

Temporal dynamics of fine roots under long-term exposure to elevated CO₂ in the Mojave Desert

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Summary

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- Deserts are considered 'below-ground dominated', yet little is known about the impact of rising CO₂ in combination with natural weather cycles on long-term dynamics of root biomass. This study quantifies the temporal dynamics of fine-root production, loss and standing crop in an intact desert ecosystem exposed to 10 yr of elevated CO₂.
- We used monthly minirhizotron observations from 4 yr (2003–2007) for two dominant shrub species and along community transects at the Nevada Desert free-air CO₂ enrichment Facility. Data were synthesized within a Bayesian framework that included effects of CO₂ concentration, cover type, phenological period, antecedent soil water and biological inertia (i.e. the influence of prior root production and loss).
- Elevated CO₂ treatment interacted with antecedent soil moisture and had significantly greater effects on fine-root dynamics during certain phenological periods. With respect to biological inertia, plants under elevated CO₂ tended to initiate fine-root growth sooner and sustain growth longer, with the net effect of increasing the magnitude of production and mortality cycles.
- Elevated CO₂ interacts with past environmental (e.g. antecedent soil water) and biological (e.g. biological inertia) factors to affect fine-root dynamics, and such interactions are expected to be important for predicting future soil carbon pools.

Introduction

Quantifying below-ground carbon fluxes and stocks presents a great challenge to understanding and predicting changes to the terrestrial carbon cycle. Arid, semi-arid, and hyper-arid ecosystems cover *c.* 47% of the terrestrial land surface (Reynolds *et al.*, 2001) and are considered below-ground dominated (Burke *et al.*, 1998). However, little is known about the impacts of rising CO₂ and variation in precipitation and temperature on root biomass and below-ground carbon cycling in deserts. Fine roots (<2 mm in diameter) are critical to understanding such below-ground dynamics because they are integral to plant uptake of water and nutrients, and their generally short lifespan allows for observations of the temporal dynamics of productivity.

Several studies show increased below-ground productivity under elevated CO₂ (Matamala & Schlesinger, 2000; Kimball *et al.*, 2002; Norby *et al.*, 2004; De Graff *et al.*, 2006; LeCain *et al.*, 2006; Iversen *et al.*, 2008; Morgan *et al.*, 2011; Norby & Zak, 2011). However, a negative effect was found by Bader *et al.* (2009), and Phillips *et al.* (2006) and Ferguson & Nowak (2011) found no sustained difference in production, loss, or turnover of fine roots in species growing in the Mojave Desert free air CO₂ enrichment (FACE) experiment. However, Ferguson & Nowak

(2011) found several time periods where elevated CO₂ plots had higher rates of fine-root production than ambient plots. Their results are based on ANOVA-type analyses of minirhizotron data of fine-root dynamics, and they found time-period was the only consistently significant factor that explained variation in production, loss and standing crop, and CO₂ treatment interacted with time to influence standing crop. The goal of our study was to quantify direct and indirect effects of elevated CO₂ on temporal dynamics of fine-root production and loss of two dominant shrub species and the plant community as a whole at the Nevada Desert FACE experiment.

Plant growth and senescence is a complex function of environmental drivers experienced over the growing season and even previous seasons (Noy-Meir, 1973; Austin *et al.*, 2004; Huxman *et al.*, 2004; Ogle & Reynolds, 2004). The temporal scale over which plant and community processes respond to changes in environmental drivers varies from seconds to weeks or months. For example, stomata can react within seconds (Lambers *et al.*, 2008), whereas a soil nitrogen pulse can lag the causal rain event by days or weeks because of the comparatively slow changes in the microbial community or fine-root structure (Cui & Caldwell, 1997). Such lag effects may underlie the transitory effects of elevated CO₂ on fine-root dynamics that were previously reported by Ferguson & Nowak (2011).

Moreover, plant reaction times to a change in an environmental driver are quite variable, and plants may produce roots even under unfavorable conditions (Reynolds *et al.*, 1999; Wilcox *et al.*, 2004; Peek *et al.*, 2005) or fail to produce roots after a break in drought conditions (Lauenroth *et al.*, 1987; Ivans *et al.*, 2003). This type of response may be attributed to what we refer to as 'biological inertia', which is analogous to the concept of inertia in physics whereby objects in motion tend to stay in motion and those at rest stay at rest. The biological inertia analogy predicts that root systems currently growing tend to continue growing and those that are dormant tend to stay dormant. This inertia effect could be a major factor controlling the complex temporal dynamics previously reported for fine roots (Ferguson & Nowak, 2011). Unique to this study, we quantify biological inertia by categorizing previous production and loss rates into four levels (zero, low, medium, and high rates), and we use these levels to model current rates.

The phenological environment of a plant also influences its response to environmental stimuli (Epstein *et al.*, 1999; Dyer *et al.*, 2011). For example, responses to changes in soil water content may differ by phenological period, and phenological period also may interact with CO₂ treatment level. The phenological periods that we explore are based on established seasonal climate patterns and 'typical' plant-growth periods. A phenological effect differs from a biological inertia effect because the previous root state can vary across individuals and years, whereas phenological periods are fixed across individuals and years.

Moreover, because root production and loss are integrated physiological and morphological responses that likely reflect cumulative effects of past environmental conditions, we are interested in how production and loss on a given day respond to environmental conditions of that day and to previous conditions. Several studies of desert plant and ecosystem processes suggest that many processes are correlated with past environmental conditions such as antecedent precipitation or soil water (Ogle & Reynolds, 2004; Burgess, 2006; Potts *et al.*, 2006; Zeppel *et al.*, 2007; Cable *et al.*, 2008). Thus, we explored the response of root production and loss to antecedent soil water content.

Finally, because fine-root production and loss were measured for individual roots, we interpreted the change in standing crop as an integrator of production and loss and thus used it to help inform the processes affecting production and loss. This linkage is achieved by a simple dynamic model for standing crop that obeys mass balance (i.e. changes in standing crop resulting from the balance between production and loss) and explicitly couples the three types of dynamic root data.

Thus, this study addresses five research questions: (1) Does CO₂ treatment directly affect fine-root production and loss? (2) Does CO₂ treatment interact with phenological period and antecedent soil water to indirectly affect fine root dynamics? (3) How does CO₂ interact with biological inertia to indirectly affect fine-root dynamics? (4) Do these direct and indirect effects of elevated CO₂ differ among the dominant shrubs (*Larrea tridentata* and *Ambrosia dumosa*) and the community as a whole? (5) Do the

direct and indirect effects of elevated CO₂ depend on the soil depth at which roots occur? To address these questions, we developed a statistical model that incorporated the effects of CO₂ treatment, cover type, phenological period, biological inertia, antecedent soil water, and depth. We show that CO₂ primarily affects fine-root production and loss via its interactions with phenological period, antecedent soil water content, and biological inertia.

