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Greater ecosystem carbon in the Mojave Desert after ten years exposure to elevated CO₂

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Carbon dioxide is the main greenhouse gas inducing climate change. Increased global CO₂ emissions, estimated at 8.4 Pg C yr⁻¹ at present, have accelerated from 1% yr⁻¹ during 1990–1999 to 2.5% yr⁻¹ during 2000–2009 (ref. 1). The carbon balance of terrestrial ecosystems is the greatest unknown in the global C budget because the actual magnitude, location and causes of terrestrial sinks are uncertain²; estimates of terrestrial C uptake, therefore, are often based on the residuals between direct measurements of the atmospheric sink and well-constrained models of ocean uptake of CO₂ (ref. 3). Here we report significant terrestrial C accumulation caused by CO₂ enhancement to net ecosystem productivity in an intact, undisturbed arid ecosystem^{4–8} following ten years of exposure to elevated atmospheric CO₂. Results provide direct evidence that CO₂ fertilization substantially increases ecosystem C storage and that arid ecosystems are significant, previously unrecognized, sinks for atmospheric CO₂ that must be accounted for in efforts to constrain terrestrial and global C cycles.

Arid and semiarid ecosystems are significant components of the terrestrial C budget; they cover 47% of the terrestrial surface⁹, represent the fifth largest pool of soil organic C (208–241 Pg; ref. 10) and exhibit large increases in net primary productivity (NPP) in response to small changes in water availability¹¹. The Nevada Desert Free-Air CO₂ Enrichment Facility (NDEFF) was established in 1997 to better understand the sensitivity of arid ecosystems to increasing atmospheric CO₂ ([CO₂]). Soil organic C and nitrogen are concentrated in the top 0.1 m and no significant differences in soil C and N were observed between CO₂ treatments in 1999 (ref. 4). Above- and belowground biomass and soils to 1 m were harvested by plant-cover type after ten years of continuous treatment. Soils were the dominant pool of C and N and contents were significantly greater under elevated [CO₂] across all cover types (Fig. 1 and Supplementary Tables 1–5). Mean total ecosystem organic C under elevated CO₂ was 1,170 g C m⁻² with a 90% credible interval of 1,062–1,285 g C m⁻², compared with 1,030 g C m⁻² (credible interval of 937–1,130 g C m⁻²) under ambient conditions. Differences were owing solely to soil organic C; no differences were observed in plant pools. This contrasts with more mesic grassland and forested ecosystems that observed increases in plant biomass after two to nine years of exposure to elevated [CO₂] (ref. 12). Mass balance analysis of the carbon

isotope composition ($\delta^{13}\text{C}$) of C entering the soil after a change in CO₂ sources in 2003 was -26.2‰ (Fig. 2), indicating $\sim 70\%$ of accrued soil organic C originated from aboveground (-27.1‰) compared with belowground (-24.0‰) sources. Comparisons of the relative contribution of different C sources to accrued soil organic C between elevated and ambient [CO₂] treatments are not possible, however, as the $\delta^{13}\text{C}$ of CO₂ for ambient CO₂ treatments remained constant throughout the experiment.

Flux estimates of net ecosystem productivity (NEP) are problematic in aridlands¹³, thus our harvest provides the first direct measure of long-term enhancements to NEP stimulated by elevated [CO₂]. Estimates of the spatial extent of aridlands range from 2.65×10^9 ha (ref. 10) to 4.89×10^9 ha (ref. 9) and plant cover in arid biomes has increased 11% as atmospheric CO₂ increased from 1982 to 2010 (ref. 14). Assuming that responses observed over this ten-year study are representative of other arid ecosystems, then enhancements to NEP in arid and semiarid lands caused by elevated CO₂ could range from 0.37 to 0.68 Pg C yr⁻¹. This enhancement of NEP is equivalent to 4–8% of current global CO₂ emissions of 8.4 Pg C yr⁻¹ and 15–28% of current terrestrial uptake estimates of 2.4 Pg C yr⁻¹ (ref. 1). The recent generation of representative concentration pathways (RCPs) for climate simulations predict that atmospheric [CO₂] will reach levels used in this experiment (513 $\mu\text{mol mol}^{-1}$) between 2045 (RCP8.5) and 2063 (RCP4.5; ref. 15) and CO₂ enhancement of NEP reported here could account for 4–8% and 2–4% of predicted total emissions for RCP4.5 (9.0 Pg C yr⁻¹) and RCP8.5 (19.0 Pg C yr⁻¹), respectively, at that time. Although extrapolations such as this can be problematic, as evidenced by the range in atmospheric [CO₂] trajectories proposed in the RCPs and possible interactions between elevated [CO₂] and other global change factors beyond the goals of this experiment, such as increased atmospheric N deposition, changes in precipitation regimes and warming, they do point out the potential for CO₂ stimulation of NEP in arid regions to impact global [CO₂].

