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香蕉枯萎病综合防控研究进展

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国家香蕉产业技术体系建设专项(批准号: CARS-31)、全国重点实验室项目(批准号: NKLTCB202306)和海南省自然科学基金(批准号: 323QN277)资助

摘要 香蕉是世界重要的果粮兼用作物, 为近5亿人口的主粮, 我国是第一大消费国和第二大生产国. 香蕉产业在兴边富民、乡村振兴中发挥重要作用, 但枯萎病的暴发严重制约了产业的发展. 本文概述了香蕉枯萎病研究现状, 综述了目前我国在枯萎病综合防控技术上取得的进展, 包括土壤枯萎病菌的快速检测技术、土壤调理、抗病品种选育、拮抗微生物应用及配套栽培技术等. 这为示范与推广枯萎病综合防控技术, 提高中国香蕉产业的国际竞争力, 促进产业健康可持续发展奠定基础.

关键词 香蕉枯萎病, 病原菌检测, 抗病品种, 拮抗微生物, 土壤调理, 栽培技术

香蕉是多年生草本植物, 属芭蕉科(Musaceae)芭蕉属(*Musa*)[1], 是发展中国家的主要粮食作物, 也是典型的热带亚热带水果. 果实富含蛋白质、碳水化合物、胡萝卜素、尼克酸、络氨酸等营养组分, 可预防人体高血压和心血管疾病等, 尤其是5-羟色胺有助于睡眠, 因此香蕉被誉为“来福果”“智慧果”“爱情果”“快乐果”[2]. 香蕉起源于东南亚国家, 已有三千多年的栽培历史, 在全球138个国家和地区广泛种植[3], 鲜果贸易量位居榜首[4]. 2021年全球香蕉收获面积达533.69万公顷[5], 总出口量为2458.43万吨, 进口量为23337.65万吨[6]. 我国香蕉种植面积位居世界第六, 产量居第二[7], 已成为热作产业一产产值最高的产业, 在推动热区农业产业结构调整、增加农民收入、乡村振兴中发挥重要的支撑作用[8,9].

香蕉枯萎病又称巴拿马病、黄叶病, 由尖孢镰刀菌古巴专化型土壤真菌(*Fusarium oxysporum* f. sp. *cubense*, 简称Foc)引起[10], 是全球香蕉毁灭性土传真菌病害[11], 可使植株自下而上黄化萎蔫、假茎纵裂、维管束褐变至整株枯亡[12], 主要通过雨水、灌溉、种苗、土壤、农机农具传播[13], 病原菌含量随香蕉多年连作在土壤中逐年累积. 尚无有效的化学农药和优质高抗香蕉品种, 造成重大的农业经济损失[14], 直接影响蕉农收入, 是世界香蕉产业发展的重大难题. 近年来, 国内外学者围绕香蕉枯萎病及其病原菌致病机理开展了深入的研究, 并在枯萎病病原菌种类、香蕉抗病品种鉴定和育种方法等领域取得了阶段性进展, 但对香蕉枯萎病致病基因挖掘、抗性资源评价与抗病基因鉴定、抗病育种选育等领域研究进展依然缓慢, 尤

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其是单一的防控技术仍难以遏制枯萎病蔓延的主要因素[15]. 本文重点综述了枯萎病综合防控策略, 为提升中国香蕉产业的国际竞争力, 促进全球香蕉产业的健康可持续发展提供经验.

