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Effects of elevated carbon dioxide on primary productivity in a Mojave Desert ecosystem

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EFFECTS OF ELEVATED CO₂ ON PRIMARY PRODUCTIVITY

IN A MOJAVE DESERT ECOSYSTEM

by

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A dissertation submitted in partial fulfillment of the requirements for the

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ABSTRACT

Effects of Elevated CO₂ on Primary Productivity in a Mojave Desert Ecosystem

by

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Growth and gas exchange are predicted to be most responsive to future atmospheric CO₂ concentrations within arid ecosystems. It is hypothesized that elevated CO₂ will result in enhanced seasonal growth, increased leaf area and extension of the growing season via increased water-use efficiency (WUE). Greater WUE could result in increased survivorship and productivity of desert shrubs, and may increase the importance of this biome in the global carbon budget. Elevated CO₂ is also expected to influence future species distribution and abundance, which could alter structure and function, especially in arid ecosystems. For these reasons, we measured aboveground production, gas exchange, and water relations of species from different functional types in order to evaluate how future atmospheric CO₂ concentrations may affect desert shrubs. Elevated CO₂ significantly enhanced growth and gas exchange of the dominant evergreen perennial during an exceptionally wet year, but had less effect on spring- and summer-active drought-deciduous shrubs. During dry years, growth and seasonal carbon assimilation rates were much reduced across all functional types. Overall it appears that
water availability strongly interacts with CO$_2$ concentration to affect growth and gas exchange. As such, unpredictable and infrequent rainfall patterns typical of the desert southwest may prevent significant CO$_2$ affects on growth in dry years. However, predictions of increased atmospheric CO$_2$ concentrations and rainfall in the desert southwest may have important implications for the future productivity of the region.
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CHAPTER 1

OVERVIEW OF PLANT PRODUCTIVITY UNDER ELEVATED CO₂

Since the dawn of the Industrial Revolution, measurable increases in greenhouse gases have resulted due to human consumption of fossil fuels. One gas in particular, carbon dioxide (CO₂), is of interest to scientists studying ecosystem responses to climate change. With the atmospheric concentration of CO₂ predicted to double from pre-industrial levels during this century (Keeling et al. 1995), a growing concern is how plant growth, reproduction, and species distributions will be affected. It is known that most species respond to elevated CO₂ via increased photosynthesis, biomass, and water-use efficiency (Bazzaz 1990). However, detailed analyses of how intact desert ecosystems react under controlled CO₂ concentrations are lacking. Terrestrial vegetation is an important sink for atmospheric CO₂, and understanding how plants may respond to increased CO₂ levels is necessary for predicting future changes in ecosystem productivity.

An effective method for determining potential responses to a changing environment is to grow individuals under current and predicted levels of a variable and compare their responses. In this way response to the treatment, in this case elevated CO₂, can be analyzed for significance, and predictions of future plant performance can be made. Using this approach, Bowes (1991) demonstrated that increased levels of atmospheric
CO₂ result in enhanced growth and higher photosynthetic rates. Because CO₂ enters the leaves by simple diffusion, it follows that increased atmospheric concentrations lead to higher rates of diffusion into the leaves, all else being equal. Nonetheless, increases in photosynthesis under elevated CO₂ are expected to be species-specific, and should differ due to interspecific variation in the ability to concentrate CO₂ at the site of carboxylation (Hatch 1992). These dissimilar responses to elevated CO₂ may equate to contrasting gains in carbon across functional types, which could alter the structure and function of ecosystems. For example, the higher stomatal conductance values in C₃ vs. C₄ species may be reduced under elevated CO₂ and lead to higher water-use efficiency (WUE), which may equate to higher gains in primary productivity (Teare et al. 1973). In desert ecosystems, greater WUE may result in positive net photosynthesis longer into the dry season, thus increasing the overall carbon gain in this system.

Prior phenological work in North American deserts has shown that water, nitrogen, and temperature interact to influence leaf demography and morphology (Cunningham et al. 1979, Nilsen et al. 1986a, Lajtha and Whitford 1989, Smith et al. 1997). Desert environments are primarily water limited, and phenological constraints on primary production occur because of the unpredictable rainfall (Beatley 1974, Smith et al. 1997). Lags in canopy development behind photosynthetic capacity following major precipitation events constrain carbon gain in desert perennials (Comstock and Ehleringer 1986). Alternatively, as growing seasons progress and soils dry, reductions in photosynthetic rates prior to reductions in leaf number creates physiological constraints on carbon gain (Comstock and Ehleringer 1986). In addition to these constraints on deciduous species, evergreens also exhibit slower growth and reduced leaf number as
they become water stressed during the dry season (Cunningham et al. 1979, Lajtha and Whitford 1989). further reducing carbon assimilation in this ecosystem. Under elevated CO₂, increased WUE and longer leaf retention may reduce phenological constraints on productivity, resulting in greater seasonal growth for Mojave Desert plants. However, relaxation of water stress may promote higher nitrogen limitations on gas exchange (Smith et al. 1997). Furthermore, while C₃ plants may initially be more responsive to elevated CO₂ than C₄ plants, with time they often exhibit photosynthetic down-regulation (Sage 1994, Huxman et al. 1998a, 1998c), which could be viewed as a new constraint on productivity under elevated CO₂.

Primary productivity under elevated CO₂ may differ proportionally between growth and reproduction for species from contrasting functional groups. Annuals have relatively high growth rates because germination, growth and reproduction are all constrained to a single growing season. By contrast, perennials may forgo reproduction in a season and use all acquired resources for growth, maintenance and storage. Under elevated CO₂, annuals are predicted to respond to increased photosynthate levels via an increase in reproductive output instead of increased growth (Hunt et al. 1991). Perennials, on the other hand, which must maintain tissues/structures through non-growing seasons, tend to put proportionally more photosynthetic resources into roots, shoots, and leaves. Tradeoffs in growth vs. reproduction in one season may affect the productivity of a perennial in the following season, depending on whether the increased photosynthate is used to create resource acquisition structures (roots, leaves) or ephemeral reproductive structures (flowers, nectar, seeds) (Bazzaz 1997). Increase in primary productivity in both annuals and perennials grown under elevated CO₂ are expected, but allocational
patterns to maintenance, growth, and reproduction may differ. It will be important to
determine what patterns evolve since they will surely influence plant distribution,
abundance, and overall community composition.

As previously stated, elevated atmospheric CO₂ has been shown to result in increased
water-use efficiency (WUE) in many plants (Bazzaz 1990), allowing for greater leaf
production at the whole plant level. Enhanced leaf production subsequently increases the
demand for nutrients, including nitrogen and phosphorous. Thus, to support a greater leaf
area, especially in nutrient poor habitats, it would seem advantageous to conserve
nutrients by withdrawing them prior to leaf drop. Nutrient resorption then is a way of
sequestering plant nutrients that might otherwise become unavailable to the plant after
leaf abscission (Killingbeck 1993). Increased nutrient resorption may help to offset the
resource limitations that presumably may occur due to increased growth under elevated
CO₂.

Extremes in abiotic factors near the soil surface play an important role in limiting
seedling establishment in deserts (Beatley 1967, Smith and Nowak 1990). However,
such limitations may be relaxed when interactions with variables such as water or
elevated CO₂ occur (Polley et al. 1996, Huxman et al. 1998b, Centritto et al. 1999,
Humphrey and Schupp 1999). Initial data collected by S. Zitzer indicates seedling
survival for Larrea and Ambrosia is greater under elevated atmospheric CO₂ than
ambient (69% vs. 40%, respectively) (Personal communication). In addition, seedling
survival rates for both species were greater in open locations than beneath shrub
canopies. Seedlings establishing in interspaces may benefit from reduced mortality via
reduced competition for water or other limiting resources. In another study, Vilela and
Ravetta (2000) found that shading *Prosopis* seedlings increased their mortality by increasing shoot:root ratios and reducing total biomass. However, contrary to the many potential competitive interactions between seedlings and mature plants, much is also known about the beneficial effects that nurse plants have on seedlings (Smith et al. 1997). Interactions between seedlings and mature plants can be competitive or facilitative, but these can also change over time. While interspace microhabitats may afford greater water availability to seedlings through reduced competition with mature plants, they may also induce higher leaf temperatures and hence higher conductance and transpiration rates.

In *Larrea*, the dominant evergreen shrub of warm desert regions throughout the southwestern United States, phenology, photosynthesis, and growth are influenced strongly by tissue water potential (Oechel et al. 1972). It has been stated that the productivity of *Larrea* and desert systems in general is limited by low standing biomass and leaf area (Chew and Chew 1965, Webb et al. 1983, Smith et al. 1997). In fact, *Larrea* leaves typically have maximum lifespans no longer than 18 months (Chew and Chew 1965, Lajtha and Whitford 1989). In addition to leaf demography, canopy architecture of *Larrea* in the Chihuahuan and Mojave Deserts has been found to improve WUE by promoting reduced self-shading during periods when conditions are most favorable for photosynthesis (Neufeld et al. 1988). It is possible elevated CO₂ may enhance some of these features, such as WUE or leaf area index (LAI), and increase productivity by either increasing leaf longevity or leaf production. Through careful quantitative analyses I will determine if increases in primary production under elevated CO₂ are the result of increased photosynthesis or increased leaf area. In addition to
Larrea, the effect of elevated CO₂ on other functional types of the NDFF will also be an important component of this project.

The research presented in the following chapters was conducted on *in situ* plants at the Nevada Desert FACE Facility (NDFF) located within the Nevada Test Site (NTS) in southern Nevada. At the NDFF plants were sampled within three ambient CO₂ (360 μmol mol⁻¹) and three 1.5x ambient CO₂ (550 μmol mol⁻¹) treatment rings, each 25 m in diameter. Additionally, three ambient CO₂ level treatment rings lacking blowers and acting as non-blower controls were also sampled. For complete description of the NDFF see Jordan *et al.* (1999). Four species naturally occurring at the NDFF were used for field examinations of phenological and physiological constraints on primary production. These species are common to this desert ecosystem, and include: (1) *Larrea tridentata*, an evergreen shrub; (2-3) *Ambrosia dumosa* and *Lycium pallidum*, spring-active, drought-deciduous shrubs; and (4) *Krameria erecta*, a summer-active, drought-deciduous shrub. These functional groups (evergreen, spring- and summer-active deciduous) represent a broad spectrum of the potential physiological responses to elevated CO₂. Presently, desert lands are increasing rapidly (Dregne 1991) and it is therefore critical that we understand how deserts may respond to the increase in greenhouse gases predicted for this century. Because desert ecosystems already represent a significant portion of the earth’s terrestrial system, and are predicted to be among the most responsive ecosystem-types to elevated CO₂ (Strain and Bazzaz 1983), analyses of this nature will help improve our understanding of how global climate change may influence the desertification process.
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CHAPTER 2

NUTRIENT RESORPTION IN NATURALLY OCCURRING DESERT SHRUBS EXPOSED TO FREE-AIR CO₂ ENRICHMENT (FACE)

This paper will be submitted to New Phytologist and is presented in the format of that journal. The complete citation is:

Summary

- Leaf nutrient resorption enables plants to sequester resources that might otherwise become unavailable. Future CO$_2$ concentrations ([CO$_2$]) may increase growth but decrease resource availability, which in turn could affect nutrient resorption.

- We compared resorption efficiency (percent of a nutrient resorbed from green leaves) and proficiency (terminal nutrient concentration in senesced leaves) of N, P, Cu, Mn and Zn in two deciduous shrubs (*Ambrosia dumosa* and *Lycium pallidum*) growing *in situ* under ambient (~375 μmol mol$^{-1}$) or elevated (~550 μmol mol$^{-1}$) CO$_2$ at the Nevada Desert FACE Facility.

- Nitrogen resorption efficiency and proficiency were greater in *Ambrosia*, regardless of [CO$_2$]. All treatments completely resorbed P. Both Cu and Mn showed some accretion, while Zn resorption was most proficient in *Lycium*, regardless of [CO$_2$]. Resorption proficiency of Cu and Mn were higher in *Ambrosia* under elevated vs. ambient CO$_2$.

- Although nutrient resorption patterns were not consistent with respect to [CO$_2$] during a near-average rainfall year, enhanced plant production under elevated CO$_2$ during exceptionally wet years may induce greater resorption in nutrients that are currently incompletely resorbed, but it may also result in a greater limitation for nutrients that are completely resorbed at the current CO$_2$ concentration.

Key words: *Ambrosia*; elevated CO$_2$; FACE; *Lycium*; Mojave Desert; plant growth; resorption efficiency; resorption proficiency
Introduction

Leaf nutrient resorption enables plants to conserve resources, and may be especially important in unpredictable environments such as deserts. Several factors are known to influence nutrient resorption, including water availability (Hocking, 1982), timing of leaf abscission (Killingbeck et al., 1990; del Arco et al., 1991), and microhabitat (Pugnaire & Chapin, 1993; Killingbeck & Whitford, 2001). Resorption can also vary temporally within individuals or populations (Killingbeck et al., 1990; May & Killingbeck, 1992), and resorption of specific nutrients may be related to their concentration, or the concentration of other nutrients, within green leaves (Chapin & Kedrowski, 1983; Nordell & Karlsson, 1995; Killingbeck & Whitford, 2001). The intensity of nutrient resorption or accretion appears to be nutrient specific, perhaps reflecting the availability of a given nutrient in the environment.

Although plant growth in deserts is primarily limited by low water availability (Smith et al., 1997), nutrient limitations do occur (Romney et al., 1978; Gutierrez & Whitford, 1987; Fisher et al., 1988; Ehleringer et al., 1998). Resorption, the withdrawal of nutrients from senescing plant tissues, conserves nutrients that would otherwise be lost in shed litter (Aerts, 1996; Killingbeck, 1996). Nutrient resorption can be expressed either as an efficiency (the difference between green and senesced leaf [N] divided by green leaf [N]), or a proficiency (the terminal concentration of a nutrient in senesced leaves; Killingbeck, 1996). These measures are complementary, with a difference in efficiency not necessarily indicating a difference in proficiency and vice versa. The process of nutrient resorption may be particularly important in arid ecosystems where inherently slow litter decomposition rates lower soil nutrient availability (Comanor & Staffeldt,
If some nutrients currently have high resorption levels due to this limitation, and if elevated CO₂ stimulates growth and nutrient demands (while reducing litter quality), limitations may intensify if there are no new inputs.

Elevated atmospheric CO₂ increases primary production in many plant species (Bazzaz, 1990). This is particularly the case in desert ecosystems, where Smith et al. (2000) measured a doubling of aboveground production in Mojave Desert shrubs growing at 550 μmol mol⁻¹ CO₂ during a high rainfall year. Because increased production under elevated CO₂ is predicted to intensify nutrient demands while at the same time slowing litter decomposition and nutrient recycling (e.g., higher leaf C:N ratios; Strain & Bazzaz, 1983), plants will either have to increase resorption or receive new inputs of nutrients. This prediction for stronger nutrient limitation under elevated CO₂ may not be valid, however, if elevated CO₂ does not enhance plant production or change the timing of leaf drop. When growth is not enhanced under high CO₂, as was found for Mojave Desert shrubs during a dry year (Smith et al., 2000), there may be no stimulus for increased resorption of nutrients.

Nutrient resorption has been examined in desert plants from a variety of growth forms and habitats (Killingbeck, 1992, 1993, 1996; Killingbeck & Whitford, 2001), but it has never been measured in naturally-occurring desert shrubs growing under elevated CO₂. The macronutrients N and P are frequently chosen for analysis because of their importance to plant growth (Chapin, 1980). Additionally, high resorption and accretion has been shown for the micronutrients Cu, Mn and Zn in other ecosystems (Killingbeck, 1985; Killingbeck & Costigan, 1988). These micronutrients could play a role in
resorption of other key elements such as N. but little is known about how they are resorbed or accreted in desert perennials under elevated CO$_2$.

In this study, we measured nutrient resorption efficiencies and proficiencies in two species of drought-deciduous desert shrubs grown under ambient and elevated CO$_2$. Specifically, we tested the hypotheses that nutrient resorption (1) efficiency and (2) proficiency increase under elevated CO$_2$. We tested our hypotheses by measuring plant growth and quantifying [N], [P], [Cu], [Mn] and [Zn] in the green and senesced leaves of two naturally-occurring deciduous shrubs, *Ambrosia dumosa* A. Gray (Asteraceae) and *Lycium pallidum* Miers (Solanaceae), growing at the Nevada Desert Face Facility. We also tested the hypothesis that the resorption of leaf nutrients is related to green leaf attributes by examining the relationship of resorption efficiency and proficiency to green-leaf SLA. [N], [P], [Cu], [Mn] and [Zn].

