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Review 综 述

内生真菌与宿主植物协同调控砷胁迫作用机制研究进展

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摘 要：丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)和深色有隔内生真菌(dark septate endophytes, DSE)是植物根系中最主要的两大类内生真菌，均可与植物根系形成菌根共生体，在促进植物生长，提高重金属等胁迫抗性方面发挥着重要作用。砷(arsenic, As)及砷化合物具有较强的毒性，可在植物中富集，造成生物链毒害。本团队一直致力于内生真菌与药用植物生长、活性物质合成，砷吸收、积累关系的研究，并取得了一定的进展。结合团队现有研究和前人研究成果，本文分析归纳了砷胁迫条件下，AMF定殖对宿主植物生长和砷吸收、积累的影响；详细阐述了砷胁迫条件下，宿主植物生理活动、抗氧化系统、激素水平、转录水平响应AMF调控的变化。其后，从宿主植物细胞内、外两个方面总结内生真菌与宿主植物协同调控砷胁迫的作用机制，归纳为“生长稀释效应”“菌丝隔离”“螯合过滤”“菌根固定化(mycorrhizal immobilization)”“转运体抑制效应”“生物转化作用”和“保宿主、降氧化”等7项作用机制，并绘

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制了不同机制之间的作用关系图。DSE-宿主植物调控砷胁迫的研究相对较少，对已有研究进行梳理归纳，发现DSE增强宿主植物砷耐性机制与AMF类似。本文对研究内生真菌与宿主植物协同调控砷胁迫作用机制，解决土壤砷污染问题，实施生态农业或中药材生态化种植，降低植物关键部位砷积累具有重要的参考价值。

关键词：砷；丛枝菌根真菌；深色有隔内生真菌；胁迫抗性；生长稀释效应；菌根固定化机制

Synergistic mechanism of endophytic fungi and host plants against arsenic stress

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Abstract: Arbuscular mycorrhizal fungi (AMF) and dark septate endophytes (DSE) are the two key types of root symbiotic fungi that enhance plant growth and resistance of plants to heavy metal stress. Arsenic (As) and As compounds are highly toxic, which accumulate in plants and then enter biologic chain. Our team has been committed to the study of relationship between endophytic fungi and the growth, synthesis of active substances, and arsenic absorption and accumulation of medicinal plants and has made some progress. According to our previous research outcomes and available research results, we summarized the role of AMF colonization in the growth and As uptake and accumulation in host plants under As stress, expounded the responses of host plants to AMF regulation under As stress in terms of physiological activities, antioxidant system, hormone level, and transcription level. In addition, 7 synergistic regulatory mechanisms involved in improving the As resistance were summarized at cellular level: ‘growth dilution effect’, ‘isolation of hyphae’, ‘chelating and filtration’, ‘mycorrhizal immobilization’, ‘transporter inhibition’, ‘biotransformation’, and ‘protecting the host and reducing oxidative stress’. The interaction among mechanisms was plotted. There are limited studies on the regulation of As stress by DSE-host plants. We found that the mechanism of DSE in enhancing arsenic tolerance of plants is similar to that of AMF. Our work has important reference value for studying synergistic antagonistic mechanism of endophytic fungi and host plants against As stress, alleviating As-polluted soil, implementing ecological agriculture or ecological planting of Chinese medicinal materials, and reducing As accumulation in key parts of plants.

Keywords: arsenic; arbuscular mycorrhizal fungi; dark septate endophytic; stress resistance; growth dilution effect; mycorrhizal immobilization mechanism

砷(arsenic, As)是我国土壤重金属污染的主要元素之一。据 2014 年发布的全国土壤环境质量调查显示，2.7%的土壤样品被砷污染[1]。砷是一种剧毒类金属，被世界卫生组织和国际癌症研究机构列为高毒致癌物[2]。砷的毒性与其存在形态和生物种类有着密切关系，无机砷的毒性远高于有机砷，对人和动物而言，As(III)的毒性又远高于 As(V)，但对植物则相反[3]。土壤砷污染不仅毒害作物，降低作物的产量及品质，还可通过食物链对生态系统和人类健康造成威胁。本团队的研究中也发现，高砷土壤背景不但会损害三七(*Panax notoginseng*)生长，还可通过富集作用危害药用和食用安全[4]。目前，业界认为采用包括砷超富集植物、砷耐性微生物等在内的多生物手段是修复砷污染土壤或降低植物砷吸收、积累的有效方式之一。

