

柑橘黄龙病与柑橘木虱发生危害与 防控技术研究七十年进展*

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摘 要 柑橘黄龙病 (Citrus huanglongbing) 是世界柑橘生产中最具毁灭性的病害, 其病原为韧皮部杆菌, 其中亚洲种 (*Candidatus Liberibacter asiaticus*, CLas) 分布最广、危害最为严重。该病主要通过媒介昆虫柑橘木虱 *Diaphorina citri* 传播, 目前已在我国 12 个省份发生, 并呈现北扩趋势, 防控形势严峻。本文系统综述了柑橘黄龙病的病害特征、发病机制、流行规律, 以及媒介昆虫柑橘木虱的生物学特性与传毒机制; 进而从物理、化学、生物及生物技术等多个维度, 全面剖析了针对黄龙病病原和媒介昆虫柑橘木虱的各类防控策略的效果与局限性。此外, 结合当前研究现状, 对未来柑橘木虱与柑橘黄龙病的研究方向进行了展望, 旨在为柑橘黄龙病的有效防控提供理论依据和技术参考, 保障柑橘产业的健康发展。

关键词 柑橘木虱; 柑橘黄龙病; 亮腹釉小蜂; 昆虫病原真菌; 理化诱杀; 绿色防控技术

Advances in research on the occurrence, damage and control of the citrus huanglongbing pathogen and the Asian citrus psyllid over the past 70 years

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Abstract The citrus huanglongbing (HLB) pathogen is one of the most devastating diseases affecting global citrus production, and poses a serious threat to the sustainable development of the citrus industry worldwide. The Asian citrus psyllid (*Diaphorina citri*), the primary vector of HLB, plays a critical role in the spread of the disease. This paper elaborates on the pathogenic understanding of HLB, including its history, symptoms, and damage, and delves into the biological characteristics, behavioral patterns, and damage mechanisms of the Asian citrus psyllid. It also reviews integrated management strategies for this pest, including physical, chemical, and biological control methods, providing a comprehensive analysis of HLB control strategies. Furthermore, areas for future research on the Asian citrus psyllid and HLB are proposed.

Key words *Diaphorina citri*; huanglongbing; *Tamarixia radiata*; entomopathogenic fungi; physicochemical trapping; green prevention and control

柑橘黄龙病 (Citrus huanglongbing, HLB) 是当前全球范围内柑橘产业面临的最具毁灭性的病害, 对世界各地的柑橘生产造成了持续且严

重的威胁 (Bové, 2006)。该病害主要通过专性媒介昆虫——柑橘木虱 *Diaphorina citri* (又称亚洲柑橘木虱) 进行传播。柑橘木虱的传播是导致

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HLB 在果园中扩散、造成树体系统性感染（表现为叶片黄化、果实畸形、树势衰退直至整体枯死）和巨额经济损失的首要原因（Bové, 2006; Zheng *et al.*, 2018）。

柑橘是我国重要的经济作物，2024 年全国种植面积超过 300 万 hm^2 ，产量超过 6 000 万吨，稳居世界第一位（Zhou, 2020; Pérez-Hedo *et al.*, 2025）。近年来，受气候变化、种苗调运及农业生态系统变动等多重因素影响，柑橘黄龙病疫情在我国呈现显著北扩和内迁趋势，传统防治手段如化学农药喷洒不仅面临效果递减、抗性加剧的

困境，也带来环境残留和非靶标伤害等次生问题。在此背景下，深入理解柑橘木虱的生物学特性、病原-媒介-寄主互作机制，并发展多策略融合的绿色综合治理体系，已成为当前研究的重点。本文系统梳理了柑橘黄龙病发生与传播的关键环节，概括了包括物理防治、生物防治、化学防治以及新兴生物技术在内的柑橘黄龙病与柑橘木虱的多种防控策略（表 1），客观评价了各项技术的应用潜力与局限，并对未来研究方向做出展望，旨在为我国柑橘黄龙病和柑橘木虱的可持续治理提供系统参考和思路借鉴。

表 1 柑橘黄龙病及柑橘木虱的防治策略
Table 1 Control strategies of citrus huanglongbing and *Diaphorina citri*

防治对象 Control target	防治策略 Control strategy		防治效果 Control effect	参考文献 Reference
柑橘黄龙病 Citrus huanglongbing (HLB)	高温热处理 Heat treatment		显著抑制 CLas 含量，但存在复发现象 Heat treatment significantly suppresses the CLas titer, but relapse can occur	林孔湘和郑儒钰， 1964; Hoffman <i>et al.</i> , 2013; 张建桃等, 2019
	抗生素 Antibiotics	氨苄西林、苄青霉 素钠 Ampicillin sodium, carbenicillin disodium	抑制 CLas，嫁接传毒率为 16.9%±16.2% Antibiotics exhibits inhibitory activity against CLas, with a graft transmission rate of 16.9%±16.2%	Zhang <i>et al.</i> , 2014
	小分子药物 Small molecule drug	化合物 P684-2850 Compounds P684-2850	抑制率为 99.6% Compound P684-2850 exhibited 99.6% inhibition of CLas	Zhang <i>et al.</i> , 2021b
		布罗波尔 Bronopol	靶向抑制 IMPDH，干扰 CLas 的增殖，抑 制常数（K _i ）为 234 nmol/L Bronopol inhibits CLas proliferation by targeting IMPDH, with an inhibition constant (K _i) of 234 nmol/L	Nan <i>et al.</i> , 2020
		抗菌肽 SAMP Antimicrobial peptide SAMP	CLas 显著减少，病株长势恢复，新叶无黄 龙病症状 Treatment with the antimicrobial peptide SAMP resulted in a significant reduction in CLas titer, concurrently restoring plant growth and resulting in new leaves that were asymptomatic for huanglongbing	Huang <i>et al.</i> , 2021
		小肽 APP3-14 Peptide APP3-14	田间试验单季防控效率达 80% In field trials, the peptide APP3-14 exhibited a control efficacy of 80% per season	Zhao <i>et al.</i> , 2025
	免疫诱导剂 Immune inducers	油菜素内酯 Brassinosteroids	1 年降低病菌含量约 98.62% Treatment with brassinosteroids resulted in a reduction of approximately 98.62% in CLas titer within one year	Canales <i>et al.</i> , 2016
		赤霉素 Gibberellins	缓解黄龙病症状 Gibberellins treatment alleviates the symptoms of huanglongbing	Ma <i>et al.</i> , 2022

续表 1 (Table 1 continued)

