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Research Advances in Chili Pepper Anthracnose

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Tianjiao Sun was born in Turpan, Xinjiang. China, in 1995. She obtained a master's degree from Hunan Agricultural University. She currently studying at the Horticulture College of Hunan Agricultural University. His main research direction is Elucidating Mechanisms of Anthracnose Resistance and Innovating Germplasm in Pepper.

Abstract: Anthracnose in chili pepper, caused by pathogenic fungi of the genus *Colletotrichum*, primarily affects pepper fruits and leaves. It has become a significant fungal disease in chili pepper production, causing global yield losses of 15%–50% and posing serious constraints to industry development. Currently, the complex species diversity of *Colletotrichum* pathogens and incomplete elucidation of key pathogenic mechanisms have limited the development of efficient control strategies.This review summarizes research advances in pathogen identification and diversity, infection cycle and pathogenic mechanisms, host resistance and genetic breeding, disease epidemiology, and integrated management techniques including chemical and biological control. Future research directions are also discussed, aiming to provide insights for in-depth studies and effective management this disease.

Keywords: Anthracnose in chili pepper; *Colletotrichum*; Pathogen diversity; Disease resistance genes; Integrated management

Introduction

Chili pepper anthracnose, caused by fungi of the genus *Colletotrichum* spp., is one of the globally destructive diseases, often resulting in yield losses of 15%–50% [1]. According to the Food and Agriculture Organization of the United Nations (FAO) statistics, China's chili pepper cultivation area reached 18,857 ha in 2023, with a total production of approximately 33.909 million tons[2]. In recent years, the northward shift of China's rainfall belt has intensified anthracnose damage during the fruit ripening stage in major producing provinces like Henan, Shandong, and Hebei, prompting a migration of the dry and processing pepper industries to more

climatically suitable regions[3]. Traditional classification methods relying on morphology and single-gene ITS markers are prone to species misidentification. Furthermore, the complex species diversity of the pathogens and incomplete elucidation of key pathogenic mechanisms have constrained the development of efficient control strategies to some extent. This review systematically summarizes the latest research advances in chili pepper anthracnose, covering pathogen identification and diversity, infection cycle and pathogenic mechanisms, host resistance and genetic breeding, disease epidemiology, and integrated management techniques including chemical and biological control. Future research directions are also discussed, aiming to provide a scientific basis for in-depth studies and effective management of this disease.

1 Pathogen Diversity of Chili Pepper Anthracnose

1.1 Global Pathogen Complex of Chili Pepper Anthracnose

The classification system of the genus Colletotrichum underwent systematic revision starting in 2009 based on multi-gene phylogenetic analyses. Integrating sequences of genes such as *ITS*, *GAPDH*, *CHS-1*, *ACT*, *TUB2*, *CAL*, *SOD2*, and APN2, along with morphological characteristics, significantly improved species identification accuracy [4]. Currently, 24 species pathogenic to chili pepper have been identified globally, with 15 species reported in China [5]. The core pathogen complexes include: *Colletotrichum scovillei* (previously identified as *C. acutatum*); *Colletotrichum truncatum* (previously identified as *C. capsici*); *Colletotrichum siamense* (previously identified as *C. gloeosporioides*). Based on comprehensive literature reports, the global distribution of these major pathogens is summarized in Table 1.

Table 1: Global distribution of major *Colletotrichum* spp. causing chili pepper anthracnose

Colletotrichum Species	Countries	References
C. truncatum	Australia, India, China, South Korea, Malaysia, USA, Vietnam, Thailand, Nigeria, Pakistan, Indonesia	[6-19]
C. scovillei	China, Brazil, South Korea, Malaysia, Indonesia, Japan, Philippines, Vietnam, Thailand, India, USA	[8,9,10,12,13,16,17,20,22,23,24,25,26,27,28,29,30]
C. siamense	Australia, India, Brazil, Malaysia, Vietnam, Thailand, South Korea, USA, China, Indonesia	[6,7,9,10,12,13,14,16,17,19,20,23,27,29]
C. coccodes	Brazil, Bulgaria, India, South Korea, Nigeria, USA, Vietnam	[13,15,23,29,31,33]

C. boninense	Brazil, India	[29,31]
C. dematium	South Korea	[23]
C. brevisporum	Brazil, Vietnam, China	[10,20,27,34]
C. fructicola	India, China, Malaysia, Vietnam	[7,10,12,27,29,35]

