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专论与综述

种子内生菌增强宿主植物重金属抗性的功能机制研究进展

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摘　要：种子是植物的繁殖器官，其内定殖有一定数量的内生菌，种子内生菌通过垂直传播成为新生植物组织内最早定殖的微生物，对连续几代植物内生菌群落的形成起着决定性作用，并在植物抗逆方面发挥着重要作用。本文对种子内生菌与宿主植物重金属抗性之间的关系及其功能机制进行综述，并对下一步研究方向予以展望。

关键词：种子内生菌，重金属抗性，抗性机制，抗性基因

Functional mechanism of seed endophytes enhancing heavy metal resistance of host plants: a review

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Abstract: Seed is the reproductive organ of plants, and there are a certain number of endophytes colonized in the seed. The seed endophytes become the earliest colonized microorganisms in the tissue of new plants through vertical propagation, which plays a decisive role in the formation of endophytic community of successive generations of plants, and plays an important role in plant stress resistance. In this paper, the relationship between seed endophytes and heavy metal resistance of host plants and their functional mechanisms are reviewed, and the future research directions are prospected.

Keywords: seed endophyte, heavy metal resistance, resistance mechanism, resistance gene

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土壤重金属污染是一个全球性问题，全球近12%的农业生产受到重金属污染的不利影响，人类生存因此受到极大威胁[1-2]。重金属污染如此令人担忧是其持久性和生物累积性，重金属长期存在于环境中，不能通过任何物理、化学或生物手段完全降解；然而一些微生物可以通过促进植物生长及微生物介导的氧化或还原反应改变金属的化学状态，从而改变金属的生物利用度及其潜在毒性[3]。

内生菌是定殖于宿主植物内部但不引起宿主植物明显症状改变的微生物。它们在营养上依赖于宿主，反过来，内生菌通过影响宿主植物代谢从而促进植物生长、增强其抗逆能力[4]。种子是多种内生菌的载体，能通过垂直传播将其传递给子代植物，种子内生菌作为建立植物内生菌群的基础，能为宿主植物的生长发育和植物保护提供许多益处，已有研究表明部分种子内生菌能赋予子代植物重金属抗性[5-7]，从而增强其对重金属污染环境的适应性[8-9]。

1 种子内生菌

种子作为植物的繁殖器官，其内定殖有一定数量的内生菌。种子与内生菌之间是一种共生关系，种子内生菌对于植物具有重要的生理学意义，如果种子萌发，所有子代幼苗都会继承亲本植物内生菌[10-11]。这些内生菌能够增强种子的活力、发芽率和恢复力，改善植物的生长和发育，从而赋予植物对生物胁迫和非生物胁迫的耐受性[12-14]。过去采用传统内生菌分离培养方法，不能够分离和培养出大量的未知种子内生菌。随着16S rRNA基因测序[15]、下一代测序(Next Generation Sequencing，NGS)[16-17]、Phylochip G3分析(第二基因组)[18]等测序新技术的广泛应用，人们相继发现了大量的种子内生菌及其群落的变化规律。种子内生菌的多样性令人惊叹，包含多达9 000个微生物种类和20亿个细菌[19-20]。最常见的种子内生细菌门有变形菌门(*Proteobacteria*)、放线菌门(*Actinobacteria*)、厚壁菌门(*Firmicutes*)和拟杆菌门(*Bacteroidetes*)[21-22]。常见内生真菌门是子囊菌门(*Ascomycota*)和担子菌门(*Basidiomycota*)[23]。郭建秀等对青藏高原高寒草甸8种植物种子内生菌进行研究，发现种子内存在115个细菌属和135个真菌属，其中变形杆菌门细菌和子囊菌门真菌在各植物种子中占优势[24]。Chen等从丹参种子中发现17门39纲微生物，他们对比了玉米、豆类种子内生菌，发现3种植物的种子核心菌群有重叠，其中包括细菌泛菌属(*Pantoea*)、假单胞菌属(*Pseudomonas*)、鞘氨醇单胞菌属(*Sphingomonas*)和真菌链格孢属(*Alternaria*)[22]。

