微生物学通报
Microbiology China
tongbao@im.ac.cn
http://journals.im.ac.cn/wswxtbcn

Nov. 20, 2021, 48(11): 4296−4305
DOI: 10.13344/j.microbiol.china.210075

专论与综述

豆类炭疽病病原物种类及其发生研究进展

刘勇 叶鹏盛[*] 曾华兰 孙小芳 何炼 华丽霞 蒋秋平 何晓敏 王明娟 张敏

四川省农业科学院经济作物育种栽培研究所 四川 成都 610300

摘 要：炭疽病是重要的世界性植物病害，造成大豆、绿豆等品质变劣，产量损失严重。本文综述了国内外大豆炭疽病的发生情况、炭疽菌种类及其特征，为了解该病的流行病学和科学防治提供理论依据。

关键词：大豆，炭疽病，病原菌，分生孢子

Research progress on pathogen species and occurrence of bean anthracnose

LIU Yong YE Pengsheng[*] ZENG Hualan SUN Xiaofang HE Lian HUA Lixia JIANG Qiuping HE Xiaomin WANG Mingjuan ZHANG Min

Industrial Crop Research Institute of Sichuan Academy of Agricultural Sciences, Chengdu, Sichuan 610300, China

Abstract: Anthracnose is a major plant disease prevalent around the globe, which causes quality deterioration and serious yield losses of soybean and mungbean. This paper summarized the occurrence, pathogen species, and characteristics of soybean anthracnose at home and abroad, aiming to provide a theoretical basis for understanding the epidemiology and scientific control of this disease.

Keywords: soybean, anthracnose, pathogen, conidium

大豆炭疽病是由炭疽菌属(*Colletotrichum* Corda)的一些真菌种引起的，主要有由平头炭疽菌等病原菌引起的 8 种症状类型，普遍发生于巴西、印度、美国南部及中国等。潮湿温暖条件下，炭疽病病害症状明显，病情严重度增加，导致美国南部地区种子产量损失 16%−26%，泰国大豆产量损失 30%−50%，印度大豆产量损失甚至可达 100%，导致大豆减产 16%−100%[1]。1996−2007 年，大豆炭疽病造成阿根廷、巴西、中国和美国等 8 个大豆主要生产国产量损失达 2 540 万 t，其中，产量损失最大的是中国，累计达 1 660 万 t，其次是美国和印度，分别累计 490 万 t 和 117 万 t[2]。2003−2005 年大豆炭疽病成为美国 15 个南部州地区的十大重要大豆病害之一，是重要的世界性植

Foundation items: Sichuan Provincial Breeding Project (2021YFYZ0021); Project of Sichuan Beans and Cereals Innovation Team of Chinese National Modern Agricultural Industry Technology System (SCCXTD-2020-20); Modern Agricultural Discipline Construction and Promotion Project (2021XKJS110)
***Corresponding author:** E-mail: yeps@163.com
Received: 22-01-2021; **Accepted:** 05-03-2021; **Published online:** 12-05-2021
基金项目：四川省育种攻关项目(2021YFYZ0021)；国家现代农业产业技术体系四川豆类杂粮创新团队项目(SCCXTD-2020-20)；现代农业学科建设推进工程项目(2021XKJS110)
*通信作者：E-mail：yeps@163.com
收稿日期：2021-01-22；接受日期：2021-03-05；网络首发日期：2021-05-12

物病害[3]。

根据前人的研究，能够引起大豆炭疽病的病原菌有：平头炭疽菌(*Colletotrichum truncatum*)[4]，有性态未知；短孢炭疽菌(*C. brevisporum*)[5]，有性态未知；毁灭炭疽菌(*C. destructivum*)[6-7]，有性态(*Glomerella glycines*)；胶孢炭疽菌(*C. gloeosporioides*)[8-10]，有性态(*G. cingulata*)；球炭疽菌(*C. coccodes*)[11]，有性态未知；禾生炭疽菌(*C. graminicola*)[12]，有性态(*G. graminicola*)；剪炭疽菌(*C. cliviae*)[13]；兰生炭疽菌(*C. chlorophyti*)；黑线炭疽菌(*C. dematium*)等。大豆炭疽病是种传病害，可以侵染任何生育期的大豆，从种子至苗期再到收获期均可发病，感染种子使其变色且可能失去发芽能力[14]，也可能在发芽期间死亡[15]，苗期引起大豆死苗，成株期可危害茎秆、豆荚，造成植株过早落叶，导致大豆品质变劣[16]、产量下降[17-19]。

炭疽病的控制管理包括减少侵染源、施用杀菌剂、非寄主轮作和种植无致病性种子，病害循环和侵染过程包括越冬孢子的初次侵染、孢子萌发、分生孢子盘和孢子的产生，或病株组织菌丝体对植物的初次侵染、附着胞和侵染钉的发育、宿主组织的渗透和菌丝定殖[20]。因此，掌握引起大豆炭疽病的病原物种类及其特征，明确不同大豆产区引起大豆炭疽病的炭疽菌种类和分布是了解该病流行病学和指导综合防治策略的基础，对确保化学防治的成功和培育抗炭疽病大豆品种至关重要，为该病的科学防治提供理论依据。因此，本文对国内外大豆炭疽病的发生情况、炭疽菌种类及其特征进行了综述和讨论。

1 平头炭疽菌(*Colletotrichum truncatum*)

1961 年，由平头炭疽菌引起的大豆炭疽病首次报道发生于巴西的南里奥格兰德州并迅速流行于塞拉多草原等中西部大草原地区[21]，随着 2001 年大豆锈病病原菌 *Phakopsora pachyrhizi* 传入巴西，大豆开始定期喷洒农药，炭疽病作为一种继发性病害持续存在，长期对大豆产量造成严重的损失，据报道，巴西北部大豆炭疽病发病率每增加 1%便造成 90 kg/hm^2 的产量损失[22]。在 21 世纪 10 年代，大豆炭疽病再次发生于巴西并造成重大损失[23]。目前的重大损失报告可能与病原菌固有的种间或其他变异性、气候和文化因素有关，也可能与主要商业大豆品种的基因构成变化有关。因此，学者们不断开展研究来阐明致病因子的性质和分布等[24]。

