

# Controls over nitric oxide and ammonia emissions from Mojave Desert soils

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**Abstract** Emissions of reactive N compounds produced during terrestrial N cycling can be an important N loss pathway from ecosystems. Most measurements of this process focus on NO and N<sub>2</sub>O efflux; however, in alkaline soils such as those in the Mojave Desert, NH<sub>3</sub> production can be an important component of N gas loss. We investigated patterns of NO and NH<sub>3</sub> emissions in the Mojave Desert and identified seasonal changes in temperature, precipitation and spatial heterogeneity in soil nutrients as primary controllers of soil efflux. Across all seasons, NH<sub>3</sub> dominated reactive N gas emissions with fluxes ranging from 0.9 to 10 ng N m<sup>-2</sup> s<sup>-1</sup> as compared to NO fluxes of 0.08–1.9 ng N m<sup>-2</sup> s<sup>-1</sup>. Fluxes were higher in April and July than in October; however, a fall precipitation event yielded large increases in both NO and NH<sub>3</sub> efflux. To explore the mechanisms driving field observations, we combined NO and NH<sub>3</sub> soil flux measurements with laboratory manipulations of temperature, water and nutrient conditions. These experiments showed a large transient NH<sub>3</sub> pulse (~70–100 ng N m<sup>-2</sup> s<sup>-1</sup>) following water addition, presumably driven by an increase in soil NH<sub>4</sub><sup>+</sup> concentrations. This was followed by an increase in NO production, with maximum NO flux rates of 34 ng N m<sup>-2</sup> s<sup>-1</sup>. Our study suggests that immediately following water addition NH<sub>3</sub> volatilization proceeds at high rates due to the absence of microbial competition for NH<sub>4</sub><sup>+</sup>; during this period N gas loss is

insensitive to changes in temperature and soil nutrients. Subsequently, NO emission increases and rates of both NO and NH<sub>3</sub> emission are sensitive to temperature and nutrient constraints on microbial activity. Addition of labile C reduces gaseous N losses, presumably by increasing microbial immobilization, whereas addition of NO<sub>3</sub><sup>-</sup> stimulates NO and NH<sub>3</sub> efflux.

**Keywords** Nitrification · Microbial activity · Biological soil crust · *Larrea tridentata*

## Introduction

In the presence of sufficient water, N is thought to limit productivity in many arid environments; however, our understanding of the processes that control N availability in these systems is still limited (Verstraete and Schwartz 1991). Relative to internal storage and turnover, N losses from deserts are small (Rundel and Gibson 1996), yet understanding these fluxes is intrinsic to the understanding of long-term ecosystem N dynamics. In comparison to other terrestrial environments, N loss mechanisms such as leaching are typically small in deserts. For example, fluxes for the Mojave Desert have been approximated at < 2 kg N ha<sup>-1</sup> year<sup>-1</sup> for leaching and erosion losses combined (Rundel and Gibson 1996). This means that in such environments, understanding gaseous emissions will be necessary for closure of the N cycle.

To date, studies have focused on measuring emissions of NO and N<sub>2</sub>O to quantify gaseous N loss from soils; however, many arid environments have highly alkaline soils, meaning that NH<sub>3</sub> volatilization may be an important and largely unstudied N loss term (Dawson 1977; Schaeffer et al. 2003). Measurements in the Mojave Desert indicate

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that N<sub>2</sub>O efflux is highly variable both spatially and temporally and is unlikely to be a substantial form of N loss (Billings et al. 2002) and NO and NH<sub>3</sub> emissions are predicted to dominate trace N gas fluxes. Multiple studies have identified nitrification and denitrification as sources of NO (e.g. Davidson et al. 1993; Firestone and Davidson 1989; Parton et al. 2001; Skiba et al. 1993), with fluxes regulated by factors that include the concentration of inorganic N (NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>), soil moisture, temperature, accessibility of labile C, and physical soil properties (Hall et al. 1996; Parton et al. 2001; Skiba et al. 1993). Similar to NO production from nitrification, rates of NH<sub>3</sub> volatilization should be sensitive to soil conditions that influence NH<sub>4</sub><sup>+</sup> concentrations and turnover in the soil (Nelson 1982; Schlesinger and Peterjohn 1991). Given this overlap in substrate use between nitrification and NH<sub>3</sub> volatilization, it is important to not only quantify rates and controls over NH<sub>3</sub> production from desert soils, but also identify the relationships between soil fluxes of NH<sub>3</sub> and NO.

Turnover of N in arid ecosystems is characterized by brief periods of intense biological activity following precipitation events (Austin et al. 2004; Belnap et al. 2005; Noy-Meir 1973). Rates of N cycling during these periods are controlled by abiotic factors, especially temperature, as well as soil nutrient availability (Fernandez et al. 2006; Gallardo and Schlesinger 1995). Arid environments have high spatial heterogeneity in soil resources, resulting in variation in N dynamics across the landscape, with patterns often associated with the accumulation of soil nutrients beneath shrubs (Schlesinger et al. 1996).

In addition to being sensitive to the size and composition of the soil N pool, microbial transformations of N also depend on C availability. C provides fuel for heterotrophic microbial processes including N mineralization and immobilization, and therefore natural variations in soil C as well as C additions have been shown to influence soil N dynamics (Gallardo and Schlesinger 1995; Schaeffer et al. 2003; Zaady et al. 1996). It is clear that C, N, and water availability influence N transformations that lead to production of N gases, but what remains unclear is whether these factors exert similar controls over both NO and NH<sub>3</sub> emission and whether our understanding of NO efflux from less alkaline systems still holds for systems with high rates of NH<sub>3</sub> volatilization.

