果 树 学 报 2021,38(4):603-612
Journal of Fruit Science

DOI:10.13925/j.cnki.gsxb.20200385

荔枝霜疫病的研究进展

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摘 要:荔枝霜疫霉(*Peronophythora litchii* Chen ex Ko et al)引起的荔枝霜疫病是我国荔枝生产和贮藏运输过程中为害最严重的病害,极大地威胁着我国荔枝产业的健康发展。该病可为害荔枝嫩叶、嫩枝、花穗及果实,流行年份对荔枝产量影响极大。笔者主要从荔枝霜疫病的症状、病原菌的分类和生物学特性、发生与流行、致病机制及防治策略等方面进行综述,并提出今后研究的趋势和待解决的问题,为该病原菌的深入研究和病害防控提供参考。

关键词:荔枝霜疫病;荔枝霜疫霉;致病机制;病害防治

中图分类号:S667.1 **文献标志码:**A **文章编号:**1009-9980(2021)04-0603-10

Research progress in studies on the downy blight disease in litchi

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Abstract: Litchi (*Litchi chinensis* Sonn.) is one of the most important tropical and subtropical fruits in China. However, litchi downy blight caused by *Peronophythora litchii* greatly threatens the healthy development of Chinese litchi industry, which is the most serious disease in litchi production, storage and transportation. Litchi downy blight damages tender leaves, twigs, flowers and fruits, leading to enormous yield loss in the epidemic years. Litchi downy blight usually occurs in April and May. At this time, the weather humidity and rainfall are high, which is suitable for the growth and infection of *P. litchii.* If it rains continuously for two days, it could cause epidemic of this disease. Usually, oospores is the source of primary infection, while sporangia and zoospores can act as the sources of secondary infection. *P. litchii* always produces sporangia and zoospores rapidly, so serious secondary infection will happen when the weather is suitable for this disease. *P. litchii* belongs to oomycetes that are diploid organisms, and the genome sequencing results of *P. litchii* was officially published in 2016, with a genome size of about 58 MB and a GC content of 49%. Bioinformatics analysis showed that there were 30 NLPs [necrosis- and ethylene-inducing protein 1 (Nep1)-like proteins], 14 CRN effector molecules (crinkler protein) and 245 specific RXLR effectors in *P. litchii*. The genome sequencing and CRISPR/Cas9 genome editing system have greatly accelerated the research on the molecular pathogenesis of *P. litchii*. In the past five years, it has made a series of progresses on molecular mechanism of zoosporogenesis, oospore formation and pathogenesis of *P. litchii*. In the aspect of functional genomics, A Puf RNA-binding protein encoding gene *PlM90* plays a key role in sexual and asexual differentiation of *P. litchii*; M90 is conserved in oomycete and up-regulated in oospores and sporangia in *P. litchii* and *P. infestans*. The silencing of *PlMAPK10* decreases the growth rate, production of sporangia, activity of extracellular laccase and the pathogenicity of *P. litchii*. The heat shock transcription factor PsHSF1 of *Phytophthora sojae*, also regulates the pathogenicity and laccas-

收稿日期:2020-09-11 **接受日期:**2020-12-30

基金项目:国家自然科学基金(31701771);现代农业产业(荔枝龙眼)技术体系(CARS-32);广东省自然科学基金(2020A1515011335)