2 种子内生菌赋予宿主植物重金属抗性

种子是植物内生菌的重要来源，从种子开始，在植物萌发和发育过程中，种子携带的内生菌可以分布到植物的根和地上部分[25-26]。López-López等发现几乎所有从菜豆(*Phaseolus vulgaris*)种子中分离的内生菌都能够在根部被发现，这表明种子传播的内生菌能够在幼苗中繁殖并持续存在[27]。在重金属污染环境中，通过种子垂直传播给下一代的部分内生菌菌株，能够显著增强宿主植物的重金属抗性，这在植物重金属污染环境适应过程中发挥着重要作用[6]。例如，李柯等研究表明，在高浓度重金属铅胁迫下，侵染内生真菌*Epichloë guerinii*的德兰臭草(*Melica transsilvanica*)种子比未侵染内生真菌的种子萌发率更高，其子代植物幼苗生物量更大[28]。同样，Mastretta等证明了接种抗镉内生菌的烟草种子可以在镉胁迫下生长，该种子内生菌降低了镉暴露对烟草的重金属毒性[7]。Johnston-Monje等发现来源于玉米种子的内生菌，可通过固氮、分泌铁载体、合成1-氨基环丙烷-1-羧酸(1-Aminocyclopropane-1-Carboxylic Acid，ACC)脱氨酶等功能刺激宿主植物，使其能够快速适应包括重金属胁迫在内的恶劣环境条件[29]。Sánchez-López等发现，在复合重金属(锌、镉、铜)胁迫下，植物*Crotalaria* *pumila* 连续 3 代种子中都具有相似的内生细菌群落，部分菌株具有重金属抗性，并且还表现出有机酸生成、磷酸盐溶解能力和ACC脱氨酶活性[5,29-30]。Truyens 等研究表明，在镉胁迫下拟南芥(*Arabidopsis thaliana*)连续几代种子内生菌比无镉胁迫的种子内生菌具有更显著的重金属抗性，以及生产更多 ACC 脱氨酶的能力；这些研究表明某些内生菌可以垂直传播给下一代并赋予其重金属抗性，对植物适应重金属胁迫环境具有重要意义[9]。

3 种子内生菌赋予植物重金属抗性的机制

3.1 促进宿主植物生长，提高植物对重金属的耐受性

3.1.1 产植物激素等促进宿主植物生长

种子内生菌能够分泌 ACC 脱氨酶，抑制乙烯合成前体 ACC、解除因重金属胁迫增加的乙烯对种子萌发及植物生长的抑制[31]。Truyens 等发现长期生活在镉/镍污染稻田的禾草细弱剪股颖(*Agrostis capillaris*)种子内生枯草杆菌属(*Bacillus* sp.)和泛菌属(*Pantoea* sp.)细菌，它们表现出更高的ACC脱氨酶活性和产生更多的铁载体、吲哚-3-乙酸(Indole-3-Acetic Acid，IAA)，将其接种在镉暴露的细弱剪股颖幼苗上可以促进幼苗生长、增加其生物量，并赋予植物较强的镉抗性[32]。此外，Truyens 等还发现，种子内生根瘤菌(*Rhizobium*)可在拟南芥中世代垂直传递，并通过产生 ACC 脱氨酶、铁载体、吲哚乙酸等增加拟南芥的生物量，从而增强其重金属抗性[8]。

3.1.2 促进植物对营养元素的吸收

种子内生菌具有改善宿主植物养分获取的功能特性，通过磷溶解、植酸矿化、固氮作用为植物提供氮、磷元素，通过分泌铁载体促进植物对铁的吸收和其他微量元素的吸收[5]。龙葵(*Solanum nigrum* L.)种子内生菌嗜线虫沙雷氏菌(*Serratia nematodiphila*)具有转运金属的通道蛋白，能促进植物对锰、锌、铁等营养元素的吸收[33]。Sánchez-López 等发现种子内生菌甲基杆菌(*Methylobacterium* sp.)具有固氮基因，可以向生长在重金属污染矿渣上的宿主植物 *Crotalaria pumila* 提供氮素，增强其重金属抗性；*Crotalaria pumila* 种子内生芽孢杆菌(*Bacillus* sp.)可以通过增加有机酸产量和增强解磷能力，从而增强宿主植物对重金属锌、镉、铜的抗性[30]。

