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异养硝化好氧反硝化菌的研究方法及脱氮增强策略研究进展

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摘要：随着水体氮污染问题日益严峻,异养硝化好氧反硝化(HN-AD)菌因其能实现同步硝化反硝化而备受关注.该技术突破了传统分段处理限制,兼具高效、适应性强等优势,但实际应用仍面临脱氮不稳定、菌群稳定性差及代谢机制不明等挑战.本文系统梳理了 HN-AD 菌的研究方法现状,包括功能菌的分离筛选及脱氮影响因素的研究手段,探讨了现代组学技术在揭示其代谢途径中的应用潜力.重点评述了 6 种关键强化脱氮的技术:细菌固定化,多菌种共培养,高效菌株选育,中间产物调控,电子传递优化及群体感应干预,阐明了其提升脱氮效率的作用机制.最后,对 HN-AD 菌的未来研究方向进行了展望,以期为该技术从实验室研究向工程化应用的转化提供一定参考.

关键词：异养硝化；好氧反硝化；研究方法；强化脱氮；污水处理
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Research progress on heterotrophic nitrification-aerobic denitrification bacteria: methods and enhanced nitrogen removal strategies. CHE Xiang-qian[1], LIN Na[1], JIN Xin-min[1], YANG Qian-gang[1], LIANG Sheng-na[1], FENG Fang[2], QIN Fen-ju[2*], ZHANG Wen-chao[2**] (1.Lukong Environmental Protection Technology Co., Ltd., Suzhou 215000, China；2.School of Chemistry and Life Sciences, Suzhou University of Science and Technology, Suzhou 215009, China). *China Environmental Science*, 2025,45(12)：6617~6630

Abstract：With the escalating problem of nitrogen pollution in aquatic ecosystems, heterotrophic nitrification-aerobic denitrification (HN-AD) bacteria have gained considerable attention due to their capability for simultaneous nitrification and denitrification. This technology presents benefits over conventional segmented treatment, such as high efficiency and strong adaptability. Nevertheless, there are still issues with the actual applications of HN-AD bacteria, such as unstable nitrogen removal, poor microbial community stability, and uncertain metabolic mechanisms. In this paper, the research methods applied in HN-AD studies, encompassing the techniques for isolation, screening of functional strains, as well as factors influencing nitrogen removal, were comprehensively reviewed. The application of modern omics technologies in elucidating HN-AD metabolic pathways was also discussed. Six key strategies for nitrogen removal enhancement were analyzed in detail: bacterial immobilization, co-cultivation of multiple strains, breeding of high-efficiency strains, regulation of intermediate metabolites, optimization of electron transfer, and quorum sensing interference. Furthermore, their underlying mechanisms for improving nitrogen removal efficiency was also systematically elucidated. Finally, the prospective research directions for HN-AD bacteria were put forward, aiming to provide valuable insights for translating this technology from laboratory research to engineering applications.

Key words：heterotrophic nitrification；aerobic denitrification；research methods；enhanced nitrogen removal；wastewater treatment

随着经济社会的飞速发展,工业、农业和生活污水中氮含量急剧增加,严重破坏水环境生态系统.过量的氮对水生生物具有直接毒性,还会导致水体富营养化,危及生态系统稳定,并对人类健康造成威胁[1-3].因此,高效去除污水中的氮刻不容缓.目前常用的脱氮方法包括物理法、化学法和生物法,其中生物脱氮具有经济和二次污染小等优势,已成为应用最广泛的脱氮方法[4-5].然而,传统的生物脱氮技术包括自养硝化和厌氧反硝化两个过程,由于二者对有机底物和溶解氧的需求截然不同,导致脱氮必须分段进行,工艺复杂,成本高且反应耗时[6-7].

近年来,具有异养硝化和好氧反硝化(HN-AD)能力的细菌因展现出独特的应用潜力而成为生物脱氮领域的研究热点[8-10].这类细菌可在有氧条件下于单一反应器内利用有机碳实现同步硝化/反硝化过程,将氨氮转化为含氮气体,从而达到脱氮目的[11].

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与传统自养硝化菌和厌氧反硝化菌相比,HN-AD 菌的优势在于:①同时完成硝化和反硝化反应,节省占地面积和投资成本;②来源丰富,种类多样,耐受性较好;③生长速率快,脱氮速率较高;④减少 pH 值调节成本,产生的酸和碱可相互中和;⑤几乎无中间产物积累[9,12].自 1983 年 Robertson 首次分离出好氧反硝化细菌以来,世界各地的学者在HN-AD菌的筛选、脱氮机制研究和实际应用方面进行了广泛研究.目前已从各种环境中筛选到多种 HN-AD 菌,如不动杆菌(*Acinetobacter* sp.)[13-15],假单胞菌(*Pseudomonas* sp.)[16-17],粪产碱杆菌(*Alcaligenes faecalis*)[18-19]等.由于 HN-AD 菌种类繁多,不同菌株脱氮过程的催化酶系及编码基因各不相同,其氮代谢过程非常复杂.

当前,对HN-AD菌的研究多集中于实验室阶段,虽然部分菌株在反应器中表现出良好的脱氮效果[20-21],但尚未达到大规模实际应用水平,主要原因在于菌株代谢调控、环境因素影响、菌群稳定性等引起的脱氮效率问题.为此,研究人员开发了多种手段,如外源添加药剂、微生物固定化、菌群协作等[22-24].目前,关于 HN-AD 功能菌的研究综述多聚焦于菌株分离筛选、脱氮代谢路径与关键酶系统,以及脱氮过程的影响因素等方面,而针对该类菌脱氮效果的强化策略仍缺乏系统性总结.本文从 HN-AD 菌常用的研究方法、强化脱氮的手段等方面评述了近年研究成果,并对今后的研究方向进行展望,以期为深入了解 HN-AD 菌的代谢机制,提高其实际应用效果提供参考.