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es activities of *P. sojae*. However, the relationship between MAPK10 and HSF1 in oomycetes needs further studies. Kong reported that PlBZP32 was involved in the oxidative response, sporangium production, cyst germination and plant infection of *P. litchii*. However, it is not clear whether the regulation of PlBZP32 on sporangium production is directly related to *PlMAPK10*. Wang found that there were two hybrid histidine kinases (PlHK1, PlHK2) and one response regulator (PlRR1) in the two-component signaling pathway of *P. litchii*. Among them, PlHK1 and PlHK2 fused an additional phosphate domain at the C-terminal. These three genes were up-regulated in the infection stage of *P. litchii* and responded to oxidative stress and osmotic stress at transcriptional level. In the functional studies of effector proteins, Kong knocked out the pectin acetylesterase gene *PAE5* of *P. litchii* through CRISPR/Cas9 technology. Phenotypic analysis of the PAE5 mutants showed that this gene was involved in the infection process of *P. litchii*, and the ectopic expression of *PAE5* in tobacco could promote the infection of *Phytophthora capsici* on tobacco, indicating that PlPAE5 could suppress the resistance of plants and promote infection. Situ obtained three cell death-inducing RXLR effectors, Avh23, Avh133 and Avh142, through large-scale screening by transient expression system in *Benthamiana thaliana*. Among them, the knockout mutants of *PlAvh142* significantly decreased the virulence of *P. litchii*, while overexpression of *PlAvh142* enhanced the virulence of *P. litchii*. This indicated that PlAvh142 had dual functions: on one hand, it can be recognized by plants to induce plant immune response, on the other hand, it functioned as a virulence factor. Virus-induced gene silencing assays showed that cell death triggered by PlAvh142 was dependent on the plant transduction components SGT1 (suppressor of the G2 allele of skp1), RAR1 (require for Mla12 resistance) and HSP90 (heat shock protein 90). The interaction between effector and litchi determined the occurrence of disease, however, it is rarely known in litchi-*P. litchii* interaction. That will be one of the key points for further studies, which will reveal the molecular basis of *P. litchii* infection and provide potential targets for disease control in the future. Different litchi cultivars showed various resistances to *P. litchii*. For example, the resistance of Heiye is higher than that of Guiwei. But so far, no resistance gene and high resistant cultivar were reported in litchi. Therefore, the control of litchi diseases must rely on agricultural control, chemicals and biocontrol, but not on resistant cultivar. Several biocontrol bacteria, fungi and actinomyces were found, such as *Paenibacillus polymyxa*, *Pseudomonas*, *Photobacerium*, *Eupenicillium brefeldianum*, *Aspergillus clavatonanicus*, *Penicillium janthinellum*, *Talaromyces flavus* and *Streptomyces* sp. DF-5. Further study revealed that several species produced volatile organic compounds (VOCs) to suppress the infection of *P. litchii*. Overall, this paper reviewed the identification, classification, biological characterization and pathogenesis of *P. litchii*. We also summarized the symptoms, occurrence, epidemic and control strategy of the disease, putting forward the study trend and problems to be solved. We hope this review would provide reference for the further studies on the pathogen and the control of this disease.

Key words: Litchi downy blight; *Peronophythora litchii*; Pathogenesis; Disease control

荔枝(*Litchi chinensis* Sonn.)是一种亚热带常绿果树,由于其营养丰富、味道鲜美,深受国内外消费者的喜爱,在中国、泰国、越南、南非、澳大利亚、美国及马达加斯加等国均有种植[1]。我国荔枝分布于广东、广西、海南、福建、四川、云南、贵州和台湾等省区,种植面积超过53.3万hm^2,高产年份的总产量超过300万t,总产值超过300亿元[2];其中广东和广西作为我国最大的产区,种植面积和产量分别约为27万hm^2、118万t和20万hm^2、87万t。但是,荔枝霜疫霉(*Peronophythora litchii* Chen ex Ko et al)引起的荔枝霜疫病(曾称荔枝霜疫霉病或荔枝霜霉病)严重威胁着我国荔枝产业的健康发展,是荔枝生产

及采后为害最为严重、影响最为广泛的病害。该病可以侵染嫩叶、嫩枝、花穗及果实，引起大量花穗和果实腐烂，一般年份可造成10%~30%的产量损失，流行年份可造成80%的产量损失，在广东、广西和四川发生尤为严重[3]。笔者对荔枝霜疫病的症状、病原的分类地位和生物学特性、病害发生与流行、病害防治以及病原菌的基因组与致病机制进行了系统性总结，以期为该病害的进一步研究提供参考。

1　荔枝霜疫病的症状

荔枝霜疫病多发生于荔枝果实转色至成熟阶段，但幼果、嫩叶、嫩枝及花穗等也可被为害。嫩叶发病会形成不规则褐色病斑，而成熟叶片受侵染则仅沿中脉出现褐色斑点。花穗受害则变褐腐烂，随后干枯脱落。果实发病时，初形成褐色病斑，无明显边缘，病斑发展迅速，可导致全果变褐，果肉发酸、糜烂，流出酸汁液；若连续阴雨或空气湿度大时，病果表面长出白色的霉层；幼果感病后很快脱落，造成大量落果[4-6]。

