

RESEARCH ARTICLE

Soil NH₃ emissions across an aridity, soil pH, and N deposition gradient in southern California

Alexander H. Krichels^{1,2,3,*} , Peter M. Homyak¹ , Emma L. Aronson⁴ , James O. Sickman¹, Jon Botthoff², Aral C. Greene¹ , Holly M. Andrews⁵ , Hannah Shulman⁴, Stephanie Piper⁶, and G. Darrel Jenerette^{2,6} 

Soil ammonia (NH₃) emissions are seldom included in ecosystem nutrient budgets; however, they may represent substantial pathways for ecosystem nitrogen (N) loss, especially in arid regions where hydrologic N losses are comparatively small. To characterize how multiple factors affect soil NH₃ emissions, we measured NH₃ losses from 6 dryland sites along a gradient in soil pH, atmospheric N deposition, and rainfall. We also enriched soils with ammonium (NH₄⁺), to determine whether N availability would limit emissions, and measured NH₃ emissions with passive samplers in soil chambers following experimental wetting. Because the volatilization of NH₃ is sensitive to pH, we hypothesized that NH₃ emissions would be higher in more alkaline soils and that they would increase with increasing NH₄⁺ availability. Consistent with this hypothesis, average soil NH₃ emissions were positively correlated with average site pH ($R^2 = 0.88$, $P = 0.004$), ranging between $0.77 \pm 0.81 \mu\text{g N-NH}_3 \text{ m}^{-2} \text{ h}^{-1}$ at the least arid and most acidic site and $24.2 \pm 16.0 \mu\text{g N-NH}_3 \text{ m}^{-2} \text{ h}^{-1}$ at the most arid and alkaline site. Wetting soils while simultaneously adding NH₄⁺ increased NH₃ emissions from alkaline and moderately acidic soils ($F_{1,35} = 14.7$, $P < 0.001$), suggesting that high N availability can stimulate NH₃ emissions even when pH is less than optimal for NH₃ volatilization. Thus, both pH and N availability act as proximate controls over NH₃ emissions suggesting that these N losses may limit how much N accumulates in arid ecosystems.

Keywords: Ammonia, Drylands, Nitrogen, pH, Rewetting, Nitrogen limitation

1. Introduction

Soil ammonia (NH₃) emissions are seldom reported in nutrient budgets but may be an important nitrogen (N) loss pathway that contributes to ecosystem N limitation (Schlesinger and Peterjohn, 1991; Soper et al., 2016). In general, ecosystem N limitation is established when N inputs (e.g., biological N fixation or atmospheric N deposition) are outpaced by outputs (e.g., hydrologic and gaseous N losses; von Sperber et al., 2017; Vitousek et al., 2021). However, in N-limited ecosystems, high biological demand

for N may constrain N losses, such that even small N inputs accumulate until primary productivity is no longer N limited (Vitousek and Field, 1999; von Sperber et al., 2017; Vitousek et al., 2022). Therefore, for ecosystem N limitation to persist, N losses must occur even when primary productivity is limited by N and biological N demand is high (von Sperber et al., 2017; Vitousek et al., 2022). In this sense, soil NH₃ emissions may operate as *demand-independent* N losses (i.e., N losses that are uncontrollable by biological processes; von Sperber et al., 2017; Vitousek et al., 2022) because NH₃ volatilization can rapidly convert NH₄⁺ to gaseous NH₃ when dry soils wet up, exporting N before it can be assimilated by plants (Schlesinger and Peterjohn, 1991; Soper et al., 2016). While the emission of other N trace gases (e.g., nitric oxide [NO] and nitrous oxide [N₂O]) can also occur as demand-independent N losses (Homyak and Sickman, 2014; Eberwein et al., 2020; Krichels et al., 2022), the factors that control NH₃ emissions from natural ecosystems have been relatively less studied and it is less clear how interactions among these factors control them. Understanding which factors control NH₃ losses from soils can help understand why ecosystems become limited by N and help reconcile why some ecosystems may experience substantial N losses even when they remain N limited (Wang et al., 2014; von Sperber et al., 2017).