Materials and Methods

Our study was conducted during the 2001 growing season at the Nevada Desert Free-Air CO$_2$ Enrichment (FACE) Facility (NDFF), located on the Nevada Test Site in southern Nevada, USA. In addition, we used archived green-leaf and litter data from a wet El Niño year (1998) to compare with the dry year in 2001. Site characteristics and CO$_2$-delivery performance at the NDFF have been summarized by Jordan *et al.* (1999). The species examined, *Ambrosia dumosa* and *Lycium pallidum*, are the dominant drought-deciduous shrubs at the NDFF. They occur naturally within six, 25-m circular plots, three of which are continuously fumigated at a set point of 550 µmol mol$^{-1}$ CO$_2$, and three of which receive ambient air (~370 µmol mol$^{-1}$ CO$_2$) via the FACE system.
(Hendrey & Kimball, 1994). Additionally, three ambient plots without the FACE system were established as controls on the potential effects of the CO₂ delivery system. Plant growth and gas exchange parameters measured to date at the NDFF have not significantly differed between the ambient FACE and non-FACE control plots, thus we will only present data from the ambient and elevated FACE plots.

For 1998 data, green leaf N concentration (mg g⁻¹) was determined from ~ 0.5 g samples collected during gas exchange campaigns on 18-19 June (Lycium: n = 2 ambient and 4 elevated CO₂ plants) and 20-21 September (Ambrosia: n = 3 ambient and 6 elevated CO₂ plants). Samples were dried at 60°C to constant mass and analyzed using a kjeldahl digestion to extract N. Bulk leaf litter collected in trays under Lycium was used to determine N resorption proficiency (the terminal concentration of a given nutrient in senesced leaves) on a mass basis (mg g⁻¹). Litter was not collected under Ambrosia in 1998, thus precluding measurement of resorption efficiency and proficiency that year. Lycium litter was analyzed at the Desert Research Institute, Reno NV, using an elemental analyzer attached to a mass spectrophotometer. Mean annual values for green-leaf and leaf litter N concentrations were determined, and resorption efficiency was calculated as:

\[
\text{green leaf } [N] - \text{leaf litter } [N] \\
\text{green leaf } [N] \\
X 100
\]

Values of green leaf N, resorption efficiency, and proficiency were compared using one-way ANOVA (SAS, 1989), with CO₂ treatment as the independent variable.

Refined methods were used in 2001 to determine resorption efficiency and proficiency because carbon can be resorbed during senescence, thus changing nutrient concentrations within the leaf, and measures based on bulk mass instead of leaf area cannot account for resorbed carbon. In each plot we collected ~ 0.5 g of green leaves from three to five
randomly chosen *Ambrosia* and *Lycium* shrubs during the peak growing season in spring (April 4-5). Green leaves were collected from all sides of each shrub. We increased sample sizes over 1998, but due to the limited number of plants we could sample without interfering with other studies at the NDFF, total sample sizes were: *Ambrosia* - 13 ambient and 15 elevated plants; *Lycium* - 14 ambient and 15 elevated plants. We collected leaves from the same individuals at the late stage of leaf senescence by lightly shaking them off several branches into plastic bags (June 3 – five ambient *Ambrosia*, twelve elevated *Ambrosia*, eleven ambient *Lycium*, and 13 elevated *Lycium*: June 9 – four ambient *Ambrosia*, two ambient *Lycium*, and one elevated *Lycium*: June 17 – three ambient *Ambrosia*, three elevated *Ambrosia*, one ambient *Lycium*, and one elevated *Lycium*: July 6 – one ambient *Ambrosia*). Senesced leaves from a given individual were all collected on the same day so as not to introduce within-shrub variation in leaf litter nutrient content. We found leaf nutrient contents and calculated values of resorption within a specific treatment did not significantly differ over the collection period, so data were pooled within a species by [CO₂]. For the 2001 data, nutrient resorption efficiency was calculated as above except using nutrient content on a leaf area basis (mg/cm²: Killingbeck & Whitford, 2001). Resorption proficiency remained the terminal concentration (% for macronutrients; mg/kg for micronutrients) of a given nutrient in senesced leaves, with low nutrient concentrations in senesced leaves indicating high resorption proficiency, and vice versa.

Upon collection, leaf samples were immediately placed in plastic bags and kept cool until leaf area was determined shortly thereafter. We scanned leaves with a flatbed scanner (Hewlett Packard model 5370C) and then measured leaf area (cm²) using
imaging software (Scion Image software, Beta 4.0.2, Scion Corporation, USA). Samples were dried at 60°C to a constant mass and nutrient analyses were completed in the Soil, Water, and Plant Testing Laboratory at New Mexico State University. A kjeldahl digestion was used to extract N, and a microwave-assisted acid digestion using concentrated nitric acid and 30% hydrogen peroxide was used to extract P, Cu, Mn and Zn. Nitrogen was measured with a Technicon AutoAnalyzer, and P, Cu, Mn, and Zn were measured with a Perkin Elmer inductively coupled plasma spectrophotometer.

Leaf area and dry mass were used to calculate specific leaf area (SLA; leaf area per unit leaf mass) in order to examine its relationship to resorption efficiency and proficiency. Statistical comparisons of SLA, green-leaf nutrients, and nutrient resorption efficiency and proficiency of each species x CO₂ treatment were analyzed by plot means (n=3 per [CO₂]) using SAS (SAS, 1989). We used ANOVA when the assumption of normality was met and the Kruskal-Wallis distribution-free statistic when the data were not normally distributed. Paired comparisons of specific variables were made with Fisher’s LSD multiple means comparison for normally distributed data, and with the Mann-Whitney U-test when data were not normally distributed. We also used linear regression (based on pooled values of a given species x CO₂ treatment) to examine the relationship between resorption efficiency and proficiency, and green-leaf SLA, N, P, Cu, Mn and Zn.

Results

Green Leaves

Green-leaf N did not differ by CO₂ growth environment for either *Ambrosia dumosa* (*P* = 0.16) or *Lycium pallidum* (*P* = 0.22) in 1998 (Table 2.1). The [N] of green leaves
was significantly higher in both species at ambient vs. elevated CO₂ in 2001 ($P < 0.05$ in both cases). In 2001, green-leaf SLA did not differ by species or [CO₂] ($P > 0.05$). There was no CO₂ effect on [P] within either species, but [P] was higher in *Ambrosia* than *Lycium* at both [CO₂] ($P < 0.05$). Both [Cu] and [Mn] did not differ within or between species by [CO₂]. *Ambrosia* [Zn] was significantly higher under elevated CO₂, while [Zn] did not differ in *Lycium*. Additionally, green-leaf [Zn] was significantly higher in *Ambrosia* than *Lycium* at both CO₂ concentrations. New shoot production was higher in *Ambrosia* than *Lycium* at both CO₂ concentrations. New shoot production was

Table 2.1. Mean specific leaf area (SLA), nitrogen concentration (N %), phosphorus concentration (P %), and copper (Cu), manganese (Mn) and zinc (Zn) concentrations in green leaves of *Ambrosia dumosa* and *Lycium pallidum* growing under ambient and elevated [CO₂] during 1998 and 2001. Numbers in parentheses are standard error of the mean. Means in vertical columns with different letters are significantly different at $P < 0.05$.

<table>
<thead>
<tr>
<th>Species</th>
<th>[CO₂] (ppm)</th>
<th>SLA (cm² g⁻¹)</th>
<th>N (%)</th>
<th>P (%)</th>
<th>Cu (mg kg⁻¹)</th>
<th>Mn (mg kg⁻¹)</th>
<th>Zn (mg kg⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ambrosia</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>370</td>
<td>2.4(0.2)a</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>550</td>
<td>2.5(0.2)a</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>2001</td>
<td>370</td>
<td>129(32)a</td>
<td>4.5(0.1)b</td>
<td>0.27(0.02)a</td>
<td>7.2(1.9)a</td>
<td>46.1(4.8)a</td>
<td>31.0(3.2)ad</td>
</tr>
<tr>
<td></td>
<td>550</td>
<td>135(23)a</td>
<td>3.9(0.2)cd</td>
<td>0.24(0.02)a</td>
<td>8.9(2.4)a</td>
<td>32.7(4.5)a</td>
<td>40.5(3.1)b</td>
</tr>
<tr>
<td><strong>Lycium</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>370</td>
<td>1.3(0.1)e</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>550</td>
<td>1.5(0.2)e</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>2001</td>
<td>370</td>
<td>118(14)a</td>
<td>4.0(0.1)c</td>
<td>0.16(0.004)b</td>
<td>7.0(1.2)a</td>
<td>48.1(5.9)a</td>
<td>21.8(1.7)e</td>
</tr>
<tr>
<td></td>
<td>550</td>
<td>116(16)a</td>
<td>3.6(0.1)d</td>
<td>0.15(0.01)b</td>
<td>10.8(3.7)a</td>
<td>42.0(5.5)a</td>
<td>26.0(1.2)cd</td>
</tr>
</tbody>
</table>
not measured in *Lycium* during 1998, and did not differ between CO₂ growth environments in 2001. *Ambrosia* shoot production was significantly greater under elevated compared to ambient CO₂ in both 1998 and 2001 (D. Housman, in review).

### Resorption Efficiency

N resorption efficiency could not be measured for *Ambrosia* during 1998 due to a lack of leaf litter data, and did not differ between ambient (30%) and elevated (34%) CO₂-grown *Lycium*. In 2001 we found no within-species effect of [CO₂] on resorption efficiency of N (Fig. 2.1a). However, N resorption efficiency in *Ambrosia* (82%) was significantly higher than *Lycium* (62%) when averaged over both [CO₂]. The resorption efficiency of P was relatively high across all treatments, and did not differ within species by growth [CO₂] (Fig. 2.1a). Resorption of Cu did not differ in *Ambrosia*, but fluctuated considerably. The ambient-grown *Ambrosia* accreted Cu during senescence (7.2 mg kg⁻¹ in green leaves vs. 17.1 mg kg⁻¹ in senesced leaves; Fig. 2.1b). Manganese was accreted in all treatments, with no significant difference in efficiencies within or between species (Fig. 2.1b). Resorption efficiency of Zn was similar across treatments (Fig. 2.1b).

### Resorption Proficiency

Resorption proficiency of N in *Lycium* did not differ between ambient (0.91%) and elevated (0.92%) [CO₂] in 1998. In 2001, N resorption was less proficient than in 1998, and did not differ within either species by CO₂ treatment, although *Ambrosia* was significantly more proficient than *Lycium*, regardless of the [CO₂] (Fig. 2.2a). We found
no CO₂ effect on resorption proficiency of P within either species, but again the species differed, this time with ambient-grown Lycium more proficient at resorbing P compared with...

Figure 2.1. Mean nutrient resorption efficiencies of Ambrosia dumosa and Lycium pallidum grown at ambient (hatched bars) or elevated (solid bars) [CO₂]: (a) Macronutrients (N and P); (b) Micronutrients (Cu, Mn and Zn). Negative resorption values indicate accretion of that nutrient in senesced leaves. Letters by error bars, when present, represent significantly different means (P < 0.05). Error bars represent 1 SE.

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to both *Ambrosia* treatments (Fig. 2.2a). All species x CO\(_2\) combinations had P resorption proficiencies indicative of essentially complete resorption (Killingbeck, 1996). Copper resorption proficiency differed between treatments, with significantly lower
proficiency in ambient-grown *Ambrosia* due to accretion in that treatment (Fig. 2.2b).

Manganese resorption proficiency was significantly higher in elevated- vs. ambient-
grown *Ambrosia*, and was higher for *Lycium* than *Ambrosia*, regardless of the CO₂
treatment (Fig. 2.2b). Zinc resorption proficiency showed no CO₂ effect in either species.
but *Lycium* resorption of Zn was more proficient than *Ambrosia*, regardless of [CO₂]
(Fig. 2.2b).

Figure 2.2. Mean nutrient resorption proficiencies of *Ambrosia dumosa* and *Lycium pallidum* grown at ambient (hatched bars) or elevated (solid bars) [CO₂]; (a) Macronutrients (N and P); (b) Micronutrients (Cu, Mn, and Zn). Dashed lines indicate resorption proficiencies considered to represent complete resorption (Killingbeck 1996). Letters by error bars, when present, represent significantly different means (P < 0.05). Error bars represent 1 SE.

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Copper

Manganese

Zinc

Resorption proficiency (mg kg⁻¹)

Ambrosia

Lycium

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Table 2.2. Partial $R^2$ from linear regressions indicating relationships between resorption (efficiency or proficiency) and green-leaf SLA. [N], [P], [Cu], [Mn] and [Zn] in *Ambrosia dumosa* and *Lycium pallidum* growing under ambient and elevated [CO$_2$] in 2001. For each measure of resorption, only variables that were significantly related to that measure in at least one treatment are presented. Regressions were performed on each species x [CO$_2$] separately; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. All significant relationships were positive except for those noted with a dash (-) after the probability asterisk(s).

<table>
<thead>
<tr>
<th>Parameter</th>
<th><em>Ambrosia</em> (ambient)</th>
<th><em>Ambrosia</em> (elevated)</th>
<th><em>Lycium</em> (ambient)</th>
<th><em>Lycium</em> (elevated)</th>
</tr>
</thead>
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<tr>
<td><strong>N resorption efficiency</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Green leaf N</td>
<td>0.99***</td>
<td>0.98***</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Green leaf P</td>
<td>-</td>
<td>-</td>
<td>0.97***</td>
<td>0.94***</td>
</tr>
<tr>
<td><strong>P resorption efficiency</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Green leaf N</td>
<td>0.99***</td>
<td>0.99***</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Green leaf P</td>
<td>-</td>
<td>-</td>
<td>0.99***</td>
<td>0.98***</td>
</tr>
<tr>
<td><strong>Cu resorption efficiency</strong></td>
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<td></td>
<td></td>
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<tr>
<td>Green leaf Cu</td>
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<td>-</td>
<td>0.76***</td>
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<tr>
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<td>-</td>
<td>0.80***</td>
<td>-</td>
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</tr>
<tr>
<td>SLA</td>
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<td>-</td>
<td>0.89***</td>
<td>-</td>
</tr>
<tr>
<td>Green leaf N</td>
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<td>-</td>
<td>0.82***</td>
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</tr>
<tr>
<td>Green leaf Zn</td>
<td>-</td>
<td>0.69***</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Green leaf N</td>
<td>-</td>
<td>0.91***</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Green leaf P</td>
<td>-</td>
<td>-</td>
<td>0.92***</td>
<td>-</td>
</tr>
<tr>
<td>Green leaf Zn</td>
<td>-</td>
<td>-</td>
<td>0.96***</td>
<td>-</td>
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<tr>
<td><strong>N resorption proficiency</strong></td>
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<td></td>
</tr>
<tr>
<td>SLA</td>
<td>-</td>
<td>-</td>
<td>0.95***</td>
<td></td>
</tr>
<tr>
<td>Green leaf P</td>
<td>0.98***</td>
<td>0.93***</td>
<td>0.96***</td>
<td>-</td>
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<tr>
<td><strong>P resorption proficiency</strong></td>
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<td></td>
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<tr>
<td>SLA</td>
<td>-</td>
<td>-</td>
<td>0.94***</td>
<td></td>
</tr>
<tr>
<td>Green leaf N</td>
<td>-</td>
<td>0.90***</td>
<td>-</td>
<td>0.94***</td>
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<tr>
<td>Green leaf P</td>
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<td>-</td>
<td>0.96***</td>
<td>-</td>
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<td><strong>Cu resorption proficiency</strong></td>
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<td>SLA</td>
<td>0.75***</td>
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<td>-</td>
</tr>
<tr>
<td>Green leaf Cu</td>
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<td>0.70***</td>
<td>0.81***</td>
<td>-</td>
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<tr>
<td>Green leaf P</td>
<td>-</td>
<td>-</td>
<td>0.84***</td>
<td>-</td>
</tr>
<tr>
<td><strong>Mn resorption proficiency</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Green leaf N</td>
<td>0.97*</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Green leaf P</td>
<td>-</td>
<td>-</td>
<td>0.97***</td>
<td>-</td>
</tr>
<tr>
<td>Green leaf Mn</td>
<td>-</td>
<td>0.91***</td>
<td>0.98***</td>
<td>-</td>
</tr>
<tr>
<td><strong>Zn resorption proficiency</strong></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>SLA</td>
<td>0.84***</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Green leaf N</td>
<td>-</td>
<td>0.83***</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Green leaf P</td>
<td>-</td>
<td>-</td>
<td>0.97***</td>
<td>0.77***</td>
</tr>
</tbody>
</table>
Relationship between resorption and green-leaf attributes

The strongest regression-based relationship in 2001 was between green-leaf [P] and N resorption proficiency (Table 2.2). Green-leaf [P] explained > 93% of the variation in N resorption proficiency for three out of four treatments. For explaining resorption efficiency of N, green-leaf [N] was most important for *Ambrosia* while green-leaf [P] was most important for *Lycium*. Specific leaf area was not a consistent predictor of any resorption parameter, although SLA did explain > 94% of the variation in both N and P resorption proficiency of *Lycium* under elevated CO$_2$. Although there were no consistent predictors of Cu, Mn and Zn resorption efficiency or proficiency, every green-leaf variable we measured explained a significant amount of the variation in at least one resorption parameter (Table 2.2).

