

Does a decade of elevated [CO₂] affect a desert perennial plant community?

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Summary

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- Understanding the effects of elevated [CO₂] on plant community structure is crucial to predicting ecosystem responses to global change. Early predictions suggested that productivity in deserts would increase via enhanced water-use efficiency under elevated [CO₂], but the response of intact arid plant communities to elevated [CO₂] is largely unknown.
- We measured changes in perennial plant community characteristics (cover, species richness and diversity) after 10 yr of elevated [CO₂] exposure in an intact Mojave Desert community at the Nevada Desert Free-Air CO₂ Enrichment (FACE) Facility.
- Contrary to expectations, total cover, species richness, and diversity were not affected by elevated [CO₂]. Over the course of the experiment, elevated [CO₂] had no effect on changes in cover of the evergreen C₃ shrub, *Larrea tridentata*; alleviated decreases in cover of the C₄ bunchgrass, *Pleuraphis rigida*; and slightly reduced the cover of C₃ drought-deciduous shrubs.
- Thus, we generally found no effect of elevated [CO₂] on plant communities in this arid ecosystem. Extended drought, slow plant growth rates, and highly episodic germination and recruitment of new individuals explain the lack of strong perennial plant community shifts after a decade of elevated [CO₂].

Introduction

Elevated [CO₂] enhances photosynthesis, water-use efficiency, and biomass accumulation in many species (Nowak *et al.*, 2004a; Ainsworth & Long, 2005). However, the dynamics of plant communities can seldom be predicted from individual plant responses, and few studies have examined how intact plant communities respond to elevated [CO₂]. Prediction of community responses might be simplified if functional groups responded in predictable ways to elevated [CO₂] based on their underlying physiology and phenology. For example, C₃ species are expected to realize greater benefits in productivity from elevated [CO₂] than C₄ species (Bowes, 1993), which would, in turn, alter the composition of mixed C₃–C₄ communities and thus ecosystem function (Polley *et al.*, 2012). By contrast, we have little comparative information about how evergreen and deciduous species may respond to elevated [CO₂].

Whether plants respond by species or as functional groups, it is likely that elevated [CO₂] will modify resource limitations and potentially alter competitive interactions. Altered competition will affect the persistence and representation of particular species in a community, with effects on relative dominance, species richness, and species diversity. Previous work measuring diversity under elevated [CO₂] has not yielded a consistent response; studies have reported that diversity increased (Niklaus *et al.*, 2001;

He *et al.*, 2002), decreased (Zavaleta *et al.*, 2003), or remained the same (Navas *et al.*, 1995; Morgan *et al.*, 2007). The variability in community responses suggests that initial species composition and higher-level interactions are key elements in elevated [CO₂] community responses (He *et al.*, 2002; Davis & Ainsworth, 2012). The complex interplay among species interactions (competition, facilitation, and herbivory; Reich *et al.*, 2001; Nowak *et al.*, 2004a), resource limitations (water and nutrient availability), and species or functional group presence and relative representation (Curtis & Wang, 1998; Bradley & Pregitzer, 2007) make studies of intact ecosystems the best predictors of community responses to elevated [CO₂]. Therefore, there is a great need for *in situ* long-term studies to understand how individual species and plant communities may respond to rapidly changing [CO₂] in the Earth's atmosphere.

Despite the clear value of community-level experiments, few studies have assessed the effects of elevated [CO₂] on diversity parameters. At many free-air CO₂ enrichment (FACE) sites, the long life span of perennials and the necessity of maintaining intact, unmanaged vegetation have precluded community-level analyses (Nowak *et al.*, 2004a). Thus, most experiments evaluating community responses to elevated [CO₂] have involved short-lived species in old fields, grasslands, and annual communities (Morgan *et al.*, 2004a; Ramseier *et al.*, 2005; Polley *et al.*, 2012). There is a particular dearth of studies addressing effects of

