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专论与综述

微生物镉解毒机制及微生物-植物互作修复研究进展

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摘　要：镉(cadmium, Cd)是引起粮食减产的主要金属之一，具有高溶解性及高迁移性，易被植物吸收和积累。微生物长期在镉胁迫的条件下进化出一系列的镉解毒机制。微生物对镉的解毒包括抑制 Cd(II)的进入、促进 Cd(II)的外排，以及将进入胞内的 Cd(II)进行“扣押”。微生物的 Cd(II)钝化是通过细胞吸附和胞外沉淀将游离态的 Cd(II)进行钝化，这类微生物具有较强的土壤镉污染治理潜力。本文主要介绍微生物的镉解毒机制、微生物-微生物互作、微生物-植物互作机制及其在镉污染生物修复中应用的最新研究进展。

关键词：镉；微生物镉解毒；镉钝化；微生物修复；微生物-植物互作

Research progress in microbial detoxification of cadmium and bioremediation based on microorganism-plant interaction

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Abstract: Cadmium (Cd) is one of the major hazardous pollutants threatening grain production. Cd(II) with good dissolubility and high mobility tends to be absorbed and accumulated by plants. Microorganisms have evolved detoxification mechanisms under Cd(II) stress, which include the inhibition of Cd(II) uptake, activation of Cd(II) efflux, and sequestration of Cd(II) into cells. A variety of microorganisms have been reported to immobilize Cd(II) by biosorption

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and extracellular precipitation. These microorganisms exhibit great potential to bioremediate cadmium-contaminated soils. This review summarizes the molecular mechanisms of microbial detoxification of cadmium, microbial interaction, and microorganism-plant interaction, and then introduces the latest research progress in the bioremediation of cadmium contamination by microorganisms.

Keywords: cadmium; microbial detoxification of cadmium; cadmium immobilization; bioremediation; microorganism-plant interaction

镉(Cd)是一种银白色的金属，位于元素周期表的第五周期 IIB 族，在自然界中主要以二价镉[Cd(II)]形式存在[1]。镉具有半衰期长、高迁移性和易被作物吸收聚集的特点，对生物体有较强的毒害作用。镉对生物体的毒害作用主要体现在 3 个方面：(1) Cd(II)与巯基具有较强的亲和力，抑制了体内关键酶的正常代谢；(2) Cd(II)与其他金属阳离子具有类似的离子属性，因此会破坏胞内离子平衡，并且取代一些蛋白中的必需金属离子如 Zn(II)、Cu(II)和 Fe(II)，导致蛋白的结构和活性发生变化；(3) Cd(II)进入细胞后会引起氧化压力，导致 DNA 损伤进而诱发畸变和癌变[2]。将游离的 Cd(II)吸附和沉淀，起到了镉钝化的作用，是环境中镉污染的主要修复方式，也使镉钝化微生物在镉污染修复方面具有较好的应用前景。

由于镉在电池、染料、涂料、电镀、镉量子点材料、合金、稳定剂和核裂变制造等现代工业中广泛应用，使得封存在矿石中的镉在水体和土壤中大量积累[3]。全球土壤镉含量调查显示，中国、韩国和日本是镉生产量最高的国家，其中我国镉产量占世界总镉产量的六分之一[4]。我国受镉污染的农田土壤面积已达 2.8×10^9 m^2[5]，其中海南农作物土壤中 Cd 含量超过我国土壤一级标准(GB15618—2018)风险筛选值的点位率达到 20.93%[6]，而湖南东部城市长沙和株洲等地镉含量均较高，最高可达 8.87 mg/kg[7]。稻田镉污染已成为制约我国水稻安全生产和农业可持续发展的主要因素，严重威胁农产品质量安全和人民健康。因此，寻找有效的镉修复方法成为亟待解决的问题。微生物修复具有易于培养、经济环保、增强土壤健康等优点，日益受到人们的关注[8-11]。长期生存于镉污染环境中的微生物已经进化出相应的镉解毒和钝化机制，本文综述微生物对 Cd(II)的解毒和钝化机制，并介绍其在镉污染修复中的研究现状。

1 微生物镉解毒机制

微生物长期在含 Cd(II)的环境中生存，已经进化出一系列的解毒机制，如图 1 所示，主要的镉解毒过程包括抑制 Cd(II)摄入、促进 Cd(II)外排、胞内 Cd(II)结合、损伤修复和胞外 Cd(II)吸附沉淀。

1.1 Cd(II)摄入和外排

减少 Cd(II)的摄入和促进 Cd(II)的外排，是微生物减少 Cd(II)毒性，维持体内 Cd(II)平衡的重要方式。Cd(II)可以通过二价阳离子吸收通道进入胞内，这类通道属于 zinc-regulated transporter/iron-regulated transporter protein (ZIP)家族的 Zn(II)转运蛋白，这类蛋白包括细菌中的 ZupT[12]和酵母菌中的 Zrt 和 Irt[13]。Cd(II)还可以通过 Mn(II)转运蛋白(MntABC 和 MntH)[14-15]、Hg(II)转运蛋白(MerCEFT)等进入胞内[16] (表 1 和图 1)。

