

基于根际微生物的作物土传病害绿色防治研究进展

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摘要: 土传病害是当前制约作物生产、危害食品安全的主要病害类型。根际微生物组作为“植物的第二基因组”，在防治作物土传病害方面展现出巨大潜力。利用根际微生物防治土传病害具有绿色、高效、普适性等优势，已成为当前根际微生物领域的研究热点。本文首先介绍了根际微生物及其在防治作物土传病害方面的潜力；随后结合最新研究成果，系统总结了微生物防治土传病害的7种机制，并将其归纳为以下3种途径：(1) 微生物-病原菌的直接互作；(2) 微生物-作物的直接和间接互作；(3) 微生物-微生物的间接互作。此外，本文综述了当前根际微生物在防治作物土传病害中的应用情况。最后，分析了利用根际微生物防治土传病害面临的研究难点，并探讨了未来可能的解决路径，以期为推动土传病害的绿色防控提供参考。

关键词: 根际微生物；土传病害；抗病机制；多组学

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Green control of soil-borne crop diseases: advances in rhizosphere microbe research

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Abstract: Soil-borne diseases are currently the most significant type of plant disease restricting crop production and threatening food safety. The rhizosphere microbiome, often regarded as the “second genome of plants”, has shown considerable potential in controlling soil-borne crop diseases. The use of rhizosphere microbes to control soil-borne diseases offers many advantages, such as being environmentally friendly, efficient, and broadly applicable, which makes it a hot topic in rhizosphere microbe research. In this review, we first introduced rhizosphere microbes and their potential for controlling soil-borne crop diseases. Subsequently, by integrating the latest research advances, we systematically summarized seven mechanisms of microbial control against soil-borne diseases and categorized them into three pathways: (1) direct interactions between microbes and pathogens; (2) direct and indirect interactions between microbes and plants; (3) indirect interactions among microbes. Furthermore, we reviewed the current applications of the rhizosphere microbes in controlling soil-borne crop diseases. Finally, we analyzed the key research challenges in using rhizosphere microbes for soil-borne disease control and discussed potential solutions, aiming to provide references for advancing the green control of soil-borne diseases.

Keywords: rhizosphere microbe; soil-borne disease; mechanism of disease resistance; multi-omics

据估计, 全球人口将于 21 世纪 80 年代中期达到约 103 亿的峰值^[1]。要养活如此庞大的人口群体, 预计到 2050 年世界粮食总产量需在 2010 年的基础上增长 35%–56%^[2]。作物产量易受多种生物和非生物因素影响, 如干旱^[3]、高温^[4]、土壤酸化^[5]、铝毒^[6]等非生物胁迫, 以及病害^[7]、虫害^[8]等生物胁迫。据统计, 全球因作物病害导致的农作物产量损失超过 30%, 经济损失高达数千亿美元, 其中土传病害的危害尤为突出^[9]。为有效防控作物病害、减少粮食产量

损失, 寻找高效的病害防治技术一直是农业发展中亟待解决的难题。传统土传病害防治主要依赖化学和物理方法。值得注意的是, 化学方法虽直接、有效, 但通常会杀灭土壤中其他有益微生物类群、破坏土壤生态系统平衡, 长期使用还会导致病原菌产生耐药性; 此外, 化学农药极易在土壤和作物中残留, 不仅污染环境, 还会引发食品安全问题, 最终危害人类健康^[10]。物理方法如日晒, 通常见效较慢且效果受气候条件制约, 土壤蒸汽灭菌则存在田间实施难度

大、成本较高等问题^[11]。从长远角度和综合成本考虑, 化学和物理方法存在一定局限性。因此, 探索绿色、高效、适用性广的病害防治技术十分必要, 也符合现代农业高质量发展的需求。

在农业土壤生态系统中, 尤其是作物根际区域栖息着种类繁多、功能各异的微生物类群。尽管土壤中存在部分可能引发作物病害的病原菌, 但大量研究表明有益根际微生物在作物绿色防控中具有高效性和功能多样性。这些根际微生物能通过固氮^[12]、解磷^[13]、解钾^[14]、产铁载体^[15]以及分泌吲哚-3-乙酸(indole-3-acetic acid, IAA)^[16]等机制促进作物生长从而增强作物抗病性。此外, 根际微生物还能通过直接分泌抗菌类物质抑制病原菌生长^[17]或激活植物免疫系统^[18]等机制提高作物的抗病能力。这些研究为利用根际微生物缓解作物土传病害提供了重要策略。

近些年, 随着高通量测序和多组学技术的发展, 根际微生物的物种多样性和功能潜力得到更系统的认识。越来越多的研究已从根际微生物群落水平深入到抗病机制层面, 这也揭示了根际微生物在作物土传病害绿色防控中的巨大潜力。因此, 本综述旨在系统总结根际微生物在作物土传病害绿色防治中的最新研究进展, 梳理根际微生物防治土传病害的主要机制以及利用根际微生物技术防治土传病害的现状, 为利用微生物防治作物土传病害提供理论参考。

1 根际微生物及其在作物土传病害的防治潜力

根际是指从植物根系表面至周围数毫米范围内的土壤所形成的微域环境。受植物根系分泌物的影响, 栖息在根际环境的微生物(即根际微生物, 包括细菌、真菌、病毒等类群)极为活跃, 还能通过一系列次级代谢产物反向调控宿主植物的生长发育^[19-20]。大量证据证实, 根际

微生物在宿主植物的整个生育周期中都发挥着重要作用^[21]。因此, 根际微生物组也被认为是“植物的第二基因组”, 受到广泛关注^[22]。

在农业生产中作物病害普遍发生, 常见的病害主要有土传病害^[23]、气传病害^[24]、种传病害^[25]和虫传病害^[8]等, 其中土传病害是农业生产中最常遇到、也是最被关注的一类作物病害。常见的土传病害包括番茄青枯病^[26-27]、黄瓜枯萎病^[28]、马铃薯疮痂病^[29]、水稻纹枯病^[30]等。例如, 青枯病是由茄科罗尔斯通氏菌(*Ralstonia solanacearum*, 以下简称“青枯菌”)引起的土传细菌性病害, 可侵染 54 个科超过 450 种植物且寄主范围持续扩大, 其中茄科作物(番茄、辣椒、马铃薯等)受害最为严重, 在马铃薯重发区产量损失可高达 100%^[7,31]。枯萎病是由镰孢菌属(*Fusarium*)引起的土传真菌性病害, 能致使 150 多种作物感染枯萎病, 其中尖孢镰孢菌(*Fusarium oxysporum*)能分化为 120 多种特殊形式, 每种都有独一无二的寄主植物^[32]。越来越多的证据表明, 根际微生物能通过多种机制直接或间接地提高作物的抗病性^[27,33-34]。例如, 接种链霉菌(*Streptomyces* sp.) NEAU-383 的孢子悬浮液和发酵提取物能显著防治番茄青枯病, 防治效率分别为 85.2% 和 95.1%^[27]。最新研究发现, 12 株 *Streptomyces* 细菌分别与 100 株细菌构成的合成群落联合处理防治番茄青枯病, 平均生防效率从单独使用时的 48.73% 提升至 70.56%^[34]。可见, 根际微生物对作物病害的防效显著, 因此深入研究其作用机制对于从不同角度提高作物抗病性至关重要。

