

# Effects of elevated CO<sub>2</sub> on fine root dynamics in a Mojave Desert community: a FACE study

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## Abstract

Fine roots ( $\leq 1$  mm diameter) are critical in plant water and nutrient absorption, and it is important to understand how rising atmospheric CO<sub>2</sub> will affect them as part of terrestrial ecosystem responses to global change. This study's objective was to determine the effects of elevated CO<sub>2</sub> on production, mortality, and standing crops of fine root length over 2 years in a free-air CO<sub>2</sub> enrichment (FACE) facility in the Mojave Desert of southern Nevada, USA. Three replicate 25 m diameter FACE rings were maintained at ambient ( $\sim 370 \mu\text{mol mol}^{-1}$ ) and elevated CO<sub>2</sub> ( $\sim 550 \mu\text{mol mol}^{-1}$ ) atmospheric concentrations. Twenty-eight minirhizotron tubes were placed in each ring to sample three microsite locations: evergreen *Larrea* shrubs, drought-deciduous *Ambrosia* shrubs, and along systematic community transects (primarily in shrub interspaces which account for  $\sim 85\%$  of the area). Seasonal dynamics were similar for ambient and elevated CO<sub>2</sub>: fine root production peaked in April–June, with peak standing crop occurring about 1 month later, and peak mortality occurring during the hot summer months, with higher values for all three measures in a wet year compared with a dry year. Fine root standing crop, production, and mortality were not significantly different between treatments except standing crop along community transects, where fine root length was significantly lower in elevated CO<sub>2</sub>. Fine root turnover (annual cumulative mortality/mean standing crop) ranged from 2.33 to 3.17 year<sup>-1</sup>, and was not significantly different among CO<sub>2</sub> treatments, except for community transect tubes where it was significantly lower for elevated CO<sub>2</sub>. There were no differences in fine root responses to CO<sub>2</sub> between evergreen (*Larrea*) and drought-deciduous (*Ambrosia*) shrubs. Combined with observations of increased leaf-level water-use efficiency and lack of soil moisture differences, these results suggest that under elevated CO<sub>2</sub> conditions, reduced root systems (compared with ambient CO<sub>2</sub>) appear sufficient to provide resources for modest aboveground production increases across the community, but in more fertile shrub microsites, fine root systems of comparable size with those in ambient CO<sub>2</sub> were required to support the greater aboveground production increases. For community transects, development of the difference in fine root standing crops occurred primarily through lower stimulation of fine root production in the elevated CO<sub>2</sub> treatment during periods of high water availability.

*Key words:* belowground standing crop, CO<sub>2</sub>, desert, FACE, fine roots, mortality, production, turn over

*Received 31 March 2005; revised version received 2 September 2005; accepted 7 September 2005*

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## Introduction

The increase in atmospheric CO<sub>2</sub> concentration during the last 250 years is well documented (Keeling & Whorf, 2004) and will continue to accelerate at least for the next several decades (Houghton *et al.*, 2001). This increase will affect plant processes on molecular to ecosystem

levels because of their sensitivity to their surrounding CO<sub>2</sub> concentration (Mooney *et al.*, 1991; Grodzinski, 1992; Bowes, 1993). Knowledge of plant and ecosystem responses to elevated CO<sub>2</sub> is crucial for an understanding of the potential global impacts of this change in the Earth's atmospheric environment (Körner, 2000).

Root systems are critical in providing water and nutrients to plants, and most of the absorptive surface is accounted for by fine roots ( $\leq 1$  mm diameter). As C availability increases in enriched CO<sub>2</sub> conditions, water and nutrient resources will more likely limit production than C. Increased photosynthesis under elevated CO<sub>2</sub> is often accompanied by increased fine root biomass (Rogers *et al.*, 1994; Curtis & Wang, 1998). Such larger root systems often display increased rates of production and mortality on an individual plant basis or areal basis (Pregitzer *et al.*, 2000; Wan *et al.*, 2004), although turnover relative to the size of the root system may not necessarily be changed (Pritchard *et al.*, 2001a). While increased root mass implies greater allocation of C belowground that can facilitate plant resource acquisition, it may not necessarily increase the root:shoot ratio (Canadell *et al.*, 1996; Tingey *et al.*, 2000). In a review of CO<sub>2</sub> enrichment studies, Stulen & den Hertog (1993) found that increased root:shoot ratios, while not always observed, were most likely to occur where water and nutrients are limiting, allowing the plant to explore a greater soil volume to acquire these resources. Water and nutrient limitations are two conditions which characterize deserts. Deserts have also been hypothesized to be the terrestrial ecosystem in which the greatest increases in primary production would occur with rising CO<sub>2</sub>, because of increases in water-use efficiency (Strain & Bazzaz, 1983; Melillo *et al.*, 1993). The importance of understanding responses to increasing CO<sub>2</sub> in deserts is underlined further by their large global extent, which is steadily increasing (Dregne, 1991).

There are a number of technical difficulties with realistic exposures of plants to elevated CO<sub>2</sub> to study their responses, and in particular belowground responses, which are more difficult to observe. Free air CO<sub>2</sub> enrichment (FACE) facilities have been developed to eliminate potential artifacts because of enclosure in small chambers, and to allow CO<sub>2</sub> exposure studies to take place in intact ecosystems with mature plants rather than in simplified communities with small plants such as seedlings (Hendrey, 1993). Minirhizotrons have become an important tool for nondestructive study of plant roots as they allow repeated observation and measurement of large numbers of individual roots to track their production, growth, and mortality (Johnson *et al.*, 2001). In this study, we used minirhizotrons in a FACE facility to address the following hypotheses about

fine root responses to elevated CO<sub>2</sub> in a desert environment:

1. Fine root length standing crop will increase, because increased C availability and/or water-use efficiency will result in greater plant size and possibly higher root:shoot ratios.
2. Rates of fine root production and mortality (length per unit time) will increase because of the increased size of the fine root systems.
3. These responses will be greater for an evergreen shrub (*Larrea tridentata*) than for a drought-deciduous shrub (*Ambrosia dumosa*), because of more continuous exposure of leaves (the primary site of CO<sub>2</sub> absorption) to higher CO<sub>2</sub> concentrations.

