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Restricted nitrous oxide emissions by ammonia oxidizers in two agricultural soils following excessive urea fertilization

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Abstract

Purpose Nitrogen (N) fertilizer placement in bands is a widely accepted agricultural practice to increase N use efficiency. An excessive ammonium concentration in a fertilizer band can increase osmotic stress on ammonia oxidizers and potentially affect nitrification and resultant nitrous oxide (N_2O) emissions, which is of great significance for soil function and climate change. The objectivity of this study was to identify the effects of excessive ammonium concentration on N_2O emissions and ammonia oxidizers in two agricultural soils.

Materials and methods In this study, we established a 56-day soil microcosm receiving a series of high concentrations of urea at 600, 900, and 1200 mg N kg^{-1} (termed as N600, N900, and N1200, respectively), which simulated high ammonium levels in the center or proximity of a fertilizer band in two types of agricultural soils (fluvo-aquic soil and anthrosol). The mineral N concentrations, net nitrification rate, and N_2O emissions were measured during the incubation. In addition, the abundances of bacterial and archaeal *amoA* were determined by using real-time quantitative PCR.

Results and discussion Urea fertilization simultaneously increased the net nitrification rate and N_2O emission at the early stage of incubation in both soils, suggesting N_2O production was mainly from ammonia oxidation. Ammonia oxidizing bacteria (AOB) but not archaea (AOA) abundance was stimulated following urea fertilization and was positively correlated with N_2O emission, indicating the dominant role of AOB in ammonia oxidation and N_2O production in fertilized soils. The cumulative N_2O emission was significantly higher in N1200 and N900 than N600 in both soils, but no further increase was observed in N1200 in the anthrosol. This implies restricted N_2O production of ammonia oxidizers at excessive ammonium concentrations in the anthrosol. In the two soils treated with no N addition, the abundances of AOA *amoA* increased along the incubation time.

Conclusions The present study collectively suggested that excessive urea-N addition was more effective in inhibiting N_2O emission in the anthrosol than in the fluvo-aquci soil. AOB rather than AOA dominated the soil nitrification and N_2O emissions under high N addition in both soils. The band fertilization regime may reduce the loss of N fertilizer from nitrification without necessarily increasing N_2O emissions.

Keywords Agricultural soils · Ammonia-oxidizing archaea · Ammonia-oxidizing bacteria · High ammonium concentration · Nitrification · Nitrous oxide

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1 Introduction

Band application of ammonium-based fertilizer, such as urea, has been widely used to promote nitrogen use efficiency (NUE) and crop yields (Grant et al. 2011; Chen et al. 2016). Compared to the broadcast application, the banded placement of urea could enhance winter wheat yield by 12.5–15.4% (Chen et al. 2016). A marked feature of band fertilization is the resulting excessive ammonium concentrations in some areas of the soil, usually near a plant. In a newly fertilized band, ammonium concentrations can reach several hundred to more than 2000 mg N kg^{-1} (Angus et al. 2014; Venterea et al. 2015; Deppe et al. 2016), which would impose high osmotic stress on soil microbes and could potentially lead to a shift in the composition and activity of the soil microbial community (Angus et al. 2014), including soil nitrifiers. The band application of ammonium-based N fertilizers could inhibit the soil nitrifying microorganisms due to the toxic effect of high ammonium concentration in the fertilizer band (Engel et al. 2010; Hartmann et al. 2015).

Nitrification is a critical step in global N cycling, which converts ammonia (NH_3) to nitrate (NO_3^-) via nitrite (NO_2^-). Ammonia oxidation is the first and rate-limiting step of nitrification, which is primarily performed by ammonia oxidizing archaea (AOA) and bacteria (AOB) in the terrestrial system (Leininger et al. 2006; Norton and Stark 2011; Prosser and Nicol 2012; Yang et al. 2013; Zhang et al. 2015) despite a recent report of complete nitrification by *Nitrospira* bacteria (Daims et al. 2015). In an agricultural system, however, the nitrification process can significantly reduce NUE by conversion of ammonium to nitrate and increase nitrous oxide (N_2O) production, either as a direct product of ammonia oxidation or by providing nitrate for denitrification (Butterbach-Bahl et al. 2013).

N_2O is a potent greenhouse gas with a global warming potential 298 times higher than carbon dioxide (CO_2) (IPCC 2007; Di and Cameron 2016). Agricultural soils are widely accepted as the major sources of N_2O, accounting for approximately 65% of the total N_2O emissions (Ma et al. 2015; Wang et al. 2016b). The application of chemical N fertilizers, such as urea and ammonium sulfate, is an important cause of enhanced N_2O emissions in agricultural systems (Cui et al. 2013; Lin et al. 2017). In general, the N_2O emission was positive correlated with additional rate of urea-N (Huang et al. 2014; Van and Maeda, 2018). However, in a microcosm incubation, Deppe et al. (2017) found that N_2O emission decreased with increasing N addition within the range of 450 to 5000 mg NH_4^+–N kg^{-1} soil, and soil nitrification was completely blocked under 5000 mg NH_4^+–N kg^{-1} soil. It has been suggested that soil N_2O emission is mainly contributed by nitrification in the soils under aerobic conditions with < 70% water-filled pore space (WFPS) (Ma et al. 2015; Liu et al. 2016a; Wang et al. 2016a; Hink et al. 2017), while denitrification is more important in N_2O production with higher WFPS (Bateman and Baggs 2005). While, in an incubation experiment with 600–1200 mg bovine urine-N kg^{-1} soil, the N_2O emission was significantly and positively correlated with soil NO_2^- (Venterea et al. 2015). Nitrification-derived N_2O emission is from enzymatic production by AOB (Kozlowski et al. 2014), and biotic or abiotic reaction associated with AOA (Stieglmeier et al. 2014). Compared to AOA, the AOB produces higher yields of N_2O when oxidizing the same amount of ammonium (Hink et al. 2017).

