

# 滨海湿地生态系统中古菌驱动的氮循环

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**摘要:** 滨海湿地是全球生产力最高的生态系统之一, 位于海洋与陆地的交界处, 承接大量含氮物质的输入, 氮循环活跃, 对全球氮储库平衡及气候变化具有关键的调节作用。古菌是滨海湿地微生物群落的重要组成部分, 然而其生态作用曾长期被忽视。随着新型生物学技术的发展, 古菌的多样性及其生态功能逐渐被揭示, 显示出其在氮循环中扮演着重要角色。本文综述了滨海湿地中古菌的分布和多样性, 重点探讨了古菌在固氮、硝化、反硝化和硝酸盐铵化等关键氮循环过程中的驱动作用。此外, 针对古菌在全球气候变化减缓中的应用, 本文还探讨了利用古菌群落减少滨海湿地氧化亚氮排放的设想。

**关键词:** 滨海湿地生态系统; 古菌; 氮循环; 氧化亚氮

## Archaea-driven nitrogen cycling in coastal wetland ecosystems

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**Abstract:** Coastal wetlands, among the most productive ecosystems on Earth, are situated at the

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interface between land and ocean, receiving substantial nitrogen inputs. These ecosystems exhibit active nitrogen cycling and play a crucial role in global nitrogen budgets and climate regulation. Archaea constitute a critical component of the microbial communities in coastal wetlands, yet their ecological significance was overlooked. The advancements in novel biological technologies have unveiled the diversity and ecological functions of archaea, highlighting their significant contributions to nitrogen cycling. This review summarizes the distribution and diversity of archaea in coastal wetland ecosystems, with a particular focus on their roles in key nitrogen cycling processes such as nitrogen fixation, nitrification, denitrification, and nitrate ammonification. In addition, for the application of archaea in global climate change mitigation, we explore the idea of using archaeal communities to reduce nitrous oxide emissions from coastal wetlands.

**Keywords:** coastal wetland ecosystem; archaea; nitrogen cycling; nitrous oxide

滨海湿地处于海陆交界地带, 是一个多圈层、多区域强烈交互的复杂区域, 包括河口、红树林、盐沼、潮汐盐湿地和新生潮汐湿地等<sup>[1]</sup>。受海陆交互作用的影响, 滨海湿地的生态环境较为脆弱<sup>[2]</sup>, 但在全球生物地球化学循环、海岸线保护、生物多样性维护等方面具有重要的生态系统服务功能<sup>[3-4]</sup>。氮循环是滨海湿地最关键的元素循环之一, 在全球范围内, 滨海湿地作为内陆与海洋生态系统之间的缓冲区, 在氮的转化和迁移过程中发挥着重要作用<sup>[5]</sup>。由于海洋和陆地之间营养物质的周转循环, 滨海湿地的氮循环十分活跃, 在全球氮储库收支和气候变化中发挥着关键作用<sup>[6]</sup>。其中, 滨海湿地产生的氧化亚氮(nitrous oxide, N<sub>2</sub>O)排放量占海洋总排放量的 50% 以上, 对气候变化具有显著影响<sup>[7]</sup>。

微生物在生物地球化学循环中起着关键作用, 同时对地球生态系统的平衡也至关重要。近年来, 随着新型生物学技术的发展和数据分析方法的不断进步, 科学家们对环境微生物群落组成的认识已经不再局限于细菌, 也转向了对古菌分布和生态功能的研究<sup>[8-9]</sup>。作为地球上最古老的生命形式之一<sup>[10]</sup>, 古菌最初被发现于火山口、盐湖和热液口等极端环境中<sup>[11-13]</sup>。由于其细胞结构与细菌相似, 古菌曾一度被视为原核生物的一个分支。直到 1977 年, Woese

等<sup>[14]</sup>基于 16S rRNA 基因序列的系统发育分析, 提出了以产甲烷菌(methanogens)为代表的“第三域”的概念, 并首次使用“古菌(archaeobacteria)”这一术语, 明确将其与细菌(bacteria)区分开来。他们指出, 产甲烷菌的表型具有明显的古老性, 并认为其生态特征与推测的 30 亿–40 亿年前地球环境条件极为契合<sup>[14]</sup>。1990 年, Woese 等<sup>[15]</sup>进一步提出了“三域系统”, 正式确立了古菌(archaea)、细菌(bacteria)和真核生物(eukarya)三大生物域的分类体系。在早期的古菌分类体系中, 仅包含泉古菌门(*Crenarchaeota*)和广古菌门(*Euryarchaeota*) 2 个门类<sup>[15-16]</sup>。随着系统发育研究的深入, 泉古菌门被重新定义为嗜热多形菌门(*Thermoproteota*), 以更准确反映其系统发育地位<sup>[17]</sup>。近年来, 基于系统发育和基因组分析, 高通量测序、宏基因组学组装和分箱技术揭示了许多新的古菌门。目前, 古菌至少包括 4 个主要的超门: 广古菌门、TACK、Asgard 和 DPANN<sup>[18]</sup>。古菌门的数量从最初的 2 个扩大到现在的至少 27 个<sup>[19]</sup>, 开启了古菌研究的新纪元。

古菌曾被认为主要分布于极端环境中, 但研究已证明古菌也广泛存在于大气、土壤、水体等普通生态系统中, 甚至在人类肠道、口腔和皮肤中均有检出<sup>[20]</sup>。此外, 滨海湿地生态系统也被证实是古菌的重要栖息地, 但由于其低丰度且培养困难, 目前对古菌在生物地球化学

循环中的作用研究仍较少<sup>[21-22]</sup>。随着生物技术的发展和应用,加快了对古菌多样性、代谢机制和相互作用等领域的研究进程<sup>[19]</sup>,发现古菌也可能是氮循环的重要驱动者(图 1)。因此,本文对滨海湿地生态系统中古菌群落结构以及驱动的氮循环主要过程进行评述,并对滨海湿地中古菌未来研究发展方向进行分析和展望。

## 1 古菌在滨海湿地生态系统的分布与多样性

古菌曾被认为是滨海地区微生物的次要组成部分。然而,最近的研究表明古菌是滨海湿地生态系统的重要组成部分。尽管滨海湿地生态系统中存在大量古菌,但对古菌在滨海地区氮循环中的作用研究较少,这主要是因为古菌丰度较低且实验室培养困难<sup>[23]</sup>。滨海湿地不同生境的古菌丰度和群落组成具有高度变异性,受地理位置和植被状况的影响尤为显著。在滨海湿地生态系统中,古菌的数量占比在有植被的湿地(如红树林 1.0%–41.3%、盐沼 5.5%–29.3% 和海草 6.0%–16.0%)高于无植被的湿地(如河口

1.4%–14.1%、潮间带滩涂 0.3%–10.0%)<sup>[23]</sup>。除植被状况外,深度也是影响滨海湿地生态系统的因素。尽管微生物的细胞密度随着沉积物深度的增加而降低,并向缺氧的次表层靠近,但次表层沉积物中古菌的丰度远高于表层<sup>[22,24]</sup>,且占比可达 37%<sup>[25]</sup>,这表明古菌比其他微生物更能适应缺氧环境,且对能量的需求更低。除此之外,温度、盐度、pH、有机质含量和含氧量等环境条件也会影响古菌的群落结构<sup>[26-29]</sup>。多项研究对滨海湿地中古菌群落结构进行了调查<sup>[24,28,30-46]</sup>,并对不同类型滨海湿地(包括盐沼、河口、潮间带、红树林等)中相对含量大于 5% 的古菌进行了汇总(图 2)。