## Methods

### Study site

The study site is at the Nevada Desert FACE Facility (NDFF), located at 36°49'N, 115°55'W in the Mojave Desert of southern Nevada at the US Department of Energy's Nevada Test Site (Fig. 1). It is situated at ~960 m elevation in the middle of a broad bajada (alluvial fan) along the southern end of Frenchman Flat. The soil is an Aridosol derived from calcareous alluvium with textures of the <2 mm fraction ranging from loamy sands in the shallow A1 horizon (0–0.16 m) to coarse sands in the subsoil horizons. With the exception of the surface soil horizon, the <2 mm fraction is structureless. The rock content is variable but often quite high. The soil surface is a mosaic of plants and their litter and of exposed soil features. Two prominent soil features are a 'desert pavement', which consists of exposed rocks where the fine soil particles have been washed or blown away, and a well-developed biological soil crust, which consists of lichens, mosses, and other autotrophic microorganisms that grow near the soil surface (Belnap & Lange, 2001). The vegetation of the site is characteristic of the northern Mojave Desert and is dominated by two xerophytic shrubs: evergreen *Larrea tridentata* (creosote bush) and drought-deciduous *Ambrosia dumosa* (bur-sage). Other important plants include the shrubs *Lycium andersonii*, *Krameria parviflora*, and *Ephedra nevadensis*, and the native perennial grasses *Pleuraphis rigida* and *Achnatherum hymenoides*. The introduced annual grass *Bromus madritensis* ssp. *rubens* is also present, as well as a variety of annual and perennial herbs.

Six 25 m diameter FACE plots were used in this study. The plots are surrounded by a plenum pipe, from which thirty-two 2 m tall vertical PVC pipes release air (Jordan *et al.*, 1999). Three of these six plots are fumigated with



**Fig. 1** Free-air CO<sub>2</sub> enrichment plots at NDFF. The short white tubes are insulated caps covering the minirhizotron tubes. (Photo taken by Travis Huxman.)

ambient air ( $\sim 370 \mu\text{mol mol}^{-1} \text{CO}_2$ ), while the other three are treated with CO<sub>2</sub>-enriched air to maintain a target concentration of  $550 \mu\text{mol mol}^{-1}$ . This FACE technology design was developed by the Brookhaven National Laboratory (Hendrey, 1993).

#### *Minirhizotron installation*

Within each of the six 25 m diameter plots, twenty-eight 57 mm OD polycarbonate minirhizotron tubes were installed between July and September 1998 at a 30° angle from vertical and to a vertical depth of 1 m. The tubes were installed from a suspended platform to avoid soil compaction from trampling (Phillips *et al.*, 2000). The tubes were placed to sample three different microsites: *Larrea* shrubs, *Ambrosia* shrubs, and systematic transects through the plant community which primarily sampled shrub interspaces. Four *Larrea* and four *Ambrosia* shrubs were selected in each plot (Fig. 2). Under each of these shrubs, one minirhizotron tube was installed so that the end of the tube at 1 m depth was directly under the center of the shrub. Another tube was installed parallel to this, with the end of the tube at 1 m depth directly under the edge of the shrub canopy. Where the radius of the shrub canopy was <30 cm, the second tube was installed 30 cm away from the first tube. Additionally, four tubes were installed along each of three radial transects in each plot. Where possible, these tubes were installed at 2 m intervals along the

community transects. However, the locations of the tubes had to be shifted sometimes to avoid crushing shrubs with the suspended installation platform or because large rocks prevented tube installation. Given the low canopy cover in this desert vegetation, community transect tubes are located primarily within shrub interspaces.

Ideally, minirhizotron installation would have occurred before the onset of fumigation (April 28, 1997) to establish pretreatment comparisons among the FACE plots. This was not possible as construction of the suspended platforms delayed the initiation of minirhizotron installation until about 10 weeks after this time. However, complete pretreatment censuses of the above-ground vegetation in each FACE plot confirmed there were no significant differences in evergreen shrubs, deciduous shrubs, perennial grasses, cacti, perennial forbs, or total plant density among treatments (Jordan *et al.*, 1999). The extensive replication of minirhizotron tubes within plots minimizes the possibility of spurious differences because of within-plot sampling error.

#### *Fine root imaging and analysis*

After a 4–6 months settling period following minirhizotron installation, video images were taken along the top side of the tubes in the FACE plots every four weeks between January 12, 1998 and January 10, 2000 using a minirhizotron camera system (Bartz Technology Corp.,

