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琯溪蜜柚炭疽病刺盘孢属种类鉴定及其致病性研究

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摘 要:【目的】明确引起琯溪蜜柚炭疽病的刺盘孢属种类及其致病力差异,为该病害的有效防控提供科学依据。**【方法】**采集福建省平和县13个乡镇琯溪蜜柚炭疽病典型病样进行组织分离,利用形态学和分子生物学等方法对分离菌株进行种类鉴定及致病性研究。**【结果】**共获得350株刺盘孢属真菌,从中选取培养性状有较大差异的58株刺盘孢属真菌进行形态学观察和多基因(ITS、*ACT*、*TUB2*、*GAPDH*及*GS*)系统发育分析,结果表明,其分属于胶胞炭疽菌复合种下的胶孢炭疽菌(*Colletotrichum gloeosporioides*)和果生炭疽菌(*C. fructicola*)、博宁炭疽菌复合种下的喀斯特炭疽菌(*C. karstii*)、平头炭疽菌复合种下的平头炭疽菌(*C. truncatum*)、*C. magnum*复合种下的短孢炭疽菌(*C. brevisporum*)以及*C. orchidearum*复合种下的兰花炭疽菌(*C. cliviicola*)。采用叶片和枝条有伤接种孢子悬浮液法,结果表明,除兰花炭疽菌(*C. cliviicola*)外的其他5种刺盘孢属真菌都可使琯溪蜜柚叶片和枝条致病,但致病力存在明显差异。病原菌菌丝生长速率、附着胞形成率与致病力相关性分析发现,相关系数分别为0.373 3和0.364 1,表明菌丝生长速率及附着胞形成率与致病力之间均呈弱相关性。**【结论】**琯溪蜜柚炭疽病的病原菌有胶孢炭疽菌、果生炭疽菌、喀斯特炭疽菌、短孢炭疽菌、平头炭疽菌(*C. truncatum*),其中胶孢炭疽菌(*C. gloeosporioides*)为病原优势种,果生炭疽菌、喀斯特炭疽菌、短孢炭疽菌和平头炭疽菌是新病原,证实了福建省琯溪蜜柚炭疽病病原菌具有多样性。不同病原菌的菌丝生长速率及附着胞形成率与致病力均呈弱相关性。

关键词:琯溪蜜柚;炭疽病;刺盘孢属真菌;致病性

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Identification and pathogenicity of *Colletotrichum* species associated with Guanximiyou pomelo anthracnose

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Abstract:【Objective】Guanximiyou pomelo (*Citrus grandis*) is a famous and popular *Citrus* species for its sweet and excellent nutrients native to Pinghe county of Fujian province, China. In Guanximiyou pomelo, anthracnose caused by *Colletotrichum* spp. is a serious disease limiting its production. In 2018, the disease seriously affected over 60% of Guanximiyou pomelo trees in an orchard in Pinghe county. The Guanximiyou pomelo anthracnose mainly damages leaves, twigs and fruits. In the edge, tip or middle of damaged leaves develop brown spots, which form a "V" shape then withering and falling off after the diseased leaves die. The damaged twigs show spots from the petiole and the base of axillary bud to the bottom of twigs. On fruit, symptoms appear as green, irregular and sunken lesions in the young stage, that turn to brown rot and then falling off in mature stage. This study aimed to clarify the species of *Colletotrichum* spp. associated with Guanximiyou pomelo anthracnose and determine the pathogenic characteristics of the pathogens, so as to provide a better acknowledge for the diversity of the pathogen species and scientific basis for the prevention and control of the disease in Fujian province.【Methods】

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A survey of anthracnose disease was conducted in 13 Guanximiyou pomelo orchards from 2019 to 2021 in Pinghe county, Fujian province. The leaves, twigs and fruit with symptoms were collected from the pomelo trees and were used as disease samples. The *Colletotrichum* spp. were isolated by the plant tissue isolation method. 4×4 mm diseased tissues were surface-sterilized with 70% ethanol for 30 s, 0.1% mercuric chloride for 60 s, washed three times in sterile water and dried on sterilized filter paper, then placed onto potato dextrose agar (PDA) plates and incubated under 28 ℃ in the dark. The single mycelium was used for purifying strains, and pure cultures were stored in PDA at 4 ℃. The colony characteristics, conidia morphology and appressorium for representative strains of the identified *Colletotrichum* spp. were recorded. The *Colletotrichum* spp. genomic DNA was extracted using a fungus genomic DNA extraction kit, which was identified through partial rDNA-ITS (ITS), actin (*ACT*), beta-tubulin (*TUB2*), glyceraldehyde-3-phosphate dehydrogenase (*GAPDH*), and glutamine synthetase (*GS*) region sequence. Phylogenetic tree based on the combined ITS-*ACT*-*TUB2*-*GAPDH*-*GS* sequences was constructed by maximum like-lihood method with MEGA 7.0. The conidia suspension of 58 representative *Colletotrichum* spp. were used in the pathogenicity tests to inoculate twigs and leaves of Guanximiyou pomelo according to Koch's postulate. Correlation analysis of mycelial growth rate, appressorium formation rate and pathogenicity were determined by Pearson method.【Results】A total of 350 strains with the similar morphology to *Colletotrichum* spp. were isolated from the collected samples infected by the Guanximiyou pomelo anthracnose disease. *C. gloeosporioides* species complexes, *C. boninense* species complexes, *C. truncatum* species complexes, *C. magnum* species complexes and *C. orchidearum* species complexes were identified based on morphological characteristics and ITS sequencing. Colony observation showed that there were significant differences in aerial and substrate mycelia's color among the five *Colletotrichum* species complexes. *C. gloeosporioides* species complexes, *C. boninense* species complexes, *C. truncatum* species complexes, *C. magnum* species complexes and *C. orchidearum* species complexes had thirteen, thirty, one, nine, five different colony characteristics, respectively. Conidia of *C. truncatum*, and *C. orchidearum* species complexes were significant different from the other three *Colletotrichum* species complexes. Conidia of *C. orchidearum* species complexes was curve and rounded at both ends, which was sickle and acuminate at both ends by *C. truncatum* species complexes, and the other three *Colletotrichum* species complexes were cylindrical, rounded at both ends or top end rounded, base end raised. To classify the taxonomic status of the *Colletotrichum* spp., the multi-genes (ITS, *ACT*, *TUB2*, *GAPDH* and *GS*) were used to build phylogenetic tree of 58 *Colletotrichum* isolates with different colony characteristics. Among the 58 *Colletotrichum* isolates, one was identified to be *C. gloeosporioides*, twelve were *C. fructicola*, thirty were *C. karstii*, nine were *C. brevisporum*, five were *C. cliviicola* and one was *C. truncatum*. Pathogenicity tests revealed that the above five *Colletotrichum* spp. induced lesions on both twigs and leaves of Guanximiyou pomelo, with *C. cliviicola* being the sole non-pathogenic exception. The strains isolated from infected sites were identical to the strains inoculated. The pathogenicity of *C. gloeosporioides* was slightly stronger than *C. fructicola*, but significantly stronger than the other three species. BZMYTJ20 demonstrated significantly stronger pathogenicity than JFMYTJ53, while DXMYTJ5 had no pathogenicity in leaf infection assays, although they all belonged to *C. karstii*. The mycelial growth rates of those pathogens ranged from 6.27 to 13.53 $mm \cdot d^{-1}$. *C. gloeosporioides* was the fastest, followed by *C. fructicola*, *C. brevisporum* and *C. truncatum*, while *C. karstii* was the slowest. The appressorium formation rate of those pathogens ranged from 33.65% to 82.52%; *C. gloeosporioides* was the highest, followed by *C. brevisporum*, *C. fructicola* and *C. karstii*, and *C. truncatum* was the lowest. By analyzing the correlation between mycelium growth rate and ap-

pressorium formation rate and pathogenicity, the correlation coefficient r = 0.373 3 and 0.364 1, so it was clear there were some positive correlation between mycelial growth rate, appressorium formation rate and pathogenicity.【Conclusion】Based on colony and morphological characteristics, phylogenetic analysis of the multiple genes (ITS, *ACT*, *TUB2*, *GAPDH* and *GS*) and pathogenicity, the pathogens of Guanximiyou pomelo anthracnose disease in Fujian were identified as 5 species, including *C. gloeosporioides*, *C. fruticola*, *C. karstii*, *C. brevisporum* and *C. truncatum*, among which *C. gloeosporioides* was the dominant. *C. fruticola*, *C. karstii*, *C. brevisporum* and *C. truncatum* were first identified as the Guanximiyou pomelo anthracnose pathogen in Fujian province, which confirmed that the pathogens of Guanximiyou pomelo anthracnose tended to be diversified and differentiated in Fujan province. There were great differences in the growth rate of mycelium, appressorium formation rate and pathogenicity among different *Colletotrichum* species, and there was some positive correlation between mycelial growth rate, appressorium formation rate and pathogenicity. This study can provide theoretical data for the diversity research and sustainable prevention and control of Guanximiyou pomelo anthracnose in Fujan province.

