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Review 综述

柑橘溃疡病生防微生物的作用机制研究及应用进展

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摘　要：柑橘是中国目前重要的经济作物之一，在种植过程中会受到诸多病害的威胁。柑橘溃疡病作为柑橘种植最常见的病害，对柑橘产业的发展造成了极大的危害。化学药物的长期使用导致病原菌耐药性增强、柑橘果实表面农药残留和环境污染等问题，微生物防治因其安全无污染等优点日益受到关注。本文总结了近 10 年柑橘溃疡病生防微生物的来源和种类，分析了生防微生物的作用机制，评价了生防菌剂的开发及其田间防效，梳理了柑橘溃疡病微生物防治现存的问题，为柑橘溃疡病的生防微生物研究提供参考。

关键词：柑橘溃疡病；生防微生物；作用机制；生防菌剂

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Research progress in the mechanism and application of biocontrol microorganisms for citrus canker

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Abstract: Citrus is one of the most important economic crops in China at present. During the cultivation, it is threatened by multiple diseases. Citrus canker, as the most common disease in citrus cultivation, has caused great harm to the development of the citrus industry. The long-term use of chemical control agents has led to problems such as enhanced resistance of pathogenic bacteria, chemical residues on the surface of citrus fruits, and environmental pollution. Microbial control has attracted increasing attention due to its safety and pollution-free advantages. This review summarizes the sources and species of biocontrol microorganisms for citrus canker in the past decade, analyzes the biocontrol mechanisms of these microorganisms, evaluates the development and field control effects of biocontrol agents, and points out the problems existing in the microbial control of citrus canker, providing a reference for the research on biocontrol microorganisms for citrus canker.

Keywords: citrus canker; biocontrol microorganism; mechanism of action; biocontrol agent

柑橘是我国及世界范围内重要的果树作物之一，在果品生产和农业经济中具有重要地位[1]。柑橘溃疡病是一种分布广泛的细菌性病害，在多地柑橘产区均有发生，已成为影响柑橘稳定生产的重要限制因素之一[2-3]。柑橘溃疡病由柑橘黄单胞菌柑橘亚种(*Xanthomonas citri* subsp. *citri*, Xcc)引起，侵染叶片、枝梢和果实，导致病斑形成、叶片脱落及果实外观品质下降[2,4]。在温暖潮湿条件下病害易流行，通过风雨、昆虫、农事操作及苗木调运等方式扩散[5-6]。目前主要依赖铜制剂和部分化学杀菌剂进行防治[7]，易对生态环境和农产品安全造成不良影响[8-9]。近年来微生物防治越来越受到重视，该防控方式是利用有益微生物或其代谢产物抑制病原菌、减轻病害的发生[10-11]。不同类型的生防微生物从柑橘叶际、内生组织、根际土壤等不同生态位中分离筛选，通过直接抑制病原菌生长、竞争营养资源和定殖空间、诱导宿主防御反应以及干扰病原菌毒力调控过程等多种途径发挥作用[12]。生防微生物在自然环境中的定殖能力、防效稳定性及其与施用方式和环境条件之间的关系是其发挥防病效果的关键，目前研究仍以菌株筛选和室内抑菌试验为主，在田间条件下保持稳定防效的生防菌剂数量十分有

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限。本文对近年来柑橘溃疡病微生物防治相关研究进行梳理，从生防微生物的来源、类型和作用机制等方面加以总结，并对生防菌剂田间应用进行分析与展望，以期为后续研究和开发提供参考。

1 柑橘溃疡病生防微生物的种类与来源

1.1 生防微生物的主要种类

目前已报道的柑橘溃疡病生防微生物以细菌为主，主要包括芽孢杆菌属(*Bacillus*)、假单胞菌属(*Pseudomonas*)和放线菌等类群[13]。细菌因分离培养相对容易、繁殖速度快、环境适应性较强且较易制剂化，成为研究热点。其中，*Bacillus* 因可形成耐逆芽孢并产生多种抗菌活性物质备受关注[14]；*Pseudomonas* 和链霉菌属(*Streptomyces*)等类群则分别在定殖竞争、铁载体分泌和次级代谢产物合成等方面具有较高开发潜力[15]。此外，一些肠杆菌属(*Enterobacter*)、伯克霍尔德氏菌属(*Burkholderia*)和梭菌属(*Clostridium*)等其他细菌也被报道具有一定拮抗活性[16-19]。有关菌株来源涵盖叶际、内生组织、根际土壤及特殊生态环境等，但不同来源菌株在抗逆性、定殖能力和代谢特征上存在明显差异。

