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植物与微生物对重金属的抗性机制及联合修复研究进展

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摘 要 人类活动导致重金属污染逐步扩大，生物为了适应重金属污染而产生的抗性能够应用于重金属修复. 相比于物理化学修复，植物和微生物修复更具环保性、经济性. 对植物和微生物的重金属抗性机制和相关基因，以及植物-微生物联合修复技术与应用进行综述. 植物与微生物抗重金属过程均由多个基因控制，污染地区的原位植物和微生物具有更好的环境适应能力和应用潜力，是抗性资源挖掘的理想来源. 当前，基因组学手段成为挖掘生物重金属抗性资源的关键手段，同时基因的水平转移以及基因编辑技术的应用极大地丰富了抗性资源及表达. 此外，植物-复合微生物联合作用提高了修复可行性和效率. 微生物通过促生作用、分泌酸性物质、增加植物中重金属运输、螯合、抗氧化等相关基因表达来增强植物修复能力，但内生菌辅助植物修复重金属机制尚不明确. 目前常用复合菌剂包括多种根际促生菌、细菌-真菌、根际菌-内生菌组合，但其应用受到接种方式和施用条件的影响. 由于污染环境的复合性和复杂性，未来多功能基因表达技术的开发和复合植物-微生物修复机制研究将会成为焦点.（图1 表5 参90）

关键词 重金属污染；抗性基因；基因挖掘；基因水平转移；植物-复合菌株修复

Advances in the mechanism of heavy metal resistance and combined remediation of plants and microorganisms

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Abstract A series of resistance systems against heavy metals has evolved in many organisms because of the extensive pollution of heavy metals by anthropogenic disturbance, which may have applications for the remediation of heavy metal contamination. Compared with traditional and physicochemical remediation, plant and microbial remediations are more suitable for ecological remediation as they are more environmentally friendly and less expensive. We reviewed the gene resources and molecular mechanisms of heavy metal resistance in plants and microorganisms, and summarized the technology and application of plant-microorganism remediation. The resistance process of heavy metals within plants and microorganisms is encoded by multiple genes. The *in-situ* plants and microorganisms in polluted areas present greater environmental adaptability and higher applicable potential, and are ideal materials for developing resistance resources. Genomics has become an excellent tool for mining resistant gene resources. It is promising to find that horizontal gene transfer and gene editing technology enriches the heavy metal resistant resources, and also increases the expression of resistance. Moreover, higher repair feasibility and efficiency can be possibly achieved by plant-microorganism combined systems. Microorganisms enhance the remediation capacity of plants by promoting growth, secreting acidic substances to dissolve heavy metals, and amplifying the genetic expression of heavy metal transport, chelation, antioxidants, and other resistance processes in plants. However, the mechanism of endophyte-assisted phytoremediation remains unclear. To date, composite microbial

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agents, such as multiple plant growth-promoting rhizobacteria, bacterial-fungal combinations, and rhizosphere microorganism-endophyte combinations, are commonly used, but their application is affected by the inoculation methods and application conditions. In general, diverse and complex pollution environments require the development of cross-species and multi-gene editing techniques, and future remediation should focus on the resistance mechanism of compound plant-microorganism synergistic remediation.

Keywords heavy metal pollution; resistance gene; gene mining; horizontal gene transfer; compound plant-microorganism remediation

随着人类生产生活的不断发展，重金属进入生态系统的来源增加且过程加快[1]. 虽然一些金属包括Cu、Zn、Fe和Mn等[2]是生物体必需的微量元素，但是过量的这些金属元素一旦进入生物体内，将对动物、植物、微生物和人类的正常生理功能和机体产生损伤. 由于生物体中非特异性运输系统对重金属不敏感，即使在体内重金属含量较高的情况下生物依然会吸收重金属，导致重金属积累产生毒性[3]. 而一些非生物必需的金属元素例如Cd、Pb等进入生物体后将产生更大的毒害作用. 例如，重金属除了对细胞直接毒害[4]，还产生活性氧（reactive oxygen species，ROS）[3]，对整个新陈代谢过程造成氧化损伤. 重金属对整个生命系统的影响已经延伸到从形态到结构、从代谢到功能、从微观到宏观等各个方面，修复重金属污染成为环境生物学领域最为关注的热点问题之一.