There is evidence for the niche specialization of ammonia oxidizers driven by ammonium concentration, in addition to other environmental factors including soil pH (Nicol et al. 2008; Offre et al. 2009; Zhang et al. 2012; Lu and Jia 2013; Xi et al. 2017), temperature (Tourna et al. 2008), and water content (Wang et al. 2015, 2017). AOB activity is generally considered to be favored at high ammonium concentrations, while AOA appear to grow better with low ammonium supply through slow mineralization of organic matter (Di et al. 2009; Verhamme et al. 2011; Carey et al. 2016; Xiang et al. 2017; Tzanakakis et al. 2018). Therefore, it is commonly observed that AOB rather than AOA activity is stimulated in agricultural soils following ammonium-based fertilization (Jia and Conrad 2009; Xia et al. 2011; Ouyang et al. 2016). However, an excessive ammonium concentration in the soil solution will increase osmotic stress and may cause a negative impact on ammonia oxidizers and the consequent nitrification activity (Bello et al. 2019). Indeed, studies have revealed the inhibition of AOA by a high level of NH_4^+–N (> 5 mM), and additionally, AOB did not respond positively to the increased concentration (Ouyang et al. 2017). An incubation experiment conducted by Acton and Baggs (2010), who reported that soil nitrification decreased with increasing from 360 to 1400 NH_4^+–N kg^{-1} soil. This potential "toxic effect" from high ammonium concentrations (Sui et al. 2014) could limit the nitrifier activity and related processes, including N_2O production, in agricultural soils and be the underlying reason for enhanced NUE by band fertilization.

The objective of this study was to investigate the effect of excessive ammonium concentrations on the ammonia oxidizers in the soil and the consequent nitrification and N_2O emissions in two contrasting agricultural soils. We hypothesize that (a) AOB rather than AOA would dominate nitrification and N_2O emissions following urea fertilization and (b) excessive concentrations of urea-N will limit the nitrification and resultant N_2O emission in the two soils.

2 Materials and methods

2.1 Site description and soil samples

The two soils used in this study were collected from Jiangyan County (JY) in Jiangsu Province (32° 24′ N, 120° 05′ E) and

Guangde County (GD) in Anhui Province (31° 01′ N, 119° 26′ E), respectively; both are located in the middle and lower reaches of the Yangtze River, China. The average annual temperatures of JY and GD are 14.0 and 15.4 °C, and the mean annual precipitations are 990 and 1330 mm, both respectively. Rice-wheat rotation is the dominating cropping system in the both sites, whereas the soils at the JY and GD sites are classified as fluvo-aquic soil and anthrosol, respectively, according to Chinese Soil Taxonomy (Cooperative Research Group on Chinese Soil Taxonomy, 2001). Soils were collected from the 0–20 cm soil layer by mixing ten random cores, which were then air-dried and passed through a 2.0-mm sieve. The basic properties of the two soils are shown in Table S1 (Electronic Supplementary Material – ESM).

2.2 Soil microcosm incubation

Soil microcosms were conducted in 120-ml serum bottles containing 20 g of soil (oven-dry equivalent). The soil samples were pre-incubated at 25 °C in the dark for one week to stabilize the soil microbial community at 40% water-filled pore space (WFPS). After pre-incubation, all the samples were adjusted to 60% WFPS by adding water or a urea solution. Four treatments with three replicates were conducted by amending 0, 600, 900, and 1200 mg urea-N kg^{-1} in dry soil into the soil and were termed as N0, N600, N900, and N1200, respectively. The concentrations used in this study represent different N levels in a fertilizer band after dilution due to diffusion and plant uptake (Venterea et al. 2015; Deppe et al. 2016, 2017). The serum bottles were covered with polyethylene film with five pin holes to allow free air exchange and were incubated at 25 °C in the dark for 8 weeks. Distilled water was added every 3 or 4 days to maintain the soil moisture at 60% WFPS if necessary.

2.3 N_2O sampling and analysis

Twenty-four serum bottles (2 soil types × 4 treatments × 3 replicates) were set up for gas sampling. Three replicate gas samples were from each treatment were collected from the serum bottles kept for the 56 days of incubation. Gas sampling was performed after 1, 2, 4, 7, 10, 14, 17, 21, 28, 42, and 56 days. Prior to gas sampling, the headspace air in the bottle was thoroughly flushed with ambient air. The serum bottles were then capped immediately with silicone rubber stoppers and incubated for 5 h at 25 °C in the dark. Gas samples of 20 ml were taken from the headspace of bottles using 20-ml syringes. After gas sampling, the rubber stoppers were removed and polyethylene films were replaced to recover the bottle. The concentrations of N_2O were determined using a gas chromatograph (Agilent 7890A, Agilent technologies, CA, USA) while the N_2O emission rate was calculated by the difference between 0 and 5 h (He et al. 2016; Liu et al. 2016a). A cumulative N_2O emission was calculated according to the equation reported by He et al. (2016) as follows:

$$F = \rho \times \frac{V}{A} \times \frac{\Delta c}{\Delta t} \times \frac{273}{273 + T}$$

$$E = \sum \frac{F_i + F_{i+1}}{2} \times (ti + ti + 1)$$

where F is the N_2O emission rate (μg N kg^{-1} h^{-1}), ρ is the density of N_2O under the standard state (1.25 kg m^{-3}), V is the headspace volume of serum bottle (m^3), A is the area of serum bottle (m^2), $\frac{\Delta c}{\Delta t}$ is the change in N_2O concentration between the incubation times of 0 and 5 h, and T is the incubation temperature (°C). E is the cumulative emission of N_2O (μg N kg^{-1}), and F_i and F_{i+1} are the N_2O emission rates at times of t_i and t_{i+1}, respectively.