Materials and Methods

Field data

Minirhizotron data were collected at the Nevada Desert FACE Facility (NDDFF) located on the US Department of Energy's Nevada National Security Site (formerly Nevada Test Site) north of Las Vegas in the Mojave Desert. The Mojave Desert is one of the driest regions in North America with an average of 140 mm of precipitation each year. Rainfall each year is highly variable; during the 10 yr experiment (1997–2007), maximum and minimum hydrological year (October to September) precipitation totals were 328 mm (1997–1998) and 47 mm (2001–2002), respectively. Precipitation during the study is shown in Fig. 1. Vegetation of the site is characteristic of the Mojave Desert and dominated by the evergreen shrub *Larrea tridentata* (Sessé & Moc. ex DC) Coville (creosote bush) and the drought-deciduous shrub *Ambrosia dumosa* (A. Gray) Payne (bur-sage). Vegetation is

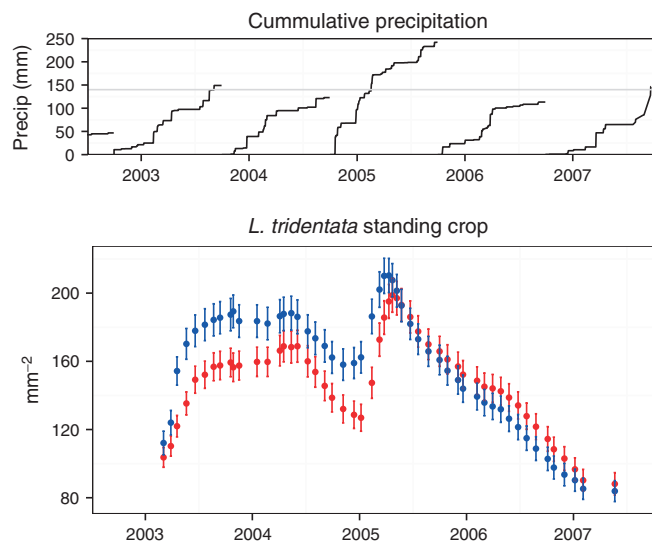


Fig. 1 Top: cumulative hydrological year precipitation during the years of the study. The horizontal gray line represents mean total annual precipitation. Bottom: *Larrea tridentata* standing crop of fine roots over time. After a drought during 2001 and 2002, *L. tridentata* standing crop at the beginning of 2003 was low. During the subsequent spring, standing crop increased for both ambient (red circles) and elevated (blue circles) treatments, but the elevated CO₂ treatment added comparatively more fine-root standing crop. The subsequent loss of roots in late 2004 was more extreme under ambient CO₂. However, ambient standing crop converged to the elevated standing crop during the El Niño event of 2005, when standing crop peaked. During the subsequent dry spell, both treatments had similar loss rates. *Ambrosia dumosa* and the entire community had similar patterns as those for *L. tridentata*.

sparse with < 20% of surface area covered by shrubs and perennial plants (Jordan *et al.*, 1999).

The NDDF data used in this study consists of six plots, each a ring of 23 m diameter. Plots were assigned to one of two treatments: blowers that elevated atmospheric CO₂ to 550 ppm (elevated CO₂), and blower controls (ambient CO₂). Each treatment was applied to three replicate plots. The CO₂ treatments were applied 24 h per day each day of the year, except during periods of low temperature (to avoid adverse effects of air movement on plant energy balance) and high wind (to reduce CO₂ consumption). During the period of minirhizotron observations (2003–2007), elevated CO₂ averaged 511 ppm and ambient CO₂ averaged 375 ppm. The CO₂ application protocol necessitated an on-site automated weather station that recorded air temperature, wind speed, wind direction, humidity, and precipitation amounts.

A total of 28 minirhizotron tubes were installed in each plot and were distributed among three cover types (*L. tridentata*, *A. dumosa*, and community). Two minirhizotron tubes were placed under four individuals (i.e. 'replicates') of each of the two shrub species for a total of 16 tubes per plot, providing fine-root data on the two dominant species. The remaining 12 tubes were arranged into three transects (i.e. 'replicates') that were systematically located along radii from the plot center (Philips *et al.*, 2006), providing data on the entire plant community.

Digital images (40 kb resolution) captured via a Bartz Technology field computer (Bartz Technology Corp., Santa Barbara, CA, USA) were analyzed by manually tracing individual roots using ROOTRACKER (David Tremmel, Duke University, Durham, NC, USA); production and loss are expressed as root length per image area (mm⁻¹ d⁻¹) (Ferguson & Nowak, 2011). Typical of minirhizotron studies, the timing of fine-root production (i.e. appearance of a new root) can be directly observed but timing of mortality cannot. Instead, actual mortality (i.e. loss of metabolic functions) occurred at some unknown time before observed root loss (i.e. when the root has decayed sufficiently to be classified as dead). We use 'loss' instead of 'mortality' here to emphasize this distinction.

Observations of root production, loss and standing crop were made approximately every 4 wk from January 28, 2003 until May 22, 2007 (52 sampling dates). Each tube was divided into 23 non-overlapping 11.5 mm × 9.1 mm frames (Ferguson & Nowak, 2011), and then grouped and averaged into four depth categories (0–25, 25–50, 50–75, and 75–100 cm after adjusting for the 30° tube angle). The grouping was used because some frames were unobservable because of scratched tubes or rock obstructions and because grouping mitigated the large number of zeros and reduced the data set to a computationally tractable size. When converting continuous data to categorical, four categories are often used because four categories maintain a high degree of flexibility (i.e. a cubic effect of depth could still be estimated) but still keep the number of categories manageably small. Finally, we divided observed average production or loss by tube standing crop so that data are rates of production and loss per unit of standing crop. An example of observed temporal dynamics in standing crop of *L. tridentata* is given in Fig. 1.

Replicate tube observations were subsequently averaged to obtain a single value per each plot, cover type, depth and sampling date combination for several reasons. First, covariate information such as soil moisture was available only at the plot level. Second, extremely long Markov Chain Monte Carlo (MCMC) simulation times were exacerbated by microsite variability when data were not aggregated across tubes within each plot. Third, aggregation reduced the percentage of zero observations, which improved model behavior. Finally, because the experiment is intended to evaluate treatment effects at the landscape level and because treatment replicates are at the plot level, bypassing the computational difficulties of using the full dataset is justified.

To quantify the role of biological inertia, we categorized production rates into four states based on observed quantiles within each cover type. The first state corresponds to prior production being zero, and the other three states correspond to previous production being low, medium or high, where these categories are defined by the observed 33.3% and 66.6% quantiles of all observed production rates for each cover type. The loss inertia term is defined similarly, and inclusion of previous rates in the model can mathematically be thought of as a discretized autoregressive model of order one.