elevated $[\text{CO}_2]$ on aridland ecosystems, which represent substantial amounts of global land cover. Community responses to elevated $[\text{CO}_2]$ may be stronger in arid regions because desert plants may be particularly responsive to elevated $[\text{CO}_2]$ conditions as a result of improved water-use efficiency (Melillo *et al.*, 1993). Species richness in deserts is often low because of environmental constraints (Kier *et al.*, 2005) and could be further reduced with increasing $[\text{CO}_2]$ as a result of competition with invasive species (Smith *et al.*, 2000). In addition, aridland plant community responses to elevated $[\text{CO}_2]$ may be complicated by episodic droughts common to desert regions, which could limit desert plants' ability to respond to elevated $[\text{CO}_2]$ (Morgan *et al.*, 2004b; Jasoni *et al.*, 2005; Housman *et al.*, 2006). Previous research has found short-term, positive effects of elevated $[\text{CO}_2]$ on above-ground or below-ground plant growth in the Mojave Desert but only in wetter years (Housman *et al.*, 2006; Ferguson & Nowak, 2011). However, elevated $[\text{CO}_2]$ did not affect perennial plant standing biomass both above and below ground at the end of the 10 yr FACE experiment (Newingham *et al.*, 2013). Although there was no effect of elevated $[\text{CO}_2]$ on final standing biomass, it is possible that there were changes in plant community characteristics under elevated $[\text{CO}_2]$ over the course of the experiment.

We examined plant community changes in an undisturbed Mojave Desert perennial plant community exposed to 10 yr of elevated $[\text{CO}_2]$. Plant community shifts were assessed by examining changes in cover, species richness, and species diversity. We predicted that elevated $[\text{CO}_2]$ would increase cover through higher canopy production of the dominant species, which would decrease species richness and diversity over time. We also predicted that C_3 shrub species would respond more strongly to elevated $[\text{CO}_2]$ than a C_4 bunchgrass, and that the dominant evergreen shrub, *Larrea tridentata*, would have a stronger response to elevated $[\text{CO}_2]$ than drought-deciduous shrubs and perennial grasses.

Materials and Methods

Experimental site

The Nevada Desert FACE Facility (NDFF) is located in southern Nevada on the Nevada National Security Site (formerly Nevada Test Site; $36^{\circ}46'12.009''\text{N}$, $115^{\circ}57'54.173''\text{W}$, 970 m). Mean annual precipitation is *c.* 146 mm, with most precipitation occurring as winter rainfall and episodic summer monsoonal rains. The NDFF consisted of nine circular plots, each 23 m in diameter, within native plant communities in the Mojave Desert. CO_2 was distributed using FACE technology, and plots were spaced at least 100 m apart to avoid CO_2 contamination in untreated plots. Three plots received continuous exposure to elevated $[\text{CO}_2]$ ($550 \mu\text{mol mol}^{-1}$ target; 'elevated') except when air temperature fell below 4°C or wind speed (5 min average) exceeded 7 m s^{-1} , resulting in an average daytime $[\text{CO}_2]$ of $544 \mu\text{mol mol}^{-1}$ and a 24 h average $[\text{CO}_2]$ of $513 \mu\text{mol mol}^{-1}$. Three plots received ambient air ($[\text{CO}_2]$ averaged $375 \mu\text{mol mol}^{-1}$ through the FACE infrastructure; 'ambient'), and three control plots did not have

the FACE infrastructure ('nonblower controls'). Previous results suggest there is no difference between ambient $[\text{CO}_2]$ and nonblower control plots at the NDFF (Nowak *et al.*, 2001). Suspended walkways with an attached sampling platform were used to eliminate disturbance of plants, biological soil crusts, and soils (Jordan *et al.*, 1999). Carbon dioxide fumigation commenced in April 1997 and ended in June 2007. Owing to extreme drought conditions in the final year of the experiment, we irrigated all plots in March 2007 with *c.* 30 mm of water to stimulate perennial green-up before terminating the experiment. This was necessary to break drought dormancy and allow for the final experimental harvest.

