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CRITICAL REVIEW

Research advances of ammonia oxidation microorganisms in wastewater: metabolic characteristics, microbial community, influencing factors and process applications

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Abstract

Ammonia oxidation carried out by ammonia-oxidizing microorganisms (AOMs) is a central step in the global nitrogen cycle. Aerobic AOMs comprise conventional ammonia-oxidizing bacteria (AOB), novel ammonia-oxidizing archaea (AOA), which could exist in complex and extreme conditions, and complete ammonia oxidizers (comammox), which directly oxidize ammonia to nitrate within a single cell. Anaerobic AOMs mainly comprise anaerobic ammonia-oxidizing bacteria (AnAOB), which can transform NH_4^+-N and NO_2^--N into N_2 under anaerobic conditions. In this review, the unique metabolic characteristics, microbial community of AOMs and the influencing factors are discussed. Process applications of nitrification/denitrification, nitritation/denitrification, nitritation/anammox and partial denitrification/anammox in wastewater treatment systems are emphasized. The future development of nitrogen removal processes using AOMs is expected, enrichment of comammox facilitates the complete nitrification performance, inhibiting the activity of comammox and NOB could achieve stable nitritation, and additionally, AnAOB conducting the anammox process in municipal wastewater is a promising development direction.

Keywords Ammonia-oxidizing bacteria · Ammonia-oxidizing archaea · Complete ammonia oxidizers · Anaerobic ammonia-oxidizing bacteria

Introduction

Ammonia oxidation is a central process in the global nitrogen cycle. This process can be divided into aerobic ammonia oxidation and anaerobic ammonia oxidation (anammox). Correspondingly, microorganisms responsible for ammonia oxidation can be divided into two categories (Fig. 1): aerobic ammonia-oxidizing microorganisms (AOMs), which consist of ammonia-oxidizing bacteria (AOB) [1, 2], ammonia-oxidizing archaea (AOA) [3], and complete ammonia oxidizers (comammox) [4, 5], and anaerobic AOMs, which comprise anaerobic ammonia-oxidizing bacteria (AnAOB) [6]. AOMs are widely distributed in natural and artificial systems, including rivers, lakes, oceans, soils and wastewater treatment systems, and they participate in the ammonia transformation process [7–10]. As an artificial system, wastewater treatment systems have the function of removing nutrient, and play important roles in protecting the aquatic ecological environment and preventing eutrophication [11].

AOMs widely exist in wastewater treatment systems and play a major role in nitrogen removal. The aerobic ammonia oxidation process, as performed by aerobic AOMs, is the first and rate-limiting step of nitrification, which is very important for nitrogen removal. In wastewater treatment systems, nitrogen removal can be achieved through various processes, such as nitrification/denitrification, nitritation/denitrification, nitritation/anammox and partial denitrification/anammox. Nitrification/denitrification is the conventional and most widely used nitrogen removal method in wastewater treatment plants (WWTPs), while nitritation/denitrification can reduce the aeration energy consumption

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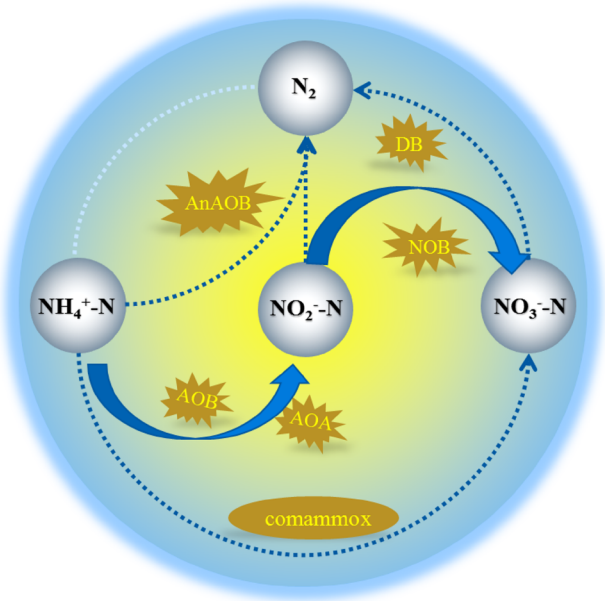

Fig. 1 Ammonia oxidation pathway and functional microorganisms during nitrogen cycle

AOB—ammonia-oxidizing bacteria; AOA—ammonia-oxidizing archaea; comammox—complete ammonia oxidisers; AnAOB—anaerobic ammonia-oxidizing bacteria; NOB—nitrite oxidizing bacteria ; DB—denitrificationg bacteria

and carbon source requirement. According to the different nitrite sources, the anammox process, as performed by AnAOB, can be divided into two pathways: nitritation/anammox and partial denitrification/anammox [2]. Anammox can reduce the carbon source and aeration requirements with the advantages of a high NH_4^+-N removal load and low sludge yield. It has been successfully applied for nitrogen removal to high strength ammonia wastewater, such as sludge fermentation liquid and landfill leachate [12, 13]. Moreover, it has been reported that AnAOB occupy a certain abundance and play an important role in nitrogen removal in WWTPs [14]. Anammox is also a promising technology for carbon and energy neutralization in wastewater treatment systems.

