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专论与综述

细菌铁载体拮抗植物病原真菌及促生作用研究进展

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摘　要：铁载体是微生物在缺铁条件下分泌的小分子有机化合物，以获取铁元素维持其生长。细菌分泌的铁载体在拮抗植物病原菌和促进植物生长方面具有重要作用。本文总结了细菌铁载体拮抗植物病原真菌的营养和生态位竞争、诱导植物诱导性系统抗性、扰乱病原菌铁稳态的机制，以及促进植物生长的作用，以解释细菌分泌的铁载体在多功能微生物菌剂研制中的重要作用。
关键词：铁载体；细菌；拮抗作用；促生作用

Bacterial siderophores antagonize phytopathogenic fungi and promote plant growth: a review

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Abstract: Siderophores are small organic molecules produced by microorganisms under iron-limiting conditions which enhance the uptake of iron to microorganisms. Bacterial siderophores play an important role in antagonizing plant pathogens and promoting plant growth. In this paper, we summarized the mechanisms of bacterial siderophores against plant pathogenic fungi, such as nutrient competition, niche competition, eliciting inducible systemic resistance in plants, and disrupting the iron homeostasis of pathogens, and the plant growth-promoting effect of the siderophores, aiming at clarifying the potential of bacterial siderophores in the development of multifunctional microbial agents.
Keywords: siderophores; bacteria; antagonism; promoting growth

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铁是植物和土壤微生物必需的微量元素，其参与植物光合、呼吸作用和电子传递等过程，也是微生物基本细胞过程的辅助因子[1-2]。在土壤环境中虽然全铁含量较高，但由于含氧量及 pH 等因素影响，其基本上以生物不能利用的低溶解性铁氧化物形式存在，生物有效性十分低[3]。一般来说，在植物根际微环境中，土壤中游离的铁(10^{-15}–10^{-17} mol/L)远低于植物最佳生长(10^{-9}–10^{-4} mol/L)和微生物(10^{-6} mol/L)维持其生长所需的铁元素[4-5]。因此，在自然土壤环境中，生物对铁营养的竞争十分激烈。

微生物为解决铁素营养问题，几乎所有已知根际细菌能够通过铁载体获取铁营养[6]。铁载体(siderophore)是一种对 Fe^{3+}具有高亲和力且分子量小于 1 kDa 的低分子量化合物；细菌铁载体主要通过非核糖体肽合成酶(non-ribosomal peptide synthetase, NRPS)、聚酮类化合物(polyketides, PKS)模块或者 NRPS/PKS 非依赖性途径合成铁载体[1]。细菌铁载体的类型、结构多样，根据其官能团性质可分为主要由真菌和细菌分泌的异羟肟酸型，主要由细菌分泌的儿茶酚型，主要由根瘤菌、葡萄球菌等细菌和毛霉菌等真菌分泌的羧酸盐型，以及混合型铁载体等[4-7]。其中，细菌等分泌的铁载体具有通过铁竞争等作用防治植物病害和促进植物营养吸收双重功效[4]。本文从细菌分泌的铁载体在拮抗植物病原真菌的作用机制及促进植物生长作用角度，来解释在多功能微生物菌剂研制中细菌分泌铁载体的重要作用。

