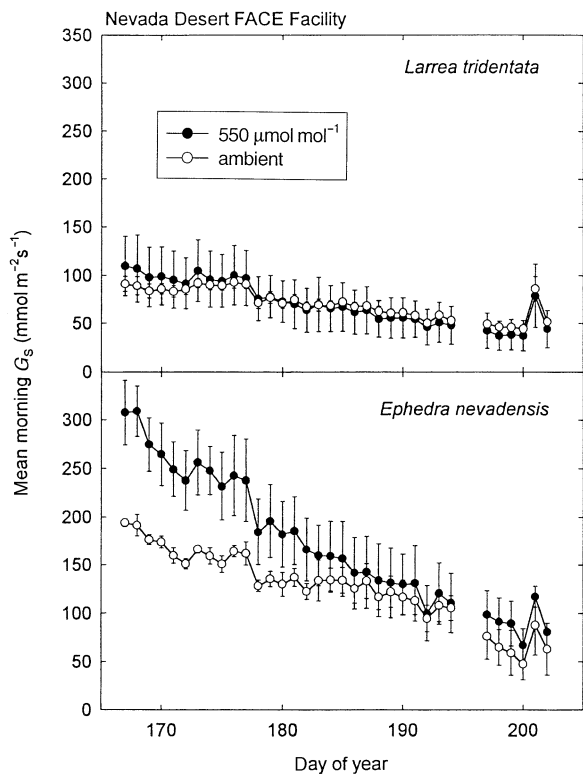


Fig. 2 Whole branch stomatal conductance (G_s) calculated from sap flux measurements in a Free Air CO_2 Enrichment (FACE) study from 16 June to 21 July 1998. Values are expressed on a leaf area basis. Bars represent ± 1 SE, using true replication ($n=3$).

G_s (Fig. 2, $P > 0.05$, repeated measures anova), or g_s from gas exchange measurements during June and July (Fig. 3). In *Ephedra*, CO_2 did cause a shift in mean LSR (actually photosynthetic surface area of whorls of green stems per unit basal sapwood area). This species produced less surface area per unit cross-sectional sapwood area under elevated CO_2 , such that the ratio was $0.08 \pm 0.02 \text{ m}^2 \text{ cm}^{-2}$ in the high CO_2 treatment, as opposed to $0.12 \pm 0.02 \text{ m}^2 \text{ cm}^{-2}$ under ambient conditions ($P < 0.05$, t -test). Expressing fluxes on a surface-area basis also reduced the variability within treatments, and a treatment effect became apparent (Fig. 2, $P < 0.05$, repeated measures anova). Notably, this effect is the opposite of what is expected under the typical high CO_2 scenario: conductance was actually higher under high CO_2 .

Glasshouse experiment

Values for θ in the glasshouse pots are given in Fig. 4. Measurement of soil water content began five days after water was withheld. At the first soil water content measurement, the elevated CO_2 pots already

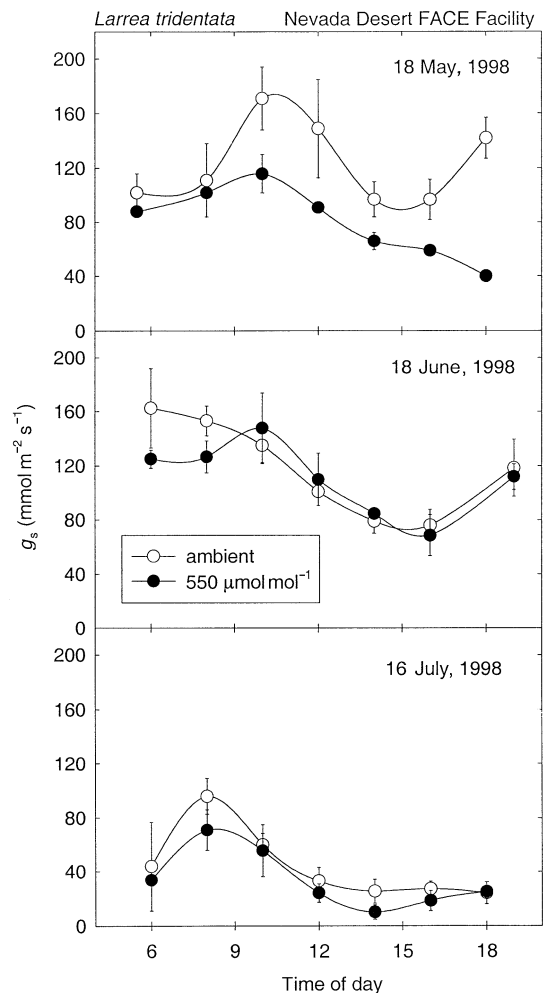


Fig. 3 Diurnal values of leaf-level stomatal conductance (g_s) on three dates in a Free Air CO_2 Enrichment (FACE) study. Bars represent ± 1 SE, using true replication ($n=3$).