植物作为初级生产者，是生态系统物质流动的"入口"；微生物数量众多且分布广泛，参与各种元素的生物地球化学循环. 随着重金属污染广泛扩散，为了稳定和平衡体内重金属含量，生物在适应重金属环境的过程中产生了一系列复杂的抗重金属系统，进化出了或简或繁的抗重金属特征，包括趋避、直接排出、减弱生物毒性和降低自身敏感度等[5]. 把植物和微生物这两类不同生态功能的生物结合起来修复重金属污染已成必然. 鉴于重金属污染早已引起全球关注[6]，传统矿冶产业遗留问题与新型电子产业和新材料的发展使全球很多区域的重金属污染加剧，修复工作需加大力度[7]. 过去建立起来的物理化学修复方法处理效果虽然明显，但治理成本较高，且易产生二次污染[8]. 近十年来新兴生物修复手段发展迅速，它不但成本较低、没有二次污染，还能提高生态系统服务功能[9]. 其中植物修复已经渐成规模，但修复成效需与微生物结合，形成植物-微生物联合修复技术[6]. 特别是分子及基因技术的发展将已知的抗重金属基因应用于修复工作，一方面基因的水平转移能够提高生物修复性能，另一方面植物与微生物相互作用、二者协同修复更加高效[10]，这将成为未来的发展方向.

抗重金属基因是宝贵的进化产物，对生物修复研究具有重要生态学意义和应用价值，利用这些已知序列的编码基因预测其同源基因，可以为生物适应进化研究以及抗性功能基因应用作基础. 近年来，随着分子生物技术的不断发展、成本降低，越来越多的重金属抗性基因被人们所知[11]. 虽然污染毒害及抗性过程研究较为深入，但对抗性基因及其在植物-微生物联合修复中的应用还缺乏梳理和总结. 为此，本文对植物与微生物的抗性相关基因归类，总结二者联合修复过程机制及其应用，旨在为进一步探索生物抗重金属机制、促进生物修复技术的发展和应用提供系统性的信息支持.

1 植物与微生物的重金属抗性及其资源挖掘

1.1 重金属抗性机制与相关基因

长期生活于高浓度重金属环境中，生物体的生长代谢和氧化防御系统必将受到影响[12]，因此它们通过一系列过程调控和平衡体内重金属浓度，表现出重金属抗性，包括直接抗性和间接抗性. 直接抗性是指生物解毒和消除重金属的过程，包括：（1）趋避作用：植物通过转运蛋白（例如*ZIP*和*NRAMP*蛋白家族）（表1）对运输重金属的特异性有效地控制重金属在植物体内的运输过程[13]；或是通过根分泌物改变金属形态从而降低吸收[14]；（2）隔离作用：生物在细胞壁或者液泡（植物与真菌）中储存大量重金属（表2），降低其对机体（其他细胞器）的损伤[2]；（3）主动排出：生物依靠主动外排系统将重金属排出细胞[15]；（4）钝化作用：细胞内的重金属与其他物质结合，减少其流动性和毒性. 间接抗性是指减少重金属对机体造成氧化损伤[16]，有研究表明植物体内抗氧化基因的表达上调抵御了氧化损伤，间接增强了其对重金属的抗性[12].

生物对重金属的抗性并非依靠单一的解毒过程. 对于不同的植物或微生物种类、生长时期、器官和不同重金属，抗重金属基因和过程都会有不同的组合方式[17-19]. 抗性基因在不同植物中也存在特异性表达，表现为不同的抗重金属相关基因在不同植物或不同基因表达量中产生的金属敏感性不同. 此外，抗重金属过程虽然可以由单个基因编码控制，但也需要其他不同的基因共表达从而产生抗性，例如植物体内起钝化作用的植物螯合素（phytochelatins，PCs）就需要螯合素合成酶基因（*PCS*）、γ-谷氨酰半胱氨酸合成酶基因（*GSH1*）和谷胱甘肽合成酶基因（*GSH2*）的共同参与[20].