1.2 Species Composition, Endemic Pathogens, and Novel Species Discoveries in China

Systematic isolation and identification from diseased chili pepper samples across 29 provinces in China (yielding 1,285 isolates), combined with morphological and multi-gene phylogenetic analyses (ITS/ACT/CAL/CHS-1/GAPDH/TUB2/HIS3), revealed 15 *Colletotrichum* species pathogenic to chili pepper in China. *C. fioriniae*, *C. fructicola*, *C. siamense*, *C. scovillei*, and *C. truncatum* were the most prevalent. Novel species first described include: *C. conoides* (Nanjing, Jiangsu), *C. grossum* (Haikou, Hainan), *C. liaoningense* (Xingcheng, Liaoning) [9]. From rotten chili pepper fruits in Sichuan Province, 88 isolates representing 7 Colletotrichum species were obtained. Phylogenetic analysis based on morphology and multi-locus sequences detected a novel species described as *C. sichuanensis* [10]. In October 2021, approximately 60% of chili pepper fruits (cv. Lamb chili) in Yunnan Province, China, exhibited typical anthracnose symptoms. Multi-locus phylogenetic analysis distinctly differentiated isolate YN296-2 as *C. jiangxiense*, distinguishing it from all other species within the *Colletotrichum* species complexes[36]. Morphological characteristics of these endemic novel species are detailed in Table 2.

Table 2: Taxonomic characteristics of novel *Colletotrichum* species endemic to China

Colletotrichum Species	Region	Colony Appearance	Growth Rate（mm/day）	Conidiophores	Conidia		Appressoria		References
				Length × Width（μm）	Shape	Length × Width（μm）	Shape	Length × Width（μm）	
C. conoides	Jiangsu	Greyish white aerial mycelium; reverse pale grey to medium grey,	13.25–13.75 (Mean 13.5)	22–30 × 3.5–5	Cylindrical to clavate, both ends obtuse, granules evenly	13.0–17.5 × 5.0–6.5（Mean 15.9×5.9）	Single or clustered, medium to dark brown, ellipsoidal to irregular, margins lobate	4.0–11.5 × 6.0–10.5（Mean 8.35×7.1）	[9]

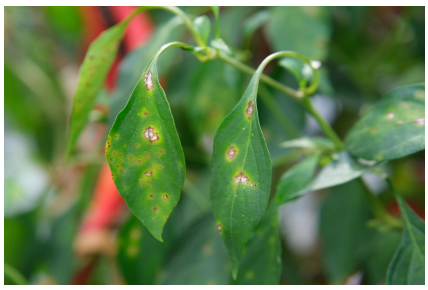
		margin white			distributed		or deeply incised		
C. grossum	Hainan	White aerial mycelium; reverse pale grey, margin white	12.25–13.0（Mean 12.6）	22–32 × 3–3.5	Cylindrical to clavate, one end acute, granules concentrated at tip	14.5–20.5 × 5.0–7.5（Mean 16.8 × 6.3）	Single, medium brown, ovoid to irregular, margins lobate	5.5–11.5 × 4.0–10.5（Mean 8.65 × 6.1 ）	
C. liaoningense	Liaoning	Pale grey aerial mycelium; reverse medium to dark brown, margin white	12.0–12.75（Mean 12.4）	27–30 × 3.5–4.5	Cylindrical to clavate, one end acute, granules concentrated at tip	14.0–18.5 × 5.0–7.5（Mean 16.3 × 6.1 ）	Single, medium to dark brown, ellipsoidal to irregular, margins lobate	3.5–5.0 × 2.5–4.5（Mean 4.1 × 2.9）	
C. sichuanensis	Sichuan	Initially white, maturing to pale grey aerial mycelium; reverse pale grey, sparse mycelium	6.1–6.4（Mean 6.3 ± 0.1）	Branched cylindrical, apex slightly swollen	Cylindrical, both ends obtuse	15–18.9 × 5.4–6.5（Mean 16.9 × 6.2）	Light to dark brown, irregular to lobate	8.1–12.4 × 5.4–8.8（Mean 10.2 × 6.8）	[10]
C. jiangxiense	Yunnan	Dense cottony aerial mycelium, white to grey, margin with orange conidial masses; reverse olive green with pale orange margin	约 12.9	11.5–20 ×1–2.5	Cylindrical, ends obtuse or one acute	13–19 × 4–6（Mean 15.2 × 5.2）	Light to dark brown, circular/ellipsoidal/irregular	-	[36]

2 Pathogen-Host Interaction

2.1 Disease Cycle and Pathogenesis

Colletotrichum spp. can infect all parts of the chili pepper plant throughout its growth cycle. During vegetative growth, leaves and stems are infected. Leaf symptoms typically include circular or irregular necrotic lesions with greyish-white to light brown centers and dark brown margins (Figure 1A, D). Severe infections cause lesions to coalesce, leading to leaf death and abscission. Stem infections produce brown, sunken lesions or cankers (Figure 1B, E), which can girdle the stem, causing systemic wilting of upper foliage. The most damaging phase occurs during fruit ripening and post-harvest storage, particularly under high humidity conditions such as rainy seasons. Infected fruits initially develop small, water-soaked spots that rapidly expand into circular or nearly circular, deep brown to black, sunken necrotic lesions (Figure 1C, F). This stage causes significant pre-harvest fruit drop and post-harvest decay, leading to substantial yield and quality losses [37, 38].