showed greater soil moisture than ambient. An 800-mL re-watering brought values in both treatments to similar levels; however, the two treatments rapidly separated again as more water was withdrawn by the larger seedlings in the ambient chamber (Fig. 4, Table 1). These measurements were conducted in the upper portion of the pot, 20 cm from the soil surface, representing the upper rooting zone. Measurements were replicated in the lower portion of the pots at 70 cm; however, there were no treatment differences or variations in soil moisture with time ($P > 0.05$) during the course of the experiment. Thus, roots appeared to be concentrated in the upper portion of the pots.

The explanation for greater soil moisture under elevated CO_2 appears to be two-fold: (i) the seedlings in the elevated CO_2 treatment were smaller (Table 1); and (ii) LSR was reduced in the high CO_2 treatment, such that

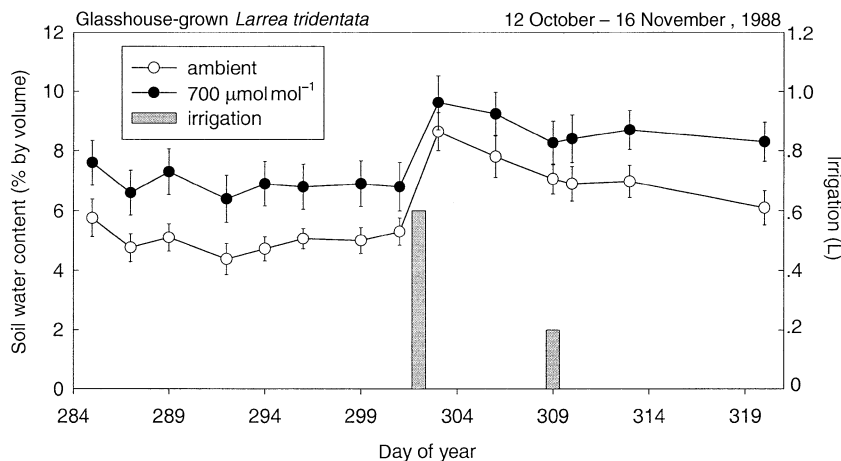


Fig. 4 Soil water content at 20 cm in pots containing *Larrea tridentata* seedlings during a glasshouse experiment. The solid bars indicate the amount of applied water according to the right axis. Bars represent ± 1 SE.

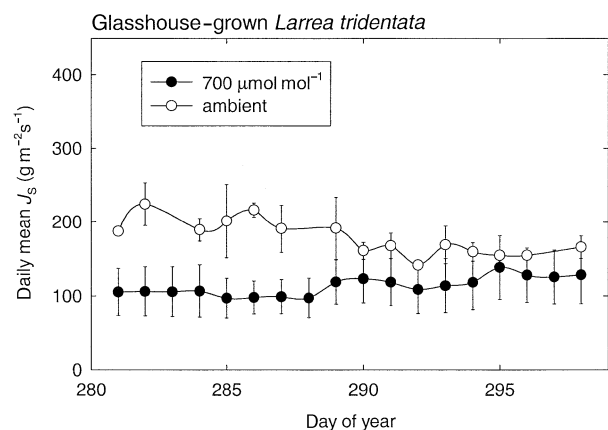


Fig. 5 Daily mean sap flux (J_s) on a cross-sectional wood area basis in a glasshouse experiment from 8 to 25 October 1998. Values are given during a period of drying soil after water was withheld from potted seedlings. Bars represent ± 1 SE.

