

土壤溶磷微生物溶磷、解磷机制研究进展

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摘 要: 土壤磷素存量较大, 但其中约 95% 不能被植物直接吸收利用, 土壤中磷素供给不足常常是制约作物生长发育的重要原因之一。活化土壤中的难溶性磷、增强土壤有效磷的供给能力, 一直是人们关注的重要问题, 并对农业可持续性发展具有重要意义。土壤溶磷微生物(phosphate solubilizing microorganisms, PSMs)是土壤磷循环中的重要一员, 能够通过酸解作用、酶解作用等将无效磷转化为有效磷供植物吸收, 从而促进植物生长发育。通过 PSMs 改善土壤磷素营养是一项有利于资源节约、环境友好的重要农业措施, 其应用前景十分广阔。因此, 深入了解 PSMs 溶磷、解磷机制对于提高土壤磷素利用效率和提高作物产量具有十分重要的作用。本文对土壤溶磷微生物的种类、无机矿物磷溶解途径以及溶磷微生物依靠酶解作用对有机磷的矿化等方面进行了综述, 并对该领域的研究发展方向进行了展望。

关键词: 溶磷微生物(PSMs); 溶磷机制; 解磷机制; 有机磷; 无机磷

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Advances in Mechanisms of Soil Phosphorus Solubilization and Dissolution by Phosphate Solubilizing Microorganisms

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Abstract: Phosphorus storage in soil is large, but about 95% of them cannot be directly absorbed by plants. Insufficient supply of phosphorus in soil is often one of the important reasons that restrict crop growth and development. It is always an important issue to activate the insoluble phosphorus and enhance the supply of available phosphorus in the soil, which is of great significance for the sustainable development of agriculture. Phosphate solubilizing microorganisms (PSMs) are important members of the soil phosphorus cycle. They can convert the ineffective phosphorus into an effective form for plant absorption through acid and enzymatic hydrolysis, and promote plant growth and development. Improving soil phosphorus nutrition through PSMs is an important agricultural measure and has a broad application prospect in resource conservation and environmental protection. An in-depth understanding of the phosphorus solubilization and dissolution mechanisms of PSMs would improve the efficiency of soil phosphorus utilization and increase crop yield. Herein, the types of PSMs in soil, the dissolution pathways of inorganic phosphorus, and the mineralization of organic phosphorus by enzymatic hydrolysis were reviewed, and the research prospect in this field was also discussed.

Key words: phosphate solubilizing microorganisms (PSMs); phosphorus solubilization mechanism; phosphorus

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dissolution mechanism; organic phosphorus; inorganic phosphorus

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磷是植物正常生长发育所必需的矿质元素,参与植物呼吸作用、细胞分裂、能量转化和生物合成等重要的生理生化过程。土壤中的磷以无机磷和有机磷两种形式存在,虽然存储量大,但其中约 95% 的磷不能被植物直接吸收利用^[1]。据统计,全世界约有 43% 的耕地土壤缺乏能被植物吸收利用的有效磷,而我国土壤中缺少有效磷的耕地占 70% 以上^[2]。为保证农业生产需求,人们常常通过大量施用磷肥来弥补有效磷的供应^[3]。但植物对其利用率较低,当季利用率仅有 5%~25%,肥料中 80% 以上的磷与土壤中的 Fe^{3+} 、 Ca^{2+} 、 Mg^{2+} 、 Al^{3+} 等阳离子结合为难溶性的磷酸盐,不能被植物吸收利用,这使磷成为植物生长发育的限制因素^[4-5]。农业生产用磷肥开采自磷酸岩,而按目前的开采速度,全球磷酸岩储量将在 50~100 年内耗尽^[6]。此外,磷肥的大量使用又会导致土壤养分失衡,诱发微量元素如铁、锌的缺乏。因此,如何提高土壤磷的利用率成为热点问题之一,溶磷微生物(phosphate solubilizing microorganisms, PSMs)作为土壤磷循环中的重要成员也成为研究焦点。

1 土壤磷素及溶磷微生物

土壤中不能被植物吸收利用的磷分为有机态磷和无机态磷。有机态磷来源于动植物和人类活动等,主要包括磷脂、植酸类、核酸、磷蛋白等,需通过矿化作用分解为无机磷才能供植物吸收利用。无机态磷主要包括土壤中难溶的矿物态磷,如 Ca-P 、 Fe-P 、 Al-P 化合物等形式,需将其溶解为可溶性的磷酸根离子后才能被植物吸收^[7]。

