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ELEVATED ATMOSPHERIC CO_2 DOES NOT CONSERVE SOIL WATER IN THE MOJAVE DESERT

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Abstract. Numerous studies, including those of desert plants, have shown reduced stomatal conductance under elevated atmospheric CO_2. As a consequence, soil water has been postulated to increase. Soil water was measured for >4 yr at the Nevada Desert Free Air CO_2 Enrichment (FACE) Facility to determine if elevated atmospheric CO_2 conserves soil water for a desert scrub community in the Mojave Desert. We measured soil water in the top 0.2 and 0.5 m of soil with time domain reflectometry and to 1.85 m with a neutron probe for the three treatments at Desert FACE: elevated CO_2 (550 μmol/mol), blower control (ambient CO_2), and non-ring treatments. The treatment main effect was not significant in any analyses of variance. Although the treatment × date interaction was significant for soil water in the top 0.5 m of soil, the expected greater soil water for elevated CO_2 vs. ambient CO_2 only occurred on one sampling date. In contrast, soil water for that same depth was significantly lower under elevated CO_2 on six dates. Thus, we infer that increased water use from increased primary productivity (and therefore leaf area) under elevated CO_2 offset the decreased water use from reduced stomatal conductance, and hence soil water was not conserved under elevated CO_2 in the Mojave Desert, unlike other ecosystems.

Key words: desert ecosystems; elevated atmospheric CO_2; evapotranspiration; Free Air CO_2 Enrichment; Larrea tridentata; *Mojave Desert; soil water balance.*

INTRODUCTION

A common response of plants to elevated atmospheric CO_2 is decreased stomatal conductance (Bazzaz 1990, Bowes 1993), which has led to speculation that plant water use would decrease in a future, high-CO_2 world. Recent meta-analyses have shown reductions in stomatal conductance at elevated CO_2 to be common (Wand et al. 1999), but not always significant, especially among trees (Curtis and Wang 1998). These observations of reduced conductance and dramatically increased plant water-use efficiency at elevated CO_2 led to the prediction that water-limited ecosystems would be the most responsive to increasing CO_2 (Strain and Bazzaz 1983, Melillo et al. 1993). Indeed, photosynthesis and primary production in desert ecosystems appear to be highly responsive to elevated CO_2, at least when soil resources such as water and nitrogen are available (Smith et al. 2000, Naumburg et al. 2003).

Reduced water use by plants could, in turn, alter the hydrologic water balance of an ecosystem and result in greater levels of soil water. For example, in annual grasslands of California, reductions in stomatal conductance and transpiration (Jackson et al. 1994) led to higher soil water under elevated CO_2 (Fredeen et al. 1997, Hungate et al. 1997). Similar increases in soil water have been observed in tallgrass prairie (Ham et al. 1995) in open-top chamber studies as well as for wheat and sorghum under Free Air CO_2 Enrichment (FACE) (Kimball et al. 2002). However, this simple scaling from stomatal conductance to ecosystem water use is tempered by potential changes in canopy leaf temperature and leaf area (Field et al. 1995). For example, counteracting effects of reduced conductance, increased canopy temperature, and increased leaf area resulted in very little effect (<2%) on cotton evapotranspiration under FACE (Kimball et al. 2002).

Because water is the primary limiting factor in desert ecosystems (Smith and Nowak 1990), conservation of soil water under elevated CO_2 may be especially important in driving community and ecosystem responses in arid lands. Thus, the primary objective of this study was to determine if soil water was conserved under elevated CO_2 in the Mojave Desert, which is the driest ecosystem in North America. Our general hypothesis was that elevated CO_2 would result in increased soil water. Specifically, we had two predictions: (1) enhancements in soil water would be greatest early in the experiment, when the effect of stomatal conductance

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alone was most pronounced, but may fade over time as enhanced plant production (and leaf area) in response to elevated CO_2 would counteract lower transpiration rates at the leaf level; and (2) soil water would primarily be enhanced in the rooting zone (below 0.15 m), with surface soils showing little CO_2 response due to the importance of direct evaporation in the water balance of those soils.

