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Photosynthesis in an invasive grass and native forb at elevated CO$_2$ during an El Niño year in the Mojave Desert

Abstract Annual and short-lived perennial plant performance during wet years is important for long-term persistence in the Mojave Desert. Additionally, the effects of elevated CO$_2$ on desert plants may be relatively greater during years of high resource availability compared to dry years. Therefore, during an El Niño year at the Nevada Desert FACE Facility (a whole-ecosystem CO$_2$ manipulation), we characterized photosynthetic investment (by assimilation rate-internal CO$_2$ concentration relationships) and evaluated the seasonal pattern of net photosynthesis (A_{net}) and stomatal conductance (g_s) for an invasive annual grass, *Bromus madritensis* ssp. *rubens* and a native herbaceous perennial, *Eriogonum inflatum*. Prior to and following flowering, *Bromus* showed consistent increases in both the maximum rate of carboxylation by Rubisco (V_{Cmax}) and the light-saturated rate of electron flow (J_{max}) at elevated CO$_2$. This resulted in greater A_{net} at elevated CO$_2$ throughout most of the life cycle and a decrease in the seasonal decline of maximum midday A_{net} upon flowering as compared to ambient CO$_2$. *Eriogonum* showed significant photosynthetic down-regulation to elevated CO$_2$ late in the season, but the overall pattern of maximum midday A_{net} was not altered with respect to phenology. For *Eriogonum*, this resulted in similar levels of A_{net} on a leaf area basis as the season progressed between CO$_2$ treatments, but greater photosynthetic activity over a typical diurnal period. While g_s did not consistently vary with CO$_2$ in *Bromus*, it did decrease in *Eriogonum* at elevated CO$_2$ throughout much of the season. Since the biomass of both plants increased significantly at elevated CO$_2$, these patterns of gas exchange highlight the differential mechanisms for increased plant growth. The species-specific interaction between CO$_2$ and phenology in different growth forms suggests that important plant strategies may be altered by elevated CO$_2$ in natural settings. These results indicate the importance of evaluating the effects of elevated CO$_2$ at all life cycle stages to better understand the effects of elevated CO$_2$ on whole-plant performance in natural ecosystems.

Keywords FACE · *Bromus* · *Eriogonum* · Elevated CO$_2$ · Photosynthesis · Stomatal conductance · Mojave Desert · Nevada Test Site · NDFF

Introduction

Performance of desert ephemerals during high-rainfall years is critical to long-term persistence of these functional types in arid lands (Beatley 1974; Monson and Szarek 1981). High photosynthetic rates during favorable periods allow for sufficient flowering and belowground growth that can replenish seed banks and/or promote the ability to perennate (Smith et al. 1997). During these high-rainfall years (such as an El Niño year), ephemeral plant growth and seed set may be limited less by soil moisture than by the availability of nitrogen in soils (Smith et al. 1997). How wet years and rising CO$_2$ concentrations may interact and affect the growth of desert ephemerals is uncertain. Desert plants have been hypothesized to increase leaf water use efficiency at elevated CO$_2$, which may promote growth and seed set, but this CO$_2$ fertilization response may be relaxed by a potential nitrogen limitation (Strain and Bazzaz 1983). Since most leaf nitrogen is held in the photosynthetic apparatus of C$_3$ plants (Evans and Seemann 1989), how elevated CO$_2$ during wet years may affect photosynthesis and whole-plant performance is important to understand (Huxman et al. 1998c) in order to predict the response of desert ecosystems to climate change.

Levels of atmospheric CO$_2$ expected to occur within this century stimulate C$_3$ photosynthesis in a number of plant species from a wide variety of plant growth forms

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(Curtis 1996). At elevated CO_2, net photosynthesis (A_{net}) is stimulated by increases in the rate of carboxylation as a result of increased efficiency of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) action and decreased energy drain through photorespiration (Bowes 1993). Increased A_{net} at elevated CO_2 often results in a high leaf carbohydrate supply that can invoke a feedback limitation on the photosynthetic apparatus (Azcon-Bieto 1983; Tissue et al. 1993). Such a feedback re-adjusts the relative partitioning of nitrogen between the component reactions of photosynthesis, such that at elevated CO_2, the abundance and/or activity of Rubisco decreases (Sage 1990). This decrease in Rubisco content at elevated CO_2 can in turn act to release nitrogen from investment in leaves, allowing potential re-allocation to other plant structures/functions that impact whole-plant function (Sage 1994).

Elevated CO_2 results in increased carbon gain and growth rates, despite photosynthetic down-regulation (Curtis and Wang 1998), most likely as a result of a number of other stimulatory effects of elevated CO_2 on whole plants (Bowes 1993). Down-regulation and subsequent re-adjustments of N within the whole plant may allow the limited plant N content to be distributed across greater leaf area, which could result in greater whole-plant carbon gain at elevated CO_2. This would occur at elevated CO_2 despite similar instantaneous rates of photosynthesis on a leaf area basis at elevated and ambient CO_2. Decreases in stomatal conductance at elevated CO_2 can potentially improve plant water balance during dry periods, promoting photosynthesis later in the day than in ambient conditions where midday stomatal closure limits CO_2 assimilation (Hamerlynck et al. 1997). Elevated CO_2 may also offset high temperature damage to the photosynthetic apparatus, which can limit carbon gain in arid ecosystems (Huxman et al. 1998a; Hamerlynck et al. 2000a; Taub et al. 2000). At low light, elevated CO_2 promotes A_{net} to an even greater extent than at high light, despite the down-regulation, changing the diurnal pattern of carbon gain (Harley 1995). All these factors may contribute to an increase in growth at elevated CO_2, despite re-adjustments in the photosynthetic apparatus. However, these alterations in function have different implications for plant performance in deserts.