Five phenological periods are defined by the months October–November, December–February, March–April, May–June, and July–September. Each phenological period within a hydrological year (October 1 to the following September 31) had at least two and at most five sampling dates per year. These phenological periods correspond to autumn, winter, spring, early summer, and late summer, respectively, and represent distinctive periods of plant growth and seasonal precipitation and temperature (Rundel & Gibson, 1996). Winter corresponds to early green-up of leaves and initiation of fine-root growth. Spring characteristically has maximal fine-root production and microbial decomposition of previously expired roots. Early summer is defined by recently produced fine roots but continued loss of older roots. During late summer, the soil water content is low and drought-deciduous shrubs and annuals are senescing and losing leaves, and fine-root production and loss also tend to be low. During the fall dormancy phase, fine-root production is negligible and loss is generally lower than late summer.

Measurements of integrated soil water over two depths increments (0–20 and 0–50 cm) were made approximately once a month with soil moisture probes (time-domain reflectometer (TDR) and neutron probes). Because minirhizotron and soil water observation dates were not always concordant, we modeled soil water content to estimate a daily time-series of soil water values. We fitted the observed soil water and precipitation data to the one-dimensional soil water budget (SWB) model of Kemp *et al.* (1997) that incorporates transpiration, evaporation and infiltration. Evaporation was modeled using daily solar radiation and air temperature. Transpiration was a function of vapor pressure deficit, leaf area index and soil water potential. Water infiltration from precipitation events followed a 'bucket model' where the top soil layer is filled to the water holding capacity and any residual moisture drains to the layer below.

We augmented the SWB model to allow for transport between layers using the Darcy–Richards equation. For each date with observed soil water data, we used the observed data as the starting point for the model and ran the model forward in time to predict soil water values up to the next date when soil water measurements were made. This model fitted the observed soil water data well enough ($R^2 = 0.66$) to scale an interpolation between soil moisture observations, even with intervening precipitation events. We then estimated a daily time-series of soil water content over the 0–50 cm profile.

Data synthesis approach

Over the 4-yr study period, which included periods of both high and low precipitation (Fig. 1), a large percentage of observations were associated with zero production or loss. Data that were non-zero, which indicated some amount of recordable production or loss, were highly skewed. These data attributes required a flexible modeling approach and prompted our choice to use a hierarchical Bayesian approach, which provides a useful framework when traditional statistics do not provide an easy solution. We fitted the same model to each cover type and parameters are estimated separately for each cover type.

The model structures for production and loss were identical, and for brevity, we only describe the production model. To address the large number of zeros and skewed values, we assumed zero-inflated lognormal models for observed production rates. To simplify notation, for observation j ($j = 1, 2, \dots, 1224$), let p_j represent the observed average production rate for a given plot, cover type, depth and sampling date. The likelihood for p_j is defined by the mixture distribution:

$$p_j \sim \begin{cases} 0 & \text{with probability } 1 - \pi_j \\ \text{Log Normal}(\mu_j, \sigma^2) & \text{with probability } \pi_j \end{cases} \quad \text{Eqn 1}$$

The probability of observing zero production is $(1 - \pi_j)$, where observed zeros result from either the production really being zero, or it being so low that it was not detected. Thus, we assume that π_j (probability of observing non-zero production) is related to the expected (or latent) log production rate (μ_j) via a logistic link function:

$$\text{logit}(\pi_j) = \alpha_0 + \alpha_1 \mu_j \quad \text{Eqn 2}$$

Next, μ_j is described by a hierarchical mixed effects model that includes depth ($d = 1, 2, 3$, or 4 for 0–25, 25–50, 50–75, and 75–100 cm), treatment ($t = 1$ or 2 for ambient or elevated), inertia ($i = 1, 2, 3$, or 4 for zero, low, medium, or high prior production), plot ($r = 1, 2, 3$ per treatment), hydrological year ($hy = 1, 2, \dots, 5$ for 2002–2003 through 2006–2007), phenological period ($s = 1, 2, \dots, 5$ for October–November, December–February, etc.), sampling occasion ($o = 1, 2, \dots, 5$) within a hydrological year and phenological period, and antecedent soil water (A). Thus, the model for μ_j is:

$$\begin{aligned} \mu_j = & \beta_0 + \beta_D[d_j] + \beta_{HY}[hy_j] + \beta_S[s_j] + \beta_{T,R}[t_j, r_j] \\ & + \beta_{I,T}[i_j, t_j] + \beta_{HY,S,O}[hy_j, s_j, o_j] \\ & + \beta_{SW}[t_j, s_j]A_j \end{aligned} \quad \text{Eqn 3}$$

For the effects vectors of depth (β_D), hydrological year (β_{HY}), phenological period (β_S), we constrained each vector to sum to zero so that the intercept (β_0) is identifiable (Gelman & Hill, 2007). We also employed sum-to-zero constraints for the inertia by treatment ($\beta_{I,T}$) matrix, and row and column sum-to-zero constraints on hydrological year by phenological period by date ($\beta_{HY,S,O}$) effects matrices. We computed the treatment main effect by summing over the inertia effects in $\beta_{I,T}$. Sum-to-zero constraints are not required for the antecedent soil water effect (β_{SW}) because it multiplies a continuous covariate. We allowed β_{SW} to vary by treatment and phenological period to account for potential effects of elevated CO_2 and variation in plant phenology on the response to soil water availability.

We next defined antecedent soil water (A_j) for each observation j . $SW_{j,1}$, $SW_{j,2}$, $SW_{j,3}$, and $SW_{j,4}$ denote the average soil water contents (v/v) in the top 0–50 cm for 0–2, 2–6, 6–14, and 14–22 wk before observation j , respectively. These time-periods were determined from preliminary analyses. We defined A_j as the weighted mean of the four soil water variables:

$$A_j = \sum_{k=1}^4 \gamma_k SW_{j,k} \quad \text{Eqn 4}$$

The weights (γ_k) are assigned a Dirichlet (1,1,1,1) prior to ensure that $0 \leq \gamma_k \leq 1$ and $\sum_{k=1}^4 \gamma_k = 1$. This prior has expected weights equal to 1/4, which corresponds to each antecedent period having equal influence. The importance of soil water conditions experienced during each time block k before observation j is described by the estimates of γ_k , and the strength and direction of antecedent soil water effects is captured by the estimates of β_{SW} in equation 3.

