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Review 综述

六价铬的微生物还原机制及其环境影响研究进展

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摘　要：六价铬[hexavalent chromium, Cr(VI)]是广泛存在于电镀、冶金、染料制造等工业废水中的重金属污染物，具有强氧化性、高生物毒性且水溶性好，是水体和土壤污染的重点治理对象。传统 Cr(VI)污染防治技术见效较快，但存在成本高、二次污染问题严重以及处理效果易受环境条件影响等弊端。相比之下，借助微生物还原 Cr(VI)以降低其环境危害的生物处理技术具有能耗低、环境友好且可持续性强等优势，日益成为 Cr(VI)污染治理的热点。本文系统介绍了微生物还原 Cr(VI)的核心机制，涵盖关键还原酶、胞内与胞外电子传递途径、调控基因表达以及微生物群落的生态适应策略。同时，深入探讨了反硝化与硫循环等能量代谢过程在 Cr(VI)还原中的协同效应，揭示多污染物共存条件下的电子竞争与代谢通路调节机制。针对不同环境因子(如 pH 值、温度、Cr 浓度、电子供体类型)，归纳了调控微生物还原效率的措施，并结合典型案例分析了微生物修复技术在实际应用中的脱毒效率、群落变化及生态重构表现。最后，本文展望了合成生物学在工程菌株构建、多组学技术在代谢通路解析、人工智能(artificial intelligence, AI)与原位传感技术在动态调控中的应用前景，提出了以“智能识别-自适应响应-多功能协同”为核心的微生物修复发展方向，为 Cr(VI)污染原位治理提供理论基础与技术支撑。

关键词：六价铬；微生物还原；铬酸盐还原酶；反硝化耦合；原位修复；生态恢复；工程菌；多组学技术

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Research progress in bioreduction mechanisms for hexavalent chromium and environmental implications

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Abstract: Hexavalent chromium [Cr(VI)] is a widespread and highly toxic heavy metal contaminant commonly found in industrial effluents from electroplating, metallurgy, and dye manufacturing. Due to its strong oxidizing nature, high solubility, and severe biological toxicity, Cr (VI) is recognized as a priority contaminant to be managed in aquatic and terrestrial environments. Although conventional treatment technologies can rapidly reduce Cr(VI) concentrations, they often entail high costs, pose risks of secondary pollution, and are susceptible to environmental fluctuations. Bioreduction of Cr(VI) has emerged as a promising alternative, offering advantages such as low energy requirements, environmental compatibility, and operational sustainability. This review provides a comprehensive overview of the core mechanisms underlying Cr(VI) bioreduction, which involve key chromate reductases, intracellular and extracellular electron transfer pathways, gene regulatory networks, and adaptive strategies of microbial communities under stress. Furthermore, we discuss the synergistic contributions of metabolic pathways, such as denitrification and sulfur cycling, to elucidate electron competition and pathway modulation in complex multi-contaminant systems. Subsequently, we analyze the effects of environmental parameters including pH, temperature, Cr concentration, and electron donor types on bioreduction efficiency. Representative studies are discussed to illustrate detoxification performance, community succession, and ecological restoration outcomes under field conditions. Finally, this review envisions future advances in microbial remediation through the application of synthetic biology to construct engineered microbial strains, the use of multi-omics technologies to elucidate metabolic pathways, and the integration of artificial intelligence (AI) with in situ sensing technologies for dynamic regulation. It further outlines a developmental framework centered on “intelligent detection-adaptive response-multifunctional coordination”, providing both a theoretical foundation and technological guidance for the in situ remediation of Cr(VI) contamination.

Keywords: hexavalent chromium; bioreduction; chromate reductase; denitrification coupling; *in situ* remediation; ecological restoration; engineered microbes; multi-omics

环境中的六价铬[hexavalent chromium, Cr(VI)]主要以铬酸盐(chromate, CrO_4^{2-})和重铬酸盐(dichromate, $Cr_2O_7^{2-}$)的形式存在，其毒性强且来源广泛[1]。铬污染的来源可分为人为源和自然源，人为源主要包括农业生产、有色冶金、化工生产等，自然源则主要涉及铬的地球化学循环[2]。Cr 作为工业中常用的原料，在广泛应用的同时也带来了严重的污染问题。通常，每生产 1 t 铬大约会产生 2.5−3.0 t 的铬渣，铬渣积累会严重污染周边土壤及水体[3]。中国是铬渣生产量最大的国家，Gao 等[4]在 2011 年的研究报告中指出，我国生产铬盐的企业约有 25 家，年生

产能力达到 32.9 万 t，铬渣年排放量达到 45 万 t，且未处理的铬渣储存量超过亿吨。铬渣管理不当易造成泄漏，严重污染土壤及水体环境。我国部分地区土壤及水体中 Cr 污染情况如表 1 所示。