防治对象 Control target	防治策略 Control strategy		防治效果 Control effect	参考文献 Reference
柑橘黄龙病 Citrus huanglongbing (HLB)	抗性苗木育种 Resistant scion breeding	杂交育种、基因工 程改造 Hybridization breeding, genetic engineering	-	Deng <i>et al.</i> , 2019; Ma <i>et al.</i> , 2022
柑橘木虱 <i>Diaphorina citri</i>	植物检疫 Plant quarantine		-	-
	农业防治 Cultural control	科学规划种植 Scientific planting planning	-	-
		合理控梢 Proper shoot management	-	-
	生物防治 Biological control	亮腹釉小蜂 <i>Tamarixia radiata</i>	单头可杀死超 500 头柑橘木虱, 防治率达 95% A single <i>Tamarixia radiata</i> individual is capable of eliminating more than 500 <i>Diaphorina citri</i> nymphs, with a control rate reaching 95%	Michaud, 2004
		球孢白僵菌 <i>Beauveria bassiana</i>	LT ₅₀ 为 4.4-5.2 d The median lethal time (LT ₅₀) of <i>Beauveria bassiana</i> against <i>Diaphorina citri</i> was 4.4-5.2 d	代晓彦等, 2014
		粘质沙雷氏菌 <i>Serratia marcescens</i>	对于柑橘木虱致死率达 80%以上 <i>Serratia marcescens</i> induced mortality in over 80% of treated <i>Diaphorina citri</i>	Hu <i>et al.</i> , 2024
	物理防治 Physical control	灯光诱捕 Light trapping 色板诱捕 Colored sticky card trapping	-	桑文等, 2018
	化学防治 Chemical control	啉虫脒 Acetamiprid	48 h 致死率可达 100% Treatment with acetamiprid resulted in 100% mortality of <i>Diaphorina citri</i> within 48 h	王吉锋等, 2019
		螺虫乙酯 Spirotetramat	有效抑制若虫发育 Spirotetramat effectively inhibits the development of <i>Diaphorina citri</i> nymphs	Demard and Diepenbrock, 2025
	RNA 干扰 RNA interference	蜕皮激素基因 Ecdysone-related genes	干扰后, 第 7 天若虫死亡率达 75%, 若虫 羽化率降低 1 倍, 同时增加对噻虫嗪和氯 氰菊酯的敏感性 Silencing ecdysone-related genes via RNAi led to 75% mortality of <i>Diaphorina citri</i> nymphs and a two-fold decrease in emergence rate by day 7; it also enhanced the susceptibility of the psyllids to thiamethoxam and cypermethrin	Zhang <i>et al.</i> , 2023a
	海藻糖酶基因 Trehalase gene	干扰后, 48 h 若虫最高死亡率达 60%, 羽 化后畸形率 20%-30% Silencing the trehalase gene via RNAi resulted in a peak nymphal mortality of 60% within 48 h, and a malformation rate of 20%-30% in emerged adults	Yu <i>et al.</i> , 2021	

1 柑橘黄龙病

1.1 柑橘黄龙病的概述

柑橘黄龙病, 别名“黄梢病”、“青果病”, 是一种由韧皮部杆菌属细菌引起的病害, 根据韧皮部杆菌病原的地理分布、热敏感性不同, 可以将黄龙病病菌分为 3 种: 美洲种 (*Candidatus Liberibacter americanus*, CLam)、亚洲种 (*Candidatus Liberibacter asiaticus*, CLas) 和非洲种 (*Candidatus Liberibacter africanus*, CLaf) (Villeanoux *et al.*, 1993; Jagoueix *et al.*, 1994; Planet *et al.*, 1995; Garnier *et al.*, 2000; do Carmo Teixeira *et al.*, 2005), 其中由 CLas 所引起的病害在全球柑橘产业中造成的损失尤为严重 (Bové, 2006)。

我国最早于台湾地区及广州潮汕地区发现柑橘黄龙病 (Reinking, 1919; Zhou, 2020), 感病的枝条、叶片黄化而不转绿, 故被称为“黄龙病”。1995 年, 在第 13 届国际柑橘病毒病学家会议中, 该病害被正式命名为“柑橘黄龙病” (Bové, 2006)。自 2020 年起, 柑橘黄龙病被列入我国一类农作物病虫害名录。

在病害研究的早期阶段, 黄龙病曾被视为一种生理性病害。1956 年, 林孔湘 (1956) 通过嫁接试验证实其传染性, 推测病原为病毒。随后, 因四环素类抗生素可抑制病害症状, 该病原被归类为类菌原体 (*Mycoplasma-like organism*, MLO) (陈作义等, 1979)。1979 年, 利用电子显微镜观察发现病原菌具有厚度不均的单位膜, 被认为符合类立克次体 (*Rickettsia-like organism*, RLO) 的特征 (柯冲等, 1979)。直到 1991 年, 研究进一步揭示该病原体具有肽聚糖层结构, 最终确认其为革兰氏阴性细菌 (柯冲等, 1991)。

1.2 柑橘黄龙病的危害与流行

柑橘黄龙病感染植株后表现出多种典型症状, 主要包括: 斑驳型黄化, 其叶片黄化区域通常界限不清晰, 多自叶片基部或边缘开始, 逐渐向叶尖或中部扩展; “红鼻子”果, 即果实显著变小、畸形、不对称, 成熟时果皮着色不均, 果肉味苦、品质劣变; 树势衰退, 表现为植株生长

迟缓、树冠稀疏, 并伴随缺锌症状、枯枝和落叶等现象 (Bové, 2006; Zheng *et al.*, 2018)。

目前, 柑橘黄龙病已在亚洲、非洲、南美洲、北美洲及欧洲等多个地区暴发, 对全球柑橘产业造成严重威胁, 每年造成数百亿美元的经济损失, 严重影响柑橘产业的健康可持续发展 (Pérez-Hedo *et al.*, 2025)。由于亚洲种 (CLas) 具有较强的耐热性和传播能力, 已从亚洲扩散至美洲及非洲部分地区, 成为优势致病种; 非洲种 (CLaf) 主要分布于撒哈拉以南非洲和部分印度洋岛屿; 而美洲种 (CLam) 正逐渐被 CLas 所取代 (da Graça *et al.*, 2022; Gasparoto *et al.*, 2022)。