Increases in total ecosystem C at the NDEFF under elevated [CO₂] are the direct result of CO₂ fertilization effects on photosynthesis. Plants grown under elevated [CO₂] had photosynthetic rates 1.3–2.0 times greater than those grown under ambient [CO₂] (ref. 5). Further, integrated leaf-level C gain for the dominant shrub *Larrea tridentata* was 170 g C m⁻² yr⁻¹ and 118 g C m⁻² yr⁻¹ greater in wet and dry years under elevated [CO₂], respectively⁵. Increased

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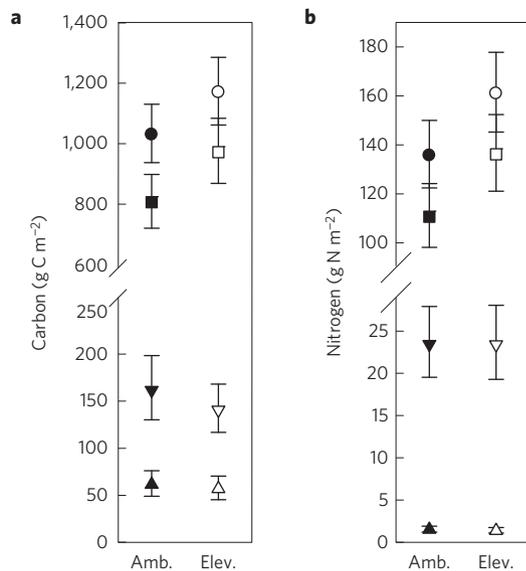


Figure 1 | Ecosystem C and N under ambient and elevated CO₂.

a,b, Posterior means and 90% credible intervals (error bars) for aboveground (filled uptriangle, open uptriangle) and belowground (filled downtriangle, open downtriangle) plant biomass, soils (filled square, open square) and total (filled circle, open circle) ecosystem C (**a**) and N (**b**) under ambient (Amb.) and elevated [CO₂] (Elev.). Estimates are derived by summing cover-weighted values for individual cover types (Supplementary Information). Mean soil (Bayesian p -value = 0.002, 0.002) and total ecosystem (p = 0.021, 0.004) were significantly different between CO₂ treatments for C and N, respectively.

photosynthesis and leaf-level C gain in all years, however, translated to increases in aboveground NPP in only wet, but not dry, years^{11,13}.

The absence of [CO₂] treatment differences in plant C and N pools at final harvest seems to contradict the measured increases in photosynthesis and NPP under elevated [CO₂]. This observation, in fact, highlights a primary mechanism for the observed increase in soil organic C, as well as a fundamental difference in the response between arid and more mesic ecosystems. Arid ecosystems are characterized by rapid increases in NPP and biomass in response to stochastic increases in water availability¹¹. The greatest enhancement in NPP and growth of plants under elevated [CO₂] at the NDFP occurred when moisture was most available. The final harvest at NDFP occurred during a dry year, indicating that peaks in production that occur under elevated [CO₂] when moisture is readily available cannot be sustained during intervening drought. Hence, additional biomass senesced, increasing C inputs into soil as litter. High rates of above- and belowground plant biomass turn-over are common in arid ecosystems; turnover of aboveground biomass at NDFP may occur every two to six years based on measurements of aboveground NPP of 10–30 g C m⁻² s⁻¹ at a nearby site¹³ and total aboveground biomass can turn over every 1.5 yr based on NPP and standing biomass estimates in the Chihuahuan Desert¹⁶.

