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封面图说: 水杉是中国特有树种, 国家一级保护植物, 有植物王国“活化石”之称, 是 1946 年由中国的植物学家在湖北的利川磨刀溪发现的。水杉曾广泛分布于北半球, 第四纪冰期以后, 水杉属的其他种类全部灭绝, 水杉确在中国川、鄂、湘边境地带得以幸存, 成为旷世奇珍。水杉耐水, 适应力强, 生长极为迅速, 其树干通直挺拔, 高大秀颀, 树冠呈圆锥形, 姿态优美, 枝叶繁茂, 入秋后叶色金黄。自发现后被人们在中国南方广泛种植, 成为著名的绿化观赏植物, 现在中国水杉的子孙已遍及中国和世界 50 多个国家和地区。

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## 湖泊氮素氧化及脱氮过程研究进展

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**摘要:**自然界中氮的生物地球化学循环主要由微生物驱动,由固氮作用、硝化作用、反硝化作用和氨化作用来完成。过去数十年间,随着异养硝化、厌氧氨氧化和古菌氨氧化作用的发现,人们对环境中氮素循环认识逐步深入,提出了多种脱氮途径新假说。对湖泊生态系统中氮素的输入、输出及其在水体、沉积物和水土界面的迁移转化过程进行了概括,对湖泊生态系统中反硝化和厌氧氨氧化脱氮机理及脱氮效率的最新研究进展进行了探讨,并对以后的氮素循环研究进行了展望。

**关键词:**湖泊;硝化;反硝化;厌氧氨氧化;古菌氨氧化;生物脱氮

### The research progresses on biological oxidation and removal of nitrogen in lakes

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**Abstract:** In recent decades, environmental problems such as water eutrophication, climate change, acid precipitation and nitrogen pollution have become increasingly problematic. This has resulted in the transformation processes of the nitrogen cycle becoming a hot topic within scientific research. This article reviews the mechanism of nitrogen input/output within lake ecosystems and summarizes the migration and transformation of nitrogen within water, sediments, and the interface between the two. The latest research progress on several predominant nitrogen oxide processes in lake ecosystems are elaborated in detail. These processes include traditional nitrification, Archaeal ammonia oxidation, anaerobic ammonia oxidation and heterotrophic nitrification,

The traditional nitrification process predominantly includes the ammonium oxidation process and nitrosation dominated by bacteria. The predominant Archaeal ammonia oxidation process is driven by ammonium oxidation Archaea, which belong to Crenarchaeota. Anaerobic ammonium oxidation is the process where ammonia is oxidized by nitrite under anaerobic or hypoxic conditions, and eight strains have been confirmed. At present, anaerobic ammonium oxidation reactions have been widely observed in fresh water systems. As is commonly known, there are essential differences in the way energy is utilized between heterotrophic nitrification and autotrophic nitrification, but the microbial enzyme systems are similar. The discrepancies between heterotrophic nitrification and bacteria ammonium oxidation during the oxidation of ammonium to nitrate have been compared here. This paper expounds in detail the types of strains, biological diversity, distribution characteristics and activity in the nitrogen transformation processes mentioned above. The main enzymes and genes which participate in the process of ammonia oxidation have also been described and analyzed.

The main biodenitrification reactions in lake ecosystems, namely heterotrophic denitrification and anaerobic ammonium

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oxidation denitrification, have also been reviewed here. Recent literature shows that the ratio of nitrogen loss by heterotrophic denitrification to total nitrogen input is substantially variable for various aquatic ecological systems. The ratio is about 63% for marine environments, 0%—50% for freshwater lakes, 10%—60% for estuaries and 1%—36% within aquaculture water. The main environmental factors affecting heterotrophic denitrification have been presented, including dissolved oxygen, pH, temperature, nitrate and organic carbon. These factors are also the main reasons for the differences in heterotrophic denitrification effect. Not only has the mechanism of anaerobic ammonium oxidation denitrification been discussed, but also its denitrification effect on aquatic ecological systems. Recent studies reveal that the ratio of nitrogen loss caused by anaerobic ammonium oxidation to total nitrogen loss fluctuates greatly for different habitats with the ratio ranging from 0%—67%. The main environmental factors affecting the denitrification efficiency of anaerobic ammonium oxidation include dissolved oxygen, temperature and nitrate concentration. Until recently, there has been a paucity of research on anaerobic ammonium oxidation in freshwater systems.