We coupled production, loss and standing crop by a dynamic model that obeys mass-balance constraints. Let $C_j(t)$ represent the observed standing crop and explicitly denote dependence on time (t) separately from the index (j') of all remaining variables. The likelihood for $C_j(t)$ is given by:

$$C_j(t) \sim \text{Normal}(\mu_{C,j'}(t), \sigma_C^2) \quad \text{Eqn 5}$$

The mean ($\mu_{C,j'}(t)$) is given by the discretized differential equation that is linked to the previously observed standing crop and the predicted production and loss rates ($\hat{p}_{j'}(t)$ and $\hat{l}_{j'}(t)$):

$$\mu_{C,j'}(t) = C_j(t - \Delta t) + C_j(t - \Delta t) \cdot (\hat{p}_{j'}(t) - \hat{l}_{j'}(t)) \cdot \Delta t \quad \text{Eqn 6}$$

Δt is the time interval (weeks) between measurements, and $\hat{p}_{j'}(t) = \exp(\mu_j)$, where μ_j is given in eqn 3, and similarly for $\hat{l}_{j'}(t)$, where the loss rate model is identical to the production rate model.

Finally, noninformative $Normal(0, \sigma=100)$ priors were assigned to all fixed effects ($\alpha_0, \alpha_1, \beta_0, \beta_{I,T}, \beta_D, \beta_S, \beta_T, \beta_{SW}$) in Eqns 2 and 3; the priors are substantially wider than the corresponding marginal posterior distributions. Random effects ($\beta_{HY}, \beta_{HY,S,O}, \beta_{T,R}$) were assigned normal priors with zero mean and variance components $v_{HY}^2, v_{HY,S,O}^2$, and $v_{T,R}^2$. Because there were only a small number of levels associated with each factor (hydrological year, date within phenological period and hydrological year, and plot within treatment), standard deviations ($v_{HY}, v_{HY,S,O}, v_{T,R}$) for each random effect were assigned folded Cauchy priors to avoid posterior distributions with unrealistically heavy right tails (Gelman, 2006). Wide uniform priors were assigned to standard deviations in production rate, loss rate, and standing crop likelihoods (e.g. σ and σ_C). The model was implemented in the Bayesian software package JAGS (Plummer, 2003) and three parallel MCMC chains were run for 100 000 iterations, Convergence was evaluated according to Gelman & Rubin (1992) diagnostics.

Results

To assess statistical significance, we used an $\alpha=0.1$ level and present 90% credible intervals (CIs). In the process of building our model, we initially included several additional covariates that were found to be nonsignificant (90% CIs for coefficients containing zero), and we removed those terms from the model presented above. Treatment-by-depth, treatment-by-phenological period, antecedent soil moisture weight-by-depth, and antecedent soil moisture weights-by-phenological period were initially considered and found to be either nonsignificant or resulted in unstable mixing of the MCMC. Surprisingly, antecedent temperature effects were also non-significant, regardless of the phenology effect being included in the model or not. We fitted a model,

without the phenology effect and included an interaction between antecedent temperature and antecedent soil moisture, and although these interaction terms were statistically significant, that model did not perform as well as the phenology model and was less interpretable, leading us to prefer the model using phenology.

Model fit

Our model explained a significant amount of variability ($R^2 \approx 70 - 80\%$) in the observed production and loss rates within each cover type (see Fig. 2 for *L. tridentata* model fits). The standing crop model explained a larger amount of variability in observed standing crop ($R^2 \approx 99\%$) (Fig. 2). However, because total production and loss between successive sampling dates is small compared with the standing crop, a simple model for standing crop that includes only previous standing crop and zero production and loss amounts in the discretized model in eqn 6 explains $\approx 70\%$ of standing crop variability. When the sub-models for production and loss are included, an additional $\approx 30\%$ of standing crop variability is explained.

To further assess model fit, we followed Gelman & Hill (2007) and examined plots of predicted log loss rates, log production rates and standing crop versus their observed values along with the 90% CIs of those predictions (Fig. 2). Because predicted points lay on or near the one-to-one line with relatively high R^2 values (Fig. 2), we concluded that the model described the mean response well. Because coverage rates ($\approx 92\%$) of posterior prediction intervals were above the desired 90%, we conclude that the model also sufficiently quantified variability in the response. Prediction intervals not overlapping the one-to-one line could indicate potential bias. For example, low loss rates were not as well predicted as high rates, and 14 observations during the

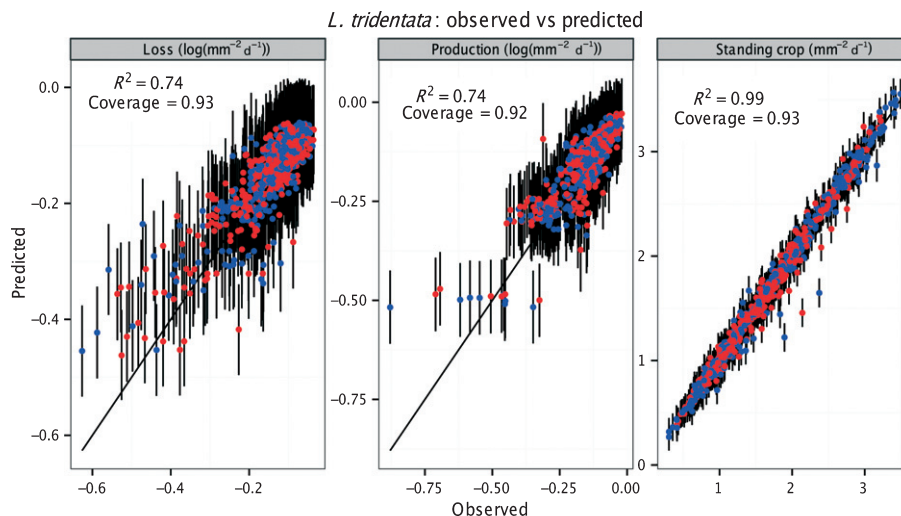


Fig. 2 Observed versus predicted data for *Larrea tridentata*: log(loss) (left panel), log(production) (middle panel), and standing crop (right panel); all observations are in units $\text{mm}^{-2} \text{d}^{-1}$. The diagonal black line is the one-to-one line; vertical lines (whiskers) associated with each point are 90% credible intervals for the predicted value. R^2 of model fits and the percentage of data points whose credible intervals overlap the one-to-one line ('coverage') are also shown. Results for *Ambrosia dumosa* and the community data were similar. The standing crop model fits the data well because total production and loss between successive sampling dates is small compared to standing crop, and past standing crop alone explains $\approx 70\%$ of standing crop variability. When sub-models for production and loss are included, most of the remaining 30% of standing crop variability is explained. Treatment: ambient, red symbols; elevated, blue symbols.

winter of 2003–2004 with low production rates are not well estimated (Fig. 2).

Posterior parameter estimates

Because effects parameters were constrained to sum to zero for categorical covariates, it is not surprising that some posterior CIs overlap zero. However, if a covariate was statistically significant, then at least one of its levels will be different than zero (i.e. at least one level of the covariate has a CI that does not overlap zero). Effects parameters should be interpreted as the change in the rate of production (or loss) that would otherwise be expected.