Discussion

To our knowledge, this is the first study of nutrient resorption in desert shrubs grown under elevated CO$_2$. Our hypothesis, that elevated CO$_2$ would enhance resorption efficiency and proficiency, was not supported in the shrubs or years we examined. The leaves of perennial plants in the northern Mojave Desert have been found to contain relatively high (3-4%) N concentrations (Romney *et al.* 1974; Wallace *et al.* 1974), and the nitrogen availability of soils is sufficient to support rapid growth even during years with abundant rainfall (Wallace *et al.* 1978). This apparent lack of an N limitation may explain why resorption did not increase under elevated CO$_2$ as we predicted. However, for some other nutrients, the resorption levels at ambient CO$_2$ already indicate essentially complete resorption is taking place, and thus we would not expect to find increased
proficiency under high CO₂. For P in particular, Wallace and Romney (1972) found it was an important limiting factor in the productivity of northern Mojave Desert, which supports the highly proficient resorption we measured for P, regardless of [CO₂].

In 2001 we found no increase in N resorption efficiency under elevated CO₂ (Fig. 2.1), even though green-leaf [N] was significantly lower in the elevated- vs. ambient-grown plants of both species (Table 2.1). This decrease in [N] at elevated CO₂ occurred without an increase in production in Lycium, perhaps as a result of increased photosynthesis at elevated CO₂ without a concomitant increase in growth. Thus, increased growth does not appear to be the sole cause for decreased nutrient content under elevated CO₂. And even though green-leaf [N] decreased under elevated CO₂, we found no difference in resorption proficiency of N between CO₂ treatments for either species (Fig. 2.2). Similar findings have been seen elsewhere (Norby & Cotrufo, 1998; Norby et al., 2001), and suggest the hypothesis of reduced litter quality (as measured by C:N) under elevated CO₂ should not be held as a universal tenet.

Several other studies have also failed to show within-species differences in N resorption efficiency under elevated CO₂ (see meta-analysis by Norby et al., 2001). The N resorption efficiencies we report in 1998 for Lycium (29% ambient and 33.5% elevated CO₂) are lower than the mean value (50%) reported for numerous perennials from a variety of habitats (Aerts, 1996). 1998 was an extremely wet year in the Mojave Desert, with an extended growing season and high soil N availability. In 2001, a more typical rainfall year, values of N resorption were 11-35% higher than that mean value. These findings suggest reduced resorption efficiency in high rainfall years, although it is possible this is due to the different sampling methodologies between years. Nonetheless,
P resorption efficiencies (79-90%) are also higher than the mean (52%) reported by Aerts (1996). Furthermore, resorption efficiencies of N and P in *Ambrosia* and *Lycium* at both CO₂ concentrations exceed those reported for several other desert shrubs and trees from the more mesic Chihuahuan Desert (Killingbeck, 1993; Killingbeck & Whitford, 2001). Overall, these higher efficiencies support the hypothesis that nutrient resorption should be greater in species located within relatively nutrient-poor habitats.

We observed no differences in green-leaf [P]. P resorption efficiency, or P resorption proficiency as a function of [CO₂] for either species. Phosphorus resorption proficiency in both species was below 0.05%, a concentration considered to represent essentially complete resorption of P (Killingbeck, 1996). These high resorption values agree with the findings of Wallace and Romney (1972) that P is a limiting factor in the Mojave Desert. Moreover, the high P proficiencies we measured were not consistent with proficiencies measured in N, probably due to limitations of the former nutrient. Differences in resorption proficiencies reveal the effects of CO₂ enrichment on leaf nutrients are nutrient-specific. Thus, it will be important for future studies and predictive models to take into account the interaction of CO₂ and specific nutrients in order to more accurately predict plant responses to global change.

For the micronutrients, we observed negative resorption efficiencies in some treatments (Fig. 2.1), indicating accretion of these nutrients in the senesced leaves. For example, [Cu] was 2.5 times higher in the senesced vs. green leaves of *Ambrosia* at ambient [CO₂]. *Ambrosia* leaves also had higher [Mn] at senescence compared to those in green leaves (2.6 and 2.5 times higher in ambient and elevated CO₂, respectively). Likewise, senesced *Lycium* leaves had higher [Mn] than green leaves at both [CO₂] (1.5-
1.7 times higher, respectively). This accretion may be the result of lower nutrient mobility, or perhaps due to lack of a driving force for their conservation, the latter of which could be caused by sufficient availability in the soil. To our knowledge, there are no published values for complete resorption of these micronutrients, and the fact that micronutrients are by definition only required in small quantities suggests not much are needed.

Linkages between green-leaf nutrient concentration and resorption have been found in species from the Chihuahuan Desert (Killingbeck & Whitford. 2001), evergreen and deciduous taiga trees (Chapin & Kedrowski. 1983), and eastern U.S. deciduous trees grown under elevated CO₂ (Norby et al., 2000). We found resorption efficiency and proficiency were strongly related to green-leaf attributes (Table 2.2), but not necessarily as we might expect. It was green-leaf [P], not [N], which explained a significant amount of the variation in N resorption proficiency for 3 out of 4 treatments. Moreover, although green-leaf [P] explained a significant amount of the variation in P resorption efficiency of both Lycium treatments, it was green-leaf [N] that explained variation in P resorption efficiency of Ambrosia at both [CO₂]. Although green-leaf SLA explained a significant amount of the variation in several resorption factors, it did not do so consistently across treatments, and so there does not appear to be a consistent leaf area affect on nutrient resorption parameters as a function of [CO₂].

Nutrient resorption can be highly influenced by the timing of leaf abscission. Past work has shown that Populus leaves that senesced on earlier dates had lower resorption efficiencies of N, P and Cu (Killingbeck et al., 1990). Uncharacteristic or sudden changes in environmental conditions (e.g., unusually dry conditions, early frost, etc.) may
lead to early abscission, making realized resorption considerably lower than potential resorption (Killingbeck et al., 1990; Norby et al., 2000). We found that the timing of leaf abscission did not differ in *Ambrosia* or *Lycium* as a function of CO$_2$. Nevertheless, the timing of leaf abscission was negatively correlated with the [N] of senesced leaves, and positively correlated with the [P], [Cu], [Mn] and [Zn] of senesced leaves. However, the timing of leaf abscission did not explain a significant amount of the overall variation in resorption proficiency for any of the nutrients that we measured (N = 10%; P = 2%; Cu = 15%; Mn = 10%; Zn = 37%). Perhaps the short duration of time (~ two weeks) over which senescence took place in *Ambrosia* and *Lycium* precluded a significant effect of time on resorption.

Green leaves collected from *Ambrosia* and *Lycium* at the NDFF during a wet El Niño year (1998) did not differ in [N] by CO$_2$ treatment. Moreover, data on *Lycium* leaf litter in 1998 showed lower N resorption efficiencies compared to 2001 and no difference in N resorption proficiency (0.9%N ±0.1 in both CO$_2$ treatments) based on a bulk mass basis. This suggests N limitation may have been reduced during the high rainfall year of 1998. Still, plant production was greater in 1998, and mean resorption efficiencies were slightly higher in 1998 vs. 2001, regardless of CO$_2$ concentration (ambient CO$_2$ = 0.9% N in 1998 vs. 1.1% N in 2001; elevated CO$_2$ = 0.9% N in 1998 vs. 1.0% N in 2001). This suggests more N may be removed from pre-senescent leaves in high rainfall years, when the overall growth is greater at both [CO$_2$].

For some nutrients resorption is not expected to increase above current levels because those levels already represent essentially complete resorption. For example, P is strongly limiting in desert shrubs growing in calcareous soils (Lajtha & Schlesinger, 1988). such
as those at the NDFF. Because P showed essentially complete resorption in both species at ambient CO₂, it would not be expected to become more proficient under elevated CO₂. Indeed, we found no significant increase in P resorption proficiency when plants were grown under high CO₂. It also seems unlikely that P proficiency would increase any further under elevated CO₂ because the average amount of P currently retained within senesced leaves is miniscule (< 0.05%). Nevertheless, the resorption proficiencies of some nutrients we examined (e.g., N) did not show complete resorption at ambient CO₂, and only two nutrients (Cu and Mn) demonstrated significantly higher resorption proficiencies under elevated CO₂. Thus, while there may be the potential for increased resorption proficiency under future CO₂ concentrations, it may be dependent on plant growth and timing of drought stress, and could be nutrient-specific. Ultimately, whether or not nutrient resorption efficiencies and proficiencies of desert shrubs change in the future will likely depend upon how elevated CO₂ and water availability interact to affect plant growth and nutrient demands. If elevated CO₂ substantially increase growth over the long term, nutrient limitations could occur unless nutrient availability increases via increased resorption or inputs into this ecosystem.

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CHAPTER 3

FUNCTIONAL ECOLOGY OF SHRUB SEEDLINGS AFTER A NATURAL RECRUITMENT EVENT AT THE NEVADA DESERT FACE FACILITY

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Abstract

Seedling recruitment is an important determinant of community structure in desert ecosystems. Positive growth responses to increasing atmospheric CO₂ concentrations ([CO₂]) are predicted to be substantial in desert plants, suggesting recruitment could be stimulated. However, to date no studies have addressed the response of perennial plant recruitment in natural populations of desert shrubs exposed to elevated CO₂. Beginning in April 1997, we employed Free-Air Carbon Dioxide Enrichment (FACE) to increase atmospheric [CO₂] in an undisturbed Mojave Desert ecosystem from ambient (~360 µmol mol⁻¹ CO₂) to ~550 µmol mol⁻¹. From 1997 to 2001 we seasonally examined survival, growth, gas exchange, chlorophyll fluorescence, and water potential responses of a cohort of *Larrea tridentata* and *Ambrosia dumosa* seedlings that germinated in Fall, 1997. Recruitment density of *Larrea* was not influenced by [CO₂], but *Ambrosia* density roughly doubled under elevated CO₂ (0.87 vs. 0.40 seedlings m⁻²). Mortality was greatest for both species during the first summer (1998), despite above-average rainfall the previous winter-spring. Significant [CO₂] × time and species × time interactions revealed survival tended to be greater at elevated CO₂ and for *Ambrosia* (28%) vs. *Larrea* (15%). Microsite (understory or interspace) alone had no influence on survival within either species. Significant species, microsite, and species × microsite effects on growth (seedling height, stem diameter and canopy size) were found, but elevated CO₂ had minimal impact on these parameters. Photosynthetic rates (*A*ₘₐₓ) for both species were higher at elevated [CO₂] during certain seasons, but not consistently so. *Ambrosia* had significantly greater photochemical efficiency of photosystem II (F'ᵥ/F'ₘ) than *Larrea*, but we found no CO₂ effect on F'ᵥ/F'ₘ for either species. These results suggest increased
atmospheric [CO₂] can enhance survival and carbon assimilation of aridland shrub seedlings during favorable growing conditions, but it may not counteract the effects of prolonged drought on seedling mortality.

Keywords: *Ambrosia dumosa;* Mojave Desert: elevated CO₂: FACE: *Larrea tridentata;* seedling survival

Introduction

The Mojave Desert is the most arid desert ecosystem in North America. It is characterized by high summer temperatures, low humidity, and unpredictable precipitation (Rundel & Gibson 1996). Extremes in abiotic factors near the soil surface play an important role in limiting the establishment of desert perennials (Smith & Nowak 1990). However, such limitations to establishment may be relaxed under elevated CO₂ (Polley *et al.* 1996; Huxman *et al.* 1998a). Increased atmospheric [CO₂] enhances water-use efficiency in many plant species (Bazzaz 1990), and may help to reduce the effects of drought-induced mortality in desert plant species. With global atmospheric CO₂ levels expected to double in this century (Keeling *et al.* 1995), some models predict arid ecosystems may in fact demonstrate the largest relative increase in primary productivity (Melillo *et al.* 1993). Along with an increase in individual growth, differences in population-level performance and species distributions and interactions may also occur (Bazzaz 1990). These changes may reflect inherent differences in carbon assimilation rates between functional types (Smith *et al.* 1997), and could result in markedly greater productivity and significant changes in structure within water-limited ecosystems.
Most desert plants germinate following set precipitation and/or temperature thresholds (Barbour 1968; Beatley 1974; Bowers 1994; Marone et al. 2000; Smith et al. 2000b). Once germinated, survival and growth depend on water, nutrient and light availability, all of which can vary by microsite (Walker et al. 2001). In many arid and semiarid regions, nurse plants enhance survival and growth by reducing abiotic stress (Franco & Nobel 1989; McAuliffe 1988; Smith & Nowak 1990; Brittingham & Walker 2000; Walker et al. 2001), but they may also increase biotic stress via increased competitive interactions (Hunter 1989; Vilela & Ravetta 2000). In general, desert shrub interspaces impose greater abiotic stress than understory microsites due to their higher irradiance and surface temperatures, lower nutrient availability, and often reduced infiltration of rainfall. Ultimately, the magnitude of the stress encountered depends on the species’ ability to avoid or tolerate stressful conditions.

In the current study, we examined the effect of elevated atmospheric CO₂ concentration and microsite on survival, growth, gas exchange, chlorophyll fluorescence, and water relations of seedlings representing two dominant Mojave Desert species: the evergreen shrub *Larrea tridentata* D.C. (Cov.) (Zygophyllaceae) and the drought-deciduous shrub *Ambrosia dumosa* A. Gray (Payne) (Asteraceae). We predicted that elevated CO₂ and understory microsites would enhance seedling (1) survival, (2) growth, (3) photosynthesis, (4) chlorophyll fluorescence, and (5) plant water potential. We tested these predictions at the Nevada Desert FACE Facility (NDFF), an ecosystem-scale elevated CO₂ experiment, by measuring seedlings within interspace and understory microsites during periods of high and low seasonal water stress.
Materials and Methods

The Study Site

A Free-Air CO₂ Enrichment (FACE) facility was established in an undisturbed Mojave Desert plant community during the winter of 1996-97. Continuous fumigation at a set point of 550 μmol mol⁻¹ CO₂ began in three 25 m diameter plots on April 28, 1997. Three similar plots were established that receive ambient CO₂ (360 μmol mol⁻¹) via the FACE apparatus. Additionally, three plots at ambient CO₂ and without the FACE apparatus were established. Other studies concurrent with ours have shown that the presence of the FACE apparatus does not affect soil moisture, leaf conductance or leaf temperature (Nowak et al. 2001), thus, excluding density data, we will only present results from the ambient (n = 3) and elevated (n = 3) CO₂ FACE plots. System performance and plant community composition are summarized in Jordan et al. (1999).

Access to plants within each plot is via a specially designed walkway and suspended platform that prevents soil and plant disturbance. The perennial plant community is dominated by the evergreen shrub Larrea tridentata, the drought-deciduous shrubs Ambrosia dumosa, Krameria erecta, Lycium andersonii, and L. pallidum, and the C₄ bunchgrass Pleuraphis rigida.

Recruitment, Survival and Growth

During a typical year, Mojave Desert shrubs break bud in late February to early March and produce viable seed crops by late April to June. Conversely, February to May 1997 produced only 6 mm of rainfall, resulting in minimal seed production prior to the initiation of fumigation with CO₂. However, above-normal rainfall in June resulted in a
flush of growth and large seed crop that was produced under elevated [\(\text{CO}_2\)]. A significant recruitment event for *Ambrosia* and *Larrea* occurred in early fall, 1997 following 45 mm of September rainfall. We assume that germination of seed produced under elevated \(\text{CO}_2\) during late July and August represented a significant portion of that recruitment event, especially in *Larrea*, which has no carryover of viable seeds between years (Boyd & Brum 1983). In October and November 1997 whole plots were surveyed for all *Larrea* seedlings, and 60-degree sections of each plot for *Ambrosia* due to their ca. 10-fold greater density. Seedling microsite (i.e., interspace or understory) was not recorded during the initial surveys; however, in November 1997 we selected 10 *Ambrosia* and 10 *Larrea* seedlings in interspace and understory microsites within each plot (n = 30 seedlings per species x microsite x [\(\text{CO}_2\)]) to track survival and growth. Survivorship (percent survival of the original cohort) was analyzed using the repeated measures ANOVA procedure of SAS (SAS Institute 1989), with Species nested within Plot x Microsite x \(\text{CO}_2\) as the subject factor, Time as the repeated factor, and Species, Time, \(\text{CO}_2\), Microsite and their interactions as model effects. To determine treatment-level survival differences, *a posteriori* tests of means were compared using the Tukey-Kramer Method (Sokal & Rohlf 1997).