除了PCs、金属硫蛋白（metallothioneins，MTs）、有机酸和无机酸等常见抗性系统，最新的研究表明防御素（defensin）在生物抗重金属方面也起着作用. 植物防御素虽然早有报道，但是远不及其他机制研究透彻[21].

1.2 植物与微生物抗性资源挖掘与应用

1.2.1 抗性资源挖掘 近现代的重金属污染加剧，迫使一批生物进化出具有明显重金属抗性的性状，合理利用这些抗性资源，是重金属修复技术发展和应用的有效保障，其中抗重金属超积累植物和野生菌株具有良好前景和挖掘价值. 超积累植物（hyperaccumulator）能够向地上部分转移更多的重金属，利用螯合、隔离、解毒和抗氧化作用减轻重金属毒害并将其储存在体内，是理想的植物修复材料[13]，常存在于金属矿区及其周边地区. 但目前已经发现的超富集植物多为小型草本、

表1 植物抗重金属基因与机制

Table 1 Genes and mechanisms of plant resistance to heavy metals

基因 Gene	重金属 Heavy metal	机制或抗性过程 Mechanism or resistant process	物种 Species	参考文献 Reference
HMAs	Zn, Cd	P型ATP酶转运金属、介导重金属在液泡隔离 P-type ATPase transports metals into the vacuole for sequestration	*Arabidopsis thaliana* Rice (*OsHMA3*) Soybean (*GmHMA3*)	[22] [23] [24]
Atcys-3A	Cd	合成半胱氨酸 Synthesis of cysteine	*Arabidopsis thaliana*	[25]
GSH1	—	γ-谷氨酰半胱氨酸合成酶 γ-glutamylcysteine synthetase	*Arabidopsis thaliana*	[20, 26]
GSH2	—	谷胱甘肽合成酶 Glutathione synthetase	*Arabidopsis thaliana*	
GR	—	谷胱甘肽还原酶 Glutathione reductase	*Arabidopsis thaliana*	
APS	—	ATP硫酸化酶 ATP sulfurylase	*Arabidopsis thaliana*	
CTS	—	硫醚合成酶 Cystathionine synthase	*Arabidopsis thaliana*	
SAT	—	丝氨酸乙酰转移酶 Serine acetyltransferase	*Arabidopsis thaliana*	
PCS	Cd, As, Zn	植物螯合素合成酶 Phytochelatin synthase	*Arabidopsis thaliana* (*AtPCS1*)	
arsC	As	As(Ⅴ)还原为As(Ⅲ)，利用膜电位将As泵出 As(Ⅴ) is reduced to As(Ⅲ) and pumped out by membrane potential	*Arabidopsis thaliana*	[20]
ACR3	As	重金属隔离至液泡 Metal is sequestrated into the vacuole	Fern *Pteris vittata*	[27]
TaVP1	Cd	液泡中的H^+-焦磷酸酶 H^+-pyrophosphatase in vacuole	Wheat	[28]
AtCAX	Cd, Mn	增加液泡膜对金属的选择透过性和运输能力 Increasing selective permeability and transport of metals	*Arabidopsis thaliana, Nicotiana tabacum*	[29]
Cu/Zn-SOD, POD1, GR1, GPX1, GST1	Cd	抗氧化酶合成（超氧化物歧化酶、过氧化物酶、谷胱甘肽还原酶、谷胱甘肽过氧化物酶等） Synthesis of antioxidant enzymes (e.g. superoxide dismutase, peroxidase, glutathione reductase, glutathione peroxidase etc.)	*Miscabthus sacchariflorus*	[30]