平头炭疽病由荷兰学者于 2009 年再次鉴定[25]，并指出该病原菌是引起大豆炭疽病最主要的病原菌[26]。在 PDA 培养基上病原菌菌落颜色为浅灰色到深灰色，孢子堆为橙色或米橙色，培养 7 d 后菌落直径为 3.0−9.0 cm。该病菌表现出 3 种类型的产孢方式，即由菌丝末端的分生细胞形成分生孢子、分生孢子盘形成分生孢子以及直接由可育的刚毛形成分生孢子。分生孢子单胞，镰状，透明，无隔膜(图 1)，平均大小为(19.0−26.5) μm×(3.0−4.5) μm。

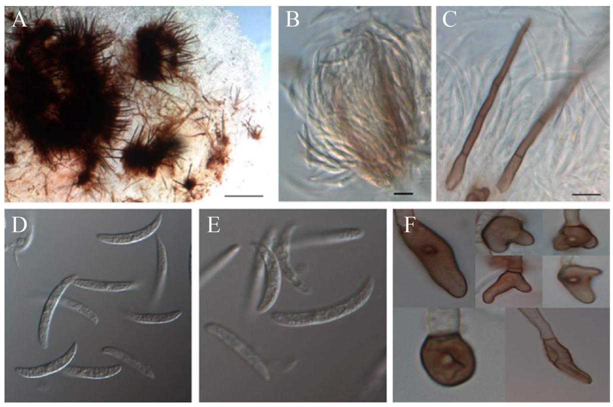

图 1 平头炭疽菌在显微镜下的形态学特征[24]

Figure 1 Morphological characteristics of *Colletotrichum truncatum* under the microscope[24]

注：A：分生孢子盘；B：分生孢子盘和分生孢子；C：刚毛和分生孢子；D、E：分生孢子；F：附着胞。比例尺：A：100 μm；B–F：10 μm

Note: A: Acervuli; B: Acervuli and conidia; C: Setae and conidia; D, E: Conidia; F: Appressoria. Scale bars: A: 100 μm; B–F: 10 μm

2 兰生炭疽菌(*Colletotrichum chlorophyti*)

2012 年，美国科学家 Yang 等首次报道 *C. chlorophyti* 侵染大豆引起大豆炭疽病[27]，随后 2013 年发现该菌可以侵染大豆种子[28]。2017 年，我国河北检验检疫局京唐港办事处植物检疫实验室从进口的乌拉圭大豆的残留茎秆上分离并鉴定出该菌，为我国口岸首次截获[29]。2019 年，Sun 等[30]研究发现该菌侵染我国北苍术。

在 PDA 培养基上，该菌菌落圆形，边缘整齐，呈灰白色，气生菌丝毡状或绒状，紧贴培养基生长，培养 3 d 后菌丝开始变黑，7 d 后黑色菌落满皿(图 2A、2B)；厚垣孢子在培养 3 d 后开始产生，单生或串生于菌丝顶端或中间，黄褐色至黑褐色，多数球形，光滑，平均大小为 7.5 μm×7.5 μm (图 2C)；分生孢子单胞，无色，新月形或镰刀状，一端尖锐，另一端较钝，平均大小为 19.4 μm×3.6 μm (图 2D)，无附着胞产生[27]。

3 胶孢炭疽菌(*Colletotrichum gloeosporioides*)

由胶孢炭疽菌引起的炭疽病是大豆豆芽最严重的病害之一[31]。2013 年，胶孢炭疽菌首次被报道侵染马来西亚大豆，造成茎弯曲生长或环绕，顶梢枯死，随后叶片和茎上形成黑色病斑，豆荚被感染则出现红棕色病斑[9]。发病后期，病斑中出现大量的表皮尖刺，在相对湿度较高的时期出现黏液样的分生孢子团。

病原菌 PDA 培养物最初为白色，随后逐渐变为灰褐色、粉红色、红褐色(图 3A)；在相对湿度较高的环境下培养一段时间后，产生针状花絮子囊孢子，大小为(13−26) μm×(4−8) μm；培养 12 d 后产生分生孢子，分生孢子直，圆柱形，透明，无隔，两端圆形，大小为(8−16) μm×(2−6) μm (图 3C)[9-10]。

4 毁灭炭疽菌(*Colletotrichum destructivum*)

大豆是阿根廷最主要的作物，由毁灭炭疽菌引起的大豆炭疽病同大豆黑斑病、大豆紫斑病和大豆叶斑病等病害在大豆生长后期发生严重，造成重大损失[32]。大豆炭疽病病原菌侵染豇豆，造成其叶和茎的蛋白质含量从 34.91%降至 20.40%、脂肪含量从 5.42%降低至 2.15%[33]，种子中蛋白质损失 28.95%、碳水化合物和脂肪损失 22.55%[34]。

病原菌菌落正面由灰黑色变为黑色，而背面则由棕色变为深黑色；菌落生长呈放射状、圆形、脂肪状、颗粒状，气生菌丝稀疏，最初呈白色(图 4A)；气生菌丝中散布有大量的针状突起，呈圆形或近圆形，深褐色，具刚毛(图 4B)；分生孢子单细胞，透明，圆柱形，微弯，大小为(13.2–20.2) μm×(3.1–5.2) μm (图 4C)[35]。

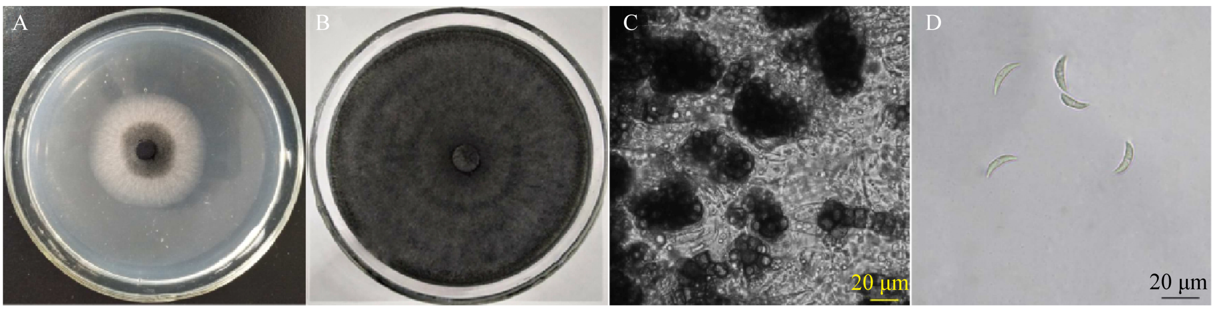

图 2 兰生炭疽菌形态特征[27]

Figure 2 Morphology of *Colletotrichum chlorophyti*[27]

