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# Plant interactions in a Mojave Desert shrubland exposed to elevated atmospheric $CO_2$ during two years of contrasting rainfall

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# ABSTRACT

Seasonal and interannual droughts characteristic of deserts have the potential to modify plant interactions as atmospheric $CO_2$ concentrations continue to rise. At the Nevada Desert FACE (free-air $CO_2$ enrichment) facility in the northern Mojave Desert, the effects of elevated atmospheric $CO_2$ (550 vs. ambient ~360 $\mu$mol mol$^{-1}$) on plant interactions were examined during two years of high and low rainfall. Results suggest that $CO_2$ effects on the interaction between native species and their understory herbs are dependent on the strength of competition when rainfall is plentiful, but are unimportant during annual drought. Seasonal rainfall for 1999 was 23% the long-term average for the area, and neither elevated $CO_2$ nor the low production of herbaceous neighbors had an effect on relative growth rate (RGR, d$^{-1}$) and reproductive effort (RE, # flowers g$^{-1}$) for *Achnatherum hymenoides* (early season perennial $C_3$ grass), *Pleuraphis rigida* (late season perennial $C_4$ grass), and *Larrea tridentata* (evergreen $C_3$ shrub). In contrast, 1998 received 213% the average rainfall. Consequently, the decrease in RGR and increase in RE for *Achnatherum*, whose period of growth overlaps directly with that of its neighbors, was exaggerated at elevated $CO_2$. However, competitive effects of neighbors on *Eriogonum trichopes* (a winter annual growing in shrub interspaces), *Pleuraphis* and *Larrea* were not affected by elevated $CO_2$, and possible explanations are discussed. Contrary to expectations, the invasive annual neighbor *Bromus madritensis* ssp. *rubens* had little influence on target plant responses because densities in 1998 and 1999 at this site were well below those found in other studies where it has negatively affected perennial plant growth. The extent that elevated $CO_2$ reduces the performance of *Achnatherum* in successive years to cause its loss from the plant community depends more on future pressure from herbaceous neighbors and less on the extent that $CO_2$ enhances *Achnatherum* growth during periods of severe drought.

## INTRODUCTION

Rising atmospheric $CO_2$ concentrations are expected to enhance primary productivity 50% in arid regions of the world with a doubling of $CO_2$ (Strain and Bazzaz, 1983; Mooney et al., 1991; Melillo et al., 1993). Recent findings support this prediction (Smith et al., 1987, 2000; Chapter 5), yet how $CO_2$-induced increases in productivity will alter plant interactions and the resulting species composition of desert plant communities remains speculative (Yoder et al., 2000; Smith et al., 2000). The role that competition plays in shaping plant communities in less productive environments has itself been a polemical issue for decades (Grime, 1973, 1979; Tilman, 1982, 1988; Fowler, 1986; Goldberg and Novoplansky, 1997). In addition, plant responses to $CO_2$ enrichment vary widely among species (Poorter, 1993; Poorter et al., 1996; Poorter and Navas, 2003) and will be difficult to ascertain because desert species represent a diversity of functional types physiologically and phenologically adapted to periodic drought (DiMichele et al., 1987; Smith et al., 1997). Thus, predicting the effects of elevated $CO_2$ on plant interactions is especially challenging in deserts and requires studies of a variety of interacting species within their natural environments.

Growth of desert plants is primarily limited by water, which occurs in infrequent and unpredictable rainfall pulses alternating with periods of severe drought stress. The extent that $CO_2$ alters plant interactions may depend on whether it reduces or enhances competitive effects during resource pulses and alters plant performance and survival during subsequent interpulse intervals (i.e., seasonal or annual drought) when resources are in short supply (*sensu* Goldberg and Novoplansky, 1997). Elevated $CO_2$ may accentuate competition when soil moisture is not limiting by increasing growth rates of some species at the expense of those with little or no growth response to elevated $CO_2$ (Reekie and Bazzaz, 1989; Bazzaz et al., 1989). Alternatively, elevated $CO_2$ may offset competitive effects by enhancing or extending soil moisture for plant growth during periods of drought (Catovsky and Bazzaz, 1999; Owensby et al., 1999; Knapp et al, 2001; Morgan et al., 2001). The outcome of plant interactions as atmospheric $CO_2$ continues to rise may shift toward species with traits that improve competitive ability for limited resources or withstand periodic drought, rather than traits that promote individual $CO_2$ responsiveness (Catovsky and Bazzaz, 2003).

The distinctive relationship between Mojave Desert perennials and their understory herbs is an ideal system for understanding the effects of elevated atmospheric $CO_2$ on plant interactions in an arid environment. Enhanced establishment of short-lived species beneath perennial plant canopies, also known as the "fertile island" effect, is well documented in deserts of southwestern North America (Went, 1942; Muller, 1953; Muller and Muller, 1956; Halvorsen and Patten, 1975; Patten, 1978; Schmida and Whitaker, 1981; Samson, 1986). In contrast, negative effects of these herbs on the performance of the perennials whose space they share have been recently recognized (Holzapfel and Mahall, 1999; Schenk et al., 2003; Chapter 3). Short-lived winter annuals of warm deserts, which predominantly use the $C_3$ photosynthetic pathway (Mulroy and Rundel, 1977; Syvertsen et al., 1976), maintain high rates of photosynthesis and growth before the onset of soil moisture stress and high temperatures. Species that have rapid growth rates and use the $C_3$ photosynthetic pathway typically exhibit the strongest growth responses to elevated $CO_2$ (Poorter and Navas 2003); hence, winter annuals may further decrease the performance of associated perennial species as atmospheric $CO_2$ continues to rise. Furthermore, non-native species such as the annual grass *Bromus madritensis* ssp. *rubens*, which has invaded the Mojave and Sonoran deserts, increases shoot growth at elevated atmospheric $CO_2$ more than its native ecological counterparts (Smith et al. 1997, 2000). *Bromus* rapidly extracts resources and grows faster than native Mojave Desert annual species (Chapter 2), and can reduce perennial plant growth rates by establishing in the understory before perennials become active (Chapter 3). Therefore, rising $CO_2$ concentrations may alter plant community structure by enhancing the ability of non-native species to reduce growth of native perennial grasses and shrubs even further.