表2 细菌与真菌的抗重金属基因及其机制

Table 2 Genes and mechanisms of bacteria and fungi resistance to heavy metals

	基因 Gene	重金属 Heavy metal	机制或抗性过程 Mechanism or resistant process	物种 Species	参考文献 Reference
细菌 Bacteria	*czc*	Zn, Cd, Co	编码RND蛋白，质子作用推动阳离子主动外排系统避免重金属在细胞内积累 Encoding RND proteins, and mediating proton driven efflux to avoid the accumulation of heavy metals in cells	*Pseudomonas aeruginosa* (*czcD, czcA, czcB, czcC*)	[18, 31-32]
	czr	Zn, Cd	编码RND蛋白 Encoding RND proteins	*Pseudomonas aeruginosa* (*czrSRCBA*)	[33]
	ncc	Ni, Cd, Co	编码RND蛋白 Encoding RND proteins	*R. metallidurans*	[18, 34-35]
	cnr	Ni, Zn, Co	编码RND蛋白 Encoding RND proteins	*R. metallidurans*	[18]
	cop	Cu	编码P型ATP酶，参与重金属从细胞质向周质运输 Encoding P-type ATPase and participating in the transport of heavy metal from cytoplasm to periplasm	*E.coli* (*EcpcoA*) *Pseudomonas syringae* (*PscopA*)	[15]
	cus	Cu	编码HME-RND中的Cus蛋白家族，有氧条件下与CopA、CueO共同解毒 Encoding Cus protein family of the HME-RND, whose detoxification together with CopA and CueO under aerobic condition	*E. coli* (*CusCFBA*)	[36]
	rbgR	Cr	编码CDF蛋白 Encoding CDF proteins	*E. coli*	[18]
	nreB	Ni	编码NreB蛋白 Encoding NreB proteins	*Achromobacter xylosoxidans*	[37]
	cnrT	Ni	编码CnrT蛋白 Encoding CnrT proteins	*Ralstonia* sp.	[37]
	ars	As	As(V)还原为As(III)，利用膜电位将As泵出 As(Ⅴ) is reduced to As(Ⅲ) and pumped out by membrane potential	*Thermoplasma acidophilum* *E. coli*	[38-39]
	cadA	Cd	通过P型ATP酶主动外排Cd Active efflux of Cd through P-type ATPase	*Staphylococcus aureus*	[40]
	mer	Hg	与Hg吸收相关蛋白MerP蛋白、黄素蛋白 MerP protein and flavoprotein related to Hg absorption	*Pseudomonas aeruginosa*	[39, 41]
	sodA	—	超氧化物歧化酶的合成 Synthesis of superoxide dismutase	*Pseudomonas aeruginosa*	[42]
真菌 Fungi	*CUP1*	Cu	—	*Yeast*	[43]
	crpA	Cu	合成P型ATP酶 Synthesis of P-type ATPase	*Aspergillus nidulans*	[44]
	HMA	Cd	Cd在酵母液泡的运输 Transporting Cd in yeast vacuole	*Yeast*	[24]
	ACR3	As	将重金属固着在液泡 Metal into the vacuole for fixation	*Yeast*	[27]
	ZRC1	Zn	重金属液泡隔离 Metal into the vacuole for sequestration	*Saccharomyces cerevisiae*	[45]
	GSH1	Zn, Cd	合成谷胱甘肽 Synthesis of glutathione	*Saccharomyces cerevisiae*	[46]

生物量有限，因此在实际应用中存在一定局限. 转基因技术能够实现超积累特性在生物量大的植物中表达，进而通过杂交、育种、基因编辑技术提高植物修复效率[47]，例如将优良抗性基因转入非食用经济作物（木材等），对于土地重金属修复和利用有着重要意义[47].

实验室研制的工程菌剂虽然能高效修复重金属污染，但在实际应用过程中受到立地条件限制. 从野外污染区域中分离出来的微生物明显具有更高的环境适应能力，高抗性野生

菌株的挖掘拓宽了优良抗性基因选择，从而在实际修复过程中实现最优的菌剂组合. 微生物修复现有的研究主要涉及：（1）利用可培养手段获得具有高抗重金属表型的微生物，或通过诱变增强其抗性；（2）利用基因组学挖掘表型背后的抗性基因通路，帮助构建工程菌株[48]. 随着测序技术的发展，基因组学已经成为主流的研究手段，推动着抗重金属微生物资源库的构建和扩大.