During our survival surveys we also collected data on growth, including plant height, stem diameter, canopy area, and canopy volume. Plant height was measured to the nearest 0.1 cm from the soil surface to the tallest shoot tip. Stem diameter was measured to the nearest 0.1 mm with digital calipers, and averaged for two perpendicular measures. Canopy area, measured in \(\text{cm}^2\), was the largest canopy width multiplied by its perpendicular width. Plant canopy volume (\(\text{cm}^3\)) was calculated as:
Due to mortality, we tracked growth on different individuals within the same cohort of seedlings over the course of the study. Unlike the survival data, growth data were analyzed by date using the general linear models procedure of SAS (SAS Institute 1989) with height, diameter, canopy area and canopy volume tested by Species nested within Plot x Microsite x [CO₂].

Gas Exchange

We measured light-saturated CO₂ assimilation rates (A_{max}) on three individuals per species per microsite during the spring and summer seasons of 1999 and 2000. Light response curves were measured using a Li-Cor 6400 open-flow gas exchange system (LiCOR Inc., Lincoln, NE, USA) with a red LED light source. Irradiance was increased from 0, 50, 100, 200, 500, 750, 1000, 1500, to 2000 μmol m⁻² s⁻¹ under constant block temperatures during each field measurement period, while [CO₂] was set at the seedlings growth [CO₂]. For each species and sampling period we used the method described in Potvin & Lechowicz (1990) to determine if individual treatment response curves differed significantly from a curve generated by all four combinations of CO₂ x microsite. If a significant difference was found, pairwise comparisons were made to detect differences between specific microsite x CO₂ treatments. Light curves found to be significantly different were then tested with the general linear models procedure of SAS (SAS Institute 1989) to determine if the differences were attributable to the maximum, light-saturated photosynthetic rate (A_{max}) and/or initial, light-limited quantum yield (\varphi) portion of the curves.
Chlorophyll Fluorescence

Photochemical efficiency of seedlings in both CO\textsubscript{2} concentrations and microsites was examined via chlorophyll fluorescence for the same individuals used in the gas exchange measurements. In 1999 and 2001 light-adapted chlorophyll fluorescence ($F'_{v}/F'_{m}$) was measured in the morning (before 1000 h) and midday (1100 - 1300 h) using a portable pulse-amplitude modulated (PAM) fluorimeter (Model FMS2, Hansatech Instruments Ltd, Norfolk, UK). In 1999, data were collected once in spring and summer, and analyzed using the general linear models procedure of SAS (SAS Institute 1989) to determine the effects of treatment, species, time and their interaction on $F'_{v}/F'_{m}$. In 2001 data were collected multiple times over the growing season and analyzed with a repeated measures ANOVA to compare $F'_{v}/F'_{m}$ by [CO\textsubscript{2}], microsite, and species over time.

Water Potential

To examine the relationship between $A_{\text{max}}$ and midday water potential ($\Psi$), three offplot seedlings per microsite were clipped for each species. It was necessary to use offplot seedlings due to the long-term nature of the NDFF and the risk of seedling mortality after clipping. We measured $\Psi$ using a pressure chamber (Model 3000, Soil Moisture Equipment Corporation, Santa Barbara, CA, USA), and then used ANOVA to test the effect of microsite on $\Psi$. 

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Results

Climate

The 1998 growing season (Hydrologic year Oct 97 – Sept 98) was an anomalously wet El Niño year in which the NDFF received 329 mm of precipitation (2.4 times the annual mean: Table 3.1), resulting in high plant productivity (Smith et al. 2000a). In 1998 soil volumetric water content (0-50 cm) reached its highest values over the course of our study (8-9%), but did not differ by microsite (Table 3.1; $P > 0.05$). The following hydrologic year (1999) was a dry La Niña cycle with below average precipitation (77 mm

Table 3.1. Seasonal precipitation and mean percent soil moisture (0-50 cm) at the Nevada Desert FACE Facility. Seasons are based on mid-month dates (ex. Summer: June 15 - September 15). Numbers in parentheses represent ± 1 SE.

<table>
<thead>
<tr>
<th>Year</th>
<th>Season</th>
<th>Precipitation (mm)</th>
<th>Soil Moisture (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Interspace</td>
<td>Understory</td>
</tr>
<tr>
<td>1997-1998</td>
<td>Fall</td>
<td>42</td>
<td>4.2 (0.2)</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>119</td>
<td>6.7 (0.6)</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>101</td>
<td>8.9 (0.3)</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>67</td>
<td>6.5 (0.2)</td>
</tr>
<tr>
<td>1998-1999</td>
<td>Fall</td>
<td>13</td>
<td>5.0 (0.1)</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>4</td>
<td>4.9 (0.1)</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>46</td>
<td>5.5 (0.2)</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>14</td>
<td>5.1 (0.1)</td>
</tr>
<tr>
<td>1999-2000</td>
<td>Fall</td>
<td>29</td>
<td>5.6 (0.2)</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>75</td>
<td>6.9 (0.3)</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>4</td>
<td>6.8 (0.2)</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>18</td>
<td>5.7 (0.1)</td>
</tr>
<tr>
<td>2000-2001</td>
<td>Fall</td>
<td>6</td>
<td>5.2 (0.1)</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>71</td>
<td>7.7 (0.3)</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>9</td>
<td>5.5 (0.1)</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>16</td>
<td>3.9 (0.1)</td>
</tr>
</tbody>
</table>
vs. a long-term average rainfall of 129 mm) and this resulted in much lower soil moisture values (4.6-5.6%; Table 3.1). In the 2000 and 2001 growing seasons precipitation was again below average (98 and 102 mm, respectively), and soil volumetric water content did not significantly differ by microsite (Table 3.1. P > 0.05). We found no CO₂ effect on soil moisture during any season or year of our study (data not shown).

The coolest year of the study was the El Niño year of 1998, when mean annual temperature was 13.2 °C, even though the low/high monthly temperatures in December (2.1 °C) and August (28.0 °C) were similar to the long-term average. The warmest year of the study was 2000, with a mean temperature of 16.2 °C and low/high mean monthly temperatures again occurring in January (5.2 °C) and July (29.0 °C). 1997, 1999 and 2001 exhibited temperatures similar to the long-term average.

Recruitment, Survival and Growth

There was significantly greater recruitment of Ambrosia (0.55 m⁻²) compared to Larrea (0.06 m⁻²) seedlings in Fall, 1997 (Table 3.2). Within the FACE plots, Ambrosia seedling density under elevated CO₂ was significantly higher compared to ambient CO₂ (0.87 vs. 0.40 seedlings m⁻²; Table 3.2). However, there was also significantly more adult biomass for Ambrosia in the elevated CO₂ plots, resulting in similar seedling densities per unit adult biomass for both [CO₂] (53.8 and 47.3 seedlings m⁻² kg adult⁻¹ in ambient and elevated CO₂, respectively). For Larrea within the FACE plots, we found no difference in seedling densities between CO₂ treatments during 1997 (0.06 vs. 0.05 seedlings m⁻² in ambient and elevated plots, respectively), although there was a trend towards greater seedling densities in the elevated CO₂ plots per kg adult biomass. After
four years, *Ambrosia* seedling densities were similar to adult *Ambrosia* densities, while *Larrea* seedling densities dropped to ~20% of adult *Larrea* density (Table 3.2).

Table 3.2. Influence of elevated CO\(_2\) and adult shrub densities on seedling densities of *Ambrosia dumosa* and *Larrea tridentata* at the Nevada Desert FACE Facility. Numbers in parentheses represent ± 1 SE. A (*) indicates the mean for the elevated CO\(_2\) treatment significantly differs from the mean directly above it (\(P < 0.05\)). Ambient CO\(_2\) values represent pooled means from blower and non-blower control plots, which did not significantly differ (\(P > 0.05\)).

<table>
<thead>
<tr>
<th>Species</th>
<th>[CO(_2)]</th>
<th>Seedling density (m(^{-2}))</th>
<th>Adult density (m(^{-2}))</th>
<th>Adult mass (kg m(^{-2}))</th>
<th>Seedling density per kg adult</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1997</td>
<td>2001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em></td>
<td>Amb</td>
<td>0.40 (0.01)</td>
<td>0.01 (0.02)</td>
<td>0.15 (0.02)</td>
<td>0.01 (0.001)</td>
</tr>
<tr>
<td></td>
<td>Elev</td>
<td>0.87 (0.21)*</td>
<td>0.30 (0.12)</td>
<td>0.31 (0.05)</td>
<td>0.02 (0.01)</td>
</tr>
<tr>
<td><em>Larrea tridentata</em></td>
<td>Amb</td>
<td>0.06 (0.02)</td>
<td>0.01 (0.004)</td>
<td>0.05 (0.01)</td>
<td>0.04 (0.01)</td>
</tr>
<tr>
<td></td>
<td>Elev</td>
<td>0.05 (0.01)</td>
<td>0.01 (0.005)</td>
<td>0.05 (0.002)</td>
<td>0.04 (0.005)</td>
</tr>
</tbody>
</table>

Repeated measures ANOVA revealed significant differences in overall final survival between species (Table 3.3; \(P < 0.05\)), with 28% survivorship in *Ambrosia* vs. 15% in *Larrea*. A significant [CO\(_2\)] x time interaction indicated survivorship was higher under elevated CO\(_2\) during part of our four-year study (Table 3.3; \(P < 0.05\)). There was also a highly significant species x time interaction (Table 3.3; \(P < 0.0001\)), with mean survivorship greater in *Ambrosia* vs. *Larrea* at each survey after Spring, 1998.

Survivorship of *Ambrosia* seedlings to the first spring was relatively high (98%) and
showed no treatment effect (Fig. 3.1; Table 3.3). During Summer 1998, survivorship decreased significantly for ambient-grown plants (98 to 52%) despite above-normal rainfall the previous winter-spring. At this same time, survivorship of elevated-grown *Ambrosia* only declined to 85%. However, following the dry summer of 1999, *Ambrosia* seedling survivorship in elevated CO$_2$ decreased from 68 to 48%. This survivorship for elevated-CO$_2$-grown *Ambrosia* seedlings was not significantly different than the 30% survivorship for ambient-grown plants. From Summer 1999 to Fall 2001, a generally

Table 3.3. Seedling survival of *Ambrosia dumosa* and *Larrea tridentata* at the Nevada Desert FACE Facility. Shown are repeated-measures ANOVA degrees of freedom, F-ratios and level of significance ($P < 0.05$: bold-type).

<table>
<thead>
<tr>
<th>Main effects and interactions</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>CO$_2$</td>
<td>1.16</td>
<td>1.33</td>
<td>0.2650</td>
</tr>
<tr>
<td>Species</td>
<td>1.16</td>
<td>4.52</td>
<td><strong>0.0495</strong></td>
</tr>
<tr>
<td>Canopy</td>
<td>1.16</td>
<td>0.15</td>
<td>0.7042</td>
</tr>
<tr>
<td>Time</td>
<td>8.128</td>
<td>175.28</td>
<td><strong>&lt;0.0001</strong></td>
</tr>
<tr>
<td>CO$_2$ x Canopy</td>
<td>1.16</td>
<td>0.01</td>
<td>0.9369</td>
</tr>
<tr>
<td>CO$_2$ x Species</td>
<td>1.16</td>
<td>1.59</td>
<td>0.2258</td>
</tr>
<tr>
<td>CO$_2$ x time</td>
<td>8.128</td>
<td>2.39</td>
<td><strong>0.0197</strong></td>
</tr>
<tr>
<td>Species x Canopy</td>
<td>1.16</td>
<td>0.00</td>
<td>0.9563</td>
</tr>
<tr>
<td>Canopy x Time</td>
<td>8.128</td>
<td>0.86</td>
<td>0.5493</td>
</tr>
<tr>
<td>Species x Time</td>
<td>8.128</td>
<td>4.42</td>
<td><strong>&lt;0.0001</strong></td>
</tr>
<tr>
<td>CO$_2$ x Species x Canopy</td>
<td>1.16</td>
<td>0.13</td>
<td>0.7215</td>
</tr>
<tr>
<td>CO$_2$ x Species x Time</td>
<td>8.128</td>
<td>1.08</td>
<td>0.3794</td>
</tr>
<tr>
<td>CO$_2$ x Canopy x Time</td>
<td>8.128</td>
<td>0.16</td>
<td>0.9951</td>
</tr>
<tr>
<td>CO$_2$ x Species x Canopy x Time</td>
<td>16,128</td>
<td>0.69</td>
<td>0.7991</td>
</tr>
</tbody>
</table>

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Figure 3.1. Survivorship of *Ambrosia dumosa* (top) and *Larrea tridentata* (bottom) seedlings growing within interspace and understory microsites at ambient and elevated CO$_2$ at the Nevada Desert FACE Facility. Circles represent ambient CO$_2$, triangles elevated CO$_2$. Open symbols indicate interspace and closed indicate understory. Data are presented as plot means (± 1 SE).
below-normal rainfall period, survivorship of *Ambrosia* declined slowly, with no significant \([\text{CO}_2]\) or microsite effect, resulting in an overall survivorship of 28%.

Survivorship of *Larrea* seedlings through the relatively wet first spring (1998) was also high (98%), with no significant treatment effects found (Fig. 3.1; Table 3.3). As in *Ambrosia*. Summer 1998 survivorship showed a marked decline despite above-normal precipitation the previous winter-spring. There were trends towards greater survivorship within interspace microsites through Fall of 1998, but by the Fall of 1999 survivorship rates in both \([\text{CO}_2]\) and microsites was near 25%. During the final two years of our study, overall *Larrea* survivorship declined to 14% of the original cohort.

*Ambrosia* showed significant differences in growth (i.e., height, stem diameter and canopy volume) by microsite (Table 3.4), but \([\text{CO}_2]\) had a minimal impact on these parameters. In Spring 1999, *Ambrosia* growing in the interspaces of both \(\text{CO}_2\) treatments had larger stem diameters and canopy volumes than understory plants, although understory plants tended to be taller (Fig. 3.2). While canopy volume was significantly greater (9.8 vs. 3.2 cm³) in understory vs. interspace individuals following the 1997-1998 El Niño, beginning in 2000 canopy volume tended to be greater within interspaces. Nonetheless, *Ambrosia* biomass consistently decreased during summer due to the drought-deciduous habit of shedding leaves and some stems.

*Larrea* growth was not significantly effected by \([\text{CO}_2]\) or microsite (Fig. 3.3; Table 3.4). However, after four years *Larrea* growth did show similar trends as *Ambrosia* in having greater stem diameter and canopy volume within interspace microsites. In contrast to the drought-deciduous habit of *Ambrosia*, the evergreen *Larrea* did not show a
consistent reduction in seedling size during the summer, although seedlings within a
given microsite tended to be smaller in size than Ambrosia seedlings from the same

Figure 3.2. Height, stem diameter, canopy area, and canopy volume of Ambrosia dumosa
seedlings in interspace and understory microsites at elevated and ambient CO₂ at the
Nevada Desert FACE Facility. Circles and triangles represent ambient and elevated CO₂,
respectively. Open and closed symbols indicate interspace and understory microsites,
respectively. Data are presented as plot means (± 1 SE).

cohort. The only significant difference we observed in Larrea growth throughout the
study was a greater canopy area for ambient-grown seedlings within interspaces during
Spring 2000 (Fig. 3.3). Throughout the four-year study only slight herbivore damage was
recorded in either species, and few individuals “disappeared” as a result of complete consumption.

Figure 3.3. Height, stem diameter, canopy area, and canopy volume of *Larrea tridentata* seedlings in interspace and understory microsites at elevated and ambient CO₂ at the Nevada Desert FACE Facility. Symbols are as in Fig. 2.

Gas Exchange & Quantum Yield

In Spring 1999, photosynthetic light response curves did not significantly differ in *Ambrosia* (Table 3.5: Figure 3.4a). This lack of any significant difference may reflect the low water stress during spring, which resulted in high *A<sub>max</sub>* in all treatments. Light response curves did significantly differ for *Ambrosia* during Summer 1999, with the understory x elevated CO₂ treatment having greater carbon assimilation rates beyond an
irradiance of 600 μmol m$^{-2}$ s$^{-1}$ than any other treatment (Table 3.5; Figure 3.4b). A comparison between pooled ambient and elevated CO$_2$ light curves for *Ambrosia* during summer was not significant ($P > 0.05$); however, a pairwise comparison of light response

table 3.4. Seedling growth of *Ambrosia dumosa* and *Larrea tridentata* at the Nevada Desert FACE Facility. Shown are F-ratios and the level of significance ($P < 0.05$; bold type).

