

Increases in Desert Shrub Productivity under Elevated Carbon Dioxide Vary with Water Availability

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ABSTRACT

Productivity of aridland plants is predicted to increase substantially with rising atmospheric carbon dioxide (CO₂) concentrations due to enhancement in plant water-use efficiency (WUE). However, to date, there are few detailed analyses of how intact desert vegetation responds to elevated CO₂. From 1998 to 2001, we examined aboveground production, photosynthesis, and water relations within three species exposed to ambient (around 38 Pa) or elevated (55 Pa) CO₂ concentrations at the Nevada Desert Free-Air CO₂ Enrichment (FACE) Facility in southern Nevada, USA. The functional types sampled—evergreen (*Larrea tridentata*), drought-deciduous (*Ambrosia dumosa*), and winter-deciduous shrubs (*Krameria erecta*)—represent potentially different responses to elevated CO₂ in this ecosystem. We found elevated CO₂ significantly increased aboveground production in all three species during an anomalously wet year (1998), with relative production ratios (elevated:ambient CO₂) ranging from 1.59 (*Krameria*) to 2.31 (*Larrea*). In three below-average rainfall years (1999–2001), growth was much reduced in all species, with only *Ambrosia* in 2001 having significantly higher production under elevated CO₂. Integrated photosynthesis (mol CO₂ m⁻² y⁻¹) in the three species was 1.26–2.03-

fold higher under elevated CO₂ in the wet year (1998) and 1.32–1.43-fold higher after the third year of reduced rainfall (2001). Instantaneous WUE was also higher in shrubs grown under elevated CO₂. The timing of peak canopy development did not change under elevated CO₂; for example, there was no observed extension of leaf longevity into the dry season in the deciduous species. Similarly, seasonal patterns in CO₂ assimilation did not change, except for *Larrea*. Therefore, phenological and physiological patterns that characterize Mojave Desert perennials—early-season lags in canopy development behind peak photosynthetic capacity, coupled with reductions in late-season photosynthetic capacity prior to reductions in leaf area—were not significantly affected by elevated CO₂. Together, these findings suggest that elevated CO₂ can enhance the productivity of Mojave Desert shrubs, but this effect is most pronounced during years with abundant rainfall when soil resources are most available.

Key words: *Ambrosia dumosa*; desert productivity; elevated carbon dioxide; *Krameria erecta*; *Larrea tridentata*; Mojave Desert; photosynthesis; water-use efficiency.

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INTRODUCTION

Photosynthetic rate and biomass production increase in most ecosystems under elevated

atmospheric concentrations of carbon dioxide (CO_2) (Drake and others 1997; Nowak and others 2004a). Nonforest terrestrial ecosystems (that is, deserts, tundra, grasslands, and savannas) account for approximately 36% of the global carbon (C) budget (Allen-Diaz and others 1996), and although deserts alone occupy nearly one-third of the terrestrial biosphere (Noble and others 1996), their productivity is among the lowest of any ecosystem type (Smith and others 1997). Even so, deserts are predicted to be among the most responsive ecosystem types to elevated CO_2 due to improved water-use efficiency (WUE, Melillo and others 1993).

Studies of plant responses to elevated CO_2 have revealed inconsistent enhancement in plant growth parameters due to annual fluctuations in water availability and temperature (Drake and others 1996; Koch and Mooney 1996; Owensby and others 1996) and age-related responses (Hättenschwiler and others 1997; Idso 1999). Elevated CO_2 reduces stomatal conductance in some desert perennials (Nowak and others 2001), which may ease water stress and promote increased growth. The water savings realized through reduced conductance under elevated CO_2 could increase leaf area and extend the growing season in water-limited regions (Strain and Bazzaz 1983), making desert ecosystems potentially less "surface-limited" in terms of leaf area (Smith and others 1997). However, adequate inputs of precipitation necessary for growth are highly variable from year to year in desert systems. Moreover, when sufficient rainfall does occur, enhanced demand for other resources may elicit new limits to plant production, such as nutrient limitations (Romney and others 1978; Smith and others 1997).

The timing of phenological events in the Mojave Desert is driven largely by precipitation and temperature (Ackerman and Bamberg 1974; Beatley 1974; Turner and Randall 1987; Esler and Rundel 1999). Prior phenological work has also shown that water, nitrogen (N), and temperature interact to influence leaf demography and morphology of woody perennials in North American deserts (Cunningham and others 1979; Nilsen and others 1986; Lajtha and Whitford 1989). Deciduous desert shrubs typically have early-season phenological constraints on C gain because canopy development often lags behind peak photosynthetic performance (Comstock and others 1988), whereas later in the growing season, water-stress-induced reductions in photosynthetic capacity occur prior to reductions in leaf area and thus result in physiological constraints on productivity (Comstock and Ehleringer 1986). Evergreen species may also show similar lags in leaf

development and photosynthetic performance after precipitation inputs as well as in stress-induced reductions in C assimilation as soil moisture declines (Cunningham and others 1979; Lajtha and Whitford 1989). However, phenological constraints for evergreen shrubs may be less than that of deciduous shrubs because the former are more drought tolerant and retain leaves that can respond immediately to unpredictable precipitation. Thus, individual species and functional types may respond quite differently to elevated CO_2 due to differences in phenological responses to water availability (Kemp 1983; Turner and Randall 1987) and inherent physiological differences in the ability to concentrate CO_2 at the site of carboxylation (Bowes 1993).

We examined how the productivity of woody perennials in the Mojave Desert responds to elevated CO_2 as a function of infrequent and unpredictable precipitation inputs that characterize this ecosystem. We focused on three species of shrubs that differ in seasonal phenology, examining new shoot production, leaf area, and photosynthetic gas exchange over 4 years during a long-term CO_2 experiment at the Nevada Desert Free-Air CO_2 Enrichment (FACE) Facility. Because plant growth is not CO_2 saturated under current atmospheric concentrations, we hypothesized that elevated CO_2 would increase photosynthesis as a result of greater WUE, leading to enhanced leaf area and aboveground production (Hypothesis 1). Due to known enhancements in WUE under elevated CO_2 , we hypothesized the stimulatory effects of elevated CO_2 on relative plant production (elevated:ambient CO_2) would be greatest in drier years when water was most limiting (Hypothesis 2). Phenologically, we hypothesized that retention of leaf area into the dry season is greater under elevated CO_2 as a consequence of prolonged water availability resulting from the enhancement of WUE (Hypothesis 3). Water availability is vital to our predictions, because year-to-year variability in precipitation is expected to strongly interact with CO_2 to affect gas exchange, nutrient availability, and productivity. We therefore tested these hypotheses over a 4-year period of one high rainfall year followed by three relatively dry years.