1 产铁载体细菌在多功能微生物菌剂中的作用

微生物菌剂由于其具有良好的生防效果和促生作用被广泛研究与应用，而且能有效避免农药等引起的环境问题。目前，对细菌微生物菌剂研究应用较多的是枯草芽孢杆菌[8-10]等，但其构成的单一菌剂由于复杂的根际环境使其田间定殖效果较差，导致菌剂功能不稳定[11]。然而，高通量测序技术的发展使人们对植株整个根际微生物群落结构有了清晰的认识，因此，基于高通量测序的合成功能菌群构建成为微生物菌剂的发展方向[12-13]。铁载体具有十分丰富的化学结构，不同种属的微生物分泌的铁载体不同，同一微生物在不同环境条件下的铁载体也差异较大[14]，而且同一微生物也可同时分泌不同类型铁载体[15]，一些微生物虽不能分泌铁载体，但其可识别利用其他微生物的铁载体[16]。由此可见，不同种属微生物对铁的获取存在替补作用，以最大效率获取铁[16-17]。同时，铁载体在促进植物营养元素吸收方面具有重要作用[18-19]。因此，认识与利用微生物铁载体的特异与非特异性，以及对铁的摄取、转运与吸收利用过程，可以促进对微生物-微生物和微生物-植物之间互作行为的认识，为提高对多功能微生物菌剂研制中合成功能菌群构建过程的理解以及综合发挥微生物次级代谢产物的作用提供理论依据。

目前，研究者主要通过铬天青 S (chrome azurol S, CAS)检测法筛选产铁载体菌株，许多研究表明产铁载体菌株对病原真菌具有抑制作用和促进植物生长的作用，如假单胞菌[20-22]、芽孢杆菌[23-25]等，但铁载体在其中的作用机制及作用大小仍需进一步研究。

2 细菌分泌铁载体对病原菌的拮抗作用机制

拮抗细菌通过分泌肽、抗生素、几丁质酶，以及根际定殖占据生态位、形成生物膜、竞争营养物质等作用方式抑制病原真菌[26]。细菌分

泌的铁载体也通过多种作用机制拮抗植物病原真菌,其不同类型铁载体发挥作用的方式可能不同。在具有拮抗作用的菌株中，产生的铁载体以儿茶酚型和异羟肟酸型为主,其中细菌主要为儿茶酚型，真菌主要为异羟肟酸型(表 1)。铁载体发挥的拮抗作用可能与对 Fe^{3+}螯合能力有关,而且儿茶酚型对 Fe^{3+}的亲和性大于异羟肟酸型[4] (图 1)。部分儿茶酚型铁载体也表现出直接抑制拮抗菌株增殖的效果，但其为细菌之间相互作用，细菌与真菌之间相似的抑制作用仍需研究[28]。

表 1 具有拮抗作用的产生铁载体的微生物(2018−2022)

Table 1 Antagonistic producing-siderophore microorganisms (2018−2022)

Siderophore-producing microorganism	Pathogens	Types of siderophore	References
Bacillus siamensis Gxun-6	*Fusarium oxysporum*	–	[27]
Pseudomonas chlororaphis YL-1	Gram-positive, Gram-negative bacteria	Pyoverdine	[28]
Penicillium chrysogenum (CAL1)	*Ralstonia solanacearum*, *Xanthomonas oryzae* pv. *Oryzae*	Hydroxamate	[29]
Pseudomonas spp., *Leclercia adecarboxylata*, *Citrobacter youngae*, *Enterobacter cloacae*	*Rhizoctonia solani*, *Phythium* sp., *Fusarium oxysporum*	Hydroxymate/Catecholate	[30]
Bacillus spp.	Banana wilt disease	Catecholate/Salicylate	[31]
Streptomyces sp. S29	*Botrytis cinerea*	Desferrioxamines/Hydroxamate	[32]
Bacillus licheniformis DS3	*Aspergillus niger*, *Alternaria solani*, *Fusarium solani*, *Fusarium oxysporium*	Hydroxymate	[33]
Bacillus amyloliquefaciens	*Pseudomonas syringae* pv. *tomato*	Catecholate	[34]
Paenibacillus triticisoli BJ-18	*Escherichia coli*, *Staphylo coccus aureus*, *B. subtilis*	Fusarinines	[35]
Bacillus subtilis MF497446, *Pseudomonas koreensis* MG209738	*Cephalosporium maydis*	Hydroxymate/Catecholate	[25]
Pseudomonas spp.	*Fusarium oxysporum* f. sp. *phaseoli*, *Stemphylium botryosum*, *Sclerotinia sclerotiorum*	–	[36]
Brevibacillus brevis GZDF3	*Candida albicans*	–	[37]
Aureobasidium pullulans L1	*Monilinia laxa*	–	[38]
Trichoderma yunnanense 2-14F2, *Beauveria pseudobassiana* 2-8F2	*Ralstonia solanacearum*	Hydroxymate	[39]
Penicilium asturianum	*Neofusicoccum kwambonambiense* XKD-1	Hydroxymate	[40]
Pseudomonas aeruginosa Gxun -2	*Fusarium oxysporum* f. sp. *cubense*	–	[41]
Escherichia coli	*Aspergillus nidulans*	Hatecholate	[42]
Bacillus subtilis SHT-15	*Verticillium dahliae*	Hatecholate	[24]
Bacillus amyloliquefaciens	*Botryosphaeria dothidea*	Hydroxymate/Catecholate	[23]