¹ Environmental Sciences, University of California, Riverside, CA, USA

² Center for Conservation Biology, University of California, Riverside, CA, USA

³ USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM, USA

⁴ Microbiology and Plant Pathology, University of California, Riverside, CA, USA

⁵ Evolution, Ecology, and Organismal Biology, University of California, Riverside, CA, USA

⁶ Botany and Plant Sciences, University of California, Riverside, CA, USA

* Corresponding author:
Emails: alexander.krichels@usda.gov;
alexander.krichels@ucr.edu

Soil pH regulates NH₃ emissions by controlling the partitioning between ammonium (NH₄⁺) and NH₃; alkaline conditions (pK_a = 9.3) deprotonate NH₄⁺ producing NH₃ (i.e., NH₃ volatilization; Avnimelech and Laher, 1977; Schlesinger and Peterjohn, 1991; McCalley and Sparks, 2008; Soper et al., 2016). At the landscape scale, soil pH is regulated by multiple state factors (Jenny, 1980), with precipitation playing a dominant role (Slessarev et al., 2016). In general, wet regions accelerate weathering of base cations, lowering soil buffering capacity and pH, whereas dry regions constrain weathering, favoring alkaline soils (Slessarev et al., 2016), and, therefore, increasing the potential for NH₃ volatilization. Indeed, among the highest NH₃ emissions from nonagricultural ecosystems have been measured in alkaline drylands (McCalley and Sparks, 2008), especially after dry soils are wetted (Peterjohn and Schlesinger, 1990; McCalley and Sparks, 2008). Wetting dry soil frees N from microbial biomass, minerals, and aggregates (Birch, 1958; Austin et al., 2004; Kim et al., 2012), thereby flushing soil pores with N-bearing substrates—including NH₄⁺—that favor N emissions before the N can be biologically assimilated (Peterjohn and Schlesinger, 1990; Homyak and Sickman, 2014; Eberwein et al., 2020; Krichels et al., 2022). Yet, wetting-induced NH₃ emissions are seldom measured in dryland ecosystems, limiting our ability to understand the factors that control emissions and their potential to regulate ecosystem N limitation.

Besides pH, soil N availability can also control NH₃ volatilization, with NH₃ emissions increasing with increasing soil NH₄⁺ concentrations (Avnimelech and Laher, 1977). NH₄⁺ fertilization produces large NH₃ fluxes in agricultural systems (Pan et al., 2016; Ma et al., 2021), suggesting that NH₄⁺ inputs, including those from atmospheric N deposition, may also increase soil NH₃ emissions in unfertilized systems so long as pH is optimal (Schlesinger and Peterjohn, 1991; McCalley and Sparks, 2008; Sun et al., 2014). However, atmospheric N deposition can also acidify soils (Falkengren-Grerup, 1989; Fenn et al., 1996), which can limit NH₃ volatilization and, therefore, how much N could be lost as NH₃. Because wetting-induced NH₃ emissions have been measured in only a handful of drylands, the effects of aridity, pH, and N availability on NH₃ emissions and overall N limitation status remain largely uncharacterized, leading us to ask: How do soil pH and NH₄⁺ supply interact to control NH₃ emissions?

To address this question, we measured in situ NH₃ emissions in response to adding water and NH₄⁺ to soils from 6 sites in southern California dryland ecosystems that vary in soil pH, aridity, and atmospheric N deposition. Extending a transect eastward from the edge of greater Los Angeles, CA, soil pH increases from moderately acidic conditions close to the city to more alkaline conditions further east (**Table 1**). Simultaneously, soils across this gradient are exposed to over 16 kg N ha⁻¹ yr⁻¹ near Los Angeles—with localized studies measuring up to 29 kg N ha⁻¹ yr⁻¹ (Sickman et al., 2019)—and as low as 3 kg N ha⁻¹ yr⁻¹ further inland (Schwede and Lear, 2014; National Atmospheric Deposition Program, 2022; **Table 1**). We

hypothesized that NH₃ volatilization would increase with soil pH and that wetting alkaline soils with NH₄⁺ solutions would reduce substrate limitation of NH₃ volatilization and lead to higher NH₃ emissions.