The field component of this study was designed to characterize the role of reactive N gas emissions in desert N cycling, specifically addressing the relative importance of NO and NH<sub>3</sub> efflux. These measurements provided us with baseline data on temporal and spatial variation in the size and composition of reactive N gas efflux. In the laboratory, we focused on the response of NO and NH<sub>3</sub> emissions to a simulated rain event and examined how changing temperature, C and N availability altered this

response. We hypothesized that: (1) emissions of both NO and NH<sub>3</sub> would increase following water addition and fluxes would remain elevated for several days, but that the magnitude and timing of this response would be different for the two gas species; (2) the direct role of biological processes, nitrification and denitrification, in NO production as compared to the indirect role of biological processes in NH<sub>3</sub> production would result in NO efflux being more sensitive to temperature, with higher NO fluxes occurring at higher temperatures; and (3) NO and NH<sub>3</sub> emissions following water addition would increase with the addition of N and decrease with the addition of C due to similar responses to changes in N mineralization and immobilization. In addition, we predicted that the higher resource availability in “islands of fertility” associated with the dominant shrub *Larrea tridentata* (Romney et al. 1980; Titus et al. 2002) would yield consistently higher rates of NO and NH<sub>3</sub> efflux. In contrast, lower resource availability in interspace soils should make effluxes from these areas generally lower and more sensitive to changes in nutrient conditions.

## Materials and methods

### Study site

Field measurements and soil collections were conducted at the Mojave Global Change Facility located in Nye County, Nevada (36°49'N, 115°55'W), 90 km northwest of Las Vegas, Nevada, USA at an elevation of 970 m. The site lies within the Nevada test site (NTS), administered by the USA Department of Energy (DOE) 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 summers >47°C. The site is a *Larrea tridentata*—*Ambrosia dumosa* plant community and has intact biological soil crusts covering ~20% of the soil surface (Titus et al. 2002). Soils are Aridisols derived from calcareous alluvium with a loamy sand texture (89% sand, 6% silt and 5% clay). Subsoils lack a caliche layer, resulting in well-drained soils. Soil pH at the site ranges from 9 to 11 (Evans unpublished data) and soils are spatially heterogeneous in nutrients, texture and infiltration (Romney et al. 1980).

### Field measurements

Field measurements were made using soil collars, which were 25.5 cm in diameter, 15 cm tall, and were installed approximately 7.5 cm into the soil profile in June 2004.

There were a total of 16 soil collars, four in each of the following cover types: under the evergreen shrub *L. tridentata* (creosote bush), under the C<sub>4</sub> bunchgrass *Pleuraphis rigida* (big galletta), soil interspace with visible biological soil crust, and soil interspace with no visible crust. Visibility of the biological soil crust was determined qualitatively by the presence or absence of lichen and moss. Instantaneous flux measurements of NO, NO<sub>y</sub> (all oxidized forms of N) and NH<sub>3</sub> were made once in each collar during 2-week periods in October 2004, April 2005, and July 2005 (only ten collars were sampled in April and 12 in October). All measurements were made between mid morning and late afternoon. In addition to background flux measurements, a large natural rain event (37.8 mm) in October 2004 enabled us to make pre- and post-rain event measurements (fluxes were measured in three collars per cover type prior to the rain event and all 16 collars after the rain event). Due to logistical constraints, the post-rain event measurements were spread across several days and each collar was sampled once during a 6-day period.

#### Soil profile collection

Intact soil profiles were collected on 17 April 2005 in areas with visible biological soil crust, no visible biological soil crust and soils beneath *L. tridentata*. Eight soil profiles were collected in each soil type. PVC pipes measuring 25.5 cm in diameter and 15 cm in depth were driven 7.5 cm into the ground using a rubber mallet. They were then excavated such that a stiff canvas cloth could be placed under the piping, ensuring the integrity of the profile. The soil cores were then placed in plastic tubs filled with 3–5 cm sand, installed in a custom-designed transport container and driven with minimal disturbance to Cornell University where they were stored in a greenhouse at 21°C. After arrival at Cornell, paraffin wax was used to seal the sand surface surrounding the PVC-encased soil profile. This set-up allowed a system where water could drain naturally from the profile and collect in the sand below.

#### Laboratory incubations

We conducted two laboratory incubation experiments in growth chambers (CMP 3244, Conviron). Environmental conditions for both experiments were 12-h day length, photosynthetically active radiation of 350 μmol m<sup>-2</sup> s<sup>-1</sup>, and 20% relative humidity. One month prior to the first set of experimental measurements, the soil profiles were moved from the greenhouse and into the growth chambers where half were incubated at 17.5°C and half at 35°C.

At the time of measurement, each profile received distilled water in the form of a 20-mm rain event and NO and NH<sub>3</sub> flux measurements were made before (day 0), within

30 min of watering (day 1), and 1, 2 and 5 or 6 days after the water addition.

The soil cores were then stored in a greenhouse (21°C) for 3 months before a second laboratory incubation experiment was conducted. One month prior to the second experiment all cores were transferred to growth chambers and incubated at 35°C. Again each core received a 20-mm rain event; however, this time half of the cores also received a N addition in the form of 20 μg KNO<sub>3</sub>-N g<sup>-1</sup> dry soil, approximately 5 times the ambient concentration of inorganic N in the soil, and the other half received a C addition in the form of 400 μg dextrose-C g<sup>-1</sup> dry soil. Nutrient addition amounts were calculated using an average dry mass per soil core of 7 kg and additions were based on concentrations used by Schaeffer et al. (2003) when measuring N cycling responses of Mojave Desert soils to nutrient additions. NO and NH<sub>3</sub> flux measurements were made before (day 0), within 30 min of watering (day 1), and 1, 2 and 5 or 6 days after the water and nutrient addition.

#### Reactive N gas flux measurements

N gas fluxes (NO, NO<sub>y</sub>, and NH<sub>3</sub>) were measured using selective thermal and chemical decomposition converters to reduce or oxidize all reactive N trace gases (e.g., oxidized forms and NH<sub>3</sub>) to NO. During measurement, a sealed top constructed of UV-transparent material (FEP Teflon) was placed over the collar. The collar top had two Teflon ports and a small mixing fan to ensure natural turbulent conditions within the collar. This system is open to the atmosphere, which minimizes induced pressure differences associated with chamber-based measurement techniques.

