Frontiers in the microbial processes of ammonia oxidation in soils and sediments

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Abstract

Purpose Two recent discoveries in nitrogen (N) cycling processes, i.e., archaeal ammonia oxidizers and anaerobic ammonia (ammonium) oxidation (anammox), have triggered great interest in studying microbial ammonia oxidation processes. The purpose of this review is to highlight recent progress in ammonia oxidation processes in soils and sediments, and to propose future research activities in this topic.

Results and discussion Aerobic ammonia oxidation and anammox processes are linked through the production and consumption of nitrite, respectively, thereby removing the reactive N (NH_4^+ , NO_2^- , NO_3^-) from soil and sediment ecosystems. Ammonia oxidizing microorganisms are widely distributed in soils and sediments, and increasing evidence suggests that ammonia oxidizing archaea and bacteria are functionally dominant in the ammonia oxidation of acid soils and other soils, respectively. The widespread occurrence and great variation in the abundance of anammox bacteria indicate their heterogeneous distribution and niche differentiation. Therefore, the worldwide distribution of both microbial groups in nature has stimulated researchers to investigate the physiology and metabolism of related groups, as well as appraising their contribution to N cycling.

Conclusions We summarized the current progress and provided future perspectives in the microbiology of aerobic and anaerobic ammonia oxidation in soils and sediments. With increasing concern and interest in soil and sediment ammonia oxidation processes, studies in the microbial mechanisms underlying nitrification and anammox, as well as their interactions, are essential for understanding their contribution to the loss of N either through nitrate leaching or N-related gas emissions.

Keywords Aerobic ammonia oxidation • Anaerobic ammonium oxidation (anammox) • Microbial processes • Nitrogen management

1 Introduction

Nitrification is a central process of the global nitrogen (N) cycle, influencing the N balance in agricultural ecosystems through emissions of the greenhouse gas, nitrous oxide and nitrate leaching. Two recent discoveries have improved our understanding of nitrification, i.e. archaeal ammonia oxidizers and the anaerobic ammonia (ammonium) oxidation (anammox) process. For over 100 years, ammonia oxidizing bacteria (AOB) have been considered as the only group mediating the first and rate-limiting step of nitrification, i.e. ammonia oxidation (Kowalchuk and Stephen 2001). Recent advances in metagenomic and sequencing techniques discovered that ammonia oxidizing archaea (AOA) appeared to be the most potential drivers in regulating aerobic ammonia oxidation, especially in acid biomes (Prosser and Nicol 2008; He et al. 2012). Moreover, the discovery of anammox process and related bacteria in the early 1990s offered new insight into the mechanism of anaerobic ammonia oxidation, which challenged the traditional view that denitrification was the only pathway leading to N loss (Jetten et al. 1998). It has been documented that anammox may contribute up to 50 % of N loss in marine systems (Dalsgaard and Thamdrup 2002; Kuenen 2008). Both processes of archaeal ammonia oxidation and anammox have been relatively well characterized in the marine ecosystem in terms of distribution, diversity and physiology, while more work is needed for understanding their significance and contribution to N cycling in soil and sediment ecosystems.

Ammonia oxidizing archaea (AOA) were firstly recognized as a member of Crenarchaea and were later proved to be a separate archaeal phylum named

Thaumarchaea (Brochier-Armanet et al. 2008). In contrast to the molecular features of AOB, AOA are better adapted to energetically stressful conditions, partly due to their tetraether-based lipid membrane. On the other hand, all the known anammox bacteria are related to *Planctomycete*. However, unlike *Planctomycete*, they contain a unique anammoxosome structure with special membrane (ladderane lipids) which can function in cell energy conservation due to their denser cell membrane than conventional membrane lipids (Kartal et al. 2012). Owing to the unique features in their cellular and molecular components, AOA and anammox bacteria developed high survival ability under harsh environmental conditions.

The biological N cycle is a complex process mediated by a wide range of microorganisms that interact with each other. Of these, the interaction of aerobic ammonia oxidation and anammox processes is one example, linking through the production and consumption of nitrite, respectively, and thereby removing the fixed N from the system (Fig. 1). The novel findings of AOA and anammox bacteria have shed new light on N transformations, especially under oxygen-limited conditions, such as at the oxic/anoxic interface. Therefore, the purpose of this review was to present a snapshot of the achievements of microbial mediated ammonia oxidation under both aerobic and anaerobic conditions by addressing the ecological niches, distribution and function of ammonia oxidizers and anammox bacteria, and thus to propose future perspectives in the field.

