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茶树炭疽病菌侵染研究进展

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摘　要　为了解茶树响应炭疽病及抗炭疽病的遗传机理,本研究搜集了茶树炭疽病的发病规律与症状、茶树炭疽病原菌分类鉴定、炭疽菌侵染过程及其机制等在茶树上的研究成果,并结合其他植物上的相关报道进行总结。结果发现:茶树炭疽病致病菌多样,侵染致病过程复杂,导致致病菌鉴定困难。同时,茶树致病菌的侵染分子机制研究较少,在其它植物中主要与真菌代谢酶类、效应蛋白及真菌毒素等有关,但具体完整的分子调控机制仍不明确。后续需继续对侵染机制和寄主茶树-炭疽病原菌互作机制进行研究,加强田间病害检测技术的研究与推广,以期为茶树炭疽病的发病机制及早期判断、综合防治提供有效帮助。

关键词　茶树; 炭疽病; 分类鉴定; 发病规律; 侵染
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Research progress on tea anthracnose pathogen infection

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Abstract　To understand the genetic mechanism of response and resistance to anthracnose of tea plant, this study collected and summarized the progress on the pathogenesis and symptoms of tea plant anthracnose, the classification and identification of tea plant anthracnose pathogens, the infection process and mechanism of anthracnose, combined with the related reports on other plants. The results showed that: The pathogenic fungi of tea anthracnose were diverse and the infection process was very complicated, which resulted in difficult to identification of pathogenic fungi. Meanwhile, there were few studies on the molecular mechanism of infection to tea plants. However, existing studies were mainly related to fungal metabolic enzymes, effector proteins and mycotoxins in other plants, the molecular regulatory mechanism was still unclear. It is necessary to further study the infection mechanism and the interaction between host tea plant and anthracnose pathogens, and strengthen the field disease detection technology, so as to provide effective help for the infection regulation and its early diagnose, and comprehensive control of tea anthracnose.

Keywords　tea plant; anthracnose; identification; infestation

茶树(*Camellia sinensis* (L.) O. Kuntze)喜阴喜湿,在生长过程中易受到真菌、细菌、类菌原体、藻类、线虫和地衣苔藓等各种病原物的危害,我国茶树病害的种类约有130种,其中真菌病害就多达72 种[1]。炭疽病主要是由炭疽菌属(*Colletotrichum*)诱发,是危害茶树的重要真菌病害,在我国众多茶

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区多有发生[1]。目前对于茶树-炭疽病整体互作机制的研究仍不深入，特别是有关茶树炭疽病侵染机制的研究仍较少。因此，本研究总结了茶树炭疽病的发病规律、病原菌的鉴定方法，并结合其它植物上炭疽菌的侵染机制等相关研究，提出了茶树炭疽病侵染和致病机制以及茶树-炭疽病互作的研究方向，为今后茶树炭疽病的深入研究提供思路。

1　茶树炭疽病发病规律

茶炭疽病发病初期叶尖或叶缘产生暗绿色水渍状小点，后逐渐变为焦黄色，最终呈现出灰白色；病斑为半圆或不规则形，后期出现散生黑色粒点、无轮纹，发病后期叶片会枯死脱落，严重时导致茶树整株死亡[2]（图 1）。由于炭疽菌属病原菌的极端破坏性和广泛性，已被列为世界上十大最重要的植物病原真菌之一[3]。

影响炭疽病发生的重要气候因素是降雨和温度。当环境温度达到 20～30 ℃、相对湿度达到 80% 以上时，最有利于炭疽病原菌生长[1]。因此，炭疽病在梅雨季节或秋雨绵绵时节发生最严重。品种差异也会影响茶树对炭疽病的抗性，‘铁观音’‘福云 6 号’‘龙井 43’等品种更容易感染炭疽病[4-5]。Orrock 等[6]发现，‘Fairhope’‘Big Leaf’‘Small Leaf’3 个品种的病害程度都要低于‘Georgian’。除此之外，施肥等茶园管理措施也会影响炭疽病的发生，配方施肥或多施磷钾肥的茶园更容易受炭疽病困扰[2]。

