The effect of long-term exposure to elevated CO_2 on nitrogen gas emissions from Mojave Desert soils

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[1] In arid regions, emissions of nitrogen (N) gases are important to long-term soil fertility and regional atmospheric chemistry, making alterations in N gas emissions an important aspect of ecosystem response to climate change. Studies at the Nevada Desert FACE Facility suggest that rising atmospheric CO_2 concentrations impact ecosystems N dynamics in the Mojave Desert; our objective was to identify whether those responses translate into changes in trace N gas emissions. We measured soil fluxes of reactive N gases (NO, NO_y, NH_3) and N_2O in plots receiving long-term fumigation with ambient and elevated (550 ppm) CO_2. Reactive N gas emissions were significantly lower under elevated CO_2 during high soil moisture conditions in the spring and fall. The strongest responses occurred in the islands of fertility created by the dominant shrub *Larrea tridentata*, where fluxes were 3–5 ng N m^{-2} s^{-1} lower in elevated CO_2 plots. Changes in total N gas emissions were driven by reduced NO and NH_3 emissions, with smaller changes in NO_y efflux and little to no production of N_2O. Lower N gas emissions under elevated CO_2 reflect changes in plant and microbial demand for N, suggesting increased uptake or immobilization coupled with decreased rates of N mineralization and nitrification. This response of N gas efflux to elevated CO_2 in the growing season suggests that in deserts, elevated CO_2 promotes ecosystem retention of N during periods of peak biological demand. Concomitantly, exposure to elevated CO_2 alters inputs of new reactive gases into the atmosphere, potentially impacting local atmospheric processes.

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1. Introduction

[2] In arid ecosystems, gaseous nitrogen (N) fluxes are often a substantial proportion of annual N loss, directly affecting its long-term bioavailability [*McCalley and Sparks*, 2008; *Peterjohn and Schlesinger*, 1990]. Therefore, an essential part of understanding the impact of global climate change on arid regions is evaluating how the magnitude and composition of N emissions will respond to future environmental conditions, including rising atmospheric CO_2 concentrations. This is of particular importance given the role of N availability in determining growth responses to increased CO_2 [*Hungate et al.*, 2003; *Reich et al.*, 2006]. In arid regions, responses to elevated CO_2 are highly correlated to water availability, with the strongest increases in productivity under elevated CO_2 occurring during periods of high precipitation [*Naumburg et al.*, 2003; *Smith et al.*, 2000]. It is likely that during these periods when strong CO_2 effects are physiologically possible, bioavailability of soil N acts as a secondary constraint on the utilization of higher CO_2 concentrations [*Hooper and Johnson*, 1999]. This means that a long-term change in the bioavailability of N under elevated CO_2 is likely to be an important variable in the response of desert communities to rising atmospheric CO_2.

[3] Gaseous N species emitted from soil directly impact key atmospheric processes associated with climate and air quality. Nitrogen gases produced in desert soils include nitric oxide (NO), a group of other reactive nitrogen oxides including HONO, HNO_3, NO_2 and organic oxides, which are categorized as NO_y, ammonia (NH_3) and nitrous oxide (N_2O). Nitrogen oxides are necessary precursors driving ozone formation in the troposphere, a strong greenhouse gas and detrimental pollutant [*Crutzen*, 1979; *Intergovernmental Panel on Climate Change* (*IPCC*), 2007], nitrous oxide is a potent greenhouse gas with 180 times the global warming potential of CO_2 [*Lashof and Ahuja*, 1990], and NH_3 par-

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ticipates in atmospheric aerosol production and cloud formation, influencing the attenuation of radiation and, therefore, the cooling of the Earth's surface [*IPCC*, 2007].

[4] The production of nitrogen gases in desert soils occurs through several different pathways. Ammonia emissions are the result of chemical transformations of mineralized NH_4^+ under the basic soil conditions prevalent in arid regions [*Schlesinger and Peterjohn*, 1991]. Nitric oxide and N_2O efflux are products of the microbe-mediated processes of nitrification and denitrification [*Firestone and Davidson*, 1989], with NO production in arid ecosystems resulting primarily from nitrification [*Hartley and Schlesinger*, 2000; *Smart et al.*, 1999]. There is variability across desert ecosystems in the prevalence and importance of N_2O emissions resulting from denitrification, in the Sonoran desert post-precipitation pulses of N_2O have been shown to be an important aspect of the N cycle [*Peterjohn and Schlesinger*, 1991], whereas in biological soil crust communities on the Colorado Plateau denitrification rates and population abundance of denitrifying bacteria are extremely low [*Johnson et al.*, 2007]. In desert soils, nitrogen oxides and NH_3 may also be produced at high surface soil temperatures yielding substantial summertime losses, especially following precipitation [*McCalley and Sparks*, 2009].

[5] Changes in ecosystem N dynamics under elevated CO_2 have the potential to alter gaseous N fluxes in desert ecosystems. Elevated CO_2 can impact N emissions by changing N inputs from fixation, microbial metabolism of N including nitrification, mineralization and immobilization and by altering plant N uptake or litter quality. Responses are likely to be strongest if elevated CO_2 alters NH_4^+ pool dynamics, the primary control over both NH_3 volatilization and the production of NO through nitrification [*Parton et al.*, 2001; *Schlesinger and Peterjohn*, 1991]. In addition to direct responses to change in N availability, studies in arid ecosystems have found that N gas fluxes are responsive to additions of labile C, suggesting that alterations in root exudates under elevated CO_2 could also affect N gas emissions. In laboratory studies additions of labile C decrease reactive N gas emissions from Mojave Desert soils [*McCalley and Sparks*, 2008], a response that is consistent with studies showing increases in microbial demand for and uptake of N following labile C addition [*Gallardo and Schlesinger*, 1995; *Schaeffer et al.*, 2003].