与细菌相比，真菌在柑橘溃疡病防治中的研究较少，多集中于其次级代谢产物的抗菌活性上。其中部分内生真菌和极端环境来源真菌产生的抗 Xcc 活性代谢物具有较高开发潜力[20-21]。然而，真菌类资源在培养成本、储运要求、环境适应性和田间稳定性等方面存在较多限制[11,22]。

噬菌体具有宿主特异性强、裂解效率高和对非靶标微生物影响小等优势[23]，在柑橘溃疡病防控中作用独特[24]。其中部分裂解性噬菌体可通过直接裂解 Xcc 显著降低病原菌数量，但其宿主谱较窄，且易受紫外线、高温和极端 pH 等环境因素影响[25-26]，田间持效性有限[27]。

总之，柑橘溃疡病生防微生物呈现出以细菌为主、真菌和噬菌体为补充的格局，不同类型生防因子在来源、作用特征和应用定位上各具优势，共同构成了柑橘溃疡病绿色防控的微生物资源基础。

1.2 生防微生物的主要来源

柑橘溃疡病生防微生物的来源与其防控功能和应用场景密切相关。由于 Xcc 主要在叶片、枝梢和果实表面存活，并通过气孔或伤口侵入寄主组织，因此不同生态位来源的生防微生物在作用方式、定殖能力和应用适配性上存在差异[12]。

叶际微生物是柑橘溃疡病生防资源的重要来源。由于病原菌 Xcc 主要通过气孔或伤口侵入叶片组织并在叶面扩展，叶际环境构成了其关键侵染生态位[13]。叶际微生物更适合通过叶面喷施等方式直接作用于病原菌。此类菌株通常可通过快速占据叶面生态位、竞争营养资源和定殖空间、分泌抗菌活性物质等方式抑制 Xcc 在叶片表面的存活和扩展。研究表明，叶际来源的枯草芽孢杆菌(*Bacillus subtilis*)和铜绿假单胞菌(*Pseudomonas aeruginosa*)等菌株在体外和田间试验中均表现出明显的拮抗性[28-29]，其中 *B. subtilis* 可将柑橘溃疡病发病率降低约 60%[30-31]。叶际环境开放性强，易受紫外辐射、降雨冲刷及温湿度变化影响，因此叶际菌株的田间持效性通常依赖于其表面附着能力、抗逆性、生物膜形成能力以及剂型保护效果。

内生微生物由于能够在植物组织内部稳定定殖[32]，在柑橘溃疡病防控中表现出不易受环境影响的优势，其防控作用主要体现在提前占据潜在侵染位点、与病原菌竞争组织内部生态位，以及诱导寄主系统抗性等方面[14,33-34]。研究表明，从多种柑橘植物中分离得到解淀粉芽孢杆菌(*Bacillus amyloliquefaciens*)、*Bacillus subtilis* 等菌株，在叶片接种试验中对柑橘溃疡病发病实现近完全控制，部分处理甚至发病率为 0[35]。

内生菌能在病原菌侵入前占据潜在侵染位点，并通过诱导宿主系统抗性提高植株整体抗病能力[32]。此外，内生菌产生的活性代谢产物(如抗菌肽、挥发性物质)在抑制病原菌方面也发挥重要作用[10,18,35]。然而，内生菌的应用仍存在筛选效率低、宿主特异性强及规模化生产难度大等问题。

根际微生物通常不直接接触叶面 Xcc，可通过调控植物根际微生态及诱导系统抗性(induced systemic resistance, ISR)增强植物对病原菌的整体防御能力来实现防控。研究表明，以芽孢杆菌和假单胞菌为代表的根际微生物可通过分泌铁载体、抗菌物质及信号分子调节植物免疫反应来提高抗病性[17,36-38]。由于其作用间接，其防控效果通常依赖于菌株在根际的定殖稳定性及宿主响应程度。

除上述主要来源外，一些特殊生态环境的微生物(如海洋或极端环境菌株)[39-40]因产生结构新颖的抗菌活性物质，在拓展生防资源多样性方面具有潜在价值，但这类微生物在柑橘体系中的生态适应性及定殖能力仍有待进一步验证。已报道的代表性生防微生物归纳见表 1。

表1　针对柑橘溃疡病的代表性生物防治剂及其功效和作用机制

Table 1　Representative biocontrol agents against citrus canker and their efficacy and mechanisms

