

• 综 述 •

微生物抗汞的分子机制及其在汞污染土壤修复中的应用前景

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摘 要: 汞污染土壤对环境 and 人类健康构成了重大威胁。抗汞微生物具备在无机汞和有机汞胁迫条件下存活的能力, 并能有效减少汞的含量和毒性。相比传统的物理和化学修复方法, 微生物修复技术因其成本低、效果显著且对环境影响较小, 近年来备受关注。本文系统阐述了微生物抗汞的分子机制, 重点探讨了其在与植物互作联合修复汞污染土壤中的应用潜力, 并揭示了微生物在促进转基因植物修复汞污染中的关键作用, 为汞污染土壤的生物修复提供了理论基础和科学依据。

关键词: 微生物; 抗汞分子机制; 汞污染土壤; 生物修复

Molecular mechanisms of microbial mercury resistance and their prospective applications in remediation of mercury-contaminated soils

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Abstract: Mercury (Hg)-contaminated soil poses a significant threat to the environment and

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human health. Hg-resistant microorganisms have the ability to survive under the stress of inorganic and organic Hg and effectively reduce Hg levels and toxicity. Compared to physical and chemical remediation methods, microbial remediation technologies have garnered increasing attention in recent years due to their lower cost, remarkable efficacy, and minimal environmental impact. This paper systematically elucidates the molecular mechanisms of Hg resistance in microbes, with a focus on their potential applications in phytoremediation of Hg-contaminated soils through plant-microbe interactions. Furthermore, it highlights the critical role of microbes in enhancing the effectiveness of transgenic plants for Hg remediation, aiming to provide a theoretical foundation and scientific basis for the bioremediation of Hg-contaminated soils.

Keywords: microorganisms; molecular mechanisms of mercury resistance; mercury-contaminated soil; bioremediation

汞(mercury, Hg)是唯一在常温常压下以液体形态存在的有毒重金属,其在环境中主要以元素汞、无机汞和有机汞这3种形式存在^[1]。汞主要来源于自然释放,如火山爆发、含汞矿物和土壤风化等;以及人为活动,如矿山开采、金属冶炼、氯碱工业、垃圾焚烧和化肥农药的广泛使用^[2]。大气中的汞通过大气环流并经干、湿沉降以 Hg^{2+} 形式进入土壤中^[3]。土壤中的 Hg^{2+} 可被厌氧微生物转化为毒性和生物利用度更高的甲基汞(MeHg)^[4-6]。MeHg 在生物体中具有极高的生物蓄积能力,并通过食物链放大,最终在人体内累积,严重威胁人类健康,是最危险的汞化合物之一^[7-8]。随着全球工业的快速发展,环境中 Hg 的释放量显著增加,导致土壤汞污染日益严重,尤以矿山和工厂周围的土壤汞污染最为严重。受汞矿分布及工业发展状况影响,全球土壤总汞浓度呈现出北半球高、南半球低的趋势,而中国土壤总汞浓度则表现为南高北低的特点^[9-10]。据报道,贵州省铜仁汞矿区土壤总汞浓度范围为 1.06–631.31 mg/kg,土壤 MeHg 浓度为 0.05–2.92 mg/kg,给生态系统和人类健康带来重大风险^[11]。汞作为一种全球性污染物,已引起了国内外的高度关注。我国生态环境部于 2017 年推动履行《关于汞的水俣公

约》,旨在解决与汞污染相关的全球性问题^[12-13]。

目前,汞污染土壤修复主要集中在传统的物化方法上,例如客土覆盖、污染土壤移除、土壤淋洗、电动修复、化学沉淀、萃取、电渗析等。这些方法虽然有一定效果,但存在成本高昂、操作费力、受环境制约大、破坏土壤结构以及容易造成二次污染等缺点^[14]。此外,这些技术通常只适用于小规模的重度污染场地,而汞污染往往能够从点源扩散到较远的地方,影响居民区和农业区,这些大面积污染区域不便采用传统修复技术^[15]。因此,迫切需要一种经济、高效、环保且可持续的修复方法。近年来,随着微生物技术的不断发展,微生物修复技术得到了越来越多的关注^[16]。土壤重金属微生物修复技术是利用细菌、真菌和少数藻类通过吸收、沉淀和转化等方式减小土壤中重金属污染物毒性和含量的过程,具有成本低、修复效果好、对环境友好等优势^[17]。目前,国内外学者已从汞污染环境中分离筛选出对汞化合物具有抵抗能力的微生物,并研究了其抗汞机制,发现它们具有去除汞的能力,可用于修复汞污染土壤^[18]。然而,关于抗汞微生物及其在汞污染土壤修复中的应用的综述较少。因此,本文将重点阐述抗汞微生物的抗汞分子机制,并概

述其在修复汞污染土壤中的应用, 以期汞污染土壤的生物修复提供理论支持和科学依据。

1 环境中的抗汞微生物

抗汞微生物是指能够在含有高浓度汞的环境中存活和繁殖, 并通过吸收、转化或外排环境中的汞化合物, 减小汞对其毒害的微生物, 包括细菌、真菌、藻类等^[19]。抗汞微生物能将汞从剧毒形式转化为低毒形式, 其数量与环境中的汞污染规模成正比^[20]。目前, 利用抗汞微生物来减轻汞对生态系统的毒害正逐步受到研究者的青睐。例如, 假单胞菌属(*Pseudomonas* sp.)、克雷伯氏菌属(*Klebsiella* sp.)、鞘氨醇单胞菌属(*Sphingomonas* sp.)、沙雷氏菌属(*Serratia* sp.)、芽孢杆菌属(*Bacillus* sp.)、肠杆菌属(*Enterobacter* sp.)等抗汞细菌已被发现在修复土壤汞污染中具有广阔的前景^[21]。酿酒酵母菌(*Saccharomyces cerevisiae*)、绿僵菌(*Metarhizium anisopliae*)、丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)等抗汞真菌也可以通过吸附和积累汞化合物来减少汞污染土壤中的汞含量^[22]。此外, Urik 等^[23]发现, 丝状真菌, 特别是黑曲霉(*Aspergillus niger*)和枝孢菌(*Cladosporium* sp.)具有巨大的挥发除汞能力, 在黑暗中静态培养 7 d 后, 它们挥发了培养基中近 80% 的汞。少数藻类, 如蓝藻(*Cyanobacteria*), 也展示出对汞具有一定的耐受性和富集能力^[24]。环境中存在种类繁多的抗汞微生物, 它们在汞胁迫下进化出多种抗汞机制, 且不同物种的抗汞途径各具特异性。这些微生物在修复土壤汞污染方面展现出巨大潜力, 深入研究其抗汞机制对于汞污染治理和环境保护具有重要指导作用。