The 118–170 g C m⁻² yr⁻¹ increase in leaf-level C gain observed here under elevated [CO₂] without consistent, concurrent increases in aboveground NPP suggests a second mechanism for the observed increases in soil organic C; significant increases in belowground allocation of C. Belowground biological activity beneath shrubs, as estimated by soil respiration, can be 60% greater under elevated compared with ambient [CO₂], but this increase is occurring without significant differences in fine-root standing crop, turnover rates⁶, or root respiration¹⁷. Thus, this increase in belowground biological activity is probably due to increases in soil microbial activity or population size, and that increased rhizodeposition and

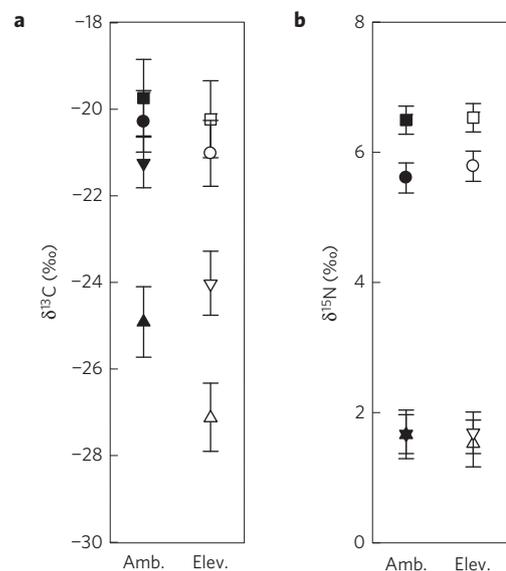


Figure 2 | Ecosystem C and N isotope composition under ambient and elevated CO₂.

a,b, Posterior means and 90% credible intervals (error bars) for aboveground (filled uptriangle, open uptriangle) and belowground (filled downtriangle, open downtriangle) plant biomass, soils (filled square, open square) and total (filled circle, open circle) ecosystem δ¹³C (**a**) and δ¹⁵N (**b**) under ambient (Amb.) and elevated [CO₂] (Elev.). Estimates are derived by summing cover-weighted values for individual cover types (Supplementary Information). Mean δ¹³C was significantly different between treatments for above- and belowground biomass (Bayesian p -value < 0.0001) and total carbon (p = 0.066). No significant differences were observed between treatments for δ¹⁵N.

subsequent assimilation and stabilization by the soil microbial community is a significant mechanism for increased C inputs to the soil under elevated [CO₂]. Rates of rhizosphere C deposition have been shown to increase 56–74% under elevated [CO₂] in diverse ecosystems^{18,19} and labile compounds immobilized into microbial residues can be a major source of stable C and N in soils²⁰. A previous study⁸ demonstrated that plant photosynthates are assimilated by rhizosphere microbial communities within 1 h of exposing *L. tridentata* to ¹³C-labelled CO₂, highlighting the tight linkage between plants, rhizodeposition and microbes in this arid ecosystem as well as the ability of C to rapidly transfer from the site of photosynthesis to the soil without increases in plant biomass or turnover rates. The C:N ratio of accumulated C and N observed here (5.5, total soil C:N = 7.3) is consistent with accumulation of bacterial and fungal residues (C:N from 4:1 to 10:1), an observation supported by increased amounts of fungal and bacterial biomarkers under elevated [CO₂] (A.K. and R.D.E., manuscript in preparation). Thus, root exudation and microbial stabilization may be more important determinants of belowground C balance in arid ecosystems than the input of fine-root litter found in more mesic ecosystems¹². The patterns observed at the NDFP are congruent with observations from the semiarid shortgrass steppe²¹, where elevated [CO₂] stimulated aboveground production of only 33% over five years but caused a doubling of rhizodeposition over the same time period.

Mean organic N was 161 g N m⁻² (credible interval of 145–178 g N m⁻²) under elevated [CO₂] in contrast to 136 g N m⁻² (credible interval of 122–150 g N m⁻²) for controls (Fig. 1). The N cycle in arid ecosystems is open with relatively high rates of N input that are balanced by similar rates of loss from soil emissions, thus small changes in either inputs or losses can significantly alter ecosystem N storage. The observed differences in N can therefore result from increased N₂ fixation or atmospheric deposition,