Finally, some research prospects have been proposed regarding improving the denitrification efficiency within actual sewage treatment and also small niche anaerobic ammonium oxidation research. The author also proposes to strengthen research on the separation and enrichment of bacterial cultures, gene expression as well as the characterization of protein activation of novel nitrogen transformation bacteria in order to provide more useful information on new nitrogen cycles.

**Key Words:** lake; nitrification; denitrification; anaerobic ammonia oxidation; archaeal ammonia oxidation; biological nitrogen removal

氮是地球上丰度最高的元素之一,为湖泊生态系统中重要的营养限制因子,也是生命构成的重要元素。随着人类工农业生产活动的增强,全球氮循环模式已被人为改变,人类活动造成的江河、湖泊等水体的氮输入明显增加,很多湖泊都出现了沉重的氮负荷,这势必影响水生生态系统的结构和水生生物的组成,从而直接影响内陆湖泊水环境安全。从20世纪80年代至今,我国富营养化湖泊所占的比例由61%增加到了88.6%,已成一个严峻的环境问题<sup>[1]</sup>。近年来人们对水体氮循环的认识经历了两次重大突破,即细菌厌氧氨氧化作用和氨氧化古细菌(AOA, ammonia-oxidizing archaea)的发现<sup>[2]</sup>,伴随着这些新发现以及氮素污染的日益严峻,迫切需要对天然水体的脱氮机理及脱氮效应做更深入的研究。

## 1 氮素在湖泊生态系统中的循环

氮素在湖泊生态系统内的循环是开放循环,主要包括5个过程,即固氮、硝化、反硝化、厌氧氨氧化和氨化作用,氮素循环过程如图1所示,这些过程主要发生在大气-水界面、水体内、水体-沉积物界面,以及沉积物内部等。