2　荔枝霜疫霉的形态特征、生物学特性与发生规律

荔枝霜疫霉在自然界中存在菌丝、孢子囊、游动孢子、休止孢、雄器、藏卵器及卵孢子等多种生物学形态，其中该菌无性繁殖产生的孢子囊和游动孢子可在短时间内引起再侵染，而有性生殖形成的卵孢子主要发挥越冬和适应不良环境的作用[4]。荔枝霜疫霉菌丝为白色，起初菌丝透明无隔膜，随着菌丝生长，颜色加深，产生隔膜。菌丝于10~30 ℃均可生长，生长适宜温度为20~28 ℃，pH值为4~8。以胡萝卜培养基或马铃薯蔗糖琼脂培养基为基础，添加多菌灵、咪鲜胺、异菌脲、利福平和制霉菌素使其质量浓度分别至10、2、200、10和50 mg·L^{-1}所配制成的选择性培养基，可有效分离荔枝霜疫霉[7]。

孢囊梗生长方式为多级有限生长，锐角分枝，一般形成7~20多个孢子囊，孢子囊成熟后遇水立即脱落。孢子囊无色或褐色，柠檬形，大小为(17~40) μm×(15~24) μm，顶端有乳状突[8-9]。孢子囊直接萌发产生芽管，发芽孔有1个或多个；间接萌发释放游动孢子，游动孢子肾脏形，侧生双鞭毛。孢子囊的萌发形式和萌发率主要受温度调控，荔枝霜疫霉孢子囊萌发温度等于或小于孢子囊形成温度，16~24 ℃时主要萌发形成游动孢子，而在26~32 ℃的温度条件下主要萌发形成芽管。游动孢子在20~24 ℃最适萌发，最适pH为7~9；且孢子囊释放游动孢子以及游动孢子的萌发均需在水中[10-11]。

荔枝霜疫霉为同宗配合，有性器官为藏卵器和雄器。藏卵器球形或近球形，无色；雄器有穿雄生、底生和侧生3类；卵孢子球形，无色，(23~33) μm×(17~27) μm；当温度为28 ℃、pH值为5、光暗交替时，卵孢子的萌发率最高，可达49.68%[4]。

荔枝霜疫病在广东多发生于4、5月份，此时降雨量大，湿度大，适合病原菌生长，只要连续下雨2 d，便可造成流行；6月下旬至7月上旬，气温显著升高，雨量显著减少，病情会明显减轻；8、9月在落地烂果的果皮内侧和患病枝条处形成卵孢子，以卵孢子和菌丝在病叶、病果和土壤中越冬，成为次年的初侵染源[4]。广西、四川和云南等地与广东省发生规律类似，而海南省的气候并不适合荔枝霜疫病的发生，目前海南省也没有大规模流行的报道。荔枝霜疫霉侵染速度快，病原菌侵染2~3 d后会出现明显的症状，并产生孢子囊进行再侵染[12]。温度、露时及其交互作用可显著影响荔枝霜疫霉孢子囊萌发及寄主发病的严重程度，相同温度下露时越长发病越重；露时相同，温度为25 ℃时，最有利于果实上病害的发生[13]。

3　荔枝霜疫霉的分类地位

荔枝霜疫霉的无性生殖结构与假霜霉(*Pseudoperonospora*)相似，因此1959年报道为荔枝霜霉(*Pseudoperonospora* sp.)，1961年Chen基于其有性生殖近似疫霉属而无性生殖近似霜霉属，建立霜疫霉属(*Peronophythora*)，其模式种为*P. litchii* Chen[4]。1978年Ko等[14]在台湾重新鉴定此菌时，基于此菌易于分离培养，孢囊梗为多级有限生长，与菌丝有区别，建立一新科——霜疫霉科(Peronophythoraceae)。近年来的基因组和转录组测序数据表明，荔枝霜疫霉具有与疫霉菌(*Phytophthora*)较为相近的序列特征，故建议归属疫霉[15-16]。但目前还没有将荔枝霜疫霉组合到疫霉属的正式报道，表明该菌的归属仍存在一定争议。鉴于该菌孢囊梗分枝为二分叉式与疫霉合轴式分枝区别较大，而更接近于霜霉；孢囊梗的生长方式为多级有限生长，与疫霉的无限生长和霜霉的有限生长方式均有所不

同；因此建议在没有其他更多依据的情况下，该菌的分类地位仍归属于霜疫霉属。

4 荔枝霜疫霉的致病机制研究

荔枝霜疫霉属于二倍体病原卵菌，基因敲除难度较大。再者，荔枝生产国多为热区的发展中国家，因此相对其他重要病原卵菌，荔枝霜疫霉的致病机制研究起步较晚且仅有少量基因功能的研究报道（表1）。

