

DE-FG03-00ER63049 FINAL TECHNICAL REPORT

Biotic Processes Regulating The Carbon Balance Of Desert Ecosystems

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EXECUTIVE SUMMARY

This project provided the funding to operate and maintain the Nevada Desert FACE Facility. This support funds the CO₂ system repairs and maintenance, basic physical and biological site information, and personnel that are essential for the experiment to continue. We have continued to assess the effects of elevated CO₂ on three key processes: (1) leaf- to plant-level responses of desert vegetation to elevated atmospheric CO₂; (2) ecosystem-level responses; and (3) integration of plant and ecosystem processes to understand carbon balance of deserts. Our focus is the seminal interactions among atmospheric CO₂, water, and nitrogen that drive desert responses to elevated CO₂ and explicitly address processes that occur across scales (biological, spatial, and temporal). Some key results to date include:

- Elevated CO₂ increases dominance of an exotic annual grass, which in turn could alter the ecology of the Mojave Desert by causing an increase in fire frequency and intensity.
- The increase in primary production in response to elevated CO₂ is greater than that observed in any other ecosystem. However, the magnitude of this increase is strongly and positively related to rainfall inputs to the system for most species.
- Strong, seasonally transient effects of elevated CO₂ on leaf photosynthesis play a major role in this constraint of productivity. Contrary to expectations, phenological patterns of canopy development and of leaf gas exchange were not changed by elevated CO₂.
- We predicted that reduced transpiration rates at elevated CO₂ would result in greater water storage. Reduced stomatal conductance and transpiration have been observed, but soil moisture has not been conserved under elevated CO₂.
- Recruitment of new plants was enhanced under elevated CO₂ during a wet year, but this initial enhancement decreased during the following 3 years of drought conditions.
- Elevated CO₂ has decreased plant-available N and increased gaseous N loss. Isotopic evidence points to altered patterns of microbial activity and plant N acquisition. Greenhouse studies found effects of elevated CO₂ on nutrient uptake kinetics.
- Litter produced in wet years decomposed faster than that produced in a dry year, but elevated CO₂ has had no significant effect on litter decomposition.
- In contrast to the large aboveground productivity response, root production and turnover have not been significantly affected by elevated CO₂ in either wet or dry years.
- Both *Larrea* and *Ambrosia* produce roots with higher specific root length under elevated CO₂, but only *Ambrosia* roots had consistently higher respiration rates. For *Larrea* root respiration, other factors such as root age and soil water availability appear to interact with elevated CO₂.
- Elevated CO₂ has increased CO₂ loss from soils in interspace locations and under *Larrea* canopies, but not under *Ambrosia* canopies. However, the interactive effects of soil temperature and moisture on soil respiration have not been elucidated for these 3 microsite locations.

Clearly, the key results indicated above would not have been possible without the existence of the NDFF (and hence the operations funding), although some of the scientific studies that lead to these results were also supported by other grants.

FINAL TECHNICAL REPORT

Key Research Results

Constraints on primary production and reproduction

Studies designed to ascertain morphological and photosynthetic constraints on primary production of desert plants at elevated CO₂ were initiated in 1997 and continue to date. Perennial plant species that are being studied include the C₃ evergreen shrub *Larrea tridentata*, C₃ drought-deciduous shrubs *Ambrosia dumosa* and *Lycium andersonii*, C₃ winter-deciduous shrub *Krameria erecta*, C₃ perennial grass *Achnatherum hymenoides*, and C₄ perennial grass *Pleuraphis rigida*. 1998 was an extremely wet year characterized by high primary production, whereas 1999-2002 were anomalously dry years. The cumulative increase in new shoot biomass for *Larrea* was significantly higher at elevated CO₂ in 1998, but no significant difference in stem growth occurred between CO₂ treatments in the dry years of 1999-2001 (Smith *et al.* 2000). The deciduous shrub *Ambrosia* also showed substantial new shoot production at elevated CO₂ in the wet 1998, but not in the 2 driest of the 3 subsequent dry years (Hamerlynck *et al.* 2002, Housman *et al.* submitted). The winter-deciduous *Krameria* had a consistent, but not significant, increase (~60%) in shoot production in wet and dry years. We monitored new root production during the same growth period and saw no evidence that plants shifted to new root production in the dry year (see below). Naturally-recruited shrub seedlings showed slightly enhanced survival and gas exchange activity at elevated CO₂, particularly during wet-to-dry transitions (Housman *et al.* 2003). These results taken together indicate that the increase in primary production in response to elevated CO₂ is greater than that observed in any other ecosystem, but the magnitude of this increase is strongly and positively related to rainfall inputs to the system.