1 香蕉枯萎病的发生和危害

香蕉枯萎病发生可追溯到20世纪初, 1874年首次发现在澳大利亚昆士兰州, 后迅速蔓延至全球各地, 如印度尼西亚、菲律宾和马来西亚等国[16]. 20世纪中叶, 在中美洲和南美洲香蕉种植区暴发, 特别是在洪都拉斯、尼加拉瓜和哥斯达黎加等国家, 造成当地蕉园大量荒废、香蕉出口市场几乎崩溃. 随着国际贸易的发展, 香蕉枯萎病快速传播至亚洲、非洲和加勒比地区, 严重威胁亚洲的菲律宾和印度尼西亚, 非洲的坦桑尼亚和乌干达, 以及加勒比地区的牙买加、特立尼达和多巴哥等国家的香蕉种植业[17], 最近发现已蔓延至哥伦比亚等国家[18]. 许多国家不得不采取紧急措施, 如销毁感染植株、限制香蕉运输和贸易等. 我国于1967年首次在台湾地区发现该病害, 随后十年香蕉种植面积减少7.36万亩(1亩=666.67 m^2)[19], 期间广东产区因枯萎病蔓延弃种香蕉, 后在福建、广西、海南、云南等地也报道枯萎病发生[20]. 截至2019年, 我国各香蕉主产区均发现香蕉枯萎病[21].

香蕉枯萎病菌根据其侵染品种可分为3个生理小种, 尤其是4号生理小种(Foc4)几乎可感染所有的栽培品种[22], 于2021年被我国列为农业植物检疫性有害生物[23]. 在没有寄主的情况下, 以厚垣孢子的形式在土壤中存活长达30年[22,24]. 由于Foc4在热带、亚热带地区均有发现, 遗传分化为热带4号生理小种(TR4)和亚热带生理小种(STR4)[25]. Carvalhais等人[26]开发了一种基于木质部分泌基因的分子诊断技术, 可准确辨别TR4和STR4菌株. Zheng等人[27]通过单核苷酸多态性揭示了世界各地Foc TR4可分为3个亚谱系, 发现国内外毒株之间存在一定的相关性. 其次, 影响香蕉枯萎病发生的因素较多, 不同香蕉品种和生育期具有显著的抗病差异, 宿根蕉根系发达较新植蕉更具抗性[28]. 冬季低温香蕉因蒸腾作用减少枯萎病害发展[29]. 强降雨天气可致香蕉枯萎病发病率增加4倍以上, 特别是洪水内涝等灾难导致香蕉根系机械断裂, 加剧病害发生[30]. 而土壤含水量高、通气性不良等也会减弱香蕉的抗性[31].

2 香蕉枯萎病综合防控技术

针对香蕉枯萎病防控的世界性难题, 2008年获农业部、财政部批准建立国家香蕉产业技术体系(以下称“香蕉体系”), 整合了全国香蕉主产区的育种、种苗、栽培、植保等领域专家, 围绕香蕉枯萎病等重要病害防控与绿色生产关键技术研发任务, 系统开展了香蕉抗病资源收集评价与筛选、抗病品种选育、土壤调理与拮抗微生物施用的研究, 筛选出一批抗性种质资源, 育成“宝岛蕉”“中热1号”等抗枯萎病突破性新品种(图1B), 创建“五位一体”香蕉枯萎病综合防控体系(图1A), 配套良种良法, 实现了枯萎病可防可控.

2.1 香蕉枯萎病菌快速检测为综合防控技术提供指导

国内外专家研究了香蕉枯萎病菌在土壤中的存活方式和消长规律, 分析了枯萎病菌在不同类型土壤中的流行与发病特征, 明确了抗感病品种、轮作方式、防控模式与香蕉枯萎病菌含量的相关性[32]. 由于香蕉枯萎病菌潜伏期长、感病植株前期症状不明显, 建立快速检测技术是早期监测枯萎病菌蔓延的关键. 传统多使用培养基菌落平板稀释法检测土壤中香蕉枯萎病菌. 随着现代分子生物学技术的发展, 聚合酶链反应(polymerase chain reaction, PCR)技术具有特异性强和灵敏性高等优势[33]. 林鹰等人[23]基于Foc 1和Foc TR4基因组序列设计特异性引物, 建立四重PCR检测技术, 基因组DNA含量仅需5×10^{-3} ng时, 就可以灵敏地检测到病原菌, 大大地提高枯萎病菌的检出效率, 且重复性好, 对感病土壤可操性强. 而实时荧光定量PCR技术(quantitative real-time PCR, qRT-PCR)借助荧光染料可精准定量土壤中病原菌含量[34]. 环介导等温扩增技术(loop-mediated isothermal amplification, LAMP)不受仪器限制, 能够现场检测土样结果, 不需考虑污染物影响, 反应效率高且稳定, 多用于基层及检疫部门[32]. 此外, 免疫反应也可用于检测土壤香蕉枯萎病病原菌的含量[35]. 在设施农业政策的引领下, 现代智能技术更多地运用于作物病害监控, 以提高预测时效和精度, 利用人工智能、卫星遥感等能够监测病害发生的节点和环境因子动态变化情况[36]. 其次, 建立支持向量机模型、随机森林算法和人工神经网络技术, 结合无人机多光谱图像, 可对香蕉枯萎病发生地和非发生地进