While the down-regulation response of the photosynthetic apparatus to elevated CO_2 appears to occur in a large number of species in a variety of growth situations, a number of environmental and phenological effects impact the relative response (Huxman et al. 1998a, 1998c; Hamerlynck et al. 2000b). Resource status is very important in regulating the photosynthetic response (McConnaughay et al. 1993). Both drought and nitrogen limitation can diminish the relative down-regulation of the photosynthetic assembly at elevated CO_2. Thus, for species growing in a natural setting, with a heterogeneous resource supply throughout ontogeny, a general release of nitrogen away from Rubisco for other uses in the plant may not always occur. In addition, stimulation of

carbon gain may be diminished by the availability of soil resources over the season, limiting total potential carbon gain. Controlling for these factors in glasshouse and growth chamber experiments may be especially difficult (Kennedy 1995), and may have led to the generalizations that have been made thus far. Such factors may be especially important for understanding CO_2 effects on photosynthesis in deserts, where soil resources are available only over a short time period and therefore limit plant growth. Responses of photosynthesis to elevated CO_2 must be made in the context of whole-plant growth in a natural setting in order to adequately understand plant responses to elevated CO_2 (Wolfe et al. 1998).

During the 1997–1998 hydrologic year (1998 growing season), the southwestern United States experienced a pronounced El Niño event. This resulted in a region-wide bloom of ephemeral plants and concomitant high primary production after several dry years of low relative production. This event thus provided us with an excellent opportunity to investigate how desert ephemerals may respond to elevated CO_2 under natural environmental conditions. We evaluated the seasonal pattern of photosynthesis and water use for two plant species growing exposed to elevated CO_2 in a natural ecosystem in the Mojave Desert. We evaluated *Bromus madritensis* ssp. *rubens* (an invasive annual grass) and *Eriogonum inflatum* (a native herbaceous perennial) at the Nevada Desert Free-Air CO_2 Enrichment (FACE) Facility, located on the Nevada Test Site in the Mojave Desert. We tested the hypothesis that plants at elevated CO_2 would down-regulate photosynthesis and thus maintain similar maximum light-saturated rates of net photosynthesis throughout a season (between CO_2 treatments). However, the reductions in stomatal conductance and potential water savings of growth at elevated CO_2 would result in increased daily rates of carbon gain as a function of greater gas exchange activity after midday and prolonged soil resource status into the summer dry season. We hypothesized that the pattern would be consistent across phenology for the two species studied. Changes in the patterns of carbon capture and water use over a season in these two species is important to understand with respect to elevated CO_2, as the interaction between native and invasive species at elevated CO_2 in natural settings is poorly understood (Dukes 2000) but may be particularly relevant to ecosystem function in the Mojave Desert (Smith et al. 2000).

Materials and methods

Study facility

The Nevada Desert FACE Facility (NDFF) is located on the Nevada Test Site (36°49′ N, 115°55′ W, 970 m), a National Environmental Research Park operated by the US Department of Energy. This area is a pristine portion of the Mojave Desert, which has been free from livestock grazing for about 50 years. The average precipitation is 138±62 mm, falling mostly as rain during winter months (Hunter 1994), but the Mojave Desert can receive unpredictable rain during any portion of the year (Bowers 1987).

The NDFF consists of nine ringed plots (each 491 m²); three plots are maintained at 550 µmol mol⁻¹ CO_2, while the remaining six plots are controls for the CO_2 enhancement and application assembly. The NDFF maintains continuous CO_2 enrichment, except when the 5-min wind speed average exceeds 7.0 m s⁻¹ (during the primary portions of this study) or when nocturnal temperature falls below 0°C, so that elevated CO_2 treatment conditions occur greater than 95% of the time. The plants are accessed from an overhead moveable walkway system that allows sampling without disturbing soil in the plots. A more extensive facility description is available in Jordan et al. (1999).

Experimental species

Bromus madritensis ssp. *rubens* (red brome; hereafter referred to as *Bromus*) is an exotic annual grass that is prominent across the northern Mojave Desert (Hunter 1991; Brooks 1998) and may be particularly responsive to growth at elevated CO_2 (Huxman et al. 1999; Smith et al. 2000). The density of *Bromus* on the Nevada Test Site has increased over the last century (Hunter 1991), possibly replacing a number of perennial shrubs, most likely through an alteration in early season soil water, as in *B. tectorum* (Harris 1967; Harris and Wilson 1970). Both *Bromus* species cause a buildup of litter and standing dead material and increase fire frequency in the desert Southwest (Mayeux et al. 1994; Brooks 1998). Thus, *Bromus* may play an important role in facilitating a transition from the current arid scrub/steppe landscapes to an annual-grass-dominated landscape in the Intermountain Region (Smith et al. 1987; Sage 1996). *Eriogonum inflatum* (hereafter referred to as *Eriogonum*) is a herbaceous perennial rosette-forming species that is common throughout the Mojave Desert and Great Basin (Smith and Osmond 1987).

Plant sampling

We selected between one and three individuals of *Bromus* and *Eriogonum* from each of six treatment plots (3-full FACE assembly with CO_2 enhancement and 3-full FACE assembly without CO_2 enhancement). Both species were selected at random from open-intercanopy spaces, greater than 1 m from any perennial plant. The photosynthetic characteristics of these plants were assessed using assimilation rate-internal CO_2 concentration (A-C_i) analysis twice during their life cycle: prior to and just following anthesis (this was a fairly early point in the period of inflorescence development for *Eriogonum*, which can produce flowers over a 4-month period). In addition to the A-C_i analysis, the diurnal pattern of carbon assimilation and stomatal conductance to water vapor was determined every week once leaves were large enough to permit gas exchange measurements, and continued until most of the vegetative leaf area had senesced.