Microbial type	Representative genus/species	Source	Biocontrol efficacy (range)	Evaluation system	Application method	Key mechanism	References
Bacteria	*Bacillus* spp. (*B. subtilis*, *B. velezensis*, *B. amyloliquefaciens*, *B. tequilensis*, *B. pumilus*)	Soil, phyllosphere, endophyte	50%−100% (detached leaves), 30%−70% (greenhouse/field)	*In vitro* assay, detached leaves, greenhouse pot experiment, field trial	Foliar spraying, leaf inoculation	Secretion of lipopeptides; defense enzyme activation; biofilm inhibition	[16,28-31, 35-37, 41-53]
	Pseudomonas spp. (*P. aeruginosa*, *P. geniculata*, *P. protegens*)	Phyllosphere	50%−80%	Greenhouse pot experiment	Leaf inoculation, root irrigation	Secretion of antibiotics; biofilm inhibition; induction of ISR	[17,28, 54-56]
	Enterobacter sp. (GN223), *Kosakonia cowanii*	Endophyte	40%−50% (field)	Field trial	Leaf inoculation	Endophytic colonization; metabolite-mediated antibacterial activity; induction of ISR	[16,18,46, 57-58]
	Acinetobacter baumannii	Soil	55.20%	Greenhouse pot experiment	Foliar spraying	Secondary metabolites; strong environmental adaptability	[59]

(待续)

(续表1)

Microbial type	Representative genus/species	Source	Biocontrol efficacy (range)	Evaluation system	Application method	Key mechanism	References
	Serratia marcescens, *Vibrio diazotrophicus*	Soil	80%−95% (*in vitro* assay)	*In vitro* assay, greenhouse pot experiment	Fermentation broth inoculation	Secretion of antibiotics; induction of ISR	[60]
	Lactobacillus sp. Kx48, *Gluconobacter* sp. Kx15	Phyllosphere	40%−50% (field)	Greenhouse pot experiment, field trial	Foliar spraying	Phyllosphere colonization; niche competition	[19]
Fungi	*Diaporthe* sp. HT-79, *Diaporthe* WZMG-Y-12, *Schizophyllum* WZMG-J-8-1, *Fusarium* LJZ-Y-20	Phyllosphere	MIC: 0.007 8−10 mg/mL	*In vitro* assay, greenhouse pot experiment	Foliar spraying	Biofilm inhibition; cell membrane disruption	[61-63]
	Aspergillus unguis	Endophyte	MBC: 200 μg/mL	*In vitro* assay	Metabolites	Cell membrane disruption	[63]
	Pseudogymnoascus sp. LAMAI 2784	Antarctic soil	97.40%	*In vitro* assay, greenhouse pot experiment	Foliar spraying	Production of dichlorinated selenides; cell membrane disruption; increased membrane permeability	[39]
	Aspergillus terreus	Deep sea	BIC: 0.078 mg/mL, superior to $CuSO_4$ (0.312 5 mg/mL)	*In vitro* assay, greenhouse pot experiment	Foliar spraying	Biofilm formation inhibition; cell membrane disruption; ROS accumulation	[40]
Phage	Phage XacF1	Soil	Lesions were significantly reduced	Detached leaves	Leaf inoculation	EPS reduction; reduced motility; virulence attenuation	[64]
	Phage XacN1	Soil	XacN1 infected 9 of 10 *X. citri* strains from Japan	*In vitro* assay	Co-culture	Infection and lysis of Xcc, with possible biofilm disruption by lysins	[24]

MIC: Minimum inhibitory concentration; MBC: Minimum bactericidal concentration; BIC: Biofilm inhibitory concentration.