表1　部分地区土壤、水体的铬污染状况

Table 1　Chromium pollution status in soils and water bodies in some regions

Environmental recipients	Sites	Chromium concentration (mg/kg soil, mg/L water)	Regulatory standards
Soil	Farmland survey site in Hubei Province[5]	156	150 mg/kg, soil environment quality risk control standard for soil contamination of agriculture land (GB 15618—2018)[6]
	Farmland survey site in Guangxi Province[7]	372	150 mg/kg, soil environment quality risk control standard for soil contamination of agriculture land (GB 15618—2018)[6]
	Agricultural area in Hunan Province[8]	297	
	Urban area in Hunan Province[9]	1 281	
	Zhejiang Province former electroplating site[10]	1 374	30 mg/kg, soil environment quality risk control standard for soil contamination of development land (GB 36600—2018)[11]
	Hunan former ferroalloy plant[12]	3 410	
Groundwater	Former alloy plant site in Hunan Province[13]	0.1−61.3	0.10 mg/L, class IV water, standard for groundwater quality (GB/T 14848—2017)[14]
	Zhejiang Province former electroplating site[10]	189	
	Hunan former ferroalloy plant[12]	109	
	Chromium slag dumping site in Henan Province[15]	82	0.05 mg/L, class III water, standard for groundwater quality (GB/T 14848—2017)[14]
	Former industrial area in Shanghai[16]	0.086	
	Survey site in Guangzhou[17]	0.052	
Surface Water	Surface water in the gold mining area of Shandong Province[18]	0.075 1	0.05 mg/L, class IV water, environmental quality standards for surface water (GB 3838—2002)[19]
	Specific water area of Taihu Lake[20]	0.076	0.05 mg/L, class III water, environmental quality standards for surface water (GB 3838—2002)[19]
	Fengtai Bridge section of the Huaihe River Basin[21]	0.147	
	Pingwei Power Plant section of the Huaihe River Basin[21]	0.113	
	Huaihe River Basin Baligou certain area[21]	0.334	
	Xijia Gou section of the Huaihe River Basin[21]	0.149	
	Longzi River section of the Huaihe River Basin[21]	0.147	
	Xinjia Wan section of the Huaihe River Basin[21]	0.111	
	A specific river basin in central Guangdong Province[22]	2.164	

Cr(VI)氧化性强且水溶性好，在环境中的迁移能力强，可快速渗透土壤并污染地下水，其在自然界中的迁移情况如图 1 所示[23]。Cr(VI)可通过饮水、皮肤接触及呼吸过程进入人体，引起细胞氧化应激、DNA 断裂、膜损伤等毒性反应，已被证实具有致癌、致畸、致突变的效应[24-26]。因而，Cr(VI)作为环境中常见且毒性极强的重金属污染物已被美国环境保护署及中国生态环境部列为优先管控的毒性物质。

化学还原沉淀法、离子交换法、电化学还原法及物理吸附法均是在工业中常用的 Cr(VI)治理方法，但这些较为传统的治理方法存在能耗高、副产物产量大、pH 条件严格及稳定性差等问题，因而难以满足绿色、可持续的处理理念，且在复杂的实际应用场景中难以稳定发挥效果[27-28]。相较之下，微生物修复具有处理成本较低、环境适应性强、生态影响小等优势，因而日益成为研究的热点[29-30]，表 2 介绍了部分 Cr(VI)还原菌的特点及其还原能力。多种环境微生物可在酶催化作用下通过胞内和胞外电子传递体系还原 Cr(VI)，将其转化为毒性更低的三价铬[trivalent chromium, Cr(III)][35]。此外，微生物还可通过调整代谢、激活抗氧化系统及分泌胞外聚合物(extracellular polymeric substances, EPS)等过程增强自身对环境中重金属胁迫的适应能力[36]。

组学技术(如宏基因组、转录组、蛋白质组及代谢组)与合成生物学的发展促使研究者可在分子、细胞及群落层面解析 Cr(VI)还原过程中的基因调控机制与代谢途径[37-40]，进而构建 Cr(VI)还原效率高且环境适应性好的工程菌株，并设计可进行智能化调控的微生物修复系统[41-42]。为系统把握该领域的研究进展，本文综述了微生物还原 Cr(VI)的关键酶系统、电子转移体系、基因调控过程及环境响应机制，介绍了 Cr(VI)还原与其他能量代谢途径的相互作