注：A：在 PDA 培养基上培养 3 d 的菌落；B：在培养基上培养 7 d 的菌落；C：厚垣孢子；D：分生孢子

Note: A: Colonies on PDA medium (3 d); B: Colonies on PDA medium (7 d); C: Chlamydospores; D: Conidia

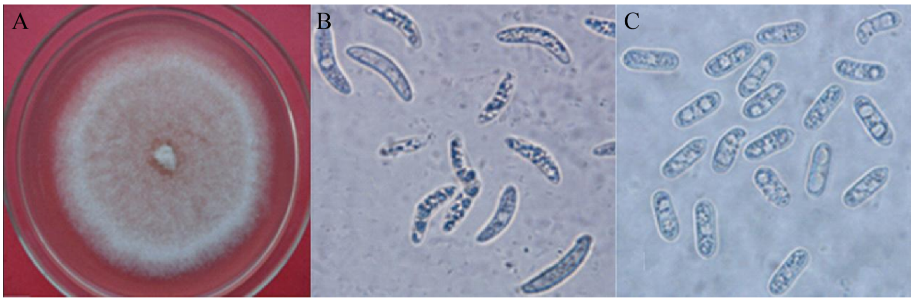

图 3 胶孢炭疽菌形态特征[10]

Figure 3 Morphology of *Colletotrichum gloeosporioides*[10]

注：A：在 PDA 培养基上的菌落；B：子囊孢子形态；C：分生孢子形态

Note: A: Colonies on PDA medium; B: The ascospore morphology of *C. gloeosporioides*; C: The conidial morphology of *C. gloeosporioides*

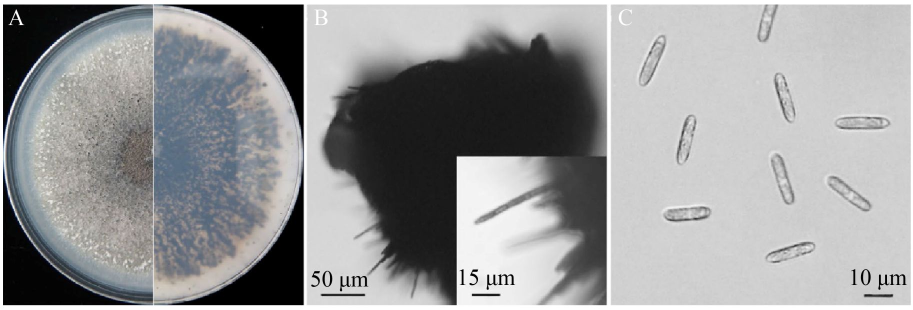

图 4 毁灭炭疽菌形态特征[35]

Figure 4 Morphology of *Colletotrichum destructivum*[35]

注：A：在 PDA 培养基上的正反面菌落形态；B：分生孢子盘和刚毛；C：分生孢子

Note: A: Colony morphology at the obverse and reverse sides on PDA medium; B: Acervuli and setae; C: Conidia

5 球炭疽菌(*Colletotrichum coccodes*)

1998 年，由球炭疽菌引起的大豆炭疽病首次报道发生于美国[11]，该病原菌宿主范围广，危害严重，以茄科作物为主，对作物种子的侵染率达 14%。据调查，在苘麻-大豆种植田块，该菌侵染大豆，在植株上产生黑斑，坏死茎上形成菌核，造成大豆产量损失可达 23%[36]。同时，该菌还被报道侵染辣椒[37]和豌豆[38]，造成严重的产量损失。

病原菌在 PDA 培养基上的菌落最初为白色(图 5A)，随着培养时间的延长逐渐变黑(图 5B、5C)，16 d 后产生大量黑色的小菌核(图 5D)；分生孢子透明、无隔，圆柱状、有水滴状小斑点，两端圆形，孢子大小为(15.5−21.3) μm×(3.6−5.3) μm；附着胞椭圆形至卵球形，不规则分裂或弯曲[39]。

6 禾生炭疽菌(*Colletotrichum graminicola*)

禾生炭疽菌较少被报道侵染大豆，其主要侵染玉米茎和叶，是引起玉米叶枯炭疽病和茎腐炭疽病的半营养真菌，造成玉米产量严重损失[40]。该菌侵染宿主引起炭疽病主要通过 3 个阶段，首先是入侵前宿主表面形成附着胞，然后通过营养生长定殖在宿主活细胞内，最后造成宿主细胞死亡出现发病症状[41-42]，形成窄直形或椭圆形水浸状病斑，随着病情发展，病斑变为褐色至淡红褐色，最后变暗褐色至黑色，茎或叶表面上生有小黑点(分生孢子盘)。有时病斑合并成相当大的暗褐色至亮黑色、稍凹陷的斑块或条斑。研究发现，添加脲酶抑制剂乙酰羟肟酸可保护作物免受

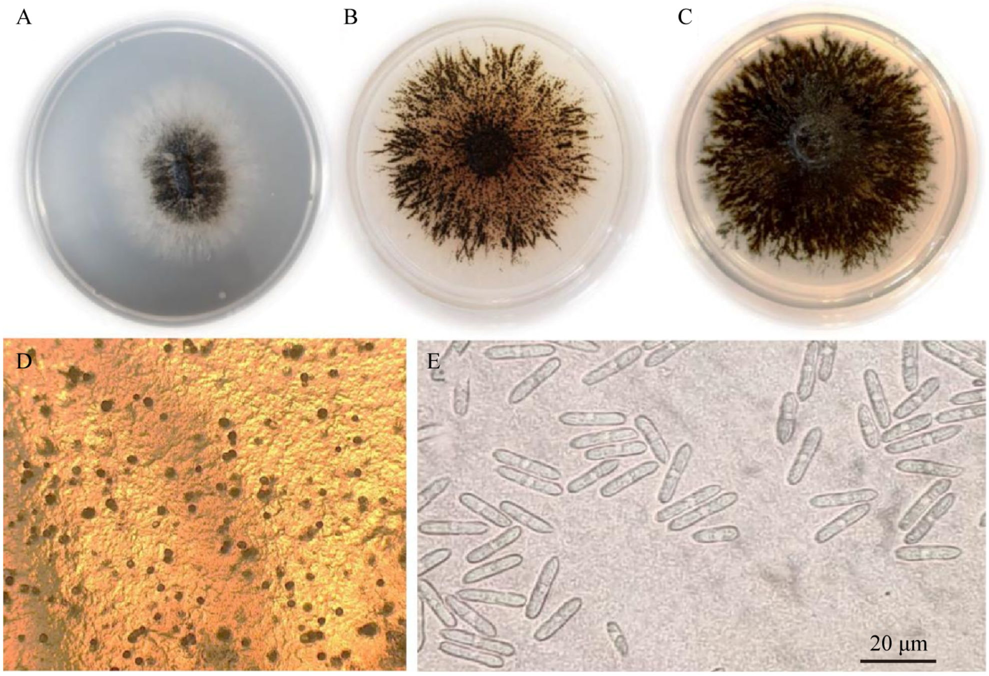

图 5　球炭疽菌形态特征[39]

