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Perspective

Resistance to Anthracnose Rot Disease in *Capsicum*

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Abstract: Pepper (*Capsicum* spp.) is an important vegetable crop worldwide with high economic and nutritional value. The *Capsicum* genus comprises more than 30 species, of which *C. annuum*, *C. chinense*, *C. baccatum*, *C. frutescens*, and *C. pubescens* are the five domesticated ones. Anthracnose fruit rot, caused by *Colletotrichum* spp., is one of the most destructive fungal diseases of pepper. In this review, we compiled up-to-date information from 40 publications on anthracnose resistance in *Capsicum* species. In total, 375 accessions were described as showing different levels of resistance against *Colletotrichum* spp. These accessions belonged to different species, including *C. annuum* (160), *C. baccatum* (86), *C. chacoense* (4), *C. chinense* (90), and *C. frutescens* (16), as well as 19 accessions of which the species were not reported. High levels of resistance were mainly present in *C. baccatum* and *C. chinense*. For some of the resistant accessions, resistance genes or quantitative trait loci (QTL) were reported. Using associated molecular markers, we located 31 QTLs and 17 resistance-related genes in the recently published *Capsicum* genomes, including *C. annuum* CM334 version 1.6, *C. chinense* version 1.2, and *C. baccatum* version 1.2. Our results could be helpful for making use of some reported accessions in the breeding of pepper cultivars with resistance to anthracnose rot disease.

Keywords: *Capsicum* spp.; anthracnose; *Colletotrichum* spp.; resistance; screening; QTL; in silico mapping; breeding

Citation: Cui, L.; van den Munckhof, M.C.; Bai, Y.; Voorrips, R.E. Resistance to Anthracnose Rot Disease in *Capsicum*. *Agronomy* **2023**, *13*, 1434. https://doi.org/10.3390/agronomy13051434

Academic Editor: Imre J. Holb

Received: 14 April 2023
Revised: 9 May 2023
Accepted: 14 May 2023
Published: 22 May 2023

1. Introduction

The *Capsicum* species, or pepper, is commonly used as a vegetable and a spice. The economic importance of pepper is highlighted by its global annual production in 2017 of approximately 31.5 million tons for fresh pepper and 3.6 million tons for dried pepper [1]. Although pepper originates from South America, most of the world's production currently takes place in Asia, which contributes to more than 65% of the total.

Capsicum belongs to the Solanaceae family. Currently, 38 *Capsicum* species are recognized, including the five important domesticated species: *C. annuum*, *C. baccatum*, *C. chinense*, *C. frutescens*, and *C. pubescens* [2,3]. The *Capsicum* species is diploid (n = 12). Its genome is, in general, quite complex, and contains a large amount of repetitive DNA sequences, which has resulted in genome sizes above 3 Gb [4,5]. Because of the large genome size, the development of reference sequences has been delayed compared with other Solanaceous crops, for instance, tomato (900 Mb, Tomato Genome Consortium) [6] and potato (844 Mb, Potato Genome Sequencing Consortium) [7]. Until now, five *Capsicum* genomes have been completely sequenced, of which three are *C. annuum* and the others are *C. baccatum* and *C. chinense* [4,5,8]. The five pepper genomes are *C. annuum* cv. CM334 (3.06 Gb with 34,903 annotated genes); cv. Zunla-1 (3.35 Gb), a wild accession Chiltepin of *C. annuum* var. *glabriusculum* (3.48 Gb); *C. baccatum* PBC81 (3.9 Gb); and *C. chinense* PI 159236 (3.2 Gb).

Anthracnose is a major disease of pepper caused by a complex of *Colletotrichum* species, mainly occurring in the (sub-)tropics during the wet season. The prevalence of anthracnose is usually associated with a high amount of inoculum in the soil, which is the primary source of infection. Secondary spread occurs rapidly through conidial dispersion in air or

surface water, or even by insects such as fruit flies (*Dacus* spp.) [9,10]. *Colletotrichum* is able to infect pepper plants at all developmental stages. The major species causing anthracnose in seedlings, leaves, and stems is *C. coccodes* [11,12]. The most prevalent and virulent species causing fruit rot are *C. scovillei* (previously known as *C. acutatum*), *C. siamense* (previously known as *C. gloeosporioides*), and *C. truncatum* (previously known as *C. capsici*) [13–17]. The taxonomy of *Colletotrichum* species has recently been revised based on pathogenicity and multi-gene phylogenetic analyses [18]. Typical anthracnose fruit rot symptoms, found on both green and ripe fruit, are black sunken necrotic tissues with water-soaked rings of wet acervuli [19] (Figure 1), leading to a loss of market value. The annual yield loss of pepper due to anthracnose has been reported to vary from 10% [20] to 50% [21], and can sometimes even be as high as 80% [22].

Figure 1. Typical anthracnose symptoms after pinprick inoculation with *C. siamense* (previously known as *C. gloeosporioides*) on a red ripe fruit of chili.

Control measures against anthracnose include the application of chemical fungicides, seed sterilization or cleaning, crop rotation, and biological control [23,24]. The frequent application of fungicides leads to environmental pollution and promotes the development of fungicide-resistant *Colletotrichum* strains [25,26]. As an alternative, growing resistant cultivars is considered to be the most effective and economic method to combat this disease. However, unlike for several other major pepper diseases, no commercial anthracnose-resistant cultivars have been released. The main factor that hinders anthracnose resistance breeding is the polygenic nature of the resistance and large variation in pathotypes [27]. Nevertheless, a vast number of *Capsicum* accessions have been evaluated worldwide, and anthracnose resistance has been identified in domesticated species including *C. annuum*, *C. baccatum*, *C. chinense*, and *C. frutescens* [28–31]. In addition, a few accessions from the wild species *C. chacoense* were reported to be resistant [30]. Genetic studies on some of these resistant accessions have identified monogenic (both dominantly and recessively inherited) and polygenic factors contributing to resistance, with the latter representing the most common type of resistance [15,21,25,26,28,32–34].