–：文中无数据

– : No data in the reference.

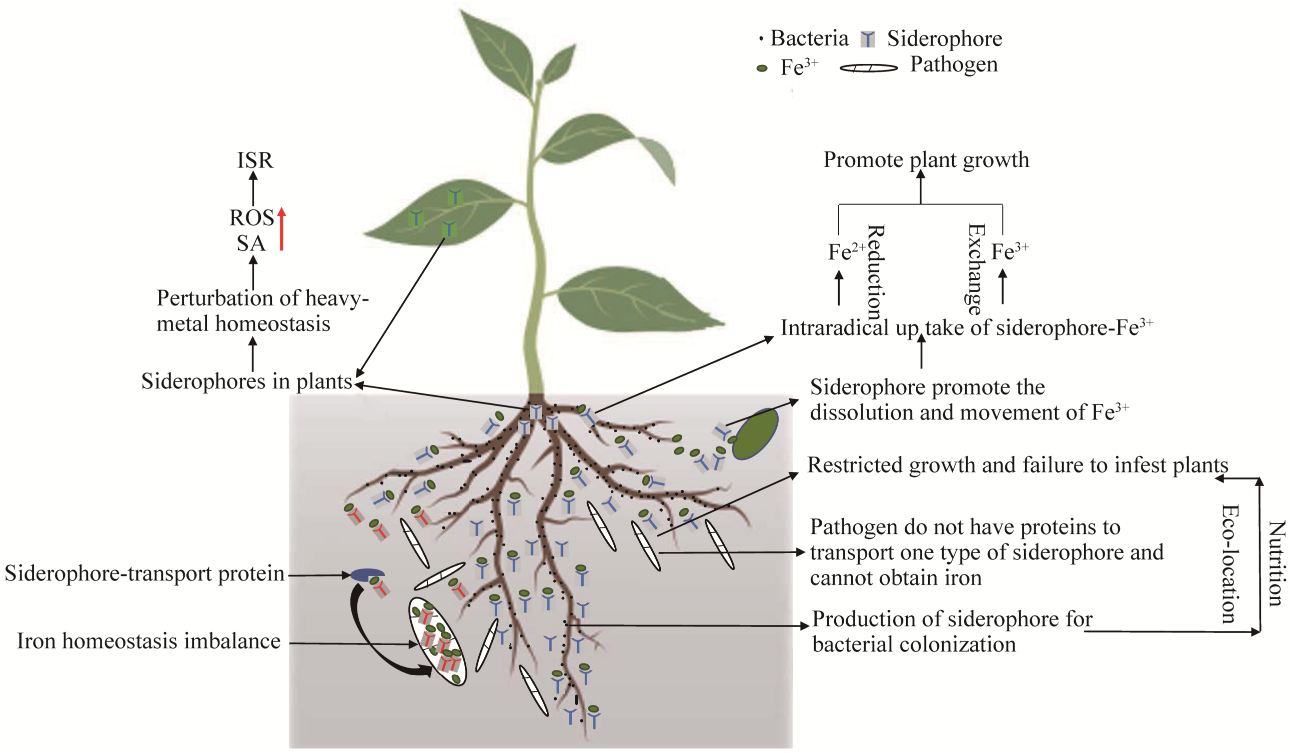

图 1　细菌铁载体对病原菌拮抗机制及促生作用示意图

Figure 1　Schematic diagram of the antagonistic mechanism of siderophore-producing by bacteria on pathogenic bacteria and promoting growth.