Experimental plots were located in an intact *L. tridentata* – *Ambrosia dumosa* desert scrub community, which has been closed to the public and livestock grazing for over 50 yr. The five most common perennial species included a C_3 evergreen shrub (*Larrea tridentata* (DC.) Coville), C_3 drought-deciduous shrubs (*Ambrosia dumosa* (A. Gray) Payne, *Lycium andersonii* A. Gray, and *Lycium pallidum* Miers), and a C_4 bunchgrass (*Pleuraphis rigida* Thurber.). Other perennial shrubs, grasses, and forbs ('other species') comprised the remainder of the plant community. Perennial plants that were clearly dead were identified to species when possible, and unidentifiable dead individuals were placed in an unidentifiable dead plants category. Our study focused on long-term above-ground responses by perennial species as a proxy for community structure. While annual plant communities are an important component of this ecosystem, their presence or absence in response to fluctuating resources warrants separate consideration and is discussed elsewhere (Smith *et al.*, 2013).

Measurements and calculations

We recorded the species, height (h), widest canopy diameter (c_1), and the canopy diameter perpendicular to the widest diameter (c_2) for each individual plant in every plot at the beginning of the experiment (June 1997–September 2000) and in 2007 just before the final experimental harvest. In the initial measurements, 7072 plants were measured; in 2007, 5780 plants were measured. There were differences in sampling date by treatment for the initial measurements; elevated $[\text{CO}_2]$ plots were measured between June 1997 and August 1998, ambient $[\text{CO}_2]$ plots were measured between September 1997 and February 1999, and nonblower control plots were measured between December 1997 and September 2000. We plotted the average sampling date for each plot against total cover, species richness, and *Larrea* cover. There was no trend associated with the average date of sampling, so we concluded that the sampling date differences at the beginning of the experiment did not bias our results.

The initial and final canopy cover for each individual was calculated as the area of an ellipse ($\pi \times 0.5c_1 \times 0.5c_2$) and then summed to estimate total cover per ring per species. After estimating their cover, the identifiable and unidentifiable dead plants were placed in a 'dead plants' category for analysis. Dead plants were not measured in three plots (two elevated, one ambient) during the initial sampling period, so the average cover of dead plants from the six other plots in the initial sampling period were

used to replace the missing values. Absolute cover for the five dominant species, dead plants, and 'other species' was calculated, as well as the relative cover (cover for each species or category divided by total perennial plant cover in the plot). Species richness was defined as the total number of perennial species observed, while diversity was calculated from the cover data using the Shannon diversity index. Both species richness and diversity excluded dead plants.

Statistical analyses

The split-plot experimental design was identical for all dependent variables, and all data were analyzed using mixed-effects ANOVA. The [CO₂] treatment was applied to entire plots. Each variable was sampled at two time points within each plot (initial and final). Therefore, all models contained [CO₂] treatment as a fixed effect (tested over plot within [CO₂] treatment), a fixed effect of time, and an interaction between [CO₂] treatment and time (both tested over the interaction between time and plot). We also estimated the differences between final and initial values for each [CO₂] treatment as *a priori* contrasts. A significant [CO₂] treatment effect alone may indicate that there were pre-existing differences among plots. Therefore, a significant

treatment × time interaction or differences in the *a priori* contrasts within each treatment across time were necessary to suggest elevated [CO₂] effects. Analyses were conducted using SAS 9.2 (SAS Institute 2002–2008, Cary, NC, USA), and details unique to each analysis are included below.

Because we were particularly interested in how the five most common species individually responded to [CO₂] treatments, we also analyzed the cover of each of the five most common species, dead plants, and 'other species' in mixed-effects ANOVAs individually as already described. Effects of time and [CO₂] treatment on total cover, species richness, and species diversity were also analyzed in separate mixed-effects ANOVAs as already described. Species diversity was back-transformed to species number equivalents for descriptive purposes. A species number equivalent is the number of equally represented species that would yield the diversity index value (Jost, 2006).