2 微生物抗汞机制

抗汞微生物多来源于汞污染环境, 并在高浓度汞胁迫下进化出多种抵抗和去除汞的机

制, 包括胞外隔离(胞外吸附和生物沉淀)、生物积累以及生物转化(图 1)^[25-26]。这些微生物根据其种类和特定的环境条件, 能够单独或协同利用上述机制来应对汞污染。

2.1 微生物对重金属的细胞外隔离

微生物通过胞外吸附和生物沉淀将重金属隔离在细胞外, 阻止重金属进入细胞, 从而抵抗其毒害作用^[26]。这种胞外隔离不仅减少了汞对微生物的直接毒害, 还可有效地固定环境中的汞, 降低其生态毒性^[27-29]。其中, 微生物分泌的带负电荷的胞外聚合物如胞外多糖(exopolysaccharides, EPS)在汞的胞外吸附进程中发挥着重要作用^[30]。EPS 分子结构中包含多种阴离子官能团(如羧基、羟基、巯基等), 这些官能团能够以非特异性方式结合 Hg^{2+} 等重金属阳离子, 将其吸附至细胞壁表面, 从而减少汞的毒害^[31]。Oyetibo 等^[32]证实亚母酵母菌(*Yarrowia* spp.)分泌的 EPS 可与 Hg^{2+} 结合形成 EPS-Hg 复合物; Kalpana 等^[33]发现产 EPS 的蜡样芽孢杆菌(*Bacillus cereus*) VK1 能够在 LB 培养基中吸附约 80.22 μg 的 Hg^{2+} , 在响应面分析法优化的 M9 基础培养基中吸附约 295.53 μg 的 Hg^{2+} 。

此外, 微生物产生的初级或次级代谢产物可与重金属离子结合形成稳定沉淀, 进一步降低重金属的毒性^[34]。例如, 细菌代谢产生的多种硫化物可与汞离子形成稳定的 HgS 沉淀, 从而减少甚至消除汞的毒性^[35]。研究显示, *Pseudomonas* sp. AN-B15 可通过将 Hg^{2+} 转化为 HgS 和 Hg -巯基来去除 Hg^{2+} ^[36], 而肺炎克雷伯菌(*Klebsiella pneumoniae*) M426 通过释放有机硫化物气体将溶液中的汞转化为沉淀^[37]。此外, 微生物还可通过光合作用、尿素水解、氨化、反硝化等途径实现微生物诱导碳酸盐沉淀, 产生的 CO_3^{2-} 可与多种重金属离子结合形成沉淀, 如 HgCO_3 、 CdCO_3 等^[38]。