As many of these genetic studies were performed prior to the release of the genome sequences, the locations of the genes/quantitative trait loci (QTLs) were not reported in relation to a common genome or map, and are hence hard to compare. Therefore, we aimed to provide a comprehensive overview of current knowledge on anthracnose resistance in pepper in terms of the source and genetics of the identified resistance, as well as the chromosomal locations of the reported anthracnose resistance genes and QTLs. This effort could provide a new starting point for making use of the identified resistant sources in breeding programs.

2. Bioassays for Evaluating Anthracnose Resistance

A key factor for success in breeding for anthracnose resistance is the methods used for inoculation and evaluation. Inoculation can be performed on fruits, either detached or still on the plant, or on whole plants (Table 1). To determine foliar resistance, pepper plants at various growth stages have been inoculated with conidial suspension via foliar spray [35,36]. For fruit bioassays, two approaches are widely used: the fruit is either not wounded or wounded prior to inoculation [19,37]. The wound inoculation ensures direct entry of the spores without considering the cuticle and epidermis as the primary defense

barrier [25,38]. This can be achieved either via a so-called pinprick method [39,40] or via a microinjection procedure [16,41]. Non-wound inoculation delivers the conidia spores onto the fruit either via droplets (detached fruits) or via spraying (in planta or detached) [42,43].

Most screening studies have been based on bioassays of detached fruits at different maturity stages, mainly the mature green and ripe stages (Table 1). In *Capsicum* species, fruit maturity is a well-documented factor that influences the expression of anthracnose resistance. Genetic analyses in populations derived from *C. chinense* PBC932 and *C. baccatum* PBC80 have revealed that resistance in mature green and ripe fruit is controlled by different genes [22,28,43,44]. Mongkolporn et al. [44] reported that detached fruits of accession PBC932 at the mature green stage were more resistant than at the ripening stage. Two linked genes are responsible for resistance at the mature green and ripe fruit stages [22]. In contrast, the ripe fruit of accession PBC80 was more resistant than the mature green fruit [28,43]. In PBC80, resistance at the ripe fruit stage is controlled by a dominant gene, while an independent recessive gene mediates resistance in mature green fruit [28,43].

For evaluating anthracnose resistance, various assessment methods have been used by different research groups (Table 1). For example, a high resistance score has been based on four aspects: low incidence (the proportion of diseased plants/fruits of the total number of plants/fruits assessed) [39,45], low severity (lesion size as a proportion of fruit size) [31,36,46], low infection rate (the fraction of inoculations resulting in a lesion) [26,47], and low AUDPC value (the area under the disease progress curve) [16,48]. In some studies, different aspects are combined. For example, disease severity and incidence were converted to the disease severity index [44,49–51], while in other studies, lesion diameter was measured as well as the infection rate [25], disease incidence [26], and AUDPC [48].

Table 1. Inoculation and evaluation methods used in previous studies to evaluate anthracnose resistance and susceptibility.

Pathogen [a]	Bioassay [b]	Inoculation Method [c]	Disease Evaluation Method [d]	Phenotypic Responses [e]	Reference
C. scovillei	1	1	DSI	R (1–<3); IR (3–<6); S (6–9)	[52]
	2	1/2	DSI	HR (0); R (0.1–1.9); MR (2.0–2.9); S (3.0–4.9); HS (5)	[30]
	4	4	Infection rate	R (infection rate < 10%)	[53]
	3	3	DI	HR (0–<10%); R (10–<20%); MR (20–<40%); S (40–<70%); HS (>70%)	[45]
	3	3	DSI, AUDPC, IP, LP	R (low value for AUDPC, and high values for IP and LP)	[16]
C. brevisporum	3	3	DSI	HR (1); R (3); MR (4); MS (6); S (8); HS (10)	[41]
	5	3	DSI based on LS	R (<10%); MR (11–20%); S (21–40%); HS (>41%)	[36]
	6	1	DSI based on LS (foliar)	1 (SL); 2 (>1 mm); 3 (1%); 4 (5%); 5 (10%); 6 (25%)	[36]
	7	2	DSI based on LS	R (0–1.0); MR (1.1–2.0); MS (2.1–3.0); S (3.1–4.0); HS (4.1–5.0)	[40]
C. capsici	-	4	DSI based on DI	I (0%); R (1–5%); MR (6–25%); S (26–50%); HS (51–100%)	[51]
	7	1	DSI based on LS	R (<20%); MR (21–40%); MS (41–60%); S (>60%)	[46]
	6	1/2	DSI based on LS	SL (0); R (0.1–10%); MR (10.1–25%); MS (25.1–50%); S (50.1–75%); HS (75.1–100%)	[31]
C. coccodes	6	1/5	DSI and AUDPC	Index (0–5)	[54]
C. siamense	3	3	DSI	HR (1); R (3); MR (4); MS (6); S (8); HS (10)	[55]
C. siamense	8	6/3	DSI and AUDPC	HR (1); R (3); MR (4); MS (6); S (8); HS (10)	[48]
C. capsid, *C. siamense*	7	2	DSI based on DI	I (0); R (1); MR (2); S (3); HS (4)	[39]
C. scovillei	2	3	Lesion diameter and infection frequency		[26,47]
C. capsici, *C. siamense*	3	2			[25]
C. siamense	2	3	LI		[56]
C. scovillei, *C. capsici*, *C. siamense*, *C. truncatum*	8	1/3	DSI based on LS	HR (0); R (1); MR (3); MS (5); S (7); HS (9)	[28,44,49,50,57]
Colletotrichum spp.	3	1	DI, lesion diameter, LGR, AUDPC, IP	R (low values for AUDPC, DI, lesion diameter, and LGR; high values for IP)	[58]

[a] *C. scovillei* (previously known as *C. acutatum*), *C. siamense* (previously known as *C. gloeosporioides*), and *C. truncatum* (previously known as *C. capsici*). [b] 1: detached immature green fruit; 2: detached mature green fruit; 3: detached mature green and ripe fruits; 4: immature green and ripe red fruits on plants; 5: detached (im)mature fruits; 6: chili plants; 7: detached ripe fruits; 8: unripe and ripe fruit detached/on plants. [c] 1: spray; 2: pinpricking wounding; 3: microinjection; 4: natural field inoculation; 5: soil-drench method; 6: dropping spores on the pericarp. [d] Disease incidence (DI): percentage of fruit infected with inoculation sites at which lesion diameter > 4 mm; lesion growth rate (LGR): the measurement of lesion growth over time and calculated in mm/day; incubation period (IP) and latent period (LP): the number of days from inoculation to the appearance of symptoms; lesion incidence (LI): percentage of inoculation sites at which lesions $\leq$ 4 mm in diameter; percent lesion size (LS): lesion size as a proportion of fruit size; DSI: disease severity index; AUDPC: area under the disease progress curve. [e] Codes are interpreted from the original studies. Immune: I; symptomless: SL; highly resistant: HR; resistant: R; intermediate resistance: IR; moderately resistant: MR; susceptible: S; highly susceptible: HS. Between brackets, the original phenotypic classes or measurements are shown.