To make a measurement, outside air is passed, at 1 l min<sup>-1</sup>, through a large-volume (750 ml) charcoal filter to scrub out reactive N and then through the collar and into the measurement system. Air concentrations of reactive N at the time of measurement were <0.5 p.p.b. NO and <2 p.p.b. NH<sub>3</sub> making it unlikely that changes in the diffusion gradients caused by scrubbing incoming air were large enough to alter soil fluxes. The measurement system consists of two conversion cells that reduce NO<sub>y</sub> (total oxidized N) and total reactive N (NO<sub>y</sub> + NH<sub>3</sub>) to NO, respectively, and a chemiluminescence NO detector. Each converter can be isolated by Teflon valves and independent measurements can be made for NO (no conversion), NO<sub>y</sub> (NO<sub>y</sub> converter only), and total reactive N (NH<sub>3</sub> + NO<sub>y</sub> conversion). Fluxes were calculated based on steady-state concentrations using the equation  $C \times q/A$  where  $C$  is concentration (nmol l<sup>-1</sup>),  $q$  is the flow rate (l s<sup>-1</sup>) and  $A$  is area (m<sup>2</sup>) of the soil surface, and NH<sub>3</sub> fluxes were calculated by subtracting the NO<sub>y</sub> flux from the total reactive N

flux. Measurements of NO, NO<sub>y</sub> and NH<sub>3</sub> were made sequentially and total measurement time averaged 20–30 min. The NH<sub>3</sub> conversion cell consists of a 30-cm length of nickel-chromium alloy tubing (INCONEL 600) passed through a mini tube furnace (model F21125; Barnstead International) heated to 825°C. Laboratory calibrations of the converter have shown 86% conversion efficiency for NH<sub>3</sub> with no influence on NO concentration. The NO<sub>y</sub> 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<sub>2</sub> (30 ml min<sup>-1</sup>) 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<sub>2</sub> and HONO and conversion efficiencies between 78 and 99% for other components of NO<sub>y</sub> (i.e., peroxyacetyl nitrate, alkyl nitrate, HNO<sub>3</sub> and other forms of NO<sub>y</sub> usually formed in the atmosphere).

After conversion (or directly in the case of the NO only measurement), air is passed through an NO analyzer (model CLD 770; Ecophysics). The CLD 770 detects light from the chemiluminescence reaction between NO and O<sub>3</sub>:



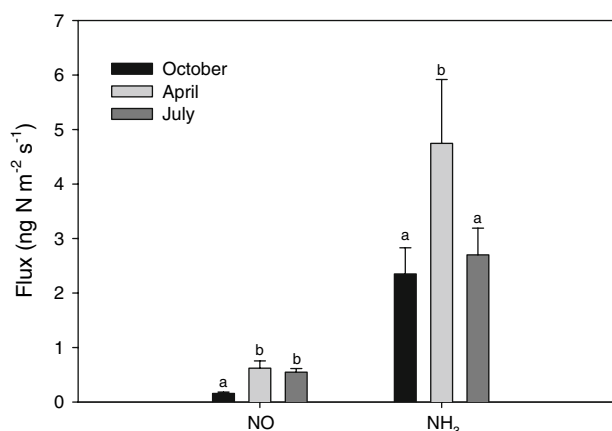
The analyzer avoids interferences (a common problem with many NO analyzers) using a pre-reaction chamber where O<sub>3</sub> is used to consume NO before entering the reaction chamber. Because the rate of reaction with NO is very fast and the reaction with most interference compounds is relatively slower, two sequential runs (the first utilizing the pre-reaction cell and second going directly to the sample cell without pre-reaction) allows for the quantification of NO independent of all interferences and gives instrument a detection limit of 50 p.p.t.v. The instrument was calibrated by sequential dilution of an NO standard (Scott Specialty Gases, Irvine, Calif.) daily.

### Statistical analysis

We used analysis of variance (PROC MIXED, SAS 9.1) with a Tukey post hoc test to determine the effects of season, cover type, and precipitation on field fluxes of NO and NH<sub>3</sub> as well as the effects of temperature, cover type and water/nutrient addition on NO and NH<sub>3</sub> fluxes through time under laboratory conditions. All analyses were performed using SAS statistical software (Cary, N.C.). Statistical significance was determined at  $\alpha = 0.05$ . Errors are presented as  $\pm 1$  SE.

## Results

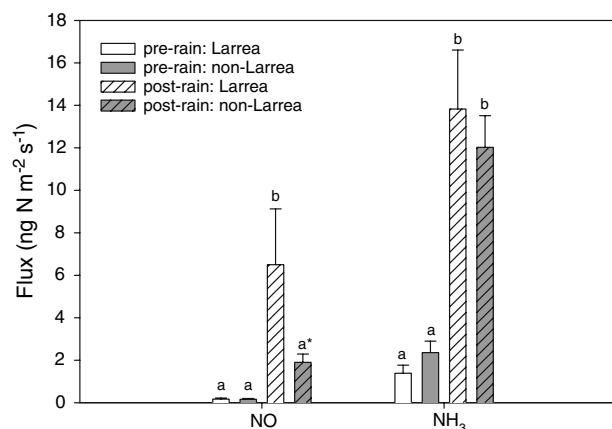
NH<sub>3</sub> and NO fluxes from dry soils varied significantly with season, NH<sub>3</sub> fluxes were significantly higher in April than