[6] Few studies that address the impacts of elevated CO_2 on soil N dynamics have quantified changes in gaseous N emissions; however, the responses of N gas fluxes should reflect ecosystem changes under elevated CO_2. The general patterns of belowground responses to elevated CO_2 including increased respiration, N immobilization and microbial N demand all suggest that elevated CO_2 has the potential to reduce gaseous losses due to increased retention of N by the microbial community [*de Graaff et al.*, 2006; *Zak et al.*, 2000]. Plant responses, including increased growth and nitrogen demand under elevated CO_2 as well as increased root exudation, could also result in lower N gas emissions. Alternatively, increased litter inputs or N fixation rates under elevated CO_2 could have the opposite effect, yielding larger N gas losses.

[7] At the Nevada Desert FACE Facility (NDFF), where an intact Mojave Desert ecosystem has been exposed to elevated CO_2 concentrations of 550 ppm since 1997, multiple studies have documented alterations in the N cycle under elevated CO_2 [*Billings et al.*, 2002a, 2002b, 2004; *Jin and Evans*, 2007; *Schaeffer et al.*, 2007]. The aim of this study was to identify whether arid ecosystem responses to elevated CO_2 translate into changes in N gas fluxes and to use that information to further our understanding of the effects of elevated CO_2 on soil N cycling and atmospheric feedbacks in arid ecosystems.

[8] We hypothesized that during the growing season, changes in plant and microbial activity under elevated CO_2 would decrease trace N gas fluxes, reflecting increases in demand for and retention of N. However, during times of the year when abiotic processes dominate trace N gas efflux and physical environmental conditions are the primary drivers of N gas fluxes, emissions were hypothesized to be insensitive to changes in atmospheric CO_2. Within this seasonal variation in the response of N gas production to elevated CO_2, we predicted that spatial patterns in soil resources and plant responses to elevated CO_2 should be evident, with changes in N gas emissions under elevated CO_2 being larger in the "islands of fertility" created by the dominant shrub *Larrea tridentata* [*Schlesinger et al.*, 1996; *Titus et al.*, 2002].

2. Site Description

[9] Measurements were conducted at the Nevada Desert FACE Facility located in Nye County, Nevada (36°49′N, 115°55′W), 90 km northwest of Las Vegas, NV USA at an elevation of 970 m. The site lies within the Nevada Test Site, administered by the U.S. Department of Energy and has been protected from recreation and grazing disturbances for approximately 50 years [*Jordan et al.*, 1999]. Mean annual rainfall is 140 mm and precipitation occurs primarily as winter storms and as short, localized summer events. Temperatures range from winter minima of −10°C to summer temperatures >47°C. The site is a *Larrea tridentata – Ambrosia dumosa* plant community, approximately 20% of the site area is covered by perennial plants and the rest is bare soil, with intact biological soil crusts covering 35–60% of the soil surface [*Jordan et al.*, 1999]. Soils are Aridisols derived from calcareous alluvium with a loamy sand texture. Subsoils lack a caliche layer, resulting in well-drained soils. Soil pH, measured in water, at the site ranges from 8 to 9 and soils are spatially heterogeneous in nutrients, texture and infiltration [*Jordan et al.*, 1999; *Romney et al.*, 1980].

[10] The site was established in April 1997 and consists of nine 23 m diameter plots, three control plots that are fumigated with ambient CO_2 concentrations (~380 ppm) and three elevated CO_2 plots fumigated with approximately 1.5 × ambient CO_2 concentrations (550 ppm) and three plots that receive no fumigation. Three-dimensional performance analysis of the CO_2 enrichment in elevated CO_2 plots show a concentration range of 512–583 ppm within a plot [*Jordan et al.*, 1999] and annual variation in CO_2 concentration at the center of the fumigated rings of 515 ± 66 ppm CO_2 from 1997–2006 and 463.6 ± 84.8 in 2007 when nighttime fumigations were discontinued. (Nevada Desert FACE CO_2 performance statistics available at http://www.unlv.edu/Climate_Change_Research/NDFF/co2_treatment.htm.) Few differences have been detected between the fumigated and nonfumigated controls therefore measurements in this study only include the fumigated plots [*Billings et al.*, 2003a,

2003b; *Weatherly et al.*, 2003]. Fumigations are delivered using the FACE technology developed by Brookhaven National Laboratory [*Hendrey and Kimball*, 1994; *Jordan et al.*, 1999]. Plots are designed with an elevated platform system that allows researchers access without touching the soil surface, thus limiting disturbance of biological soil crusts and alterations to the soil system through compaction [*Jordan et al.*, 1999]. The elevated CO_2 treatment ended in June 2007 and two-thirds of each plot was harvested between August and November 2007.

3. Methods

3.1. Sampling and Experimental Design

[11] Soil fluxes were measured using collars, 25.5 cm diameter and 15 cm tall that had been installed approximately 7.5 cm into the soil in February 1999 [*Billings et al.*, 2002a]. Collars were perforated belowground to allow for penetration by roots and lateral movement of water. There were a total of eight collars located in each plot, two in each of the following cover types: under the evergreen shrub *L. tridentata* (creosote bush), adjacent to the drought deciduous shrub *Lycium* spp., adjacent to the C_4 bunchgrass *Pleuraphis rigida* (big gaelleta), and in plant interspaces. Collars could not be located directly beneath either *Lycium* or *Pleuraphis* individuals without damaging the plants, therefore measurement locations associated with these cover types visibly resembled those found in plant interspaces. When collars were relocated at the end of the March 2007 sampling period into the third of each plot that would remain unharvested at the end of fumigation, cover type distribution was changed to increase replication of shrub microsites, with four collars each located under *L. tridentata* and in plant interspaces.