滨海湿地生态系统中常见的古菌类群包括深古菌门(*Bathyarchaeota*)、广古菌门、嗜热多形菌门、乌斯古菌门(*Woesearchaeota*)和 *Promethearchaeota*,它们的相对丰度通常占古菌总量的 95% 以上<sup>[22-23]</sup>。其中,深古菌门是滨海地区丰度最高的优势菌群,主要活跃在缺氧的表层沉积物中,其相对丰度可达到 60% 以上<sup>[22,47]</sup>。例如,在巴西卡多佐岛国家公园底部沉

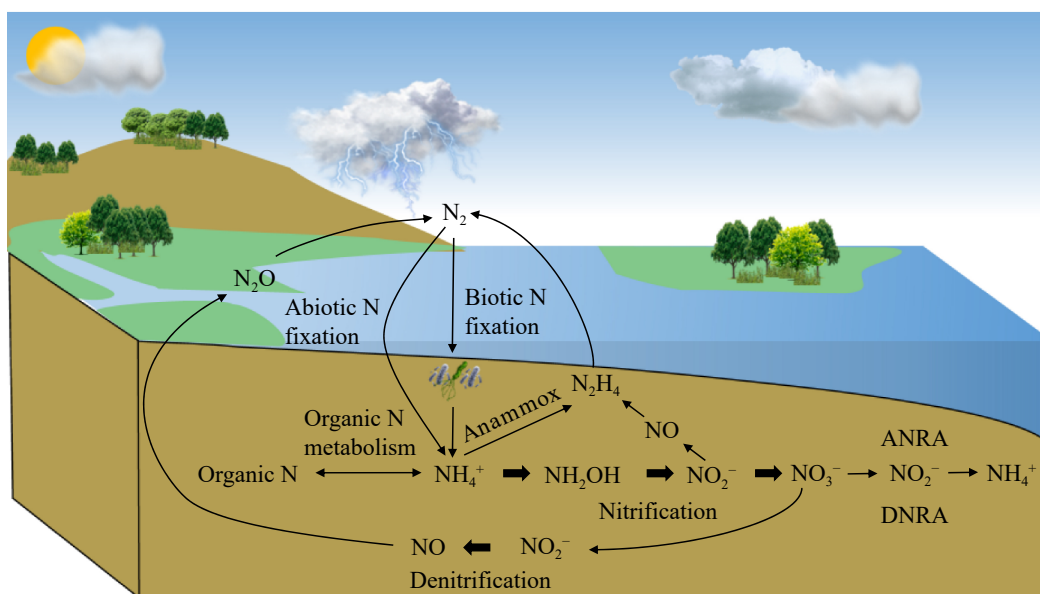


图1 滨海湿地生态系统氮循环路径

Figure 1 Diagram depicting a nitrogen cycle pathway for coastal wetland ecosystems.

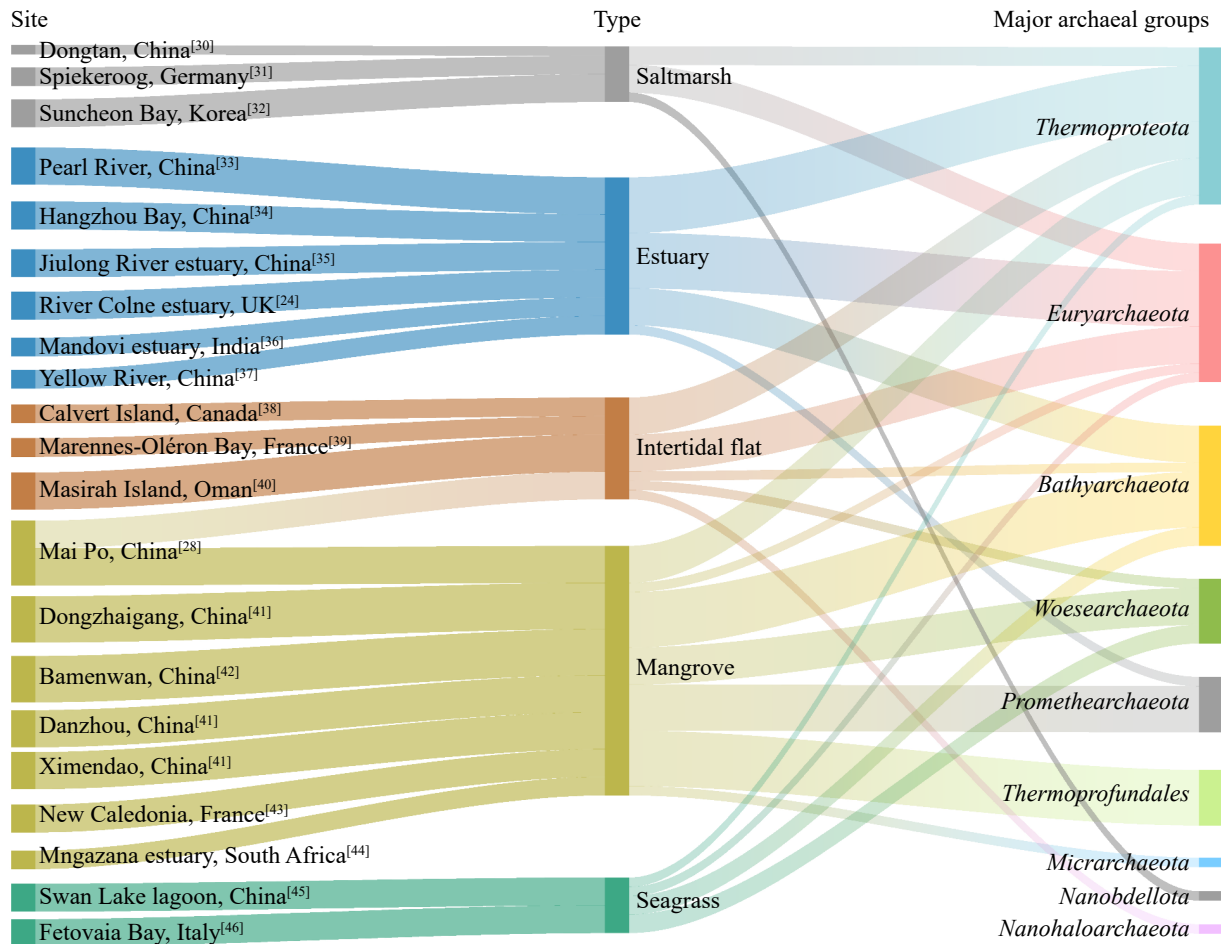


图2 不同类型滨海湿地的古菌分布

Figure 2 Distribution of archaea in different coastal wetland ecosystems.