在我国, 柑橘黄龙病呈现向北、向内陆蔓延的趋势, 已蔓延至广东、广西、台湾、福建、浙江、江西、湖南、云南、贵州、海南、四川、江苏 12 个省 (自治区) (江宏燕等, 2018; Zhou, 2020)。2013 年江西赣州暴发黄龙病, 导致约 5 000 万株柑橘树因病被清除, 造成重大经济损失。近年来, 随着媒介昆虫柑橘木虱持续向北扩散 (张阳等, 2021; 文刚等, 2024), 长江中上游柑橘主产区面临黄龙病入侵的风险显著增加, 而江苏南部等长江下游新阻截前沿区的设立, 进一步凸显了黄龙病北扩态势的严峻性, 对我国柑橘产业的可持续发展构成严重威胁。

1.3 柑橘黄龙病的防控

1.3.1 物理防控 柑橘黄龙病病菌对高温敏感, 因此在生产实践中常采用光照、湿热空气或红外辐照等方式对病苗进行脱毒处理。在 40-50 °C 条件下进行热处理可显著降低病苗中的病原菌载量, 同时提升其次生代谢物含量, 增强植株活力 (林孔湘和郑儒钰, 1964; Hoffman *et al.*, 2013; 黄秀等, 2021; 张建桃等, 2019)。然而, 受设备限制, 高温处理尚未能大规模应用于田间病株脱毒, 目前多与茎尖嫁接技术结合, 用于无毒苗木的培育。

除培育无毒苗木外, 及时清除病树也被证实可有效延缓病害扩散。林孔湘 (1956) 在广东开展的试验表明, 清除病树的果园 3 年后发病率为 31.9%, 而未清除病树的果园发病率高达 72.6%。类似地, 广东阳春柑橘产区通过严格执行病树移

除等综合防控措施, 将黄龙病发病率从 3.9%降至 0.3% (Zheng *et al.*, 2018)。广西当前正大力推行以“彻底清除病树”与“木虱统防统治”为核心的防控策略, 结合柑橘黄龙病科普宣传、病树清理/病虫统防统治补贴等工作, 保障广西沃柑产区高质量发展 (钱开胜, 2024)。福建永春通过建立无病毒容器育苗中心, 良种率达 98%以上, 同时结合防护网生态隔离、全国快速灭杀木虱等措施, 打造的“永春模式”被列为柑橘黄龙病防控主推技术, 在全国范围推广宣传 (尤有利和潘慧明, 2025)。

1.3.2 抗生素防治 抗生素处理被证实可一定程度上缓解黄龙病症状。早在 20 世纪 70 年代, 我国科学家便发现四环素、土霉素和青霉素处理可以抑制黄龙病的症状, 但四环素仅能暂时抑制症状, 无法彻底清除病原 (广西柑桔黄龙病研究小组, 1975)。随着研究深入, 更多高效抗生素被筛选出来, 如氨苄西林、苄青霉素钠和头孢氨苄等。其中, 氨苄西林可通过诱导热休克蛋白 (Heat shock proteins, HSPs) 表达、激活防御基因以增强寄主免疫力, 并调节内生菌群落结构, 提高放线菌门等有益菌群的丰度 (Yang *et al.*, 2022a)。美国已批准使用土霉素和链霉素防控黄龙病, 但出于抗生素残留、环境污染及抗药性等考虑, 在我国尚未批准抗生素用于柑橘黄龙病防治。研究表明, 随着青霉素处理含量的升高, 柑橘叶片中的 CLas 含量逐渐降低, 但是长期使用会破坏病树的根际细菌群落结构, 降低解磷细菌等有益菌的丰度 (黄洋等, 2021)。

1.3.3 纳米制剂 纳米材料凭借其独特的物理化学性质, 在柑橘黄龙病防控中展现出应用潜力。喷施纳米银制剂可破坏病原菌细胞膜完整性, 导致胞内物质外泄, 从而改善病株生理状态, 提高叶绿素含量与坐果率, 抑制 CLas 繁殖 (Umair Raza *et al.*, 2023)。纳米锌制剂与水杨酸、过氧化物或 2S 白蛋白联用也可显著降低 CLas 含量 (Ghosh *et al.*, 2018; Mendis *et al.*, 2019; Naranjo *et al.*, 2020)。

尽管纳米材料在柑橘黄龙病防治中展现出良好的应用潜力, 但其田间应用的稳定性、安全性及递送系统仍需进一步优化, 以确保在有效抑

制 CLas 的同时, 最大限度降低对非靶标生物及环境的潜在影响。

1.3.4 小分子药物 小分子药物防治策略基于病原基因组靶点筛选, 通过特异性结合致病关键位点, 精准抑制 CLas 而不影响非靶标生物, 为开发绿色农药提供了新途径。

在转运系统抑制剂方面, 转位酶 SecA 作为细菌特有的分泌系统组分, 常被作为药物筛选的特异性靶点 (Akula *et al.*, 2011)。化合物 P684-2850 和 P684-3808 可与 CLas 的 SecA 蛋白形成稳定氢键, 阻碍其与 ATP 结合, 从而抑制 CLas 生长 (Zhang *et al.*, 2021b)。CLas 的 ZnuABC 基因编码锌转运系统, 负责吸收外界 Zn^{2+} 以满足自身代谢需求 (Duan *et al.*, 2009), 小分子化合物如 ZINC15670529 可通过与 ZnuA1 活性位点残基形成氢键, 阻断 Zn^{2+} 的吸收 (Saini *et al.*, 2021)。

鸟嘌呤核苷酸合成是病菌存活的核心过程, 其中肌苷-5'-单磷酸脱氢酶 (Inosine-5'-monophosphate dehydrogenase, IMPDH) 负责将肌苷-5'-单磷酸氧化为 5'-单磷酸黄嘌呤 (Xanthosine 5'-monophosphate, XMP), 而鸟苷-5'-单磷酸合成酶 (Guanosine-5'-monophosphate synthase, GMPS) 进一步将 XMP 转化为鸟苷-5'-单磷酸 (Guanosine-5'-monophosphate, GMP) (Goncheva *et al.*, 2022), 布罗波尔、双硫仑、叶酸及 AZD1152 等小分子化合物可分别通过抑制 IMPDH 和 GMPS 活性, 阻碍 CLas 存活 (Nan *et al.*, 2020, 2021)。

此外, 根皮素、苯溴马隆、己烷雌酚可以与 CLas 细胞渗透压相关蛋白 LdtR 形成复合物, 抑制细菌细胞壁的合成 (Pagliai *et al.*, 2014)。抗菌肽 (Antimicrobial peptides, AMPs) 作为一类广泛存在于自然界的小肽, 可通过作用于细胞膜/壁、抑制肽聚糖合成或形成孔隙以杀灭病原 (Zhang *et al.*, 2021a)。有研究表明 MaSAMP、D4E1、Plantaricin JLA-9、Darobactin 以及 Urechistachykinin II 等抗菌肽对 CLas 均具有抑制潜力 (Stover *et al.*, 2013; Huang *et al.*, 2021; Wang *et al.*, 2022)。借助人工智能辅助筛选, Zhao (2025) 利用人类肠道菌小肽数据库筛选出