[12] In order to best represent gas fluxes within a FACE plot while minimizing disturbance to soils, known spatial patterns of soil nutrients were taken into consideration when choosing soil collar location and size. In the Mojave Desert, soil nutrients are highly correlated with the distribution and characteristics of the dominant shrub species, particularly *L. tridentata*, with spatial autocorrelation of nutrients matching average shrub canopy diameter (typically 1–2 m) [*Schlesinger et al.*, 1996]. Biologically essential elements such as N and P are typically 2–3 times higher under shrub canopies than in plant interspaces and there is low spatial variability in the difference between shrub and interspace soils [*Schlesinger et al.*, 1996]. A 25.5 cm diameter soil collar likely represents a relatively uniform sample of soil nutrient characteristics within a soil type, with eight collar locations providing for replication of both interspace and shrub soil characteristics within a plot.

[13] Reactive N gas flux measurements (NO, NO_y, and NH_3) were made as part of 5 sampling trips during the CO_2 fumigation period (April 2005, July 2005, July 2006, January 2007, and March 2007) and 4 sampling trips after the end of the CO_2 fumigation (July 2007, October 2007, January 2008, and April 2008). Nitrous oxide measurements were made starting in July 2006. An 8.7 mm rain event interrupted sampling during July 2005, resulting in prerain and postrain measurements for the elevated CO_2 treatment, but only postrain measurements for the control treatment. In March 2007, sampling was conducted before and approximately 36 h after a 30 mm artificial rain event was applied to the plots. All nitrogen was removed from the irrigation water using a resin filtration system and total dissolved inorganic nitrogen content of precipitation is typically <0.3 mg/L. Soil moisture (0–30 cm) was monitored from October 2006 through January 2008 using time domain reflectrometry (Dynamax, Inc, Houston, TX, USA). Moisture data is not available for the 2005 and spring 2008 measurement periods, however, 2005 was an El Nino year with above average precipitation and 2008 was a below average precipitation year, suggesting high and low soil moisture respectively during these spring growing seasons.

3.2. Reactive N Gas Flux Measurements

[14] Nitrogen gas fluxes (NO, NO_y, and NH_3) were measured using a flow-through chamber design and selective thermal and chemical decomposition converters to reduce or oxidize all reactive nitrogen trace gases (e.g., oxidized forms and ammonia) to NO. During measurement, a transparent top with two ports was placed over the soil collar. One port remained open to the atmosphere, which minimizes induced pressure differences associated with closed chamber based measurement techniques. A transparent lid design was chosen to minimize shading of the soil, which in this ecosystem can cause large changes in soil temperature, directly affecting N gas emissions [*McCalley and Sparks*, 2009].

[15] To make a measurement, outside air was passed, at 1 L min^{-1}, either directly to the measurement system to quantify background air concentrations, or through the soil collar and then to the measurement system to quantify soil emissions. The measurement system consisted of two conversion cells that converts NO_y (total oxidized N) and total reactive N (NO_y + NH_3) to NO, respectively, and a chemiluminescence NO detector (Thermal Electron Corporation 42*i*-TL). Each converter can be isolated by Teflon valves and independent measurements made for NO (no conversion), NO_y (NO_y converter only), and total reactive N (NH_3 + NO_y conversion). Fluxes were calculated based on steady state concentrations using the equation C * q/A where C is concentration (nmol L^{-1}), q is the flow rate (L s^{-1}) and A is area (m^2) of the soil surface. Concentrations used for calculation were soil chamber minus air concentrations for any particular measurement. Ammonia fluxes were calculated by subtracting the total NO_y value from the total reactive N value. Measurements of NO, NO_y and NH_3 were made sequentially and total measurement time averaged 20–30 min.

[16] The NH_3 conversion cell consists of a 30 cm length of nickel-chromium alloy tubing (INCONEL 600) passed through a mini tube furnace (Lindburg/Blue MiniMite Tube Furnace) heated to 825°C. Laboratory calibrations of the converter have showed a 86% conversion efficiency for NH_3 with no influence on NO concentration. The NO_y converter is a heated glass catalytic converter that contains a 60 cm piece of 1/4″ gold tube heated to 300°C. A small flow of H_2 (30 mL min^{-1}) is introduced just prior to the heated region to facilitate the reduction of oxidized N to NO. Laboratory calibration tests have shown a 100% conversion of NO_2 and HONO and conversion efficiencies between 78–99% for other components of NO_y (i.e., peroxyacetyl nitrate, alkyl nitrate, HNO_3 and other forms of NO_y).