AOMs have various metabolic characteristics and are influenced by environmental factors, which results in distinct microbial community structures in different wastewater treatment systems (Table 1). In this review, the metabolic characteristics and factors influencing the AOM community are discussed; the microbial abundance in different habitat are summarized; and the future development of ammonia removal technologies based on AOMs are prospected.

Metabolic mechanism and influencing factors of AOMs

The ammonia oxidation process performed by different AOMs involves different pathways and intermediates (Fig. 2), AOB and AOA have similar ammonia oxidation mechanisms to the nitrite pathway, comammox can independently complete the whole nitrification process in single cell, and AnAOB can transform NH_4^+-N and NO_2^--N into N_2 under anaerobic condition.

Ammonia-oxidizing bacteria

Metabolic characteristics

In 1890, Monteiro et al. discovered the first AOB, *Nitrosomonas europaea*, confirming the existence of AOMs and the ammonia oxidation process in natural environments [1]. In 1993, AOB were isolated and identified based on the 16S rRNA gene sequencing method, which has subsequently become the main method to evaluate the phylogeny of AOB [15]. To date, known AOB genera include *Nitrosospira*, *Nitrosomonas*, *Nitrosococcus, Nitrosolobus* and *Nitrosovibrio*, from the phylum *Betaproteobacteria*, as well as *Nitrosococcus*, from the phylum *Gammaproteobacteria* [16]. Studies have shown that AOB affiliated with *Betaproteobacteria* are widely distributed in the natural environment, while *Nitrosomonas* is the main functional AOB for nitrification in wastewater treatment systems [17, 18], Conversely, AOB affiliated with *Gammaproteobacteria* are found only in marine and salt lake environments [19].

As shown in Fig. 2a, during ammonia oxidation metabolism, AOB first convert ammonia into NH_2OH using ammonia monooxygenase (AMO), with the ammonia substrate acting as an energy and reducing agent [20]. This is the rate-limiting step, and the substrate used by AMO is NH_3, rather than NH_4^+, because AMO can only catalyze non-ionic

Table 1 The AOM abundance in different habitats as detected through molecular methods

AOMs	Habitat	Abundance	Microbial method	References
AOB	WWTPs	4.625×10^4–9.99×10^9 copies/sludge	qPCR	[22]
	Biofilter	5.20×105–1.10×106 copies/mL	qPCR	[23]
	Constructed wetland	5.30×10^4–3.10×10^7 copies/mL	qPCR	[24]
	Activated sludge	2.43%	16S rRNA gene HTS	[25]
	Biofilm	10.6%	16S rRNA gene HTS	[16]
	Biofilm	3.44%	16S rRNA gene HTS	[2]
	BCO system	13.1%	16S rRNA gene HTS	[26]
	Biofilm	19.41%	FISH	[28]
	BABE reactor	8%	FISH	[29]
	IFAS system	0.98%	16S rRNA gene HTS	[27]
	Bacterial-algal symbiosis system	2.8%	Metagenomics	[30]
AOA	WWTPs	limit of detection–1.90×10^7 copies/g sludge	qPCR	[22]
	Biofilter	7.40×10^3–1.30×10^4 copies/mL	qPCR	[23]
	Constructed wetland	4.10×10^6–4.20×10^7 copies/mL	qPCR	[24]
Comammox	RBC system	1.8–19.4%	Metagenomics	[72]
	WWTPs	0.02–0.36%	Metagenomics	[73]
	Nitrogen removal system	0.5–17%	Metagenomics	[74]
AnAOB	WWTPs	10^5–10^7 copies/mL	qPCR	[86]
	WWTPs	0.11%	Metagenomics	[14]
	Ana-EGSB	6–13%	16S rRNA gene HTS	[87]
	DEAMOX system	0.53%	16S rRNA gene HTS	[2]
	Bacterial-algal symbiosis system	1.3%	Metagenomics	[30]
	IFAS (A^2O)	2.49%	Metagenomics	[103]

qPCR quantitative PCR, *HTS* high-throughput sequencing, *BCO* biological contact oxidation, *DEAMOX* denitrifying ammonium oxidation, *BABE* bioaugmentation batch enhanced reactor, *RBC* rotating biological contactor system, *Ana-EGSB* anaerobic expanded granular sludge bed