积物层中, 深古菌门占古菌总数的 70% 以上<sup>[48]</sup>; 在中国九龙江河口沉积物中, 深古菌门约占总古菌的 60%<sup>[49]</sup>。广古菌门中底栖古菌目 (*Thermopfundales*) 也是最常见的古菌类群之一。在巴西卡多佐岛沉积物层中, 底栖古菌目占古菌总数的 5%–53%<sup>[48]</sup>; 在新喀里多尼亚沉积物中, 底栖古菌目占古菌总数的 43%<sup>[43]</sup>。在天津渤海湾沿岸地区的研究中发现, 深古菌门和广古菌门这 2 种菌群占古菌群落总丰度的 70% 以上<sup>[50]</sup>。产甲烷菌也是广古菌门中最重要的类群之一。例如, 在印度喀拉拉邦红树林生态系统中, 甲烷杆菌纲 (*Methanobacteria*)、甲烷球菌纲 (*Methanococci*) 和甲烷微菌纲 (*Methanomicrobia*)

分别占古菌总数的 5%、8% 和 35%<sup>[51]</sup>。嗜热多形菌门是好氧古菌, 其在好氧环境和表层沉积物中的丰度明显高于相同地点的底层沉积物<sup>[28]</sup>。研究表明, 在印度西海岸, 嗜热多形菌门是丰度最高的门 (44%–74%)<sup>[52]</sup>; 在印度孙德尔本斯红树林表层沉积物中, 嗜热多形菌门也是优势菌门<sup>[53]</sup>。此外, 巴斯古菌门在红树林和盐沼生态系统中的丰度高于其他生态系统<sup>[54]</sup>。例如, 在中国的大亚湾和东寨港的红树林沉积物中, 巴斯古菌门占总古菌的 10%–27%<sup>[55–56]</sup>。 *Promethearchaeota* 也是滨海湿地沉积物的重要组成部分, 且与深古菌门类似, *Promethearchaeota* 在沉积物底层的丰度比表层更高<sup>[42,57]</sup>。

## 2 滨海湿地生态系统中古菌驱动的氮循环

近年来,古菌在氮循环中的重要作用逐渐被认识,尤其是在固氮(nitrogen fixation)、硝化(nitrification)、反硝化(denitrification)等过程中的贡献<sup>[7]</sup>。古菌群落不仅在滨海湿地的氮循环中发挥着核心作用,而且在减少温室气体  $\text{N}_2\text{O}$  排放方面具有潜力<sup>[58]</sup>。Fu 等<sup>[50]</sup>研究表明,在牡蛎礁生态修复过程中,古菌群落的变化对氮的去除和温室气体减排具有重要影响。这些发现为未来探索古菌在湿地生态系统中的应用提供了新的视角。古菌可以驱动除亚硝酸根氧化和厌氧氨氧化(anaerobic ammonium oxidation, Anammox)之外的大部分氮循环过程(图 3)。然而,在滨海湿地的氮循环过程中,实际的氮循环过程受到多种因素的调控。例如,盐度<sup>[59]</sup>、pH<sup>[60]</sup>、溶解氧浓度<sup>[1,61]</sup>等环境因素都会影响古菌是否能够表达相关功能基因,并实际执行代谢功能。虽然古菌的基因组中可能编码固氮、硝化等相关功能基因,但这些基因的存在并不意味着古菌一定能在所有环境条件下执行这些代谢功能<sup>[62-63]</sup>。因此,古菌是否能够发挥这些作用,仍需通过

实验验证和更多的生态学研究来进一步明确。

### 2.1 固氮过程

古菌等大多数微生物可以从无机氮(如铵、 $\text{NH}_4^+$ 、或硝酸盐、 $\text{NO}_3^-$ )及有机氮中吸收氮源<sup>[64]</sup>。然而这些氮源在生物圈内供不应求,维持生命的大部分氮源是来自大气中的氮库<sup>[65]</sup>。固氮作用可以分为非生物固氮(abiotic nitrogen fixation, ANF)和生物固氮(biotic nitrogen fixation, BNF)。在非生物固氮中,氮气( $\text{N}_2$ )在闪电等高能条件下与氧气反应生成一氧化氮(nitric oxide, NO),随后进一步氧化形成二氧化氮(nitrogen dioxide,  $\text{NO}_2$ ),  $\text{NO}_2$  溶解于水后转化为  $\text{NO}_3^-$  和亚硝酸盐( $\text{NO}_2^-$ )<sup>[66]</sup>。生物固氮则是通过古菌或细菌等微生物携带的固氮酶将空气中的  $\text{N}_2$  还原为氨( $\text{NH}_3$ )。尽管大气中氮库储存量大,但氮的生物有效性主要依赖于生物固氮过程<sup>[67]</sup>。固氮酶(nitrogenase)主要包括钼-铁(Mo-Fe)、钒-铁(V-Fe)和铁-铁(Fe-Fe)这 3 种类型,其中的钼、钒和铁等金属离子主要起催化作用,分别由 *nifDK*、*vnfDGK* 和 *anfDGK* 基因编码<sup>[68]</sup>,而含铁的电子转运蛋白[固氮酶还原酶(nitrogenase reductase)]则由 *nifH*、*vnfH* 和 *anfH* 基因编码<sup>[69]</sup>(图 4)。固氮作用耗能较大,每固定 1 mol 氮需要消耗 16 mol

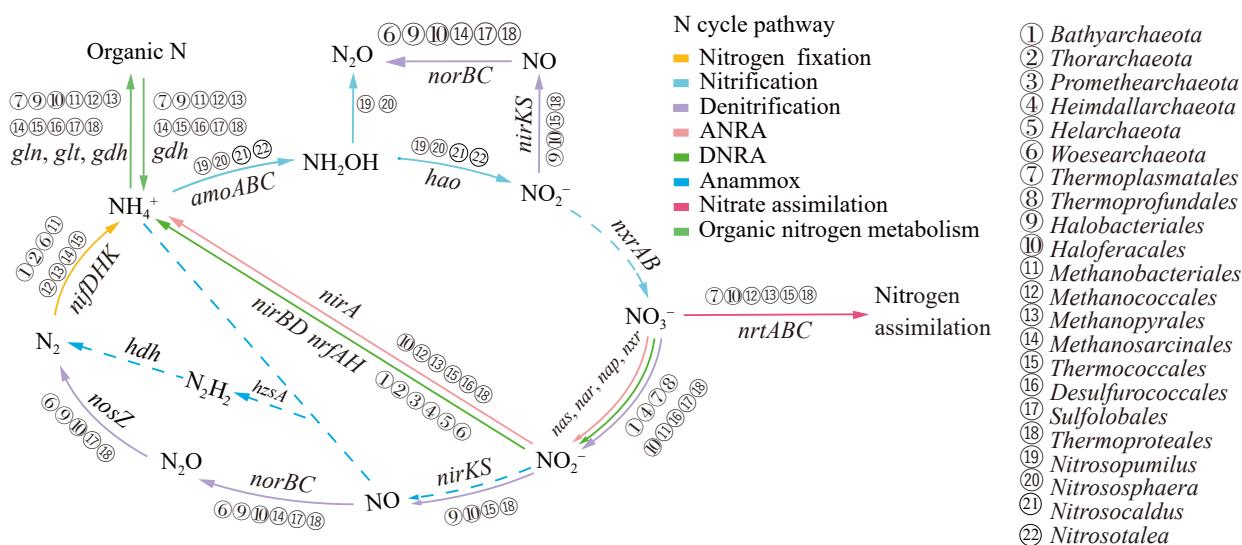


图3 滨海湿地生态系统古菌驱动的氮循环过程

Figure 3 Archaea-driven nitrogen cycle process in coastal wetland ecosystems.