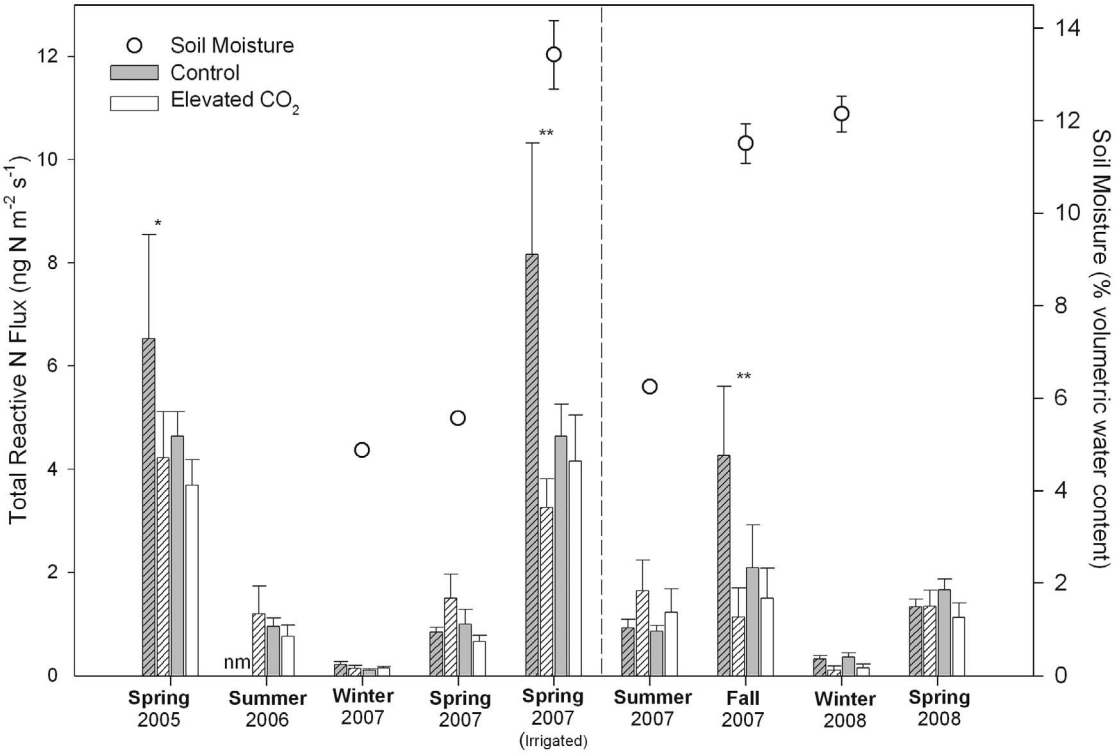

Figure 1. Total reactive N gas fluxes from soils exposed to ambient and elevated CO_2 treatments. Hatching indicates measurements made under the dominant shrub *L. tridentata*; plain bars are measurements made in nonshrub influenced soils (nm, not measured). The dashed line demarks the end of the CO_2 fumigation period. Differences between control and elevated CO_2 within a sampling period are indicated (** indicates $p < 0.05$; * indicates $p < 0.1$). Average soil moisture for all plots is included from winter 2007 to winter 2008; moisture data are not available for the remaining dates.

[17] After conversion (or directly in the case of the NO only measurement), air is passed through an NO analyzer (Thermo Electron Corporation, Model 42*i* TL). This instrument detects light from the chemiluminescence reaction between NO and O_3:

$$NO + O_3 \rightarrow NO_2 + O_2 + h\upsilon$$

The analyzer avoids interferences from other gas species by using a prereaction chamber where O_3 is used to consume NO before entering the reaction chamber. Because the rate of reaction with NO is very fast and the reaction with most interference compounds is relatively slower, two sequential runs (the first utilizing the prereaction cell and second going directly to the sample cell without prereaction) allows for the quantification of NO independent of all interferences. Using a 120 s averaging period, the instrument has a detection limit of <50 pptv and zero noise of 25 ppt, resulting in a detectable flux limit of 0.01 ng N m^{-2} s^{-1}. The instrument was calibrated daily by sequential dilution of an NO standard (Scott-Marin, Riverside, CA).

3.3. N_2O Flux Measurements

[18] Fluxes of N_2O were measured using a closed chamber method in which collars were sealed with a transparent, gas tight lid fitted with a septum. Natural variation in soil temperature in this ecosystem is closely linked to solar radiation. Soil temperature analyses of incubations with transparent lids and opaque lids show that use of transparent lids yields soil temperature changes within the chamber that most closely match ambient soil conditions. Both opaque and transparent lids reduce temporal variation in soil temperature, likely due to reduced incoming solar radiation caused by opaque chamber sides (C. K. McCalley and K. L. Sparks, unpublished data, 2010).

[19] Three gas samples were collected over a 2 h period in preevacuated 22 mL vials and analyzed at Cornell University using a gas chromatograph fitted with an electron capture detector (Shimadzu GC-2014). Chamber volume was calculated using the average of 4 depths measurements made in the field. Fluxes were calculated based on the rate of increase in concentration over time, in cases where the concentration increase was not linear over the entire 2 h incubation time, fluxes were calculated using the slope of the initial linear period. Measurements when N_2O concentration did not change over time were assigned a value of zero and included in all statistical analyses.

3.4. Statistical Analysis

[20] We used analysis of variance (PROC MIXED, SAS 9.1) with Tukey post hoc tests to test significant effects of elevated CO_2 on N gas emissions (N_{total}, NO, NO_y, NH_3, and