2 柑橘溃疡病生防微生物的作用机制

2.1 产生抑菌活性物质直接作用于病原菌

柑橘溃疡病生防机制中产生抑菌活性物质是一种直接作用方式。生防微生物分泌的抗生素、脂肽、酶类及其他活性物质可干扰病原菌的代谢过程、抑制其生长繁殖、损伤细胞结构完整性，从而降低 Xcc 的侵染能力，实现病害防控[37,44,61,65]。因此，该类机制的研究多围绕抗 Xcc 活性物质的筛选鉴定、主要成分解析及作用靶点展开，其中脂肽类、抗生素类、环二肽类及真菌次级代谢产物对细胞膜完整性、生物膜形成、活性氧积累和胞内物质外渗的影响是关注重点。拮抗菌株通常能同时产生聚酮化合物、非核糖体肽及挥发性有机化合物等多类活性物质，这种多组分协同作用有助于增强抑菌效果的稳定性。*Bacillus* 产生的脂肽类代谢物是研究较多的直接抑制因子。*Bacillus amyloliquefaciens* 产生的伊枯草素和泛革素类物质能特异性破坏 Xcc 细胞膜完整性，可引起 78.5% 左右的病原菌胞内物质外渗，显著高于化学药剂处理组(53.2%)[37]，从而抑制病原菌的正常生长；Lin 等[61]从柑橘内生真菌间座壳属(*Diaporthe* sp.) HT-79 中分离获得的亚油酸可通过破坏细胞膜结构并诱导活性氧积累抑制病原菌生长；Wattana-Amorn 等[66]从 *Streptomyces* sp. strain 22-4 菌株中分离得到的环二肽类化合物对 Xcc 表现出明确的抑制作用。这些研究为理解生防微生物的抑菌机制提供了依据。

此外，微生物挥发性有机化合物(microbial volatile organic compounds, mVOCs)也是抑菌的重要活性物质。研究表明，来源于 *Bacillus*、*Pseudomonas* 及部分真菌微生物的挥发物可在无直接接触条件下对多种植物病原菌生长产生抑制作用，其机制与影响细胞膜结构、干扰能量代谢及调控信号传导过程有关[67]。mVOCs 具有易扩散、非接触作用和信号调节等特点，相关研究涉及活性挥发物鉴定、抑菌谱评价、病原菌膜结构与能量代谢变化，以及植物防御反应激活等多方面[67]。另外，mVOCs 作为信号分子也参与植物-微生物互作过程，采用拟南芥[68]、黄瓜[69]、葡萄[70]和番茄[71-72]等体系研究，发现 mVOCs 能诱导植物抗氧化系统及防御相关基因表达，增强宿主抗性，推测 mVOCs 在柑橘叶际环境中可通过“非接触调控”方式参与柑橘溃疡病防御，值得深入研究。

2.2 营养与生态位竞争

除直接抑制之外，生防微生物也可通过竞争致病菌的营养与生态位发挥防控作用。即通过限制 Xcc 对碳源、氮源、铁元素等关键养分及定殖位点的获取，降低其在叶际、伤口或组织内的存活与侵染能力[12]。与单纯抑菌作用相比，该机制更强调生防微生物在寄主表面的适应和定殖过程，因此叶际存活能力、伤口部位优先占位、铁载体介导的铁营养竞争以及生物膜形成等，是近年来评价竞争型生防菌的重要内容[52,54,73-74]。从功能层级来看，竞争抑制较直接抑菌机制更依赖于生防微生物在寄主表面的稳定定殖能力。研究表明，*Bacillus* 和 *Pseudomonas* 具有与铁载体合成和营养竞争相关的功能基因，从而增强其在生态位竞争中的优势[75-76]，这是部分 *Bacillus* 和 *Pseudomonas* 能够在多次田间试验中保持生防效果的重要原因之一；另外，生防菌可通过快速繁殖形成空间占位效应，降低病原菌的定殖率，并在叶片表面形成稳定的生物膜结构，增强自身黏附性和抗逆性。如 *Bacillus amyloliquefaciens* 通过分泌脂肽类抗生素形成空间占位效应，在柑橘叶际微环境中可降低 Xcc 定殖率达 62.3%[37]。相比叶际微生物，内生生防菌能够直接定殖于植物组织内部，通过消耗宿主体内可利用营养、占据潜在侵染通道，并与宿主形成相对稳定的共生关系，在病原菌入侵前或侵染早期形成防

御屏障，如内生菌特基拉芽孢杆菌(*Bacillus tequilensis*)可在柑橘叶片伤口处优先定殖，有效抢占生态位，从而抑制 Xcc 的繁殖[35]。然而，营养与生态位竞争机制通常需要一定的时间窗口才能充分发挥作用，其生防效果高度依赖于微生物的定殖时机、环境适应性及施用方式。