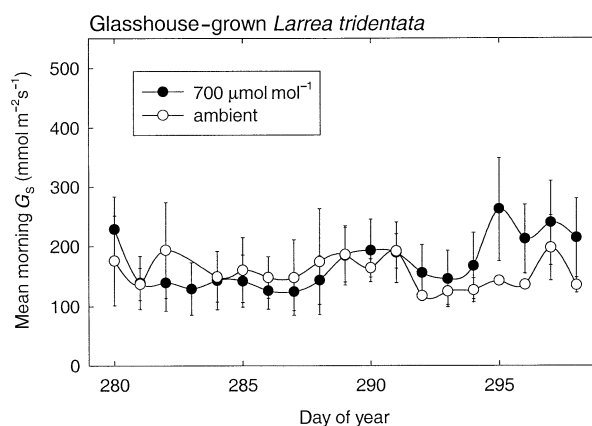


Fig. 6 Whole branch conductance (G_s) calculated from sap flux measurements in a glasshouse experiment from 7 to 25 October 1998. Values are given on a leaf-area basis. The experiment was conducted during a period of drying soil after water was withheld from potted seedlings. Bars represent ± 1 SE.

the ratio was $0.08 \pm 0.01 \text{ m}^2 \text{ cm}^{-2}$ under elevated CO_2 and 0.20 ± 0.05 in ambient air ($P < 0.05$, heteroscedastic t -test). On a sapwood area basis, J_s was lower under high CO_2 under moist conditions, although this effect was confounded with soil moisture as the soil dried (Fig. 5, $\alpha = 0.05$, repeated-measures anova) and the pre-dawn shoot water potential dropped from -2.5 to -3.8 MPa. In Fig. 6, the flux is expressed as G_s per unit leaf area. The shift in LSR brought G_s to similar levels in both treatments ($P > 0.05$, repeated measures anova).

Leaf-level g_s measurements taken three times during this dry-down show similar trends, i.e. no apparent CO_2 effect late into the drying period (Fig. 7). Early in the experiment, before water was withheld, the first set of diurnal measurements showed higher g_s in the elevated CO_2 treatment ($P < 0.05$), similar to the pattern recorded for *Ephedra* under moist conditions in the field (Fig. 2).

Values of leaf-level g_s compared favourably to G_s , although a sufficiently high number of low values was not available in the glasshouse to show a linear relationship (Fig. 8). At the NDFF, a strong linear relationship was found under both ambient and elevated CO_2 as a result of the low values in July ($P < 0.05$); however, there was a trend for values to fall below the 1:1 line during the high values in June, particularly under ambient conditions (Fig. 8).

Discussion

Two categories of CO_2 responses were observed in this study. For field-grown *Larrea*, LSR was not affected by elevated CO_2 , and stomatal closure at high CO_2 was observed only under very moist conditions after mid-morning (Fig. 3). For field-grown *Ephedra* and glass-

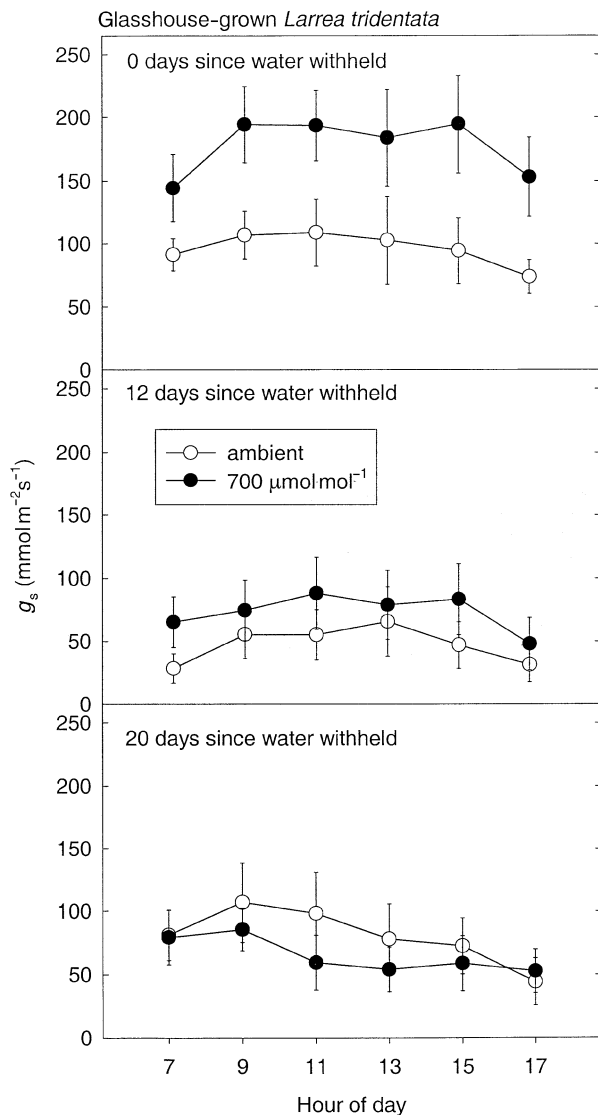


Fig. 7 Diurnal values of leaf-level stomatal conductance (g_s) on three dates during a glasshouse experiment. Bars represent ± 1 SE.