2. Methods

2.1. Sites description

We studied 6 sites spanning a soil pH gradient in southern California, labeled alphabetically in order of increasing pH (**Table 1**)—A was the most acidic and F was the most alkaline. Across the soil pH gradient, acidic soils generally had higher annual precipitation (Slessarev et al., 2016), with the site closest to Los Angeles averaging approximately 279 mm yr⁻¹ and the most eastern site in Joshua Tree National Park averaging approximately 101 mm yr⁻¹ (Daly et al., 2007). Vegetation at the most acidic site (site A) is dominated by chamise (*Adenostoma fasciculatum*), whereas creosote shrubs (*Larrea tridentata*) dominate the increasingly alkaline sites B, C, D, E, and F. At all sites, soils are relatively coarse-textured, characterized as sandy loams through gravelly sands covering a mix of taxonomies (see Table S1). Soil NH₄⁺ concentrations were lowest in site E (1.62 ± 1.10 μg N g⁻¹) and highest in site F (12.2 ± 6.73 μg N g⁻¹); concentrations did not follow patterns in atmospheric N deposition (**Table 1**).

Because of the proximity of our sites to Los Angeles, the sites fall along an atmospheric N deposition gradient; the highest N deposition rates occur near Los Angeles in the most acidic soils (**Table 1**). Because atmospheric N deposition can acidify soils (Falkengren-Grerup, 1989; Fenn et al., 1996), it is possible that, together with the effect of aridity on soil pH (Jenny, 1980), this anthropogenic factor also contributes to the observed gradient in soil pH across our sites.

2.2. Experimental design

We measured NH₃ emissions after adding water or NH₄⁺ to soils from sites A and F in August 2018 and from sites B, C, D, and E in June 2020. While environmental conditions likely differed between the 2 sampling periods, soils from all sites were dry prior to wetting (<3.6% gravimetric water content). Wetting-induced soil NH₃ emissions were measured from underneath 4 shrubs to capture the islands of fertility, where soil nutrients are concentrated (Peterjohn and Schlesinger, 1990) and where previous work has shown high gaseous N emission rates (Eberwein et al., 2020; Krichels et al., 2022). All 4 shrubs were within a 10-m radius and were separated from one another by at least 1 m. At each of the 4 shrubs, we installed 2 polyvinyl chloride collars (20-cm diameter × 10-cm height; inserted 5 cm into the ground) under each of the canopies. One collar underneath each shrub was wetted with 500-mL deionized water, corresponding to approximately a 7-mm rainfall event, within the range of historically occurring rain events at the sites (mean rain event in 2019 and 2020 at site F = 6.4 mm; <https://doi.org/10.21973/N3V66D>). The other collar was wetted with a solution of ammonium chloride corresponding to 15 kg NH₄⁺-N ha⁻¹, an N input rate within the range of annual atmospheric N deposition in drylands in southern California

Table 1. Location, soil pH, annual precipitation (Daly et al., 2007), soil inorganic N, atmospheric N trace gas concentrations (see Supplemental Methods), and modeled atmospheric N deposition rates (Schwede and Lear, 2014; National Atmospheric Deposition Program, 2022) at each of the 6 sites from this study

Variable	A	B	C	D	E	F
Lat	33.9696	33.9221	33.8961	33.9440	33.9041	33.6487
Long	−117.2994	−116.7577	−116.6868	−116.3949	−115.7233	−116.3776
Mean annual precipitation (mm)	279	299	246	145	101	142
Soil pH	5.77 ± 0.50	6.65 ± 0.25	7.00 ± 0.36	7.19 ± 0.27	7.50 ± 0.34	8.36 ± 0.19
Soil NO ₃ [−] (μg N g ^{−1})	6.60 ± 3.73	5.48 ± 3.46	7.08 ± 3.95	2.75 ± 1.11	2.76 ± 1.81	17.4 ± 25.0
Soil NH ₄ ⁺ (μg N g ^{−1})	10.7 ± 6.59	8.92 ± 5.67	8.37 ± 3.39	7.86 ± 8.34	1.62 ± 1.10	12.2 ± 6.73
Ambient NH ₃ concentration (ppb)	6.3	4.2	3.6	2.4	1.4	NA
Ambient NO _x concentration (ppb)	19.7	9.9	4.2	2.2	1.5	NA
Modeled N deposition (kg N ha ^{−1})	16.9	9.3	8.2	4.5	3.0	4.2

NA indicates that data are missing from a site.

