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油菜菌核病研究进展

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[摘 要] 菌核病是危害油菜生产的主要病害之一。结合已有文献与本研究室的研究结果,文章就核盘菌的致病过程和致病机理、油菜菌核病抗病资源筛选、抗病育种现状、抗性遗传规律、抗病 QTL 定位及抗性基因发掘等方面进行了总结和展望。

[关键词] 油菜;菌核病;致病机理;分子机制;抗病育种

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Advance in *Sclerotinia* stem rot of rapeseed

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Abstract: *Sclerotinia* stem rot caused by fungal pathogen *Sclerotinia sclerotiorum* is one of the most devastating diseases in rapeseed production. Combining with the existing research literature and the findings of our lab, the review summarized and prospected the researches in infection process and pathogenesis mechanism of *S. sclerotiorum*, disease-resistant resources, breeding progress, inheritance of resistance, resistant QTL loci, and resistance genes in rapeseed.

Key words: rapeseed; *Sclerotinia* stem rot; pathogenesis; molecular mechanism; resistance breeding

油菜是重要的油料作物,在食品、冶金、机械等多种行业应用广泛,经济价值高。核盘菌(*Sclerotinia sclerotiorum*)是一种广谱性病原真菌,可寄生于 70 多科 400 多种植物,由其引起的菌核病是油菜的一大主要病害^[1]。在中国,菌核病可引起油菜减产 10%~80%^[2];在澳大利亚,菌核病导致油菜年均减产 24%^[3];在北美双低油菜主要种植区域^[4]以及欧洲油菜种植区^[5-7]该病的危害也日趋严重,加之全球气候变化,更可能加速该病害的流行^[8]。化学杀菌剂的使用对该病害有一定防控效果,但效率却依赖于施用时间、植株发育阶段及环境等条件^[9],且

提高了生产成本^[4],还会引发环境污染等问题。因此,选择和培育抗病品种是控制油菜菌核病最经济有效的途径^[10-11]。本文参照国内外及本课题组的研究成果,综述了核盘菌的致病机理,并从抗源筛选、抗性遗传规律探索、抗病分子机制解析等方面总结了油菜菌核病目前的研究状况,以期为油菜菌核病的抗性改良提供参考。

1 核盘菌的致病过程及致病机理

1.1 致病过程

核盘菌经典的侵染循环路径主要是菌核在土

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壤、染病茎秆或种子中越冬、越夏,当外界环境适宜时,菌核可萌发产生菌丝或子囊孢子。子囊孢子成熟后从子囊中弹出,借气流传播,飘落到植株的叶片或花瓣上,在营养和环境条件适宜时萌发形成菌丝,侵入植物体,使植物受侵部位的细胞、组织坏死,形成水渍状病斑并腐烂,再蔓延到其他健康植株,最后

在患病部位尤其是茎秆中形成菌核。对油菜而言,其菌核病的发病符合这个过程(图 1)。核盘菌在油菜花期来临前萌发,通过产生子囊孢子附着在油菜花瓣,继而以花瓣为营养基质生长萌发产生菌丝,菌丝再随着花瓣的凋零飘落到油菜的叶片或茎秆上,开始实现对油菜的侵染^[12]。