2.3 诱导植物系统抗性

除直接抑制与竞争机制外，生防微生物还能诱导植物产生系统抗性(ISR)或系统获得性抗性(systemic acquired resistance, SAR)，调控寄主防御响应，增强对柑橘溃疡病的整体抵御能力[77]。与前 2 类机制不同，诱导抗性并不直接作用于 Xcc，而是激活柑橘自身的防御系统，降低宿主后续侵染的敏感性，构建持续且广谱的防卫反应，具有提高田间防控稳定性的优势。相关研究不再仅关注病斑减少或防效高低，而是进一步转向解析生防微生物如何激活柑橘防御信号通路，如水杨酸、茉莉酸等信号途径，以及防御酶活性、防御相关基因表达和诱导抗性持续时间等指标。生防菌表面的鞭毛蛋白、脂多糖等结构组分，以及其分泌的脂肽类化合物和部分挥发性有机物等代谢产物可作为激发子被植物细胞膜上的模式识别受体感知，触发免疫信号转导，激活下游防御反应，增强植株对病原菌的抗性[78]。诱导系统抗性通常伴随着多条植物防御信号通路的激活，其中水杨酸和茉莉酸通路在抗细菌性病害中发挥核心作用。Riera 等[17]发现根际细菌北澳伯克霍尔德氏菌(*Burkholderia territorii*) A63、金属伯克霍尔德氏菌(*Burkholderia metallica*) A53 及膝形假单胞菌(*Pseudomonas geniculata*) 95 可通过激活水杨酸信号通路，诱导水杨酸羧甲基转移酶、苯丙氨酸脱氨酶编码基因的表达，增强柑橘对 Xcc 的抗性。通过该机制产生的防控效果、诱导强度和持续性受微生物定殖水平、施用时期以及环境条件等多因素的影响。

2.4 干扰病原菌群体感应与毒力调控

群体感应(quorum sensing, QS)是细菌通过分泌并感知可扩散信号因子(diffusible signal factor, DSF)、*N*-酰基高丝氨酸内酯类信号分子(*N*-acyl homoserine lactones, AHLs)等信号分子来调节毒力因子表达、细胞运动、生物膜形成、胞外多糖合成及协同侵染行为和协调群体行为的调控机制[79]。该机制不以减少病原菌数量为核心，而是通过干扰病原菌的通讯机制，使 Xcc 在寄主表面或组织内处于“低毒力、低侵染效率”的状态，体现了生防微生物的系统调控作用。这一方向的关键在于从杀灭病原菌转向削弱病原菌致病力，因此 Xcc 的 DSF 信号系统、致病因子调控基因簇(regulation of pathogenicity factors, rpf)调控网络，以及生物膜形成、胞外多糖产生、运动性和毒力基因表达等，成为机制解析的重要切入点。在 Xcc 中，由 *rpf* 基因簇调控合成的信号因子 DSF 是核心群体感应信号分子[80-81]。生防微生物可通过抑制信号分子合成、降解或修饰信号分子、阻止信号分子与受体蛋白结合等多种作用方式干扰 Xcc 的群体感应系统，即群体感应淬灭。贪铜菌属(*Cupriavidus* sp.) HN-2 分泌的内酯酶可水解 AHLs 信号分子的内酯键，降低病原菌信号分子在微环境中的有效浓度并使其失活[82]；部分假单胞菌[如 *Pseudomonas* sp. SJ02、嗜昆虫假单胞菌(*Pseudomonas entomophila*)等]能够降解 DSF 信号分子或干扰其传导路径，进而抑制 Xcc 的毒力基因表达[83-84]。从防控策略角度看，群体感应干扰代表了一种“去毒力化”调控路径，可抑制病斑扩散，同时降低病原菌因快速进化而产生抗性的风险，提升病害防控的稳定性。

从柑橘溃疡病发生过程来看，上述机制分别作用于 Xcc 侵染循环的不同环节。抑菌活性物质主要降低病原菌存活和增殖能力；营养与生态位竞争限制其在叶面、伤口等关键位点的初始定殖；诱导寄主系统抗性，增强其抗病能力；群体感应干扰则削弱 Xcc 的毒力表达和侵

染效率。因此，生防微生物对柑橘溃疡病的防控并非单一抑菌过程，而是由病原菌抑制、定殖阻断、寄主防御激活和毒力削弱等多环节共同实现(图 1)。然而，这些作用如何在复杂田间环境中稳定表达，并最终转化为可推广的防控效果，仍有赖于菌剂设计与应用技术的优化。