Desert species that are affected the least by their understory herbs during resource pulses and withstand periods of drought between pulses are likely to persist as atmospheric $CO_2$ continues to rise (*sensu* Goldberg, 1990). *Larrea tridentata* is a dominant evergreen shrub that is insensitive to neighboring annuals (Chapter 4) because it is physiologically active throughout the year, even when soil water potentials drop well below those tolerated by winter annuals (Oechel et al., 1972; Franco et al., 1994; Hamerlynck et al., 2000). Root systems of annuals typically occur in shallow soil depths (Cable, 1969), and thus annuals should have little effect on *Larrea* whose root system allows it to take advantage of soil moisture at greater lateral and vertical depths than neighboring plants (Gile et al., 1998). In addition, *Larrea* uses the $C_3$ photosynthetic pathway and may take advantage of elevated $CO_2$-induced increases in water use efficiency later in the season after herbs have senesced. Growth of the early season $C_3$ grass *Achnatherum hymenoides* is concurrent with activity of winter annuals, thereby placing *Achnatherum* in direct competition with annuals (Chapter 3), and dormancy occurs at the onset of high summer temperatures. The ability of *Achnatherum* to withstand competition with its neighbors under elevated $CO_2$ will depend less on its tolerance to neighbor-induced water stress and more on its ability to increase growth belowground and extract deep soil moisture that is unavailable to shallow rooted annual species (Yoder et al., 2000). The late season $C_4$ grass *Pleuraphis rigida* has a shallow root system that overlaps completely with winter annuals and other short-lived species (Chapter 3; Robberecht et al., 1983). $C_4$ species are typically less responsive to increased $CO_2$, and *Pleuraphis* carbon uptake is dependent on favorable soil water potentials (Nobel, 1980; Nobel and Zhang, 1997); hence, reduction in *Pleuraphis* performance by neighbors may be pronounced as $CO_2$ increases because of the rapid and earlier growth of neighbors before *Pleuraphis* becomes active.

The objective of this study was to determine whether an increase in atmospheric $CO_2$ reduces the performance of native Mojave Desert species by enhancing the competitive effect of neighboring herbaceous plants. First, the establishment of short-lived herbs associated with perennial plant canopies and open spaces between perennials was measured at ambient and elevated $CO_2$, and secondly differences in the establishment of neighbors on the growth and reproduction of the perennials with which they were associated were evaluated. The responses of perennials to the abundance of the entire understory community were tested separately from those of only *Bromus madritensis* neighbors. Finally, these questions were examined in years of contrasting rainfall because the effects of interannual water stress on plant physiological processes may overshadow the benefits of increased water use efficiency under elevated atmospheric $CO_2$ (Smith et al., 2000).

## MATERIALS AND METHODS

### *Nevada Desert FACE Facility*

A free-air $CO_2$ enrichment (FACE) facility was constructed and fumigation began in spring 1997 at the Nevada Test Site in southern Nevada. The Nevada Desert FACE facility (NDFF) is the first of its kind developed in a natural desert biome (Jordan et al., 1999) and is desired over open-top chambers because it is minimally intrusive to above- and belowground microclimate and large enough to include the spatial heterogeneity in vegetation and soil nutrients characteristic of deserts. The vegetation at the NDFF is a *Larrea tridentata-Ambrosia dumosa-Lycium* spp. desert scrub community, and soils are Aridosols derived from calcareous alluvium without a developed caliche layer (Jordan et al. 1999). The NDFF itself is composed of nine 23-m diameter circular plots (491 $m^2$ each): three plots are blower-controls maintained at ambient $CO_2$ (360 $\mu mol\ mol^{-1}$), three have elevated $CO_2$ (550 $\mu mol\ mol^{-1}$), and three additional plots have no $CO_2$ flow apparatus (ring control). Only plants within the blower-control and elevated plots were the focus of this study as shoot-level responses to ambient and non-ring plots have been shown to be statistically indistinguishable (Jordan et al., 1999; Smith et al., 2000, Nowak et al. 2001), and initial herbaceous plant densities measured in this study were not significantly different between the two treatments at the beginning of the experiment (data not shown).

*Target perennial and neighborhood measurements*

Natural establishment of herbaceous forbs and grasses beneath perennial plants was measured in 1998 and 1999, which were unusually wet and dry years for the region, respectively. In addition, growth and reproduction of four native Mojave Desert species were measured as a function of the natural variation in establishment of these herbs around them. Three individuals of each species, hereafter referred to as targets, were selected and measured within each of the six FACE plots during 1998 and 1999: creosote bush, *Larrea tridentata* (DC.) Cov.; indian rice grass, *Achnatherum hymenoides* (Roemer & Schultes) Barkworth; and galleta grass, *Pleuraphis rigida* Thurber. These perennial species represent a range of functional types (*Larrea* = evergreen $C_3$ shrub; *Achnatherum* = early season $C_3$ grass; and *Pleuraphis* = late season $C_4$ grass) and collectively comprise a large proportion of the perennial plant abundance (4.4%, 19.6%, and 31.0%, respectively; Jordan et al., 1999). Because manipulation of plants was restricted in an effort to maintain the long-term integrity of the site, only plants that had few or no perennial plant neighbors within a 1-m radius were selected to minimize competition effects. Plants of a fourth species, the native winter annual *Eriogonum trichopes* Torrey were selected in the open spaces between perennials during 1998 to test the same hypotheses of elevated $CO_2$ and neighbor effects on plant performance. Density and aerial cover of herbaceous species, which are hereafter referred to as neighbors, were measured monthly using four 25 cm × 20 cm transparent grids with 1 $cm^2$ demarcations placed at cardinal directions at the base of each *Achnatherum, Pleuraphis, Larrea* and *Eriogonum* individual (total sampling area per individual target=0.20 $m^2$). The peak aerial cover was determined for each neighbor species and summed across neighbor species to approximate the competitive effect on each target.