内生真菌(endophytic fungi, EF)是指一类定殖于健康植物组织及细胞内，不会对植物引起明显病害症状的微生物[5]，在促进宿主植物营养吸收、增强胁迫抗性等方面发挥重要作用，主要包括丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)和深色有隔内生真菌(dark septate endophytes, DSE)两大类[6]。AMF 是迄今发现与植物关系最为密切的互惠内生真菌，能与 90%的植物根系形成菌根共生体[7]，可在植物根细胞内产生“泡囊”“丛枝”“菌丝圈”等典型结构[8]。DSE 是重金属污染环境根系中普遍存在的一类小型内生真菌，菌丝颜色较深，具有明显的横隔，可在植物细胞中形成微菌核典型结构[9-11]。

众多研究证实，AMF、DSE 在改善根际土壤微生物群落结构、抑制病原微生物损害，促进宿主植物营养成分吸收，提高重金属、干旱、高盐胁迫抗性等方面发挥着重要作用[8,11-13]。本团队研究结果显示，AMF、DSE 种类、定殖密度与三七、滇黄精、阳春砂仁生长、活性物质含量之间存有高度正相关[6,9,11]，并从其根系中离出了多株砷、铅(Pb)、镉(Cd)耐性菌株，其中来源于三七的菌株 Pn-12、Pn-13 对 As(V)的耐性高达 1 600 mg/L[6]；来源于滇黄精的菌株 DT-5、MZ-11 对 As(V)的耐性高达 1 200 mg/L，EC_{50}值分别为 1 281 mg/L 和 1 108 mg/L。比较来看，关于 AMF-宿主植物协同调控砷胁迫作用机制的研究报道较多，而对 DSE-宿主植物协同调控的研究多处于探索阶段。

本文基于团队研究成果，综合分析了内生真菌 AMF、DSE 与宿主植物协同调控砷胁迫作用机制，对利用 AMF、DSE 等微生物手段解决土壤砷污染问题，实施生态种植，降低砷积累提供了技术参考和理论支持。

1　砷胁迫条件下，AMF 对宿主植物生长及砷吸收、积累的影响

砷在土壤中常以无机态形式存在，包括五价氧化态砷酸盐 As(V)和三价还原态亚砷酸盐 As(III)，并以 As(V)为主。无机砷又可通过微生物等生物甲基化过程，进一步生成有机砷化合物一甲基砷(monomethyl arsenic, MMA)和二甲基砷(dimethyl arsenic, DMA)等[14]。当植物根系吸收砷并积累到一定程度后，植物生长受到抑制，生长发育延迟，生物量下降，植株矮小、叶片失绿、根数量减少、根尖发褐或发黑，直至植株死亡[15]。笔者发现，土壤砷酸盐浓度过高(100 mg/kg)，三七叶片发黄，萎蔫脱落，极易死亡，但三七砷耐性机制尚不明确。

一些长期生长在砷污染环境中的植物，形成了一系列砷抗性机制，包括“外排机制”“螯合作用”“细胞壁的储存作用”“液泡区隔作用”“抗氧化系统防御作用”等[15-16]。

植物对砷的耐受限度受植物品种、砷化学形态及浓度的影响，大部分农作物、经济作物或药用植物对砷耐受性较低，在高砷土壤背景下，其生长或代谢产物合成受到严重影响。利用共生内生真菌增强植物砷胁迫抗性，降低砷在关键部位积累是目前实施生态种植常最采用的手段之一。

1.1 砷胁迫条件下，AMF 对宿主植物生长的影响

综合表 1 可知，AMF 可通过增强宿主抗氧化防御，促进营养物质吸收，增大生物量，扩大 P/As(V)吸收比率，降低砷吸收和积累等方式来提高植物砷耐性，且因 AMF 种类不同，调控效果差异显著。Chen 等[21]研究发现，砷胁迫下，分别接种摩西斗管囊霉(*Funneliformis mosseae*)、苏格兰斗管囊霉(*F. caledonium*)和根内根孢囊霉(*Rhizophagus intraradices*)均能显著增加蜈蚣草(*Pteris vittata* L.)叶片和根系磷浓度，提高 P/As 比率。而后有研究证实，砷胁迫下，接种 AMF 显著提升棉花(*Gossypium hirsutum* L.)[23]、烟草(*Nicotiana tabacum* L.)[25]、紫花苜蓿(*Medicago sativa* L.)[28]、刺槐(*Robinia pseudoacacia* L.)[32]等吸收微量元素及水分的能力，从而显著促进宿主植物生长和根系发育。此外，AMF 种类与增强砷耐性效果之间关系密切。Yu 等[18]研究表明，分别接种 *F. mosseae* 和幼套近明球囊霉(*Claroideoglomus etunicatum*)均增加玉米(*Zea mays* L.)生物量和磷浓度(*F. mosseae*>*C. etunicatum*)，减少地上部的砷积累(*F. mosseae*≈*C. etunicatum*)