3.1.3 促进植物的光合作用

种子内生菌对宿主植物的光合作用有积极影响，能够通过增加色素含量、提高植物对铁元素的摄取能力等作用促进重金属胁迫下植物的光合作用。Wan 等通过对龙葵种子的研究发现，在重金属镉胁迫下，种子内生菌显著提高了植物叶片中的类胡萝卜素和叶绿素 a、b 含量[33]。同样地，Mirzahossini 等发现在镍胁迫下，种子内生香柱菌(*Epichloë*)显著提高了高羊茅(*Tall fescue*)中的总叶绿素含量，从而促进光合作用；种子内生菌分泌的铁载体能增加植物对铁元素的吸收，铁元素是叶绿素合成有关酶的组成成分，铁元素增加可以提高叶绿素含量，从而促进植物光合作用[34-36]。Sánchez-López 等发现 *Crotalaria pumila* 种子内生菌甲基杆菌含有编码捕光复合体的基因以及参与叶绿素和类胡萝卜素合成的基因，能够在重金属胁迫下促进植物光合作用[5]。

3.1.4 协同增强植物抗氧化系统(Antioxidantsystem，AOS)

种子内生菌可以通过降低电解质和脂质过氧化水平，调节植物抗氧化酶[如过氧化氢酶(CAT)、超氧化物歧化酶(SOD)、谷胱甘肽过氧化物酶(GSH-PX)、抗坏血酸过氧化物酶(APX)]活性以及脂质过氧化(丙二醛形成)，减轻重金属诱导植物氧化胁迫导致的细胞膜损伤和氧化应激损伤[33,37]。Zhang 等发现醉马草(*Achnatherum inebrians*)种子内生菌通过改善宿主植物抗氧化防御系统，主要通过影响抗氧化酶活性、增加丙二醛和脯氨酸的含量提高其对重金属镉的抗性[38]。龙葵种子内生真菌可通过提高抗氧化酶活性赋予宿主植物重金

属抗性，有利于其抵御重金属镉的毒害[33]。

3.2 种子内生菌可通过降低植物体内重金属含量从而减轻其植物毒性

3.2.1 通过外排或内生菌胞内积累降低重金属对植物的胁迫强度

种子内生菌可以通过外排重金属离子使其在细菌细胞外沉淀、转运到细菌胞内积累或者通过生物活性吸附来降低重金属对宿主植物的毒害作用。芽孢杆菌(*Bacillus* sp.)作为种子内生菌已在玉米、水稻、番茄、花生、菜豆、西葫芦、葡萄、阿拉伯咖啡等植物中发现[39]。芽孢杆菌能够利用腺嘌呤核苷三磷酸(ATP)水解释放的能量，通过P型ATP酶外排泵逆浓度梯度向细菌胞外输送重金属离子，使其在细胞外沉淀以减轻重金属对种子内生菌及宿主植物的毒性[40-41]。同样地，水稻种子内生菌嗜麦芽窄食单胞菌(*Stenotrophomonas maltophilia*)中存在防御结瘤分裂(Resistance-Nodulation-Cell Dicision，RND)家族外排泵，是由周质膜蛋白组成的三元复合体，可以直接从种子内生菌细胞中泵出重金属阳离子[42]。种子内生不动杆菌(*Acinetobacter*)和沙雷氏菌(*Serratia*)可以通过调节与镉吸收和转位相关的离子通道来促进镉在胞内的积累[43-44]。水稻种子内生菌可以通过生物活性吸附，即通过较慢的活性代谢过程将重金属镉转运到内生菌细胞中，以减轻重金属对宿主植物的毒害作用[45]。