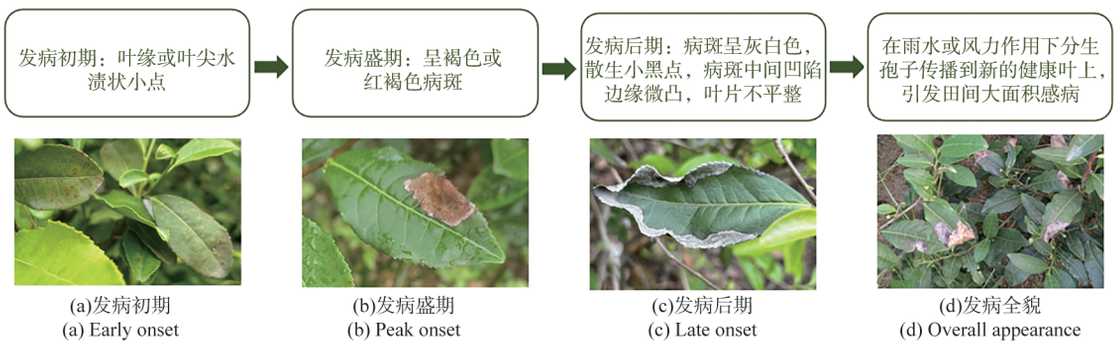

图 1　炭疽病发展过程

Fig. 1　Anthracnose development process

2　炭疽病原菌分类与鉴定

2.1　致病菌种类

我国各个产茶省份均有茶树炭疽病发生。Liu 等[7]从福建和浙江等 7 个省份的茶树炭疽病叶中仅分离鉴定到 6 个炭疽菌种，其中有已知种 *C. camelliae*、*C. fructicola*、*C. gloeosporioides*、*C. siamense* 和新发现种 *C. henanense* 和 *C. jiangxiense*，并认为 *C. camelliae* 是茶树炭疽病优势菌种，且具有寄主特异性。而 Wang 等[8]则从中国 15 个茶叶生产省的炭疽病病叶中分离得到 106 株炭疽病原菌，分布于 9 个已知种（*C. camelliae*、*C. cliviae*、*C. fioriniae*、*C. fructicola*、*C. karstii*、*C. siamense*、*C. aenigma*、*C. endophytica* 和 *C. truncatum*），1 个新发现种（*C. wuxiense*）和 1 个未鉴定种；其中 *C. camelliae*、*C. fructicola* 和 *C. siamense* 3 株致病菌株与 Liu 等[7]发现的一致，而 *C. camelliae* 在各茶区的病叶中被分离得到，危害多个茶树品种，是茶树炭疽病优势致病菌种[9]。Orrock 等[6]对在美国茶树中分离出的炭疽病原菌进行形态学和序列分析，发现该病菌与中国流行的 *C. camelliae* 分离株具有亲缘关系。中国台湾地区于 2021 年首次报道了由 *C. fructicola* 引起的茶树炭疽病[10]。

除了炭疽菌属（*Colletotrichum*）外，座盘孢属（*Discula*）是茶炭疽病的另一病原真菌。它起初在上世纪的日本被发现[11]，后被归入到炭疽菌属中[12]。但该菌的分生孢子要小于炭疽菌，形态结构有差异，且在 PDA 培养基上不产生附着胞结构。通过对不同真菌 28S rDNA 的 D1～D2 区域构建系统发育树分析，将其重新修订为座盘孢属[11]。基于形态学鉴定和内转录间隔区（ITS）测序，‘龙井 43’中也有该属炭疽菌的报道[8]，而日本的高花青素茶树品种‘Sunrouge’对座盘孢属病菌引发的炭疽病具有一定抗性[13]。