METHODS

Study site

This research was conducted at the Nevada Desert FACE Facility (NDFF), a state-of-the-technology research facility that is designed to study responses of an undisturbed Mojave Desert ecosystem to increasing atmospheric CO_2 (Jordan et al. 1999). The NDFF consists of nine study plots, each 23 m in diameter: three elevated CO_2 FACE rings (target CO_2 concentration 550 μmol/mol), three blower-control rings (at ambient CO_2), and three non-ring control plots (also at ambient CO_2). This experimental design yields two comparisons of interest: first is the comparison of FACE and blower-control treatments to determine the effect of elevated CO_2, and second is that between the blower-control and non-ring treatments to determine the effect of the FACE apparatus. In this paper, we generally refer to the three treatments as elevated CO_2, ambient CO_2, and non-ring, respectively.

The array of study plots is located on a broad alluvial fan in vegetation that is characterized by *Larrea tridentata* (DC.) Cov., an evergreen shrub that can grow over 1 m in height. Other important shrubs include drought-deciduous *Lycium andersonii* A. Gray and *Ambrosia dumosa* (A. Gray) Payne. Abundant perennial grasses include the C_3 tussock grass *Achnatherum hymenoides* (Roemer & Schultes) Barkworth (formerly *Oryzopsis hymenoides*) and the C_4 tussock grass *Pleuraphis rigida* Thurber (formerly *Hilaria rigida*). Up to 75 species of annual and perennial forbs may occur, depending on amount and seasonality of rainfall (Jordan et al. 1999).

The Desert FACE experiment began on 28 April 1997 with a step increase from ambient CO_2 (~370 μmol/mol) to a set point of 550 μmol/mol for the three elevated CO_2 plots. The Desert FACE experiment has operated continuously at 24 h/d, 365 d/yr since initiation of the experiment, except for system maintenance, when wind or cold-temperature thresholds were exceeded, or when the control system was damaged (primarily from lightning strikes). Mean CO_2 concentration at mid-canopy level in the center of the plot is very close to the target value of 550 μmol/mol (Jordan et al. 1999). Since initiation of the experiment in April 1997, precipitation has varied greatly, from very wet at ~240% of the long-term average during the 1998 El Niño to below average for 1999, 2000, 2001, and 2002 (83%, 76%, 79%, and 37% of long-term average, respectively).

Soil water sampling

A total of 16 time domain reflectrometry (TDR) probes (Dynamax, Inc., Houston, Texas, USA) were installed in each of the nine plots. Half of the probes were 0.2 m long, and the other half were 0.5 m long. All probes were pushed into the soil from the surface; thus, 0.2 m probes measured soil water content for the 0–0.2 m portion of the soil profile, and 0.5 m probes measured the 0–0.5 m depth profile. TDR probes were installed in two microsite locations: a pair of 0.2- and 0.5-cm probes was installed under the canopy of four randomly selected *Larrea* plants in each plot, with another pair installed nearby in the interspace between perennial plants. TDR probe installation occurred during the summer and fall of 1997 and was completed ~6 mo after initiation of the treatments. TDR soil water measurements began in November 1997 for the 0.2-m probes and in February 1998 for 0.5-m probes, and have continued at ~2-wk intervals. We present data through mid-August 2002 in this paper. Initially, 44% of the 0.5-m probes were not fully inserted into the soil because rocks in the soil impeded installation. For these probes, we corrected the soil water measurement based on the proportion of the probe length in air because the dielectric constant of air (1) is much less than that of water (80) (Topp 1993). By December 1999, all these TDR probes had been relocated in their respective microsite location so that they were fully inserted into the soil.