2.1　细菌分泌铁载体通过营养、生态位竞争抑制病原菌

在自然环境中，即使存在铁沉淀物，细菌分泌的铁载体具有对铁的竞争性生长抑制作用，并且其抑制作用大于通过溶解铁促进竞争者生长的作用[43]。由于铁的形态单一、生物有效性极低，细菌分泌特异性铁载体螯合植物根际的铁，病原真菌因不具有识别细菌产生的铁载体而无法吸收植物根际的铁，病原真菌生长受损无法入侵植物[44-45]。Lambrese 等[46]研究发现 *Kosakonia radicincitans* 产生的铁载体在 60 mg/L 时对膨胀青霉、灰霉病菌、根霉、链格孢菌的分生孢子萌发和菌丝生长均有抑制作用。Wang 等[47]从滇重楼根际分离到 16 株产铁载体菌株，其只有在铁限制培养基中才对白色念珠菌具有抑制活性。细菌产生的铁载体除了抑制病原真菌生长，还会导致病原真菌出现生长形态改变。例如，Yu 等[48]从番茄根际土分离到一株丁香假单胞杆菌(*P. syringae*) BAF.1，纯化后的铁载体在限铁条件下对尖孢镰刀菌的抑制率达 95.24%，显著抑制孢子萌发、破坏孢子超微结构，菌丝生长变形、弯曲、分枝增加。由此可见，细菌铁载体作为次生代谢产物，可能在生物防治中发挥作用。

同时，细菌分泌的铁载体并不直接参与病原真菌竞争铁，其可以促进细菌菌株的定殖能力，通过间接作用达到抑菌目的。Wensing 等[49]研究发现大豆叶表菌株 *P. syringae* pv. syringae

22d/93 产生的铁载体含量较大豆细菌性叶斑病菌大，同时与其产铁载体突变株比较发现，铁载体不直接参与抑制病原菌，而是通过增加拮抗菌株在叶际的附生适应性，以达到迅速占据生活空间的目的。Arif 等[50]将铜绿假单胞菌(*P. aeruginosa*)的铁载体受体基因 *pfeA* 和 *fpvA* 在木豆根瘤菌 IC3123 和 ST1 中克隆和表达，与亲本菌株相比，携带 *pAKEnt* 和 *pAKFpvA* 基因的菌株在接种花生和木豆植株后表现出更好的根际定殖能力。铁营养的竞争优势增加了细菌在复杂环境中的适应能力，保证了其在定殖中的优势，对整个生态位点的占据也成为其抑制病原真菌的重要机制之一。

总而言之，铁是影响细菌分泌铁载体的关键因子，而在铁缺乏时细菌产生的铁载体对病原真菌表现出更好的抑制作用。这说明铁载体介导的铁营养竞争是抑制病原真菌生长的机制之一，但竞争结果取决于铁载体的铁亲和力、产生的铁载体的数量，以及铁载体的物种特异性[51]。同时，由于铁载体对 Fe^{3+}的高亲和性，通过竞争 Fe^{3+}来抑制病原真菌生长可能为主要的作用机制。

2.2 细菌分泌铁载体诱导植物产生诱导性系统抗性

植物本身具有抵御生物和非生物胁迫的机制，在非胁迫环境中生长的健康植株，其防御系统并未被激活，只有受到特定信号分子刺激时才激活防御系统。植物面对缺铁胁迫会产生诱导性系统抗性(induced systemic resistance, ISR)，这表明感知铁耗竭是植物识别环境胁迫的一种机制[5,52]。在植物与病原真菌相互作用过程中，植物使用铁抑制策略来降低病原体的致病性或局部增加铁水平产生活性氧(reactive oxygen species, ROS)抑制病原菌[51]。同时植物铁的缺乏会导致苯丙烷途径基因的上调，如香豆素[53]等酚类物质不断积累，这些物质具有改善植物铁营养并保护植物免受病原真菌侵害的双重功能[54]。