Relative growth rates of the targets (RGR) were determined by monitoring plant growth monthly beginning in March and ending when plants senesced. For *Achnatherum* and *Pleuraphis*, two tillers were selected per plant and tagged at the base with a loose band of colored tape. The length of each leaf per tiller was measured at each sampling time. The relationship between leaf mass and leaf length was determined using leaves harvested and measured for mid-day xylem pressure potential; this relationship was used to estimate the total leaf biomass on each tiller every time measurements were collected. For *Larrea*, four terminal twigs, each approximately 2 cm long, were tagged with tape. Twig length and the number of leaflet pairs were measured at each sampling time. Similar to the grasses, *Larrea twig* mass was estimated using twigs that were harvested from plants for mid-day xylem pressure potential. *Eriogonum* cover was estimated using the same transparent 1 $cm^2$ grid used for aerial cover of neighbors, and mass was estimated from plant cover measured similarly on individuals harvested outside of the rings. RGR was calculated for all target species (*Achnatherum*, *Pleuraphis*, *Larrea* and *Eriogonum*) according to Blackman (1919), which used the means of the $\log_e$-transformed masses to avoid bias in the estimates (Hoffmann and Poorter, 2002). Targets that experienced herbivory or whose tags fell off were omitted from analysis.

### *Target plant shoot physiology*

Instantaneous gas exchange and water potentials were measured on targets at the same time growth measurements were collected. A single terminal twig for *Larrea*, the most-recently fully expanded leaf for *Achnatherum* and for *Pleuraphis*, and a leaf from the basal rosette of *Eriogonum* were selected from each plant for gas exchange measurements. Net photosynthesis and stomatal conductance to water vapor were measured with a portable open photosynthesis system (Li-Cor 6400, Li-Cor, Inc., Lincoln, Nebraska) by stratifying $CO_2$ treatments through the day between 0800 and 1500 h. Leaf temperatures were maintained within an average ± 2° C (standard deviation) of prevailing air temperatures, and saturating photon flux density (1.5 mmol $m^{-2}$ $s^{-1}$ supplied by a red-blue LED light source). Mid-day water potentials ($\Psi_{mid}$) were measured on each plant during the same time period on the following day gas exchange was measured by excising the plant tissue and placing it in a Scholander-type pressure chamber (PMS Instrument Co., Corvallis, Oregon).

### *Statistical analyses*

Establishment of herbaceous neighbors was analyzed using univariate and multivariate techniques performed with SAS statistical software (SAS Institute, Inc.; Cary, NC; version 6.12). The main and interactive effects of $CO_2$ and microsite on cover, density and plant size of the entire neighbor community were tested in separate two-way ANOVAs for each year. MANOVA was used to test $CO_2$ and microsite effects on the combination of species' cover responses for each year. A single multivariate outlier was identified by examining Mahalanobis distances and removed. When the chi-square test of homogeneity of within covariance matrices was significant ($\alpha=0.10$), the within covariance matrices was used in the discriminant function (Morrison, 1976). Following the MANOVA, each species was evaluated in separate two-way ($CO_2$ and microsite) ANOVAs using a sequential Bonferonni procedure to control family-wise Type I-error rate (Quinn and Keough 2002).

Target plant RGR, RE and physiological responses were analyzed separately for each year and each species using a two-way ANOVA procedure using $CO_2$ as a qualitative factor and neighbor cover as a quantitative factor (Fernandez, 2001a). Mid-day xylem pressure potential, net assimilation rate and stomatal conductance for each target were plotting through time (in days), and the average seasonal values used in ANOVAs were determined as the integrated area under each curve using the trapezoidal rule and dividing by the time interval that the measurements were collected. *Bromus* effects on RGR and RE were also analyzed in a two-way ANCOVA using $CO_2$ as a qualitative factor, *Bromus* cover as a quantitative factor, and cover of all other neighbors as the covariate (Fernandez, 2001b). The covariate × $CO_2$ interaction was not significantly different for any of the ANCOVAs performed; thus, this analysis was appropriate for addressing *Bromus* effects. For univariate tests, violation of the assumption of equal variance was examined in residual plots and using Levene's test for equal variance. Violation of normality was examined in normality plots and tested according to D'Agostino (1971).

Heteroscedastic data were $\log_{10}$-transformed to meet the assumption of equal variance (Box and Cox, 1964).

## RESULTS

### *Establishment of plant neighbors*

Seasonal rainfall in 1997/1998 was 219% the long-term average, the majority falling during January through March (140 mm) compared with the period October through December (22 mm). In contrast, 1998/1999 rainfall was only 23 % of average (13 mm during October though December, 4 mm during January through March). Consequently in spring 1998, plant density was greatest beneath *Larrea* compared with the other microsites *(P*=0.01), but aerial cover was not different among microsites (*P*=0.24, Table 1). $CO_2$ decreased plant densities in 1998 (*P*=0.02) but did not significantly alter total aerial cover (*P*=0.47). These lower densities at elevated $CO_2$ were reflected early in the growing season in 1998 (data not shown) with 226 ± 22 plants $m^{-2}$ and 80 ± 11 plants $m^{-2}$ for ambient and elevated plots, respectively ($P<0.01$; averaged over only perennial microhabitats measured in early February). In 1999, density was lowest beneath *Achantherum* (*P*=0.04) compared to the other microsites (open microsite was not sampled due low plant production). Total aerial cover did not increase significantly with $CO_2$ enrichment in spring 1999, although the lack of significance was likely due to patchiness in distribution and abundance resulting in large variation among plots during this dry year (*P*=0.10 and 0.14 for density and cover, Table 1).

Elevated $CO_2$ and microsite significantly affected the aerial cover of the most common neighbor species in 1998 (89-96% of total cover depending on microsite) based on MANOVA (Wilk's Lambda, *P*=0.02 and <0.01, respectively). Separate univariate ANOVAs demonstrated that the most abundant annual neighbor, *Eriogonum trichopes,* had the lowest cover beneath *Larrea* microhabitats, and elevated $CO_2$ reduced cumulative cover overall. *Lepidium lasiocarpum* and *Vulpia octoflora*, in contrast, had greatest cover beneath *Larrea* microhabitats, but did not respond to elevated $CO_2$. The invasive annual grass, *Bromus madritensis* ssp. *rubens*, had greater cover with $CO_2$ enrichment and beneath perennials compared to open microhabitats. In contrast, no native annual plants germinated in 1999. Only *Bromus* was found beneath *Larrea* canopies and the small perennial bunchgrass *Erioneuron pulchellum* grew beneath *Achnatherum* and *Pleuraphis* (open microhabitat was not measured in 1999). MANOVA results indicate no significant $CO_2$ effect in 1999 (Wilk's Lambda, *P*=0.50), but microsite did have a significant effect on the cumulative cover of these species ($P<0.01$).