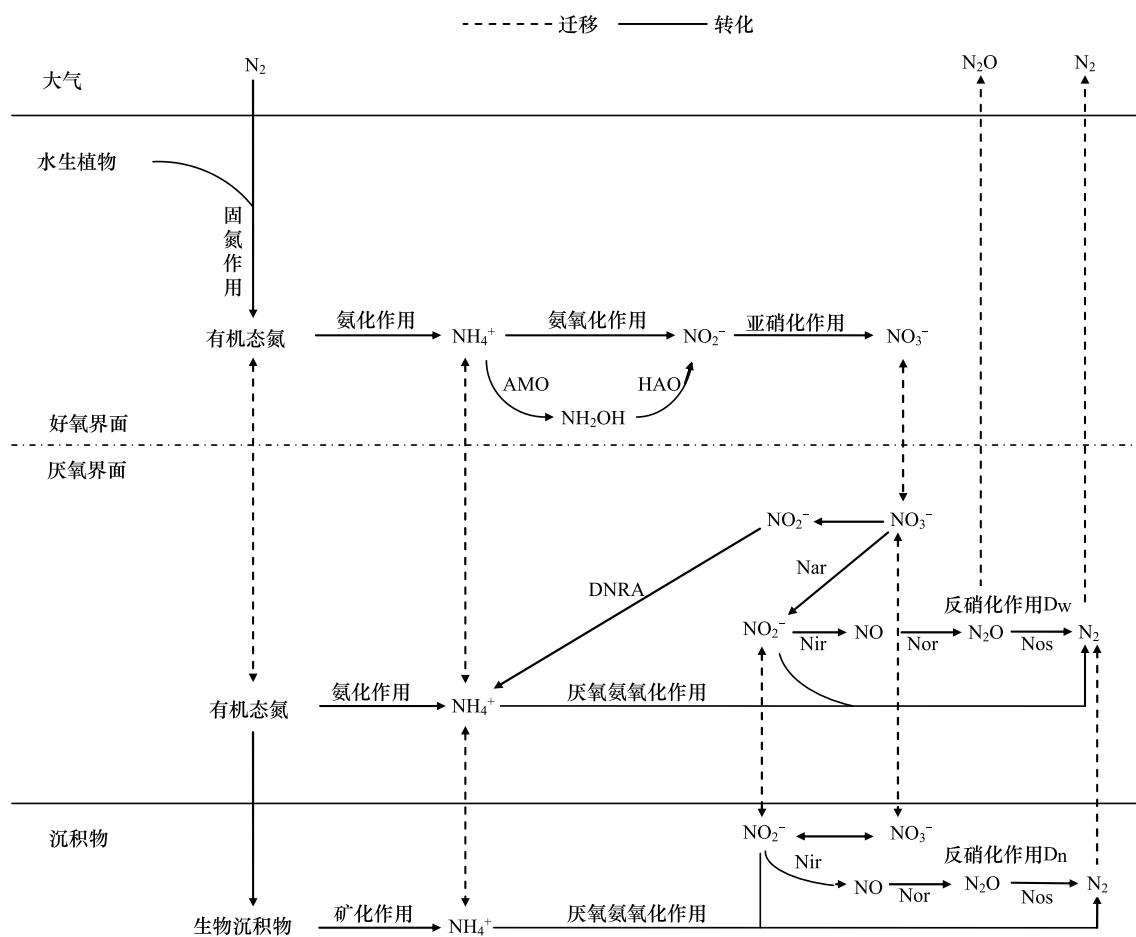
### 1.1 氮素在大气-水界面的迁移转化

湖泊生态系统中氮素的输入过程主要有为排放、生物固氮和大气沉降等方式。反硝化会导致湖泊氮素输出,在不受人为干扰的自然界中,生物固氮是补偿该输出的主要途径。对于氮素污染严重的富营养化湖泊,生物固氮的量很少,其输入效应基本可忽略。而氮输出方式首先是水生生物将氮素转化为自身生物量,经人工捞取或收获后离开湖泊生态系统。其次,氮素经生物脱氮后以N<sub>2</sub>O、N<sub>2</sub>等气体形式进入气相。最后一部分氮损失是通过氨氮挥发作用逸出湖泊系统。

### 1.2 氮素在湖泊生态系统内的氧化作用

#### 1.2.1 细菌的氨氧化

外源氮素进入湖泊生态系统经矿化或氨化转变成NH<sub>4</sub><sup>+</sup>。早在19世纪90年代Winogradsky首次发现在好氧条件下将NH<sub>4</sub><sup>+</sup>经NO<sub>2</sub><sup>-</sup>氧化为NO<sub>3</sub><sup>-</sup>,随之该过程被定义为硝化作用<sup>[6]</sup>。虽然硝化作用只改变无机氮的存在形式,不影响氮的收支,但是它连接氨化与反硝化作用,实现了有机氮降解。一般认为硝化作用分为两个步骤进行:氨氧化和亚硝酸盐氧化。而典型的氨氧化过程被认为是一个主要由变形菌纲中的一小部分细菌种群所

图1 湖泊生态系统中氮素循环示意图<sup>[3-5]</sup>Fig. 1 Nitrogen cycle in ecosystem of Lakes<sup>[3-5]</sup>

AMO 代表氨单加氧酶; HAO 代表细菌羟胺氧化还原酶; Nar 代表硝酸盐还原酶; Nir 代表亚硝酸盐还原酶; Nor 代表氧化氮还原酶; Nos 代表氧化亚氮还原酶; -----迁移; ——转化

进行的专性好氧化能的自养过程<sup>[7]</sup>。通常认为氨氧化是  $NH_4^+$  先经氨氧化细菌 (AOB, Ammonia Oxidation Bacteria) 的氨单加氧酶 (AMO, Ammonia monooxygenase) 作用转化为羟氨 ( $NH_2OH$ )，再经氨氧化细菌的羟氨氧化酶 (HAO, Hydroxylamine Oxidase) 作用转化为  $NO_2^-$ 。参与这个过程主要菌种有亚硝酸单胞菌属 (*Nitrosomonas*)、亚硝酸球菌属 (*Nitrosococcus*) 及亚硝酸螺菌属 (*Nitrosospira*) 等。亚硝酸盐氧化是  $NO_2^-$  在亚硝酸氧化菌 (NOB, Nitrite Oxidation Bacteria) 的亚硝氧化还原酶 (NOR, Nitrite Oxidoreductase) 催化作用下被氧化为  $NO_3^-$ ，参与这个过程主要菌种有硝化杆菌属 (*Nitrobacter*)、硝化球菌属 (*Nitrococcus*) 等。