一些研究发现铁载体介导了植物与微生物之间的识别与防御反应。Aznar 等[55]基于铁载体对铁的强螯合能力阐明了一种铁载体作用机制：在去铁铵(deferoxamine, DFO)处理过的拟南芥叶中，铁的分布状态被扰乱，触发局部缺铁信号，根中金属转运蛋白 IRT1 上调响应该信号，导致根中金属离子稳态的扰动，活性氧、水杨酸(salicylic acid, SA)和胼胝质积累以及防御基因激活。该 ISR 过程来自叶到根的传递，同样植物病原菌产生的铁载体(chrysobactin, CB)在叶中会引起根中铁缺乏，并激活 SA 介导的信号通路，导致 *PR1* 基因表达[56]。这些诱导性系统抗性(ISR)反应只在未螯合铁的铁载体状态下起作用，在拟南芥叶中 *AtFER1* 基因表达可以被纯化的铁载体 CB 激活，而 Fe-CB 螯合物不能激活该基因[57]。Betoudji 等[58]研究了一种合成的类似于不动杆菌属(*Acinetobacter* spp.)产生的铁载体，其对病原菌 *P. syringae pv tomato* DC3000 具有抗菌活性，同时在直接施于根部后发现 SA 途径的基因 *PR1* 表达上调，并抑制了病原菌的入侵，该作用来自于根部到叶的传递。在水稻中，Fe^{3+}和活性氧在稻瘟病菌侵染的水稻叶鞘表皮细胞的菌丝内部和周围集中聚集，而去铁胺 DFO 处理后显著抑制了 Fe^{3+}和活性氧积累引起的细胞死亡[59]。

铁载体诱导的系统抗性是植物生长和防御之间的平衡，铁吸收相关基因 *IRT1* 和 *FRO2* 的表达调节 PRE1-IBH1-HBI1 模块是关键[44,60]。然而是否能够触发植物对病原菌的系统抗性，取决于铁载体的类型能否诱发植物缺铁反应[55,61-62]。

2.3 细菌分泌的铁载体通过扰乱病原菌铁稳态发挥抑制作用

对于绝大多数微生物而言，铁是必需的微量元素，其可通过多种途径摄取铁，但过多铁离子则会引起Fenton反应和Haber-Weiss反应，产生羟基自由基，自由基会对DNA、蛋白质、细胞膜和脂质等造成损伤，对细胞产生毒害作用[63-64]。维持铁离子在微生物胞内的稳态对微生物生长极其重要[51]。

微生物铁稳态的维持由铁摄取、转运、存储共同作用[63]。真菌通过胞外铁载体吸收铁，胞内铁载体有助于铁的储存和运输[65]。对铁-铁载体的转运则是通过特定转运蛋白，其中部分转运蛋白具有高度特异性，如白色念珠菌仅存在一种底物特异性转运蛋白(CaArn1p/CaSit1p)；部分具有非特异性，例如酿酒酵母蛋白MirA转运异源铁载体肠杆菌素[66]。

外源铁载体可能导致铁吸收稳态机制遭受破坏，SreA是一种GATA型铁载体合成转录抑制因子，其在高铁条件下共同抑制参与铁载体生物合成的基因如*mirA*等；缺乏SreA导致与铁载体结合的铁摄取的失调[67-69]。由此产生的铁过载，部分被细胞内铁载体所缓冲，导致氧化应激增加；编码抗氧化酶，如超氧化物歧化酶和过氧化氢酶的基因被上调可能抵消这种效应[70]。