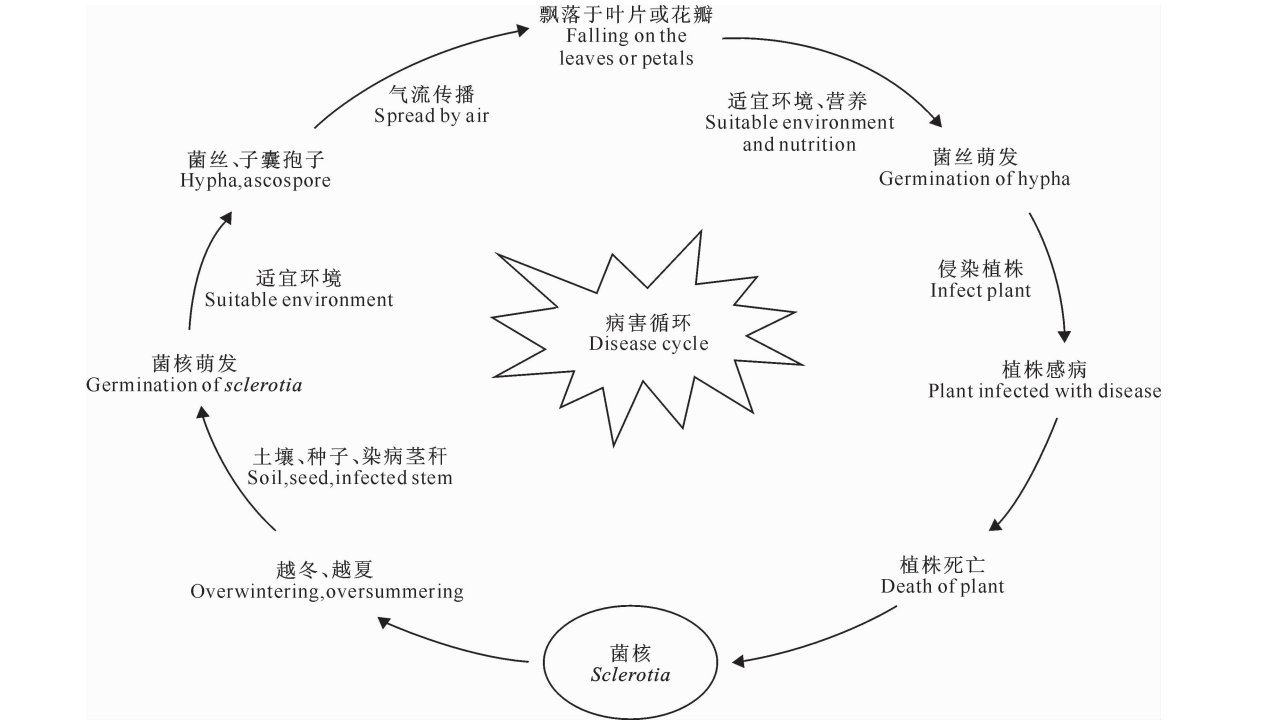


图 1 油菜菌核病的病害循环

Fig. 1 Disease cycle of *Sclerotinia sclerotiorum* in rapeseed

1.2 致病机理

目前,对核盘菌的致病机理尚缺乏系统全面的阐述,但研究表明细胞壁降解酶和草酸的分泌对核盘菌的致病有十分重要的作用^[13-18]。核盘菌能分泌多种作用于寄主表皮的水解酶,如多聚半乳糖醛酸酶(Polygalacturonase, PG)、纤维素酶(Cellulase)、半纤维素酶(Hemicellulase)、果胶酶(Pectinase)、蛋白酶(Protease)、角质酶(Cutinase)、葡聚糖酶(Dextranase)等酶类,攻破寄主表层防护,降解细胞壁,侵染组织,为病菌提供营养,便于菌丝入侵和病菌繁殖^[13-16,19]。核盘菌分泌的草酸是其关键致病因子之一^[17]。研究发现,草酸通过以下方式在核盘菌的致病过程中发挥作用:①酸化、腐败寄主组织^[20];②与细胞壁中胶层的 Ca^{2+} 结合形成草酸钙结晶损坏细胞壁结构^[21-22],与 Mg^{2+} 螯合使叶绿素合成受阻和核糖体功能退化^[23],与二价金属离子结合改变膜透性,导致电解质外渗,使细胞生理机能退化^[24-25];③

影响寄主氧化还原环境,促进寄主的氧化爆发,破坏寄主体内平衡,诱发细胞程序性死亡^[26-31];④为病菌分泌水解酶营造适宜的 pH 环境^[15,24-25],抑制与寄主抗病性相关的酶^[15,32];⑤刺激保卫细胞对 K^{+} 的吸收及对淀粉的降解,影响其细胞膜的渗透性,使保卫细胞功能失调,促使气孔张开,引发叶片发生脱水等症状,利于病菌入侵^[33]。然而,有学者发现了分泌草酸毒素能力强,但致病力却极弱的核盘菌菌株^[34-35],表明草酸并非核盘菌的惟一致病因子,核盘菌存在更复杂的致病机理,尚待进行更深入和系统的研究。