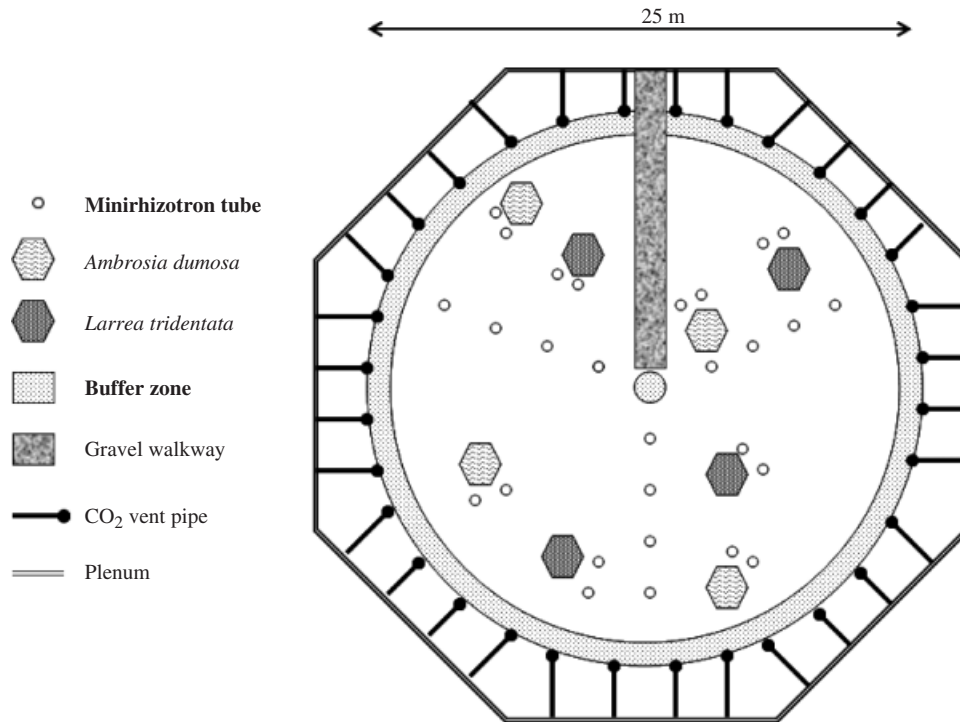


Fig. 2 Minirhizotron placement in the free-air CO<sub>2</sub> enrichment (FACE) plots. Each plot had 8 *Ambrosia* tubes, 8 *Larrea* tubes, and 12 community transect tubes.

Santa Barbara, CA, USA). A mechanical advancing camera handle was used that insured co-registration of video images at multiple sample times (Johnson & Meyer, 1998). The image frame area was  $14.3 \times 10.6 \text{ mm}^2$ . Images were taken at increments of 4 cm vertical depth between the surface and 1 m depth. The images were processed using MSU ROOTs software (Enslin *et al.*, 1994). Each root was given a unique identification number, and its length and width were determined by tracing with the computer mouse. As described by Johnson *et al.* (2001), error checking computer programs were used to examine for 14 different types of classification, measurement, and recording errors for each image at a single sample time and across sample times. In addition, independent re-analyses of six tubes were performed on five occasions to determine the precision of the root data from the images. These demonstrated >99% overlap in individual root presence, and precision (mean absolute difference) in length and width measurements of 0.6 and 0.04 mm, respectively, indicating the high quality and repeatability of the root measurements.

This process provided measurements of root number and length per unit frame area ( $\text{m m}^{-2}$ ) at repeatable locations along the minirhizotron tubes. Measurements were pooled over all tubes within each FACE plot and microsite type. At each sampling time, fine root standing crop was measured by the length of all fine roots

present, production over the 4-week sampling interval was measured by the length of newly appeared roots plus length extension of roots already present, and mortality over the sampling interval was measured by the length of disappeared roots plus length decreases of roots already present. Over the 2-year course of the study, >100 000 video images were analyzed and the appearance, growth, and the fate of 23 634 individual roots were tracked, totaling 125 679 root observations and measurements.

Repeated-measures analysis of variance (ANOVA) in PROC GLM of SAS (SAS-Institute, 1999) was used to test for effects of CO<sub>2</sub>, time, and CO<sub>2</sub> × time interactions on fine root standing crop, production, and mortality to 1 m depth in each of the three microsites (*Ambrosia*, *Larrea*, and community transect). Similarly, repeated-measures ANOVAs were performed to test for effects of microsite, time, and microsite × time interactions on standing crop, production, and mortality within each of the CO<sub>2</sub> treatments. Specific time contrasts comparing the two years (sample periods 1/12/98–1/12/99 and 1/13/99–1/10/00) were also performed. Because the FACE plots were the actual experimental units to which the CO<sub>2</sub> treatments were applied, the ANOVAs were performed on plot means for each variable and microsite. The Greenhouse–Geisser adjustment was used to account for possible nonsphericity in the repeated-

measures ANOVAS (SAS-Institute, 1999). In addition, mean annual fine root standing crop ( $\text{m m}^{-2}$  frame area) and cumulative production and mortality ( $\text{m m}^{-2}$  frame area  $\text{year}^{-1}$ ) were calculated for each of the two years (periods of 1/12/98–1/12/99 and 1/13/99–1/10/00). We calculated a turnover index ( $\text{year}^{-1}$ ) by dividing cumulative mortality by mean annual standing crop for each year, and used repeated-measures ANOVA to test for effects of year and CO<sub>2</sub> on turnover for each microsite, and year and microsite for each CO<sub>2</sub> treatment.

#### Test for effects of minirhizotrons on root density

To determine whether the presence of a minirhizotron tube affected the fine root density in the immediate vicinity, we excavated 14 additional minirhizotron tubes outside the FACE plots each year in May of 1998, 1999, and 2000. These tubes had been installed in May 1997 to a depth of 1 m. A back-hoe was used to dig a trench next to each tube, and the soil was carefully removed to expose the side of the tube along the trench wall. Five bulk soil samples were collected along the top surface of each tube at various depths using a  $44 \times 44 \times 92 \text{ mm}^3$  open-sided metal box with sharpened edges that was driven into the trench wall. Additional samples were collected at 5.4, 16.2, 32.4, and 54.0 cm horizontal distances away from the minirhizotron tubes to test for effects of the tube presence on fine root density. Fine roots were wet sieved from these bulk soil samples, dried, and weighed. To eliminate the contribution of any inorganic material clinging to the roots, the dried roots were ground and combusted in a muffle furnace at 450 °C for 4 h, and the ash weight was

subtracted from the original weight to give ash-free root dry weight.

#### Results

The roots observed (23 634 individual roots) were very fine, with >90% of the 125 679 root observations indicating a diameter <0.3 mm (Fig. 3). Fine root length production peaked in April, May, or early June of both years at all three microsities (Fig. 4). Peak fine root standing crop lagged about a month behind peak production, with peak values ranging from ~30 to 60  $\text{m m}^{-2}$  frame area. Peak mortality lagged 1–2 months behind peak standing crop, with maximum mortality during the hot summer months. 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 in 1999. Calendar year 1998 had 300 mm of rainfall (Fig. 5), over twice the normal amount, with profuse germination and growth of winter annuals; in contrast, 1999 had 94 mm of rainfall, about two-thirds of normal, with very little winter precipitation, which led to an almost complete absence of winter annual plant cover (Smith *et al.*, 2000). A smaller peak of fine root production occurred after a sizable rain event in late September during this dry year (Figs 4 and 5).