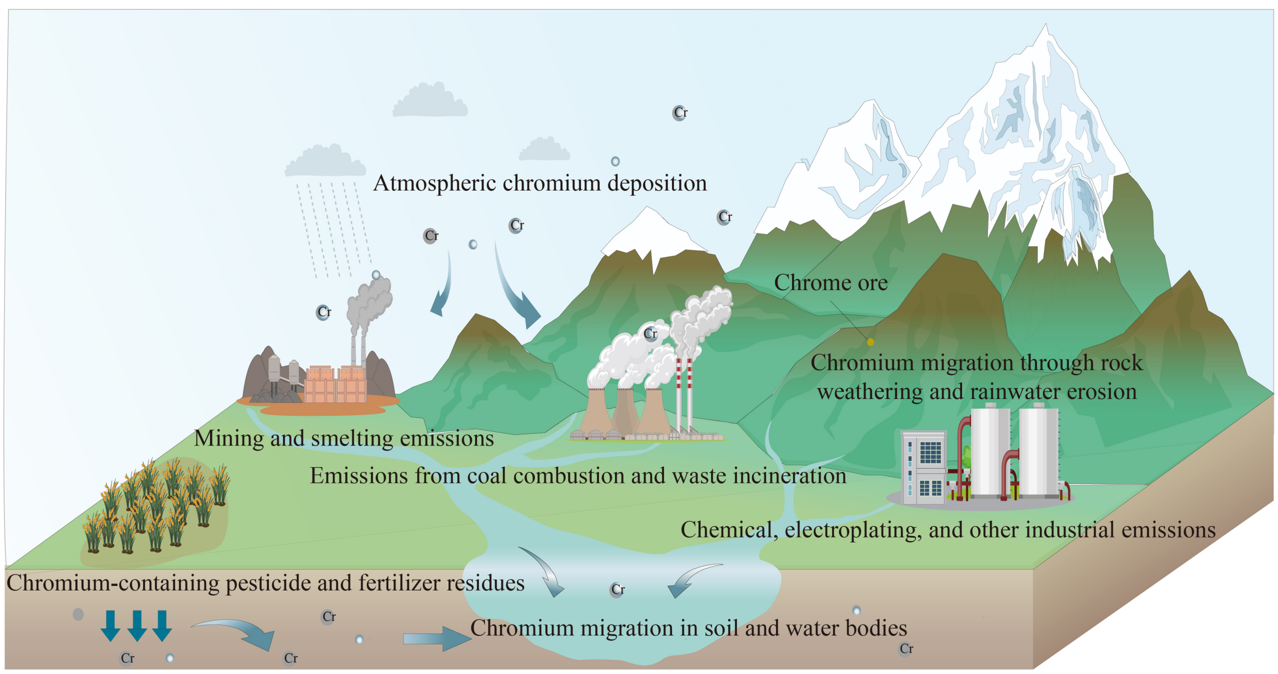

图1　铬污染及其迁移

Figure 1　Chromium contamination and its transport.

表2 部分Cr(VI)还原菌的特点及还原能力

Table 2 Characteristics and reduction capabilities of certain Cr(VI) reduction bacteria

Species	Characteristics	Cr(VI) reduction ability
Bacillus spp.[31]	Gram-positive, aerobic or facultatively anaerobic, spore-forming bacteria that are widely distributed in soil and aquatic environments	Certain strains can adapt to high-chromium environments by reducing the highly toxic Cr(VI) to the less toxic Cr(III) through enzymatic activities (such as chromate reductase) or extracellular secretions
Halomonas spp.[32]	Gram-negative, halophilic bacteria that are tolerant to high-salinity environments and commonly found in marine habitats or salt lakes	Certain strains exhibit chromium resistance and are capable of reducing Cr(VI) *via* enzymatic or non-enzymatic pathways, while maintaining their activity even under saline-alkaline conditions
Pseudomonas spp.[33]	Gram-negative, aerobic bacteria with diverse metabolic capabilities, widely distributed in soil and aquatic environments, and exhibiting strong environmental adaptability	Various *Pseudomonas* species, such as *Pseudomonas aeruginosa*, are capable of reducing Cr(VI) to Cr(III) *via* chromate reductase or the electron transport chain, and can tolerate high concentrations of chromium contamination
Bacillus pumilus[3]	Gram-positive, aerobic, spore-forming bacteria that are capable of withstanding extreme conditions, such as radiation and desiccation	They exhibit highly efficient Cr(VI) reduction capabilities, which can be achieved through intracellular enzymatic processes or surface adsorption, making them suitable for applications in bioremediation
Exiguobacterium spp.[34]	Gram-positive bacteria that are psychrotolerant and alkali-tolerant, and are widely distributed in extreme environments	Certain strains exhibit high tolerance to Cr(VI) and are capable of reducing Cr(VI) through enzymatic reactions or adsorption by extracellular polysaccharides
Cellulosimicrobium cellulans[34]	Gram-positive bacteria capable of degrading cellulose, commonly found in soil and plant residues	They are capable of reducing Cr(VI) to Cr(III) through the secretion of reductive compounds or enzymes, and possess dual capabilities for organic matter degradation and heavy metal remediation