自然界中,土壤溶磷微生物是土壤磷循环中的重要一员,能将无效磷转化为有效磷供植物吸收。溶磷菌的活动不仅能为植物提供足够的有效磷,还能分泌生长素等植物生长调节剂促进植物生长^[8]。此外,部分溶磷菌还可以分泌嗜铁素^[9]、抗生素以及 ACC 脱氢酶等^[10]。同时,也有部分溶磷菌能提高重金属土壤的生物修复效率^[11]。研制环境友好型的溶磷菌菌肥^[12],并将其替代传统化肥,可减少环境污染、改良土质、增加土壤肥力。

溶磷微生物主要包括溶磷细菌(phosphate solubilizing bacteria, PSB)、溶磷真菌(phosphate solubilizing fungi, PSF)和溶磷放线菌(phosphate so-

lubilizing actinomycete, PSA)。在土壤中,溶磷细菌占 PSMs 总量的 1%~50%^[13],主要有芽孢杆菌属(*Bacillus*)、假单胞菌属(*Pseudomonas*)、欧文氏菌属(*Erwinia*)和沙雷氏菌属(*Serratia*)等;溶磷真菌仅占 0.1%~0.5%^[14],主要有青霉菌属(*Penicillium*)、曲霉菌属(*Aspergillus*)、AM 菌根属(*Arbuscular mycorrhiza*)等;溶磷放线菌主要有链霉菌属(*Streptomyces*)和小单胞菌属(*Micromonospora*)等^[14]。

溶磷菌的溶磷、解磷过程十分复杂,其潜在机制也因菌种不同而各不相同。其可能机制如图 1 所示,主要包括有机酸酸解作用、酶解作用和释放 H^+ 等^[15]。其相关溶磷、解磷效率^[16-19]如表 1 所示。目前,对 PSMs 溶磷、解磷机制认识的局限性限制了溶磷菌及相关菌肥的广泛应用。

2 无机矿物磷溶解途径

无机矿物磷的溶解主要与 PSMs 中小分子有机酸的分泌有关^[20]。PSMs 产生的有机酸包括葡萄糖酸、草酸、酮基葡萄糖酸、苹果酸、柠檬酸等^[21-22]。PSMs 菌种不同,其产酸的种类和含量也各不相同,溶磷能力也不一样^[23]。将柠檬酸和草酸添加到土壤中,能有效提高土壤的溶磷效率。关连珠等^[24]发现,草酸和植酸酶的使用能显著提高土壤有效磷的含量。

溶磷菌分泌的有机酸能够降低土壤 pH,促进微溶的矿质磷溶解(包括磷酸钙和磷灰石等)^[25];同时能与 Fe^{3+} 、 Ca^{2+} 、 Mg^{2+} 、 Al^{3+} 等阳离子螯合,即有机酸离子与 Pi 在土壤中竞争(直接物理竞争或静电竞争)相同的吸附位点^[26],释放磷酸根离子。已有研究报道,欧文氏菌(*Erwinia*)对磷矿石的高效溶解是由于葡萄糖在葡萄糖脱氢酶(glucose dehydrogenase, GDH)催化下发生直接氧化反应(非磷酸化氧化)产生葡萄糖酸^[27-28];而葡萄糖酸通过介导直接酸化途径溶解磷矿石,使其在葡萄糖酸含量相对较低的情况下,也能释放大量的 Pi ^[29]。此外,根据菌种的不同,有的溶磷微生物可将葡萄糖酸进一步氧化为 2-酮基葡萄糖酸。相比葡萄糖酸,2-酮基葡萄糖酸具有更高的溶磷效率^[30]。

一些 PSMs 在 GDH 相关基因突变失活后不能溶解石灰性土壤中的难溶磷酸盐^[31]。吡咯喹啉醌(pyr-roloquinoline quinone, PQQ)作为 GDH 的辅酶,

表 1 溶磷微生物的溶磷、解磷相关指标^[16-19]