Gas exchange measurements strongly suggest seasonally transient responses to elevated atmospheric CO₂, which should constrain ecosystem productivity. First, enhancements in photosynthesis of the perennial plants were more pronounced in wet seasons than during dry periods (Hamerlynck *et al.* 2000b); enhanced photosynthetic rates were also observed for the dominant species of ephemeral plants in 1998 (Huxman & Smith 2001). Second, significant down-regulation of photosynthesis occurred only during wet seasons in *Larrea* (Huxman *et al.* 1998c). In a cross FACE-site comparison, we found the species at the NDFP showed a similar biochemical response to elevated CO₂ as do herbaceous and tree species from more mesic FACE sites. We also found that elevated CO₂ enhances photosynthetic activity of desert perennials under both heat (Huxman *et al.* 1998b, Hamerlynck *et al.* 2000b, Taub *et al.* 2000) and cold (Loik *et al.* 2000) stress conditions.

One of our interests is to determine if the purported water savings attributed to elevated CO₂ translates into increased leaf area retention. We examined morphological versus physiological constraints by carefully monitoring seasonal patterns of photosynthetic gas exchange (including assessments of CO₂-saturated photosynthetic capacity) and leaf area development and loss. The timing of peak canopy development did not change under elevated CO₂, including no observed extension of leaf longevity into the dry season in the deciduous species (Housman *et al.* submitted). Similarly, seasonal patterns in CO₂ assimilation did not change, except for *Larrea*. Therefore, phenological and physiological patterns that characterize Mojave Desert perennials – early season lags in canopy development behind peak photosynthetic capacity, coupled with reductions in late-season photosynthetic capacity prior to reductions in leaf area – were not significantly affected by elevated CO₂.

Annual plants were extensively studied during the wet year (1998), but were all but absent from NDFP in 1999, and were moderately present in 2000-2002. Repetitive harvests in all plots, in a variety of understory conditions, were performed on four dominant annual species: *Bromus madritensis* ssp. *rubens* (invasive grass), *Vulpia octoflora* (native grass), *Eriogonum trichopes* (native dicot), and *Lepidium lasiocarpum* (annual mustard). Native annuals responded to elevated CO₂ with fewer, larger plants, whereas the exotic *Bromus* exhibited both larger plant size and higher plant density at elevated CO₂ (Smith *et al.* 2000). *Bromus* biomass was enhanced in beneath-shrub microhabitats to an even greater extent than in interspaces. Despite much higher seed rain at elevated CO₂, our results from both

controlled-environment and field (FACE) conditions indicate that *Bromus* produces smaller seeds of lower quality (Huxman *et al.* 1998a, 1999b), which in turn produce seedlings with reduced initial growth rates (Huxman *et al.* 1998a, 2001). Results from native annuals, such as *Vulpia*, do not show lower seed quality. Therefore, the interplay between seed rain and seed quality responses to elevated CO₂ are complex and will take multiple generations of plant growth and seed production to determine potential long-term annual plant responses to elevated CO₂.