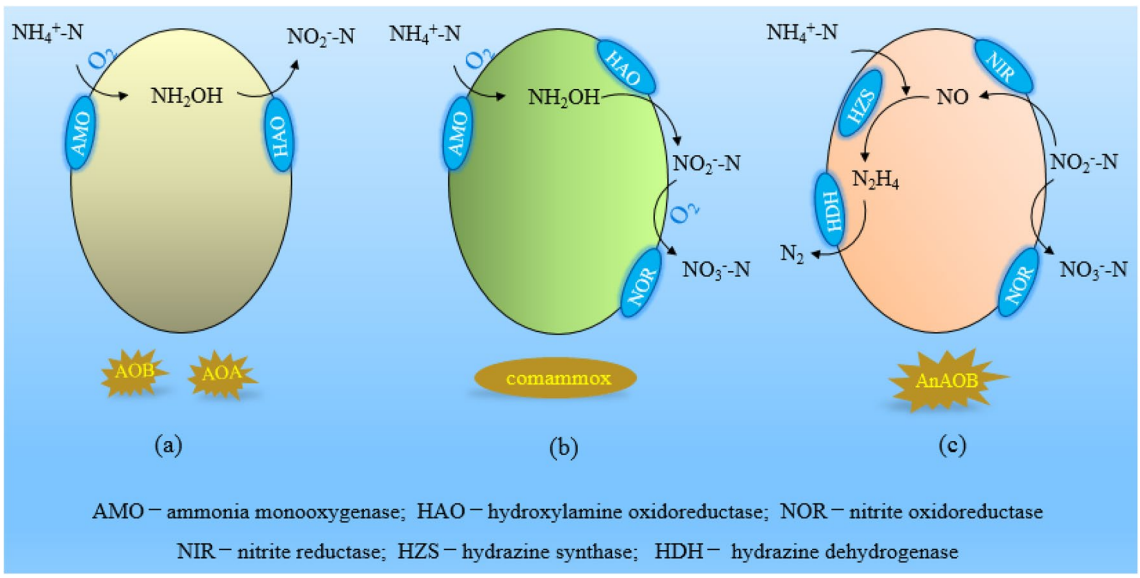

Fig. 2 Ammonia oxidation process conducted by different AOMs and enzymes. **a** AOB&AOA; **b** comammox; **c** AnAOB

ammonia oxidation, but not NH_4^+ oxidation. This is also the main reason ammonia oxidation has become a rate-limiting step for nitrification. The second step in ammonia oxidation is the transformation of NH_2OH into NO_2^--N under the action of hydroxylamine oxidoreductase (HAO). Thus, the process of ammonia oxidation to nitrite is completed through the cooperative action of the AMO and HAO enzymes [21]. In addition, nitrite-oxidizing bacteria (NOB) further convert NO_2^--N into NO_3^--N to complete nitrification, and NOB include *Nitrobacter*, *Nitrococcus*, *Nitrospina* and *Nitrospira* [16].

AOB show a high abundance in wastewater systems when detected by the quantitative real-time polymerase chain reaction (qPCR) method. In the activated sludge of WWTPs, Gao et al. detected the AOB *amoA* gene with an abundance ranging from 4.625×10^4 to 9.99×10^9 copies/g sludge [22]. In a biofilter system, the AOB abundance ranged from 5.20×10^5 to 1.10×10^6 copies/mL [23]. Sims et al. found that the AOB were present in a constructed wetland at 5.30×10^4–3.10×10^7 copies/mL [24]. Many researchers have used 16S rRNA gene high-throughput sequencing to detect the relative abundance of AOB. Zhang et al. studied the activated sludge in an anaerobic/oxic/anoxic system and found that *Nitrosomonas* and *Nitrospira* were present at proportions of 0.92% and 1.51%, respectively [25]. Zhao et al. enriched the AOB *Nitrospira* and *Nitrosomonas* to 9.31% and 1.29% in a biofilm nitrification system, respectively [16]. Zhang et al. detected *Nitrosomonas* and *Nitrospira* at proportions of 7.95% and 5.15% in a biological contact oxidation system [26]. In an anoxic/oxic biofilm system, the *Nitrospira* was detected at a proportion of 3.44% [2]. In an IFAS system, *Nitrosomonas* occupied 0.98% of the total bacteria [27]. Fluorescence in situ hybridization (FISH) has also been used to detect the relative abundance of AOB. Using the FISH method, Zhao et al. detected AOB at 19.41% in a nitrification biofilm system with a pre-A_2NSBR process [28], while an increase in AOB from 4 to 8% was observed in a bioaugmentation batch enhanced reactor [29]. Zhang et al. detected that *Nitrosomonas* was dominant with 2.8% in a bacterial–algal symbiosis system through metagenomic analysis [30].