METHODS

Research was conducted at the Nevada Desert FACE Facility (NDFF) located within the Nevada Test Site, southern Nevada, USA ($36^{\circ}49'N$,

115°55'W, 965–970 m elevation). Three shrubs common to this ecosystem were chosen: *Larrea tridentata* (evergreen), *Ambrosia dumosa* (drought-deciduous), and *Krameria erecta* (winter-deciduous). We sampled naturally occurring individuals within three ambient (37.9 ± 1.4 Pa CO₂) and three elevated CO₂ plots (set point: 55.0 Pa; mean: 54.4 ± 3.2 Pa at temperatures $>4^{\circ}\text{C}$). Each plot is 25 m in diameter and surrounded with a plenum and 32 riser tubes that deliver ambient or elevated [CO₂] air; an additional three ambient plots lacking the CO₂ delivery system act as blower controls. We found no significant difference between the ambient-air and blower control plots for any of the parameters measured, so we present only data on the former. Adult shrub densities for *Larrea*, *Ambrosia*, and *Krameria* in the plots are 0.05, 0.11, and 0.04 plants m⁻², respectively. For a complete site description, including species composition, density, cover, and the FACE delivery system, see Jordan and others (1999).

Aboveground morphological attributes were measured on three marked shoots per shrub for three shrubs per species per plot. Permanent marks were placed near a shoot terminus prior to the start of the growing season using a nontoxic permanent marker. For each marked shoot, shoot diameter, length (from the mark to shoot tip, including any side branches), and leaf number were recorded every 2–4 weeks during the active growing season. Growth data (diameter + length) were converted to measures of shoot biomass via regressions derived from shoots harvested during gas-exchange campaigns. Separate length versus biomass regressions were used for elevated and ambient CO₂ grown plants.

For each marked shoot, we calculated peak and total annual leaf area development during a wet (1998) and dry (2001) year based on leaf counts, using the relationship of leaf number to leaf area created from stems harvested during gas exchange campaigns. To determine the percent of maximum yearly canopy development at each sampling period, we divided the leaf area of each stem at each sampling period by the maximum leaf area for that stem in that year, and we plotted these data as the percent of maximum leaf area using plot means. Detailed seasonal patterns are not reported for the intervening very dry years (1999, 2000) due to extremely low production in these years (see Smith and others 2000).

Over the 1998 and 2001 growing seasons, diurnal gas exchange was measured at biweekly to monthly intervals on one stem per shrub for three shrubs per species within a single ambient and

elevated CO₂ plot. Because of the time required to access the pivoting walkways in each plot—see Jordan and others (1999) for a description of these walkways—we could not conduct multispecies diurnals on all six plots, resulting in pseudoreplication for this set of measurements.

Instantaneous WUE for each species \times CO₂ treatment was calculated using the ratio of photosynthesis to stomatal conductance at 0900 hours because of the strong correlation between daily integrated photosynthesis and midmorning photosynthetic rates (Naumburg and others 2003). We estimated annual photosynthetic carbon assimilation (mol CO₂ m⁻² y⁻¹) by plotting mean daily integrated photosynthesis (A_{day}) values and integrating the area under each curve for each species \times CO₂ treatment. These data gave us a single estimate for each species under ambient and elevated CO₂ from which we then calculated the relative enhancement ratio (elevated:ambient CO₂) of annual photosynthesis under elevated CO₂.

Statistical Analyses

We examined the main effects and interactions of CO₂, species and year using mixed-model analysis of variance (ANOVAs), (SAS Institute, Cary, NC, USA). Annual aboveground production was tested from 1998 to 2001 using plot means ($n = 3$ plots per CO₂ treatment, consisting of $n = 3$ plants per species per plot and $n = 3$ shoots per plant). Due to brief growing seasons in 1999 and 2000, peak and total leaf area, leaf [N], and WUE data were tested across a relatively wet (1998) and dry (2001) year only, using plot means for peak and total leaf area from all plots and $n = 3$ plants per species for a single plot for leaf [N] and WUE data collected from the diurnal gas exchange measurements. For each species, we also analyzed canopy development (that is, annual leaf area development) during 1998 and 2001, using CO₂, date, and their interaction as model effects. When overall significant differences were found, we used Tukey–Kramer post hoc tests (Sokal and Rohlf 1997) to compare means. All data were checked for violation of statistical assumptions and appropriately transformed if necessary. Due to high inherent variability at this desert site, we report $P < 0.10$ as significant. For photosynthetic enhancement ratios, because each species had only a single value for annual photosynthesis at ambient and elevated CO₂, we could not statistically analyze this parameter as we could other variables and thus only report the ratio.

Table 1. Hydrologic Year Precipitation for the Nevada Desert Free-Air CO₂ Enrichment (FACE) Facility and Percent of Long-term Mean Precipitation for Each Year

Hydrologic Year	Total Precipitation (mm)	Pre- growing Season	Growing Season	Post-growing Season	Mean Soil Moisture (%)
1998	309 (239%)	135 (44%)	107 (35%)	67 (22%)	6.6 (4.2–8.9)
1999	107 (83%)	17 (16%)	47 (44%)	43 (40%)	5.1 (4.9–5.5)
2000	98 (76%)	56 (57%)	24 (24%)	18 (18%)	6.3 (5.6–6.9)
2001	102 (79%)	70 (69%)	16 (16%)	16 (16%)	5.6 (3.9–7.7)

Total precipitation from October 1 of the preceding year to September 30 of the year is shown.

Also shown is precipitation during the pre-growing season (October 1–February 28), growing season (March 1–June 30), and post-growing season (July 1–September 30), with percent of hydrologic year rainfall in parentheses.

Mean site soil moisture and seasonal range of soil moistures at 0–0.5 m (in parentheses) during the year are from Nowak and others 2004b.

RESULTS

Annual Variations in Precipitation

The 1998 growing season was characterized by an exceptionally wet El Niño year, with 2.4-fold higher rainfall than the long-term average (129 mm); it was followed by three below-average rainfall years that were 76–83% of the long-term mean (Table 1). The 1998, 2000, and 2001 hydrologic years (that is, October 1 of the preceding year to September 30 of that year) had the typical seasonal precipitation pattern, with the greatest percentage of rainfall occurring during the fall and winter time period that precedes the time of major growth for perennials. In the 2001 hydrologic year, 70% of the precipitation was received before March. In contrast, 1999 was an exceptionally dry pre-growing season, with only 17 mm of rainfall during the first 5 months of the hydrologic year (Table 1). Soil volumetric moisture in the surface 50 cm (TDR) as well as surface 1.85 m (neutron probe) depth profiles did not significantly differ between ambient and elevated CO₂ plots over the course of our study (Nowak and others 2004b), so we report overall site means only (Table 1).