3.2.2 通过分泌铁载体、有机酸、蛋白质等与重金属形成络合物或溶解重金属，将有毒金属离子转化为毒性较低或无毒的形式

游离重金属离子对植物细胞毒害性极强，种子内生菌可以分泌螯合剂与重金属离子结合，改变重金属的活性状态，以减轻重金属离子对植物的毒害作用[42,46]。十字花科植物种子内生镰刀菌(*Fusarium* sp.)可以通过产生金属草酸盐来固定有毒的金属和类金属物质，或者在类黑色素聚合物上与重金属形成螯合作用[25,47-48]。种子内生真菌可以促进德兰臭草胚根分泌大量的酚类物质与铅螯合，减少宿主植物根部对铅的吸收[28]。Malinowski等研究发现，种子内生香柱菌(*Epichloë* spp.)侵染会导致高羊茅植物根系分泌物中酚类物质含量增加，酚类物质螯合重金属，使重金属的生物活性降低[49]。大肠埃希菌(*Escherichia coli*)被报道为种子内生菌[50]，有研究表明大肠埃希菌能够产生有机汞裂解酶将有机汞裂解成汞离子(Hg^{2+})，再产生汞还原酶将剧毒离子Hg^{2+}转化为毒性较小的挥发性氧化汞(HgO)，从而减轻重金属毒性[51-52]。Dimkpa等研究表明种子内生菌链霉菌属(*Streptomyces* spp.)在重金属镉/镍胁迫下铁载体产量增加，铁载体可以帮助植物获得足够的铁与有毒重金属离子竞争[5,53]，还可以结合培养基中的金属离子阻止它们扩散到细胞中，以此来保护内生菌及其宿主植物免受金属毒性的影响[54]。

总而言之，种子中的内生菌在重金属胁迫条件下以增加生物量和降低重金属毒性来促进植物生长[55-58]，种子内生菌-植物-重金属之间的相互影响简要总结如图1所示。

4 内生菌重金属抗性基因

重金属抗性基因通过编码重金属转运蛋白(包括ATP酶外排泵和外排跨膜蛋白)、参与重金属解毒过程、参与重金属耐受信号转导等功能赋予种子内生菌重金属抗性，从而增强宿主植物对重金属的耐受性。Nies对微生物中重金属抗性系统提出了详细的见解，重金属转运重要蛋白质家族有ABC、P-type[b]、A-type[c]、RND、HoxN、CHR、MIT、CDF[59]。*nik*、*cop*、*mer*、*chr*、*czc*、*nccMdt*和*znt*基因的表达与细菌对重金属的抗性有关[60-61]。全基因组测序、金属组学、蛋白质组学和转录组学的整合可用于预测金属在微生物中引发的毒性和防御机制[62]。基因组测序和RT-qPCR分析表明，与LZ-C蛋白紧密相关的湖生戴尔福特菌(*Delftia lacustris*)的*Chr*、*Czc*和*Mer*家族基因相关的基因与重金属耐受性密切相关，*MerR*家族基因