Khan等[42]发现外源细菌铁载体增加导致真菌菌落减小，菌丝长度增加，菌丝分枝增多，胞内铁含量的增加,活性氧和丙二醛增加，过氧化氢酶活性增加、抗坏血酸过氧化物酶活性降低，并证实可通过真菌转运蛋白MirA转运异源铁载体;由此可见，细胞内过多的铁蓄积扰乱了ROS的生理平衡，导致氧化应激，抗氧化酶系统无法恢复平衡，导致不可逆转的真菌抑制作用。对细菌而言，外源铁载体pyochelin增加了大肠杆菌培养物中的ROS水平[71]。铁载体转运蛋白对异源铁载体的识别与利用是微生物之间合作和竞争行为的表现,对不同铁载体受体蛋白的深入认识将促进对微生物之间相互作用的认识,促进对铁载体发挥抑制病原真菌作用机制的认识。

3 细菌铁载体对植物的促生作用

植物对铁元素的吸收策略，一种为以双子叶植物为代表的通过提高质膜上H^+-ATPase活性从而促进质子向根际分泌，降低土壤pH、改善铁的溶解性，然后通过与膜结合的Fe^{3+}-螯合还原酶还原Fe^{3+}离子，随后将Fe^{2+}吸收到根细胞中；另一种则是禾本科植物通过分泌植物型铁载体吸收利用铁元素[3,72]。在植物根际土壤微环境及植物组织内部定殖了大量共生细菌，而植物通过根系分泌物影响微生物群落结构，根际及根组织内细菌则通过产生植物生长素等激素、增加植物营养(固氮、溶磷、解钾)、产生铁载体等作用促进植物生长发育[73]。

根际及根组织内定殖的细菌在促进植物铁吸收中具有重要作用，与非无菌土壤种植的植物相比，在无菌土壤中生长的向日葵和玉米生长不良，组织内铁含量较低[74]。当植物在无菌土壤中生长时，油菜、红花苜蓿的铁获取和生长显著减少，但在无菌土壤中添加Fe-EDDHA可以恢复正常生长[75]。假单胞菌定殖于拟南芥根际，分泌挥发性有机化合物(volatile organic compounds, VOCs)诱导ISR和铁获取相关转录因子MYB 72的激活，并增强根的铁获取能力[61]。Sharma等[76]研究表明，接种球形节杆菌(*Arthrobacter globiformis*)后诱导缺铁敏感玉米过氧化物酶和脯氨酸增加，提高了植株的生物

量，以及对铁和磷的吸收、蛋白质和叶绿素的含量。Gao 等[77]从铁高效苹果砧木根际分离到假单胞 SP3，其在低铁砧木碱性土壤中生长时，植株的生物量、根系发育和铁浓度增加。这说明促生功能菌通过多种代谢途径影响植物营养吸收功能。

同时，有研究表明植物铁吸收的增加与细菌分泌的铁载体密切相关[78-79]。尽管目前细菌分泌的铁载体如何促进植物铁吸收的机制尚不明确，但有研究者提出了植物可以从微生物铁载体中获得铁的两种可能机制[80-81]：(1) 具有高氧化还原电位的微生物铁载体可以被还原向植物的运输系统提供 Fe^{2+}；在这种机制中，假设微生物分泌的 Fe^{3+}-铁载体被运输到植物根部的质外体，可能会发生铁载体的减少，所以 Fe^{2+}被困在质外体中，导致根中的铁浓度较高。(2) 微生物铁载体可以螯合土壤中的铁，然后与植物铁载体进行配体交换，这种机制取决于微生物和植物铁载体的稳定性常数和浓度，以及根环境的 pH 和氧化还原条件。植物在面临缺铁胁迫状态时，根际产铁载体微生物丰度显著增加，表现出与植物分泌的酚类物质相似的微生物群落结构变化，表明微生物分泌的铁载体在改善植物铁营养中效果显著[82]。拟南芥植株中的荧光假单胞菌(*P. fluorescens*) C7R12 产生的铁载体 apo-pyoverdine 可恢复缺铁培养基中植株的生长状况，其铁载体正向调节与发育和铁获取/重新分配相关基因的表达，同时抑制防御相关基因的表达[83]。产铁载体细菌菌株(siderophore producing bacterial strains, SPBs)单独接种，以及与土壤结合施用铁时，花生鲜重和干重相对增加的最大值分别为 63%和 86%，SPBs+Fe 土壤施用的组合应用使花生的总铁吸收量增加了 24.14%−49.75%，而 SPBs+Fe 叶面施用处理的增加量为 14.73%−45.72%[84]。Ghavami 等[85]从油菜根际分离的产铁载体菌株 *Micrococcus yunnanensis* YIM 65004(T)和 *Stenotrophomonas chelatiphaga* LPM-5(T)，它们显著促进了油菜和玉米的根部和地上部的重量，以及植株铁的含量。