Plant Production

For all three shrub species in 1998, and *Ambrosia* in 2001, new shoot production under elevated CO₂ was significantly greater than that under ambient CO₂ (Figure 1, Table 2). For example, during the wet year (1998), mean peak biomass production for *Larrea* was 244 and 562 mg shoot⁻¹ at ambient and elevated CO₂, respectively; for *Ambrosia*, 22 and 48 mg shoot⁻¹ at ambient and elevated CO₂, respectively; and for *Krameria*, 29 and 45 mg shoot⁻¹ at ambient and elevated CO₂, respectively (Figure 1). In the subsequent, below-average rainfall years (1999–2001), all shrubs had much smaller incre-

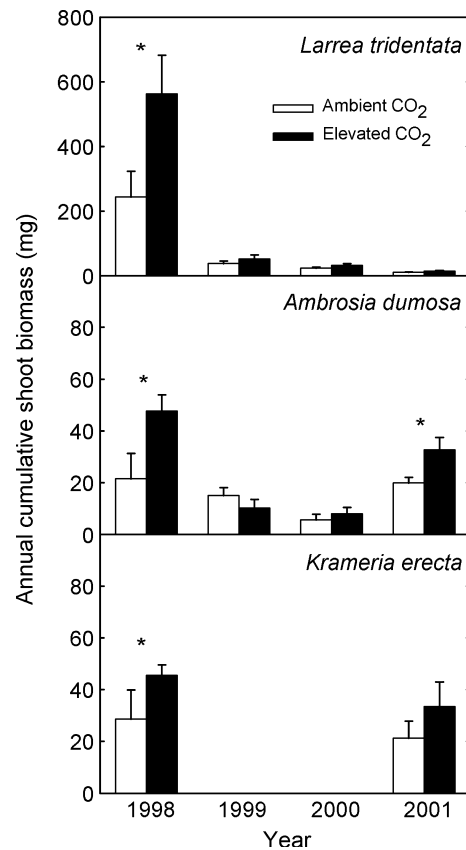


Figure 1. Cumulative shoot production of *Larrea tridentata* (top), *Ambrosia dumosa* (middle), and *Krameria erecta* (bottom) from 1998 to 2001 at the Nevada Desert FACE Facility. Open bars represent ambient CO₂; filled bars represent elevated CO₂. Error bars represent ± 1 SE. Asterisks indicate significantly greater production under elevated CO₂ at $P < 0.10$. Note different ordinate scales. Due to sampling constraints, *Krameria* was not measured in 1999 and 2000.

ments of growth, and some individuals lost biomass through abscission of smaller stems, resulting in a significant CO₂ \times year interaction (Table 3). Still,

Table 2. Relative Enhancement Ratios (Elevated: Ambient CO₂) for Aboveground Production, Peak and Total Leaf Area Produced Per Measured Shoot, Leaf Nitrogen Concentration, Annual Integrated CO₂ Assimilation, and Average Instantaneous Water-use Efficiency (WUE) for Three Shrub Species at the Nevada Desert FACE Facility during Above- (1998) and Below-average (2001) Rainfall Years

Species	Year	Production	Peak Leaf Area	Leaf Area	Leaf Nitrogen content	Photosynthesis	WUE
<i>Larrea tridentata</i>	1998	2.31	2.96	1.18	0.91	1.26	1.38
	2001	1.31	0.93	0.92	0.87	1.37	1.80
<i>Ambrosia dumosa</i>	1998	2.22	1.00	1.06	0.92	2.03	1.23
	2001	1.64	1.24	1.28	0.81	1.32	1.76
<i>Krameria erecta</i>	1998	1.59	1.60	1.10	0.79	1.42	1.40
	2001	1.57	1.58	1.33	0.94	1.43	1.33

Instantaneous WUE values are from measurements reported in Naumburg and others (2003) and were determined during the day at 0900 hours because photosynthetic rates at that time were highly correlated with daily integrated photosynthesis.

Table 3. ANOVA Results for Aboveground Production of Three Shrub species during 4 Years at the Nevada Desert FACE Facility

Main Effects and Interactions	df	F	P
[CO ₂]	1, 37	5.60	0.0233
Species	2, 37	42.93	<0.0001
Year	3, 37	45.20	<0.0001
Species × CO ₂	2, 37	0.46	0.6378
Year × CO ₂	3, 37	2.80	0.0532
Year × Species	4, 37	25.38	<0.0001
Year × Species × CO ₂	4, 37	0.81	0.5271

Shown are degrees of freedom (df), F-ratios, and level of significance ($P < 0.10$ in boldface type).

new shoot production was significantly greater in *Ambrosia* under elevated CO₂ in 2001 (mean peak biomass production = 21 and 33 mg shoot⁻¹ at ambient and elevated CO₂, respectively; Figure 1), and *Ambrosia* had greater growth than *Larrea*, resulting in a significant species × year interaction (Table 3). Furthermore, relative aboveground production ratios (that is, aboveground production at elevated CO₂ divided by that at ambient CO₂) were, with only one exception (*Ambrosia* in 1999), stimulated under elevated CO₂ regardless of annual rainfall (Table 2). Overall, elevated CO₂ resulted in a 1.59- to 2.31-fold enhancement across the three species in aboveground production during 1998, whereas biomass enhancement in 2001 was smaller, ranging from 1.31 in *Larrea* to 1.64 in *Ambrosia* (Table 2).

Enhancement of leaf area production under elevated CO₂ was inconsistent with that of shoot production, indicating that some enhancements in aboveground production were due to increased stem rather than leaf production. Peak leaf production in 1998 was 2.96-fold greater in *Larrea*, 60% greater in *Krameria*, and not different in

Ambrosia under elevated versus ambient CO₂; in 2001 peak leaf production was 24% greater in *Ambrosia*, 58% greater in *Krameria*, and not significantly different in *Larrea* at elevated CO₂. Although *Larrea* had the highest peak leaf production during 1998 and lowest during 2001, resulting in a significant species × year interaction, *Krameria* and *Ambrosia* differed in peak leaf production by [CO₂], resulting in a significant species × CO₂ interaction (Table 4). *Larrea* showed the greatest relative enhancement in total annual leaf area production during the high rainfall year, whereas *Ambrosia* and *Krameria* had greater total annual leaf area enhancement in a relatively low rainfall year (Table 2). Similar to peak leaf production, total annual leaf area production had significant species × CO₂ and species × year interactions (Table 4).