Table 1 Phosphorus solubilization and dissolution indicators of PSMs

PSMs	Strains	Organic acid produces	Changes of pH	Source of insoluble	Enzyme type	Amount of P solubilized/(mg·L ⁻¹)
PSB	<i>Enterobacter</i> sp.	Acetic, citric, gluconic	ND	TCP	Acid phosphatase	258.6
	<i>Enterobacter ludwigii</i>	Gluconic, oxalic, citric	7.0→4.0	TCP	ND	600
	<i>Pantoea agglomerans</i>	Gluconic, oxalic, citric	7.0→3.2	TCP	ND	575.16
	<i>Azospirillum</i> sp.	Acetic, citric, gluconic	ND	TCP	ND	218.1
	<i>Pseudomonas fluorescens</i>	Gluconic, oxalic, 2-ketogluconic, lactic, succinic, formic, citric, malic	7.0→4.0	TCP, MRP, URP, NCRP	Acid phosphatase, phosphonoacetate hydrolase	1 312
	<i>Pseudomonas</i> sp.	Lactic, isocitric, tartaric, pyruvic	7.0→4.9	TCP, MRP, URP, NCRP	Acid phosphatase, phytase	19.5
	<i>Bacillus</i> sp.	Acetic, citric, gluconic, malic, quinic	7.0→4.0	TCP	Phytase, D-α-glycerophosphatase	298.3
	<i>Burkholderia</i> sp.	Acetic, citric, gluconic, lactic, succinic, propionic, oxalic	7.0→3.5 6.6→4.9 6.6→4.0	TCP	Acid phosphatase	384.28, 433.81, 499.85
	<i>Acinetobacter</i> sp.	Gluconic, oxalic, 2-keto-gluconic, lactic, malic, formic	7.0→4.2	TCP, URP, MRP and NCRP	ND	414
	<i>Aspergillus niger</i>	Citric, gluconic, oxalic, lactic	7.0→3.2	Rock P	ND	392
PSF	<i>Penicillium</i> sp.	Citric, gluconic, oxalic, succinic, glycolic, malic	7.0→3.3 6.3→3.2	Tilemsi RP, TCP, RP, aluminum P	ND	381, 39.2~86.1
	<i>Trichoderma</i> sp.	Citric, lactic, succinic, tartaric	5.4→4.3	Rock P	ND	9.31
PSA	<i>Streptomyces</i> sp.	Oxalic, citric, succinic	7.0→5.0	TCP, aluminum P	ND	87.5~148.1

注: TCP, 磷酸三钙; MRP, 马苏里岩磷酸盐; URP, 乌代浦岩磷酸盐; NCRP, 北卡罗来纳岩磷酸盐; ND, 不确定。
Notes: TCP, tricalcium phosphate; MRP, Mussoorie rock phosphate; URP, Udaipur rock phosphate; NCRP, North Carolina rock phosphate; ND, not determined.

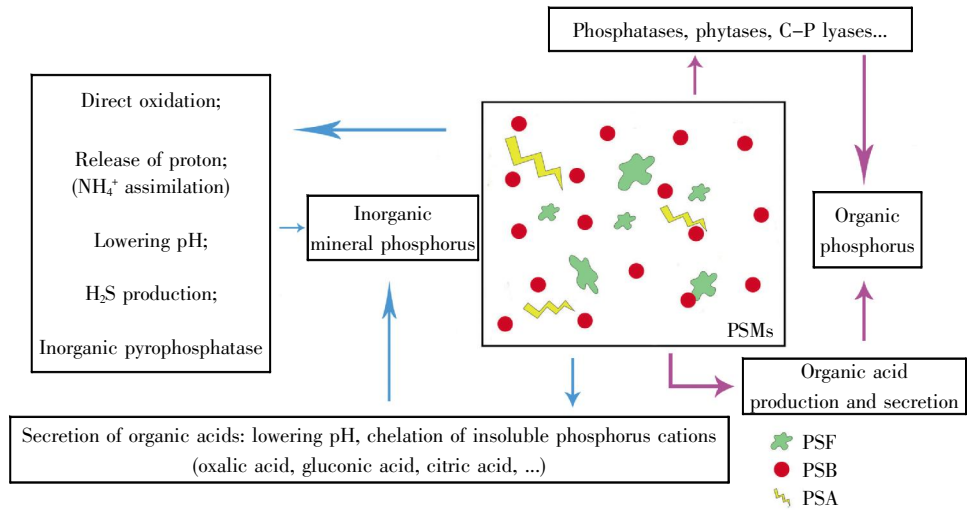


图 1 溶磷微生物(PSMs)溶解难溶性磷的潜在机制

PSF: 溶磷真菌; PSB: 溶磷细菌; PSA: 溶磷放线菌。

Fig.1 Potential mechanisms for the solubilization of insoluble phosphorus by PSMs

PSF: Phosphate solubilizing fungi; PSB: Phosphate solubilizing bacteria; PSA: Phosphate solubilizing actinomycete.

