Science of the Total Environment 635 (2018) 240–248

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Vertical distribution of ammonia-oxidizing microorganisms across a soil profile of the Chinese Loess Plateau and their responses to nitrogen inputs

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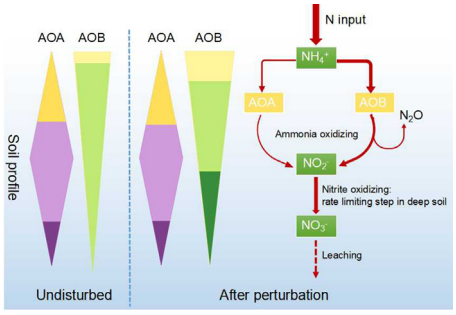
HIGHLIGHTS

- Deep soils on China's Loess Plateau are frequently exposed to perturbations and N inputs.
- AOA and AOB control the rate-limiting step of nitrification.
- There were different AOA and AOB distribution along the loess soil profile.
- N inputs increased AOB abundance and diversity, but had limited effects on AOA.
- High N inputs may lead to nitrate accumulation in deep loess soils.

GRAPHICAL ABSTRACT



Shapes indicate the distribution pattern of AOA and AOB abundance along the soil profile, and colors indicate their community diversity.

ARTICLE INFO

Article history:
Received 6 January 2018
Received in revised form 1 April 2018
Accepted 7 April 2018
Available online xxxx

Editor: P Holden

Keywords:
Soil erosion
Deep soil
Ammonia-oxidizing archaea
Ammonia-oxidizing bacteria
Nitrous oxide
Nitrite accumulation

ABSTRACT

Ammonia-oxidizing archaea (AOA) and bacteria (AOB) oxidize ammonia into nitrite, the first and rate-limiting step of microbial nitrification, and exert major controls over soil nitrogen transformations. The Loess Plateau in northwest China is characterized with deep soils that are often exposed to the surface and reactive nitrogen (N) inputs due to erosion and human removal of the surface soil. However, few have examined the distribution of AOA and AOB along the profile of Loess Plateau soils and their responses to N inputs. We examined the abundance and diversity of AOA and AOB along the soil profile (0–100 cm) and their responses to two levels of N inputs (low at 10, and high at 100 μg N g^{-1} soil) in a 55-d incubation experiment. While AOB were most numerous in the surface soil (0–20 cm), AOA were most abundant in the subsoils (20–40 and 40–60 cm), suggesting a niche differentiation between AOA and AOB along the soil profile. High N input increased AOB nearly ten-fold in the upper two layers of soils (0–20 and 20–40 cm) and sixteen to twenty-five fold in the deeper soil layers (40–60, 60–80 and 80–100 cm). However, it only increased AOA by 7% (40–60 cm) to 48% (20–40 cm). In addition, potential nitrification rate and N_2O emissions correlated only with AOB. Finally, high N input significantly increased AOB diversity and led to nitrite accumulation in deep soil layers (60–80 and 80–100 cm). Together, our results showed that high N input can significantly alter the diversity and function of ammonia-oxidizing microbes in the deep soil of Loess Plateau, suggesting the need to examine the generality of the observed changes and their potential environmental impacts.

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https://doi.org/10.1016/j.scitotenv.2018.04.104
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1. Introduction

Human activities have profoundly altered the global nitrogen (N) cycle, with anthropogenic N inputs overtaking natural N fixation in recent years (Green et al., 2004; Gruber and Galloway, 2008; Erisman et al., 2013). Most anthropogenic N enters the terrestrial ecosystems in the form of NH_4^+ and soil microbes convert NH_4^+ into mobile NO_3^- through the nitrification process, which may lead to NO_3^- leaching into water and/or N_2O (a potent greenhouse gas) emissions (Gruber and Galloway, 2008; Fang et al., 2009; Dai et al., 2013). Transformation of ammonia to nitrite through oxidation is the first and rate-limiting step of microbial nitrification, which is conducted by ammonia monooxygenase (Rotthauwe et al., 1997; Konneke et al., 2005). Although ammonia oxidation has long been considered to be performed by only a few phylogenetically restricted microorganisms in the phylum of *Proteobacteria*, isolated strains and metagenomic evidences confirmed the presence of ammonia-oxidizing archaea (Konneke et al., 2005; Schleper et al., 2005; Hatzenpichler et al., 2008). AOA frequently outnumber their AOB counterparts (Leininger et al., 2006) and are predominant in nutrient-poor environments like unfertilized (Shen et al., 2008) or acidic soils (Gubry-Rangin et al., 2010; Zhang et al., 2012), indicating their important role in terrestrial N cycling. There is an increasing interest in the distribution of ammonia-oxidizing microorganisms (AOM) in deep soils because deep soils (25–100 cm) contain ca. two thirds of total soil N (Batjes, 1996) and 35–58% of total microbial biomass (Fierer et al., 2003; Schutz et al., 2010). Previous studies have shown that bacterial *amoA* genes declined significantly with depth while archaea *amo*A genes were more abundant in deeper soil horizons, resulting in a maximal AOA to AOB ratio in soil layers between 40 and 60 cm (Leininger et al., 2006; Zhu et al., 2011). Yet, how AOA and AOB communities along the soil profiles respond to new N inputs have rarely been studied, particularly in systems where deep soil exposure is routine.