Influencing factors

The metabolic process and growth rate of AOB in wastewater treatment systems are influenced by the available substrates, such as ammonia and free ammonia (FA), and the environmental factors, including dissolved oxygen (DO) and temperature.

(1) Ammonia and FA. AOB have a relatively wide range of ammonia tolerance, with *Nitrosospira* usually being more sensitive to high ammonia concentrations [31]. FA refers to non-ionic ammonia. The balance between ammonia and FA mainly depends on the pH of the wastewater. FA can inhibit AOB and nitrite-oxidizing bacteria (NOB); however, AOB are less sensitive to FA. A low FA concentration can seriously disrupt the activity of NOB, while AOB have a relatively stronger tolerance to FA than NOB [32, 33]. It has been found that when the FA concentration is between 1 and 5 mg/L, the nitrite oxidation process is inhibited, but the ammonia oxidation reaction is not [34].

(2) DO. Oxygen is the electron acceptor of the ammonia oxidation reaction; thus, it is one of the key factors affecting the metabolic process of AOB [35]. AOB have a stronger affinity for DO than NOB, and nitritation can be attained by limiting the growth of NOB with a low DO concentration to cause nitrite accumulation [36]. Some researchers have found that low DO will not affect the ammonia oxidation process because low DO facilitates the growth of AOB, thereby increasing their total abundance [15, 37]. Groeneweg et al. suggested that since AOB have a higher affinity for DO than NOB, the AOB have a competitive advantage in low-DO wastewater [38]. A study by Laanbroek et al. showed that the saturation coefficient of AOB for DO is 0.2–0.4 mg/L [39]. Fitzgerald et al. found that the genus *Nitrosomonas* was responsible for nitrification under a low DO concentration [35].

(3) Temperature. In the range of 5–35 °C, the ammonia oxidation reaction rate will increase with the increasing temperature. Researchers have reported that when the temperature is higher, the AOB growth rate is faster than that of NOB [40, 41]. The research results of Lopez-Palau et al. show that the appropriate temperature for the ammonia oxidation reaction is 33–37 °C, because AOB activity is the strongest in this temperature range, and the appropriate temperature control strategy is successfully applied to attain nitritation [42]. However, the activity of NOB is reported stronger when temperature is below 15 °C [43].

Ammonia-oxidizing archaea

Metabolic characteristics

In 2004, Venter et al. first found the AMO gene (*amoA*) sequence in the macrogenome of archaea in Sargasso sea area [44]; therefore, it is possible that some archaea could drive ammonia oxidation reactions. Subsequently, the sequences of three subunits of the AMO gene of *Crenarchaeota* were found in the macrogenome: *amoA*, *amoB* and *amoC*, with the transcription levels of the above three genes positively correlated with the ammonia concentration in the environment [45]. In 2005, Treusch et al. also found *amoA*

gene of AMO when analyzing the genomes of soil archaea [46]. In 2005, the first strain of archaea *Nitrosopumilus maritimus* SCM1 was successfully isolated and pure cultured. This strain has AMO genes of *amoA*, *amoB* and *amoC*; uses NH_3-N as the only nitrogen and energy source; and fixes CO_2 for inorganic autotrophic growth, which indicate AOA owns the similar ammonia oxidation capacity with AOB (Fig. 2a) [3]. In 2007, AOA were divided into a new archaeal phylum termed *Thaumarchaeota* [47]. Currently, AOA mainly include *Nitrosopumilus maritimus*, *Nitrosopumilus maritimus* SCM1, *Nitrososphaera gargensis*, *Cenarchaeum symbiosum*, *Nitrososphaera gargensis, Cenarchaeum symbiosum* and *Nitrosocaldus yellowstonii* [48, 49]. Overall, research shows that AOA are widely distributed in aquatic ecological environments [47, 50, 51].

AOA show a high ammonia oxidation capacity and abundance in various wastewater treatment systems [52, 53]. AOA were first detected in the activated sludge of 9 WWTPs in the USA by Park et al. in 2006 [54]. In 2009, Zhang et al. collected samples from two WWTPs in Hong Kong and detected the ammonia oxidation activity of AOA [55]. AOA were detected with an abundance reaching to 1.90×10^7 copies/g sludge in a wastewater treatment system [22]. AOA were also detected in a biofilter system with an abundance of 7.40×10^3–1.30×10^4 copies/mL [23]. Sims et al. detected AOA with an abundance of 4.10 × 106–4.20 × 107 copies/mL in a constructed wetland system [24].

Influencing factors

The sewage treatment system relies on the ammonia oxidation reaction to remove ammonia nitrogen. Researchers have found AOA in many sewage treatment systems. In some sewage treatment systems, the amount of AOA far exceeds that of AOB. However, different from AOB, AOA cannot be found in all systems with good ammonia nitrogen removal performance. Researchers have made many guesses about the factors influencing the existence of AOA, including ammonia substrate, DO and temperature.