1 HN-AD 菌脱氮的研究现状及瓶颈

HN-AD 菌具有多样化的氮代谢路径.研究表明,HN-AD 菌可能通过同化、异化、硝化、反硝化等不同生物转化途径分解氮源[25].多条氮代谢路径也可在同一株菌中同时出现.如 Huang 等[26]证明 *Pseudomonas putida* Y-9 在好氧条件下可同步进行硝酸盐同化、异化硝酸盐还原成铵和反硝化三重代谢途径,这种特性赋予其强大的环境适应性.通常,HN-AD 菌的好氧同化过程可将废水中的有机物和氮素同时去除,将不同形式氮素转化为细胞有机氮[27],其同化效率受菌属类别和培养条件等影响.而且,该途径虽能暂时去除水体中的氮,但可能因菌体死亡后氮的再释放导致脱氮不彻底.通过异化作用,HN-AD 菌可以将水体中的无机氮素转化为含氮气体(NO、N_2O、N_2),从而将无机氮素有效脱除,但其易受环境条件(C/N、溶解氧等)限制,导致脱氮效率不稳定[12].高 C/N 可能促进同化作用(菌体生长优先),而低 C/N 可能更依赖异化反硝化,但后者可能因碳源不足导致代谢受阻,总脱氮效率下降[9].多数菌种的最适 C/N 为 8~15,如 *Acinetobacter* sp. ND7 的最适 C/N 为 8[28], *Ralstonia pickettii* J4 在 C/N=15 时 NH_4^+-N 去除效果最佳[29]. HN-AD 菌脱氮效率的变化本质上是菌株功能异质性与环境互作复杂性的体现,需通过机制研究与工艺优化协同提升.

在复杂水环境中,往往存在多种污染物,HN-AD 菌在实现异养硝化和好氧反硝化脱氮的同时,还可以实现多种新污染物的协同去除,如一些毒性有机污染物、磷、金属离子等.HN-AD 菌生长快,通常需要有机物提供碳源,在去除氮素的同时实现有机物的降解.如 *Diaphorobacter* sp. PDB3 能利用有机污染物苯酚作为碳源,在优化条件下可使苯酚降解率和总有机碳降解率达 90%以上,氨氮实现全部去除[30].苯酚浓度过高,则会对菌产生抑制作用.另有研究证明持久性有机污染物布洛芬也可以作为脱氮细菌的碳源,布洛芬与总氮的同步去除结果表明二者去除效率高度相关[31].部分水体,如水产养殖废水、制药厂废水中常有抗生素等有机药物分子残留.Liang 等[32]分离得到的菌株 *Achromobacter* sp. JL9,可在低 C/N 废水中展现出优异的磺胺甲恶唑(SMX)降解与氮转化协同能力,SMX 降解速率常数与 C/N、SMX 初始浓度及溶解氧浓度呈显著相关性.值得注意的是,部分 HN-AD 菌还能实现单一反应器中的同步脱氮除磷,这一发现为解决传统工艺中的微生物种群竞争和丰度变化导致的脱氮除磷效率波动问题提供了新的思路.Yang 等[33]分离鉴定出一株具有高效异养硝化、好氧反硝化及聚磷能力的新菌株 *Pseudomonas putida* NP5,并实现了关键氮磷代谢酶的成功表达.目前已知的具有同步脱氮除磷能力的 HN-AD 菌主要涉及假单胞菌属(*Pseudomonas*)、副球菌属(*Paracoccus*)和不动杆菌属(*Acinetobacter*)等[10,33-34],但其具体氮磷代谢机制及代谢网络调控尚不明确.另外,Junfeng Su 团队还筛选到多株兼具 HN-AD 和生物矿化能力的菌株,

实现了氨氮、磷酸盐、Ca^{2+}或重金属离子的同步去除[14,35].

HN-AD 菌作为强化菌株在污水处理系统中已展现出一定的应用潜力.研究表明,通过向移动床生物膜反应器(MBBR)中直接接种 HN-AD 菌种,可使总氮去除率从 30.4%显著提高至 80.7%[21].将 *Acinetobacter* sp. T1 接种至猪场废水处理的好氧池中时,出水化学需氧量 COD、NH_4^+-N 和总氮的去除率均明显提升[36].尽管 HN-AD 菌的前景广阔,但其实际应用目前尚未实现大规模推广,其瓶颈和核心难点主要在于:(1)代谢机制与调控的复杂性:代谢途径多样,关键酶活性调控难度大[37].(2)环境适应性挑战:实际污水成分复杂,重金属、盐分等可能抑制菌群活性,同时脱氮活性且易受环境条件影响(C/N、溶解氧、pH 值等)[8,38-39].(3)菌群稳定性问题:低 C/N 条件下,土著微生物与 HN-AD 菌的碳源竞争加剧,导致竞争抑制,而且生物膜形成能力差的菌株易流失,也难以维持稳定的菌群结构[7,40].以上多种因素共同影响了 HN-AD 菌在应用中的脱氮稳定性,因此需从脱氮机理解析和实际应用优化两方面协同推进,以推动其规模化应用.

2　HN-AD 菌的研究方法

2.1　HN-AD 功能菌的分离与筛选方法

富集培养是获得纯培养物的重要步骤.为有效分离特定细菌,需设法使其在混合菌群中占有足够的比例,控制好营养条件.实际操作中,通常从活性污泥或底泥等富含目标菌的生境取样,经预处理之后接种至富集培养基.随后,将其经梯度稀释后涂布于固体分离培养基上,多次分离纯化,获得 HN-AD 细菌.分离培养基包括异养硝化培养基(NM)和好氧反硝化培养基(DM),固体分离培养基中一般加入 1%溴百里酚蓝(BTB)作为指示剂,选取出现蓝色晕圈的菌落[41].对获得的菌种进行形态学和分子生物学鉴定:包括菌落形态观察,革兰氏染色鉴定,并通过电镜分析获得细菌的微观形态特征;扩增细菌的 16S rRNA 基因,测序,在 NCBI 数据库中进行 BLAST 相似性比对分析,确定其种属名,采用 MEGA 软件构建系统发育树[42-43].

2.2　脱氮过程的影响因素研究方法

HN-AD 菌的脱氮性能评价依赖对不同氮指标的测定,包括 NH_4^+-N、NO_3^--N、NO_2^--N 和总氮(TN).以上指标的测定均依据《水和废水监测分析方法》采用分光光度法完成[41,44].