抗蛋白水解肽 APP3-14, 该肽可通过抑制柑橘体内 MYC2 蛋白的泛素化降解以杀灭 CLas。

小分子药物通过精准靶向 CLas 的关键代谢通路与功能蛋白, 实现对病菌的特异性抑制, 为黄龙病绿色防控提供了全新思路。同时, 抗菌肽作为天然小分子活性物质, 通过破坏病菌细胞膜结构发挥杀菌作用, 进一步丰富了靶向防控的技术体系。未来需进一步优化小分子药物的田间稳定性与递送效率, 推动其从实验室研究走向实际应用, 以充分发挥其精准防控的潜力。

1.3.5 免疫诱导剂 免疫诱导剂可通过激活柑橘自身免疫系统或调节防御信号通路, 增强对 CLas 的耐受力。水杨酸作为一种植物激素, 在提高植物抗逆性和免疫防御能力等方面发挥重要作用。研究表明, 在耐病柑橘品种中水杨酸含量显著高于感病品种 (Zou *et al.*, 2019), 提高水杨酸含量能激活柑橘防御酶系统, 显著降低 CLas 滴度 (Soares *et al.*, 2022)。然而 CLas 可通过表达水杨酸羟化酶降解水杨酸, 从而抑制植株防御反应 (Stansly *et al.*, 2014; Nehela and Killiny, 2020)。因此, 开发其他免疫诱导剂有助于更好地诱导柑橘植株获取抗黄龙病的系统抗性。喷施油菜素内酯可诱导超氧化物歧化酶、谷胱甘肽过氧化物酶等相关防御基因表达, 增强抗病性并抑制 CLas 增殖 (Canales *et al.*, 2016)。使用赤霉素则通过抑制植株体内活性氧积累缓解柑橘黄龙病的症状 (Ma *et al.*, 2022)。

1.3.6 抗性育种 抗性育种通过筛选天然耐病种质、杂交育种及基因工程手段改良柑橘品种的抗性, 是黄龙病可持续防控的重要策略。在天然耐病资源筛选方面, 多种柑橘近缘种和品种表现出对黄龙病的较强耐病性, 如澳洲指橙 *Microcitrus australasica*、十里香 *Murraya paniculata* 等。澳洲指橙具有多个显著抗菌特性的潜在抗菌肽和特定的氧化还原控制系统, 在感染黄龙病后, 体内抗菌肽表达上调, 氧化还原调控系统及 PR1 蛋白等防御反应增强 (Alves *et al.*, 2022; Weber *et al.*, 2022; Younas *et al.*, 2025), 使其对黄龙病具有高度抗性。橘枳杂交种 US-897 在感染黄龙病后无明显症状, 淀粉和胼胝质堆积减少, 植株防御反应增强 (Deng *et al.*, 2019)。通过过表达

免疫调控基因或抗菌肽基因等转基因手段, 可增强植株抗病性, 加速抗性品种培育。在柑橘中过表达拟南芥 *NPR1* 基因, 可抑制 CLas 诱导的过度免疫反应, 减轻愈伤组织和活性氧积累, 进而提高对 CLas 的抗性 (Peng *et al.*, 2021; Ma *et al.*, 2022)。过表达 *PUB21DN* 基因则可通过稳定 MYC2 蛋白激活茉莉酸途径, 进而帮助植株抵抗 CLas (Zhao *et al.*, 2025)。

尽管抗性育种仍面临周期长、基因调控复杂等挑战, 其环境友好性和持续效果使其成为黄龙病综合治理的核心方向。结合分子标记辅助选择与多组学技术, 有望加速抗病基因挖掘与品种选育进程。

2 柑橘木虱

2.1 柑橘木虱的生物学特性及形态特征

柑橘木虱寄主范围广泛, 主要危害芸香科植物, 如九里香和柑橘等 (Westbrook *et al.*, 2011; 任素丽等, 2018b)。其最适生长温度为 25-28 °C, 雌虫交配后 1 d 即可开始产卵, 单雌产卵量最高可达 800 粒, 在南方地区每年可发生 11-14 代, 世代重叠现象显著 (Wenninger and Hall, 2007)。柑橘木虱属不完全变态昆虫, 在 25-30 °C 条件下, 完成整个生活史需 15-47 d, 包括卵期 (2-4 d)、1-5 龄若虫期 (11-15 d) 和成虫期 (Liu and Tsai, 2000; 任素丽, 2016)。

柑橘木虱卵呈椭圆状, 顶端尖细, 末端钝圆且具短柄, 多集中产于嫩芽、嫩叶及芽茎交界处; 1 龄若虫体呈扁椭圆形, 具红色复眼, 无翅芽; 2 龄若虫于胸部第 2 节出现翅芽; 3 龄若虫翅芽明显增大, 前缘伸至复眼后缘, 后缘达腹部第 3 节, 触角末端变黑; 4 龄若虫翅芽前缘超过复眼, 后缘超过腹部第 3 节, 前后翅错位明显; 5 龄若虫体色加深、体纹清晰, 触角除基节外均为黑色, 末端具 2 根刚毛; 成虫初羽化时为白色, 随后体色逐渐加深, 取食时虫体与叶面成 45°角 (阮传清等, 2012; 任素丽, 2016)。

柑橘木虱复眼发达, 视觉灵敏, 具有较强的趋光能力 (Mann *et al.*, 2011a), 尤其对蓝光 (460 nm)、绿光 (530 nm)、黄光 (580 nm) 具

有显著正趋性,而对于红光(690 nm)反应较弱(Wenninger *et al.*, 2009; Paris *et al.*, 2017; 王飞凤等, 2020; 丁鹏等, 2024),夜间因光照减弱,其活动频率显著低于白天(Wenninger and Hall, 2007)。柑橘木虱通常取食茎、叶、叶柄(许鑫等, 2018),但更偏好于嫩芽上取食并产卵,可能与嫩叶具有更高的营养物质含量以及柑橘木虱对于黄绿光的趋性有关(Wenninger *et al.*, 2009; Sétamou *et al.*, 2016; Cifuentes-Arenas *et al.*, 2018)。