(Fenn et al., 2006; Eberwein et al., 2020). The collars were separated from each other by at least 50 cm to avoid cross-contamination of wetting solutions.

2.3. NH₃ emissions

We used passive NH₃ samplers to estimate soil NH₃ emissions in soil chambers at our sites. Immediately after adding water or NH₄⁺ solution to soil collars, a chemically pretreated NH₃ sampler (Ogawa pads; Ogawa USA, Pompano Beach, FL) was placed on the ground inside the chamber and sealed by fitting a rubber lid on top of the collar; the sampler was housed within a vented plastic container to prevent contact with the soil and contamination. Collar lids were then covered with aluminum foil to minimize heating from solar radiation. To minimize the chance that NH₃ would saturate our passive samplers and to capture discrete periods of NH₃ emissions, we replaced the NH₃ samplers with new ones at predetermined time intervals. In 2018, passive samplers were deployed to collect NH₃ from 0 to 15 min, 15 min to 12 h, and 12 h to 24 h postwetting. The chambers were open for approximately 10 s when new passive samplers were installed, which allowed some NH₃ to escape (based on our 15-min emission rates [Figure S1], we estimate less than 0.1% of the total NH₃ emitted escaped from site F while the chambers were open). Because the samplers did not saturate with NH₃ in 2018 (reaching as high as 50 μg N-NH₃ out of a theoretical maximum of 290–875 μg N-NH₃; Roadman et al., 2003), passive samplers were installed for 2 intervals in 2020: 0 to 15 min and 15 min to 24 h postwetting. All 8 collars within a given site were wet within a 30-min period starting at approximately 9:00 in the morning. For each site, 4 NH₃ samplers were used as blanks; they were placed adjacent to collars in sealed plastic bags to prevent the adsorption of atmospheric NH₃.

To measure how much NH₃ accumulated on each passive sampler, the samplers were extracted in 8 mL of deionized water overnight and analyzed for NH₄⁺ at the University of California, Riverside, Environmental Sciences

Research Laboratory (<https://envisci.ucr.edu/research/environmental-sciences-research-laboratory-esrl>). The NH₄⁺ concentration of this solution was measured using a colorimetric assay (SEAL methods Environmental Protection Agency 126-A) with a SEAL AQ-2 discrete analyzer (SEAL analytical, Mequon, WI). To calculate total NH₃ fluxes for each chamber, we summed the amount of NH₃ collected on each NH₃ sampler (minus NH₃ from the blanks) incubated within each chamber. The sum of NH₃ was then divided by the time the chamber was closed (approximately 24 h) to estimate NH₃ emission rates. Because NH₃ may have been emitted throughout the 24-h incubation and rates of NH₃ absorption to the passive samplers are concentration-dependent, it is unlikely that the passive samplers collected all the NH₃ within a chamber for a given sampling period. However, passive samplers work well during short chamber incubations (Yu and Elliott, 2017) and have been successfully deployed to measure the fluxes of nitric oxide (Osborne et al., 2022). As such, while we acknowledge that our measurements likely underestimate NH₃ fluxes, they provide a reasonable estimate of how NH₃ emissions vary across sites and allow for comparisons among sites in response to adding N.

2.4. Statistical analyses

All statistical analyses were conducted using R 3.6.1 (R Core Team, 2019). We used analysis of variance to determine whether NH₃ emissions differed between sites and in response to adding NH₄⁺; NH₃ emissions were the response variable, while site and N addition were the predictor variables. Model residuals were assessed for normality using Shapiro–Wilk’s tests; log transformations were applied to NH₃ emissions. We used linear regression to determine whether soil pH was related to average NH₃ emissions in response to water addition from each site. Log-transformed average NH₃ emissions from each site were included as the response variable, and average soil pH at each site was included as the predictor variable.