Fine root growth

The effects of elevated CO₂ on fine root dynamics at the NDFF were measured using 28 minirhizotron tubes under *Larrea tridentata* and *Ambrosia dumosa* shrubs and along systematic transects in each of three ambient CO₂ and three 550 ppm CO₂ FACE plots (Phillips *et al.* 2000). We monitored fine root length production, turnover, and standing crop every 4 weeks in 1998 and 1999. Fine root production peaked in April or May of both years at all tube locations (Fig. 1). Peak fine root standing crop lagged about a month behind peak production.

Peak turnover lagged 1-2 months behind peak standing crop, with maximum turnover during the hot summer months. Rainfall in 1998 was about 3.5 times the normal annual amount, with profuse germination and growth of winter annuals. In contrast, 1999 had only about half the normal annual rainfall, with very little winter precipitation, and an almost complete absence of winter annual plant cover. Peak standing crop for 1999 was only about 60% of peak standing crop for 1998, reflecting poorer soil moisture conditions for root growth and the lack of annuals. There were no consistent differences among CO₂ treatments in fine root standing crop, production, or turnover under *Larrea* or *Ambrosia*. For transect tubes, there were no consistent CO₂ treatment differences in fine root production or turnover; however, fine root standing crop was consistently lower in the elevated CO₂ treatment, with significant differences in June-July 1998, and February-June and October 1999. Other studies at NDFF have found decreased leaf conductance under CO₂ enrichment for several perennials, including *Larrea* (see below). We speculate that higher water use efficiency associated with elevated CO₂ and decreased conductance may allow sufficient water uptake with slightly smaller amounts of fine roots. For tubes under *Larrea*, there was a tendency for a deepening of the root systems under elevated CO₂, with decreases in the 20-40 cm depth class and increases in the 40-60, 60-80, and 80-100 cm depth classes during the wet year of 1998. This trend did not persist into 1999, which was much drier.

Root and soil respiration

Elevated atmospheric CO₂ influences fine root physiology and structure in the two native shrubs of the Mojave Desert, *Larrea tridentata* and *Ambrosia dumosa*. Respiration rates (measured on both root dry weight and root length bases) and specific root length (m g⁻¹) were measured in individual roots during three consecutive but very different hydrologic years at the NDFF. In 2000-01, a year receiving ~75% of precipitation, root respiration rates and specific root lengths were significantly greater with elevated CO₂ in both species. Root respiration rates were generally greater with elevated CO₂ for *Ambrosia* in both a drought year with only ~35% of precipitation (2001-02) and a near-normal precipitation year (2002-2003) (Fig. 2). Results for *Larrea* have been more mixed during the drought year, but because the treatment effects for *Larrea* are consistent within a sampling date, we suspect that plant water status or root age may influence the CO₂ response and are investigating these effects in both field and controlled environment studies. For both species, specific root length is greater with elevated CO₂. Changes in root form and function suggest altered patterns of carbon use with elevated CO₂ in these two Mojave Desert shrubs. In contrast, controlled environment studies have shown no effect of elevated CO₂ on root respiration for grasses (Yoder *et al.* 2000).

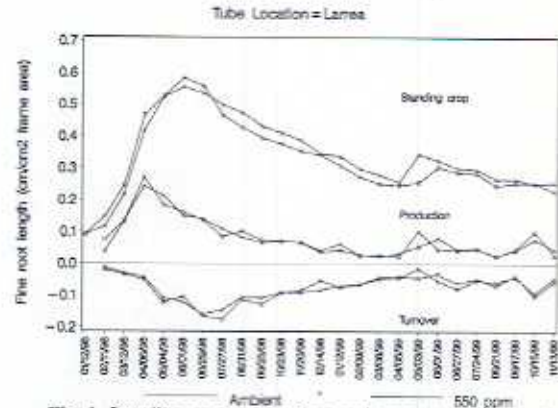


Fig. 1. Standing crop, production, and turnover of fine roots at the NDFF from Jan 1998 through Nov 1999.