表 1 砷胁迫下，接种 AMF 对宿主植物生长及砷积累的影响

Table 1 Effects of AMF on the growth and arsenic accumulation of host plants under the stress of arsenic

Plants	AMF	Arsenic concentration in each treatment group	Effects on plant growth and arsenic absorption and accumulation
Zea mays L.	*Funneliformis mosseae*, *Diversispora spurcum*	2.02 mg/kg	Enhanced the antioxidant defense of leaves; Limited arsenic transfer from roots to shoots; Reduced arsenic accumulation in shoots; Promoted the uptake of phosphorus and sulfur[17]
	Claroideoglomus etunicatum, *Septoglomus constrictum*, *F. mosseae*	0, 25, 50, 100 mg/kg	The biomass and phosphorus concentration increased with the inoculation of *F. mosseae* and *C. etunicatum* (*F. mosseae*>*C. etunicatum*) and the arsenic accumulation decreased in shoots (*F. mosseae*≈*C. etunicatum*). Inoculation with *S. constrictum* produced a negative effect on biomass[18]
	F. mosseae	1 204.99 mg/kg	Root length and dry weight significantly increased with the inoculation of *F. mosseae*, as well as the decrease of arsenic concentration in stems[19]
	C. etunicatum	5, 30 mg/L	Reduced the accumulation of arsenic in stems and leaves, and the arsenic transfer to shoots; Increased the types and quantities of organic acids secreted by roots[20]
Pteris vittata L.	*F. caledonium*, *Rhizophagus intraradices*, *F. mosseae*	106 mg/kg	Increased the dry weight of leaves and roots; Elevated P/As ratio in roots and leaves; limited arsenic transfer from roots to leaves[21]
	C. etunicatum	5, 30 mg/L	Reduced the secretion of organic acids in the root system; Promoted the absorption and transport of arsenic; Elevated the ratio of As (III)/As (V); Improved the transfer rate of arsenic from the roots to the shoots[20]
	F. mosseae	75 mg/L	Increased dry weights of leaves and roots and the concentration of phosphorus and arsenic[22]

(待续)

(续表 1)

Plants	AMF	Arsenic concentration in each treatment group	Effects on plant growth and arsenic absorption and accumulation
Nicotiana tabacum L.	*F. mosseae*	0, 1, 30 mg/kg	Promoted the growth and development metabolism under arsenic stress. Regulated the synthesis and secretion of reduced glutathione (GSH); Reduced the accumulation of arsenic in the plant[25]
	F. mosseae	8.5 mg/kg	Increased GSH content in *N. tabacum* tissue, thus affecting the content of metal-induced chelator; Reduced arsenic content in leaves and roots of the adult plants[26]
Medicago truncatula Gaertn.	*F. mosseae*	0, 10, 50, 100, 200 mg/kg	Increased the absorption of phosphorus in *M. truncatula*; Reduced arsenic accumulation in stems and roots; Improved dry weight of stems and roots[27]
Medicago sativa L.	*F. mosseae*	0, 25, 100 mg/kg	Increased dry weight and the level of total phosphorus; Reduced arsenic transfer to shoots[28]
Pityrogramma calomelanos (Linnaeus) Link *Melastoma malabathricum* L. *Tagetes erecta* L.	*F. mosseae*, *R. intraradices*, *C. etunicatum*	(243±13) μg/g	Inoculation with these AMF can reduce arsenic accumulation in *P. calomelanos* and *T. erecta*, but had no significant effect on their growth However, these AMF significantly promoted the growth and arsenic accumulation of *M. malabathricum*[29]
Holcus lanatus L.	*F. mosseae*, *F. caledonium*	353 mg/g	Significantly reduced arsenic uptake in *H. lanatus*; Inhibits phosphate transport system[30]
Solanum lycopersicum L.	*F. mosseae*	0, 25, 50, 75, 150 mg/kg	The biomass and phosphorus uptake of *S. lycopersicum* were significantly increased at 25, 50 and 75 mg/kg, respectively. Increased the P/As ratio of roots and aerial parts; Decreased arsenic concentration in stems[31]
Robinia pseudoacacia L.	*R. intraradices*	0, 100, 200 mg/kg	Enhanced the growth and root development; Regulated phytohormone concentrations and ratios[32]
Pisum sativum L.	*F. mosseae*	0. 30, 60, 90 mg/kg	Promoted the nutritional uptake; Increased the biomass and antioxidant enzyme activity; Reduced arsenic concentration in soil by sequestering arsenic in subterranean parts of symbionts, thereby enhancing antioxidant and osmotic protection mechanisms[33]
Lens culinaris L.	*F. mosseae*	0, 2, 5 mg/L	Root phosphorus concentration decreased with the increase of arsenic concentration; Reduced arsenic concentration in edible part of *L. culinaris*[34]

