2025, 65(2): 515-523
CSTR: 32112.14.j.AMS.20240442
DOI: 10.13343/j.cnki.wsxb.20240442

微生物学报
Acta Microbiologica Sinica
http://journals.im.ac.cn/actamicrocn

Review 综述

外生菌根真菌及其助手细菌联合解磷的研究进展

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摘　要：植物的各项新陈代谢活动需要大量磷素，然而土壤中有效磷含量往往不到全磷的 0.1%，难以满足植物的生长发育。外生菌根真菌与菌根助手细菌二者联合体系能够显著提高土壤磷的植物有效性，促进外生菌根体系对磷的高效吸收。本文分类讨论了外生菌根真菌与菌根助手细菌二者联合对难溶性无机磷、可溶性有机磷和难溶性有机磷这 3 种主要土壤磷源的溶解矿化能力及其机制。其中，对于难溶性无机磷，外生菌根真菌主要通过调控菌根助手细菌的有机酸和质子代谢促进其溶解；对于可溶性有机磷，外生菌根真菌主要是提高自身及菌根助手细菌相关磷酸酶的活性，以加速其矿化；而对于难溶性有机磷，外生菌根真菌首先通过刺激菌根助手细菌分泌有机酸，将其溶解为可溶态有机磷，然后再对其进行有效矿化。此外，本文还对联合体系中分泌相关代谢物与启动信号交换的分子机制进行了讨论，展望了联合体系解磷在未来的研究前景。

关键词：外生菌根真菌；菌根助手细菌；土壤磷素；有机酸；磷酸酶；植酸酶

资助项目：国家自然科学基金(32171754)；江苏高校优势学科建设工程资助项目
This work was supported by the National Natural Science Foundation of China (32171754) and the Priority Academic Program Development (PAPD) of Jiangsu Higher Education Institutions.

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Received: 2024-07-19; Accepted: 2024-11-05; Published online: 2024-12-24

Research progress of synergistic interactions between ectomycorrhizal fungi and mycorrhizal helper bacteria in phosphorus solubilization

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Abstract: Plants require a large amount of phosphorus for metabolic processes. However, the available phosphorus in the soil is typically less than 0.1% of total phosphorus, which is difficult to meet the growth and development of plants. The symbiosis system of ectomycorrhizal fungi and mycorrhizal helper bacteria can significantly improve the availability of soil phosphorus and promote the efficient uptake of phosphorus by plants. In this review, we discussed the solubilization and mineralization of chelated inorganic phosphorus, soluble organic phosphorus, and chelated organic phosphorus by ectomycorrhizal fungi and mycorrhizal helper bacteria. Ectomycorrhizal fungi mainly promote the solubilization of chelated inorganic phosphorus by regulating the organic acid and proton metabolism of mycorrhizal helper bacteria. They accelerate the mineralization of soluble organic phosphorus by enhancing the activities of related phosphatases in themselves and in mycorrhizal helper bacteria. Ectomycorrhizal fungi may first stimulate the mycorrhizal helper bacteria to secrete organic acids for solubilizing chelated organic phosphorus into soluble phosphorus before mineralization. Moreover, we explored the molecular mechanisms of metabolite signal exchange and secretion in the symbiosis system and outlined the prospects for studying the interactions between ectomycorrhizal fungi and mycorrhizal helper bacteria in promoting plant phosphorus uptake.

Keywords: ectomycorrhizal fungi; mycorrhizal helper bacteria; soil phosphorus; organic acids; phosphatase; phytase

土壤中的磷素(phosphorus, P)参与植物生长发育的多个过程，在植物代谢过程中起着十分重要的作用[1-2]。目前，我国土壤中可供植物直接利用的正磷酸盐(如 HPO_4^{2-}、$H_2PO_4^-$磷酸盐)含量往往不到全磷的 0.1%[3]。一方面，磷属于不可再生资源，全球磷储量有限，磷矿开采难度大；另一方面，过量施用磷肥导致更多的磷未经植物利用便流失到土壤中，迅速转变成非正磷酸盐的形式大量积累，磷肥的快速流失大大限制了陆地植物的生产力。植物通过改变根系形态结构与生物化学性质(如根系分泌物)，以及与菌根真菌共生等方式，促进根部磷素吸收[4-6]。