Soil respiration provides an integrative measure of belowground respiratory activity and is an essential component of ecosystem carbon budgets. Because increased primary production and greater belowground carbon allocation under elevated atmospheric CO₂ may increase rates of soil respiration, we measured soil respiration using a continuous, open flow gas exchange system. Soil respiration in the interspace among plants showed a strong diurnal pattern in total belowground respiration, combined with slightly higher hourly efflux within elevated CO₂ treatments. Continued measurements during the 1999-2000 season resulted in a range of net daily soil CO₂ flux from -3.10 ± 3.36 to 57.6 ± 59.2 mmol m⁻² d⁻¹. There was a consistent trend toward higher soil CO₂ flux in elevated rings, and this effect was most pronounced when temperatures were high. Small differences in net daily CO₂ flux resulted in substantial differences in total soil CO₂ loss over time: when net daily CO₂ flux was summed over the 1999-2000 season, elevated ring interspace soil averaged approximately 1.4 times the CO₂ loss of ambient ring interspace soil (Fig. 3)

Water balance

A large number of interrelated water balance studies are being conducted at the NDFP because of the importance of water balance and water limitations on ecosystem function in desert ecosystems and because of consistent reports of reduced water use by plants at elevated CO₂. We have assessed plant water status with water potential measurements, stomatal conductance with gas exchange systems, branch-level transpiration with sap-flow gauges, and soil moisture content with TDR probes (to 50 cm depth) and neutron access tubes (to 2 m depth). In concert with photosynthesis, stomatal conductance (g_s) and water potentials were also recorded over both diurnal and seasonal time courses. Elevated CO₂ caused a reduction in g_s (relative to controls) during moist but not dry conditions (Hamerlynck *et al.* 2000b, Nowak *et al.* 2001). Lower g_s during the growing season under elevated CO₂ was associated with higher predawn water potential during subsequent summer months. However, we saw no differences in leaf temperature of these microphyllous species as a function of CO₂ (Nowak *et al.* 2001).

We assessed branch-level water loss of *Larrea* and the leafless shrub *Ephedra nevadensis* using the sap-flow technique to test if lower stomatal conductance scales to lower transpiration at the canopy level (Pataki *et al.* 2000). Sap flow per unit xylem conducting area (J_s) was similar at elevated and ambient CO₂ for *Larrea*, whereas *Ephedra* had substantial reductions in sap flow at elevated CO₂. Results from our shoot growth measurements indicate higher leaf area in *Larrea* at elevated CO₂, which suggests that this increase in leaf area compensates for lower leaf-level transpiration rates at elevated CO₂ in *Larrea* (in a separate experiment, we found no effect of elevated CO₂ on root hydraulic conductance of *Larrea* seedlings; Huxman *et al.* 1999a). Leaf

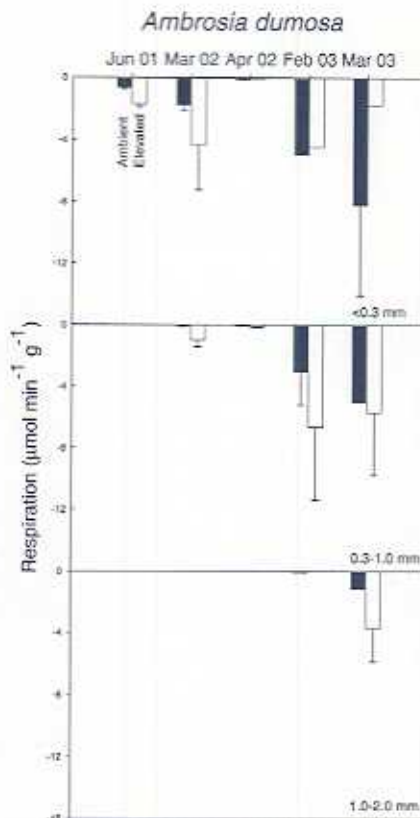


Fig. 2. Field measurements of root respiration during dry (2001 & 2002) and average (2003) years at the NDFP for 3 different size classes of fine *Ambrosia dumosa* roots with diameter <0.3 mm (top), 0.3-1.0 mm (middle), and 1.0-2.0 mm (bottom).