### *Target plant growth and reproduction*

Growth measurements of target plants began in March for both years and ended when targets senesced (June, 1998 for *Eriogonum* and *Achnatherum*; August, 1998 for *Pleuraphis* and *Larrea*; June, 1999 for *Achnatherum* and *Pleuraphis*; and August, 1999 for *Larrea*). Different metrics for relative growth rate (RGR) were measured for each species due to their contrasting growth forms, and reproductive effort (RE) was not quantified in 1999 for *Achnatherum* and *Pleuraphis* because inflorescence production was negligible for this dry year (Fig. 1). RGR for *Eriogonum* individuals measured in the open marginally declined (linear effect, *P*=0.07) and RE significantly increased with increasing herbaceous neighbor cover in 1998 (quadratic effect, $P<0.01$, Fig. 1). However, $CO_2$ had no overall effect on either *Eriogonum* RGR or RE (*P*=0.80 and 0.39, respectively).

RGR and RE for *Achnatherum*, *Pleuraphis* and *Larrea* were analyzed separately for each year (Fig. 1). In 1998, the decline in *Achnatherum* RGR and the increase in RE associated with increasing neighbor cover was intensified with $CO_2$ enrichment (Neighbor cover × $CO_2$, $P=0.03$ and $P < 0.01$ for RGR and RE, respectively) resulting in lower overall RGR ($P=0.02$) and higher RE ($P<0.01$) at elevated $CO_2$. Greater RE (flowers $g^{-1}$) was due to declining biomass and not to a change in the number of flowers produced at elevated $CO_2$. *Achnatherum* RGR declined slightly, but not significantly, with an increase in neighbor cover during 1999 ($P=0.10$), and $CO_2$ had no effect on *Achnatherum* RGR in this dry year ($P=0.61$). In 1998, *Pleuraphis* RGR declined with an increase in neighbor cover ($P=0.05$), and RGR was higher at elevated compared with ambient $CO_2$ ($P<0.01$). A decline in RE with increasing neighbor cover was significant for *Pleuraphis* in 1998 (linear effect, $P<0.01$), but $CO_2$ fumigation had no overall effect on RE ($P=0.17$). In 1999, *Pleuraphis* RGR did not change with increasing neighbor cover ($P=0.16$) or between $CO_2$ treatments ($P=0.34$). Finally, *Larrea* RGR was not statistically different between $CO_2$ treatments in either year ($P=0.12$ and 0.28, respectively). However, a significant interaction occurred for *Larrea* in 1998 ($P=0.05$) with an increase in RGR as neighbor cover increased under elevated $CO_2$. RE was significantly lower for *Larrea* at the elevated $CO_2$ treatment compared with ambient $CO_2$ in 1998 ($P=0.02$).

The cover of *Bromus madritensis* ssp. *rubens* neighbors (*Brma*$_{cov}$) generally did not have an effect on RGR or RE after accounting for the aerial cover of all other neighbors (ANCOVA, Table 3). Only *Larrea* RGR and RE in 1998 marginally increased ($P=0.06$ and 0.04) with an increase in *Brma*$_{cov}$.

*Target plant shoot physiology*

Mid-day water potentials of the target species generally declined with an increase in cover of neighbors and increased under elevated $CO_2$ in 1998, but neighbor cover and $CO_2$ effects diminished in 1999 (Fig. 2). During 1998, average seasonal mid-day xylem pressure potentials integrated through the season ($\Psi_{mid}$) were significantly higher for *Eriogonum* under elevated compared with ambient $CO_2$ treatments ($P<0.01$). This $CO_2$ effect for *Eriogonum* $\Psi_{mid}$ occurred when neighbor cover was low but disappeared when neighbor cover increased ($CO_2$ × neighbor cover, $P<0.01$, Fig. 2). Low neighbor cover for *Achantherum* grown at elevated $CO_2$ coupled with higher $\Psi_{mid}$ at elevated $CO_2$ ($P=0.01$) resulted in an overall negative relationship between $\Psi_{mid}$ and neighbor cover ($P<0.01$). *Pleuraphis* $\Psi_{mid}$ also declined with an increase in neighbor cover ($P=0.03$) but was only slightly higher at elevated compared to ambient $CO_2$ ($P=0.06$). *Larrea* $\Psi_{mid}$ declined slightly with an increase in neighbor cover ($P=0.06$) and was significantly higher at elevated $CO_2$ in 1998 ($P<0.01$). In 1999, $\Psi_{mid}$ did not change as a function of the scant neighbor cover in 1999 for *Achnatherum* ($P=0.59$), or *Larrea* ($P=0.43$), but decreased for *Pleuraphis* ($P=0.02$). $CO_2$ had no effect on $\Psi_{mid}$ for any of these perennial targets ($P=0.60$, 0.92, and 0.18, for *Achnatherum*, *Pleuraphis* and *Larrea*, respectively).

Seasonal $A_{net}$ declined as $\Psi_{mid}$ decreased in 1998 for *Eriogonum*, *Pleuraphis* and *Larrea* (linear effect, $P<0.01$, $P=0.02$, and $P<0.01$, respectively). $A_{net}$ was significantly higher at elevated $CO_2$ for *Eriogonum* ($P=0.03$), *Achnatherum* ($P=0.01$), and *Larrea* ($P<0.01$) in 1998. Seasonal $g_s$ also declined as a function of $\Psi_{mid}$ for *Eriogonum* in 1998 (linear effect, $P=0.05$), and was significantly lower at elevated $CO_2$ for *Eriogonum* ($P=0.02$) and *Pleuraphis* ($P<0.01$). In contrast to 1998, seasonal $A_{net}$ and $g_s$ did not change as a function of $\Psi_{mid}$ in 1999 for *Achantherum* ($P=0.89$ and 0.28), *Pleuraphis* ($P=0.14$ and 0.09) or *Larrea* ($P=0.59$ and 0.84).

However, elevated $CO_2$ significantly increased $A_{net}$ in 1999 for *Achantherum* and *Pleuraphis* (both $P<0.01$) and significantly decreased $g_s$ for *Achnatherum* and *Larrea* in 1999 (both $P<0.01$).