The CO<sub>2</sub> repeated-measures ANOVAS showed significant ( $P < 0.05$ ) effects of time, but no significant CO<sub>2</sub> × time interactions for fine root length standing crop, production, and mortality at all three microsities (*Ambrosia*, *Larrea*, community transect) (Table 1). Contrasts between years showed that standing crop, production, and mortality were significantly greater in the

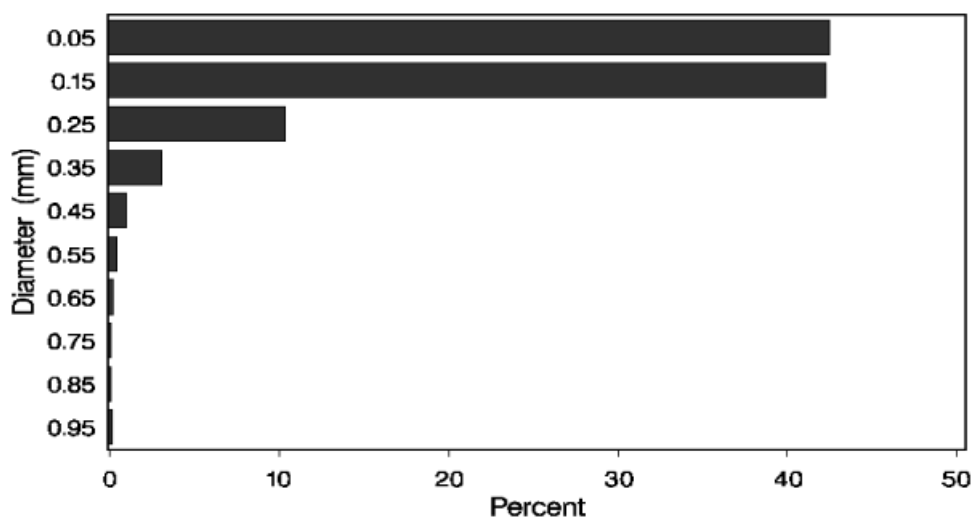
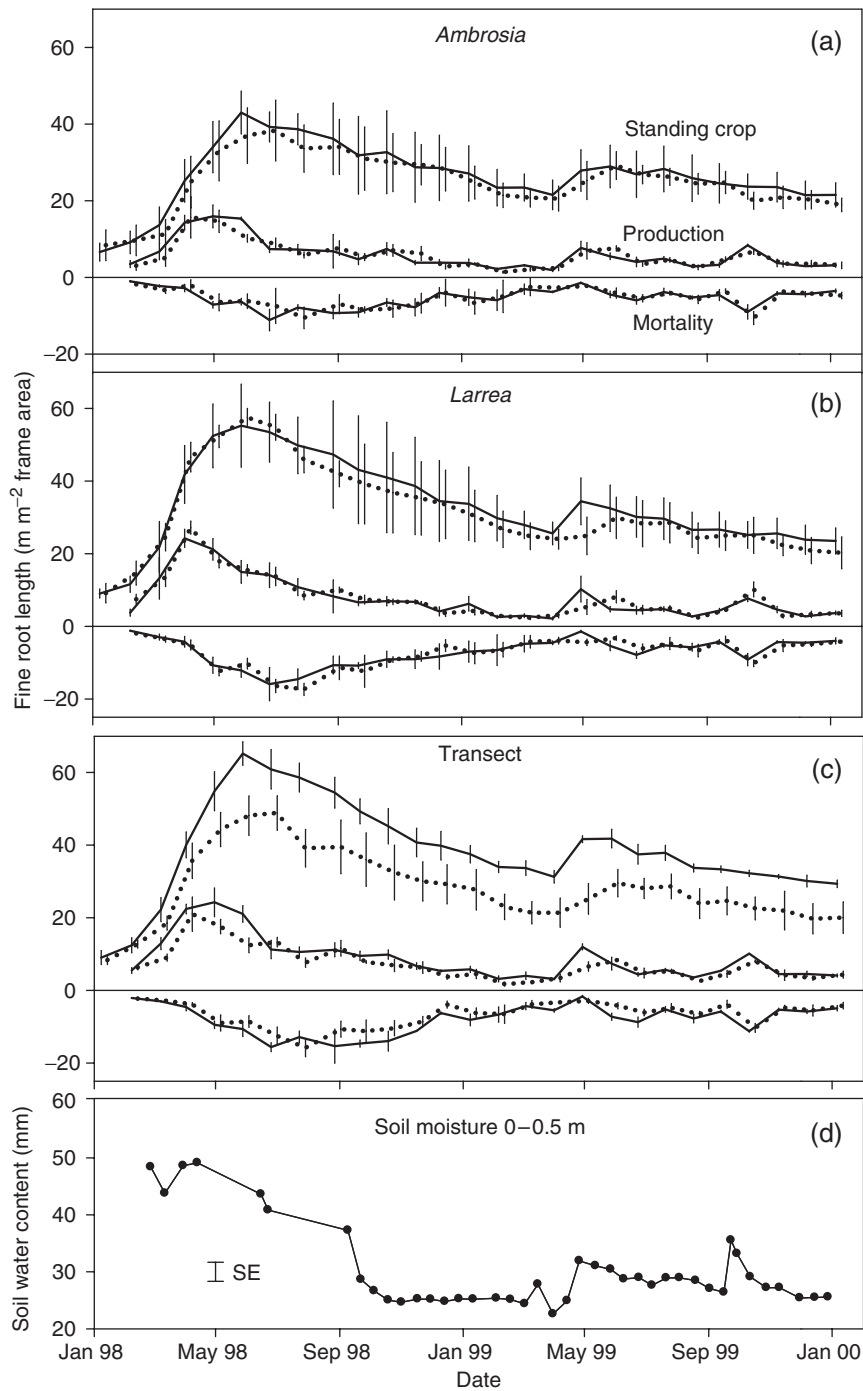


Fig. 3 Distribution of fine root diameter measurements (125 679 observations of 23 634 individual roots), over the 2-year observation period.