综上所述，不同茶产区、品种和发病时期所分离得到的炭疽病原菌及优势致病菌有所不同，也导

致病原菌鉴定困难。

2.2 病原菌鉴定

2.2.1 形态学鉴定

炭疽菌的传统鉴定方法主要是形态学鉴定，即依据菌落颜色和直径，色素的产生，菌丝生长速率，菌体形态特征、分生孢子盘、分生孢子和附着胞形态及大小、刚毛有无及形态等特征，并结合病原菌寄主范围进行鉴定[14]。研究表明，炭疽菌属菌落大多呈白色，气生菌丝致密，边缘整齐（图2），分生孢子透明、单孢、圆柱状。而*C. acutatum*因密生粉红色孢子，菌落呈粉红色，分生孢子形状呈梭型[7,15]。*D. theae-sinensis*的分生孢子透明，呈梭形或倒卵形[15]。炭疽菌的附着胞多为暗褐色，形态为梨形或姜瓣形，同属不同种的菌株在菌丝生长速度、产孢情况、分生孢子及附着胞形态大小等方面存在一定差异[16]。但形态学鉴定不能准确区分形态相似的同属菌种，在田间应多与病叶形态观察结合，从而初步判定诱发田间植物发病的病原菌。

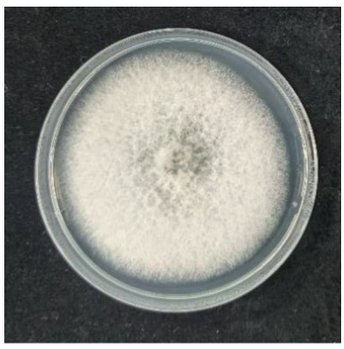

图2 胶孢炭疽菌菌落形态

Fig. 2 Colonial morphology of *Colletotrichum gloeosporioides*

2.2.2 单基因序列分析

rDNA-ITS序列具有广泛的序列多态性，常应用于真菌的分子鉴定和属内种间或种内差异较明显的菌群间的系统发育关系分析[17]。雷娇娇等[18]和彭成彬等[19]通过形态学鉴定和rDNA-ITS测序，明确了贵阳花溪九安和福建省4个茶区的茶树炭疽病优势病原菌为*C. gloeosporioides*。而从福建其他地区的不同品种茶树上分离得到的8株病原菌中只有1个菌株为*C. gloeosporioides*，其余7个菌株为*C. fructicola*；且这7株*C. fructicola*存在种内碱基突变或缺失，与*C. gloeosporioides*遗传距离相近[14]。然而，炭疽菌形态特征复杂多变，种内ITS序列相对一致，不表现多态性，可能会导致病原菌鉴定有误，且GenBank中存在错误序列，因此单基因ITS序列的鉴定结果也存在一定的不准确性[20]。

2.2.3 多基因序列分析

随着研究深入，多基因结合可以提高病原菌种类鉴定的准确率[21]。用于茶树炭疽菌种类鉴定的基因位点有钙调蛋白（Calmodulin，CAL）、几丁质合成酶（Chitin synthase 1，CHS-1）、3-磷酸甘油醛脱氢酶（Glyceraldehyde-3-phosphate dehydrogenase，GAPDH）、ITS、肌动蛋白（Actin，ACT）、β-微管蛋白（β-tubulin 2，TUB2）、谷氨酰胺合成酶（Glutamine synthetase，GS）、交配型基因（*ApMAT*）和超氧化物歧化酶-2（Superoxide dismutase-2，SOD2）[20]。刘威等[22]经过多基因分析，发现福州市不同品种茶树病叶上的5株病原菌株均为*C. siamense*。Lu等[23]利用多基因序列分析结合形态学特征，在浙江地区的茶树上鉴定得到2个菌种*C. camelliae*和*C. fructicola*，且*C. camelliae*的致病力更强。张莉等[24]通过ITS-GAPDH-CAL比对拼接后构建系统进化树，确定分离得到的病原菌株为*C. camelliae*。Chen等[15]结合形态学分析和ITS、TUB2多基因序列分析，首次报道了在我国重庆地区由*C. acutatum*引起的茶树炭疽病。贡长怡等[16]收集了中国12个省份的炭疽病叶并进行病原菌分离，结合形态学和多基因序列聚类分析发现供试株均为*C. gloeosporioides* complex，包括*C. fructicola*、*C. camelliae*、*C. siamense*和*C. aenigma*，其中*C. camelliae*分离频率最高。