<table>
<thead>
<tr>
<th>Effect</th>
<th>Height</th>
<th>Stem Diameter</th>
<th>Canopy Area</th>
<th>Canopy Volume</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>P</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>CO$_2$</td>
<td>1.02</td>
<td>0.3152</td>
<td>0.15</td>
<td>0.6989</td>
</tr>
<tr>
<td>Species</td>
<td>61.36</td>
<td>&lt;0.0001</td>
<td>425.63</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Canopy</td>
<td>27.89</td>
<td>&lt;0.0001</td>
<td>41.45</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Time</td>
<td>26.93</td>
<td>&lt;0.0001</td>
<td>12.79</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>CO$_2$ x Canopy</td>
<td>2.87</td>
<td>0.0921</td>
<td>0.16</td>
<td>0.6900</td>
</tr>
<tr>
<td>CO$_2$ x Species</td>
<td>2.08</td>
<td>0.1511</td>
<td>1.11</td>
<td>0.2939</td>
</tr>
<tr>
<td>CO$_2$ x Time</td>
<td>0.26</td>
<td>0.9766</td>
<td>0.24</td>
<td>0.9619</td>
</tr>
<tr>
<td>Species x Canopy</td>
<td>11.97</td>
<td>0.0007</td>
<td>29.80</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Canopy x time</td>
<td>0.44</td>
<td>0.8955</td>
<td>1.00</td>
<td>0.4304</td>
</tr>
<tr>
<td>Species x Time</td>
<td>1.35</td>
<td>0.2242</td>
<td>1.77</td>
<td>0.1116</td>
</tr>
</tbody>
</table>

curves between interspace and understory *Ambrosia* within the ambient CO$_2$ plots was significant ($P < 0.0001$), revealing greater carbon assimilation rates for interspace seedlings. A pairwise comparison between interspace and understory *Ambrosia* seedlings within the elevated CO$_2$ treatment was also significant ($P < 0.0001$), indicating
understory seedlings had higher photosynthetic rates above 600 μmol m⁻² s⁻¹, while interspace seedlings had significantly higher Φ (P < 0.05).

A Summer 1999 test of overall group effect in Larrea was not possible due to the small number of photosynthetically active seedlings within the ambient CO₂ plots.

Figure 3.4a-d. Photosynthetic light curves for Ambrosia dumosa (top) and Larrea tridentata (bottom) in interspace and understory microsites at ambient and elevated CO₂ at the Nevada Desert FACE Facility in Spring (left) and Summer (right) of 2000. Curves are: interspace, ambient CO₂ (—); understory, ambient CO₂ (—-); interspace, elevated CO₂ (•••); and understory, elevated CO₂ (——).

The test for an overall group effect for Larrea light response curves in Spring 1999 was significant (Table 3.5; Figure 3.4c). A pairwise comparison between interspace and
Table 3.5. Mean maximum photosynthesis ($A_{\text{max}}$) and quantum yield ($\varphi$) for *Ambrosia dumosa* and *Larrea tridentata* seedlings at the Nevada Desert FACE Facility. Numbers in parentheses represent $\pm 1$ SE. Different superscripts indicate significant ($P < 0.05$) within-species treatment differences for a parameter during that season.

<table>
<thead>
<tr>
<th>Season</th>
<th>[CO$_2$]</th>
<th>Microsite</th>
<th>$A_{\text{max}}$</th>
<th>$\varphi$</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ambrosia dumosa</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1999 Spring</td>
<td>360</td>
<td>interspace</td>
<td>41.0 (23.1)$^a$</td>
<td>0.047 (0.022)$^a$</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>360</td>
<td>understory</td>
<td>29.5 (13.7)$^a$</td>
<td>0.029 (0.016)$^a$</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>550</td>
<td>interspace</td>
<td>30.0 (13.6)$^a$</td>
<td>0.030 (0.015)$^a$</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>550</td>
<td>understory</td>
<td>39.1 (36.2)$^a$</td>
<td>0.045 (0.047)$^a$</td>
<td>2</td>
</tr>
<tr>
<td>Summer</td>
<td>360</td>
<td>interspace</td>
<td>1.1 (0.3)$^a$</td>
<td>0.021 (0.016)$^a$</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>360</td>
<td>understory</td>
<td>0.4 (0.6)$^a$</td>
<td>0.017 (0.023)$^a$</td>
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</tr>
<tr>
<td></td>
<td>550</td>
<td>interspace</td>
<td>2.1 (1.1)$^a$</td>
<td>0.006 (0.001)$^a$</td>
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</tr>
<tr>
<td></td>
<td>550</td>
<td>understory</td>
<td>6.7 (4.8)$^a$</td>
<td>0.006 (0.004)$^a$</td>
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</tr>
<tr>
<td>2000 Spring</td>
<td>360</td>
<td>interspace</td>
<td>5.3 (1.6)$^a$</td>
<td>0.019 (0.014)$^a$</td>
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</tr>
<tr>
<td></td>
<td>360</td>
<td>understory</td>
<td>4.6 (1.4)$^a$</td>
<td>0.010 (0.003)$^a$</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>550</td>
<td>interspace</td>
<td>5.9 (4.2)$^a$</td>
<td>0.015 (0.007)$^a$</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>550</td>
<td>understory</td>
<td>6.6 (4.0)$^a$</td>
<td>0.029 (0.017)$^a$</td>
<td>3</td>
</tr>
<tr>
<td><em>Larrea tridentata</em></td>
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<td></td>
<td></td>
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<td>1999 Spring</td>
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<td>interspace</td>
<td>6.4 (0.2)$^a$</td>
<td>0.014 (0.009)$^a$</td>
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<tr>
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<td>0.013</td>
<td>1</td>
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<td></td>
<td>550</td>
<td>interspace</td>
<td>15.6 (3.2)$^b$</td>
<td>0.022 (0.005)$^a$</td>
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<tr>
<td></td>
<td>550</td>
<td>understory</td>
<td>16.5 (7.9)$^b$</td>
<td>0.025 (0.017)$^a$</td>
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</tr>
<tr>
<td>Summer</td>
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<td>interspace</td>
<td>0.9</td>
<td>0.004</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>360</td>
<td>understory</td>
<td>0.3</td>
<td>0.005</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>550</td>
<td>interspace</td>
<td>0.5 (0.5)$^a$</td>
<td>0.010 (0.004)$^a$</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>550</td>
<td>understory</td>
<td>1.0 (0.8)$^a$</td>
<td>0.002 (0.0004)$^a$</td>
<td>2</td>
</tr>
<tr>
<td>2000 Spring</td>
<td>360</td>
<td>interspace</td>
<td>6.5 (2.9)$^a$</td>
<td>0.028 (0.003)$^a$</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>360</td>
<td>understory</td>
<td>7.6 (0.9)$^a$</td>
<td>0.037 (0.018)$^a$</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>550</td>
<td>interspace</td>
<td>1.9 (1.5)$^a$</td>
<td>0.018 (0.018)$^a$</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>550</td>
<td>understory</td>
<td>5.0 (4.7)$^a$</td>
<td>0.034 (0.018)$^a$</td>
<td>3</td>
</tr>
</tbody>
</table>

understory *Larrea* at elevated $\text{CO}_2$ was not significant ($P > 0.05$). A comparison between interspace and understory *Larrea* within the ambient $\text{CO}_2$ plots was not possible due to a small sample sizes resulting from photosynthetic inactivity in some individuals.

However, the pairwise comparison between pooled ambient and elevated $\text{CO}_2$ light

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response curves was highly significant (P < 0.0001), indicating elevated CO₂-grown Larrea had greater light-saturated photosynthetic rates during spring (Table 3.5; Figure 3.4c).

Within elevated CO₂ plots, a comparison between microsites revealed no significant difference in Aₘₐₓ, but significantly higher φ for interspace compared to understory Larrea seedlings (Table 3.5). A comparison between pooled ambient and elevated light response curves in summer was not significant (P > 0.05), indicating Larrea did not differ in overall carbon assimilation rates late in the growing season (Figure 3.4d). In Spring 2000, mean Aₘₐₓ and φ did not significantly differ between any CO₂ x microsite treatment for either species (Table 3.5; P > 0.05).

Chlorophyll Fluorescence

In Spring 1999, F′₀/F′ₘ values did not differ for either species by [CO₂], microsite, or their interaction (Fig. 3.5; P > 0.05). However, there were differences between species, with Ambrosia F′₀/F′ₘ values significantly higher compared to Larrea (Fig. 3.5; P < 0.01). During Summer 1999, F′₀/F′ₘ did not significantly differ within or between species by [CO₂], microsite or their interaction (Fig. 3.5; P > 0.05).

A full-season F′₀/F′ₘ data set was not obtained in 2000 due to equipment problems, but in 2001 a repeated measures ANOVA revealed no significant difference in Larrea morning or midday F′₀/F′ₘ values by [CO₂], microsite or their interaction (Fig. 3.5; P > 0.05 in all cases). Repeated measures ANOVA also indicated Ambrosia morning F′₀/F′ₘ values did not differ by [CO₂], but were significantly greater in interspace vs. understory microsites (Fig. 3.5; P < 0.05). Between-species analysis revealed significantly higher
morning $F'_{v}/F'_{m}$ values in *Ambrosia* compared to *Larrea* over the course of the growing season (Fig. 3.5; $P < 0.0001$).

Figure 3.5. Morning and midday $F'_{v}/F'_{m}$ for *Ambrosia dumosa* (top) and *Larrea tridentata* (bottom) in 1999 and 2001 at the Nevada Desert FACE Facility. Open bars: interspace, ambient CO$_2$; Coarse-dashed bars: understory, ambient CO$_2$; Filled bars: interspace, elevated CO$_2$; Fine-dashed bars: understory, elevated CO$_2$.

**Water Potential**

Spring 1999 offplot *Ambrosia* seedlings within interspace microsites had significantly higher $\Psi$ than understory *Ambrosia* seedlings (-1.5 MPa vs. -2.2 MPa; Table 3.5; $P < 0.05$). By summer, *Ambrosia* $\Psi$ had dropped significantly in both microsites, and did not
differ between the interspace and understory (Table 3.6; \( P > 0.05 \)). For *Larrea*,
interspace vs. understory \( \Psi \) comparisons were not available during 1999. However, in
Spring 2000 we found significantly lower \( \Psi \) in interspace compared to understory *Larrea*
(-5.9 MPa vs. -4.0 MPa; Table 3.6; \( P < 0.01 \)), but no significant difference in *Ambrosia*
\( \Psi \) by microsite. The following year (2001) both species had significantly higher late
season water potentials within interspace microsites (Table 3.6; \( P < 0.05 \) in each case).

Table 3.6. Mean midday water potential (\( \psi \)) for *Ambrosia dumosa* and *Larrea tridentata*
seedlings at the Nevada Desert FACE Facility. (*) and (**) indicate water potential is
significantly different from the value directly above it at \( P < 0.05 \) or \( P < 0.01 \)
significance levels, respectively.

<table>
<thead>
<tr>
<th>Year</th>
<th>Season</th>
<th>Microsite</th>
<th>( \psi ) (MPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>Spring</td>
<td>interspace</td>
<td>-1.5</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>understory</td>
<td>-2.2*</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>interspace</td>
<td>-5.6</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>understory</td>
<td>-4.1</td>
</tr>
<tr>
<td>2000</td>
<td>Spring</td>
<td>interspace</td>
<td>-6.6</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>understory</td>
<td>-5.7</td>
</tr>
<tr>
<td>2001</td>
<td>Summer</td>
<td>interspace</td>
<td>-2.8</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>understory</td>
<td>-4.4*</td>
</tr>
</tbody>
</table>

*Ambrosia dumosa*

<table>
<thead>
<tr>
<th>Year</th>
<th>Season</th>
<th>Microsite</th>
<th>( \psi ) (MPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>Spring</td>
<td>interspace</td>
<td>-1.9</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>understory</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>interspace</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>understory</td>
<td>-7.4</td>
</tr>
<tr>
<td>2000</td>
<td>Spring</td>
<td>interspace</td>
<td>-5.9</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>understory</td>
<td>-4.0**</td>
</tr>
<tr>
<td>2001</td>
<td>Summer</td>
<td>interspace</td>
<td>-2.6</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>understory</td>
<td>-4.0*</td>
</tr>
</tbody>
</table>

*Larrea tridentata*

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Discussion

Seedling recruitment in deserts is highly variable owing to inconsistent rainfall events that produce only episodic germination (Beatley 1967; Jordan & Nobel 1979; Marone et al. 2000). Temperature extremes, both high and low, affect the subsequent survival of individuals through processes such as photoinhibition (Huxman et al. 1998a), heat stress (Nobel 1984), and freeze-induced xylem cavitation (Pockman & Sperry 1997). Biotic factors, including seed bank size (Childs & Goodall 1973), granivory and herbivory (Soholt 1973; McAuliffe 1986), rodent burrowing (Hunter et al. 1980), resource competition (Fonteyn & Mahall 1978; Hunter 1989), and facilitation (Jordan & Nobel 1979; Brittingham & Walker 2000) also affect recruitment and survival of desert plants. Nevertheless, drought is the primary limitation on recruitment (Smith et al. 1997). Our study, as well as others (Tschaplinski et al. 1995; Centritto et al. 1999), found elevated CO$_2$ does not consistently improve the drought tolerance of seedlings, although this result is not universal (Polley et al. 1996). Perennial seedling survival and growth under elevated CO$_2$ is still dependent upon adequate soil moisture to sustain physiological processes following germination, although water-use efficiency should be increased through decreases in stomatal conductance (Nowak et al. 2001).

Many plant species respond to increased CO$_2$ via increased photosynthesis, WUE, and biomass (Bazzaz 1990). At the NDFF, a 50% increase in atmospheric CO$_2$ concentration doubled new shoot growth in adult Larrea during the wet year of 1998, but showed no effect during a dry year (Smith et al. 2000a). Annual plants also showed dramatically increased growth at elevated CO$_2$ during the wet year, particularly in understory microsites (Smith et al. 2000a). Nevertheless, allocation patterns among shoots, roots,
and leaves can differ over the lifespan of long-lived shrubs, potentially resulting in age-dependent growth responses to elevated CO\textsubscript{2}. Increases in biomass under elevated CO\textsubscript{2} may be sustained in the long-term for some species, but they may also be short-lived due to photosynthetic down-regulation (Huxman et al. 1998b), or even absent in other species (Smith et al. 1987). Thus, the response to [CO\textsubscript{2}] we measured within seedlings represents only a small, albeit important, part of the life cycle.

Past studies have shown understory microsites facilitate the survival of many desert plants (Franco & Nobel 1988; Brittingham & Walker 2000; Walker et al. 2001). It has also been shown that seedlings growing in the understory of nurse plants benefit from increased nutrient availability and reduced intensity of radiation (Jordan & Nobel 1979; Walker et al. 2001). Understory microsites can also have greater water availability than interspaces (Walker et al. 2001), and lower herbivory (McAuliffe 1986), making them more favorable for recruitment. Nevertheless, tradeoffs to establishment in the understory can occur, and may include increased competition with the nurse plant for water or nutrients (Hunter 1989), and decreased survival due to increased root:shoot ratios (Vilela & Ravetta 2000) or the burrowing activity of small rodents. We found enhanced plant water status (as measured by $\Psi$) in summer for both species within interspace microsites, suggesting that interspaces, although potentially inferior in terms of nutrient availability, can have lower late-season water stress, which should promote greater survival. Unfortunately, our survival data do not support this hypothesis, indicating that other factors such as summer surface temperatures may adversely affect seedling survival within interspace microsites.
An El Niño weather pattern at the onset of our study resulted in high rainfall and soil moisture, and, coupled with a considerably cooler mean temperature, likely contributed to the overall low seedling mortality during the 1998 growing season. In contrast, survivorship of both species at ambient [CO₂] declined sharply by Fall 1998 to <60%. At the same time, understory Larrea averaged less than 30% survivorship in both CO₂ concentrations. It appears this large mortality event was associated with high summer temperatures at the soil surface. In 1999 below-average rainfall reduced survivorship even further – of a total rainfall of 80 mm, only four rainfall events were in excess of 10 mm and two were in excess of 20 mm, so most precipitation received in 1999 was not converted into deep storage and was therefore unavailable for root uptake. Overall, the 1998-99 hydrologic year saw only 60% of the long-term average rainfall which, coupled with high summer temperatures at the soil surface, resulted in heavy seedling mortality independent of species, [CO₂] and microsite. Fall 1999 survival declined from the previous survey by 3.5% for ambient-CO₂-grown Ambrosia and 20% for elevated-grown Ambrosia, but by 2000 survivorship for both species leveled off. Thus, it appears some threshold in age or size was reached in 2000, after which mortality became minimal. Perhaps the return to near-average rainfall (126 mm vs. a long-term average of 129 mm) was enough to sustain physiological processes at a maintenance level for both species. The Fall 2000 and Spring 2001 surveys also revealed declines in survivorship for both species, but these were not significantly different by [CO₂] or microsite within either species. Overall, the highest survivorship was for interspace Ambrosia seedlings growing under elevated CO₂. Their 37% survivorship was 10% higher than survivorship of Ambrosia in any other treatment. Moreover, in that same microsite Larrea survivorship
was lowest (7%). Therefore, over a four-year period, *Ambrosia* experienced 20% higher survival than *Larrea* within interspace microsites at elevated CO₂. Although *Ambrosia* has been shown to more readily colonize interspaces than does *Larrea* (McAuliffe 1988), our results suggest future [CO₂], coupled with adequate rainfall, could enhance survival of *Ambrosia* within interspace microsites and potentially alter community structure in the Mojave Desert.