Results

During initial sampling, 30 species of perennial grasses, forbs, cacti, and shrubs were observed across all plots, while 23 species were observed in 2007 (Table 1). Total cover, species richness, and species diversity significantly decreased over the course of the

Table 1 Perennial plant species observed at the Nevada Desert Free-Air CO₂ Enrichment (FACE) facility during initial (1997–2000) and final (2007) sampling

Species	Common name	Growth form	Initial	Final
<i>Achnatherum hymenoides</i>	Indian ricegrass	Bunchgrass	EAC	EA
<i>Acamptopappus shockleyi</i>	Shockley's goldenhead	Subshrub	EAC	EAC
<i>Ambrosia dumosa</i>	White burrobush	Shrub	EAC	EAC
<i>Androstaphium breviflorum</i>	Pink funnel lilly	Forb	E	
<i>Argemone corymbosa</i>	Prickly poppy	Forb	EA	
<i>Astragalus tidestromii</i>	Tidestrom's milkvetch	Forb	EAC	AC
<i>Atriplex canescens</i>	Fourwing saltbush	Shrub	A	A
<i>Baileya multiradiata</i>	Desert marigold	Forb	EAC	EAC
<i>Delphinium parishii</i>	Desert larkspur	Forb	AC	
<i>Encelia virginensis</i>	Virgin River brittlebush	Shrub	E	
<i>Ephedra nevadensis</i>	Nevada jointfir	Shrub	EAC	EAC
<i>Eriogonum inflatum</i>	Desert trumpet	Forb	EAC	E
<i>Grayia spinosa</i>	Spiny hopsage	Shrub	AC	EAC
<i>Hymenoclea salsola</i>	Cheeseweed	Subshrub	A	A
<i>Krameria erecta</i>	Littleleaf ratany	Shrub	EAC	EAC
<i>Krascheninnikovia lanata</i>	Winterfat	Subshrub/shrub	EAC	EAC
<i>Larrea tridentata</i>	Creosotebush	Shrub	EAC	EAC
<i>Lycium andersonii</i>	Anderson's wolfberry	Shrub	EAC	EAC
<i>Lycium pallidum</i>	Pale wolfberry	Shrub	EAC	EAC
<i>Mirabilis pudica</i>	Four o'clock	Forb	EAC	AC
<i>Opuntia basilaris</i>	Beavertail pricklypear	Cactus	EAC	EAC
<i>Opuntia echinocarpa</i>	Staghorn cholla	Cactus	EAC	EAC
<i>Opuntia ramosissima</i>	Pencil cactus	Cactus	EC	EAC
<i>Pleuraphis rigida</i>	Big galleta	Bunchgrass	EAC	EAC
<i>Polygala subspinosa</i>	Spiny milkwort	Subshrub/shrub	EAC	EAC
<i>Psoralea fremonti</i>	Indigo bush	Shrub	EAC	EAC
<i>Sphaeralcea ambigua</i>	Desert globemallow	Forb/subshrub	EAC	
<i>Sphaeralcea grossulariifolia</i>	Gooseberry leaf globemallow	Forb/subshrub	AC	
<i>Stephanomeria pauciflora</i>	Wirelettuce	Forb/subshrub	EAC	EA
<i>Thamnosma montana</i>	Turpentine-broom	Subshrub	A	

A letter indicates that the species was present in a [CO₂] treatment for the listed time period, where 'E' is for elevated [CO₂], 'A' is for ambient [CO₂], and 'C' is for the nonblower control.

experiment, but the decreases between the initial and final sampling were similar for all [CO₂] treatments (Table 2; Fig. 1).