3 柑橘溃疡病生防菌剂的应用现状与发展趋势

3.1 生防菌剂的应用现状

目前已报道的柑橘溃疡病生防菌剂主要包括单菌剂、复合菌剂以及生防微生物与化学或天然活性物质联合构建的复配制剂等类型。单菌剂是目前研究与应用最广泛的类型，主要以芽孢杆菌(*Bacillus*)、类芽孢杆菌(*Paenibacillus*)、假单胞菌(*Pseudomonas*)及放线菌等为代表。其中，枯草芽孢杆菌(*Bacillus subtilis*)、解淀粉芽孢杆菌(*Bacillus amyloliquefaciens*)和贝莱斯芽孢杆菌(*Bacillus velezensis*)等芽孢杆菌具有较强环境适应性、芽孢形成能力及多种抗菌活性物质合成能力，在柑橘溃疡病防控中研究最多。这类菌株能够产生伊枯草菌素(iturin)、丰原素(fengycin)和表面活性素(surfactin)等脂肽类物质，对 Xcc 具有显著抑制作用，同时兼具一定诱导植物抗性和叶际定殖能力[37,44-45]。此外，部分类芽孢杆菌属(*Paenibacillus*)、假单胞菌属(*Pseudomonas*)和链霉菌属(*Streptomyces*)菌株也表现出良好的防控潜力[28,85-86] (表 2)。

柑橘溃疡病的发生主要集中于叶际环境，具有开放性强、波动剧烈等特点，生防菌不仅需要快速定殖，还需具备持续抑菌能力以及一定的环境耐受性，单一生防菌很难达到预期效果。近年来，复合菌剂逐渐受到重视。与单菌剂相比，复合菌剂通过整合不同功能菌株实现协同防控。例如，将具有快速定殖能力的菌株与高抑菌活性菌株进行组合，可同时实现生态位竞争与持续抑菌作用；芽孢杆菌与木霉(*Trichoderma*)等真菌复配可兼顾病原抑制和植物健康促进功能[87]。一些产品已开始采用“细菌+真菌”或“多菌种协同”的组合模式，如 *Bacillus subtilis* 与哈茨木霉(*Trichoderma harzianum*)复配菌剂[88]，以及多黏类芽孢杆菌(*Paenibacillus polymyxa*)与其他促生菌联合体系等[89]。

除复合菌剂外，生防微生物与低剂量铜制剂、植物源活性物质或有机载体联合构建的复配制剂也受到关注。这类体系旨在降低传统化学药剂使用量，同时提高防效稳定性。研究表明，芽孢杆菌与铜制剂联合使用后可在减少铜剂施用量的同时维持较高防效，从而降低环境风险[90]；利用海藻酸钠、多糖类物质或有机肥载体对生防菌进行包埋和缓释处理可提高菌剂田间稳定性[88-89,99]。从应用转化角度看，病害绿色防控材料的开发并不局限于生防微生物本身，柑橘果皮黄酮提取物对多种植物病原真菌具有显著抑制作用，其中多甲氧基黄酮是主要活性成分，表明从天然活性物质中筛选抑菌成分作为绿色防控材料同样具有重要意义[100]，也提示生防微生物菌剂与植物活性成分协同应用具有进一步开发潜力。因此，柑橘溃疡病生防菌剂的发展趋势已由“单一菌株应用”逐步向“复合体系构建”转变。目前针对柑橘溃疡病的商品化菌剂相对有限，现有产品多以广谱芽孢杆菌类生防菌为核心，主要作为化学防治的辅助措施。

3.2 生防菌剂的发展趋势

当前柑橘溃疡病生防菌剂应用仍面临从室内效果向田间稳定防效转化不足的问题。其原因主要包括：叶际环境开放，紫外辐射、降雨冲刷及温湿度波动容易影响生防菌存活和定殖；室内抑菌效果与田间防效之间存在差距，单一菌株难以同时完成快速定殖、持续抑菌、诱导抗性和环境适应等多种功能；现有菌剂在剂型稳定性、施用时期、施用浓度以及与铜制剂等常规措施的配套应用方面仍不成熟。结合柑橘溃疡病的发生特点及叶际生态环境特征，后续研究可重点关注 4 方面。(1)在资源挖掘层面，