其中，外生菌根(ectomycorrhizal, ECM)真菌能够与大部分温带和北方松柏科树种形成广泛、多样的共生结构，显著改善植物根系从土壤中

获取养分的能力，提供宿主植物所需磷素的20%–100%[7-8]。外生菌根真菌定殖于宿主植物根尖，可以形成菌丝套或鞘，以及作为植物和外生菌根真菌之间资源交换场所的哈蒂氏网；还可以形成根外菌丝和地上部大型子实体结构，二者分别承担着从土壤中探索、提取、转移资源和繁殖、传播的功能[9]。研究表明，外生菌根根外菌丝表面以及子实体内部都存在大量功能性细菌，即菌根助手细菌(mycorrhiza helper bacteria, MHB)，对菌根共生体的功能具有积极作用[10]。已有大量研究分离获得多种菌根助手细菌，如荧光假单胞菌(*Fluorescent pseudomonads*) BBc6R8、枯草芽孢杆菌(*Bacillus subtilis*) MB3、水拉恩氏菌(*Rahnella aquatilis*) HX2、罗勒氏杆菌(*Ralstonia basilensis*) AB301921、链霉菌(*Streptomyces* sp.) AcH505、德沃斯氏菌(*Devosia* sp.) ZB163 等[11-14]。这些原本分布于土壤中的细菌受菌根真菌分泌到体外的糖类(棉子糖、海藻糖、果糖、葡萄糖等)、有机酸类(柠檬酸、琥珀酸等)、氨基酸(天冬氨酸、谷氨酸、亮氨酸等)、挥发性化合物(5,6,7-三氢-7-羟基-3-并基苯并呋喃、2,5-二异丙基吡嗪等)等的吸引[15]，沿根外菌丝逐渐向菌根际移动，接触、吸附到真菌菌丝表面，生长并形成生物膜后定殖在菌丝表面；或随着外生菌根真菌子实体的形成，逐渐迁移最终定殖在子实体内[16]，辅助外生菌根真菌完成其生态功能。外生菌根真菌能显著改变菌根际部分细菌的群落组成及相对丰度[17]，塑造对实现其生态功能有利的细菌群落。

外生菌根真菌为了提高在不良环境中获取营养元素的效率，往往选择性地招募具有相关功能的菌根助手细菌辅助其完成生态功能。与腐生真菌相比，外生菌根真菌在整个生长过程中菌丝际土壤的细菌丰度更高，且二者的细菌群落组成存在显著差异。在鸡油菌(*Cantharellus cibarius*)子实体中普遍存在不同种类根瘤菌，以根瘤菌-鸡油菌的共存模式辅助菌丝生长和子实体形成[18]。本文论述了外生菌根真菌在磷素缺乏情况下，如何分泌特定代谢物与解磷细菌建立联合体系，并对土壤中不可直接利用的难溶性无机磷、可溶性有机磷和难溶性有机磷等磷源进行联合解磷。

1 外生菌根真菌代谢物启动真菌-细菌双向信号，促进宿主植物生长

外生菌根真菌与细菌的相互作用由多个阶段的信号交换组成，其中小分子信号物质主要由真菌分泌[19]。外生菌根真菌分泌的代谢物一方面影响自身的生长，另一方面也介导真菌-细菌相互作用(bacterial-fungal interactions, BFI)。Uehling 等[20]研究表明，在真菌与细菌尚未接触的前共生阶段，磷饥饿状态的真菌分泌铁载体、赤糖酸、乳酸、脂肪酸等多种代谢物作为初始信号，供细菌识别并作为营养物质利用，以促进细菌趋化与增殖。细菌则向周围环境分泌次级信号，被真菌边缘菌丝感知，加速真菌菌丝生长速率、磷酸戊糖代谢和呼吸作用[21]。这种双向信号被感知并开启了二者联合体系的建立，以增强解磷能力。同时，二者联合体系促进了参与宿主植物中碳固定、糖代谢和氨基酸生物合成等过程的蛋白质表达量上调，如组蛋白、ATP 合酶等。这些差异表达蛋白能与种子发育和非生物胁迫耐受性相关的其他蛋白质或海藻糖、木糖醇等代谢物相互作用，共同调节宿主植物糖代谢和次生代谢物的生物合成，从而促进植物养分获取和改善植物生长状况[22]。