可见茶炭疽病病原菌复杂多样，不同茶树品种、不同地区、不同发病进程和不同鉴定技术等获得的优势致病菌有所不同，为茶树抗炭疽病的机制研究增加了难度。

3 炭疽病侵染机制研究

宿主植物与病原的互作可以从病原菌侵染过程和植物的抗性免疫反应这2个方面进行研究。一旦病原菌识别穿透寄主植物，就很难根除病原感染[25]，因此研究炭疽病菌侵染机制很有必要。目前，茶炭疽病的相关研究主要集中在茶树抗性方面，本研究收集整理了其他植物中炭疽病原菌的侵染机制研究，以期对茶树炭疽病侵染研究提供参考。

3.1 炭疽菌的侵染过程

在风力和雨水等媒介下，炭疽菌分生孢子附着

到嫩叶背面的茸毛上，待环境条件适宜，分生孢子萌发，形成芽管；芽管先端形成附着胞，通过表皮的气孔或伤口处实现侵染定殖，导致叶片发病，逐渐形成病斑[26]。

炭疽病病原菌对茶树叶片的吸附是致病过程中的重要环节，其中附着胞的形成尤为关键。它吸附在叶片表面吸取营养，保护孢子直至其穿透寄主细胞[27]，并合成高浓度的胞内渗透活性物质以产生巨大压力。研究炭疽病病原菌附着胞形成的分子机制有助于提高对寄主茶树-真菌相互作用的分子机制的认识[28]。病原菌也会代谢产生酶类物质，如果胶酶（Pectinase）、纤维素酶（Cellulase）和角质酶（Cutinase）等，酶类物质会降解茶树的角质层和细胞壁的各类物质，更利于病菌侵染[3]。李晓丽等[29]通过共聚焦显微拉曼技术研究发现炭疽病菌的侵染会导致茶树叶片细胞壁拉曼光谱位移，强度与发病前存在显著差异，从而证明炭疽病原菌的侵染会导致叶片细胞壁化学成分发生明显变化。

一些重要的真菌信号通路，如异三聚体鸟嘌呤核苷酸结合蛋白（G 蛋白）[30-31]、环磷酸腺苷（cAMP）[32]和丝裂原活化蛋白激酶（MAPK）[33-35]等是附着胞形成和功能行使所必需的，黑色素对支撑附着胞结构的完整性和介导附着胞内压积累以穿透寄主具有重要作用。在附着胞形成的过程中，黑色素合成途径上的漆酶基因 *Cglac3* 的表达显著上调[36]；*Colac2* 调控附着胞黑色素和分生孢子色素积累，突变后导致炭疽菌致病力丧失[37]。目前已有较多有关炭疽菌附着胞形成的研究，但多集中在单一基因的作用，尚未能够明确解析其调控通路，表 1 中列举了近 5 年的部分报道。总的来说，参与炭疽菌附着胞形成的通路众多，作用机理复杂，具体的调控机制仍有待进一步挖掘。

表 1　近 5 年有关炭疽菌附着胞形成的相关研究报道

Table 1　Related research reports on the formation of appressorium of anthracnose in recent 5 years

参与途径 Involved pathway	具体调控机制 Regulation mechanism	参考文献 Reference
MAPK 信号通路 Mitogen-activated protein kinase signaling pathway	*CgMCK1* 编码 MAPKKK 蛋白，敲除突变体未能形成附着胞；*CgSte50*、*CgSte11* 和 *CgSte7* 参与调控 CgMPK1 的磷酸化，缺失突变体产生缺陷，丧失附着胞形成和致病性；*CgMsb2* 参与了丝裂原活化蛋白激酶 CgMk1 的磷酸化，*CgSho1* 不能单独激活 CgMk1，而是与 *CgMsb2* 合作激活 CgMk1。	[38]-[40]
cAMP 信号途径 Cyclic adenosine monophosphate	突变体不产生附着胞，外源添加 cAMP 或过表达 cAMP 信号途径，*ΔCgCMK1* 也不能恢复形成附着胞能力。	[41]
G 蛋白 G protein	*CgRGS3* 缺失突变体产孢率和附着胞形成率下降，黑色素产量降低。	[42]
活性氧 Reactive oxygen species	*CgCdc42* 参与活性氧（ROS）相关基因调控，突变体产生异常附着胞，致病力减弱；*CgNOXB* 和 *CgNOXR* 参与调节菌丝尖端和附着胞中 ROS 的产生和分布，控制肌动蛋白纤维（F-actin）的特化重塑，并参与真菌细胞壁的生物合成。	[43]-[44]
精氨酸合成途径 Arginine synthesis pathway	*CgCPS1* 通过编码氨甲酰磷酸合成酶参与精氨酸的生物合成，突变体附着胞形成缺陷。	[45]
组蛋白修饰 Histone modification	*CgHOS2*、*CfGcn5*、*CfSet1* 和 *CfSnt2* 参与组蛋白 H3 的去乙酰化，缺失突变体无法形成附着胞。	[46]-[49]
黑色素形成 Melanin formation	*CgNVF1* 参与黑色素形成（突变体菌丝白化，附着胞无法形成）。	[50]
其他 Others	*CgCAP20* 影响功能性附着胞发育，减少未成熟附着胞对寄主的渗透；*CgCOM1* 调控分生孢子萌发、胚管发育、附着胞形成和菌丝生长；*CgEnd3* 调控附着胞形成、黑化、胀压积累、附着胞穿透能力；*CgFim1* 参与附着胞中的肌动蛋白动力学和环状结构形成，以及影响菌丝尖端中肌动蛋白细胞骨架的极性；*CoMTF4* 在附着胞发育过程中的植物源性信号转导中发挥作用；*Cglac13* 参与 *C. gloeosporioides* 芽管和附着胞的形成、菌丝生长和木质素降解的调控；*CfCpmd1* 缺失突变体菌丝生长缓慢，无法形成附着胞。	[51]-[56]