(1) Ammonia substrate.

Presence of the ammonia substrate is the main factor determining the community structure of AOA. Compared with AOB, AOA have an extremely low substrate concentration threshold and semi-saturation coefficient, and have a strong adaptability to low ammonia concentrations [56, 57]. Specifically, a low ammonia concentration is conducive to the growth of AOA, who could contribute more to the ammonia oxidation process [58, 59]. In general, AOA are more dominant than AOB at a low concentration of ammonia because of their high affinity for ammonia [57, 60]. AOA were also detected in wastewater treatment system with high ammonia concentration, however, the relative abundance is generally lower than that of AOB [54, 55].

(2) Temperature

Temperature is another important factor affecting the structure and abundance of the ammonia-oxidizing microbial community. The response range of AOA to temperature (0.2–97 °C) is much wider than that of AOB, which indicates that AOA could exist in complex and extreme conditions; some studies indicate that AOA still keep high ammonia oxidation activity at 84–85 °C[61]. However, it has been shown that the diversity of AOA declines at low temperature [62]. Some studies have shown that AOA are more resistant to low temperature than AOB [63].

(3) DO

AOA have a wide range of adaptability to DO (0.1–6 mg/L) [64, 65]. Low DO can promote the growth of AOA, which have a competitive advantage over AOB at a low oxygen concentration. AOA have a high affinity for DO, which can explain their dominance at a low oxygen concentration [48, 54]. AOA occupy a significantly different ecological distribution location from AOB.

Complete ammonia oxidizers

Metabolic characteristics

It has long been believed that nitrification is completed by two different types of AOMs under aerobic conditions. AOB or AOA first use oxygen to oxidize ammonia to nitrite, which is then further oxidized to nitrate by NOB [66]. In 2006, Costa et al. predicted the existence of complete ammonia oxidizers (comammox) that can independently complete the whole nitrification process [67]. Using kinetic prediction of the optimal metabolic path length, the authors postulated that such a microorganism would have a characteristically low growth rate and high cell yield. In 2015, the complete ammonia oxidation process and functional microorganisms of comammox were discovered and confirmed [4, 5]. Daims et al. enriched and cultured biofilms that could oxidize ammonia nitrogen into nitrate [4]. In this study, FISH and PCR verified that the AMO gene (*amoA*) of AOB and AOA could not be detected in the enriched cultures, only the NOB *Nitrospira* was detected; thus, it was speculated that this kind of *Nitrospira* may have the ability to oxidize both ammonia and nitrite. Moreover, functional macrogenome analysis show that *Nitrospira* not only has the gene for the key nitrite oxidation enzyme, nitrite oxidoreductase (NOR), but also the genes for the characteristic enzymes of ammonia oxidation, AMO (*amoA*) and HAO. This *Nitrospira* also showed the ability to convert ammonia nitrogen into nitrate, as Fig. 2b presents, so it was considered to be a novel microorganism harboring whole ammonia oxidation process and was named *Candidatus* Nitrospira inopinata. In the same year, van Kessel et al. also reported the existence of comammox. Using sludge collected from an aquaculture trickling

filter wastewater treatment system [5]. FISH showed that *Nitrospira* occupied 15% of the community, while further analysis indicated that along with the NOR gene necessary for nitrite oxidation, the detected *Nitrospira* species also contained *amoA* and HAO genes that catalyze the ammonia oxidation process. Therefore, these *Nitrospira* species, which were named *Candidatus* Nitrospira nitrosa and *Candidatus* Nitrospira nitrificans, have the ability to fully oxidize ammonia. So far, all the identified comammox belong to *Nitrospira* lineage II and their genomes contain the genes for AMO (*amoA*), HAO and NOR, which can complete nitrification in single comammox cell [4, 68]. According to phylogenetic analysis of *amoA* gene, comammox microorganisms can be divided into clade A and clade B. The evolution rate of ammonia oxidation-related proteins of clade B is significantly faster than that of clade A, and the two types of bacteria are significantly different in their substrate metabolism, energy transfer and environmental adaptability [69, 70].

Comammox are widely detected in wastewater treatment system. Roots et al. found that comammox became the dominant AOMs in a nitrification reactor with low DO [71]. In a rotating biological contactor system, the relative abundance of comammox was 1.8–19.4%, all belonging to clade A, which was higher than that of NOB [72]. Wang et al. found that the abundance of comammox in activated sludge of WWTPs was 0.02–0.36% (mainly belonging to *Candidatus* Nitrospira nitrosa), which was far higher than that of AOA and AOB [73]. Cotto et al. found that the relative abundance of comammox in a biofilm system (17%) was higher than that in an activated sludge system (0.5–3.0%), and that they mainly belonged to *Candidatus* Nitrospira nitrosa [74].