Leaf number per unit stem length showed a recurring pattern in *Ambrosia*, where for every year except 1999 individuals had significantly lower leaf numbers per unit stem length under elevated CO₂ (3.7 and 2.6 leaves cm⁻¹ stem length in ambient versus elevated CO₂, respectively; $P < 0.05$), indicating the greater aboveground production in 1998

Table 4. ANOVA Results for Peak and Total Leaf Area, Leaf Nitrogen Content, and WUE for Three Shrub Species during 1998 and 2001 at the Nevada Desert FACE Facility

Main Effects and Interactions		<i>df</i>	<i>F</i>	<i>P</i>
Peak Leaf Area	[CO ₂]	1, 24	24.48	<0.0001
	Species	2, 24	17.58	<0.0001
	Year	1, 24	55.02	<0.0001
	Species × CO ₂	2, 24	15.40	<0.0001
	Year × CO ₂	1, 24	0.27	0.6050
	Year × Species	2, 24	69.55	<0.0001
	Year × Species × CO ₂	2, 24	1.67	0.2102
Total Leaf Area	[CO ₂]	1, 24	67.95	<0.0001
	Species	2, 24	130.16	<0.0001
	Year	1, 24	22.13	<0.0001
	Species × CO ₂	2, 24	84.01	<0.0001
	Year × CO ₂	1, 24	0.24	0.6319
	Year × Species	2, 24	16.09	<0.0001
	Year × Species × CO ₂	2, 24	0.32	0.7287
Leaf Nitrogen Content	[CO ₂]	1, 165	15.00	0.0002
	Species	2, 165	22.54	<0.0001
	Year	1, 165	18.88	<0.0001
	Species × CO ₂	2, 165	0.02	0.9773
	Year × CO ₂	1, 165	0.01	0.9115
	Year × Species	2, 165	8.77	0.0002
	Year × Species × CO ₂	2, 165	1.03	0.3598
WUE	[CO ₂]	1, 42	29.78	<0.0001
	Species	2, 42	13.71	<0.0001
	Year	1, 42	62.23	<0.0001
	Species × CO ₂	2, 42	0.18	0.8333
	Year × CO ₂	1, 42	1.66	0.2044
	Year × Species	2, 42	7.70	0.0014
	Year × Species × CO ₂	2, 42	0.93	0.4031

Shown are (*df*), *F*-ratios, and level of significance (*P* < 0.10 in boldface type).

and 2001 at elevated CO₂ was due to greater stem production. *Larrea* under elevated CO₂ had fewer leaves per unit stem length in April 2000 (6.0 and 4.6 leaves cm⁻¹ stem length in ambient versus elevated CO₂, respectively; *P* < 0.05), but this difference disappeared by May (4.6 and 4.2 leaves cm⁻¹ stem length in ambient versus elevated CO₂, respectively; *P* > 0.10). No other species showed significant differences in this variable.

Leaf Nitrogen Content, Canopy Development, and Gas Exchange

Leaf N content per unit mass was significantly greater under ambient versus elevated CO₂ (Table 4). All three species significantly differed in leaf N, with highest mean values in *Ambrosia*, intermediate values in *Larrea*, and lowest values in *Krameria*. Years also significantly differed, with higher leaf N content in the dry (2001) versus wet

(1998) year. A significant species × year interaction resulted from increased leaf N in *Ambrosia* and *Krameria* in 2001, whereas *Larrea* showed no change. In 1998, leaf N values were 2.43 and 2.20% (*Larrea*), 2.36 and 2.16% (*Ambrosia*), and 1.92 and 1.52% (*Krameria*) in ambient and elevated CO₂, respectively. In 2001, leaf N values were 2.37 and 2.07% (*Larrea*), 3.45 and 2.79% (*Ambrosia*), and 2.22 and 2.08% (*Krameria*) in ambient and elevated CO₂, respectively.

Canopy development for all three shrubs during relatively wet (1998) and dry (2001) years generally were not significantly different between ambient and elevated CO₂ treatments (Figures 2, 3). We found no significant CO₂ × time interaction for *Larrea* canopy development in 1998 (Figure 2; *P* > 0.10), and development of canopy leaf area for ambient CO₂ paralleled that for elevated CO₂, with both treatments peaking in October 1998. In 2001, timing of peak canopy development also did not

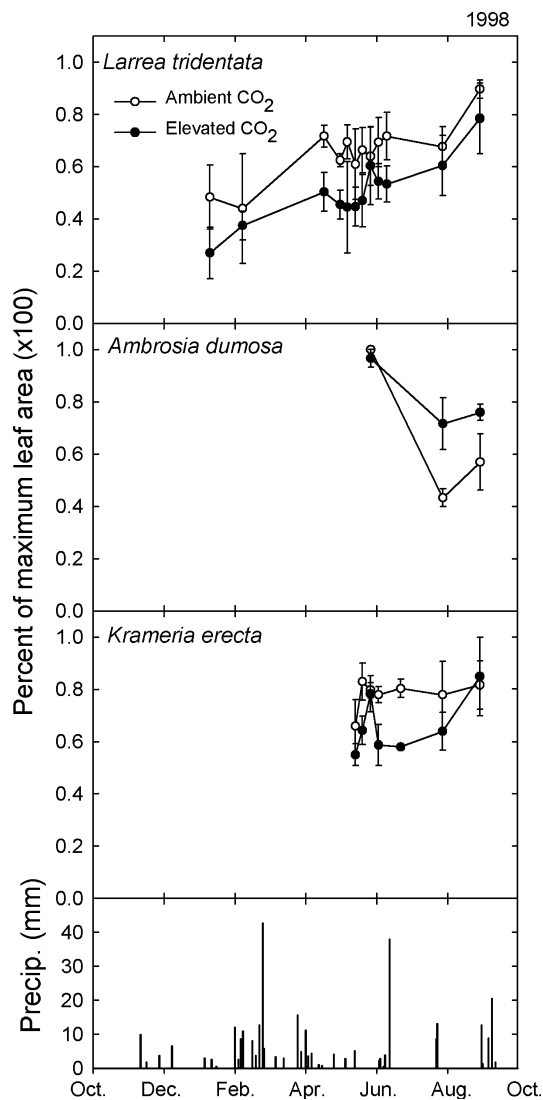


Figure 2. Canopy development, as percent maximum leaf area per shoot, for three shrub species at the Nevada Desert FACE Facility during a relatively wet year (1998): *Larrea tridentata* (top), *Ambrosia dumosa* (middle), and *Krameria erecta* (bottom). Open circles represent ambient CO₂; filled circles represent, elevated CO₂. Error bars represent ± 1 SE. Shown at bottom are precipitation events during the hydrologic year. Note: Mean peak leaf area for shoots measured under ambient and elevated CO₂, respectively, were 14.1 and 41.7 cm² (*Larrea*), 1.7 and 1.7 cm² (*Ambrosia*), and 2.0 and 3.2 cm² (*Krameria*).