2.4 Soil sampling and analysis

The samples for each treatment were destructively collected in triplicate on days 0, 7, 14, 21, 28, 42, and 56 for inorganic N and soil pH measurements. In total, 168 bottles (2 soil types × 4 treatments × 3 replicates × 7 sampling points) were prepared. Subsamples of 2 g soils on days 0, 7, 28, and 56 were collected and stored at − 80 °C for DNA extraction. A total of 4 g of each soil (on a dry weight basis) was shaken with 20 ml of 2 M KCl solution in 100-ml centrifuge tubes for 1 h. The suspensions were then filtered through Whatman No. 42 papers. The NH_4^+–N, and NO_2^- plus NO_3^-–N concentrations were measured on a continuous flow analyzer (Skalar SAN++, The Netherland). Soil pH (soil/water = 1:2.5) was measured with a pH detector.

The net nitrification rate (n) was calculated according to the equation suggested by Shi et al. (2016).

$$n\,(dt1{-}dt2) = \frac{(NO_2^-\,plus\,NO_3^-{-}N)dt2{-}(NO_2^-\,plus\,NO_3^-{-}N)dt1}{t}$$

where $(NO_2^-$– plus NO_3^-–$N)_{dt1}$ is the soil NO_2^-– plus NO_3^-–N concentration at days $t1$, $(NO_2^-$– plus NO_3^-–$N)_{dt2}$ is the concentration of NO_2^-– and NO_3^-–N at days $t2$, and t is the days between d_{t2} and d_{t1}.

2.5 DNA extraction and quantification by real-time quantitative PCR

Soil DNA was extracted from 0.5 g of soil using the FastDNA SPIN kit for soil (MP Biomedicals, CA, USA) according to the manufacturer's protocol. Total soil DNA concentration was determined using a NanoDrop spectrophotometer (NanoDrop Technologies, DE, USA).

The quantification of AOA and AOB *amoA* copies was determined using CrenamoA23F/CrenamoA-2R and amoA-1F/amoA-2R (Zhao et al. 2015), respectively. The qPCR

was performed on a CFX96 Optical Real-Time Detection System (Bio-Rad Laboratories, CA, USA). Each 20-μl reaction mixture included 10 μl 2 × SYBR Premix Ex Taq (Takara Biotechnology, Shiga, Japan), 0.5 μM of each primer, 1 μl of DNA template, and 8 μl of deionized water. Extracted DNA was diluted multiple times to test the potential inhibition of the PCR by a humic substance, and 10-fold diluted DNA was used as the qPCR template. The standard curves were generated using the known copy numbers of plasmid DNA containing AOA or AOB *amoA*. For all assays, the amplification efficiencies ranged from 90 to 105% and R^2 ranged from 0.996 to 0.999.

2.6 Data analysis

The statistical analysis was performed using the SPSS 19.0 software for Windows (IBM Co., Armonk, NY, USA). One-way analysis of variance (ANOVA) was conducted to assess the significant difference in the means of N_2O emissions, soil inorganic N concentration, net nitrification rate, and *amoA* abundances among treatments for each soil, followed by the least significant difference (LSD) test at a 5% level. Correlations between *amoA* abundances and soil inorganic N concentration or N_2O emission rate were assessed by the Pearson's correlation procedure.

3 Results

3.1 Soil N_2O emission

The N_2O emission rates were generally low (0.01–0.08 μg N kg^{-1} h^{-1}) in the N0 treatment without N fertilization (Fig. 1 a and b). The emission rates of N_2O were significantly stimulated upon urea fertilization and higher in the fluvo-aquic soil than in the anthrosol ($p < 0.05$). It is noted that in the fluvo-aquic soil, the lag period before the emission rate peaked was longest in N1200, followed by N900 and N600. The N_2O emission rate in fertilized treatments dropped to the same level as N0 at the incubation endpoint, except for N1200 where the emission rate was still higher than N0. In the anthrosol, the same trend was observed, wherein N1200 required more time to reach the maximum N_2O emission rate than N600 and N900 after the addition of urea.

The fertilization of urea significantly increased the cumulative N_2O emissions in both soils following the 56-day