Figure 5　Morphology of *Colletotrichum coccodes*[39]

注：A：在 PDA 培养基上培养 5 d 的菌落；B、C：在 PDA 培养基上培养 10 d 的菌落；D：PDA 培养基上形成的菌核；E：分生孢子

Note: A: Colony on PDA after 5 days; B, C: Colonies on PDA after 10 days; D: Microsclerotia formed on PDA; E: Conidia

该病原菌侵染，从而降低炭疽病发病率[43]。

禾生炭疽菌分生孢子盘黑褐色，呈盘形或垫状，盘上密生棍棒状单细胞的分生孢子梗，无色至淡褐色，平滑，疏松排列成栅栏状(图 6A)；梗顶生分生孢子，分生孢子有镰刀形和卵圆形 2 种[44]。镰刀形孢子有时略直，单胞无色，大小为(12−16) μm×(2.5−5.5) μm (图 6B)；卵圆形孢子单胞无色，大小为(9.8−41.5) μm×(2.3−7.7) μm[45]。

7　剪炭疽菌(*Colletotrichum cliviae*)

2017 年，由剪炭疽菌引起的大豆炭疽病首次报道发生于巴西[13]，侵染大豆造成叶片和茎坏死，病斑平均大小为 4.26 mm。该病原菌使大豆种子发芽率降低 44%−55%，对大豆豆荚的致病性低于平头炭疽菌，在大豆茎上病斑显著小于由平头炭疽菌侵染形成的病斑[46]。在巴西，该菌还被报道侵染利马豆[47-48]和芒果[49]。同时，通过国内

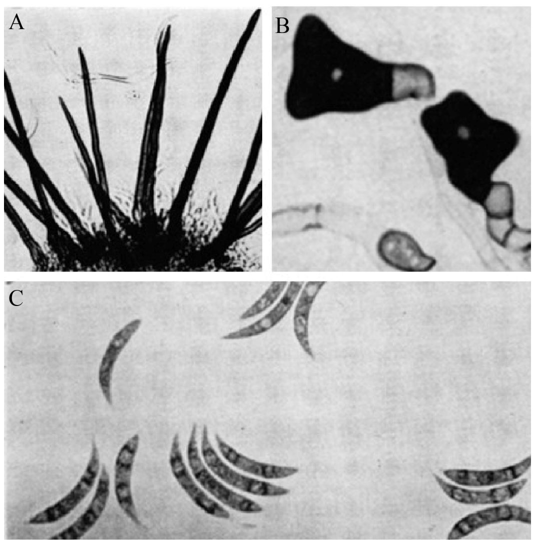

图 6　禾生炭疽菌形态特征[45]

Figure 6　Morphology of *Colletotrichum graminicola*[45]

注：A：分生孢子盘(135×)；B：附着胞(750×)；C：分生孢子(670×)

Note: A: Acervulus (135×); B: Appressoria (750×); C: Conidia (670×)

外分离菌的单倍型多样性分析和真菌寄主范围测定表明，剪炭疽菌可能为巴西高原地区特有。

剪炭疽菌在 PDA 培养基上形成灰色到深灰色的菌落(图 7A)，生长迅速，即使在 30−33 °C 的条件下其生长速度也显著快于平头炭疽菌，培养 7 d 后菌丝占满直径为 9 cm 的培养皿，并已经出现分生孢子；分生孢子单胞，透明，无隔，圆柱形，末端钝，平均大小为 14.80 μm×4.44 μm (图 7C−7E)；附着胞叶状或圆齿状，大小为 (10−19) μm×(4−9) μm[46]。

8　短孢炭疽菌(*Colletotrichum brevisporum*)

2020 年，中国江苏南通市首次报道短孢炭疽菌侵染大豆引起大豆炭疽病，发病率达 65%，造成大豆产量较 2019 年降低 28%−35%[5]。病原菌侵染大豆，造成茎和叶中出现不规则的棕色坏死病变，并明显萎蔫。该病原菌在中国桑树[50]、巴西利马豆[48]和拉丁美洲岛国甜椒[51]等作物报道过，其形态特征与 Damm 等[52]报道的短孢炭疽菌一致。

短孢炭疽菌在吐温-20 培养基上，菌落直径较小，大约为 9.21 mm；在 PDA 培养基上，菌落中心为灰白色，边缘白色，菌丝有隔膜。分生孢子圆柱形，单胞，平均长度为 15 μm (图 8)[5]。

9　展望

南美地区是世界上大豆种植最多的区域，世界上 50%以上的大豆产于巴西和阿根廷，并不断向亚马逊南部延伸[54]。该区域面积约为 5 360 万 hm^2 [55-56]，多为大豆净作或小麦-大豆连作栽培，易发生炭疽病。中国大豆常年种植面积为 841.3 万 hm^2。在我国，大豆炭疽病的发生南方重于北方，尤其是对南方鲜食大豆的生产造成严重影响，高发病田块病荚率可达 50%以上[4]，严重影响了鲜食大豆的产量和外观品质，进而造成重大的经济损失。近年来由于雨水增多，大豆炭疽