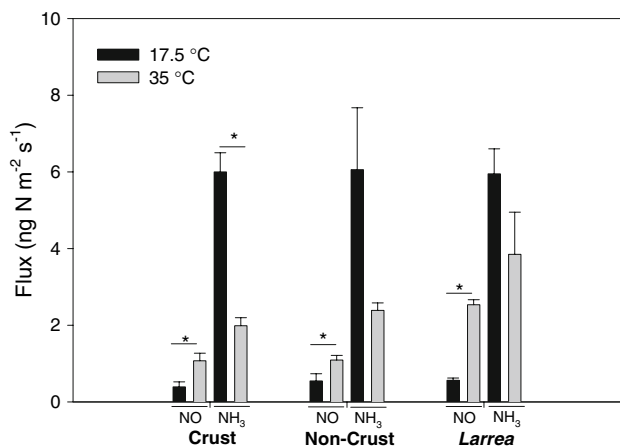
**Fig. 1** Seasonal patterns of NO and NH<sub>3</sub> efflux from dry Mojave Desert soils (different letters indicate significant differences between flux measurements for a particular gas species)

in either October ( $P = 0.02$ ) or July ( $P = 0.04$ ), while NO fluxes were significantly lower in October than in either April ( $P = 0.002$ ) or July ( $P = 0.006$ ) (Fig. 1). Variation in fluxes among cover types did not influence seasonal patterns; therefore cover types were pooled for clarity. Total losses of reactive N in the spring were double those measured in the fall, and although NO fluxes were elevated in the summer, overall summer N gas losses were only marginally larger than those measured in the fall. NH<sub>3</sub> was the dominant reactive N gas species emitted from dry soils. NH<sub>3</sub> fluxes ranged from 0.9 to 10 ng N m<sup>-2</sup> s<sup>-1</sup> whereas NO fluxes were smaller, with values ranging from 0.08 to 1.6 ng N m<sup>-2</sup> s<sup>-1</sup>.

Following a natural rain event there was a significant increase in soil fluxes of NO ( $P = 0.002$ ) and NH<sub>3</sub> ( $P < 0.0001$ ) (Fig. 2). Increases in soil emissions were



**Fig. 2** Soil NO and NH<sub>3</sub> fluxes before and after a natural rain event in the Mojave Desert (different letters represent significant differences between flux measurements within a gas species, the asterisk above the non-Larrea post-rain NO flux indicates that there is a trend ( $P = 0.07$ ) towards a difference between pre and post-rain values)



**Fig. 3** The effect of temperature and cover type on NO and NH<sub>3</sub> efflux from dry Mojave Desert soil (asterisks indicate a significant differences between 17.5 and 35°C)

substantial; post-rain NO and NH<sub>3</sub> fluxes were 8–40 and 5–10 times higher than pre-rain fluxes, respectively. There was a significant rain by cover type interaction for NO efflux ( $P = 0.02$ ); post-rain fluxes of NO were significantly higher in soils under *L. tridentata* than in soils from the other cover types ( $P = 0.0009$ ). Similar to dry soils, NH<sub>3</sub> dominated post-rain reactive N gas fluxes, with 4 times higher efflux compared to NO.

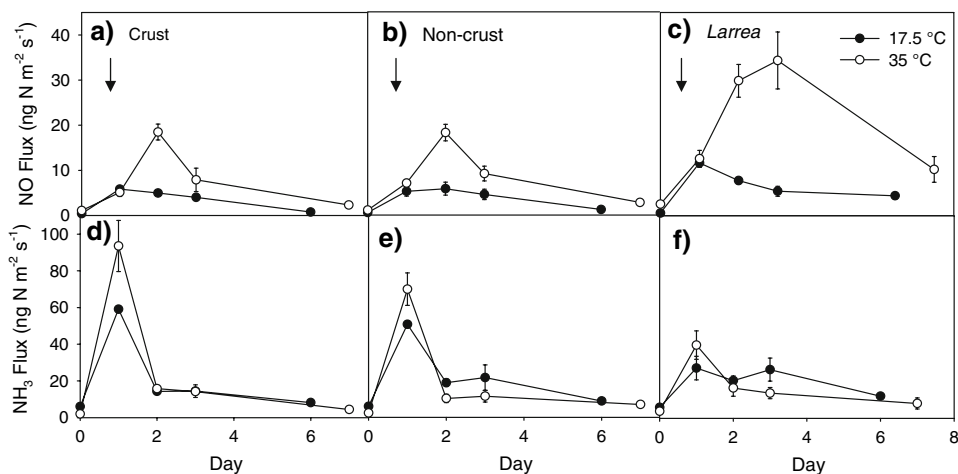
Under laboratory conditions, temperature had an opposing effect on NO compared to NH<sub>3</sub> emission from dry soils (Fig. 3). In all soils, NO emissions were higher from soils incubated at 35°C compared to 17.5°C ( $P < 0.04$ ), whereas NH<sub>3</sub> emissions were significantly higher at 17.5°C from crust soils ( $P = 0.001$ ) and there was a trend towards this pattern in non-crust soils ( $P = 0.1$ ). At both incubation temperatures, NH<sub>3</sub> efflux was higher than NO efflux. This difference was particularly pronounced at 17.5°C, where soil fluxes of NH<sub>3</sub> were more than 10 times greater than NO fluxes. In contrast, at 35°C

there was only a 1.5–twofold difference between NH<sub>3</sub> and NO efflux. In terms of overall magnitude of emission, interspace soils (crust and no crust soils) exhibited nearly double the total reactive N gas fluxes at 17.5°C compared to those measured at 35°C. In contrast, emissions from soils derived from under *L. tridentata* were similar ( $\sim 5\text{--}6 \text{ ng N m}^{-2} \text{ s}^{-1}$ ) regardless of temperature.