图 1 香蕉枯萎病防控技术及抗病品种. A: "五位一体"香蕉枯萎病综合防控技术体系; B: 选育的香蕉枯萎病抗病优质新品种
Figure 1 Control technologies and varieties of bananas resistant to *Fusarium* wilt disease. A: Integrated control system of "Five-in-One"; B: new high-quality varieties of bananas resistant to *Fusarium* wilt disease

行识别[37]. 例如, 利用卫星遥感成功建立了基于二元逻辑归类评估香蕉枯萎病侵染区的方法[38]. 检测技术的不断更新为及时发现病原, 有效实施隔离和遏制香蕉枯萎病措施提供了指导.

2.2 土壤调理是综合防控技术的基础

有研究表明, 土壤pH与香蕉枯萎病发病率、香蕉病情指数呈极显著相关性. Foc TR4喜好的酸性环境对土壤肥力有效性具有较强的破坏力[39], 提高土壤酸碱度可限制病菌对微量元素的摄入, 增强微生物群落的竞争关系[40]. Stover[29]发现抑病型蕉园土壤pH为中性或微碱性. 本团队多年来对不同主产区核心蕉园监测发现, 85%蕉园土壤pH小于5.5, 土壤有机质和钙镁钾离子含量偏低, 增施有机肥可提高土壤有机质含量, 提升酸性土壤阳性离子的交换能力[41], 改善土壤微生物多样性, 减少镰刀菌含量. 王春梅等人[42]利用石灰、油茶茶枯粉、微生物菌肥处理提高蕉园土壤微生物菌门丰度和植株的抗枯萎病能力. 香蕉体系专家樊小林提出"以肥治酸-改土-减污"和"以肥沃土-培肥-抗病"的理念, 通过施用碱性肥料优化土壤微生物种群结构, 增加细菌、放线菌丰度, 有效防控了香蕉枯萎病的发生[43]. 朱小花等人[44]增施虾肽氨酸肥提高香蕉枯萎病防控效果达96.6%. 通过在土壤中混加保水剂改善土壤结构和养分供应, 可增强土壤通气性和保水保肥能力, 提高防治效果, 沈宗专等人[45]发现, 氨水熏蒸可降低Foc TR4发病指数, 提高香蕉产量. 黄新琦等人[46]在海南蕉园应用强还原土壤灭菌法成功抑制了枯萎病的蔓延. Chen等人[47]发现, 芽胞杆菌可显著提高土壤微生物对羧酸及聚合物的利用效率, 产生不同纤维素酶改善土壤微生物的多样性. 因此, 通过平衡施肥调节土壤理化性质, 可有效改善香蕉生长环境, 增强其抗病能力, 抑制香蕉枯萎病蔓延.