Key words: Guanximiyou pomelo; Anthracnose; *Colletotrichum* spp.; Pathogenicity

琯溪蜜柚[Guanxi honey pomelo（*Citrus grandis*）]是福建省重要的柑橘属经济作物，平和县种植面积达48 333.33 hm^2，为中国琯溪蜜柚第一大种植县。作为中国名特优柚类品种，蜜柚产业对福建省平和县的经济发展起着至关重要的作用[1-2]。琯溪蜜柚炭疽病是由刺盘孢属（*Colletotrichum* spp.）真菌引起的一种重要病害，在平和县琯溪蜜柚种植区普遍发生，病重果园发病率超过60%，主要危害叶片、枝梢、花及果实[3]。叶片受害通常发生在叶缘、叶尖或主脉，产生褐色病斑，病部枯死后多呈“V”字形，最后枯萎脱落；枝梢受害一般从叶柄、基部腋芽处开始产生病斑，随后发展至枝条，枝条自上而下枯死；染病花蕾呈褐色腐烂状，导致落花；果实受害初期出现暗绿色油渍状不规则病斑，幼果易脱落，成熟果变褐腐烂并导致落果，还可在贮藏期发生，引起果实腐烂[4]。

据国内外报道，引起柑橘类作物炭疽病的病原种类有胶孢炭疽菌复合种、尖孢炭疽菌复合种、平头炭疽菌复合种、博宁炭疽菌复合种、长真孢炭疽菌复合种、*C. orchidearum*复合种、*C. magnum*复合种和热带生炭疽菌（*C. tropicicola*）单系种等[5-7]。其中，胶孢炭疽菌复合种下的胶孢炭疽菌（*C. gloeosporioides*）是目前报道最多的种，在世界柑橘产区均可发生，为柑橘炭疽病的主要病原菌，对柑橘产业危害最大[8-10]。

刺盘孢属真菌种类繁多，具有多个复合种群，复合群下有多个单系种，种间形态差异微小，单独依据形态学特征对刺盘孢属真菌进行分类鉴定存在较大的困难[11-12]；刺盘孢属真菌的ITS序列保守性过强，对于多数近缘种构建的系统发育树在关键进化节点支持率低，ITS在该属的系统分类研究中同样存在一些局限性[13]。近年来，以形态特征为基础，结合致病性测定与多基因联合聚类分析的多相法已被广泛应用于柑橘炭疽病病原菌的分类研究[14-15]。Wang等[7]采用形态特征观察结合多基因系统发育分析和致病性测定，将华盛顿脐橙炭疽病病原菌鉴定为胶孢炭疽菌（*C. gloeosporioides*）、果生炭疽菌（*C. fructicola*）、澳大利亚炭疽菌（*C. australianum*）、喀斯特炭疽菌（*C. karstii*）和可可炭疽菌（*C. theobromicola*）。

笔者课题组前期研究发现，引起琯溪蜜柚炭疽病的病原菌为胶孢炭疽菌（*C. gloeosporioides*）[3]，但目前尚未见关于该病的病原种类多样性及致病力分析方面的研究报道。为明确琯溪蜜柚炭疽病的病原种类多样性，笔者在本研究中采集琯溪蜜柚炭疽病典型病样进行刺盘孢属真菌分离、形态特征观察及多基因系统发育分析，并对其进行致病性测定研究。研究结果可为深入研究琯溪蜜柚炭疽病的病原菌致病机制以及制定行之有效的防治措施提供理论依据。

1　材料和方法

1.1　材料

2019年至2021年，在福建省平和县13个乡镇

的琯溪蜜柚炭疽病发生严重的果园进行系统调查，观察蜜柚炭疽病在新梢抽发期及果实膨大期的田间症状特点。采集具有典型症状的发病样品，将不同发病症状的样品分别用塑封袋密封并于当天带回实验室及时分离。

1.2 方法

1.2.1 菌株分离纯化 在新鲜病样的病健交界处切取4 mm×4 mm大小的组织块，依次用70%乙醇表面消毒30 s，0.1%升汞消毒60 s，无菌水漂洗3次，于无菌滤纸上晾干后，置于PDA平板上，28 ℃恒温黑暗培养，待长出菌落后，挑取菌落边缘单菌丝于新的PDA平板上进行纯化。将纯化后的菌株分别置于PDA斜面上4 ℃保存和滤纸片上−20 ℃保存备用。

1.2.2 培养性状和形态特征观察 挑取各菌株的菌丝接种至PDA平板中央，28 ℃黑暗培养，每天记录观察菌落的生长情况并测量菌落直径。待菌株长满平板时将其表面划伤诱导产孢，用接种针挑取分生孢子于滴有无菌水的载玻片上，在光学显微镜下观察分生孢子的形态特征。取60 μL分生孢子悬浮液滴于无菌凹槽载玻片上，置于25 ℃黑暗培养12 h，在光学显微镜下观察附着胞形态特征，同时计算附着胞形成率。附着胞形成率/%=附着胞形成孢子数/调查总孢子数×100。

1.2.3 多基因系统发育分析 刮取PDA平板上28 ℃培养7 d的菌丝，用SK8259试剂盒提取供试菌株基因组DNA，用于PCR扩增的模板。采用引物ITS1/ITS4[16]、ACT-512F/ACT-783R[17]、Bt2a/Bt2b[18]、GDF/GDR[19]和GSF1/GSR2[20]分别扩增菌株的内转录间隔区（ITS）序列及β-微管蛋白（TUB2）、肌动蛋白（ACT）、3-磷酸甘油醛脱氢酶（GAPDH）和谷氨酰胺合成酶（GS）基因的部分序列，具体引物信息见表1。PCR反应体系和扩增程序参考前人的研究方法[16-20]。将PCR扩增产物在1%的琼脂糖凝胶上电泳，在紫外灯下，切取目的片段，使用凝胶纯化试剂盒（AXYGEN）纯化回收DNA片段。所有引物由生工生物工程（上海）股份有限公司合成，并完成测序。

在GenBank（https://www.ncbi.nlm.nih.gov/）数据库使用BLAST搜索比对，下载与本研究中相似性较高的刺盘孢属真菌序列作为参考（具体菌株编号及序列登录号见表2）。使用DNAMAN9.0软件对本研究中得到的基因序列与GenBank中下载的刺盘孢属真菌序列进行多重比对和分析，必要时用MEGA 7.0对序列进行手工校正。采用软件PhyloSuite v1.2.2将所有比对好的ITS、*ACT*、*TUB2*、*GAPDH*和*GS*基因序列首尾串联。采用最大似然法（Maximum Likelihood，ML），使用MEGA 7.0构建系统发育树，用自展检验法以1000次重复计算分支支持率。

表1 基因引物名称及序列

Table 1 Gene primer name and sequence

基因名称 Gene name	引物 Primer	序列（5'−3'） Sequence (5'−3')
ITS	ITS1	TCCGTAGGTGAACCTGCGG
	ITS4	TCCTCCGCTTATTGATATGC
ACT	ACT-512F	ATGTGCAAGGCCGGTTTCGC
	ACT-783R	TACGAGTCCTTCTGGCCCAT
TUB2	Bt2a	GGTAACCAAATCGGTGCTGCTTTC
	Bt2b	ACCCTCAGTGTAGTGACCCTTGGC
GAPDH	GDF	GCCGTCAACGACCCCTTCATTGA
	GDR	GGGTGGAGTCGTACTTGAGCATGT
GS	GSF1	ATGGCCGAGTACATCTGG
	GSR1	GAACCGTCGAAGTTCCAC

1.2.4 致病性测定及致病力评估 根据柯赫氏法则将分离获得的刺盘孢属真菌进行致病性测定，采用孢子悬浮液刺伤接种离体叶片和枝条、活体叶片。以健康无伤、成熟度好、大小相近的琯溪蜜柚嫩叶和枝条以及健康幼苗为接种材料，洗去表面灰尘后用75%乙醇表面消毒，无菌水冲洗3次，自然风干。用无菌昆虫针（Φ=0.5 mm）刺伤嫩叶和枝条表面（深度约1 mm），向伤口表面喷洒孢子悬浮液（浓度为1×10^6孢子•mL^{-1}），每个菌株接种叶片9枚，枝条9个，3次重复，以接种无菌水为对照。待悬浮液自然风干后将离体叶片和枝条置于塑料盒中，放入25 ℃、12 h/12 h光暗交替、相对湿度90%的人工气候箱保湿培养，蜜柚苗接种后置于温室大棚。期间观察并记录发病情况，发病后从病斑上再分离、纯化菌株。采用十字交叉法测量病斑直径，根据不同分离株的病斑大小，评估致病力。

1.2.5 病原菌菌丝生长速率、附着胞形成率与致病性相关性分析 利用Excel对菌丝生长速率、附着胞形成率与致病力相关性进行分析，$0<|r|\leqslant0.3$，无相关性；$0.3<|r|<0.8$，弱相关性；$|r|\geqslant0.8$，强相关性。

2 结果与分析

2.1 刺盘孢属真菌分离纯化

从平和县13个乡镇（小溪镇、山格镇、文峰镇、

表 2　本研究用于系统发育分析的菌株序列信息

Table 2　List of isolates of *Colletotrichum* species used for phylogenetic analyses in this study