3. Sources of Anthracnose Resistance in *Capsicum* Germplasm

Breeding for resistance to anthracnose in pepper was started in the early 1990s by Korean and Indian chili breeders [59]. Their breeding programs mainly relied on moderate resistance obtained from *C. annuum* sources (cv. Perennial and Chungryong), which is the most widely cultivated *Capsicum* species [59,60]. Aiming to identify resistance at a high level, disease tests have been performed worldwide in a large number of *Capsicum* accessions. In total, 375 resistant accessions have been identified in the cultivated *Capsicum* species corresponding to *C. annuum* (160), *C. baccatum* (86), *C. chinense* (90), and *C. frutescens* (16) as well as in the wild species *C. chacoense* (4) and 19 accessions of unreported species [28–31] (Tables 2 and S1).

Table 2. Summary of identified sources of *Capsicum* accessions resistant to *Colletotrichum* species.

***Colletotrichum* Species** [a]	***Capsicum* Species** [b]					
	C. annuum	***C. baccatum***	***C. chacoense***	***C. chinense***	***C. frutescens***	***Capsicum* spp.**
C. scovillei	18	46	4	21	7	-
C. capsici	76	22	-	13	8	4
C. siamense	31	18	-	41	-	15
C. coccodes	1	-	-	-	1	-
C. brevisporum	-	-	-	15	-	-
C. dematium	7	-	-	-	-	-
C. truncatum	9	-	-	-	-	-
Colletotrichum spp.	18	-	-	-	-	-
Total	160	86	4	90	16	19

[a] *C. scovillei* (previously known as *C. acutatum*); *C. siamense* (previously known as *C. gloeosporioides*), and *C. truncatum* (previously known as *C. capsici*); resistance to multiple species (*Colletotrichum* spp.), including *C. capsica* (syn. *C. truncatum*), *C. siamense*, and *C. scovillei* was identified in 18 *C. annuum* accessions. [b] *Capsicum* spp. denotes that the *Capsicum* species was not mentioned in the corresponding reports; "-" no such report. *Capsicum* accessions resistant to *Colletotrichum* spp. were summarized from the following references: [13,16,25,26,28,30,31,35,36,39,41,44–49,51–56,59,61–70].

In these screening, six *Colletotrichum* species were used, of which three (*C. scovillei*, *C. truncatum*, and *C. siamense*) are prevalent worldwide and three (*C. coccodes*, *C. brevisporum*, and *C. dematium*) are common in Asia [19]. In most of the screens, a single *Colletotrichum* species was used. In a few cases, *C. annuum* accessions were evaluated against multiple *Colletotrichum* spp., leading to the identification of 18 accessions with broad resistance (Table 2).

In order to avoid redundant screenings in future studies, we summarize and present accessions identified as susceptible (Table S2). This panel included 255 accessions of the following species: *C. annuum* (167 accessions), *C. baccatum* (31), *C. chinense* (38), and *C. frutescens* (19).

4. Breeding for Anthracnose Resistance in *Capsicum*

Some of the resistant accessions of *C. annuum*, *C. baccatum*, and *C. chinense* listed in Table 2 have been used as donors for anthracnose resistance (Table 3). However, the resistance identified in *C. baccatum* is difficult to transfer into elite *C. annuum* lines, as an interspecific crossing barrier exists between both species [52]. As a result, one or multiple bridge crosses or embryo rescues are necessary in order to introgress the resistance into *C. annuum* [67]. For example, hybrids of *C. baccatum* PBC80 with elite *C. annuum* cultivars have been obtained with the aid of embryo rescue [71]. On the other hand, resistance in the accessions of *C. annuum* and *C. chinense* is generally easier to introduce into existing *C. annuum* lines.

The development of resistant cultivars can be facilitated with prior knowledge of the genetic basis of resistance and associated molecular markers for marker-assisted selection (MAS). The very first genetic map of anthracnose resistance in pepper was derived from an interspecific population between *C. annuum* and a resistant *C. chinense* accession,

PRI95030 [25] (Table 3). More recent genetic maps have been constructed and genetic analysis has been conducted in several populations derived from the main resistance sources, including *C. chinense* PBC932 [15]; *C. baccatum* PBC80 [34], PBC81 [29,72], PI594137 [47], and 881045 (Cbp) [33]. In addition, genetic studies have also been based on resistance obtained from *C. annuum* sources including cv. Perennial, cv. Chungryong, cv. Punjab Lal, and accessions 83–168, which are not highly resistant (Table 3). Results from these genetic studies indicate that the estimated inheritance of resistance depends not only on the *Colletotrichum* species and methods used for inoculation, but also on the fruit stages and the other parental lines used in the study (Table 3). For example, a single recessive gene model was suggested for the resistance of *C. chinense* PBC932 against *C. truncatum* (previously known as *C. capsici*) infection at different maturity stages in a cross with *C. annuum* cv. Bangchang (Table 3) [22], while polygenic resistance against *C. scovillei* was found at the mature green and ripe fruit stages in crosses between PBC 932 and *C. annuum* 9955-15 [72] or 77013 [15]. The inheritance of *Colletotrichum* spp. resistance derived from *C. baccatum* accessions PBC80, PBC81, and PI594137, from either intraspecific populations or an interspecific cross with *C. annuum*, was shown to be controlled by single or multiple genes at different maturity stages [28,29,43,47]. In contrast, monogenic resistance was found to be responsible for resistance to *C. truncatum* (previously known as *C. capsici*) in *C. annuum* accessions 83–168 [73], and to *C. scovillei* in *C. baccatum* accessions PI594137 [47] and PBC80 [34].