2.3 抗性品种选育和应用是枯萎病综合防控的核心

选育抗病品种是香蕉枯萎病防控的根本途径. 但全球香蕉种质资源系统挖掘和评价不足, 抗病种质资源稀缺, 野生抗性资源少且难以直接利用. 目前国内外主要香蕉种质资源保存机构有广东省农业科学院果树研究所国家种质香蕉圃、中国热带农业科学院国家热带果树种质资源圃、广西农业科学院(特色蕉类为主)、云南省红河热带农业科学研究所(野生蕉为主)、印度国家香蕉研究中心、比利时鲁汶大学香蕉种质交换中心[48]. 我国非香蕉原产地, 野生种[49]、野生近缘种[50]等香蕉资源少, 遗传基础狭窄, 多样性不足. 国内研究学者对抗性品种收集、鉴定始于20世纪90年代, 从162份香蕉种质资源中鉴定出2份高抗、58份抗病和

44份中抗Foc R1材料. 1996~2016年, 黄秉智等人[51]筛选出22份高抗、15份抗病、38份中抗Foc TR4的种质资源. 易干军团队[52]对37个主栽香蕉品种AAB类开展系统抗性评价. Xu等人[53]发现“云蕉1号”对Foc TR4拮抗能力较“桂蕉1号”“巴西蕉”强. 陈业渊和魏守兴等人制定了《香蕉种质资源描述规范》用于香蕉种质资源评价鉴定[54], 这为抗病香蕉品种遗传改良提供了基础.

现种植的香蕉品种多由小果野蕉*Musa acuminata*(A基因组)和野蕉*Musa balbisiana*(B基因组)通过种内和种间杂交形成的二倍体、三倍体和四倍体杂交种[55]. 主栽培品种易感Foc TR4, 且多为三倍体, 育性差、杂交育种难, 导致抗性品种选育周期长, 难度大. 目前主要采用引种、芽变、组培苗变异、人工诱变等育种技术提高品种的适应性和抗病性. 国际上公认的香蕉抗性杂交品种“Goldfinger(*Musa* AAAB, 编号FHIA-01)”由洪都拉斯农业研究所(Fundación Hondureña de Investigación Agrícola, FHIA)利用Prata Ana三倍体香蕉和SH3142二倍体香蕉杂交选育而成, 具有抗枯萎病、高产及良好农艺性状等特性, 被国际香大蕉改良网络(International Network for Improvement in Banana and Plantains, INIBAP)列为优异种质[56,57]. 多年来, 在国家香蕉体系专家联合攻关下, 选育出“宝岛蕉”“中热1号”“桂蕉9号”和“粉杂1号”等抗(耐)病香蕉新品种[58,59]. “宝岛蕉”是在“新北蕉”种质(Formosana, GCTCV-218)的基础上, 通过“组培诱变→毒素筛选→病圃筛选→大田筛选→多点试种→综合决选”选育而成的具有中抗、优质、丰产且遗传稳定的新品种[60], 是我国首个国审抗枯萎病香蕉品种, 也是“十三五”第一批热带南亚热带作物主导品种和“十四五”农业农村部主导品种, 目前占抗病品种种植面积的40%以上, 已成为我国重病蕉园的主要更新种植品种, 近两年累计推广面积达120万亩以上. 金志强团队[61]利用巴西蕉未成熟雄花胚性愈伤经^{60}Co-γ射线辐射诱导结合毒素筛选、抗性标记等方法育成的抗枯萎病和优良性状兼备的突变体“中热1号”, 为迄今首个以辐射诱变育成的高抗枯萎病Foc TR4且丰产优质的新品种. 广西韦绍龙等人[62]利用芽变选育出首个自主培育的抗(耐)Foc TR4新品种“桂蕉9号”, 在广西、云南、海南等主产蕉区推广50万亩. 广东省农业科学院果树研究所从“广粉1号”实生苗中育成的“粉杂1号”, 是当前商业种植中唯一抗香蕉枯萎病的粉蕉品种, 重病蕉园发病率控制在5%以下, 荣获“2021年中国农业农村十大重大新品种”. 许林兵等人[63]对GCTCV-218进行多代抗性鉴定试验, 育成农艺性状、经济效益良好的中高抗Foc TR4香蕉品种“南天黄”. 谢艺贤团队[64]从“农科1号”芽变株中选育出“热科1号”是株型矮化、产量和抗枯萎病能力稳定的新品种. 上述选育的抗(耐)病品种不仅增强了环境适应性, 也解决品种抗病性状退化、产区分化等问题, 为枯萎病防控提供了多元化的品种储备.