We further explored the decrease in cover during the study by examining the five most common individual species. The relative cover of *Ambrosia* and *Pleuraphis* decreased while *L. pallidum*, *L. andersonii*, and *Larrea* increased over time; the ‘other species’ group did not change substantially during the study (Tables 3, 4; Fig. 2). There were treatment effects within these larger trends. *Ambrosia dumosa* relative cover decreased more in elevated [CO₂] than in nonblower control and ambient [CO₂] (Tables 3, 4; Fig. 2). *Lycium andersonii* and *L. pallidum* relative cover increased in nonblower control and ambient [CO₂] plots over time but not under elevated [CO₂] (Tables 3, 4; Fig. 2). By contrast, the ‘other species’ group had little change in cover for any treatment, and no differences were noted over time relative to [CO₂] treatment (Tables 3, 4; Fig. 2). The absolute and relative cover of *Larrea* tended to increase during the study, but this increase occurred in all CO₂ treatments, although it was greatest in nonblower control and elevated [CO₂] plots (Tables 3, 4; Fig. 2). *Pleuraphis* relative cover decreased during the study (Tables 3, 4), but the relative cover of *Pleuraphis* decreased less in elevated [CO₂] plots than in nonblower control or ambient [CO₂] (Fig. 2). Overall, the patterns for the drought-deciduous shrubs and ‘other species’ grouped together suggest that elevated [CO₂] negatively impacted their cover relative to *Pleuraphis* during the study (Fig. 2).

Discussion

We found that elevated [CO₂] had no effect on total cover, species richness, and species diversity in our long-term desert FACE experiment. Other studies have found no plant community responses to elevated [CO₂], although many have been shorter-term or in less natural ecosystems (Navas *et al.*, 1995; Morgan *et al.*, 2007; Davis & Ainsworth, 2012). Yet other studies have found that elevated [CO₂] can negatively affect species richness, diversity, or both (Zavaleta *et al.*, 2003; Dawes *et al.*, 2011). These plant community responses to elevated [CO₂] are likely mediated by precipitation and soil moisture (Niklaus & Körner, 2004). The NDFE was the most arid FACE site, representing an area with extremely low annual precipitation. Arid plant community responses to elevated [CO₂] may be quite different from

Table 2 ANOVA for total cover, species richness, and species diversity across treatment (nonblower control, ambient [CO₂], and elevated [CO₂]) and time

Effect	df	Cover		Species richness		Species diversity	
		F	P	F	P	F	P
Treatment	2	0.7	0.550	0.4	0.712	1.6	0.278
Time	1	23.8	0.003	16.9	0.006	49.3	0.001
Treatment × time	2	1.0	0.410	1.0	0.439	0.3	0.722

Degrees of freedom (df) represent numerator degrees of freedom; denominator degrees of freedom were 6 for all effects. Bold values are statistically significant at $\alpha = 0.05$.

semiarid community responses as a result of extreme water (and potentially nutrient) limitations and highly fluctuating rates of productivity (Shaw *et al.*, 2005) in these pulse-dominated systems. Notably, higher soil moisture has been observed under elevated [CO₂] in semiarid ecosystems (Niklaus *et al.*, 1998; Morgan *et al.*, 2001), but there was no effect of elevated [CO₂] on soil moisture at the NDFE over the long term (Nowak *et al.*, 2004b).