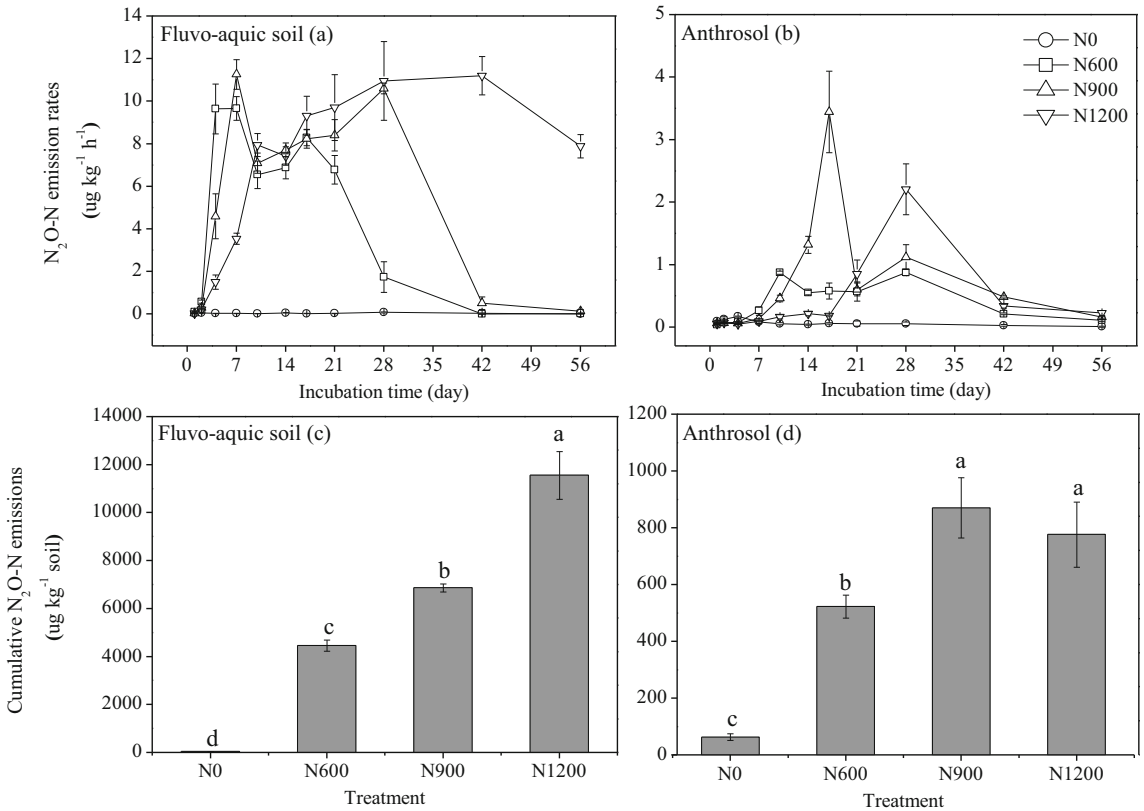

Fig. 1 Changes in the N_2O emission rate (**a**, **b**) and cumulative N_2O emissions (**c**, **d**) during 56-day incubation in the fluvo-aquic soil (**a**, **c**) and the anthrosol (**b**, **d**) fertilized with urea at different concentrations. N0, N600, N900, and N1200 represent urea concentrations of 0, 600, 900, and 1200 mg N kg^{-1} soil, respectively. Data are the means with standard deviations ($n = 3$)

incubation, compared to the N0 treatment (Fig. 1 c and d). In the fluvol-aquic soil, the cumulative N_2O emission increased with increasing addition rate of urea-N ($p < 0.05$). In the anthrosol, the cumulative N_2O emission was significantly higher in N900 and N1200 than in the N600 treatment. However, no significant difference was observed in the cumulative N_2O emission between the N900 and N1200 treatments; cumulative N_2O emission was significantly higher in the fluvo-aquic soil than in the anthrosol.

3.2 Soil inorganic nitrogen and net nitrification rate

The soil NH_4^+ concentration was low (6.9–11.0 mg N kg^{-1}) in the N0 treatment throughout the incubation (Fig. 2 a and b). Due to rapid hydrolysis of urea, the soil NH_4^+–N concentrations significantly increased following urea fertilization and decreased with time in both soil types. In the fluvo-aquic soil, the NH_4^+ decreased sharply after day 7, reaching to the same level with N0 treatment after 21, 28, and 56 days for N600, N800, and N1200, respectively (Fig. 2a). On the other hand, NH_4^+ concentrations decreased more gradually in the anthrosol with urea addition and were always higher than in the N0 treatment throughout incubation (Fig. 2b). Nevertheless, a similar trend was observed wherein the NH_4^+ concentrations in the anthrosol were highest in N1200, followed by N800 and N600 during the incubation period after day 7 (Fig. 2b).

For the both soils, higher levels of urea fertilization led to significantly higher production of soil NO_2^- and NO_3^-–N at the end of 56-day incubation ($p < 0.05$) (Fig. 2c, d). In the anthrosol, the soil NO_2^- and NO_3^-–N concentration was lower in the N1200 than in the N600 and N900 during the first 28 days of incubation, indicating that soil nitrification was partly inhibited by addition of 1200 mg urea-N kg^{-1} soil. For the fluvo-aquic soil, urea addition increased the net nitrification rate at the interval of d0–d7 and d7–d14, compared to the N0 treatment (Table 1). For the anthrosol, the net nitrification rate decreased from 2.40 to − 0.02 mg kg^{-1} soil day^{-1} with increasing urea-N rate from 600 to 1200 mg kg^{-1} at the interval of d0–d7. At the later stage of incubation (d28–d56), no significant difference was found in the net nitrification rate among the fertilized treatments.

3.3 Abundances of AOA and AOB

In the present study, the abundances of AOA and AOB responded differently to high urea-N addition (Fig. 3). Following the 56-day incubation, the AOA abundances