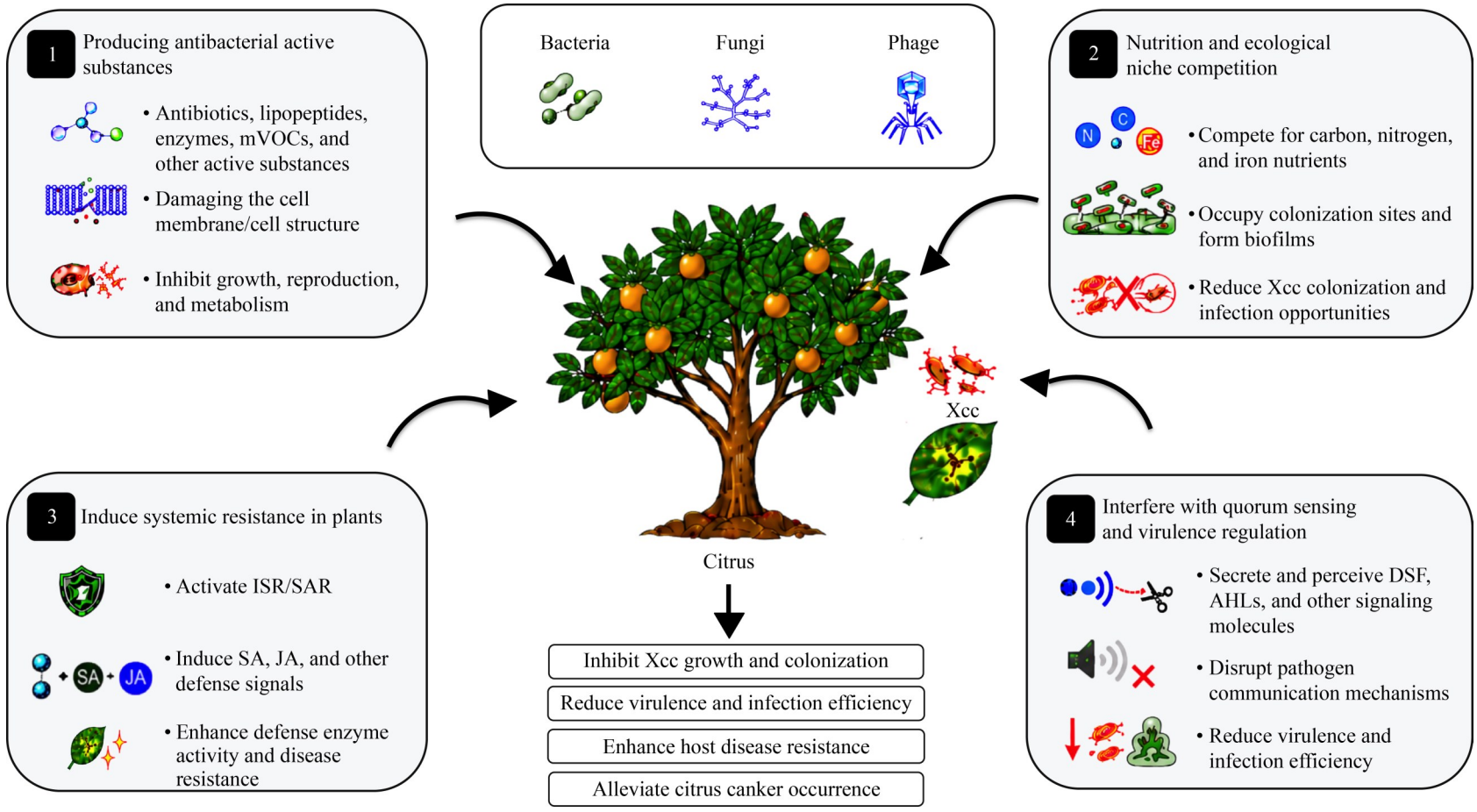


图1　柑橘溃疡病生防微生物的主要作用机制示意图

Figure 1　Schematic diagram of the main mechanisms of biocontrol microorganisms against citrus canker.