促进 Cd(II)的外排是微生物减少 Cd(II)毒害的有效方式。研究表明膜蛋白家族成员与 Cd(II)

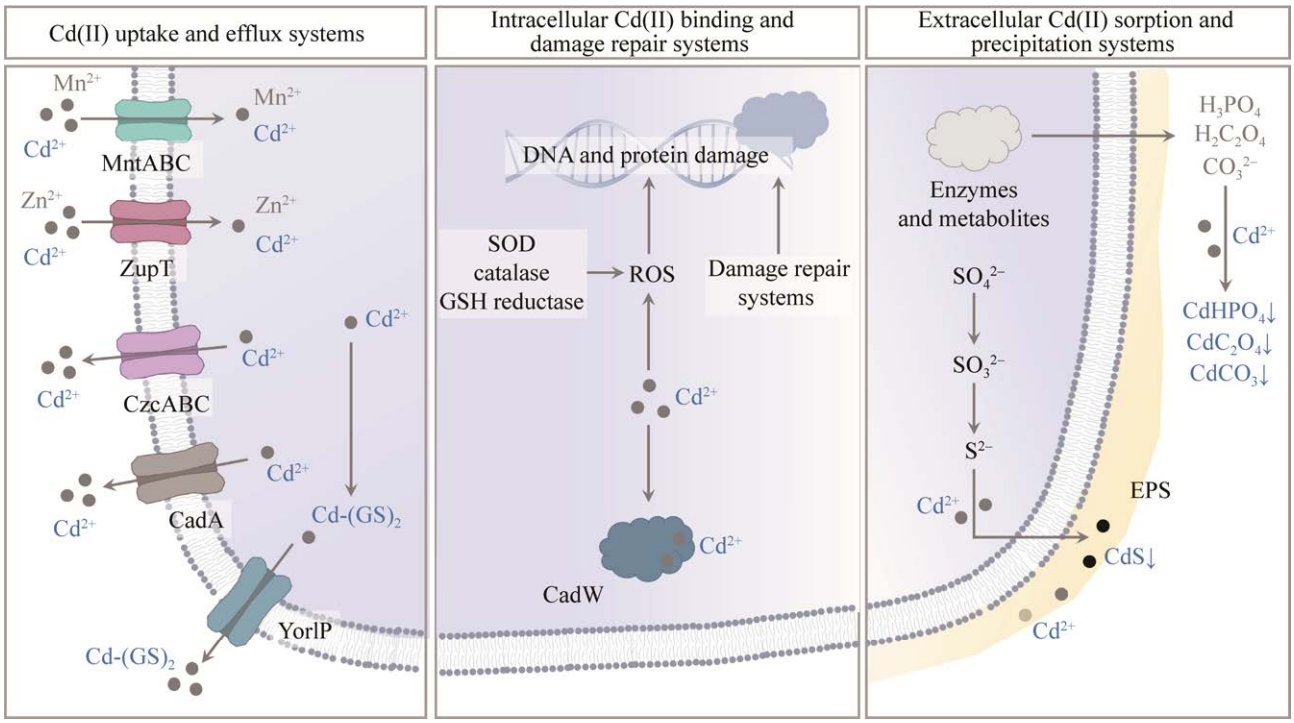

图 1 微生物对镉解毒示意图 微生物镉解毒机制分为镉摄入和外排、胞内结合与修复、胞外吸附与沉淀. MntABC、ZupT、CzcABC、CadA 和 YorlP 蛋白参与 Cd(II)的转运；超氧化物歧化酶、过氧化氢酶和谷胱甘肽还原酶降低胞内氧化压力，损伤修复系统修复 DNA 和蛋白损伤；CadW 蛋白参与胞内 Cd(II)结合；细菌产生胞外多糖参与胞外 Cd(II)吸附；硫酸盐还原途径产生的 S^{2-}与 Cd(II)在胞外形成 CdS 沉淀；代谢产物磷酸、草酸和碳酸盐参与胞外 Cd(II)沉淀

Figure 1 A scheme model of cadmium detoxification in the microbe. The mechanism of Cd(II) detoxification in the microbe includes Cd(II) uptake and efflux, intracellular Cd(II) binding and damage repair, and extracellular Cd(II) sorption and precipitation. MntABC, ZupT, CzcABC, CadA, and YorlP proteins are involved in the Cd(II) transport. Superoxide dismutase (SOD), catalase, and glutathione (GSH) reductase reduce intracellular oxidative stress, and the damage repair system repairs DNA and protein damage. CadW protein is involved in intracellular Cd(II) binding. Microbes produce exopolysaccharides (EPS) to absorb extracellular Cd(II). The S^{2-} produced by the sulfate reduction pathway produces extracellular CdS precipitates with Cd(II). Metabolites phosphoric acid, oxalic acid, and carbonate participate in extracellular Cd(II) precipitation.