菌种名 Species name	分离物编号 Isolate No.	寄主 Host	来源 Origin	基因序列登录号 GenBank accession number				
				ITS	*ACT*	*TUB2*	*GAPDH*	*GS*
C. gloeosporioides	CG1	*Punica granatum*	Albania	MT300326	MT332146	MT332145	MT332147	MT332150
	ZH3	/	China	MT476850	MT500918	MT501094	MT501050	MW344714
	C-47	*Capsicum annuum*	India	MG282160	MG729649	MG383569	MG729659	MG729657
	JFMYTJ34	**Guanximiyou pomelo**	**China**	**PQ624726**	**PQ603050**	**PQ616674**	**PQ616558**	**PQ616616**
C. fructicola	ZH6	*Cyclocaryay paliurus*	China	MT476840	MT500908	MT501084	MT501040	MW344704
	HNLD-10	Strawberry	China	MK629873	MK675237	MK681417	MK675259	MK681395
	YCH32	*Jasminum nudiflorum*	China	MT626035	MT741778	MT683674	MT741781	PQ046875
	AHMYTJ2	**Guanximiyou pomelo**	**China**	**PQ624695**	**PQ603019**	**PQ616643**	**PQ616527**	**PQ616585**
	NSMYTJ4	**Guanximiyou pomelo**	**China**	**PQ624697**	**PQ603021**	**PQ616645**	**PQ616529**	**PQ616587**
	WZMYTJ7	**Guanximiyou pomelo**	**China**	**PQ624700**	**PQ603024**	**PQ616648**	**PQ616532**	**PQ616590**
	BZMYTJ23	**Guanximiyou pomelo**	**China**	**PQ624714**	**PQ603038**	**PQ616662**	**PQ616546**	**PQ616604**
	GQMYTJ26	**Guanximiyou pomelo**	**China**	**PQ624717**	**PQ603041**	**PQ616665**	**PQ616549**	**PQ616607**
	LXMYTJ29	**Guanximiyou pomelo**	**China**	**PQ624720**	**PQ603044**	**PQ616668**	**PQ616552**	**PQ616610**
	SGMYTJ35	**Guanximiyou pomelo**	**China**	**PQ624727**	**PQ603051**	**PQ616675**	**PQ616559**	**PQ616617**
	XZMYTJ37	**Guanximiyou pomelo**	**China**	**PQ624729**	**PQ603053**	**PQ616677**	**PQ616561**	**PQ616619**
	WFMYTJ40	**Guanximiyou pomelo**	**China**	**PQ624732**	**PQ603056**	**PQ616680**	**PQ616564**	**PQ616622**
	WFMYTJ48	**Guanximiyou pomelo**	**China**	**PQ624740**	**PQ603064**	**PQ616688**	**PQ616572**	**PQ616630**
	GQMYTJ55	**Guanximiyou pomelo**	**China**	**PQ624747**	**PQ603071**	**PQ616695**	**PQ616579**	**PQ616637**
	CLMYTJ59	**Guanximiyou pomelo**	**China**	**PQ624750**	**PQ603074**	**PQ616698**	**PQ616582**	**PQ616640**
C. karstii	HUNTJLYC8	*Camellia oleifera*	China	MF615464	MF615469	MF615484	MF615474	MF615479
	OCAC4	*Small cardamom*	India	KJ813595	KJ813445	KJ813470	KJ813545	KJ813570
	GZAAS5.09501	*Citrus sinensis*	China	JQ247629	JQ247653	JQ247641	JQ247605	JQ247618
	DXMYTJ5	**Guanximiyou pomelo**	**China**	**PQ624698**	**PQ603022**	**PQ616646**	**PQ616530**	**PQ616588**
	AHMYTJ11	**Guanximiyou pomelo**	**China**	**PQ624704**	**PQ603028**	**PQ616652**	**PQ616536**	**PQ616594**
	DXMYTJ13	**Guanximiyou pomelo**	**China**	**PQ624705**	**PQ603029**	**PQ616653**	**PQ616537**	**PQ616595**
	CLMYTJ15	**Guanximiyou pomelo**	**China**	**PQ624707**	**PQ603031**	**PQ616655**	**PQ616539**	**PQ616597**
	GQMYTJ18	**Guanximiyou pomelo**	**China**	**PQ624710**	**PQ603034**	**PQ616658**	**PQ616542**	**PQ616600**
	BZMYTJ20	**Guanximiyou pomelo**	**China**	**PQ624711**	**PQ603035**	**PQ616659**	**PQ616543**	**PQ616601**
	XXMYTJ21	**Guanximiyou pomelo**	**China**	**PQ624712**	**PQ603036**	**PQ616660**	**PQ616544**	**PQ616602**
	AHMYTJ22	**Guanximiyou pomelo**	**China**	**PQ624713**	**PQ603037**	**PQ616661**	**PQ616545**	**PQ616603**
	SGMYTJ25	**Guanximiyou pomelo**	**China**	**PQ624716**	**PQ603040**	**PQ616664**	**PQ616548**	**PQ616606**
	WZMYTJ28	**Guanximiyou pomelo**	**China**	**PQ624719**	**PQ603043**	**PQ616667**	**PQ616551**	**PQ616609**
	GQMYTJ32	**Guanximiyou pomelo**	**China**	**PQ624723**	**PQ603047**	**PQ616671**	**PQ616555**	**PQ616613**
	WFMYTJ33	**Guanximiyou pomelo**	**China**	**PQ624724**	**PQ603048**	**PQ616672**	**PQ616556**	**PQ616614**
	WZMYTJ34	**Guanximiyou pomelo**	**China**	**PQ624725**	**PQ603049**	**PQ616673**	**PQ616557**	**PQ616615**
	BZMYTJ36	**Guanximiyou pomelo**	**China**	**PQ624728**	**PQ603052**	**PQ616676**	**PQ616560**	**PQ616618**
	NSMYTJ38	**Guanximiyou pomelo**	**China**	**PQ624730**	**PQ603054**	**PQ616678**	**PQ616562**	**PQ616620**
	NSMYTJ41	**Guanximiyou pomelo**	**China**	**PQ624733**	**PQ603057**	**PQ616681**	**PQ616565**	**PQ616623**
	WZMYTJ42	**Guanximiyou pomelo**	**China**	**PQ624734**	**PQ603058**	**PQ616682**	**PQ616566**	**PQ616624**
	XZMYTJ43	**Guanximiyou pomelo**	**China**	**PQ624735**	**PQ603059**	**PQ616683**	**PQ616567**	**PQ616625**
	JFMYTJ44	**Guanximiyou pomelo**	**China**	**PQ624736**	**PQ603060**	**PQ616684**	**PQ616568**	**PQ616626**
	GQMYTJ45	**Guanximiyou pomelo**	**China**	**PQ624737**	**PQ603061**	**PQ616685**	**PQ616569**	**PQ616627**
	XZMYTJ46	**Guanximiyou pomelo**	**China**	**PQ624738**	**PQ603062**	**PQ616686**	**PQ616570**	**PQ616628**
	CLMYTJ47	**Guanximiyou pomelo**	**China**	**PQ624739**	**PQ603063**	**PQ616687**	**PQ616571**	**PQ616629**
	WZMYTJ49	**Guanximiyou pomelo**	**China**	**PQ624741**	**PQ603065**	**PQ616689**	**PQ616573**	**PQ616631**

注：本研究所获得菌株加粗表示。

Note: The isolates obtained in this study are expressed in bold.

表 2 （续） Table 2 (Continued)

菌种名 Species name	分离物编号 Isolate No.	寄主 Host	来源 Origin	基因序列登录号 GenBank accession number				
				ITS	*ACT*	*TUB2*	*GAPDH*	*GS*
	XZMYTJ50	**Guanximiyou pomelo**	**China**	**PQ624742**	**PQ603066**	**PQ616690**	**PQ616574**	**PQ616632**
	LXMYTJ51	**Guanximiyou pomelo**	**China**	**PQ624743**	**PQ603067**	**PQ616691**	**PQ616575**	**PQ616633**
	SGMYTJ52	**Guanximiyou pomelo**	**China**	**PQ624744**	**PQ603068**	**PQ616692**	**PQ616576**	**PQ616634**
	JFMYTJ53	**Guanximiyou pomelo**	**China**	**PQ624745**	**PQ603069**	**PQ616693**	**PQ616577**	**PQ616635**
	BZMYTJ56	**Guanximiyou pomelo**	**China**	**PQ624748**	**PQ603072**	**PQ616696**	**PQ616580**	**PQ616638**
	BZMYTJ58	**Guanximiyou pomelo**	**China**	**PQ624749**	**PQ603073**	**PQ616697**	**PQ616581**	**PQ616639**
	LXMYTJ60	**Guanximiyou pomelo**	**China**	**PQ624751**	**PQ603075**	**PQ616699**	**PQ616583**	**PQ616641**
C. brevisporum	YYGXZ07	Pepper	China	KU319458	KU319457	KU319453	KU319456	KU319455
	JXHTC19	*Dalbergia odorifera*	China	MF993572	MG515612	MG515615	MN737614	MN737615
	GZAAS5.09545	*Citrus medica*	China	JQ247623	JQ247647	JQ247635	JQ247599	JQ247611
	XXMYTJ1	**Guanximiyou pomelo**	**China**	**PQ624694**	**PQ603018**	**PQ616642**	**PQ616526**	**PQ616584**
	AHMYTJ6	**Guanximiyou pomelo**	**China**	**PQ624699**	**PQ603023**	**PQ616647**	**PQ616531**	**PQ616589**
	LXMYTJ8	**Guanximiyou pomelo**	**China**	**PQ624701**	**PQ603025**	**PQ616649**	**PQ616533**	**PQ616591**
	WFMYTJ14	**Guanximiyou pomelo**	**China**	**PQ624706**	**PQ603030**	**PQ616654**	**PQ616538**	**PQ616596**
	SGMYTJ16	**Guanximiyou pomelo**	**China**	**PQ624708**	**PQ603032**	**PQ616656**	**PQ616540**	**PQ616598**
	XZMYTJ17	**Guanximiyou pomelo**	**China**	**PQ624709**	**PQ603033**	**PQ616657**	**PQ616541**	**PQ616599**
	XXMYTJ30	**Guanximiyou pomelo**	**China**	**PQ624721**	**PQ603045**	**PQ616669**	**PQ616553**	**PQ616611**
	SGMYTJ31	**Guanximiyou pomelo**	**China**	**PQ624722**	**PQ603046**	**PQ616670**	**PQ616554**	**PQ616612**
	XXMYTJ39	**Guanximiyou pomelo**	**China**	**PQ624731**	**PQ603055**	**PQ616679**	**PQ616563**	**PQ616621**
C. cliviicola	S37	*Morus alba*	China	KY986892	KY986904	MF033886	KY986898	MK585943
	C-77	*Capsicum annuum*	India	MG282172	MG729670	MG383581	MG729674	MG729673
	DXMYTJ3	**Guanximiyou pomelo**	**China**	**PQ624696**	**PQ603020**	**PQ616644**	**PQ616528**	**PQ616586**
	AHMYTJ9	**Guanximiyou pomelo**	**China**	**PQ624702**	**PQ603026**	**PQ616650**	**PQ616534**	**PQ616592**
	JFMYTJ10	**Guanximiyou pomelo**	**China**	**PQ624703**	**PQ603027**	**PQ616651**	**PQ616535**	**PQ616593**
	WFMYTJ27	**Guanximiyou pomelo**	**China**	**PQ624718**	**PQ603042**	**PQ616666**	**PQ616550**	**PQ616608**
	XXMYTJ54	**Guanximiyou pomelo**	**China**	**PQ624746**	**PQ603070**	**PQ616694**	**PQ616578**	**PQ616636**
C. truncatum	BJ-3	*Clausena lansium*	China	MK629874	MK675238	MK681418	MK675260	MK681396
	C-3	*Capsicum annuum*	India	MG204564	MG703483	MG204619	MG703491	MG703489
	OOC72	*Allium cepa (onion)*	India	KJ486149	KJ485890	KJ485927	KJ486075	KJ486112
	GQMYTJ24	Guanximiyou pomelo	China	PQ624715	PQ603039	PQ616663	PQ616547	PQ616605
C. plurivorum	LFN0016	Soybean	Brasil	MK142673	KT696277	MK188482	MK139901	–
	GX018	*Diospyros kaki*	China	MN092338	MN092324	MN092341	MN092335	–
C. dematium	JZB330314	*Prunus avium*	China	OL378294	OL471275	OL471279	OL471273	–
C. okinawense	PC7	*Carica papaya*	China	OQ642143	OQ723039	OQ723040	OQ723038	–
	PP3	Papaya	China	MK649935	MK790071	MK790073	MK790069	–
C. acutatum	19301A	*Olea europaea* cv. Galega Vulgar	Portugal	PP508294	PP506870	PP506921	PP506775	–
	43380	*Prunus dulcis* (almond)	Australia	MT254972	MT305716	MT270256	MT305691	–
Curvularia lunata	A112	*Saccharum* sp.	Brazil	MT683262	MT757139	MT820144	MW091454	–