2.2 柑橘木虱的发生及危害

柑橘木虱在我国最早于 1907 年在台湾地区被发现,随后相继于 1927 年和 1934 年在澳门和广东地区发现,并逐渐扩散至广西、福建、江西、云南、湖南及浙江等多个省(自治区),呈现向北和向内陆迁移的趋势,这一扩散路径与柑橘黄龙病的传播态势基本一致(王晓亮等, 2016)。柑橘木虱的扩散受温度、风力和海拔等多种环境因子的影响。研究表明,成虫短距离飞行能力约为 60 m,若借助风力等外界条件,12 d 内可扩散至 2 km 范围内(Lewis-Rosenblum *et al.*, 2015)。温度不仅显著影响其种群数量变动,还与成虫的飞行活动时间呈正相关关系(邝凡等, 2017; Martini *et al.*, 2018)。

柑橘木虱成虫和若虫通常在嫩芽部位刺吸汁液,导致新叶扭曲畸形。其取食易诱发煤污病,覆盖叶片表面,影响植株光合作用,抑制正常生长。更为严重的是,其作为柑橘黄龙病传播媒介的生态行为极大地加剧了危害程度。除嫁接传播病苗外,带菌柑橘木虱的迁移和取食是柑橘黄龙病在健康植株间传播的主要途径。柑橘木虱在取食感染植株获菌后,往往表现出对健康植株更强的趋性,这种行为特性是导致黄龙病在果园内迅速扩散的重要原因之一。

2.3 柑橘木虱的防控

2.3.1 植物检疫 植物检疫是防止柑橘木虱及其传播的柑橘黄龙病通过人为活动远距离扩散的重要防线和措施。由于其虫体小、隐蔽性强,尤其是卵和低龄若虫极易随带虫的苗木、接穗、果实及其他芸香科寄主植物的调运而传播,因

此,建立和严格执行严格的植物检疫制度至关重要。

2.3.2 农业防治 农业防治主要通过栽培与管理措施降低田间柑橘木虱虫口密度,主要包括:1、科学规划种植。柑橘果园周围避免零散种植芸香科植物,减少有利于柑橘木虱繁殖扩散的环境,果园间可通过种植防护林建立隔离带,阻断柑橘木虱在果园之间迁徙;2、田间管理。合理施肥,科学抹控夏梢、秋梢,减少虫口数量,冬季清园,减少越冬虫口密度。

2.3.3 生物防治 生物防治是利用天敌生物、微生物以及植物源产物等防治农业害虫的手段,具有环境友好、可持续等优点,是害虫可持续治理中最有效、应用前景最广的防治手段之一(代晓彦等, 2014)。

柑橘木虱的天敌包括捕食性天敌(如异色瓢虫 *Harmonia axyridis*、龟纹瓢虫 *Propylea japonica*、亚非草蛉 *Chrysopa boninensis*、黄猊蚁 *Oecophylla smaragdina* 和管蛛科蜘蛛 *Hibana velox*)及寄生性天敌(如亮腹釉小蜂 *Tamarixia radiata*、阿里食虱跳小蜂 *Diaphorencyrtus aligarhensis*) (Michaud, 2004; Navarrete *et al.*, 2013; 代晓彦等, 2014)。六斑月瓢虫 *Menochilus sexmaculata* 和龟纹瓢虫因对柑橘木虱成虫及若虫均有较强捕食能力,在我国应用广泛。亮腹釉小蜂主要寄生柑橘木虱的若虫阶段,田间释放可以显著压制柑橘木虱种群密度(Milosavljević *et al.*, 2021; Xu *et al.*, 2025)。

当无法大规模释放寄生蜂防治柑橘木虱的时候,昆虫病原真菌因其可大规模生产的特点,成为防治柑橘木虱的主要生物防治技术。目前,已被证实对柑橘木虱具有杀灭作用的昆虫病原真菌有球孢白僵菌 *Beauveria bassiana*、玫烟色棒束孢 *Isaria fumosorosea*、金龟子绿僵菌 *Metarhizium anisopliae* 和爪哇虫草 *Cordyceps javanica* 等(桑文等, 2018; Ou *et al.*, 2019; Xu *et al.*, 2025)。随着生物防治研究的深入,研究发现苏云金杆菌 *Bacillus thuringiensis* 除了防治鳞翅目害虫外,还可以杀灭柑橘木虱若虫(Dorta *et al.*, 2020);粘质沙雷氏菌 *Serratia marcescens* 可通过诱导活性氧介导的肠道细胞凋亡对柑橘

木虱具有较高的灭杀效果 (Hu *et al.*, 2024)。

利用植物源产物来防治柑橘木虱的研究很多,尤其是番石榴及其挥发物、菊科植物(薇甘菊 *Mikania micrantha*、假臭草 *Praxelis clematidea*)。目前,已发现多个番石榴品种对于柑橘木虱具有驱避作用,并利用网布覆盖证实其挥发物是驱避柑橘木虱的主要原因 (Zaka *et al.*, 2010)。将番石榴挥发物提取的 α -copaene、二甲基二硫醚制成诱剂后可以显著排斥亚洲柑橘木虱,并激活植物的防御反应 (Ling *et al.*, 2022)。岑伊静等 (2005) 发现,在薇甘菊、蜆蛄菊 *Wedelia chinensis*、假臭草 3 种菊科植物中,薇甘菊对于柑橘木虱的驱避作用最强,且不受柑橘木虱性别差异的影响。同时通过提取假臭草花的挥发物,发现其同样具有驱避作用,最高驱避率可达 100% (王奇志等, 2018)。最近研究发现,蜘蛛毒液中存在一种神经毒素 ω/κ -HxTx-Hv1h,通过雪花莲凝集素递送系统喷施后,可以显著提高柑橘木虱的死亡率且不会对雄蜂造成影响 (Miranda *et al.*, 2024),具有新型生物杀虫剂的开发潜力。

2.3.4 物理防治 物理防治作为柑橘木虱绿色防控体系的重要组成部分,通过隔离、拦截等非化学手段阻断其在田间的扩散与繁殖途径,有效降低种群密度和柑橘黄龙病传播风险。主要防治手段包括灯光诱捕、色板诱捕、反光膜驱避以及防虫网阻隔等 (桑文等, 2018)。利用柑橘木虱的趋光特性,田间应用蓝色和绿色的 LED 光源可显著提高柑橘木虱的诱集效果 (丁鹏等, 2024)。色板诱捕因成本低、操作简便而被广泛使用,利用昆虫对颜色的趋性使用不同色板诱捕可取得不错的防治效果。田间试验结果显示,黄板对柑橘木虱的诱杀效果优于其他颜色捕虫板,下午 12:00-16:00 为黄板诱捕柑橘木虱的最佳时间,且黄板悬挂高度为 150 cm、间距 4-5 m 可最大化提高诱捕效果 (Sétamou *et al.*, 2012, 2014; 赵政等, 2018)。防虫网可有效阻隔柑橘木虱及其他害虫(如蚜虫、潜叶蛾和粉虱)接触植株,选用透气透光的防虫网还能促进植株健康生长(张小凤等, 2017)。