2 根际微生物防治作物土传病害的主要机制

当作物遭受土传病原菌侵害时, 根际微生物可通过多种机制帮助作物抵御病害。总体而言, 根际微生物抵御作物土传病害的机制有 7 种, 可归纳为 3 个途径: (1) 微生物-病原菌的直接互

作(与病原菌竞争生态空间和养分、合成和分泌抗菌类物质); (2) 微生物-作物的直接和间接互作(激活作物的免疫系统、促进作物养分吸收、提高作物非生物胁迫抗性); (3) 微生物-微生物的间接互作(抑制病原菌辅助菌的生长、促进抗病菌株的抗病能力)(图 1)。早期研究主要集中在微生物-病原菌的直接互作方面, 主要是微生物通过与病原菌竞争生态空间和养分, 或合成和分泌抗菌物质来直接抑制病原菌的生长。随着研究深入, 微生物-作物的互作机制逐渐被揭

示, 根际微生物能够通过激活作物的免疫系统、促进养分吸收、提高作物非生物胁迫抗性来增强作物的抗病性。近年来, 随着测序技术的发展和培养组学的兴起, 微生物-微生物的间接互作研究也取得了新进展: 一方面, 根际微生物通过抑制病原菌辅助菌间接削弱病原菌的生长; 另一方面, 根际微生物通过促进抗病菌株的抗病能力来增强对病害的防控效果。尽管这 3 个途径的作用对象不同, 但在根际微生物实际抗病过程中上述 3 种途径可能共同发挥作用。

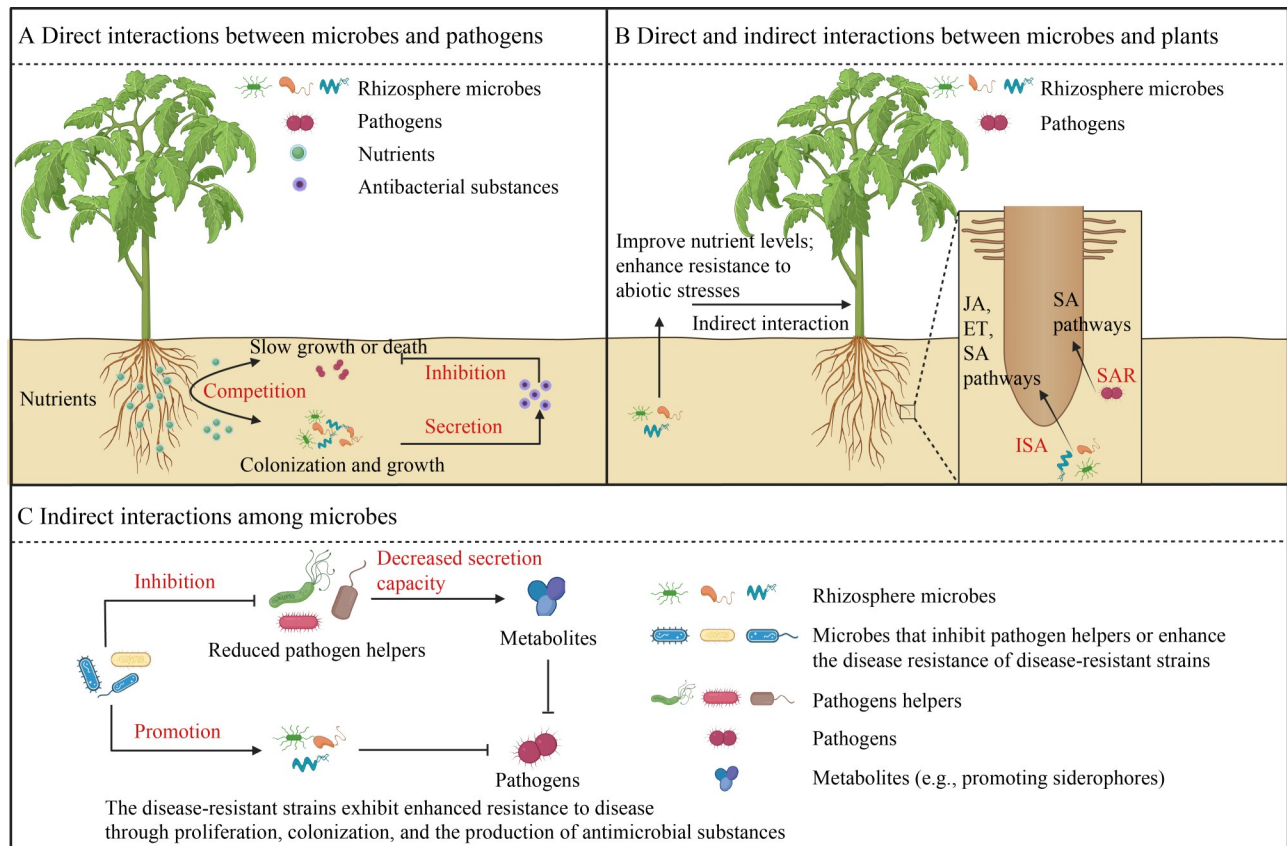


图1 根际微生物防治作物土传病害的主要途径和机制。A: 微生物-病原菌的直接互作; B: 微生物-作物的直接和间接互作; C: 微生物-微生物的间接互作。SAR: 获得性系统抗性; ISR: 诱导系统抗性; JA: 茉莉酸; SA: 水杨酸; ET: 乙烯。

Figure 1 The main pathways and mechanisms of rhizosphere microbes control against soil-borne diseases in crops. A: Direct interactions between microbes and pathogens; B: Direct and indirect interactions between microbes and plants; C: Indirect interactions among microbes. SAR: Systemic acquired resistance; ISR: Induced systemic resistance; JA: Jasmonic acid; SA: Salicylic acid; ET: Ethylene.

2.1 微生物与病原菌的直接互作

2.1.1 与病原菌竞争生态空间和养分

作物根际生态位中的空间资源有限, 因此具有重叠生态位的微生物之间对生存空间的竞争极为激烈。一些根际微生物凭借其较强的趋化性和运动能力能够快速占据根际生态位空间, 阻碍病原菌附着于作物根系, 从而达到防治病害的目的^[35-37]。例如, 密旋链霉菌 (*Streptomyces pactum*) Act12 可以增强韩国假单胞菌 (*Pseudomonas koreensis*) GS 的运动性和趋化性, 使其快速定殖在番茄根际^[36]。与青枯菌具有生态位重叠的细菌能够降低病原菌成功入侵番茄根际的概率, 进而降低盆栽试验中番茄青枯病的发病率^[38]。与肠道微生物通过营养阻断保护宿主免受病原体入侵类似, 根际微生物组可通过竞争养分阻断病原菌入侵植物根系, 尤其是在多种资源共存的环境中, 若某一资源被耗尽, 具有“快速切换”能力的微生物可通过迅速利用第二种资源获得竞争优势^[39-40]。例如, 稀缺的铁元素是微生物间竞争的关键资源之一, 有益微生物通过分泌不能被病原菌吸收的铁载体获取土壤中的 Fe^{3+} , 而病原菌难以获取铁元素, 其生长因此受到抑制^[41]。研究发现油菜假单胞菌 (*Pseudomonas brassicacearum*) R401 能通过分泌铁载体限制青枯菌吸收铁元素, 从而抑制青枯菌生长^[42]。总之, 根际土壤中的养分有限, 若要利用营养阻断的方式抑制病原菌, 需要准确确定特定病原菌与根际微生物的代谢需求和营养需求。由于涉及多个微生物之间的互作, 该研究具有很大挑战性。