为了实现 HN-AD 菌的最大脱氮效率,有必要对其培养环境中的单因素变量进行优化,这一任务可以通过统计方法来完成.响应面方法(RSM)作为一种经验统计建模技术,因其能够有效分析多变量之间的交互作用并预测出最优条件[45],常被用于工艺优化研究.例如,Qiao 等[46]采用三水平(−1、0、1)Box-Behnken 因子设计研究了氮浓度、温度和溶解氧对细菌脱氮速率的影响,通过分析其二次效应和双向交互作用,预测了最佳脱氮条件,结果发现在最优参数下,硝态氮的去除速率为 11.25mg/(L·d),与模型预测值(11.44mg/(L·d))高度吻合.类似地,Zhang 等[47]成功使用 RSM 法优化了固定化菌株 *Paracoccus* sp. QD-21 去除氨氮的条件,优化后的参数为振荡速率 147.31r/min,温度 36°C, C/N 8.72, pH 8.此外,菌株 *Alcaligenes faecalis* WT14 在 RSM 预测的最佳条件下,可实现 55.9mg/(L·d)的氨氮去除率[18].需要注意的是,该方法预测的准确性取决于实验设计的合理性和数据的质量.

生物脱氮的动力学研究对于理解菌株的生理特性及脱氮过程的机制至关重要[48],其主要关注微生物在脱氮过程中的生长、底物降解、产物生成以及环境因素对这些过程的影响.如 Logistic 模型常用于描述细菌生长动力学[49-50],Gompertz 模型用于拟合细菌对氮素的去除过程,以确定底物浓度与去除时间之间的关系[43,49].利用修正的 Gompertz 模型拟合 HN-AD 菌 *Pseudomonas aeruginosa* SNDPR-01 对氮磷的去除过程,根据拟合获得的细菌对氮素的最大降解速率和迟滞时间等参数,可推断该菌株的异养硝化和好氧反硝化过程与磷酸盐代谢相关[43].底物浓度对异养硝化好氧反硝化整体性能产生显著影响.由于底物过量引起的抑制可通过 Haldane 基质抑制动力学模型来描述[51-52].汪诺等[51]采用 Haldane 模型,拟合了不同氨氮浓度对菌株生长及基质降解特性的影响,结果发现随氨氮浓度升高,菌株的适应期延长,最大比生长速率降低,表明高氨氮对菌株具有抑制作用.而单一底物的低浓度限制过程可用 Monod 方程来描述,用于计算底物的半饱和浓度和最大底物利用

率[46].在该模型中,仅将 NH_4^+-N 视为底物,但实际上 HN-AD 菌同时利用氮源和碳源,二者均被视为限制性底物.此时单一底物的 Monod 模型可能无法精确预测底物降解性能.因此,Zheng 等[53]进行了修正,采用多底物动力学模型(如 Contois-Contois 模型,Monod-Contois 模型)来描述细胞生长及不同底物的生物降解过程,从而为菌株在实际废水处理中的应用提供具体指导.

2.3 功能基因与分子机制的研究方法

HN-AD 细菌种类繁多,其产酶体系存在一定差异,代谢途径也呈现多样性,导致脱氮机制较为复杂,因此其作用机制尚未完全阐明.目前,主要通过测定氮循环中间产物或终产物、关键酶活性,相关基因扩增,及多组学技术来研究其脱氮途径.

关键酶活性测定可帮助从酶学角度理解其脱氮途径[27,54].HN-AD 菌脱氮过程中的关键酶主要包括氨单加氧酶(AMO)、硝酸盐还原酶(NAR)、羟胺氧化还原酶(HAO)和亚硝酸还原酶(NIR)等,分别通过测定反应混合物中氯化铵的氧化、硝酸盐还原为亚硝酸盐、羟胺和亚硝酸盐的量来确定[55-56].氮同位素示踪技术可帮助进一步明确氮转化路径.如赵等[54]利用高精度的气相色谱－同位素比值质谱技术(GC-IRMS)同位素示踪技术,发现菌株 MP15 可通过硝化作用将 NH_4^+-N 转化为 $^{15}N_2O$.

一些研究通过基因特异性聚合酶链式反应(PCR)扩增鉴定了参与硝化和反硝化的部分基因(如 *nirS*、*nirK*、*hao* 和 *napA*)[28],但 PCR 扩增未获得这些常见基因并不代表其不具有 HN-AD 能力,可能存在新基因或替代的氮代谢途径,因此需要结合其他方法全面分析脱氮机理.组学技术(包括基因组学、转录组学、蛋白质组学和代谢组学)在 HN-AD 菌的研究中发挥了重要作用,为揭示其代谢机制、功能基因表达、蛋白质功能及代谢网络提供了全面的工具和方法.基因组学技术通过对 HN-AD 细菌的全基因组测序和注释,可鉴定与氮代谢相关的功能基因,分析其代谢途径,如硝化、反硝化、同化硝酸盐还原等,还可以揭示不同菌株之间的功能差异和进化关系.比如对 *Marinobacter alkaliphilus* SBY-1 进行全基因组测序,注释,识别出主要的氮代谢功能基因,并预测其氮代谢途径为:NO_3^--N→NO_2^--N→NO→N_2O → N_2[57].对一株克雷伯氏菌(*Klebsiella* sp.)的基因组分析揭示了可能参与氮同化和异化途径的基因,并通过实时定量 PCR(qRT-PCR)分析了不同氮源条件下基因表达水平的变化[58].

转录组学通过分析基因的表达水平,揭示了 HN-AD 细菌在不同环境条件下的基因调控网络[22,59-60].Yang 等[22]通过转录组分析发现群体感应信号分子影响硝化、反硝化基因(*amo*, *nas*, *nir* 等)表达.采用 RNA-Seq 转录组分析技术鉴定了 *Pseudomonas aeruginosa* P-1 对 Cd^{2+}和 Pb^{2+}胁迫响应的机制及关键基因,发现参与双组分系统和膜转运蛋白的差异表达基因上调[59].蛋白质组学常用于鉴定与氮代谢相关的关键酶及环境胁迫下的蛋白质表达变化[61-62].如 Ma 等[61]根据蛋白组分析结果详细阐述了磺胺甲恶唑对细菌相关通路的抑制及细菌的适应性策略,为理解细菌在抗生素压力下的响应机制提供了重要参考.Zhang 等[63]利用代谢组学分析揭示了与氨去除相关的代谢物,证明菌株单培养与共培养两种系统之间存在显著的代谢差异.整合代谢组学、蛋白质组学和 RNA 干扰分析,发现共培养系统的 HN-AD 过程与吲哚乙酸(IAA)密切相关.因此,多组学联合分析可以帮助更全面地揭示 HN-AD 菌的氮代谢机制[64].