的转运有关，这些蛋白包括 resistance-nodulation-division (RND)家族、ATP binding cassette (ABC)家族、heavy metal efflux (HME)家族和 cation diffusion facilitator (CDF)家族[2,30] (表 1)。细菌中研究较多的 Cd(II)外排系统包括革兰氏阳性细菌，如 *Staphylococcus aureus*、*Bacillus subtilis* 和 *Listeria* 中的 Cad 系统[23-25]，以及革兰氏阴性细菌，如 *Alcaligenes eutrophus* CH34 中的 Czc 系统[17] (图 1)。Cad 系统由操作子 *cadCA* 组成，包含蛋白 CadA 和 CadC。CadA 为 P-type ATPase，CadC 属于 ArsR/SmtB 家族的负调控转录调控因子[23]。ArsR/SmtB 家族的金属感应蛋白是原核生物中最常见的金属调控蛋白，调控金属抗性蛋白如金属外排、转运蛋白和还原酶、金属隔

表 1 微生物中的镉转运与结合蛋白

Table 1 Cadmium transport and binding protein in microbe

功能 Function	蛋白家族 Protein family	来源 Source	参考文献 Reference
Cd(II) uptake proteins			
CzcD	P-type ATPase	*Alcaligenes eutrophus* CH34	[17]
MntABC	ABC family	*Bacillus subtilis*	[14]
MntH	ABC family	*Bacillus subtilis*	[14]
MerCEFT	ABC family	*Pseudomonas* K-62	[16]
ZupT	ZIP family	*Escherichia coli*	[12]
Zrt	ZIP family	*Saccharomyces cerevisiae*	[13]
Irt	ZIP family	*Saccharomyces cerevisiae*	[13]
Cd(II) binding proteins			
CadW		*Pseudomonas* sp. B7	[18]
MerP	ABC family	*Pseudomonas* K-62	[16]
Glutathione		*Pichia kudriavzevii*	[19]
Metallothionein		*Synechococcus* PCC 7942	[20]
Glycoprotein		*Lactobacillus plantarum* L67	[21]
LECBP		*Lentinula edodes*	[22]
Cd(II) efflux proteins			
CadA	P-type ATPase	*Staphylococcus aureus*, *Bacillus subtilis* and *Listeria*	[23-25]
TolC	RND family	*Escherichia coli*	[26]
CzcABC	P-type ATPase	*Alcaligenes eutrophus* CH34	[17]
CzcP	P-type ATPase	*Cupriavidus metallidurans* CH34	[27-28]
CzcE	CDF family	*Acinetobacter baumannii*	[29-30]
Others			
CadC		*Staphylococcus aureus*, *Bacillus subtilis* and *Listeria*	[23-25]
CzcR		*Alcaligenes eutrophus* CH34	[17]

离蛋白的表达[31-32]。Czc 系统由 CzcA、CzcB、CzcC、CzcD 和 CzcR 这 5 个蛋白组成，CzcABC 是跨质膜和细胞膜的外排蛋白。CzcD 可以缓慢地吸收 Cd(II)，从而将胞外的 Cd(II)信号传递给转录阻遏因子 CzcR[17]。随后在该系统中还发现了 CzcP 和 CzcF 两个 Cd(II)外排蛋白[27-29]。在酵母细胞中，Cd(II)的外排则与谷胱甘肽代谢有关。进入酵母细胞中的 Cd(II)通过谷胱甘肽代谢途径形成 Cd-$(GS)_2$ 复合物[19] (图 1)。属于 ABC 家族的膜转运蛋白 Ycf1 可以直接将 Cd-$(SG)_2$ 复合物转运至液泡中，从而减少镉毒害[33]。此外，细胞膜上的外排蛋白 Yorlp 则可以将细胞质中的 Cd-$(GS)_2$ 复合物转运至胞外[19] (图 1)。

1.2 胞外 Cd(II)吸附沉淀

微生物的代谢产物硫酸盐、碳酸盐、磷酸盐、草酸盐或者氢氧根离子可以与 Cd(II)形成不可溶性的镉沉淀。比如硫酸盐还原菌产生的 H_2S 气体可以与 Cd(II)在胞外形成 CdS 沉淀[34-35]；产脲酶的细菌可以催化尿素形成碳酸盐，从而形成碳酸镉沉淀[36]；土壤中促进磷酸盐或可溶性磷产生的细菌可以与 Cd(II)形成磷酸镉沉淀，

如 *Citrobacter* 具有抗镉的酸性磷酸酯酶，可分解有机-2-磷酸甘油，产生 HPO_4^-，进而与 Cd(II)形成磷酸镉沉淀[37]；此外，可以分泌草酸盐的细菌或者真菌能与 Cd(II)形成草酸镉沉淀[38](图 1)。