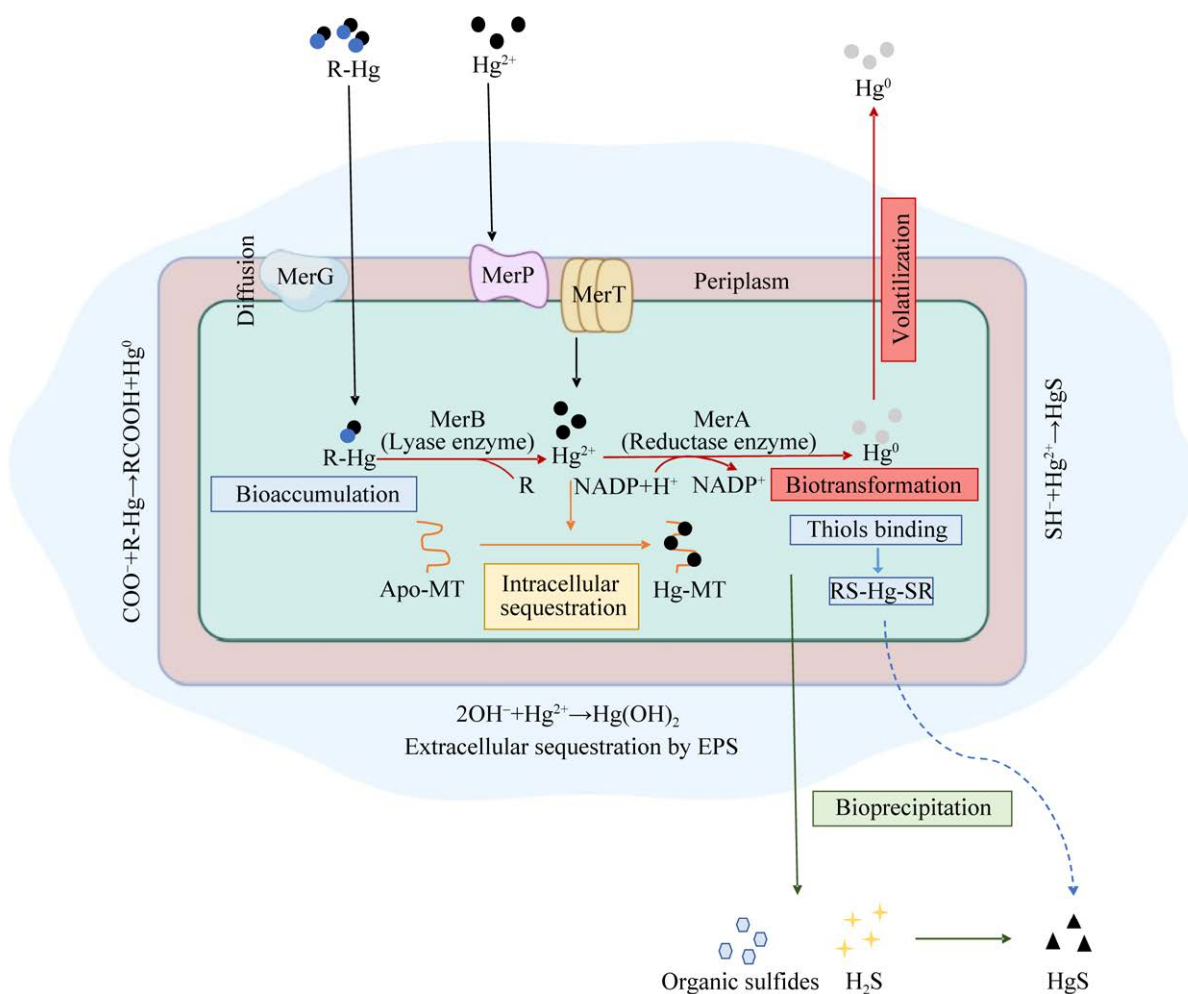


图 1 微生物抗汞机制 R 为烷基。

Figure 1 Microbial mechanisms of mercury resistance. R refers to alkyl groups.

微生物对汞的细胞外隔离是其抵抗汞胁迫及去除汞污染的重要机制，包括微生物分泌的EPS 对汞的吸附作用和代谢产物对汞的沉淀作用。尽管许多微生物已显示出通过胞外吸附和生物沉淀修复汞污染的潜力，但深入研究这些机制有助于最大化微生物在汞污染修复中的应用潜力。

2.2 微生物硫醇化合物螯合作用促进重金属细胞内生物积累

与胞外隔离不同的是,生物积累是指微生物吸收环境中的汞,并将其存储在细胞内部^[39],形成汞-微生物复合物。金属硫蛋白(metallothionein,

MT)和植物螯合素(phytochelatin, PC)等硫醇化合物在微生物细胞对汞的生物积累过程中起着至关重要的作用^[40-41]。MT 和 PC 均富含半胱氨酸,其半胱氨酸上的硫醇基团可以螯合金属阳离子,结合形成 HM-MT 和 HM-PC 络合物^[42-43]。研究发现,转入 *mt* 基因的 *mt-1* 转基因大肠杆菌(*Escherichia coli*)能够在培养基中积累高达 100.20 $\mu\text{mol/L}$ 的汞,MT 的金属封存特性在汞污染修复中具有广阔的前景^[44]。

汞可大量积累于真菌体内，圆红冬孢酵母 (*Rhodotorula toruloides*)、大型真菌(*Macrofungi*)、膝曲弯孢 (*Curvularia geniculata*) 和青霉菌

(*Penicillium*)等都被发现具有很强的汞积累能力^[45-48]。Gordeeva 等^[46]发现氯碱厂和冶金厂周围生长的蘑菇体内汞浓度甚至高于其生长土壤中的汞浓度,具有很强的积累能力。目前,也有一些具备汞积累能力的细菌被发现。例如,从金矿开采地点分离的南海假芽孢杆菌(*Fictibacillus nanhaiensis*)和东洋芽孢杆菌(*Bacillus toyonensis*)的汞积累率分别高达 82.25%和 81.21%^[49]。来自海洋环境中的 *Pseudomonas* sp. S1 对无机汞的积累量为 133.33 mg/g^[50]。*Enterobacter* sp. EMB21 通过将汞积累在细胞内,能去除培养基中 99% 的汞^[51]。综上所述,微生物在汞积累方面展现出卓越潜力,使其成为汞污染修复的理想选择。

2.3 微生物 *mer* 操纵子介导的生物转化

抗汞微生物通过其独特的代谢机制,可将环境中的 Hg^{2+} 高效转化为挥发性的 Hg^0 , 从而实现汞的去除。目前,相关机制的研究主要聚焦于细菌^[23]。研究表明,细菌主要通过调控位于质粒、Tn21 转座子、基因组 DNA 或整合子上的 *mer* 操纵子来催化汞的挥发^[52]。细菌 *mer* 操纵子由一系列与抗汞功能相关的基因组成,控制汞的转运、转化过程(表 1)^[59]。细菌 *mer*

操纵子分为抵抗无机汞的窄谱型 *mer* 操纵子(*merR*、*merT*、*merC*、*merF*、*merP*、*merA* 和 *merD*)以及抵抗无机汞和有机汞(MeHg 和苯汞)的广谱型 *mer* 操纵子(*merR*、*merT*、*merP*、*merE*、*merA*、*merB*、*merG* 和 *merD*)^[60]。

细菌 *mer* 操纵子介导的汞生物转化机制包括细菌对汞的捕获、转运和转化过程(图 2)。由 *merA* 基因编码的汞还原酶(MerA)和由 *merB* 基因编码的有机汞裂解酶(MerB)是 *mer* 操纵子中负责催化汞形态转化的 2 个关键蛋白^[26]。MerA 存在于细菌细胞质中,是一种黄素蛋白,参与 *mer* 操纵子的窄谱机制,它以 NAD(P)H 为电子供体将 Hg^{2+} 还原为 Hg^0 , 并扩散至细胞外^[19]。当细胞外存在汞离子时,正调控因子 *merR* 基因的产物在与操纵子结合的部位发生扭曲折叠,允许 RNA 聚合酶进入进行 *merT*、*merP* 和 *merA* 基因转录^[57]。位于质膜外的周质 Hg^{2+} 结合蛋白 MerP 的半胱氨酸残基 Cys17 和 Cys14 与 Hg^{2+} 结合,形成 S-Hg 中间体,然后转移到跨细胞膜的汞转运蛋白 MerT 上的半胱氨酸残基上,MerT 将 Hg^{2+} 从位于膜周质侧的 2 个半胱氨酸残基转移到位于胞质侧的 2 个半胱氨酸残基上,使 Hg^{2+} 转运至细胞内^[61-62]。