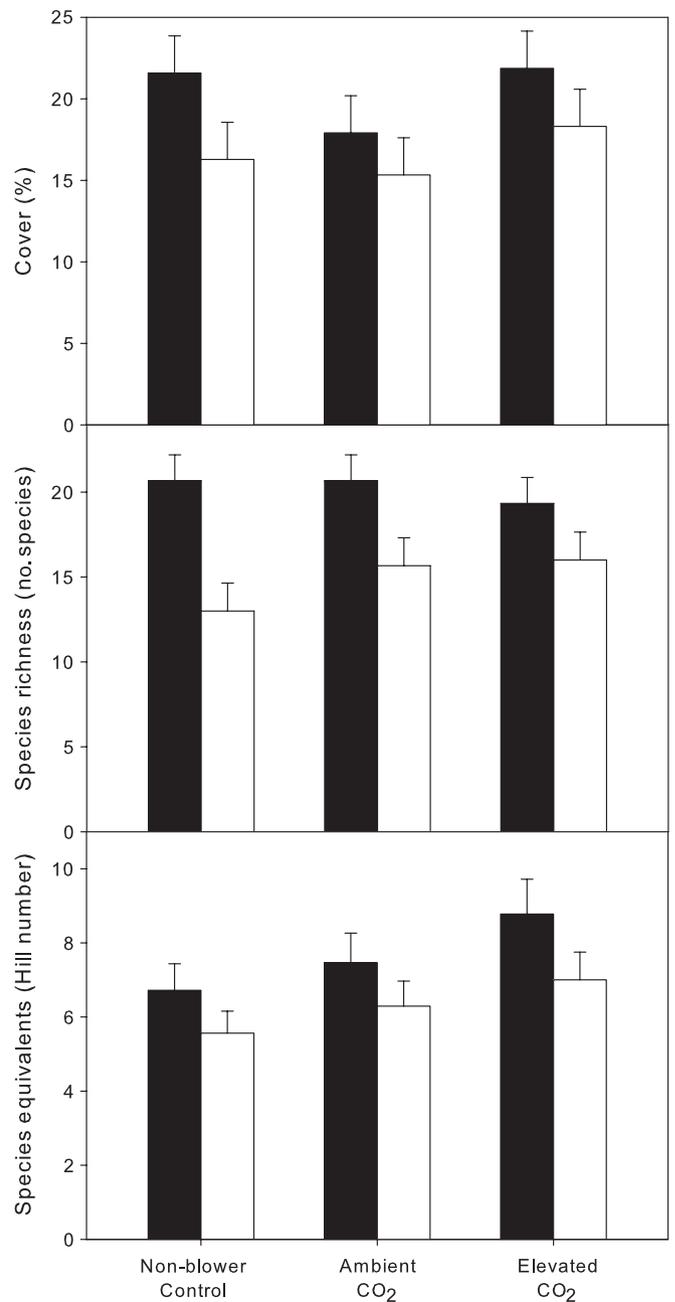


Fig. 1 Percentage cover, species richness, and diversity (expressed as species number equivalents) for all species treated with nonblower controls, ambient [CO₂], and elevated [CO₂] at initial (closed bars) and final (open bars) sample points (1997–2007). For percentage cover, species richness, and diversity, the only significant effect was time at $\alpha = 0.05$. Values are mean \pm SE.

Previous work during four consecutive years (1998–2001) at the NDFF revealed significant increases in photosynthetic rate (Naumburg *et al.*, 2003) and productivity (Housman *et al.*, 2006) with elevated $[\text{CO}_2]$ in wet years and small or no changes in normal or dry years for *Larrea*, *Ambrosia*, and *Krameria erecta*. Based on these short-term responses, we incorrectly predicted there would be an overall increase in long-term cover with elevated $[\text{CO}_2]$. Long-term data from other FACE sites have exposed similar incongruities between short-term physiological data and long-term changes in cover or biomass (Navas *et al.*, 1995). We propose that enhanced plant growth in elevated

Table 3 ANOVA table for the effects of treatment (nonblower control, ambient $[\text{CO}_2]$, and elevated $[\text{CO}_2]$) and time on the absolute (percentage of plot) and relative (each species relative to total plant cover) cover of the five most common species, dead plants, and other species