2.3.5 化学防治 鉴于化学农药见效快,化学防治仍是当前防治柑橘木虱的主要手段,常用的化

学农药包括有机磷类、有机氯类、新烟碱类、拟除虫菊酯类、阿维菌素类、氨基甲酸酯类杀虫剂以及昆虫生长调节剂等 (Boina and Bloomquist, 2015; 付佩珊等, 2019)。研究表明,77.5%敌敌畏与 5%啉虫脒复配可以在 48 h 内实现 100%致死率 (王吉锋等, 2019); 22%高效氯氟·噻虫嗪、10%吡虫啉和 4.5%高效氯氰菊酯兼具杀灭效果和持效性 (宋晓兵等, 2015); 螺虫乙酯可有效抑制若虫发育,与吡丙醚复配可延长持效期 (Demard and Diepenbrock, 2025)。然而,化学农药的广泛使用易导致抗药性发展、环境污染及农产品安全等问题。常用于防治柑橘木虱的拟除虫菊酯类农药,对于传粉昆虫西方蜜蜂 *Apis mellifera* 具有一定的毒杀作用,急性触杀的 LD_{50} 为 0.022-0.051 $\mu\text{g}/\text{头}$,远低于高毒剂量的标准,此外化学农药的使用,会影响蜜蜂的学习、记忆和定位等行为 (Belzunces *et al.*, 2012; 刘琼琼, 2019)。王吉锋等 (2019) 通过测试 13 种常用的化学农药对于柑橘木虱的田间防治效果,发现田间柑橘木虱种群对于化学农药均已产生不同程度的抗性。化学农药的滥用会通过提高柑橘木虱农药作用靶点的突变频率,如钠离子通道 VGSC-L925M、乙酰胆碱酯酶 *AchE*-N88S、 γ -氨基丁酸受体 *GABAR*-A270V 等 (高一凡, 2024; Liu *et al.*, 2025),加速柑橘木虱抗药性的形成,不仅加大实际生产的防治难度和成本,更会陷入“滥用-突变-再滥用”的恶性循环。

2.3.6 生物技术防治——基于 RNA 干扰技术的核酸农药 RNA 干扰 (RNA interference, RNAi) 技术通过特异性沉默关键基因表达实现对靶标害虫的精准防控,具有高度物种特异性,对非靶标生物安全,是害虫综合管理的前沿策略。研究表明,喷施基于 RNAi 的核酸农药,例如,靶向 RR-2 亚家族的外壳蛋白 8、表皮蛋白以及己糖激酶的 RNAi 制剂,可破坏柑橘木虱几丁质合成,抑制若虫蜕皮,导致柑橘木虱死亡 (Yang *et al.*, 2022b; Lu *et al.*, 2024; Yuan *et al.*, 2025a)。营养代谢对于昆虫的生长发育具有重要的作用。研究表明,抑制海藻糖酶基因会导致柑橘木虱体内海藻糖积累和葡萄糖减少,抑制若虫蜕皮并导致成虫畸形及死亡率上升 (Yu *et al.*, 2021); 抑制糖

转运蛋白及蔗糖水解酶活性,会影响糖转运和渗透平衡过程,导致柑橘木虱腹部出现肿胀、死亡等表型 (Santos-Ortega and Killiny, 2018; Liu *et al.*, 2025)。

蜕皮激素对于柑橘木虱生长繁殖具有重要意义,通过 RNAi 的核酸农药,干扰蜕皮激素合成通路的 *Halloween* 基因表达,会降低蜕皮激素滴度,抑制卵巢发育,同时还会增加柑橘木虱对于噻虫嗪和氯氰菊酯的敏感性 (Zhang *et al.*, 2023a), 类似表型在干扰蜕皮激素受体及超气门蛋白基因中也被观察到 (Zhang *et al.*, 2023b), 说明蜕皮激素是调控柑橘木虱生长发育的重要基因,也是防治的关键靶点,可通过靶向干扰蜕皮激素通路防控柑橘木虱。此外,靶向液泡 ATP 酶,不仅可以导致柑橘木虱体重减轻、死亡,还会通过诱导中肠上皮细胞凋亡而抑制体内 CLas 的滴度 (Guo *et al.*, 2023)。

RNAi 技术通过干扰柑橘木虱的关键基因,展现出良好的防治效果。然而,制约 RNAi 在生产实践中应用的最重要的因素是 RNAi 的效率问题。因此,如何保证核酸农药的关键物质 dsRNA 在实践中稳定不被降解是目前仍需克服的一大问题。研究表明,利用层状双氢氧化物负载 dsRNA 喷施在叶片上,显著提高 dsRNA 附着叶片的稳定性以及 RNAi 效率 (Cheng *et al.*, 2024); 星形聚阳离子纳米颗粒和纳米壳聚糖能有效穿透柑橘木虱体壁递送 dsRNA (Lu *et al.*, 2024; Yuan *et al.*, 2025b)。除了使用纳米材料作为递送系统的载体外,使用柑橘衰退病毒 (Citrus tristeza virus, CTV) 作为生物载体也是一种具有应用前景的策略。CTV 能在柑橘韧皮部长期、稳定地存活而不引起明显症状,利用其作为生物载体表达靶向 dsRNA 也展现出应用潜力。目前已成功使用 CTV 表达组织蛋白酶、细胞色素 P450 的 dsRNA 用于防治柑橘木虱,均取得不错的防治效果 (Ibanez *et al.*, 2023; Kishk *et al.*, 2024)。

3 柑橘黄龙病-柑橘木虱-柑橘三者互作机制

柑橘木虱的若虫和成虫均可通过取食感病

植株韧皮部获取 CLas, 其中 2-5 龄若虫的获菌效率显著高于成虫,这可能与其取食频率高、持续时间长有关,且体内 CLas 含量随龄期增长而增加 (Hung *et al.*, 2004; 任素丽等, 2018a)。研究表明,仅 4-5 龄若虫和成虫能够传播黄龙病,2-3 龄若虫虽可获取病原菌但不具备传病能力;同时各龄期若虫获取病菌后,可终身携带 CLas (Mann *et al.*, 2011b; Wu *et al.*, 2018)。目前,柑橘黄龙病的传播主要依赖带菌成虫取食健康植株实现水平传播。其垂直传播效率较低:经卵传播至后代的效率约为 4%,通过交配传至雌虫的效率仅为 2%-3%,且经交配获菌的雌虫不再进一步传播 (Pelz-Stelinski *et al.*, 2010; Mann *et al.*, 2011b)。因此,防治柑橘木虱已成为阻断柑橘黄龙病蔓延的关键措施。