细菌分泌的铁载体促进植物铁吸收作用也可能与其铁载体增加土壤中生物有效铁含量有关[13,57,86-87]。Sarwar 等[88]从花生根际分离到产铁载体菌株 20 株并将其接种于土壤后发现，MGS-11、MGS-14 和 MGS-91 这 3 个菌株的产铁载体量最多(>60% SU)，在培养第 32 天时土壤中有效铁的释放量分别比对照增加 82%、71%和 69%。Liu 等[89]研究表明根系分泌物和微生物铁载体在促进铁溶解方面具有协同作用。微生物作为植物的第二基因组，其在植物生长发育中发挥着重要作用。产铁载体菌株在促进植物铁吸收中的作用可能为植物吸收铁营养的第 3 种策略，铁载体可能通过多种途径促进植物吸收铁元素，如改善土壤中铁的生物有效性、促进植物相关基因的表达、改善其他金属元素的可利用性等。

4 小结与展望

根际和根组织内细菌在植物病害生物防控中发挥着重要作用，其通过分泌多种抑菌物质，以及引起植物本身抗性而抑制病原真菌入侵植物。面对细菌分泌的抑菌物质，病原真菌也会分泌某些物质降解抑菌物质，如新洋葱伯克霍尔德菌(*Burkholderia cenocepacia*)对褐根病菌(*Phellinus noxius*)产生拮抗作用时，在细菌分泌 pyochelin 这类铁载体后，真菌则产生 dehydroergosterol peroxide，可以将 pyochelin 和 ent-pyochelin 修饰成酯化物，导致铁载体螯合能力及拮抗作用降低[90]。同时，许多病原菌本身也能分泌铁载体，其不仅在维持病原菌铁稳

态方面发挥重要作用，也可通过共享机制吸收细菌分泌的铁载体[46]，部分病原菌分泌的铁载体在维持病原菌致病性方面也具有重要作用[56,91-92]。这说明了多功能、多途径防控植物病害中的重要性。

总而言之，细菌的拮抗和促生效果取决于其在植物根际或根内的定殖能力，但单一微生物菌剂的定殖及功能稳定性差，而复合微生物菌剂在定殖及功能方面具有更强的稳定性。铁载体作为微生物铁吸收的重要途径之一，其运输依靠铁载体转运蛋白的相互识别，对不同菌株之间铁-铁载体运输利用的认识，将促进微生物合成菌群的构建。细菌分泌的铁载体结构的多样性，使得筛选具有拮抗植物病原真菌作用的铁载体菌株时比较困难，对铁载体结构的解析，对不同病原菌铁载体转运蛋白的认识，有助于高效筛选具有抑制病原菌的产铁载体菌株。

在植物与微生物互作中，植物在缺铁时会分泌酚类物质促进产铁载体细菌富集，以改善根际铁营养状况。然而，产铁载体细菌促进植物铁营养吸收机制，以及外源施入铁载体或者产铁载体菌株如何改变根际微生物群落结构仍需进一步研究。

铁载体多种功效的特性有助于促进对植物–微生物及微生物–微生物之间竞争与合作的认识，为促进植物铁吸收利用[3]、种间协同进化研究[93]、多功能微生物菌肥研制及应用提供新见解。

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