Cd(II)还可以通过静电相互作用、离子交换和络合吸附等方式被钝化在细胞表面[35,39]。比如细菌产生的胞外多糖(exopolysaccharide, EPS)可以结合 Cd(II)，存在于多糖中的可电离官能团如氨基、羧基、羟基、磷酸盐和硫酸盐等，是影响胞外多糖吸附能力的主要物质[35,40-41](图 1)。此外，细菌 *Pseudomonas putida* 在其 EPS 表面产生的巯基是结合 Cd(II)的重要位点[42]。

1.3 胞内 Cd(II)结合

面对 Cd(II)压力，有些微生物会产生金属结合蛋白，将进入胞内的 Cd(II)钝化或者“扣押”，进而减少 Cd(II)对 DNA 及蛋白的损伤[18]。如表 1 所示，细菌中富含半胱氨酸的金属硫蛋白(BmtA)就是一种最常见的 Cd(II)结合蛋白。*Synechococcus* PCC 7942 中的 SmtA 为一种典型的 BmtA 蛋白，该蛋白包含 4 个半胱氨酸和 2 个组氨酸保守位点，可以结合 Cd(II)和其他金属离子[20,43]。SmtB 为 SmtA 编码基因的阻遏调控蛋白，当 Cd(II)存在时可以解除这种阻遏现象，进而激活 SmtA 编码基因的转录[44]。在 *Pseudomonas* sp. B7 中，鉴定到一种新型的 Cd(II)结合蛋白 CadW，其 Cd(II)保守结合位点为 123 位 His 残基[18] (图 1)。此外，在 *Lactobacillus plantarum* L67 和 *Lentinula edodes* 中，glycoprotein 和 LECBP 分别被证实为 Cd(II)结合蛋白[21-22]。

1.4 DNA 和蛋白质损伤修复

Cd(II)进入微生物细胞内，使胞内氧化自由基增加，从而引起氧化压力，导致脂质过氧化和 DNA 损伤。细菌中的谷胱甘肽(GSH)、超氧化物歧化酶(SOD)、过氧化氢酶(CAT)和谷胱甘肽还原酶等都参与到了降低胞内氧化压力的过程中(图 1)。为了降低氧化压力，*Rhizobium* sp. 将乙醛转化成乙醇[45]，还有些细菌将乙二醛转化为乳酸[46]。

在 Cd(II)胁迫下，细菌中也进化出了一系列与 DNA 和蛋白损伤修复相关的基因。在 Cd(II)诱导条件下，错配修复基因 *mutLS*、碱基切除修复基因 *Nudix* 家族和重组修复基因 *rec* 家族等 DNA 修复相关基因上调表达[47]。Wu 等[48]发现，*Alishewanella* sp. WH16-1 细菌中的 RuvCAB 蛋白能够修复因 Cd(II)引起的 DNA 损伤，而且调控蛋白 RuvR 调控该 DNA 损伤修复系统的转录。此外，与蛋白合成和修复相关的蛋白也受 Cd(II)的诱导，如核糖体蛋白 S1、天冬氨酸转氨酶和能量代谢蛋白(磷酸甘油酸激酶、NADH 脱氢酶、琥珀酸脱氢酶黄素蛋白和无机焦磷酸酶)和热休克蛋白(HtpG、HSP12、GroEL 和 DnaK)等[32,49-51]。

2 微生物与微生物互作促进镉钝化

自然界中的微生物存在着协同、共生、互惠、寄生或竞争的生存方式，它们通过分子和遗传信息的传递来进行相互作用。这种相互作用与微生物的次级代谢物、群体感应系统、生物被膜形成和细胞信号转导等有关[52]。生物被膜是吸附 Cd(II)的重要物质，White 等[53]发现，几种硫酸盐还原菌共培养产生的生物被膜中含有更多的可结合 Cd(II)的蛋白和 EPS。Li 等[54]发现多种细菌产生的生物被膜吸附 Cd(II)的量，比单一菌株产生的生物被膜中的镉累积量增加了 25%–30%。将 *Bacillus cereus* DS16、*Actinomyces meyeri* CIP 13148、*Escherichia coli* O157:H7 和 *Pseudomonas fluorescens* CP003194 菌株混合培养后，与单独培养条件相比，混合

菌株产生更多的生物被膜，进而赋予细菌更高的 Cd(II)吸附效率[55]。我们前期研究发现了 1 株产生物被膜的 *Comamonas* sp. A23 和 1 株产硫化氢的 *Enterobacter* sp. A11，两菌组合后显著提高了生物被膜的含量，从而提高了菌株去除溶液中镉离子的能力[35]。