2.1.2 合成和分泌抗菌类物质

根际微生物通常通过合成和分泌抗菌类物质直接抑制病原菌生长来达到防治作物病害的作用。根际微生物在代谢活动中分泌的抗菌类物质主要有脂肽(如表面活性素、多黏菌素)^[17,43]、抗生素(如聚酮类抗生素、吩噻嗪类抗生素)^[44-45]、裂解酶(如几丁质酶、纤维素

酶)^[44,46-47]、挥发性有机物(如 6-戊基- α -吡喃酮、 α -蒎烯、3-萜烯等)^[48-49]等。例如, 对 2 个抗青枯病和黑胫病能力存在差异的烟草品种进行根际微生物组的宏基因组分析时发现, 抗病品种根际微生物组中氢氰酸合成酶、绿脓菌素生物合成以及 arthrofactin 型环脂肽合成酶等生防功能相关基因的丰度更高^[50]。此外, 宏基因组与代谢组联合分析表明, 在烟草短期连作条件下, 根际中镰孢菌属的类群富集会土壤生物碱含量显著上升, 而生物碱已被广泛证实具有抗菌活性^[51]。最近研究发现, 解淀粉芽孢杆菌 (*Bacillus amyloliquefaciens*) TG1-2 的培养滤液及其产生的表面活性素能够在 RNA 和蛋白质水平上均下调大丽轮枝菌 (*Verticillium dahliae*) 的 NatA 复合物 (N-terminal acetyltransferase A complexes, NatA) 的 2 个亚基 *VdArd1* 和 *VdNat1* 的表达, 抑制该复合物的积累, 进而削弱热激蛋白 83 (heat shock protein 83, Hsp83) 分子伴侣的乙酰化水平, 致使 Hsp83-Sti1-Hsp70 共伴侣复合物解离, 最终导致蛋白质泛素化降解和真菌凋亡, 有效抑制病原菌的生长^[52]。总之, 根际微生物产生的抗菌类物质可同时防治多种病原菌, 而同一病原菌也可受多种抗菌物质抑制, 可见根际微生物防治作物病害兼具高效性和广谱性的特点。

2.2 微生物与作物的直接和间接互作

2.2.1 激活作物的免疫系统

为了抵御病原菌产生的负面影响, 植物自身会启动一系列免疫反应。植物主要通过激活获得性系统抗性 (systemic acquired resistance, SAR) 和诱导系统抗性 (induced systemic resistance, ISR) 2 种途径来启动免疫反应。其中, SAR 由病原菌触发, 必需信号分子是水杨酸 (salicylic acid, SA); ISR 则由有益根际微生物诱导, 通常被认为依赖于茉莉酸 (jasmonic acid, JA) 或乙烯 (ethylene, ET) 信号通路, 但越来越多的证据表明, 一些 ISR 也依赖于 SA 信号通路的参与^[53]。例如, *P. brassicacearum* NA13 不仅能直接抑制

病原菌尖孢镰孢菌 (*Fusarium oxysporum* f. sp. *conglutinans*), 还能通过调控 ET、JA 和 SA 信号通路关键基因的表达增强白菜对枯萎病的系统抗性, 如 ET 信号通路的关键调控因子组成型三重反应基因 (constitutive triple response 1, *CTR1*) 表达显著下降, 与增强防御反应相关的病程相关蛋白 1 (pathogenesis-related protein 1, PR1) 和病程相关蛋白 4 (pathogenesis-related protein 4, PR4) 基因显著上调^[18]。类似地, 小麦水培试验同样证实, 接种固氮鞘氨醇单胞菌 (*Sphingomonas azotifigens*) 和沙漠糖芽孢杆菌 (*Rhizobium deserti*) 能通过特异性上调 JA 信号通路以及 SA 信号通路相关基因的表达, 如与转录激活因子髓细胞组织增生蛋白 2 (myelocytomatosis oncogenes 2, MYC2) 相关以及与 PR1 相关的基因表达显著上调, 激活黄瓜花叶病毒感染小麦的诱导性系统抗性^[54]。此外, 根际微生物还能通过影响植物的代谢通路来增强抗病性。例如, 转录组和非靶向代谢组分析发现, 巨大普里斯特氏菌 (*Priestia megaterium*) JR48 能产生苯丙酮酸增强植物的苯丙氨酸代谢, 并协同 SA 信号激活植物过氧化物酶基因表达, 催化单木质醇聚合为木质素多聚体的 H、G、S 亚基, 从而通过增加木质素含量提高植物对辣椒疫霉的抗性^[55]。一项针对玉米茎基腐病抗感品种的多组学分析 (16S rRNA 基因/ITS 扩增子、宏基因组、基因组、转录组及非靶向代谢组) 发现, 部分芽孢杆菌虽不能直接抑制禾谷镰孢菌 (*Fusarium graminearum*) 生长, 却可通过特异性上调萜烯合酶 6 (terpene synthase 6, TPS6) 与酪氨酸脱羧酶 1 (tyrosine decarboxylase 1, TYDC1) 基因的表达, 激活玉米体内的倍半萜、异喹啉生物碱和甜菜碱等合成途径; 代谢组分析进一步证实, 该类芽孢杆菌通过促进玉米内源小檗碱 (一种天然异喹啉生物碱) 的合成, 从而提升玉米对茎基腐病的抗性^[56]。在已报道的微生物抗病机制中激活植物的免疫系统与合成和分泌抗菌类物质是目前最常报道的 2 种机制。

2.2.2 根际微生物促进作物养分吸收

除了激活作物免疫系统外, 促进作物养分吸收也是提高作物抗病性的关键环节。适宜的养分水平是作物构建有效防御体系的基础^[57-58]。例如, 在大豆中不同形态的磷通过促进磷的周转驱动大豆根际微生物组成发生变化, 进而通过免疫激活、胼胝质沉积等机制增强大豆对尖孢镰孢菌的防御能力^[59]。