Figure 1. Characteristic symptoms of anthracnose on chili pepper fruit (A, D), leaves (B, E), and stems (C, F)



A

B

C

D

E

F

The core infection process of Colletotrichum spp. begins with conidia recognizing hydrophobic signals on the host surface, germinating to form germ tubes that differentiate into melanized appressoria at their tips. This structure accumulates osmotic regulators like glycerol, generating enormous turgor pressure (5–8 MPa) to drive the mechanical penetration of the pepper cuticle by the penetration peg [39]. Notably, *C. scovillei* forms unique dendritic penetration pegs on chili pepper fruits – intermediate structures composed of thick-walled hyphal branches with sharp tips for efficient cuticle penetration, a structure formed exclusively on chili fruit cuticles [40].

Infection strategies subsequently diverge:Intramural necrotrophy (e.g., *C. truncatum*): Hyphae expand between the cuticle and cell wall, secreting toxins like colletotrichin to induce rapid host cell necrosis (within 24 hours), bypassing a biotrophic phase[41].Hemibiotrophy (e.g., *C. siamense*): After penetration, slender primary hyphae develop and maintain a biotrophic phase inside cells for 3–5 days, during which effector proteins suppress host immunity. This phase transitions to thick secondary necrotrophic hyphae that secrete pectinases and cellulases to destroy tissue and spread[42].

2.2 Key Pathogenicity-Related Genes

The pathogenicity of chili pepper anthracnose fungi is intricately regulated by a multi-gene network, involving infection structure development, nutritional strategy transition, and activation of key signaling pathways. Studies show that the NADPH oxidase complex encoded by *CsNox2* and *CsNoxR* genes is crucial for penetration peg formation. Knockout mutants (*Δcsnox2, Δcsnoxr*) form appressoria but fail to penetrate intact pepper epidermis, resulting in loss of pathogenicity [43]. Pathogenesis post-penetration heavily relies on conserved MAPK signaling pathways: *CsPMK1* (Fus3/Kss1 homolog) regulates appressorium formation and lipid mobilization via the homeobox transcription factor CsHOX7; its deletion causes delayed conidial germination and complete loss of infectivity [44]. *CsSTE7* (MAPKK) deletion leads to defects in appressorium formation and loss of pathogenicity [45]. Cell wall integrity pathway components *CsMck1* (MAPKKK), *CsMkk1* (MAPKK), and *CsMps1* (MAPK) collectively regulate hyphal growth, stress response, and infectious hypha development; mutants of all three lose pathogenicity [46]. The adaptor protein CsSte50, a key regulator of the MAPK cascade, is essential for pathogenicity; its deletion causes impaired conidial germination, absence of appressorium formation, and complete loss of virulence [47].

2.3 Host Resistance Mechanisms in Chili Pepper

Chili pepper resistance to anthracnose involves both preformed (passive) and inducible (active) defense mechanisms [48]. Passive defense relies on pre-existing structural barriers and antimicrobial compounds. Research indicates strong resistance to non-wound inoculation, suggesting *Colletotrichum* cannot effectively penetrate the intact cuticle [49]. In the resistant accession *Capsicum baccatum*PBC80, the fruit epidermis provides initial defense via cuticle and cell walls. Post-infection, localized cell wall thickening occurs, and high concentrations of reactive oxygen species (ROS) and phenolic compounds directly inhibit pathogen expansion [50]. Mature fruits exhibit stronger resistance than immature fruits due to increased phenolic content (e.g., chlorogenic acid, caffeic acid) and reinforced cell wall structure [51]. The CaAMP1 protein strongly inhibits *Colletotrichum* spore germination and hyphal extension in vitro [52]. These barriers effectively hinder spore attachment, penetration, and initial colonization.