为了研究菌株互作促进生物被膜产生的机制，Boyer 等[56]发现，*Pseudomonas aeruginosa* 产生的酰基-高丝氨酸内酯(AHLs)能够诱导 *Burkholderia cepacia* 菌株参与生物被膜形成相关基因的表达。Stoner 等[57]发现 *Pseudomonas aeruginosa* 分泌的胞外多糖 Psl 可以促进 *Streptococcus salivarius* 生物被膜的产生。Ch'ng 等[58]发现 *Staphylococcus aureus* 为 *Enterococcus faecalis* 的有氧呼吸过程提供了血红蛋白，进而促进 *Enterococcus faecalis* 生物被膜的产生。采用差异蛋白质组学和代谢组学分析技术，我们发现在相互作用去除镉的过程中，A23 菌株促进了 A11 菌株中 4-羟基苯乙酸降解产生琥珀酸的代谢途径，并发现琥珀酸为两菌互作的关键信号分子；另外，体外加入琥珀酸促进菌株 A23 产生更多的生物膜来钝化镉离子[35]。

在研究 *Enterobacter* sp. A11 和 *Comamonas* sp. A23 互作提高镉离子去除机制的过程中，我们还发现在镉胁迫下，共培养菌株中肠杆菌 A11 的 H_2S 代谢、琥珀酸合成、金属离子转运和 TCA 循环等途径被激活；体外加入琥珀酸促进菌株 A11 产生更多的 H_2S，形成 CdS 沉淀来钝化镉离子，因此除了生物被膜之外，硫化氢也是两菌互作钝化镉离子的重要因子[35]。

3 微生物降低植物体内镉含量的机制

人类接触镉胁迫的途径主要来自镉超标农产品的食用，因此，农田土壤镉污染是我们最关注的污染问题。土壤是微生物的大本营，在镉污染环境中，微生物与植物之间同样进化出一系列的镉钝化互作机制。微生物与植物互作钝化镉的机制，包括降低农田土壤植物可利用态镉含量和影响植物镉解毒蛋白的活性(图 2)。

3.1 微生物降低农田土壤植物可利用态镉含量

微生物通过自身细胞吸附作用、代谢产物螯合和沉淀的方式来钝化镉，从而使土壤中生物可利用态镉的含量降低，进而降低植物的镉含量。研究表明 *Methylobacterium oryzae* CBM20 通过产生 1-aminocyclopropane-1-carboxylate deaminase (ACC)、poly-β-hydroxybutyrate (PHB)、生物被膜和胞外多糖等与 Cd(II)结合，从而降低土壤中生物可利用态的镉含量[59]。硫酸盐还原菌 SRB1-1 或 A11 产生的 H_2S 可与 Cd(II)形成 CdS 沉淀[35,60]，而细菌 *Bacillus* sp.可产生磷酸盐与 Cd(II)反应生成难溶性的 $CdPO_4$ 沉淀，进而钝化土壤中的生物可利用态镉[61]。此外，提高土壤 pH 将可溶性 Cd(II) 转化为 $Cd(OH)_2$ 沉淀是另一种重要的土壤钝化手段，如 *Serratia liquefaciens* CL-1 和 *Bacillus thuringiensis* X30 可以通过代谢升高土壤的 pH，从而减少土壤中可溶性镉的含量[62]。

3.2 微生物影响植物镉转运和镉结合蛋白的活性

微生物可以通过调节植物激素水平影响植物中 Cd(II)转运基因的表达(图 2)。研究发现脱落酸可以抑制植物中 Fe(II)吸收蛋白 IRT1 的活性，从而限制 Cd(II)的摄入[63]。因此，施加产脱落酸的细菌可以减少植物对 Cd(II)的吸收[64]。Zhou 等[65]还发现不产脱落酸的 Cd(II)抗性细菌 *Enterobacter asburiae* NC16 抑制了小麦中脱落酸分解途径，使小麦中脱落酸含量升高，从而