南胜镇、坂仔镇、安厚镇、大溪镇、霞寨镇、五寨乡、九峰镇、芦溪镇、国强乡、长乐乡）的18个蜜柚果园和3个蜜柚苗圃中共采集256份具有炭疽病典型症状的样品（叶片165份、果实48份和枝梢43份）。通过组织分离共获得367株分离物，经对培养性状和形态特征观察后初步分析鉴定，共有350株刺盘孢属真菌。根据分离菌株的形态特征和ITS序列分析主要有5类复合种，其中220株为胶孢炭疽菌复合种、76株为博宁炭疽菌复合种、29株为*C. magnum*复合种、15株为*C. orchidearum*复合种，10株为平头炭疽菌复合种，其分离频率分别为62.86%、21.71%、8.29%、4.29%和2.86%。

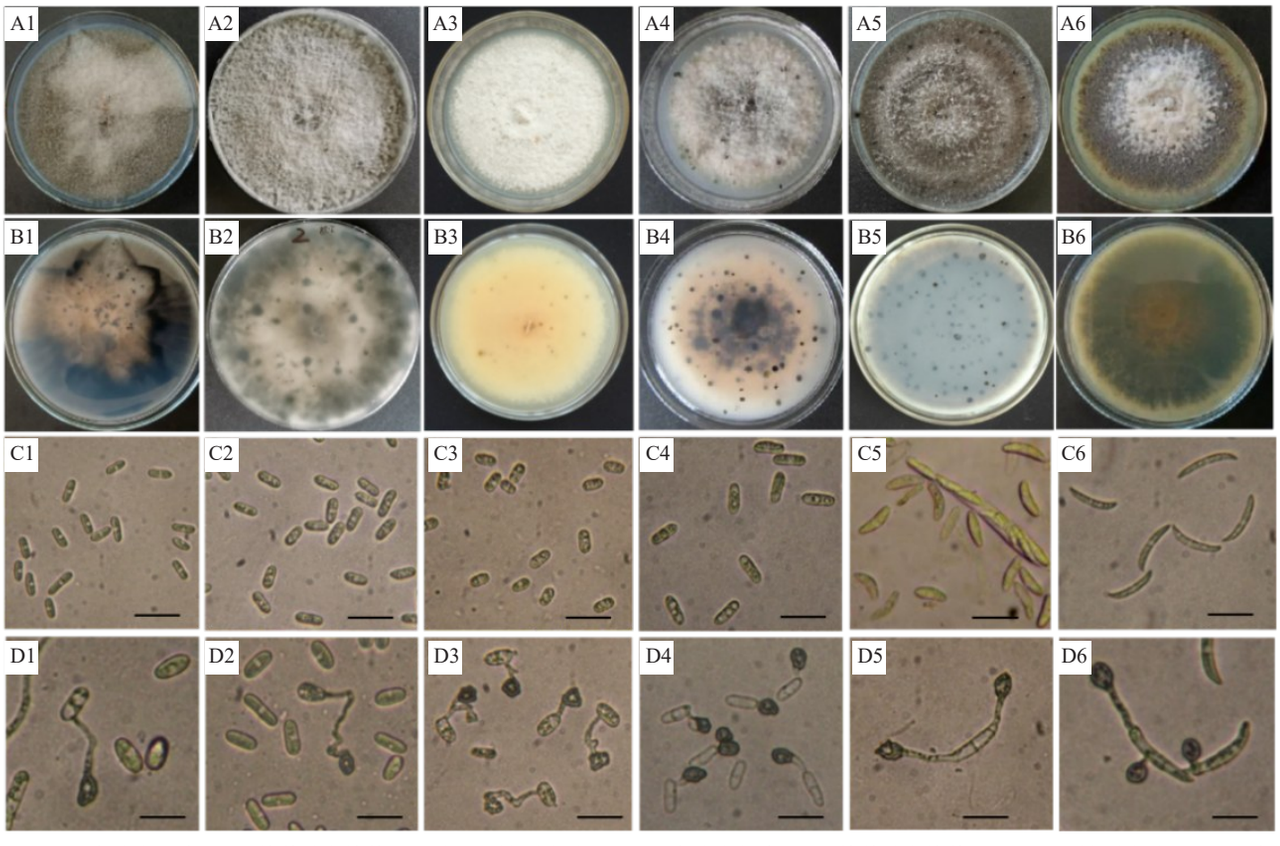
2.2 刺盘孢属真菌形态特征鉴定

胶胞炭疽菌复合种：其中有128株在PDA培养

基上的培养性状、分生孢子均一样。代表菌株JFMYTJ34菌落为深灰色，气生菌丝发达（图1-A1），背面明显可见扇形的角边区，中间橘黄色，边缘深灰色（图1-B1）。培养10 d左右可产生砖红色分生孢子堆，分生孢子单胞，无色，圆柱形，两端钝圆，有1~2个油球，大小为（12.0~18.8）μm×（4.0~6.2）μm（图1-C1）；附着胞单生或散生，深褐色，近圆形或不规则形，边缘整齐，大小为（8.0~16.5）μm×（4.0~8.5）μm（图1-D1）。另外92株在PDA培养基上的培养性状存在差异，菌落颜色为灰白色至灰色等12种不同的培养特征。代表菌株AHMYTJ2在PDA培养基上生长迅速，菌落灰白色，边缘整齐光滑，气生菌丝发达、绒毛状（图1-A2），背面浅灰色至浅橄榄灰色（图1-B2）。分生孢子堆橙红色，分生孢子光滑，无色，有油球，单胞，圆柱状、棍棒状，两端钝圆，基部偶有平截，大小为（13.0~17.0）μm×（4.0~6.0）μm（图1-C2）；附着胞单生或散生，浅褐色，椭圆形、棒状或不规则状，边缘完整，大小为（4.0~17.0）μm×（3.0~8.0）μm（图1-D2）。

博宁炭疽菌复合种：76株菌的培养性状差异较大，有30种不同的培养性状。代表菌株BZMYTJ20在PDA培养基上生长较慢，菌落乳白色，气生菌丝稀疏，绒毛状或卷毛状（图1-A3），背面浅褐色（图1-B3）。分生孢子堆橙色，分生孢子透明，无隔膜，圆柱状，顶部钝圆，基部脐状突起，大小为（12.0~17.0）μm×（5.5~7.5）μm（图1-C3）；附着胞单生或散生，浅棕色至深褐色，形状多样，多数为不规则型，边缘完整，大小为（8.6~11.0）μm×（6.0~8.5）μm（图1-D3）。

*C. magnum*复合种：各菌株间培养性状存在较大差异，有9种不同的培养特征。代表菌株XX-



A1~A6. 代表菌株在PDA培养基上培养10 d的正面菌落状态；B1~B6. 代表菌株在PDA培养基上培养10 d的反面菌落状态；C1~C6. 代表菌株的分生孢子；D1~D6. 代表菌株的附着胞；1. JFMYTJ34；2. AHMYTJ2；3. BZMYTJ20；4. XXMYTJ1；5. DXMYTJ3；6. GQMYTJ24。标尺=20 μm。

A1-A6. Front views of 10 d PDA culture of representative strains; B1-B6. Back views of 10 d PDA culture of representative strains; C1-C6. Conidia of representative strains; D1-D6. Appressorium of representative strains; 1. JFMYTJ34; 2. AHMYTJ2; 3. BZMYTJ20; 4. XXMYTJ1; 5. DXMYTJ3; 6. GQMYTJ24. Scale=20 μm.

图1　刺盘孢属真菌代表菌株的培养性状及形态特征

Fig. 1　Colony and morphological characteristics of representative strains belonging to six *Colletotrichum* spp.

MYTJ1在PDA培养基上菌落灰白色，气生菌丝发达（图1-A4），背面橘红色伴有黑色小点（图1-B4）。分生孢子橙红色，圆柱形，两端钝圆，大小为（13.0~19.0）μm×（4.0~5.5）μm（图1-C4）；附着胞单生，棕色到深棕色，椭圆形、棒状或不规则形，边缘完整，大小为（7.0~15.5）μm×（5.0~8.0）μm（图1-D4）。

*C. orchidearum*复合种：各菌株间培养性状差异较大，有5种不同的培养特征。代表菌株DXMYTJ3在PDA培养基上生长较快，菌落颜色灰褐色至墨绿色，中间形成环状轮纹圈，气生菌丝发达（图1-A5），背面深灰色至灰色（图1-B5）。分生孢子无色，单胞，椭圆形、弧形，两端钝圆，中间偶有缢缩，大小为（13.0~19.0）μm×（4.0~7.0）μm（图1-C5）；附着胞浅褐色至褐色，椭圆形或棒状，边缘偶有凸起，大小为（9.0~15.0）μm×（3.0~13.0）μm（图1-D5）。

平头炭疽菌复合种：10株在PDA培养基上的培养性状、分生孢子均一样。代表菌株GQMYTJ24在PDA培养基上生长较慢，菌落卡其色至橙黄色，气生菌丝不发达（图1-A6），背面杏黄色至桔黄色（图1-B6）。分生孢子镰刀型，光滑，无色，单胞，两端尖，中间有1个油球，大小为（20.0~27.0）μm×（2.0~4.0）μm（图1-C6）；附着胞浅褐色，椭圆形或卵圆形，边缘完整，大小为（7.0~18.0）μm×（5.0~11.0）μm（图1-D6）。