Species	Effect	df	Absolute cover		Relative cover	
			F	P	F	P
<i>Ambrosia dumosa</i>	Treatment	2	2.7	0.148	2.9	0.133
	Time	1	25.3	0.002	12.3	0.013
	Treatment \times time	2	1.6	0.276	1.2	0.369
<i>Larrea tridentata</i>	Treatment	2	0.8	0.502	0.9	0.449
	Time	1	6.9	0.040	56.6	<0.001
	Treatment \times time	2	2.3	0.180	1.7	0.267
<i>Lycium andersonii</i>	Treatment	2	1.3	0.350	2.5	0.165
	Time	1	14.2	0.009	9.4	0.022
	Treatment \times time	2	5.6	0.043	7.8	0.021
<i>Lycium pallidum</i>	Treatment	2	0.0	0.963	0.3	0.747
	Time	1	0.4	0.555	15.9	0.007
	Treatment \times time	2	2.2	0.188	1.7	0.265
<i>Pleuraphis rigida</i>	Treatment	2	2.0	0.219	1.8	0.237
	Time	1	28.4	0.002	35.5	0.001
	Treatment \times time	2	3.1	0.117	2.9	0.134
Dead plants	Treatment	2	2.8	0.140	1.2	0.368
	Time	1	3.6	0.106	12.3	0.013
	Treatment \times time	2	0.3	0.745	0.5	0.632
Other species	Treatment	2	0.3	0.725	0.3	0.758
	Time	1	10.1	0.019	0.1	0.795
	Treatment \times time	2	0.2	0.806	0.3	0.746

Degrees of freedom (df) represent numerator degrees of freedom; denominator degrees of freedom were 6 for all effects. Bold values are statistically significant at $\alpha = 0.05$. Italicized values are statistically significant at $\alpha = 0.10$.

Table 4 Table of initial and final absolute cover (%) and SEs of the five most common species, dead plants, and other species under nonblower control ambient $[\text{CO}_2]$, and elevated $[\text{CO}_2]$ treatments for initial and final sampling periods

Time	Treatment	<i>Ambrosia dumosa</i>	SE	<i>Larrea tridentata</i>	SE	<i>Lycium andersonii</i>	SE	<i>Lycium pallidum</i>	SE	<i>Pleuraphis rigida</i>	SE	Other species	SE	Dead plants	SE
Initial	Control	1.3	0.6	5.3	0.7	3.3	0.4	1.7	0.7	5.3	0.7	4.7	1.6	1.4	0.2
Initial	Ambient	1.4	0.6	4.0	0.7	2.5	0.4	1.8	0.7	2.7	0.7	5.5	1.6	0.9	0.2
Initial	Elevated	3.3	0.6	4.2	0.7	2.8	0.4	2.0	0.7	2.7	0.7	6.8	1.6	1.0	0.2
Initial	All	2.0	0.4	4.5	0.4	2.8	0.2	1.9	0.4	3.6	0.4	5.7	0.9	1.1	0.1
Final	Control	0.8	0.6	5.4	0.7	3.0	0.4	1.8	0.7	1.5	0.7	3.7	1.6	1.7	0.2
Final	Ambient	1.0	0.6	4.2	0.7	2.5	0.4	2.1	0.7	1.0	0.7	4.6	1.6	1.1	0.2
Final	Elevated	2.5	0.6	5.1	0.7	2.2	0.4	1.9	0.7	1.3	0.7	5.3	1.6	1.5	0.2
Final	All	1.5	0.4	4.9	0.4	2.6	0.2	1.9	0.4	1.3	0.4	4.5	0.9	1.5	0.1

$[\text{CO}_2]$ during wet years was counteracted by plant death and substantive biomass loss through canopy dieback (Miriti *et al.*, 2007; McAuliffe & Hamerlynck, 2010) in ensuing low rainfall years. Indeed, total cover decreased from initial to final sampling in all treatments, probably because initial sampling took place during higher than average rainfall conditions. Surprisingly, these changes were not influenced by $[\text{CO}_2]$.

Few clear-cut patterns have emerged when examining plant responses to elevated $[\text{CO}_2]$ by functional group (Poorter & Navas, 2003; Nowak *et al.*, 2004a; Ainsworth & Long, 2005). We predicted that C_3 species would respond more favorably than C_4 species to elevated $[\text{CO}_2]$ based on improvements in WUE in C_3 plants. However, there was no evidence that C_3 species consistently benefited from elevated $[\text{CO}_2]$ to cause a shift in C_3 – C_4 dominance. On the contrary, our results suggest that C_3 deciduous shrubs may have reduced performance and the C_4 bunchgrass relatively better performance in elevated $[\text{CO}_2]$ conditions in the Mojave Desert. Considering *L. tridentata* did not respond in the same way as the other C_3 plants, this work adds to the body of