greater retention of N through decreased gas emissions from volatilization, nitrification and denitrification, or transfer of N from below our sampling zone into the top 1 m of soil. Rates of atmospheric deposition in this region are $0.5\text{--}1.0\text{ g N m}^{-2}\text{ yr}^{-1}$, whereas another study²² recently determined the mean rate of N_2 fixation in aridlands is $1\text{ g N m}^{-2}\text{ yr}^{-1}$, strongly suggesting that the differences in accumulation rates observed here are at the lower region of the credible interval. Increased rates of heterotrophic N_2 fixation were observed under elevated $[\text{CO}_2]$ (ref. 23), but rates are not great enough to solely account for the observed treatment differences. Changes in rooting dynamics and plant N acquisition below the 1 m depth examined in this experiment may have also contributed to the observed differences. Nitrate readily leaches in coarse soils and the greatest concentrations are often observed at depths of 1 m or greater²⁴. Nutrient acquisition by dominant shrubs can occur to 5 m (ref. 25) and seasonal patterns and observed treatment differences in leaf $\delta^{15}\text{N}$ of *L. tridentata*⁷ are consistent with patterns observed with plant use of nitrate at depth²⁶; effectively transferring N from depth to the top 1 m of soil. Finally, elevated $[\text{CO}_2]$ may increase total ecosystem N over time by increasing rates of N retention by plants and microbes, thereby decreasing rates of gaseous loss²⁷. This hypothesis is supported by experimentation; volatilization is the primary source of N loss at the NDFP (refs 4,28) and experimental addition of C (ref. 27) or elevated $[\text{CO}_2]$ (ref. 28) greatly decreased gaseous N emissions, thus facilitating retention of N in the soil. Reliable estimates of annual N fluxes in arid ecosystems are problematic due to their episodic occurrence. The observed differences in ecosystem N content observed here are probably due to a combination of each of the above factors, and separating their relative roles requires further experimentation beyond the goals of this study.

The progressive N-limitation hypothesis predicts increased N limitations to NPP as ecosystems accumulate C, but this has not yet been observed at the NDFP. $[\text{CO}_2]$ enhancement and direct C-addition studies demonstrate that microbial activity at the NDFP is limited by available C (refs 23,27) and increased C inputs accelerate rates of soil N transformations, thus increasing N mineralization and inorganic N availability^{7,29}. Soil organic matter in arid ecosystems is largely recalcitrant⁷, but increased litter and rhizodeposition under elevated $[\text{CO}_2]$ have caused an increase in microbial biomass and diversity, especially for fungi⁸ that are more efficient at using recalcitrant substrates. This is accompanied by an increase in the diversity of substrates used by the microbial community as well as the activities of enzymes involved in N and C cycling²⁹.

Assessing the location and magnitude of terrestrial C sinks is challenging because of their spatial and temporal complexity. Previous efforts to estimate C uptake by the terrestrial surface often focused on easily identified sinks such as forest regrowth and typically did not consider non-forested ecosystems or physiological enhancements to photosynthesis and growth caused by increasing $[\text{CO}_2]$. Despite suggestions that the strength of global C sinks has recently declined or remained static, recent mass balance analyses of global C indicate that uptake of CO_2 by oceans and the land surface has accelerated over the past 50 yr (ref. 2), highlighting the uncertainties present in our knowledge of the global C cycle. Results from this ten-year experiment clearly demonstrate two critical areas that must be considered to develop a more comprehensive understanding of the fates of atmospheric CO_2 . First, non-forested ecosystems must be accounted for in studies of terrestrial sinks; arid and semiarid lands are the most widespread terrestrial biomes and the enhancements in NEP in response to elevated $[\text{CO}_2]$ observed here indicate their importance as a significant C sink. Second, increases in C storage observed here were the result of $[\text{CO}_2]$ enhancements to photosynthesis, subsequent increases in plant biomass during wet years followed by greater senescence in dry

years and increased rhizodeposition. Thus, more mechanistic detail is necessary in models predicting plant, rhizodeposition and NEP responses to elevated $[\text{CO}_2]$ (ref. 30). Consideration of both factors will in turn allow us to better constrain terrestrial C dynamics and ultimately the global C cycle.