3. Results

Over the 24 h after adding water to soils, NH₃ emission rates averaged $6.51 \pm 10.9 \mu\text{g N-NH}_3 \text{ m}^{-2} \text{ h}^{-1}$ ($\pm$ standard deviation) across all sites (**Figure 1**). Soil NH₃ emissions differed among sites ($F_{5,34} = 11.0$, $P < 0.001$); they were highest at the most alkaline site (site F; $24.2 \pm 16.0 \mu\text{g N-NH}_3 \text{ m}^{-2} \text{ h}^{-1}$) and lowest at the most acidic site (site A; $0.77 \pm 0.81 \mu\text{g N-NH}_3 \text{ m}^{-2} \text{ h}^{-1}$). Overall, site-averaged NH₃ emissions were positively correlated with soil pH (adjusted $R^2 = 0.88$, $P = 0.004$, **Figure 2A**). The positive relationship between NH₃ emissions and pH was also present when results from 3 other studies measuring NH₃ emissions from nonagricultural ecosystems were included in the model (adjusted $R^2 = 0.92$, $P < 0.001$, **Figure 2B**, Table S1).

Wetting with NH₄⁺ solutions increased NH₃ emissions relative to adding only water over the 24 h post-wetting ($F_{1,34} = 14.7$, $P < 0.001$). In our most alkaline site (F), NH₃ emissions were 3 times higher in NH₄⁺-amended soils ($73.4 \pm 39.7 \mu\text{g N-NH}_3 \text{ m}^{-2} \text{ h}^{-1}$) than in soils wetted with only water ($24.2 \pm 16.0 \mu\text{g N-NH}_3 \text{ m}^{-2} \text{ h}^{-1}$), but at our most acidic site (A) emissions were only 1.3 times higher in NH₄⁺-amended soils ($1.03 \pm 1.71 \mu\text{g N-NH}_3 \text{ m}^{-2} \text{ h}^{-1}$) than in soils wetted with only water ($0.77 \pm 0.81 \mu\text{g N-NH}_3 \text{ m}^{-2} \text{ h}^{-1}$; **Figure 1**). NH₃ emissions from NH₄⁺-amended soils were also positively correlated with average soil pH (adjusted $R^2 = 0.81$, $P = 0.009$, **Figure 2C**).

4. Discussion

By measuring NH₃ emissions in soils across a gradient in pH, aridity, and atmospheric N deposition, we show that NH₃ emissions generally increase in more alkaline and arid soils, supporting our hypothesis that NH₃ emissions would increase with soil pH. However, adding NH₄⁺ increased NH₃ emissions in all but the most acidic site, suggesting that increasing N availability can overcome pH limitation of NH₃ emissions in slightly acidic soils. Below, we discuss how these controlling factors on soil NH₃ emissions may contribute to varying N losses from ecosystems that range in soil pH, atmospheric N deposition, and precipitation.

Soil NH₃ emissions were positively correlated with site pH whether soils were wetted with water or NH₄⁺ solution, consistent with pH operating as a proximate control over NH₃ emissions (Avnimelech and Laher, 1977). However, these emissions varied substantially within each site (e.g., 0.77 ± 0.81 in site A and $24.2 \pm 16.0 \mu\text{g N-NH}_3 \text{ m}^{-2} \text{ h}^{-1}$ in site F), likely due to microscale variation in soil and environmental factors known to govern trace gas emissions (e.g., soil moisture, temperature, texture, and substrate availability; Firestone and Davidson, 1989). While accounting for more soil and environmental factors could have improved the observed within-site variation in NH₃ emissions, we were still able to detect an effect of pH on NH₃ emissions across our landscape-scale pH gradient, suggesting it is a dominant control. Indeed, the most