**Fig. 4** Fine root standing crop, production, and mortality ( $\text{m m}^{-2}$  frame area) for the three microsites: (a) *Ambrosia*, (b) *Larrea*, and (c) community transect. The ambient  $\text{CO}_2$  treatment ( $\sim 370 \mu\text{mol mol}^{-1}$ ) is shown with a solid line and the elevated  $\text{CO}_2$  treatment ( $550 \mu\text{mol mol}^{-1}$ ) is shown with a dotted line. Errors bars show the mean  $\pm$  standard error for the 3 free-air  $\text{CO}_2$  enrichment plots in each treatment. Sampling took place on the same dates for both  $\text{CO}_2$  treatments, but they have been offset  $\pm 3$  days to avoid overlap of error bars on the graph. (d) Soil water content (mm) in the top 0.5 m as measured by TDR probes (see Nowak *et al.* (2004b) for details). For simplicity, only the ambient  $\text{CO}_2$  treatment is shown here as Nowak *et al.* (2004b) found no significant  $\text{CO}_2$  treatment effect in soil moisture.

wet year (1998) than the dry year (1999) at all microsites, except for *Ambrosia* standing crop where the less dramatic difference was nearly significant ( $P = 0.063$ , Table 1). There were no significant differences among CO<sub>2</sub> treatments in fine root length standing crop, production, or turnover under *Ambrosia* or *Larrea* (Fig. 4a,b; Table 1). For community transect tubes, fine root standing crop was significantly lower ( $P = 0.047$ ) in elevated

CO<sub>2</sub>; however, there were no consistent CO<sub>2</sub> treatment differences in fine root length production or mortality (Fig. 4c, Table 1).

The microsite repeated-measures ANOVAs also found significant effects of time, but no significant effects of microsite or microsite × time interactions on standing crop, production, or mortality of fine root length at either CO<sub>2</sub> level (Table 1). Contrasts between years indicated significantly greater standing crop, production, and mortality in the wet year than the dry year for both CO<sub>2</sub> treatments, except for standing crop in the ambient CO<sub>2</sub> treatment, which was nearly significant ( $P = 0.064$ , Table 1).

Cumulative fine root production and mortality both exceeded mean standing crop for each of the 2 years (Table 2), indicating dynamic root systems. Fine root turnover indices (annual cumulative mortality/mean standing crop) ranged from 2.33 (SE = 0.06) to 3.17 (SE = 0.26) year<sup>-1</sup> (Table 2), corresponding to average fine root life spans of 4–5 months. This measure of relative fine root turnover was significantly higher ( $P = 0.034$ ) in elevated CO<sub>2</sub> compared with ambient CO<sub>2</sub> only for community transect tubes. The index was consistently smaller in the dry year 1999, which

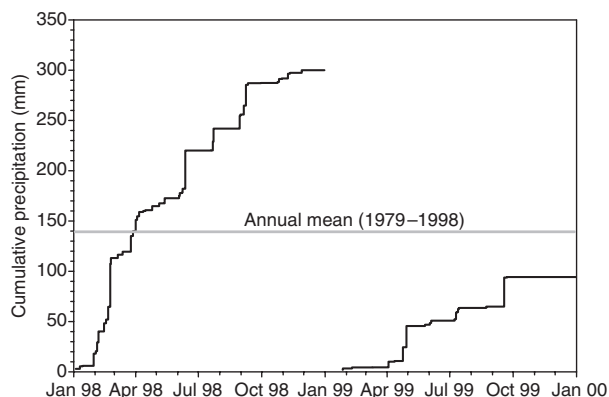


Fig. 5 Cumulative precipitation for calendar years 1998 and 1999 at the Nevada Desert free-air CO<sub>2</sub> enrichment facility.

Table 1 Summary of repeated measures analyses of variance for effects of time, CO<sub>2</sub> (370, 550 μmol mol<sup>-1</sup>) and microsite (*Ambrosia*, *Larrea*, community transect) on fine root standing crop, production, mortality, and annual turnover index

Source	Standing crop – P value			Production – P value			Mortality – P value		
	<i>Ambrosia</i>	<i>Larrea</i>	Community transect	<i>Ambrosia</i>	<i>Larrea</i>	Community transect	<i>Ambrosia</i>	<i>Larrea</i>	Community transect
Time	<b>0.0023</b>	<b>0.0020</b>	<b>0.0003</b>	<b>0.0003</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0038</b>	<b>0.0022</b>	<b>0.0008</b>
Time × CO <sub>2</sub>	0.90	0.70	0.45	0.56	0.48	0.22	0.53	0.76	0.56
CO <sub>2</sub>	0.81	0.85	<b>0.047</b>	0.86	0.97	0.17	0.94	0.90	0.18
Year	0.063	<b>0.011</b>	<b>0.0076</b>	<b>0.0036</b>	<b>0.0018</b>	<b>0.0002</b>	<b>0.0054</b>	<b>0.0007</b>	<b>0.0043</b>

Source	Standing crop – P value		Production – P value		Mortality – P value	
	CO <sub>2</sub> = 370	CO <sub>2</sub> = 550	CO <sub>2</sub> = 370	CO <sub>2</sub> = 550	CO <sub>2</sub> = 370	CO <sub>2</sub> = 550
Time	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0001</b>	<b>0.0001</b>
Time × microsite	0.53	0.35	0.31	0.25	0.53	0.58
Microsite	0.33	0.57	0.21	0.24	0.22	0.20
Year	0.064	<b>0.020</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0032</b>	<b>0.0005</b>

Source	Annual turnover index – P value			Annual turnover index – P value		
	<i>Ambrosia</i>	<i>Larrea</i>	Community transect	Source	CO <sub>2</sub> = 370	CO <sub>2</sub> = 550
Year	0.14	0.09	0.27	Year	<b>0.0047</b>	0.12
Year × CO <sub>2</sub>	0.99	0.67	0.76	Year × microsite	0.81	0.99
CO <sub>2</sub>	0.27	0.38	<b>0.034</b>	Microsite	0.73	0.93

Time represents the 27 four-week sample times (no production or mortality data for the first sample time), while year represents specific contrasts between 13 sample times (periods of 1/12/1998–1/12/1999 vs. 1/13/1999–1/10/2000). Statistically significant ( $P < 0.05$ ) results are shown in bold type.