To introgress anthracnose resistance into a *C. annuum* line, backcrossing is one of the most important techniques used in breeding [74]. Successful resistant lines have been obtained from the backcrossing of resistant sources of *C. baccatum* and *C. chinense* with a recurrent elite *C. annuum* cultivar. At the AVRDC (the World Vegetable Center), five *C. annuum* lines, namely AVPP1102-B, AVPP0513, AVPP0719, AVPP0207, and AVPP1004-B, were found to be promising in terms of fruit yield and tolerance to anthracnose [45]. Two *C. annuum* varieties from IVEGRI (the Indonesian Vegetables Research Institute), Lembang-1 and Tanjung-2, have been reported to possess moderate resistance [75]. There have been multiple anthracnose-resistant *C. annuum* lines reported in India, including PBC-380, BS-20, BS28, Taiwan-2, Pant C-1 [31], LLS, VI047018 (derived from *C. chinense* PBC932), Breck-2, VI046804 (derived from *C. baccatum* PBC80), Breck-1, Jaun, and VI046805 (derived from *C. baccatum* PBC81) [76].

Table 3. *Capsicum* accessions used in anthracnose resistance breeding.

Genetic Source		Resistance Level [a]	Population		*Colletotrichum* spp. [b]	Inoculation Method	Genetic Mechanism [c]		Reference
***Capsicum* spp.**	**Accession**		**Type**	**Susceptible Parent**			**Mature Green**	**Ripe**	
C. annuum	Chungryong	MR	F_2, BC_1	*C. annuum* PI244670	*C. dematium*, *C. siamense*	Detached pinpricking	Partial dominant *	Partial dominant *	[59,68]
	Perennial	MR	F_2, BC_1, BC_2	*C. annuum* 'Kolascai E-14'	*C. truncatum*	-	Polygenic	na	[60,68]
	83–168	MR	F_2, BC_1	*C. annuum* 'KKU-Cluster'	*C. capsici*	Detached dropping	Single dominant	na	[73]
	Punjab Lal	R	F_2	*C. annuum* 'PT 12-3'	*C. scovillei*, *C. capsici*	Detached pinpricking	Polygenic	Polygenic	[77]
	GBUEL104	HR	F_2, BC_1, BC_2	*C. annuum* GBUEL103	*C. scovillei*	Detached microinfection	Two dominant QTLs *	Two dominant QTLs *	[41]
C. chinense	PRI95030	HR	F_2	*C. annuum* 'Jatilaba'	*C. siamense*, *C. capsici*	Detached pinpricking	na	Polygenic	[25]
	PBC932	R	F_2, BC_1, BC_3	*C. annuum* '9955-15'	*C. scovillei*	Detached microinfection	Two dominant genes *	Polygenic recessive *	[72]
	PBC932	HR	F_2, BC_1	*C. annuum* 'Yeoju', 'Bangchang'	*C. capsici*		Single recessive *	Single recessive *	[22,26]
	PBC932	R	BC_1	*C. annuum* '77013'	*C. scovillei*		Polygenic dominant *	Polygenic dominant *	[15]
C. baccatum	PI594137	R	F_2, BC_1	*C. baccatum* Golden-aji	*C. scovillei*	Detached microinfection	Single dominant	na	[47]
	PBC80	HR	F_2, BC_1	*C. baccatum* CA1316	*C. scovillei*		Single recessive *	Single dominant *	[28,34,43]
	PBC81	HR	F_2, BC_1	*C. annuum* SP26, Matikas	*C. scovillei*, *C. capsici*		Polygenic *	Polygenic *	[29,78]
	881045 (Cbp)	R	F_2	*C. baccatum* Golden-aji	*C. scovillei*		na	Polygenic	[33]

[a] Highly resistant: HR; resistant: R; moderate resistance: MR. [b] *C. scovillei* (previously known as *C. acutatum*), *C. siamense* (previously known as *C. gloeosporioides*), and *C. truncatum* (previously known as *C. capsici*). [c] * resistance in mature green and ripe fruit controlled by distinct genes; na: genetic information not available as mapping has not been performed.

5. Location of Anthracnose Resistance on the Pepper Genome

Knowledge on the localization of resistance genes and QTLs is of utmost importance when it comes to the development of markers linked to the resistance, subsequent gene introgression, and identification of allelic variants present in novel (wild) material. Many studies have been devoted to this aim, and their output, including resistant sources, *Colletotrichum* strains, linkage maps, and linked/flanking markers, is summarized in Table S3. However, for many of the genes and QTLs reported to date, their localization on the corresponding genome is not available due to the lack of reference sequences at the time of their first report. With the availability of the three pepper genomes [4,5,8], we attempted to map previously reported genes and QTLs on the chromosomes (Tables 4 and S3, Figure 2). After retrieving the reported sequences of associated markers, primer pairs, fragments, and genes, in silico mapping was performed on the corresponding genomes (*C. annuum* CM334 version 1.6, *C. chinense* version 1.2, or *C. baccatum* version 1.2) using BLASTN (nucleotide-to-nucleotide BLAST) in TBtools software [79]. For BLASTN, sequences of two categories were used. The first category is for AFLP markers and other PCR markers for which sequences of the amplified fragments are known. Amplicon sequences (>100 bp) were used, and the chromosome with the most likely hit (E-value below 1×10^{-5}) was chosen. The second category is for when the amplicon sequences are unknown. Primer sequences of about 20 bp were used and the setting was then set for short query sequences with an E-value threshold of 1000. When multiple markers could be used for one QTL, the chromosome anchored by the majority of markers was chosen. Some QTLs could not be anchored since their flanking markers had hits on different chromosomes.

In total, 56 QTLs were reported from 11 studies (Table 4), and 31 of them were anchored using the in silico mapping approach. The BLAST hits (markers flanking and/or within the QTL regions) were found across all 12 *Capsicum* spp. chromosomes (Tables 4 and S3, Figure 2).