## DISCUSSION

Neighbor effects on plant growth were pronounced during 1998 compared with 1999, years which received more than two times and less than one fourth the average seasonal rainfall, respectively. Neighbor-induced inhibition of target growth with an approximately 50% increase in atmospheric $CO_2$ occurred for *Achnatherum*, whose period of growth overlaps completely with that of its understory herbs. In contrast, the relationship between neighbors and drought-tolerant *Larrea*, the late season *Pleuraphis*, and the winter annual *Eriogonum* in open microhabitats did not change at elevated $CO_2$ for reasons that are explored below. Elevated $CO_2$ studies have predicted responses of plant mixtures on the basis of differences in growth rates (Poorter, 1993; Poorter et al., 1996), $C_3/C_4$ physiology (Bazzaz and Carlson, 1984; Carter and Peterson, 1983; Reynolds, 1996), phenology (Chiarello and Field, 1996), and differences in growth forms such as grasses vs. forbs or shrubs (Chiarello and Field, 1996; Polley et al., 1996) and legumes vs. grasses (Grünzweig and Körner, 2001). Results of this study suggest that the adaptations that allow desert species to persist during periods of both high resource availability and severe drought provide insight into the appearance and functioning of mixed plant communities in a high $CO_2$ world. Based on the two-phase resource dynamics hypothesis (Goldberg and Novoplansky, 1997), the extent that elevated $CO_2$ intensifies plant interactions during periods of resource pulses and the extent that elevated $CO_2$ growth enhancement during interpulse periods can alleviate competitive effects experienced during pulse periods may determine the appearance of desert plant assemblages in the future.

*Achantherum* was the only species whose neighbor effects on growth were accentuated at elevated $CO_2$. Yet how herbaceous neighbors impacted *Achantherum* growth remains unclear because the peak aerial cover of neighbors was the same between $CO_2$ treatments. However, rapid growth and resource extraction of neighbors early in the season or shifts in biomass toward belowground tissues may explain the enhanced competitive ability at elevated $CO_2$ of these predominantly $C_3$ annual species and requires additional research attention (Poorter et al., 1996). Interestingly, the declines in *Achnatherum* mid-day water stress between $CO_2$ treatments did not mirror the accentuated decline in growth at elevated compared with ambient $CO_2$ in 1998. Thus, neighbors may have depleted resources other than water during this year of above-average rainfall (e.g., soil N), or *Achnatherum* adjusted its physiology or allocation to offset greater water depletion by neighbors at elevated $CO_2$. Neighbor-induced declines in *Achnatherum* RGR reflect proportional declines in canopy leaf area because tiller number and specific leaf area ($cm^2\ g^{-1}$) did not change with elevated $CO_2$ (data not shown). With this in mind, overall mid-day water stress for *Achnatherum* was in part alleviated through lower stomatal conductance at elevated $CO_2$ throughout the season (Nowak et al., 2001). Greater leaf level carbon uptake at elevated $CO_2$ was potentially allocated belowground thereby reducing the mid-day water stress expected at high neighbor cover. Although root growth was not measured in this study, root biomass and whole root system N uptake increased for *Achnatherum* fumigated with 1000 $\mu mol\ mol^{-1}$ $CO_2$ in a greenhouse study, thus potentially countering the negative effects associated with plant competition (Yoder et al., 2000). In addition, extension of roots into deeper soils at elevated $CO_2$ has been measured for other species at this site during 1998 (D. L. Phillips et al., unpublished data) and would allow *Achantherum* to reduce mid-day water stress by accessing moisture beyond the soil depths used by winter annuals. Shifts in biomass allocation to roots among competing plants in response to elevated $CO_2$ has been found elsewhere (Pritchard et al., 2001) and requires further study in this arid system.

In contrast to *Achnatherum*, elevated $CO_2$ had little effect on the interactions between understory herbs and *Pleuraphis*, *Larrea* or *Eriogonum* in 1998. Neighbor-induced water stress increased and net assimilation rates decreased to the same extent for *Pleuraphis* growing at both $CO_2$ treatments, thus elevated $CO_2$ did not exacerbate neighbor competitive effects as originally predicted for this late season grass. *Pleuraphis* growth began as neighbors senesced, but a late spring rain storm (38 mm on June 12, 1998) replenished soil moisture in the top 20 cm of soil, where *Pleuraphis* roots generally predominate, to a level resembling soil moisture when annuals were first active (Nowak et al., in press). Elevated $CO_2$ also did not accentuate the interaction between *Eriogonum* growth and winter annual neighbors possibly due to nutrient limitation common in the spaces between shrubs (Titus et al., 2003), which is known to restrict a strong $CO_2$ response to annual species neighbors (Zangerl and Bazzaz, 1984). In contrast, *Larrea* RGR was positively related to neighbor cover, which suggests that microsite conditions were enhanced for both neighbors and targets (i.e., positive facilitation), but disentangling plant canopy effects on resources from plant responses will require manipulative experiments in the future (Holzapfel and Mahall, 1999).

Competitive effects disappeared irrespective of $CO_2$ treatments during 1999 because rainfall was insufficient to germinate most herbaceous understory species; only low densities of *Bromus* and the small perennial grass *Erioneuron* established beneath the canopies of *Larrea* and the perennial grasses, respectively. Weak competitive effects of winter annuals on Mojave Desert perennials have also been shown when delayed addition of water in early spring resulted in low winter annual biomass (Chapter 3). Each species had similar phenologies between $CO_2$ treatments; thus, any $CO_2$-induced water savings due to lower transpiration did not extend the growth period into drought as has been found in other studies (Volk et al., 2000; Grünzweig and Körner, 2001). Furthermore, plant canopies in this study were too poorly developed in 1999 for differences in stomatal conductance (i.e, for *Achantherum* and *Larrea*) to confer any significant water savings as has been reported for this site (Nowak t al., in press). Drought stress overwhelmed any benefits that increased $CO_2$ may have had on physiology and growth and is consistent with other studies at this site (Pataki et al., 2000; Smith et al., 2000; Huxman and Smith, 2001; Nowak et al., 2001; Naumberg et al., 2003).