用，分析了 pH、温度、共存污染物等因素对还原效率的影响，并结合典型修复案例探讨了微生物还原 Cr(VI)过程中的环境适应策略，最后从功能菌构建、多组学分析、智能调控及功能设计角度探讨了微生物还原 Cr(VI)的工程应用前景，旨在为生物技术修复重金属污染提供理论支撑和技术参考。

1 Cr(VI)微生物还原机制

微生物还原 Cr(VI)涉及酶催化、电子传递、代谢调整、群落适应及演化等多个层次，是一个复杂的协同调控过程[43]。其中，电子传递过程中的电子供体是指在微生物代谢过程中能够提供电子的物质，电子通过呼吸链或发酵途径传递给电子受体以驱动能量和还原力的生成；微生物的代谢途径不同所需的电子供体也不同，如异养微生物以有机物(如糖类)作为电子供体，自养微生物以无机物[如硫化氢(hydrogen sulfide, H_2S)]作为电子供体[44]。

微生物还原 Cr(VI)的过程不仅体现了微生物对环境胁迫的适应能力，也为调控微生物修复过程提供了生物基础。以下从 6 个维度系统阐述 Cr(VI)的微生物还原机制。

1.1 关键还原酶系统

Cr(VI)的还原首先依赖多种特异性还原酶的催化作用。黄素单核苷酸(flavin mononucleotide, FMN)依赖型黄素还原酶(flavin reductase, ChrR)可利用还原型辅酶Ⅱ [nicotinamide adenine dinucleotide phosphate (reduced form), NAD(P)H]供能，在细胞内将电子准确传递至 Cr(VI)，将其还原[45]；硝基还原酶 A (nitroreductase A, NfsA)能够参与多种氧化还原过程[46]；而外膜细

胞色素 A (outer membrane cytochrome A, OmcA)等作为跨膜细胞色素可参与细胞外的电子传递以还原 Cr(VI)[47]；老黄酶家族作为古老的NAD(P)H 脱氢酶类，也可间接参与 Cr(VI)转化[48]。这些酶的协同催化作用是实现 Cr(VI)高效还原的关键。

1.2 电子传递与基因调控途径

在典型厌氧菌如硫还原地杆菌(*Geobacter sulfurreducens*)中，导电菌毛(electrically conductive pilus, PilA)和多血红素胞外细胞色素，如外膜细胞色素 Z (outer membrane cytochrome Z, OmcZ)可构成电子通路，将电子从细胞内传递至细胞外，进而还原胞外 Cr(VI)[49]。这一过程也受到一系列基因的调控，如编码金属排铬蛋白的基因 *chrA* 和编码跨膜金属转运泵的基因 *czcA* 可在 Cr(VI)诱导下表达[50-51]。在 Cr(VI)胁迫下，多数菌株也会激活与还原过程相关的基因表达，如编码铬酸盐还原酶 R 的基因 *chrR*、编码硝基还原酶 A 的基因 *nfsA*，以增强对电子供体的利用能力并提高 Cr(VI)还原速率[52]。这些基因对微生物的 Cr 适应性演化具有重要作用。

1.3 微生物类型与生态策略

闵祺等[53]研究发现，已有多种兼性厌氧微生物可还原 Cr(VI)，如奥奈达湖希瓦氏菌(*Shewanella oneidensis*)可以乳酸作为电子供体还原 Cr(VI)；土壤中的葡萄球菌属(*Staphylococcus*)可在胞内酶的催化作用下还原 Cr(VI)，并将其转化为 Cr(III)沉淀[54]；杂色云芝(*Trametes versicolor*)是一类存在于土壤中的白腐真菌，其分泌的胞外酶呈酸性，不仅可调节根际 pH，还可通过有机酸络合促进 Cr(III)沉降[55-56]。这些微生物在生态位中发挥着不同作用，且其 Cr 还原机制均表现出对环境的高度适应性。

1.4 代谢网络重构与 EPS 响应

Cr(VI)具有强氧化性，会导致细胞氧化应激并扰乱能量代谢，在与环境的相互作用中，微生物演化出代谢重构机制来适应 Cr(VI)环境[57]。唐晨[58]研究发现 Cr(VI)刺激可促使菌体戊糖磷酸途径(pentose phosphate pathway, PPP)与三羧酸循环(tricarboxylic acid cycle, TCA)通量增强，进而促进还原当量 NAD(P)H 的生成；同时促进超氧化物歧化酶(superoxide dismutase, SOD)、过氧化氢酶(catalase, CAT)等抗氧化酶的表达以减少活性氧对细胞的氧化损伤[59-60]。此外，Cr(VI)还可促进微生物分泌 EPS，不仅有利于吸附和络合金属离子，还可为微生物还原 Cr(VI)提供良好的环境条件[61]。EPS 响应机制可起到保护作用，同时促进 Cr(III)沉淀。