3 HN-AD 菌的脱氮增强策略

3.1 微生物固定化

微生物固定化是解决菌株定殖难、易流失、适应时间长、碳源不足等问题的有效方法.该技术通过吸附、共价结合、交联、膜封装、包埋等方法将微生物固定到载体上[65],为微生物的生长和繁殖提供附着位点[66].固定化载体一般可分为无机载体、有机载体和复合载体.近年来,HN-AD 菌的固定化技术研究取得了一定进展,如具有较大比表面积的生物炭[67];具有磁性和生物相容性的纳米 Fe_3O_4[68];具有良好机械强度和化学稳定性的聚乙烯醇等高分子材料[69],均被成功应用,显著提升了脱氮稳定性.考虑到天然和合成有机聚合物的混合物具有更好的机械强度和扩散性优势,Shi 等[13]将固态碳源玉米芯和 HN-AD 菌 *Acinetobacter Pittii* SY9 共包埋于聚乙烯醇-海藻酸钠微胶囊中,并填充至序批式反应器(SBR).结果发现该多孔微胶囊能有效延缓碳源释放(可持续 120d),同时系统

对总氮的去除率超过 90%.即使在 C/N 低至 2.8 的情况下,也能确保生物微胶囊 SBR 的高 HN-AD 性能,具有广阔的应用前景.聚乙烯醇-海藻酸钠复合物载体具有多孔结构,利于微生物附着,外部结构紧密,可有效防止微生物流失.在实际废水处理中,应用附着 HN-AD 菌株 QD-21 的载体使氨氮去除率提高了 63.31%[47].

固定化还可以提高细菌对环境因子的耐受能力.如硅藻土固定菌株后,由外至内形成了溶解氧梯度,内部微氧区缓解了氧气对硝酸盐还原酶的抑制,使固定化菌株对高溶解氧的耐受能力显著高于游离菌,脱氮效率更高[73].选择载体时,需综合考虑材料特性、可获得性、成本及环保性等因素.Li 等[70]采用静电纺丝技术制备纳米纤维载体,与游离细菌相比,固定化的 HN-AD 细菌生长更快,同步硝化-反硝化效率更高,且可回收利用(图 1(a)).该方法制备简便、快速、易修饰,载体比表面积大,孔隙连通,生物相容性好,应用潜力显著.

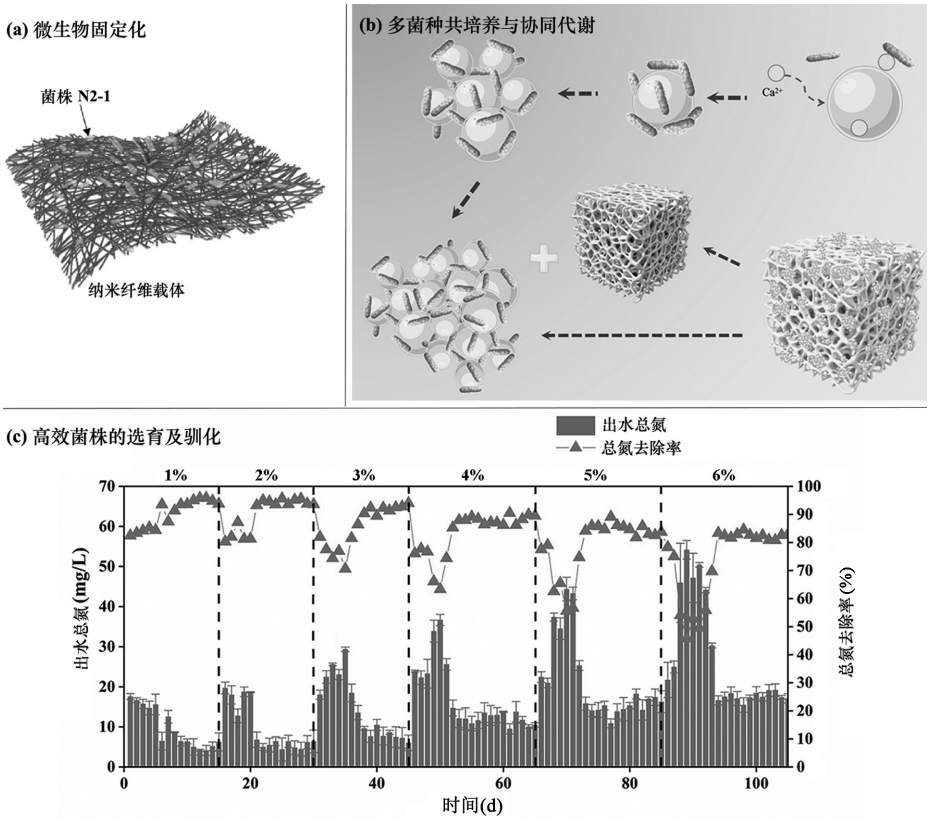


图 1　不同措施强化 HN-AD 脱氮的研究实例

Fig.1　Research cases of different strategies to enhance HN-AD nitrogen removal

(a)微生物固定化: 以纳米纤维为载体负载HN-AD菌,表现出高效同步硝化-反硝化能力(引自文献[70],经Elsevier出版社许可使用);(b)协同代谢: HN-AD菌与原壳藻形成的菌-藻共生系统,可同时高效去除 NH_4^+-N, PO_4^{3-}-P、总氮和 Ca^{2+}(引自文献[71],经 Elsevier 出版社许可使用);(c)驯化: 梯度盐度驯化对系统总氮去除的影响(引自文献[72],经 Elsevier 出版社许可使用).

部分载体除了作为吸附剂和微生物附着体外,还可以通过其自身的物理或化学特性强化 HN-AD 菌脱氮性能.如低温椰壳生物炭可加速电子传递,促进酶与氮磷底物之间的氧化还原反应,这是提高复合 HN-AD 菌氮磷去除效率的重要原因[10].生物炭通过提供成核点促进了好氧污泥颗粒化,增强了微生物多样性,从而减轻了有毒化合物对硝化细菌和反硝化细菌的抑制作用,使反应器的稳定性和污染物去除性能得到了改善[67].Ma 等[74]将茶生物炭、纤维素和层状双氢氧化物(LDH)制备成复合材料,然后与菌丝球结合形成复合菌丝球,用于固定 HN-AD 菌株 Y1 和纤维素降解菌株 ZY7,其中纤维素用于提供辅助碳源,其他材料具有高生物相容性和高吸附容量等优点,支持细菌高效脱氮除磷.