CLas 被柑橘木虱摄取后,在其体内经历增殖、循环与扩散过程:CLas 经由口针进入中肠,于中肠上皮细胞内快速增殖,继而通过胞吞/胞吐方式穿越肠道屏障进入血淋巴,进而扩散至脂肪体、肌肉、卵巢和精巢等组织,最终到达唾液腺,随取食时唾液一同注入健康植株 (Ammar *et al.*, 2011; 任素丽等, 2018a; Lin *et al.*, 2022)。CLas 在柑橘木虱不同组织含量同样存在差异,以中肠含量最高,其次是唾液腺、血淋巴 (许长藩等, 1988; Guo *et al.*, 2024),这与 CLas 在柑橘木虱体内增殖和传播的关键部位一致。

感染 CLas 后,柑橘木虱的生理行为、营养状态和免疫反应均产生不同程度的变化。当柑橘木虱携带 CLas 后,其取食行为会发生改变,带菌柑橘木虱取食植物韧皮部的时间显著缩短,而分泌唾液的时间显著延长,这也有利于 CLas 由柑橘木虱体内向植株转移,促进自身的传播 (Cen *et al.*, 2012; Luo *et al.*, 2015; Liu *et al.*, 2024)。在营养代谢方面,CLas 感染会促进柑橘木虱对植物代谢产物的吸收,并激活表皮蛋白表达,加速若虫发育进程,从而缩短病原菌在柑橘木虱体内的循环周期,提高传播效率 (Killiny *et al.*, 2017; Yuan *et al.*, 2025a)。营养代谢发生变化的同时也会伴随着生长发育的变化。研究表明,CLas 可通过调控 Kr-h1-JH-20E 信号通路影响柑橘木虱卵巢发育并促进产卵,该过程受到 miRNA 含量

变化的调控 (Nian *et al.*, 2024, 2025)。免疫方面, 柑橘木虱感染 CLas 后, 成虫中肠细胞凋亡水平较高, 若虫中肠凋亡水平较低, 体内自噬相关基因被显著激活 (Ghanim *et al.*, 2016; Mann *et al.*, 2018; Yuan *et al.*, 2025c)。

柑橘黄龙病的流行是 CLas、柑橘木虱和寄主植物三者之间复杂互作的结果, 不仅涉及直接的病原传播, 还包含生理、生态及分子层面的相互调控, 共同推动病害的流行。CLas 定殖于柑橘韧皮部后, 会引发植物系统性生理紊乱。一方面, CLas 通过分泌效应蛋白 (如 SDE4405) 激活柑橘体内细胞自噬反应, 抑制柑橘的免疫反应, 进而降低柑橘对柑橘木虱的抗性以促进自身的传播 (Shi *et al.*, 2023); 另一方面, 影响柑橘的生理代谢, 导致淀粉、胍胍质大量积累, 并破坏激素信号通路 (如茉莉酸和水杨酸平衡)。CLas 感染后, 会改变柑橘的挥发性有机化合物, 其中 α -蒎烯、 γ -蒎烯含量的升高会吸引柑橘木虱取食感病柑橘 (黄克志等, 2024)。

4 结论

柑橘黄龙病及其媒介昆虫柑橘木虱的持续危害对全球柑橘产业构成了严峻挑战。过去 70 年的研究在病原学、媒介生物学及综合治理技术方面取得了系列重要进展。在病原学上, 柑橘黄龙病病原从早期被误判为生理性病害或病毒, 逐步明确为韧皮部限制性革兰氏阴性细菌, 并进一步区分为亚洲种、非洲种和美洲种, 其中亚洲种 (CLas) 因其强适应性和传播力成为全球优势致病种。在防控策略上, 防控理念逐渐由依赖化学农药的单一干预, 转变为以“预防为主、绿色综合”为导向的多元治理体系, 涵盖了从无毒苗木、农业管理、生物防治到新兴的纳米材料、小分子药物和 RNA 干扰技术等多个层面。

然而, 当前的研究与实践仍面临诸多瓶颈: 首先, 由于 CLas 不可离体培养, 极大地限制了对致病机理和病原-寄主互作的深入解析; 化学农药的长期不合理使用导致柑橘木虱抗药性日益突出, 且带来环境残留风险; 此外, 许多新兴技术 (如 RNAi、纳米制剂、抗菌肽等) 仍面临田间稳定性、递送效率和成本效益的挑战; 最

后, 抗病种质资源匮乏且育种周期漫长, 难以应对病害快速扩散的紧迫需求。

5 未来研究方向

基于对各项防控技术潜力和局限性的分析, 未来的研究应着力于突破现有瓶颈, 实现从基础研究到田间应用的有效衔接。具体方向如下:

5.1 抗病种质创新与育种技术的精准化

培育抗黄龙病或耐病的柑橘品种是从植株源头上阻断柑橘黄龙病的关键策略, 但其面临育种周期长、基因调控网络复杂等挑战。未来研究应: 1. 深入解析抗病机制。加强对柑橘属及其近缘野生种中抗病基因资源的挖掘, 结合基因组学、转录组学等组学技术, 大规模鉴定抗性相关基因及等位变异, 拓展种质筛选范围, 重点阐明如澳洲指橙等高抗种质中抗菌肽表达调控、免疫信号通路 (如水杨酸/茉莉酸通路) 互作的具体分子机制, 为基因编辑提供精准靶标; 2. 创新研发育种技术。利用根癌农杆菌介导的上胚轴遗传转化、CRISPR/Cas9 等基因编辑手段, 精准敲除或修饰“感病基因”, 或导入/优化“抗病基因”, 可显著缩短育种周期, 加快抗病品种选育进程。

5.2 面向田间应用的绿色农药与技术优化

化学农药长期不合理使用已导致抗药性增强、环境残留及防治成本上升等问题, 因此开发高效、低毒、环境兼容的新型绿色农药至关重要。未来研究需针对性地: 1. 攻克药物递送与稳定性的瓶颈。纳米制剂和 RNA 生物农药在农业害虫防控中显示出良好潜力, 但其田间应用仍面临挑战。未来除继续筛选致死效应强、抗性风险低的高效靶基因外, 需重点优化递送系统 (如星形聚阳离子、层状双氢氧化物), 重点突破其田间持效性与环境安全性评价, 以推动新型绿色农药的大规模应用; 2. 筛选高效的植物源农药。从天然植物中提取对柑橘木虱或黄龙病病原菌具抑制活性成分, 研发植物源农药, 并通过结构修饰提升其活性与稳定性。探索其与化学农药或其他生物制剂的复配方案, 可实现协同增效并延缓抗性发生; 3. 推动小分子药物与抗菌肽的实用