1.5 还原机制的进化适应与系统生物学解读

在持续的 Cr(VI)暴露中，部分微生物可表现出显著的适应性[62]。例如，沙雷氏菌属(*Serratia*) S2 菌株与芬克纤维微菌(*Cellulosimicrobium funkei*) AR8 菌株在 Cr 胁迫下会促进 ChrR 蛋白、ChrA 蛋白及 SOD 等功能蛋白表达以降低 Cr(VI)的生物毒性，同时还可通过调整能量代谢、促进膜排毒及信号传导形成较为稳定的金属耐受型代谢模式[62-63]。通过系统生物学分析可以发现，该代谢调控表现出“代谢-转运-抗氧化”的三元协同特征，这为进一步构建工程菌提供了基因靶点，也为人为调控微生物代谢促进 Cr(VI)还原提供了依据。

1.6 微生物 Cr(VI)还原动力学模型

微生物还原 Cr(VI)的过程可通过动力学模型进行模拟[64]。在低浓度范围内多数菌株还原 Cr(VI)符合一级动力学模型，温度、pH 及电子供体浓度等会显著影响反应的速率常数[64-65]；当 Cr(VI)浓度升高到一定值时，生物毒性增强，会显著抑制微生物的生命活动，部分体系的还原反应呈现零级反应特征[2]。碳源的种类也会影响 Cr(VI)的还原速率，因而可通过调整碳源优化 Cr(VI)的还原过程。

2 Cr(VI)还原与反硝化及硫酸盐还原过程的耦合机制

现实情况中 Cr(VI)污染环境较为复杂，微生物对 Cr(VI)的生物转化并非依赖单一的电子供体，且常与反硝化、硫循环等能量代谢途径相耦合[66]。微生物细胞内 Cr(VI)和硝酸根(nitrate ion, NO_3^-)的还原过程常共享相同的电子供体系统，且在多污染环境中共存的其他重金属也会影响微生物的代谢途径并调控功能基因表达[67]。本文将从氧化还原调控、共存污染物干扰、代谢途径选择到硫代谢介导的间接还原机制系统探讨 Cr(VI)与反硝化及硫酸盐还原过程的协同机制。

2.1 氧化还原调控机制与电子供体竞争

Yaashikaa 等[68]研究发现反硝化菌中的施氏假单胞菌(*Pseudomonas stutzeri*)可将 NO_3^-还原为 N_2，同时可将 Cr(VI)还原为 Cr(III)，但 NO_3^-和 Cr(VI)均为强电子受体，会竞争有限的电子供体，进而影响各自的还原效率[69]。因此，为优化对二者的去除效果，可调控 NO_3^-/Cr(VI)摩尔比例及碳源投加量，使反硝化与 Cr(VI)还原先后进行，从而减弱抑制作用，提升还原速率及处理稳定性。

2.2 共污染物干扰与协同机制

在多种金属污染共存的环境中，如三价砷[arsenic(III), As(III)]、二价铅[lead(II), Pb(II)]、二价镉[cadmium(II), Cd(II)]等离子会影响酶活性、干扰膜转运或通过诱导细胞发生应激反应，从而抑制 Cr(VI)还原[70]。值得注意的是，某些毒性物质，如 As(III)也可激活其自身的排毒系统，如亚砷酸盐外排泵 B (arsenite efflux pump B)，同时提升对 Cr(VI)的耐受水平，表现出交叉激活效应[71]。在 Cr(VI)与 As(III)共存的环境中，菌株不仅可通过双金属共代谢途径在氧化 As(III)的过程中协同还原 Cr(VI)，还能通过自身排毒机制提高对有害离子的耐受能力[72]。

2.3 耦合代谢途径建模与调控优化

通过代谢流分析可以发现，在厌氧菌的代谢过程中 Cr(VI)与 NO_3^-共享还原型烟酰胺腺嘌呤二核苷酸 (reduced nicotinamide adenine dinucleotide, NADH)的生成与利用途径，电子流量在反硝化与 Cr(VI)还原途径间动态分配[73-74]。乳酸作为电子供体不仅可提供还原力，还可调节胞内 pH 并参与能量供应，通过控制乳酸浓度及碳氮比可实现 Cr(VI)与 NO_3^-的最优去除效果，基于此可采取有效调控措施提高修复过程的可控性与代谢效率[39,75]。