*Bromus* production in this study was inadequate (13% and 18% total biomass at ambient and elevated $CO_2$, respectively; Zitzer et al., unpublished data) to negatively affect native Mojave Desert species as in other studies (Holzapfel and Mahall, 1999; Schenk et al., 2003; Chapter 3). Based on its potential to increase under elevated $CO_2$ (Smith et al., 2000), *Bromus'* impact may be more pronounced following successive years with above-average precipitation (Beatley, 1966; Hunter 1991) or following wildfire and subsequent colonization (Beatley, 1966; Brown and Minnich, 1986). Native warm desert perennial and annual species are slow to re-establish or disappear entirely after wildfire, yet *Bromus madritensis* reestablishes and dominates quickly into burned areas (Brown and Minnich 1986). The implications of species-specific responses to rising $CO_2$ concentrations such as non-native species like *Bromus madritensis* are twofold: increased frequency and severity of wildfires in North American deserts (Mayeux et al., 1994; Sage, 1996; Brooks, 1999) and displacement of native species associated with greater production and competitive ability of non-native annual grasses (Brooks, 2000; Chapter 2). Further study is necessary at this site to determine whether increased dominance occurs at elevated $CO_2$ and has a negative long-term impact on perennial plant performance and survival.

In conclusion, elevated $CO_2$ has the potential to shift the outcome of plant interactions between target plants and understory herbs but depends upon the degree of overlap between the periods of growth for coexisting species and the resource dynamics during the period that species interact. These results are consistent with the two-phase hypothesis of resource pulses in unproductive environments (Goldberg and Novoplansky, 1997) where competition between understory herbs and *Eriogonum*, *Achnatherum* and *Pleuraphis* occurred during a period of resource pulse (i.e., 1998, also see Chapter 3) and was intensified under elevated $CO_2$ for *Achnatherum*. The extent that elevated $CO_2$ impacts future desert plant communities depends more on the cumulative effects of neighbor pressure on plant performance across consecutive wet years and less on the extent that $CO_2$ enhances growth during periods of severe drought.

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Table 1. Density and aerial cover (mean ± SE) of herbaceous plants measured in four microsites (*Larrea*, *Pleuraphis* and *Achnatherum* canopies or in open) at elevated and ambient $CO_2$ concentrations. *P*-values for ANOVA statistics test $CO_2$ (df=1, 64), microsite (df=3,64) and $CO_2$ × microsite (df=3,64) effects.

| | Density ($m^{-2}$) | | Cover ($dm^2\ m^{-2}$) | |
|---|---|---|---|---|
| | 1998 | 1999 | 1998 | 1999 |
| *Larrea* | | | | |
| Ambient | 328 ± 48 | 23 ± 11 | 27 ± 3 | 1 ± 1 |
| Elevated | 242 ± 26 | 89 ± 46 | 31 ± 7 | 2 ± 1 |
| *Pleuraphis* | | | | |
| Ambient | 237 ± 29 | 7 ± 3 | 29 ± 5 | 1 ± 1 |
| Elevated | 194 ± 29 | 18 ± 6 | 27 ± 5 | 3 ± 1 |
| *Achnatherum* | | | | |
| Ambient | 211 ± 36 | 8 ± 4 | 24 ± 5 | 2 ± 1 |
| Elevated | 141 ± 27 | 11 ± 4 | 16 ± 5 | 2 ± 1 |
| Open | | | | |
| Ambient | 186 ± 34 | No plants | 25 ± 3 | No plants |
| Elevated | 154 ± 48 | | 23 ± 5 | |
| | *P*-values | | | |
| $CO_2$ | 0.023 | 0.10 | 0.47 | 0.14 |
| Microsite | 0.01 | 0.04 | 0.24 | 0.80 |
| $CO_2$ × Micro | 0.86 | 0.22 | 0.69 | 0.48 |

Table 2. Peak cover of common herbaceous species at ambient and elevated $CO_2$ in mixed communities occupying open and perennial canopy microsites during 1998 and 1999.

| | | | | 1998 | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Microsite | | | | Univariate *P*-values | | |
| | [$CO_2$] | Open | *Achy* | *Plri* | *Latr* | $CO_2$ | Micro | C*M |
| *Eriogonum trichopes*[nf] | Amb | 36 | 35 | 31 | 1 | 0.03 | <0.01 | 0.70 |
| | Elev | 28 | 13 | 22 | 2 | | | |
| *Lepidium lasiocarpum*[nf] | Amb | 3 | 6 | 9 | 20 | 0.71 | <0.01 | 0.11 |
| | Elev | 4 | 3 | 14 | 17 | | | |
| *Vulpia octoflora*[ng] | Amb | 0 | 1 | 1 | 3 | 0.33 | <0.01 | 0.56 |
| | Elev | 0 | 0 | 1 | 3 | | | |
| *Bromus madritensis*[ig] | Amb | 1 | 1 | 2 | 1 | 0.01 | 0.03 | 0.66 |
| | Elev | 2 | 2 | 5 | 5 | | | |
| *Chaenactis carphoclinia*[nf] | Amb | 1 | 1 | 2 | 0 | 0.56 | 0.07 | 0.76 |
| | Elev | 2 | 1 | 1 | 0 | | | |
| | | | | 1999 | | | | |
| | [$CO_2$] | Open | *Achy* | *Plri* | *Latr* | $CO_2$ | Micro | C*M |
| *Erioneuron pulchellum*[ng] | Amb | No | 3 | 2 | 0 | 0.40 | <0.01 | 0.21 |
| | Elev | plants | 3 | 3 | 0 | | | |
| *Bromus madritensis*[ig] | Amb | No | 0 | 0 | 1 | 0.45 | <0.01 | 0.45 |
| | Elev | plants | 0 | 0 | 2.5 | | | |

[nf] native forb

[ng] native grass

[ig] invasive grass

Table 3. *P*-values for ANCOVAs (separate tests for each target species × year treatment combination) testing for effects of *Bromus madritensis* ssp. *rubens* neighbors (*Brma*$_{cov}$) on target species RGR and RE. Neighbor cover excluding *Brma*$_{cov}$ was included in the statistical model as the covariate. *Achnatherum* and *Pleuraphis* had no *Bromus* neighbors during the dry year of 1999 nor did they produce sufficient flowers to test RE.