### 1.2.2 古菌的氨氧化

嗜温泉古菌 (*Crenarchaeota*) 在全球氮循环过程中起着重要作用。研究发现海洋泉古菌具有氨氧化能力，并将其鉴定为氨氧化古菌 (Ammonia-oxidizing archaea, AOA)。氨可以由氨氧化古菌在古菌氨单加氧酶的催化条件下被氧化<sup>[8]</sup>，古菌氨单加氧酶的 *am oA* 基因普遍存在于海洋中，包括强光带、深层缺氧区以及海洋和江口的沉积物中<sup>[9]</sup>。与普通氨氧化细菌相比，水体和沉积物中氨氧化古菌的 *am oA* 基因很少重叠相似，具有丰富的生物多样性<sup>[10]</sup>，而氨氧化细菌的 *am oA* 基因数则相对较少，氨氧化古菌氨单加氧酶的 *am oA* 基因的拷贝数高于氨氧化细菌<sup>[11]</sup>。目前在水体<sup>[12]</sup>、沉积物<sup>[13]</sup>、以及陆水生动物的组织<sup>[14]</sup>中均已发现了氨氧化古菌的存在。环境中存在的绝大多数中温古菌为氨氧化古菌，这些菌类可能在氮素循环过程中起着重要作用<sup>[15-16]</sup>。

### 1.2.3 厌氧氨氧化

有学者发现氨的氧化过程不仅可以在有氧条件下进行,还可以在厌氧-缺氧的条件下通过厌氧氨氧化菌的作用被亚硝酸盐氧化,定义为厌氧氨氧化<sup>[17]</sup>。它主要包括两步:第一步是部分氨氮在氨氧化菌的作用下氧化为  $\text{NO}_2^-$ ,然后  $\text{NO}_2^-$  作为电子受体在亚硝酸盐还原酶的作用下被还原为  $\text{NH}_2\text{OH}$ ,第二步是在厌氧氨氧化菌的作用下,剩余的氨氮作为电子供体与第一步生成  $\text{NH}_2\text{OH}$  在联胺水解酶(Hydrazine hydrolase, HH)的作用下形成联胺( $\text{N}_2\text{H}_4$ ), $\text{N}_2\text{H}_4$  在联胺氧化酶(Hydrazine-oxidizing enzyme, HZO)作用下最终被氧化生成  $\text{N}_2$ 。自从在海洋环境中发现了厌氧氨氧化作用存在之后,厌氧氨氧化作用迅速成为海洋氮素研究的热点问题。湖泊的厌氧氨氧化作用目前还了解得较少,但自 Schubert 等首次在湖泊生态系统中发现厌氧氨氧化作用以后<sup>[18]</sup>,该氧化反应已备受关注。最近研究表明,河流沉积物中也有厌氧氨氧化发生,其菌种为 *Candidatus “Brocadia anamm oxidans”*<sup>[19]</sup>。将该沉积物引入厌氧反应器进行富集培养后,得到的菌种却为 *Candidatus “Scalindua”*,这可能是各菌种生长条件差异引起的物种演替,也说明污水处理研究成果并不能简单地类推到自然环境研究中。已确认的厌氧氨氧化细菌有 5 种<sup>[20]</sup>,最早发现的 anammox 菌被临时定名为 *Candidatus “Brocadia anamm oxidans”*<sup>[21]</sup>、*Candidatus Brocadia fulgida*<sup>[22]</sup>;后来又先后发现了 *Candidatus “Kuenenia stuttgartiensis”*<sup>[23]</sup>;*Candidatus “Scalindua sorokinii”*; *Candidatus “Scalindua brodae”*<sup>[24]</sup> 和 *Candidatus “Scalindua wagneri”*<sup>[25]</sup>,它们均属于浮霉状菌门(Planctomycetales)中的 Brocadiales 目。近年来在北极永冻层,污水处理系统等很多其它生态系统中也证实存在厌氧氨氧化<sup>[26-28]</sup>。徐昕荣在污水处理系统中发现了新的厌氧氨氧化细菌,由于同源性较低的,其分类地位仍未确定<sup>[29]</sup>。在海洋中也发现了厌氧氨氧化菌新种 *Candidatus “Anamm oxoglobus propionicus”*<sup>[30]</sup>、*Candidatus “Jettenia asiatica”*<sup>[31]</sup>,新菌种的不断发现预示着厌氧氨氧化现象远比人们认知的更加广泛。由于厌氧氨氧化菌的多样性对全球氮循环的影响突出,迫切需要对其进行更深入的研究。