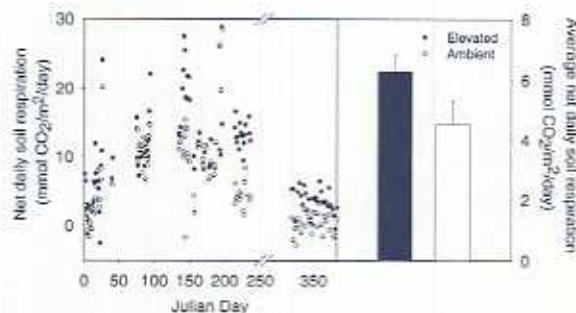


Fig. 3. (A) Net daily soil respiration data from elevated and ambient rings. Each point represents the average of soil respiration data from three rings. Data span the time period from May 1999 through July 2000. (B) Net daily flux data from ambient and elevated rings averaged over 128 days of system operation.

area compensation does not occur in the leafless *Ephedra*, and thus canopy-level transpiration rates are lower at elevated CO₂.

These results from branch-level measurements are supported by our measurements of soil moisture (Nowak *et al.* submitted). Results over four years of soil moisture data indicate no overall significant differences in soil moisture content at any depth. Although we observed treatment differences on some dates during the experiment for soil water in the top 0.5 m depth profile, on only 1 date was soil moisture in the elevated CO₂ treatment significantly greater than that in the ambient CO₂ treatment. For all other dates, either these 2 treatments were not significantly different, or occasionally during wetter time periods, soil moisture was greater under ambient CO₂. Thus, elevated CO₂ did not result in the conservation of soil moisture in the Mojave Desert.

Nutrient cycling

The dominant mechanism of N input into many arid ecosystems is N₂-fixation by biological soil crusts (Evans & Johansen 1999, Evans & Lange 2001), and these crusts have been particularly responsive to global change (Evans *et al.* 2001a). Four dominant crust cover types have been characterized at the NDFP according to the dominant species: (1) moss; (2) the lichen *Collema*; (3) the cyanobacterium *Microcoleus*; and (4) *Collema-Microcoleus*. N₂-fixation by the moss cover type was negligible under both ambient and elevated CO₂ (Billings *et al.* 2003a). Rates of N₂-fixation were greatest for crusts dominated by *Collema*, but activity at elevated CO₂ was only 60% of that observed under ambient conditions. In contrast, nitrogenase activity by crusts dominated by *Microcoleus* increased over 300% under elevated CO₂. The organisms responsible for N₂-fixation in *Microcoleus* crusts are heterotrophic bacteria that live in the cyanobacterial sheaths. The greatest impact of elevated CO₂ on N₂-fixation by biological soil crusts and subsequent ecosystem inputs may be an indirect effect caused by the increase in higher-plant productivity and annual cover that will shade autotrophic lichens. Thus, the dominant source of N input may shift from autotrophic fixation by lichens to heterotrophic fixation by *Microcoleus*-dominated crusts and free-living organisms.

Plant δ¹⁵N values provide a strong indication of a change in nitrogen dynamics caused by elevated CO₂ (Billings *et al.* 2002a). Fractionation does not occur with nitrogen uptake at the low concentrations typical of desert soils (Evans 2001), and no changes have been observed in root dynamics under elevated CO₂ (see above), so the dramatic shift in δ¹⁵N observed with elevated CO₂ must be caused by changes in soil N dynamics. The δ¹⁵N of plant-available nitrogen is a function of many variables, including the δ¹⁵N of substrates used by microbial populations during mineralization, rates of microbial transformations and immobilization, and gaseous loss from inorganic N pools. Changes in any of these factors should alter the δ¹⁵N of plant-available N and subsequently plant δ¹⁵N. Therefore, a significant shift in plant δ¹⁵N is a conclusive indicator of changes in the N cycle.