In the *C. chinense* accession PBC932, a major QTL for resistance to *C. scovillei* on the bottom of chromosome 5 was consistently detected in different studies [80–83]. The interval is flanked by the markers P5in-2266-404 and P5in-2268-978 within a physical distance of 164 kb in the physical map [82]. Additionally, many other QTLs were identified in the study of Sun et al. [15], of which four were likely located on chromosomes 3 (AnRGo12), 5 (AnRGO5_AnRGT5), 7 (AnRgo7), and 10 (AnRGo10/AnR_{GD}10). For resistance to *C. capcisi*, three QTLs were found, with two of them mapped to chromosomes 9 (QTLUL) and 11 (QTL-L4) [84].

In *C. baccatum* PBC80, monogenic resistance to *C. truncatum* (previously known as *C. capsici*) was found that could be inherited either dominantly or recessively [22,26]. In the study of Suwor et al. [81], a major contributing QTL (LG12) against *C. scovillei* was identified that could be anchored to chromosome 12.

In *C. baccatum* PBC81, many QTLs were identified in three independent studies [72,85,86]. In the study of Lee et al. [86], one QTL (CcR9) for resistance to *C. truncatum* (previously known as *C. capsici*) could be mapped to chromosome 3, while the other one (CaR12.2) for resistance against *C. scovillei* could be mapped to chromosome 12. Three QTLs (RA80f6_r1, RA80f6_g1, and RA80f6_g2) conferring *C. scovillei* resistance were mapped to chromosomes 4, 8, and 3, respectively [72].

In *C. baccatum* var. *pendulum* 881045, Kim et al. [33] found more than 15 QTLs contributing the resistance to *C. scovillei*. A major QTL, An9.1, could be mapped to the top of chromosome 1. A few minor QTLs could be assigned to chromosomes 3 (An8.1/An8.2), 4 (An4.1), 6 (An7.2–7.4), and 10 (An 13.1).

In *C. chinese* PRI195030, four QTLs were detected [25], of which only two could be mapped, including the QTLs H1 on chromosome 2 for *C. scovillei* resistance and B1 on chromosome 7 for resistance to *C. truncatum* (previously known as *C. capsici*) and *C. scovillei*. Other QTLs could not be assigned to any chromosomes since their associated markers are mapped to different chromosomes.

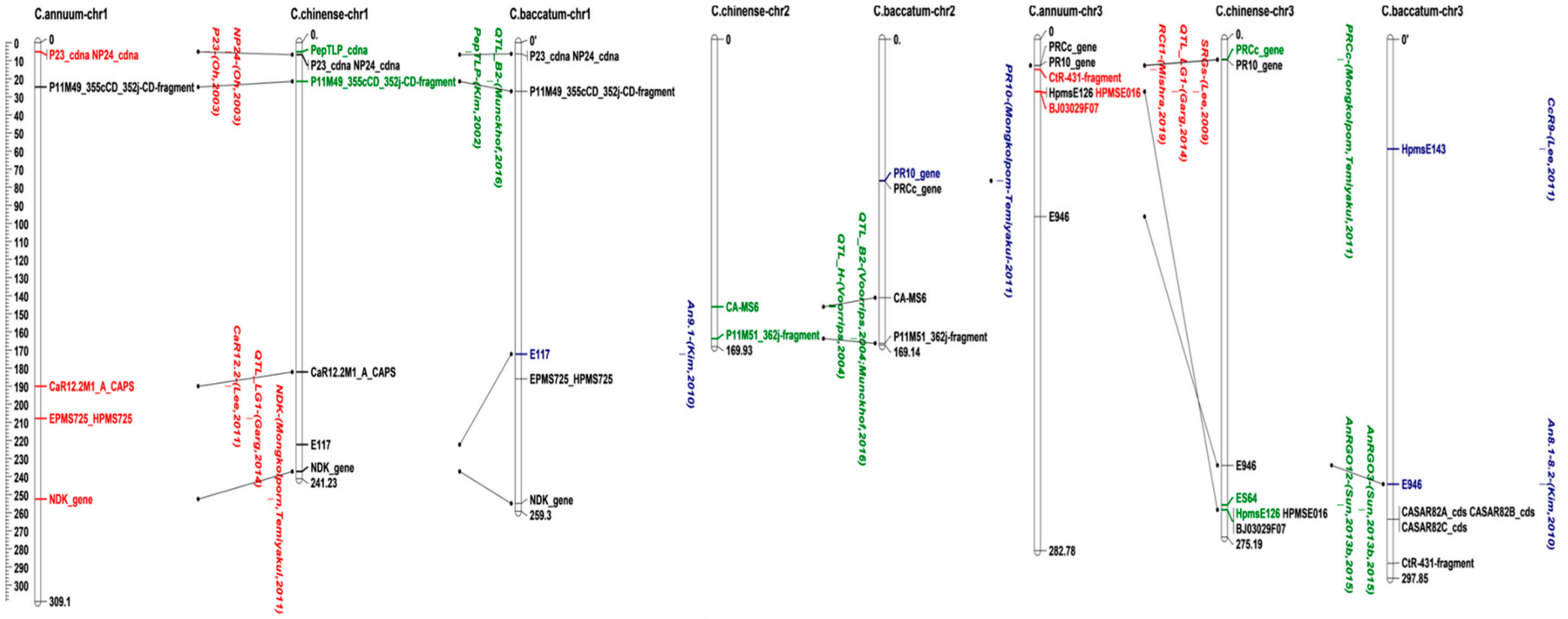
Table 4. Published QTL studies on anthracnose resistance.