2.3 刺盘孢属真菌多基因系统发育分析

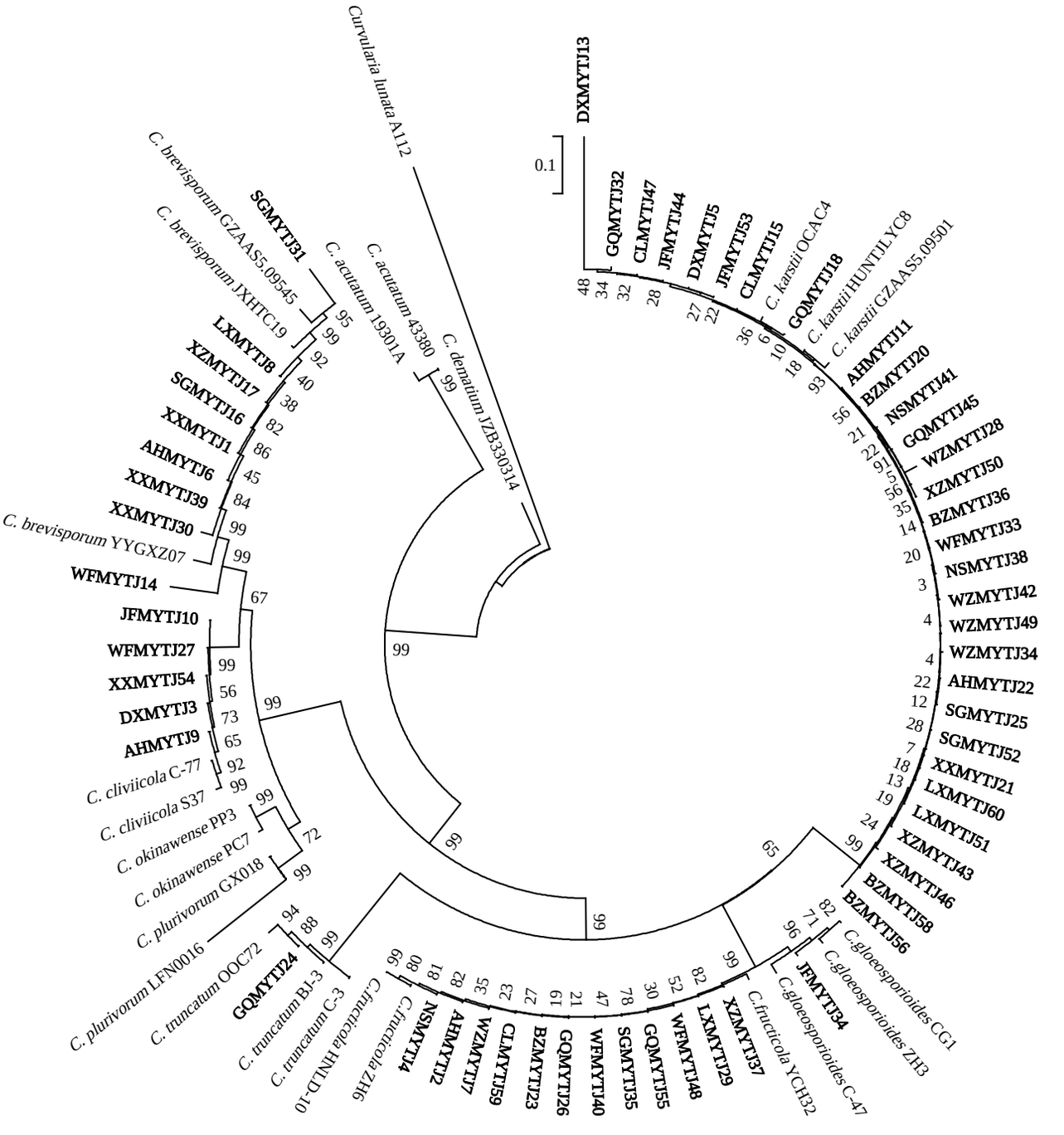
从胶孢炭疽菌复合种、博宁炭疽菌复合种、*C. magnum*复合种、*C. orchidearum*复合种和平头炭疽菌复合种中各选取13株、30株、9株、5株和1株培养性状有较大差异的代表菌株共58株刺盘孢属真菌进行多基因系统发育分析。分别提取DNA作为模板，扩增其ITS、*ACT*、*TUB2*、*GAPDH*和*GS*序列并测序，得到大小分别为500、250、500、300和1000 bp左右的特异性片段。将5个基因按顺序首尾相连（ITS-*ACT*-*TUB2*-*GAPDH*-*GS*），以菌株*Curvularia lunata*为外类群，采用MEGA 7.0构建系统发育树。结果表明（图2），58株刺盘孢属真菌在系统发育树上聚类为6个不同的分支，其中菌株JFMYTJ34与胶孢炭疽菌（*C. gloeosporioides*）单独聚类为一个小分支，GQMYTJ26等12株与果生炭疽菌（*C. fructicola*）聚类为一个分支；BZMYTJ20等30株与喀斯特炭疽菌（*C. karstii*）聚类为一个大分支；XXMYTJ1等9个菌株聚类为短孢炭疽菌（*C. brevisporum*），AHMYTJ9等5株聚类为兰花炭疽菌（*C. cliviicola*），菌株GQMYTJ24与平头炭疽菌（*C. truncatum*）聚类为一个分支。结合培养性状和分生孢子形态特征结果，从平和县琯溪蜜柚炭疽病样品中分离获得的刺盘孢属真菌分属于6个种，分别为胶孢炭疽菌（*C. gloeosporioides*）、果生炭疽菌（*C. fructicola*）、喀斯特炭疽菌（*C. karstii*）、短孢炭疽菌（*C. brevisporum*）、兰花炭疽菌（*C. cliviicola*）和平头炭疽菌（*C. truncatum*）。

2.4 致病性测定

选取培养性状有较大差异的58株刺盘孢属真菌菌株（同多基因系统发育分析），采用孢子悬浮液刺伤接种离体的叶片和枝条。致病性测定结果表明，不同菌株对健康蜜柚叶片和枝条的致病情况不同（表3），其中胶孢炭疽菌（*C. gloeosporioides*）JFMYTJ34及12株果生炭疽菌（*C. fructicola*）接种后病原菌迅速侵入有伤口的蜜柚组织，7 d后达到发病高峰期，叶片病斑呈浅灰褐色至深褐色、近圆形，略微凹陷（图3-K~M），枝条病斑呈淡褐色至深褐色，椭圆形至梭形，稍微下陷，病健交界分明（图3-B~D），症状表现与田间植株症状一致。9株喀斯特炭疽菌（*C. karstii*）接种3 d后开始出现水渍症状病斑，9 d后达到发病高峰期，叶片病斑呈灰白色椭圆形，稍凸起（图3-N~O），枝条病斑呈浅褐色稍下陷（图3-E~F）。9株短孢炭疽菌（*C. brevisporum*）接种3 d后开始出现青褐色水渍小斑，随后病斑迅速扩大，9 d后叶片病斑可穿透背面使叶片变软（图3-P~Q），枝条病斑逐渐发展至整个枝条并使其腐烂（图3-G~H）。平头炭疽菌（*C. truncatum*）GQMYTJ24接种5 d后开始出现青色水渍小斑，病斑逐渐扩大，向下凹陷，10 d后枝条上的病斑都出现干枯症状（图3-I，R）。21株喀斯特炭疽菌（*C. karstii*）、5株兰花炭疽菌（*C. cliviicola*）及对照不发病。

从5种致病的刺盘孢属真菌中各选取一株致病性最强的代表菌株进行健康蜜柚盆栽幼苗叶片有伤接种，结果表明，这些代表菌株均能使叶片产生干枯的病斑，发病率为100%。接种3 d后叶片开始出现轻微症状，与田间发病初期症状一致，7 d后症状加重，叶片病斑面积扩大，不同种的刺盘孢属真菌产生的病斑大小差异明显，与田间发病中、后期症状一致（图4）。

对以上离体接种和盆栽接种发病的组织取样进行病原菌再分离，得到的病原菌经形态学和分子生



本研究获得的菌株加粗表示。

The isolates obtained in this study are expressed in bold.

图 2　58 株刺盘孢属真菌基于 *ITS*、*ACT*、*TUB2*、*GADPH*、*GS* 序列的多基因系统发育树

Fig. 2　Phylogenetic tree of 58 *Colletotrichum* species based on the combined *ITS-ACT-TUB2-GAPDH-GS*

物学鉴定，结果与接种的病原菌菌株完全一致。结果表明，胶孢炭疽菌（*C. gloeosporioides*）、果生炭疽菌（*C. fructicola*）、喀斯特炭疽菌（*C. karstii*）、短孢炭疽菌（*C. brevisporum*）和平头炭疽菌（*C. truncatum*）5种刺盘孢属真菌均是引起福建琯溪蜜柚炭疽病的病原菌。

2.5　病原菌菌丝生长速率、附着胞形成率及致病力分析

5种致病的刺盘孢属真菌菌丝生长速率在6.07~13.53 mm·d^{-1}之间（表3），其中胶孢炭疽菌（*C. gloeo-*

表 3 琯溪蜜柚炭疽病病原菌菌丝生长速率、附着胞形成率及叶片病斑长度

Table 3 Mycelial growth rate and appressorium formation rate of pathogens, lesion lengths of Guanximiyou pomelo leaves