2.4 有益微生物添加是枯萎病综合防控的强有力补充

土壤微生物被称为第二大基因组, 在植物生长发育及病害发生过程中发挥重要作用. 微生物群落失衡, 加剧枯萎病的发生及蔓延. 随着绿色农业发展需求, 利用环境功能微生物防控香蕉枯萎病已成为当前研究的热点. 目前报道具有香蕉枯萎病防效的微生物有真菌、细菌和放线菌等, 多以木霉、芽胞杆菌、链霉菌为主[65~68]. 复合微生物制剂的施用可利用植物自身微生物与病原菌进行空间和营养竞争, 或合成生物活性化合物阻断枯萎病的发生. 有报道, 香蕉根际微生物群落直接影响枯萎病的发生, 发病根系土壤瓜氨酸等代谢物参与富集驱散自解毒细菌[69], 而拮抗菌的添加和生物肥料的施用可提高土壤有益微生物丰度, 降低病原菌含量, 有效抑制枯萎病暴发和促进香蕉生长. Jing等人[70]从抑病蕉园分离的紫色链霉菌JBS5-6可破坏Foc TR4细胞结构, 抑制菌丝生长和孢子萌发, 降低了香蕉枯萎病菌的侵染, 控制效率达64.94%. 南京农业大学沈其荣团队[71]通过施用木霉改善生物肥料改变微生态环境, 提高香蕉生物量, 降低枯萎病菌的数量. Tao等人[72]发现, 解淀粉芽胞杆菌W19与土著益生菌群互作增强了土壤的抑病能力. 本团队前期分离了大量的拮抗功能菌株, 建立了微生物资源保藏库, 鉴定出抑制Foc TR4的关键代谢产物. Yun等人[73]从药用植物大叶仙茅中筛选得到高抗Foc TR4的放线菌5-10, 分泌物可使菌丝萎缩和破裂. Qi等人[74]从干热河谷土壤中分离得到强抑菌活性的丁香链轮丝菌SCA3-4. Chen等人[75]从南海软珊瑚中分离得到的链霉菌新种JCM 34965, 产生的Niphimycin C化合物可抑制病原真菌线粒体复合体酶的活性, 破坏线粒体结构和功能, 诱导细胞凋亡. 胡一凤[76]对比分析健康和感染枯萎病香

蕉植株, 发现内生放线菌NJQG-3A1对多种致病菌有明显的抑制效果, 可提高根部微生物群落的丰度. 因此, 配合施用拮抗菌和土壤消毒剂可改善土壤中的微生物群落结构, 形成抵御Foc TR4入侵的生物屏障, 降低病原菌的侵染[77].