differ between ambient-CO₂ and elevated-CO₂ grown *Larrea* (Figure 3; $P > 0.10$), with peak canopy development occurring in May. Due to constraints imposed by sampling multiple species within a given time period, *Ambrosia* canopy development was not measured during the main portion of the 1998 growing season, but late-season canopy development did not differ by CO₂ or the CO₂ \times time interaction (Figure 2; $P > 0.10$). In 2001, peak

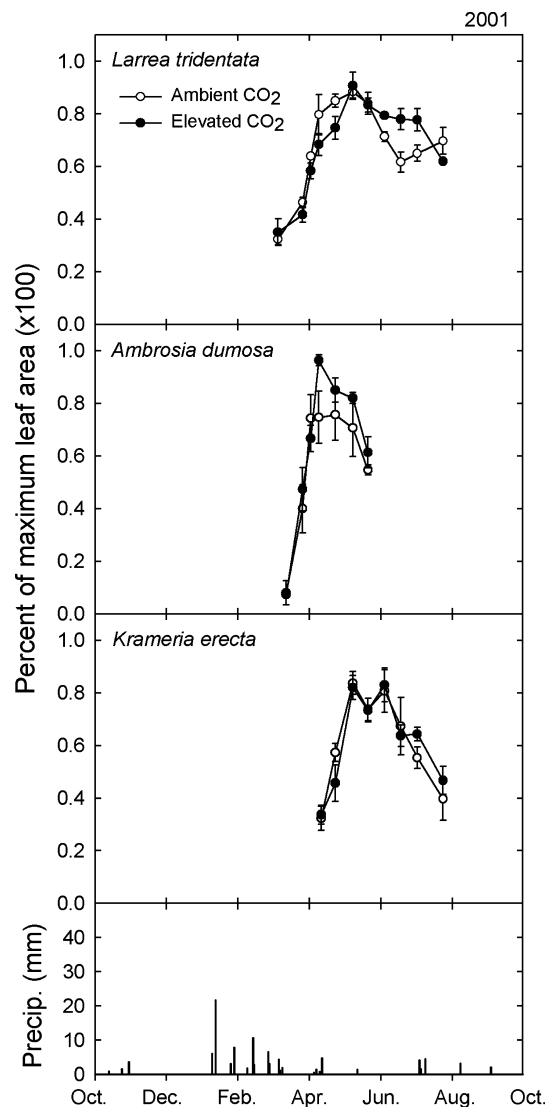


Figure 3. Canopy development, as percent maximum leaf area per shoot, for three shrub species at the Nevada Desert FACE Facility during a relatively dry year (2001). All legends are as in Figure 2. Shown at bottom are precipitation events during the hydrologic year. Note: Mean peak leaf area for shoots measured under ambient and elevated CO₂, respectively, were 1.4 and 1.3 cm² (*Larrea*), 2.1 and 2.6 cm² (*Ambrosia*), and 1.2 and 1.9 cm² (*Krameria*).

canopy development in *Ambrosia* occurred in April and did not significantly differ in its timing between CO₂ treatments (Figure 3; $P > 0.10$), and there was also no significant CO₂ \times time interaction on canopy development ($P > 0.10$). In 1998, timing of peak canopy development did not differ in *Krameria* by CO₂ treatment, although a CO₂ \times time interaction indicated that the 37% greater canopy leaf area at ambient versus elevated CO₂ during July and August was significant (Figure 2). In 2001, we

found no significant difference in canopy development for *Krameria* between CO₂ growth environments (Figure 3).

Integrated photosynthesis during 1998 averaged 53.6 and 67.8 mol CO₂ m⁻² y⁻¹ for ambient- and elevated-CO₂ grown *Larrea*, respectively, indicating a 26% enhancement of annual CO₂ assimilation at elevated CO₂ (Table 2). In the below-average rainfall year of 2001, integrated photosynthesis in *Larrea* averaged only 27.1 and 37.0 mol CO₂ m⁻² y⁻¹ for ambient and elevated CO₂ plants, respectively. However, the greater disparity in integrated photosynthesis between CO₂ treatments during the drier year resulted in a 37% enhancement in annual CO₂ assimilation at elevated CO₂. Integrated photosynthesis in *Ambrosia* during 1998 averaged 20.6 and 41.7 mol CO₂ m⁻² y⁻¹ at ambient and elevated CO₂, respectively, resulting in an approximate two fold enhancement in carbon assimilation at elevated CO₂. As with *Larrea* in 2001, *Ambrosia* in both CO₂ treatments in 2001 showed reduced annual CO₂ assimilation (18.9 and 25.1 mol CO₂ m⁻² y⁻¹, respectively). *Krameria* in 1998 had integrated photosynthesis values of 28.0 and 39.9 mol CO₂ m⁻² y⁻¹ at ambient and elevated CO₂, respectively, indicating a 42% enhancement in annual photosynthesis at elevated CO₂ (Table 2). Annual CO₂ assimilation in *Krameria* during 2001 was also reduced in both CO₂ environments (17.6 and 25.2 mol CO₂ m⁻² y⁻¹, respectively), but it had a similar enhancement at elevated CO₂ to that during 1998 (Table 2).

In all species, we previously reported diurnal C assimilation was higher under elevated versus ambient CO₂, and photosynthetic rates at 0900 hours (peak daily rate) were strongly correlated with daily integrated photosynthesis (Naumburg and others 2003). Instantaneous WUE at 0900 hours was significantly higher under elevated versus ambient CO₂ (Table 3) as a result of both higher CO₂ assimilation and lower conductance, the latter of which occurred only in *Larrea* during periods of relatively high soil moisture. WUE was also significantly greater during a relatively low (2001) versus high (1998) rainfall year, and differed by species, with both *Larrea* and *Krameria* having higher WUE than *Ambrosia*. A significant species × year interaction resulted from a greater absolute increase in overall WUE for *Krameria* versus *Larrea* in 2001. The enhancement ratios (elevated:ambient CO₂) for WUE were considerably higher during 2001 versus 1998 for both *Larrea* and *Ambrosia*, whereas the summer-active *Krameria* showed little difference in WUE enhancement ratios between years (Table 2).