Study	QTL	Flanking Marker(s)	LOD [a]	R^2 [b]	In Silico Mapping Chromosome	*Colletotrichum* Species	Resistant Source		Fruit Stage [c]	Trait [d]
							Capsicum Species	Accession		
[25]	B1	E37M51_184cCD	3.9–9.3	16.3–77.1	7	*C. capsici*, *C. scovillei*	*C. chinense*	PRI95030	F	LA, IF
	B2	P11M49_355cCD_352jCD P11M51_362j E37M51_184cCD E37M51_251j P11M51_280	2.7–4.7	30.2–51.8	1 2 7 10 12	*C. scovillei*				
	H1	P11M51_362j	2.9–3.7	13.4–20.5	2	*C. capsici*				LD
	G1	P11M50_137j, P14M58_199jCD	2.8	7.6	-					
[85]	QTL_LG1	hpms1-166, hpms1-274 hpms1-155			7 8	*C. scovillei*	*C. baccatum*	PBC81	GF, RF	DI, TLD
	QTL_LG7	hpms2-24			-					
	QTL_LG9	hpms1-216, hpms1-274			-					
	QTL_LG10	AF039662			-					
[84]	QTL-UL	G31			9	*C. capsici*	*C. chinense*	PBC932	GF	LA
	QTL_L4	G28			11					
	QTL_L3	G41			-					
[33]	An9.1	E117	4.6	14.4	1	*C. scovillei*	*C. baccatum* var. *pendulum*	881045	F	DA
	An8.1-8.2	E946	4–4.1	2–8.4	3					
	An8.1-8.2	E946	4–4.1	2–8.4	3					DR
	An4.1	E1540	3.1	0.6	4					-
	An7.2-7.4	E672, E384	2.5–3.8	4.9–37.5	6					DR
	An13.1	E246	2.9	15.4	10					DA
	An3.1-3.3	E63M82_270, E65M81_450	2.7–3.6	12.8–30.1	-					DR
	An5.1	E74M79_370, E77M81_320	2.9	3.9	-					
[33]	An6.1	me02em03_04, me02em02_05	2.8	0.9	-	*C. scovillei*	*C. baccatum* var. *pendulum*		F	DR
	An7.1	E76M83_250, E65M80_420	3.4	11.3	-					DA
	An7.5	E77M83_320, E75M83_450	3.9	6.9	-					
	An8.3	E70M84_380, E71M79_295	3.3	15.2	-					DR
	An8.4	E71M79_330, E67M79_250	3.8	20.5	-					
	An9.2	E76M83_350, E75M81_480	3	10.8	-					DA
[29]	CaR12.2	CaR12.2M1_A_CAPS CaR12.2M1_B_CAPS	7.8–9.6	11.9–20.5	1 12	*C. scovillei*	*C. baccatum*	PBC81	GF, RF	TLD
	CcR9	HpmsE143	13.4–15.9	57.5–78.9	3	*C. capsici*				DI, TLD, OLD
	CaR12.1	EtagMcag11, EtccMcga05	4.7	17.9	-	*C. scovillei*			RF	TLD
	CcRC	EaacMcgc02, EaatMccg07	6.7	10.6	-	*C. capsici*				DI

Table 4. *Cont.*

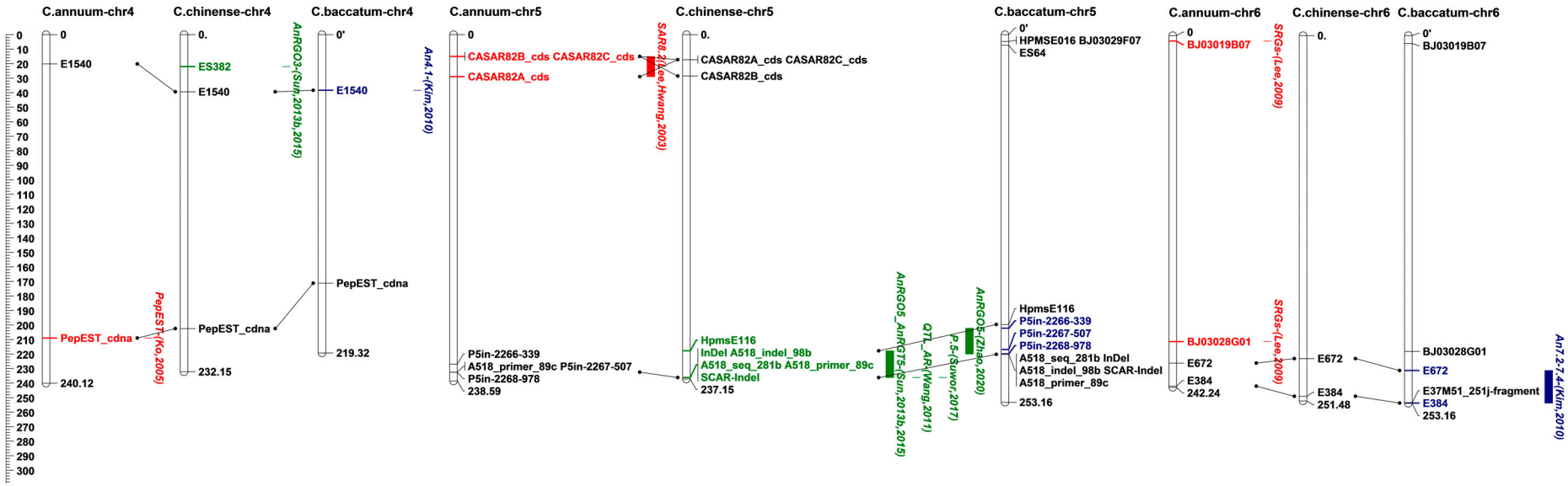
Study	QTL	Flanking Marker(s)	LOD [a]	R^2 [b]	In Silico Mapping Chromosome	*Colletotrichum* Species	Resistant Source		Fruit Stage [c]	Trait [d]
							Capsicum Species	Accession		
[77]	QTL_LG1	EPMS725_HPMS725	3.4–5.8	16.7–71	1	*C. scovillei*	*C. annuum*	Punjab Lal	GF, RF	IP
		HPMSE016			3					
	QTL_LG2	HPMSE051	2.1–4.9	7.2–18	9					
	QCcR-ifp-iivr-1.1	CAMS020, HPMSE016	3.5	14.2	-	*C. capsici*				IP, LA
	QCcG-la.iivr1.1	HPMS725, CAMS644								
[80]	QTL_AR	A518_InDel_98b, A518_seq_281b, A518_primer_89c			5	*C. scovillei*	*C. chinense*	PBC932	GF	OLD
[15]	$AnR_{GO}3$	HpmsE126	2.3	2.9	3	*C. scovillei*	*C. chinense*	PBC932	GF	OLD
		ES382			4					
	$AnR_{GO}12$	ES64, Epms745	2.7	3.1	3					
	$AnR_{GO}5\_AnR_{GT}5$	InDel-HpmsE116, InDel	31.9–32.3	60.5–62.4	5					OLD, TLD
	$AnR_{GO}7$	HpmsE057	2.2	2.5	7					OLD
	$AnR_{GO}10$, $AnR_{GD}10$	C2_At4g03400, Gp20068	2.2–2.3	2.9–4.7	10					OLD, DI
	$AnR_{GD}5$, $AnR_{RO}5$, $AnR_{RT}5$, $AnR_{RD}5$	HpmsE116	2.7–12.3	9.3–33.2	-				GF, RF	DI, OLD, TLD
	$AnR_{GD}12$	ES118, ES181	2.8	5.4	-				GF	DI
[81]	P.5	SCAR-InDel			5	*C. scovillei*	*C. chinense*	PBC932	GF	LD
	LG12	SSR-HpmsE032			12		*C. baccatum*	PBC80		
[82]	$AnR_{GO}5$	P5in-2266-404, P5in-2268-978	24.4	69.3	5	*C. scovillei*	*C. chinense*	PBC932	GF	TLD
[72]	RA80f6_r1	SNP_305/331	4	17.7	4	*C. scovillei*	*C. baccatum*	PBC81	GF, RF	IP
	RA80f6_g1	SNP_541/571	5.2	20.2	8					
	RA80f6_g2	SNP_228/218	3.5	12.8	3					