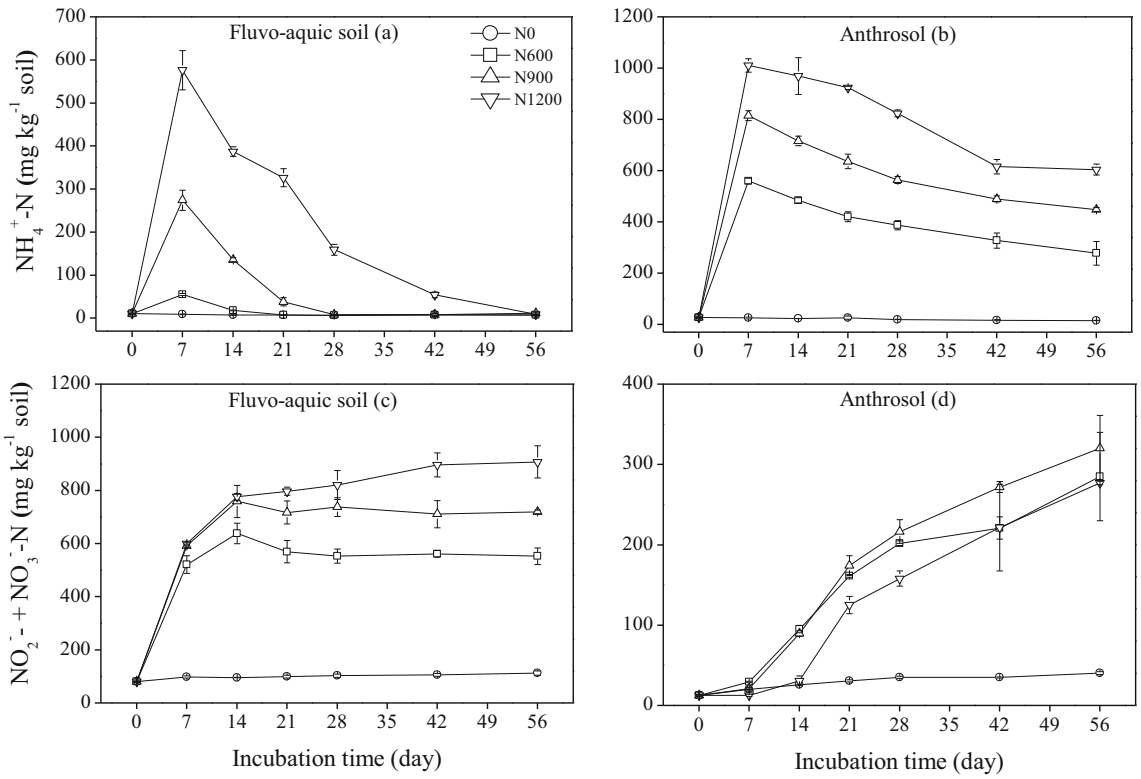

Fig. 2 Changes in NH_4^+–N (**a**, **b**), and NO_2^- – plus NO_3^-–N (**c**, **d**) during 56-day incubation in the fluvo-aquic soil (**a**, **c**) and the anthrosol (**b**, **d**) fertilized with urea at different concentrations. N0, N600, N900, and N1200 represent urea concentrations of 0, 600, 900, and 1200 mg N kg^{-1} soil, respectively. Data are the means with standard deviations (n = 3)

Table 1 Net nitrification rate during incubation for 56 days in the fluvo-aquic soil and the anthrosol fertilized with urea at different concentrations

Soils	Time intervals	Net nitrification rates (mg kg^{-1} soil day^{-1})			
		N0	N600	N900	N1200
Fluvo-aquic soil	d0~d7	2.51 ± 0.57 c	62.93 ± 4.75 b	73.10 ± 0.89 a	74.14 ± 0.79 a
	d7~d14	(− 0.33) ± 0.09 c	16.73 ± 5.55 b	23.78 ± 8.64 a	25.25 ± 1.85 a
	d14~d28	0.52 ± 0.41 b	(− 6.05) ± 1.90 c	(− 1.50) ± 2.51 b	3.16 ± 3.09 a
	d28~d56	0.33 ± 0.28 b	(− 0.02) ± 1.11 b	(− 0.64) ± 0.25 b	3.11 ± 2.15 a
Anthrosol	d0~d7	1.09 ± 0.02 b	2.40 ± 0.11 a	1.19 ± 0.22 b	(− 0.02) ± 0.18 c
	d7~d14	0.79 ± 0.04 c	9.38 ± 0.65 a	9.84 ± 0.50 a	2.59 ± 0.89 b
	d14~d28	0.65 ± 0.10 c	7.64 ± 0.22 b	9.06 ± 1.07 a	9.09 ± 0.67 a
	d28~d56	0.19 ± 0.06 b	2.96 ± 1.96 a	3.70 ± 1.46 a	4.26 ± 0.09 a

N0, N600, N900, and N1200 represent urea concentrations of 0, 600, 900, and 1200 mg N kg^{-1} soil, respectively. Different lowercase letters in the same row indicate significant difference at $p < 0.05$. Data are the means with standard deviations ($n = 3$)

slightly increased in the fluvo-aquic soil in the N0 and N600 treatments but remained at the same level at day 0 in N900 and N1200 (Fig. 3a). In the anthrosol, the AOA abundances significantly increased only in the N0 treatment without fertilization but remained at the same level in N600 and significantly decreased ($p < 0.05$) in N900 and N1200 (Fig. 3b).

The AOB abundances, in contrast, significantly increased following urea fertilization compared to the N0 treatment (Fig. 3 c and d). However, no significant differences were observed between different levels of nitrogen fertilization in both soils. The AOB/AOA ratios ranged from 0.32 to 2.79 and from 0.28 to 46.02 in the fluvo-aquic and paddy soils, respectively (Fig.