共同参与葡萄糖等碳源的无机磷代谢, 并起着重要的调控作用^[31]。焦子伟等^[32]将水生拉恩氏菌(*Rahnella aquatilis*) HX2 菌株的 *pqq* 基因簇导入大肠杆菌(*Escherichia coli*) DH5α, 结果显示: 工程菌株 DH5α 能分泌更多的有机酸, 特别是葡萄糖酸, 与原菌株相比, 工程菌株 DH5α 拥有更强的

溶解矿质磷能力。类似的还有分离自洋葱假单胞菌(*Pseudomonas cepacia*)的矿物磷酸盐溶解基因 *gabY*^[33], 其与 *pqq* 基因没有明显同源性, 可在直接氧化途径表达或(和)调控中发挥替代作用, 增加溶磷能力^[27, 34]。

有些 PSMs 只有在 NH₄⁺存在时才能溶解无机

磷酸盐。Halder 等^[35]发现有的固氮菌需要 NH_4^+ 的存在才能溶解羟基磷灰石; Asea 等^[36]发现, 相比于以 NO_3^- 为唯一氮源, 以 NH_4^+ 为唯一氮源时, 培养介质 pH 显著降低, 溶磷菌溶磷量显著增加。 NH_4^+ 同化作用过程中, 利用 ATP 转换时产生的能量, 通过质子泵释放 H^+ , 使 pH 降低, 从而有助磷的溶解^[20, 37]。土壤 pH 与溶磷效率有一定的相关性, 但 pH 的下降并不是微生物溶磷的必要条件^[38]。

此外, 有一些 PSMs 在土壤难溶磷的溶解过程中起着补充作用。例如: 土壤中的硫杆菌(*Thiobacillus*)通过产生的 H_2S 与 Fe-P 化合物反应生成 FeSO_4 , 从而释放出磷酸根离子^[39]; 桔灰青霉菌(*Penicillium aurantiogriseum*)不分泌有机酸, 通过吸收 Ca^{2+} , 从而释放磷酸根以溶解钙磷酸盐^[40]; 还有些 PSMs 产生的胞外多糖能够显著增强溶磷作用, 并通过呼吸作用产生 CO_2 , 导致 pH 降低, 使部分磷酸盐溶解^[41]。有研究表明: 溶磷微生物分泌的磷酸酶也能够溶解无机难溶磷, 如已经确定的无机磷酸酶——焦磷酸水解酶, 它可以将焦磷酸盐水解为磷酸盐离子, 且其酶活性在一定范围内随 pH 增高而增加^[42]。

3 有机磷溶解途径

有机磷的矿化主要依靠酶解作用, 这些酶包括磷酸酶、植酸酶、C-P 裂解酶、核酸酶等^[43]。其中, 磷酸酶和植酸酶(肌醇六磷酸酶)最为常见, 它们的底物主要存在于土壤中^[44]。

磷酸酶包括酸性磷酸酶、碱性磷酸酶、磷酸二酯酶和无机焦磷酸酶等, 能水解磷酸酯键释放无机磷酸。根据底物特异性, 磷酸酶还可进一步分为特异性磷酸酶和非特异性磷酸酶。磷酸单酯酶可以从磷酸单酯化合物中解离磷酸基团; 而磷酸二酯酶可以水解核酸中的磷酸二酯键。植酸酶可通过催化肌醇六磷酸中磷酸单酯键的水解, 释放出肌醇磷酸酯和无机磷酸酯^[45]。C-P 裂解酶裂解有机磷酸酯的 C-P 键。D- α -甘油磷酸酶是一种稀土磷酸酶, 由其催化的反应产物被鉴定为甘油和无机磷酸盐^[46]。此外, 有报道指出许多酶都可以作为有机磷酸酯清除剂, 从核苷酸和糖磷酸中释放无机磷酸盐^[47]。

磷酸酶随着 pH 的变化, 显示出不一样的催化能力。在 pH 小于 6 时, 酸性磷酸酶占优势; pH 大于 7 时, 碱性磷酸酶更普遍。根据已分离出来的磷酸酶基因及其特征, 人们将非特异性磷酸酶