2 Ecophysiology, distribution and function of aerobic ammonia oxidizers in soils

and sediments

2.1 Niche specialization of ammonia oxidizers in soils and sediments

Since the first report of AOA in soils (Leininger et al. 2006), subsequent investigations on the diversity and abundance of AOB and AOA in soil ecosystems have demonstrated numerical abundant AOA in soils, irrespective of nutrient contents (He et al. 2007; Shen et al. 2008, 2011), soil types (Chen et al. 2010; Yao et al. 2013) and agricultural management practices (Ying et al. 2010, 2013). The abundance and composition of AOB and AOA in many soils have suggested that AOA functionally dominated ammonia oxidation in acid soils, while they were outcompeted in neutral and alkaline soils by AOB (Di et al. 2009; Shen et al. 2012). For example, acid soils amended with inorganic fertilizers and organic manure showed higher copy numbers of archaeal *amoA* gene compared with AOB, and there were positive correlations between the gene copy numbers and the potential nitrification rate (He et al. 2007). However, though a similar trend for the abundance ratio of AOA/AOB was observed in another alkaline soil, there was no significant correlation between the AOA gene copy number and the potential nitrification rates (Shen et al. 2008). These two contrasting results, combined with other recent findings on the ecological distribution of AOA, indicated two significant features for AOA: nitrification capacity; and niche specialization (Prosser and Nicol 2008; He et al. 2012). In terms of nitrification capacity, available knowledge suggested that AOA may have a mixotrophic or heterotrophic lifestyle as demonstrated through genomic sequence annotation of *N.maritimus* and a microcosms study of an acidic forest soil (Walker et al. 2010;

Levicnik-Höfferle, et al. 2012; Chen et al. 2013). This kind of feature confers AOA with the ability of utilizing organic carbon, and even some small organic molecules (Tourna et al. 2011; Stahl and de la Torre 2012). However, not all the Thaumarchaeota with *amoA* gene could perform CO₂ fixation or ammonia oxidation due to little information available on the physiological feature of AOA ammonia mono-oxygenase (AMO) (Stahl and de la Torre 2012), suggesting that correlation analysis between AOA *amoA* gene abundance and ammonia oxidation rates should be processed with caution.

Sediments share some features with soils, while they are distinct from soils due to the substantial difference of many factors, such as dissolved oxygen (DO) levels and salinity. Thanks to the introduction of molecular approaches to the microbiology of sediments, molecular surveys have shown that AOA are also widely distributed in the sediments of freshwater lakes, wetlands, estuarine and rivers, indicating their more widespread distribution than AOB in sedimentary environments (Francis et al. 2005). Contrasting the niche segregation of AOB and AOA in soils, a number of factors were involved in structuring the abundance and distribution of these two groups in sediments, such as salinity (Francis et al. 2005; Santoro et al. 2008), NH₄⁺ concentration (Liu et al. 2013), trophic status (Herrmann et al. 2009), pH (Wang et al. 2011) and organic carbon content (Liu et al. 2013). For example, AOA appeared to be dominant in river sediments with lower pH but higher organic carbon and NH₄⁺ concentration (Liu et al. 2013). Among these factors, salinity was shown to be a main factor influencing AOA community structure (Francis et al. 2005) as well as spatial

distribution (Sahan and Muyzer 2008) in saline biome.

Although field surveys based on molecular methods provide large amounts of information indicating the potential importance of AOA, culture-based analyses and stable isotope probing (SIP) experiments present more robust and direct evidence supporting AOA niche preference (Lehtovirta-Morley et al. 2011; Zhang et al. 2012). For example, the culture *N.devanaterra* was the only isolated AOA that is restricted to the growth pH range of 4.0 to 5.5, showing its favorable feature of lower pH (Lehtovirta-Morley et al. 2011). Through incubating different acidic soils with $^{13}\text{C}\text{-CO}_2$, a significant incorporation of ^{13}C -labeled carbon source into the *amoA* gene were detected for AOA, but not for AOB (Zhang et al. 2012). Furthermore, meta-analysis of a wide pH range of soils based on different scales with 454 barcoded pyrosequencing approaches clearly showed AOA specific adaptation to lower pH soils, further indicating the apparent preference for lower pH of AOA (Gubry-Rangin et al. 2011; Hu et al. 2013).