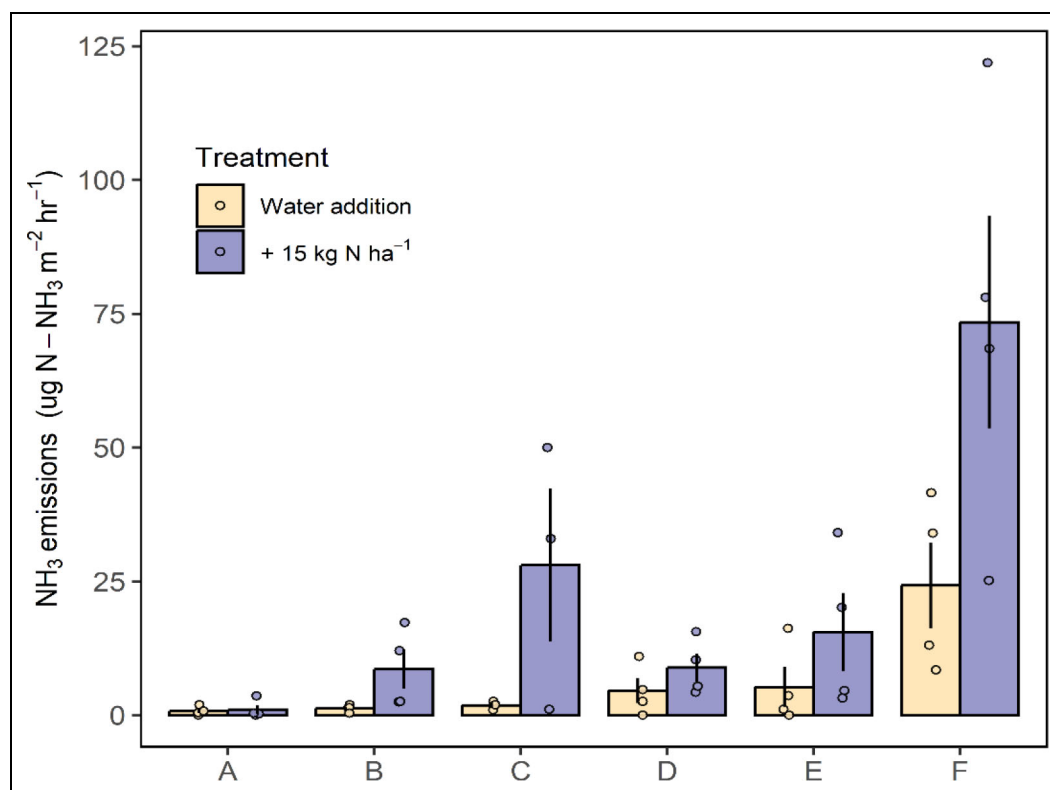


Figure 1. Average soil ammonia (NH₃) emissions at each site after adding water or 15 kg N-NH₄⁺ ha⁻¹ addition. Bars represent the mean NH₃ emissions, lines the standard error of the mean ($n = 4$ per site), and dots represent individual measurements. Sites are arranged in order of pH, with site A being the most acidic and site F the most alkaline.