**Table 2** Summary of fine root (0–1 mm diameter) annual standing crop, production, and mortality ( $\text{m m}^{-2}$  frame area), and turnover index ( $\text{year}^{-1}$ )

Period	CO <sub>2</sub> (ppm)	Microsite	Mean standing crop ( $\text{m m}^{-2}$ )	Cumulative production ( $\text{m m}^{-2}$ )	Cumulative mortality ( $\text{m m}^{-2}$ )	Turnover index ( $\text{year}^{-1}$ )
1/12/98–1/12/99	370	<i>Ambrosia</i>	29.8 (6.2)	100.9 (16.9)	80.4 (11.7)	2.77 (0.20)
		<i>Larrea</i>	40.4 (10.2)	141.2 (29.4)	116.6 (20.4)	2.99 (0.24)
		Community transect	44.7 (1.9)	156.3 (8.4)	127.8 (12.2)	2.87 (0.28)
	550	<i>Ambrosia</i>	28.1 (5.8)	95.8 (16.6)	78.9 (12.9)	2.88 (0.19)
		<i>Larrea</i>	39.5 (5.6)	142.5 (8.0)	120.9 (3.6)	3.16 (0.35)
		Community transect	34.0 (4.3)	128.0 (16.0)	106.1 (10.6)	3.17 (0.27)
1/13/99–1/10/00	370	<i>Ambrosia</i>	24.7 (4.6)	53.8 (7.3)	59.4 (11.5)	2.40 (0.04)
		<i>Larrea</i>	27.8 (4.7)	57.7 (6.8)	67.7 (13.7)	2.41 (0.08)
		Community transect	34.5 (0.9)	72.0 (3.5)	80.2 (0.5)	2.33 (0.06)
	550	<i>Ambrosia</i>	23.0 (2.7)	52.7 (5.5)	58.5 (8.7)	2.52 (0.13)
		<i>Larrea</i>	25.0 (4.4)	58.0 (7.7)	68.1 (10.4)	2.77 (0.22)
		Community transect	23.9 (3.7)	59.4 (6.0)	67.0 (9.2)	2.85 (0.33)

Values are means (SE) for three FACE plots. FACE, free-air CO<sub>2</sub> enrichment.

lacked winter annuals; this difference was significant for ambient CO<sub>2</sub> ( $P = 0.0047$ ), but not quite significant for elevated CO<sub>2</sub> ( $P = 0.12$ , Table 1).

We did not find any evidence that the minirhizotron tubes influenced fine root density. In our excavated tubes, bulk soil samples adjacent to the tubes did not significantly differ in fine root biomass density (ash-free dry weight per volume of soil) from samples 5.4–54.0 cm away.

## Discussion

### Temporal patterns

The seasonal patterns of fine root length standing crop, production, and mortality were similar across microsites, CO<sub>2</sub> treatments, and years (Fig. 4). There was a rapid rise in fine root production and standing crop during the first several months of 1998, which are likely a result of germination of winter annuals in the favorable moisture conditions for that year, as well as rapid root growth in perennials. Part of this early pattern could be the result of recovery from the disturbance of minirhizotron installation (Joslin & Wolfe, 1999), although the tubes had 4–6 months to recover before the first images were taken. Also, levels of fine root length standing crop, production, and mortality were higher in the wet year of 1998 than the dry year of 1999 (Fig. 4), as would be expected in a water-limited system. Additional fine root production pulses occurred in May–June and October 1999 in all microsites (Fig. 4a–c) after rainfall increased soil moisture levels (Fig. 4d). The ambient CO<sub>2</sub> production peak occurred in May 1999, while the elevated CO<sub>2</sub> peak was delayed until early June (Fig. 4a–c). All three microsites also exhibited

a peak in fine root mortality at the same time in October 1999, which counteracted the root production pulse.

### Effects of elevated CO<sub>2</sub>

Based on our results, we reject the hypotheses of increasing fine root standing crop and production in response to elevated atmospheric CO<sub>2</sub> concentration for this desert system. Indeed, fine root standing crop was significantly reduced by elevated CO<sub>2</sub> for the community transects. In glasshouse studies, Yoder *et al.* (2000) found no significant effect of elevated CO<sub>2</sub> (1000 ppm) on root surface area for three Mojave Desert grass species. At NDFF, elevated CO<sub>2</sub> was associated with greater aboveground production (Smith *et al.*, 2000; Nowak *et al.*, 2004a; Housman *et al.*, 2005). Increasing aboveground production without a concomitant increase in root length implies a decreased ecosystem root:shoot ratio under elevated CO<sub>2</sub> conditions. Previous studies on responses of root:shoot ratios to elevated CO<sub>2</sub> have had mixed results, demonstrating increases, no change, and occasionally decreases (Curtis & Wang, 1998; Arnone *et al.*, 2000; Tingey *et al.*, 2000).

The repeated-measures ANOVA found significant reductions in fine root standing crop in response to elevated CO<sub>2</sub> for the community transects over the 2-year period, but no statistically significant differences in production or mortality. However, some differences in one or both of these processes had to occur to produce the differences in standing crop. Compared with ambient CO<sub>2</sub>, cumulative reductions in fine root production in the elevated CO<sub>2</sub> treatment during March–June of 1998 were responsible for the initial development of the fine root standing crop difference that was then maintained throughout the study (Fig. 4c). This occurred

during a time of high soil moisture (Fig. 4d) in this very wet year, when root growth was rapid. Fine root production pulses also occurred in May and October 1999 after precipitation events increased soil moisture levels (Fig. 4c,d). In the community transects, production responses were also lower at these times for the elevated CO<sub>2</sub> treatment compared with ambient. Thus, it appears that at the community level, elevated CO<sub>2</sub> led to lower responsiveness of fine root production at times of high water availability, ultimately resulting in decreased fine root standing crop.