表2 柑橘溃疡病的生防菌剂

Table 2 Biological control agents for citrus canker

No.	Microbial agent type	Strains and other components used	Target diseases and pests	Publication date	References
1	Compound microbial agent	*Bacillus pumilus*, *Trichoderma viride*	Citrus canker, citrus root-knot nematode	2025-05-27	[87]
2	Compound microbial agent	*Bacillus subtilis*, *Trichoderma harzianum*, and organic fertilizer carrier	Citrus canker	2019-11-15	[88]
3	Compound microbial agent	*Beauveria bassiana*, *Paenibacillus polymyxa*, fermented citrus peel and aged tangerine peel products, sodium alginate, polyvinyl alcohol	Citrus canker	2025-04-29	[89]
4	Compound microbial agent	*Bacillus subtilis*, copper-based formulation	Citrus canker	2019-09-27	[90]
5	Single-strain agent	*Desmospora profundinema* GS1	Citrus canker, peach crown gall, tobacco bacterial wilt, rice bacterial blight, pear fire blight, bacterial fruit blotch of cucurbits, soft rot of Chinese cabbage	2025-05-13	[91]
6	Single-strain agent	*Bacillus subtilis*	Citrus canker	2025-01-28	[92]
7	Compound microbial agent	*Bacillus mucilaginosus*, *Bacillus subtilis*	Citrus canker, citrus green mold, citrus Huanglongbing, citrus root-knot nematode	2024-02-09	[93]
8	Compound microbial agent	*Amycolatopsis* sp., *Bacillus velezensis*, *Penicillium oxalicum*, *Lactiplantibacillus plantarum*	Citrus canker	2023-11-03	[94]
9	Compound microbial agent	*Trichoderma harzianum*, pesticides, and chemical fertilizers	Citrus canker	2022-10-11	[95]
10	Compound microbial agent	*Burkholderia* sp., *Bacillus pumilus*	Citrus canker, wax gourd wilt, cucumber damping-off, or tomato bacterial wilt	2022-07-01	[96]
11	Single-strain agent	*Paenibacillus polymyxa*	Citrus canker	2022-01-18	[97]
12	Single-strain agent	*Paenibacillus polymyxa*	Citrus canker	2021-08-31	[98]

注重从柑橘叶际、内生及根际等关键生态位中筛选兼具定殖能力与多功能特性的优势菌株，并结合高通量测序与功能验证手段，解析其在天然微生物群落中的生态位及互作关系，为功能菌群构建提供基础。(2)在机制研究层面，应加强对多种作用机制协同关系的解析，明确直接抑菌、生态位占据和诱导抗性等作用在病害防控过程中的协同效果。叶际定殖能力决定生防菌能否在病原菌侵染位点稳定存在，抑菌活性影响其对 Xcc 的直接抑制效果，诱导抗性则关系到植株整体防御水平。这些功能模块的分工与协同，将为合成菌群(synthetic microbial community, SynCom)的合理设计提供依据。(3)在菌剂开发与应用层面，应加强剂型优化与施用技术研究，例如通过包埋、缓释或添加保护剂等方式提高生防菌在叶面环境中的存活率和持效性，同时系统评估其与低剂量铜制剂或其他绿色防控措施的协同效果，构建更加稳定和可操作的综合防控体系。(4)在评价体系方面，应建立从体外筛选、温室验证到田间试验的分

级评价体系，特别是加强多区域、多年份条件下的田间验证，以提高不同研究结果之间的可比性和应用指导价值。

近年来，SynCom 在植物病害生物防控中受到关注。虽然目前直接针对柑橘溃疡病的 SynCom 研究仍较少，但柑橘其他病害研究已提供了一定参考。例如，*Trichoderma* 与 *Bacillus* 组成的跨界合成菌群可通过调控根际微生物组、抑制病原真菌并激活植物防御反应，缓解柑橘黄龙病与根腐病复合危害[101]；柑橘溃疡病相关研究也发现，抗病材料中富集的溶杆菌属(*Lysobacter*)具有潜在生防作用[102]。在上述基础上，基于功能互补构建 SynCom 有望成为提升柑橘溃疡病生物防控稳定性的关键路径。通过整合具有定殖优势、抑菌活性及诱抗能力的不同功能菌株可构建如下功能组合模式：(1)定殖优势菌株，主要来源于叶际或内生环境，具备较强的表面附着能力和生物膜形成能力，用于快速占据叶面生态位，阻止病原菌初始定殖；(2)高效抑菌菌株，以芽孢杆菌、放线菌等为代表，能够产生脂肽类抗菌物质或其他次级代谢产物，直接抑制 Xcc 的生长；(3)诱导抗性菌株，多来源于根际或内生微生物，通过激活植物防御信号通路(如水杨酸或茉莉酸途径)增强植株整体抗病能力。在实际应用中，上述功能菌株可根据具体需求进行组合，并通过优化剂型(如包埋、缓释等)及施用方式(如叶面喷施与根际处理结合)，构建“地上-地下协同”的防控体系。

总之，柑橘溃疡病生物防治的发展，应从单一生防微生物的应用转向多功能合成菌群的应用。后续研究不仅关注菌株在室内是否具有较强抑菌活性，还应综合考虑其叶际或根际定殖能力、抑菌物质产生能力、诱导抗性效果、环境适应性、剂型稳定性及与现有防控措施的兼容性。通过资源挖掘、机制解析、菌剂开发及田间应用之间的紧密衔接推动生防微生物由实验研究向应用转化，为柑橘产业绿色可持续发展提供重要支撑。

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