Influencing factors

The comammox have the characteristics of high ammonia affinity, low oxygen adaptability, low growth rate and metabolic diversity.

(1) Ammonia and nitrite substrate. When the ammonia substrate is limited, the specific growth rate of *Candidatus* Nitrospira inopinata, which has a high ammonia affinity, is more advantageous than that of AOA and AOB [75]. However, when the ammonia substrate is sufficient, the maximum specific growth rate of AOB is significantly higher than that of AOA and *Candidatus* Nitrospira inopinata, giving AOB a survival advantage. Thus, comammox bacteria are more suitable for survival in sewage treatment systems with a low ammonia concentration [5, 74, 76]. Conversely, *Candidatus* Nitrospira inopinata has a low substrate affinity for nitrite [75], and its nitrite semi-saturation coefficient is similar to that of *Nitrobacter* and 16.7–49.9 times higher than that of *Nitrospira* [71, 77].

(2) DO. Oxygen plays an important role in the metabolism of comammox. *Candidatus* Nitrospira nitrosa was found as the dominant nitrifier in a low-DO wastewater treatment system, and a study found that this comammox is able to survive in a micro oxic environment. Hence, comammox could be enriched by controlling low DO (< 1 mg/L).

Anaerobic ammonia-oxidizing bacteria

Metabolic characteristics

In 1977, Broda predicted that there should be an autotrophic bacterium that could conduct nitrogen removal [78]. In 1995, Mulder et al. confirmed this metabolic process in a denitrifying fluidized-bed reactor [6]. Under strict anaerobic conditions, NH_4^+-N and NO_2^--N are transformed into N_2 during this process, with NH_4^+-N used as the electron donor and NO_2^--N acting as the electron acceptor. The specific biochemical reaction procedure are shown in the Fig. 2c, part of NO_2^--N are oxidized to NO_3^--N by nitrite oxidoreductase (NOR), another part of NO_2^--N are reduced into NO through nitrite reductase (NIR), and then the NO and NH_4^+-N are transformed into N_2H_4 under the action of hydrazine synthase (HZS), finally, N_2H_4 is oxidized to N_2 with hydrazine dehydrogenase (HDH) [79– 82]. AnAOB mainly include *Candidatus kuenenia*, *Candidatus scalindua*, *Candidatus brocadia*, *Candidatus jettenia*, *anammoxoglobus*, *Brasilis anammoximicrobium* at genus level [83, 84]. The AnAOB that conduct anammox are autotrophic bacteria with slow growth rate of 7–14 days or even longer [85].

Most AnAOB genera are detected in wastewater treatment systems and play an important role in nitrogen removal. Through metagenomic analysis, Li et al. detected AnAOB with an abundance of 0.11% in actual WWTPs [14]. Wang et al. found that AnAOB are widespread in conventional WWTPs with 10^5–10^7 copies/mL using qPCR [86]. Zhao et al. enriched the AnAOB *Ca.* Brocadia to an abundance of 0.53% in an attached biofilm system [2]. Jin et al. found that *Ca.* Brocadia accumulated to a relative abundance of 6–13% in an anaerobic expanded granular sludge bed [87].

Influencing factors

(1) Substrate. NH_4^+-N and NO_2^--N are the substrates for of anammox. Some studies suggest that the activity of AnAOB is less affected by the concentration of NH_4^+-N. For example, the anammox process is not affected below 1000 mg/L NH_4^+-N, but excessive NH_4^+-N will produce FA, which, along with free nitrous acid (FNA), inhibits AnAOB activity [88, 89]. AnAOB are more sensitive to the NO_2^--N concentration [90, 91]. Some studies indicate that *Ca.* Brocadia

is able to live in environments with relatively higher nitrite concentrations, while *Ca*. Kuenenia can only live in environments with lower NO_2^--N concentrations. The effect of nitrite on the activity of anammox bacteria varies according to the type of AnAOB. The effects of NH_4^+-N and NO_2^--N on anammox are mainly caused by FA and FNA. It has been reported that the minimum inhibitory concentration of FA is 2 mg/L, while the inhibitory concentration of FNA is 1.5–213.0 μg/L, with FNA exerting a more obvious inhibitory effect on anammox than FA [8]. Due to different experimental operating conditions, inoculated sludge and microbial community structure, the inhibitory concentrations of FNA and FA also differ in different systems.

(2) Temperature. Within a certain temperature range, the activity of AnAOB is improved when the temperature is increases. Studies have shown that AnAOB exhibit the highest activity in the range of 35–40 °C. When the temperature is higher than 40 °C or lower than 15 °C, the anammox activity rapidly decreases [92, 93]. High temperature has a particularly adverse impact on AnAOB, with inhibition or even death occurring over 40 °C [94, 95].