A total of three neutron probe tubes were installed in a systematic fashion within each plot during the late spring and summer of 1999. Tubes were placed only in interspaces between shrubs and located approximately halfway along three radii: one orientated due south and the other two at 120° from due south. Neutron probe measurements began in September 1999 and have continued at ~4-wk intervals; data through mid-August 2002 are included in this paper. Measurements were made at 0.15 m soil depth and then at 0.2 m depth increments to a soil depth of 1.75 m.

To facilitate the comparison of soil water data for different increments of soil depth, we converted the TDR and neutron probe measurements of soil water from volumetric percent soil water to an equivalent depth of water (mm). For neutron probe measurements, we followed the procedures in Anderson et al. (1987) to determine the total amount of water in the soil profile from the surface to a depth of 1.85 m (i.e., half the 0.2 m depth increment past the 1.75 m depth reading). For TDR measurements, we used an analogous procedure based on the length of the probe.

Statistical analyses

TDR data were analyzed with a $3 \times 2 \times 108$ and $3 \times 2 \times 95$ split-split-plot analyses of variance (ANO-

TABLE 1. Results from split-split-plot analysis of variance for total amount of soil water in the top 0.2 m of soil, the top 0.5 m, and between 0.2 and 0.5 m soil depth.

	Top 0.2 m			Top 0.5 m			0.2–0.5 m		
Factor	df	F	P	df	F	P	df	F	P
Whole plot treatment	2, 6	0.1	0.956	2, 6	0.6	0.566	2, 6	0.8	0.493
Microsite location	1, 6	17.7	0.006	1, 6	0.1	0.736	1, 6	3.1	0.102
Treatment × microsite	2, 6	0.4	0.710	2, 6	1.6	0.284	2, 6	1.5	0.262
Sampling date	107, 1251	180.1	<0.001	94, 1076	99.0	<0.001	94, 1071	30.2	<0.001
Treatment × date	214, 1251	0.8	0.944	188, 1076	2.6	<0.001	188, 1071	2.0	<0.001
Microsite × date	107, 1251	5.6	<0.001	94, 1076	0.8	0.958	94, 1071	0.6	0.999
Treat. × microsite × date	214, 1251	0.4	1.000	188, 1076	0.6	0.999	187, 1071	0.6	1.000

Note: Soil water was measured by time domain reflectometry.

VA) for the 0.2-m and 0.5-m TDR probes, respectively. The three whole-plot treatments were the main effects, the two microsite locations (interspace vs. canopy) were the split-plot factor, and the 108 and 95 sampling dates were the split-split-plot factor. Neutron probe data (both for individual depths and for total water in the soil profile) were analyzed with 3 × 34 split-plot ANOVAs, where the three whole-plot treatments were the main effects and the 34 sampling dates were the split-plot factor. ANOVAs were computed by PROC MIXED in SAS for Windows version 8.2 (2002). For both TDR and neutron probe soil water measurements, the nine study plots were considered the experimental units, and the four TDR probes for each microsite location as well as the three neutron probes were treated as subsamples that were averaged together before the ANOVA was computed. Mean comparisons for significant factors in the ANOVAs were made with the ''lsmeans/diff'' command in SAS. $P \leq 0.05$ was considered significant.

RESULTS

Over all sampling dates, soil water in the top 0.2 m of soil was not significantly different among the three treatments (elevated CO_2, ambient CO_2, and non-ring control) (Table 1, Fig. 1). The only factors in the ANOVA that were significant were microsite location, sampling date, and the microsite location × date interaction term. Examining the microsite × date interaction term first, the interspace microsite was significantly wetter than the canopy microsite for 45 of 108 sampling dates (42% of sampling dates), and 78% of dates with significant differences occurred during the fall through spring (October through April) time period. In contrast, the interspace microsite was significantly drier than the canopy on only one sampling date. No significant differences between microsite locations occurred on the remaining 62 dates. Next we examined the significant microsite main effect, and over all sampling dates, the top 0.2 m of soil in the interspace between shrubs had, on average, 1.3 mm more water than that under *Larrea* canopies. For the 45 sampling dates when the interspace was significantly wetter, the interspace microsite averaged 2.5 mm more water than the canopy in the top 0.2 m of soil.