炭疽菌有2种侵染模式：一种是菌丝侵入寄主细胞后立即吸取营养，并立即产生次级菌丝危害寄主细胞，从而进入死体营养型阶段（图3(a)）；菌丝可穿透鲜嫩部位表层，潜伏1～2周后，缓慢形成病斑[57]。另一种是菌丝侵入细胞后，先大范围侵染寄主细胞，待占领了大量寄主细胞后，再由密布的初级菌丝产生大量次级菌丝，进而显现扩大病斑（图3(b)）。油茶炭疽菌（*C. fructicola*）也可从叶片表面气孔直接进入植物体内，而不穿透角质层[58]。

3.2 炭疽病侵染致病分子机制

炭疽病侵染在其它植物中主要与真菌代谢酶类、效应蛋白及真菌毒素等有关。

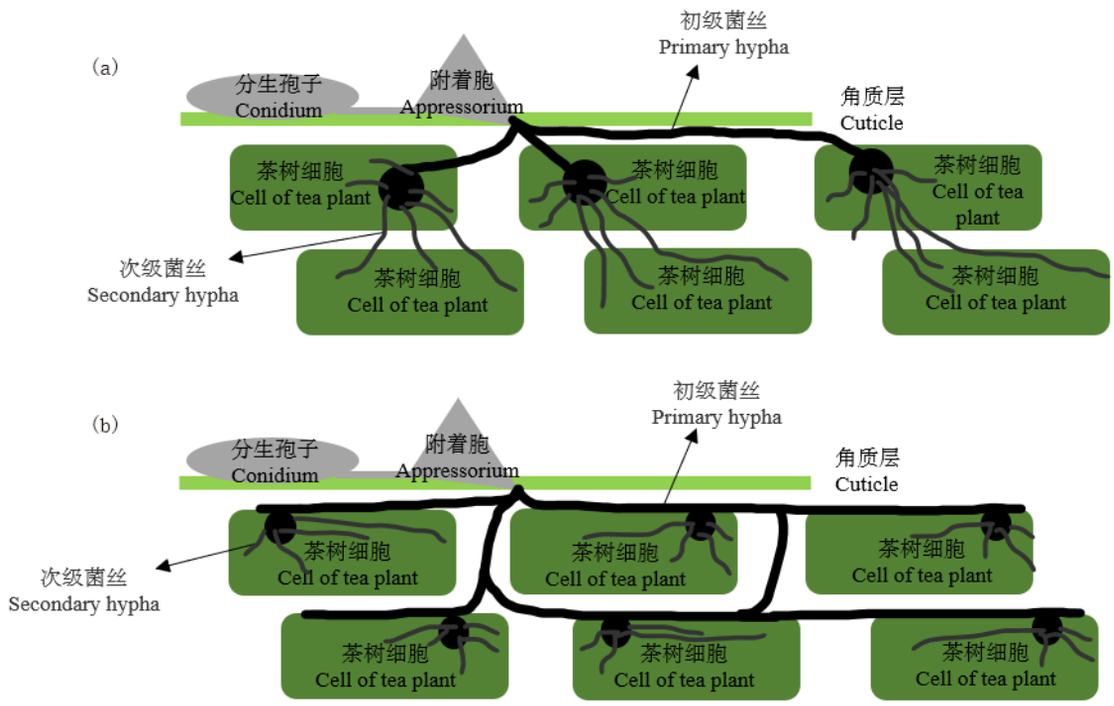

图3 炭疽菌2种侵染过程简易示意图

Fig. 3 Simple diagram of two infection processes of *Colletotrichum*

3.2.1 真菌代谢酶类

炭疽菌在侵染过程中代谢产生的酶类能够降解茶树叶片的角质层和细胞壁，降低茶树抵抗病原菌侵染的能力。*C. gloeosporioides*在附着胞形成侵染钉阶段分泌角质酶水解寄主细胞的角质多聚物从而突破叶片表皮实现侵染[59-61]，且不同的菌株产生的角质酶存在分化现象[62]；而缺失分泌角质酶能力的*C. gloeosporioides*突变体不能对健康番木瓜进行侵染致病[63]。此外，研究发现*C. gloeosporioides*在油茶和香蕉中的致病力还受到纤维素酶、果胶酶和漆酶的影响[64-65]。在微生物侵染植物的过程中，果胶酶可以降解植物细胞壁便于微生物在植物体内定殖，同时释放单糖或寡糖提供营养[66]。外源添加果胶酶和纤维素酶会加速受炭疽病胁迫的植物体病情发展，但不会增加寄主范围[67]。炭疽菌的果胶酸裂解酶基因*pelA*和*pelB*是重要的致病因子，敲除后炭疽菌对鳄梨和番茄等植物的侵染能力明显下降[68-69]。

3.2.2 效应蛋白

效应蛋白也是植物病原真菌的重要致病因子之一，在炭疽菌侵染植物体的过程大量合成。炭疽菌属效应蛋白的数量和种类因菌种而异，但约20%的核心效应蛋白存在于每个炭疽菌物种中，70%的保守效应蛋白具有直系同源物，每个炭疽菌属物种