表 1 细菌 *mer* 操纵子中不同基因及其功能

Table 1 Different genes in the bacterial *mer* operon and their function

Genes	Coded Protein	Location	Functions	References
<i>merA</i>	Hg^{2+} reductase	Cytoplasm	Conversion of Hg^{2+} to Hg^0	[26]
<i>merB</i>	Organomercurial lyase	Cytoplasm	Lysis of C-Hg bond	[26]
<i>merP</i>	Periplasmic Hg^{2+} binding protein	Periplasm	Transfer of Hg^{2+} to integral membrane proteins	[53]
<i>merT</i>	Hg^{2+} transport protein	Inner membrane	Transport of Hg^{2+}	[54]
<i>merC</i>	Hg^{2+} transport protein	Inner membrane	Transport of Hg^{2+}	[54]
<i>merF</i>	Hg^{2+} transport protein	Inner membrane	Transport of Hg^{2+}	[54]
<i>merE</i>	MeHg transport protein	Inner protein	Uptake of organo-mercurials into cytoplasm	[55]
<i>merG</i>	Phenylmercury resistance protein	Periplasm	Resistance to phenyl-mercury by efflux mechanism	[56]
<i>merR</i>	Regulator protein	Cytoplasm	Positively regulates the <i>mer</i> operon	[57]
<i>merD</i>	Regulator protein	Cytoplasm	Negatively regulates the <i>mer</i> operon	[58]

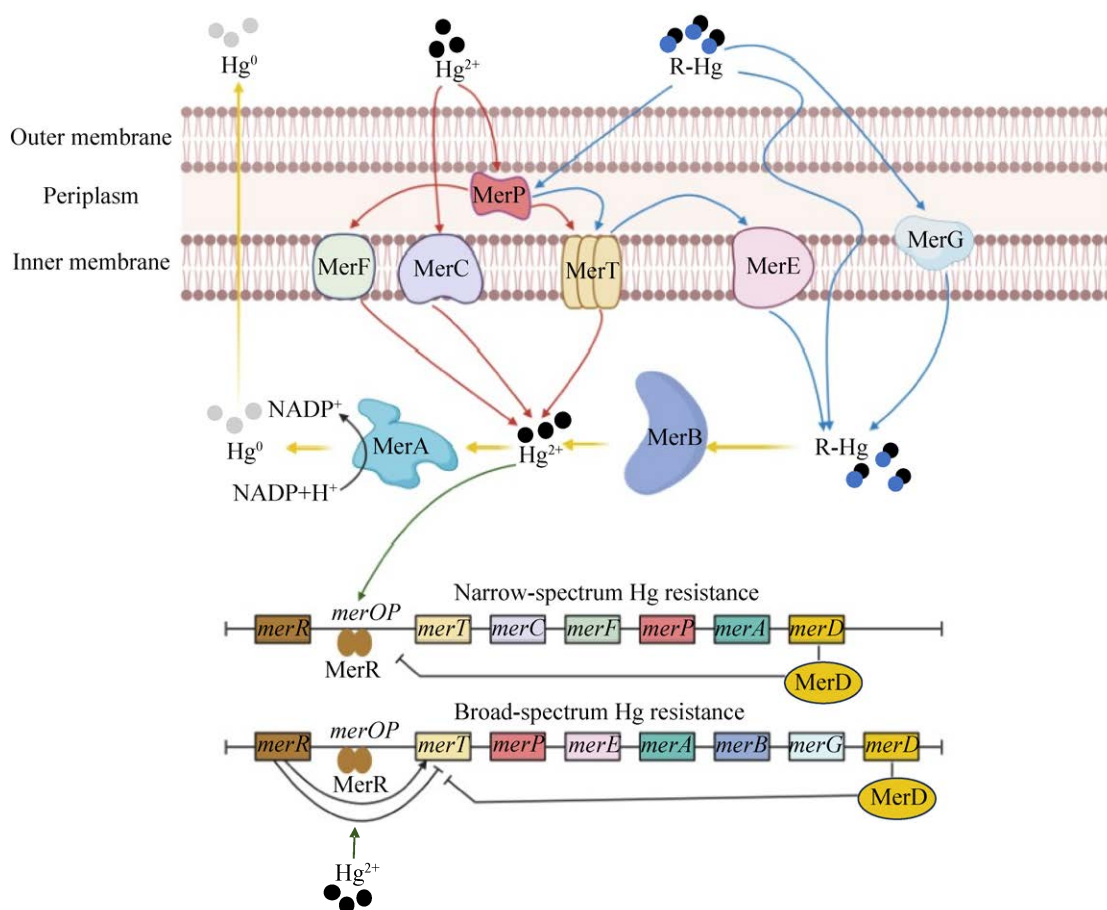


图2 细菌 *mer* 操纵子对无机汞(窄谱)和有机汞(广谱)抗性机制 R 为烷基。

Figure 2 Mechanism of bacterial *mer* operon resistance to inorganic mercury (narrow spectrum) and organic mercury (broad spectrum). R refers to alkyl groups.

随后, Hg^{2+} 通过 MerT 上的半胱氨酸基团直接传递至细胞内 MerA 氨基末端结构域中的 2 个半胱氨酸残基, 并经由分子间传递进一步转移至 MerA 活性位点的 2 个半胱氨酸残基, 最终在 NAD(P)H 的作用下被还原为挥发性 Hg^0 [63-64]。

MerB 存在于细菌细胞壁中, 参与 *mer* 操纵子的广谱机制, 通过裂解碳-汞键催化有机汞化合物的去甲基化。有机汞因具有脂溶性而不需要经过 MerT、MerP 的转运就可以直接进入细胞质内, 此外 MerP、MerT、MerE、MerG 也可以参与有机汞的转运 [53]。有机汞进入细胞质后与 MerB 去质子化的 Cys159 和 Cys96 结合, 由

Asp99 提供质子打开 C-Hg 键, 释放出有机部分, 而 Hg^{2+} 与 Cys96 和 Cys159 的硫醇基形成以汞为中心的三角形中间物质, 随后 S-Hg 键被临近的 MerA 蛋白 C 端的 Cys559 与 Cys558 取代, 使 MerB 上的 Hg^{2+} 快速传递至 MerA 的活性部位, 进而还原为 Hg^0 [65]。

mer 操纵子的表达受 *merR* 基因编码的 Hg^{2+} 依赖性反式作用激活物-阻遏蛋白(MerR)的调节。MerR 在没有 Hg 的情况下抑制操纵子的表达, 并在存在 Hg 时通过与 Hg 结合而失去对操纵子的抑制作用 [66]。MerR 蛋白 C 端的汞结合域能与汞形成独特的平面配位三角结构, 不仅