2 外生菌根真菌与菌根助手细菌对难溶性无机磷的解磷策略

2.1 外生菌根真菌与菌根助手细菌对难溶性无机磷的溶解能力

难溶性无机磷约占土壤无机磷的 99%，在石灰性土壤中以羟基磷灰石或氟磷灰石为主，酸性土壤中以铁铝氧化物及氢氧化物结合态磷为主。虽然外生菌根真菌对难溶性无机磷有溶解能力，但其效率难以满足宿主植物对磷的大量需求。徐冰等在研究纯培养条件下 9 种外生菌根真菌对磷矿粉的活化情况时发现，不同种类的外生菌根真菌对磷矿粉的溶解矿化效率为 2.97%–8.32%[23]。此外，硬皮马勃属(*Scleroderma*)、空团菌属(*Cenococcum*)、豆马勃属(*Pisolithus*)、牛肝菌科(*Boletaceae*)等的 10 种外生菌根真菌对磷酸铝、磷酸铁、磷酸三钙等难溶性磷酸盐的溶磷率仅为 0.1%–5.47%[24-25]。同时，研究发现，在自然森林土壤中，磷灰石区共富集了 17 种外生菌根真菌以及假单胞菌属(*Pseudomonas*)、鞘氨醇单胞菌属(*Sphingomonas*)、芽孢杆菌属(*Bacillus*)和类芽孢杆菌属(*Paenibacillus*)为主的优势细菌[26]，这可能与外生菌根真菌对溶磷相关细菌的招募密切相关。Koele 等[27]研究发现，双色蜡蘑(*Laccaria bicolor*)单独存在时不具备溶解磷灰石的能力，但其菌丝表面能够大量定殖具备高效解磷能力的伯克霍尔德菌(*Burkholderia glathei*)，二者共接种时分泌大量有机酸，可增强解磷作用，促进磷素吸收，从而提高宿主植物生物量。本课题组 Zhang 等也研究发现，以磷酸三钙为磷源，苦粉孢牛肝菌(*Tylopilus neofelleus*)与芽孢杆菌(*Bacillus* sp.) B5 联合处理可显著提高可溶性磷含量，且该含量是单独接种处理总和的 5 倍[28]。因此，外生菌根真菌与菌根助手细菌联合作用对土壤难溶性无机磷有更强的溶解能力。

2.2 外生菌根真菌与菌根助手细菌联合解难溶性无机磷的机制

酸化是土壤微生物溶解无机磷的主要机制。钟传青发现，巨大芽孢杆菌(*Bacillus megaterium*) P17 在以黄麦岭磷矿粉、黄金卡黄磷矿粉为唯一磷源时的发酵液能产生柠檬酸、琥珀酸、乳酸及乙酸等有机酸，通过螯合磷矿粉中的金属离子，使磷游离出来[29]。此外，有学者认为，质子的释放同样能增溶难溶性无机磷。Park 等在研究荧光假单胞菌(*Pseudomonas fluorescens*) RAF15 对难溶性磷酸盐的增溶作用时，认为质子的释放是分泌有机酸之外的另一个溶磷机制，有机酸的解离以及伴随铵同化所产生的质子释放在土壤中，导致溶磷反应的平衡向更利于溶解的方向移动[30]。如表 1 所示，大量实验表明外生菌根真菌能够通过上调菌根助手细菌的多种有机酸合成、降解与分泌过程相关基因的表达，如葡萄糖酸脱氢酶基因(*gcd*)、甲基柠檬酸裂合酶基因(*prpB*)、吡咯并喹啉醌合酶基因(*pqqC*)、谷氨酸-γ-半缩醛脱氢酶基因(*pcd*)、二氢硫辛酰胺脱氢酶基因(*lpd*)等，促进胞外环境酸化，并富集细菌氨基酸代谢、碳水化合物代谢、能量代谢、膜转运等通路，联合改善宿主植物对难溶性无机磷的利用[27-28,31]。

3 外生菌根真菌与菌根助手细菌对可溶性有机磷的解磷策略

3.1 外生菌根真菌与菌根助手细菌对可溶性有机磷的矿化能力

据报道，相比正磷酸盐环境，生长在有机磷环境的土生空团菌(*Cenococcum geophilum*)和大毒滑锈伞(*Hebeloma crustuliniforme*)菌丝体中植酸酶活性显著提高，表明部分外生菌根真菌可能通过产生解磷相关酶对有机磷进行水解，

表1　联合培养下菌根助手细菌的有机酸代谢变化

Table 1　Changes in the organic acid metabolism of mycorrhizal helper bacteria under co-cultivation with ectomycorrhizal fungi

Organic acid	Source	Performance in the combined treatment	References
Gluconic acid	*Burkholderia cepacia*	The content of gluconic acid increases. The expression of the glucose dehydrogenase gene (*gcd*) is up-regulated. The biomass of the host plant and the mycorrhizal infection rate increase	[27]
Lactic acid	*Bacillus* sp.	The expression of the lactate metabolism-related genes (*gapA*, *pckA*) is up-regulated. The amino acid metabolism pathway, energy metabolism pathway and membrane transport pathway are enriched	[28]
Gluconic acid, succinic acid, oxalic acid and tartaric acid	*Pseudomonas aeruginosa*	The expression of the acid-producing genes (*gcd*, *pqqA-F*, *mps*, *gabY*) is up-regulated	[31]