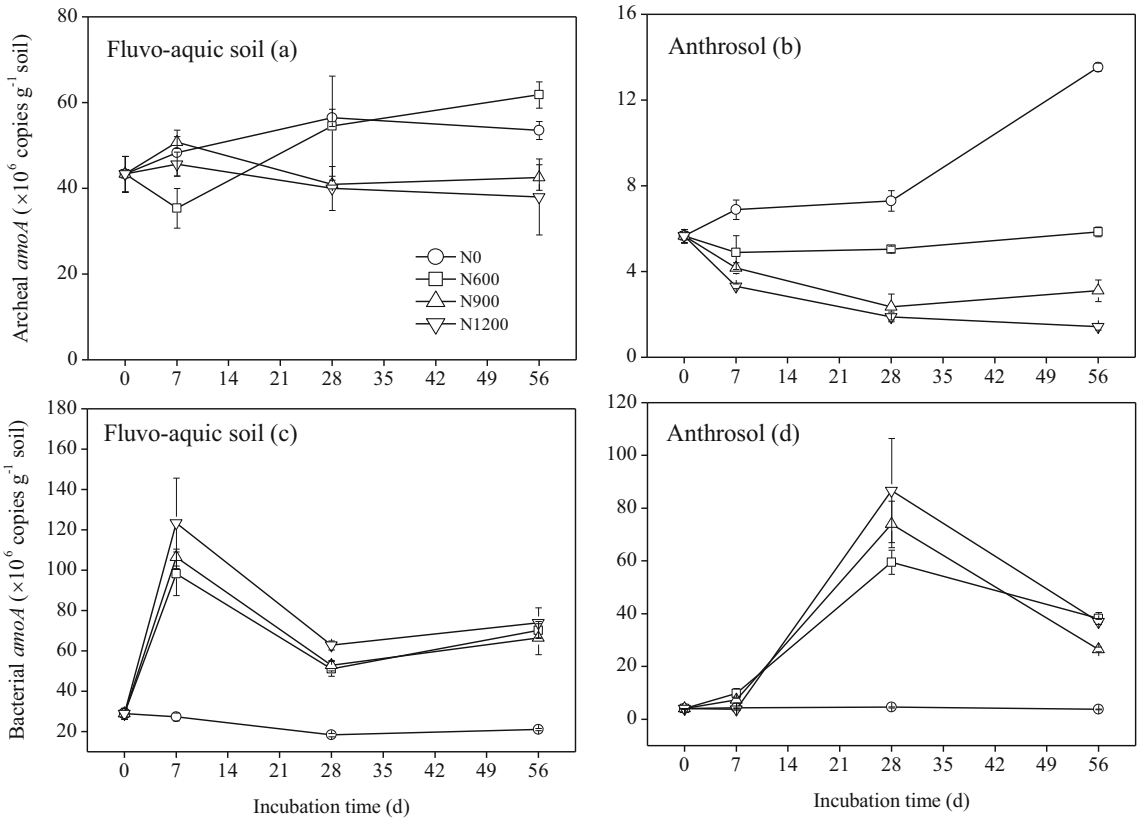

Fig. 3 Changes in AOA (**a**, **b**), AOB (**c**, **d**) abundance during 56-day incubation in the fluvo-aquic soil (**a**, **c**) and the anthrosol (**b**, **d**) fertilized with urea at different concentrations. N0, N600, N900, and N1200 represent urea concentrations of 0, 600, 900, and 1200 mg N kg^{-1} soil, respectively. Data are the means with standard deviations ($n = 3$)