1.2.2　植物与微生物技术与应用　植物与微生物的重金属抗性有相似之处，功能基因的水平转移（horizontal gene transfer, HGT）或者基因编辑技术实现不同物种间重金属抗性表达、修复性能提高. 原核生物中广泛存在重金属抗性基因的HGT[49-50]，除了细菌之间，细菌与蓝藻的抗性基因也可以是水平转移，但每种基因表达的功能在不同物种之间存在差异，不同物种抗重金属系统协同作用将得到“1+1>2”的抗重金属效率[18]. 尽管真核生物中基因水平转移不常见[51]，但最新的研究表明内生菌与植物间的基因能够发生水平转移[52]. 具有较强抗性的植物能够通过基因水平转移增加其内生菌的抗重金属能力[53]，真菌中的抗性基因也能够水平转移给细菌[54]. HGT不仅丰富了物种基因多样性，增加了生物修复的材料，还为污染修复抗性种质的培育提供基础. 尤其是内生菌与植物之间的HGT，它能够为植物或微生物修复提供更好的资源与性能，但目前关于这方面的研究还较为缺乏.

和HGT类似，基因编辑技术实现了重金属抗性基因在不同植物中的稳定遗传和表达[55]，增加重金属蓄积能力、提高植物生物量和修复重金属的种类[8, 56]. 目前，基因编辑技术已经成功完成植物-植物、微生物-微生物、植物-微生物之间的基因重组：（1）在拟南芥中转入来自大蒜的*AsPCS1*基因，能够增加金属硫蛋白和重金属结合能力、液泡隔离作用，从而提高拟南芥的金属吸附和耐受重金属的能力[57]；（2）原核生物中的抗重金属基因多存在于质粒或转座子上[58-59]，基因重组后的细菌和真菌均能够提高重金属耐受性能[60]，此外，通过与已经报道的抗性基因对比等方法可以挖掘更多重金属抗性基因资

表3　植物、微生物修复技术

Table 3　Plant and microbial remediation technologies

修复模式 Remediation mode	改良剂种类 Type of soil conditioner	修复过程 Remediation process	参考文献 Reference
高抗性植物＋土壤改良剂 Resistant plant + soil amendment	有机肥、生物炭、pH改良剂 Organic fertilizer, biochar, pH ameliorant	增加重金属吸收、改变土壤环境更适于高抗性植物生长 Increasing heavy metals absorption and making soil environment more suitable for the growth of highly resistant plants	[61-62]
高抗性植物＋螯合剂 Resistant plant + chelating agent	EDTA、DTPA、柠檬酸盐 EDTA, DTPA, citrate	增加植物吸收重金属过程 Increasing the absorption of heavy metals by plants	[63]
抗性微生物＋土壤改良剂 Resistant microorganism + soil amendment	生物炭、有机肥、陶粒、脱落酸 Biochar, organic fertilizer, ceramsite, abscisic acid	增加微生物吸收、固定重金属效率 Increasing the absorption and fixation efficiency of heavy metals by microorganisms	[64]

EDTA：乙二胺四乙酸. DTPA：二乙烯三胺五乙酸.

EDTA: Ethylene diamine tetraacetic acid.DTPA: Diethylenetriamine pentaacetic acid.