Direct effect of elevated CO₂ The main effect of CO₂ treatment was found by summing across previous rates in the interaction of CO₂ and biological inertia. The main effect of elevated CO₂ was not significant in all situations except for *L. tridentata* production where elevated CO₂ significantly increased production rate; the 90% CI for the difference between the elevated and ambient CO₂ effect coefficients was 0.23–0.80.

Interaction of CO₂ with antecedent soil moisture and phenological period Even with antecedent soil water content and previous production and loss patterns included in the model, both production and loss differed by phenological period (Fig. 3). Phenological trends (β_S , Eqn 3) for loss rates in *A. dumosa* and *L. tridentata* are higher than otherwise expected in late summer and autumn, but lower than otherwise expected in spring. Production rate trends are less clear, but for both *A. dumosa* and *L. tridentata*, late summer production was lower than expected, whereas production was higher than expected in spring (*A. dumosa*) and early summer (*L. tridentata*). An interaction between phenology and CO₂ treatment was not found to be significant and thus was not included in the final model.

We expected production to be positively correlated with antecedent soil water content, but the effect (β_{SW} , Eqn 3) was

positive only during late summer, autumn and winter for *A. dumosa* and *L. tridentata* (Fig. 4). Conversely, a negative effect of antecedent soil water was estimated for spring and early summer, suggesting that greater past soil water content led to reduced production during these periods. The CO₂ treatment interacted with antecedent soil water in some instances such that spring (*A. dumosa* and *L. tridentata*) and early summer (*L. tridentata*) production β_{SW} estimates were significantly more negative under elevated compared with ambient CO₂. Loss rates followed a similar trend: spring (*A. dumosa*, *L. tridentata* and community) and early summer (*A. dumosa* and community) loss β_{SW} estimates were significantly more positive under elevated CO₂. Posterior means for β_{SW} for community production and loss rates followed the same trend as *A. dumosa* and *L. tridentata*, but higher levels of uncertainty (wider 90% CIs) in autumn and winter led to statistically insignificant effects, although a few were negative with smaller 90% Cs (spring and early summer).

We explored the importance of soil water at different periods into the past via antecedent weight parameters (γ , Eqn 4). The prior for γ has each prior time-period being equally important (i.e. prior weights $\gamma_k = 1/4$ for each time-period, k). The posterior results for γ , however, suggest a lag response to moisture. For *A. dumosa*, production is most strongly coupled ($\gamma > 1/4$) with the first and last antecedent soil water periods, and weights for intermediate time periods (prior 2–6 and 6–14 wk) were significantly $< 1/4$ (Fig. 5). For *L. tridentata*, weights for production were smallest (γ_2) in the prior 2–6 wk, significantly larger for 0–2 wk, and largest for the past 6–14 and 14–22 wk. Weights for the community were more uncertain (wider CIs), but suggest that water conditions during the previous 2 wk are less important than conditions experienced further in the past; the greater uncertainty is likely a result of relatively few non-zero antecedent soil water effects (β_{SW}).

Antecedent soil moisture weights for loss rates were similar to weights associated with production rates. For *A. dumosa* and *L. tridentata*, the previous 0–2 and 14–22 wk had high weights ($\gamma > 1/4$), whereas intermediate periods had low weights (γ near

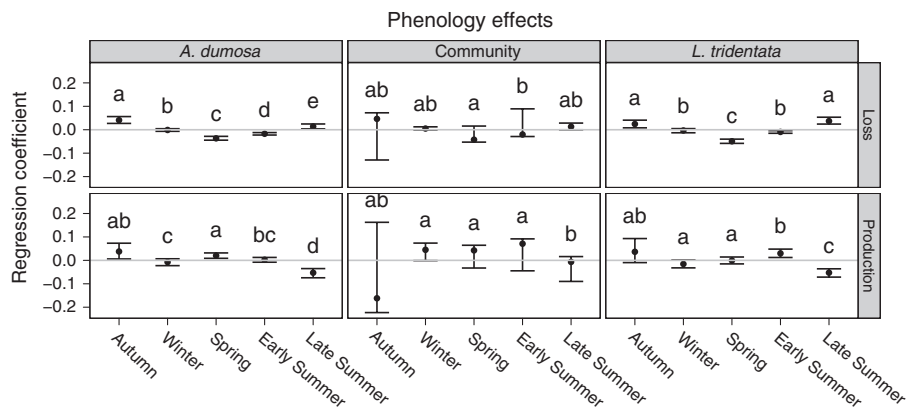


Fig. 3 Posterior means and 90% credible intervals for phenology effects, β_S , on *Ambrosia dumosa* (left panels), community (middle panels), and *L. tridentata* (right panels) fine-root loss (upper panels) and production (lower panels) during different phenological periods. Means with different lower case letters within a panel indicate significant differences among the five phenological periods. If all credible intervals in a panel overlap the horizontal gray line at zero, then there is no phenological effect on production or loss for a particular species.