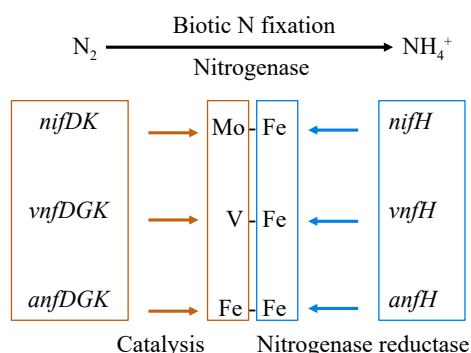


图4 由固氮酶催化的生物固氮过程

Figure 4 Biotic nitrogen fixation catalyzed by nitrogenase.

三磷酸腺苷(adenosine triphosphate, ATP), 因此被认为是自然生态系统生产力的限制因素<sup>[70-71]</sup>。

滨海湿地生态系统的微生物固氮速率通常较低, 但在不同区域和环境条件下表现出一定的差异性, 受外源性氮输入、有机质供应、环境梯度(如盐度和 pH)以及菌群组成等多重因素的综合影响<sup>[72]</sup>。有研究测量得出菲茨罗伊河口的固氮速率为  $0.99\text{--}1.09\ \mu\text{mol N}/(\text{m}^2\cdot\text{h})$ , 且位置和季节对其影响不大<sup>[73]</sup>; 墨西哥湾的小泻湖的固氮速率相对较高, 为  $1.6\text{--}2.6\ \mu\text{mol N}/(\text{m}^2\cdot\text{h})$ <sup>[74]</sup>。滨海湿地生态系统中常见的固氮古菌主要包括产甲烷古菌(甲烷杆菌纲、甲烷球菌纲和甲烷微菌纲)和厌氧甲烷氧化古菌(anaerobic methanotrophic archaea subgroup 2, ANME-2), 它们广泛存在于缺氧环境中<sup>[64,75-76]</sup>。Mo-Fe 固氮酶在固氮产甲烷菌中占优势<sup>[75]</sup>, 其中噬乙酸甲烷八叠球菌(*Methanosarcina acetivorans*)的基因组中包含 *nif*、*vnf* 和 *anf* 基因, 是古菌中唯一含有 3 种固氮酶的菌群<sup>[77]</sup>。除产甲烷古菌和厌氧甲烷氧化古菌外, 近年来也在其他古菌中发现了固氮相关基因。例如, 李猛团队在深圳福田红树林沉积物中的深古菌门和索尔古菌门(*Thorarchaeota*)基因组中发现了 *nifH* 基因<sup>[78-79]</sup>, 乌斯古菌门中也含有 *nifH* 基因<sup>[80]</sup>。古菌在滨海湿地中的固氮作用不容小觑。例如, 在美国佛罗里达的大沼泽地土壤中, 古菌相关的 *nifH* 基因序列占 *nifH* 总基

因序列的 6%–44%; 而在 *nifH* 转录本中, 古菌来源的转录本占比 2%–49%<sup>[81]</sup>。需要注意的是, 虽然部分古菌基因组编码了固氮酶(如 *nifH* 基因), 但这些基因的存在并不意味着古菌在所有环境条件下都能进行氮固定。在滨海湿地生态系统中, 固氮相关基因的存在可能反映了这些古菌的代谢潜能, 而实际的固氮功能则受多种因素的调控, 包括环境条件(如盐度、pH)和微生物群落的相互作用<sup>[72,82]</sup>。因此, 基于基因组分析推测氮代谢潜能时, 需要特别注意这一潜能并不总是转化为实际的代谢功能。另外, 与古菌相比, 细菌固氮菌只在无其他氮源的情况下才会表达固氮酶<sup>[64,75,83]</sup>, 而固氮甲烷氧化菌可以与甲烷厌氧氧化(anaerobic oxidation of methane, AOM)联合体中的细菌共享氮源<sup>[83-84]</sup>。

## 2.2 硝化作用

硝化作用包括氨氧化微生物将  $\text{NH}_4^+$  转化为  $\text{NO}_2^-$ , 以及亚硝酸盐氧化微生物将  $\text{NO}_2^-$  转化为  $\text{NO}_3^-$ 。氨氧化是硝化作用的第一步和限速步骤, 也是滨海湿地氮循环的重要组成部分<sup>[85-86]</sup>。氨单加氧酶(ammonia monooxygenase, AMO)是氨氧化过程中第一步反应的核心催化酶, 其编码基因 *amoA* 可用于评估不同环境中的氨氧化效率, 解析功能微生物的群落组成及其生物多样性<sup>[7]</sup>。羟胺氧化还原酶(hydroxylamine oxidoreductase, HAO)由 *hao* 基因编码, 是氨氧化过程中另一关键酶, 负责将氨氧化产生的中间产物羟胺( $\text{NH}_2\text{OH}$ )进一步转化为  $\text{NO}_2^-$ <sup>[7]</sup>。尽管长期以来氨氧化过程被认为仅由氨氧化细菌(ammonia-oxidizing bacteria, AOB)驱动, 但近年来的分子生物学研究表明, 部分古菌具有与细菌相似的 *amoA* 基因, 随后通过基因转录手段间接证明了氨氧化古菌(ammonia-oxidizing archaea, AOA)也具有氨氧化功能, 可以在好氧条件下与 AOB 共同负责氨氧化<sup>[87-89]</sup>。利用不同生物钟模型进行的系统基因组学和分子定年分析表明, 古菌中的氨氧化作用至少在 10 亿年前开始出现<sup>[90-91]</sup>。目前, 将  $\text{NO}_2^-$  氧化为  $\text{NO}_3^-$  的功能仅在亚硝酸

盐氧化细菌(nitrite-oxidizing bacteria, NOB)和新发现的存在于硝化螺菌属(*Nitrospira*)的完全氨氧化细菌(complete ammonia-oxidizing bacteria, Comammox)中发现<sup>[92]</sup>。

滨海湿地生态系统中, AOA 的主要优势菌包括嗜热多形菌门的亚硝化侏儒菌属(*Nitrosopumilus*)、亚硝化球形菌属(*Nitrososphaera*)、亚硝化暖菌属(*Nitrosocaldus*)和 *Nitrosotalea*<sup>[93]</sup>。研究表明, 滨海湿地中 AOA 的数量往往比 AOB 高出一个数量级<sup>[93-96]</sup>。另一方面, 室内培养结果显示, 一些 AOA 菌株对  $\text{NH}_4^+$  的半饱和常数远低于 AOB 菌株<sup>[97-98]</sup>。在氮浓度较低的渤海北部和长江口地区, AOA 中的 *amoA* 基因比氮浓度较高的地区丰度更高<sup>[99]</sup>, 这表明在营养缺乏的环境中, AOA 对底物具有更强的亲和力, 可能比 AOB 具有竞争优势<sup>[100]</sup>。然而, *amoA* 基因、转录 RNA 和编码蛋白的丰度并不足以解释细菌和古菌的氨氧化活性<sup>[101]</sup>。与 AOB 相比, AOA 具有更低的生长速率和更低的细胞特异性氨氧化活性, 这表明尽管 AOA 在数量上占优势, 但在氨氧化的贡献上不如 AOB<sup>[102-104]</sup>。Wang 等<sup>[5]</sup>研究发现, 我国环渤海地区 4 种典型滨海湿地(稻田、河口、浅滩和芦苇湿地)中 AOB 的氧化能力均显著高于 AOA, 且 AOA 群落结构较 AOB 更为稳定。Zhu 等<sup>[105]</sup>也对渤海地区滨海湿地的 AOA 和 AOB 的潜在活性进行了研究, 结果表明 AOB 的活性可能由相关功能基因决定, 而 AOA 的活性与自身丰度有关。AOA 的存在与温度和氧浓度有关, 已有研究证实热带地区河口生态系统的硝化作用随低氧浓度和  $\text{H}_2\text{S}$  的存在而减弱<sup>[106]</sup>。然而, 也有一些 AOA 可以在无氧环境中通过自身产氧维持其氨氧化功能<sup>[107]</sup>。AOA 还倾向于在较低 pH 环境中生存, 在一些酸性土壤中是主要的氨氧化驱动者<sup>[63,95]</sup>。此外, 由于 AOA 含有与重金属运输和调节相关的基因, 它在被污染的和富营养的河口环境中可以发挥更重要的作用<sup>[108]</sup>。综合来看, 在极端环境或贫营养条件下, AOA 相较于 AOB 显示出更强的生