2 油菜菌核病抗性资源的筛选及抗病育种

2.1 抗病资源的筛选与鉴定

优良的抗源对作物抗病育种有至关重要的作用,因此学者们对甘蓝型油菜资源进行了系统而全

面的菌核病抗性鉴定,发现甘蓝型油菜对菌核病的抗性存在差异,但并未找到免疫或者高抗材料^[36-39],因此学者们尝试在甘蓝型油菜的近缘物种中发掘优良抗源。早在 20 世纪末,中国农业科学院油料作物研究所等对 2 000 余份芸薹属材料进行了鉴定,发现芥菜型油菜抗性最强,并选出约 6% 的高抗种质^[37]; Li 等^[38]和 Barbetti 等^[39]报道了在芥菜型油菜中存在较好的抗病资源,如澳大利亚的 *Brassica juncea* JM06018、*Brassica juncea* JM06006 和中国的 *Brassica juncea* 2 等材料。也有学者报道芸薹属中的埃芥对菌核病具有很强的抗性^[40]。芸薹属中的甘蓝,尤其是野生甘蓝拥有很强的菌核病抗性^[41-42];此外,还有学者在十字花科植物中寻找抗病资源,发现 *Erucastrum cardaminoides*、*Diplotaxis tenuisiliqua* 和 *Erucastrum abyssinicum* 等野生型十字花科植物具有高抗菌核病的性能^[43]。这些研究尽管均未找到完全免疫的材料,但明确了不同芸薹属物种对菌核病的抗性存在明显差异,甘蓝型油菜的近缘物种中存在抗性较强的资源,这对甘蓝型油菜的抗菌核病育种具有较大的应用价值。

2.2 抗菌核病育种

受限于油菜中抗病资源的缺乏,国内育种工作者通过传统育种方式选育出了一批具有部分抗性的甘蓝型油菜品种,如中双 2 号^[44]、中油 821^[45]、中双 4 号^[46]、中双 9 号^[47]、湘油 11 号和湘油 15 号^[48]、中双 11 号^[49]等;针对北美油菜种植,先锋育种公司也培育出了对菌核病抗性显著提高的杂交春油菜品种 Pioneer Brand® 45S51 和 Pioneer Brand® 45S52^[50]。虽然有学者曾采用无花瓣育种^[51]、诱变育种^[52]和基因工程育种^[53-55]等方式来培育抗菌核病的油菜,但目前尚没有通过此类途径获得抗菌核病品种的报道。由此看来,要培育高抗菌核病的油菜必须依赖于优良抗源的发掘和先进育种技术的应用。

3 油菜菌核病的抗性遗传规律

由于没有找到高抗菌核病的油菜资源,人们只能采用具有部分抗性的油菜来研究菌核病的抗性遗传规律。早期研究发现,甘蓝型油菜 BC₁F₁ 与 BC₂F₁ 代具有明显偏亲本较强抗性的特性,其抗性表现为部分显性^[56]。随后有学者发现,油菜菌核病抗性主要受核基因控制,由多个基因共同作用,抗性遗传由基因的加性效应和非加性效应共同控制,且加性遗传方差大于显性遗传方差^[57-59]。何昆燕

等^[60]利用六世代分析模型研究了甘蓝型油菜的菌核病抗性遗传规律,发现抗性受 2 对主基因的控制,并受多基因修饰,基因效应及其互作随病情发展呈加性至显性的动态变化。近年来对油菜抗菌核病 QTL 定位的研究结果表明,油菜的菌核病抗性为数量性状,受多基因共同作用,各抗病位点间以加性效应为主,存在一定的上位性,且可能存在与环境的互作^[61]。本研究小组在对甘蓝的抗病位点定位研究中也发现了同样的规律^[62-63]。综上可知,各研究得出的结论不尽相同,这预示着油菜菌核病抗性遗传机制的复杂性,但可以确定的是,油菜菌核病抗性为数量性状,其抗性遗传受多基因控制,并倾向于认为加性效应在油菜菌核病的抗性遗传中起着主要作用。