3.2　多菌种共培养与协同代谢

与单一菌株相比,混合菌株往往可通过菌株间

的协同作用,提高其环境适应性,从而在实际应用中使整个微生物群体更稳定[75].细菌种间交流可以增强生物量产量和胞内酶活性,并且混合细菌群落的多样化代谢途径和能力可能促进更彻底的氮去除[46,67,76-77].研究表明,接种HN-AD菌群可使移动床生物膜反应器(MBBR)的启动周期从 39d 大幅缩短至 15d,氨氮耐受浓度由 200mg/L 显著提升至1000mg/L,总氮去除率从 30.4%提高至 80.7%[21].实际污水环境(如垃圾渗滤液[77]、海水养殖废水[78]、生活废水[76]、活性污泥等)以其多样的微生物群落、高氮含量和复杂的环境条件为特征,不仅为 HN-AD 菌提供了天然的富集来源,还确保了菌株的环境适应性.当然,不同生态系统中微生物优势种属及之间的共存模式对氮转化的贡献也存在差异[79].Huang 等[78]从海水养殖废水中分离鉴定了 25 种新的嗜盐 HN-AD 细菌,发现 *Marinomonas communis* 与 *Halomonas titanicae*、*Marinomonas communis* 与 *Cobetia marina* 等组合在形成细菌群落时,因种间共存与合作,表现出比单一物种更优越的脱氮效率、环境适应性和生物量生产能力.枯草芽孢杆菌(*Bacillus subtilis*)、施氏假单胞菌(*Pseudomonas stutzeri*)和红球菌(*Rhodococcus* sp.)的协同作用显著提升了生活污水中的总氮和有机碳去除效率[76].Chen 等[2]将分离自化工废水和养猪废水的 HN-AD 混合菌进行了多代驯化,优化群落结构,使不动杆菌属的丰度从16.9%增加到 80%,使中试规模中 NH_4^+-N 去除效率超过 90%.共培养还可以促进细胞代谢能力和碳源代谢活性.如链霉菌 PYX97 和 TSJ96 菌株的共培养增强了氮去除(去除了 96.40%的总氮)和有机碳去除率(去除了 92.13%的溶解性有机碳)[5].

除了上述提到的多种脱氮菌共培养形成的复合菌剂可以增强脱氮效果外,将HN-AD细菌与其他功能菌共培养,也可以形成协同效应,提升脱氮和多种协同效果.近年来,细菌-藻类共生系统在废水处理和资源利用方面的优势已得到普遍认可[80-81],可用于高效脱氮除磷.将蛋白核小球藻(*Chlorella pyrenoidosa*)与 HN-AD 细菌结合,一方面可以增强小球藻对氨氮的耐受性,促进小球藻对二氧化碳的处理;另一方面,小球藻可为 HN-AD 细菌提供溶解氧,满足其对氧气和碳源的需求,从而增强 HN-AD 细菌-小球藻共生系统的脱氮和除磷能力[80].微藻辅助的 HN-AD 共生系统的营养物去除性能显著受光照强度、盐度和接种微藻生物量的影响[82].也有研究将微藻与HN-AD复合菌剂混合创建共生系统,其具有耐受性强、去除效率高的优点,可用于水产养殖废水等高氨氮、高有机质等废水的处理.微藻的加入提高了 HN-AD 功能菌群(以不动杆菌属、假单胞菌属和副球菌属为主)的丰度以及功能基因(如 *Nas*)的表达[24].Zhang 等[14]分离出了一株同步实现 HN-AD 和微生物诱导碳酸盐沉淀(MICP)的菌株,将其与粘附于聚氨酯海绵上的微藻混合,形成细菌-藻类共生动态海绵生物修复系统[71].藻类通过光合作用为细菌的HN-AD过程提供好氧环境,同时呼吸作用产生的 CO_2 和吸附的 Ca^{2+}促进了钙沉淀的形成,而细菌利用 MICP 固定 Ca^{2+}则有助于缓解微藻的光抑制(图1(b)).

3.3 高效菌株的选育及驯化

获得高效菌株并提高菌株活性对生物脱氮效果具有决定性作用.目前获取高效HN-AD菌株的途径主要是通过大规模筛选,或者对已有菌株进行驯化和改造.由于复杂的环境可形成耐毒性高的菌种,因此通常可从特定环境中分离筛选具有较高环境适应性的菌株,如耐高氨氮、耐低温、耐盐、耐重金属等特性的菌株[16-17,83].例如,从市政污泥中分离得到的 *Acinetobacter* sp. ND7,在好氧条件下表现出优异的脱氮性能,其对铵态氮、亚硝酸盐氮、硝酸盐氮的最大比去除速率分别为 5.74,4.17 和 3.63mg/(L·h)[28].从海洋沉积物中分离出一株具有 HN-AD 能力的嗜盐细菌 *Vibrio diabolicus* SF16,在处理含盐废水时表现出较好的脱氮效果,对铵态氮和总氮的平均去除效率分别高达 97.14%和 73.92%[84].Yang 等[17]从污水处理厂的活性污泥中分离出一株耐六价铬(Cr^{6+})的高效 HN-AD 菌株 *Pseudomonas putida* LX1,其在 25mg/L Cr^{6+}条件下能够实现>80%的铵态氮去除率,且无硝酸盐氮和亚硝酸盐氮积累.从冬季的河水中筛选到一株耐盐耐低温的 HN-AD 菌,为 *Acinetobacter* sp.,在盐度为 40g/L,15℃的条件下,仍能维持生长及一定的脱氮效果,在处理海水养殖尾水中具有较好的表现[85].目前,国内外关于高效HN-AD菌的筛选研究日益增多,表 1 列举了部分已报道的案例.