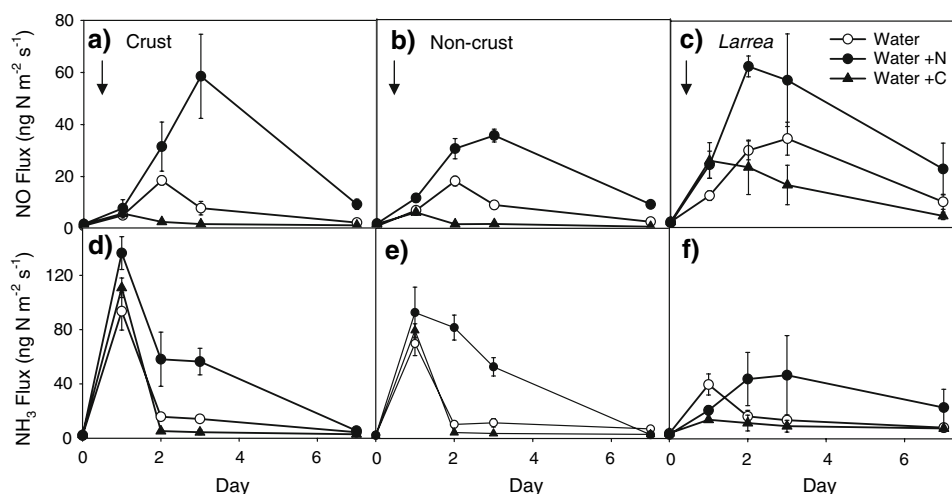
The addition of water to soil profiles caused significant changes in emissions of NO ( $P < 0.0001$ ) and NH<sub>3</sub> ( $P < 0.0001$ ) (Fig. 4). Immediately following water addition (day 1), there was a large, transient NH<sub>3</sub> pulse. This pulse was particularly pronounced in crust and non-crust soils where fluxes averaged 94 and 70 ng N m<sup>-2</sup> s<sup>-1</sup>, respectively. NO fluxes also increased following water addition; however, this response was delayed relative to the NH<sub>3</sub> response, with fluxes peaking 1 to 2 days after the addition of water. Peak post-water fluxes of NO were highest in *Larrea* soils; with maximum NO effluxes of 34 ng N m<sup>-2</sup> s<sup>-1</sup> as compared to 18 ng N m<sup>-2</sup> s<sup>-1</sup> in interspace soils.

There were significant interactions between the response of reactive N gas emissions to soil wetting, cover type ( $P < 0.0001$ ) and incubation temperature ( $P < 0.0001$ ) (Fig. 4). Crust and non-crust soils had similar patterns of NO and NH<sub>3</sub> efflux following water addition and this response was different from that observed from *Larrea*-influenced soils. The NH<sub>3</sub> pulse observed immediately following soil wetting was substantially higher in interspace soils as compared to *Larrea*-influenced soils, with interspace fluxes approximately double those measured from *Larrea* soils. NO efflux showed the opposite pattern, with peak fluxes from *Larrea* soils being double those measured from interspace soils. All cover types exhibited similar responses to increasing temperature from 17.5 to 35°C, with higher incubation temperature yielding higher post-water fluxes of both NH<sub>3</sub> and NO. Temperature had a particularly strong effect on post-water NO efflux: peak

**Fig. 4a–e** Response of NO and NH<sub>3</sub> efflux to a pulse water addition at two temperatures (20-mm water addition is indicated by arrows). **a, d** flux from soils with a visible biological soil crust; **b, e** flux from soils with no visible biological soil crust; **c, f** flux from soils collected beneath *Larrea tridentata*



**Fig. 5a–f** The influence of C and N availability on the response of NO and NH<sub>3</sub> efflux to a pulse water addition (20-mm water addition is indicated by arrows). **a, d** flux from soils with a visible biological soil crust; **b, e** flux from soils with no visible biological soil crust; **c, f** flux from soils collected beneath *L. tridentate*



NO fluxes from soils incubated at 35°C were 3 times those from soils incubated at 17.5°C.

C (dextrose) and N (KNO<sub>3</sub>) had a significant effect on post-wetting fluxes of NO ( $P < 0.0001$ ) and NH<sub>3</sub> ( $P < 0.0001$ ) (Fig. 5). N addition stimulated both NO and NH<sub>3</sub> efflux in all soils, prolonging the period of elevated NH<sub>3</sub> emissions from one to several days and more than doubling the maximum NO efflux for all cover types. In contrast, C addition caused a dramatic reduction in reactive N gas emissions, especially from crust and non-crust soils.

As with the water addition, crust and non-crust soils showed a similar response to nutrient additions, while *Larrea*-influenced soils responded differently. The effect of cover type is apparent when comparing the response of soil NO efflux to labile C additions (Fig. 5, closed triangles). In crust and non-crust soils, treatment with C virtually eliminated the post-water NO pulse and caused NH<sub>3</sub> emissions to rapidly return to baseline levels following the simulated rain event. In contrast, treatment of *Larrea* soils with labile C did not have a large effect on the magnitude of NO or NH<sub>3</sub> emissions; however, it did cause a shift in the timing of the response, with fluxes peaking on day 1 instead of day 3.

## Discussion

This study simultaneously quantified soil emissions of NO and NH<sub>3</sub> and indicated that in alkaline soils, such as those found in the Mojave Desert, NH<sub>3</sub> is the dominant form of reactive trace N gas loss. Our estimates of NH<sub>3</sub> volatilization also suggest that the acid trap method employed in previous studies underestimate instantaneous NH<sub>3</sub> emissions. Field fluxes of NH<sub>3</sub> from dry soils were 1.5–3.5 times those measured by Billings et al. (2002) and were similar in magnitude to those measured in wet soils by

Schaeffer et al. (2003). Additionally, our range of post-wetting NH<sub>3</sub> pulses of  $\sim 28$ – $140$  ng N m<sup>-2</sup> s<sup>-1</sup> were comparable to the maximum pulse of  $\sim 112$  ng N m<sup>-2</sup> s<sup>-1</sup> reported in Schaeffer and Evans (2005) for the Colorado Plateau.