2.4 硫循环与间接还原途径解析

韩卉[76]在厌氧污泥还原 Cr(VI)的研究中发现，适量硫酸盐可促进 Cr(VI)还原，过量则会起到抑制作用。硫酸盐还原菌(sulfate-reducing bacteria, SRB)对 Cr(VI)的间接还原是指其代谢产物硫离子(sulfide ion, S^{2-})对 Cr(VI)的还原作用，该过程可稳定 Cr(VI)，降低其迁移能力和生物毒性[77-79]。SRB 的代谢产物 H_2S 与 Cr(VI)反应生成硫化铬[chromium(III) sulfide, Cr_2S_3]沉淀，且该过程常与铁还原菌协同形成 Cr-Fe-S 三元耦合沉淀体系，不仅可以稳定 Cr(VI)，也提高了还原体系的电子缓冲能力[80-81]。当电子供体不足时二者为竞争关系，此时硫循环则会抑制 Cr(VI)还原。

2.5 硫代谢基因调控机制

SRB 通过关键硫还原基因的表达将硫酸根(sulfate ion, SO_4^{2-})还原为 H_2S，同时可促进 Cr(VI)沉淀。此外，普通脱硫弧菌(*Desulfovibrio vulgaris*)能够合成具有 Cr(VI)还原能力的细胞色素 c，且 H_2S 代谢速率与 Cr(VI)初始浓度呈正相关，表现出硫酸盐还原与 Cr(VI)还原的协同促进效应[78,82]。在 Cr(VI)胁迫下，微生物还可通过激活抗氧化基因保护细胞生存，并通过促进 EPS 合成来络合还原产物 Cr(III)等金属离子[59,81]。此外，在 As(III)、三价铁[ferric ion, Fe(III)]、NO_3^-等多重污染体系中 SRB 群落表现出高度的

动态调节能力，部分菌属可通过调整对电子受体的亲和性来调节电子流分配，进而保证 Cr(VI)还原的电子供应[83]。

3 Cr(VI)还原的环境影响因素与修复效果评估

3.1 pH 值与温度条件调控

微生物还原 Cr(VI)的过程对环境条件较为敏感，pH 和温度会影响酶的稳定性以及电子传递效率[27,84]。张敏等[81]的研究发现菌株还原 Cr(VI)的适宜 pH 范围为 7.0−9.0，pH 值过低不仅会造成部分酶失活，还会增强 Cr(VI)的生物毒性。适宜的温度范围有助于提升酶活性，温度过高或过低均会影响还原效果。例如，Das 等[85]的研究发现 35 ℃是解淀粉芽孢杆菌(*Bacillus amyloliquefaciens*)还原 Cr(VI)的最适温度，高于 45 ℃或低于 30 ℃都会显著抑制菌株生长。在工程应用中，调控 pH 与温度不仅可以提高细菌活性和 Cr(VI)转化效率，还能促进 Cr(III)沉淀，使其形成稳定胶体[86]。

3.2 Cr(VI)初始浓度与电子供体类型

Cr(VI)浓度是影响其生物毒性的关键因子[57]。当 Cr(VI)浓度超过 200 mg/L 时可能导致微生物细胞发生肿胀、变形和破裂等损伤，采用阶段化培养可增强菌群对 Cr(VI)的耐受水平[87-88]。电子供体类型会显著影响 NAD(P)H 的生成速率及呼吸链活性，其中乳糖、葡萄糖等可促进 Cr(VI)还原过程，而麦芽糖则可能起到抑制作用[65]。乳酸可在乳酸脱氢酶(lactate dehydrogenase, LDH)作用下进行供能并起到缓冲作用，葡萄糖可驱动 PPP 通路生成 NAD(P)H。此外，曹威等[2]研究发现季氨基结构也可作为 Cr(VI)还原的电子供体。

3.3 群落响应机制与多菌协同作用

在微生物还原 Cr(VI)的过程中，其群落响应机制涉及微生物种群演替及功能基因激活等方面。高通量测序和宏基因组学研究发现，初始阶段假单胞菌门(*Pseudomonadota*)与芽孢杆菌门(*Bacillota*)的微生物处于主导地位，负责 Cr(VI)识别与部分还原[89]；随着修复过程的推进，放线菌门(*Actinomycetota*)、拟杆菌门(*Bacteroidota*)等耐金属且 EPS 分泌能力强的菌属逐渐增多，这一过程也使得合成金属转运蛋白、抗氧化酶及多糖合酶等的功能基因被激活[90]。生态网络分析表明，在 Cr(VI)生物还原过程中菌群之间存在电子共享、协同代谢的稳定关系网，为 Cr(VI)污染修复提供了有序的微环境。

3.4 金属共污染与协同/拮抗效应

在多种金属污染的场地，Cr(VI)与 As(III)、五价砷[arsenic(V), As(V)]、Cd(II)等离子之间存在复杂的相互作用。例如，细菌表面 Cd(II)可能会抑制其对 As(V)的吸附[91-92]。As(III)可激活 ArsB 蛋白、亚砷酸盐转运蛋白 3 (arsenite transporter 3)等外排蛋白，间接提高微生物对 Cr(VI)的耐受性，表现出“协同效应”[93]；而 Cd(II)可能会造成膜损伤，某些金属离子也可能会与 Cr(VI)竞争酶的结合位点，从而对 Cr(VI)还原过程产生“拮抗作用”[94]。基于此，在工程菌株的构建中可尝试使 Cr(VI)还原与其他金属耐受基因共同表达，从而实现共污染环境的协同治理。