DISCUSSION

It has been well documented that elevated atmospheric CO₂ can enhance plant WUE (Bazzaz 1990; Bowes 1993), leading to predictions that future CO₂ concentrations will reduce water limitations and enhance net primary production in water-limited ecosystems (Mooney and others 1991; Melillo and others 1993). Increased productivity under elevated CO₂ has been found in many ecosystem types (Nowak and others 2004a), including forests (DeLucia and others 1999; Norby and others 2002), grasslands (Owensby and others 1996), and deserts (Smith and others 2000). However, the duration of this enhancement is highly variable, lasting from only a few years in arctic vegetation exposed to a step-change increase in [CO₂] (Oechel and Vourlitis 1996), to decades in evergreen oaks exposed to a natural high [CO₂] source (Hättenschwiler and others 1997). Yearly changes in abiotic factors (for example, water and nutrient availability) can also contribute to variability in plant productivity under elevated CO₂ (Loustau and others 2001). Likewise, biotic factors such as invasive species and anthropogenic activities (for example, grazing or soil disturbance events) may interact with atmospheric CO₂ concentration to alter productivity, especially in dry ecosystems (Belnap 1995; Smith and others 2000; Ehleringer 2001). At the Nevada Desert FACE Facility over a 4-year period, we found elevated CO₂ increased C assimilation rates, aboveground growth, and WUE in desert shrubs as hypothesized. However, contrary to our second hypothesis, the greatest relative increases in these variables were not in dry years, when we expected that enhancements in WUE would have been greatest (Table 2).

In the high rainfall year (1998), we found significantly more new shoot production (around 2,400 g m⁻² in *Larrea*, 490 g m⁻² in *Ambrosia*, and 380 g m⁻² in *Krameria*) at elevated CO₂ (Figure 1, Table 2). In contrast, the stimulation of aboveground productivity by elevated CO₂ in all three species was lower during the subsequent below-average rainfall years (in 2001: around 60 g m⁻² in *Larrea*, 340 g m⁻² in *Ambrosia*, and 280 g m⁻² in *Krameria*). We also witnessed some individual plants that senesced smaller stems, perhaps due to localized xylem cavitation or as an adaptation to maintain water balance (Orshan 1954; Smith and others 1997). Nonetheless, the ratios of elevated-to-ambient production usually indicated positive enhancement of growth under elevated CO₂, and the overall CO₂ effect was significant (Table 3). The generally lower enhancement of production under

elevated CO₂ for *Krameria* may be the result of its phenology—summer-active *Krameria* is expected to have greater respiratory losses due to higher temperatures and hence lower net annual C assimilation. Mean annual temperatures were coolest in the high-growth year (13.2°C, with the minimum and maximum monthly temperatures similar to the long-term average) and near the long-term average (16.2°C) during the three subsequent dry years. Likewise, rainfall the year prior to our study was similar to the long-term average, so the increase in aboveground production we measured in 1998 was not due to anomalous rainfall in the previous year altering soil nutrient pools or potentially “setting up” meristems for a high-growth year. Measures of root growth at the NDFP have not shown a significant difference in belowground shrub production under elevated CO₂ (D. Phillips and R. Nowak, unpublished data), so our findings are not due to shifts in biomass allocation from above- to belowground structures.

Primary production in *Larrea*, and desert productivity in general, is limited by low standing biomass and leaf area (Chew and Chew 1965; Webb and others 1983; Smith and others 1997). Low water availability is typically considered the primary cause for low leaf area and productivity in desert ecosystems (Smith and others 1997), but N availability also limits production of desert perennials (Ettershank and others 1978; Fisher and others 1988). The greater stimulation of aboveground production under elevated CO₂ in the high rainfall year (1998) could be due to greater N availability when soil moisture is high, permitting plants to exploit elevated CO₂ concentrations and hence increase growth under ample water conditions. Indeed, we have observed this positive N effect on growth of annual plants at the NDFP, which showed the largest increases in standing biomass under elevated CO₂ within higher N microsites (Smith and others 2000). Billings and others (2002) found that elevated CO₂ increased microbial activity and enriched pools of plant-available N at the NDFP in 1998, with subsequently reduced soil N availability in elevated CO₂ plots in 1999. Even though we found a 6% (*Larrea*) to 21% (*Krameria*) decline in leaf N under elevated CO₂ (Table 2) and pronounced photosynthetic down-regulation in *Larrea* (Huxman and others 1998), higher CO₂ assimilation was still achieved, perhaps because of the reduced need for Rubisco at higher CO₂ concentrations (Wong 1979; Conroy 1992). Overall, our results over 4 years with variable rainfall substantiate that soil water and nutrient availability interact to control production in this ecosystem.

Gas exchange measurements indicated annual integrated photosynthesis was higher under elevated CO₂ in both above- (30–51%) and below-average (24–30%) rainfall years, approaching the 43% increase in CO₂ concentration that the shrubs were exposed to over the course of our study. Instantaneous WUE was also greater under elevated CO₂; but unlike annual integrated photosynthesis, WUE was increased to a greater extent in dry years. Nevertheless, these higher photosynthetic rates did not always equate to significant increases in biomass; in fact, what we observed over 4 continuous years of CO₂ fertilization in the Mojave Desert is a fairly consistent enhancement in photosynthetic C assimilation under elevated CO₂, but highly variable investment of that C into new shoot biomass. Apparently C is lost to other non-growth pathways such as production of secondary compounds, maintenance respiration, or from roots via exudation. Even though the 18% increase in leaf area for *Larrea* under elevated CO₂ during 1998 suggests greater water use, no significant difference in overall canopy conductance occurred between ambient and elevated CO₂ (Pataki and others 2000). Additionally, *Larrea* typically had higher stem water potentials at elevated versus ambient CO₂, whereas *Ambrosia* and *Krameria* showed no consistent response to atmospheric CO₂ with respect to water potential (data not shown). Our finding of increased photosynthesis without increased production in some years is consistent with the notion that new shoot growth is more sensitive to water deficits than is photosynthetic C assimilation (Hsiao 1973).

We did not measure greater leaf retention into the dry season under elevated versus ambient CO₂ (Figures 2 and 3). Instead of phenological shifts, peak and total annual leaf production were typically higher at elevated CO₂ during the growing season. We hypothesized that higher WUE at elevated CO₂ would result in greater retention of leaf area into the summer dry season, particularly in the deciduous species, but the data do not support this hypothesis. The lack of differences in plant water potential at elevated versus ambient CO₂ for the deciduous shrubs did not result in differential leaf retention, as declining water potential is the primary driver of leaf fall in the dry season in desert shrubs (Smith and others 1997). However, there were more subtle changes in leaf phenology as a function of [CO₂]. In *Larrea*, increased leaf production results in greater carryover of leaves into the next growing season because of its evergreen life form. From a morphological standpoint, canopy development did change in *Ambrosia*, with typically

longer leaf internodes and hence more "open" shoots under elevated CO₂. This decline in leaf:stem ratio indicates that the extra C fixed under elevated CO₂ goes more to stem rather than leaf production, resulting in greater C storage in woody tissues. However, we do not have independent C-allocation data to support this premise.