Plant-available N has been continuously measured at the NDFP since winter 1998/99 using ion-exchange resin bags. Available N has been low because of below-normal precipitation, but significant differences in the amount and relative forms of N have been observed (Billings *et al.* 2002a). Inorganic-N in elevated CO₂ plots was only 60% of that observed under ambient conditions. The relative amount of inorganic-N occurring as nitrate also decreased from 51% under ambient CO₂ to <35% under elevated CO₂. These differences in available N occur despite no differences in net mineralization rates between ambient and elevated CO₂ in long-term laboratory incubations. Thus, the decrease in inorganic-N caused by elevated CO₂ results from decreased rates of gross N mineralization, greater microbial immobilization, an increase in gaseous N loss, or greater plant assimilation. Ongoing experiments suggest that it is probably a combination of each of these factors. We tested the role of C versus N limitations on microbial activity by applying C and N in a full factorial experiment (Schaeffer *et al.* 2003). Application of C increased microbial respiration from 55 to over 300%, and decreased inorganic-N within the soil from 90 to 95% in different spatial locations at the NDFP. This indicates that soil microbes are C-limited and the addition of C increased immobilization.

Potential and actual rates of gaseous N-loss have increased under elevated CO₂. NH₃ loss via volatilization has been measured since May 1999 (Billings *et al.* 2002b). Rates of volatilization were 36% greater under elevated CO₂ during spring of 2000, but differences were not significant on other sampling dates. Elevated CO₂ has resulted in a 200% increase in potential denitrification as assessed by the denitrification enzyme assay. Denitrification has been measured since May 1999 using direct measures of N₂O flux and the acetylene block method to assess total loss. N₂O has yet to be detected on any sampling date.

The initial rate of litter decomposition (first 4 months of exposure) and litter-mediated nutrient cycling assessed over the entire 2000 hydrologic year using mesh bags of representative leaf/twig litter mixtures composited separately for the wet El Niño 1998 hydrologic year and the relatively dry 1999 hydrologic year showed no effect of production under elevated CO₂ on decomposition but a strong effect of year-to-year climate variability (Weatherly *et al.* 2003). Litter produced in the wetter year decomposed almost three times faster (25% of initial mass present in 4 months) than litter produced in the drier year (18%), and this effect was mainly due to differences in species make-up of the litter that was produced in 1998 and 1999. Litter produced in the wetter year contained higher proportions of more rapidly decomposing *Lycium pallidum* and *Lycium andersonii* leaves and lower proportions of slowly decomposing *Larrea tridentata* leaves, than did litter produced in the dry year (which showed the converse pattern in litter species composition). Rates of litter decomposition calculated after 12 months of exposure were still greater for litter produced in the wet year (35 vs. 30%). Greater litter production in the wet year (30 vs. 12 g m⁻²), with further stimulation of production in the wet year in plots maintained under elevated CO₂ (36 vs. 25 g m⁻²), tended to increase the amount of litter (g m⁻² yr⁻¹), C and N decomposed (or released) in ecosystems under elevated CO₂. Elevated CO₂ did result in increased C:N ratios of composited litter mixtures (Weatherly *et al.* 2003) but did not result in significant changes in litter chemical quality when viewed at the individual species level (Billings *et al.* 2003b). Long-term (up to two years of exposure) decomposition measurements continue in all NDFR rings. Overall, elevated CO₂ has had no effect on litter mediated nutrient cycling

System Operations Results

During 2002, the CO₂ concentration of the 3 elevated CO₂ FACE rings averaged ~550 ppm during the time periods when the control system was operational, which was its set-point. CO₂ concentration over the entire time period, including conditional shut-downs of the system control, was ~515 ppm. Approximately 2,200 tons of liquid CO₂ were used. In contrast, the average CO₂ concentration of the 3 ambient FACE rings was ~370 ppm over the last year. Results for 2001 were similar to those in 2002. In February 2003, the source of CO₂ was changed and will provide an opportunity to better understand carbon uptake.