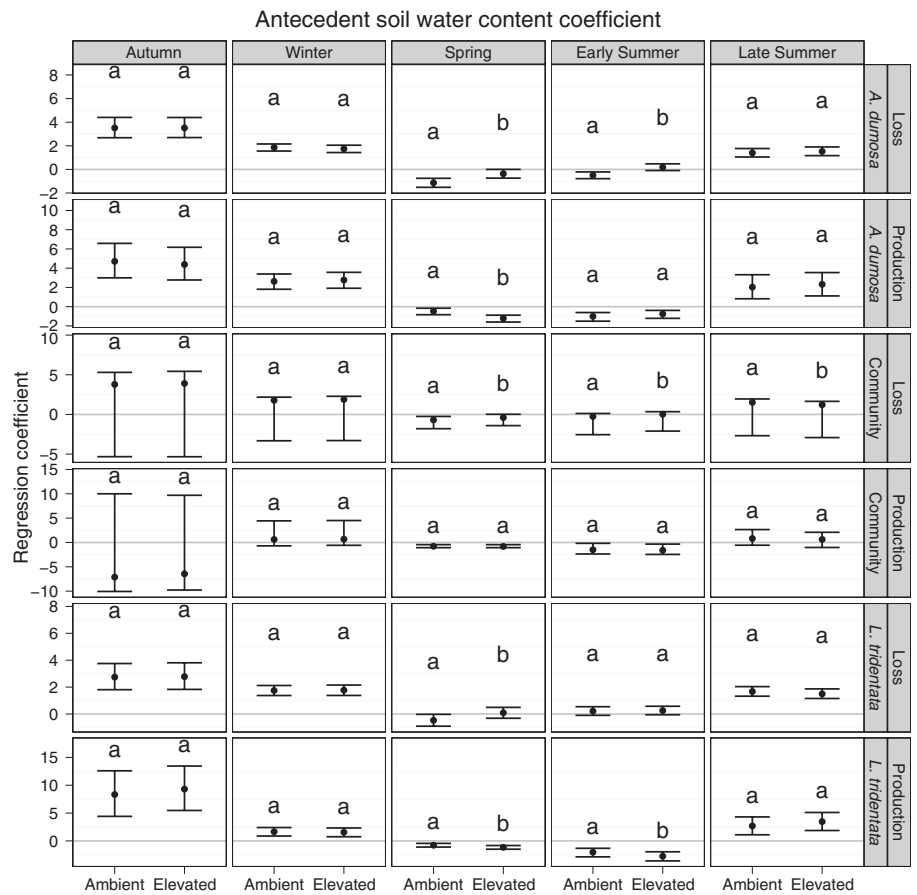


Fig. 4 Posterior means and 90% credible intervals for antecedent soil water coefficients, β_{SW} , for fine-root loss and production for all three cover types during different phenological periods for ambient and elevated CO_2 treatments. Credible intervals that overlap zero indicate that antecedent soil water does not significantly influence production or loss for that particular combination of cover type, phenological period, and CO_2 treatment. Means with different lower case letters within a panel indicate significant differences between CO_2 treatments.

0.05). For *L. tridentata*, soil water conditions 0–2 and 14–22 wk into the past were equally important for loss (γ_1 and γ_4 were not statistically different). For *A. dumosa*, soil water conditions during the previous 14–22 wk were about twice as important as those during the previous 0–2 wk ($\gamma_4 = 0.62$ and $\gamma_1 = 0.35$, respectively). Because community antecedent soil water effects (β_{SW}) were generally not significantly different than zero (results not shown), each antecedent soil water period had similar effects on fine-root production and loss.

Interaction of CO_2 with biological inertia For the inertia response, both production and loss followed the same trend with strong negative effects for prior zero and strong positive effects for previous low levels, but mixed positive or zero effects for previous medium and mixed negative or zero effects for previous high levels (Fig. 6). If the previous rate was zero, then the current rate is less than would otherwise be expected ($\beta_{I,T}$, except for loss rates in the community transects and production rates for the community and *L. tridentata* under elevated CO_2). If the previous rate was low, this always has a positive (amplifying) effect on current production or loss. Previous medium rates either had a positive effect (*L. tridentata* production and loss) or did not notably influence current rates (zero effect for *A. dumosa* and community). If the previous rate was high, the inertia effect is zero or negative, denoting a de-amplification of current rates, as occurred under ambient CO_2 for *L. tridentata* production and loss and

community loss. Furthermore, the inertia effect differed between CO_2 treatment levels in some instances. For production, significant treatment effects only occurred for *L. tridentata* whereby the inertia effects under elevated CO_2 were significantly higher (greater amplification) for previous zero production and previous high production compared with the ambient CO_2 inertia effects. For loss, CO_2 treatment only affected *A. dumosa* and community inertia terms such that the previous low effect was reduced under elevated CO_2 and the previous high effect was increased under elevated CO_2 (community only).

Cover type differences Here we summarize differences among cover types highlighted in the previous sections. Different cover types have similar trends for antecedent soil moisture coefficients, with elevated CO_2 yielding lower production and higher loss coefficients in spring and early summer. However, CO_2 treatment did not significantly affect early summer production in *A. dumosa* and loss in *L. tridentata* (Fig. 3). The trend in the antecedent soil moisture weights (γ) was essentially the same for both species for fine-root loss (Fig. 4). However, production weights, differed somewhat between species such that soil moisture conditions in the previous 6–22 wk were most important for *L. tridentata* whereas recent conditions (0–2 wk) and conditions 14–22 wk into the past were most important for *A. dumosa*.

The difference in CO_2 treatment response between the two dominant shrubs was most pronounced in the inertia coefficient.

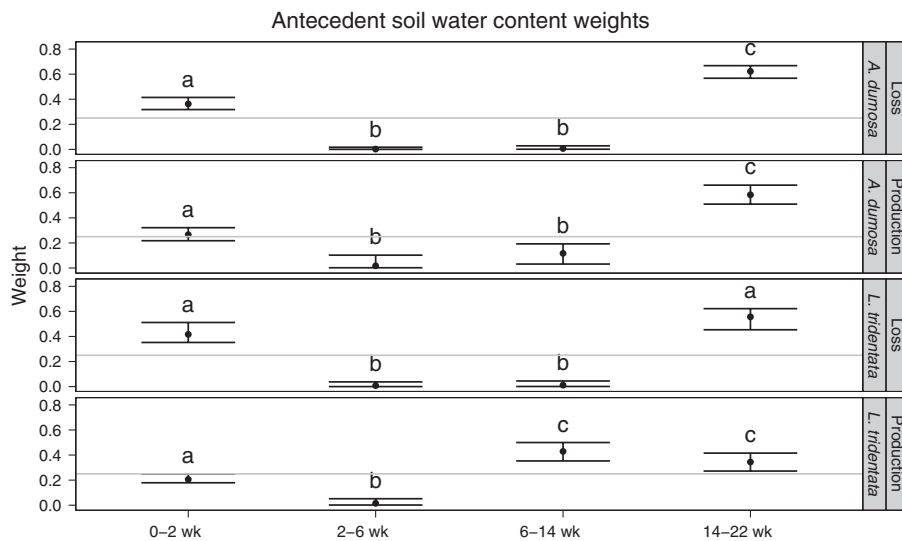


Fig. 5 Posterior means and 90% credible intervals for antecedent soil water weights, γ , for fine-root loss and production of *Ambrosia dumosa* (upper two panels respectively) and *Larrea tridentata* (lower two panels respectively) for different time periods before the observation. The gray horizontal line denotes the expected value the weights (1/4) based on the prior distribution; if all periods overlap 1/4, then data do not suggest any period or antecedent soil water is more influential than any other. Means with different lower case letters among the four antecedent weights.