存适应性, 因而成为这些环境中的主要氨氧化功能微生物。

## 2.3 反硝化作用

反硝化作用是指在厌氧条件下将  $\text{NO}_3^-$  还原为  $\text{N}_2$  的过程, 该过程并不总是以  $\text{N}_2$  为最终产物, 也可能导致 NO 和  $\text{NO}_2$  的释放<sup>[109]</sup>。完整的反硝化过程需要 4 种关键酶: 硝酸盐还原酶[同化型硝酸盐还原酶(assimilatory nitrate reductases, Nas)、膜结合型硝酸盐还原酶(membrane-bound nitrate reductase, Nar)、周质硝酸盐还原酶(periplasmic nitrate reductase, Nap)和亚硝酸盐氧化还原酶(nitrite oxidoreductase, Nxr)]、亚硝酸盐还原酶(nitrite reductase, Nir)、一氧化氮还原酶(nitric oxide reductase, Nor)和一氧化二氮还原酶(nitrous oxide reductase, Nos)<sup>[110]</sup>。随着生活污水和工业废水大量排入滨海湿地生态系统, 沉积物中积累了显著的含氮污染物负荷<sup>[111]</sup>。反硝化作用作为滨海湿地氮循环中的一个关键环节, 对于系统中氮的去除发挥着至关重要的作用。据统计, 超过半数的溶解性无机氮在滨海湿地生态系统中是通过反硝化过程得到有效去除的<sup>[112]</sup>。反硝化过程通常由生长在低氧或缺氧条件的兼性厌氧菌驱动<sup>[113]</sup>。除细菌外, 一些古菌甚至真核生物也可以进行反硝化作用<sup>[64,113]</sup>。一些嗜盐古菌, 如富盐菌属(*Haloferax*)、盐盒菌属(*Haloarcula*)和需苏打线菌属(*Natrinema*)<sup>[110,114]</sup>, 以及一些极端嗜热古菌, 如需氧热棒菌(*Pyrobaculum aerophilum*)<sup>[115]</sup>等, 都被研究证实存在反硝化功能。此外, Asgard 超门的海姆达尔古菌门(*Heimdallarchaeota*)也被证实含有编码参与反硝化的酶<sup>[116]</sup>。

反硝化过程的第一步是  $\text{NO}_3^-$  还原。许多古菌能够通过同化或异化途径还原  $\text{NO}_3^-$ , 硝酸盐异化还原(dissimilatory nitrate reduction to ammonium, DNRA)比硝酸盐同化还原(assimilatory nitrate reduction to ammonium, ANRA)更频繁<sup>[117]</sup>。绝大多数反硝化古菌仅以  $\text{NO}_3^-$  为电子受体<sup>[118-120]</sup>, 也有古菌可以同时以  $\text{NO}_3^-$  和  $\text{NO}_2^-$  为

电子受体, 例如地中海富盐菌 (*Haloferax mediterranei*)<sup>[117,121]</sup>。硝酸盐还原酶有 4 种类型, 包括 Nas、Nar、Nap 和 Nxr。研究表明, 具有 NO<sub>3</sub><sup>-</sup> 还原功能的需盐小杆菌纲 (*Halobacteria*)、热原体纲 (*Thermoplasmata*) 和嗜热多形菌纲 (*Thermoprotei*) 等均在滨海湿地地区广泛存在<sup>[92,122]</sup>。在滨海湿地红树林沉积物中也发现了深古菌门和底栖古菌目基因组中的 *nar* 基因<sup>[79,123]</sup>。此外, 产甲烷菌热自养甲烷热杆菌 (*Methanothermobacter thermautotrophicus*) 中也含有与细菌 Nas 同源的硝酸盐还原酶和基因<sup>[124]</sup>。

NO<sub>2</sub><sup>-</sup> 还原是反硝化过程的限速步骤<sup>[125]</sup>, 该过程受到 *nirK* 编码的铜亚硝酸盐还原酶 (Cu-nitrite reductase, Cu-Nir) 和 *nirS* 编码的 cd<sub>1</sub> 型亚硝酸盐还原酶 (cd<sub>1</sub>-nitrite reductase, cd<sub>1</sub>-Nir) 2 种 Nir 的催化作用<sup>[126]</sup>。反硝化古菌中也含有编码这 2 种酶的基因。例如, 乌斯古菌门<sup>[80]</sup>和广古菌门的死海盐盒菌 (*Haloarcula marismortui*) 和反硝化富盐菌 (*Haloferax denitrificans*) 含有 *nirK* 基因, 而嗜热多形菌门的 *P. aerophilum* 含有 *nirS* 基因<sup>[64]</sup>。对 *H. marismortui* 和淋病奈瑟氏球菌 (*Neisseria gonorrhoeae*) 的 *nirK* 基因编码的 Cu-Nir 进行蛋白序列分析, 结果表明其亲缘关系较近, 这可能是因为 *nirK* 基因发生了横向基因转移<sup>[127-128]</sup>。研究表明, *P. aerophilum* 中具有与膜结合的呼吸型 Nir, 该酶以甲萘酚为电子供体, 因此具有不同于细菌 cd<sub>1</sub>-Nir 的亚细胞定位和还原剂, 此外, *P. aerophilum* 中参与反硝化作用的其他还原酶也是以甲萘酚为电子供体的膜结合酶<sup>[129]</sup>。在菲茨罗伊河口, *nirS* 的丰度和多样性比 *nirK* 高, 且 *nirS* 丰度与反硝化潜能正相关<sup>[73]</sup>, 这表明河口地区 *nirS* 型反硝化菌相比 *nirK* 型更重要。

NO<sub>3</sub><sup>-</sup> 和 NO<sub>2</sub><sup>-</sup> 的还原可以与甲烷厌氧氧化进行耦合, 该过程被称为反硝化厌氧甲烷氧化 (denitrifying anaerobic methane oxidation, DAMO), 由 DAMO 细菌 (NC10 门) 和 DAMO 古菌 [anaerobic methanotrophic archaea subgroup 2d