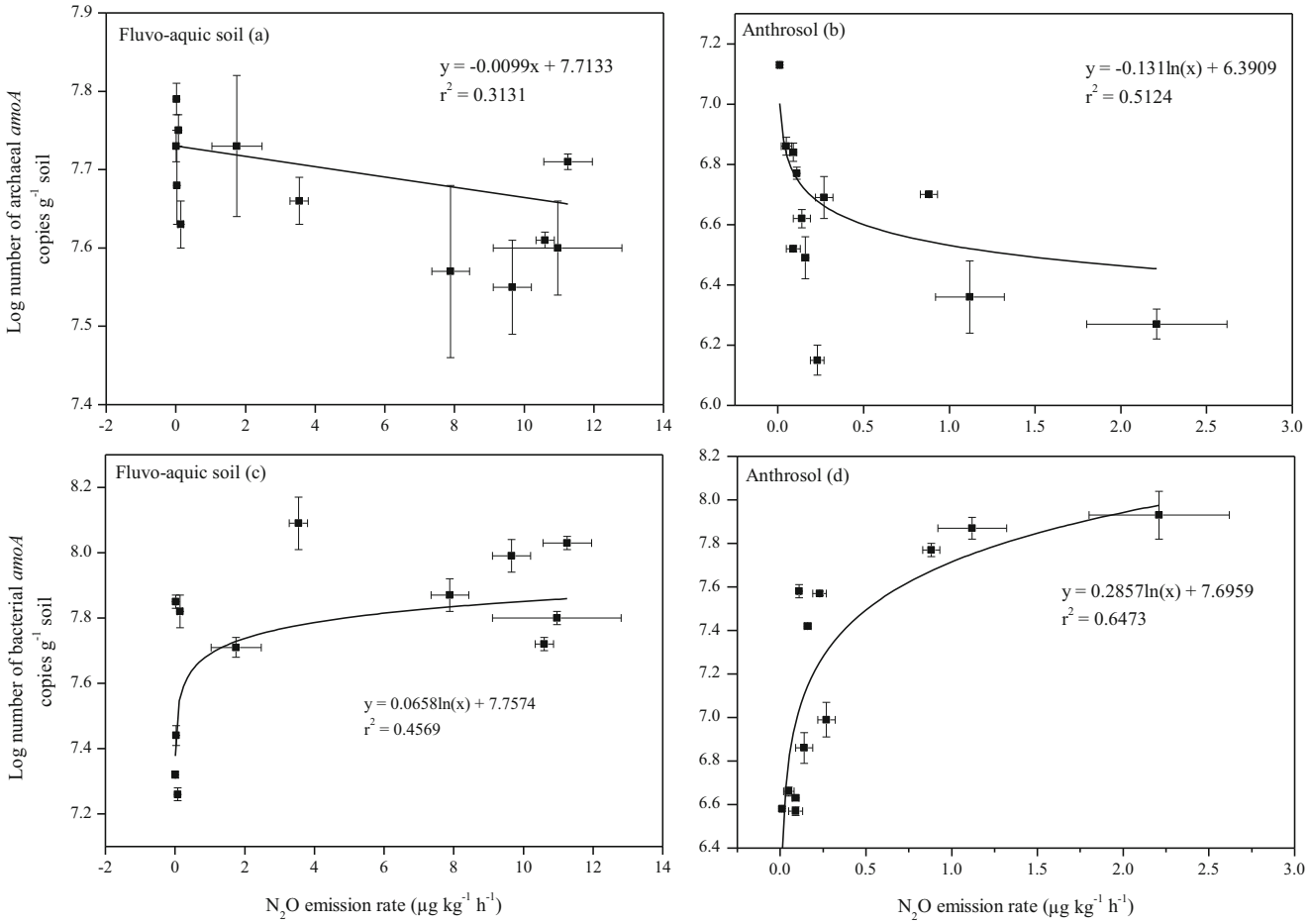

Fig. 4 Relationship of N_2O emission rates with AOA (**a**, **b**) and AOB (**c**, **d**) abundances in the fluvo-aquic soil (**a**, **c**) and the anthrosol (**b**, **d**) fertilized with urea at different concentrations

S2 – ESM). The addition of urea significantly increased the AOB/AOA ratios in the both soils.

3.4 Relationships between nitrification and N_2O emissions with ammonia oxidizer abundance

A significant positive relationship was observed between nitrite and nitrate concentration and AOB abundance in fertilized soils ($p < 0.05$), whereas nitrite and nitrate concentration were negatively correlated with AOA abundance (Table S2 - ESM). Similarly, in both soils following urea fertilization, the N_2O emission rate was positively correlated to AOB but not to AOA abundance (Fig. 4 a and b).

4 Discussion

The results of the present study showed that in the initial stage of incubation, an increase in N_2O emission was primarily due to the nitrification process in both soils under our aerobic microcosm incubation; this was strongly indicated by the concurrence of enhanced nitrification rates and N_2O emissions following urea addition (Table 1; Fig. 1). Other pathways, represented by denitrification, might have also contributed to the N_2O production in our soils but were unlikely to be dominant under our aerobic incubation condition. A previous study has conducted similar microcosm incubations in an agricultural soil under 60% WFPS and revealed negligible N_2O production derived from denitrification (Hink et al. 2017). In the present study, soils were also incubated under 60% WFPS condition, favorable for aerobic nitrification but not ideal for anaerobic denitrifier activity (Bateman and Baggs 2005; Avrahami et al. 2002; Hu et al. 2015a; Liu et al. 2016b). Nitrifier denitrification is also an important pathway in the production of soil N_2O (Wrage et al. 2001). In the fluvo-aquic soil, N600 treatment still maintained a high level of N_2O emission but had a low NH_4^+ concentration in the days 14–28, indicating that the N_2O production maybe through nitrifier denitrification in this study. High-level addition of urea-N usually leads to an accumulation of NO_2^- and then increases the soil N_2O emission produced by nitrifier denitrification (Venterea et al. 2015; He et al. 2016). Ma et al. (2015) reported that in a fluvo-aquic soil, addition of urea-N inhibited transformation of NO_2^- to NO_3^- and stimulated the

accumulation of NO_2^-, thus resulting in an increase in N_2O emission. Therefore, the soil N_2O may be derived from coupled nitrification and denitrification in our incubation experiment. However, further studies would be needed to assess the contribution of NO_2^- to N_2O emission by using ^{15}N tracer method.

Our study further displayed niche differentiation of archaeal and bacterial ammonia oxidizers for N_2O emissions. At the N0 condition without urea addition, both soils appeared to show AOA rather than AOB activities, as the AOA abundances increased with the incubation time while the abundances of AOB remained unchanged throughout the incubation time (Fig. 3). This is consistent with the previous revelation of high AOA activity in soils where NH_4^+ being limited and derived mainly from mineralization of soil organic N (Di et al. 2010a, b; Cui et al. 2013; Ouyang et al. 2016; Wang et al. 2016a, b; Guo et al. 2017; Hink et al. 2018). However, following the urea addition, only AOB growth was induced, which supports previous studies on agricultural soils (Jia and Conrad 2009; Di et al. 2010a; Xia et al. 2011; Dai et al. 2013; Shen et al. 2014; Zhang et al. 2017). Our results therefore strongly suggested that AOB played a dominant role in ammonia oxidation and N_2O production under urea-amended conditions and was further demonstrated by a positive and significant correlation between AOB abundance and the N_2O emission rate (Fig. 4; Table S2 - ESM). This niche differentiation of active ammonia oxidizers by different NH_4^+ concentrations resulted in different consequences of N_2O emission in soils, as AOA and AOB are the major N_2O source under the N limited condition and those following urea supply, respectively.

A higher concentration of urea would potentially lead to more N_2O production from ammonia oxidizers, i.e., AOB, in our soils (Mahmood and Prosser 2006; Di and Cameron 2011). However, for the anthrosol, there was no significant difference in the cumulative N_2O emission between the N900 and N1200 treatments (Fig. 1d), indicating that factors other than N availability should have limited N_2O production under high ammonium concentration. One possible explanation is the high osmotic stress imposed by the excessive ammonium concentration in the soil, which might affect the enzymatic kinetics of AOB. This is supported by a more delayed emergence of the maximum N_2O emission rate observed in soils receiving a higher concentration of urea (Fig. 1 a and b). Another one maybe that high NH_4^+ concentration is toxic to soil nitrifiers (Deppe et al. 2017), thus resulting in a lower N_2O emission in N1200 than in N600 and N900 at the early stage of incubation. The enzymatic production of N_2O by AOB could be suppressed by excessive levels of N addition at the early stages of incubation, similar to a previous study (Van and Maeda 2018) and apparently relieved with decreasing ammonium concentration at a later stage. Additionally, some AOB can adapt to the increasing soil NH_4^+ concentration (Yang et al. 2013). Previous study has showed that we should not rule out the potential competition of AOA for N_2O production in soils receiving less fertilization input. For instance, the AOA abundance was higher in N600 compared to both N900 and N1200, implying its potential activity in N600. Since the AOA yields less N_2O than AOB by converting the same amount of ammonia (Hink et al. 2017), the significantly less N_2O emissions in N600 compared to both the N900 and N1200 regimes could be the consequence of competition for NH_4^+ from AOA in ammonia oxidation. This could particularly be the case in the anthrosol, as the production of nitrite and nitrate occurred at similar rate between differently fertilized microcosms.

