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Distinct drivers of activity, abundance, diversity and composition of ammonia-oxidizers: evidence from a long-term field experiment

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ABSTRACT

Ammonia oxidation, the primary and rate-limiting step of nitrification, is mediated by both ammonia-oxidizing archaea (AOA) and bacteria (AOB). However, the dominant environmental driver of the activity, abundance, diversity and composition of ammonia-oxidizers has not been well understood enough, and the relative contribution of AOA and AOB to nitrification is still under debate. Soils treated with different fertilization regimes in an over 35-year field experiment were collected to explore the variation in function and structure of ammonia-oxidizer communities and corresponding driver. The highest nitrification activity (44.49 mg N kg^{-1} soil d^{-1}) was found in only organic fertilizer (O) treated soil, whereas the lowest activity (2.81 mg N kg^{-1} soil d^{-1}) was observed in only mineral fertilizer (NPK) treated soil. Moreover, as 1-octyne was employed to discriminate AOA- and AOB-supported nitrification, AOA dominated (93.53%) the nitrification in the Control soil, while AOB contributed dominantly (84.73–89.10%) in all of the organic amended soils, and NPK-treated soil showed an almost equal contribution to AOA (45.79%) and AOB (54.21%). Compared with the Control soil, AOA abundance increased in soils with organic and low chemical fertilizer but decreased in only chemically treated soil, whereas the AOB abundance in all fertilized soils was greatly enhanced. The AOA activity was linearly dependent on AOA abundance, whereas the AOB activity was exponentially correlated with AOB abundance. The sequences of AOA and AOB in the Control soil were mostly affiliated with group I.1b *thaumarchaeota* and genus *Nitrosospira* clusters 3a.1. Soil treated with NPK increased the abundance of AOA that belonged to group I.1a-associated lineage, whereas more abundant AOB was related to *Nitrosospira* clusters 3a.2 and 8b. In contrast, the O-treated soil showed more abundant AOB that belonged to *Nitrosospira* clusters 3b and 8b. As revealed by aggregated boosted tree analysis, the soil ammonium (NH_4^+) content was identified as the dominant driver of activity and diversity of AOA, and soil pH was considered to be the major influencing factor in abundance and composition of AOA; the AOB composition was mainly affected by soil NH_4^+ content, the relative activity and diversity by soil pH, and the relative abundance by soil electrical conductivity (EC). Collectively, different fertilization regimes will result in variations in activity, abundance, diversity and composition of ammonia-oxidizers with distinct drivers. Our research could be helpful to identify better strategies for the mitigation of nitrate production in agricultural soils.

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1. Introduction

Nitrification is a critical aerobic process in the global nitrogen cycle, influencing the fate of nitrogen in terrestrial ecosystems and often promoting the leaching of nitrate and the release of nitrous oxide from soils. The primary and rate-limiting step, ammonia oxidation, has traditionally been thought to be catalysed through the ammonia-oxidizing archaea (AOA) of *Thaumarchaeota* phylum (Brochier-Armanet et al., 2008) and bacteria (AOB) of β- and γ-classes of *Proteobacteria* (Head et al., 1993), despite recent evidence indicating complete nitrification by *Nitrospira* bacteria that are present in the environment (Daims et al., 2015). Furthermore, an accurate molecular assessment approach of the genetic potential for ammonia oxidation has been established with the development

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of techniques to examine the functional *amoA* gene, which encodes the α-subunit of the key enzyme ammonia monooxygenase in both AOA and AOB. These developments provide an opportunity to assess soil ammonia-oxidizer communities' ecology and function in response to environmental change.

Fertilization, which is a commonly used agricultural practice for improving plant nutrition and achieving high yield, strongly influences the soil environment. Environmental factors that influence AOA and AOB are well known and have been extensively investigated. Numerous individual experimental studies have suggested that AOA and AOB communities are mainly shaped by the soil pH (Nicol et al., 2008; Gubry-Rangin et al., 2011; Hu et al., 2013) and substrate (ammonia/ammonium) (Avrahami et al., 2002; Martens-Habbena et al., 2009; Verhamme et al., 2011). Moreover, soil salinity (Erguder et al., 2009; Zhang et al., 2015), organic carbon (Jiang et al., 2014), carbon/nitrogen ratio (Lu et al., 2015), moisture content (Hu et al., 2015), temperature (directly affected by the soil structure) (Tourna et al., 2008), and soil texture (Wessen et al., 2011) also exert significant influences on the activity, abundance, diversity and composition of ammonia-oxidizing communities in soil. These investigations have provided insights into the processes of ammonia oxidation and have improved our understanding of how ammonia-oxidizers will respond to environmental change. However, the relative importance of these soil characteristics in controlling ammonia-oxidizer communities in natural environments, especially in anthropogenically disturbed agricultural ecosystems, is still unclear.

The relative contribution of AOA and AOB to soil nitrification remains largely unsolved. Although previous studies have shown that AOA is generally more abundant than AOB in soils (Leininger et al., 2006; He et al., 2007; Nicol et al., 2008; Shen et al., 2008), the ammonia oxidation rate may be not necessarily directly linked to current AOA and AOB populations (Nicol et al., 2008). In some agricultural soils, AOA is found to play a more critical role than AOB in ammonia oxidation (Gubry-Rangin et al., 2010; Zhang et al., 2012). However, a contrary conclusion has been presented in several studies (Xia et al., 2011; Ai et al., 2013; Ouyang et al., 2016), which demonstrated that the changes in ammonia oxidation activity are associated with the abundance and composition of AOB community, but not with those of AOA. Similar results were reported in a meta-analysis by Carey et al. (2016), who revealed that AOB is more responsive to nitrogen addition than AOA in land-use or soil management. Recently, a study by Taylor et al. (2013) demonstrated that ammonia oxidation activity of AOB is quickly and irreversibly inhibited by 1-octyne, whereas AOA is more resistant than AOB, and therefore 1-octyne can be used to distinguish AOA- and AOB-supported nitrification.