etunicatum)，而接种缩隔球囊霉(*Septoglomus constrictum*)对生物量和砷积累的影响不大，可见 *F. mosseae*、*C. etunicatum* 和 *S. constrictum* 在增强玉米砷耐性上，*F. mosseae* 和 *C. etunicatum* 效果更佳。本团队前期研究发现，*R. intraradices* 对三七生长促进效果显著优于 *C. etunicatum*。

1.2 砷胁迫条件下，AMF 对宿主植物砷吸收、积累的影响

植物主要通过根系从土壤中吸收砷，并对砷形式存有一定的偏好性，一般为，As(III)>As(V)>DMA>MMA，其中主要以 As(III)和 As(V)的形式进入植物细胞，随后 As(V)在砷酸还原酶催化

下转化为 As(III)，然后 As(III)通过特定的转运体被泵出细胞或形成 As(III)-硫醇复合物，并被隔离在液泡中[16]。Li 等[35]研究显示，接种 AMF 可将无机砷甲基化为 MMA、DMA 或将 As(V)还原为 As(III)。Ultra 等[36]、Li 等[37]在向日葵(*Helianthus annuus* L.)、水稻(*Oryza sativa* L.)中得到了验证，发现在根系中分别接种聚丛根孢囊霉(*R. aggregatum*)和 *R. intraradices* 可以在土壤和植株中检测到有机砷，推测是因 AMF 参与无机砷的甲基化进程，将高毒的无机砷甲基化为较低毒的有机砷，降低毒性。此外，接种 AMF 均倾向于将转化的砷释放到环境中，而不是将其转移到植物组织中[35]。

根系是植物吸收砷的主要器官，也是最主要的积累部位，其次是茎、叶、芽等地上部分[15]。前期团队研究显示，施加 AMF (*R. intraradices*, *C. etunicatum*)、DSE (球孢枝孢霉 *Cladosporium sphaerospermum*、枝孢样枝孢霉 *C. cladosporioides*)可以降低三七对砷的吸收、积累。刘凯洋等[23]研究发现，砷胁迫下，分别接种 *R. intraradices* 和 *F. mosseae* 可降低棉花地下部和地上部的砷浓度，显著下调转移系数，抑制砷向地上部转移。Degola 等[26]以烟草和 *F. mosseae* 为研究对象得到了类似结果。但不同 AMF 对不同植物吸收积累效果明显不同，Zhan 等[17]研究发现，接种 *F. mosseae* 会导致玉米根系和枝条砷浓度增加。

2 砷胁迫条件下，植物生理活动、抗氧化系统、植物激素浓度、转录水平等响应 AMF 调控的变化

2.1 砷胁迫条件下，植物生理活动响应 AMF 调控的变化

在砷胁迫条件下，植物在营养成分吸收、生物量改变、根系形态和根际微环境理化性质变化等相关生理活动方面均会响应 AMF 调控而改变。

在增强营养成分吸收、促进成长方面，菌根可在砷胁迫下快速生长，增大根系与土壤的接触面积，使植物从土壤中吸收更多的磷、氮、钾、钙等营养元素及水分，从而促进植物生长，但也会导致植物吸收更多砷，毒害作用增强[38]。此外，交错的庞大菌丝网对不同植物间的养分和水分进行再分配，是宿主植物获取有效养分、水分的另一条重要途径[39]。

在改变根际土壤微环境理化性质方面，接种 AMF 会改变土壤酸碱度(pH)、氧化还原电位、根系分泌物等微环境理化性质及根际微生物群落结构，从而降低砷等重金属离子的移动性和生物有效性，进而增强宿主植物对砷等重金属的胁迫抗性[39]。研究证实，AMF 广泛定殖会增加土壤 pH，降低根际重金属浓度，通过降低重金属的生物有效态离子浓度，达到提高植物的重金属耐受性的目的[38-39]。