2.5　栽培管理是枯萎病综合防控的配套技术

香蕉长期连作造成肥料利用率降低, 土壤微生态环境失衡[78,79]. 大量试验表明, 香蕉与韭菜[80,81]、冬瓜[82]、辣椒[83]、甘蔗[84]、南瓜等非寄主作物进行轮作、间作减少了尖孢镰刀菌的含量, 但轮作限制了香蕉的经济效益[83], 增加土壤酸杆菌目细菌的相对丰度, 加剧病原菌危害[85]. 间套作有利于改善香蕉连作对土壤理化性质、微生态环境失衡的影响. 李燕培[86]发现, 香蕉套作红薯可提高土壤pH和酶活, 调节土壤细菌与真菌的群落组成. 刘满意等人[87,88]通过香蕉套作白三叶草提高土壤肥力, 降低病原菌丰度, 重塑土壤微生物群落结构. 目前, 采用香蕉轮作/套种韭菜是较为常见的香蕉枯萎病防控种植模式, 用乙酸乙酯萃取韭菜提取液可抑制枯萎病菌的生长[89]. 其次, 研究人员发现厌氧土壤灭菌法可减少土壤病原菌传播风险[90~92]. 郭标等人[93]研发香蕉宽窄行宜机化栽培模式, “实现耕种管收”便捷作业, 提高蕉园通风透光, 增加香蕉与葫芦科、茄科、旋花科等植物间套作的可操作性, 降低枯萎病发生, 改善香蕉的产量和品质. 云南省在设施化新型农业的背景下[92], 发展“山地云蕉”特色产业, 搭配玉米、咖啡立体种植, 可减轻病害的影响[58]. 李虹等人[94]提出, 改良土壤pH、精准施肥、配套花生间作的综合防控方法有效地抑制香蕉枯萎病蔓延, 减少化肥用量, 提高香蕉产量. 因此, 采取合理的栽培措施是抑制枯萎病菌传播的重要途径.

3　存在的问题及展望

近年来, 香蕉枯萎病大面积暴发, 使得土壤生态系统失衡, 种植成本增加, 经济损失巨大, 导致广西、云南、海南等地香蕉种植面积锐减. 其次, 枯萎病寄主的专化性使各产区蕉农多种植某一抗性品种, 造成香蕉品种多样化减少[13]. 由此, 亟需探索一种有效的防控措施. 香蕉体系专家创新了香蕉枯萎病综合防控技术体系, 制定香蕉枯萎病防控技术规范[95]. 近年来, 香蕉枯萎病防控虽然取得一些进展, 但随着病原菌的进化和传播方式的转变, 仍面临一些挑战, 如品种多样性不足、抗性品种表现不稳定、室内实验效果达不到田间生产要求、高效栽培技术推广难度大等. 因此, 未来研究应继续探索新的防治策略和方法, 例如, (ⅰ) 改进病原菌的诊断技术. 深入探究病原菌传播的机制和途径, 开发更快捷准确的病原菌检测方法, 及时发现病害并采取相应的防控措施. (ⅱ) 推进抗病育种技术的研发. 目前仍缺乏主导性、突破性、广适性抗病新品种, 应以农艺性状市场接受度和品种质量为导向, 突破高产优质抗病品种选育的新技术. (ⅲ) 挖掘高效广谱的功能微生物. 由于生态环境复杂多变, 仍需筛选高效广适的功能菌株, 应对病原菌产生的抗药性. (ⅳ) 加强种植环境管理. 综合考虑不同地区的气候、土壤和栽培条件等因素, 研发配套的栽培技术体系. (ⅴ) 促进国际合作. 利用联合国粮农组织(Food and Agriculture Organization, FAO)、国际植物保护组织(International Plant Protection Convention, IPPC)等国际组织加强病害监测和预警能力, 加强科研成果的交流和共享, 整合资源, 共同应对全球性香蕉枯萎病的危害. 综合研发和运用多种手段和策略, 支撑香蕉产业的健康可持续发展.

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Research progress on the integrated control of *Fusarium* wilt disease in banana

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Banana is an important fruit crop consumed by approximately 500 million people worldwide. China is the largest consumer and the second largest producer of bananas. The banana industry is crucial for the growth and development of the countryside. However, the outbreak of *Fusarium* wilt disease has seriously restricted the development of the banana industry. This review summarized the research progress on the integrated prevention and control technology, including the rapid pathogen detection, soil conditioning, resistance cultivar breeding, antagonistic microorganism application, and cultivation technology. The key technologies for integrated prevention and control lay a foundation for better management of the banana *Fusarium* wilt disease. This may help improve the competitiveness of China's banana industry in the international market while promoting its healthy and sustainable development.

banana *Fusarium* wilt, pathogenic detection, disease-resistant varieties, antagonistic microorganisms, soil conditioning, cultivation technologies

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