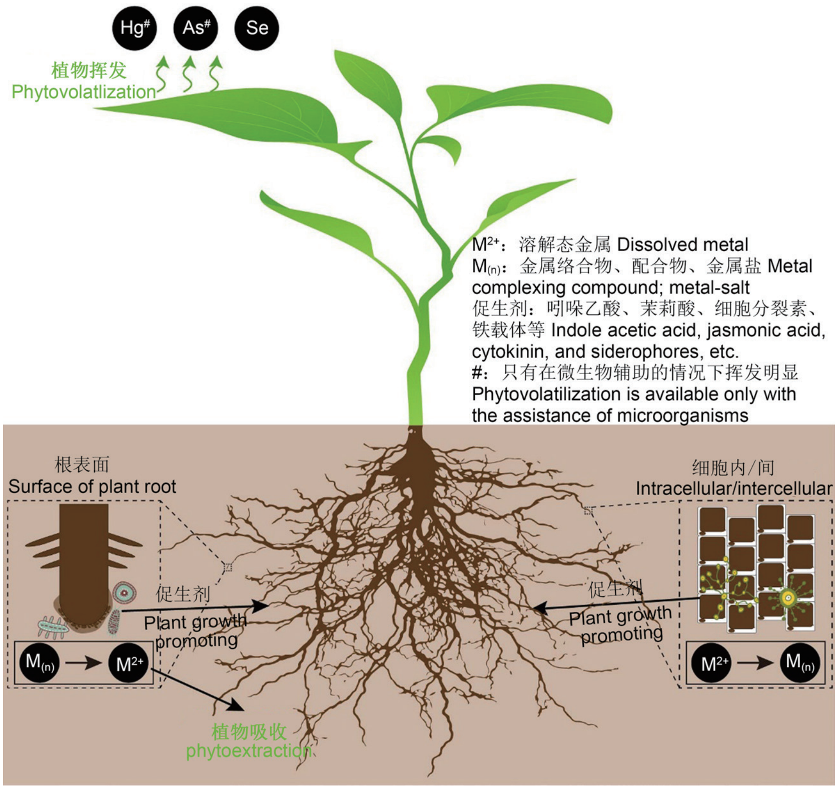

图1　植物-微生物重金属污染修复过程.

Fig. 1　Process of plant-microbial remediation of heavy metal pollution.

源；(3) 铜绿假单胞菌中的抗重金属基因*PpczcCBA*在烟草体内重组表达后，显著减少植物对Cd的积累[32]. 但是在实际应用中，高抗性植物与菌株受到环境条件影响，往往修复效果不佳. 为了解决这一问题，通常以土壤改良剂或是外源添加剂、生物炭等辅助修复，能够有效提高重金属修复效率[61] (表3).

2 植物与微生物联合修复机制与应用

2.1 植物-微生物联合修复机制

植物-微生物联合抗性的研究主要包括植物与根际微生物、内生菌的协同作用，促生根际微生物 (plant growth promoting rhizobacteria，PGPR) 是目前研究较多的一类. 大量研究表明，PGPR能够通过固氮、溶磷、分泌生长激素增加根、茎生物量，促进植物生长并改变植物对重金属的利用率[65-67]；还能分泌有机酸来促进植物对重金属吸收 (图1). 在草本植物[68]和玉米等作物[69]种子中添加促生根际微生物，均能观察到明显的促生作用和重金属耐受性.

植物-内生菌修复是最近兴起的技术[63]，与PGPR类似，内生菌也能促进植物生长并减少重金属对植物的毒害作用，除此之外它还与植物抗病能力相关. 早有研究在Cd超积累植物龙葵中分离出沙雷氏菌LRE07，它对Cd有较强抗性，能够高效率吸收Cd和Zn并解毒[70]. 此外，内生菌还能引发植物的防御免疫系统[71]，通过螯合作用降低重金属的生物利用性和移动性[72]. 除了对重金属解毒外，内生菌也能溶解无机磷酸盐、产生植物生长素和铁载体促进植物生长、增加生物量[73]. 虽然早已发现内生菌的存在，也有证据表明内生菌具有更加强大的重金属抗性和蓄积能力[71]，但对其抗性机理知之甚少[74]，尤其是多种菌群共同作用的机理.

从分子层面来说，现已经探明的微生物辅助和促进植物修复主要有4种机制 (表4)：(1) 提高植物吸收重金属能力. 微生物刺激植物，增加植物自身分泌生长激素的基因表达来促进植物生长 (尤其是根部)，从而增加重金属吸收面积和总量；(2) 提高植物抗氧化能力. 例如增加谷胱甘肽代谢的相关基因表达；(3) 与物质运输、能量相关基因上调，将重金属运输至非敏感区域；(4) 解毒过程相关酶的基因上调从而增加植物的重金属耐受能力.