house-grown *Larrea*, high CO_2 caused a reduction in the allocation of leaf area (green stem length in *Ephedra*) per unit cross-sectional wood area. A reduction in LSR results in increased leaf-specific conductivity such that more water may be transpired per unit leaf-area at the same water potential gradient (Tyree & Ewers 1991; Pataki *et al.* 1998a). Thus, both G_s and g_s were unaffected or were increased under high CO_2 (Figs 2,6,7). Previously, elevated CO_2 studies on temperate tree species have found small or no changes in LSR (Pataki *et al.* 1998b).

In addition to stomatal effects, leaf-area reductions imply that increases in aboveground biomass under

elevated CO_2 may also be less than anticipated. Although decreases in LSR do not necessarily translate into reductions in total biomass, in the glasshouse study where whole plant leaf-area could be directly measured, the CO_2 -grown plants produced 60% less total leaf area than ambient-grown plants. The 45% reduction in total biomass under elevated CO_2 (Table 1) was likely to be due to photosynthetic down-regulation, which was measured in these seedlings in a separate study more than a year prior to this experiment (Huxman *et al.* 1998). At this time, biomass data showed a trend toward lower biomass under elevated CO_2 , although this effect was not yet significant (Huxman *et al.* 1999).

Total biomass data were not available for *Ephedra*; however, an analysis of green stem length and diameter values indicated that the reduction in surface area under elevated CO_2 was caused by a 13% reduction in mean stem length ($P < 0.05$, *t*-test) rather than a change in diameter ($P > 0.05$, *t*-test). *Ephedra* is a long-lived evergreen, although partial stem abscission may be initiated during dry conditions, with the production of new stems during the moist growing season (Addicott 1982). Thus, some green stems were likely to have been produced entirely during the course of the experiment. An increase in this fraction may be expected in later years of CO_2 fumigation.

Reductions in leaf area and subsequently total water uptake may result in increased soil moisture availability under elevated CO_2 conditions. In the glasshouse experiment, this appeared to be the case (Fig. 4). Thus, the g_s data in Fig. 7 showed more rapid stomatal closure during soil drying in the CO_2 treatment, despite similarities in the relative change in soil moisture (Fig. 4). It is unclear whether the increased g_s in the elevated CO_2 treatment under moist conditions (Fig. 7, upper panel) is a consequence of the hydraulic effects of decreased LSR, or the greater soil moisture availability. In either case, the large reduction in g_s during the drying period, which exceeded the reductions in the ambient treatment, resulted in similar values in both treatments in dry conditions, similar to effects of elevated CO_2 on field-grown *Ephedra* (Fig. 2). Causally, this response may be related to higher VPD under dry conditions, which has been shown to increase stomatal sensitivity to high CO_2 in some species (Bunce 1998).

Although sap flux-derived G_s in glasshouse *Larrea* occasionally showed higher conductance in the elevated CO_2 treatment, this effect was nonsignificant ($\alpha = 0.05$) in contrast with the 8 October diurnal g_s measurements (Fig. 7). However, this was the only instance in which the two methods disagreed. In general, sap flux-derived G_s yielded very similar values to g_s , with differences generally falling within the standard error of the 1:1 line (Fig. 8). One notable exception was a tendency toward