植物生长必需的营养元素有 17 种。此外, 一些元素 (如硒、硅、铝) 虽非必需元素, 但对植物生长具有显著益处。在农业生产中, 土壤缺乏植物可利用态养分是最为普遍的现象, 这也是影响作物产量以及作物病害发生率的主要因素之一。一些根际微生物类群能够通过直接增加土壤可利用态养分含量, 或间接改善植物根系构型, 增强作物对养分的吸收能力, 涉及的养分包括氮^[12,60]、磷^[13]、钾^[14,61] 等大量元素, 铁^[15]、锰^[62]、锌^[63] 等微量元素, 以及硒^[64] 等有益元素。例如, 草酸杆菌科 (*Oxalobacteraceae*) 的细菌会在玉米根际土壤中大量富集, 通过调节玉米侧根发育增加其地上部植株的氮含量^[60]。此外, 以 γ -变形菌 (*Gammaproteobacteria*) 为主的固氮细菌定殖于玉米茎木质部并进行固氮作用, 同样能显著增加玉米植株的氮积累量^[12]。在磷吸收方面, 恶臭假单胞菌 (*Pseudomonas putida*) MTCC 5279 通过分泌以葡萄糖酸为主的有机酸溶解难溶性无机磷酸盐, 并上调玉米根系中磷转运蛋白基因的表达, 从而显著增强玉米根系和地上部植株的磷积累量^[13]。在铁吸收方面, *Pseudomonas* sp. 1502IPR-01 能分泌铁载体 pyoverdine 螯合土壤中不溶性的 Fe^{3+} , 从而显著增加花生幼叶和根际的活性铁含量^[15]。总之, 根际微生物主要通过提高土壤养分的有效性、重塑根系构型以及调控根系养分转运相关基因的表达来增强植物对养分的吸收, 这也间接强化了植物对病原菌的抵抗能力。

2.2.3 根际微生物提高作物非生物胁迫抗性

非生物胁迫不仅会挑战作物的生存耐受性,还会影响其对病害的易感性。健康状况良好的作物能够有效抵御胁迫,并抑制病原菌侵染;反之,易感作物在胁迫环境下其抗病能力会大幅削弱,从而为病原菌的入侵与致病创造有利条件^[65]。因此,提高作物对非生物胁迫的抗性已成为增强其整体抗病能力的有效途径。

干旱、高温、土壤酸化和铝毒等是农业生产中常见的非生物胁迫,尤其是在华南地区。研究证实,根际微生物通过产生有机酸(如脯氨酸、草酸、苹果酸、苯甲酸)^[6]、胞外多糖(如海藻糖)等渗透保护剂^[66]、植物激素(如生长素、赤霉素)^[67]提高土壤 pH^[68],诱导作物产生抗氧化剂(如过氧化氢酶、过氧化物酶等酶促成分以及核黄素、抗坏血酸等非酶促成分)^[68],调控相关基因的表达^[4]等途径增强作物对非生物胁迫环境的抗性。例如,在干旱胁迫下,贝莱斯芽孢杆菌(*Bacillus velezensis*) GH1-13 通过激活水稻中的 JA 信号通路来上调活性氧(reactive oxygen species, ROS)清除基因(如抗坏血酸过氧化物酶基因(ascorbate peroxidase, *OsAPX*)和过氧化氢酶基因(catalase, *OsCAT*)等的表达,降低水稻中 ROS 的积累从而增强其抗旱性^[3]。高温胁迫下,接种变形球囊霉(*Diversispora versiformis*)能上调黄瓜中大多数热休克蛋白基因(heat shock protein 70 gene, *CsHsp70s*)和质膜内在蛋白基因(plasma membrane intrinsic proteins gene, *CsPIPs*)的表达,阻止蛋白质聚集和折叠并提高水的跨膜运输能力,保护黄瓜细胞免受热休克的影响^[4]。当遭受铝胁迫时,根内根孢囊霉(*Rhizophagus intraradices*, 原名 *Glomus intraradices*)等 3 株丛枝菌根(arbuscular mycorrhizae, AM)真菌通过与蓖麻共生增加蓖麻根系分泌苯丙素、聚酮、有机酸等物质的含量,其中苯丙素类物质可清除 ROS 减轻氧化损伤,柠檬酸等有机酸可螯合根际中的 Al^{3+} 形成稳定复合物,减少植物根系对 Al^{3+} 的吸收,从而缓解铝胁迫对植物的毒害^[6]。

此外,红城红球菌(*Rhodococcus erythropolis*)与铜绿假单胞菌(*Pseudomonas aeruginosa*)构建的合成群落通过提高水稻根系过氧化物酶活性、增加铝转运蛋白基因(aluminum transporter 1, *NRAT1*)的表达以及提高水稻根际 pH 来抵抗酸性铝毒胁迫;此外,该菌群通过富集根际解磷细菌加速有机磷矿化,其中 *R. erythropolis* 在铝胁迫下形成由聚磷酸盐(polyphosphate, polyP)组成的寡体,该结构参与磷的储存、pH 稳态、渗透调节以及营养胁迫条件下的应激反应,进一步缓解由土壤低 pH 导致的有效磷缺乏问题^[68]。早期研究也表明,接种根内根孢囊霉 BGC JX04B 可通过诱导番茄根系中磷酸盐转运蛋白基因(如 phosphate transporter 1-5, *SIPT1-5*)的表达,增加低 pH 条件下番茄地上部的磷含量和磷吸收总量^[5],同时激活作物抗氧化防御系统和相关基因表达来协助作物抵御胁迫的危害。

2.3 微生物与微生物的间接互作

2.3.1 抑制病原菌辅助菌的生长

一些微生物能与植物病原菌互作从而增强其致病性,此类微生物被定义为病原菌辅助菌。例如, Li 等^[69]从分离的 160 株细菌中发现,有 50.6% 能显著促进青枯菌生长,其中突尼斯叶杆菌(*Phyllobacterium ifriqiyense*) LM1 和副氧化微杆菌(*Microbacterium paraoxydans*) LM2 在体内、体外试验中均增加了青枯菌数量,且体内试验中增加量高达 946.7%,还使番茄青枯病发病程度至少增加 62.5%。此外,芽孢杆菌也可能作为辅助菌促进青枯菌生长,这与之前的研究结果截然相反^[41]。利用这一特性,根际微生物能通过抑制病原菌辅助菌间接降低病原菌对作物的危害。例如,根际细菌通过间接抑制青枯菌辅助菌 *P. ifriqiyense* LM1 和 *M. paraoxydans* LM2 来降低青枯菌密度,进而降低番茄青枯病发病率^[69]。这种间接抑制机制可能源于病原菌辅助菌产生的代谢物和铁载体,这些物质能被病原菌利用从而促进其生长^[41,70-72]。例如,定殖于小麦种子内部的可遗传微生物在种子发芽后会迁

移至新生根际, 成为根际微生物群落的一部分(即种子传播的根际微生物组), 这些微生物能产生葡萄糖、果糖、烟酸和核黄素等物质供土壤中的特定共生细菌利用, 避免与其他细菌竞争养分而增强共生细菌的生长能力^[72]。同样地, 芽孢杆菌属的菌株产生的促进性铁载体能被青枯菌利用, 提高青枯菌吸收土壤中铁素的能力, 使番茄植株根际青枯菌数量和病情指数增加^[41]。目前已知的病原菌辅助菌相对较少, 关于这些类群促进病原菌生长的机制研究得还不够透彻。因此通过阻断病原菌辅助菌与病原菌之间的作用途径抑制作物病害这种方式还存在较大难度, 仍需深入研究。