在根系形态变化方面，植物根系是植物与重金属持续接触的重要器官，也是植物吸收水分和养分的重要器官。根毛如同过滤器，有选择地吸收金属离子，除储存在根系中外，部分转移至茎和叶中[38]。砷胁迫会抑制植物生长、根系发育，而接种 AMF 可有效缓解这一胁迫，从而促进根系发育，提高总根数、根直径、根面积、根体积、根叉数和根尖数的生长量[23,40]。根系功能的优化是 AMF 促进营养成分吸收的先决条件，尤其在重金属胁迫条件下[23]；此外，AMF 还可强化根系细胞壁木质化，使宿主植物根尖表皮变厚、细胞层数增多，影响金属离子进入根系的进程[38-39]。

2.2 砷胁迫条件下，植物抗氧化系统响应 AMF 调控的变化

研究证实，砷胁迫条件下，植物发生应激反

应，产生大量活性氧(reactive oxygen species, ROS)，导致细胞器损伤，甚至死亡[38]。Sharma 等[41]研究证实，在砷胁迫条件下，接种 *R. intraradices* 和 *C. etunicatum* 可通过改善植物抗氧化防御系统，如增强抗坏血酸过氧化物酶(aseorbateperoxidase, APX)、超氧化物歧化酶(superoxide dismutase, SOD)、过氧化物酶(peroxidase, POD)和过氧化氢酶(catalase, CAT)等活性，降低过氧化氢水平，防止膜过度氧化，减少氧化损伤，从而提高植物对砷的胁迫抗性。在抵御砷胁迫抗性中，增加 As(III)螯合化合物还原性谷胱甘肽(reduced glutathione, GSH)水平，减少 GSH 的再循环也是植物的有效策略之一[42]。而 AMF 的定殖不但会通过自身合成 GSH，还可调控植物增加 GSH 前体物质硫酸盐转运体的表达，从而共同提高 GSH 水平[43]。

2.3 砷胁迫条件下，植物激素浓度响应 AMF 调控的变化

植物激素是植物生长发育的关键调节因子，一个平衡的激素系统可以促进根的生长，生物量增加，胁迫抗性增强，从而加速生物修复过程[38,44]。Abd_Allah 等[45]认为，AMF 可稳定非生物胁迫引起的激素水平波动。Zhang 等[32]进一步研究发现，刺槐-*R. intraradices* 共生体系通过调节砷胁迫下的植物激素比来协调激素平衡，从而减缓植物生长发育，维持正常水分平衡，提高植物细胞渗透压，进而提高刺槐幼苗砷胁迫抗性。Bi 等[46]研究表明，*F. mosseae* 在玉米根系中定殖可以显著提高根系中吲哚乙酸和细胞分裂素浓度，并降低脱落酸浓度，从而改变根系的生长发育，推测与砷胁迫抗性有关。

2.4 砷胁迫条件下，植物转录水平响应 AMF 调控的变化

砷胁迫条件下，AMF 通过调节宿主植物与砷吸收、转运、转化相关基因表达，从而影响宿主植物对砷的吸收、迁移和积累[39,47]。研究表明，砷可影响高亲和磷酸盐转运蛋白基因和具有砷外排泵功能的基因表达量，且蒺藜苜蓿(*Medicago truncatula* Gaertn.)高亲和磷酸盐转运蛋白基因 *GiPT* 表达量与 *R. intraradices* 根外菌丝对 As(V)的摄取密切相关[48]；李景龙等[49]研究发现，*R. intraradices* 通过上调砷酸盐还原酶基因(*RiarsC*)的表达量，从而提升 As(V)还原为 As(III)的比例，提高砷胁迫抗性和解毒能力。此外，AMF 可通过下调磷酸盐摄取系统表达、上调宿主植物植物螯合素基因的表达，从而达到降低砷吸收、积累的目的。如，*R. intraradices* 诱导下大麦(*Hordeum vulgare* L.)中砷酸盐的摄取响应 *HvPht1* 下调表达而减少[50]；*R. intraradices* 的定殖明显上调白刺花[*Sophora davidii* (Franch.) Skeels]根和叶中植物螯合素基因 *SvPCS1* 的表达，使白刺花根和叶细胞中砷浓度降低[51]。

3 AMF 与宿主植物协同调控砷胁迫抗性机制

3.1 砷胁迫条件下，AMF 与宿主植物“外部”协同调控机制

综合现有研究发现，砷胁迫条件下，AMF 与宿主植物的“外部”协同调控机制可归纳为“生长稀释效应”、“菌丝隔离”和“螯合过滤”3 项发生在细胞外相对宏观的作用机制(图 1)。