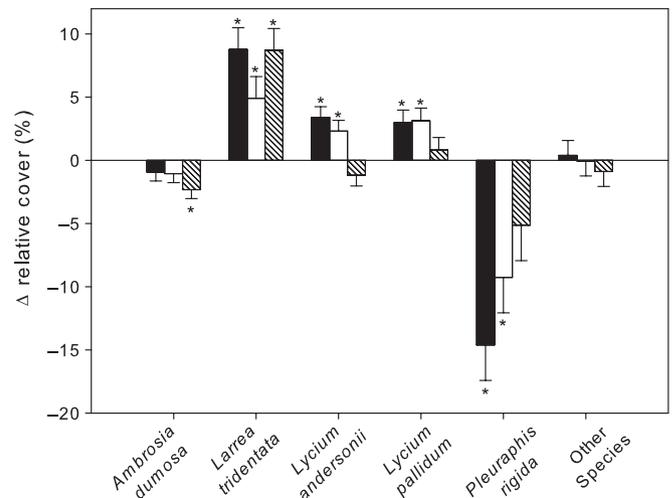


Fig. 2 Change in relative cover for the five most common species – *Ambrosia dumosa*, *Larrea tridentata*, *Lycium andersonii*, *Lycium pallidum*, and *Pleuraphis rigida* – and other species over the study period treated with nonblower controls (closed bars), ambient $[\text{CO}_2]$ (open bars), and elevated $[\text{CO}_2]$ (hatched bars). The asterisk indicates statistically significant differences from initial to final biomass (1997–2007) within species and treatment at $\alpha = 0.05$. Values are means \pm SE.

literature suggesting that photosynthetic pathway is not a chief determinant of response to elevated $[\text{CO}_2]$ (Nowak *et al.*, 2004a; Ainsworth & Long, 2005). *Pleuraphis* was the only C_4 plant and bunchgrass that we examined, making comparative conclusions about this functional type and photosynthetic pathway untenable. Although the relative cover of *Pleuraphis* decreased over the study, this decrease was ameliorated under elevated $[\text{CO}_2]$, suggesting that canopy dieback and mortality were less severe. This contrasts with other studies, which have found that grasses have a competitive disadvantage under elevated $[\text{CO}_2]$ (Shaw *et al.*, 2005).

The episodic germination and establishment of long-lived plants in the Mojave Desert limit the scope of the species diversity and species richness patterns that we report. Our initial measurements took place during a pronounced wet cycle, which temporarily increased species richness through the appearance of shrub seedlings. Housman *et al.* (2003) reported that neither germination nor mortality of shrub seedlings was ultimately influenced by elevated $[\text{CO}_2]$, although initial seedling survivorship of *Larrea* and *Ambrosia* was higher in elevated $[\text{CO}_2]$. All seedlings died during the study period, which prohibited any increase in species richness. Definitive answers on the effects of elevated $[\text{CO}_2]$ on desert perennial plant recruitment must involve observations during rare periods when perennial plants establish in the Mojave Desert, which did not occur during the decade of our study.

Contrary to predictions, elevated $[\text{CO}_2]$ did not affect total cover, species richness, or species diversity, even though we found small effects of elevated $[\text{CO}_2]$ on the cover of individual species that could eventually alter the overall plant community over longer timescales. We propose that the lack of strong plant community responses to elevated $[\text{CO}_2]$ may be explained by the long-term steady state of this desert ecosystem, which has slow plant growth and rare perennial recruitment events. Indeed, perennial plant cover of *c.* 17% at the NDFP is a function of low precipitation and recurring drought, and elevated $[\text{CO}_2]$ may have little influence on this dynamic. It is likely that overall plant cover will remain low, particularly if precipitation in the region decreases in response to climate change (Seager *et al.*, 2007). Our results provide the first information about the effects of elevated $[\text{CO}_2]$ on aridland perennial communities, which comprise a large and growing portion of global land cover.

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