2.2 Habitat-associated phylotypes of ammonia oxidizers in soils and sediments

Extensive molecular surveys of *amoA* genes showed that AOA are ubiquitous in various environments, indicating its dominant role in global N cycling. In line with these findings are phylogenetic pattern studies of AOA associated with different environmental factors (Fernandez-Guerra and Casamayor 2012; Cao et al. 2013). Remarkably, the pH-associated selection of AOA phylotypes is one of the most popular arguments, which has been corroborated by metagenomic methods at

different biogeographical scales (Gubry-Rangin et al. 2011; Hu et al. 2013), as well as culture-based physiological studies (Lehtovirta-Morley et al. 2011). However, most of the previous studies focused on a small number of land use types or a single habitat, which raises the question of how other possible factors govern the distribution of AOB and AOA globally. Recently, multi-factorial drivers (land use, soil type, climate and N deposition) were highlighted for their importance in shaping microbial niche segregation of AOB and AOA (Yao et al. 2013). Moreover, *amoA* sequences retrieved from mangrove and estuary sediments showed the presence of niche-specific AOA phylotypes, which were influenced by variable environmental factors. This multi-factorial driving phenomenon was proven further by a meta-analysis survey of ~6000 deposited *amoA* sequences covering 11 different habitats worldwide (Fernandez-Guerra and Casamayor 2012), depicting a global picture of habitat-associated phylogenetic community patterns of AOB and AOA. Furthermore, it was found that AOB and AOA in soils and sediments showed an earlier burst of diversification compared with other habitats, indicating that these two guilds under this condition were phylogenetically more diverse than those in other habitats, including marine ecosystems. However, the mechanism underlying this feature is still very limited and future research is needed with emphasis on multi-factorial drivers, except pH and ammonium, for elucidating the niche habitat of AOB and AOA.

2.3 Inhibition of ammonia oxidation and nitrifier-mediated N₂O production

Since the recognition of AOA capacity for ammonia oxidation, the extent to which

AOA contribute to soil nitrification became a key issue for global N cycling, which resulted in the quest of how to differentiate the role of AOB and AOA in the ammonia oxidation process. Nitrification inhibitors, as the most frequently used tools in reducing N loss, are therefore playing an key role in distinguishing AOB and AOA contributions to soil nitrification (Offre et al. 2009; Zhang et al. 2012). For example, a short-term soil incubation study showed that octyne had no effect on the growth of AOA, while it inhibited AOB, indicating its potential function in discriminating archaeal and bacterial nitrification in short-term assays (Taylor et al. 2013). As previously shown, dicyandiamide (DCD) and acetylene (C_2H_2) are extensively used inhibitors of nitrification by merit of their ability to inactivate ammonia oxidation activity mediated by the dominated microbial ammonia oxidizer (Di et al. 2009; Shen et al. 2012; Zhu et al. 2013). However, a comparison of six different reagents including four nitrification inhibitors, one antibiotic and one NO-scavenger, showed that DCD was the weakest inhibitors on AOA with nearly 1 mM for EC_{50} (Shen et al. 2013). Furthermore, due to the intrinsic difference in the cellular structure of AOB and AOA, the response of these two functional guilds to diverse nitrification inhibitors was variable (Lehtovirta-Morley et al. 2013). Considering the different susceptibilities to inhibitors, caution should be exercised when assessing the relative role of AOB and AOA in nitrification after applying inhibitors (Shen et al. 2013).

Nitrous oxide (N_2O), as an especially potent greenhouse gas, and the microbial-mediated emission process, has been receiving increasing attention. Denitrification and nitrification are considered to be the main steps responsible for the

production of N_2O under anaerobic and aerobic conditions (Wrage et al. 2001; Bateman and Baggs 2005), respectively. However, the relative role of the nitrifier denitrification process is increasingly being noticed, which may contribute a considerable proportion to N_2O production (Wrage et al. 2004; Kool et al. 2010). More interestingly, recent research showed that the production of N_2O through NH_3 oxidation pathways increased as O_2 availability decreased, indicating a significant source of N_2O production under limited O_2 conditions (Zhu et al. 2013). These authors further suggested that ammonium fertilizer instead of urea would be better as N fertilizers in mitigating N_2O emissions. This phenomenon could be related to the ureolytic N metabolic traits of AOA (Lu and Jia 2013) or the highly insensitive capacity of AOA to oxygen (Pett-Ridge et al. 2013). However, there is no research linking the microbial function of ammonia oxidizers to N_2O production in field experiments, which was mainly demonstrated through pure cultures studies (Santoro et al. 2011). In the context of global climate change, the microbial mechanisms underlying N_2O production through the ammonia oxidation pathway still remain elusive, yet more studies are required to elucidate the relative contribution of AOB and AOA to N_2O emissions.