When pathogens breach passive defenses, chili pepper activates active defense responses via the innate immune system, centered on two cascading signals:

PAMP-triggered immunity (PTI) and effector-triggered immunity (ETI). PTI is initiated when pathogen-associated molecular patterns (PAMPs) are recognized by plant pattern recognition receptors (PRRs), inducing MAPK signaling activation, Ca^{2+} influx, and ROS burst. This subsequently regulates defense gene expression via salicylic acid (SA) or jasmonic acid (JA)/ethylene (ET) pathways [53]. ETI is triggered when resistance proteins (e.g., NLR-type proteins) directly recognize pathogen effectors, leading to a hypersensitive response (HR) involving programmed cell death at infection sites to limit pathogen spread. The *CbAR9* gene in *C. baccatum*PBC80 encodes a CC-type NLR protein; its overexpression significantly enhances resistance to anthracnose and activates pathogenesis-related *(PR*) gene expression (*PR1, PR2, PR10*), restricting pathogen diffusion [54]. This process is finely regulated by hormone signaling networks and transcription factors: SA signaling dominates resistance to hemibiotrophic pathogens, activating *PR* genes and systemic acquired resistance (SAR) [55]. JA/ET pathways synergistically combat necrotrophic infections. Key transcription factors (WRKY, NAC, AP2-EREBP) act as regulatory hubs by integrating hormone signals – e.g., WRKY33 positively regulates JA/ET signaling to promote defensin *PDF1.2* expression [56], while CaWRKY50 negatively regulates SA signaling [55]. C2H2 zinc finger proteins (e.g., CanZF40/46) coordinate defense gene expression like lipoxygenase (*LOX*) via JA/ET pathways [57]. Furthermore, activation of ripening-specific genes like PepEST (a JA-induced esterase) and the phenylpropanoid pathway (key genes *4CL, CCoAOMT*) strengthens the multi-layered synergistic defense network in fruit resistance [58, 59].

3 Germplasm Resources Resistant to Chili Pepper Anthracnose

Resistance to chili pepper anthracnose exhibits significant species specificity and fruit developmental stage dependency. Commercial cultivars of *C. annuum* are generally susceptible, while broad-spectrum resistance primarily resides in wild relatives *C. baccatum* and *C. chinense*[60]. Several core germplasms with broad-spectrum, high-level resistance have been identified (Table 3), showing significant pathogen specificity, fruit stage dependency, and genetic diversity.

Table 3: Core resistant germplasms and their resistance characteristics

Colletotrichum Species	Resistant Accession	Pepper Species	Resistance Level	Key Genetic Mechanism	Resistance Stability	Validation Population	References
C. scovillei	PBC80	*C. baccatum*	HR	Green fruit: Recessive gene *Co4*; Red fruit: Dominant gene *Co5* (independently inherited)	Immunity throughout growth stages	F2, BC1	[61]
	PBC81	*C. baccatum*	HR	Polygenic control	Broad-spectrum	F2, BC1	[62]

	PBC932	*C. chinense*	R	Green fruit: 2 dominant genes; Red fruit: 2 recessive genes	Stage-specific	BC1	[63]
	GBUEL104	*C. annuum*	HR	Dominant effect > Additive effect	Green/Ripe fruit dominant	F2, BC1, BC2	[64]
	Pi594137	*C. baccatum*	R	Single dominant gene	Broad-spectrum (stronger than PBC81/932)	F2, BC1	[65]
	0038-9155	*C. annuum*	HR	Green fruit: 2 complementary dominant genes; Red fruit: 2 recessive duplicate epistatic genes	Stage-independent inheritance	F2, BC1, BC2	[66]
	PBC932	*C. chinense*	HR	Single recessive gene col (Green & Red fruit)	Zero lesion, complete resistance	F2, BC1	[67]
	PBC81	*C. baccatum*	HR	Polygenic control	Broad-spectrum	F2, BC1	[68]
C. truncatum	83–168	*C. annuum*	MR	Single dominant gene	Delays infection	F2, BC1	[69]
	Punjab Lal	*C. annuum*	R	Single dominant gene	Multi-pathogen resistance	F1、F2、BC1	[70]
	Daepoong-cho	*C. annuum*	HR	Single recessive gene (allelic to PBC932 col)	Suppresses initial infection	F2、BCR、BCS	[71]
	PRI95030	*C. chinense*	HR	Major QTL B1 (Explains 57.3% variation)	Broad-spectrum	F2	[19]
C. siamense	UENF1718/UENF1797	*C. baccatum*	HR	Stage-specific genes	Symptom-free at all stages	-	[72]