Due to the unpredictable nature of Mojave Desert rainfall, seedling emergence, survival and growth are not necessarily well correlated over time. The more conservative response of *Larrea* to soil resource availability is suggested by the relatively uniform size-class distribution above a height of 30 cm at the NDFF (Jordan *et al.* 1999). Additionally, because heavy, late-summer rainfall is apparently necessary for *Larrea* germination (Boyd & Brum 1983), and because this rainfall pattern followed by periods with sufficient soil moisture to sustain survival occurs very sporadically in the Mojave Desert, high mortality and low recruitment are common (Went & Westergaard 1949; Barbour 1968). On the other hand, *Ambrosia* possesses a normal size class distribution and has a higher density than *Larrea* at the NDFF. This suggests more frequent establishment of *Ambrosia*, which was supported by a subsequent recruitment event during Fall 1999 in which only *Ambrosia* seed germinated. Moreover, the increased survivorship of elevated-CO₂-grown *Ambrosia* during the high rainfall period in 1998 (Fig. 3.1) suggests future recruitment may be significantly enhanced at elevated [CO₂] during periods with favorable precipitation.

We predicted higher water potentials in the understory, but instead found Ψ were significantly higher for interspace *Ambrosia* seedlings in Spring, 1999 (Table 3.6). Even
so, there were no significant differences in $A_{\text{max}}$ at that time between Ambrosia seedlings in either microsite (Table 3.5), indicating that water availability alone is not a good predictor of carbon assimilation rates. These findings are not conflicting, given that both microsites had relatively low water stress during spring, with mean $\psi$ differences between treatments, although significant, less than one MPa. The microsite difference in $\psi$ disappeared with increased summer water stress, and photosynthetic rates declined, although understory Ambrosia grown at elevated CO$_2$ had $A_{\text{max}}$ three times higher than those in any other treatment.

Larrea seedlings grown at elevated CO$_2$ had significantly higher $A_{\text{max}}$ than ambient-grown plants in Spring 1999, indicating elevated CO$_2$ did increase photosynthetic rates during the relatively cool and moist part of the year. Elevated CO$_2$ has also previously been shown to reduce the effects of extreme high temperature and drought on photosynthetic capacity of Larrea seedlings grown in a glasshouse (Hamerlynck et al. 2000a). At the NDFF, a drop in $\psi$ during the dry period was coupled with a drop in $A_{\text{max}}$ within all treatments to a level near the light compensation point for photosynthesis. Thus, photosynthetic rates for Larrea seedlings did not remain higher under elevated CO$_2$ further into the dry season. This result also holds true for adult Larrea at the NDFF (Hamerlynck et al. 2000b). We found no evidence to support our hypothesis that Larrea carbon assimilation rates would be higher in the understory x elevated CO$_2$ treatment.

Comparing functional types, the decrease in photosynthetic rate from the wet to dry season was much larger for the drought-deciduous Ambrosia due to its higher springtime $A_{\text{max}}$. This higher $A_{\text{max}}$ in Ambrosia compared to Larrea is expected based on their functional types (Smith & Nobel 1986; Rundel & Gibson 1996), and represents an
opportunistic strategy for increased carbon gain in the former during conditions favorable for growth. This probably explains the difference we observed between species for $A_{\text{max}}$; lower $A_{\text{max}}$ in Larrea presumably reflects lower leaf nitrogen content, a trait common in species that maintain photosynthetically active leaf canopies year-round (Field & Mooney 1986; Reich et al. 1991).

Seedling $\psi$ in 2001 again indicated understory microsites can be subject to greater water stress than interspace sites. This hypothesis was supported by greater $F'_{\psi}/F'_{\text{m}}$ values within interspace microsites. Between species, higher morning $F'_{\psi}/F'_{\text{m}}$ values in Ambrosia (0.77) compared to Larrea (0.67) were consistent with higher rates of carbon assimilation in the former.

The functional types presented here represent contrasting strategies for growth and survival in arid ecosystems. Larrea is evergreen, while Ambrosia is drought-deciduous and produces leaves only after sufficient winter-spring rains. This latter habit represents an opportunistic strategy in which higher photosynthetic rates are achieved, but over a shorter period of time, and with a lower WUE. Lower photosynthetic rates and stomatal conductance in Larrea serve as adaptations to conserve soil moisture and maintain a year-round canopy. In regions with unpredictable precipitation, such as the Mojave Desert, the evergreen habit may partially compensate for lower photosynthetic rates via a more rapid photosynthetic response to rainfall events (Caldwell 1985; Smith et al. 1997). However, the trade-off is that Larrea maintains leaf area during the hot, dry summer months, which can result in greater mortality of seedlings compared to the deciduous Ambrosia. Taken as a whole, our results suggest future atmospheric CO$_2$ concentrations
may positively enhance survival of some desert shrubs more than others, potentially changing species’ abundances and the structure of this desert ecosystem.

Conclusions

We found significant effects of species, time, [CO$_2$] x time and species x time, revealing seedling survival tended to be greater in elevated CO$_2$ plots and for *Ambrosia* compared to *Larrea*. The primary difference in survival appeared during the first summer dry season after germination, but prior to pronounced drought conditions. CO$_2$-related differences occurred during the first significant drop in survivorship, but then were less apparent once survivorship became uniformly low following a major drought cycle. Microsite had a greater effect on growth parameters (height, diameter, etc.) than did [CO$_2$], but alone it had no significant influence on survival. Chlorophyll fluorescence revealed few CO$_2$ effects within either species, but noticeable differences between species. This disparity in interspecific $F'_v/F'_m$ values reflects inherent differences between species in light utilization and, coupled with differences in survival, suggests the future photosynthetic performance of these species may be enhanced under elevated CO$_2$. However, it appears any enhancement of photosynthetic rates in response to elevated [CO$_2$], or within a particular microsite, will be limited to periods with sufficient water availability. These findings suggest future increases in atmospheric [CO$_2$], coupled with periods of increased water availability, may result in greater carbon gain and survival for seedlings of some desert shrub species. These results do not suggest, however, that elevated CO$_2$ will enhance seedling growth or survival during periods of prolonged drought. Therefore, elevated CO$_2$ may have its greatest effect on desert shrub...
recruitment and subsequent community structure if it is accompanied by increased 
summer rainfall, which has been predicted by some General Circulation Models (Taylor 
& Penner 1994).

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CHAPTER 4

SHRUB PRODUCTIVITY IN A DESERT ECOSYSTEM EXPOSED TO FREE-AIR CO₂ ENRICHMENT

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Abstract

The productivity of aridland plants is predicted to increase with rising atmospheric CO₂ concentrations, mainly due to enhancement in plant water-use efficiency. However, there are few detailed analyses of how intact desert vegetation responds to elevated CO₂. From 1998-2001 we quantified aboveground production, photosynthesis, and water relations within naturally occurring shrubs exposed to either ambient (~375 μmol mol⁻¹) or elevated (550 μmol mol⁻¹) CO₂ concentrations at the Nevada Desert Free-Air CO₂ Enrichment (FACE) Facility in the Mojave Desert, USA. Three functional types were sampled that represent potentially different responses to elevated CO₂ - evergreen (Larrea tridentata), drought-deciduous (Ambrosia dumosa) and winter-deciduous (Krameria erecta). Elevated CO₂ significantly increased aboveground production in Larrea and Ambrosia during a wet El Niño year (1998), with relative production ratios (elevated:ambient CO₂) of 2.31 and 2.22, respectively. In three below-average rainfall years (1999-2001) growth was reduced in all species, with only Ambrosia in 2001 having significantly higher production under elevated CO₂. The relative production ratio for Krameria in a wet year (1.59) was similar to that in a dry (1.57) year. Shoot water potentials (ψ) did not consistently differ between CO₂ treatments for any species, however ψ were higher under elevated CO₂ in three out of four years when species were pooled by CO₂ treatment. Integrated seasonal photosynthesis (mmol m⁻² season⁻¹) was 1.26 to 2.03-fold higher under elevated CO₂ in the wet year (1998), and 1.32 to 1.43-fold higher after three years with low rainfall. Instantaneous WUE was also higher in shrubs grown under elevated CO₂. The timing of peak canopy development did not change under elevated CO₂, including no observed increase in leaf longevity. Similarly, seasonal
patterns in CO₂ assimilation did not change, except for Larrea where peak photosynthetic rates occurred earlier under high CO₂. Overall, 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 elevated CO₂ can substantially enhance productivity of Mojave Desert shrubs, but this effect is most pronounced during years with high rainfall when soil resources are most available.

Keywords: Ambrosia dumosa, Desert productivity, Elevated CO₂, Krameria erecta, Larrea tridentata, Photosynthesis, Water potential.

Introduction

Photosynthetic rates and biomass production are predicted to increase in many ecosystems under the higher CO₂ concentrations predicted for later this century (Bazzaz 1990). However, studies of plant responses to elevated CO₂ are revealing inconsistent enhancement in these parameters due to fluctuations in water availability and temperature between years (Drake et al. 1996; Koch and Mooney 1996; Owensby et al. 1996) and age-related responses to elevated CO₂ (Hättenschwiler et al. 1997; Idso 1999). While forests store ~80% of all aboveground organic carbon (Kirschbaum et al. 1996), and studies have shown significant increases in productivity of young fast-growing trees under elevated CO₂, it is unclear whether these increases will be sustained (DeLucia et al. 1999; Oren et al. 2001). Non-forest terrestrial ecosystems (i.e., deserts, tundra,
grasslands and savannas) account for ~36% of the global carbon budget (Allen-Diaz et al. 1996), and although deserts alone account for nearly one-third of the terrestrial biosphere (Noble et al. 1996), their productivity is among the lowest of any ecosystem type (Schlesinger 1997; Smith et al. 1997). Even so, deserts are predicted to be among the most responsive biomes to elevated CO$_2$ due to increased water-use efficiency (WUE) (Melillo et al. 1993). Our study examines how productivity of the dominant woody perennials in the Mojave Desert responds to elevated CO$_2$ as a function of infrequent and unpredictable precipitation inputs that characterize this ecosystem.

Elevated CO$_2$ increases shrub productivity and invasive species success in the Mojave Desert during years with abundant rainfall (Smith et al. 2000). It also reduces stomatal conductance in some desert perennials (Nowak et al. 2001), which serves to decrease water stress and may enhance growth. The water savings realized through reduced conductance under elevated CO$_2$ might extend the growing season in water-limited regions (Strain and Bazzaz 1983), and could increase leaf area, hence making desert ecosystems less “surface-limited” (Smith et al. 1997). Nevertheless, adequate inputs of precipitation are necessary for growth to occur, and these inputs are highly variable in desert systems. Moreover, when adequate rainfall does occur the enhanced demand for resources may elicit new checks on production, such as nutrient limitations (Romney et al. 1978; Smith et al. 1997).

The timing of phenological events in the Mojave Desert is driven largely by precipitation, temperature, and soil moisture (Ackerman and Bamberg 1974; Beatley 1974; Turner and Randall 1987; Esler and Rundel 1999). Prior phenological work has shown that water, nitrogen, and temperature interact to influence leaf demography and
morphology of woody perennials in the North American deserts (Cunningham et al. 1979; Nilsen et al. 1986; Lajtha and Whitford 1989). Water is typically the primary factor limiting productivity of desert vegetation (Smith et al. 1997), and its availability strongly influences such growth parameters as stem elongation. If increased WUE under elevated CO₂ results in enhanced growth in desert perennials, longer internodes and more open plant canopies might be expected. These longer internodes may reduce self-shading, increase light interception, and subsequently affect gas exchange and water relations (Neufeld et al. 1988). Even so, deciduous desert shrubs typically have early-season phenological constraints on carbon gain because canopy development often lags behind peak photosynthetic performance (Comstock et al. 1988), while later in the growing season reductions in photosynthetic capacity (prior to reductions in leaf area) result in physiological constraints on productivity (Comstock and Ehleringer 1986). Evergreen species also exhibit lags in leaf development and performance following rainfall, as well as reductions in photosynthesis as soil moisture declines (Cunningham et al. 1979, Lajtha and Whitford 1989). It seems likely individual species and functional types will respond differently to elevated CO₂ due to inherent physiological differences in the ability to concentrate CO₂ at the site of carboxylation (Bowes 1993) and differences in phenological responses to water availability (Kemp 1983; Turner and Randall 1987).

Here we report results from a long-term experiment examining the effects of elevated CO₂ on a Mojave Desert ecosystem; in this study we examined new shoot production, photosynthetic gas exchange, and water relations in several species of shrubs that differ in seasonal phenology. We predicted that elevated CO₂ would increase aboveground
shrub production and photosynthesis, and lower water stress as measured by shoot water potential ($\psi$). Due to known enhancements in WUE under elevated CO₂, we predicted the stimulatory effects of elevated CO₂ on shrub growth would be greatest in drier years, except during times of severe drought when we would anticipate the CO₂ effect to be suppressed. Therefore, we expected the greatest stimulation of relative plant production (elevated:ambient CO₂) to occur in moderate rainfall years, with wet years having less of a CO₂ effect. Additionally, we predicted higher $\psi$ under elevated CO₂ due to enhanced WUE, although this may not occur if leaf area, and hence transpiration, are substantially increased. Water availability is vital to our predictions, as year-to-year variability in precipitation is expected to strongly interact with CO₂ to affect the productivity and gas exchange of Mojave Desert shrubs. We therefore compared the above functional parameters over a cycle of wet-dry years that typifies this arid ecosystem.

**Materials and Methods**

Research was conducted at the Nevada Desert Free-Air CO₂ Enrichment (FACE) Facility (NDFF) located on the Nevada Test Site in southern Nevada, USA (36°49'N, 115°55'W, 965-970 m elevation). Three shrubs common to this ecosystem were chosen for study: *Larrea tridentata* (evergreen); *Ambrosia dumosa* (drought-deciduous); and *Krameria erecta* (winter-deciduous). We sampled naturally occurring individuals within three ambient (375 ± 18 μmol mol⁻¹ CO₂) and three elevated CO₂ plots (set point: 550; mean: 537 ± 41 μmol mol⁻¹ CO₂), each 25 m in diameter. These plots are individually ringed with a plenum and 32 riser tubes that deliver ambient or elevated air, while an additional three ambient plots lacking the CO₂ delivery system act as controls. We found
no significant difference between the ambient FACE and control (non-FACE) plots for any of the parameters measured, so we only present data on the former. For a complete site description of the NDFF, including species composition, cover, and the FACE delivery system see Jordan et al. (1999).

Aboveground morphological attributes were measured on three marked shoots per shrub from three shrubs per species per plot. Marks were placed near a shoot terminus prior to the start of the growing season using a Sharpie permanent marker (Sharpie, Sanford North America, Bellwood, IL., USA). For each marked shoot, shoot diameter, length (from mark to shoot tip, including any side branches), leaf number, and reproductive output were collected every 2-4 weeks during the active growing season. Growth data were converted to measures of shoot biomass via regressions derived from shoots harvested during gas-exchange campaigns. Separate length vs. biomass regressions were used for elevated and ambient CO\textsubscript{2} grown plants. We compared yearly aboveground production of the marked shoots for each species-by-CO\textsubscript{2} treatment using the ANOVA procedure of SAS (SAS 1989). Because we are limited in our ability to destructively harvest at the NDFF, we could not allometrically scale individual shoot growth data to whole-canopy shoot production.

For each marked shoot we calculated leaf area 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. We also examined the effect of elevated CO\textsubscript{2} on canopy openness, using leaf number per unit shoot length as a proxy for self-shading. These data were compared for each species-by-CO\textsubscript{2} treatment using ANOVA.
Reproductive output was measured in 2001 as reproductive allocation (RA), defined as: \[\text{RA} = \frac{\text{shoot reproductive biomass}}{\text{total shoot biomass}} \times 100\]. Reproductive biomass was calculated by counting all buds, flowers, and fruits on each tagged shoot and multiplying by mean dry mass of each structure derived from off-plot harvests. Comparisons of RA were made for each species-by-CO$_2$ treatment using one-way ANOVA. We also compared RA between species within a given CO$_2$ treatment to determine if species-specific shifts in reproductive allocation occur under elevated CO$_2$.