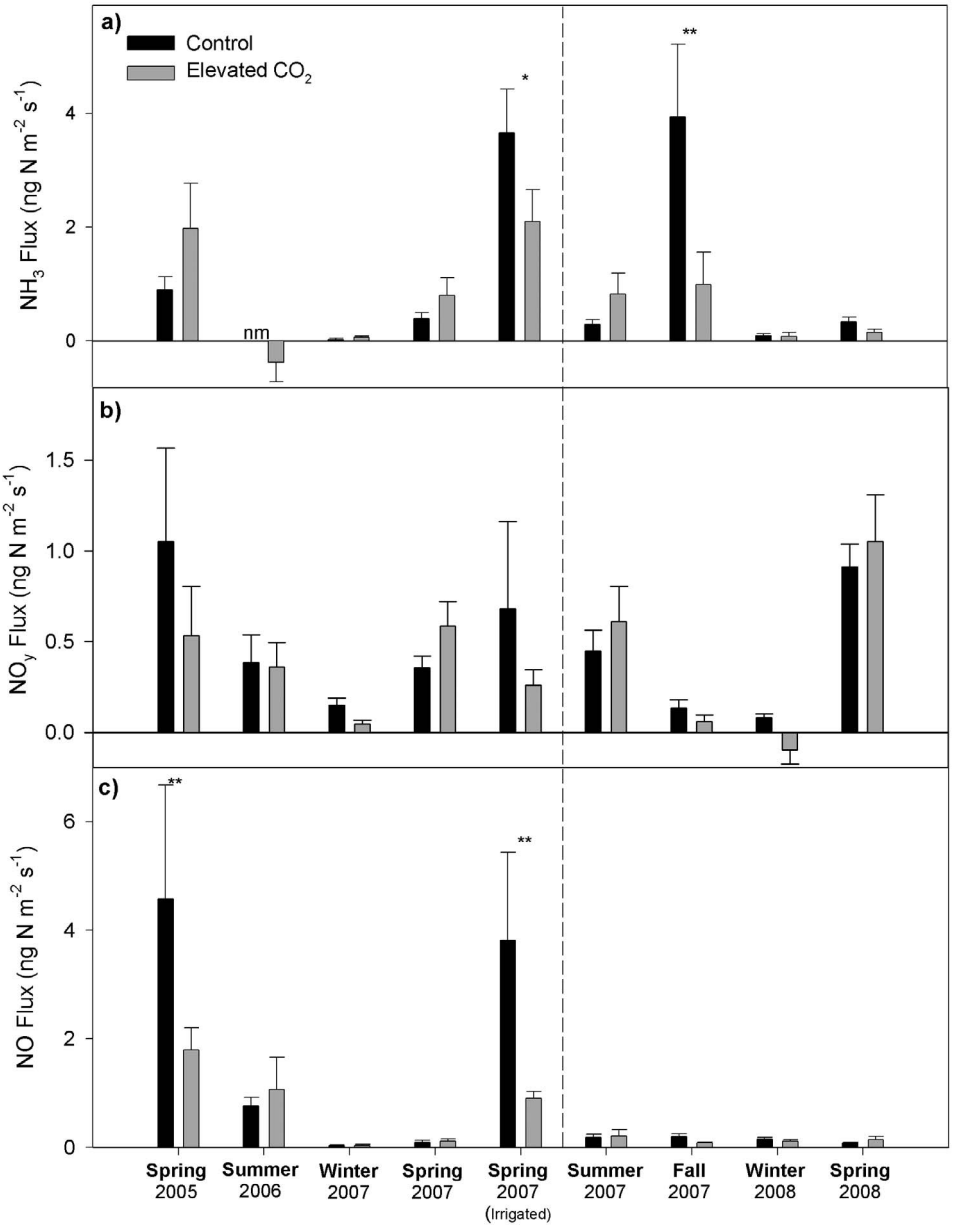

Figure 2. Response of (a) NH_3, (b) NO_y, and (c) NO emissions from *L. tridentata* soils exposed to ambient and elevated CO_2 treatments (nm, not measured). The dashed line demarks the end of the CO_2 fumigation period. Differences between control and elevated CO_2 within a sampling period are indicated (** indicates $p < 0.05$; * indicates $p < 0.1$).

N_2O) as well as the significance of season and cover type. Statistical analyses were done with all four cover types and then repeated with interspace soils combined with *Lycium* and *Pleuraphis* cover types when there were no significant differences between interspace, *Lycium* and *Pleuraphis* cover types. Only the combined cover type results are presented. Replicate collar measurements from each plot were averaged for statistical analysis except for the summer rain event data that had incomplete replication across plots. Data were log transformed to account for nonnormal distributions when necessary. All analyses were performed using SAS statistical software (Cary, NC). Due to small sample sizes (n = 3 FACE rings per treatment) statistical significance was determined at $\alpha = 0.1$. Errors are presented as ±1 SE.

4. Results

[21] Across CO_2 treatments there were significant fixed effects of time of year ($p < 0.001$) and cover type ($p < 0.08$) on reactive N gas loss. Reactive N gas emissions ranged from 0–18 ng N m^{-2} s^{-1}, with pulses as high as 78 ng N m^{-2} s^{-1} following a summer rain event and were similar in magnitude to previous measurements made at this site [*McCalley and Sparks*, 2008]. Fluxes were highest in the spring and fall when temperatures were moderate (average daily tempera-

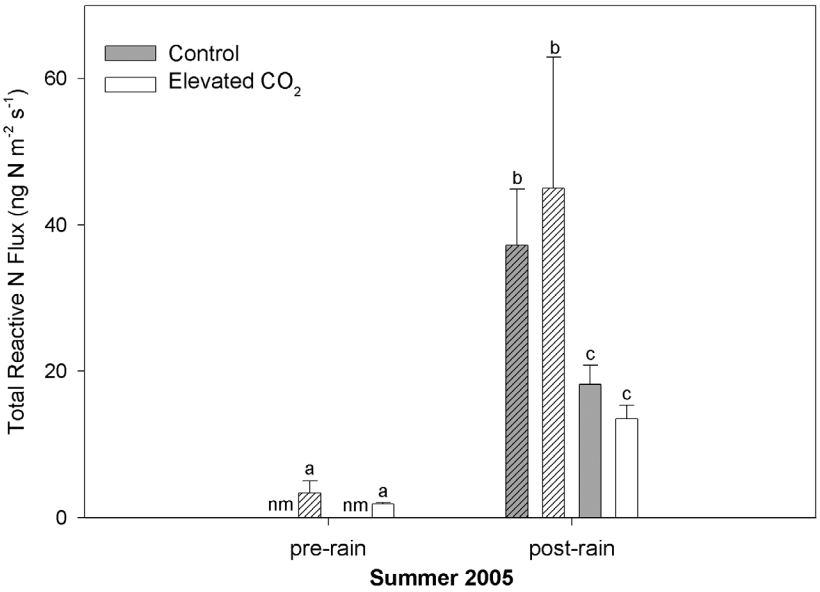

Figure 3. Total reactive N gas fluxes before and after a natural rain event (8.7 mm). Hatch marks indicate measurements made under the dominant shrub *L. tridentata*; plain bars indicate measurements made in nonshrub influenced soils. Precipitation occurred during the sampling period, limiting replication and treatment representation of prerain fluxes (nm, not measured). Letters indicate significant differences in reactive N gas efflux ($p < 0.05$).