除了缺乏完全免疫或高抗资源外,在分子水平上对油菜菌核病抗性的不完全阐述也是限制相关研究的一大因素。为此,学者们从 DNA、RNA 以及蛋白质水平上对油菜的抗菌核病基因进行了发掘,以期解析油菜抗菌核病的分子机制。

3.1 抗病 QTL 的定位

在 DNA 水平上,学者们主要采取 QTL 定位途径来寻找抗病相关基因(表 1)。刘春林等^[64]采用 RAPD 标记构建图谱与 F₂ 单株苗期叶片抗性结合的方式检测到 3 个抗病主效 QTL,但未能提供该图谱与甘蓝型油菜各连锁群的对应关系,导致其所鉴定的抗病 QTL 难以与其他类似研究进行比较。何昆燕^[65]和 Yin 等^[66]各自利用 3 种不同的鉴定方法对同一个甘蓝型油菜 DH 群体进行多年、多环境下的抗病性鉴定,分别检测到 18 和 21 个抗病 QTL,但可能由于鉴定方法的不完全相同,两者鉴定出的 QTL 重叠较少。Zhao 等^[2]在甘蓝型油菜 F_{2,3} 家系中鉴定出 3 个苗期和 3 个成株期抗病 QTL,但苗期与成株期抗病 QTL 之间未检测到重叠,随后其又利用叶柄接种法在 2 个 DH 群体中分别获得 11 和 2 个抗病位点,单个 QTL 能解释的最高表型变异度为 22%,并在 N12 和 N02 连锁群上的 QTL 区域检测到同源区段^[67]。本研究室利用甘蓝型油菜 DH 群体在 N12 和 N02 上鉴定出抗病 QTL,并发现 2 个 QTL 区域之间存在同源性^[68]。近来,一些研究者通过不同的抗性鉴定方法在不同的群体中也鉴定出了一些抗病 QTL,这些 QTL 多数分布在甘蓝型油菜的 A 亚基因组上,少数存在于 C 亚基因组,其中单个 QTL 能解释的最大变异度达到 42%^[67,69-72]。在最近的一篇报道中,研究者将重要

的 QTL 位点锁定在了甘蓝型油菜的 A9 和 C6 染色体上,通过生物信息学手段并结合 RT-PCR 验证的方法,确定了一个吲哚硫代甲基转移酶(Indole glu-

cosinolate methyltransferase, IGMT) 编码基因 (*BnIGMT5.a*),该基因为 C6 上 QTL 区间中的候选抗病基因^[61]。

表 1 甘蓝型油菜的抗菌核病 QTL

Table 1 Resistant QTLs against *Sclerotinia sclerotiorum* of *Brassica napuse*

群体 Population	组合 Cross	接种方法 Inoculation method	抗性指标 Resistance index	QTL 数 QTL number	QTL 所在连锁群 Linkage group	贡献率 % Variation	参考文献 Reference
F ₂	085 (R)×Xiangyou13 (S)	A	1	3	LG4, LG8, LG14	13.9~29.2	[64]
		A	1	3	LG5(N7), LG12(LG11)	9.5~41.5	
		B	3	3	LG3(N6), LG4(N7), LG5(N7)	11.3~24.7	
DH	DH821 (R)×Bao604 (S)	B	3	3	LG1(N1), LG2(N12), LG5(N7),	8.7~42.2	[65]
		E	4	12	LG9 (N10), LG10 (N3), LG12 (LG11), LG15, LG19		
		B	3	10	N4, N7, N10, N11, N12	10.2~36.2	
DH	DH821 (R)×Bao604 (S)	C	3	10	N1, N3, N4, N6, N17, LG11	11.6~15.1	[66]
		E	1	1	N12	17.3	
		A	1	3	LG3, LG12, LG17	13.6~23.2	
F _{2:3}	NingRS-1 (R)×Hui5200 (S)	B	1	3	LG7, LG10, LG15	17.4~39.8	[2]
DH	RV289 (R)×P1804 (S)	D	2	11	N2, N3, N5, N12, N14, N16, N19	5.9~22.0	[67]
DH	Major (S)×Stellar (R)	D	2	2	N3	11.1~22.7	[67]
DH	PHI2004HS1 (S)× 04DHS11418 (R)	F	1	8	N1, N7, N9, N11, N12, N18, N19	6.3~10.1	[70]
BC ₁ F ₂	M83 (R)×APL01 (S)	A	3	1	N1, N9, N13	5.0~6.4	[71]
		C	3	1	N3, N8, N9	5.4~5.7	
DH1	ZY821 (R)×Bao604 (S)	C	1	3	A1, A7, C3	—	[69]
DH3	ZY821 (R)×Westar (S)	C	1	2	C6, C9	—	
DH4	DH3 (R)×Westar (S)	C	1	2	A3, A7	—	
DH6	DH3 (R)×Digger (S)	C	1	2	A1, A6	—	
DH7	DH1 (R)×Digger (S)	C	1	1	A6	—	
DH	J7005 (R)× Huashuang5 (S)	A	3	9	A3, A9, C8	3.18~13.07	[72]
		C	2	23	A1, A2, A3, A6, A7, A9, C2, C6, C8	2.91~41.6	
DH	J7005 (R)× Huashuang5 (S)	A	1	3	A3, A9, C5	7.91~15.86	[61]
		C	1	10	A1, A2, A3, A6, A8, A9, C6, C7, C8	3.43~32.61	