The representative *C. baccatum* accession PBC80 exhibits immunity throughout the growth cycle against 13 strains of both *C. scovillei* and *C. truncatum* (gene stacking: green fruit recessive *co4* + red fruit dominant *co5*) [61]. The broadest-spectrum accessions PBC81 and PI594137 confer stable resistance to multiple pathogens via polygenic or single dominant gene control [65, 68]. While *C.*

baccatum shows strong resistance to *C. truncatum* and *C. siamense*, *C. scovillei* can partially overcome resistance in the green fruit stage. The *C. chinense* accession PBC932 achieves zero-lesion immunity to *C. truncatum* (single recessive col gene) [67], but its resistance to *C. scovillei* is stage-specific (green fruit: two dominant genes; red fruit: two recessive genes) [63]. PRI95030 possesses resistance to both *C. siamense* and *C. truncatum* via a major QTL *B1* (explaining 57.3% lesion variation) [19]. Among C. annuum cultivars, a few highly resistant sources exist, such as GBUEL104 (Brazil) [64], Daepoong-cho (Korea) [71], and Punjab Lal (India) [70], which achieve resistance via dominant or recessive major genes but require interspecific introgression for improvement. These resources combine resistance stability with agronomic value; for instance, the hybrid DP-37×Putra chili 4 achieved synergistic improvement in disease resistance (lesion area <5%), yield (1273 g/plant), and pungency (31,236 SHU) [73].

4 Genetics and Mapping of Anthracnose Resistance in Chili Pepper

Genetic studies reveal that resistance to different pathogens is controlled by major genes, QTLs, or gene clusters, exhibiting significant pathogen species specificity and fruit ripening stage dependency. Major resistance sources are concentrated in wild species *C. baccatum* and *C. chinense.* Resistance introgression into cultivated *C. annuum* is accelerated through interspecific hybridization and marker-assisted selection (MAS). Reported molecular markers associated with anthracnose resistance traits for MAS are listed in Table 4.

Table 4: Key QTLs/genes mapped for chili pepper anthracnose resistance

Colletotrichum Species	Resistant Accession	QTL	Linkage Group/Chromosome	Molecular Marker (Type)	Marker Interval / Position	References
C. scovillei	*C. baccatum* 'PBC81'	CaR12.2	LG12	AFLP	HpmsE032～EataMcgc01	[68]
	C. baccatum 'PBC81'	ARG_4a	LG4	SNP	chr4_161.7～chr4_207.43	[74]
		ARG_4b	LG4	SNP	chr4_196.86	
		ARG_12	LG12	SNP	chr12_36.95～chr12_39.89	
		ARR_11	LG11	SNP	chr11_232.44～chr11_234.14	
	C. baccatum 'PBC80'	-	LG12	SSR	HpmsE032	[75]
	C. chinense 'PBC932'	-	P5	SCAR/InDel	SCAR-InDel	

	C.baccatum var. pendulum 881045	An9.1	P1	AFLP	meD2emD3_2	[76]
		RA80rP2、RA80rP3.1、RA80rHP1	LG4	SNP	BACSNP-4-63～BACSNP-4-60	
	C. baccatum 'PBC80'	RA80rP3.2	LG12	SNP	BACSNP-12-61～BACSNP-12-58	[77]
		RA80rHP2	LG9	SNP	BACSNP-3-84～BACSNP-3-87	
		AnRGO5、AnRGT5、AnRGD5、AnRRO5、AnRRT5	P5	InDel	InDel～HpmsE116	[63]
	C. chinense 'PBC932'	AnRGO5	P5	KASPar	P5L_P_81～P5L_P_137	[78]
		AnRGO5	P5	KASPar、InDel	P5in-2266-404～P5in-2267-978	[79]
		RA806_r1	P4	SNP	SNP_305～331	
	C. baccatum 'PBC80'	RA806_g1	P8	SNP	SNP_541～571	[80]
		RA806_g2	P3	SNP	SNP_228～218	
	6 个 *C. chinense* 种质：IT229207、 IT236717、IT261436、IT261448、IT284059 、IT305437	-	Ch01,、Ch02,、Ch03, Ch05、Ch08、Ch09	SNP	ChCh01: 37,429,407 bp (CA01g29280) Ch02: 146,421,570 bp (CA02g17350) Ch03: 1,918,096 bp (CC-NBS-LRR) Ch05: 未指定位置 (PRP 基因)	[81]
	C. baccatum 'PBC80'	CcR9	LG9	AFLP	HpmsE143～EtgtMcgt10	[54]
C. truncatum	*C. annuum* 'Punjab Lal'	RCt1	-	ISSR、AFLP	CtR-431 、 CtR594	[70]
	C. annuum 'Punjab Lal'	QCoG-la.livr1.1		SSR	HPMS725～CAMS644	

C. baccatum 'PBC81'	CcR9	LG9	AFLP	HpmsE143～EtgtMcgt03	[68]
	CcRC	LGC		EaacMcgc02～EaatMccg07	
C. chinense 'PBC932'	RA932g、RA932r	LG2	SNP	CAP_T39318_0_1_1042 ～CAP_ T22290_0_1_429	[77]
C. chinense 'PBC932'	QTLUL	P9		G31	[82]
	QTL-L4	P11		G28	