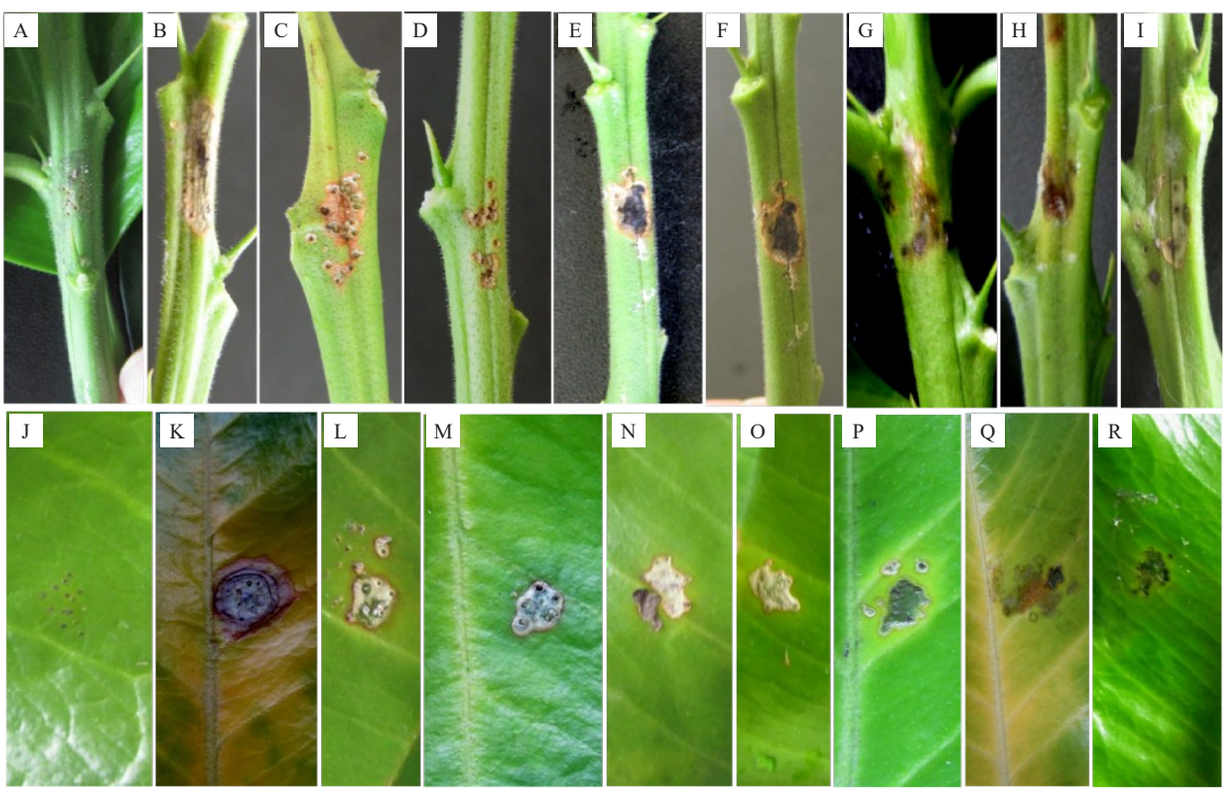
菌株种名 Species	菌株编号 Isolates number	菌丝生长速率 Mycelial growth rate/（mm·d^{-1}）	附着胞形成率 Appressorium formation rate/%	叶片病斑长度 Lesion lengths of leaves/mm	来源 Source
胶孢炭疽菌 *C. gloeosporioides*	JFMYTJ34	13.53±0.21 Aa	82.52±0.48 Aa	18.30±0.20 Aa	九峰镇蜜柚枝梢 Guanximiyou pomelo twigs from Jiufeng town
果生炭疽菌 *C. fructicola*	AHMYTJ2	12.07±0.12 Cd	69.56±2.69 CDe	18.17±0.35 Aa	安厚镇蜜柚叶片 Guanximiyou pomelo leaves from Anhou town
	NSMYTJ4	10.07±0.12 FGhi	59.25±3.25 GHhi	18.07±0.25 Aa	南胜镇蜜柚果实 Guanximiyou pomelo fruits from Nansheng town
	WZMYTJ7	10.27±0.12 EFgh	55.01±1.30 HIij	16.93±0.15 BCcd	五寨乡蜜柚枝梢 Guanximiyou pomelo twigs from Wuzhai town
	BZMYTJ23	10.47±0.12 Eg	46.61±1.65 JKl	14.67±0.15 Fg	坂仔镇蜜柚叶片 Guanximiyou pomelo leaves from Banzai town
	GQMYTJ26	12.67±0.12 Bc	55.91±2.75 HIij	15.67±0.15 Ef	国强乡蜜柚枝梢 Guanximiyou pomelo twigs from Guoqiang town
	LXMYTJ29	11.47±0.12 De	58.19±2.86 HIhi	16.33±0.06 De	芦溪镇蜜柚果实 Guanximiyou pomelo fruits from Luxi town
	SGMYTJ35	13.07±0.12 Bb	52.00±3.27 IJjk	16.37±0.21 De	山格镇蜜柚枝梢 Guanximiyou pomelo twigs from Shan’ge town
	XZMYTJ37	10.07±0.12 FGhi	55.35±2.74 HIij	16.83±0.06 Cd	霞寨镇蜜柚叶片 Guanximiyou pomelo leaves from Xiazhai town
	WFMYTJ40	12.87±0.35 Bbc	52.00±3.27 IJjk	14.47±0.15 Fg	文峰镇蜜柚果实 Guanximiyou pomelo fruits from Wenfeng town
	WFMYTJ48	12.07±0.12 Cd	59.30±1.72 GHhi	15.83±0.35 Ef	文峰镇蜜柚果实 Guanximiyou pomelo fruits from Wenfeng town
	GQMYTJ55	8.67±0.25 KLno	62.80±3.61 EFgh	17.13±0.06 BCbc	国强乡蜜柚枝梢 Guanximiyou pomelo twigs from Guoqiang town
	CLMYTJ59	11.13±0.06 Def	52.85±1.28 IJjk	15.73±0.06 Ef	长乐乡蜜柚叶片 Guanximiyou pomelo leaves from Changle town
喀斯特炭疽菌 *C. karstii*	AHMYTJ11	6.27±0.12 Or	62.80±3.61 EFgh	15.57±0.06 Ef	安厚镇蜜柚枝梢 Guanximiyou pomelo twigs from Anhou town
	DXMYTJ13	8.27±0.15 LMp	48.39±2.99 JKkl	5.03±0.12 Mn	大溪镇蜜柚叶片 Guanximiyou pomelo leaves from Daxi town
	CLMYTJ15	8.67±0.15 KLno	64.29±2.38 DEfg	11.17±0.31 GHh	长乐乡蜜柚果实 Guanximiyou pomelo fruits from Changle town
	GQMYTJ18	9.27±00.12 Jm	61.42±3.25 FGgh	9.87±0.31 IJk	国强乡蜜柚叶片 Guanximiyou pomelo leaves from Guoqiang town
	BZMYTJ20	6.07±0.31 Or	62.80±3.61 EFgh	17.37±0.21 Bb	坂仔镇蜜柚果实 Guanximiyou pomelo fruits from Banzai town
	WFMYTJ33	8.13±0.06 MNpq	45.32±4.02 Kl	5.83±0.25 Lm	文峰镇蜜柚叶片 Guanximiyou pomelo leaves from Wenfeng town
	WZMYTJ34	6.27±0.12 Or	68.95±2.39 CDef	14.47±0.15 Fg	五寨乡蜜柚果实 Guanximiyou pomelo fruits from Wuzhai town
	XZMYTJ46	7.87±0.12 Nq	47.19±2.31 JKl	4.83±0.25 Mn	霞寨镇蜜柚枝梢 Guanximiyou pomelo twigs from Xiazhai town
	JFMYTJ53	9.53±0.12 HIkl	44.95±1.82 Kl	3.77±0.06 No	九峰镇蜜柚枝梢 Guanximiyou pomelo twigs from Jiufeng town
短孢炭疽菌 *C. brevisporum*	XXMYTJ1	9.27±0.06 Jm	81.69±1.33 Aab	17.13±0.15 BCbc	小溪镇蜜柚叶片 Guanximiyou pomelo leaves from Xiaoxi town
	AHMYTJ6	11.33±0.58 Def	78.96±2.78 ABab	15.73±0.15 Ef	安厚镇蜜柚枝梢 Guanximiyou pomelo twigs from Anhou town
	LXMYTJ8	9.33±0.12 Ilm	76.53±2.56 ABcd	10.27±0.06 Ij	芦溪镇蜜柚叶片 Guanximiyou pomelo leaves from Luxi town

注：同列不同大写字母表示不同菌株在 0.01 水平差异极显著，不同小写字母表示不同菌株在 0.05 水平差异显著。

Note: Different capital letters in the same column indicate extremely significant differences among different strains at the 0.01 level, Different small letters indicate significant differences at the 0.05 level.

表 3 （续） Table 3 (Continued)

菌株种名 Species	菌株编号 Isolates number	菌丝生长速率 Mycelial growth rate/（mm·d^{-1}）	附着胞形成率 Appressorium formation rate/%	叶片病斑长度 Lesion lengths of leaves/mm	来源 Source
	WFMYTJ14	8.67±0.12 KLmo	78.81±2.83 ABab	11.27±0.21 Gh	文峰镇蜜柚叶片 Guanximiyou pomelo leaves from Wenfeng town
	SGMYTJ16	9.67±0.15 GHjk	68.97±2.19 CDef	8.83±0.25 Kl	山格镇蜜柚果实 Guanximiyou pomelo fruits from Shan’ge town
	XZMYTJ17	8.87±0.15 JKn	77.10±2.58 ABbc	10.83±0.25 GHi	霞寨镇蜜柚果实 Guanximiyou pomelo fruits from Xiazhai town
	XXMYTJ30	11.07±0.12 Df	68.48±3.18 CDef	9.63±0.15 Jk	小溪镇蜜柚叶片 Guanximiyou pomelo leaves from Xiaoxi town
	SGMYTJ31	9.73±0.12 GHkl	72.77±1.55 BCde	10.73±0.21 Hi	山格镇蜜柚叶片 Guanximiyou pomelo leaves from Shan’ge town
	XXMYTJ39	9.93±0.12 FGij	69.35±2.02 CDe	9.77±0.06 Jk	小溪镇蜜柚叶片 Guanximiyou pomelo leaves from Xiaoxi town
平头炭疽菌 *C. truncatum*	GQMYTJ24	8.33±0.42 LMop	33.65±2.57 Lm	4.83±0.15 Mn	大溪镇蜜柚叶片 Guanximiyou pomelo leaves from Daxi town
对照 Control	CK	/	/	0.00±0.00	/