2.3.2 促进抗病菌株的抗病能力

在微生物-微生物的互作中根际微生物不仅能抑制病原菌辅助菌的生长, 还可通过强化抗病微生物的抗病能力来提高其生防效果。其核心机制在于: 一种微生物可为另一种抗病微生物提供增殖所需的关键因子^[73], 或刺激其产生抑制病原菌的抗菌类物质^[34,74]; 此外, 还可促进抗病微生物定殖于作物根际^[75]。例如, *P. putida* H3 产生的琥珀酸能促进难培养抗病细菌尼尔菌(*Niallia* sp.) RD1 的生长, 两者在根际互作时通过增加 *Niallia* sp. RD1 的丰度提高番茄抗青枯病能力^[73]。产酶溶杆菌(*Lysobacter enzymogenes*) OH11 通过其 IVA 型分泌系统分泌效应蛋白 Le1519, 该蛋白与保护假单胞菌(*Pseudomonas protegens*) Pf-5 中抗真菌抗生素 2,4-二乙酰基藤黄酚(2,4-diacetylphloroglucinol, 2,4-DAPG)生物合成途径的特异性转录阻遏物 PhIF 结合, 从而激活菌株 *P. protegens* Pf-5 产生 2,4-DAPG^[74]。异形根孢囊霉(*Rhizophagus irregularis*) 可使 *B. velezensis* 沿着菌丝网络迁移, 有助于其在番茄根际定殖^[75], 从而保护番茄免受灰霉病侵害。总之, 微生物-微生物的互作能通过多种机制增强有益根际微生物抗土传病害的能力, 但目前鲜有报道根际微生物间相互作用的具体机制。

3 根际微生物防治作物土传病害的现状

利用根际微生物防治作物病害的方式主要有 3 种(表 1): (1) 单一抗病菌株的生物防治; (2) 人工合成微生物群落的生物防治; (3) 真菌-细菌跨界互作的生物防治。早期研究主要集中在利用单一菌株的高效抗病特性来控制作物病害, 但随着研究发现单一抗病菌株应用存在局限性, 因此人工构建合成群落和细菌-真菌跨界互作逐渐成为防治作物病害的方式。

3.1 单一抗病菌株的生物防治

在农业生产中, 单一抗病菌株通常因其对作物病害具有高效防治作用而被广泛应用, 其中芽孢杆菌属^[97]、木霉菌属(*Trichoderma*)^[98] 是已被商业化的细菌和真菌类群。利用单一抗病菌株防治土传病害的研究早在 20 世纪 50 年代就已有初步进展。早在 1955 年, Dunleavy^[99] 发现一株枯草芽孢杆菌(*Bacillus subtilis*) 能够有效防治甜菜腐烂病。此后, 越来越多的研究人员开始研究单一抗病菌株防治作物土传病害的效果, 大量研究证实单独使用某些细菌或真菌可以有效防治病害^[76-80,100]。例如, 从 159 株菌中筛选出的 *B. amyloliquefaciens* OR2-30 通过产生伊枯草菌素抑制禾谷镰孢菌分生孢子的形成和萌发, 诱导禾谷镰孢菌产生 ROS, 缩短玉米茎腐病的病斑长度^[77]。然而, 单一菌株的抗病效果大多是在可控的实验室条件下验证的, 无法真实反映田间应用情况, 抗病效果不可预测和重复^[101]。田间土壤生态环境极其复杂, 种植温度^[81]、土壤类型^[102]、作物品种^[103-104]、土著微生物^[105] 等因素限制单一菌株在作物根际定殖和生长, 难以发挥菌株的最佳抗病性能。例如, *B. subtilis* PTA-271 可以减轻葡萄球菌枯死病, 但其发挥作用的温度仅在 28 °C; 此外, *B. subtilis* PTA-271 在沙质土壤中定殖和存活能力随接种时间延长而降低^[81,102]。基于以上原因, 现在大多数微生物防治技术研究已从单一菌株研究转移到合成微生物群落研究中。

表1 根际微生物防治土传病害的作用方式

Table 1 The mode of action of microbial technology in controlling soil-borne diseases

作物 Crops	病原菌 Pathogens	抗病微生物 Disease-resistant microbes	作用机制和生防方式 Mechanism of action and biological control methods	参考文献 References
辣椒 <i>Capsicum annuum</i>	辣椒疫霉菌 <i>Phytophthora capsici</i>	铜绿假单胞菌 Pa608 <i>Pseudomonas aeruginosa</i> Pa608	单菌生防:产生的 α -蒎烯和3-萜烯能够抑制辣椒疫霉菌的生长 Single-strain biocontrol: the strain Pa608 inhibits the growth of <i>Phytophthora capsici</i> by producing α -pinene and 3-carene	[49]
油菜 <i>Brassica rapa</i> var. <i>oleifera</i>	核盘菌 <i>Sclerotinia sclerotiorum</i>	苏云金芽孢杆菌 4F5 <i>Bacillus thuringiensis</i> 4F5	单菌生防:同时激活水杨酸、乙烯和茉莉酸信号通路,触发油菜的诱导系统抗性 Single-strain biocontrol: the strain activates the salicylic acid, ethylene, and jasmonic acid signaling pathways simultaneously, thereby triggering induced systemic resistance in <i>Brassica rapa</i> var. <i>oleifera</i>	[76]
玉米 <i>Zea mays</i>	禾谷镰孢菌 <i>Fusarium graminearum</i>	解淀粉芽孢杆菌 OR2-30 <i>Bacillus amyloliquefaciens</i> OR2-30	单菌生防:产生的脂肽(伊枯草菌素)抑制病原真菌分生孢子的形成和萌发、诱导活性氧的产生并导致菌丝体细胞死亡 Single-strain biocontrol: the strain OR2-30 inhibits the growth of <i>F. graminearum</i> by secreting iturin to suppress conidial formation and germination, inducing the production of reactive oxygen species, and causing mycelial cell death	[77]
番茄 <i>Solanum lycopersicum</i>	茄科罗尔斯通氏菌 <i>Ralstonia solanacearum</i>	恶臭假单胞菌 IsoF <i>Pseudomonas putida</i> IsoF	单菌生防: <i>P. putida</i> IsoF 借助四型b亚型分泌系统以接触依赖的方式将毒素递送至病原菌内,并入侵现有生物膜,从而保护番茄植株免受病原菌的侵害 Single-strain biocontrol: the strain IsoF utilizes its type IVB secretion system to deliver toxins into pathogens in a contact-dependent manner and invade existing biofilms, thereby protecting tomato plants from pathogenic infection	[78]
蒺藜苜蓿, 豌豆 <i>Medicago truncatula</i> , <i>Pisum sativum</i>	根丝丝霉 <i>Aphanomyces euteiches</i>	寡雄腐霉 M1 <i>Pythium oligandrum</i> M1	单菌生防:诱导植物体内合成抗菌异黄酮类化合物和苯丙类化合物,并调整根际微生物群落 Single-strain biocontrol: the strain M1 enhances the overall disease resistance of plants by activating the synthesis of endogenous antimicrobial compounds (isoflavonoids and phenylpropanoids) and modulating the rhizosphere microbial community	[79]
豌豆 <i>P. sativum</i>	终极腐霉 <i>Globisporangium ultimum</i>	棘孢木霉 ZNW <i>Trichoderma asperellum</i> ZNW	单菌生防:在病原菌的菌丝体上寄生并诱导宿主植物系统性抗性 Single-strain biocontrol: the strain ZNW parasitizes the mycelium of the pathogen and triggers induced systemic resistance in the host plant	[80]

(待续)

(续表 1)