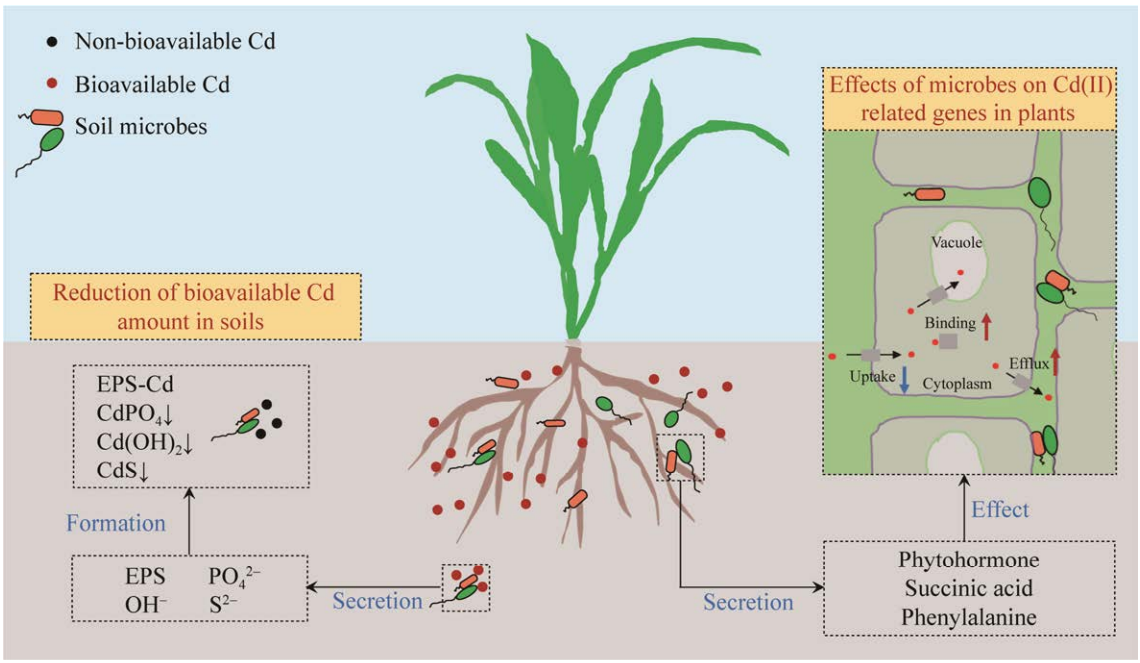

图 2 微生物降低植物中的镉含量 微生物降低植物中镉含量的机制分为减少土壤中生物可利用态镉含量和影响植物中镉相关基因. 微生物分泌的胞外多糖钝化土壤中的 Cd(II)，分泌的磷酸盐、氢氧根和 S^{2-}与土壤中的 Cd(II)形成沉淀；微生物分泌的植物激素、琥珀酸和苯丙氨酸影响植物中镉摄入、结合和外排基因的表达水平

Figure 2 Microbe reduces cadmium content in the plant. The mechanism of microbe reduces cadmium content in plants, including the reduction of bioavailable Cd amount in soils and the effects on Cd(II) related genes in plants. Exopolysaccharide (EPS) secreted by microbes immobilized Cd(II) in soils, and the secretion of phosphate, hydroxide, and S^{2-} are used to precipitate Cd(II) in soils; Phytohormones, succinic acid, and phenylalanine secreted by microbes affect the expression levels of genes related to Cd(II) uptake, binding, and efflux in plants.

提高 IRT1 蛋白的活性。此外，乙烯同样与植物在镉环境中的生存存在相关性。*Pseudomonas fluorescens* UW4 可以通过 1-aminocyclopropane-1-carboxylate 脱氨酶降解乙烯合成的前体物质 1-aminocyclopropane-1-carboxylate，进而最终通过降低乙烯的水平来减少 Cd(II)对莴苣的胁迫[66]。

我们前期研究发现，*Enterobacter* sp. A11 和 *Comamonas* sp. A23 共培养菌剂可进入水稻根内，分布于根内的维管组织和细胞间隙中，并影响水稻的金属离子转运、植物激素信号转导、碳固定和光合作用等，这 2 株菌会激活水稻中的超敏反应、防御感应系统和 MAPK 信号途径来增强水稻对 Cd(II)的抗性；此外，这 2 株菌产生的琥珀酸可以激活水稻根部 Cd(II)结合蛋白(HIP28-2 和 CDI8)和 Cd(II)外排蛋白(BCP1)的表达，抑制 Cd(II)摄入蛋白(COPT4 和 HKT6)的表达，从而减少水稻中镉的含量；但 2 株菌产生的另一种代谢产物苯丙氨酸则可以通过激活水稻根部 Cd(II)结合蛋白(HIP28-1、HIP28-4、BCP2 和 CDI8)的表达来抑制 Cd(II)摄入蛋白(NRAM5 和 HKT6)的表达，以减少水稻中镉的含量[67]。然而，是否还存在其他的诱