3.5 原位修复过程的环境反馈与功能评估

Cr(VI)的微生物修复成效主要取决于 Cr(VI)的去除率，但也应关注修复过程中的环境反馈。微生物原位修复通常伴随局部氧化还原电位下降、碳源富集及微生物自养/异养比例调整等过程，因而可通过监测 pH、溶解氧、Cr(VI)/Cr(III)浓度等的变化及群落演替对修复过程进行多维评估[95]。同时，也可通过高通量测序的香农指数(Shannon index)、多样性热图及功能基因丰度变化来量化修复过程中的微生物生态响应[96]。

4 典型修复案例与生态影响分析

4.1 土壤原位修复工程示范

安徽合肥某电镀厂受到重度 Cr(VI)污染，土壤中 Cr(VI)的初始质量比为 98 mg/kg，通过接种 *Staphylococcus* sp. 优势土著菌并联合施用有机肥处理 21 d 后，Cr(VI)被完全还原[54]。在这一过程中，土著菌可通过 EPS 与胞内酶 ChrR 等的协同作用实现 Cr(VI)高效还原与 Cr(III)络合沉淀。随着 Cr(VI)被还原，土壤理化性质得到改善，微生态环境的稳定性不断提高，为实现 Cr(VI)污染的长效治理提供了重要支撑。

4.2 地下水 Cr(VI)-NO_3^-协同去除

宋纪斌[97]在乳化油强化治理地下水 Cr(VI)和硝酸盐污染的研究中发现，乳化油可起到促进 Cr(VI)及硝酸盐还原的作用；此外，在实验的第 6 天，土著微生物对 Cr(VI)单一污染的去除率仅为 54%，但在 Cr(VI)与硝酸盐的复合污染下对 Cr(VI)的去除率可达 95%；在这一过程中，硝化与 Cr(VI)还原可共享呼吸链及电子供体，且硝酸根作为更易被利用的电子受体，促进了体系内电子的转移过程，进而对 Cr(VI)的还原具有促进作用，显著提升了治理效率。Lin 等[98]研究发现，乳化油可对菌群结构演替产生深远影响，进而影响 Cr(VI)还原。

4.3 植物-微生物联合修复

李顺灵等[99]通过中试试验将铬污染土壤、秸秆及复合菌剂等混合进行好氧发酵，并种植高羊茅等对铬有富集作用的植物，修复一个月后土壤 Cr(VI)浸出浓度由 55.1 mg/L 降至 0.5 mg/L 以下，2 个月后 Cr(VI)浸出浓度可降至 0.308 mg/L，甚至检测为零，展现出植物-微生物联合修复 Cr(VI)污染的良好成效。在这一过程中微生物与植物构建起根际复合修复体系，接种菌可促进根际分泌有机酸及根部 EPS 形成，从而增强对 Cr(III)的络合能力，且通过分析植物体内金属转运蛋白的表达水平发现重金属主要富集于根部[100]。

4.4 多源污染场地的耦合治理案例

代兴丽[101]在金属污染废水治理研究中通过一株肠杆菌同步进行 Cr(VI)还原与 As(III)氧化，将其分别转化为毒性更低的 Cr(III)和 As(V)；该研究发现，投加 As(III)可明显提升该菌对 Cr(VI)的抗性，单独投加 Cr(VI)时该菌对其还原率为 64.5%，同时投加 Cr(VI)与 As(III)时 Cr(VI)的还原率可达 93.0%，且该菌也表现出更高的 Cr(VI)还原速率及 As(III)氧化速率。

5 技术发展趋势与未来展望

5.1 工程菌株构建与模块化设计

目前，微生物修复 Cr(VI)的技术受限于菌株环境适应性较弱及代谢通路受阻等方面，合成生物学为构建工程菌提供了重要支撑[102-104]。合成生物学将生物视为“可编辑的模块”，通过对模块进行设计和重构来改造微生物，如将铬还原酶、排铬蛋白、抗氧化蛋白及导电结构蛋白整合表达，从而构建出同时具备 Cr(VI)还原、抗胁迫及电子输出功能的工程菌[105-106]。此外，还可通过规律成簇的间隔短回文重复序列系统及相关蛋白(clustered regularly interspaced short palindromic repeats, CRISPR-associated, CRISPR-Cas)系统(如 Cas9)对特定位置的基因进行剪切、插入等操作，并结合自动化 DNA 装配技术快速构建工程菌并调控其表达[107]。在未来，以“可控表达+可感知+环境响应”为目标设计和构建的工程菌有望对复杂的动态污染体系实现高效生物修复。