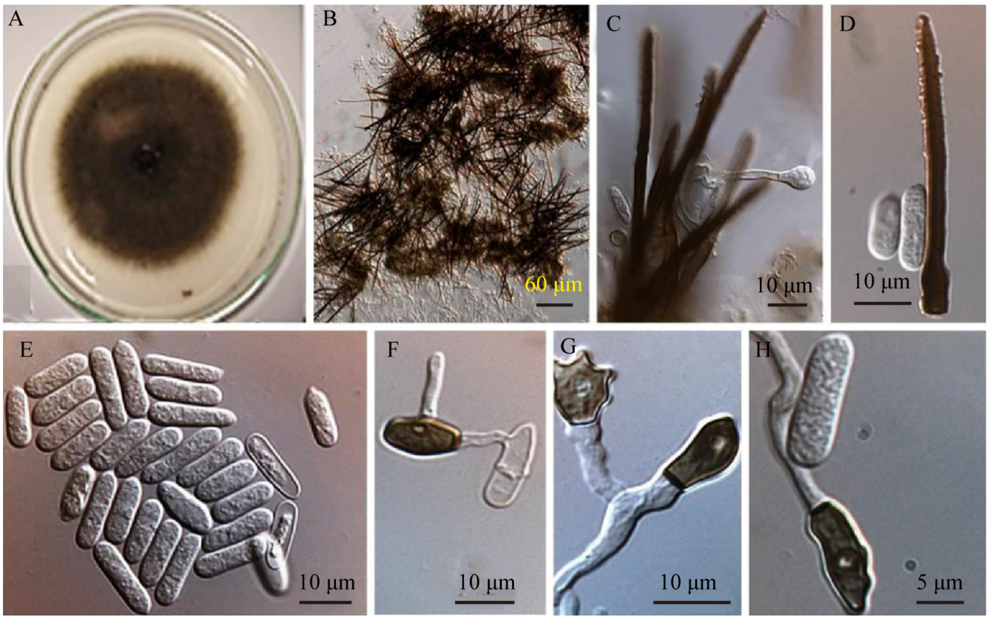

图 7　剪炭疽菌形态特征[46]

Figure 7　Morphological characteristics of *Colletotrichum cliviae*[46]

注：A：菌落形态；B：刚毛子座；C 和 D：刚毛；E：大量分生孢子；F：萌发的分生孢子；G、H：形状各异的附着胞

Note: A: Fungal colony morphology; B: Stroma setose; C and D: Setae; E: Conidial mass; F: Germinated conidia; G, H: Appressoria of varied shapes

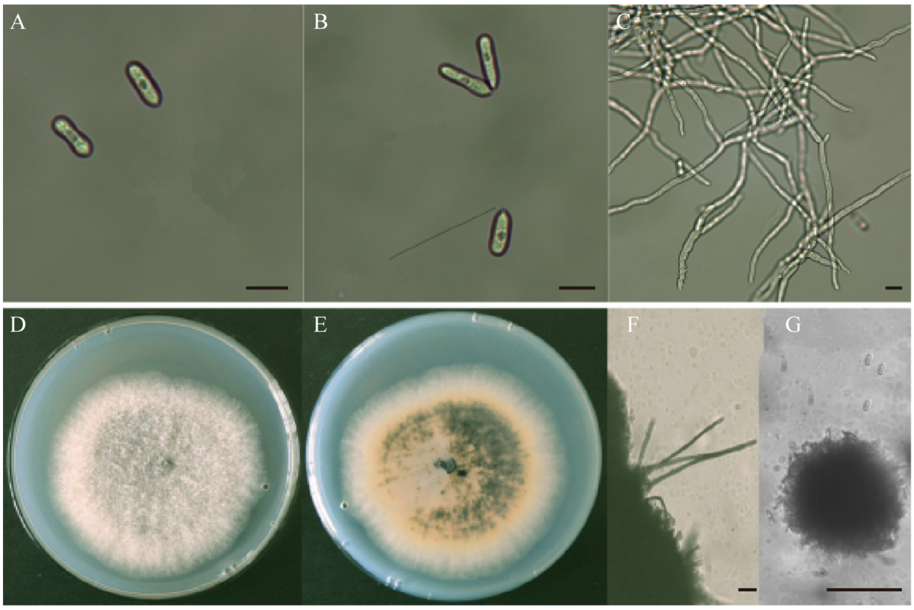

图 8 短孢炭疽菌形态特征[5]

Figure 8 Morphological characteristics of *Colletotrichum brevisporum*[5]

注：A−C：分生孢子和菌丝形态，标尺为 10 μm；D−E：在 PDA 培养基上菌落形态；F：刚毛，标尺为 10 μm；G：无性繁殖体，标尺为 100 μm

Note: A−C: Morphology of *C. brevisporum* conidia and mycelia, bar: 10 μm; D−E: PDA culture; F: Setae, bar: 10 μm; G: Conidiomata, bar: 100 μm

病在我国南方鲜食大豆产区有明显加重的趋势；2020 年 3 月该病造成江苏大豆产量损失 28%−35%，是威胁大豆生产的重要病害[57]。

截至目前，国内外大豆炭疽病的主要病原是平头炭疽菌，其次是球炭疽菌、毁灭炭疽菌、禾生炭疽菌和胶孢炭疽菌[58]。在我国，大豆炭疽病的主要病原仍是平头炭疽菌[57,59]，其次是兰生炭疽菌[29]和胶孢炭疽菌[60]。目前有关大豆炭疽病的研究文献较多，但研究多集中在大豆炭疽病病害症状的识别与病原菌分离[18,27,59]、大豆品种抗病性鉴定[57]、大豆炭疽病防治[61]等方面，曾华兰等也在大豆炭疽病发生和抗病性鉴定方面进行了初步的探索，描述了大豆炭疽病的症状类型及发生情况，提出了相应的防治措施[62]，研究证实由平头炭疽菌引起的大豆豆荚炭疽病是造成四川大豆减产、品质下降的主要病害。大豆炭疽菌分子类群和不同菌株的排他性或半排他性聚集与其地理来源存在着较强的相关性[63]，由不同病菌引起的大豆炭疽病症状表现各不相同，发生规律也有所差异。目前，有关大豆炭疽病病原菌的形态学鉴定和分子生物学鉴定缺乏一定的研究，而研究表明，不同致病力的炭疽病分离菌株均可以造成严重的炭疽病，这可能与目前大豆栽培品种抗病能力较差有关[24]，因此亟需筛选和培育抗病的大豆品种，而选育和利用抗性品种的前提是筛选得到优异的抗性资源[57]。目前我国尚无对炭疽病的免疫品种，因此，明确引起大豆炭疽病的主要病原物、生物学特征及发生发展规律，有利于在病害发生关键环节对其进行有效的防治，降低成本投入。研究证实选育推广抗病品种是防治大豆炭疽病最经济有效的方法，而品种的抗病性评价是筛选抗原和选育抗病品种不可缺少的手段[64]。因此，本团队制定了四川省地方标准《大豆品种抗炭疽病性鉴定技术规程》，连续多年对来自四川和重庆的鲜食大豆品种材料进行了大豆炭疽病的抗性评价，鉴定出中抗材料 3 份，中感材料 22 份，感病材料 6 份[64]。本结果可作为针对性地