含有4.1%～15.6%的物种特异性效应蛋白[70]。不同的候选效应蛋白(Candidate effector proteins, CEPs)发挥不同作用,分别在附着胞、初生活体菌丝和活体-死体营养转换阶段表达[71]。根据它们的亚细胞定位,效应蛋白可以分为在细胞外空间起作用的质外体效应蛋白和在宿主细胞内起作用的细胞内效应蛋白[72]。

在病原菌相关分子模式触发免疫(PAMP-triggered immunity, PTI)中,植物识别病原菌上的保守分子,从而诱发识别PAMP的植物模式识别受体(PRR)与膜定位的受体样激酶(RLK)、受体样细胞质激酶(RLCK)缔合以传导防御信号并触发免疫应答[73]。而病原菌则分泌效应蛋白调节和阻断植物信号传导,抑制寄主的PTI防御系统,阻止植物体抗性基因识别和防御这些毒性效应蛋白,同时触发效应因子诱导的免疫反应(Effector-triggered immunity, ETI),随后病原菌又产生新的效应蛋白,攻击寄主的防御系统[74-76]。

CEC3、NIS1和EC92作为核心保守效应蛋白,在多个菌种中均能够诱导细胞死亡[77-79]。CgDN3在*C. gloeosporioides*、*C. higginsianum*和*C. orbiculare*中分离并在侵染某个阶段特异表达,具有促进侵染的作用,敲除*CgDN3*基因的突变体的致病力显著下降[71,80]。此外,*C. truncatum*中的CtNUDIX[81]、*C. lentis*的CtToxB[82]和*C. gloeosporioide*的CFEM(Common in fungal extracellular membrane)效应蛋白Cghn13279和Cghn13471[83],*C. higginsianum*的ChEC91[84]等效应蛋白均可诱导寄主细胞坏死;其中CtNUDIX可能调控病原菌的活体-死体营养阶段转换,而ClToxB则可能是对寄主起作用的选择性毒素。禾谷炭疽菌(*C. graminicola*)的关键效应蛋白CgEP1含有功能性核定位信号和DNA结合结构域,可能参与调控寄主基因转录活性[85]。*CgBASP2*基因通过调控菌丝生长和机械穿透力调控*C. gloeosporioides*的侵染能力[86]。过表达效应蛋白PXLR131能够增强*C. gloeosporioides*的致病性[87]。