One of such system is the Loess Plateau in northwest China, which has very deep loess originated from eolian dust deposition (An et al., 1991; Sun, 2002). The Plateau was once a high and flat plain, but now >70% of the area is a gully-hill dominated region owing to massive soil erosion largely caused by intense human activities over the past millennia (Zhao et al., 2013). Currently, over 60% of the Loess Plateau is subjected to severe soil and water erosion, with average annual soil losses amounting to 2000–2500 t km^{-2} (Shi and Shao, 2000; Wei et al., 2000). Consequently, deep soil layers are frequently exposed to the surface and are thus susceptible to changes in environmental factors such as temperature increase and N inputs through fertilization and/or deposition.

More importantly, deep soils on the Loess Plateau are often characterized with high organic C and ideal soil structure for plant growth (Gao et al., 2017). To reduce soil erosion and/or compensate cropland losses due to urbanization, there is a large-scale initiative to erase small hills and level the ground (Department of land and resources of Shaanxi Province, 2014). Large amounts of chemical N are subsequently applied to the newly exposed subsurface soils to ensure crop yields (Wei et al., 2000). However, AOM communities along the soil profile and their responses to new N inputs have not been investigated. These knowledge gaps critically hinder the capacity of agronomists and environmental scientists to predict the behavior of reactive N inputs and design environmentally-friendly N management regimes. Thus, we conducted an exploratory experiment to determine 1) the abundance and diversity of ammonia-oxidizing microorganisms along a Loess Plateau soil profile, and 2) how AOA and AOB in different soil layers respond to new N inputs.

2. Materials and methods

2.1. The sampling site and soil sampling

The sampling site is located at the Yunwu Mountain National Nature Reserve, northeast of Guyuan City, Ningxia Hui Autonomous Region of China (106°23′E, 36°15′N). The Reserve is situated in the middle of the Loess Plateau at an elevation of 1800–2100 m and has a total area of 6660 ha, with a hilly landscape and deeply incised gullies. The site has a typical semiarid climate and the annual precipitation is about 425 mm with 60%–75% occurring in July, August and September. The mean annual air temperature is 8.6 °C, with the lowest in January (−6.5 °C) and the highest in July (22.8 °C). The soil is a montane grey-cinnamon soil, Calci-Orthic Aridisol, according to the Chinese taxonomic system, which is equivalent to a Haplic Calcisol in the FAO/UNESCO system. The vegetation is a typical semiarid grassland on the Loess Plateau and primarily consists of *Stipa grandis*, *S. przewalskyi*, *S. bungeana*, *Artemisia sacrorum*, and *Thymus mongolicus*.

Soil samples were collected on July 30, 2016. The standing plants and surface residues were removed from the surface right before the soil sampling. An auger (10 cm diameter) was used to collect soil samples to a depth of 100 cm at intervals of 0–20, 20–40, 40–60, 60–80 and 80–100 cm. Soil cores were placed in sterile bags and immediately transported on ice to the laboratory in Nanjing Agricultural University (Nanjing, China) within three days. Soil samples were pre-treated by sieving through a 2 mm mesh to remove stones, roots and soil animals. Each soil sample was divided into two subsamples: one was stored at 4 °C for chemical analyses and an incubation experiment (see details below), and the other was stored at −80 °C for analyses of gene abundance.

2.2. The soil microcosm incubation experiment

The laboratory microcosm incubation experiment was initiated within 2 weeks after the field soil sampling and was set up in a full factorial design, including five soil depths (0–20, 20–40, 40–60, 60–80 and 80–100 cm) and three N levels: Control with no N addition (0 N), low N (LN, 10 μg NH_4^+-N per gram dry soil) and high N (HN, 100 μg NH_4^+-N per gram dry soil). This resulted in 15 different treatment combinations and each treatment combination was replicated 12 times. For each replicate, exact 40 g of soil (dry weight equivalent) was weighed into a 250 ml plastic bottle. After 7-d pre-incubation, soil moisture was adjusted to 60% of the field water-holding capacity (WHC) by adding deionized water or ammonium sulfate solution. The microcosms were capped with loose-fitting lids to allow air exchange, and were incubated at 25 °C in the dark. Distilled water was added twice or thrice a week to maintain 60% WHC. During the 55-d incubation, destructive samplings with three replicates of each treatment were performed on day 3, 10, 25 and 55. Each replicate was divided into two parts with one for the determination of extractable soil N and soil microbial biomass C (MBC), and another for characterization of the AOM abundance and community composition by qPCR and T-RFLP analyses.

2.3. Soil parameters

The age of each soil sample was estimated through determining the mean radiocarbon (^{14}C) conventional age (years BP; Stuiver and Polach, 1977) and $^{13}C/^{12}C$ ratio (‰) at Xi'an Accelerator Mass Spectrometry Center (3MV AMS), Xian, China, and the results were converted to years following the method described by Talma and Vogel (1993). Total soil C (TC) and N (TN) concentrations were determined by an elemental analyzer (Elementar Vario Micro Cube, Germany). Ammonium (NH_4^+) and nitrate (NO_3^-) concentrations in soil extracts were measured by a segmented flow analyzer (Skalar SAN Plus; Skalar Inc., Breda, The Netherlands). Soil MBC was estimated using the chloroform fumigation extraction method (Vance et al., 1987). Briefly, 12.5 g of soil was fumigated with ethanol free chloroform for 48 h and then extracted with 50 ml of 0.5 M K_2SO_4 (shaken for 30 min). Another 12.5 g of soil was extracted immediately with 0.5 M K_2SO_4 (shaken for 30 min) without fumigation and used as the control. Dissolved organic C (DOC) in the extracts was determined with a TOC analyzer (Elementar Vario Micro

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