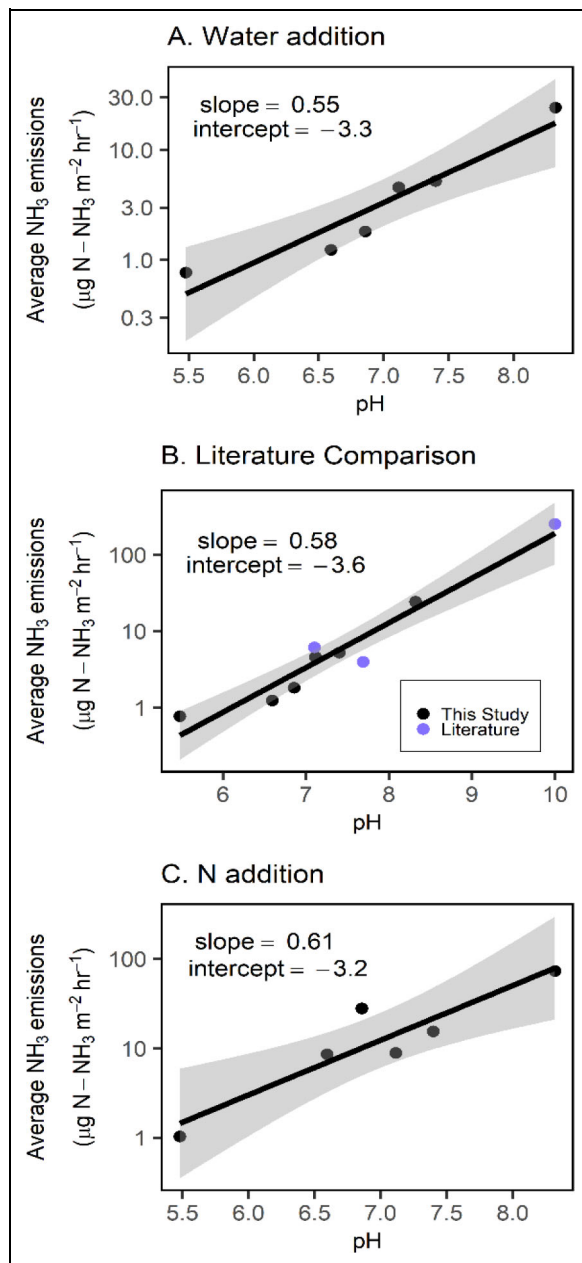


Figure 2. Relationship between mean soil pH and mean log-transformed ammonia (NH₃) emissions over the 24 h after wetting (A and B) or 15 kg N-NH₄⁺ ha⁻¹ addition (C) at each site. Lines show the linear regression between mean soil pH and mean log-transformed NH₃ emissions at each site. Shaded gray areas represent the 95% confidence interval for statistically significant linear regressions ($P < 0.05$). Panel B includes NH₃ emissions and soil pH from 3 studies conducted in nonagricultural ecosystems (Table S1). We used pH 10 as the average pH for the study by McCalley and Sparks (2008) that reported a range in pH from 9 to 11.

alkaline site in our gradient (F) produced the most NH₃ over 24 h postwetting (**Figure 1**) with the emissions being over 20 times higher than in woody clusters within a remnant grassland (pH = 7.1; Soper et al., 2016) and 4 times higher than in deserts (pH = 7.69; Schlesinger and

Peterjohn, 1991; **Figure 2B**; Table S2). However, emissions at our most alkaline site were 10 times lower than wetting-induced emissions from the highly alkaline Mojave Desert (pH = 9–11; Table S2; McCalley and Sparks, 2008), consistent with increasingly alkaline soils driving higher rates of NH₃ volatilization. Furthermore, our results align well with other studies measuring NH₃ emissions, illustrating a consistently positive relationship between soil pH and NH₃ emissions (**Figure 2B**), and reinforcing the role of pH as a major control over NH₃ emissions. This consistent positive relationship between pH and NH₃ emissions may also be most pronounced in coarse-textured desert soils—like those in our study sites—that are often characterized by low cation exchange capacity, favoring deprotonation of NH₄⁺ to NH₃ over the binding of NH₄⁺ to soil surfaces (Schlesinger and Peterjohn, 1991). Altogether, our measurements suggest that arid and alkaline soils with low cation exchange capacity are particularly susceptible to losing N via NH₃ volatilization.

While NH₃ emissions were highest in the most alkaline and arid site, adding NH₄⁺ still increased NH₃ emissions in all but the most acidic site, where low pH (5.8) likely constrained NH₃ volatilization (Avnimelech and Laher, 1977). However, adding NH₄⁺ still increased NH₃ emissions in moderately acidic soils (pH = 6.7), suggesting that adding NH₄⁺ can shift the equilibrium between dissolved NH₄⁺, NH₃, and H⁺ in soil pore water to produce more NH₃ so long as H⁺ concentrations are not exceedingly high (Avnimelech and Laher, 1977; Sun et al., 2014). Our data show that adding N shifted this equilibrium when soil pH was somewhere between 5.8 and 6.7, suggesting that in sites with high rates of atmospheric N deposition, NH₃ may be emitted even in moderately acidic soils if excess N overcomes pH restrictions on NH₃ volatilization.