导植物 Cd(II)吸收与转运的物质，以及它们之间的相互作用机制仍值得进一步研究。

4 镉污染的微生物修复

4.1 吸附和沉淀

细菌细胞表面或者产生的 EPS 中的大量带负电荷官能团赋予了它们较强的 Cd(II)吸附能力，这些官能团包括羟基、羧基、磷酰基和氨基[68]。*Pseudomonas*、*Enterobacter*、*Bacillus* 和 *Lactobacillus* 等细菌已被发现通过吸附的方式修复 Cd(II)污染[17,35,69-72]。真菌的细胞壁上含有带负电荷的物质如葡聚糖、甘露聚糖、纤维素、几丁质和蛋白质等，也是吸附 Cd(II)的优良材料[73]。藻类细胞壁含有大量果胶质、纤维素和多种多糖，使其具有多孔结构和较大的表面积，并且细胞表面带负电的官能团使其对 Cd(II)也具有较强的吸附能力[74]。莱茵衣藻、狐尾藻、涠洲马尾藻和小球藻等吸附 Cd(II)的研究均有报道[75-78]。目前，利用微生物细胞作为吸附材料进行 Cd(II)污染水体修复已经取得了良好的效果。*Rhodobacter sphaeroides* 在 Cd(II)浓度为 10 mg/L 的废水中对 Cd(II)的去除率为 97.92%[79]。产生物被膜的 *Scenedesmus obliquus* FACHB-12 在 Cd(II)浓度为 3 mg/L 水体中的 Cd(II)去除效率为 61.8%[80]。*Phanerochaete chrysosporium* 处理 Cd(II)污染废水的最大吸附能力可为 104.8 mg/g[81]。此外，细菌产生的带有负电荷的纳米材料，比如硒纳米和碲纳米等也具有良好的 Cd(II)吸附能力[82-83]。

微生物产生的金属硫蛋白、植物螯合肽(主要由藻类和真菌产生)和纳米材料是钝化 Cd(II)的有效螯合剂。研究发现，过表达金属硫蛋白和植物螯合肽的细菌表现出良好的 Cd(II)钝化能力[84-85]。Zhou 等[43]制备的金属硫蛋白 SmtA 与生物合成的硒纳米材料 SmtA-SeNPs 对 Cd(II)和 Pb(II)均具有高效的吸附能力，其中对 Cd(II)的最大吸附量为 506.3 mg/g。

微生物产生的 H_2S 气体或者有机酸可以与 Cd(II)形成沉淀，从而减少生物可利用态 Cd(II)的含量。在 Xia 等[86]的研究中发现硫酸盐还原菌 *Alishewanella* sp. WH16-1 能够产生 H_2S 气体，并且在含 Cd(II)条件下形成 CdS 沉淀。将这株菌与海藻酸钠固定化后应用于 Cd 污染土壤中，菌株 WH16-1 使土壤中生物可利用态 Cd 含量降低了 50%，使稻米中 Cd 含量下降了 78.3%[87]。另一株产 H_2S 气体的 *Enterobacter* sp. A11，在 *Comamonas* sp. A23 存在的条件下产生更多的 H_2S 气体，并使其 Cd(II)去除率从 11%升高到 97.4%，将这种混合菌剂应用到 Cd(II)污染土壤后使土壤中生物可利用态 Cd 和小白菜中 Cd 含量显著下降[35]。

4.2 微生物与化学材料联用

将微生物与化学材料联合使用，在保证了微生物材料 Cd(II)吸附能力的同时，增强了微生物对不利环境的抗性，而且方便将吸附重金属后的微生物材料从环境中分离。海藻酸钠、海藻酸钙、聚砜、聚丙烯酰胺、聚氨酯和二氧化硅等都是良好的微生物固定材料[88]。目前，用镉吸附菌剂与磁性纳米颗粒制得的新型生物修复剂也已经被应用于镉污染水体的修复中，这些磁性纳米材料包括聚乙烯醇磁性材料(Fe_3O_4@Cu/PVA)、磁性氧化石墨烯(MGO)、壳聚糖磁珠等。将 *Pseudomonas* sp. H117 与聚乙烯醇磁性材料(Fe_3O_4@Cu/PVA)包埋，使其镉去除效率提高 7.09%[89]。用壳聚糖磁珠固定 *Aspergillus sydowii* 后，使其 Cd(II)吸附量从 40.94 mg/g 提高到 56.4 mg/g[90]。此外，生物炭与镉吸附菌剂包埋材料也是一种良好的镉去除材料，比如 *Phoma* sp. ZJ 与生物炭包埋处理 Cd(II)污染废水[91]，以及生物炭包埋 *Pseudomonas* sp.

NT-2[92]、*Enterobacter* 和 *Klebsiella*[93]等镉吸附菌剂，均展现出良好的 Cd(II)去除能力。生物炭既可以作为微生物减小镉毒害的保护剂，也可为微生物提供生长所需的营养物质，从而增强了微生物的镉钝化能力。合适的固定材料和包埋技术将是决定微生物吸附剂能否广泛应用的关键因素之一。

4.3 微生物增强超富集植物对镉的去除

微生物协同超富集植物的修复方式是重金属污染土壤原位修复的重要方式。微生物分泌的铁载体、有机酸和生物表面活性剂等可以增加生物可利用态金属的含量和移动性，使其更容易被植物吸收。很多根际微生物分泌的氨基酸、脱落酸、吲哚乙酸、赤霉酸、胞外多糖、细胞分裂素和挥发性化合物可以促进植物生长，进而增强植物的修复能力[94-95]。植物也会为微生物提供栖息的场所，并且释放一些碳水化合物、羧酸和氨基酸等物质为微生物提供营养[96-97]。*Serratia marcescens* HB-4 菌株与鱼腥草联合使用，可以使鱼腥草的镉吸附量提高 44.27%[98]。此外，*Pseudomonas fluorescens* 与白杨、*Rahnella* sp. JN6 与小白菜、*Paecilomyces lilacinus* NH1 与龙葵等联合使用，均显著提高植物 Cd 修复的效果[99-101]。这种微生物与植物联合修复的方法不仅可以克服植物生长缓慢和土壤中生物可利用态金属含量低等植物修复中遇到的问题，还可以解决微生物不容易稳定定殖的难题。