(ANME-2d)] 参与介导<sup>[130]</sup>。与 DAMO 细菌不同的是, DAMO 古菌只能还原 NO<sub>2</sub><sup>-</sup>, 不能将产生的 NO<sub>2</sub><sup>-</sup> 进一步还原为 NO、NO<sub>2</sub> 或 N<sub>2</sub><sup>[131]</sup>。然而, DAMO 古菌可以将产生的小部分 NO<sub>2</sub><sup>-</sup> 转化为 NH<sub>4</sub><sup>+</sup>, 防止 NO<sub>2</sub><sup>-</sup> 的积累和引起毒性<sup>[132]</sup>。滨海湿地生态系统由于陆源营养物质和有机物的输入, 通常具有较高的 NO<sub>3</sub><sup>-</sup> 和 NO<sub>2</sub><sup>-</sup> 可利用性, 使其成为 DAMO 过程发生的首选生境<sup>[133]</sup>。在湿地潮间带地区沉积物中发现了 DAMO 细菌和 DAMO 古菌的共存, 且 DAMO 古菌的生物多样性高于 DAMO 细菌, DAMO 古菌的活性也略高于 DAMO 细菌<sup>[134-135]</sup>。这表明 DAMO 过程在潮间带沼泽甲烷和硝酸盐汇中的重要性, 也可能说明 DAMO 古菌在滨海湿地生态系统中的贡献比 DAMO 细菌更大。另外, 受氧气水平的影响, NC10 细菌和亚硝酸盐依赖型 DAMO 在水-沉积物界面较高, 而 ANME-2d 和硝酸盐依赖型 DAMO 则占据更深的层<sup>[134]</sup>。

NO 是 NO<sub>2</sub><sup>-</sup> 还原的产物, 在其生成后立即被 Nor 还原为 N<sub>2</sub>O。大多数反硝化细菌中 Nor 由 *norB* 和 *norC* 编码的细胞色素 b 和 c 组成, 由于其接受来自细胞色素 c 的电子, 也被称为 cNor。也有一些反硝化细菌, 如杀虫贪铜菌 (*Cupriavidus necator*), 其 Nor 以对苯二酚 (quinol) 作为电子供体, 被称为 qNor<sup>[128,136-137]</sup>。一些古菌中也含有 Nor 相关基因序列。研究表明, *P. aerophilum* 中含有 qNor 型的 Nor<sup>[115,138]</sup>, 马泽氏甲烷八叠球菌 (*Methanosarcina mazei*)<sup>[139]</sup> 和硫磺矿解糖叶菌 (*Saccharolobus solfataricus*)<sup>[140]</sup> 中也含有编码 Nor 的基因。滨海湿地中具有 Nor 的古菌主要包括乌斯古菌门、嗜热多形菌纲、甲烷微菌纲和需盐小杆菌纲等类群<sup>[80,92,122]</sup>。

反硝化过程的最后一步是将 N<sub>2</sub>O 还原为 N<sub>2</sub>, 该过程由 *nosZ* 基因编码的 Nos 催化反应。该基因广泛存在于滨海湿地, 且有研究通过宏基因组测序技术表明乌斯怀亚湾沉积物中的 *nosZ* 基因序列不仅来自细菌, 也来自古菌<sup>[141]</sup>。滨海湿地中一些古菌由于 *nosZ* 基因的缺失导致

反硝化过程并不完整, 主要以  $N_2O$  为最终产物, 如 *H. marismortui*<sup>[142]</sup>。相比之下, 其他古菌, 如需盐小杆菌纲的 *H. denitrificans* 和嗜热多形菌纲的 *P. aerophilum* 具有完整的反硝化途径<sup>[64,92,122]</sup>, 因此可以将  $N_2O$  还原为  $N_2$ 。然而 *P. aerophilum* 中形成的  $N_2O$  仍在体内积累, 主要原因是  $N_2O$  被还原的速度极其缓慢<sup>[115,136,143]</sup>。

## 2.4 硝酸盐铵化

$NO_3^-$  可以通过同化或异化还原成  $NH_4^+$ , 滨海湿地生态系统的研究主要集中在  $NO_3^-$  异化还原成  $NH_4^+$  (DNRA) 的研究<sup>[132]</sup>。该过程中  $NO_2^-$  异化还原为  $NH_4^+$  需要 *nirB* 和 *nirD* 基因编码的 Nir, 目前已经在滨海湿地沉积物中存在的索尔古菌门、深古菌门、乌斯古菌门和除奥丁古菌门(*Odinarchaeota*)外的所有 Asgard 超门中检测出 *nirB* 基因<sup>[78-80]</sup>或 Nir<sup>[144]</sup>。此外, 滨海湿地生态系统中能执行 DNRA 过程的微生物还包括化能自养型硫细菌和 DAMO 古菌<sup>[132]</sup>。 $NO_3^-$  同化还原为  $NH_4^+$  (ANRA) 的过程需要 *nirA* 基因编码的 Nir, 该基因目前已经在广古菌门和嗜热多形菌门的基因组中发现<sup>[64]</sup>。

## 2.5 有机氮代谢

有机氮代谢(organic nitrogen metabolism)主要是  $NH_4^+$  和有机氮的相互转换。硝酸盐还原和氮固定产生的  $NH_4^+$  进入细胞时, 生物体会通过特定的转运系统转运  $NH_4^+$ , 该过程需要铵转运蛋白(ammonium transporter, AMT)的作用, 然后通过谷氨酰胺合成酶-谷氨酸合成酶(glutamine synthetase-glutamate synthase, GS-GOGAT)和谷氨酸脱氢酶(glutamate dehydrogenase, GDH) 2 种途径进行有机氮代谢, 滨海湿地生态系统中具有这 2 种途径的古菌主要属于热原体门(*Thermoplasmata*)、嗜热多形菌门和广古菌门下的产甲烷菌<sup>[64]</sup>。

在 GS-GOGAT 途径中, GS 存在 3 种类型, GS II 和 GS III 只存在于真核生物或细菌中, 只有 GS I 存在于古菌中。古菌中含有编码 GS I 的

*glnA* 基因, 主要存在于广古菌门<sup>[145]</sup>。GS 在铵同化中的重要性因古菌种类而异, 在深海热球菌(*Thermococcus profundus*)和超嗜热古菌(*Pyrococcus* sp.)中未检测到 GS 活性或 GS 活性较低, 说明该反应偏向于谷氨酸的产生<sup>[146]</sup>。相比之下, 在海沼甲烷球菌(*Methanococcus maripaludis*)中无法获得 *glnA* 缺失突变株, 表明 GS 为该菌的必需酶<sup>[147]</sup>。大多数古菌的基因组都含有编码 GOGAT 小亚基或大亚基的 *gltA* 或 *gltB* 基因。大多数古菌中含有编码大亚基的 *gltB* 基因, 如 *S. solfataricus*、詹氏甲烷热球菌(*Methanocaldococcus jannaschii*)和坎氏甲烷火菌(*Methanopyrus kandleri*)<sup>[64]</sup>。此外, *Pyrococcus* sp. 中仅含有 *gltA* 基因而不含 *gltB* 基因<sup>[148]</sup>。

在 GDH 途径中, GDH 既催化谷氨酸的氧化脱氨, 又催化铵还原为 2-酮戊二酸。截至目前, 嗜热多形菌门和广古菌门的多数菌中都检测出了编码 GDH 的 *gdhA* 基因, 如激烈火球菌(*Pyrococcus furiosus*)、岸边热球菌(*Thermococcus litoralis*)、*T. profundus* 和 *S. solfataricus* 等<sup>[64]</sup>。研究中的大多数 *Pyrococcus* sp. 都表达出高水平的 GDH, 这表明 GDH 在极端微生物的铵同化中起重要作用<sup>[149]</sup>。另外, 由于 *Pyrococcus* sp. 的 GDH 同时使用还原型烟酰胺腺嘌呤二核苷酸(reduced nicotinamide adenine dinucleotide, NADH)和还原型烟酰胺腺嘌呤二核苷酸磷酸(reduced nicotinamide adenine dinucleotide phosphate, NADPH), 其性质与真核生物更相似, 而非细菌<sup>[149]</sup>。蛋白质序列分析表明, 来自 *P. furiosus* 和美未氏火球菌(*Pyrococcus horikoshii*)的 GDH 与中温细菌的关系比与嗜热古菌 *S. solfataricus* 或嗜盐古菌盐沼需盐小杆菌(*Halobacterium salinarum*)的关系更密切<sup>[149]</sup>, 这表明细菌和古菌在进化过程中可能发生 *gdhA* 基因之间的横向转移。