大量研究表明，AMF 可通过增强营养元素吸收，提高光合作用效率等途径，达到促进植物生长，提高生物量，稀释组织内砷浓度的目的[32,52]，这种因植物快速生长，产生额外生物量造成砷浓度降低的现象，称之为“生长稀释效应(growth dilution effect)”[51]。此效应已在玉米[19]、棉花[23]、蒺藜苜蓿[27]、紫花苜蓿[28]、大豆[*Glycine max* (L.) Merr.][52]中发现且证实。

“菌丝隔离”机制是指宿主植物通过根外

AMF 菌丝结构积累大量砷及砷化合物，从而降低宿主植物对重金属的吸收，减少砷积累[38,53]。在这一过程中，真菌结构表面产生的半胱氨酸、氨基酸和硫醇基等正电荷粒子会改变砷价态，并将其牢牢吸附在宿主植物根部，限制迁移[38,54]。此外，Li 等[55]研究发现，菌丝表面产生的胞外聚合物颗粒，具有羧基、胺基、羟基等官能团，可通过络合、表面沉淀、离子交换等吸附重金属，将重金属隔离在菌丝表面。

“螯合过滤”机制是指 AMF 通过根外菌丝螯合进入根系的砷离子，并储存在菌丝中，降低砷有效浓度，从而提高植物对砷的耐受力[56]。AMF 的根外菌丝和孢子可为砷离子提供结合位点，结合土壤中的砷离子，限制向地上部分转移[56-57]。Zhang 等[32]研究发现，AMF 菌丝还可通过分泌球囊霉素相关土壤蛋白及柠檬酸、草酸、戊酸、酒石酸等低分子量有机酸、黏液等物质螯合土壤中的无机砷，降低刺槐对砷的吸收。

3.2 砷胁迫条件下，AMF 与宿主植物“内部”协同调控机制

砷胁迫条件下，AMF 与宿主植物的“内部”协同调控机制可归纳为“菌根固定化(mycorrhizal immobilization)”“转运体抑制效应”“生物转化作用”和“保宿主、降氧化”4 项发生在植物细胞内相对微观的作用机制(图 1)。

“菌根固定化”机制是指 AMF-宿主植物共生体系可通过增强植物细胞壁“滞留作用”及液泡“区隔作用”固定植物根内砷，抑制砷向地上部分转移[51]。有研究表明，砷离子在进入细胞壁时，部分离子会与细胞壁上的羧基、羟基、醛基等活