A-C_i characterization

The A-C_i response of both species was determined with a programmable, open-flow gas exchange system (Li 6400, Li-Cor, Lincoln, Neb.). Block temperature was held at the typical maximum daytime temperature achieved during this study, and relative humidity (RH) at 20%. All measurements were made with a saturating red light source (PPFD=1,500 µmol m⁻² s⁻¹). The CO_2 concentration of the cuvette (C_a) was initially maintained at 200 µmol mol⁻¹ for 5 min to stimulate stomatal opening and then reduced to 75 µmol mol⁻¹. C_a was incrementally increased to 150, 250, 350, 550, 700, 800, 900, 1,200, and 2,000 µmol mol⁻¹, and gas exchange properties were logged at each C_a once the system had reached a pre-determined stability point (coefficient of variation=1%). The data from the A-C_i response was imported to Photosynthesis Assistant (Dundee Scientific Ver. 1.1.2, Dundee, UK), where V_{Cmax} (maximum rate of carboxylation by Rubisco), J_{max} (light-saturated rate of electron transport), R_d (daytime respira-

tion), and TPU (triose-phosphate utilization capacity) were determined as in Farquhar et al. (1980) as modified by Harley and Sharkey (1991) and Harley et al. (1992). In addition, the CO_2 compensation point (Γ) was determined from the least-squares regressions generated in Photosynthesis Assistant.

We determined the relative limitation of photosynthesis by stomatal behavior (RSL) from the regressions in Photosynthesis Assistant. RSL was calculated with the following equation (Farquhar and Sharkey 1982):

$$RSL = \left(\frac{A_{Ci} - A_{Ca}}{A_{Ca}} \right) \times 100 \tag{1}$$

Where A_{Ca} is the net photosynthetic rate at C_a=360 or 700 µmol mol⁻¹ CO_2 (for ambient and elevated plants, respectively) and A_{Ci} is the net photosynthesis at the C_a required to obtain a C_i equivalent to the growth CO_2 concentration of the plant.

Leaf nitrogen (on a dry mass basis: g g⁻¹) was determined for a small number of leaf samples at the onset of flowering. A fully expanded leaf from one individual of each species in each ring was taken and dried for 3 days at 70°C. Samples were ground to a fine powder and shipped to the University of Georgia where elemental analysis by sample combustion was conducted with an NA1500 C/H/N Analyzer (Carlo Erba, Milan, Italy).

Seasonal and diurnal gas exchange

For diurnal patterns of carbon assimilation and stomatal conductance to water vapor, we selected three to five individuals in a pair of FACE rings (one elevated CO_2 and one ambient CO_2). Due to the spatial layout of the NDFF, we were only able to make sufficient measurements in a single pair of rings, because using the complete NDFF set-up resulted in an insufficient number of measurements to adequately describe gas exchange over a diurnal period. We used a Li-6400 open-flow gas exchange system to conduct the diurnal measurements. Cuvette environmental conditions (temperature, PPFD, RH) were set to mimic external environmental conditions for the time period being measured, and were held consistent across the samples in the ring pairs. A series of five measurements was made over a minute once the cuvette had been placed on a leaf and the flow through the system had stabilized (usually requiring less than 3 min). The mean of these five measurements was used as the value for the individual leaf being measured. We followed the diurnal course of photosynthesis and stomatal conductance on the same leaves over the course of the day.

Statistical analysis

Because of the strong relationship between the response variables in an A-C_i analysis, the parameters derived from it were evaluated by a two-way MANOVA, using phenological stage and CO_2 as factors for each species independently. Six parameters were included in the model, each of which was generated from the A-C_i curves: V_{Cmax}, J_{max}, TPU, R_d, Γ, and RSL. Following the overall MANOVA, each parameter was evaluated independently with a two-way ANOVA, with CO_2 and phenological stage as factors in the model. Following the detection of significance (α=0.05), pairwise comparisons were constructed by Student Newman-Kuels tests.

The diurnal responses of photosynthesis and stomatal conductance were used to determine midday maximum values over the course of the season. Values measured between 0900 and 1130 hours were used to determine the midday maximum. A three-way split-plot repeated-measures ANOVA was used to test for the significance of CO_2 concentration and time for these response variables. CO_2 treatment was the whole-plot factor, CO_2 treatment×replicate was the whole-plot F-test denominator, while time and time×CO_2 treatment were the sub-plot factors, using the three-way interaction (CO_2 treatment×time×replicate) as the sub-plot F-test denominator. Of specific interest were the CO_2 treatment×time interactions, which would indicate CO_2 treatment-specific changes in plant function throughout the season.

Results

There was greater than 100 mm of precipitation over the duration of this experiment (March to May 1998) and 257.6 mm within the wet portion of the hydrologic year (October 1997 to June 1998). This acted to maintain soil moisture content (surface 50 cm) consistently around 7.5 g g^{-1}, with no significant differences between CO_2 environments over the entire period of plant activity ($P>0.05$). Over the course of this experiment, midday temperature increased from 15 to 27°C in a stepwise fashion. Minimum temperatures were typically about –4°C each night.

The elevated-CO_2 treatment significantly affected the photosynthetic characteristics (based on the six response variables used in the MANOVA) of *Bromus* and *Eriogonum* (Table 1). This was not the case for phenology, which was significant only for photosynthesis in *Eriogonum*. An interaction between CO_2 and phenology was not present on the response variables for either species. Thus, *Eriogonum* and *Bromus* differed in their response to CO_2 throughout ontogeny.