提高了汞的亲合力,还起到了区分汞与其他金属的作用^[66]。*merO* 基因位于 MerR 结合的 *mer* 位点的操作区,对 *mer* 操纵子基因的表达产生正负调控作用^[26]。汞与 MerR 结合时,MerR 构象发生改变并从 *merO* 结合位点解离,使 RNA 聚合酶能够结合并开始转录结构基因^[53]。*merD* 基因也参与调节操纵子的表达,因为它编码的调节蛋白(MerD)是 MerR 的拮抗剂,MerD 可以与 MerR 竞争 *merO* 结合位点,当汞浓度很低时,MerD 占据 *merO* 位点从而抑制 *mer* 操纵子的表达^[58,67]。

目前,抗汞细菌的分离以及细菌 *mer* 操纵子介导的汞的生物转化受到研究者的广泛关注。Mahbub 等^[68]从汞污染土壤中分离得到 *Sphingomonas* sp. SA2,发现其产生汞还原酶,并通过细菌细胞吸附和挥发去除汞。Binish 等^[69]分离得到的弗氏柠檬酸杆菌(*Citrobacter freundii*) MM7 能够在 10 d 内去除培养基中 80% 的汞,且携带 *merA* 基因。Singh 等^[70]的研究中发现摩根根菌(*Morganella* sp.) IITISM23 的 *merA* 基因呈阳性,并在菌株粗酶提取物中检测到汞还原酶活性。携带 *mer* 操纵子的抗汞细菌被发现具有很强的除汞能力,可以通过各种酶以高度特异性和有效的方式将有机汞和无机汞转化为毒性更小的挥发性的 Hg^0 ,并无需额外能量消耗即可扩散至细胞外及其周围环境,具有修复汞污染环境的巨大潜能,利用这类细菌进行汞污染场地修复是一种有前景的方法。

3 微生物在汞污染土壤修复中的应用

3.1 汞污染土壤的微生物修复

尽管实验室研究发现了大量具有汞去除能力的微生物,然而,实际应用于汞污染土壤修复的研究较少。*Pseudomonas* sp. DC-B1 和 *Bacillus* sp. DC-B2 可以显著提高土壤中的汞去

除效率^[71-72]。此外,*C. freundii* Y9 在好氧和厌氧条件下分别可以将 45.80%–57.10% (好氧)、39.10%–48.60% (厌氧)的元素汞转化为不溶性汞^[73]。沸石固定化的维罗尼假单胞菌(*Pseudomonas veronii*)可以使土壤中的气态单质汞(gaseous elemental mercury, GEM)排放量提高 10^4 倍^[74]。*Sphingomonas* sp. SA2 可以去除田间土壤中 60% 的汞^[75]。高地芽孢杆菌(*Bacillus altitudinis*) MIM12 在第 4 天和第 8 天对金矿尾矿中汞的原位生物修复效率分别为 82.10% 和 95.16%^[76]。此外,真菌在修复汞污染土壤上也发挥着重要作用。例如,接种 *Penicillium* sp. DC-F11 能够去除土壤中总汞含量的 25.89%^[48]。接种真菌(*Lecytophthora* sp.) DC-F1 并与生物炭(4%)共同作用对汞的去除率为 13.30%–26.10%^[77]。此外,通过突变或转基因改造微生物,可以极大地增强其修复汞污染土壤的能力。例如,转入 *merA* 基因的转基因 *B. cereus* BW-03 (pPW-05)能够通过挥发和生物吸附去除土壤中超过 90% 的汞^[78]。然而,这些研究主要是在可控的实验室条件或盆栽试验中进行,还需进一步田间试验验证。此外,外源抗汞微生物在土壤中的定殖、生长和活性受到土壤环境和生存竞争等因素的影响,制约了抗汞微生物在汞污染土壤修复中的应用^[79]。同时,还需关注添加抗汞微生物对土壤中汞甲基化过程以及微生物群落的影响。因此,提升微生物修复土壤汞污染的作用效果,确保其生态安全性,优化其在田间的应用,均需要进一步探索和研究。

3.2 微生物辅助植物修复汞污染土壤

植物修复是一种利用植物去除被污染环境中污染物的技术,因其成本低、易于管理、绿色环保且具有观赏价值和潜在经济效益,被认为是一种可持续的修复技术^[80]。汞污染土壤植物修复技术主要包括植物提取、植物挥发和植

物稳定等^[2]。其中,最有前景的是植物提取技术,即在汞污染土壤上种植对汞具有较强累积能力的植物,通过其根系吸收土壤中汞,并将其转移到地上部分,最后通过收割地上部分来去除土壤中的汞^[81]。该技术的关键是采用汞超富集植物,但目前尚无公认的汞超富集植物,增加了利用植物修复汞污染土壤的难度^[81]。汞的生物有效性、植物生物量及其根系深度均影响植物修复效率^[82]。为了提高植物提取的效率,常使用螯合剂来提高土壤中汞的生物有效性^[83]。但螯合剂价格昂贵,并可能对生态系统造成损害,不适合大面积受污染的土壤^[81,84]。因此,

研究者提出利用植物根际或内生细菌或真菌之间的相互作用来修复污染土壤(图 3)^[85]。

3.2.1 细菌

植物促生菌(plant growth-promoting bacteria, PGPB)是指生活在根际土壤或定殖于植物内部的,能够直接或间接促进植物生长、提高作物产量和防治病虫害的有益细菌,包括根际促生菌(plant growth promoting rhizobacteria, PGPR)、内生促生菌(plant growth promoting endophytic bacteria, PGPE)以及根瘤菌(*Rhizobium*)等^[86-87]。已有研究表明,PGPB 通过与植物建立共生关系,提高植物对重金属耐受性,强化植物对重