NO flux estimates of 0.14–2.5 ng N m<sup>-2</sup> s<sup>-1</sup> from dry soils in this study fall within the range of measurements reported for other arid and semi-arid environments. Measurements from semi-arid grassland and shrubland sites range from 0.2 to 2.8 ng N m<sup>-2</sup> s<sup>-1</sup> (Smart et al. 1999) and 2.6–5.7 ng N m<sup>-2</sup> s<sup>-1</sup> (Martin et al. 1998) for short-grass steppe ecosystems and 0.4–8.7 ng N m<sup>-2</sup> s<sup>-1</sup> across a mesquite gradient (Martin et al. 2003). In the Chihuahuan Desert, Hartley and Schlesinger (2000) measured fluxes of  $<0.3$  ng N m<sup>-2</sup> s<sup>-1</sup> in the dry season and 0.3–97 ng N m<sup>-2</sup> s<sup>-1</sup> during the wet season. Wetting of Mojave soils produced an NO pulse ranging from  $\sim 7$ – $35$  ng N m<sup>-2</sup> s<sup>-1</sup>, similar to pulses of 37 and 14 ng N m<sup>-2</sup> s<sup>-1</sup> from grassland and shrubland soils, respectively, in the Chihuahuan Desert. When looking at NO flux estimates for a range of natural ecosystems, fluxes from the Mojave Desert are larger than or comparable to estimates for temperate forests, comparable in magnitude to several flux estimates from dry soils in tropical forests and savannas (Davidson et al. 1991; Johansson et al. 1988; Rondon et al. 1993; Sanhueza et al. 1990), and lower than estimates from more mesic tropical forest and savanna ecosystems (Cardenas et al. 1993; Johansson et al. 1988; Johansson and Sanhueza 1988; Serca et al. 1994). The peak NO pulses measured in our laboratory experiment were lower than the approximately 140 ng N m<sup>-2</sup> s<sup>-1</sup> NO pulse measured by Davidson et al. (1993) in a seasonally dry tropical forest in Mexico or the 150–250 ng N m<sup>-2</sup> s<sup>-1</sup> post-rain flux measured by Johansson and Sanhueza (1988) in a tropical savanna. However, the combined NO + NH<sub>3</sub> pulse (39–112 ng N m<sup>-2</sup> s<sup>-1</sup>) following wetting of

Mojave soil in our study suggests that pulse rain events in arid environments, especially those with high alkalinity, lead to total losses of reactive N gases comparable to other systems.

The seasonal measurements of NO and NH<sub>3</sub> fluxes collected under ambient soil conditions in this study can be used to develop an estimate of the contribution of N gas emission to the annual N budget in the Mojave Desert. Assuming that each of the three seasons measured in this study represent one quarter of the total year, with the fourth quarter being winter months whose N gas production is likely to be minimal (estimated at 1/2 the N gas flux measured in October), then N gas losses in the form of NO and NH<sub>3</sub> are ~1 kg N ha<sup>-1</sup> year<sup>-1</sup>, with NH<sub>3</sub> comprising ~90% of the flux. If you factor in the considerably larger N gas pulses that occur following precipitation, an additional 0.4–0.6 kg N ha<sup>-1</sup> year<sup>-1</sup> (30–45 days of elevated fluxes) is lost as NO and NH<sub>3</sub>. Rundel and Gibson (1996) working at a similar site in the Mojave Desert estimated plant uptake at ~4.5 kg N ha<sup>-1</sup> year<sup>-1</sup> and erosion losses (including leaching) at <2 kg N ha<sup>-1</sup> year<sup>-1</sup>. These numbers suggest ~30–40% of the loss of N from this system could be in the form of gaseous NO and NH<sub>3</sub>.

In addition to providing an estimate of the contribution of NO and NH<sub>3</sub> efflux to N losses from Mojave Desert soils, the field measurements in this study enabled us to develop general characterizations of the pattern of reactive N loss from an intact arid ecosystem. Measurements made over multiple seasons suggest that throughout the year there is a continuous, small flux of reactive N gases, dominated by NH<sub>3</sub>, interspersed with short-term precipitation-induced large pulses of reactive N gases. In general, fluxes were higher in the spring than in the summer or fall (Fig. 1). These observations are consistent with the mechanism that warmer temperatures and periodic rain events stimulate nutrient turnover during the spring growing season (Fernandez et al. 2006; Rundel and Gibson 1996).

Although seasonality was a significant factor in the characterization of N gas loss from soils, spatial variability associated with cover type did not influence NO or NH<sub>3</sub> flux estimates from dry soils in this study. This may be because under dry soil conditions, fluxes were not large enough for such patterns to be detectable or, alternatively, that plant cover does not play an important role in describing spatial patterns of NO or NH<sub>3</sub> emission in this system.

A rain event in October 2004 led to considerable increases in NO and NH<sub>3</sub> emissions (Fig. 2). This is consistent with our understanding of the importance of pulse rain events in driving N dynamics and trace N gas loss in arid environments (Austin et al. 2004; Hartley and Schlesinger 2000; Martin et al. 1998; Smart et al. 1999).

Following precipitation, there was spatial variation in N gas loss associated with cover type, with NO emissions being highest from soils under *L. tridentata*. Variation in soil nutrients between shrub and interspace soils have been well documented in arid ecosystems (Schlesinger et al. 1996) including the Mojave Desert (Romney et al. 1980; Titus et al. 2002). Shrubs such as *L. tridentata* promote high resource availability and more rapid N turnover and these patterns are presumed to drive the observed spatial variability in N gas loss. We did not see spatial patterns in NH<sub>3</sub> emission, nor did we see effects of cover types other than *Larrea* on NO emissions. However, time constraints imposed by our measurement system meant that our post-rain event measurements were made over a 6-day period and day-to-day replication of a single measurement position was not possible. The largest differences across cover types in N gas emission, particularly NH<sub>3</sub> efflux, may have occurred immediately following the precipitation event.

In order to more fully elucidate the fine-scale mechanisms controlling N trace gas efflux from Mojave Desert soils we conducted a series of laboratory experiments. Multiple studies have shown that addition of water to dry soils can cause a large pulse of NO, due to the accumulation of N during dry periods and stimulation of microbial activity following soil wetting (e.g. Anderson and Levine 1987; Davidson 1992; Hartley and Schlesinger 2000; Johansson et al. 1988; Rondon et al. 1993). Consistent with this literature, water addition during our laboratory experiments (Fig. 4) resulted in a large NO pulse; however, this response was delayed relative to other studies that show NO fluxes peaking within hours of water addition (Barger et al. 2005; Davidson et al. 1991, 1993; Martin et al. 2003; Neill et al. 2005). The delayed post-wetting NO pulse we observed in Mojave soils may be related to the immediate, large pulse of NH<sub>3</sub> volatilization that occurred in these soils (Fig. 5). In experiments looking at interactions between NH<sub>3</sub> volatilization and nitrification, Praveen-Kumar and Aggarwal (1998) found that only one process, either nitrification or NH<sub>3</sub> volatilization, occurred at a time. They proposed that toxic levels of NH<sub>4</sub><sup>+</sup>/NH<sub>3</sub> inhibit nitrification especially in coarse-textured alkaline soils; however, when conditions allow for nitrification, NH<sub>3</sub> volatilization is dramatically reduced, possibly due to rapid drawdown of NH<sub>4</sub><sup>+</sup> by nitrifiers. In our system, an initial pulse of NH<sub>4</sub><sup>+</sup> following soil wetting coupled with high alkalinity may have caused NH<sub>3</sub> volatilization at the exclusion of nitrification, thus delaying the NO pulse that typically coincides with soil wetting. Alternately, the delayed NO pulse could be the result of slow recovery of the nitrifier population following drought conditions.