2.2 植物-微生物修复技术与应用

植物与微生物联合修复是近年来发展较为迅猛的一种修复方式[9]. 大量研究表明，植物-微生物共存能够促进植物的重金属抗性，具有较为理想的修复效果[65]，一方面微生物促进植物生长；另一方面，植物部分抗重金属过程也能提高这些微生物的抗重金属能力. 比起化学修复和物理修复，它能够更加“生态”地进行修复. 实际应用中，常在植物或者土壤中接种功能微生物 (表4). 接种方式 (种子接种，还有土壤接种、多种菌混合接种)、种子大小、土壤理化性质均会影响修复效果[48, 62, 72].

植物与单一抗性菌株组合的修复方法的应用最多，机理研究较为成熟 (表5). PGPR是常用的抗性菌种，有效提高植物对重金属的抗性. 除此之外，内生菌群也能表现出优异的辅助作用[83]，但内生菌受到环境影响较大且不易控制，因此应用较少. 另一种应用较多的技术则在植物-微生物组合基础上再配合外源添加物 (例如有机酸、螯合剂、促生剂、肥料) 或者改性材料 (例如生物炭、有机固体、磷酸盐副产物) 来改善环境条件从而提高修复效率[84-85]. 但这些常用的修复技术在实际应用中也存在一些问题. 有些菌根真菌与植物无法共存或者不能在实际污染的环境中存活[63]，PGPR在改善根际环境的优良能力能够解决这一问题，还能增加修复效率. 因此，植物+复合菌剂的修复模式表现出了一定应用潜力，但现有的机制研究尚为缺乏.

表4 微生物辅助植物修复重金属污染方法
Table 4 Microbial-assisted phytoremediation of heavy metal pollution

植物 Plant	接种微生物 Inoculated microorganism	重金属 Heavy metal	基因表达差异 Differences in gene expression	接种方式 Inoculation mode	参考文献 Reference
玉米 Maize B73	*Glomus intraradices* (AM fungus)	Cd	上调基因：植物激素、丝裂原活化蛋白激酶、谷胱甘肽代谢 Up-regulated genes: plant hormones, mitogen activated protein kinase, glutathione metabolism	土壤接种 Inoculation in soil	[75]
东南景天 *Sedum alfredii*	*P. fluorescens*	Cd	诱导侧根形成，增加吲哚乙酸分泌，降低脱落酸、油菜素内酯、茉莉酸等浓度 Inducing formation of lateral root, increasing secretion of indoleacetic acid and decreasing concentrations of abscisic acid, brassinolide and jasmonic acid etc.	根系接种 Inoculation in root	[76]
拟南芥 *Arabidopsis thaliana*	*Mucor* sp.	Cd, Zn, Pb	有毒金属转运、解毒基因上调 Transport of toxic metals and up-regulation of detoxification genes	土壤接种 Inoculation in soil	[77]
拟南芥 *Arabidopsis thaliana*	*Campylobacter jejuni*	—	γ-谷氨酰环转移酶2，保护植物免受重金属毒害 γ-glutamyl cyclotransferase 2 protects plants from heavy metals	植物组织接种 Inoculation in plant tissue	[78-79]
紫花苜蓿 *Medicago sativa*	*Sinorhizobium meliloti*	Cd	增加养分获取能力和生物量，重金属从根部向地上部分转移 Increasing nutrient acquisition capacity and biomass, and heavy metals transferred from the roots to the aboveground parts	根系接种 Inoculation in root	[80]
高粱 *Sorghum bicolor* L.	*Burkholderia* sp. strain S6-1, *Pseudomonas* sp. strain S2-3	Cu, Zn	增加1-氨基环丙烷-1-羧酸脱氨酶、吲哚乙酸、铁载体，促进重金属吸收 Increasing 1-aminocyclopropane-1-carboxylic acid deaminase, indoleacetic acid, and siderophores to promote the absorption of heavy metals	土壤接种 Inoculation in soil	[81]
东南景天 *Sedum alfredii*	*Pseudomonas fluorescens*	Cd	提高净光合速率，碳固定相关基因上调 Increasing the net photosynthetic rate and up-regulating carbon fixation related genes	植物整株接种 Inoculation in whole plant	[82]