### 1.2.4 异养硝化

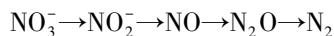
近年来,异养硝化也在自然界中被发现。有报道,尽管在一些土壤环境中没检测到自养硝化微生物存在,但却检测到  $\text{N}_2\text{O}$  和  $\text{NO}$  的释放,由此推断,这一现象可能与异养硝化细菌的异养硝化-反硝化有关<sup>[32]</sup>。自然界中异养硝化微生物种类繁多,且其可以利用的基质范围广泛。虽然它与自养硝化微生物的酶系统相似,但这两类微生物在能源利用方式上有着本质的不同。已有研究表明,异养硝化产生的  $\text{NO}_3^-$  直接来源于  $\text{NH}_4^+$ ,并不需要  $\text{NH}_4^+$  氧化为  $\text{NO}_2^-$  的中间反应过程<sup>[33]</sup>,这在一定程度上也导致了一些异养硝化作用产物亚硝酸盐积累量的偏低。另有研究者采用<sup>15</sup>N 同位素跟踪异养硝化的过程,发现异养微生物对  $\text{NH}_4^+$  没有作用,但能将有机氮直接氧化为  $\text{NO}_3^-$  而彻底跨过有机氮分解为  $\text{NH}_4^+$ ,再氧化为  $\text{NO}_2^-$  的过程<sup>[34]</sup>。早先已经在湖水、污泥、深海火山口发现了异养硝化微生物的存在<sup>[35-36]</sup>,近年来又在污水处理系统中发现了异养硝化微生物,菌种为 *Alcaligenes* sp., *Corynebacterium* sp., *Acinetobacter* sp., *Xanthomonas* sp. 和 *Bacillus* strains<sup>[37-39]</sup>。异养硝化菌主要由细菌、放线菌、真菌、藻类构成,其代谢机理和途径目前尚不明确。今后应深入研究异养硝化微生物关键酶的分离、纯化和基因表达,以及电子传递途径等,揭示它在氮素循环中所起的作用和重要性。

## 2 湖泊生态系统的生物脱氮

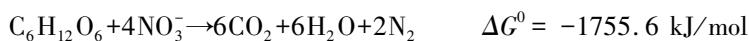
湖泊生态系统中生物脱氮作用主要为反硝化和厌氧氨氧化两种过程,多发生于沉积物的还原环境中。近年来,随着对脱氮研究的发展,对其机制提出了多种假设,如耦合硝化-反硝化过程,即脱氮过程所需的硝酸盐主要是沉积物中的氨氮经过硝化作用生成;非耦合硝化-反硝化过程,即脱氮过程所需的硝酸盐主要来自于上覆水。

### 2.1 反硝化脱氮及影响因素

反硝化作用的概念是由 Gayon 与 Dupetit 于 1882 年提出。一般认为反硝化过程经历以下几个步骤:



反应计量式如下:



在早先海洋生态系统的研究中,沉积物-水界面上进行的反硝化作用是一个重要的脱氮过程。Port Phillip 海湾沉积物反硝化损失的氮约占整个水体氮的 63%<sup>[40]</sup>。随着研究领域的不断扩大,近年来对淡水生态系统的研究也在不断的深入。太湖梅梁湾的上覆水  $\text{NO}_3^-$  浓度与非耦合硝化-反硝化( $D_w$ )显著相关,而硝酸盐释放速率对  $D_w$  的影响并不显著;梅梁湾北部河口区内耦合硝化-反硝化( $D_n$ )占总脱氮速率的比值在 39.53% 左右,开敞湖区为 69.96%,  $D_w$  占总脱氮速率的比值在 47.21%, 开敞湖区为 19.85%<sup>[41]</sup>。也有研究者计算了进、出太湖的营养元素产生量,并据此可计算出水土界面反硝化作用清除的氮约占太湖外源性输入氮的 2.03%—7.92%,是年平均净入湖氮总量的 27.0%—105.3%<sup>[42]</sup>;美国 Okeechobee 湖和瑞士 Baldegg 湖由反硝化作用清除的氮比值分别为 9%—23% 和 0.2%<sup>[43-44]</sup>。其他淡水系统中反硝化脱氮对营养氮素的去除也相当突出,我国长江口表层沉积物反硝化作用去除的无机氮每天为  $6.47 \times 10^5 \text{ kg} \cdot \text{N}$ ,是长江无机氮日输入总量的 13.8%<sup>[45]</sup>。黄河口表层沉积物的反硝化作用每天去除的无机氮约为  $4.10 \times 10^4 \text{ kg} \cdot \text{N}$ ,是黄河无机氮日输入总量的 11.22%。河口通常可清除 10%—60% 的氮负荷,反硝化脱氮在其中起到了非常重要的作用。Sertizinger 等认为养殖水体通过反硝化作用的氮损失占其总输入的 1%—36%<sup>[46]</sup>。硝酸盐可被生物固定或同化吸收而暂时从水体中去除,但生物残体最终仍通过矿化作用把硝酸盐返回到环境中去。反硝化作用能把硝酸盐彻底的从自然环境中去除,因而被公认为是去除湖泊氮素的最佳途径。

在自然条件下,影响反硝化脱氮的因素有众多,但主要是由界面上的硝化作用控制<sup>[47]</sup>。反硝化作用还需要一定量的溶解氧分压,溶解氧浓度变化会引起它的季节性变化<sup>[48]</sup>。水体的 pH 值也是影响反硝化作用一个最重要自然因素,pH 值在 9.5 以上硝化细菌受到抑制,而 pH 值在 6.0 以下时亚硝化细菌被抑制<sup>[49]</sup>。在海洋水环境中影响反硝化的主要因子是温度、 $\text{NO}_3^-$ 、有机碳<sup>[50]</sup>,在反硝化微生物活性温度范围内,温度是沉积物反硝化速率的决定因素,反硝化速率与温度呈显著性正相关<sup>[51-52]</sup>。

## 2.2 厌氧氨氧化脱氮及脱氮效率

早在 1977 年 Broda 预言厌氧氨氧化反应和厌氧氨氧化菌的存在<sup>[53]</sup>,后在 1995 年 Mulder 证实了 Broda 的预言<sup>[54]</sup>。采用 $^{15}\text{N}$  同位素示踪实验对以  $\text{NO}_2^-$  为电子受体的厌氧氨氧化进行了研究,发现了厌氧氨氧化的发生主要按以下反应式进行<sup>[55]</sup>:



海洋厌氧氨氧化反应已进行 10 余年研究,但对于该反应产生的氮气量占海洋氮气总产生量的比值还没有明确结论,这一比值估计在 30%—50% 之间<sup>[56]</sup>,甚至达到 50% 以上,比反硝化脱氮量更大<sup>[57]</sup>。应用 $^{15}\text{N}$  标记的硝酸盐和氨对海底沉积物进行的培养实验发现,厌氧氨氧化作用产生  $\text{N}_2$  导致的氮损失占全部氮损失的 24%—67%<sup>[58]</sup>。厌氧氨氧化是海洋氮损失的主要原因,在黑海和 Gulfo Dulce 海的好氧与缺氧交界通过厌氧氨氧化作用而损失的氮达 20%—40%<sup>[59]</sup>。淡水系统的研究成果很少,还不能形成较全面的认识,不过坦桑尼亚坦噶尼喀湖的研究表明,约有 13% 的氮气损失是由该反应引起<sup>[22]</sup>。不同地点的生境条件对厌氧氨氧化的除去氮素能力也有明显的影响,引起的氮素损失占总损失量比值也在 0%—67% 的较大范围内波动<sup>[2]</sup>。与反硝化作用相比,浅水中厌氧氨氧化对氮素的去除所占比重较小,但深水中情况刚好相反,厌氧氨氧化的绝对速率与水深并不相关<sup>[60]</sup>。在海洋最低含氧带中还发现反硝化形成的亚硝酸盐被厌氧氨氧化消耗殆尽,反硝化后续过程产生的氮气几乎可以忽略不计<sup>[27,59]</sup>,厌氧氨氧化脱氮目前已被认为是重要的脱氮途径。