For *C. scovillei*, wild species core accessions *C. baccatum* 'PBC81' and 'PBC80' contribute major QTLs *CaR12.2* (chr12, AFLP markers HpmsE032~EataMcgc01 → fine-mapped to a 36.95–39.89 Mbp NLR gene cluster) [64,74] and RA80rP2/RA80rP3.1/RA80rHP1 (Chr4, SNP markers BACSNP-4-63~60) [77], respectively. Resistance in 'PBC80' green fruit co-segregates completely with SSR marker *HpmsE032* (231 bp) (prediction accuracy 100%) [75]. *C. chinense* accession 'PBC932' regulates resistance in both fruit stages via a QTL cluster at the end of chromosome P5 (explaining 33.17–62.38% of green fruit resistance variation) [63]. Its key gene *AnRGO5* (within a 164 kb interval, NBS-LRR protein CA05g17730) is non-functional in susceptible materials due to structural variation [79]. The linked KASPar marker UN27353_1781 (2 cM) has a selection accuracy of 92.9% [78]. For *C. truncatum*, the CC-NLR gene *CbAR9*, cloned from *C. baccatum* 'PBC80' (located in major QTL *CcR9*, chr9) and functionally validated, activates PR gene pathways [54]. The homologous locus in 'PBC81' has a SCAR marker with 82.5% selection efficiency [62]. The dominant gene RCt1 (resistance to *C. truncatum*) in *C. annuum* 'Punjab Lal' has a conserved STS marker CtR-431 (1.8 cM) [70].

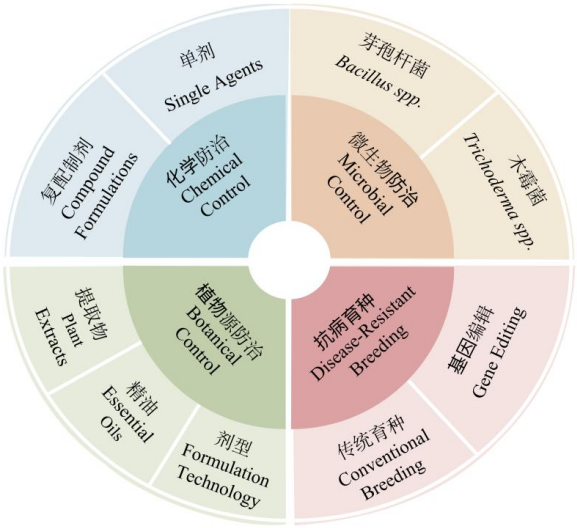
Significantly, breakthroughs have been made in understanding cross-resistance QTL mechanisms: In *C. baccatum* 'PBC81', the major resistance locus for C. scovillei (*CaR12.2* on chr12) and the major locus for *C. truncatum* (*CcR9* on chr9) are inherited independently. However, minor QTL *CaR9* (chr9) and *CcR12.2* (chr12) co-localize with the major QTLs for the other pathogen [62], revealing synergistic defense pathways. Molecular marker pyramiding strategies developed based on this (e.g., combining SCAR-InDel and SSR-HpmsE032) increased resistant genotype selection efficiency to 77.2%, significantly accelerating the introgression of resistance sources (e.g., PBC series) into cultivated types, providing theoretical and technical support for multi-pathogen resistance pyramiding breeding [75].

5 Integrated Management of Chili Pepper Anthracnose

Integrated management of chili pepper anthracnose encompasses chemical control, development of microbial-based fungicides, utilization of plant-derived fungicides,

and breeding resistant varieties. The core framework of integrated strategies is summarized in Figure 2.

Figure 2: Management Strategies for Chili Pepper Anthracnose



5.1 Chemical Control

Chemical fungicide application remains crucial for controlling large-scale epidemics before or during the initial outbreak of chili pepper anthracnose, due to its rapid action, ease of application, and high efficiency. Through in vitro toxicity assays and field trials, several highly effective fungicide classes have been identified, including picoxystrobin, thiophanate-methyl, difenoconazole, prochloraz, azoxystrobin, mancozeb, pyraclostrobin, and their combinations (e.g., difenoconazole·pyraclostrobin, fluazinam·pyraclostrobin) [83-89]. However, prolonged sole or excessive use of chemicals is widespread, readily inducing pathogen resistance and leading to significantly reduced efficacy [88].

Furthermore, due to variations in field management practices, long-term sole or excessive use is common, exacerbating the risk of pathogen resistance. Resistance studies show significant differences in baseline sensitivity to the same fungicide among different *Colletotrichum* species (e.g., *C. truncatum* vs *C. scovillei*). Fludioxonil exhibited the strongest inhibitory activity against these strains (EC_{50} values of 0.0120 μg/mL and 0.0142 μg/mL, respectively) [90], while carbendazim and difenoconazole also performed well. In Sichuan Province, *C. scovillei* showed high sensitivity to prochloraz (EC_{50} 0.0337 μg/mL), tebuconazole, and epoxiconazole, providing a basis for regionalized precise chemical application [91].