并释放少量磷酸根到环境中[32]。然而，外生菌根真菌分泌的酸性磷酸酶仅能水解磷酸单酯类有机磷，对植酸等有机磷的矿化效率较低，难以满足宿主植物对磷的大量需求。Mei 等研究表明，厚环乳牛肝菌(*Suillus grevillei*)与内生细菌拉氏西地西菌(*Cedecea lapagei*)联合接种时植酸钠矿化率是二者单独接种总和的 1.8 倍，二者联合接种可显著增加菌丝区酸性磷酸酶和碱性磷酸酶的活性，缓解宿主植物马尾松的磷胁迫，促进马尾松幼苗生长[33]。同时接种假单胞杆菌(*Pseudomonas fluorescens*) 1-42 和褐环乳牛肝菌(*Suillus luteus*) N94 可以提高根际土壤酸性磷酸酶活性和速效磷含量，显著提高宿主樟子松根、茎全磷含量，促进樟子松的生长[34]。此外，Battini 等发现细菌也可以通过提高真菌菌丝长度与密度，增强对有机磷的矿化[35]。

3.2　外生菌根真菌与菌根助手细菌联合矿化可溶性有机磷的机制

微生物在土壤溶液中矿化植酸的效率取决于它们在外部培养基中或至少在细胞壁空间中产生植酸酶的能力。除了植酸，土壤有机磷按其磷酸酯键数目可分为磷酸单酯类和磷酸二酯类，分别需由磷酸单酯酶和磷酸二酯酶的水解作用将磷酸酯键打开，释放出无机磷[36]。研究表明，外生菌根真菌可能由腐生菌进化而来，仍保留编码有机化合物降解相关的基因，能够产生多种磷酸酶，且其活性与土壤中磷酸酯类有机磷的含量呈显著正相关；随着土壤磷缺乏加剧，相关磷酸酶活性增强[37]，可显著增加有机磷的有效性。

此外，Mei 等[33]研究表明，外生菌根真菌与菌根助手细菌联合培养时，解磷酶活性显著增强，与单独处理相比，碱性磷酸酶基因和植酸酶基因分别显著上调了 7.13 倍和 9.35 倍，并且聚磷酸盐(poly-P)代谢相关的多磷酸盐激酶和外切多聚磷酸盐磷酸酶相关的基因表达也上调，表明联合体系矿化植酸钠效率提高，poly-P 代谢活跃。如表 2 所示，一方面外生菌根真菌可能通过促进菌根助手细菌的增殖、运动、定殖和分泌系统相关基因表达量显著上调，提高磷酸酶的分泌；或通过上调相关磷动员细菌的磷酸酶基因(*phoC*、*phoN*、*phoD*、*phnX* 和 *appA*)表达，并提高细菌磷酸酶活性，以达到促进有机磷矿化和吸收的功能[33,38-42]。另一方面菌根助手细菌也可以调控外生菌根真菌中与细胞呼吸和能量代谢相关通路，提高真菌的生物活性，改善菌丝对磷的活化。

表2　外生菌根真菌与菌根助手细菌联合处理的变化

Table 2　Changes in the combined treatment of ectomycorrhizal fungi and mycorrhizal helper bacteria

Main phospholytic enzymes	Performance in the combined treatment	Reference
Alkaline phosphatase	The transmembrane transport pathway is enriched. The expression of the secretion system-related genes (*SecY*, *SecG*) and proliferation-related genes (*dnaG*, *dnaN*) and phosphorus starvation protein genes (*PsiE*, *phoH*) are up-regulated	[33]
Phytase	The expression of the phytase gene (*phy*), secretion system genes (*gspF*, *vib8*), cytokinesis-related genes (*fstA*, *fstZ*), mycelial phosphate transporter gene (*GintPT*) and polyphosphate synthesizing gene (*Vct4p*) are up-regulated	[40]
Phosphatase	The enzyme activity increases with the increase of mycorrhizal colonization. The expression of ATP metabolic gene, aerobic respiration gene and transmembrane transporter gene are up-regulated	[41]
Acid phosphatase	The enzyme activity increases. The expression of genes related to flagellar movement and chemotaxis are up-regulated. The biomass of the roots and stems of the host plant increases and the expression of phosphorus transporters in roots is up-regulated	[42]