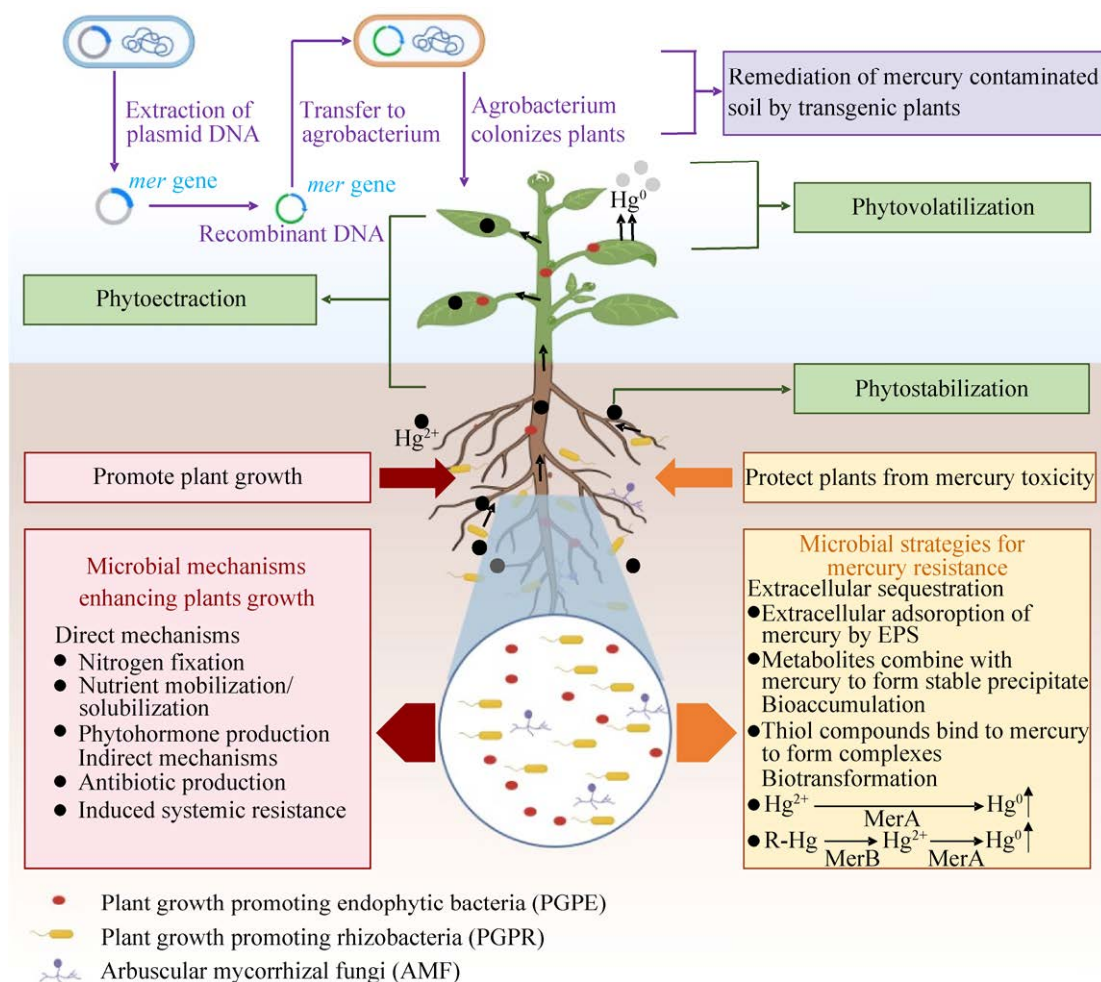


图 3 微生物辅助植物修复汞污染土壤

Figure 3 Microbial-assisted phytoremediation of mercury-contaminated soil.

金属污染土壤的修复能力^[88]。本课题组前期筛选出耐镉(cadmium, Cd)促生菌 *Serratia* sp. Y15 和 *Klebsiella* sp. Y38, 并将其应用于 Cd 污染土壤生物修复中, 结果表明, 接种 PGPB 可以提高紫花苜蓿(*Medicago sativa* L.)生物量以及对 Cd 的吸收和转运^[89]。此外, 本课题组还发现接种植物促生菌 *Pseudomonas* sp. TR1 促进了干旱胁迫下芸苔属(*Brassica oxyrrhina*)的生长以及对重金属的吸收^[90]。

PGPB 通过多种机制辅助植物修复汞污染土壤。一方面, PGPB 可以通过胞外隔离(胞外吸附和生物沉淀)、积累作用和生物转化作用降低土壤中汞的含量和毒性, 减轻汞对植物的毒性; 另一方面, PGPB 可以通过提高土壤中营养元素的生物利用度, 产生吲哚乙酸(indoleacetic acid, IAA)、细胞分裂素、赤霉素、脱落酸等植物激素直接促进植物生长, 或通过分泌抗生素, 诱导植物系统抗性间接促进植物生长^[91-93]。Singh 等^[94]发现, 从汞污染土壤中分离出的抗汞短波单胞杆菌(*Brevundimonas* sp.) IITISM22、枸橼酸杆菌(*Citrobacter* sp.) IITISM25 和 *Morganella* sp. IITISM23 能够通过产生 IAA、铁载体、1-氨基环丙烷-1-羧酸脱氨酶等促进植物生长, 还能产生 EPS 吸附 Hg^{2+} 。将这些菌株与芥菜(*Brassica juncea* L.)联合修复汞污染土壤时, 发现接种细菌提高了植物生物量和生长指标以及根部汞积累量, 增强了植物叶片中超氧化物歧化酶、过氧化氢酶、抗坏血酸过氧化物酶、过氧化物酶等抗氧化酶的活性。此外, 与未接菌土壤相比, 接种细菌的土壤中汞去除速率显著提高。

大量研究表明, PGPB 对植物在汞污染土壤上的适应能力和汞富集能力有着重要影响。例如, Mathew 等^[95]发现, 分离自汞污染地区根际土壤的发光杆菌(*Photobacterium* sp.) MELD1