For both species, daytime respiration (R_d) and CO_2 compensation point (Γ) were influenced by CO_2 environment in a similar manner: values were greater at elevated than at ambient CO_2 (Table 2, Figs. 1, 2). R_d nearly doubled for both species at elevated CO_2, regardless of phenological period, while Γ was approximately 20 μmol mol^{-1} greater at elevated compared to ambient CO_2. Phenology did not significantly affect either variable.

All parameters except the relative stomatal limitation to photosynthesis (RSL) were influenced by growth at elevated CO_2 in *Bromus*, whereas RSL was one of the few parameters influenced by CO_2 in *Eriogonum* (Table 2). CO_2 decreased RSL in *Eriogonum* by about half, regardless of phenological stage (Fig. 2). Phenology also affected RSL by decreasing the values by approximately half from pre- to post-anthesis (Fig. 2). RSL showed no consistent trend with CO_2 or phenology in *Bromus*.

The maximum rate of carboxylation by Rubisco (V_{Cmax}) was affected by elevated CO_2 in an opposite manner in the two species evaluated here. There were strong phenological and CO_2 effects on V_{Cmax} in *Bromus* such that the values decreased from pre- to post-anthesis, and were significantly greater at elevated compared to ambient CO_2 post-anthesis (Fig. 1). The decrease at flowering was greatest for *Bromus* at ambient CO_2, while V_{Cmax} during flowering at elevated CO_2 was not significantly different (pairwise) from either ambient or elevated CO_2 prior to flowering. In contrast to the pattern in *Bromus*, there was a $CO_2 \times$phenology interaction in *Eriogonum*, such that the greatest value of V_{Cmax} was in the post-anthesis ambient-grown plants (significantly greater than post-anthesis *Eriogonum* at elevated CO_2; Table 2, Fig. 2). Prior to anthesis, there were no significant differences between values for the two CO_2 environments.

V_{Cmax} is a parameter derived from gas exchange manipulations describing the maximum carboxylation

Table 1 Two-way MANOVA for parameters derived from the A-C$_i$ analysis of *Bromus madritensis* ssp. *rubens* and *Eriogonum inflatum* at the Nevada Desert FACE Facility in 1998. Factors in the model are CO_2 (ambient or elevated) and phenology (pre- or post-anthesis). Response variables used in the analysis are V_{Cmax}, J_{max}, R_d, TPU, RSL, and Γ

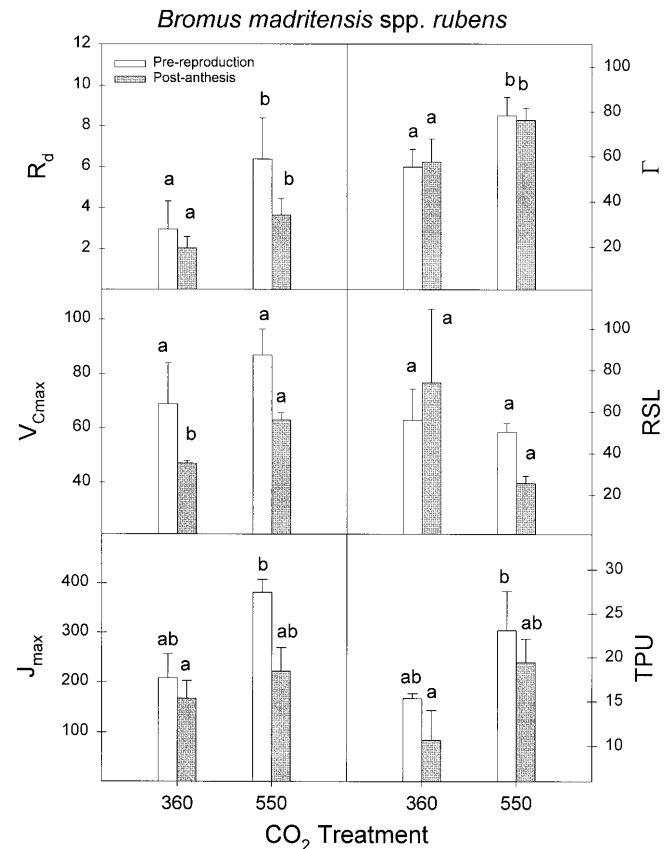| Effect	df	Wilk's lambda	P
Bromus madritensis ssp. *rubens*			
CO_2	3,6	0.033	0.03
Phenology	3,6	0.182	0.27
$CO_2 \times$phenology	3,6	0.246	0.39
Eriogonum inflatum			
CO_2	3,6	0.005	0.01
Phenology	3,6	0.005	0.01
$CO_2 \times$Phenology	3,6	0.344	0.56

Fig. 1 Parameters derived from the A-C$_i$ analysis for *Bromus madritensis* ssp. *rubens* during two phenological stages at the Nevada Desert FACE Facility during 1998. Significant differences among treatments groups are indicated by different *lowercase letters*. Data plotted are means±1 SE. Units for the different parameters are as follows: V_{Cmax}, μmol CO_2 m^{-2} s^{-1}; J_{max}, μmol electrons m^{-2} s^{-1}; R_d, μmol CO_2 m^{-2} s^{-1}; TPU, μmol CO_2 m^{-2} s^{-1}; Γ, μmol CO_2 mol^{-1}; RSL, %

efficiency of Rubisco. Biochemical samples determined from a small sample of leaves taken during the onset of flowering corroborated the parameters derived from gas exchange data (following the protocol outlined in Huxman et al. 1998c). Post-anthesis, V_{Cmax} at elevated