除自然筛选外,通过基因工程手段或诱变等方

式也可获取高性能 HN-AD 菌株.由于 HN-AD 菌种及脱氮路径的多样性,因此目前关于其基因改造的研究有限,且该类方法操作复杂,成本较高.相比之下,微生物诱变是一种高效、实用、经济、简单且安全的育种方法,可促进生物体高频变异,从而筛选出具有优良性状的生物体.Wang 等[86]通过紫外-硫酸二乙酯复合诱变获得了一株高效 HN-AD 突变菌株 Δ*Rhodococcus* sp. CPZ 24,其最大硝化和反硝化速率分别为 3.77 和 1.37mg/(L·h),相比野生菌株分别提高了 30.30%和 17.10%.

此外,提升 HN-AD 菌对复杂环境因子的抗性,保证微生物活性也尤为重要.因为脱氮微生物通常对重金属[59,87]、抗生素[61,88]等有毒污染物敏感,在胁迫条件下时,其生长或代谢功能易受抑制,进而影响脱氮效率.针对这一问题,研究人员采取驯化方法提高细菌的耐受性,使其获得优势生长.Chen 等[92]利用人工干预结合逆境驯化的方法,筛选到一株能够抵抗表面活性剂线性烷基苯磺酸(LAS)胁迫的 HN-AD 菌 *Rhodococcus* SY24.在 LAS 胁迫下,SY24 的最大硝化和反硝化速率分别比原始菌株提高了 13.80%和 8.81%,表现出显著的 LAS 耐受性和 HN-AD 潜力.Song 等[72]以高盐芥菜废水为底物,通过 105d 的梯度盐度驯化,成功在 SBR 系统中建立了 HN-AD 模式.驯化过程中,随着盐度的增加,对总氮去除率有一定影响(图 1(c)),但耐盐能力明显提升.其群落结构发生明显演替:自养硝化功能菌属逐渐消失,而耐盐异养微生物和 HN-AD 菌属成为优势菌种,表明驯化后异养硝化得到了增强.

表 1　部分异养硝化-好氧反硝化菌的脱氮特性(最佳参数)

Table 1　Nitrogen removal characteristics of selected HN-AD bacteria (optimal parameters)

菌株	来源	最优条件及脱氮性能	文献
Pseudomonas aeruginosa	活性污泥	在 C/N=10、P/N=0.1、温度 30°C、pH 值 7.5~8.5 的最佳条件下,该菌株对氨氮的去除率为 87%,对磷酸盐的去除率为 97%	[43]
Acinetobacter sp.	养猪场废水	21h 对 NH_4^+-N, NO_3^--N, NO_2^--N 的去除率分别为 84.84%、87.13%和 92.63%;可处理混合氮源.	[89]
Paracoccus denitrificans	垃圾渗滤液处理厂的活性污泥	该菌株对 NH_4^+-N, NO_3^--N 和 NO_2^--N 的去除速率分别达到 17.33,21.83 和 32.37mg-N/(L·h),并能同步去除混合氮源;厌氧条件下也能反硝化.	[90]
Pseudomonas veronii	寒冷地区冬季河水底泥	分别以 NH_4^+-N、NO_3^--N 或 NO_2^--N 为唯一氮源(105mg/L),10 ℃,处理 48h,该菌对三种氮源的去除率分别为 99.07%、96.89% 和 90.29%,且几乎无亚硝酸盐累积.	[41]
Paracoccus sp.	活性污泥	在 147.31r/min, 36 ℃,C/N 8.72, pH 值 8 最优条件下,氨氮去除率达到(94.82±0.82)%.	[47]
Sphingopyxis sp.	化工厂废水	当以 NH_4^+-N、NO_3^--N 或 NO_2^--N(300mg/L)作为单一氮源时,该菌株的最高脱氮效率分别达到 100%、91.1%和 68.5%;其最适盐度范围为 0~5%.	[91]
Ralstonia pickettii	鱼塘废水	在葡萄糖为最佳碳源、温度 30℃、C/N 15、pH 值 7、摇床转速 100r/min、初始 NH_4^+-N 浓度 50mg/L 条件下,该菌株对 NH_4^+-N 和总氮的最佳去除率分别达 98.99%和 88.86%.	[29]
HN-AD 菌群	垃圾渗滤液	当接种量为 10%、碳氮比为 15%时,该菌群对 NH_4^+-N、TN、COD 的去除率分别为 74.69%、89.23%和 83.50%.	[75]
HN-AD 菌群	化工厂和水产养殖厂废水	最适条件为:乙酸钠作为碳源、碳氮比 10、溶解氧 3.0~4.0mg/L.对 NH_4^+-N 的去除率保持在 90%以上,且对实际高氨氮废水表现出稳定的脱氮性能.	[2]

3.4　代谢中间产物的外源性添加

通常调控代谢中间产物,如添加适量羟胺、亚硝酸盐,可优化 HN-AD 菌的脱氮途径,提高脱氮效率,这也是强化 HN-AD 菌脱氮的重要途径之一.目前关于 HN-AD 的研究大多受限于中间产物的积累以及不同形式无机氮源之间的相互抑制,导致总氮消耗效率较低.羟胺(NH_2OH)和亚硝酸盐(NO_2^-)作为 HN-AD 菌代谢过程中的关键中间产物,其适量添加可提高 HN-AD 效率[93,96],但过量会导致毒性效应和代谢失衡.以羟胺和亚硝酸盐为混合氮源分离得到的 *Pseudomonas taiwanensis* EN-F2 菌株具有优异的 HN-AD 能力.额外补充羟胺能够刺激 EN-F2 菌株细胞生长,明显提高 NAR 和 NIR 的酶活性(图 2(a))[93],并促进硝酸盐/亚硝酸盐向 N_2O 转化[97].而亚硝酸盐的添加使 EN-F2 对总氮的转化率分别提升了 5.61%(铵系统)和 15.41%(硝酸盐系统),这可能源于细胞生长与氮消耗的同步加速[96].Zheng 等[60]进一步证实亚硝酸盐通过增加反硝化基因的表达、电子传递和 ATP 水平来增强反硝化作用,添加 20mg/L 亚硝酸盐使硝酸盐的还原速率提高了 3.9mg/(L·h).