表5　植物-微生物修复技术与应用
Table 5 Plant-microbial remediation technologies and applications

修复模式 Remediation mode	修复过程 Process	应用现状 Application status	参考文献 Reference
植物+土壤添加剂+抗性菌剂 Plant + soil amendment + resistant microorganism	改善环境条件、增加植物吸收重金属效率 Improving environmental conditions and increasing plant absorption of heavy metals	应用较多，机制研究较为成熟 Wide applications; the mechanism research is more mature	[62, 85]
植物+根际促生细菌 Plants + PGPR	促进植物生长、为根际促生菌提供适宜生长环境、增加重金属吸收量、减少重金属毒害作用 Promoting plant growth, increasing heavy metals absorption and reducing heavy metal toxicity	应用较多，机制研究较为成熟，但施用条件研究不足 Wide applications; the mechanism researches are more mature, but the application conditions are insufficiently studied	[86]
植物+根际促生细菌+菌根真菌 Plant + PGPR + mycorrhiza fungi	增加植物吸收重金属效率、促进植物生长 Increasing the efficiency of plant absorption of heavy metals and promoting plant growth	应用较少，机制研究较少 Less application, and less mechanism research	[63]
植物+复合土壤抗性菌剂 Plant + composite microbial agents	增加植物吸收重金属效率 Increasing the efficiency of plant absorption of heavy metals	应用较少，机制研究较少 Less application, and less mechanism research	[87]
植物+内生菌 Plant + endophyte	促进植物生长、帮助植物体内螯合重金属减少毒性 Promoting plant growth and helping plant chelate heavy metals to reduce toxicity	难以实现应用，多种菌群的修复机制尚不清楚 Hard to achieve application; the repair mechanism of multiple microorganisms is not clear	[72]

3 结论与展望

植物、微生物作为生态系统中的生产者和分解者，具有不可或缺的生态地位和意义，面对日趋严重的重金属污染，了解其复杂的抗性系统[3]并转化为技术应用是当前亟待研究的问题．作为生物适应重金属污染、物种遗传结构优化的直接证据，抗性基因是生物基因多样性和重金属修复研究的一个重要基础．尽管重金属生物修复在过去几十年时间取得了进展，但针对其分子机制理论和整个生态系统层面的前景应用也才刚刚开始．未来的研究应该重点关注以下方面：

（1）从污染环境中挖掘更多的原位抗性资源和组合模式．污染区域植物与微生物的物种共存模式更好地验证和实现了生物修复的实际应用，因此，从原位污染环境（例如矿区、尾矿库、金属冶炼厂、电子垃圾废弃地）中发现和确定新的抗性资源是植物-微生物联合修复组合的优先考量．

（2）充分利用组学研究获取未知抗性资源．分子组学的迅猛发展，使得从生物DNA、RNA、蛋白质和代谢产物中获取抗性资源成为可能．微生物潜在抗性基因挖掘可利用微生物可培养以及基因组学实现[48]．分子组学的发展拓宽了我们对优良抗性基因的选择，从而在实际修复过程中实现最优组合．

（3）不断发展基因编辑手段，为获取多重抗性提供可能．生物具有多重抗性是其生存于多种金属污染环境的必要条件[88]，但现有基因编辑技术只能够实现单一抗性基因的表达[89]．因此，在未来开发多基因的转移技术、实现多种抗性及促生长基因共表达对修复前期生物生存至关重要．

（4）开展复合生物修复体系的机制研究．单一菌株与植物联用的修复机制研究较多，虽然植物-微生物-改良剂、植物-复合微生物等复合体系具有更高效的修复效果，但其机制知之甚少尚待深入研究．

（5）植物-微生物联合修复体系的适用环境条件与阈值区间．不同立地环境条件下物种表现出的耐受能力和修复效果不同[90]，实际应用过程中应该充分考虑物种对环境的偏好性与适应能力，研究不同修复植物-微生物组合在不同环境条件下的施用效果．

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