表1 已报道的荔枝霜疫霉功能基因和效应分子

Table 1 The reported functional genes and effector of *Phytophthora litchii*

蛋白 Protein	功能 Function	参考文献 Reference
NLP蛋白家族 NLP protein family	PlNLP9、PlNLP19和PlNLP25能够诱导植物细胞死亡 PlNLP9、PlNLP19 and PlNLP25 are able to induce cell death	[15]
PlM90	参与病原菌卵孢子形成、游动孢子的释放和休止 Participate in oospore formation, zoospore releasing and encysting	[17]
PlMAPK10	参与病原菌孢无性繁殖、致病过程与胞外漆酶活性 Associated with asexual reproduction, pathogenicity and laccase activity	[18]
PlBZP32	参与病原菌无性繁殖、致病过程与抗氧化过程 Participate in asexual reproduction, pathogenesis and antioxidation	[19]
PlPAE5	参与致病过程的效应分子，调节植物抗病性 A effector associated pathogenesis and regulating plant resistance	[20]
RXLR蛋白家族 RXLR protein family	Avh23、Avh133和Avh142可以引起植物的细胞死亡 Avh23、Avh133 and Avh142 are able to induce plant cell death	[21]
PlAvh142	既能诱导细胞死亡又是病原菌的致病因子 Induce cell death, pathogen virulence factor	[21]
PlHK1、PlHK2	侵染阶段转录上调，响应渗透胁迫和氧化胁迫 Up-regulated during infection stage and under H_2O_2 or osmotic stress	[22]
PlRR1	侵染阶段转录上调，响应渗透胁迫和氧化胁迫 Up-regulated during infection stage and under H_2O_2 or osmotic stress	[22]

荔枝霜疫霉的基因组测序结果于2016正式发表，基因组大小约58 Mb，GC含量为49%。通过生物信息学分析，发现该菌有30个NLP蛋白[necrosis- and ethylene- inducing protein 1（Nep1）- like proteins]、14个CRN效应分子（crinkler protein）和245个卵菌特有的RXLR效应分子[15]。荔枝霜疫霉基因组的公布极大地促进了荔枝霜疫霉致病机制的研究。

在功能基因研究方面，Jiang等[17]基于基因沉默技术，研究了荔枝霜疫霉*PlM90*对该菌的有性和无性分化具有特异性的调控作用，*PlM90*的沉默会导致该菌的卵孢子产量大幅降低，游动孢子释放和休止孢形成延迟；致病疫霉M90在卵孢子和游动孢子囊中上调表达[23]，进一步证实了M90具有调节荔枝霜疫霉中有性孢子和无形孢子发育的功能，但M90与其他卵孢子形成相关蛋白（如G-protein-coupled receptors，importin α）之间的信号转导过程还是未知的[24-25]。卵孢子的形成是卵菌特有的有性生殖方式，以荔枝霜疫霉M90为突破口可深入研究卵菌有性繁殖的分子机制。Jiang等[18]还报道了*PlMAPK10*的沉默会导致病原菌生长减慢、孢子囊产量降低、胞外漆酶活性降低以及病原菌的致病力下降。而亲缘关系较近的大豆疫霉热激转录因子PsHSF1也调节病原菌的致病力和漆酶活性等性状[26]，卵菌MAPK10和HSF1的功能及其关系还有待进一步研究。Kong等[19]报道了荔枝霜疫霉BZP转录因子PlBZP32参与病原菌的氧化应答、孢子囊的产量、休止孢的萌发以及侵染寄主等过程，但该基因对孢子囊产量的调节是否与*PlMAPK10*有联系也不清楚。王荣波等[22]通过转录分析发现，荔枝霜疫霉双组分信号途径中存在2个杂合型组氨酸激酶（PlHK1、PlHK2）和1个响应调控蛋白（PlRR1），其中PlHK1和PlHK2的C端额外融合一个磷酸功能域，这3个基因在荔枝霜疫霉侵染阶段表达上调，并响应氧化胁迫和渗透胁迫，但该3个蛋白在荔枝霜疫霉生长发育和侵染过程中的功能仍需基于基因敲除等试验的进一步证明。