Regarding application technology optimization, chemical fungicides primarily work by disrupting pathogen cell structures (e.g., increasing membrane permeability), interfering with metabolism, or inhibiting growth. Core measures include seed treatment (e.g., copper sulfate, carbendazim) and field spraying [92]. Recent studies indicate significant synergistic effects from coformulations: 20%

fluazinam·pyraclostrobin SC (900 g/ha) achieved 82.65% control efficacy [87]; 40% difenoconazole·pyraclostrobin SC and 25% pyraclostrobin SC were most effective when applied at disease onset (88.59% and 86.99%, respectively) [88]. Among single agents, benzimidazoles (carbendazim, thiophanate-methyl), triazoles (hexaconazole, tebuconazole, epoxiconazole), and prochloraz-manganese chloride complex significantly reduced diseased fruit rates [84]. Innovations in application strategies have emerged: Using electric sprayers equipped with carbon spray booms and symmetric nozzles improved control efficacy by 4.90%~8.90%, saved 67.99% of spray solution, and reduced labor time by 55.51% [93].

5.2 Microbial-based Fungicides

Facing environmental pressures, costs, and resistance risks associated with chemical control, microbial biocontrol agents (BCAs) represent an important green strategy for managing chili pepper anthracnose. Various beneficial microorganisms exhibit significant antagonistic activity, with *Bacillus* spp. being particularly prominent. *Bacillus subtilis* KB21 produces iturin-like cyclic lipopeptides (CLPs) that combine direct inhibition of *C. scovillei* with induction of chili pepper defense gene expression [94]. *Bacillus velezensis* strains (e.g., LY7, HG-8-2, ZF438) perform exceptionally: Endophyte LY7 enhances disease resistance and promotes growth; its secreted Cupin-domain protein is a key antifungal factor [95]. HG-8-2 and its lipopeptide extracts show strong antagonism against *C. scovillei* [96]. ZF438 achieved 68.26% and 47.93% control efficacy on detached fruits and potted plants, respectively [97]. *Bacillus subtilis* subsp. endophyticus can colonize plants long-term, inhibiting pathogen growth and spore development via secreted peptide-like substances, potentially inducing plant defense enzymes [98]. *Bacillus amyloliquefaciens* strains achieved a 61.11% inhibition rate; their cell-free filtrates disrupted hyphae [99]. *Bacillus subtilis* JN032305 (on talc carrier) showed good stability and compatibility with carbendazim; seed treatment reduced disease incidence by 60% and significantly increased yield; root dipping increased root length by 120% and doubled yield; fruit spraying reduced postharvest incidence by 65.3% [100]. Furthermore, filtrates and volatile organic compounds (VOCs) from *Brevibacillus* sp. B-4359, specific strains of *Burkholderia* spp., and some actinomycete isolates (8 isolates showed 100% inhibition) also demonstrated antifungal potential [101-103].

The genus Trichoderma is a major fungal BCA. *Trichoderma koningiopsis* PSU3-2 effectively controls postharvest anthracnose (*C. siamense*) through triple synergistic mechanisms: nutrient competition and direct antagonism (79.57% inhibition), volatile organic compounds (VOCs, containing key components like 2-phenylethanol, 38.33% inhibition), and mycoparasitism mediated by high-activity chitinase and β-1,3-glucanase secretion (causing hyphal deformation and lysis). Its spore suspension (10^6 spores/mL) as a dip treatment completely suppressed lesion formation (100% efficacy) [104]. Li et al. screened 6 *Trichoderma* strains whose non-volatile metabolites achieved over 92% inhibition; some volatile metabolites also showed inhibitory activity [105]. To enhance biocontrol efficacy, optimization strategies are being explored: A 3:7 ratio of *B. velezensis* LY7 (1.0×10^8 CFU/mL)

with low-dose propiconazole (0.75 g/L) yielded optimal results [106]; Radiation mutagenesis of *B. velezensis* successfully generated mutant strains with increased inhibition rates (up to 59.9%) [107].