Table 2 A two-way ANOVA for each of the parameters from the A-C$_i$ analysis for *Bromus madritensis* ssp. *rubens* and *Eriogonum inflatum* from the Nevada Desert FACE Facility during 1998. Presented are the *F*-statistics for each parameter (* significant at α=0.05)

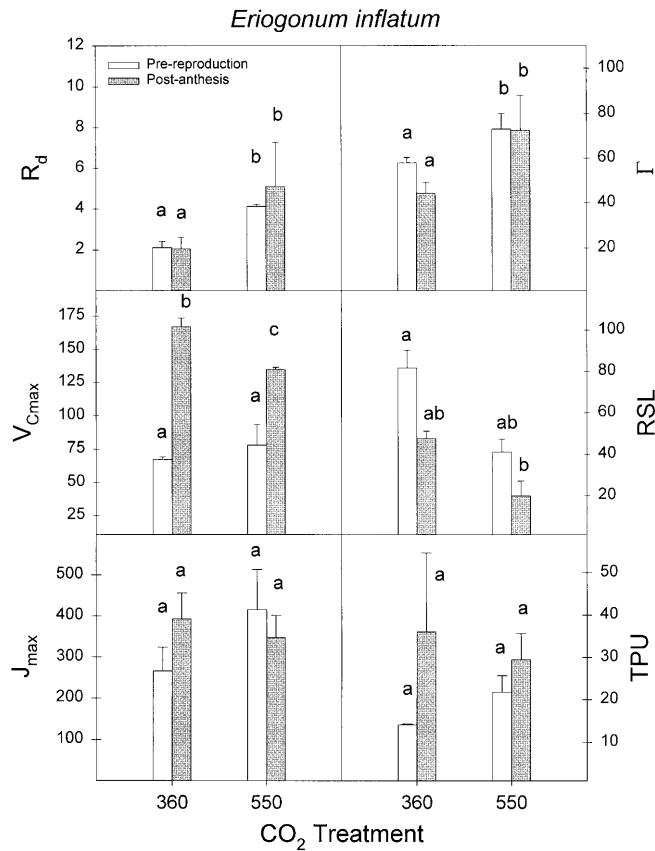| Factor	df	V_{Cmax}	J_{max}	TPU	R_d	RSL	Γ
Bromus madritensis ssp. *rubens*							
CO$_2$	1,8	4.71*	5.98*	5.53*	5.10*	2.05	6.22*
Phenology	1,8	7.10*	4.20*	1.99	1.17	0.99	0.01
CO$_2$×phenology	1,8	0.01	0.87	0.52	0.17	1.61	0.03
Eriogonum inflatum							
CO$_2$	1,8	0.48	0.59	0.49	4.46*	10.3*	6.0*
Phenology	1,8	49.8*	0.42	3.03	0.05	6.82*	1.39
CO$_2$×phenology	1,8	3.45*	1.92	0.52	0.01	0.50	0.68

Fig. 2 Parameters derived from the A-C$_i$ analysis for *Eriogonum inflatum* during two phenological stages at the Nevada Desert FACE Facility during 1998. Significant differences among treatments groups are indicated by different *lowercase letters*. Data plotted are means±1 SE. Units as in Fig. 1

Fig. 3 Maximum values of net assimilation (A_{net}) and stomatal conductance (g_s) determined from a diurnal assessment of gas exchange over the course of the 1998 growth season for *B. madritensis* ssp. *rubens* and *E. inflatum* at the Nevada Desert FACE Facility. Data plotted are means±1 SE

CO$_2$ was 34% greater than at ambient CO$_2$ for *Bromus* (Fig. 1), whereas the number of Rubisco active sites per unit chlorophyll at elevated CO$_2$ was 44% greater than at ambient CO$_2$. Leaf N for *Bromus* at this time period was 2.32±0.3 and 3.64±1.0 g g^{-1}, for ambient and elevated CO$_2$, respectively. For *Eriogonum*, the pattern was the opposite. V_{Cmax} at elevated CO$_2$ was 80% of ambient (Fig. 2) and Rubisco sites were 60% of ambient CO$_2$. Likewise, leaf N was 1.91±0.08 at elevated CO$_2$ and 2.09±0.08 at ambient CO$_2$ for this same time period in *Eriogonum*. The adherence of the gas exchange, leaf N, and Rubisco data to the same pattern suggests that the seasonal gas exchange data set may well reflect the leaf nitrogen status of these plants at ambient and elevated CO$_2$.
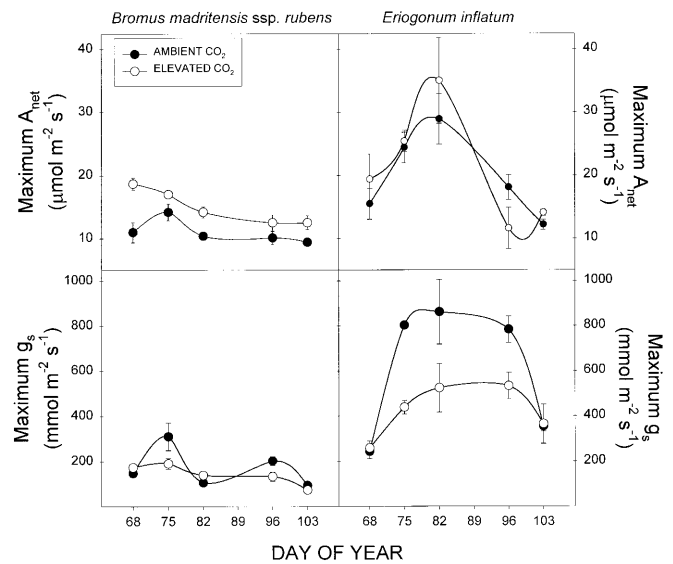
The maximum rate of electron transport (J_{max}) was also differentially affected by CO$_2$, depending upon species. For *Bromus*, there was a CO$_2$ effect (Table 2) that led to slightly greater (but not pairwise significantly different) values at elevated as compared to ambient CO$_2$ for both phenological periods (Fig. 1). However, there was a general decrease in J_{max} with the onset of reproduction, similar to the pattern in V_{Cmax} (Fig. 1). J_{max} was not significantly affected by either CO$_2$ growth environment or phenological stage in *Eriogonum* (Fig. 2). For both species, TPU behaved similarly to J_{max}. For *Eriogonum*, there were no clear effects of elevated CO$_2$ or phenology, but for *Bromus*, CO$_2$ had a significant effect. This effect led to greater J_{max} at elevated compared to ambient CO$_2$, regardless of phenological stage, with slight decreases in both treatments upon flowering (Table 2, Fig. 1).