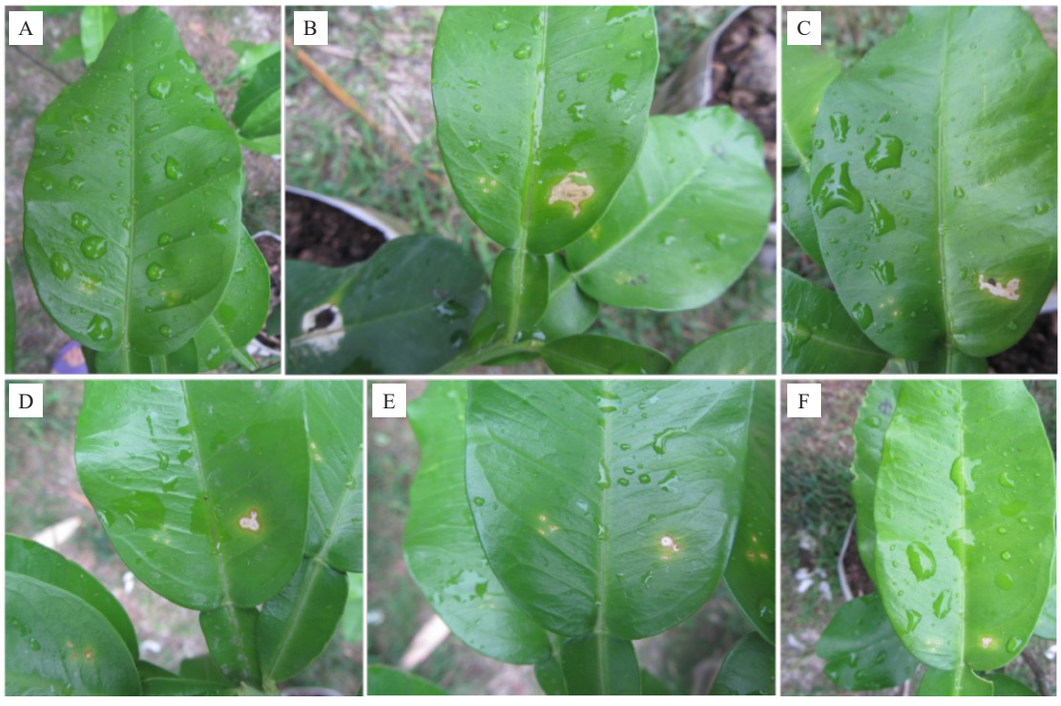


A、J. 接种清水的对照；B、K. 接种胶胞炭疽菌 JFMYTJ34 的枝条和叶片；C、L. 接种果生炭疽菌 AHMYTJ2 的枝条和叶片；D、M. 接种果生炭疽菌 NSMYTJ4 的枝条和叶片；E、N. 接种喀斯特炭疽菌 BZMYTJ20 的枝条和叶片；F、O. 接种喀斯特炭疽菌 WZMYTJ34 的枝条和叶片；G、P. 接种短孢炭疽菌 XXMYJ1 的枝条和叶片；H、Q. 接种短孢炭疽菌 WFMYTJ14 的枝条和叶片；I、R. 接种平头炭疽菌 GQMYTJ24 的枝条和叶片。

A, J. Controls inoculated with water; B, K. Inoculated twigs and leaves with *C. gloeosporioides* JFMYTJ34; C, L. Inoculated twigs and leaves with *C. fructicola* AHMYTJ2; D, M. Inoculated twigs and leaves with *C. fructicola* NSMYTJ4; E, N. Inoculated twigs and leaves with *C. karstii* BZMYTJ20; F, O. Inoculated twigs and leaves with *C. karstii* WZMYTJ34; G, P. Inoculated twigs and leaves with *C. brevisporum* XXMYJ1; H, Q. Inoculated twigs and leaves with *C. brevisporum* WFMYTJ14; I, R. Inoculated twigs and leaves with *C. truncatum* GQMYTJ24.

图 3　5 种刺盘孢属真菌代表菌株接种离体琯溪蜜柚枝条和叶片产生的症状

Fig. 3　Symptoms of Guanximiyou pomelo twigs and leaves inoculated with five *Colletotrichum* spp.



A. 接种清水的对照；B. 胶胞炭疽菌 JFMYTJ34；C. 果生炭疽菌 AHMYTJ2；D. 喀斯特炭疽菌 BZMYTJ20；E. 短孢炭疽菌 XXMYJ1；F. 平头炭疽菌 GQMYTJ24。

A. Controls inoculated with water; B. *C. gloeosporioides* JFMYTJ34; C. *C. fructicola* AHMYTJ2; D. *C. karstii* BZMYTJ20; E. *C. brevisporum* XXMYJ1; F. *C. truncatum* GQMYTJ24.

图 4 5 种刺盘孢属真菌代表菌株接种盆栽琯溪蜜柚叶片产生的症状

Fig. 4 Symptoms of Guanximiyou pomelo leaves in vivo after inoculated with representative isolates of five *Colletotrichum* spp.

sporioides）的平均生长速率最快，为 13.53 mm·d^{-1}；果生炭疽菌（*C. fructicola*）次之，平均生长速率为 11.28 mm·d^{-1}；短孢炭疽菌（*C. brevisporum*）和平头炭疽菌（*C. truncatum*）居中，平均生长速率分别为 9.76 mm·d^{-1}和 8.33 mm·d^{-1}；喀斯特炭疽菌（*C. karstii*）的平均生长速率最慢，平均生长速率为 7.81 mm·d^{-1}。5 种刺盘孢属真菌的附着胞形成率在 33.65%～82.52%之间（表 3），其中胶孢炭疽菌（*C. gloeosporioides*）最高，为 82.52%；其次是短孢炭疽菌（*C. brevisporum*），平均附着胞形成率为 74.74%；果生炭疽菌（*C. fructicola*）和喀斯特炭疽菌（*C. karstii*）居中，分别为 56.57%和 56.23%；平头炭疽菌（*C. truncatum*）最低，为 33.65%。

调查分析 5 种致病的刺盘孢属真菌接种琯溪蜜柚叶片 10 d 后的病害严重程度及病斑长度（表 3）。结果表明，不同种的刺盘孢属真菌致病力存在明显差异，胶孢炭疽菌（*C. gloeosporioides*）的致病力最强，接种叶片的平均病斑长度为 18.30 mm；其次是果生炭疽菌（*C. fructicola*），平均病斑长度为 16.35 mm；短孢炭疽菌（*C. brevisporum*）的致病力居中，平均病斑长度为 11.58 mm；平头炭疽菌（*C. truncatum*）的致病力较弱，平均病斑长度为 4.83 mm。喀斯特炭疽菌（*C. karstii*）不同菌株之间的致病力存在较大差异，菌株 BZMYTJ20 接种叶片的平均病斑长度为 17.37 mm，菌株 JFMYTJ53 接种叶片的平均病斑长度仅为 3.77 mm，而 DXMYTJ5、XXMYTJ21 和 BZMYTJ56 等菌株接种叶片后不发病。

2.6 病原菌菌丝生长速率、附着胞形成率与致病力相关性分析

对 5 种致病的刺盘孢属真菌菌丝生长速率与致病力进行相关性分析（图 5），结果表明，其相关系数 r 为 0.373 3，0.3＜|r|＜0.8，表明菌丝生长速率与致病力之间呈弱相关性。对 5 种致病的刺盘孢属真菌附着胞形成率与致病力进行相关性分析（图 6），结果表明，其相关系数 r 为 0.364 1，0.3＜|r|＜0.8，表明附着胞形成率与致病力之间呈弱相关性。

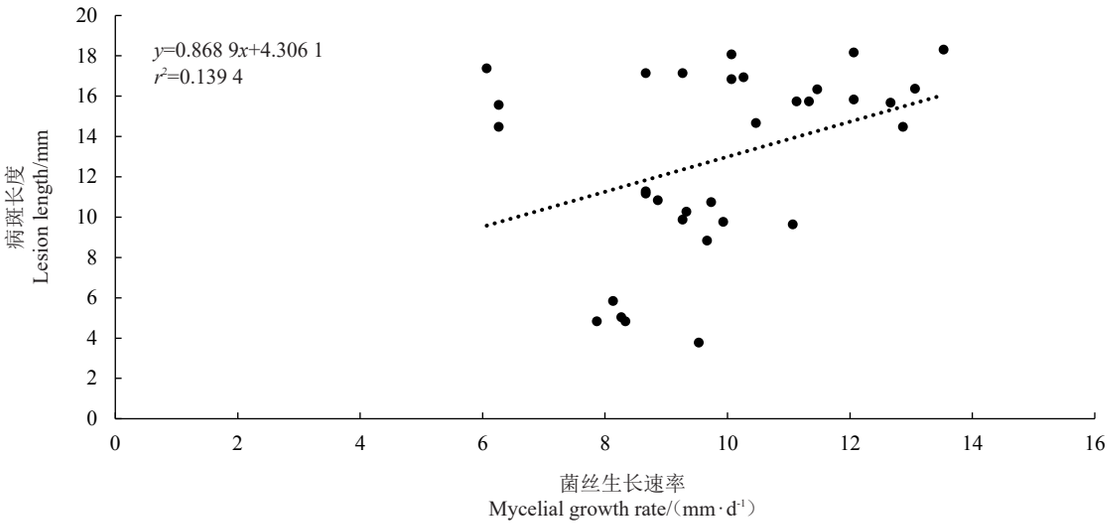


图5　5种刺盘孢属真菌菌株菌丝生长速率与致病力相关性分析

Fig. 5　Linear analysis of the relationship between pathogenicity and mycelial growth rate of five *Colletotrichum* spp.