在效应分子研究方面，Kong等[20]通过CRISPR/Cas9技术敲除了荔枝霜疫霉果胶乙酰酯酶基因*PAE5*，对突变体的表型分析表明,该基因参与病原菌的侵染过程，并且在烟草上表达PAE5会导致烟草对辣椒疫霉更加感病。Situ等[21]利用本氏烟草系统大规模筛选得到3个能引起植物细胞坏死的RXLR效应分子（Avh23、Avh133和Avh142），其中PlAvh142的敲除突变体对荔枝致病力明显减弱，过表达则使其致病力加强，表明PlAvh142具有双重功能：一方面能被植物识别引起免疫反应，另一方面又是病原菌的毒力因子。进一步研究表明，

PlAvh142引起的细胞死亡依赖于植物信号转导元件SGT1（suppressor of the G2 allele of skp1）、RAR1（require for Mla12 resistance）和HSP90（heat shock protein 90）。效应分子与病原菌的互作过程对病原菌能否成功侵染起决定性作用，上述效应分子与植物在蛋白水平的互作还是未知的，这是今后深入研究荔枝和霜疫霉相互作用的重点之一。

5　荔枝霜疫病的防治

不同荔枝品种对荔枝霜疫霉存在抗性差异，如黑叶对荔枝霜疫霉的抗性高于桂味[27]。但目前没有发现任何荔枝品种对荔枝霜疫霉是高抗的，或者说荔枝尚未有垂直抗性的报道。因此，目前荔枝病害防控依赖于化学防治和农业防治，生物防治方法仍在研究和开发中，尚未有大规模应用。

针对荔枝霜疫病的农业防治措施主要包括加强果园栽培技术管理，改善果园生态环境。具体措施有：彻底剪除病枝，修剪过密枝条，保障通风透光，降低果园湿度；保持土壤疏松透气，雨季清沟，以利排水降湿；做到科学用肥，以施有机质肥为主；合理利用药物进行疏花，果实成熟后及时采摘；采后做好清园工作，修剪枝条，控制冬梢生长，将果园的病果、烂果、落叶等集中深埋，同时清除园内的杂草。以上措施均可减少第2年荔枝霜疫霉的初侵染源[28-29]。此外，利用树盘下覆地膜的方法也可以减少落地小花、小果，以免被土面的荔枝霜疫霉感染而繁殖出更多侵染源[30]，以及通过植保站和各荔枝病虫害监测点对病原菌进行调查和监测，做好科学预报和防治工作[31]。

化学防治是荔枝霜疫病防治的主要手段，重点抓好荔枝春梢期、花蕾期、幼果期和果实发育后期，尤其是果实近成熟阶段的疫情监测与防控。具体喷施方式如下，3—4月的春梢期和花蕾期各喷药1次；坐果后从幼果期直至采收，每15 d喷药1次；若连续阴雨，则需要抢晴施药。

目前防治荔枝霜疫病常见的化学药剂有烯酰吗啉、代森锰锌，氟菌•霜霉威、肟菌•戊唑醇、丙森锌、甲霜•锰锌、氰霜唑、烯肟菌酯、烯肟菌胺、SYP-2815和苯醚菌酯等。其中，烯酰吗啉对荔枝霜疫霉的菌丝生长和孢子囊萌发具有较好的抑制效果，其EC_{50}分别为1.70和0.84 mg·L^{-1}[32]，烯酰吗啉与咪鲜胺以1∶1体积比混配可作为防治荔枝霜疫病和炭疽病的优选混配比例[33]。将560 g·L^{-1}嘧菌酯•百菌清悬浮剂用于荔枝挂果期，可提高加转色期、成熟期和储藏期果实对荔枝霜疫病的防效[34]；10 mg·L^{-1}的60%吡唑醚菌酯•代森联水分散剂对荔枝霜疫霉抑菌效果达96.98%，大田防治效果优良[35]。周俞辛等[36]在离体条件下研究了4种QoI类杀菌剂（烯肟菌酯、烯肟菌胺、SYP-2815和苯醚菌酯）对荔枝霜疫霉不同发育阶段的影响，发现这4种药剂在荔枝霜疫霉菌丝扩展和孢子囊产生阶段活性较高。生长速率法与田间药效试验方法相结合发现，10%苯醚菌酯悬浮剂对荔枝霜疫霉的EC_{50}值为0.73 mg·L^{-1}，1000 mg·L^{-1}的田间防治效果为84.92%[37]。250 mg·mL^{-1}双炔酰菌胺悬浮剂对荔枝霜疫病有较好的防治效果，最佳剂量为1500倍液，对花穗和果实霜疫霉病防效为86%~89%[38]，在荔枝挂果期至成熟前期施用4次，可有效防治荔枝霜疫病[39]。李堃娟等[40]发现在荔枝挂果期喷药3次后，68.75%氟菌•霜霉威SE 600倍液、75%肟菌•戊唑醇WG 2500倍液、66.8%丙森•缬霉威WP 800倍液、70%丙森锌WP 500倍液和68%精甲霜•锰锌WG 800倍液对果实成熟期霜疫霉病的防效分别为89.92%、91.45%、89.53%、88.11%和88.01%，因此这5种杀菌剂可在荔枝产区上轮换应用。