注:R. 抗病, S. 感病; A. 苗期离体叶片接种法, B. 成株期田间牙签接种法, C. 成株期田间菌丝琼脂块贴附法, D. 活体叶柄接种法, E. 花瓣接种法, F. 草酸浸根法; 括号中的编号代表该连锁群在 Yin 等^[66]图谱中所对应的染色体情况; “—”表示数据缺失。

Note: R. Represents resistant, S. Represents susceptible; A. Represents detached leaf inoculation, B. Represents toothpick inoculation, C. Represents mycelial plug inoculation, D. Represents petiole inoculation, E. Represents petal inoculation, F. Represents oxalic-acid soak root inoculation; Numbers in parentheses represent the linkage group in the map of the corresponding chromosomal condition in Yin et al^[66]; “—” indicates missing data.

3.2 基因表达层面对抗病基因的挖掘

在 RNA 水平上,多数研究者采用 cDNA 芯片技术来研究油菜受核盘菌侵染后诱导表达的基因,或不同抗性材料在核盘菌侵染后基因的表达差异。研究发现,受核盘菌诱导的基因主要包括:①几丁质酶(Chitinase)、葡聚糖酶、渗调蛋白(Osmotins)和凝集素(Agglutinin)等病程相关蛋白(Pathogenesis-related proteins, PRs)编码基因;②细胞色素 P450 (Cytochrome P450, CYP450)相关蛋白基因以及谷胱甘肽转移酶(Glutathione transferase)基因;③茉莉酸(Jasmonic acid, JA)生物合成和信号传递、活性氧代谢(Reactive oxygen metabolism)及氧爆反应

(Oxidative burst)相关蛋白基因;④细胞壁结构与功能相关基因;⑤蛋白激酶(Protein kinases)、分子转运蛋白和细胞发育相关基因等;⑥转录因子(锌指、WRKY、AP2 和 MYB 家族)、次生代谢物合成基因等^[73-75]。其中,初步确定的候选抗病相关基因包括:*Bn-29*、*Bn-30* 和 *Bn-10*(三者一起正调控油菜菌核病的抗性)^[76], 促分裂原活化蛋白激酶(Mitogen-activated protein kinase, MAPK) 基因^[77-78]、*Bn-MAPK7-1*、*BnMAPK7-2* 和 *BnMAPK7-3*^[79], 正调控抗性的乙烯信号转导途径(Ethylene-signaling pathway)关键调节因子 *BnEIN3*^[80], 乙烯应答转录因子(Ethylene-responsive transcriptional factors,

ERFs) *BnERF104* 和 *BnERF50* 基因^[81-82] 及多聚半乳糖醛酶抑制蛋白 (Polygalacturonase-inhibiting protein, PGIP) 基因 *Pgip1* 和 *Pgip2*^[83-84] 等。尽管众多学者都致力于揭示油菜抗病分子机制,但受 cDNA 芯片技术本身的限制,这些研究无法在整个转录组水平上对油菜接种核盘菌后基因的表达变化进行系统而全面地跟踪,因而这些研究类似于一幅拼图中的少数几个小单元,只有用更多的单元来补充和完善整幅图片后,才能明确油菜抗核盘菌的分子机制。