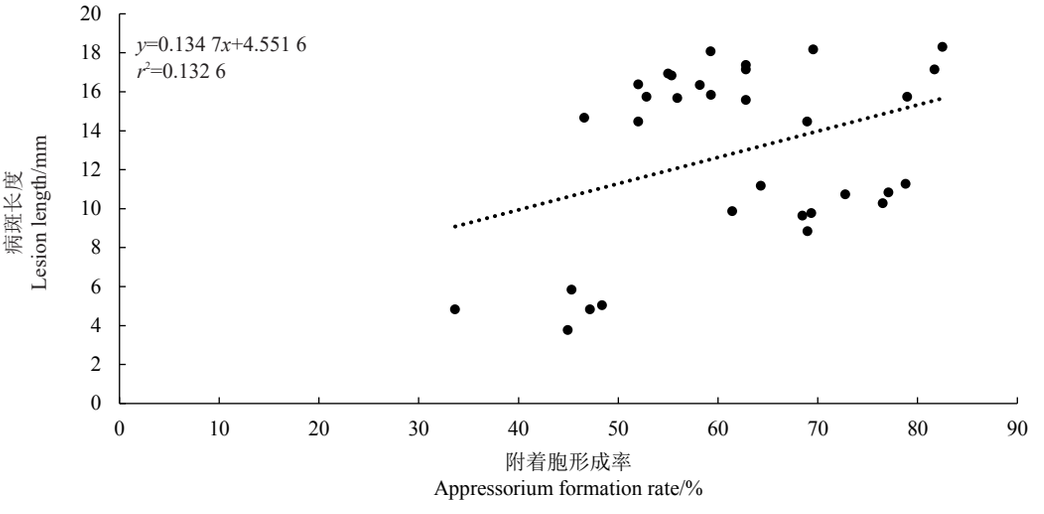


图6　5种刺盘孢属真菌菌株附着胞形成率与致病力相关性分析

Fig. 6　Linear analysis of the relationship between pathogenicity and appressorium formation rate of five *Colletotrichum* spp.

3　讨　论

炭疽病是琯溪蜜柚的主要病害之一，可在整个生育期造成严重危害，极大地影响了琯溪蜜柚产业的健康发展。刺盘孢属真菌作为柑橘炭疽病的主要病原菌，种类繁多[21]，据报道，国内外关于柑橘刺盘孢属真菌的记录有100余种，其中超过10种是柑橘炭疽病的病原菌[22]。中国2017年报道琯溪蜜柚炭疽病病原菌为胶孢炭疽菌（*C. gloeosporioides*）[3]，之后一直未见其他刺盘孢属真菌侵染琯溪蜜柚的报道。笔者课题组于2019年在福建省平和县琯溪蜜柚种植区发现该病的田间症状具有多样性，通过形态学特征观察和多基因系统发育分析，将琯溪蜜柚相关刺盘孢属真菌鉴定为5类刺盘孢复合种下的6种单系种，揭示了琯溪蜜柚刺盘孢属真菌种类的多样性。Peng等[23]在云南和贵州柑橘主产区分离到的柑橘相关刺盘孢属真菌，鉴定为胶胞炭疽菌复合种下的胶胞炭疽菌（*C. gloeosporioides*）和果生炭疽菌（*C. fructicola*）、博宁炭疽菌复合种下的博宁炭疽菌（*C. boninense*）和喀斯特炭疽菌（*C. karstii*）、*C. magnum* 复合种下的短孢炭疽菌（*C. brevisporum*）、尖孢炭疽菌复合种的西蒙氏炭疽菌（*C. simmondsii*）和*C. murrayae*，与本研究结果不尽相同。

柑橘炭疽病可由多种刺盘孢属真菌复合侵染，

国内已报道的柑橘炭疽病病原种类有胶孢炭疽菌（*C. gloeosporioides*）、果生炭疽菌（*C. fructicola*）、博宁炭疽菌（*C. boninense*）、喀斯特炭疽菌（*C. karstii*）、短孢炭疽菌（*C. brevisporum*）、平头炭疽菌（*C. truncatum*）、热带生炭疽菌（*C. tropicicola*）、暹罗炭疽菌（*C. siamense*）、普洛柏炭疽菌（*C. plurivorum*）和江西炭疽菌（*C. jiangxiense*）等，其中胶孢炭疽菌（*C. gloeosporioides*）是主要的病原菌[24-25]。国外已报道的柑橘炭疽病病原种类有胶孢炭疽菌（*C. gloeosporioides*）、果生炭疽菌（*C. fructicola*）、澳大利亚孢炭疽菌（*C. australianum*）、喀斯特炭疽菌（*C. karstii*）、尖孢炭疽菌（*C. acutatum*）、荷花炭疽菌（*C. nymphaeae*）、*C. catinaense*、*C. limonicola*、*C. helleniense* 和可可炭疽菌（*C. theobromicola*）等[21,26]。Huang 等[5]从福建琯溪蜜柚无症状的叶片中分离获得胶孢炭疽菌（*C. gloeosporioides*）和喀斯特炭疽菌（*C. karstii*），然而未对这些菌株进行致病性测定，尚不确定其是否对琯溪蜜柚致病。本研究结果发现有5种刺盘孢属真菌可引起琯溪蜜柚炭疽病，与国内外研究结果相一致，证实琯溪蜜柚炭疽病病原种类具有多样性。笔者在本研究中通过盆栽、田间活体接种试验，表明不同的病原在田间所造成的症状存在明显差异，琯溪蜜柚炭疽病不同的田间症状与病原种类的多样性息息相关，因此，进行准确的病原种类鉴定可为该病的田间症状诊断和有效防控提供重要的信息，促进蜜柚产业健康发展。

形态学观察结果表明，5种琯溪蜜柚炭疽病病原菌在PDA培养基上的培养性状存在差异，菌落生长速度快慢不一，不同菌株之间附着胞产生速度及形成率差异也较大。胶胞炭疽菌（*C. gloeosporioides*）培养性状稳定，各个菌株培养性状基本一致，菌丝生长速率最快，而喀斯特炭疽菌（*C. karstii*）培养性状极其不稳定，分离的菌株中培养性状各异，菌丝生长速率最慢；短孢炭疽菌（*C. brevisporum*）产生附着胞的速度最快且形成率最高，平头炭疽菌（*C. truncatum*）产生附着胞的速度最慢且形成率最低。琯溪蜜柚炭疽病菌的形态特征存在较大差异，表明该菌具有丰富的生理生化特性，其在侵染寄主时会引起致病力的差异，菌株的培养性状、菌丝生长速率和附着胞产生速度及形成率可能对刺盘孢属真菌的致病力起重要作用[27-28]。本研究致病力测定结果发现，5种病原菌的致病力存在较大差异，不同种刺盘孢属真菌及同种的不同菌株对琯溪蜜柚存在明显的致病力分化现象，胶胞炭疽菌（*C. gloeosporioides*）致病力最强，喀斯特炭疽菌（*C. karstii*）的平均致病力最弱，与Guarnaccia 等[21]对欧洲柑橘炭疽病病原菌致病力测定的结果一致。然而Mayorquin 等[29]对美国加利福尼亚小柑橘炭疽病的病原菌进行致病力研究发现，喀斯特炭疽菌（*C. karstii*）是该病的主要致病菌，其致病力明显强于胶胞炭疽菌（*C. gloeosporioides*），这进一步证实了不同产区柑橘炭疽病病原菌的致病力存在较大差异。笔者在本研究中还发现喀斯特炭疽菌（*C. karstii*）不同菌株之间的致病力存在较大差异，有的菌株致病力较强，有的较弱，有的不致病，Mario 等[30]研究表明，3株不同的喀斯特炭疽菌（*C. karstii*）分离株对甜橙叶片同样表现出明显的致病力差异，其中1株的致病力显著高于其他2株，但并未发现不致病的菌株，可能与选取的代表菌株数量较少有关。对5种病原菌的菌丝生长速率和致病力进行相关性分析，发现二者有一定程度的正相关关系，表明病原菌在侵染寄主的过程中菌丝生长速率越快，致病力可能越大，危害性越强。5种病原菌的附着胞形成率和致病力相关性分析证实二者呈弱相关性，表明病原菌在侵染寄主的过程中附着胞形成率与致病力相关。致病力差异还与其他多种因素相关，刺盘孢属真菌的果胶裂解酶活性及致病相关基因如MAP激酶基因 *Cgl-SLT2*、漆酶基因 *Lac1* 等对其致病力起着重要的调控作用[31-32]。因此，琯溪蜜柚炭疽病病原菌致病力差异的分子机制还有待进行深入全面的研究。

刺盘孢属真菌寄主范围广泛，同一种刺盘孢属真菌可同时侵染多种植物，造成严重的病害。来源于意大利柑橘的胶孢炭疽菌（*C. gloeosporioides*）可以侵染柑橘、杧果、辣椒、草莓、番石榴和木瓜等作物，引起炭疽病[14,33]；Prihastuti 等[34]发现果生炭疽菌（*C. fructicola*）可以引起咖啡发生炭疽病，随后其他研究表明该菌也可以侵染柑橘、李、桃、梨和猕猴桃等植物，发生炭疽病[35]；短孢炭疽菌（*C. brevisporum*）最初来源于彩叶凤梨炭疽病病叶，同时该菌可以侵染柑橘、南瓜、辣椒等经济作物，引起炭疽病[36-37]；喀斯特炭疽菌（*C. karstii*）可引起柑橘、山茶、咖啡、番茄等作物发生炭疽病病害[38]；平头炭疽菌（*C. truncatum*）是大豆、柑橘、番木瓜等作物炭疽病的病原菌[39-40]。因此，有必要进一步对上述琯溪蜜柚炭疽病刺盘孢属真菌进行其他作物的致病性测定，明确来

源于琯溪蜜柚的刺盘孢属真菌是否会侵染其他作物，以便在果园管理中防范交互感染。

4　结　论

引起福建省平和县琯溪蜜柚炭疽病的病原菌有胶孢炭疽菌（*C. gloeosporioides*）、果生炭疽菌（*C. fructicola*）、喀斯特炭疽菌（*C. karstii*）、短孢炭疽菌（*C. brevisporum*）和平头炭疽菌（*C. truncatum*），其中胶孢炭疽菌（*C. gloeosporioides*）为优势病原菌，果生炭疽菌（*C. fructicola*）、喀斯特炭疽菌（*C. karstii*）、短孢炭疽菌（*C. brevisporum*）和平头炭疽菌（*C. truncatum*）是琯溪蜜柚炭疽病的新病原。5种琯溪蜜柚炭疽病病原菌的菌丝生长速率及附着胞形成率与致病力均呈弱相关性。

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