It is important to know how long-term different fertilization regimes lead to various environmental changes in soil including effects on activity, abundance, diversity and composition of ammonia-oxidizer communities since they are important for ecosystem services. Since there remain notable knowledge gaps regarding the relative role of ammonia-oxidizers in nitrification and their environmental drivers, we conducted the present study, which collected soils from a 35-year field fertilization experiment, to estimate changes in the nitrification rate and the relative contribution of AOA and AOB under different fertilization regimes and to investigate the dominant environmental drivers influencing the activity, abundance, diversity and composition of AOA and AOB. Here we employed a series of complementary analyses (nitrification potential assay, octyne inhibition, quantitative real-time polymerase chain reaction and high-throughput 454 pyrosequencing, etc) to comprehensively analyse the AOA and AOB communities, and simultaneously set to test the following hypotheses: (i) different fertilization regimes could potentially change the ammonia oxidation activity of AOA and AOB and their relative contribution to nitrification, and (ii) environmental variables disturbed by fertilization would affect differently the different ammonia oxidizers activity, abundance, diversity and composition. Our expectation was to improve management strategies of nitrate production in agricultural soils by understanding the prevailing environmental driver for the ecological function of AOA and AOB.

2. Materials and methods

2.1. Experimental field site and soil sampling

The field site was established in 1981 at the Yangliu Long-term Experimental Station (33°37′N, 116°45′E) located in Suixi, Anhui Province, China, where a wheat-maize rotation is the current cropping system. The area has a typical temperate and monsoonal climate with an annual average temperature and precipitation of 14.8 °C and 872 mm, respectively. The soil was derived from fluvio lacustrine sediments and classified as Vertisol (IUSS Working Group WRB, 2015). At the beginning of the experiment, the soil had a pH (H_2O) of 7.6, 5.93 g kg^{-1} organic carbon, 0.78 g kg^{-1} total N, 0.47 g kg^{-1} total P, and 64.1 and 2.5 mg kg^{-1} of alkali-hydrolyzable N and available P, respectively.

Five treatments were conducted with four replicates (plot area 30 m^2) for each treatment in a randomized plot design. The treatments consisted of: (1) Control, no fertilizer; (2) NPK, only mineral NPK fertilizer (N, 525 kg ha^{-1} y^{-1}; P_2O_5, 210 kg ha^{-1} y^{-1}; and K_2O, 210 kg ha^{-1} y^{-1}); (3) O, organic-only fertilizer (composted bean cake, 7500 kg ha^{-1} y^{-1}); (4) NPKO, mineral NPK (N, 262.5 kg ha^{-1} y^{-1}; P_2O_5, 105 kg ha^{-1} y^{-1}; and K_2O, 105 kg ha^{-1} y^{-1}) plus organic fertilizer (composted bean cake, 3750 kg ha^{-1} y^{-1}); and (5) HNPKO, high rate mineral NPK (N, 420 kg ha^{-1} y^{-1}; P_2O_5, 168 kg ha^{-1} y^{-1}; and K_2O, 168 kg ha^{-1} y^{-1}) plus high rate organic fertilizer (composted bean cake, 6000 kg ha^{-1} y^{-1}). The N application rates of the NPK, O and NPKO treatments were equal to 525 kg N ha^{-1} y^{-1} by summing organic N and inorganic N inputs, whereas 840 kg N ha^{-1} y^{-1} were applied in the HNPKO treatment with an organic N to inorganic N ratio of 1:1. The mineral NPK fertilizer consisted in the application of the compound fertilizer (15-15-15, N-P_2O_5-K_2O) and urea. Organic fertilizer was made by composting soybean cake in which the water, C, N, P, and K contents were: 100–150 g kg^{-1}, 174–232 g kg^{-1}, 60–70 g kg^{-1}, 10–30 g kg^{-1}, and 20–30 g kg^{-1} respectively.

Soil samples were collected (0–20 cm) in each plot in March 2016 from 6 positions using an auger for coring and then were composited together as a single sample. Moist soils were sieved through 2-mm mesh to remove impurities and to further homogenize the samples before subdividing each for analyses. Aliquots of samples were then stored at −80 °C until molecular analysis or at 4 °C until soil moisture, nitrification potential, dissolved organic carbon (DOC), ammonium (NH_4^+) and nitrate (NO_3^-) were analysed, or were air-dried for soil total carbon (TC), total nitrogen (TN), pH and electrical conductivity (EC) analysis.

2.2. Soil properties

The soil moisture was determined by oven drying soils at 105 °C for 12 h. Soil TC and TN contents were determined by a vario MACRO cube element analyser (Elementar Analysen systeme GmbH, Hanau, Germany). The concentration of DOC was quantified with a Liqui-TOC element analyser II (Elementar Analysen systeme GmbH, Hanau, Germany) after the soil samples were extracted by K_2SO_4 (0.5 M). Soil NH_4^+ and NO_3^- were extracted with a 0.01 M $CaCl_2$ solution (1:10 of soil:solution by mass) for 30 min, and then the NH_4^+ and NO_3^- concentrations were determined using a continuous-flow

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