[a] LOD: likelihood of odds ratio; [b] R^2: percentage of phenotypic variance explained by each QTL; [c] GF: green fruit, RF: red fruit, F: fruit (undefined); [d] DI: disease incidence, TLD: true lesion diameter, OLD: overall lesion diameter, IP: Infection percentage, LA: lesion area, DR: disease rate, DA: disease area, IF: infection frequency.



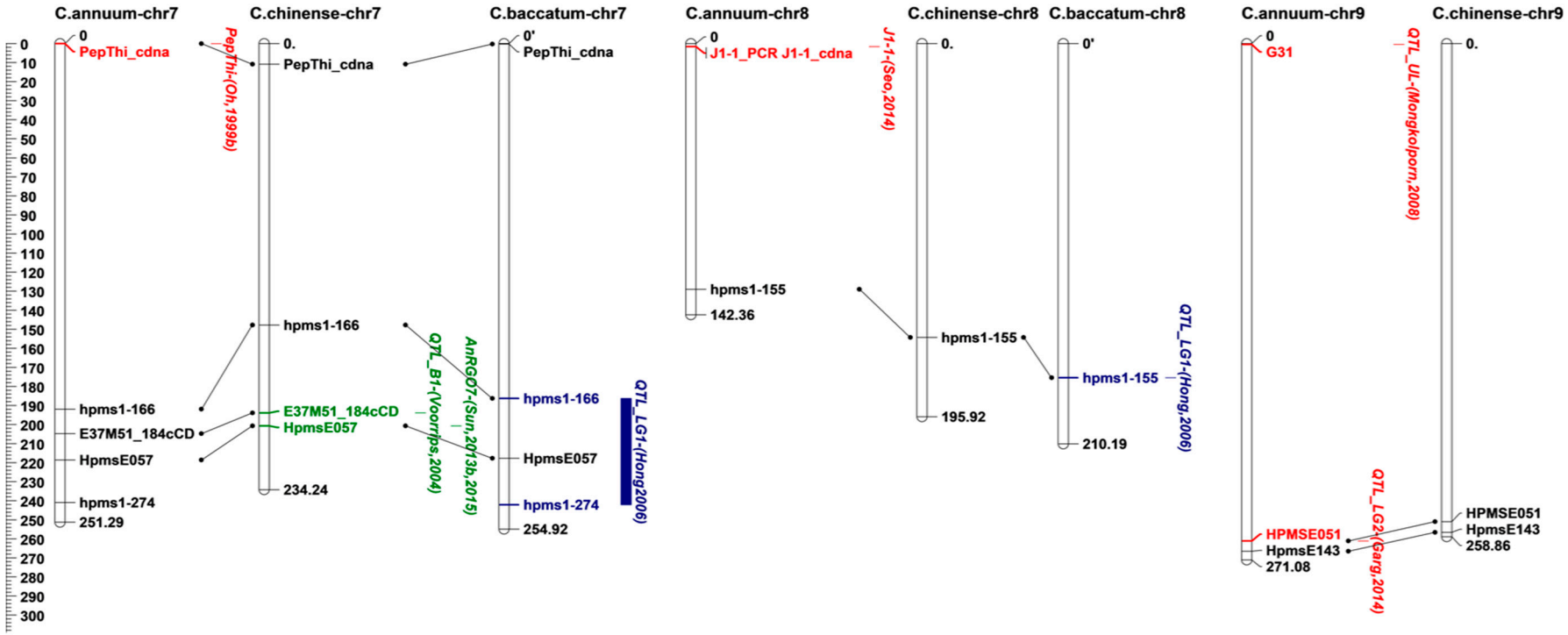
(**A**)