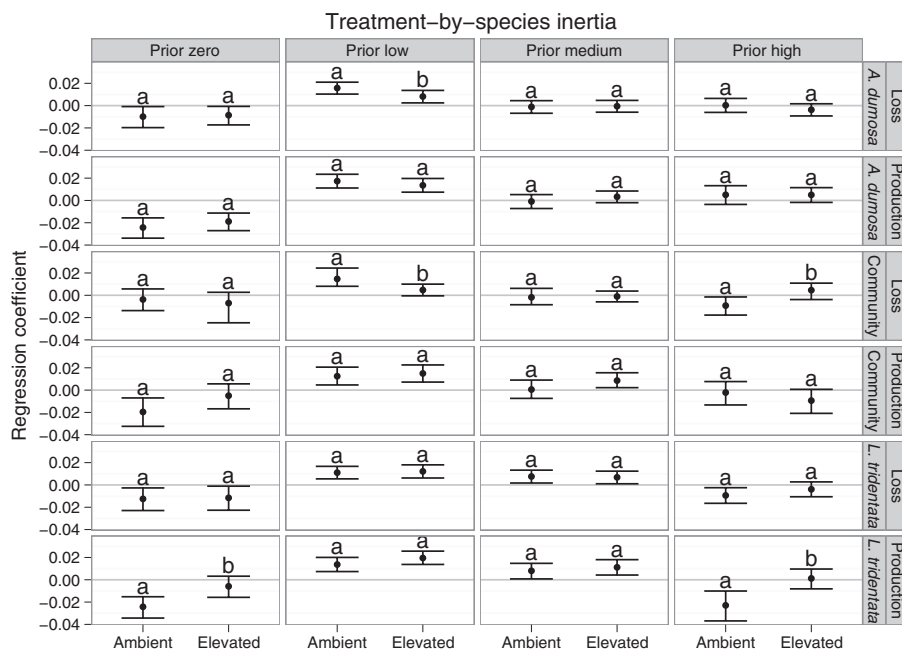


Fig. 6 Means and 90% credible intervals for the inertia effect, $\beta_{i,T}$ for fine-root loss and production of *Ambrosia dumosa* (upper panels), community (middle panels), and *Larrea tridentata* (lower panels) under both ambient and elevated CO₂ treatments. A row of credible intervals that all overlap zero indicate that biological inertia does not significantly influence production (or loss) for that particular combination of cover type and CO₂ treatment. Means with different lower case letters within a panel indicate significant differences between CO₂ treatments.

The only treatment effect for *A. dumosa* was that the loss term when prior loss was low was less positive under elevated CO₂. For *L. tridentata*, the treatment effect increased the production coefficient when previous production was zero or high. The community cover type had a decrease in loss coefficient when previous loss was low (same as *A. dumosa*) but uniquely had an increase in the loss coefficient when previous loss was high (Fig. 6).

Depth effects The depth effects (β_D , Eqn 3) were generally the same for production and loss (Fig. 7). Production and loss rates decreased significantly with depth across all cover types (i.e. depth effects were positive for the surface layer and decreased with depth with the most negative values occurring for the deepest layer). However, effects of the 25–50 and 50–75 cm depths were statistically indistinguishable for *L. tridentata* production.

The CO₂ treatment did not interact with depth, and allowing antecedent soil moisture weights to vary by depth resulted in unstable mixing of the MCMC; thus, both interactions were removed from the final model.

Discussion

Direct and indirect effects of CO₂ on fine-root dynamics

Although our modeling results reinforce earlier conclusions that elevated atmospheric CO₂ does not consistently affect production of or loss of fine roots for Mojave Desert vegetation (Phillips *et al.*, 2006; Ferguson & Nowak, 2011), our results provide new insight into how elevated CO₂ indirectly influences fine-root dynamics.

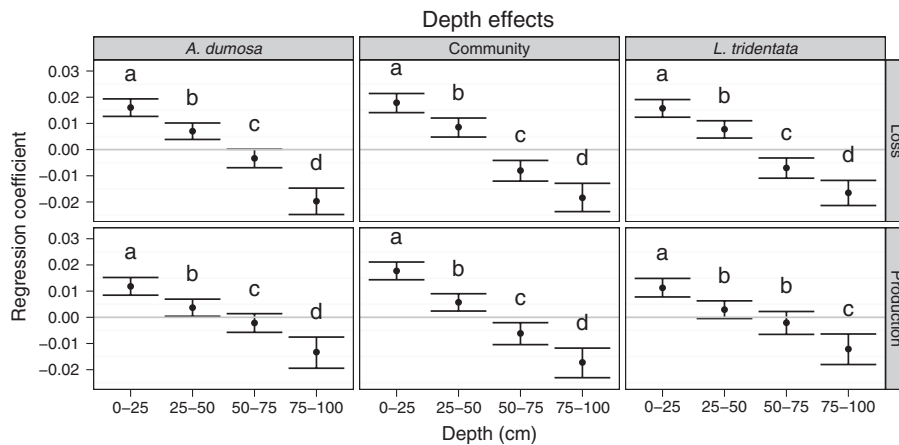


Fig. 7 Posterior means and 90% credible intervals for depth effects, β_D , of *Ambrosia dumosa* (left panels), community (middle panels), and *Larrea tridentata* (right panels) for fine-root loss (upper panels) and production (lower panels). Means with different lower case letters within a panel indicate significant differences among the four depth increments. If all credible intervals in a panel overlap the horizontal gray line at zero, then there is no depth effect on production or loss for a particular species.

Interaction of CO₂ with phenological period and antecedent soil water

The strong interaction between phenology and soil water is driven by a plant's ability to react to changes in soil water. Although observed production rates did peak during spring, as expected (data not shown), *A. dumosa* and *L. tridentata* plants were able to utilize high soil water levels for increased levels of fine-root production during late summer, autumn and winter. During spring, production rates are already high and increased soil water levels did not increase the rates further. The negative effect of antecedent soil water in early summer (Fig. 4) suggests that, before dormancy, if water had been plentiful earlier in the growing season, then a plant likely will not allocate additional carbon resources for water acquisition. More negative soil water coefficients during spring and summer under elevated CO₂ could be a result of two factors: (1) plants exposed to elevated CO₂ already have a large fine-root network because of earlier increased production and, under high soil water conditions, they do not need to increase their fine-root network; or (2) increased water-use efficiency under elevated CO₂ (Aranjuelo *et al.*, 2011) reduces the need for increased water acquisition.

As with many desert processes, fine-root production and loss rates are strongly affected by precipitation events. However, the relationship between observed fine-root production and loss versus individual precipitation events is not solely caused by direct and immediate responses. That is, substantial lag times can occur between precipitation and fine-root production and loss, as shown by the high importance of soil water experienced 14–22 wk ago (Fig. 5). The antecedent weights describing the influence of past soil water status suggest that both immediate and delayed responses occur for production and loss rates in both *A. dumosa* and *L. tridentata*. These two different time scales (i.e. immediate or short-term vs delayed or long-term) underlying fine-root loss might partly be a result of the delay between a root dying and when it has observably decayed. For example, increases

in short-term soil moisture content stimulated fine-root loss (Fig. 5), but an initial pulse of observed fine-root loss immediately following a precipitation event might be caused by rapid increases in microbial activity that decompose roots that died weeks or months earlier. The second pulse of observed loss might reflect the decay of fine roots that died immediately following the precipitation event.