在构建工程菌用于 Cr(VI)修复的同时，也应考虑工程菌和人工设计的基因元件向周围环境泄漏带来的生物安全风险，具体防控措施可分为 2 个方面：一是杀死或抑制工程菌防止其扩散；二是减少基因元件向环境中的迁移，防止环境微生物摄取和利用基因元件[108]。

5.2 多组学联合解析与数据驱动优化

对生物修复系统进行有效调控，需要深入理解菌群、功能基因及代谢产物之间的动态关系。宏基因组学可揭示群落结构与耐铬基因的分布；蛋白质组学可监测 Cr(VI)还原酶的表达水平[109]；代谢组学可通过跟踪中间代谢产物，如乳酸、NAD(P)H 等，预测代谢通路的电子流向及通量瓶颈。通过多组学分析可对修复的全过程进行优化调控，如可通过 KEGG 路径(Kyoto encyclopedia of genes and genomes pathway)识别代谢过程中的通量障碍，通过代谢网络建模(flux balance analysis, FBA)可对修复效率进行预测[110-111]。在复杂污染体系中，可基于多组学的分析数据及模型预测，对工艺进行有效调控，优化 Cr(VI)还原过程。

5.3 自适应调控与智能响应系统

在 Cr(VI)生物修复中，环境条件的变化(如 pH、温度、碳源浓度等的波动)会直接影响修复过程的稳定性，因此有必要设计和构建具备自适应反馈功能的修复体系。如将 pH/Cr 等浓度探针、基于铬响应调控蛋白 ChrP (由 *chrP* 基因编码)及铬操纵子调控区 *chrO* 基因调控的铬感应系统、比例-积分-微分(proportional-integral-derivative, PID)控制或反向传播(back propagation, BP)神经网络预测模型等应用于修复系统，可实现对电子供体流量、菌剂投加等的动态调控[112-114]。此外，人工智能(artificial intelligence, AI)辅助的修复系统可对复杂参数进行分析并输出控制策略，从而提高修复效率[115]。

5.4 多污染协同控制与群落功能冗余设计

自然环境中的 Cr(VI)污染常与 NO_3^-、As(III)、Pb(II)等污染并存，因此单因子修复策略难以满足实际的修复目标。复合反应带可实现对多种污染物的协同控制，该技术对多种功能菌进行集成应用，并结合碳源梯度控制、电子受体引导及载体固定化等技术实现 Cr(VI)、NO_3^-、SO_4^{2-}等的同步去除[116]。Lin 等[52]将菌群固定于石英胶粒等载体上，实现了 Cr(VI)的连续高效去除。

杨旭楠等[41]提出基于多组学技术的功能菌群设计思路，即在微生物群落构建中使不同物种执行相关生态功能，如电子转移、金属络合及 EPS 生成等，从而增强系统的处理效果与稳定性。为应对 Cr(VI)污染的复杂条件，未来有必要加强关于 Cr(VI)修复的微生物群落研究以推进功能群落构建。16S/18S rRNA 基因测序可用于鉴别 Cr(VI)污染环境中微生物的群落组成[117]；宏基因组学可同时获取群落物种组成和功能基因信息；宏转录组和蛋白质组可直接反映微生物群落的功能活性[118]。在掌握微生物群落信息的基础上进行功能群落构建，可实现对本土微生物的充分开发，并根据微生物群落策略组合功能互补的菌株，同时整合植物对 Cr(VI)的积累与稳定作用，形成协同增效的修复体系[119]。

6 总结与展望

Cr(VI)污染严重危害人体健康和生态系统的稳定，近年来以微生物为核心的修复技术因其绿色高效、环境友好等优势成为修复治理的重要研究方向[120]。本文从酶促反应、电子传递、功能基因到微生物的响应机制梳理了 Cr(VI)的还原过程，微生物还原 Cr(VI)不仅依赖各种还原酶的协同催化，还与排毒与导电基因的表达密切相关；同时，菌群可通过调整代谢、分泌 EPS、激活抗氧化通路等提升自身的 Cr(VI)耐受水平。

在技术应用层面，利用合成生物学可进行高性能工程菌构建，多组学技术可对微生物修复全过程进行解析，智能化修复系统则可通过生物传感、AI 控制及反馈调节机制等实现对复杂污染环境的有效治理。土壤、地下水及植物联合修复等案例已证实微生物修复 Cr(VI)污染的巨大潜力。未来，Cr(VI)生物修复的突破点可聚焦于高通量筛选高效耐铬菌、环境响应机制

探索、多维生物信息系统建立，以及在复杂污染条件下构建功能冗余的稳定生物系统。此外，Cr(VI)生物修复系统也朝着智能响应、自适应调控及多污染协同的方向发展。

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