5.3 Plant-derived Fungicides

Developing natural and safe plant-derived fungicides is an important direction for green control of chili pepper anthracnose. Extracts and active components from various plants show significant antifungal effects. Effective Plant Extracts: Methanol extracts of *Justicia procumbens* inhibited pathogen hyphal growth and spore development [108]. Allicin (from garlic) performed well; its 6% aqueous emulsion (600~1200 μg/mL) achieved field spray control efficacy comparable to 50% carbendazim WP (1000 μg/mL) [109]. 15% ginger extract also inhibited mycelial growth and spore germination at levels comparable to synthetic fungicides [110]. Plant Essential Oils (EOs): Due to their broad-spectrum antifungal properties and natural origin, EOs are a research hotspot. Litsea cubeba essential oil (LCEO) strongly inhibited *C. scovillei* spore germination (MIC 0.60 mg mL^{-1}), primarily by disrupting cell membrane structure (causing spore deformation, content leakage, membrane lipid peroxidation) and inhibiting ergosterol synthesis [111]. Clove oil (rich in eugenol) was effective in vitro and for seed treatment: 0.25% concentration significantly reduced seed infection rate (from 75.8% to 7.5%) without affecting seed germination or seedling growth [112]. Novel formulations are also being developed, such as oil-in-water nanoemulsions of thyme oil (TO) combined with licorice aqueous extract (LAE) [113].

5.4 Breeding Resistant Varieties

Developing resistant cultivars is an economically efficient strategy to control chili pepper anthracnose using genetic resistance, reducing pesticide reliance [114]. Conventional breeding has successfully developed highly anthracnose-resistant varieties like 'UNEMAT Pedro' (red fruit) and 'UNEMAT Malagueta Pantaneira' (orange-red hybrid fruit). Their fruit infection rates were significantly lower than commercial cultivars, yields increased 2-4 times, and fruit quality was excellent (distinct pungency, good storage) [115]. CRISPR/Cas9 gene editing has achieved breakthroughs in resistance breeding. By editing the susceptibility gene *CaERF28*, homozygous mutants free of foreign DNA were generated. These mutants (e.g., S1-14-1-9) showed significantly enhanced resistance, with disease indices dropping from 74.8% in wild type to <5% after fruit inoculation with Colletotrichum, while maintaining stable agronomic traits. This provides important material for developing non-transgenic resistant chili pepper varieties [116].

6 Challenges and Future Perspectives

6.1 Current Challenges

Unclear Pathogen Population Structure: Although 15 *Colletotrichum* species (including 5 novel species) have been identified in China, the population genetic structure and dominant species in different production regions remain unknown. For

instance, the epidemiology of endemic pathogens like *C. sichuanensis* in Sichuan and Yunnan is not understood, hindering targeted breeding and precise chemical control across regions.

Insufficient Depth in Resistance Mechanisms: While *Colletotrichum* infection relies on effector proteins to suppress host immunity, how these effectors specifically disrupt plant defenses is not fully resolved. The molecular basis for the significant resistance differences in the same cultivar at different fruit ripening stages also remains unclear, limiting the design of broad-spectrum resistant varieties.

Difficulty in Transferring Superior Resistance Genes: Core resistance sources like PBC80 and PBC932 are concentrated in wild species *C. baccatum* and *C. chinense*. Their introgression into cultivated *C. annuum* is hampered by reproductive barriers and linkage drag. Although 12 major QTLs (e.g., *CaR12.2*, *CcR9*) have been mapped, marker-assisted selection (MAS) efficiency is only 77.2%-92.9%, and pyramiding multiple genes entails long breeding cycles.

Limited Field Efficacy of Biocontrol Agents: Microbial preparations and plant-derived active substances show high inhibition rates in vitro, but their field efficacy is often insufficient and inconsistent. Factors limiting large-scale application include inadequate colonization ability of biocontrol agents, instability of active ingredients, and unoptimized synergistic mechanisms with chemical fungicides.

6.2 Future Perspectives

Pathogen Surveillance and Characterization: Integrate multi-locus genotyping and population genomics to establish a national repository of Colletotrichum isolates from major chili pepper production regions and develop a physiological race differentiation system. This will clarify the core pathogenic species in different regions, providing a basis for deploying resistant varieties and implementing precise chemical control.

Deciphering Effector-Host Interactions: Utilize yeast two-hybrid screening and structural biology to identify core Colletotrichum effector proteins and their cognate chili pepper immune receptors. Screen for corresponding resistance gene targets to provide new directions for gene editing-based breeding.

Advanced Resistance Breeding: Combine high-resolution genetic mapping with multi-omics analysis to precisely map fruit ripening stage-specific resistance QTLs. Develop high-throughput KASP/InDel molecular markers. Overcome interspecific hybridization barriers using embryo rescue techniques. Employ gene editing to target susceptibility genes. These approaches will enable efficient pyramiding of multiple resistance traits, significantly enhancing breeding efficiency.

Optimized Integrated Management: Develop synergistic microbial-chemical formulations to extend efficacy duration. Construct plant-derived synergistic systems to enhance environmental stability. Implement precision deployment of resistant varieties based on regional pathogen profiles. Establish a green management chain

from seed priming with beneficial microbes to postharvest preservation.

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