3 Distribution and diversity of anammox bacteria in soils and sediments

3.1 The advent of the anammox process

The mystery of ammonium loss in either marine or denitrifying bioreactor was the major biochemical enigma of N cycling, which remained elusive until a few decades

ago. This phenomenon, named anammox, was discovered from the denitrifying pilot plant fed with nitrate (Mulder et al. 1995). Thanks to the successful enrichment from a batch reactor fed with ammonium, a new fascinating group termed anammox bacteria, turn out to be the main responsible group mediating the process of anaerobic oxidation of ammonium to nitrogen gas (N_2) (Strous et al. 1999). Later on, the evidence for the presence of anammox bacteria in the environment was also detected from the Black Sea and Golfo Dulce in the Caribbean Sea with high ammonium concentration and low amounts of fixed N (Dalsgaard et al. 2003; Kuypers et al. 2003). So far, all the known anammox bacteria – including *Candidatus* Brocadia, *Candidatus* Kuenenia, *Candidatus* Scalindua, *Candidatus* Anammoxoglobus and *Candidatus* Jettenia – belong to the phylum *Planctomycetes* based on the morphological analysis and molecular methods using 16S rRNA gene and whole genomic sequencing. Insight into the redox process of anammox by analyzing anammox bacterium, *Candidatus* Kuenenia stuttgartiensis, suggested that three possible redox steps including the oxidation of nitrite (NO_2^-) to nitric oxide (NO), of NO to hydrazine (N_2H_4), and of N_2H_4 to N_2 were involved in the anammox process (Strous et al. 2006; Kartal et al. 2012). According to the reactions stated above, the role of NO and N_2H_4 in the anammox process as intermediates was established via inhibition studies and fluorescent labeling techniques (Kartal et al. 2013). Moreover, key genes and proteins including hydrazine synthase and nitrite reductase were confirmed as functional biomarkers for understanding central steps of anammox and its ecophysiological dynamics (Kartal et al. 2012). Molecular methods using both 16S

rRNA gene and selective functional genes, such as hydrazine oxidoreductase gene *hzo*, coupling with biochemical methods including ladderane lipid analysis, have greatly improved our knowledge on the distribution, diversity and function of anammox bacteria in natural environments.

3.2 The niche separation of anammox bacteria

Molecular detection of anammox bacteria in ecosystems has shown its distribution, diversity and activity in anoxic habitats, suggesting its powerful significance in global N cycling (Kuypers et al. 2003; Humbert et al. 2010). Anammox bacteria appear to be omnipresent in anoxic environments, including marine, sediments, estuaries, paddy soils and wastewater treatment plants (den Camp et al. 2006; Schmid et al. 2007; Humbert et al. 2010; Zhu et al. 2011; Wang and Gu 2013). The widespread occurrence and great variation in the abundance of anammox bacteria indicated their heterogeneous distribution and niche differentiation (Schmid et al. 2007), which further substantiated their role in biogeochemical N cycling. Accumulated knowledge on the diversity of anammox bacteria has shown lower diversity in marine ecosystems (Schmid et al. 2007), which were mostly dominated by the genus of *Candidatus Scalindua*, while non-*Scalindua* anammox bacteria were sporadically found in estuarine and coastal environments. Limited studies have been carried out in the terrestrial biome, especially in complex and diverse soils (Wang and Gu 2013). The research on a variety of habitats with 112 samples from Switzerland and France first highlighted the presence of anammox in soil environments (Humbert et al. 2010). The

occurrence of the anammox process and detection of related bacteria in the above research were mainly attributed to the water-logged oxygen-limiting conditions and high content of fixed inorganic N (NO_2^- , NO_3^- , and NH_4^+). The broad distribution of anammox bacteria in soils was attributed to the high N contents. More evidence for the existence of the anammox process in terrestrial environments were accumulated from soils either receiving slurry manure for 25 years (Zhu et al. 2011) or N-loaded peat soils (Hu et al. 2011). Both of the above studies demonstrated high biodiversity of anammox bacteria in soils than other habitats (Hu et al. 2011; Zhu et al. 2011), and more than four genera of anammox bacteria (i.e. *Brocadia*, *Kuenenia*, *Anammoxoglobus* and *Jettenia*) were commonly detected. The worldwide distribution of the anammox process in nature inspired researchers to investigate the physiology and metabolism of anammox bacteria, as well as appraising their contribution to N cycling.