目前，随着细菌中越来越多的 Cd(II)结合蛋白被发现，通过遗传手段构建转基因的超富集植物进行重金属污染修复也取得了不错的效果。将细菌中的 Cd(II)结合蛋白基因 *cadR* 转入拟南芥中可以使拟南芥的根部和茎中的镉积累量分别提高 5.2 倍和 3.5 倍[102]。将 *Saccharomyces cerevisiae* 中的金属硫蛋白基因 *CUP1* 和 *ScMTII*，*E. coli* 中的谷胱甘肽合成酶基因 *gshI* 和 *gshII*，*E. coli* 中的谷氨酰半胱氨酸合成酶基因 *ECS*，*Enterobacter cloacae* 中的 ACC-脱氢酶基因，以及 *S. cerevisiae* 中的液泡扣押基因 *YCF1* 构建到超富集植物中，可以提高超富集植物的镉吸附量[103-104]。

4.4 其他微生物修复策略

生物反应器是利用微生物进行镉去除的有用方法，基于生物被膜吸附 Cd(II)、硫酸盐还原菌沉淀 Cd(II)和产生物被膜的硫酸盐还原菌钝化 Cd(II)的生物反应器是较常用的 3 种方法。微生物电化学方法比如基于微生物电化学硫酸盐还原系统以电解水产生的氢气作为自养型硫酸盐还原菌(SRB)的电子供体，并利用含 SO_4^{2-} 的废水作为硫源，经还原产生的含 S^{2-} 水溶液作为钝化剂，进而与 Cd(II)反应生成难溶性的 CdS 沉淀[105]。此外，采用基因工程技术构建 Cd(II)修复工程菌也有相关研究，如过表达 CrMTP4 蛋白的工程衣藻 *Reinhardtii* 显著增加了对 Cd 的抗性及积累[106]；将金属结合肽 CP2 和 HP3 表面展示在 *Saccharomyces cerevisiae* 中能显著提高其对 Cd(II)和 Zn(II)的吸附能力[107]。

5 展望

由于重金属无法降解且难以从环境中提取，目前针对土壤中镉污染的主要手段还是以降低其生物有效性将其在环境中钝化，进而减少粮食作物对可溶性镉的吸收为主。镉钝化微生物大多分离自镉污染的环境中，将其作为修复手段应用到土壤污染修复中具有价格低廉、环境友好等优势。随着越来越多镉钝化微生物的鉴定及其与植物间互作机制的解析，微生物在未来镉污染修复的应用中将会发挥重要作用。虽然利用微生物进行镉污染的修复有很多优势，但同时也面临很多挑战。(1) 镉污染农田

土壤具有复杂性，常伴随着多种重金属的复合污染，如重金属镉-砷或镉-铬复合污染。重金属砷或铬会影响镉钝化微生物的活性，然而目前关于复合污染环境中微生物的镉解毒机制仍认识不足，下一步需加强微生物在复合重金属污染条件下解毒机制的探究。(2) 微生物互作促进生物被膜和硫化氢形成的机制，以及是否还有其他镉钝化机制尚不清楚。下一步建议开展微生物组和多物种生物被膜及硫化氢形成机制的研究，挖掘镉钝化功能基因，并从生物被膜的组成、结构、形成途径、调控硫化氢形成的信号分子等方面进行探究。(3) 在重金属污染环境中，微生物与植物互作具有重要的生物学意义，然而植物的代谢产物对微生物代谢的影响，以及植物中受微生物诱导的镉吸收与转运途径尚无确切的答案。下一步需推进多组学联用的方式，解析微生物与植物中调控重金属转化与解毒途径的研究，从表观特征、功能基因、代谢产物和调控途径等方面构建微生物与植物的相互作用网络。

微生物菌剂具有广阔的应用前景，但微生物污染修复方面同样也面临着诸多挑战，针对如何根据不同的环境条件去选择合适的微生物，如何让镉钝化微生物在土壤中稳定定殖，以及如何协调镉钝化优势菌与土著微生物的平衡关系等问题，未来的镉污染微生物修复中应该加强以下几个方面的研究：探究温度、pH、营养物质和其他环境因素对微生物的生存及定殖的影响；开展根际微生物、植物内生菌等植物益生菌重金属钝化的研究与应用；解析土壤-植物系统中微生物的迁移与生态健康的关系，优化土壤微生物的镉钝化功能，利用合成生物学技术构建可持续发展和促进生态健康的功能微生物。

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