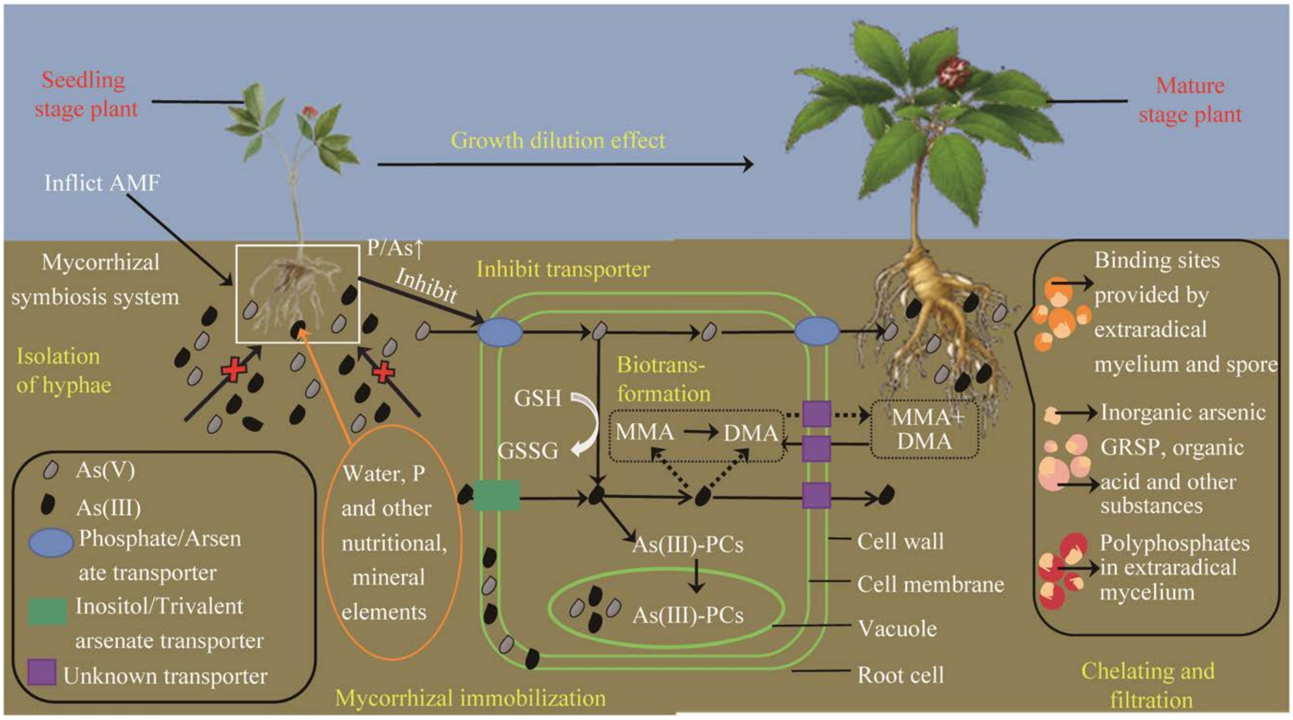

图 1　AMF-宿主植物协同调控砷胁迫作用机制

Figure 1　Synergistic mechanism of endophytic fungi and host plants on arsenic stress. AMF: Arbuscular mycorrhizal fungi; As(V): Arsenate; As(III): Arsenite; P: Phosphorus; GSH: Reduced glutathione; GSSG: Glutathione oxidized; MMA: Monomethyl arsenic; DMA: Dimethyl arsenic; PCs: Phytochelatins; GRSP: Glomalin-related soil protein.

性基团结合形成沉淀，通过细胞壁“滞留作用”，抑制重金属离子向地上部分转移，减轻毒害[56,58]。也有研究揭示，植物可以通过菌丝磷酸盐、巯基等化合物的络合作用，在根内菌丝液泡和孢子中储存重金属离子，提高根系结合重金属的能力，将重金属离子隔离在宿主植物根系中，减少重金属向地上部的迁移[56-57]。砷离子还能与植物体内的有机酸、植物螯合肽、金属硫蛋白等金属配位体发生螯合作用，将离子态的重金属转变成低毒或无毒的螯合态形式，并在植物体内呈区室化分布，从而降低原生质体中游离态重金属浓度[15]，而 AMF 的定殖则会强化这一机制[38,59]。

“转运体抑制效应”是指 AMF—宿主植物共生体系通过抑制植物根系中磷酸盐和砷酸盐共同转运体-高亲和磷酸盐蛋白(high affinity phosphate transporter)活性，降低砷吸收，从而增加宿主植物对砷的耐性[27,60]。由于磷酸盐和砷酸盐具有相同的电化学性质，存在转运体竞争关系，在 AMF 与宿主植物互作过程中，会抑制高亲和磷酸盐转运蛋白活性，减少磷酸盐和砷酸盐吸收量[27]。本团队研究结果显示，三七根系中高亲和磷酸盐蛋白 PnPht1;1、PnPht1;2、PnPht1;3 对磷酸盐偏好性优于砷酸盐，在磷充足条件下，高表达抑制三七对砷的吸收[61-62]。AMF 定殖可以通过增加茎和根 P/As 含量比来抑制砷吸收，在增强植物磷营养的同时抑制砷吸收，从而达到降低植物砷吸收、积累的目的[63]。

“生物转化作用”是指 AMF-植物共生体系通过降低植物中无机砷/有机砷浓度比例，即将无机砷转化为毒性较低的有机砷，从而降低砷对宿主植物的毒害作用[37]。Ultra 等[36,64]、Zhang 等[65]研究发现，AMF 的定殖可将 As(V)还原为 As(III)或甲基化为有机砷，随后将部分 As(III)以螯合态形式从水-甘油通道蛋白排出细胞外，降低砷积累。而植物和包括 AMF 在内的微生物均能将砷甲基化，AMF-植物共生体系的砷甲基化能力显著提高[37]。

“保宿主、降氧化”机制是指 AMF-植物共生体系通过增强宿主植物抗氧化系统，降低砷诱导的氧化应激，加快清除 ROS，保护宿主植物细胞，从而提高植物的砷胁迫抗性[38,43]。砷胁迫会引发植物氧化应激，导致过氧化氢等氧化物质浓度增加。为应对氧化应激水平的提高，宿主植物激活“配备”的抗氧化系统[41]，而 AMF 的定殖则会与宿主植物一道增强抗氧化系统。本团队研究证实，高浓度砷胁迫均会增强三七根中 SOD、POD、CAT 等抗氧化酶活性，提高 MDA、GSH 等抗氧化物质含量[4]。Zhan 等[17]研究表明，AMF 通过增强 SOD、CAT 等活性和总抗氧化能力，降低过氧化氢和丙二醛含量，从而增强玉米叶片的抗氧化防御系统。Sharma 等[41]也得到了类似结果，砷胁迫条件下，与对照相比，分别接种 *R. intraradices*、*C. etunicatum* 后小麦(*Triticum aestivum* L.)叶片的 APX、SOD、POD、CAT 等抗氧化酶活性和总抗氧化能力均大幅提升，类胡萝卜素、脯氨酸和 α-生育酚等抗氧化物质浓度均显著增加，说明 AMF 与宿主植物可通过协同调控增强抗氧化防御系统来提高砷胁迫抗性。