分为 A、B、C 三类^[48-50]。Rossolini 等^[51]从摩氏摩根氏菌(*Morganella morganii*)和斯氏普罗威登斯菌(*Providencia stuartii*)分离出具有高度同源性的 A 类磷酸酶基因, 并经研究表明这些基因垂直衍生自共同的祖先; 同时, 该团队还证实了各细菌磷酸酶家族(A、B 和 C)存在各种保守结构域和特征基序。在酸性或中性的土壤条件下, 由 *acpA*、*phoC* 和 *napA* 等基因编码的酸性磷酸酶表现出较强溶磷活性。Fraga 等^[52]从摩氏摩根氏菌(*M. morganii*)克隆了 *napA* 基因, 将其转移到洋葱伯克氏菌(*Burkholderia cepacia*) IS-16 中后, 后者酸性磷酸酶活性明显提高, 溶磷能力显著增强。

磷酸酶的产生主要是通过无机磷酸盐(Pi)浓度进行调节。当处于低 Pi 条件下时, 涉及 Pi 信号转导的操纵子调控元件被由 *PhoB* 构成的 PHO 调节因子激活, 碱性磷酸酶(*phoA* 基因编码)被大量表达; 随着 Pi 的浓度增加, 碱性磷酸酶的活性受到抑制^[53]。

大多数碱性磷酸酶受 Pi 抑制调控, 但部分酸性磷酸酶, 如摩氏摩根氏菌(*M. morganii*)和斯氏普罗威登斯菌(*P. stuartii*)产生的不被大量磷酸盐抑制的 A 类酸性磷酸酶(*phoC* 基因编码)和不被少量磷酸盐抑制的 B 类酸性磷酸酶(*napA* 基因编码), 均表现出不被高水平磷酸盐抑制的特有磷酸酶活性调控模式^[54-55]。除此之外, 磷酸乙醛水解酶和 C-P 裂解酶也仅在磷酸盐限制条件下被诱导^[56-57]。在荧光假单胞菌(*Pseudomonas fluorescens*) MF3 菌株中, 编码酸性磷酸酶的 *apo* 基因的表达受生长温度调节; 在福氏志贺氏菌(*Shigella flexneri*)中, 编码三磷酸腺苷双磷酸水解酶的 *apy* 基因, 以及其他相关等位基因均以温度调节方式表达^[58]。

小分子有机酸也可促进有机磷的矿化。Patel 等^[59]发现, 在有机酸阴离子(如葡萄糖酸盐、柠檬酸盐)的存在下, 肌醇六磷酸钙(植酸钙)的水解效率得到提高。有机酸阴离子的存在可以改善肌醇六磷酸钙盐的溶解性, 从而提高解磷效率。其增溶机理与植酸酶的水解是互补的, 有机酸阴离子通过与二价金属螯合作用提高肌醇六磷酸酶活性, 但其确切的机制仍不清楚^[60]。

4 展望

我国乃至全世界耕地土壤缺磷现象普遍较重, 土壤中磷素的固定和转化效率影响土壤磷的积累及利用。基于土壤溶磷微生物的优点, 针对

PSMs 研制相关菌肥是提高土壤有效磷含量,促进植物生长发育,发展可持续农业的重要手段之一。研制 PSMs 菌肥,我们所面临的挑战还有很多,例如:实验室培养的高效溶磷菌无法在自然环境中占据优势地位,生存能力差,溶磷、解磷能力退化或受到极大抑制。

为改善土壤磷的利用效率,对 PSMs 的溶磷、解磷机制研究必不可少。未来可从以下几个方面展开深入研究:1) 从溶磷菌在土壤中的生态关系入手,即探究土壤 pH、深度、温度和海拔等对溶磷菌的生存和溶磷、解磷能力的影响;2) 很多组合菌肥比单一菌肥有着更强的生存能力和溶磷、解磷能力,深入解析其差异,有利于制备更高效的 PSMs 菌肥;3) 分离克隆溶磷、解磷相关基因,了解其表达调控机制,利用基因工程手段改良溶磷菌株,得到更高效的溶磷菌株。

相信随着研究的深入,PSMs 菌肥能代替化肥促进植物生长,提高土壤有效磷含量,同时改善土壤环境,降低环境污染,使农业生产更好更快的发展。

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