Significant upgrades to the hardware and software that operate the FACE system were incorporated during the grant period. These upgrades have increased system reliability, *e.g.*, significantly less down time, improved alarm systems and quality control checking, more efficient CO₂ distribution enhanced protection against ultraviolet radiation degradation, and have reduced the impact of lightning strikes to the FACE hardware. A fulltime multiport sampler has been established to monitor three-dimensional CO₂ concentrations within a CO₂ treatment ring. An ambient multiport sampler has been established to monitor ambient CO₂ concentrations within the blower control rings. Additional meteorological measurements such as relative humidity, more detailed precipitation information, and PAR (photosynthetically absorbed radiation) have been incorporated into the operating system. Computer systems at NDFR have been networked and now permit Brookhaven National Laboratory to archive operational data on a daily basis.

Cumulative Impacts

NDFF publications and presentations

The following table summarizes the number of publications and professional presentations for the NDFF. Publication citations are given below in the literature citation section.

| | ≤1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | Submitted |
|----------------------------|-------|------|------|------|------|------|------|-----------|
| Publications | 1 | 3 | 7 | 8 | 6 | 3 | 7 | 3 |
| Professional presentations | 9 | 5 | 20 | 13 | 12 | 8 | -- | -- |

Other contributions to research and education

This study has and continues to provide important information to the global change community in general, and more specifically will potentially provide needed inputs for general circulation models (GCMs) in the future. Most of these models have been formulated by atmospheric physicists, but they also need important biological and ecological inputs in order to validate model behavior at the landscape scale. Responses of the terrestrial biosphere to future concentrations of atmospheric CO₂ are increasingly being incorporated into GCMs. These responses generally take the form of increases in carbon assimilation and sequestration as a result of CO₂ fertilization with concurrent reductions in water vapor fluxes due to stomatal closure. Both responses have been frequently reported in growth chamber, glasshouse, and field Free Air CO₂ Enrichment (FACE) studies, but these studies have been predominantly conducted on temperate forest or crop species. At present, GCMs are using predictive functions from mesic plant responses to simulate how arid and semiarid regions will respond to elevated CO₂ and concomitant climate change. Since the Nevada Desert FACE Facility is the only study of its kind in a desert region, we are generating important response functions that will be of considerable use to GCM modelers. Primary among these will be changes in leaf area, species composition, spectral signatures/albedo, soil water balance, and landscape energy balance. As we develop these functions, modelers have already expressed interest in using these data to enhance their models and therefore greatly refine model predictive capabilities for arid and semiarid systems.

The Nevada Desert FACE Facility (NDFF) is a magnet research facility that has been the subject of numerous 'popular science' articles in the Southwest US, which in turn has helped educate the public-at-large about elevated CO₂ and climate, and how increased atmospheric CO₂ and other global change factors might affect deserts. The NDFF has also been extensively visited by student groups, teachers, conference groups, and other types of individuals, again providing an important educational service to both professionals and the lay public in Nevada and in the region.

The NDFF maintains a web site that describes the experiments being conducted, and also provides operations and experimental data for other scientists in biology, ecology, global change research and GCM modeling (http://www.unlv.edu/Climate_Change_Research).

Contributions to human resources development

This study has contributed to human resource development in the following ways:

- provided research opportunities for 52 scientists and 16 postdoctoral fellows
- provided research training for 14 technicians and research associates
- provided research training for 30 graduate students
- provided research training for 73 undergraduate students
- provided research experience and educational materials for 2 high school science teachers;
- provided exposure to science and technology for a variety of constituents - students, pre-college teachers, policymakers, and the general public - through extensive seminars, tours, and public talks by the PI's, staff, and graduate students associated with this study.

NDFP PUBLICATIONS

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