Across nearly all day samples over the season, the maximum value of daily A_{net} was greater at elevated than at ambient CO$_2$ for *Bromus*, except for day 75, the date of maximum A_{net} in *Bromus* for the season (Fig. 3). As

Fig. 4 Diurnal values of A_{net} and g_s for *B. madritensis* ssp. *rubens* at elevated and ambient CO_2 in the Mojave Desert during the 1998 growth season. Data plotted are means±1 SE
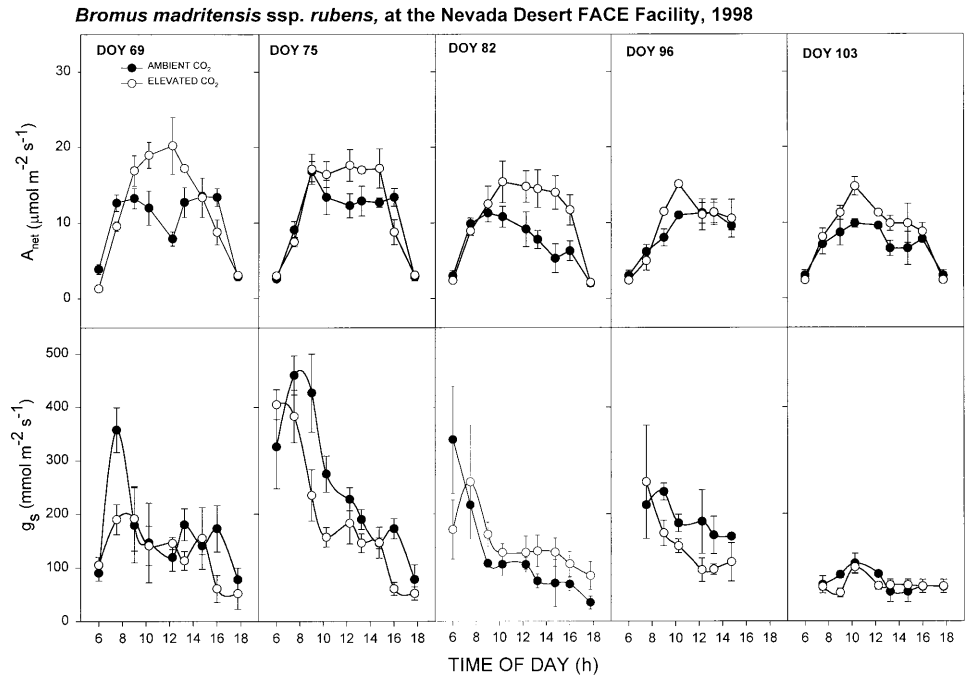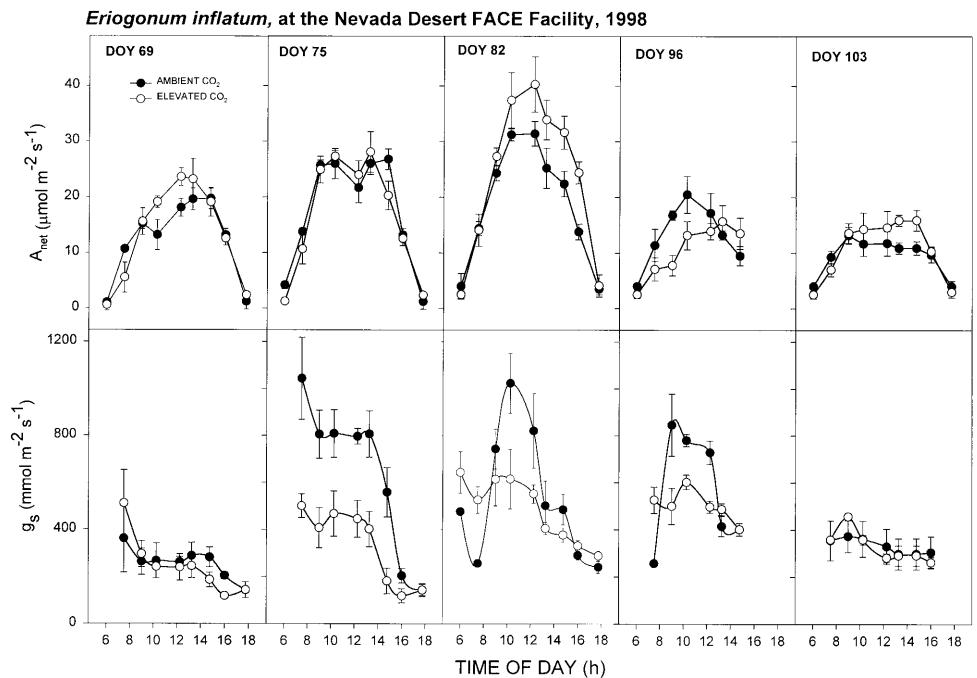