作物 Crops	病原菌 Pathogens	抗病微生物 Disease-resistant microbes	作用机制和生防方式 Mechanism of action and biological control methods	参考文献 References
葡萄 <i>Vitis vinifera</i>	小新壳梭孢 <i>Neofusicoccum parvum</i>	枯草芽孢杆菌 PTA-271 <i>Bacillus subtilis</i> PTA-271	单菌生防: 触发水杨酸和茉莉酸反应基因的表 达并且可以解毒真菌毒素(-)-terremutin 和 (R)-mellein Single-strain biocontrol: the strain PTA-271 not only triggers the salicylic acid and jasmonic acid signaling pathways in plants, but also degrades the two fungal toxins (-)-terremutin and (R)-mellein	[81]
花生 <i>Arachis hypogaea</i>	齐整小核菌 <i>Sclerotium rolfsii</i> JN3011	哈茨木霉 QT20045 <i>Trichoderma harzianum</i> QT20045	单菌生防: <i>T. harzianum</i> QT20045 通过菌丝缠 绕、寄生及解离等机制直接抑制病原真菌, 此 外, 在病原真菌胁迫下, <i>T. harzianum</i> QT20045 还能通过下调果胶酯酶家族基因表达维持花 生幼苗细胞壁的稳定, 同时上调 suppressor of mkk1/mkk2 (<i>AhSUMM2</i>) 基因表达来增强植物 抗病性 Single-strain biocontrol: the strain QT20045 directly inhibits pathogenic fungi through mechanisms such as hyphal entanglement, parasitism, and lysis. In addition, under pathogenic fungal stress, this strain can maintain the stability of peanut seedling cell walls by downregulating the expression of pectinesterase family genes and upregulating the expression of the <i>AhSUMM2</i> gene to enhance plant disease resistance	[82]
大豆 <i>Glycine max</i>	大豆疫霉菌 <i>Phytophthora sojae</i>	根内根孢囊霉 BGC BJ09 <i>Rhizophagus intraradices</i> BGC BJ09	单菌生防: <i>R. intraradices</i> 通过降低大豆植株 内 H ₂ O ₂ 增加茉莉酸含量、谷胱甘肽还原酶活 性来增强大豆对大豆疫霉的抗性 Single-strain biocontrol: the strain BGC BJ09 enhances soybean resistance to <i>P. sojae</i> by reducing H ₂ O ₂ levels, increasing jasmonic acid content, and elevating glutathione reductase activity in the plants	[83]
大豆 <i>G. max</i>	大豆疫霉菌 <i>P. sojae</i>	珊瑚球菌 EGB <i>Corallococcus</i> sp. EGB	单菌生防: <i>Corallococcus</i> sp. EGB 分泌一种新 型硫胺素酶 I (thiaminase I, CcThi1) 到胞外, 从 而分解环境中的公共硫胺素, 阻断疫霉菌获取 硫胺素, 进而抑制疫霉菌的生长 Single-strain biocontrol: the strain EGB inhibits the growth of <i>P. sojae</i> via a thiaminase I CcThi1 secreted into extracellular environment through outer membrane vesicles	[84]

(待续)

(续表1)

作物 Crops	病原菌 Pathogens	抗病微生物 Disease-resistant microbes	作用机制和生防方式 Mechanism of action and biological control methods	参考文献 References
水稻 <i>Oryza sativa</i>	尖孢镰孢菌 <i>Fusarium oxysporum</i>	贝莱斯芽孢杆菌 Bv S3 <i>Bacillus velezensis</i> Bv S3	单菌生防: <i>B. velezensis</i> Bv S3 的无菌滤液可显著降低尖孢镰孢菌孢子萌发率和菌丝生长, 并引起菌丝畸形 Single-strain biocontrol: the sterile filtrate of strain Bv S3 can significantly reduce the spore germination rate and hyphal growth of <i>F. oxysporum</i> , and cause hyphal malformation	[85]
花生 <i>A. hypogaea</i>	<i>F. oxysporum</i>	<i>Pantoea</i> sp., <i>Fictibacillus</i> sp., <i>Enterobacter</i> sp., <i>Paenibacillus</i> sp., <i>Sporosarcina</i> sp., <i>Lysinibacillus</i> sp., and <i>Pseudomonas</i> sp.	合成群落: 该合成群落由轮作花生根际富集, 但在单作花生根际中明显减少的菌株组成。体外实验表明, 该群落能够显著抑制 <i>F. oxysporum</i> 的菌丝生长。进一步将其回补至单作花生中, 可恢复植株的抗病能力。其抑菌机制可能与挥发性有机化合物 (volatile organic compounds, VOCs) 及抗生素类物质的产生有关。例如, 在轮作花生根际检测到而在单作根际中未能检出的二甲基硫醚、2,5-二甲基环己酮、6-甲基-3,5-戊二烯-2-酮等 VOCs, 即使在低浓度下也对病原菌表现出强烈抑制活性 Synthetic community: the synthetic community consists of strains that are enriched in the rhizosphere of rotated peanuts but significantly reduced in the rhizosphere of monoculture peanuts. This community can significantly inhibit the mycelial growth of <i>F. oxysporum</i> , and reintroducing it into monoculture peanuts can restore the plant's disease resistance. Its antibacterial mechanism may be related to the production of volatile organic compounds (VOCs) and antibiotic-like substances	[86]
马铃薯 <i>Solanum tuberosum</i>	<i>Fusarium</i> spp.	解淀粉类芽孢杆菌 B9D10, 恶臭假单胞菌 B65D14, 乙酸钙不动杆菌 B9H9, 变形斑沙雷氏菌 B65H4, 放线菌 B9H11 和枯草芽孢杆菌 B65D7 <i>Paenibacillus amylolyticus</i> B9D10, <i>P. putida</i> B65D14, <i>Acinetobacter calcoaceticus</i> B9H9, <i>Serratia proteamaculans</i> B65H4, <i>Actinomycetes</i> sp. B9H11, and <i>B. subtilis</i> B65D7	合成群落: 合成群落其他成员菌株促进 <i>S. proteamaculans</i> B65H4 产生己酸, 从而抑制病原真菌分生孢子萌发以及抑制菌丝生长 Synthetic community: the consortium inhibits the pathogenic fungus by promoting <i>S. proteamaculans</i> B65H4 to produce caproic acid, which suppresses conidial germination and hyphal growth	[87]

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(续表 1)