As with the top 0.2 m, soil water in the top 0.5 m of soil was not significantly different among the three treatments over all sampling dates (Table 1, Fig. 2). However, unlike the top 0.2 m, the treatment × date interaction term for the top 0.5 m was significant. For mean comparisons of treatments within sampling date, the treatments were not significantly different for 71 of 95 sample dates (75%). For the remaining 24 sample dates, the elevated CO_2 effect (i.e., the comparison of the elevated CO_2 and blower control treatments) was significant for seven dates: on only one sampling date was the elevated CO_2 treatment significantly wetter than the ambient CO_2 treatment, and for the other six dates, the elevated CO_2 treatment was significantly drier than the ambient CO_2 treatment. Another comparison of interest is that between the two types of ambient CO_2 treatments: the blower-control and non-ring control treatments (i.e., the ''blower'' effect). The non-ring control treatment was significantly wetter than the blower-control treatment for nine sample dates, but significantly drier for three sample dates. The most common treatment difference was between the elevated CO_2 and the non-ring treatments: the non-ring treatment was significantly wetter than the elevated CO_2 treatment on 20 dates.

We also examined the amount of water stored between 0.2 and 0.5 m soil depth. Results from the ANOVA (Table 1) were nearly identical to those for the top 0.5 m of soil (data not shown).

Finally, as with the shallower soil layers, soil water in the top 1.85 m of soil was not significantly different among the three treatments over all sampling dates (Table 2, Fig. 3). We also examined the amount of water stored between 0.45 and 1.85 m soil depth, and again the main plot treatment and treatment × date interaction terms were not significant (Table 2). We then analyzed the neutron probe data for each individual depth from 0.55–1.75 m soil depth, and neither the treatment main effect nor the treatment × date interaction were significant in any of these ANOVAs (results not shown). Considering that soil water recharge occurred only to a soil depth of 0.75 m in spring 2000, 0.55 m in spring 2001, and <0.55 m in spring 2002, the lack of significant differences among treatments for soil water below 0.55 m is not surprising.