Diurnal values of A_{net} and g_s for *Bromus madritensis* ssp. *rubens*, at the Nevada Desert FACE Facility, 1998

Fig. 5 Diurnal values of A_{net} and g_s for *E. inflatum* at elevated and ambient CO_2 in the Mojave Desert during the 1998 growth season. Data plotted are means±1 SE

Diurnal values of A_{net} and g_s for *Eriogonum inflatum*, at the Nevada Desert FACE Facility, 1998

the season progressed, maximum A_{net} in the ambient-CO_2 plants slowly diminished, whereas at elevated CO_2, the overall seasonal decline occurred to a lesser extent. This may be illustrated by the significant $CO_2\times$time interaction on A_{net} in the repeated-measures ANOVA (Table 3), which may also be a function of the earlier peak in rates for elevated- compared to ambient-CO_2-grown plants. An interaction between time and CO_2 also existed for *Eriogonum* (Table 3), but the pattern of CO_2 stimulation was not the same as for *Bromus*. The only point where maximum A_{net} was greater at elevated as

compared to ambient CO_2 was the single point of peak photosynthetic activity in *Eriogonum* (Fig. 3). Elevated CO_2 did not change the seasonal pattern of increase and decline in maximum A_{net} for *Eriogonum*.

The trend of CO_2 effects on maximum stomatal conductance was opposite to that for A_{net} with respect to the two species studied here. In *Bromus*, there was a significant time×CO_2 effect (Table 3), which resulted in decreased g_s at elevated CO_2 early and again later in the season. For *Eriogonum*, there was a significant $CO_2\times$time interaction that led to a decrease in maximum

Table 3 A split-plot, repeated-measures ANOVA for net assimilation (A_{net}) and stomatal conductance (g_s) for *Bromus madritensis* ssp. *rubens* and *Eriogonum inflatum* from the Nevada Desert FACE Facility during 1998. These are the mean midday maximum values taken from diurnal estimates of gas exchange. Presented are the *F*-statistics for each parameter (* significant at $\alpha = 0.05$)

Factor	df	A_{net}	g_s
Bromus madritensis ssp. *rubens*			
CO_2	4,29	21.3*	11.7*
Time (day of year)	1,8	12.1*	12.4*
$CO_2 \times$ time	4,29	2.67*	8.78*
Eriogonum inflatum			
CO_2	4,29	0.9	103.5*
Time (day of year)	1,8	23.6*	56.5*
$CO_2 \times$ time	4,29	50.4*	9.7*

g_s during the middle portion of the season, when rates at ambient CO_2 were the greatest (Fig. 3).

These patterns of A_{net} and g_s can also be illustrated by the diurnal CO_2 effects throughout the season. In *Bromus*, regardless of the day of the year, A_{net} was higher and remained higher throughout much of the day at elevated compared to ambient CO_2 (Fig. 4). Stomatal conductance (g_s) was lower at elevated CO_2 on day 75 and 96, whereas on other days, there were no consistent CO_2 effects. *Eriogonum* showed the opposite patterns, with little consistent diurnal patterns in A_{net} with respect to CO_2, but significant reductions in g_s at elevated compared to ambient CO_2 (Fig. 5).

Discussion

The gas exchange properties (A-C$_i$ relationship, seasonal A_{net}, and g_s) of two ephemeral species growing in a whole-ecosystem CO_2-manipulation experiment in the Mojave Desert during the wet 1998 El Niño year were affected differently by growth at elevated CO_2 and phenological stage. Daily maximum A_{net} was greater throughout the season at elevated as compared to ambient CO_2 in *B. madritensis* ssp. *rubens* but not in *E. inflatum*, whereas elevated CO_2 reduced maximum g_s in *Eriogonum* but not in *Bromus*. Elevated CO_2 and phenology altered the functional components of the A-C$_i$ relationship in *Eriogonum*, whereas only CO_2 was a significant factor for *Bromus*. These differential responses are contrary to our original hypotheses concerning the effects of elevated CO_2 on photosynthetic patterns at different life cycle stages for these two Mojave Desert species.

Contrary to our original hypothesis of consistent prolonged down-regulation of photosynthesis at elevated CO_2, a downward adjustment of photosynthetic investment at elevated CO_2 was only noted at one phenological stage in either species. Investment in photosynthesis was not affected by phenology in *Bromus*. For *Bromus*, the maximum rate of carboxylation by Rubisco (V_{Cmax}) was not reduced by elevated compared to ambient CO_2 at any time. In fact, post-anthesis values of V_{Cmax} were significantly greater at elevated than at ambient CO_2 and these values did not differ from either CO_2 treatment value prior to flowering (Table 2, Fig. 1). Up-regulation of photosynthesis at elevated CO_2 has been noted in *Solanum tuberosum* (Sage et al. 1989), and the pattern of increased investment in photosynthesis late in the life cycle may be important for whole-plant performance in *Bromus* in a natural setting.