tures of 15–19°C) and recent precipitation, either natural as in the Spring 2005 and Fall 2007 or artificial as in Spring 2007, resulted in high soil moisture (~11–13% volumetric water content in 2007). Naturally dry springs, including ambient measurements in 2007 and 2008 yielded soil fluxes that were similar in magnitude to summer conditions, with emissions of approximately 1 ng N m^{-2} s^{-1}. Fluxes were consistently low during winter months (≤0.3 ng N m^{-2} s^{-1}), despite high soil moisture during the winter of 2008. During periods of high N gas emissions in the spring and fall, there were significant spatial patterns in N gas loss with the highest fluxes occurring under the dominant shrub *L. tridentata* ($p < 0.05$). Spatial patterns in soil N gas emissions were not evident during other times of the year and soil microsites associated with cover types other than *L. tridentata* were not significantly different from each other and were combined for clarity.

[22] The effect of elevated CO_2 on reactive N gas emissions depended on season and was strongest in the islands of fertility created by *L. tridentata* (Figure 1). Reactive N gas emissions were significantly lower under elevated CO_2 during the spring and fall when recent precipitation, either natural or artificial, resulted in high soil moisture (Figure 1). Long-term exposure to elevated CO_2 reduced reactive N gas efflux by ~3–5 ng N m^{-2} s^{-1} under *L. tridentata* in spring 2005, fall 2007 as well as following irrigation in spring 2007, all periods when soil moisture content was high due to recent natural or artificial precipitation ($p < 0.1$). Fluxes of reactive N gases were insensitive to elevated CO_2 exposure when soil moisture was low and during the summer and winter months. Additionally there were no significant effects of elevated CO_2 on total reactive N loss from non-*Larrea* soils. The observed responses to elevated CO_2 spanned a time period before and after the end of the CO_2 fumigation, indicating that changes in N gas loss were indirect responses to elevated CO_2 exposure; however, from this experiment it is not clear how long the legacy of elevated CO_2 will impact the loss of reactive N gases.

[23] Lower rates of reactive N gas loss from *L. tridentata* soils were observed under elevated CO_2 conditions for both NO and NH_3, with the responsiveness of individual gas species to elevated CO_2 varying with season (Figure 2). The chemical species composition of the response reflected the overall composition of reactive N gas emissions during a given measurement period, with significant responses occurring in the particular chemical species that dominated overall emissions. Springtime responses to elevated CO_2 were primarily driven by lower NO efflux. In both spring 2005 and following irrigation in spring 2007 NO emissions were >60% lower in elevated CO_2 plots ($p < 0.0001$). In spring 2007, NH_3 emissions were also significantly lower under elevated CO_2 ($p = 0.08$). In the fall of 2007 changes in total reactive N gas efflux were driven by a large decrease in NH_3 emissions under elevated CO_2 ($p = 0.002$). Exposure to elevated CO_2 did not result in any changes in NO_y efflux from *L. tridentata* soils. The only significant change in NO_y was lower emissions in non-*Larrea* soils under elevated CO_2 in the spring of 2005 ($p = 0.01$); however this response was not large enough to significantly impact total reactive N losses.

[24] A summer precipitation event in 2005 resulted in a substantial pulse of reactive N gases that was insensitive to long-term exposure to elevated CO_2 (Figure 3). Due to the unpredictable nature of summer precipitation, prerain measurements are limited to a few replicates in the elevated CO_2 plots; however, the magnitude of these emissions are consistent with measurements made during other summer seasons. Following precipitation there was a substantial increase

Table 1. Mean Rates of N_2O Fluxes From Soils Exposed to Ambient and Elevated CO_2 Treatments[a]

	N_2O Flux (ng N m^{-2} h^{-1})			
	Larrea tridentata		*Non-Larrea*	
	Ambient	Elevated CO_2	Ambient	Elevated CO_2
Summer 2006	0.62 ± 0.28	0.00 ± 0.00	2.93 ± 1.17	2.63 ± 1.52
Winter 2007	5.79 ± 4.18	7.52 ± 7.52	6.82 ± 3.48	8.88 ± 3.32
Spring 2007	1.41 ± 1.07	2.80 ± 1.40	2.13 ± 0.74	1.83 ± 0.69
Spring 2007 (irrigated)	4.34 ± 2.48	2.07 ± 1.34	3.38 ± 0.84	2.77 ± 0.87
Summer 2007	1.39 ± 0.53	0.91 ± 0.49	1.18 ± 0.57	1.66 ± 1.29
Fall 2007	4.69 ± 1.05	4.31 ± 1.11	4.51 ± 1.38	2.77 ± 1.02
Winter 2008	0.17 ± 0.12	2.66 ± 1.35*	0.23 ± 0.18	1.29 ± 0.74
Spring 2008	0.71 ± 0.52	0.00 ± 0.00	0.71 ± 0.52	0.89 ± 0.65

[a]Errors are one standard error of the mean. Significance differences between control and elevated CO_2 within a sampling period are indicated by the asterisk ($p < 0.05$).

in reactive N gas efflux from both cover types with losses averaging 40.1 ± 7.6 ng N m^{-2} s^{-1} (under *Larrea*) and 16.1 ± 1.7 ng N m^{-2} s^{-1} (other cover types) (Figure 3). Postrain emissions were significantly higher under *L. tridentata* as compared to other cover types ($p < 0.01$). For all cover types there were no differences in the response to precipitation between elevated CO_2 and control plots.