3.3 蛋白质层面对抗病基因的挖掘

在蛋白质水平上,早期学者们主要是通过检测少量与植物抗逆/抗病相关蛋白在接种核盘菌前后的变化情况来判断其是否与菌核病抗性相关,如王汉中等^[85] 研究了苯丙氨酸解氨酶 (Phenylalanine ammonia-lyase, PAL)、几丁质酶、 β -1,3-葡聚糖酶 (β -1,3-dextranase)、过氧化物酶 (Peroxidase, POD) 和多酚氧化酶 (Polyphenol oxidase, PPO) 等油菜中重要的防御酶类在抗、感材料接种前后的活性变化,发现 PAL、几丁质酶和 β -1,3-葡聚糖酶、POD、PPO 与油菜对菌核病的抗性密切相关;张志元等^[86] 发现,超氧化物歧化酶 (Superoxide dismutase, SOD) 与油菜对菌核病的抗性有关。后来学者们开始采用蛋白质组学来研究油菜抗菌核病的机制和抗病基因。皇甫海燕等^[84] 对油菜抗菌核病近等基因系及其感病亲本在核盘菌侵染后的蛋白质组进行了分析,发现组成线粒体 ATP 合酶 F1 的重要亚基 F1 β 、糖酵解关键酶磷酸甘油酸激酶 (Phosphoglycerate kinase, PGK)、参与合成维生素 B1 的辅酶噻唑 (thiazole) 生物合成酶 THI1 和 1,5-二磷酸核酮糖羧化酶/加氧酶 (Ribulose-1,5-bisphosphate carboxylase/oxygenase, RuBisCO) 在油菜对菌核病的抗性反应中差异表达。Wen 等^[87] 对甘蓝型油菜抗、感品种接种核盘菌前后进行了比较蛋白组学分析,发现与抗性相关的蛋白主要在病原抗性、抗氧化作用和转录调节这几个部分发生作用,并发现一些作用于活性氧清除的胰蛋白酶抑制蛋白 (Trypsin inhibitor protein, TIP)、富含甘氨酸的细胞壁蛋白 (Glycine rich protein, GRP)、热激蛋白 (Heat shock protein, HSP) 和硫醇甲基转移酶 (Thiol methyltransferase, TMT) 在抗性品种中呈上调或特异表达。

4 油菜菌核病的研究展望

尽管科学家们对油菜抗菌核病育种及相关研究

投入了较大精力,也在取得了一定成效,但还存在一些重要问题需要解决:一是油菜中缺乏可利用的优良抗源,导致抗性位点定位的重复性差,抗病基因鉴定工作进展缓慢,其研究成果难以应用于育种实践,油菜菌核病抗性的改良难以获得突破性进展;二是寄主与核盘菌的互作机制复杂,病原菌的致病机理、寄主的抗病机制至今仍不清晰,从而限制了抗病基因的鉴定和油菜抗菌核病的分子设计育种;三是研究手段尚需改进,当前对抗病基因的鉴定研究多采用 QTL 定位或通过检验少数基因对核盘菌的响应情况来推测其与抗性的关系,难以准确鉴定出抗病基因,更无法了解寄主的抗病机制。

鉴于上述问题,笔者认为油菜菌核病研究的首要内容仍然是广泛搜寻可利用的优良抗病资源,包括油菜的近缘物种乃至十字花科其他植物。在获得优良抗源的基础上,通过远缘杂交或传统育种方式将其抗病成分转入油菜,利用其进行抗病位点鉴定的准确性必将得到有效提高,抗病机制的分析难度也将降低。随着生物学和生物信息学研究技术的快速发展,以及甘蓝型油菜、甘蓝和白菜全基因组测序的进行和完成,结合全基因组水平、转录组水平和代谢组水平的分析手段,可快速、全面、准确地解析油菜的抗菌核病机制并发掘抗病基因,这对于油菜抗菌核病的分子设计育种具有重要的实践意义。

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