Our results indicate that desert shrubs may be capable of substantial increases in photosynthesis and production at future CO₂ concentrations, although responses will vary between years and across functional types. *Larrea*, via its evergreen growth form, is capable of responding with positive C assimilation to unpredictable precipitation inputs at any time of the year (Smith and others 1997). In contrast, the deciduous shrubs *Ambrosia* and *Krameria* may not respond similarly to rainfall events as does *Larrea*. These species are less opportunistic than *Larrea*, because producing and shedding leaves is costly and must coincide with adequate rainfall for net C gain to occur. Therefore, *Ambrosia* and *Krameria* employ a strategy of higher C assimilation rates, but over a shorter period of time when soil moisture is relatively high. These deciduous species will, however, respond to late summer/early fall rainfall events when precipitation inputs are large enough to result in net C gain, as seen in 1998. These species may thus be expected to respond most strongly to elevated CO₂ if it is accompanied by increases in rainfall.

Deserts encompass a substantial and increasing portion of the terrestrial biosphere (Reynolds 2001), yet they are not nearly as productive as forests. Even so, increasing global desertification could make the acquisition and storage of C within desert ecosystems much more important in the global C budget, and there are indications that woody plants may sequester significant amounts of C in drylands (Pacala and others 2001; but see Jackson and others 2002). In any case, if precipitation increases in the desert Southwest, as some models predict (Weltzin and others 2003), rising CO₂ concentrations coupled with greater water availability would significantly enhance C inputs into these dryland ecosystems. As we continue our assessments, it is clear that drylands are important ecosystems for which we need more extensive and detailed information concerning their potential responses to global change.

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REFERENCES

- Ackerman TL, Bamberg SA. 1974. Phenological studies in the Mojave Desert at Rock Valley (Nevada Test Site). In: Lieth H, Ed. Phenology and seasonality modeling, ecological studies; vol 8. Berlin Heidelberg New York: Springer. p 215–26.
- Allen-Diaz B, Chapin FS III, Diaz S, Howden M, Puigdefábregas J, Stafford-Smith M. 1996. Rangelands in a changing climate: impacts, adaptations and mitigation. In: Watson RT, Zinyowera MC, Moss RH, Dokken DJ, Eds. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change. New York: Cambridge University Press. p 131–58.
- Bazzaz FA. 1990. The response of natural ecosystems to rising global CO₂ levels. *Annu Rev Ecol Syst* 21:167–96.
- Beatty JC. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55:856–63.
- Belnap J. 1995. Surface disturbances: their role in accelerating desertification. *Environ Monitor Assess* 37:39–57.
- Billings SA, Schaeffer SM, Zitzer S, Charlet T, Smith SD, Evans RD. 2002. Alterations of nitrogen dynamics under elevated carbon dioxide in an intact Mojave Desert ecosystem: evidence from nitrogen-15 natural abundance. *Oecologia* 131: 463–7.
- Bowes G. 1993. Facing the inevitable: plants and increasing atmospheric CO₂. *Annu Rev Plant Physiol Plant Molec Biol* 44:309–32.
- Chew RM, Chew AE. 1965. The primary productivity of a desert shrub (*Larrea tridentata*) community. *Ecol Monogr* 35:355–75.
- Comstock JP, Ehleringer JR. 1986. Canopy dynamics and carbon gain in response to soil water availability in *Encelia frutescens* Gray, a drought-deciduous shrub. *Oecologia* 68:271–8.
- Comstock JP, Cooper TA, Ehleringer JR. 1988. Seasonal patterns of canopy development and carbon gain in 19 warm desert shrub species. *Oecologia* 75:327–35.
- Conroy JP. 1992. Influence of elevated atmospheric CO₂ concentration on plant nutrition. *Aust J Bot* 40:445–56.
- Cunningham GL, Syvertsen JP, Reynolds JF, Willson JM. 1979. Some effects of soil-moisture availability on above-ground production and reproductive allocation in *Larrea tridentata* (DC) Cov. *Oecologia* 40:113–23.
- DeLucia EH, Hamilton JG, Naidu SL, Thomas RB, Andrews JA, Finzi A, Lavine M, and others. 1999. Net primary production