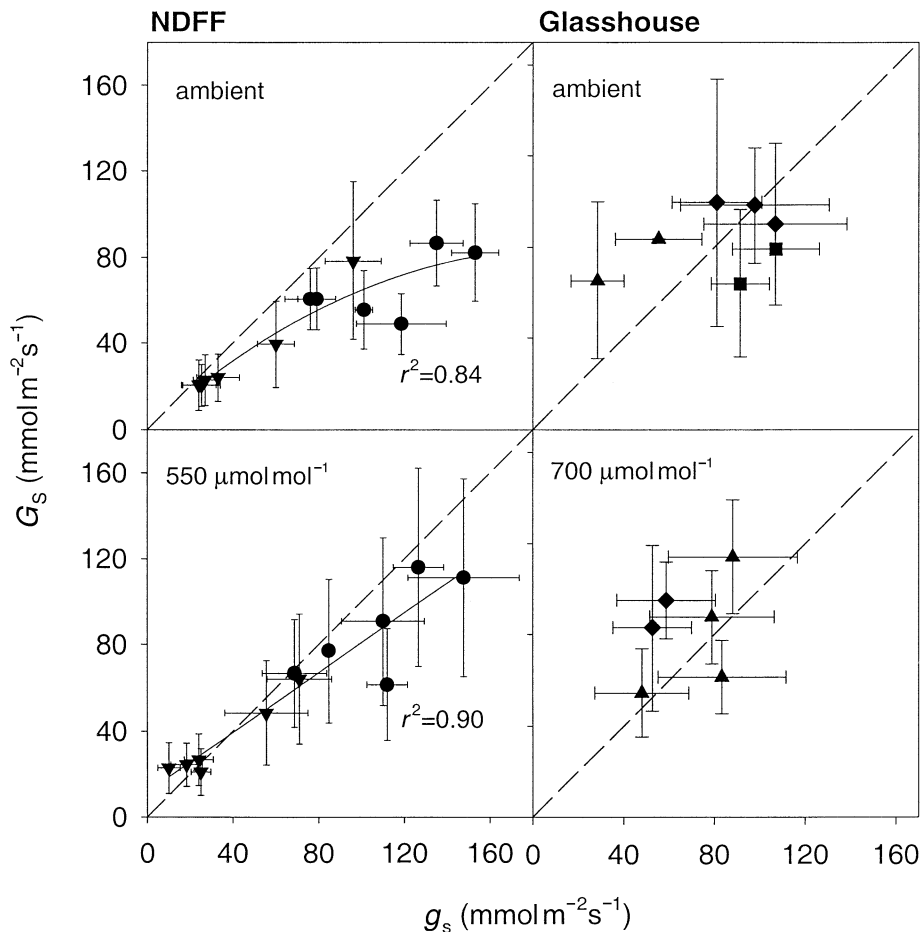


Fig. 8 Leaf-level stomatal conductance (g_s) in comparison to sap flux-derived canopy stomatal conductance (G_S) for *Larrea tridentata* during dates and times when both values were available. Measurements were taken on 18 June (●) and 16 July (▼) at the NDFF, and 8 October (■), 20 October (▲), and 28 October (◆) in the glasshouse. Bars represent ± 1 SE.

$G_S < g_s$ under ambient CO_2 conditions during the moist, high transpiration period in June, despite a strong relationship between the two sets of measurements (Fig. 8). This is indicative of leaf or aerodynamic boundary layer conductance issues more prevalent in the ambient treatment. Although leaf-to-air temperature differences, as well as CO_2 effects on leaf dimension have not been detected in *Larrea* at this site, plot-level estimates of leaf area or canopy structure that may influence boundary layer conductance are not yet available. Future measurements of these parameters may discern which CO_2 effects influence the relationship between g_s and G_S .

For both methods, the values of G_S and g_s recorded in the field were considerably higher than literature values for these species (Meinzer *et al.* 1990; Smith *et al.* 1995), particularly earlier in the season (Figs 2,3). The unusually favourable El Niño conditions provided a unique opportunity to observe potentially larger CO_2 responses than may be present in seasons of normal rainfall, as

stomatal closure under high CO_2 tends to be greater under unstressed conditions promoting high g_s (Curtis 1996; Saxe *et al.* 1998).

Leaf-level measurements in field-grown *Larrea* indicated that CO_2 -induced stomatal closure occurred under moist conditions in May. *Larrea* has also shown a 23% reduction in mid-morning stomatal conductance in response to high CO_2 during an additional period of increased water availability in the later summer period (Nowak and Jordan, unpubl. data). This is in agreement with the hypothesized similarity in the magnitude of stomatal closure with temperate evergreen tree species, $\approx 20\%$ (Field *et al.* 1995; Saxe *et al.* 1998). The stomatal closure effect occurred only in the absence of a reduction in LSR.

Larrea and *Ephedra* responded differently to elevated CO_2 in the field, with a reduction in LSR in *Ephedra* and no detectable change in LSR in *Larrea*. However, field-grown plants were fumigated for only two growing seasons, such that shifts in allometry under high CO_2

may not yet be apparent in some species, particularly for mature individuals. *Larrea* did show a reduction in LSR in the glasshouse experiment where seedlings were (i) exposed to high CO₂ since three months of age, and (ii) fumigated with a higher CO₂ concentration (700 rather than 550 µmol mol⁻¹). Thus, field-grown *Larrea* may exhibit a reduction in LSR in the future after additional years of exposure to the high CO₂ treatment. In this case, it is likely that stomatal closure under high CO₂ will be reduced or eliminated.

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