3.3 The contribution of anammox bacteria to N cycling

Current knowledge has shown the massive contribution of the anammox process to the N loss in marine sediments by ^{15}N isotope pairing, for instance: 30% N missing in the Black Sea (Kuypers et al. 2003); 35 % in Costa Rica (Dalsgaard et al. 2003); and 24 % and 67 % in the offshore sediments (Dalsgaard and Thamdrup 2002). Altogether, up to 50 % of N_2 production in marine ecosystems is associated with the anammox process (Kuenen 2008). The high rates of anammox activity detected in very diverse environments are more likely related to the sediment reactivity and the provision of

nitrate/nitrite in the pore water. Intriguingly, the interface at land–freshwater riparian zones in North China comprised anammox hotspots, where the potential rates of anammox reached the highest levels compared to other results reported so far (Zhu et al. 2013). This research group further found that this anammox active zone was ubiquitous at land–freshwater interfaces and had a positive effect on reducing N₂O production, suggesting significant implications for mitigating emissions of this greenhouse gas.

4 Future perspectives

Microbial processes involved in ammonia oxidation at aerobic/anaerobic interfaces, such as flooded paddy soils and biofilms, are complex and mainly associated with anaerobic anammox bacteria and aerobic ammonia oxidizers (bacteria and archaea). It was found that at the surface with enough oxygen, nitrite production was mainly driven by bacterial ammonia oxidizer and denitrifiers, while at deeper layers it was more related to the rates of archaeal ammonia oxidation (Lam et al. 2007; Zhu et al. 2011). The linkage between ammonia oxidation and anammox is coupled through nitrite, which is produced by aerobic ammonia oxidizers and consumed by anammox bacteria and nitrite oxidizing bacteria depending on oxygen condition (Kuenen 2008). Therefore, with the increasing concern and interest in archaeal ammonia oxidizer and anammox bacteria in N cycling, research on microbial mechanisms underlying nitrification and anammox, as well as their interactions, is essential for understanding their contribution to the loss of N, either through nitrate leaching or N-related gas

emissions.

As demonstrated above, the global N cycle is one of the most complicated processes in ecosystems, involving several key processes such as biological N fixation, nitrification, denitrification, ammonification, anammox, and dissimilatory reduction of nitrite to ammonium (DNRA). Additionally, the N cycle is closely coupled to other essential biogeochemical processes, such as carbon, phosphorus and sulfur cycles, and their integration is of pivotal importance in maintaining the health and development of ecosystems. For example, strong evidence has been obtained from genomic studies that AOA culture is involved in carbon fixation and the organotrophic growth metabolic pathway (Hallam et al. 2006; Walker et al. 2010), partially due to the mixotrophic lifestyle of AOA. Moreover, in aquatic environments, the metal oxides such as iron oxides and manganese oxides, play an important role in anaerobic ammonia oxidation as electron acceptors (Dalsgaard and Thamdrup 2002). Therefore, for future studies, microbial analysis for ammonia oxidation combined with other microbial processes, such as carbon fixation and sulfate reduction, will provide us with a more comprehensive understanding of N biogeochemical cycling.

Contributing to the rapid development of molecular techniques, microbial analyses have initiated a new area for microbial ecology using culture-independent methods based on nucleic acids, proteins and lipids. Of these, high-throughput sequencing technology, especially the next generation sequencing technique, is showing a powerful advantage in deciphering microbial abundance, distribution and composition. Particularly, large-scale sequencing techniques enable us to gain further

insight into the distribution patterns of ammonia oxidizer and anammox bacteria via generating billions of sequences and thereby to reveal their interaction with biotic and abiotic factors (Gubry-Rangin et al. 2011; Hu et al. 2013). Additionally, other advanced methods, which show promise, such as nano-scale secondary ion mass spectrometry (Nano-SIMS) and single-cell sequencing approaches, remain relatively unexplored in soil and sediment microbial ecology. In order to get a more comprehensive knowledge of ammonia oxidation, the combination of several techniques, such as stable isotope probing (SIP) and pyrosequencing, should be applied together to gain insight into the metabolic activities of microbes mediating ammonia oxidation under oxic/anoxic conditions.

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Fig.1

Fig. 1 Microbially mediated nitrogen (N) transformation pathways in soils and sediments. Ammonia oxidation and nitrite oxidation are highlighted in red, anammox process is in blue, dissimilatory reduction of nitrite to ammonium (DNRA) is in brown, denitrification is in black dash lines and ammonification is in green

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