## 2.6 氮转运

在氮循环中, 除了  $NH_4^+$  可以进入生物体外,  $NO_3^-$  也可以通过硝酸盐转运蛋白(nitrate transporter, NRT)进行转运。NRT 在细菌中有 2 种

类型<sup>[5]</sup>: 一种是 ATP 依赖的 ABC 型转运蛋白 (ATP-binding cassette transporter), 该蛋白由 1 个完整的膜亚基、1 个细胞质 ATP 结合元件和 1 个周质底物结合蛋白组成; 另一种是依赖于质子推动力的单体 NarK 型转运蛋白 (NarK-type transporter)。在古菌中仅存在第一种 NRT, 该蛋白由 *NrtABC* 基因编码。在滨海湿地中, 广古菌门的沃氏富盐菌 (*Haloferax volcanii*)<sup>[150]</sup>、*P. furiosus*<sup>[138]</sup> 以及热原体纲的嗜酸热原体 (*Thermoplasma acidophilum*)<sup>[151]</sup> 和火山热原体 (*Thermoplasma volcanium*)<sup>[152]</sup> 等古菌中均发现了硝酸盐转运蛋白的存在。

### 3 古菌对 N<sub>2</sub>O 减排的作用

N<sub>2</sub>O 是一种重要的温室气体, 其全球增温潜势 (global warming potential, GWP) 是 CO<sub>2</sub> 的 265 倍<sup>[153]</sup>。滨海湿地的氮循环对温室气体 N<sub>2</sub>O 的产生与排放, 乃至全球氮储库的收支及气候变化都发挥着重要作用<sup>[50]</sup>。为应对由温室气体排放导致的全球变暖问题, 参与滨海湿地氮循环的古菌有望成为减缓气候变化的重要生物技术手段。古菌通过 2 种主要机制减少 N<sub>2</sub>O 的排放: 一是抑制 N<sub>2</sub>O 的生成, 二是促进 N<sub>2</sub>O 的还原。

滨海湿地中的 N<sub>2</sub>O 具有多种产生途径, 古菌参与的过程主要包括反硝化过程和硝化过程。硝化过程中 N<sub>2</sub>O 的来源为 NH<sub>2</sub>OH 不完全氧化为 NO<sub>2</sub><sup>-</sup> 的副产物以及硝化菌的反硝化过程, 该过程由 AOA 和 AOB 共同参与<sup>[154-155]</sup>。研究表明, 氨氧化产生的 N<sub>2</sub>O 与土壤 pH 呈正相关, 这是由于生态位分化: AOB 的丰度随着土壤 pH 的增加而增加, 而 AOB 相较于 AOA, 每氧化 1 mol 的 NH<sub>4</sub><sup>+</sup> 会产生更多的 N<sub>2</sub>O<sup>[156]</sup>。微生物通过 N<sub>2</sub>O 还原酶将 N<sub>2</sub>O 还原为 N<sub>2</sub>, 是目前生物圈中已知的唯一 N<sub>2</sub>O 汇。NosZ 蛋白由 *nosZ* 基因编码, 分为 2 个进化分支<sup>[157]</sup>: 进化支 I (clade I) 主要存在于广古菌门, clade I 的微生物基因组中 83% 还具有 Nir 基因, 更可能是完全反硝化基因; 进化支 II (clade II) 中 51% 的微生物表现为

非反硝化作用的 N<sub>2</sub>O 还原菌, 即可以作为真正的 N<sub>2</sub>O 汇而不具有产生 N<sub>2</sub>O 的潜力<sup>[158]</sup>。有研究将 clade II 的 *nosZ* 群落与减少的潜在 N<sub>2</sub>O 排放联系起来, 也支持了 clade II 的 *nosZ* 群落对 N<sub>2</sub>O 汇的能力这一观点<sup>[159-160]</sup>。此外, 沉积物 pH 对 Nos 酶的活性具有重要影响, 较低的 pH 会抑制 Nos 酶的活性, 从而促进 N<sub>2</sub>O 的排放<sup>[161-162]</sup>, pH 值的调整在控制 N<sub>2</sub>O 排放方面起着重要作用。Lv 等<sup>[163]</sup> 的研究表明, 生物炭的引入可增强 DAMO 古菌和细菌的有效富集, *Candidatus Methanoperedens* 的丰度从 9.8% 增加到 16.1%, 增强了 DAMO 古菌介导的反向甲烷生成和硝酸盐还原过程。生物炭可能作为电子受体, 通过电子穿梭机制接受电子并将其转移到 NC10 细菌将 NO<sub>2</sub><sup>-</sup> 还原为 N<sub>2</sub><sup>[164]</sup>。这一过程显著提高了 NO<sub>3</sub><sup>-</sup> 和 NO<sub>2</sub><sup>-</sup> 的还原效率, 为 N<sub>2</sub>O 减排提供潜在途径。

针对滨海湿地中 N<sub>2</sub>O 的减排, 以下是几种可能的策略 (图 5)。(1) 提高 AOA/AOB 的丰度比。研究表明, 增加 AOA 相对于 AOB 的丰度比, 可以降低硝化作用中的 N<sub>2</sub>O 排放。可以通过使用硝化抑制剂, 如 3,4-二甲基吡唑磷酸盐 (3,4-dimethylpyrazole phosphate, DMPP), 选择性抑制 AOB 的活性, 并延缓硝化速率, 从而减少 N<sub>2</sub>O 的排放<sup>[165-166]</sup>。同时, 添加  $\alpha$ -酮酸 (如丙酮酸和草酰乙酸) 可以通过缓解 H<sub>2</sub>O<sub>2</sub> 的毒性, 增强 AOA 的氨氧化活性。尽管  $\alpha$ -酮酸不会直接促进 AOA 的异养生长, 但它通过改善 AOA 的环境条件, 间接提高了其氨氧化活性<sup>[167]</sup>。此外, 在实际应用中需要考虑微生物群落的复杂性。 $\alpha$ -酮酸的添加可能对其他微生物群体产生影响<sup>[167]</sup>, 因此需要在实际操作中控制  $\alpha$ -酮酸的浓度, 或结合其他策略, 以确保其能够更有针对性地促进 AOA 的生长, 而不会过度刺激其他微生物的生长。(2) 接种来自 clade II 的 N<sub>2</sub>O 还原菌作为潜在的 N<sub>2</sub>O 减排策略, 理论上有助于减少 N<sub>2</sub>O 排放。Clade II 中的 N<sub>2</sub>O 还原菌如脱卤厌氧黏杆菌 (*Anaeromyxobacter dehalogenans*), 已被证明