We hypothesize that there are two potential sources of N for the large NH<sub>3</sub> pulse observed immediately after the addition of water to dry, desert soil. Volatilized NH<sub>3</sub> could

come from either microbial biomass N released in response to changes in osmotic potential or from the dissolution of mineral N accumulated during the preceding dry period (Davidson et al. 1993; Miller et al. 2004; Schlesinger and Peterjohn 1991). It is likely that both are N sources; however the size of the  $\text{NH}_3$  pulse and the fact that it is highest in interspace soils where nutrient accumulation is lowest (Titus et al. 2002; Vinton and Burke 1995), suggests that microbial biomass N could be a substantial component of the initial  $\text{NH}_3$  flux. Changing osmotic conditions can result in the release of nutrients either by microbes lysing or pumping intercellular solutes into the soil solution to maintain osmotic balance (Halverson et al. 2000; Kieft et al. 1987). Experiments by Fierer and Schimel (2003) on the source of the post-rewetting  $\text{CO}_2$  pulse suggest that the primary source of N in the soil solution following rewetting is intracellular solutes expelled by microbes. It is probable that the release of N happens faster than the microbial community can respond, thus in basic soils this, in combination with  $\text{NH}_4^+$  accumulated during dry periods, appears to drive a large, transient pulse of  $\text{NH}_3$  volatilization. In our system, this pulse was much lower in *Larrea*-influenced soils suggesting that, depending on the primary source of the  $\text{NH}_3$ , these microsites either have less accumulated mineral N due to faster internal cycling or the microbial population is more resistant to changes in osmotic potential.

Following soil wetting, the composition and magnitude of N gas emissions from Mojave Desert soils were dictated largely by temperature and the nutrient status of the soil solution (Figs. 4, 5). During periods of microbial activity, inorganic N is likely consumed in the system by three processes: (1) volatilization as  $\text{NH}_3$ , (2) immobilization by microbes or plants, or (3) utilization by nitrifying and denitrifying bacteria. The first and third processes produce  $\text{NH}_3$  and NO, respectively, whereas the second process retains N in the soil, reducing rates of N gas emission. The partitioning of N among these pathways is the result of competitive interactions among microorganisms, plants and chemical reactions, with the outcome being influenced by soil conditions, in our study temperature and nutrient availability. Our results suggest that in Mojave soils, temperature altered N gas loss by influencing rates of microbial processing of N, whereas the relative availability of labile C and N determined whether the dominant fate of N was immobilization or gaseous loss. When looking at the form in which N was lost to the atmosphere, timing as well as the abundance of inorganic N appeared to be an important determinant of NO versus  $\text{NH}_3$  emission.

The importance of competitive interactions for inorganic N in determining the size and composition of trace N gas loss is reflected in the fact that fluxes of  $\text{NH}_3$  and NO differed not only in the timing of the post-wetting pulse, but

also in the response to changes in soil conditions. In dry soils, the magnitude of both NO and  $\text{NH}_3$  emission was affected by temperature; however, the direction of this response was opposite for the two gas species. The observed increase in NO efflux with an increase in temperature is consistent with temperature regulating the metabolic activity of nitrifying and denitrifying bacteria, with low activity at low temperatures leading to minimal NO efflux (Parton et al. 2001; Skiba et al. 1993). The observed positive relationship between temperature and NO emissions, especially following soil wetting, is one that has been shown in other studies (Anderson and Levine 1987; Barger et al. 2005; Martin et al. 2003; Smart et al. 1999; Williams et al. 1988) although other responses to temperature have been reported (Aneja et al. 1995; Johansson and Sanhueza 1988; Rondon et al. 1993; Serca et al. 1994).

The reduction in  $\text{NH}_3$  efflux we observed at higher temperatures in dry soils is more surprising; however, given the increase in NO production, it is likely that increased microbial activity at high temperatures increased competition for  $\text{NH}_4^+$ , reducing the amount of substrate for  $\text{NH}_3$  volatilization. In contrast to NO production, addition of water diminished the importance of temperature in determining rates of  $\text{NH}_3$  volatilization. This response is likely the result of differences in timing between the stimulation of biological activity and peak  $\text{NH}_3$  efflux. If the influence of temperature on  $\text{NH}_3$  production is largely an indirect effect of changing competitive dynamics for  $\text{NH}_4^+$ , then the large post-wetting pulse of  $\text{NH}_3$  likely occurs prior to the stimulation of microbial activity and is thus independent of direct temperature effects on the microbial community.