化。除了借助人工智能技术筛选抑制 CLas 的小分子药物和抗菌肽外,还可以在已筛选出的活性小分子(如 P684-2850)和抗菌肽(如 MaSAMP、APP3-14)基础上,深入研究其在植株体内的传导分布规律、对非靶标生物的安全性及抗药性风险,为制剂开发奠定基础;4. 优化免疫诱导剂的使用策略。由于 CLas 会通过复杂的调控机制抵抗植物自身的免疫防御机制,应探索水杨酸类似物或其他免疫诱导剂(如油菜素内酯)的协同应用,以规避病原的免疫抑制。

5.3 病原体-媒介-植物互作中的关键机制挖掘

深入揭示病原-媒介-寄主三者间互作机制,有助于发现防控新靶点与突破路径。需系统阐释 CLas 在木虱体内的定殖与传播机制,如 1. 阐明媒介传播的分子基础。重点研究 CLas 如何突破柑橘木虱中肠屏障并在唾液腺富集的分子过程,鉴定其关键效应蛋白,为开发阻断 CLas 在虫体循环的靶标药物提供依据;2. 揭示病原操纵寄主的机理。深入解析 CLas 效应蛋白如何精确干

扰柑橘生理代谢(特别是韧皮部功能)和免疫应答(如茉莉酸信号通路),为通过调控植物生理提高耐受性提供新思路。

5.4 综合治理体系的整合与区域化应用

面对单一防治技术的局限性,推行生态调控与综合治理已成为必然趋势。未来应 1. 突破天敌规模化应用瓶颈。重点研究亮腹釉小蜂等优势天敌的规模化、低成本繁殖技术和田间释放策略(包括释放时机、剂量与方法)。应注重保护与增强本地天敌种群,通过果园生草、种植蜜源或诱集植物(如马缨丹 *Lantana camara*)为其提供生境与替代食源,提升生态系统控害能力。同时,积极筛选对木虱具高致病性的昆虫病原真菌、细菌或病毒资源,并探索其与化学农药的协同兼容使用模式;2. 构建基于风险的精准防控范式。为应对黄龙病与媒介昆虫的持续威胁,笔者曾在广东建立了基于疫情风险等级的分区治理模式,构建以“预防入侵、维持无疫”为目标的全程精准防控体系(图 1),并获得了 2022 年度的广

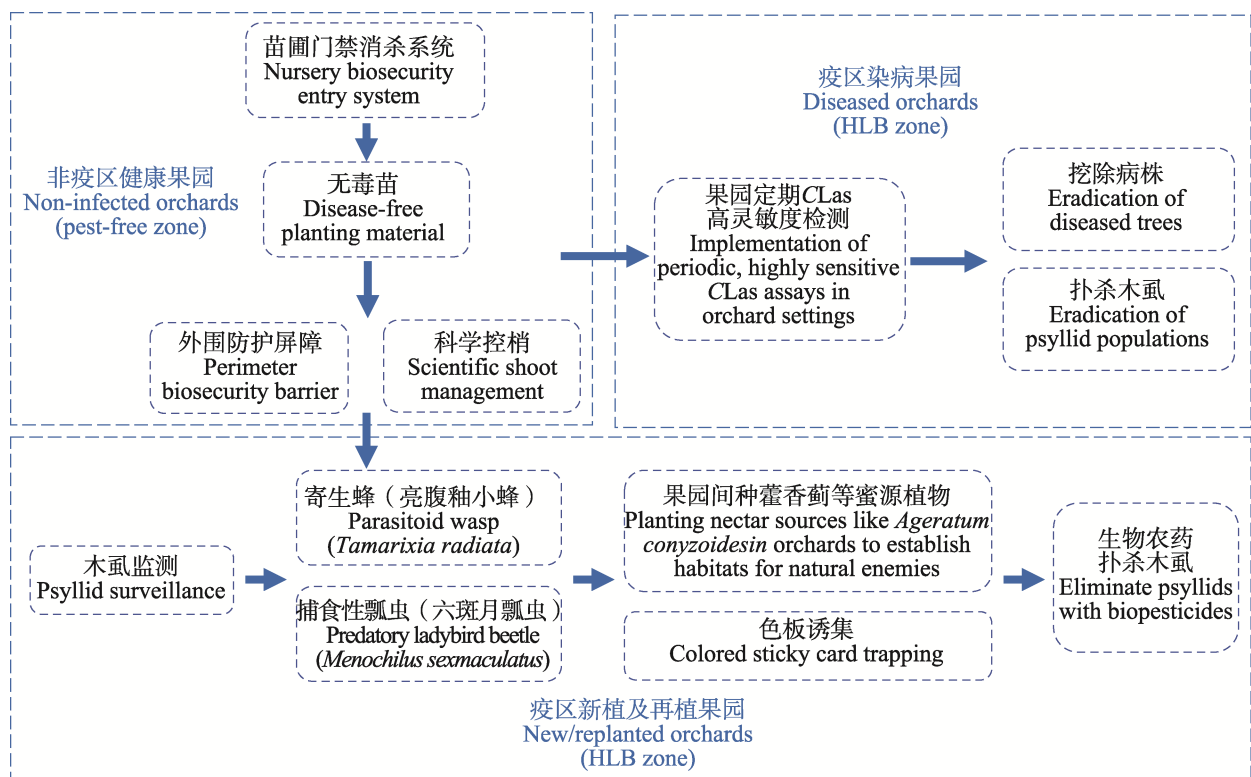


图 1 果园综合治理模式

Fig. 1 Orchard comprehensive management mode

东省科技进步一等奖。该精准防控体系包括在非疫区健康果园,集成使用无毒苗木、物理阻隔、天敌释放(寄生蜂、瓢虫等)、蜜源植物、信息素诱捕和低毒生物制剂等生态调控手段;疫区新植及再植果园需强化隔离与监测,严格管控木虱种群,提高化学防治精准度,追求快速杀灭与更高致死标准;染病果园则应聚焦传播阻断,实施药剂预处理、成虫清零与病株清除。通过农业、生物、物理与化学措施的多元协同,依托动态监测与预警支持,实现不同疫情下的绿色可持续治理,为柑橘产业系统防控黄龙病提供综合技术解决方案。

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