- of a forest ecosystem with experimental CO₂ enrichment. *Science* 284:1177–9.
- Drake BG, González-Meler MA, Long SP. 1997. More efficient plants: a consequence of rising atmospheric CO₂? *Annu Rev Plant Physiol Plant Molec Biol* 48:609–39.
- Drake BG, Peresta G, Beugeling E, Matamala R. 1996. Long-term elevated CO₂ exposure in a Chesapeake Bay wetland: ecosystem gas exchange, primary production, and tissue nitrogen. In: Koch GW, Mooney HA, Eds. Carbon dioxide and terrestrial ecosystems. San Diego: Academic. p 197–214.
- Ehleringer JR. 2001. Productivity of deserts. In: Roy J, Saugier B, Mooney HA, Eds. Terrestrial global productivity. San Diego: Academic. p 345–62.
- Esler KJ, Rundel PW. 1999. Comparative patterns of phenology and growth form diversity in two winter rainfall deserts: the succulent Karoo and Mojave Desert ecosystems. *Plant Ecol* 142:97–104.
- Ettershank G, Ettershank J, Bryant M, Whitford WG. 1978. Effects of nitrogen on primary production in a Chihuahuan desert ecosystem. *J Arid Environ* 1:135–9.
- Fisher FM, Zak JC, Cunningham GL, Whitford WG. 1988. Water and nitrogen effects on growth and allocation patterns of creosotebush in the northern Chihuahuan Desert. *J Range Manage* 41:387–91.
- Hättenschwiler S, Miglietta F, Raschi A, Körner C. 1997. Thirty years of in situ tree growth under elevated CO₂: a model for future forest responses? *Global Change Biol* 3:463–71.
- Hsiao TC. 1973. Plant responses to water stress. *Annu Rev Plant Physiol* 24:519–70.
- Huxman TE, Hamerlynck EP, Moore BD, Smith SD, Jordan DN, Zitzer SF, Nowak RS, and others. 1998. Photosynthetic down-regulation in *Larrea tridentata* exposed to elevated atmospheric CO₂: interaction with drought under glasshouse and field (FACE) exposure. *Plant Cell Environ* 21:1153–61.
- Idso SB. 1999. The long-term response of trees to atmospheric CO₂ enrichment. *Global Change Biol* 5:493–5.
- Jackson RB, Banner JL, Jobbagy EG, Pockman WT, Wall DH. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* 418:623–6.
- Jordan DN, Zitzer SF, Hendrey GR, Lewin KF, Nagy J, Nowak RS, Smith SD, and others. 1999. Biotic, abiotic and performance aspects of the Nevada Desert Free-Air CO₂ Enrichment (FACE) Facility. *Global Change Bio* 5:659–68.
- Kemp PR. 1983. Phenological patterns of Chihuahuan Desert plants in relation to the timing of water availability. *J Ecol* 71:427–36.
- Koch GW, Mooney HA. 1996. Response of terrestrial ecosystems to elevated CO₂: a synthesis and summary. In: Koch GW, Mooney HA, Eds. Carbon dioxide and terrestrial ecosystems. San Diego: Academic. p 415–29.
- Lajtha K, Whitford WG. 1989. The effect of water and nitrogen amendments on photosynthesis, leaf demography, and resource-use efficiency in *Larrea tridentata*, a desert evergreen shrub. *Oecologia* 80:341–8.
- Loustau D, Hungate B, Drake BG. 2001. Water, nitrogen, rising atmospheric CO₂, and terrestrial productivity. In: Roy J, Saugier B, Mooney HA, Eds. Terrestrial global productivity. San Diego: Academic. p 123–67.
- Melillo JM, McGuire AD, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL. 1993. Global climate change and terrestrial net primary production. *Nature* 363:234–40.
- Mooney HA, Drake BG, Luxmoore RJ, Oechel WC, Pitelka LF. 1991. Predicting ecosystem response to elevated CO₂ concentration. *BioScience* 41:96–104.
- Naumburg E, Housman DC, Huxman TE, Charlet TN, Loik ME, Smith SD. 2003. Photosynthetic responses of Mojave Desert shrubs to free air CO₂ enrichment are greatest during wet years. *Global Change Biol* 9:276–85.
- Nilsen ET, Sharifi MR, Rundel PW, Virginia RA. 1986. Influences of microclimatic conditions and water relations on seasonal leaf dimorphism of *Prosopis glandulosa* var. *torreyana* in the Sonoran Desert, California. *Oecologia* 69:95–100.
- Noble IR, Gitay H, Alwelaie AN, Hoffman MT, Saunders AR. 1996. Deserts in a changing climate: impacts. In: Watson RT, Zinyowera MC, Moss RH, Dokken DJ, Eds. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change. New York: Cambridge University Press. p 159–69.
- Norby RJ, Hanson PJ, O'Neill EG, Tschaplinski TJ, Weltzin JF, Hansen RA, Cheng WS, and others. 2002. Net primary productivity of a CO₂-enriched deciduous forest and the implications for carbon storage. *Ecol Appl* 12:1261–6.
- Nowak RS, DeFalco LA, Wilcox CS, Jordan DN, Coleman JS, Seemann JR, Smith SD. 2001. Leaf conductance decreased under free-air CO₂ enrichment (FACE) for three perennials in the Nevada desert. *New Phytol* 150:449–58.
- Nowak RS, Ellsworth DS, Smith SD. 2004a. Tansley Review: Functional responses of plants to elevated atmospheric CO₂ — do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytol* 162: 253–80.
- Nowak RS, Zitzer SF, Babcock D, Smith-Longozo V, Charlet TN, Coleman JS, Seemann JR, and others. 2004b. Elevated CO₂ does not conserve soil moisture in the Mojave Desert. *Ecology* 85:93–9.
- Oechel WC, Vourlitis GL. 1996. Direct effects of elevated CO₂ on arctic plant and ecosystem function. In: Koch GW, Mooney HA, Eds. Carbon dioxide and terrestrial ecosystems. San Diego: Academic. p 163–76.
- Orshan G. 1954. Surface reduction and its significance as a hydroecological factor. *J Ecol* 42:442–4.
- Owensby CE, Ham JM, Knapp AK, Rice CW, Coyne PI, Auen LM. 1996. Ecosystem-level responses of tallgrass prairie to elevated CO₂. In: Koch GW, Mooney HA, Eds. Carbon dioxide and terrestrial ecosystems. San Diego: Academic. p 147–62.
- Pacala SW, Hurtt GC, Baker D, Peylin P, Houghton RA, Birdsey RA, Heath L, and others. 2001. Consistent land- and atmosphere-based U.S. carbon sink estimates. *Science* 292:2316–20.
- Pataki DE, Huxman TE, Jordan DN, Zitzer SF, Coleman JS, Smith SD, Nowak RS, and others. 2000. Water use of two Mojave Desert shrubs under elevated CO₂. *Global Change Biol* 6:889–97.
- Reynolds JF. 2001. Desertification. In: Levin S, Ed. Encyclopedia of biodiversity; vol 2. San Diego: Academic. p 61–78.
- Romney EM, Wallace A, Hunter RB. 1978. Plant response to nitrogen fertilization in the northern Mohave Desert and its relationship to water manipulation. In: West NE, Skujins J, Eds. Nitrogen in desert ecosystems. Stroudsburg (PA): Dowden, Hutchinson & Ross. p 232–43.
- Smith SD, Monson RK, Anderson JE. 1997. Physiological ecology of North American desert plants. Berlin Heidelberg New York: Springer.

- Smith SD, Huxman TE, Zitzer SF, Charlet TN, Housman DC, Coleman JS, Fenstermaker LK, and others. 2000. Elevated CO₂ increases productivity and invasive species success in an arid ecosystem. *Nature* 408:79–82.
- Sokal RR, Rohlf FJ. 1997. *Biometry*. New York: W.H. Freeman.
- Strain BR, Bazzaz FA. 1983. Terrestrial plant communities. In: Lemon E, Ed. CO₂ and plants: the response of plants to rising levels of carbon dioxide. AAAS Select Symp 84. Washington (DC): American Association for the Advancement of Science. p 177–222.
- Turner FB, Randall DC. 1987. The phenology of desert shrubs in southern Nevada. *J Arid Environ* 13:119–28.
- Webb WL, Lauenroth WK, Szarek SR, Kinerson RS. 1983. Primary production and abiotic controls in forests, grasslands, and desert ecosystems in the United States. *Ecology* 64:134–51.
- Weltzin JF, Loik ME, Schwinning S, Williams DG, Fay PA, Haddad BM, Harte J, and others. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience* 53:941–52.
- Wong SC. 1979. Elevated atmospheric partial pressure of CO₂ and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C₃ and C₄ plants. *Oecologia* 44:68–74.