目前有关荔枝霜疫霉抗药性的研究较少，广东、广西、云南等地区荔枝霜疫霉菌株对烯酰吗啉抗药性的研究表明无该药的抗药性亚群体[41]。Zhou等[42]发现荔枝霜疫霉Cytb点突变F128S可以提高其对烯肟菌胺和烯肟菌酯的抗性水平，G142A/S和Y131C可使荔枝霜疫霉对4种QoI杀菌剂烯肟菌酯、烯肟菌胺、SYP-2815和苯醚菌酯产生高水平抗性，其中Y131C可引起荔枝霜疫霉对这4种药剂的上百倍抗性。调查表明，部分果农对安全用药相关技术不清楚，存在使用药剂种类单一、极少采用轮换用药以及混配不合理等问题[43]；为了避免荔枝霜疫霉抗药性的产生，应避免单一药剂在田间的长期使用，做到轮换使用，科学用药。

在生物防治研究方面，枯草芽孢杆菌BS-2、解淀粉链芽孢杆菌TB2和枯草芽孢杆菌TL2可作为荔枝霜疫霉的生防细菌，三者对荔枝霜疫霉菌丝生长和孢子囊萌发均可产生抑制作用，其中TB2和BS-2菌液抑制率可达63.34%和79.29%[32]。粘类芽孢杆菌（*Paenibacillus polymyxa*）、假单胞菌（*Pseudo-*

monas)、发光杆菌(*Photobacerium*)等生防细菌对荔枝霜疫霉有显著抑制作用[44-45]。关于生防真菌,研究发现布雷正青霉(*Eupenicillium brefeldianum*)、短棒曲霉(*Aspergillus clavatonanicus*)、微紫青霉(*Penicillium janthinellum*)等多株海洋真菌[46]和土壤菌核寄生黄蓝状菌(*Talaromyces flavus*)[47]等均对荔枝霜疫霉菌丝生长有较强的抑制作用。链霉菌*Streptomyces* sp. DF-5及其发酵液可使荔枝霜疫霉菌丝畸形和生长速率减慢[48]。采用平板稀释法对28份土壤样品进行分离纯化后获得的476株放线菌进行筛选,获得了2株可显著地抑制荔枝霜疫霉生长的放线菌,其中菌株BWL-H1的抑菌率达94.6%。

进一步对生防微生物抑制原理进行探究,发现解淀粉芽孢杆菌(*Bacillus amyloliquefaciens*)PP19、短小芽孢杆菌(*Bacillus pumilus*)PI26和乙酰微小杆菌(*Exiguobacterium* acetylicum)SI17产生的挥发性有机化合物(volatile organic compounds,VOCs)能够有效抑制荔枝霜疫霉侵染荔枝[49]。1-(2-Aminophenyl)ethanone(EA)和Benzothiazole(BTH)能够直接抑制荔枝霜疫霉在培养皿上的生长和该病原菌对荔枝的侵染,而化合物α-Farnesene(AF)能够抑制荔枝霜疫霉的侵染,但不能在体外抑制荔枝霜疫霉的生长,这表明该化合物可能通过诱导植物抗病性从而抑制病原菌侵染[49]。青霉属培养物的4'-hydroxymonocillin IV和4'-methoxymonocillin IV对荔枝霜疫霉均有抑制效果[50]。菌株BWL-H1产生的挥发性物质4-ethylphenol对荔枝霜疫霉的抑菌活性最强[51]。