[25] Emissions of N_2O were a very small component of gaseous N loss and fluxes were largely insensitive to elevated CO_2 (Table 1). Across all seasons and treatments, N_2O fluxes averaged 2.6 ± 0.3 ng N m^{-2} h^{-1} or approximately 0.0007 ng N m^{-2} s^{-1} and under most measurement conditions (211 of 365), N_2O emissions were undetectable. Maximal N_2O fluxes of 0.01 ng N m^{-2} s^{-1} occurred in the winter of 2007 and these relatively high losses were not isolated to a single cover type or CO_2 treatment. Even during this period of maximal efflux, N_2O fluxes were an order of magnitude lower than reactive N gas fluxes, indicating that N_2O emissions make a minor contribution to N dynamics in this ecosystem. Across all seasons and cover types the only response of N_2O emissions to elevated CO_2 was a very small, 7×10^{-4} ng N m^{-2} s^{-1}, flux increase under *L. tridentata* in the winter of 2008 ($p = 0.03$). Measurement biases and errors associated with the use of closed, unvented chambers for N_2O flux measurements could have impacted the magnitude of our results [*Matthias et al.*, 1978; *Hutchinson and Livingston*, 2001]; however, even a large underestimation of the actual flux is unlikely to have changed the interpretation that N_2O emissions were extremely low and therefore a minor component of the N cycle at this site.

5. Discussion

[26] Long-term exposure to elevated CO_2 decreased reactive N gas emissions from Mojave Desert soils, indicating changes in the cycling and availability of N. In the spring and fall when recent precipitation, either natural or artificial, created soil conditions that are optimal for biological activity[*Naumburg et al.*, 2003; *Huxman et al.*, 2003], long-term fumigation with elevated CO_2 yielded reductions in reactive N gas loss in the islands of fertility created by the dominant shrub *L. tridentata*. Decreased N gas loss under elevated CO_2 was characterized by large reductions in NO and NH_3, which suggests a change in NH_4^+ availability for nitrification and volatilization. We propose that these shifts in N dynamics could be driven either by decreased N supply from litter, roots or N fixation, or increased N uptake by plants or microbes.

[27] One potential mechanism for the observed reductions in gaseous N loss under elevated CO_2 is decreased N supply limiting the substrate for NH_3 volatilization and NO production during nitrification. However, studies on the dominant sources of N into these soils: litter, fine root turnover and N fixation in biological soil crusts all show that elevated CO_2 has little to no effect on these processes in the Mojave Desert. Measurements of leaf litter chemistry at the Desert FACE site show no changes in response to elevated CO_2 [*Billings et al.*, 2003b] or a small increase in C:N [*Weatherly et al.*, 2003]. Additionally, there is no evidence of changes in litter inputs or decomposition rates in this desert ecosystem following long-term exposure to elevated CO_2 [*Weatherly et al.*, 2003]. While it has been proposed that changes in fine root dynamics can provide important explanatory power in understanding responses of below-ground N cycling to elevated CO_2 [*Zak et al.*, 2000], in the Mojave Desert exposure to elevated CO_2 has not altered the fine root standing stock, production or mortality beneath shrubs [*Phillips et al.*, 2006]. Changes in new N inputs from N fixation under elevated CO_2 could also directly impact the processes that drive N gas production, yet multiple measurements of N fixation rates in this system show no changes in response to elevated CO_2 [*Billings et al.*, 2003a; *Schaeffer et al.*, 2007].

[28] The lack of a response to elevated CO_2 of multiple factors influencing N supply to desert soils suggests that changes in internal N cycling are responsible for growing season reductions in N gas loss from Mojave soils. Increased availability of labile C in soils exposed to elevated CO_2 resulting from increased rhizodeposition by shrubs [*Nguyen*, 2003] provides a mechanism by which elevated CO_2 changes resources for microbial metabolism, increasing demand for and immobilization of N, ultimately lowering gaseous N losses in the islands of fertility created by shrubs. We know that the availability of carbon substrate can limit microbial activity in the Mojave Desert [*Schaeffer et al.*, 2003], that additions of labile C sources cause increased N immobilization [*Gallardo and Schlesinger*, 1995; *Schaeffer et al.*, 2003] and decreased NO and NH_3 efflux [*McCalley and Sparks*, 2008] similar to what we see under elevated CO_2. Further, meta-analysis of the effects of elevated CO_2 on soil nutrient dynamics shows that increases in immobilization of N linked to increased microbial N demand is a common response to elevated CO_2 across a wide range of ecosystems

[*de Graaff et al.*, 2006]. While direct measurements of microbial biomass N at the Desert FACE site have provided inconsistent results showing increases [*Schaeffer et al.*, 2007] and decreases [*Jin and Evans*, 2007] under elevated CO_2, ^{15}N enrichment of *L. tridentata* leaves growing under elevated CO_2 [*Billings et al.*, 2002b] could be indicative of increased microbial activity and utilization of N by the microbial community.

[29] Changes in mineralization or nitrification rates under elevated CO_2 can also provide insights into the mechanisms contributing to shifts in reactive N gas loss. Mineralization of organic N to NH_4^+ provides the substrate for NH_3 volatilization as well as NO production through nitrification. The outcome of competition between nitrification and volatilization then drives patterns in the composition of total reactive N gas emissions and likely the observed patterns in the composition of the elevated CO_2 response [*McCalley and Sparks*, 2008]. Although there were small and inconsistent CO_2 effects on net N mineralization in the Mojave Desert [*Billings et al.*, 2002a; *Schaeffer et al.*, 2007], reductions in gross N mineralization are consistent with the observed reductions in NO and NH_3 efflux [*Jin and Evans*, 2007] as are measurements showing lower inorganic N (NH_4^+ and NO_3^-) availability under elevated CO_2 [*Billings et al.*, 2002b]. Instantaneous rates of gross nitrification show minimal responses to elevated CO_2 [*Jin and Evans*, 2007], but net measurements show a reduction beneath shrubs in the high CO_2 plots [*Schaeffer et al.*, 2007] consistent with our observations of lower NO emissions in these islands of fertility. Overall responses at the Desert FACE site suggest that reductions in reactive N gas emissions under elevated CO_2 could be associated with changes in N cycling rates including decreased mineralization and nitrification.