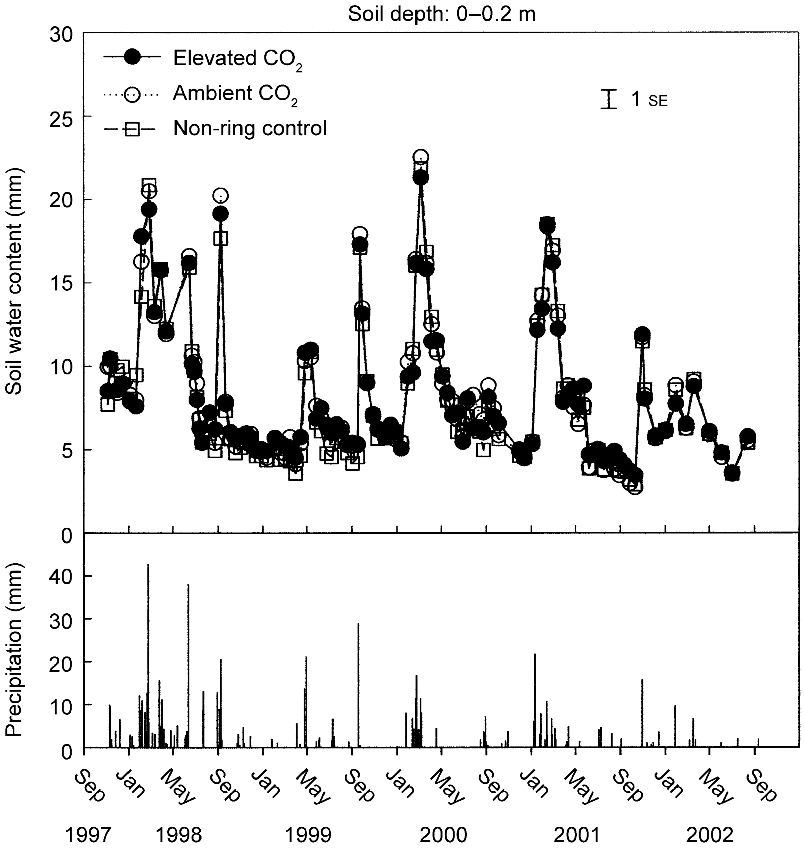

FIG 1. Top: total amount of water in the top 0.2 m of soil for elevated CO_2 (filled circles, solid line), ambient CO_2 (open circle, dotted line), and non-ring control (open squares, dashed line) treatments, averaged over both the *Larrea* and interspace microsite locations. Neither the treatment main effect nor the treatment × date interaction term was significant in the analysis of variance; the mean standard error for treatments within a date is shown for reference. Bottom: daily precipitation at the study area.

DISCUSSION

Averaged over >4 yr of soil water measurement at the Nevada Desert FACE Facility, soil water in the elevated CO_2 treatment was not significantly different from that in the ambient CO_2 treatment. If individual dates are examined, soil water under elevated CO_2 was greater than that under ambient for only one date. For all other dates, either these two treatments were not significantly different, or occasionally during wetter time periods, soil water was greater under ambient CO_2. Thus, we reject our overall hypothesis, and conclude that elevated CO_2 did not result in the conservation of soil water in the Mojave Desert. Although we do not have measurements of soil water potential to independently verify this result, the lack of significant differences in soil texture among treatments (R. S. Nowak, *unpublished data*) suggests that soil matric potentials also would not differ among treatments. Our result contrasts with greater soil water under elevated CO_2 that have been consistently, but not always significantly, observed in different grasslands (Fredeen et al. 1987, Niklaus et al. 1998, Volk et al. 2000), a scrub-oak woodland (Hungate et al. 2002), a pine forest (Schafer et al. 2002), and a deciduous tree plantation (Gunderson et al. 2002).

We have documented both decreased leaf conductance (Nowak et al. 2001) and increased plant biomass (Smith et al. 2000) for Mojave Desert plants under elevated CO_2. These CO_2 effects are largest during wetter time periods. Because leaf temperature is nearly identical under elevated and ambient CO_2 (Nowak et al. 2001), transpiration rate per unit leaf area is decreased under elevated CO_2. However, we infer that ecosystem water use, i.e., the product of leaf transpiration and leaf area across all species, was at least as great under elevated CO_2 as under ambient CO_2 because soil water was not consistently greater in the elevated CO_2 treatment. In a similar vein, we measured no significant effects of elevated CO_2 on sap flux for *Larrea tridentata* during summer 1998 (Pataki et al. 2000). Thus, we infer that increased water use from the CO_2-induced increase in leaf area is approximately proportional to decreased water use from reduced leaf conductance for a desert scrub community in the Mojave Desert.

Some evidence supports our first specific hypothesis, i.e., that enhancements of soil water would occur early