影响厌氧氨氧化反应最显著的因素是厌氧氨氧化菌的种类和数量,还有一些其他的环境因子,如有机质、温度和 pH 值等。高浓度的有机质,将与氨氮竞争电子受体,且往往有机质更易成为电子供体,从而使厌氧氨氧化的脱氮效率降低。温度和 pH 值的变化都是影响厌氧氨氧化菌的生长速率及酶活性的限制因子。在自然环境中厌氧氨氧化细菌表现出较强的温度适应范围,从 2—80℃ 均有发现。对于不同生态系统中厌氧氨氧化种群的适宜温度要符合当地自然环境,多数在 15—25℃ 为最适温度,若温度  $\geq 25^\circ\text{C}$ , 厌氧氨氧化反应速率急剧下降;若温度达到 37℃, 反应基本处于停止状态<sup>[61]</sup>。厌氧氨氧化适宜厌氧的环境,氧气对厌氧氨氧化有明显的抑制作用,当溶解氧浓度高至 5mg/L 时,厌氧氨氧化活性被完全抑制<sup>[62]</sup>。

### 3 展望

目前,固氮、硝化、反硝化作用也逐步深入到了参与微生物的酶和对应基因序列的探讨。已有报道将硝化/反硝化菌固定在共聚物载体上以增强其繁殖能力和对环境变化的耐受性。今后的重点是通过努力制备出硝化/反硝化优势菌种相容性强的载体,使硝化/反硝化菌脱氮效力有进一步提高。厌氧氨氧化的研究目前已提出了可能的生化反应模型和功能基因,且通过实验获得了厌氧氨氧化菌的主要生理学参数,但对厌氧氨氧化菌的结构与功能以及酶在新陈代谢中的作用机理尚不十分明确,而且现已鉴定出的厌氧氨氧化菌种主要集中在浮霉状菌目,难以分离和纯化,目前还未得到厌氧氨氧化菌的纯菌株,今后如能分离得到纯菌株,或发现具有厌氧氨氧化功能的其它菌种,对厌氧氨氧化而言将会是一个新的突破。今后可能要在厌氧氨氧化菌生长特性、物种多样性、生长动力学等方面加强研究,特别是加强小生境中的厌氧氨氧化过程的研究,从而明确厌氧氨氧化反应条件、中间产物等内在因素。自2005年Könneke在从海洋中分离到一株氨氧化古菌后<sup>[8]</sup>,国内对泉古菌的研究也逐步拓宽和加深,发现不同环境介质中的泉古菌16S rDNA的序列存在着明显区别<sup>[63]</sup>。以后的探索重点可能是在温泉古菌的分离培养、DNA和mRNA水平上分析温泉古菌16S rDNA基因的表达、蛋白质活性的表征上,以揭示它生态功能以及潜在的生态价值来推动氮循环研究的进步。异养硝化菌的发现已经在污水处理同步硝化反硝化工艺中有所应用,但是异养硝化速率相对较低,今后的研究应着重于如何培养和富集异养硝化菌、如何提高异养硝化的速率来实现污水中氮的去除。期望以后的探索能够将厌氧氨氧化与古菌氨氧化和异养硝化等研究相结合,弄清楚它们相互的存在关系,是否存在DO、NH<sub>4</sub><sup>+</sup>的竞争或NO<sub>2</sub><sup>-</sup>共生关系,以及它们各自引起氮损失的比例和主导地位。这些问题的答案将有助于更深入地了解自然条件下氮素的循环机理,同时促进污染湖泊生态修复技术的提高。

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