Over the growing season, diurnal gas exchange was measured at bi-weekly to monthly intervals on one stem per shrub for three shrubs per species within a single ambient and elevated CO$_2$ plot (because of the time required to access the pivoting walkways in each plot – see Jordan et al. (1999) for a description of these walkways – we could not conduct multi-species diurnals on all six plots). In 1998 and 2001 we calculated the daily integrated photosynthesis ($A_{\text{day}}$) from diurnal measurements taken every two to three hours using a LiCOR 6400 open-flow photosynthesis system (LiCOR Inc., Lincoln, NE, USA). From the 9 AM diurnal point [the data point with typically the highest stomatal conductance and photosynthesis] we calculated instantaneous water-use efficiency for each species-by-CO$_2$ treatment using the ratio of photosynthesis to stomatal conductance, and compared means with ANOVA. $A_{\text{day}}$ was plotted with relative canopy development (i.e., percent of maximum leaf area) to examine potential phenological and physiological constraints on seasonal carbon assimilation. These data were analyzed by species using a factorial ANOVA, with $A_{\text{day}}$ and canopy development as dependent variables, and CO$_2$, date, and CO$_2$*date as independent variables. In addition to daily photosynthesis, we also estimated seasonal photosynthetic carbon assimilation (mmol m$^{-2}$ season$^{-1}$) by linearly
integrating the area under the $A_{day}$ curves for each species-by-CO$_2$ treatment. From these data we calculated the relative enhancement ratio (elevated:ambient CO$_2$) of seasonal photosynthesis under elevated CO$_2$. In the above analyses, we used plot means to analyze canopy development, but for $A_{day}$ we used the single plot measurement since diurnals could only be done in one ambient and elevated CO$_2$ plot per sampling date.

At the same time gas exchange was measured in 2001, morning and midday light-adapted $F_v'/F_m'$ as well as midday dark-adapted $F_v/F_m$ chlorophyll fluorescence were measured to compare the photochemical efficiency of photosystem II under ambient and elevated CO$_2$. Fluorescence was measured with a pulse-amplitude modulated (PAM) fluorimeter (Model FMS2, Hansatech Instruments Ltd., Norfolk, UK). For light-adapted samples, initial fluorescence ($F_o'$) was determined by exposure to a modulated low-level light. This was followed by a strong saturating pulse of light used to determine maximal fluorescence ($F_m'$). $F_v'/F_m'$ was then calculated as $F_v' = (F_m'-F_o')/F_m'$. Dark-adapted fluorescence was measured at midday on leaf samples that had been without light for ~0.5 h. Chlorophyll fluorescence measurements were compared by CO$_2$ treatment for each species using ANOVA. Because the length of the growing season varies by species, not all species were measured on each sampling period. Additionally, equipment failure precluded measurements after 7 May 2001.

Plant water status, as measured by predawn or midday shoot water potential ($\Psi$), was determined for one individual per species per plot ($n=3$ per species-by-CO$_2$ treatment) using a Scholander-type pressure chamber (Model 3000, Soil Moisture Equipment Corp., Santa Barbara, CA, USA). These data were analyzed by year for each species using ANOVA, with CO$_2$ treatment as the independent variable. We also used paired t-tests to
compare pooled species $\Psi$ between CO$_2$ treatments in order to determine if there was an overall CO$_2$ effect on $\Psi$.

Results

Water Relations

The 1998 growing season (Oct. 97-Sept. 98) was an exceptionally wet El Niño year, receiving 2.4 times higher rainfall than the long-term average of 129 mm, but was followed by three below-average rainfall years that were 76-83% of the long-term mean (Table 4.1). 1999 was a dry growing season, with only 17 mm of rain falling during the first six months of the hydrologic year. We did not measure predawn water potentials in 1998, and thus present midday water potentials ($\Psi_m$) for the first year of our study and

<table>
<thead>
<tr>
<th>Hydrologic year</th>
<th>Precipitation (mm)</th>
<th>Percent of long-term average (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>309</td>
<td>239</td>
</tr>
<tr>
<td>1999</td>
<td>107</td>
<td>83</td>
</tr>
<tr>
<td>2000</td>
<td>98</td>
<td>76</td>
</tr>
<tr>
<td>2001</td>
<td>102</td>
<td>79</td>
</tr>
</tbody>
</table>
predawn water potentials ($\psi_p$) for subsequent years. For *Larrea*, $\psi_m$ was significantly higher under elevated vs. ambient CO$_2$ in 1998 ($P = 0.017$; Table 4.2). *Ambrosia* and *Krameria* showed no significant difference in water potential between CO$_2$ treatments in any year. However, pooled species $\psi_m$ in 1998 indicated significantly higher water potential under elevated CO$_2$ ($P = 0.04$). In subsequent years, the pooled species $\psi_p$ were also significantly higher under elevated CO$_2$ (Table 4.2).

Table 4.2. Mean predawn ($\psi_p$) and midday ($\psi_m$) water potentials (MPa ± 1 SD) at the Nevada Desert FACE Facility. Amb: ambient CO$_2$; Elev: elevated CO$_2$. Pooled species values are mean $\psi$ and were tested for significance using paired t-tests. Asterisks (*) indicate significantly higher $\psi$ for a species in a given year under elevated CO$_2$ at $\alpha = 0.10^*$ or 0.05**.

<table>
<thead>
<tr>
<th>Species</th>
<th>[CO$_2$]</th>
<th>1998 $(\psi_m)$</th>
<th>1999 $(\psi_p)$</th>
<th>2000 $(\psi_p)$</th>
<th>2001 $(\psi_p)$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Larrea tridentata</em></td>
<td>Amb</td>
<td>-3.6 ± 0.1</td>
<td>-4.3 ± 1.6</td>
<td>-4.5 ± 2.0</td>
<td>-4.0 ± 1.4</td>
</tr>
<tr>
<td></td>
<td>Elev</td>
<td>0.1**</td>
<td>-3.7 ± 1.6</td>
<td>-4.0 ± 1.7</td>
<td>-3.8 ± 1.7</td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em></td>
<td>Amb</td>
<td>-3.2 ± 1.1</td>
<td>-2.7 ± 1.5</td>
<td>--</td>
<td>-2.2 ± 1.6</td>
</tr>
<tr>
<td></td>
<td>Elev</td>
<td>-2.9 ± 1.0</td>
<td>-2.0 ± 0.8</td>
<td>--</td>
<td>-2.0 ± 1.1</td>
</tr>
<tr>
<td><em>Krameria erecta</em></td>
<td>Amb</td>
<td>-3.8 ± 1.1</td>
<td>-4.6 ± 2.0</td>
<td>-5.5 ± 1.7</td>
<td>-5.4 ± 1.3</td>
</tr>
<tr>
<td></td>
<td>Elev</td>
<td>-3.5 ± 1.3</td>
<td>-4.3 ± 2.1</td>
<td>-5.2 ± 1.7</td>
<td>-5.2 ± 1.4</td>
</tr>
<tr>
<td>Pooled species</td>
<td>Amb</td>
<td>-3.6</td>
<td>-3.9</td>
<td>-5.0</td>
<td>-3.9</td>
</tr>
<tr>
<td></td>
<td>Elev</td>
<td>-3.1**</td>
<td>-3.3**</td>
<td>-4.6*</td>
<td>-3.7**</td>
</tr>
</tbody>
</table>

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Growth and reproductive allocation

Under elevated CO\textsubscript{2} we found significantly higher new shoot production for \textit{Larrea} (mean peak biomass production: ambient CO\textsubscript{2}: 244 mg, elevated CO\textsubscript{2}: 562 mg) and \textit{Ambrosia} (mean peak biomass production: ambient CO\textsubscript{2}: 22 mg, elevated CO\textsubscript{2}: 48 mg) during 1998 (Fig. 4.1). Growth of \textit{Krameria} showed higher aboveground production under elevated CO\textsubscript{2} in 1998 (mean peak biomass production: ambient CO\textsubscript{2}: 29 mg, elevated CO\textsubscript{2}: 45 mg), but the difference was not statistically significant. In the subsequent, below-average rainfall years (1999-2001) all shrubs accumulated much smaller increments of growth, and some individuals were even seen to drop some of their smaller stems. There was only one significant difference between CO\textsubscript{2} treatments after 1998 – new shoot production was significantly higher in \textit{Ambrosia} under elevated CO\textsubscript{2} (mean peak biomass production: ambient CO\textsubscript{2}: 21 mg, elevated CO\textsubscript{2}: 33 mg) during 2001 (Fig. 4.1). However, relative aboveground production ratios indicate growth was (with only one exception, \textit{Ambrosia} in 1999) stimulated under elevated CO\textsubscript{2}, regardless of rainfall (Table 4.3). Elevated CO\textsubscript{2} resulted in a 1.59- to 2.31-fold enhancement in aboveground production during 1998 whereas growth enhancement in 2001 was lower across all species, ranging from 1.31 in \textit{Larrea} to 1.64 in \textit{Ambrosia} (Table 4.3).

Enhancement of leaf area under elevated CO\textsubscript{2} was less than that of shoot production (Table 4.3). \textit{Larrea} showed the greatest enhancement in leaf area between wet and dry years, while the winter-deciduous species (\textit{Krameria}) showed little difference in leaf area enhancement between years. Leaf number per unit stem length showed a recurring pattern in \textit{Ambrosia}, where for every year except 1999, individuals had significantly lower leaf numbers per unit stem length under elevated CO\textsubscript{2} (ambient CO\textsubscript{2} avg. = 3.7
leaves per cm stem length, elevated CO₂ avg. = 2.6 leaves per cm stem length; \( P < 0.05 \)).

This lower density of leaves per unit stem length under elevated CO₂ is indicative of

Figure 4.1. Cumulative shoot production of *Larrea tridentata* (top), *Ambrosia dumosa* (middle), and *Krameria erecta* (bottom) between 1998 and 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 (\( \alpha = 0.10 \)). Note different scales. Due to sampling constraints, *Krameria* was not measured in 1999 and 2000.
longer internodes and more ‘open’ shoot tips. *Larrea* under elevated CO₂ did have fewer leaves per unit stem length during the mid-2000 growing season (April, ambient CO₂ = 3.0 leaf pairs per cm vs. 2.3 leaf pairs per cm under elevated CO₂; \( P = 0.044 \)), but this difference disappeared later in the growing season (May, ambient CO₂ = 2.3 leaf pairs per cm vs. elevated CO₂ = 2.1 leaf pairs per cm; \( P = 0.37 \)). No other species showed significant differences in this variable.

Table 4.3. Relative enhancement ratios (elevated:ambient CO₂) for seasonal photosynthesis, peak leaf area (total leaf area produced per growth shoot), aboveground production, and instantaneous water-use efficiency for three functional types at the Nevada Desert FACE Facility during above- (1998) and below-average (2001) rainfall years.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Production</th>
<th>Leaf area</th>
<th>Photosynthesis</th>
<th>WUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larrea tridentata</td>
<td>1998</td>
<td>2.31</td>
<td>1.71</td>
<td>1.26</td>
<td>1.38</td>
</tr>
<tr>
<td></td>
<td>2001</td>
<td>1.31</td>
<td>0.94</td>
<td>1.37</td>
<td>1.80</td>
</tr>
<tr>
<td>Ambrosia dumosa</td>
<td>1998</td>
<td>2.22</td>
<td>1.00</td>
<td>2.03</td>
<td>1.23</td>
</tr>
<tr>
<td></td>
<td>2001</td>
<td>1.64</td>
<td>1.30</td>
<td>1.32</td>
<td>1.76</td>
</tr>
<tr>
<td>Krameria erecta</td>
<td>1998</td>
<td>1.59</td>
<td>1.51</td>
<td>1.42</td>
<td>1.40</td>
</tr>
<tr>
<td></td>
<td>2001</td>
<td>1.57</td>
<td>1.53</td>
<td>1.43</td>
<td>1.33</td>
</tr>
</tbody>
</table>

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Reproductive allocation (RA) in *Larrea* did not differ significantly between ambient (17%) and elevated (15%) CO$_2$ treatments ($P > 0.05$) in 2001. *Ambrosia* had variable RA at both [CO$_2$], resulting in no significant difference ($P > 0.05$) between ambient (18% ± 16%) and elevated (32% ± 24%) CO$_2$-grown plants. RA also did not significantly differ in *Krameria* between CO$_2$ treatments (10% ambient vs. 12% elevated CO$_2$: $P > 0.05$).

Furthermore, RA was not significantly different between species at ambient CO$_2$.

However, pairwise comparisons of the species*CO$_2$ interaction term revealed that RA for *Ambrosia* at elevated CO$_2$ was significantly higher than that for both *Larrea* and *Krameria* at elevated CO$_2$ ($P < 0.05$).

Gas exchange and canopy development

We found no significant CO$_2$-by-time interaction for *Larrea* canopy development in 1998 ($P > 0.05$). There was also no difference in $A_{day}$ by CO$_2$ or CO$_2$*time ($P > 0.05$ in both cases); however, $A_{day}$ did significantly differ over time in *Larrea* during 1998 (Fig. 4.2; $P < 0.001$). In the below-average rainfall year of 2001, elevated-CO$_2$-grown *Larrea* showed maximal $A_{day}$ prior to full canopy development, and this occurred earlier than in ambient-grown plants (Fig. 4.2), indicating a shift in peak photosynthesis under elevated CO$_2$. $A_{day}$ showed significant CO$_2$ and CO$_2$-by-time effects in 2001 ($P < 0.01$ in both cases), with higher early-season $A_{day}$ under elevated CO$_2$. In addition, there was a significant time effect on $A_{day}$ ($P < 0.0001$) due to the high rates early in the growing season.

Due to sampling constraints, *Ambrosia* relative canopy development and $A_{day}$ were not measured early in the 1998 growing season. However, mid- to late-season canopy
Figure 4.2. Canopy development vs. daily integrated photosynthesis ($A_{\text{day}}$) for *Larrea tridentata* at the Nevada Desert FACE Facility during a wet (top) and dry (bottom) year. Open circles represent ambient CO$_2$, filled circles elevated CO$_2$. Solid lines represent percent of maximum leaf area per growth shoot. dotted lines daily integrated photosynthesis. Error bars represent ±1 SE.

development did not differ by CO$_2$ or the CO$_2$-by-time interaction ($P > 0.05$). $A_{\text{day}}$ was significantly higher under elevated CO$_2$ in September ($P < 0.01$), and $A_{\text{day}}$ in both CO$_2$ treatments reduced considerably from September 20 to November 2, 1998, resulting in a highly significant time effect (Fig. 4.3; $P < 0.001$). A weakly significant ($P = 0.051$)
CO₂-by-time interaction indicated A\textsubscript{day} in \textit{Ambrosia} tended to be higher under elevated CO₂ at the end of the growing season (Fig. 4.3). In 2001, \textit{Ambrosia} peak canopy development did not significantly differ in its timing or percent development between CO₂ treatments (Fig. 4.3: \( P > 0.05 \)). There was also no significant CO₂-by-time interaction on canopy development (\( P > 0.05 \)). The timing of peak A\textsubscript{day} did not differ by CO₂ treatment (\( P > 0.05 \)), although mean A\textsubscript{day} was higher for \textit{Ambrosia} under elevated CO₂ (\( P < 0.05 \)). Finally, a significant time effect revealed A\textsubscript{day} was considerably lower in \textit{Ambrosia} during the latter part of the growing season, regardless of CO₂ concentration (\( P < 0.01 \)).

As in \textit{Larrea} during 1998, timing of peak canopy development in \textit{Krameria} did not differ by CO₂ treatment (Fig. 4.4). However, canopy development showed a significant CO₂-by-time interaction, with late-season canopy leaf area 37% higher under elevated vs. ambient CO₂. Mean A\textsubscript{day} did not significantly differ in \textit{Krameria} by CO₂, time, or their interaction (\( P > 0.05 \) in all cases). Unlike 1998, in 2001 we found no significant late-season difference in canopy development, although mean A\textsubscript{day} was significantly higher for elevated vs. ambient grown \textit{Krameria} (Fig. 4.4: \( P < 0.01 \)). There was also a significant (\( P < 0.05 \)) time effect on A\textsubscript{day}, indicating photosynthetic rates were much reduced near the end of the growing season.

Integrated seasonal photosynthesis during 1998 averaged 53.6 and 67.8 mol m\(^{-2}\) for ambient and elevated CO₂-grown \textit{Larrea}, respectively, indicating a 26% enhancement of seasonal photosynthesis under elevated CO₂ (Table 4.3). In the below-average rainfall year of 2001, \textit{Larrea} seasonal photosynthesis averaged only 27.1 and 37.0 mol m\(^{-2}\) for ambient and elevated CO₂ plants, respectively. However, the greater disparity in
Figure 4.3. Canopy development vs. daily integrated photosynthesis ($A_{day}$) for *Ambrosia dumosa* at the Nevada Desert FACE Facility during a wet (top) and dry (bottom) year. Open circles represent ambient CO$_2$, filled circles elevated CO$_2$. Solid lines represent percent of maximum leaf area per growth shoot. dotted lines daily integrated photosynthesis. Error bars represent ±1 SE.