选用抗性材料、筛选抗病品种、育出抗病增产品种的依据。本文通过明确引起大豆炭疽病的主要病原物及其特征，综述了 8 种大豆炭疽菌特征特性，有利于鉴别大豆侵染复合物，为了解该病流行病学和指导综合防治策略奠定基础，对成功开展化学防治和培育抗炭疽病大豆品种具有重要意义。

REFERENCES

[1] Wrather JA, Anderson TR, Arsyad DM, Gai J, Ploper LD, Porta-Puglia A, Ram HH, Yorinori JT. Soybean disease loss estimates for the top 10 soybean producing countries in 1994[J]. Plant Disease, 1997, 81(1): 107-110

[2] Wrather A, Koenning S. Effects of diseases on soybean yields in the United States 1996 to 2007[J]. Plant Health Progress, 2009, 10(1): 24

[3] Yang HC, Haudenshield JS, Hartman GL. *Colletotrichum incanum* sp. nov., a curved-conidial species causing soybean anthracnose in USA[J]. Mycologia, 2014, 106(1): 32-42

[4] Wang T, Zhong RS, Gao ZM. Studies on the nutritive physiological characteristics of *Colletotrichum truncatum*[J]. Journal of Fungal Research, 2006, 4(3): 91-93 (in Chinese)
汪涛，钟荣顺，高智谋．大豆炭疽病菌(*Colletotrichum truncatum*)的营养生理研究[J]. 菌物研究, 2006, 4(3): 91-93

[5] Shi XC, Wang SY, Duan XC, Gao X, Zhu XY, Laborda P. First report of *Colletotrichum brevisporum* causing soybean anthracnose in China[J]. Plant Disease, 2021, 105(3): 707

[6] Baird RE, Mullinix BG, Peery AB, Lang ML. Diversity and longevity of the soybean debris mycobiota in a no-tillage system[J]. Plant Disease, 1997, 81(5): 530-534

[7] Ramos AM, Tadic LF, Cinto I, Carmona M, Gally M. Molecular characterization of *Colletotrichum* species causing soybean anthracnose in Argentina[J]. Mycotaxon, 2013, 123(1): 457-465

[8] Chen LS, Chu C, Liu CD, Chen RS, Tsay JG. PCR-based detection and differentiation of anthracnose pathogens, *Colletotrichum gloeosporioides* and *C. truncatum*, from vegetable soybean in Taiwan[J]. Journal of Phytopathology, 2006, 154(11/12): 654-662

[9] Mahmodi F, Kadir JB, Wong MY, Nasehi A, Puteh A, Soleimani N. First report of anthracnose caused by *Colletotrichum gloeosporioides* on soybean (*Glycine max*) in Malaysia[J]. Plant Disease, 2013, 97(6): 841

[10] Xiao JW, Liu YL, Ran JX, Yang ZC. Identification of *Colletotrichum* isolates from Brazil soybean[J]. Chinese Agricultural Science Bulletin, 2011, 27(5): 333-337 (in Chinese)
肖杰文，刘月廉，冉俊祥，杨占臣．巴西大豆中炭疽菌的分离鉴定研究[J]. 中国农学通报, 2011, 27(5): 333-337

[11] Riccioni L, Conca G, Hartman GL. First report of *Colletotrichum coccodes* on soybean in the United States[J]. Plant Disease, 1998, 82(8): 959

[12] Yang HC, Haudenshield JS, Hartman GL. Multiplex real-time PCR detection and differentiation of *Colletotrichum* species infecting soybean[J]. Plant Disease, 2015, 99(11): 1559-1568

[13] Barbieri MCG, Ciampi-Guillardi M, Moraes SRG, Bonaldo SM, Rogério F, Linhares RR, Massola NS Jr. First report of *Colletotrichum cliviae* causing anthracnose on soybean in Brazil[J]. Plant Disease, 2017, 101(9): 1677

[14] Poti T, Mahawan K, Cheewangkoon R, Arunothayanan H, Akimitsu K, Nalumpang S. Detection and molecular characterization of carbendazim-resistant *Colletotrichum truncatum* isolates causing anthracnose of soybean in Thailand[J]. Journal of Phytopathology, 2020, 168(5): 267-278

[15] Gizlice Z, Carter TE Jr, Burton JW. Genetic diversity in North American soybean: I. multivariate analysis of founding stock and relation to coefficient of parentage[J]. Crop Science, 1993, 33(3): 614-620

[16] Allen TW, Bradley CA, Sisson AJ, Byamukama E, Chilvers MI, Coker CM, Collins AA, Damicone JP, Dorrance AE, Dufault NS, et al. Soybean yield loss estimates due to diseases in the United States and Ontario, Canada, from 2010 to 2014[J]. Plant Health Progress, 2017, 18(1): 19-27

[17] Backman PA, Williams JC, Crawford MA. Yield losses in soybeans from anthracnose caused by *Colletotrichum truncatum*[J]. Plant Disease, 1982, 66(11): 1032-1034

[18] Manandhar JB, Hartman GL. Anthracnose[A]//Hartman GL, Sinclair JB, Rupe JC. Compendium of Soybean Diseases[M]. St. Paul, MN: APS Press, 1999: 13-14

[19] Wrather JA, Koenning SR. Estimates of disease effects on soybean yields in the United States 2003 to 2005[J]. Journal of Nematology, 2006, 38(2): 173-180

[20] Yang HC, Hartman GL. Methods and evaluation of soybean genotypes for resistance to *Colletotrichum truncatum*[J]. Plant Disease, 2015, 99(1): 143-148

[21] Araújo AG, Café-Filho AC, Cupertino FP. Antracnose da soja na região geoeconômica do Distrito Federal[J]. Fitopatologia Brasileira, 1988, 13: 130

[22] Dias MD, Pinheiro VF, Café-Filho AC. Impact of anthracnose on the yield of soybean subjected to chemical control in the north region of Brazil[J]. Summa Phytopathologica, 2016, 42(1): 18-23

[23] Rogério F, Gladieux P, Massola NS, Ciampi-Guillardi M. Multiple introductions without admixture of *Colletotrichum truncatum* associated with soybean anthracnose in Brazil[J]. Phytopathology, 2019, 109(4): 681-689

[24] Rogério F, Ciampi-Guillardi M, Barbieri MCG, Bragança CAD, Seixas CDS, Almeida AMR, Massola NS. Phylogeny and variability of *Colletotrichum truncatum* associated with soybean anthracnose in Brazil[J]. Journal of Applied Microbiology, 2017, 122(2): 402-415

[25] Damm U, Woudenberg JH, Cannon PF, Crous P.