4 DSE 与植物协同调控砷胁迫作用机制

DSE 在重金属污染环境中有相对较高的丰度，可在高浓度铅[66]、锌(Zn)[67]、镉[68]等重金属污染环境中定殖于植物根部，但对于 DSE 增强植物砷耐性的研究及协同调控机制研究相对较少。本研究团队前期对云南省多个样地的滇黄精[9]、三七[69]DSE 定殖情况进行了系统调查，发现 DSE 平均定殖率范围分别为 29.25%–37.58%、31.67%–45.19%；纯培养条件下，部分 DSE 菌株

对砷、铅、镉具有较强的耐性。

现综合已有研究，发现 DSE 增强植物砷耐性机制与 AMF 类似。研究显示，DSE 可通过调控植物细胞壁生物合成途径，重塑组成，使细胞壁对重金属离子形成“区室化”，降低金属离子的吸收和转移，从而增强植物对重金属的耐受性[70]。此前研究团队将具有 Cd 耐性的 DSE 嗜鱼外瓶霉(*Exophiala pisciphila*)接种在玉米根部，可以显著提高其玉米镉抗性，究其原因，DSE 显著增强细胞壁镉化合物储存能力[71]。

增强抗氧化系统，降低自由基氧化损伤是 DSE 增强植物重金属胁迫抗性的重要渠道之一。Zhu 等[72]研究表明，DSE 菌丝除具有吸附重金属的能力外，还显著提高 SOD 和 POD 等抗氧化酶的活性，从而缓解了重金属胁迫引起的膜脂过氧化损伤。DSE 细胞壁中的黑色素则可增强细胞壁的机械强度，赋予细胞对重金属的结合能力，可与在重金属胁迫下产生的氧自由基形成复合体，完成氧自由基的清除[73]。DSE 还可通过类似 AMF “生长稀释效应”来降低砷等重金属浓度，如增强光合作用，促进营养元素吸收，平衡植物激素等[74-75]。Wang 等[76]研究表明，在重金属污染的土壤中，DSE 可限制根与地上部之间离子的迁移，从而降低金属离子吸收和积累。本团队从基因和蛋白的角度证实，自然抗性相关巨噬细胞蛋白基因(natural resistance-associated macrophage protein, NRAMP)和 ATP 结合盒转运蛋白(ATP-binding cassette, ABC)基因 *EpABC1*、*EpABC2*、*EpABC3* 在嗜鱼外瓶霉(*E. pisciphila*)重金属耐性中发挥着重要作用，对前者功能和转录特性分析发现，该基因的下调表达影响镉离子的吸收和转运[77]；后者表达的蛋白可以通过“液泡的区隔”和“外排”等作用机制增强宿主重金属耐性[78-79]。

5 展望

通过施加微生物菌肥来实现生态种植已是发展现代农业中的最常采用的手段之一。基于 AMF 和 DSE 的内生真菌菌肥制作方便[80]，作用高效，被认为在中药生态种植，重金属污染区及干旱、盐碱区作物栽培中具有广阔应用前景。目前，研究证实，砷胁迫条件下，AMF 定殖可以提高宿主植物的胁迫抗性，但与 AMF 种类相关，而关于 AMF-宿主植物协同调控植物砷耐性的作用机制研究仍需进一步深化，如 AMF 作用差异与种类之间的关系、所涉及的代谢通路或信号分子、所涉及的植物或 AMF 的关键酶或特异表达蛋白等。本研究团队一直致力于 AMF 调控三七砷吸收机制的研究，相关实验仍在进行中，并取得了初步进展，对于下一步的生产应具有正向促进作用，但相关调控机制仍不明确，拟根据已测得的三七砷吸收、转运因子，酶学系统变化等生理指标，相关基因表达特性分析，结合代谢组学、转录组学和蛋白组学，从生理和分子角度揭示相关调控机制。

相较 AMF，对 DSE-宿主植物协同调控砷耐性作用机制的研究鲜有报道，需借鉴 AMF 作用机制进行类比研究。由于 DSE 种类众多，可进行纯培养，在明确其作用效果和机制的基础上，更具推广价值。

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