Seasonal photosynthesis between CO$_2$ treatments during the drier year resulted in a 37% enhancement under elevated CO$_2$. Mean seasonal photosynthesis in *Ambrosia* during 1998 averaged 20.6 mol m$^{-2}$ at ambient CO$_2$ and 41.7 mol m$^{-2}$ at elevated CO$_2$, resulting....

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in a ca. 2-fold enhancement in carbon assimilation under elevated CO₂. As with *Larrea* in 2001, *Ambrosia* in both CO₂ treatments showed reduced seasonal photosynthesis (ambient CO₂: 18.9 mol m⁻², elevated CO₂: 25.05 mol m⁻²). *Krameria* in 1998 had a seasonal photosynthesis average of 28.0 mol m⁻² and 39.9 mol m⁻² at ambient and elevated CO₂, respectively, indicating a 42% enhancement in mean seasonal photosynthesis under elevated CO₂ (Table 4.3). Seasonal photosynthesis in *Krameria* during 2001 was also reduced (ambient CO₂: 17.6 mol m⁻², elevated CO₂: 25.2 mol m⁻²), resulting in similar enhancement to that in 1998 (Table 4.3).

Mean instantaneous water-use efficiency (WUE) at the 0900 h diurnal point was higher under elevated vs. ambient CO₂ (*P* < 0.05 for each species), regardless of rainfall. Relative WUE ratios (elevated:ambient CO₂) were considerably higher during a dry vs. wet year for both *Larrea* and *Ambrosia* (Table 4.3). *Krameria* showed little difference in WUE between wet and dry years.

Chlorophyll fluorescence

In 2001, morning Fₚ'/Fₘ' values in *Larrea* were significantly higher under ambient vs. elevated CO₂ in the latter part of the growing season (Fig. 4.5). No other species showed significant differences in morning Fₚ'/Fₘ' between CO₂ treatments over the 2001 growing season. Midday Fₚ'/Fₘ' only differed by [CO₂] in *Krameria*, and this was on the only date it was measured for this species (May, ambient CO₂ = 0.502, elevated CO₂ = 0.669; *P* < 0.05). In May, dark-adapted Fₚ'/Fₘ did not differ between CO₂ treatments for *Ambrosia* (mean: ambient 0.805, elevated 0.791) or *Krameria* (mean: ambient 0.798, elevated 0.824). For *Larrea*, dark-adapted Fₚ'/Fₘ did not differ between CO₂ treatments.
Figure 4.4. Canopy development vs. daily integrated photosynthesis ($A_{day}$) for *Krameria erecta* at the Nevada Desert FACE Facility during a wet (top) and dry (bottom) year. Open circles represent ambient CO$_2$, filled circles elevated CO$_2$. Solid lines represent percent of maximum leaf area per growth shoot, dotted lines daily integrated photosynthesis. Error bars represent ±1 SE.

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Figure 4.5. Morning (top) light-adapted $\frac{F_v}{F_m}$ and midday (bottom) dark-adapted $\frac{F_v}{F_m}$ chlorophyll fluorescence for *Larrea tridentata* at the Nevada Desert FACE Facility. Open circles: ambient CO$_2$; Filled circles: elevated CO$_2$. An asterisk (*) indicates fluorescence values differed significantly on that sampling date at $\alpha = 0.05$. 

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Discussion

It has been well documented that elevated atmospheric CO\textsubscript{2} can enhance plant water-use efficiency (Bazzaz 1990; Bowes 1993), leading to predictions that future CO\textsubscript{2} concentrations will reduce water limitations and enhance net primary production in water-limited ecosystems (Mooney et al. 1991; Melillo et al. 1993). Increased productivity under elevated CO\textsubscript{2} has been found in many ecosystem types (temperate forests. DeLucia et al. 1999; grasslands. Owensby et al. 1996; deserts. Smith et al. 2000). although the duration of this enhancement is highly variable, lasting from only a few years in arctic vegetation (Oechel and Vourlitis 1996) to decades in evergreen oak trees (Hättenschwiler et al. 1997). Yearly changes in abiotic factors (e.g., water and nutrient availability) may contribute to this variability in plant productivity under elevated CO\textsubscript{2} (Loustau et al. 2001). Likewise, biotic factors, including invasion and anthropogenic activities (grazing or soil disturbance events) may also interact with atmospheric CO\textsubscript{2} to alter productivity, especially in dry ecosystems (Belnap 1995; Smith et al. 2000; Ehleringer 2001). Here, we found elevated CO\textsubscript{2} increases carbon assimilation rates, aboveground growth and water-use efficiency of desert shrubs, but contrary to our predictions, the greatest relative increases in these variables are not constrained to dry years.

Primary production in *Larrea tridentata*, and desert productivity in general, is limited by low standing biomass and leaf area (Chew and Chew 1965; Webb et al. 1983; Smith et al. 1997). Low water availability is typically considered the primary check on desert ecosystem productivity (Smith et al. 1997), but nitrogen can also be limiting, as seen in the Chihuahuan Desert (Ettershank et al. 1978; Fisher et al. 1988). This limitation,
however, may not be as strong in the Mojave Desert until consecutive high rainfall years with high productivity have depleted soil N (Romney et al. 1978; Smith et al. 1997). We found a 1.31- to 2.31-fold increase in new shoot production under elevated CO$_2$ for Mojave Desert shrubs during below- and above-average rainfall years, respectively. In low rainfall years, aboveground production generally did not differ between CO$_2$ concentrations, although the ratio of elevated-to-ambient production usually indicated some positive enhancement of growth under elevated CO$_2$. Measures of root growth at the NDFF have failed to show a significant difference in belowground shrub production under elevated CO$_2$ (Phillips, unpublished data), and so our findings are not due to shifts in biomass allocation. These results do not support our initial hypothesis that elevated CO$_2$ would result in the largest stimulation of growth (relative to growth under ambient CO$_2$) in dry years, when gains in water-use efficiency should be most important. This could be due to greater N availability in the high rainfall year of 1998 permitting plants to exploit elevated CO$_2$ concentrations, and hence increase growth, under ample water conditions. Indeed, we have observed this positive N effect on growth of annual plants at the NDFF, which showed the largest increases in standing biomass under elevated CO$_2$ within higher nitrogen microsites (Smith et al. 2000).

Peak daily integrated photosynthesis ($A_{\text{day}}$) shifted in *Larrea* to an earlier date than peak canopy development in a low rainfall year under elevated CO$_2$, suggesting that while absolute productivity increased, growth was still constrained by asynchronous timing of peak photosynthesis and canopy development. Additionally, although seasonal photosynthetic rates were enhanced in all species under elevated CO$_2$, this did not necessarily equate to significant enhancements in new shoot production. Apparently
carbon is lost to other non-growth pathways such as production of secondary compounds, or from roots via exudation (we have observed an approximate doubling of soil respiration beneath Larrea shrubs; data not shown). While we observed this shift in peak A\textsubscript{day} only during a relatively dry year, we emphasize that most years in the Mojave Desert are limited with respect to water availability. Nevertheless, if early season carbon gain does become more leaf-area limited under elevated CO\textsubscript{2} it may still be partially compensated for by higher overall seasonal carbon assimilation rates.

Chlorophyll fluorescence showed no consistent patterns between species, but in a few instances differed within-species by [CO\textsubscript{2}]. The lower morning F\textsubscript{v}/F\textsubscript{m} values we measured in Larrea under elevated CO\textsubscript{2} may be the result of greater photochemical quenching and/or increased non-photochemical quenching via the xanthophyll cycle. Such findings of reduced F\textsubscript{v}/F\textsubscript{m} under elevated CO\textsubscript{2} have been seen in Eucalyptus (Roden and Ball 1996a). It is also plausible the reduced chlorophyll fluorescence we measured may be the result of feedback inhibition caused by greater starch accumulation under elevated CO\textsubscript{2} (Roden and Ball 1996b). Further studies are necessary to determine the mechanism responsible for reduced chlorophyll fluorescence in Larrea under elevated CO\textsubscript{2}.

The canopy architecture of Larrea in the Chihuahuan and Mojave Deserts enhances WUE by reducing self-shading during periods favorable for carbon gain (Neufeld et al. 1988). We speculated enhanced growth under elevated CO\textsubscript{2} might further increase WUE if this growth resulted in longer internodes that further reduced self-shading. Over the course of our study, however, we found only a single sampling date where internode lengths were significantly longer for Larrea grown under elevated CO\textsubscript{2}. Furthermore, increases in WUE under elevated CO\textsubscript{2} may be offset by greater leaf area and its attendant
increase in transpiration (Smith et al. 1999). Nonetheless, even though we measured a 71% increase in leaf area for *Larrea* under elevated CO$_2$ during 1998. WUE and $\psi$ were still significantly higher compared to ambient-grown plants.

In the high rainfall year (1998) we found significantly higher new shoot production in *Ambrosia* and moderately enhanced production in *Krameria*, both deciduous shrubs, under elevated CO$_2$. The overall lack of a statistically significant increase in *Krameria* productivity during wet and dry years may be due to the summer-active growth habit of this species, which occurs during periods of reduced water availability and higher temperatures that may diminish a CO$_2$ fertilization effect. Aboveground productivity of all three species declined during the below-average rainfall years, and we witnessed some individuals even dropping stems, perhaps as an adaptation to maintain water balance (Orshan 1954; Smith et al. 1997). Still, gas exchange measurements indicated seasonal photosynthesis was higher under elevated CO$_2$ in both above- (30-51%) and below-average (24-30%) rainfall years, approaching the 43% increase in CO$_2$ concentration that the shrubs were exposed to over the life of the experiment. Instantaneous WUE was also greater under elevated CO$_2$, due to an increase in photosynthesis without a significant change in stomatal conductance. Overall, higher photosynthetic rates did not always equate to significant increases in biomass: in fact, what we observed over four continuous years of CO$_2$ fertilization in the Mojave Desert is fairly consistent enhancement in photosynthetic carbon assimilation under elevated CO$_2$, but highly variable investment of that carbon into new shoot biomass.

Our results indicate some desert shrubs may be capable of substantial increases in photosynthesis and growth at future CO$_2$ concentrations. If precipitation increases in the
desert Southwest as some models predict (Taylor and Penner 1994). Rising CO$_2$ concentrations coupled with greater water availability may significantly enhance carbon inputs into the Mojave Desert. Still, whether or not high levels of productivity will be maintained is uncertain due to species-specific responses that may over time lead to changes in the composition and structure of this ecosystem. Smith et al. (2000) found that elevated CO$_2$ increases the success of an invasive annual (Bromus) over that of native annuals in the Mojave Desert. Furthermore, we measured higher reproductive allocation in Ambrosia under elevated CO$_2$ compared to other perennials during a dry year. And previous work has shown early survival of Ambrosia is greater compared to Larrea under elevated CO$_2$ (Housman et al. in review). The increased success of Bromus and higher early survival of Ambrosia indicate future changes in the structure and function of this ecosystem may indeed occur with rising CO$_2$.

Deserts encompass a substantial and increasing portion of the terrestrial biosphere (Reynolds 2001), yet they are not nearly as productive as forests, the primary terrestrial carbon sinks. Nonetheless, increasing global desertification could make the acquisition of carbon within arid ecosystems much more noteworthy in the global carbon budget. As we continue our assessments it is clear that drylands are an important ecosystem type for which we need more extensive and detailed information.

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CHAPTER 5

SUMMARY OF MAJOR RESULTS

Substantial increases in aridland primary production have been predicted under high CO$_2$ as a result of enhanced water-use efficiency (WUE). However, plant growth and gas exchange within arid ecosystems is highly unpredictable due to infrequent and irregular inputs of precipitation. In this four-year study at the Nevada Desert FACE Facility (NDFF), we found that in dry years, predicted increases in growth may not occur as the overriding need for water limits production, regardless of [CO$_2$]. In other words, a baseline amount of moisture is first necessary to maintain carbon balance, while new growth and reproduction occur only after sufficient additional precipitation has fallen. Thus, water savings under high CO$_2$ during years with low precipitation may be pronounced, as measured by WUE (see Chapter 4), but due to the overall low water availability and abbreviated growing season it typically does not equate to significantly greater carbon assimilation rates or production of new biomass. Conversely, when rainfall is ample, elevated CO$_2$ may significantly increase primary production of desert perennials.

Plant growth, photosynthesis, and reproduction in the Mojave Desert have the potential to increase dramatically under future CO$_2$ levels and precipitation regimes. Data from the NDFF in 1998 showed dramatic enhancement of production under high
CO$_2$ (Smith et al. 2000). While this was an exceptionally wet year, the three subsequent years were dry and had substantially reduced growth, indicating water and CO$_2$ interact to control the functioning of this ecosystem. With some models suggesting the desert Southwest will receive higher inputs of rainfall in the future (Taylor and Penner 1994), enhanced carbon gain seems likely in this ecosystem. A precipitation increase, especially in the form of winter rains, would favor winter- and spring-active shrubs, annuals, and grasses under elevated CO$_2$. It would also increase deep soil moisture storage, benefiting summer active species as well. Conversely, if summer rains increase, summer-active perennials might show more positive growth responses to high CO$_2$ while spring-active, deciduous shrubs would probably show little increase in productivity due to partial-to-complete summer dormancy in these species.

Along with increased production of perennials, native and exotic annuals also increase productivity under elevated CO$_2$, although the density and biomass of exotic species show differentially larger increases (Smith et al. 2000). These higher yields are partly due to lower construction costs for invasives compared to native species under high CO$_2$ (Nagel et al., in review). Another potential change resulting from an increased abundance of exotic grasses is a decrease in litter quality (i.e., C:N ratio) and subsequent N availability (R.D. Evans, in press). Thus, the increased success of exotic grasses in the Mojave Desert is worrisome because it could change fire cycles and ultimately alter the structure and function of this ecosystem, converting it from a native shrubland to invasive grassland.

Increases in seasonal carbon assimilation rates under elevated CO$_2$, in concert with decreases in stomatal conductance (Nowak et al. 2001), can serve to increase net primary
production in a water-limited desert ecosystem. However, when water becomes less limiting under high CO$_2$, other factors, such as low nutrient availability, can become checks on production. In the Mojave Desert, N can be a limiting factor on plant growth, although in the area of this study P may be more limiting (Wallace and Romney 1972). If future nutrient limitations occur, species or functional types capable of greater nutrient resorption prior to leaf senescence could be at a selective advantage in the long-term. However, some Mojave Desert shrubs already show essentially complete resorption of particular nutrients (Chapter 2), with the amounts left in the leaves so miniscule it is unlikely resorption could increase. or if it did, the returns would be minute. This suggests future plant growth under high CO$_2$ may be restricted unless there are new inputs or access to nutrients in this ecosystem.

The continued shifts expected to occur in the aforementioned global change variables (i.e., atmospheric [CO$_2$, water and nutrient availability) could have profound impacts of future recruitment and growth of Mojave Desert plant species. Early results from the NDFF have already found higher early survival of *Ambrosia dumosa* compared to *Larrea tridentata* under elevated CO$_2$ (Chapter 3). If these trends were to continue the future structure of this portion of the Mojave Desert could slowly go from one co-dominated by evergreen/drought-deciduous shrubs, to one more exclusive to drought-deciduous species. Still, several factors, including species interactions and response to multiple enviromental perturbations, make such predicitions highly uncertain.

The research presented here suggests the Mojave Desert ecosystem is a dynamic region with the potential for dramatically higher carbon assimiliation rates and plant productivity under future CO$_2$ concentrations. Still, several questions remain to be
answered about the interactions of elevated CO₂, water and nutrient availability, and how they influence ecosystem structure and function in the Mojave Desert. Future directions of study at the NDFF should include scaling-up from shoot to whole-plant productivity, and ultimately productivity at the ecosystem level. Planned projects involving detailed branch allometrics and mini-dome gas exchange will help tremendously in determining net ecosystem production (NEP). Likewise, development of new gas exchange protocols for measuring larger branch segments will aid in scaling from leaf to higher levels of organization. Fluctuations between predawn and midday water potentials (with values in some instances much lower at predawn) suggest hydraulic lift may be occurring and should be more fully investigated. Hydraulic lift has already been confirmed within *Larrea* and *Ambrosia* on the same watershed as the NDFF (Yoder and Nowak 1999), but it needs to be more fully examined under high CO₂. In the meantime, future water relations data should be collected at predawn to avoid the potential confounding factor of hydraulic lift and to make comparisons between CO₂ treatments and species more straightforward. Finally, data from the Mojave Global Change Facility, a sister site to the NDFF where multiple environmental variables (water, nitrogen, and crust disturbance) are being manipulated simultaneously, will aid greatly in the predictive power and understanding of aridland plant responses to elevated CO₂.

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