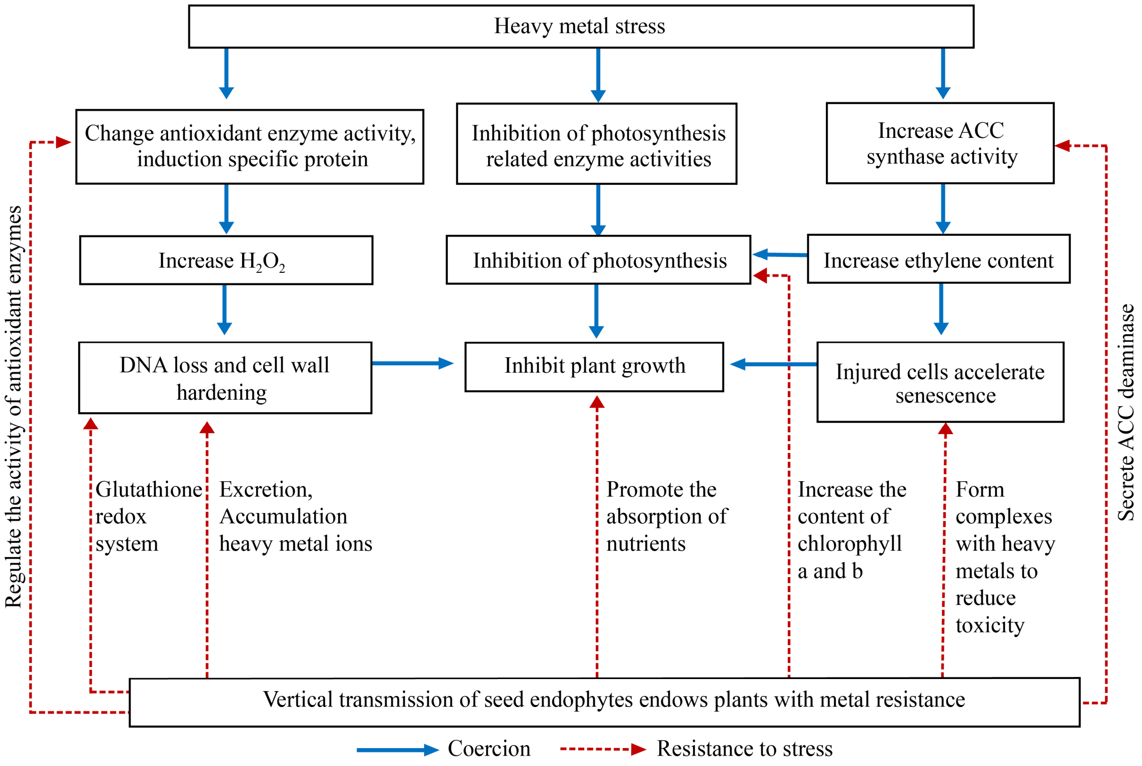

图 1　种子内生菌-植物-重金属之间的相互影响
Figure 1　Interaction between seed endophytes, plants and heavy metals

还参与许多重金属解毒活动[63]。此外，在耐镉恶臭假单胞菌(*Pseudomonas putida*) CD$_2$ 中，*czcCBA1*、*cadA2R* 和 *colRS* 这 3 个基因参与了金属外排系统，ColRS、ColR 和 ColS 参与镉耐受信号转导系统的一部分；ColRs 还通过遗传互补在多金属耐受性调节中发挥作用[64]。在大孢树粉孢菌(*Oidiodendron maius*)中发现了编码 PLAC8 家族蛋白的新基因 *OmFCR1*，该基因的表达增强了真菌对镉的耐受性[65]。金属硫蛋白基因与真菌中的氧化和重金属胁迫有关[66]。植物螯合酶(PCS)编码基因也被证明可以提高真菌对金属胁迫的耐受性[67]。Shen 等首次从转录组水平深入了解了重金属抗性真菌嗜鱼外瓶霉(*Exophiala pisciplila*)的谷胱甘肽 s-转移酶(GSTs)基因，并初步解释了其重金属抗性机制；这些 GSTs 在不同重金属胁迫下均可表达，而基因表达的上调与外瓶霉属对重金属的耐受性有关[68]。对 3 种抗金属促进植物生长菌的基因组分析表明，它们都有不同的重金属抗性基因；P 型金属转运蛋白包括 ATP 酶、CDF、HupE/UreJ 和 CHR 家族，在苜蓿根瘤菌中观察 CopA/CueO 系统和 ZntA 转运体，根瘤脓杆菌(*Agrobacterium tumefaciens*)中 CzcD 转运蛋白参与了对不同金属的抗性和动态平衡[69]。在铜抗性恶臭假单胞菌(*Pseudomonas putida*)中存在操纵子和基因簇，如 *cop*、*cus*、*czc*、*nik* 和 *asc* 系统，重金属抗性基因的测定预测了该种子内生菌对重金属的抗性[70]。

5　展望

种子内生菌对宿主植物在金属污染土壤上的生存和传代具有重要意义。研究有益的内生菌在金属胁迫生物修复中的生物技术应用，以及金属胁迫下生态位中细菌群落的多样性和结构，对于人们进一步开发利用植物修复环境污染有很大帮助。为了更好地了解重金属污染环境中种子内生菌及其宿主植物的关系，以及优化金属污染土壤的植物-微

生物联合修复技术，可以从如下几方面进行深入研究：(1) 利用荧光蛋白标记法等方法探索种子内生菌之间的相互作用，以及这些群落在植物生活史上的动态变化。(2) 从宏基因组、转录组和蛋白质组学水平，运用酶联免疫吸附试验(ELISA)、染色质免疫共沉淀测序(ChIP-Seq)等方法来发掘种子中大量未被发现的内生菌种群、表型特征，以及其在种子萌发和植物生长过程中可能发挥的作用。(3) 利用微生物分解污染物代谢基因的表达测序等方法，进一步从分子机制阐明种子内生菌增强宿主植物抗重金属胁迫的机制。随着研究的深入，我们有望发现更多的种子内生菌资源，并开发新技术，探索其深层机理和实际应用。

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