| 1998 | | Covariate | *Brma*$_{cov}$ | $CO_2$ | *Brma*$_{cov}$ × $CO_2$ |
|---|---|---|---|---|---|
| *Eriogonum* | RGR | 0.08 | 0.57 | 0.68 | 0.53 |
| | RE | <0.01 | 0.39 | 0.96 | 0.18 |
| *Achnatherum* | RGR | 0.55 | 0.37 | 0.08 | 0.75 |
| | RE | 0.05 | 0.11 | 0.07 | 0.11 |
| *Pleuraphis* | RGR | 0.06 | 0.27 | <0.01 | 0.32 |
| | RE | 0.04 | 0.16 | 0.01 | 0.11 |
| *Larrea* | RGR | <0.01 | 0.06 | 0.35 | 0.65 |
| | RE | <0.01 | 0.04 | 0.75 | 0.84 |

| 1999 | | Covariate | *Brma*$_{cov}$ | $CO_2$ | *Brma*$_{cov}$ × $CO_2$ |
|---|---|---|---|---|---|
| *Larrea* | RGR | 0.35 | 0.76 | 0.12 | 0.07 |
| | RE | 0.47 | 0.59 | 0.61 | 0.60 |

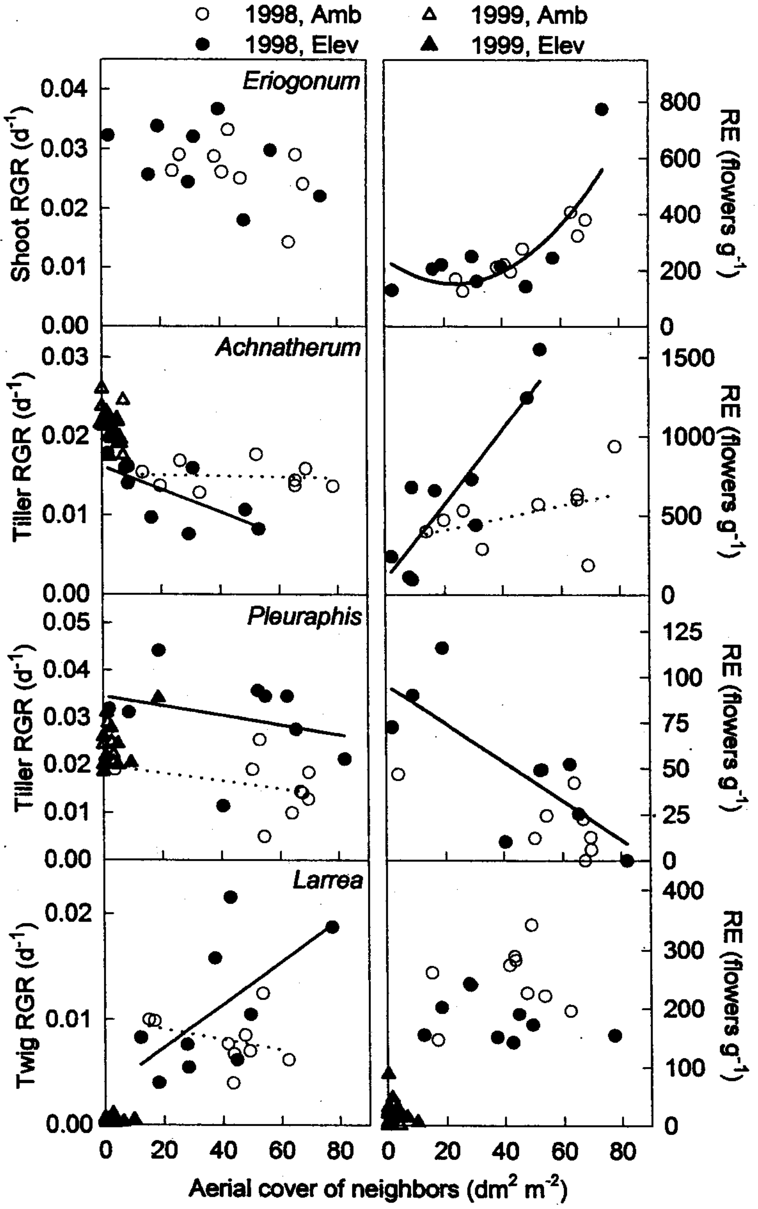
FIGURE LEGENDS

**Figure 1.** Relationships between target responses and herbaceous neighbors. Relative growth rate (RGR, left panels) and reproductive effort (RE, right panels) were measured during 1998 and 1999. Lines represent significant overall regression (bold solid line) or significant separate regressions for ambient (dotted line) and elevated $CO_2$ (solid line) during 1998 only (see text). Analyses for 1999 found no significant main or interaction effects, but data are included for comparison with 1998. *Eriogonum* did not occur in 1999, and only *Larrea* produced enough flowers in 1999 for analysis of RE for that year. Note different ordinate scales among target species.

**Figure 2.** Relationships between target $\Psi_{mid}$ and herbaceous neighbors during 1998 (left panels) and 1999 (right panels). Lines represent significant overall regression (bold solid line) or significant separate regressions for ambient (dotted line) and elevated $CO_2$ (solid line) during 1998 only (see text). Note different ordinate and abscissa scales between years.