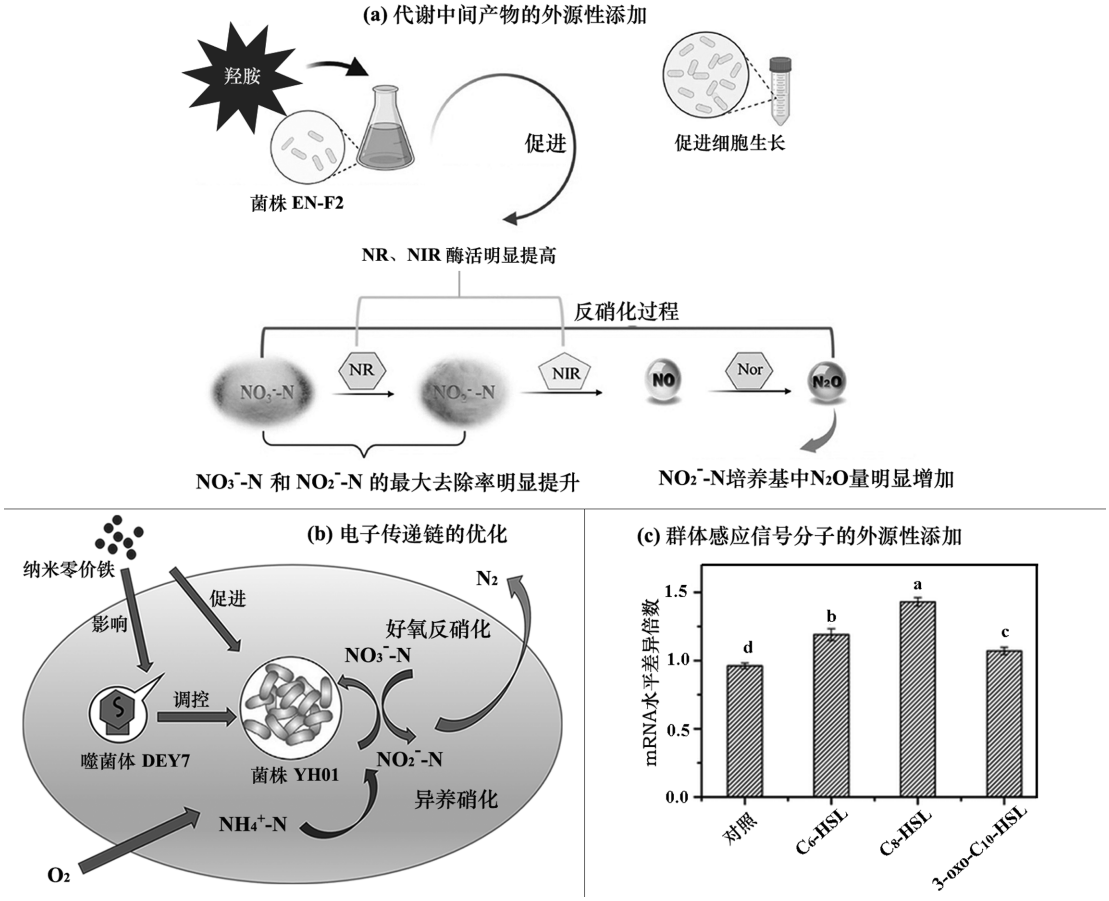


图 2 不同措施强化 HN-AD 脱氮的研究实例

Fig.2 Research cases of different strategies to enhance HN-AD nitrogen removal

(a)代谢中间产物添加:补充适量羟胺可促进关键酶活的提升,促进细胞生长(引自文献[93],经 Elsevier 出版社许可使用);(b)电子传递链的优化:纳米零价铁化学还原产生的 Fe^{2+}可作为电子供体促进生物反硝化(引自文献[94],经 Elsevier 出版社许可使用);(c)群体感应信号分子添加:脱氮过程的关键基因 *amoA* 在不同种类 AHLs 添加后的表达水平(引自文献[95],经 Royal Society of Chemistry 出版社许可使用,非商业用途)

3.5 电子传递链的优化

HN-AD 菌独特的代谢途径高度依赖电子传递链的灵活调控.优化电子传递链可提升其反硝化效率,通常通过添加电子供体(如铁、氢气)或氧化还原介体(如醌类物质、腐殖质)来实现[98].有机碳源在为微生物生长提供营养和能量的同时,也在HN-AD过程中充当电子供体,参与硝化和反硝化反应[37].因此,高效的HN-AD一般只能在较高的C/N条件下实现.那么,如何降低 HN-AD 的 C/N 需求,使微生物在有机底物有限或极端条件下高效进行生物反硝化非常关键.通过提供额外的胞外电子或者促进电子介电传导可有效解决以上问题[99-100].铁(Fe)及其化合物是安全且低毒的材料,在促进许多酶的合成和电子传递中发挥关键作用[101].不同价态的铁通过调节关键微生物群落的组装来影响硝化和反硝化的强度[102].其中,纳米零价铁常被用作污水系统添加剂去除 NO_3^--N、NH_4^+-N 和 TN 等污染物[103-104].它作为还原剂,可为 HN-AD 菌提供电子供体,促进电子转移并加速反硝化过程.在HN-AD菌与噬菌体共存系统中,50mg/L 纳米零价铁的加入最大限度地减轻了噬菌体 DEY7 对 HN-AD 菌 YH01 的抑制作用,并取得了最佳的脱氮效果(图 2(b))[94].铁-活性炭(Fe-AC)的外源添加被证明可增强好氧条件下水中土著反硝化细菌的脱氮能力,其根本原因在于 Fe-AC 系统反应生成的 Fe^0、Fe^{2+}和 H_2 为反硝化提供持续的电子供体[23].新型的铁碳材料还表现出协同效应,一方面辅助积累了与氮、碳和铁转化相关的主要功能基因,另一方面还增强了电子传递系统活性和ATP生成,从而显著提高了HN-AD菌对总氮的去除效率[105].此外,磁铁矿可通过光激发产生电子或通过增强胞外电子转移来促进微生物功能.Liu 等[106]构建了一个磁铁矿光生电子耦合 HN-AD 细

菌系统,可有效促进 HN-AD 菌生长,铵盐和硝酸盐的去除率均达到菌株单独作用时的 4 倍以上.