(3) DO. Because AnAOB are anaerobic bacteria, the influence of DO mainly inhibits the anaerobic process. When the DO concentration is too high, it is not conducive to the survival and reproduction of AnAOB, and even leads to the complete inhibition of AnAOB activity [96]. Kimura et al. found that the anammox reaction can be inhibited when the concentration of DO exceeds 2.5 mg/L; however, this inhibition is reversible, AnAOB activity being restored after the DO concentration decreases [97].

(4) Organics. As ammonia oxidation reaction is an autotrophic process without requirement of organics, the presence of excessive organics will inhibit the anaerobic ammonia oxidation process. Many researchers have reported that the participation of organics will make heterotrophic denitrifying bacteria compete out AnAOB for NO_2^-N [98, 99]. However, recent studies indicate that AnAOB and denitrifying bacteria can coexist under proper organics concentration to promote nitrogen removal. The existence of organics could provide electronics for denitrification which create necessary conditions for anammox. Wang et al. found that Thauera sp. strain SND5 could store carbon intracellularly (C/N ratio = 1) to reduce the organics which favors the growth of AnAOB [100]. Zhao et al. achieved deep nitrogen removal of 72.3% through denitrifying ammonium oxidation under C/N ratio of 2.9 [2]. Endogenous denitrification coupled with anammox was attained in AOA-O system, and the TIN effluent was 8.9 mg/L with low C/N ratio of 3.4 [101].

Aside from the above-mentioned AOMs, heterotrophic nitrification and aerobic denitrification microorganisms (HNADMs) attracted much attention with unique metabolic characteristics recently, they were proved to conduct ammonia oxidation and denitrification simultaneously at the same oxic environment [102]. HNADMs have a complex genus composition belongs to different fungus and bacteria, they are widely distributed in various environments, including extreme conditions. The application of HNADMs in wastewater treatment deserves more research in the future.

Process applications and future development

The main nitrogen removal processes performed by AOB, AOA, comammox and AnAOB in wastewater treatment systems include nitrification/denitrification, nitritation/denitrification, nitritation/anammox and partial denitrification/anammox.

Nitrification/denitrification

Traditional biological nitrogen removal from wastewater is considered to be mainly completed via nitrification/denitrification [104, 105], as shown in formulas (1) and (2).

$$NH_4^+ + 2O_2 \rightarrow NO_{3^-} + 2H^+ + H_2O, \quad (1)$$

$$NO_{3^-} + 5H^+ \rightarrow 0.5N_2 + 2H_2O + OH. \quad (2)$$

The main AOMs involved in nitrification include AOB, AOA and comammox. The nitrification process requires a longer sludge retention time (SRT); a sufficient hydraulic retention time (HRT) and DO; and appropriate environmental conditions, including temperature and pH [106]. Denitrification refers to the reduction of nitrate to N_2 by denitrifying bacteria, which use organic matter as an electron donor under anoxic conditions [107]. There are many types of denitrifying bacteria, which are all classified as heterotrophic bacteria. Compared with nitrification, the denitrification reaction is faster. In the presence of organic matter and nitrate nitrogen, denitrification can be completed quickly as long as the environmental conditions are appropriate. Furthermore, simultaneous nitrification and denitrification (SND) can be carried out in the same zone, which could reduce the required reactor volume [108, 109]. Studies indicate that aerobic granular sludge and biofilm system facilitate the nitrogen removal through SND [27, 110–112].

In the future, it would be advantageous to promote complete nitrification by comammox for treating low ammonia wastewater under low DO conditions. This could further reduce aeration energy consumption and sludge production.

Currently, the relationship between comammox and SND is lacking, which need further research.

Nitritation/denitrification

Nitritation means that the nitrification process is controlled at the nitrite production stage, which can be only conducted by AOB or AOA, as shown in formulas (3), and then nitrite is reduced to N_2 (4) [113].

$$NH_4^+ + 1.5O_2 \rightarrow NO_{2^-} + 2H^+ + H_2O, \quad (3)$$

$$NO_{2^-} + 5H^+ \rightarrow 0.5N_2 + H_2O + OH. \quad (4)$$

Compared with the traditional nitrification/denitrification process, nitritation/denitrification can reduce the aeration energy consumption by 25% and the carbon source requirement by 40% [114, 115]. In recent years, research on achieving nitritation has mainly focused on real-time control) [113], as well as parameters related to DO [39], temperature [116], intermittent aeration [117], FA and FNA [118, 119]. The purpose of these control measures is to inhibit NOB activity or wash out the NOB from the system, to control ammonia oxidation at the nitrite stage [114]. There are many successful laboratory studies on nitritation, and a pilot-scale experiment has been operated successfully [113]; however, in practical application, it is difficult to maintain stable nitritation in WWTPs as low ammonia, low temperature and fluctuating characteristics.