近些年发现了大量的新化合物可以抑制荔枝霜疫霉的侵染。如紫檀芪可以破坏荔枝霜疫霉细胞壁、质膜和细胞器等,抑制菌丝生长和孢子囊萌发[52];从荔枝果皮提取的多酚物质,花椒油活性物质桉树脑、柠檬烯、月桂烯、丁香酚、小檗碱及苦参碱和香芹酚等对荔枝霜疫霉菌都具有显著的抑制作用[53-55]。盾叶薯蓣(根)、水菖蒲甲醇提取物(干粉)以质量浓度10 mg·mL^{-1}处理7 d后对荔枝霜疫霉有抑菌活性,抑菌率分别为94.14%和98.50%;黄石斛、毛唇芋兰、葛和土牛七在甲醇提取物质量浓度为0.01 g·mL^{-1}时对荔枝霜疫霉的抑制率可达100%[56],野核桃、百部、苦参、朱砂藤、八角莲、筒鞘蛇菰甲醇提取物相同质量浓度时抑菌率超过80%,盾叶薯蓣75%乙醇提取物1.0 mg·mL^{-1}和5.0 mg·mL^{-1}处理对荔枝霜疫霉病菌丝生长的抑菌率分别为86.64%和96.15%[57]。双氢青蒿素、厚朴酚、辣椒碱、青蒿琥酯、蛇床子素以及蒿甲醚等6种植物提取物对荔枝霜疫霉均有抑制作用,其中厚朴酚的抑制效果最强,其EC_{50}值为25.4~38.5 μg·mL^{-1},平均值为31.2 μg·mL^{-1};双氢青蒿素的EC_{50}值为42.7~74.1 μg·mL^{-1},平均值为60.0 μg·mL^{-1}[58]。一种新的脱乙酰壳多糖能够诱导荔枝果实在采后对荔枝霜疫霉的抗性,且此过程与过氧化物代谢相关,脱乙酰壳多糖处理的荔枝果实可产生更多木质素和抗病相关酶类,使荔枝果实采摘后更加抗病[59];*Dickeya zeae*产生的化合物zeamines也对荔枝霜疫霉有较好的防治效果[60]。

荔枝霜疫霉的化学防治效果较好,合理施药能够及时有效阻止荔枝霜疫病的大流行,农业防治措施也有一定的应用,生防制剂的田间试验已经展开,但目前尚未有正式登记的防治荔枝霜疫病的生防制剂,因此生物防治和其他绿色防控技术的开发与推广还需要更多的投入。

6 展 望

荔枝霜疫病的发生与流行是制约我国荔枝产业发展的一大因素,因此对该病害的有效防控尤为重要。2016年以来,荔枝霜疫霉基因组测序的完成和遗传转化体系的建立推动了该病原菌功能基因和效应分子功能的研究[61],发现了M90参与病原菌的有性生殖,PlMAPK10调节病原菌漆酶活性并影响致病力,PlBZP32调节病原菌的孢子囊产量和致病力,病原菌RXLR效应分子和果胶乙酰酯酶在与植物互作过程中发挥关键作用[17-21]。在目前研究的基础上,仍需继续深入研究病原菌有性生殖、无性繁殖、致病过程以及病原微生物与寄主的互作机制,以期为病害防控提供理论基础。一方面可以通过反向遗传学鉴定荔枝霜疫霉具有重要功能的效应分子和功能基因,另一方面可以通过基于互作蛋白筛选等技术对已知的荔枝霜疫病关键致病因子进行深入研究,从而鉴定植物的抗病基因或感病因子,为病害防控提供新的靶标或为抗病育种奠定分子基础。

随着人们生活水平的提高,消费者对荔枝品质的要求越来越高,因此规范和减少化学农药的使用

已经成为科研工作者和广大种植者努力的方向。荔枝霜疫霉化学防治所用药剂虽然有多种选择，但是在使用过程中应当交替使用，并监测田间抗药性菌株的发生和分布情况，从而达到科学施药的目的。新的低毒农药和生物防治药剂的开发将为荔枝病害防治带来更多更好的选择，生物防治和农业防治新技术开发已经正在进行，而将来的田间施用可在一定程度上减少化学药剂用量。此外，RNA干扰策略能够有效地抑制病原菌的侵染过程，而该技术对荔枝霜疫霉的防效还不清楚。以关键致病基因为靶标的RNA干扰策略是潜在的病害防治新技术，筛选特异且高效的RNA干扰靶点将为病害防控提供新策略。

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