Methods

Free-air- CO_2 -enrichment (FACE) experiments allow investigators to quantify whole-ecosystem responses to elevated $[\text{CO}_2]$ in coupled plant–soil systems. The NDFP was the only FACE experiment located in an intact arid ecosystem. The NDFP was located 15 km north of Mercury, ($36^\circ 49' \text{ N}$, $115^\circ 55' \text{ W}$; elevation 965–970 m) in the northern Mojave Desert. The site consisted of nine 23-m-diameter experimental plots exposed to three fumigation treatments. Three plots were fumigated at ambient atmospheric $[\text{CO}_2]$ ($\sim 380\text{ }\mu\text{mol CO}_2\text{ mol}^{-1}$) as a blower control (ambient), three at $\sim 550\text{ }\mu\text{mol CO}_2\text{ mol}^{-1}$ (elevated) and three received no fumigation (non-blower control). Treatments began in April 1997 and continued until June 2007. Fumigations were maintained continuously throughout the experiment except when air temperatures were below 4°C or when wind speeds $> 7\text{ m s}^{-1}$ for more than 5 min. Mean $[\text{CO}_2]$ concentrations were $513\text{ }\mu\text{mol mol}^{-1}$ and $375\text{ }\mu\text{mol mol}^{-1}$ for elevated and ambient treatments, respectively, over the life of the experiment. The $\delta^{13}\text{C}$ of supplemental CO_2 was -5.4‰ until 10 February 2003 when the source CO_2 was switched to -32.0‰ for the remainder of the experiment. Dilution with ambient air resulted in $\delta^{13}\text{C}$ of CO_2 in the elevated treatment of -7.3‰ and -18.2‰ before and after the source switch, respectively. The $\delta^{13}\text{C}$ of ambient and control treatments was -8‰ throughout the experiment.

Seven cover types based on the dominant species were identified in each plot. The final harvested area for each ring was calculated from aerial photographs using image-processing software (ENVI, Exelis Visual Information Solutions). Vegetation and soils to 1 m depth were destructively harvested from two-thirds of each plot at the end of the 2007 growing season. Aboveground biomass was determined by cutting all plants at ground level and summing biomass for all individuals of each species. Belowground biomass was measured for each cover type using two approaches. First, root biomass was determined from excavated soil collected in association with specific cover types. Second, roots were collected from transects through the plot. Fine-root data were obtained from minirhizotron tubes⁶. Soils were collected under the canopies of the five most abundant plant-cover types and in plant interspaces to 1 m in depth at 0.2 m increments. Soils were collected from two microsites, centre and edge of aboveground vegetation canopies, under all cover types except *Pleuraphis rigida* (a C_4 bunchgrass). Rock and soil volumes and soil bulk densities were measured by excavation. Two square pits ($0.5 \times 0.5\text{ m}$ projected area) in each plot were excavated to 1 m in 0.2 m increments. Samples were passed through 2 mm mesh screens to separate rocks ($> 2\text{ mm}$) from soils ($\leq 2\text{ mm}$). Rock volume was quantified by measuring the amount of water displaced in a 20 l plastic container. Bulk densities were used to scale soil content measurements to an aerial basis. The mean rock and soil volumes for all plots by depth were used to correct for rock content. Plant C and N contents and stable isotope compositions were determined at the Washington State University Stable Isotope Core Facility (Pullman) using an ECS 4010 elemental analyser (Costech Analytical, Valencia) interfaced with an isotope ratio mass spectrometer (Delta PlusXP, Thermo Finnigan). Soil samples for organic C content and stable isotope composition were treated with $3\text{NH}_3\text{PO}_4$ to remove carbonates before analysis.

Final harvest data were analysed at the level of the cover type to address merging of data from the soil, aboveground and belowground samples from each sample location (see Supplementary Information for complete description of the statistical analysis methods). All C and N content data were log transformed for analysis, whereas $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data were not transformed. Data were analysed through a linear mixed-effects model with cover type and $[\text{CO}_2]$ treatment as fixed effects, and ring within treatment as a random effect. Separate models were fitted to each response variable to obtain pool and isotope estimates for each ring-cover type combination. Change in the relative proportion of the cover types was not detected during the experiment, so landscape-level estimates were calculated by summing values for soil, root and aboveground estimates for each cover type, yielding cover-type pool totals and computing weighted averages of these cover type totals to obtain the plot-level totals. All statistical models were simultaneously implemented in a Bayesian framework that allowed us to propagate uncertainty in the cover type \times pool type \times ring estimates, yielding accurate estimates (posterior means and credible intervals) of the ring, cover type by ring and treatment-level total pool estimates. The fixed effect coefficients and standard deviation terms were assigned relative standard priors and a semi-informative prior was used for the ring random effect standard deviations due to the small number of rings per treatment.

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Author contributions

S.S. and R.N. conceived the study. R.E., S.S., R.N., T.C., B.N. and L.F. designed the final harvest. R.E. and A.K. collected soils data, S.S., T.C. and B.N. collected aboveground plant data and R.N. collected belowground plant data. L.F. and T.C. determined plot area and species composition. B.H. provided elemental and isotopic analyses, and D.S. and K.O. analysed the data. All authors wrote the paper.

Additional information

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Competing financial interests

The authors declare no competing financial interests.