Inhibiting the activity of NOB and comammox bacteria could facilitate the realization and stable maintenance of nitritation. However, knowledge on how to control the metabolic characteristics of comammox is still lacking; thus, in-depth research is needed in the future.

Nitritation/anammox

The anammox reaction conducted by AnAOB is expressed in formula (5). The traditional nitrification/denitrification process must convert all ammonia into nitrate, which requires a substantial energy consumption due to the aeration process. In contrast, nitritation/anammox only needs to convert about 50% of the ammonia into nitrite, reducing the aeration energy consumption by approximately 60%. The traditional denitrification process requires organic matter as an electron donor for nitrogen removal, while in the nitritation/anammox process is completely autotrophic and does not require additional carbon source, which can reduce the carbon source requirement by 100%. Furthermore, both AOB and AnAOB are chemoautotrophic bacteria with a low sludge yield, which greatly reduces the cost of sludge disposal [120, 121].

$$NH_4^+ + 1.32\,NO_{2^-} + 0.066HCO^3- + 0.13\,H^+ \rightarrow 0.12\,N_2 + 0.26\,NO^3- + 0.066CH_2O_{0.5}N_{0.15} + 2.03\,H_2O. \quad (5)$$

Nitritation/anammox has been successfully applied to more than 110 wastewater treatment systems with high strength ammonia [122 124]. Nitritation/anammox applied to low-strength sewage is in the stage of laboratory research. Miao et al. developed a single-stage nitritation/anammox system to treat low-strength sewage under intermittent aeration conditions [125]. Jin et al. developed a two-stage nitritation/anammox process for advanced nitrogen removal from municipal wastewater [87]. Zhang et al. established a granular sludge reactor to treat low-strength sewage via the nitritation/anammox pathway [126]. Wang et al. developed an anaerobic/oxic/anoxic SBR system to achieve nitritation/anammox with treating actual domestic sewage [127].

The application of nitritation/anammox in WWTPs is a promising future development prospect [14, 128]. However, it is necessary to solve the bottleneck caused by low AnAOB activity under low-strength sewage and low temperatures. Novel methods such as biofilm, granular sludge, and new materials have been studied to improve the AnAOB activity.

Partial denitrification/anammox

During the partial denitrification/anammox process, NO_2^--N comes from the reduction of NO_3^--N, which can effectively solve the problem that NO_2^--N is difficult to obtain through nitritation. Thus, partial denitrification/anammox could reduce the aeration energy consumption by 45% and carbon source dosage by 79% [129, 130]. Ma et al. achieved mainstream nitrogen removal by coupling anammox with the partial denitrification pathway [131]. Zhao et al. developed an A/O process to achieve advanced nitrogen removal of 72.3% through the partial denitrification/anammox pathway when treating domestic sewage. In this biofilm system, the AnAOB *Ca.* Brocadia was detected at 0.53% and the typical denitrifier *Thauera* was enriched to 13.75% [2]. Zhao et al. achieved rapid start-up of partial denitrification/anammox system without seeding AnAOB, *Ca.* Brocadia was enriched with proportion of 2.49% and contributed to 37.9% of the nitrogen removal process [103]. Wang et al. proposed the method of culturing partial denitrification biofilm in side stream incubator to attain partial denitrification/anammox in mainstream [132].

The key purpose of partial denitrification/anammox is to maintain stable nitrite accumulation during denitrification, which is closely related to the microbial community structure, carbon source type, C/N ratio, pH and nitrate load. However, continuing research is needed in the future [120, 133, 134].

Certainly, nitrogen removal processes performed by AOMs are not limited to the above-mentioned pathways. Some novel pathways such as SND coupled with denitrifying phosphorus removal by Thauera sp. strain SND5 has been discovered [135]. Sulfur autotrophic denitrification-enhanced anammox without requirement of carbon source has been conducted [136]. Electricity production coupled to ammonium in a microbial fuel cell was deeply studied [137]. Integrated algae/partial-nitrification/anammox has been proposed and confirmed [30]. Development of novel efficient nitrogen removal pathways is the key research direction in the future.

Conclusion

AOB, AOA, comammox and AnAOB are widespread in wastewater treatment systems. These AOMs have different metabolic characteristics and microbial community dynamics, and they participate in the ammonia oxidation process and play important roles in nitrogen removal. It is advantageous to enrich comammox to promote the complete nitrification performance, on the contrary, inhibiting the activity of comammox and NOB could facilitate the realization and stable maintenance of nitritation. Additionally, employing the anammox process in municipal wastewater is a promising development direction; however, the bottleneck caused by low AnAOB activity due to low-strength sewage and low temperature needs to be solved in the future.

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