Relative to the emission of other N-bearing trace gases, NH₃ emissions (between 0.77 ± 0.81 and 24.2 ± 16.0 $\mu\text{g N-NH}_3 \text{ m}^{-2} \text{ h}^{-1}$) were smaller than nitrogen oxide losses measured at nearby sites. Peak NO emissions from some drylands can exceed $700 \mu\text{g N-NO m}^{-2} \text{ h}^{-1}$ (Homyak and Sickman, 2014; Eberwein et al., 2020), and peak N₂O emissions can exceed $2,100 \mu\text{g N-N}_2\text{O m}^{-2} \text{ h}^{-1}$ (Eberwein et al., 2020; Krichels et al., 2022). In contrast, average NH₃ emissions did not surpass $25 \mu\text{g N-NH}_3 \text{ m}^{-2} \text{ h}^{-1}$ in any of our sites, though some of our passive samplers exposed for only 15 min postwetting exceeded $80 \mu\text{g N-NH}_3 \text{ m}^{-2} \text{ h}^{-1}$ (Figure S1). While these rates are low compared to NO and N₂O emissions, NH₃ emissions increased after adding NH₄⁺, suggesting that NH₃ emissions may become increasingly important in systems, where NH₄⁺/NH₃ atmospheric inputs are increasing (Decina et al., 2020).

5. Conclusions

We show that in situ NH₃ emissions were highest in the most arid and alkaline soils. While soil pH is a well-established control on NH₃ volatilization, we found that increasing N availability can help overcome pH limitation of NH₃ volatilization even in moderately acidic soils. These demand-independent NH₃ losses upon wetting dry soils are particularly large in alkaline drylands, where they may

allow ecosystem N limitation to persist despite anthropogenic N inputs.

Data accessibility statement

All data presented in this study are available in the Dryad database (Krichels, 2023).

Supplemental files

The supplemental files for this article can be found as follows:

SI_Material.Docx

Acknowledgments

The authors thank the University of California Natural Reserve System (<https://doi.org/10.21973/N3V66D>) for access to field sites, Beatriz Vindiola and Delores Lucero for their help with the passive samplers, and David Lyons from the UCR Environmental Sciences Research Laboratory for help with sample analyses. They also thank the National Science Foundation (DEB 1916622 and DEB 1656062) for their support. This study was supported in part by the USDA Forest Service Rocky Mountain Research Station. The findings and conclusions in this publication are those of the author and should not be construed to represent any official USDA or U.S. Government determination or policy.

Competing interests

PMH is an associate editor at *Elementa* but did not have a role in the reviewing or handling of this manuscript. The authors declare no other competing interests.

Author contributions

Contributed to conception and design: AHK, PMH, ELA, JOS, JB, ACG, HMA, HS, SP, GDJ.

Contributed to acquisition of data: AHK, PMH, ELA, JOS, JB, ACG, HMA, HS, SP, GDJ.

Contributed to analysis and interpretation of data: AHK, PMH, GDJ.

Drafted and/or revised this article: AHK, PMH, GDJ.

Approved the submitted version for publication: AHK, PMH, ELA, JOS, JB, ACG, HMA, HS, SP, GDJ.

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How to cite this article: Krichels, AH, Homyak, PM, Aronson, EL, Sickman, JO, Botthoff, J, Greene, AC, Andrews, HM, Shulman, H, Piper, S, Jenerette, GD. 2023. Soil NH₃ emissions across an aridity, soil pH, and N deposition gradient in southern California. *Elementa: Science of the Anthropocene* 11(1). DOI: <https://doi.org/10.1525/elementa.2022.00123>

Domain Editor-in-Chief: Steven Allison, University of California Irvine, Irvine, CA, USA

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Knowledge Domain: Ecology and Earth Systems

Published: June 28, 2023 **Accepted:** April 7, 2023 **Submitted:** October 3, 2022

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