作物 Crops	病原菌 Pathogens	抗病微生物 Disease-resistant microbes	作用机制和生防方式 Mechanism of action and biological control methods	参考文献 References
番茄 <i>S. lycopersicum</i>	<i>R. solanacearum</i>	Pyoluteorin 缺陷型的保护假单胞菌 Pf-5 和贝莱斯芽孢杆菌 DMW1 Pyoluteorin-deficient <i>Pseudomonas protegens</i> Pf5 and <i>B. velezensis</i> DMW1	合成群落: 敲除 <i>P. protegens</i> Pf-5 的 pyoluteorin 合成基因, 使其能与 <i>B. velezensis</i> DMW1 互作共生, 共定殖于番茄根系并增强 <i>B. velezensis</i> DMW1 抗菌代谢物合成, 协同保护番茄免受青枯病侵害 Synthetic community: the pyoluteorin-deficient strain Pf-5 can interact with and co-colonize the tomato rhizosphere together with strain DMW1, enhance the synthesis of antibacterial metabolites by strain DMW1, and synergistically protect tomatoes from bacterial wilt	[88]
黄芪 <i>Astragalus membranaceus</i>	<i>F. oxysporum</i>	<i>Stenotrophomonas</i> sp., <i>Rhizobium</i> sp., <i>Ochrobactrum</i> sp., and <i>Advenella</i> sp.	合成群落: <i>Stenotrophomonas</i> sp. 直接抑制真菌病原体生长, 其他 3 种细菌则激活植物体内茉莉酸信号通路以及激活诱导系统抗性相关酶活性 Synthetic community: <i>Stenotrophomonas</i> sp. directly inhibits the growth of fungal pathogens, while the other three bacteria activate the jasmonic acid signaling pathway in plants and trigger induced systemic resistance by enhancing the activity of resistance-related enzymes	[89]
小麦 <i>Triticum aestivum</i>	立枯丝核菌 <i>Rhizoctonia solani</i> AG8	14 株细菌构建的 10 个合成群落 Ten synthetic communities constructed from 14 bacterial strains	合成群落: 10 个群落中的 4 个合成群落通过产生挥发性物质显著抑制 <i>R. solani</i> AG8 的生长 Synthetic community: four out of the ten synthetic communities significantly inhibit the growth of <i>R. solani</i> AG8 by producing volatile substances	[90]
西瓜 <i>Citrullus lanatus</i>	<i>F. oxysporum</i>	<i>P. aeruginosa</i> Q6 等 16 株细菌 A synthetic community of 16 bacterial strains, including <i>P. aeruginosa</i> Q6	合成群落: 通过微生物协同作用增强抗病性, 并且合成群落其他成员能够促进假单胞菌的生物膜形成 Synthetic community: the community enhances disease resistance through microbial synergy, and other members of the synthetic community can promote biofilm formation in <i>P. aeruginosa</i> Q6	[91]

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(续表1)

作物 Crops	病原菌 Pathogens	抗病微生物 Disease-resistant microbes	作用机制和生防方式 Mechanism of action and biological control methods	参考文献 References
小果野蕉 <i>Musa acuminata</i>	<i>F. oxysporum</i> f. sp. <i>cupense</i>	师岗链霉菌和印度梨形孢 <i>Streptomyces morookaense</i> and <i>Piriformospora indica</i>	微生物跨界互作: <i>S. morookaensis</i> 产生次生化合物 xerucitrinin A 和 6-戊基- α -吡喃酮, 抑制 <i>F. oxysporum</i> 的生长并减少其孢子数量, <i>P. indica</i> 防止病原菌定殖到根部 Cross-kingdom microbial interactions: <i>S. morookaensis</i> produces secondary compounds, xerucitrinin A and 6-pentyl- α -pyrone, which inhibit the growth of <i>F. oxysporum</i> and reduce its spore production. Meanwhile, <i>P. indica</i> prevents the pathogen from colonizing the roots	[48]
番茄 <i>S. lycopersicum</i>	灰葡萄孢霉 <i>Botrytis cinerea</i>	<i>B. velezensis</i> 和异形根孢囊霉 <i>B. velezensis</i> and <i>Rhizophagus irregularis</i>	微生物跨界互作: <i>B. velezensis</i> 能沿着 <i>R. irregularis</i> 真菌菌丝网络迁移并形成生物膜, 而 AM 真菌能调控芽孢杆菌产生表面活性素使二者稳定共存, 互作时能激活植物系统抗性以保护番茄免受地上部病害灰葡萄孢霉侵害 Cross-kingdom microbial interactions: <i>B. velezensis</i> can migrate along the hyphal network of <i>R. irregularis</i> and form biofilms, while AM fungi can regulate surfactant production by <i>Bacillus</i> , enabling stable coexistence between the two. During interaction, they can activate plant systemic resistance to protect tomatoes from the above-ground pathogen <i>Botrytis cinerea</i>	[75]
藏红花 <i>Crocus sativus</i>	<i>F. oxysporum</i>	皮尔瑞俄类芽孢杆菌 SR235 和云南木霉菌 SR38 <i>Paenibacillus peoriae</i> SR235 and <i>Trichoderma yunnanense</i> SR38	微生物跨界互作: <i>T. yunnanense</i> SR38 和 <i>P. peoriae</i> SR235 共培养发酵液中具有抗病性的有机酸(DL-3-苯乳酸、3-羟基癸酸、(2S)-2-异丙基苹果酸), 其含量比单一 SR38 或 SR235 菌株产生的高, 从而激活植物免疫系统 Cross-kingdom microbial interactions: the fermentation broth co-cultured with <i>T. yunnanense</i> SR38 and <i>P. peoriae</i> SR235 contains disease-resistant organic acids (DL-3-phenyllactic acid, 3-hydroxydecanoic acid, and (2S)-2-isopropylmalate), which are present in higher amounts than those produced by a single SR38 or SR235 strain, thereby activating the plant's immune system	[92]

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(续表 1)

作物 Crops	病原菌 Pathogens	抗病微生物 Disease-resistant microbes	作用机制和生防方式 Mechanism of action and biological control methods	参考文献 References
辣椒 <i>C. annuum</i>	<i>P. capsici</i>	<i>B. subtilis</i> QST713 and <i>T. harzianum</i> T-22	微生物跨界互作: <i>T. harzianum</i> T-22 和 <i>B. subtilis</i> QST713 联合处理增加辣椒中抗氧化酶以及酚类化合物含量,增强植物抵抗病原菌能力 Cross-kingdom microbial interactions: the combined treatment with <i>T. harzianum</i> T-22 and <i>B. subtilis</i> QST713 increases the content of antioxidant enzymes and phenolic compounds in peppers, enhancing the plant's resistance to pathogens	[93]
烟草 <i>Nicotiana tabacum</i>	烟草疫霉菌 <i>Phytophthora nicotianae</i>	<i>B. subtilis</i> Tpb55 and <i>T. asperellum</i> HG1	微生物跨界互作: <i>T. asperellum</i> HG1 和 <i>B. subtilis</i> Tpb55 共培养使 <i>T. asperellum</i> HG1 产生抗卵菌脂肪族化合物 2E,4E-癸二烯酸含量增加,其能抑制多种植物病原菌 Cross-kingdom microbial interactions: co-culturing <i>T. asperellum</i> HG1 and <i>B. subtilis</i> Tpb55 increase the content of the anti-oomycete aliphatic compound 2E,4E-decadienoic acid produced by <i>T. asperellum</i> HG1, which can inhibit a variety of plant pathogens	[94-95]
番茄 <i>S. lycopersicum</i>	<i>F. oxysporum</i> f. sp. <i>Lycopersici</i>	74 种不同真菌:105 种细菌(细菌:真菌的生物量比为 4:1) 74 fungal strains: 105 bacterial strains (bacterial:fungal biomass ratio of 4:1)	微生物跨界互作:此跨界合成群落能够激活番茄茉莉酸和水杨酸信号通路,并且富集几丁质酶、木葡聚糖水解酶等在内的 51 条碳水化合物活性酶(carbohydrate-active enzyme, CAZyme)相关途径 Cross-kingdom microbial interactions: the cross-kingdom synthetic community activates both jasmonic acid and salicylic acid signaling pathways in tomato and enriches 51 carbohydrate-active enzyme (CAZyme)-related pathways, including those for chitinases and xyloglucan hydrolases	[96]