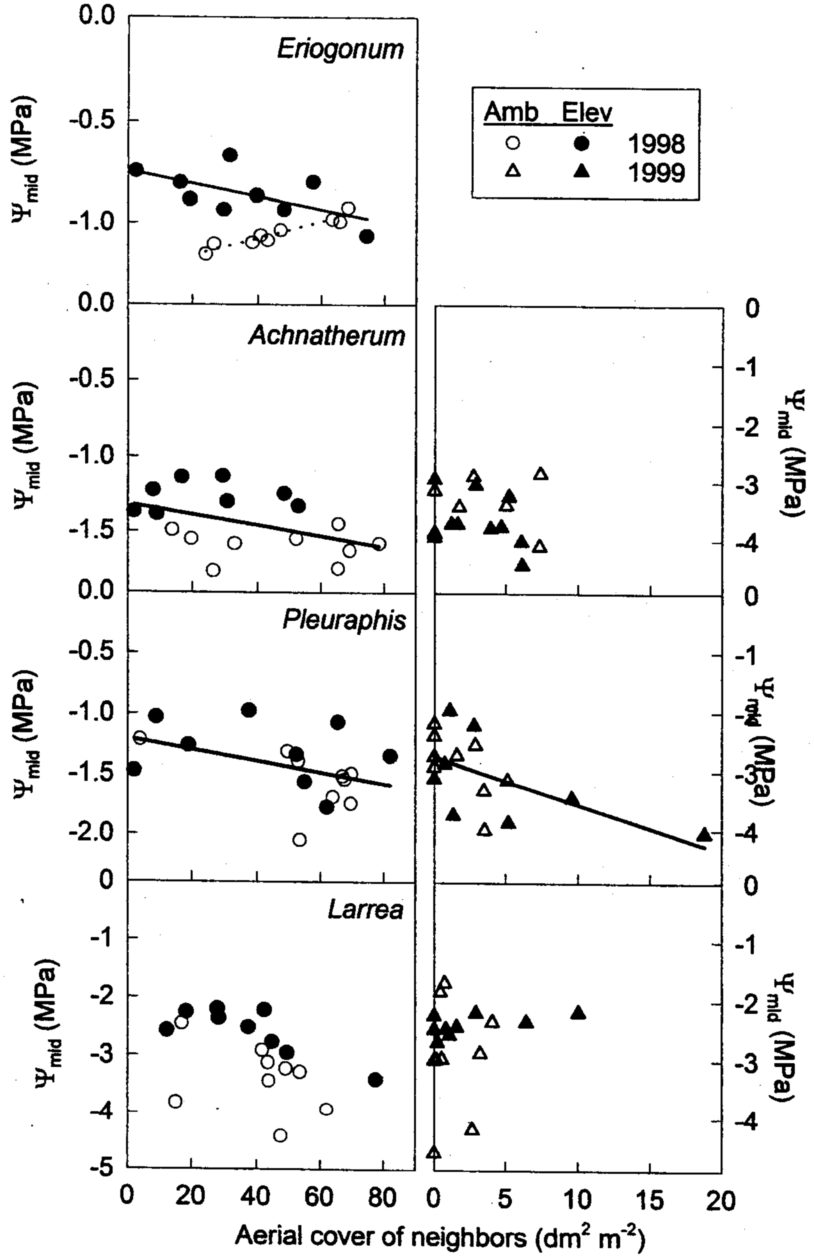
**Figure 3.** Relationships between target $A_{net}$ (upper panels) and $g_s$ (lower panels) associated with $\Psi_{mid}$ during 1998 and 1999. Lines represent significant overall regression (bold solid line) or significant separate regressions for ambient (dotted line) and elevated $CO_2$ (solid line) during 1998 only (see text). Note different abscissa scales among species.

Figure 1



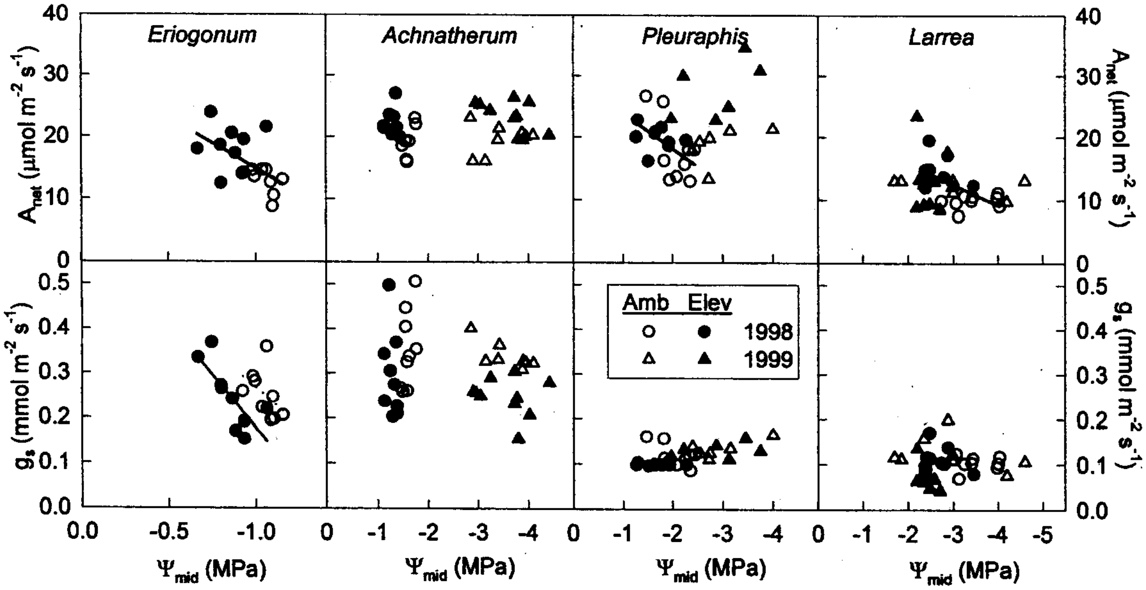
○ 1998, Amb
● 1998, Elev
△ 1999, Amb
▲ 1999, Elev
Eriogonum
Achnatherum
Pleuraphis
Larrea
Shoot RGR (d-1)
Tiller RGR (d-1)
Tiller RGR (d-1)
Twig RGR (d-1)
RE (flowers g-1)
RE (flowers g-1)
RE (flowers g-1)
RE (flowers g-1)
0.00
0.01
0.02
0.03
0.04
0.05
0
100
200
300
400
600
800
25
50
75
125
500
1000
1500
0
20
40
60
80
Aerial cover of neighbors (dm2 m-2)

Figure 2



Eriogonum
Achnatherum
Pleuraphis
Larrea
Amb Elev
○ ● 1998
△ ▲ 1999
$\Psi_{mid}$ (MPa)
Aerial cover of neighbors (dm$^2$ m$^{-2}$)
0.0
-0.5
-1.0
-1.5
-2.0
0
-1
-2
-3
-4
-5
0
20
40
60
80
0
5
10
15
20

Figure 3



Eriogonum
Achnatherum
Pleuraphis
Larrea
A<sub>net</sub> (µmol m-2 s-1)
g<sub>s</sub> (mmol m-2 s-1)
40
30
20
10
0
0.5
0.4
0.3
0.2
0.1
0.0
Amb Elev
1998
1999
0.0
-0.5
-1.0
0
-1
-2
-3
-4
-5
Ψmid (MPa)