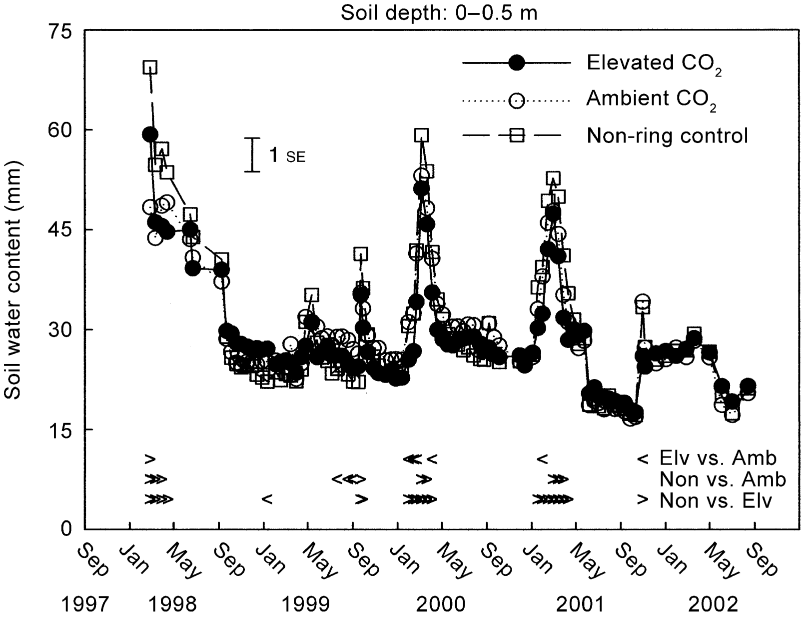

FIG 2. Total amount of water in the top 0.5 m of soil for elevated CO_2 (filled circles, solid line), ambient CO_2 (open circle, dotted line), and non-ring control (open squares, dashed line) treatments, averaged over both the *Larrea* and interspace microsite locations. The treatment × date interaction term was significant, and mean comparisons between treatments on a particular date are shown along the bottom of the graph. Significant differences between pairs of treatments (shown near the bottom right of the graph) are indicated by greater-than (>) and less-than (<) symbols; a greater-than symbol indicates that the first treatment is significantly greater than the second treatment on that date, and a less-than symbol indicates that the first treatment is significantly less than the second. The mean standard error for treatments within a date is shown for reference.

in the experiment. The only date when elevated CO_2 soil water was significantly greater than ambient CO_2 soil water was in February 1998, which was near the beginning of the experiment. The experiment began in April 1997, and spring 1998 was the first full growing season after the initiation of elevated CO_2. Decreased conductance occurs rapidly under elevated CO_2 (Bazzaz 1990, Bowes 1993) and was evident in our experiment (Nowak et al. 2001) in early spring 1998. However, annual growth of plants in our experiment was just beginning in February, and hence increased productivity induced by elevated CO_2 had not yet occurred. Thus, this transient increase in soil water under elevated CO_2 lends further support to our inference that increased leaf area offsets the decrease in conductance.

The differences among our three treatments primarily reflect water stored between 0.2 and 0.5 m soil depth. Both the top 0.5-m TDR soil water measurements and the 0.2–0.5 m measurements had significant treatment × date interaction terms, but none of the treatment terms were significant in the ANOVAs for soil water measurements above (top 0.2-m TDR) or below (0.45–1.85 m neutron probe) the 0.2–0.5 m deep soil layer. These results are generally consistent with our prediction that treatment effects would occur in the rooting zone and not in the surface soil layer. Furthermore, essentially no water moved into and back out of soil depths below 0.75 m soil depth. However, neutron probe measurements did not begin until September 1999, when the Mojave Desert had entered into a series of drought years. Although this lack of soil water movement below ~0.75 m in dry years is similar to other water balance studies in the area, soil water does infiltrate to depths >0.75 m during wet years (Yoder and Nowak 1999). Because we did not have neutron probe tubes in place during the very wet 1998 El Niño, we do not know if additional water is differentially stored below 0.75 m soil depth during very wet years.

TABLE 2. Results from split-plot ANOVA for total amount of soil water to a depth of 1.85 m and for that between 0.45 and 1.85 m soil depth.

	Top 1.85 m			0.45–1.85 m		
Factor	df	*F*	*P*	df	*F*	*P*
Whole plot treatment	2, 6	1.9	0.224	2, 6	3.0	0.127
Sampling date	33, 193	276.6	<0.001	33, 193	106.2	<0.001
Treatment × date	66, 193	0.9	0.707	66, 193	0.9	0.624

Note: Soil water was measured by neutron probe.