One explanation for the dual time-scale for production is that fine-root production increases immediately following a precipitation event, which quickly depletes plant labile carbon resources (Tissue & Wright, 1995), thus leading to a negative feedback whereby production is halted. After a period of carbon assimilation in which plant labile carbon pools are replenished, fine-root production could be restarted and continue until environmental conditions are unfavorable. A second alternative explanation is that different antecedent weights for production spans two phenological periods, with the shorter time scale being important during autumn, winter and spring whereas the longer time-scale may be important in early and late summer when soil is relatively dry and the ability to grow may depend on how much the plant grew in the preceding autumn, winter and spring. Given a wet winter with high fine-root productivity, it is reasonable to expect the early and late summer period should have low fine-root productivity owing either to an already sufficiently large fine-root network or to having exhausted limiting resources (De Soyza *et al.*, 1996). To disentangle the two competing explanations for antecedent weights, a model with weights that vary by phenological period may be necessary. We tried this interaction, but it was removed because of non-significance, and it is not clear if the non-significance is results from limited temporal replication of the study or if the first explanation is the underlying cause.

Phenological period also had different effects on fine-root production and loss (Fig. 3), which indicates that antecedent soil water content alone is not sufficient to explain seasonal variation in observed production and loss. Fine-root production rates were lower than expected in late summer for both *A. dumosa* and *L. tridentata*, but it appears that production during other periods

may be sufficiently explained by other factors that likely covary with phenological period, such as antecedent soil water and past root status. The fine-root loss cycle (high in late summer and autumn and low during spring) and low autumn productivity are consistent with plants having the greatest need for fine roots in spring to acquire soil resources when shoot growth is greatest. During autumn and winter, when many mature plants are senesced or dormant, the need for fine roots is much smaller, and hence production of new roots is not needed to support soil nutrient and water acquisition because aboveground demand is low or nonexistent. Furthermore, cooler soil and air temperatures also reduce plant metabolism (Holthausen & Caldwell, 1980), which in turn reduces the need for plants to provide resources for tissue maintenance. In addition, high fine-root mortality in winter can reduce root maintenance respiration costs, and thus improve carbon balance of plants.

Interaction of CO₂ with biological inertia

Perhaps the most interesting indirect effect of CO₂ is its interaction with biological inertia, which for *L. tridentata* under elevated CO₂ causes the shrub to start fine-root production sooner and sustain production longer than shrubs growing under ambient CO₂ (Fig. 6). For example, if *L. tridentata* fine roots were dormant (i.e. previous production was zero) during the last census (i.e. c. 4 wk ago), then current production rates are expected to be very low, or perhaps still zero under ambient CO₂, but production is expected to be significantly higher under elevated CO₂. For *A. dumosa*, elevated CO₂ plants had less root loss than ambient plants when previous loss was low. Thus, for both *L. tridentata* and *A. dumosa*, elevated CO₂ tends to increase the pool of fine roots, but the mechanism differs between species (i.e. via production vs loss responses).

We hypothesize that these inertia trends reflect lag and source-sink responses associated with labile carbon availability and allocation (Inauen *et al.*, 2012). For example, increased leaf assimilation under elevated CO₂, which has been observed for *L. tridentata* (Huxman *et al.*, 1998; Hamerlynck *et al.*, 2000; Aranjuelo *et al.*, 2011) and other species in the community (Huxman & Smith, 2001; Hamerlynck *et al.*, 2002; Ellsworth *et al.*, 2004), likely provides a favorable carbon balance that allows species such as *L. tridentata* to more readily initiate or even increase root growth at all levels of current growth rates. This favorable carbon balance may explain why *L. tridentata* initiates fine-root growth sooner and maintains it longer under elevated CO₂.

Furthermore, initiation and maintenance of fine-root growth provides an important mechanism that partly accounts for the sustained increases in assimilation under elevated CO₂ observed in *L. tridentata* (especially during dry periods) compared with *A. dumosa*, which did not sustain greater assimilation rates under elevated CO₂ (especially during dry periods) (Aranjuelo *et al.*, 2011). Increased ability of fine roots to break dormancy and initiate growth under elevated CO₂ also has positive feedback effects on shoot growth under elevated CO₂, helping *L. tridentata* access soil resources to allow faster growth rates earlier in spring under

elevated CO₂ compared with ambient CO₂ (Smith *et al.*, 2000; Housman *et al.*, 2006). Although this tendency to modify biological inertia enhances fine-root production and ultimately fine-root standing crop, high levels of fine-root production are not sustainable, especially during subsequent drought periods. Thus, fine-root standing crops for plants under elevated CO₂ eventually return to levels similar to those under ambient CO₂.

Cover type differences

In addition to the aforementioned species differences between the dominant shrubs, some important differences emerged with respect to community-level responses. For example, antecedent soil water effects at the community level were generally intermediate between the two shrub species and were more uncertain (Fig. 4). Because the community includes both *A. dumosa* and *L. tridentata*, as well as many other species, intermediate values and greater uncertainty are expected. Antecedent soil moisture effects are more variable and CIs overlap zero except for spring effects and thus the importance of different past time periods is difficult to resolve for fine-root production in the whole community (Fig. 5). This may simply be a result of the community reflecting responses of many species that respond differently to antecedent soil water and with different lag times.

Other factors affecting fine-root dynamics

Considering the importance of temperature on biological processes, especially in desert ecosystems (Strain & Chase, 1966; Bell *et al.*, 2009; Cable *et al.*, 2011), the lack of significant air temperature effects on fine-root production or loss were surprising. However, other studies have also failed to detect a correlation (Fitter *et al.*, 1999; Wilcox *et al.*, 2004) and suggest that air and soil temperatures are only indirectly related to mortality. Natural seasonal cycles of temperature may confound the statistical detection of temperature effects: similar temperature regimes may result in different growth responses depending on the time of year as well as other environmental conditions. However, other factors in our model sufficiently explain natural seasonal cycles, and the lack of a significant temperature effect appears to reflect a real air temperature insensitivity. In contrast, other biological processes in the Mojave Desert, such as soil CO₂ flux have relatively high sensitivity to temperature (Cable *et al.*, 2011). Given that diurnal, seasonal, and inter-annual temperature variation in the Mojave Desert is very large, we suspect that time of year (i.e. phenological period) and antecedent soil moisture are more reliable predictors of favorable growth periods than temperature.

Conclusions

One of the primary goals of the Nevada Desert FACE experiment is to identify possible carbon sequestration mechanisms to inform predictive global vegetation models. Transitory effects of elevated CO₂ that were noted by Ferguson & Nowak (2011) can be statistically shown to be true effects and that carbon sequestration via fine roots can occur. However, because of the

relatively short residence time of the fine-root carbon pool, carbon will eventually be incorporated into the soil carbon pool, and global change factors such as elevated CO₂ are expected to have an impact on soil carbon cycling and feedback to climate change (Davidson & Janssens, 2006; Shen *et al.*, 2009). Our study suggests that past environmental (e.g. antecedent soil water) and biological (e.g. biological inertia as represented by past root growth states) controls on root dynamics must be considered in vegetation models in order to accurately predict the outcome of such feedbacks.

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