Our results further revealed that the net nitrification rate increased with increasing the concentration of urea addition in the fluvo-aquic soil at the first 14 days of incubation (Table 1). However, in the anthrosol, higher level of N addition (N1200) decreased the net nitrification rate over 28-day incubation. This indicates a potentially high retention ratio of urea-derived ammonium not oxidized to nitrate in the early stage of incubation. Despite the gradients in urea-N concentration (600–1200 mg N kg^{-1}) applied to the soils, the nitrification rate was not drastically stimulated by the maximum urea supply. Particularly, in the anthrosol, the net nitrification rate continued at the same rate among the urea addition treatments at the later stage of incubation (d28–d56). The reason maybe that the active ammonia oxidizers in this soil might reach the maximum specific cell activity in oxidizing ammonia with sufficient ammonium (Prosser and Nicol 2012), limiting the nitrification rate in the anthrosol. This might explain the high NUE in a fertilized band of the agricultural field (Grant et al. 2001; Pfab et al. 2012), wherein the nitrification rate no longer increased with excessively high ammonium supply, resulting in a high proportion of the fertilizers being utilized in the form of ammonium by plant and other soil organisms. The transferability of microcosm incubation to field condition is limited (Venterea et al. 2015; Deppe et al. 2017). Because the urea-N content is a distinct gradient under the incubation condition, but it is a continuous gradient in the field due to diffusion and uptake by plant. In addition, the temperature and water content are constant in the microcosm incubation, whereas they are dynamic under the field condition.

It is noted that the nitrification and cumulative N_2O emission were much higher in the fluvo-aquic soil than in the anthrosol following the urea addition (Table 1; Fig. 1 c and d), and this difference in nitrification activity should be determined by soil physicochemical properties (Yao et al. 2013; Shen et al. 2014; Hu et al., 2015b), thus affecting the soil N_2O emission. Among all soil characteristics, soil pH seems to be a major factor determining the distribution and activity of ammonia oxidizers (Shen et al. 2012; Hu et al. 2014; Jiang et al. 2015; Li et al. 2018). Dai et al. (2014) reported that the soil nitrification was dependent on initial soil pH in an

incubation experiment. In the present study, the fluvo-aquic soil and anthrosol were neutral and acidic in their native states, respectively (Table S1 - ESM). The soil nitrification capacity was higher in the soil with higher pH than that in the acid soil (Shen et al. 2014; Jiang et al. 2015; Wang et al. 2015). Yuan et al. (2005) reported that fluvo-aquic soil had a higher nitrification potential than permeable anthrosol. In an microcosm incubation with 150 mg NH_4^+–N kg soil, Wang et al. (2016a) found that the cumulative N_2O emission was higher from the alluvial soil (pH = 7.8) than that from the red soil (pH = 6.2). Previous studies have shown that higher ratios of AOA to AOB abundances lowered the soil pH (Yao et al. 2013; Hu et al. 2014; Xi et al. 2017), with dominant AOA activities were constantly revealed in acidic soils, while AOB dominated the soil nitrification in the neutral-alkaline and N-rich soils (Zhang et al. 2012; Lu and Jia 2013; Jiang et al. 2015; Liu et al. 2015; Li et al. 2018). Due to the rapid hydrolysis of urea, the soil pH reached a peak value at the early stage of incubation (Fig. S1 - ESM), which would, therefore, favor AOB. In a microcosm experiment, Venterea et al. (2015) found that addition of bovine urine at 1200 mg N kg^{-1}, soil pH increased from 5.3 to 7.5 at first 2 days of incubation. We speculate that the composition as well as physiological traits of active AOB are distinct in these two soils due to long-term adaptation to the different *in situ* pH conditions. Future experiments relying on phylogenetic analysis should be conducted to test this hypothesis. Furthermore, a meta-analysis of 713 soil samples from Scotland conducted by Yao et al. (2013), who found that soil type also played an important role in shaping specific niches of ammonia-oxidizers. In our study, the AOA was negatively affected by high N addition in the anthrosol, but was not in the fluvo-aquic soil.

5 Conclusions

The present results showed the potential effect of the band fertilization regime on soil nitrification and N_2O emission. The simulated high ammonium concentrations in the present study would be common in the center or in proximity to the area under band fertilization. Despite that fact that ammonium-based fertilization would inevitably boost the soil nitrification, the resultant N_2O production does not necessarily increase with more input of ammonium-based fertilizers due to increased osmotic stress likely restricting ammonia oxidizer activity. Compared to the N0 treatment, the AOB abundance was enhanced by addition of N fertilizer, except for that in day 7 in the anthrosol, whereas the growth of AOA was not affected or decreased by high addition of urea-N. There was a delay for peak N_2O emission under the high N fertilizer addition in the both soils. The results from the present study indicated that AOB rather than AOA dominated the soil nitrification and N_2O emissions in the agricultural soils treated with high N addition. We demonstrate, in this study, the great potential of the band fertilization regime with regard to soil fertility and greenhouse gas emissions from a microbiological perspective and encourage further investigation into this trending agricultural management system.

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