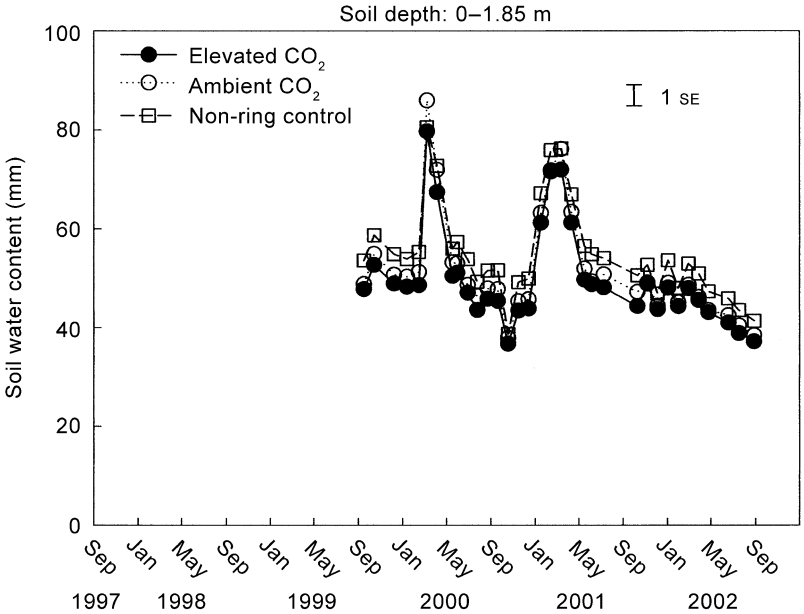

FIG 3. Total amount of water in the top 1.85 m of soil for elevated CO_2 (filled circles, solid line), ambient CO_2 (open circle, dotted line), and non-ring control (open squares, dashed line) treatments from neutron probe tubes placed in the interspace microsite location. Neither the treatment main effect nor the treatment × date interaction term was significant in the analysis of variance; the mean standard error for treatments within a date is shown for reference.

Although the FACE apparatus is thought to minimally alter microclimate (Mooney and Koch 1994), the blowers that mix and move elevated CO_2 air onto plots may slightly increase air movement over the study plot, and hence increase evaporation (Dingman 1994). This ''blower'' effect was observed for soil water in the top 0.5 m of soil for 9% of the sampling dates, but 3% of the sampling dates had the reverse (i.e., the non-ring control treatment was significantly drier than the blower-control treatment). Furthermore, this blower effect did not occur in the top 0.2 m of soil (Fig. 1), where changes in evaporation should be most evident. Thus, our soil water results do not provide strong evidence for a persistent blower effect, and hence our observed lack of overall CO_2 effects on soil water are ecologically relevant and are not an artifact of the FACE apparatus.

Interestingly, a microsite effect on soil water was observed regularly in the top 0.2 m of soil. A ''fertile resource island'' occurs in the Mojave (Titus et al. 2002) and other desert ecosystems, where the soil under the canopies of perennial plants typically have greater nitrogen and phosphorous content than soil in the interspace between plants. However, this concept of greater resource availability under canopies does not extend to water; our measurements of soil water showed less soil water under canopies, especially during the fall, winter, and spring.

In conclusion, elevated atmospheric CO_2 may not alter the hydrologic water balance in arid ecosystems. In water-limited environments, plants under current atmospheric CO_2 conditions utilize all available soil water during a year (Anderson et al. 1987, Yoder and Nowak 1999), and results from this study suggest that the perennial vegetation will continue to fully extract soil moisture from the soil profile in a future, high-CO_2 world. Therefore, while transient differences in soil water may occur, we predict that elevated atmospheric CO_2 will not stimulate a long-term increase in soil water in arid ecosystems. Rather, any water saved through decreased leaf conductance will be offset by increases in plant productivity in desert environments.

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