4　外生菌根真菌与菌根助手细菌对难溶性有机磷的解磷策略

4.1　外生菌根真菌对难溶性有机磷的矿化能力

由于有机磷具有多个正磷酸盐结构和可变质子位点，在土壤中极易吸附于金属氧化物、黏土和有机质，或者与金属阳离子螯合形成沉淀物，导致难溶性有机磷在土壤中高度积累[43]。近年来，研究表明外生菌根真菌对难溶性有机磷的矿化效率较低，且各种真菌的矿化效率具有很强的差异性。如橙黄硬皮马勃(*Scleroderma citrinum*)能对植酸钙和卵磷脂进行低效的矿化，矿化率分别为 4.5% 和 0.8%；而土生空团菌(*Cenococcum geophilum*)对植酸钙和卵磷脂的矿化率分别为 0.05% 和 1.1%[25]。因此，在自然林地土壤中，单独依靠外生菌根真菌对土壤中难溶性有机磷的矿化能力难以满足外生菌根体系对土壤磷元素的大量需求。

4.2　外生菌根真菌与菌根助手细菌解吸难溶性有机磷的理论性机制

Patel 等[44]研究表明，以肠杆菌科(*Enterobacteriaceae*)为代表的根际产酸细菌通过分泌葡萄糖酸和乙酸可增强植酸酶催化体外植酸钙的去磷酸化作用；在体外条件下，pH 调节至 6.0 的葡萄糖酸钠与植酸酶的组合能够从植酸钙释放的无机磷约为 40 μg/mL，而 pH 调节至 4.5 的乙酸或乙酸盐与植酸酶的组合能够从植酸钙释放的无机磷可达 80 μg/mL。此外，紫色酸性磷酸酶(purple acid phosphatase, PAP)、组氨酸酸性磷酸酶(histidine acid phosphatase, HAP)、β-螺旋植酸酶(β-propeller phytase, BPP)和半胱氨酸磷酸酶(cysteine phosphatase, CP)等植酸酶的矿化作用只能发生在溶液中，许多螯合形态或吸附形态的植酸盐被束缚于沉淀状态，难以酶解，需要有机酸将沉淀溶解，从固体表面脱附植酸后，才能被植酸酶水解释放出磷酸根[45-47]。由此可见，首先通过有机酸将金属螯合态植酸盐从固相中释放出来可能是植酸酶等解磷酶发挥水解作用的先决条件。根据 Turner 提出的假说，外生菌根真菌和菌根助手细菌在利用难溶性有机磷时，可能需要菌根助手细菌先合成有机酸用于增溶，随后联合外生菌根真菌分泌解磷酶用于矿化释放正磷酸盐供宿主植物吸收利用[48]。

5 总结与展望

土壤微生物通过酸解和/或酶解等方式活化土壤中被固定的磷素。外生菌根真菌往往通过分泌信号物质从周边招募具有解磷功能的细菌，并且促进细菌增殖和相关功能活性；同时，这些解磷细菌可通过促进外生菌根真菌菌丝的生长和弥补其在解磷功能上的不足，提高对土壤中磷素的解吸效率，形成“交叉喂食”的互利共生模式[49]。研究表明，外生菌根真菌可通过分泌糖类、有机酸类、氨基酸类、挥发性化合物等招募功能微生物，调节微生物组稳态，以应对复杂的外部环境和生长需求[15]。然而，对于磷缺乏状态下，外生菌根真菌所分泌用于招募具有特定功能的解磷细菌的关键化合物仍不清楚。

此外，前期研究发现，外生菌根真菌和菌根助手细菌的联合体系在磷缺乏时上调葡萄糖酸脱氢酶基因(*gcd*)、吡咯并喹啉醌合酶基因(*pqqC*)、碱性磷酸酶基因(*phoD*)等，加快三羧酸循环、糖代谢途径，促进分泌葡萄糖酸、草酸、乳酸、柠檬酸等有机酸或提高酸性磷酸酶、碱性磷酸酶、植酸酶的活性，从而活化土壤难溶性无机磷或可溶性有机磷，促进宿主植物的生长[27-28,38-42]。然而，关于外生菌根真菌与菌根助手细菌联合活化土壤难溶性有机磷的研究还鲜有报道。未来可综合运用生物化学、分子生物学、基因组学、转录组学和代谢组学等方法，探究外生菌根真菌对菌根助手细菌特异性招募的关键代谢物，分析外生菌根真菌与菌根助手细菌相互作用提高不同磷源有效性的分子机制，以进一步完善对植物-真菌-细菌三者外生菌根体系的认识。

作者贡献声明

曹耿悦：论文撰写与修改；郑庭裕、于梦雅、张杰、高鑫、赵梦婷、戴传超：参与论文内容收集与讨论；贾永：论文修改与审核。

作者利益冲突公开声明

作者声明不存在任何可能会影响本文所报告工作的已知经济利益或个人关系。

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