At post-anthesis, *Bromus* maintained high carbon fixation capacity at elevated CO_2, despite the onset of flowering. This is evident in the increasingly greater difference between elevated and ambient CO_2 for A_{net} through time (Figs. 3, 4). Increased photosynthetic rates late in the season have been noted in the tallgrass prairie (Knapp et al. 1993), but as a result of enhanced whole-plant water status, not an up-regulation of photosynthesis. Importantly, for *Bromus*, the temporal pattern of flowering relative to carbon gain potential of leaves was changed by growth at elevated CO_2. *Bromus* reached peak seed set earlier at elevated CO_2 and produced seeds of lesser quality (despite initiating flowering at similar points; T.E. Huxman, T. Charlet, S.F. Zitzer, S.D. Smith, unpublished data) but retained the ability to fix carbon after flowering. Thus the increased carbon gain potential of leaves late in the life cycle may be sequestering nitrogen resources from re-translocation to seeds. A decrease in seed N is the primary cause of that decrease in seed quality (Huxman et al. 1998b). How this decoupling of processes through phenology will affect the status of *Bromus* at elevated CO_2 with respect to future potential population dynamics is unclear, especially since *Bromus* dramatically increased in density at elevated CO_2 in 1998 (Smith et al. 2000).

Down-regulation of photosynthesis at elevated CO_2 was observed for *Eriogonum* following the initiation of flowering, similar to the general decreased investment in photosynthesis that has been seen in other species (Sage et al. 1989). V_{Cmax} was significantly lower at elevated than at ambient CO_2 (Fig. 2). This re-adjustment results in similar maximum A_{net} values across the two CO_2 growth environments through time (Figs. 3, 5). This differs from most other studies where instantaneous photosynthetic rates are greater than at ambient CO_2 despite down-regulation at elevated CO_2 (Curtis and Wang 1998). Here, the diurnal pattern of gas exchange results in increased carbon gain for the plant, but not instantaneous maximum rates, similar to that hypothesized by Harley (1995). In contrast to *Bromus*, elevated CO_2 did not appear to result in a de-coupling of the potential for carbon gain relative to flowering in *Eriogonum*.

Both species showed increases in day respiration (R_d) and CO_2 compensation point (Γ) at elevated CO_2 that were consistent across phenology (Figs. 1, 2). The increase in Γ can most likely be explained as a result of the increases in R_d. In this light, a greater proportion of energy acquired through photosynthesis is required to offset increases in respiration (increased Γ) in the leaf as a result of growth at elevated CO_2 (increased R_d). The

change in R_d is the opposite of that predicted by the general trend of a decrease in leaf N on an area basis at elevated CO_2 and a general trend among elevated-CO_2 studies (Curtis and Wang 1998). A decrease in R_d may have been expected, but instead we measured a slight increase. Estimation of R_d has been noted to be difficult (Harley et al. 1992), but the changes we measured through time are consistent with whole-plant activity in these species and the N content we measured in leaves post-anthesis. Additionally, *Bromus* showed decreases in R_d associated with senescence of leaf material and re-translocation of resources toward reproductive structures. *Eriogonum* did not show a change in R_d with phenology, as leaf function is maintained and the developing inflorescence has the ability to fix carbon independently (Osmond et al. 1987). These changes associated with R_d suggest the importance of placing potential CO_2 effects on net carbon assimilation in the context of life history strategy and plant functional type in natural ecosystems.

A decrease in relative stomatal limitations to photosynthesis (RSL), as observed in *Eriogonum*, has been noted in *Pinus taeda* (Lewis et al. 1994), in which the decrease in RSL was attributed to a decreased TPU capacity at elevated CO_2, changing the shape of the saturated region of the A-C_i curve. In *Eriogonum*, we did not see a specific effect of elevated CO_2 on TPU. However, slight decreases in V_{Cmax} and J_{max} along with non-significant changes in TPU could lead to a similar result, placing the operating C_i nearer the saturated region of the A-C_i response curve. The lack of an effect of CO_2 or phenology on RSL for *Bromus* may be due to the non-significant effects of time and CO_2 on stomatal behavior.

Bromus and *Eriogonum* represent different life history strategies that deal in different manners with the persistent drought conditions of deserts. As an annual, *Bromus* is a drought escaper that relies on seed production to persist in an episodic environment characterized by drought (Smith et al. 1997). In contrast, *Eriogonum* is a drought-evading perennial that finishes important phenological stages and senesces prior to the onset of persistent drought conditions, but can perennate with belowground structures. The species-specific response to elevated CO_2 suggests different potentials to maintain these two strategies in arid environments. The greatest relative effect of elevated CO_2 on *Bromus* was during seed development (largest difference in A_{net} and V_{Cmax}), and may have affected the ability of *Bromus* to produce seeds, reducing mean seed mass and subsequent seedling growth potential (Huxman et al. 1998b, 1999). Under field conditions, *Bromus* makes more seeds per individual and increases in density (Smith et al. 2000; T.E. Huxman, T. Charlet, S.F. Zitzer, S.D. Smith, unpublished data). How the decreased ability to produce quality seeds and changes in plant density will affect the ability of *Bromus* to persist in long protracted droughts is not clear, but understanding the long-term response of this invasive grass to elevated CO_2 and climate change will be important. *Eriogonum*, on the other hand, did not shift any characteristic relative to gas exchange or phenology, and thus maintained its important traits for persisting in the Mojave Desert at both ambient and elevated CO_2.

The results presented here have implications for the manner in which different plant types are represented in ecosystem production models and other simulations aimed at predicting the impacts of elevated CO_2. Unlike the expectation of consistent, sustained increases in A_{net} that may be expected in long-lived species of woody plants (Curtis and Wang 1998), our results suggest that changing resource conditions through ontogeny are potentially more important in shorter-lived species and for species in arid ecosystems (Huxman et al. 1998c; Hamerlynck et al. 2000b). Thus, for ecosystems where annual and short-lived perennial species are important components of the vegetation, such as deserts and annual grasslands, production models used to predict plant performance at elevated CO_2 must take into account transient periods of increased carbon gain and effects on phenology, and not simple enhancement over the duration of a growing season.

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