显著提高了长豇豆(*Vigna unguiculata* subsp. *sesquipedalis*)的生物量、根长、种子数以及根系对汞的积累量。Ustiatik 等^[96]发现, 接种华葵咸海鲜球菌(*Jeotgalicoccus huakuii*) B1 和解淀粉芽孢杆菌(*Bacillus amyloliquefaciens*) B2 提高了百慕大草(*Bermuda grass*)和印度鹅草(*Indian goosegrass*)的生物量和 Hg 的生物积累量, 用细菌-植物联合体系处理减少了加汞砂中 80% 的汞。而另一些研究表明, PGPB 降低了宿主植物对汞的吸收。接种 *Pseudomonas* sp. SAICEUPSM^T 促进了汞污染土壤中白羽扇豆(*Lupinus albus*)的生长, 却显著减少了植物枝条对汞的积累^[97]。烷基酚假单胞菌(*Pseudomonas alkylphenolica*)KL28 能够通过固定土壤中的 Hg 减轻汞对桔梗(*Platycodon grandifloras*)的毒性, 并减少汞在植物体内的积累^[98]。*Pseudomonas* sp. AN-B15 能够通过挥发和固定作用降低土壤中 Hg^{2+} 的含量和毒性, 促进植物生长, 并减少汞在根系中的积累^[36]。上述研究表明, 抗汞的 PGPB 对植物汞积累的影响是不确定的。因此, 在利用 PGPB-植物联合修复汞污染土壤时, 不宜选择可食用的作物, 以免造成资源浪费。相反, 选择能源植物或有观赏价值的植物, 不仅能够有效修复汞污染土壤, 还可提供附加的观赏和经济效益。因此, 本课题组未来将利用筛选出的抗汞细菌与能源植物协同修复汞污染土壤, 以探究该菌株在辅助植物修复汞污染土壤上的作用及潜力。

此外, 由于豆科植物与根瘤菌之间的共生关系, 利用豆科植物-根瘤菌联合修复汞污染土壤也是一种切实可行的策略。根瘤菌通过减少植物地上部对汞的吸收, 从而减轻其毒害作用, 并促进植物生长。例如, 研究表明, 白羽扇豆接种具有汞抗性的加那利群岛慢生根瘤菌(*Bradyrhizobium canariense*) L-7AH 后, 植物的

根瘤、根和簇根中都积累了大量的汞,而叶片和种子样品中未检测到汞;这表明白羽扇豆在抗汞根瘤菌的辅助下,可以有效地从土壤中去除汞,并将其固定在地下组织中,从而减少了汞的生物有效性,同时减少了对人类健康的潜在风险^[99]。因此,利用豆科植物与根瘤菌的共生体系修复汞污染土壤是一个具有前景的选择。

3.2.2 真菌

菌根真菌(mycorrhizal fungi, MF)能够定殖于植物根表面、皮层或表皮细胞,通过提供磷酸盐、硝酸盐等难以获取的营养物质,促进碳水化合物交换,并形成菌丝网络,进而在植物间传输资源和化学信号,从而促进植物生长^[100-101]。这种植物与真菌的互作对双方均有利:植物根系为真菌提供碳源和其他有机物质,而真菌通过形成菌丝网络及产生酶类物质,提高植物对养分的吸收能力^[102]。目前,关于真菌辅助植物修复汞污染的研究主要集中于 AMF 上^[85]。接种 AMF 能够在汞胁迫条件下促进植物生长并影响其对土壤中汞的吸收。例如,在土壤汞含量为 6 mg/kg 的条件下,接种商业 AMF 显著促进了香根草(*Chrysopogon zizanioides*)的生长及其对汞的积累^[103]。Kodre 等^[104]的研究表明,接种从汞污染地点分离的 AMF 的玉米(*Zea mays* L.),其根部汞积累量(439 mg/kg)显著高于未接种处理的玉米。接种 AMF 后,植物根部存在丛枝菌根结构(菌丝、丛枝、囊泡),并检测到四硫代汞复合物,其形成百分比与丛枝形成水平和汞根浓度密切正相关。这表明 AMF 可促进汞的转化,使其形成更具迁移性的化学形态,从而提高汞从土壤向根部的迁移率。此外,与未接种的对照组相比,接种商业 AMF 的多年生黑麦草(*Lolium perenne* L.)根系对汞的吸收率显著提高,而在地上部分的积累降低,显示出 AMF-植物共生体系对植物吸收污染物方式的

影响^[105]。

AMF 在汞污染土壤植物修复中的作用包括促进植物生长、提高根系对汞的吸收及降低汞向地上部分的转移,但其促进重金属从土壤转移到植物组织的具体机制尚不明确。此外,当前研究主要集中在 AMF 上,缺乏对其他代表性真菌在汞修复方面的研究。微生物-植物联合修复汞污染土壤是一种广泛研究和尝试的生物修复方法,但需要根据不同的土壤类型和环境条件选择合适的微生物-植物组合,并综合考虑其适用性和成本效益,以实现更佳的修复效果。

3.2.3 转基因植物修复汞污染土壤

通过基因工程技术将参与汞解毒的细菌基因(如细菌 *mer* 操纵子)植入受体植物中,以提高植物对汞的积累能力和效率,是目前有效的促进植物修复污染土壤的方法之一。目前,已在拟南芥(*Arabidopsis thaliana*)、烟草(*Nicotiana tabacum* L.)、东方白杨(*Populus deltoides* Bartr. ex Marsh.)、水稻(*Oryza sativa*)和番茄(*Solanum lycopersicum*)等植物中进行细菌操纵子基因转化,以提高植物去除土壤中汞的效率^[26]。然而,由于微生物、植物和动物之间密码子的偏好性差异很大,tRNA 识别特异性密码子的缺失或低可用性可能导致模式植物中外源基因表达量较低^[106-108]。应用此技术时需要根据相关植物的密码子设计合成基因,以确保其在植物中达到理想表达量表达。

在修复土壤中无机汞化合物方面,有研究从 *E. coli* 质粒中分离出编码汞还原酶 *merA* 基因,将其稳定整合到烟草基因组中,发现成功表达 *merA* 基因的烟草相较于野生型,表现出更强的挥发 HgCl_2 的能力^[109]。此外,含有 *merA* 基因的黄杨(*Buxus sinica*)转基因品系显示出更强的抵抗和挥发汞的能力^[110]。在有机汞的修复方面,细菌 *merB* 基因编码的汞裂解酶蛋白能够