As with many elevated CO<sub>2</sub> studies, decreased stomatal conductance and increased water-use efficiency at the leaf level were observed in a number of species at NDFP (Huxman & Smith, 2001; Nowak *et al.*, 2001; Hamerlynck *et al.*, 2002a; Naumberg *et al.*, 2003). We suggest that these physiological changes may allow similar (under *Larrea* and *Ambrosia* shrubs) or significantly smaller (along community transects) fine root systems to provide sufficient water uptake to support increased aboveground plant production in elevated CO<sub>2</sub> compared with ambient conditions (Nowak *et al.*, 2004a). For example, Hamerlynck *et al.* (2002a) found that elevated CO<sub>2</sub> moderated whole-plant water use in *Lycium andersonii* even when leaf growth was stimulated. This is consistent with the lack of differences in soil moisture between the ambient and elevated CO<sub>2</sub> treatments, even though aboveground production was higher in the latter, as reported by Nowak *et al.* (2004b).

Our results also lead to rejection of the hypothesis of decreased fine root mortality (length per unit time) in response to elevated CO<sub>2</sub>. However, the turnover index, which expresses fine root mortality relative to standing crop, was significantly higher in elevated compared with ambient CO<sub>2</sub> for community transect tubes, which largely sampled shrub interspaces (Tables 1 and 2). The increase in this ratio was driven by significantly lower fine root standing crop ( $\text{m m}^{-2}$  frame area) as discussed above, rather than increased annual mortality ( $\text{m m}^{-2}$  frame area year<sup>-1</sup>), which was unchanged by elevated CO<sub>2</sub> (Fig. 4). This higher relative turnover rate corresponds to shorter fine root life span under elevated CO<sub>2</sub> conditions. Eissenstat *et al.* (2000) predicted that elevated CO<sub>2</sub> may be associated with longer root life spans under certain conditions, and some studies have observed this response (Arnone *et al.*, 2000). This prediction was from a cost-benefit model for maximizing efficiency of resource acquisition by roots, and assumed that elevated CO<sub>2</sub> would result in reduced tissue N concentrations and root maintenance respiration. However, neither root N nor root respiration were reduced by CO<sub>2</sub> enrichment at our site (Apple *et al.*, 2005, personal communication), and thus, no increase in fine root life span would be expected under this model.

#### *Microsite comparisons*

As neither *Larrea* nor *Ambrosia* microsites showed any significant differences in fine root production, standing crop, or mortality under elevated CO<sub>2</sub>, we also reject the hypothesis of a greater CO<sub>2</sub> effect on roots of evergreen vs. drought-deciduous shrubs. This effect was expected because of the longer exposure of evergreen shrub leaves to atmospheric CO<sub>2</sub>. The fact that elevated CO<sub>2</sub> had no effect on fine root standing crop for the tubes under *Larrea* and *Ambrosia* shrubs, but led to a significant decrease for the community transect tubes that largely sample shrub interspaces, is interesting. Other microsite factors may play a role in determining the balance between increased aboveground biomass and increased water-use efficiency under elevated CO<sub>2</sub>, and the root systems required to meet these needs. Smith *et al.* (2000) reported that aboveground biomass increases of desert annuals to elevated CO<sub>2</sub> at our research site were greater in shrub canopy microsites than in low-fertility shrub interspaces. Titus *et al.* (2002) characterized these different microsites and found that litter, soil organic matter, and mineral nutrients (except Ca) were higher in shrub microsites than in interspaces. It is possible that greater water-use efficiency makes reduced fine root systems sufficient to provide resources for modest CO<sub>2</sub>-induced increases in aboveground production in interspaces, but not for higher fertility shrub microsites where aboveground production is more enhanced. For both ambient and elevated CO<sub>2</sub>, Nowak *et al.* (2004b) found that areas under shrub canopies had lower soil moisture in the top 20 cm than did interspaces, which indicates greater evapotranspiration in these fertile soil islands. While this argument about the relative sizes of increases in water-use efficiency and biomass may explain why fine root standing crop was somewhat smaller under elevated CO<sub>2</sub> in the community transects, the temporal development of this difference appears to arise from less stimulation of fine root production during growth pulses in times of high water availability, as discussed earlier.

All three microsites had significantly higher fine root standing crop, production, and mortality in the wetter year (Table 1, Fig. 4; *Ambrosia* standing crop was nearly significant,  $P = 0.063$ ). Dramatic increases in aboveground production for *Larrea* and *Ambrosia* in higher rainfall years have been observed at the Nevada Test Site previously (Turner & Randall, 1989) and in the current study (Housman *et al.*, 2005), which were considerably larger than those that we observed belowground. It may be that greater availability of water for root uptake allows increased aboveground production with a more modest increase in fine roots. Compared with *Larrea*,

*Ambrosia* exhibited a more muted response to wetter conditions both in aboveground shoot production (Housman *et al.*, 2005) and in fine root responses (Table 1, Fig. 4). *Ambrosia* drops its leaves and becomes dormant in dry conditions (drought evasion), which may slow the response time to increased water availability compared with the evergreen *Larrea*, which is highly drought resistant and remains photosynthetically active even in very dry conditions (Smith *et al.*, 1997; Hamerlynck *et al.*, 2002b).