氧化还原介体(RM)是一类可以可逆地被氧化和还原的有机分子,能通过改善电子传递提高反硝化速率[107],并在 HN-AD 过程中发挥类似的调节作用[39].其中,外源 RM 的氧化还原电位是关键:理想RM的氧化还原电位应介于两个半反应之间,且需避免与其他电子受体竞争.由于氨氧化是HN-AD的限速步骤,调节 AMO 的电子传递尤为重要.Wu 等[39]发现低氧化还原电位的蒽醌-2,6-二磺酸(AQDS)可以加速细胞生长,但无法改变AMO与其他氧化还原酶之间的电子竞争,因此不能促进 HN-AD.而富里酸(FA)具有合适的氧化还原电位,可构建独立电子传递系统,避免与其他受体竞争电子,从而促进氨氧化,解决 HN-AD 过程中的限速步骤.在低 C/N 条件下,添加 FA 实现了 HN-AD 效率的有效提升.

3.6　群体感应信号分子的外源性添加

群体感应(QS)是一种依赖于细胞密度的微生物细胞通讯现象,通过信号分子(如 N-酰基-L-高丝氨酸内酯,AHLs)的释放、传递和诱导发挥作用[108].在 HN-AD 细菌中,QS 系统对脱氮过程具有重要调控作用.当环境中信号分子浓度达到特定阈值时,QS 系统被激活,进而调控微生物的生长、硝化和反硝化等脱氮过程.当前,外源性添加 QS 信号分子已成为强化微生物脱氮的有效策略之一,其机制包括调节生物膜系统及胞外聚合物的分泌、脱氮菌群丰度及氮去除相关酶的活性等[109].如红树林湿地中,QS 促进了 HN-AD 细菌的生长、反硝化和生物膜形成[110].外源性信号分子的调控效果与其种类、浓度、环境因素等密切相关.王乙舒等[15]证实低温添加 10nmol/L C10-HSL 可显著缩短细菌生长的迟滞期,提高脱氮速率.而在 20 和 10℃条件下分别添加 C10-HSL 对氮素转化相关功能基因(*amoA*, *napA*)表达的增量有所差异.对 HN-AD 菌株 YB1107,添加 C4-HSL 或 C8-HSL 两种信号分子后,可促进氨氧化和生物膜形成,同时抑制好氧反硝化,共同调控微生物的生理行为[22].低浓度外源 AHLs 可促进不动杆菌 JQ1004 的生物膜形成、絮凝、胞外聚合物特性以及脱氮效果,其顺序为 C8-HSL > C6-HSL > 3-oxo-C10-HSL[95] (图 2(c)).值得注意的是,QS 影响具有两面性,适宜浓度可以促进酶表达和菌群协作,而浓度过高则可能抑制代谢活性.比如*Pseudomonas aeruginosa* 喹诺酮信号(PQS)过度分泌会显著抑制其 HN-AD 活性[56].而且,AHL 在协调细菌生长、异养硝化和好氧反硝化方面的作用似乎比 PQS 更大.目前多数关于 QS 调控的研究都是添加化学合成的信号分子,而非自然分泌的信号分子.有研究表明在好氧硝化系统中添加化学合成的信号分子与自然分泌的信号分子对细菌代谢的调控存在差异[111],二者在 HN-AD 过程中是否有差异尚需进一步研究.

4　展望

HN-AD 菌具备在好氧条件下同步完成硝化和反硝化的能力,展现出高效的脱氮性能和较强的环境适应性.然而,目前相关研究主要集中在实验室阶段,实际工程应用案例较为有限.未来研究可从以下方向进一步拓展:

HN-AD 的使用效果受到多种因素的限制,目前实际应用有限的原因主要是 HN-AD 菌加入反应器后会大大增加反应的不确定性.后续仍然需要在反应器的运行模式、长期运行及影响因素等方面投入更多精力.比如可引入智能调控系统,基于传感器和 AI 实时优化系统的工艺参数.

目前筛选出的 HN-AD 菌株主要停留在脱氮特性的初步探索,上述总结的脱氮增强手段多聚焦于效果提升,而对其代谢途径及脱氮增强的分子机制的研究仍需深入.伴随着分子生物学技术的飞速发展,可以考虑使用基因编辑技术以明确关键酶编码基因的作用和地位,或利用基因重组技术构建高效脱氮菌株,提升环境耐受力.

实际的污水环境通常较为复杂,除氮超标外还含有多种污染物,如磷、抗生素、重金属和微塑料等.因此,需系统评估HN-AD菌对这些污染物的耐受性及去除潜力.

可采用多种强化手段联用的策略,以提升污染物的协同去除效果.例如,结合生物处理与物理化学方法,如活性污泥法与高级氧化技术的联用,可同时降解多种污染物.此外,整合多种生物强化策略不仅能提高生物脱氮的效率,还可降低运行成本,实现污水处理的可持续性.具体的联合方案应根据实际废水特性、运行条件和目标脱氮效果进行优化设计.

本文总结的脱氮增强策略可在一定程度上提

升脱氮性能,但仍需综合考虑其潜在影响,包括各类添加物(如载体、电子穿梭体、QS 信号分子、外加物种等)的稳定性、成本以及对微生物群落的影响.未来研究应进一步深入探讨物种间的相互作用及群落动态变化规律,以期为调控目标HN-AD菌的生物量和活性提供科学依据.

菌株的生物安全性评估是微生物引入新环境的核心环节.病原微生物可能破坏生态平衡并威胁人类健康,因此菌株的毒性和安全性研究不可或缺.目前HN-AD菌研究普遍缺乏安全性评估,需进一步加强,比如通过药敏实验评估耐药性,通过动物模型系统评估环境筛选菌的生物毒性和安全性[112].

5 结论

HN-AD 菌因其独特的同步硝化-反硝化能力,在污水脱氮领域展现出广阔的应用前景.本文总结了当前HN-AD菌的研究方法,包括功能菌的分离筛选、脱氮动力学模型构建以及多组学技术对代谢机制的解析,并重点探讨了提升脱氮效率的强化策略.微生物固定化技术通过载体优化可增强菌株稳定性和环境耐受性;多菌种共培养利用菌种之间的协同互作显著提升脱氮性能;高效菌株选育和代谢调控(如添加中间产物、优化电子传递链)进一步提高了脱氮效率;群体感应技术则为调控菌群行为提供了新思路.然而,HN-AD 技术的实际应用仍面临挑战,未来研究需结合基因编辑、多技术联用和生态风险评估,推动其工程化应用.通过跨学科合作和系统性优化,HN-AD 技术有望成为高效、经济且可持续的污水脱氮解决方案.

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