将有机汞裂解为 Hg^{2+} [26]。Singh 等[111]将修饰后的细菌 *merBpe* 基因整合到烟草植物基因组中,发现 *merBpe* 转基因植物在相同的醋酸苯汞浓度下生长旺盛,而对照植物生长受到严重抑制甚至死亡。同时,研究还表明细菌 *merA* 基因和 *merB* 基因共同作用对有机汞解毒具有重要作用。将 *merA*、*merB* 基因整合到烟草叶绿体基因中,显著增强了烟草对汞的积累能力,转基因烟草叶片汞吸收量是野生型的 100 倍[112]。类似地,将细菌 *merA* 基因和 *merB* 基因整合到东方白杨中,发现转基因植物对醋酸苯汞具有较强的耐受性,且对有机汞化合物的解毒速度比野生型快 2–3 倍[113]。最近,番茄和水稻的 *merA/B* 转基因品系由于能够去除土壤中的汞并抑制汞在叶子、谷物和果实中的积累,被提议作为修复汞污染土壤的安全作物[114]。多项研究表明,利用细菌抗性基因构建的转基因植物可实现汞由高毒向低毒形态的转化,适用于修复汞污染场地[85]。

除了汞转化基因外,细菌 *mer* 操纵子上还含有编码汞转运蛋白的 *merC*、*merT*、*merP* 基因,这些汞转运蛋白能够特异性识别无机汞和有机汞并将其转运至细胞内[26]。细菌 *merC* 基因编码的 MerC 蛋白起到汞吸收泵的作用,转基因植物中 MerC 的表达促进了 MeHg 的转运和螯合,提高了汞在拟南芥中的根部至枝部的易位[115]。Sasaki 等[116]将来自氧化亚铁硫杆菌(*Acidithiobacillus ferrooxidans*)的 *merC* 基因导入烟草中,发现转基因植株 Hg^{2+} 的积累量是野生型的 2 倍,证实了细菌汞离子转运蛋白 MerC 在转基因植物积累 Hg^{2+} 的应用潜力。细菌 MerE 转运蛋白有助于将无机汞和有机汞转运至细胞膜上,Sone 等[117]将 *E. coli* 的 *merE* 基因导入拟南芥中,发现表达 *merE* 基因的转基因拟南芥相较于野生型,积累了更多的 MeHg 和汞离子,

并对其耐受性更强,表明 MerE 促进了 MeHg 和汞离子在拟南芥中的转运和积累。细菌 *merT* 基因编码的内膜细胞质蛋白 MerT 有助于将摄取的有机和无机汞转运到汞还原位点,Xu 等[118]将产碱假单胞菌(*Pseudomonas alcaligenes*)中的汞转运蛋白基因 *merT* 整合到拟南芥中,发现 MerT 蛋白定位于拟南芥原生质体液泡,增加了转基因拟南芥对 Hg 的耐受性,并减少了汞诱导的活性氧的产生,从而保护植物免受氧化损伤。周质汞结合蛋白 MerP 可以与 Hg^{2+} 结合,促进无机汞离子进入细胞[119]。Hsieh 等[120]通过在拟南芥中表达巨型芽孢杆菌(*Bacillus megaterium*)的 *merP* 基因,发现转基因拟南芥对汞、镉和铅具有更强的耐受性和吸收能力。

基于基因工程技术改造的植物在修复汞污染土壤方面展现出巨大的潜力,已引起多个领域的广泛关注。在评估这些转基因植物重金属提取效率时,研究人员应同时进行详尽的生态风险评估,以确保转基因植物在修复重金属污染土壤过程中的安全性和可持续性。此外,亟需加强对公众科普宣传,纠正人们对基因工程技术的误解,从而促进该技术的认可与应用。

4 总结与展望

由于汞在生态系统中无法自然降解,并会通过食物链发生生物累积及生物放大,对生态系统和人类健康构成严重威胁,因此亟需解决土壤汞污染问题。近年来,利用微生物修复土壤重金属污染的方法引起了广泛关注。抗汞微生物(包括细菌、真菌和藻类)因其减轻汞毒害的特性,展现出修复汞污染土壤的巨大潜力。本文详细阐述了抗汞微生物的机制,包括胞外隔离(胞外吸附和生物沉淀)、生物积累和生物转化等,并分析了抗汞微生物及其与植物联合体系在修复汞污染土壤中的应用潜力,同时评估了

mer 转基因植物在该领域的重要性。

利用抗汞微生物进行汞污染土壤修复是一种经济、高效、可持续且有前景的方法。然而,在实际应用之前,必须对现场的汞含量和土壤类型等背景条件进行详细评估,以选择适宜的应用技术,提高修复效率。基于抗汞微生物在汞污染土壤中的应用仍面临诸多挑战和待解决的科学问题,例如:

(1) 进行田间试验与实际应用的研究。目前,关于汞的微生物修复研究大多集中在实验室,直接将抗汞微生物应用于汞污染土壤的修复研究较少。应进一步加强田间试验,并开展该修复技术在大规模场地的实际应用研究。此外,提高利用抗汞微生物修复土壤汞污染的效率,并验证其用于汞生物修复的有效性和可行性,开发商业抗汞菌剂。

(2) 考虑土壤生态系统的复杂性。添加外源菌剂可能会影响土壤中的微生物群落结构,因此在使用外源菌剂进行土壤修复时,需要充分考虑土壤生态系统的复杂性,并进行长期监测和评估,以确保生态系统的健康。

(3) 研发二次污染防治技术。在微生物转化作用下,土壤中挥发的 Hg^0 进入大气后可能导致大气汞污染,并且 Hg^0 通过生物地球化学循环可能重新沉降于土壤。为减少再污染风险,可以将抗汞微生物与适当的吸附材料(如活性炭)结合,以增强对挥发 Hg^0 的吸附能力。此外,相较于生物转化技术,利用微生物进行汞固定(如通过胞外吸附、生物沉淀和生物积累)在生物修复中更具安全性。因此,有必要加强对抗汞微生物生物固定技术的研究与开发。

(4) 探索复合污染修复技术。由于土壤通常受到多种重金属或有机物的复合污染,应加强具有广谱修复作用的微生物和植物的筛选,并强化生物修复技术的研发和应用工作。

总之,抗汞微生物在汞污染土壤修复中展现出显著潜力,但仍需通过进一步的研究与技术开发,解决现存的科学问题和技术挑战,以实现该方法的推广和应用。

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