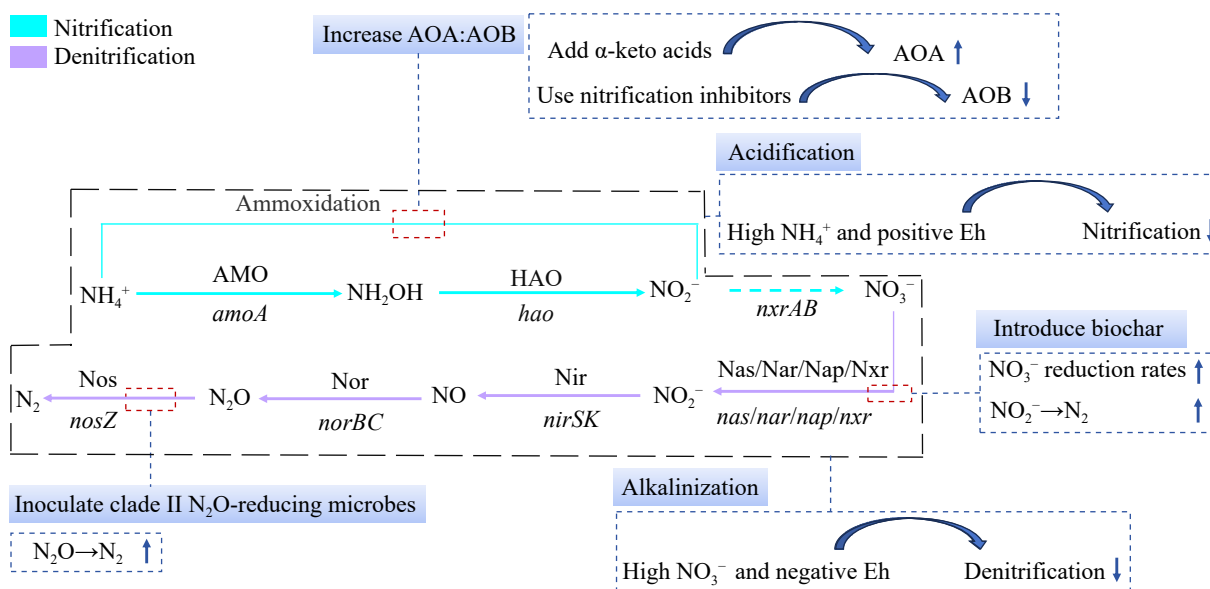


图5 滨海湿地生态系统 $\text{N}_2\text{O}$ 减排策略

Figure 5 Strategies related to  $\text{N}_2\text{O}$  emission reduction in coastal wetland ecosystems.

能够通过化学反硝化过程将  $\text{N}_2\text{O}$  还原为  $\text{N}_2$ <sup>[168]</sup>。然而, 这些菌株是否能在滨海湿地这一复杂的生态系统中成功存活并发挥作用仍需更多实验验证。考虑到滨海湿地的微生物群落复杂性, 建议未来进行实地试验以评估这些菌株的生存能力和  $\text{N}_2\text{O}$  还原效能, 并研究其对环境条件(如盐度、pH、温度等)的适应性。(3) 调节沉积物 pH。由于 pH 的改变对硝化作用和反硝化作用中  $\text{N}_2\text{O}$  排放的影响是相反的, 在实际应用中应根据具体情况选择调整策略。当沉积物中  $\text{NH}_4^+$  含量较高且氧化还原电位(Eh)值为正时,  $\text{N}_2\text{O}$  的产生主要源于硝化作用<sup>[169-170]</sup>, 此时通过酸化处理可降低  $\text{N}_2\text{O}$  的排放; 而当沉积物中  $\text{NO}_3^-$  含量较高且 Eh 为负时, 反硝化作用成为  $\text{N}_2\text{O}$  排放的主要来源<sup>[171]</sup>, 这时可以通过添加石灰进行碱化处理, 以减少  $\text{N}_2\text{O}$  的生成。(4) 引入生物炭。生物炭能够显著上调 DAMO 古菌的功能基因表达, 增强其硝酸盐还原速率, 同时提供良好的载体和微环境, 促进 DAMO 古菌与细菌的有效富集与协同作用<sup>[164]</sup>, 为温室气体减排提供潜在途径。滨海湿地古菌通过多种机制在  $\text{N}_2\text{O}$  减排中扮演

着重要角色, 采取适当的策略可有效缓解温室气体  $\text{N}_2\text{O}$  对气候变化的影响。然而, 在实际应用中需要进行更广泛的实地试验和微生物群落监测, 进一步验证这些策略在滨海湿地生态系统中的效果, 特别要考虑环境变量和微生物群落的复杂性。

## 4 总结与展望

古菌作为地球生物界三大域之一<sup>[15]</sup>, 是滨海湿地生态系统的重要组成部分<sup>[23]</sup>, 然而其生态功能长期被忽视。本文系统梳理了滨海湿地中古菌群落结构及其在氮循环中的关键作用, 并对基于古菌群落减缓  $\text{N}_2\text{O}$  排放的可行性进行了讨论。尽管古菌在生物地球化学循环中扮演着不可或缺的角色, 但其作用机制和功能探讨仍存在诸多未解之处。同时, 海岸带生态修复(例如牡蛎礁生态修复)对古菌群落及其在氮循环中的作用影响也值得关注<sup>[50]</sup>。结合当前研究动态和发展趋势, 未来研究可聚焦以下几个方面。

(1) 未分离古菌在氮代谢中的功能解析。目前, 许多参与氮循环的古菌尚未被成功分离和

培养, 限制了对其代谢途径和功能潜力的深入理解<sup>[172-174]</sup>。未来需结合共培养、直接种间电子传递、单细胞分离、高通量培养和原位环境模拟等技术, 以提升古菌的分离效率并探索其在氮循环中的功能潜力。

(2) 多组学技术在氮循环研究中的综合应用。目前, 古菌功能研究主要依赖基因组数据<sup>[50]</sup>或蛋白质组数据<sup>[175]</sup>, 较少实现两者的整合。未来需结合基因组学、转录组学、蛋白质组学等多组学技术, 系统解析古菌的氮代谢基因及其表达调控机制, 揭示其在滨海湿地生态系统中的具体作用机制。

(3) 古菌与细菌在氮循环中的功能对比研究。滨海湿地生态功能的微生物研究常将细菌与古菌混合分析, 古菌的独立贡献仍未被量化<sup>[5,39,50]</sup>。未来可通过原位实验及功能分析, 比较古菌与细菌在氮循环关键过程(如氨氧化、反硝化等)中的贡献度, 明确古菌的生态地位与重要性。

(4) 环境因子对古菌氮代谢功能的综合影响。滨海湿地环境复杂多变, 理化因子(如盐度、温度、pH、氮含量等)、植被类型(互花米草、芦苇等)、季节变化以及沉积物深度等因素都会对古菌的氮代谢功能产生重要影响<sup>[5,50,176]</sup>。然而, 目前对于这些环境因素如何共同调控古菌在氮循环中的作用机制尚不完全明了。未来研究应通过综合的野外调查和实验室模拟, 探讨多种环境因素在不同空间和时间尺度的共同作用下对古菌氮代谢功能的影响, 为滨海湿地氮循环的精准调控提供理论依据。

随着理论基础的不断积累和技术手段的进步, 古菌在滨海湿地生态系统氮循环中的作用将会得到更深入的揭示。这不仅有助于填补当前的研究空白, 也将为全球氮循环变化及 N<sub>2</sub>O 排放对气候影响的精准预测提供科学依据。

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## 作者利益冲突公开声明

作者声明不存在任何可能会影响本文所报告工作的已知经济利益或个人关系。

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