[30] Increased N uptake by plants under elevated CO_2 would also decrease substrate availability for nitrification and volatilization resulting in reductions in reactive N gas emissions. At the Desert FACE site, increases in shrub productivity and annual biomass under elevated CO_2 have been observed during periods of high water availability [*Housman et al.*, 2006; *Smith et al.*, 2000], potentially increasing plant N demand during the periods when reduced N gas loss were observed. Seasonal patterns in plant photosynthetic responses to elevated CO_2 at the Desert FACE site were similar to those observed for reactive N gas emissions, with the largest increases in carbon fixation occurring during wet springs or following large fall precipitation events [*Naumburg et al.*, 2003]. Exposure to elevated CO_2 did not extend the photosynthetically active period of shrubs into the dry season [*Naumburg et al.*, 2003], supporting the hypothesis that changes in plant N demand under elevated CO_2 and the resulting effects on reactive N gas emission are restricted to the growing season during high precipitation years.

[31] The responses to elevated CO_2 observed in this study continued for at least several months after the end of the treatment period, suggesting a CO_2 legacy effect on the mechanism driving changes in N gas efflux. Changes in substrate availability for N gas emissions due to increased plant N demand under elevated CO_2 could have a longer-term affect on soil N dynamics either through lasting changes in the available N pool or because growth increases under elevated CO_2 resulted in plants that continue to have higher N demands even when no longer exposed to higher CO_2 conditions. Alternations in substrate availability for microbial communities hypothesized to increase demand for and immobilization of N also have the potential to persist for a period following the end of CO_2 fumigation. Alternatively, these results could indicate that the responses are independent of the FACE treatment and are instead due to natural, spatial variability in N gas emissions. However, this is unlikely due to the rigorous site selection and experimental design standards for the FACE experiment [*Jordan et al.*, 1999].

[32] The Mojave Desert is not unique in that long-term exposure to elevated CO_2 can cause reductions in gaseous N loss due to alterations in microbial utilization of N. Although measurements of reactive N gas emissions under elevated CO_2 are limited, patterns similar to what we see in the Mojave Desert have been documented in other systems. When exposed to elevated CO_2 and given nutrient subsidies, grassland ecosystems in both California and Colorado exhibited increases in N immobilization coupled with substantial decreases in nitrification and NO efflux [*Hungate et al.*, 1997; *Mosier et al.*, 2003]. In the Colorado Shortgrass Steppe, N_2O emissions were also slightly lower under elevated CO_2; further suggesting reduced N availability for the microbial community. While there is a lack of data on responses of N gas loss to elevated CO_2 across a wide range of ecosystems, generalized responses of increased N immobilization [*de Graaff et al.*, 2006] and soil respiration [*Zak et al.*, 2000] could indicate widespread reduction in substrate availability for processes that yield N gas emissions.

[33] Our data suggest that while growing season emissions of reactive N gases can be substantially altered by rising atmospheric CO_2 concentrations, summertime losses, including the large pulses of N gas emissions following monsoonal rain events are not affected by elevated CO_2. Summer fluxes largely result from chemical formation of reactive N, which utilize soil stocks of N and are maximized under high soil moisture and temperature conditions [*McCalley and Sparks*, 2009]. Likely, chemical losses did not respond to elevated CO_2 because the accumulation of mineral N that typically occurs during dry periods in desert ecosystems [*Austin et al.*, 2004] meant they were not substrate limited but rather controlled by physical soil conditions, particularly temperature and moisture. On an annual basis these summertime N gas losses represent approximately 10–60% of total reactive N gas emissions, with the remaining N gas efflux mostly occurring during the growing season [*McCalley*, 2010]. Seasonal variability is driven by the fact across years summertime precipitation at this site ranges from 70% to as little as 10% of total precipitation [*Blainey et al.*, 2007]. Changes to N gas efflux under rising atmospheric CO_2 concentrations will therefore be closely linked to precipitation patterns and while climate models predict future shifts in the timing and/or amount of precipitation, there is little consensus on the nature of this change [*IPCC*, 2007].

6. Summary and Conclusions

[34] Combining seasonal measurements of reactive N gas emissions and our understanding of the response of other

ecosystem parameters to elevated CO_2 provides insight into the nature of desert responses to global change. Our results suggest that elevated CO_2 alters soil N dynamics in arid ecosystems. Reductions in NO and NH_3 efflux during periods of peak biological activity point toward increased plant N uptake and decreased N mineralization and nitrification as likely changes to soil nutrient cycling under elevated CO_2. Ultimately, these alterations in reactive N gas efflux have important implications for nutrient availability and biosphere-atmosphere interactions in arid regions. Specifically, changes in plant and microbial demand for N under elevated CO_2 reduces reactive N gas fluxes by >60% during periods of peak N demand, increasing the retention of biologically available N during critical growth periods. Given that annual emissions of reactive N gases are approximately 1 kg N ha^{-1} in the Mojave Desert [*McCalley and Sparks*, 2008; *McCalley*, 2010] a magnitude that is roughly equivalent to 20–25% of the total N taken up by plants annually and 30% of total exogenous N inputs [*Rundel and Gibson*, 1996], changes in this flux represent a biologically relevant alteration in N losses from a N-limited desert ecosystem. Of this annual N gas efflux, as much as 30% occurs during the growing season period impacted by elevated CO_2 [*McCalley*, 2010]. In El Ninõ years when growing season N gas emissions are greatest and N demand highest, elevated CO_2 reduces annual N gas loss by close to 20%. Conversely, these responses alter the flux of new reactive gases into the atmosphere, potentially impacting local atmospheric processes in otherwise pristine and remote desert regions.

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