Colletotrichum species with curved conidia from herbaceous hosts[J]. Fungal Diversity, 2009, 39: 45-87
[26] Hyde KD, Cai L, McKenzie EHC, Yang YL, Zhang JZ, Prihastuti H. *Colletotrichum*: a catalogue of confusion[J]. Fungal Diversity, 2009, 39: 1-17
[27] Yang HC, Haudenshield JS, Hartman GL. First report of *Colletotrichum chlorophyti* causing soybean anthracnose[J]. Plant Disease, 2012, 96(11): 1699
[28] Yang HC, Stewart JM, Hartman GL. First report of *Colletotrichum chlorophyti* infecting soybean seed in Arkansas, United States[J]. Plant Disease, 2013, 97(11): 1510
[29] Li HY, Jin S, Zhang XQ, Fan GH, Zhang JX, Xu YX. Identification of *Colletotrichum chlorophyti* causing soybean anthracnose[J]. Plant Protection, 2017, 43(2): 163-166 (in Chinese)
李海云，靳帅，张学勤，范光辉，张建新，许艳霞. 大豆炭疽病菌 *Colletotrichum chlorophyti* 的鉴定[J]. 植物保护, 2017(2): 163-166
[30] Sun WM, Wen XL, Qi HX, Feng LN, Cao J, Han ZL, Yang WJ, Zhang MY, Han BJ, Meng TY. First report of anthracnose of *Atractylodes chinensis* caused by *Colletotrichum chlorophyti* in China[J]. Plant Disease, 2019, 103(4): 764
[31] Lee JH, Jeong SW, Cho YA, Park S, Kim YH, Bae DW, Chung JI, Kwak YS, Jeong MJ, Park SC, et al. Determination of the variations in levels of phenolic compounds in soybean (*Glycine max* Merr.) sprouts infected by anthracnose (*Colletotrichum gloeosporioides*)[J]. Journal of the Science of Food and Agriculture, 2013, 93(12): 3081-3086
[32] Carmona M, Sautua F, Perelman S, Reis EM, Gally M. Relationship between late soybean diseases complex and rain in determining grain yield responses to fungicide applications[J]. Journal of Phytopathology, 2011, 159(10): 687-693
[33] Amadioha AC, Nwazuo ED. Alterations of biochemical composition of leaf and stem of cowpea (*Vigna unguiculata* (L.) Walp.) by *Colletotrichum destructivum* O'Gara in Nigeria[J]. Journal of Experimental Agriculture International, 2019, 33(2): 1-7
[34] Amadioha AC, Nwazuo ED. Biochemical composition of seed and husk of cowpea (*Vigna unguiculata* (L.) Walp.) infected by *Colletotrichum destructivum* O'Gara in storage[J]. Annual Research & Review in Biology, 2019, 31(1): 1-7
[35] Sun HY, Tian JM, Steinkellner S, Liang Y. Identification and characterization of *Colletotrichum destructivum* causing anthracnose on sunflower[J]. Archives of Microbiology, 2020, 202(6): 1459-1467
[36] Ditommaso A, Watson AK, Hallett SG. Infection by the fungal pathogen *Colletotrichum coccodes* affects velvetleaf (*Abutilon theophrasti*)-soybean competition in the field[J]. Weed Science, 1996, 44(4): 924-933
[37] Tyvaert L, Everaert E, Lippens L, Cuijpers WJM, França SC, Höfte M. Interaction of *Colletotrichum coccodes* and *Verticillium dahliae* in pepper plants[J]. European Journal of Plant Pathology, 2019, 155(4): 1303-1317
[38] Bellé C, Ramos RF, Moccellin R, Farias CRJ. Detection of *Colletotrichum coccodes* causing leaf anthracnose on *Pisum sativum* in southern Brazil[J]. Journal of Plant Pathology, 2020, 102(1): 255
[39] Pérez-Mora JL, Cota-Rodríguez DA, Rodríguez-Palafox EE, García-León E, Beltrán-Peña H, Lima NB, Tovar-Pedraza JM. First confirmed report of *Colletotrichum coccodes* causing black dot on potato in Mexico[J]. Journal of Plant Diseases and Protection, 2020, 127(2): 269-273
[40] Gorman Z, Christensen SA, Yan YX, He YM, Borrego E, Kolomiets MV. Green leaf volatiles and jasmonic acid enhance susceptibility to anthracnose diseases caused by *Colletotrichum graminicola* in maize[J]. Molecular Plant Pathology, 2020, 21(5): 702-715
[41] Gong AD, Jing ZY, Zhang K, Tan QQ, Wang GL, Wen DL. Bioinformatic analysis and functional characterization of the CFEM proteins in maize anthracnose fungus *Colletotrichum graminicola*[J]. Journal of Integrative Agriculture, 2020, 19(2): 541-550
[42] Torres MF, Ghaffari N, Buiate EAS, Moore N, Schwartz S, Johnson CD, Vaillancourt LJ. A *Colletotrichum graminicola* mutant deficient in the establishment of biotrophy reveals early transcriptional events in the maize anthracnose disease interaction[J]. BMC Genomics, 2016, 17(1): 1-24
[43] Benatto Perino EH, Glienke C, De Oliveira Silva A, Deising HB. Molecular characterization of the purine degradation pathway genes *ALA1* and *URE1* of the maize anthracnose fungus *Colletotrichum graminicola* identified urease as a novel target for plant disease control[J]. Phytopathology, 2020, 110(9): 1530-1540
[44] Nordzieke DE, Sanken A, Antelo L, Raschke A, Deising HB, Pöggeler S. Specialized infection strategies of falcate and oval conidia of *Colletotrichum graminicola*[J]. Fungal Genetics and Biology, 2019, 133: 103276
[45] Politis DJ. The identity and perfect state of *Colletotrichum graminicola*[J]. Mycologia, 1975, 67(1): 56-62
[46] Dias MD, Fonseca MEN, Dias-Neto JJ, Santos MDM, Pandolfo GM, Boiteux LS, Café-Filho AC. Biology, pathogenicity, and haplotype analyses of *Colletotrichum* cliviae: a novel soybean anthracnose agent in warm tropical areas[J]. Tropical Plant Pathology, 2018, 43(5): 439-451
[47] Sousa ES, Silva JRA, Assunção IP, Melo MP, Feijó FM, Silva Matos K, Andrade Lima GS, Beserra JEA. *Colletotrichum* species causing anthracnose on lima bean in Brazil[J]. Tropical Plant Pathology, 2018, 43(1): 78-84
[48] Cavalcante GRS, Barguil BM, Vieira WAS, Lima WG, Michereff SJ, Doyle VP, Câmara MPS. Diversity, prevalence, and virulence of *Colletotrichum* species associated with lima bean in Brazil[J]. Plant Disease, 2019,