几丁质是所有病原真菌细胞壁中的重要成分,并作为微生物相关分子模式(MAMPs),可被植物几丁质受体识别以激活多种由MAMP触发的免疫反应[88]。炭疽病原菌会分泌相应的效应蛋白与该受体结合进而保护几丁质免受识别,或者降解寄主几丁质酶来抑制其对病原菌几丁质的捕获。炭疽菌效应蛋白中细胞溶解酶基序(Lysin motif, LysM)结构域对于几丁质结合来说是必需的,但含有该结构域的效应蛋白的作用方式不同。LysM胞外蛋白ELP1和ELP2可能通过结合几丁质来抑制几丁质激发子激活的免疫反应[89]。*C. graminicola*产生的Cgfl能够降解植物的几丁质酶[90]。CgNLP1能够靶向抑制寄主的R2R3型转录因子HbMYB88-like的核积累[91];而CgSntf2则能够减少胼胝质沉积和H_2O_2积累,并靶向结合苹果的叶绿体PSII组装因子Mdycf39,干扰植物的防御反应[92],进而促进对寄主的侵染。

炭疽菌效应蛋白的发现与功能挖掘对于植物-炭疽菌互作机制研究具有重要意义。然而,现有研究对这些效应物在植物上的作用靶点和具体分子机制还处于较浅显的阶段,而且炭疽菌效应物在病原体-植物相互作用过程中的分泌和递送机制尚不明确。鉴定效应物并明确靶向作用模式,将为炭疽菌效应蛋白毒力功能的分子机制研究提供参考,有助于开发防治炭疽病的新策略。

3.2.3　真菌毒素

在炭疽菌的死体营养阶段,炭疽菌会通过分泌真菌毒素来促进寄主植物的坏死。真菌毒素是对植物病程有决定性影响的有毒物质[93],其作用机理复杂。目前,对炭疽菌属毒素的研究主要集中在生化成分测定以及抗病材料的初步筛选。油茶炭疽病原菌(*C. camelliae* Massee)的毒素是多聚糖类物质[94],枸杞炭疽病原菌是一种不能被透析掉的蛋白聚糖类物质[95],而西瓜炭疽菌(*C. orbiculare* (Berk.) Arx)则是一种非蛋白物质[96]。茶树的真菌毒素也可能是非蛋白物质,且提取的毒菌滤液能使茶树叶片形成病斑[97],炭疽菌毒素的代谢通路和作用机制仍有待进一步研究。

总之,炭疽菌在侵染致病过程中涉及的形态变化、物质分泌、基因调控和信号通路等机制十分复杂,在茶树中涉及的分子机制研究较少,以上3种机制是否在茶树中存在且具有一致性尚未可知。明确病原真菌间以及它们与寄主植物间的相互关系,对茶叶生产中炭疽病害的精准预判和有效防治具有重要意义。

4　研究展望

综上所述,茶树炭疽病的鉴定和侵染研究已经

取得一定进展,但有几个关键问题仍未有突破性进展。

1)炭疽菌侵染机制不够深入。尽管对于炭疽菌侵染的研究取得一定进展,但炭疽病原菌种类复杂、致病能力受多种因素影响导致侵染过程复杂,炭疽病侵染致病机制研究仍有突破的空间,而已有研究也为茶树-炭疽病互作和田间防治技术提供坚实基础。

2)茶树-炭疽病互作关系尚不明确。对于茶树-炭疽病互作关系的研究是开展生物防治和抗性育种的关键前提。尽管有关茶树对炭疽病防御机制的研究已经开展,咖啡碱通路和儿茶素通路等相关研究已取得一定进步,但茶树炭疽病防御机制相关机理的研究仍处于初步阶段。

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