Information on the lateral distribution of roots in deserts has been reported in the literature for almost a century (Cannon, 1911), although the data are spotty and the methods variable. Many studies focused on shrubs and excavated individual root systems to determine their lateral extent (Brisson & Reynolds, 1994). Some authors concluded that desert root systems are laterally extensive enough to fill the entire horizontal area and/or overlap, while others concluded there is considerable space between root systems (Barbour, 1973). Competition has been inferred by the correlation of shrub size with interplant distances and increasing regularity of spacing (Phillips & MacMahon, 1981) and by changes in water potential in response to removal of neighbors (Fonteyn & Mahall, 1978). While our data do not allow mapping of root systems to address lateral extent, overlap, and competition, it is notable that we found fine root length in the community transects, which largely sampled shrub interspaces, to be as high as under *Larrea* and *Ambrosia* shrubs. We could not reliably distinguish between fine roots of different species, including grasses and forbs, so these results do not necessarily address the degree of overlap between shrub root systems as previous excavation studies attempted to do. However, the distribution of root diameters we observed extended to very fine roots, which are likely to have been greatly undersampled when individual shrub root systems were excavated. Thus, our results indicate that for the community as a whole, very fine roots are extensively distributed in shrub interspaces as well as under shrub canopies, even though interspaces had significantly lower nutrient contents than shrub islands (Titus *et al.* 2002). Similarly, Yoder & Nowak (1999) found that for *Larrea*, *Ambrosia*, and two other shrub species, annual water extraction from beneath plant canopies was not significantly different than from shrub interspaces at the Nevada test site.

### Implications

The lack of significant increases in fine root standing crop, production, and mortality because of increased CO<sub>2</sub> is a surprising result, as is the significant decrease

in standing crop for community transects. Summarizing results for a number of FACE studies, Nowak *et al.* (2004a) reported that both aboveground and belowground production generally increased with CO<sub>2</sub> enrichment in bog, forest, and grassland ecosystems. For a FACE system in a *Pinus taeda* forest, results varied somewhat depending on the methods of analysis and the period of time covered. Using repeated-soil coring, Matamala & Schlesinger (2000) reported no significant differences because of CO<sub>2</sub> in fine root production, but an increase in live fine root standing crop biomass. With minirhizotrons, Pritchard *et al.* (2001b) found increases in root length, production, and mortality with elevated CO<sub>2</sub> that were not statistically significant, but no change in relative turnover. In an analysis of net ecosystem production (NEP) over 4 years at the same site, Hamilton *et al.* (2002) reported an 8% increase in fine root increment in the elevated CO<sub>2</sub> treatment. For a FACE system in a *Liquidambar styraciflua* forest, Norby *et al.* (2004) found that elevated CO<sub>2</sub> caused increased fine root production and peak standing crop after a delay of 2 years; fine root mortality increased with elevated CO<sub>2</sub> to a similar extent as standing crop, resulting in no change in turnover rates (year<sup>-1</sup>). In their study, the increase in fine root production constituted a large portion of the total CO<sub>2</sub>-induced increase in net primary production. In contrast, in our desert system aboveground production was significantly enhanced with CO<sub>2</sub> enrichment (Smith *et al.*, 2000; Nowak *et al.*, 2004a; Housman *et al.*, 2005), but without a corresponding response in fine roots under *Larrea* and *Ambrosia*, and with decreased fine roots along the community transects.

Unchanged or decreased fine root systems in the elevated CO<sub>2</sub> treatment may be explained by opposing effects of increased aboveground biomass and increased water-use efficiency, resulting in no net change in ecosystem water use, obviating the need for a larger root system. However, soil respiration has been observed to increase significantly in the elevated CO<sub>2</sub> plots at NDDFF (Wells *et al.*, 2001; de Soyza *et al.*, 2005), indicating increased C translocation belowground by some pathway. Our results show that this was not because of increased root growth (and subsequent mortality and decomposition), and Apple *et al.* (2005, personal communication) report that root respiration did not increase with elevated CO<sub>2</sub>. The increased soil respiration with elevated CO<sub>2</sub> may be because of increased microbial activity and respiration, for which evidence has been observed at NDDFF (Billings *et al.*, 2002, 2004) and elsewhere (Zak *et al.*, 2000). Soil microbial activity in the Mojave Desert is primarily C limited (Schaeffer *et al.*, 2003), but our results make it unlikely that the C source for increased microbial activity is root

biomass. Weatherly *et al.* (2003) showed that litter production is increased with CO<sub>2</sub> enrichment at this site, but litter decomposition is very slow in the desert, and litter accumulation is minimal in shrub interspaces where the increased soil respiration was observed. Thus, increased mycorrhizal growth (Tingey *et al.*, 1997) or root exudation (Paterson *et al.*, 1997) under elevated CO<sub>2</sub> seem to be likely sources for increased microbial respiration, as Schäfer *et al.* (2003) suggested may be the case for a *Pinus taeda* FACE system.

Taken together, the results of our study led to rejection of the hypotheses that elevated CO<sub>2</sub> would increase fine root standing crop, production, and mortality, and that these responses would be greater for evergreen than drought-deciduous shrubs. The lack of increase in fine roots to accompany observed increase in aboveground production seems best explained by increased water-use efficiency keeping ecosystem water use unchanged, thus, removing the need for a larger root system for increased water acquisition. In fertile shrub islands, where aboveground production increases were greatest, the opposing factors of higher biomass and greater water use efficiency under elevated CO<sub>2</sub> may be fairly balanced leading to no changes in fine roots. However, at the community level, including the large areas in shrub interspaces, elevated CO<sub>2</sub> increased aboveground production by a lesser amount and smaller fine root systems seemed sufficient for acquisition of belowground resources. This difference developed primarily through decreased stimulation of root production during times of high water availability in elevated CO<sub>2</sub>.

### Acknowledgements

This research was funded by an interagency agreement between the US Department of Energy (DE-AI03-96ER62288) and the US Environmental Protection Agency (RW89937719), with additional support to R.S.N. by the Nevada Agricultural Experiment Station. Operation of the Nevada Desert FACE Facility was supported by the US Department of Energy (DE-FC002-91ER5667), Brookhaven National Laboratory, the US Department of Energy National Nuclear Security Administration/Nevada Operations Office, and Bechtel Nevada. This document has been subjected to EPA review and approved for publication. Mention of trade names or commercial products does not constitute endorsement or recommendation for use. We thank Craig Biggart, Rob Coulombe, Leslie DeFalco, Scott Holub, Alan Knapp, Melissa Lucash, and Travis Spikes for assistance in installing the minirhizotron tubes, and Jay Arnone and three anonymous reviewers for comments on the manuscript. Figure 1 is reprinted from Norby *et al.* (2001), with permission of the New Phytologist Trust and the photographer, Travis Huxman.

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