Nutrient availability, especially N availability, has been identified as an important determinant of N gas loss from soils. Numerous studies have shown that N additions stimulate NO production (e.g. Cardenas et al. 1993; Hall and Matson 2003; Hartley and Schlesinger 2000; Johansson et al. 1988; Martin et al. 1998; Rondon et al. 1993; Sanhueza et al. 1990; Serca et al. 1994; Smart et al. 1999; Venterea et al. 2003). Excess inorganic N in the soil solution enhances NO loss either as a result of increased substrate availability for nitrifying and denitrifying bacteria (Davidson et al. 1993; Hartley and Schlesinger 2000; Mosier et al. 1998) or decreased consumption of NO by the microbial community (Stark et al. 2002). Our experiment added N in the form of  $\text{NO}_3^-$ , the primary substrate for denitrification as opposed to nitrification. It is possible the stimulation of NO loss by  $\text{NO}_3^-$  addition is due to increased denitrification (Cardenas et al. 1993; Rondon et al. 1993); however, most studies suggest nitrification is the primary source of NO (e.g. Davidson et al. 1993; Hartley and Schlesinger 2000; Parton et al. 2001; Smart et al. 1999; Stark et al. 2002). It is likely the addition of  $\text{NO}_3^-$  in our study reduced competition for N, either



leaving more  $\text{NH}_4^+$  available for nitrification or, as hypothesized by Stark et al. (2002), decreasing consumption of NO within the soil, increasing emission.

An alternative explanation for the observed high NO efflux following  $\text{NO}_3^-$  addition is chemodenitrification. Under acidic conditions,  $\text{NO}_2^-$  equilibrates with  $\text{H}^+$  and the resulting  $\text{HNO}_2$  can decompose under aqueous conditions to produce NO or can react with soil organic matter, also producing NO (Davidson 1992; Nelson 1982; Venterea and Rolston 2000). Abiotic production is less likely to be an important mechanism of NO production in Mojave Desert soils due to high pH; however, it has been suggested that even in highly alkaline soils, acidic microsites enable such reactions to occur (Nelson 1982). However, if the measured NO pulse was the result of direct chemical or microbial alteration of  $\text{NO}_3^-$  then one would expect an immediate pulse following N addition instead of a 1- to 2-day delay in peak NO efflux.

Fewer studies have looked at the role of C availability in determining rates of NO emission; however, in our system C addition had a strong negative influence on post-wetting NO efflux. Studies that have investigated the role of labile C in determining rates of NO efflux have reported variable responses [no response to C addition (Bakwin et al. 1990; Smart et al. 1999), increased fluxes (Slemr and Seiler 1991) and flux suppression (Matson et al. 1996)]. Increased fluxes of NO after C addition have been attributed to increased denitrification (Slemr and Seiler 1991), whereas decreases are thought to be the result of increased microbial immobilization of N (Matson et al. 1996). Increased microbial immobilization of N following labile C addition in Mojave Desert soils supports the conclusion of Schaeffer et al. (2003) that microbial activity in Mojave soil crusts is limited by the availability of labile C. Additionally, labile C has been shown to stimulate microbial immobilization of N in other arid and semi-arid ecosystems (Gallardo and Schlesinger 1992, 1995; Schaeffer et al. 2003; Schaeffer and Evans 2005; Stark et al. 2002). In the present study, the influence of C addition was much stronger in soils from interspaces between shrubs. This is likely driven by higher soil organic matter contents beneath *L. tridentata* (Ewing et al. 2007; Schaeffer et al. 2003) making microbial activity in these soils less C limited and therefore less sensitive to additional C.

In general,  $\text{NH}_3$  volatilization was less responsive than NO production to changes in nutrient availability.  $\text{NO}_3^-$  addition did not substantially alter the initial  $\text{NH}_3$  pulse following soil wetting; however, in interspace soils,  $\text{NH}_3$  emissions remained elevated for several days suggesting that this process is sensitive to changes in  $\text{NO}_3^-$  availability. This prolonged period of  $\text{NH}_3$  volatilization is likely driven by reduced competition for N leading to higher  $\text{NH}_4^+$  availability (sensu Schlesinger and Peterjohn

1991). The fact that this response did not occur in *Larrea*-influenced soils suggests higher soil C content enabled microbial immobilization of the added  $\text{NO}_3^-$  (Schaeffer et al. 2003; Zaady et al. 1996). As with  $\text{NO}_3^-$  addition, the initial pulse of  $\text{NH}_3$  following soil wetting was insensitive to changes in labile C; however, C addition did alter the rate at which fluxes returned to baseline values. Increased C availability accelerated the decline in  $\text{NH}_3$  efflux, presumably due to the same mechanism hypothesized for the suppression of NO emission. In addition to decreasing nitrification, increased N immobilization would draw down the pool of  $\text{NH}_4^+$  available for volatilization, thus reducing  $\text{NH}_3$  efflux.

The observation that the initial pulse of  $\text{NH}_3$  following water addition is insensitive to temperature, and  $\text{NO}_3^-$  and C addition suggests that following precipitation a portion of the N released into the soil solution is lost to the atmosphere before microbial activity is stimulated. During this period,  $\text{NH}_3$  volatilization proceeds uninhibited by competition for  $\text{NH}_4^+$  and therefore is insensitive to factors such as temperature and labile C that alter rates of N immobilization and nitrification. Subsequently, microbial activity is up-regulated in response to increased water availability and rates of  $\text{NH}_3$  volatilization, although still elevated over baseline levels, are constrained by microbial and presumably plant uptake of  $\text{NH}_4^+$ .

The combination of laboratory and field measurements presented in this study indicate that N gas production in the form of NO and  $\text{NH}_3$  is an important component of Mojave Desert N dynamics, with  $\text{NH}_3$  production being a significant loss term. Similar to studies addressing controls over NO production, we have found that water addition exerts a strong control over rates of  $\text{NH}_3$  emission. Although temperature and nutrient availability are important constraints on  $\text{NH}_3$  efflux, unlike NO production the sensitivity of  $\text{NH}_3$  emissions to these factors is time dependent, with initial pulses of  $\text{NH}_3$  after water addition being relatively insensitive to alterations in soil conditions. Moreover, the presence of high rates of  $\text{NH}_3$  volatilization appears to alter NO responses to water addition, delaying the post-wetting NO pulse frequently observed in other systems by several days. These results suggest both that  $\text{NH}_3$  production needs to be included in estimates of N dynamics in ecosystems with highly alkaline soils and that in these systems  $\text{NH}_3$  volatilization needs to be considered when studying controls over other processes, such as NO production, that are sensitive to concentrations of  $\text{NH}_4^+$ .

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