3.2 人工合成群落的生物防治

由于天然微生物群落过于复杂导致研究极其困难。因此 Großkopf 等^[106]提出了构建合成微生物群落模型,即 2 种及以上能共存且具有互补功能的抗病促生微生物构建得到的人工微生物群落,其构建策略主要有 2 种:“自上而下”(施加外部压力驯化筛选关键菌)和“自下而上”(代谢模型预测最优组合并验证)^[107]。随着对合成群落的深入研究发现,合成群落能很好地适

应环境变化,其功能稳定、抗病效果比单一菌株更好。例如,由 3 株芽孢杆菌组成的合成群落能够干扰真菌细胞增殖、霉菌毒素生物合成,并且上调 JA 信号标记基因 *LOX2-3* 和 *LOX4* 的表达,使 JA 含量显著增加,其降低花生病害的效果比其中任一种芽孢杆菌都好^[108]。合成群落的抗病效果并非由其菌株数量单一决定,而是高度依赖于菌株间的最佳组合;此外,在高效抗病的合成群落中任一关键菌株缺失都可能削弱合成群落的抗病功能^[87,109]。由 *P. putida*

等 5 种细菌与变形斑沙雷氏菌 (*Serratia proteamaculans*) 65H4 互作使其产生己酸显著降低马铃薯枯萎病病情指数, 但单一菌株或缺失 *S. proteamaculans* 65H4 的合成群落单独作用却对马铃薯的抗病效果不佳; 另外, 其他大型合成群落(大于 6 种细菌)的抗病效果反而低于这个组合^[87]。人工构建合成群落对于菌株的选择具有挑战性, 但由于大多数合成群落对作物的效果和稳定性比其中单一成员好, 构建可重复的复杂合成群落研究依然是生物防治方式的主要突破口。

3.3 真菌-细菌跨界互作的生物防治

真菌-细菌跨界互作在土壤环境中普遍存在, 作为一种特殊的合成群落, 其在抑制作物病害方面比单独的真菌或细菌合成群落更有效。早期研究主要关注其促进作物吸收养分方面, 尤其是 AM 真菌与根际细菌的互作。例如, 用环状尼尔菌 (*Niallia circulans*) YRNF1 与幼套近明球囊霉 (*Claroideoglossum etunicatum*) 和 *R. intraradices* 共同处理茄子提高了叶片总氮、磷、钾含量^[110]。德沃斯氏菌 (*Devosia* sp.) ZB163 与 *R. irregularis* MUCL43194 联合处理夏枯草时验证了同样的结果, 而且还增强了 AM 真菌对根系的侵染^[111]。近年来, 真菌-细菌跨界互作防治作物病害的效果及作用机制开始被陆续报道。目前研究多集中于木霉菌、AM 真菌和芽孢杆菌之间的互作, 而针对其他菌之间相互作用的研究则相对有限^[75,92-93]。在田间试验中, 在移植前 1 周预先用印度梨形孢 (*Piriformospora indica*) 处理土壤, 同时用师岗链霉菌 (*Streptomyces morookaense*) 处理香蕉幼苗, 之后将幼苗种植到处理过的土壤中, 到第二年年底香蕉植株几乎未出现枯萎病症状^[48]。哈茨木霉 (*Trichoderma harzianum*) 突变体 $\Delta Tgmfs4$ 通过调控杆菌溶素转运蛋白 (bacilysin transmembrane transporter, TgmFS4) 降低 *B. velezensis* 产生杆菌溶素进入胞内的可能性, 使哈茨木霉突变体和 *B. velezensis* 能够共存, 通过协同作用提升番茄枯萎病防治

效果^[112]。目前, 真菌-细菌跨界互作的生物防治研究尚处于起步阶段, 许多潜在机制仍不清楚, 进一步研究跨界互作机制对土传病害防治具有重要意义。由于真菌与细菌对营养偏好存在差异^[113], 未来有望通过利用真菌-细菌互作方式竞争土壤中多种类型养分, 削弱病原菌吸收养分的能力, 从而防治作物病害。

4 总结与展望

本文系统总结了根际微生物的 7 种生防机制, 包括与病原菌竞争生态空间和养分、合成并分泌抗菌类物质、激活作物的免疫系统、促进作物养分吸收、提高作物非生物胁迫抗性、抑制病原菌辅助菌的生长、增强抗病菌株的抗病能力。这些机制可进一步归纳为 3 个核心互作途径: 微生物-病原菌的直接互作、微生物-作物的直接与间接互作和微生物-微生物的间接互作。对上述机制的进一步认识有助于加深对“作物-根际微生物-病原菌”三方复杂互作关系的理解。目前, 基于根际微生物的生防手段已广泛应用于水稻、番茄、大豆等多种作物, 主要策略包括施用单一抗病菌株、构建人工合成微生物群落(细菌群或真菌群), 以及利用真菌-细菌跨界互作体系。

尽管根际微生物在增强作物抗病能力方面潜力显著, 但其田间应用仍面临若干重要挑战: (1) 绝大多数功能微生物仍处于“不可培养”状态, 且其定殖效率与生防功能易受土壤环境及作物基因型等诸多因素干扰, 导致核心微生物资源的挖掘与利用困难重重; (2) 病原菌辅助菌群以及对生防类群具促进功能的微生物虽在自然界中普遍存在, 然而微生物间的互作研究较为复杂, 相关研究起步也较晚, 其生防潜力尚未被充分认知; (3) 多组学技术已积累了海量的植物-微生物互作数据, 但如何整合作物基因组、转录组、代谢组与微生物宏基因组、宏转录组等多维数据, 并从中构建模型、提炼生物学问题, 进而系统性揭示“植物-微生物”互作的内在机制

仍是当前生物信息学面临的重要难题。此外，定向挖掘适应特定生境(如土壤理化特性与气候类型)的抗病微生物，并构建适用场景明确(如特定作物品种)、防治效果稳定的人工合成菌群也是将根际微生物研究推向田间应用的关键环节。

人工智能(artificial intelligence, AI)技术的快速发展与应用普及为突破上述瓶颈提供了全新路径。通过 AI 与多组学数据的深度融合，不仅能更深刻地揭示作物-微生物互作的内在机制，还可借助微生物互作预测模型，推断群落功能、指导合成群落的设计，进而通过实验验证驱动作物健康的核心微生物、功能基因及信号分子。与此同时，将宿主植物遗传学与微生物组数据相结合也展现出重要潜力。作物基因型与根际微生物组的结构和功能密切相关，因此深入解析宿主遗传背景对微生物组装配的影响，并在此基础上实现对微生物组的精准调控，将为高效筛选关键功能微生物提供一条极具前景的新策略。在这些前沿方法的共同推动下，有望最终实现根际微生物组的定向设计与调控，为从根本上解决作物土传病害、推动农业绿色可持续发展提供科技支撑。

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