103(8): 1961-1966

[49] Vieira WAS, Michereff SJ, Morais MA, Hyde KD, Câmara MPS. Endophytic species of *Colletotrichum* associated with mango in northeastern Brazil[J]. Fungal Diversity, 2014, 67(1): 181-202

[50] Xue LH, Zhang L, Yang XX, Huang XQ, Wu WX, Zhou XQ, White JF, Liu Y, Li CJ. Characterization, phylogenetic analyses, and pathogenicity of *Colletotrichum* species on *Morus alba* in Sichuan province, China[J]. Plant Disease, 2019, 103(10): 2624-2633

[51] Villafana RT, Ramdass AC, Rampersad SN. *Colletotrichum brevisporum* is associated with anthracnose of red bell pepper fruit in Trinidad[J]. New Disease Reports, 2019, 39(1): 11

[52] Damm U, Sato T, Alizadeh A, Groenewald JZ, Crous PW. The *Colletotrichum dracaenophilum*, *C. magnum* and *C. orchidearum* species complexes[J]. Studies in Mycology, 2019, 92: 1-46

[53] Villafana RT, Rampersad SN. Diversity, structure, and synteny of the cutinase gene of *Colletotrichum* species[J]. Ecology and Evolution, 2020, 10(3): 1425-1443

[54] United States Department of Agriculture. World agricultural supply and demand estimates 2019[EB/OL]. Washington, DC, USA: USDA, 2019. [2019-09-09]. https://www.usda.gov/sites/default/files/documents/March_2019_WASDE_Lockup_Briefing.pdf

[55] CONAB. Companhia Nacional de Abastecimento—Boletim Grãos Junho 2019[EB/OL]. Brasília, Brazil: CONAB. [2019-09-09]. https://www.conab.gov.br/info-agro/safras/graos/boletim-da-safra-de-graos

[56] Ministerio de Agricultura, Argentina. Estimaciones agrícolas al 05 de Septiembre 2019[EB/OL]. Buenos Aires, Argentina: Ministerio de Agricultura, Ganaderia y Pesca. [2019-09-09]. https://www.agroindustria.gob.ar/sitio/areas/estimaciones/

[57] Feng LL, Zhu LM, Xie H, Yang QH, Guo B, Yuan FJ. Identification of the pathogen of vegetable soybean anthracnose in Zhejiang Province and evaluation of soybean cultivars for resistance to *Colletotrichum truncatum*[J/OL]. Acta Phytopathologica Sinica, 1-15. [2021-02-20]. https://doi.org/10.13926/j.cnki. apps.000730 (in Chinese)
冯乐乐, 竹龙鸣, 谢华, 杨清华, 郭蓓, 袁凤杰. 浙江省鲜食大豆炭疽病病原分离及抗性鉴定[J/OL]. 植物病理学报, 1-15. [2021-02-20]. https://doi.org/10.13926/j.cnki.apps.000730

[58] Dias MD, Dias-Neto JJ, Santos MDM, Formento AN, Bizerra LVAS, Fonseca MEN, Boiteux LS, Café-Filho AC. Current status of soybean anthracnose associated with *Colletotrichum truncatum* in Brazil and Argentina[J]. Plants, 2019, 8(11): 459

[59] Chen WJ. Identification and control of soybean pod anthracnose[D]. Hangzhou: Master's Thesis of Zhejiang University, 2007 (in Chinese)
陈吴健. 大豆豆荚炭疽病的病原鉴定及其防治[D]. 杭州: 浙江大学硕士学位论文, 2007

[60] Sun J, Xu B, Zhou CB. Diagnoses of anthraces in legume plants in Xichang district[J]. Journal of Xichang University: Natural Science Edition, 2004, 18(4): 83-84 (in Chinese)
孙劲, 徐彪, 周长彬. 西昌地区豆科植物炭疽病的鉴定[J]. 西昌学院学报(自然科学版), 2004, 18(4): 83-84

[61] Sun ZF. Study on disease factors of soybean pod anthracnose and its control[D]. Hangzhou: Master's Thesis of Zhejiang University, 2008 (in Chinese)
孙志峰. 大豆豆荚炭疽病的发病因子及其防治研究[D]. 杭州: 浙江大学硕士学位论文, 2008

[62] Zeng HL, He L, Ye PS, Jiang QP, Hua LX, Wang MJ, Zhang M, He XM. The main diseases of soybean in Sichuan and their control measures[A]//Proceedings of the 2019 Annual Meeting of the Chinese Society for Plant Protection[C]. Guiyang: Plant Protection Society of China, 2019: 70 (in Chinese)
曾华兰, 何炼, 叶鹏盛, 蒋秋平, 华丽霞, 王明娟, 张敏, 何晓敏. 四川大豆主要病害及其防治措施[A]//中国植物保护学会 2019 年学术年会论文集[C]. 贵阳: 中国植物保护学会, 2019: 70

[63] Liu Y, Zeng HL, Hua LX, He L, Ye PS. Symptoms and occurrence of soybean Anthracnose[A]//Chen WQ. Plant Health and Pest Control[C]. Plant Protection Society of China, 2020: 1 (in Chinese)
刘勇, 曾华兰, 华丽霞, 何炼, 叶鹏盛. 大豆炭疽病菌的症状类型及其发生[A]//陈万全. 植物健康与病虫害防控[C]. 中国植物保护学会, 2020: 1

[64] Zeng HL, He L, Jiang QP, Hua LX, Li Y, He XM, Wang MJ. Resistance evaluation to soybean anthracnose of fresh soybean varieties[A]//Chen WQ. Plant Health and Pest Control[C]. Plant Protection Society of China, 2020: 1 (in Chinese)
曾华兰, 何炼, 蒋秋平, 华丽霞, 刘勇, 何晓敏, 王明娟. 鲜食大豆品种对大豆炭疽病的抗性评价[A]//陈万全. 植物健康与病虫害防控[C]. 中国植物保护学会, 2020: 1