Figure 2. *Cont.*



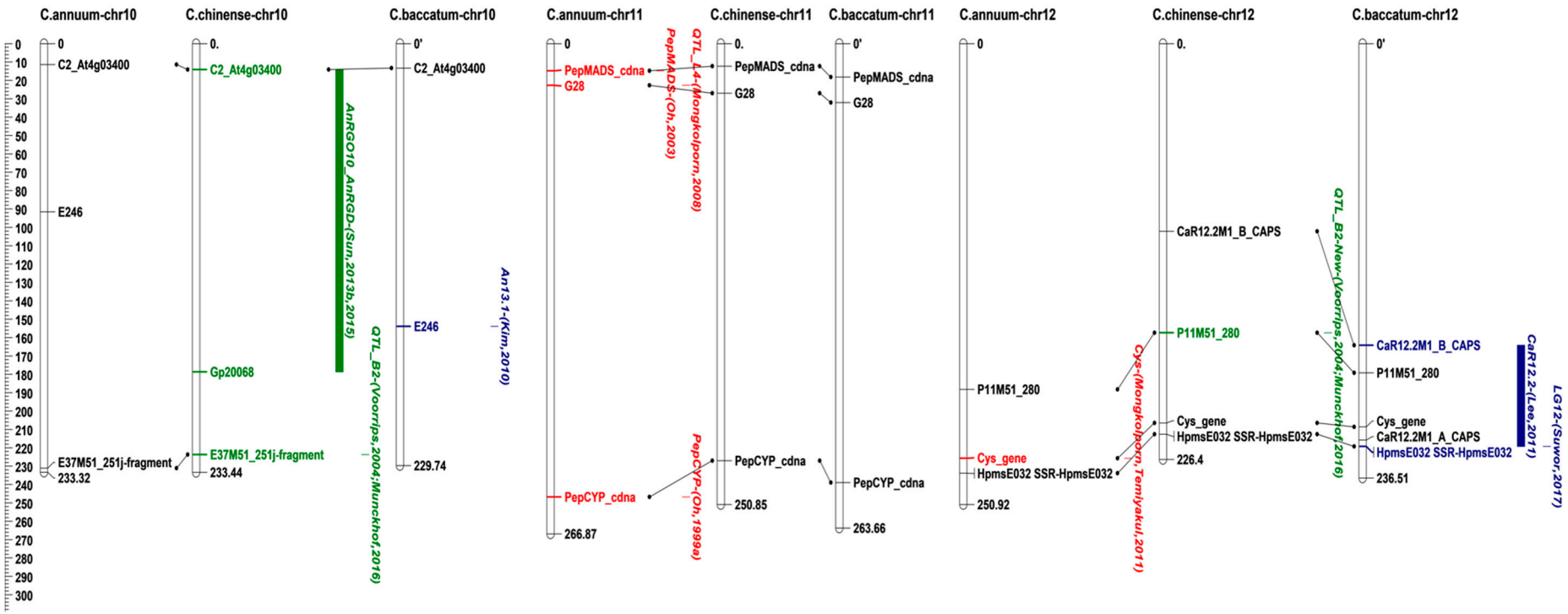
(**B**)

Figure 2. *Cont.*



(**C**)

Figure 2. *Cont.*



(**D**)

Figure 2. Anthracnose resistance-associated QTLs, genes, and fragments projected on the physical chromosomes of *C. annuum* CM334 version 1.6, *C. chinense* version 1.2, and *C. baccatum* version 1.2. Positions are in million base pairs. QTLs and genes are displayed as bars or indicators shown to the right of the chromosomes. Their names as given by the authors are maintained, and the study from which they originate is indicated between brackets. Molecular markers flanking the QTLs are indicated on the corresponding chromosomes. Synteny links are represented by black lines. Depending on the origin of resistance sources, molecular markers, QTLs, and genes are displayed in different colors (i.e., red for *C. annuum*, green for *C. chinense*, and blue for *C. baccatum*). Information was visualized using MapChart 2.3 [87]. (**A**) Physical maps of chromosomes 1–3 of *C. annuum* CM334 version 1.6, *C. chinense* version 1.2, and *C. baccatum* version 1.2; (**B**) physical maps of chromosomes 4–6; (**C**) physical maps of chromosomes 7–9; (**D**) physical maps of chromosomes 10–12.

In *C. annuum* PT-12-3, among the four reported QTLs, only QTL_LG2 could be assigned to chromosome 9 [68].

6. Defense Mechanisms of Anthracnose Resistance Caused by *Colletotrichum* spp.

The complete resistance of *C. chinense* accession PBC932 and *C. baccatum* accessions PBC80 and PBC81 is due to a hypersensitive reaction (HR) [12,22,28]. The immune response consists of slight tissue necrosis and localized cell death surrounding the inoculation site on the detached fruits [22,28,88]. The infected cells themselves have thickened cell walls or a thickened cuticle layer and have high levels of reactive oxygen species [12,88].

To understand the molecular mechanisms of defense against anthracnose, differential *Capsicum* spp.–*Colletotrichum* spp. pathosystems have been used to evaluate the expression of defense-related genes or the production of antimicrobial compounds. Based on an expression study with the *C. truncatum*-resistant accession Bhut Jolokia (obtained from a cross between *C. frutescens* and *C. chinense*), Mishra et al. [89] identified a number of defense-related genes, including *PDF1.2*, lipoxygenase *Lox3*, *PR2*, *PR5*, and transcription factors (*WRKY33* and *CaMYB*), as possibly being involved in the resistance response.

In *C. baccatum* accession PBC80, pathogen-responsive gene 10 (*PR10*) was differentially expressed upon *C. scovillei* infection [90]. This gene is located on *C. baccatum* chromosome 2 at 78.2 Mb. In *C. baccatum* accession P27 challenged with *Colletotrichum* spp., the resistant response was dependent on the ripening stage and correlated with the accumulation of the metabolites butane-2,3-diol, fructose, and phenolics, and superoxide dismutase and peroxidase activities [58].

In the incompatible interaction of *C. annuum* cv. Nokkwang with *C. siamense*, six defense-responsive genes, including cytochrome P450, a *PepCYP* gene, a thionin-like gene (*PepThi*), a defensin gene (*J1-1*) [91], a pepper thaumatin-like gene (*PepTLP*), a MADS-box gene (*PepMADS*) [92], and a pepper esterase gene (*PepEST*) [93], were reported, of which *PepCYP* was mapped towards the bottom of chromosome 11, *PepThi* on the distal top of chromosome 7, *J1-1* on the top of chromosome 8, *PepTLP* on chromosome 1 at 5.08 Mb, *PepMADS* on chromosome 11 at 14.7 Mb, and *PepEST* on chromosome 4 at 208.98 Mb. Moreover, the salicylic acid-induced protection of ripe pepper fruits of cv. Nokkwang against *C. siamense* was associated with highly expressed SA-responsive genes (*SRGs*) [94]. A *SRG*, namely BJ03029B07, was located at the top of *C. annuum* chromosome 6, and BJ03028G01 was located towards the bottom of this chromosome. Additionally, BJ03028G01 co-localized with QTL An7.2–7.4. The possible involvement of these genes in anthracnose resistance controlled by the QTL An7.2–7.4 needs to be studied. In *C. annuum* cv. Hanbyul, a systemic acquired resistance gene (*CASAR8.2*) with three cDNA clones (CASAR82A, -B, and -C) was strongly associated with resistance to *C. coccodes* [95]. This gene was mapped to the top of chromosome 5. *C. annuum* UENF 1381, in response to *C. siamense*, produced abundant amounts of antimicrobial peptides such as defensin, lipid transfer protein, and protease inhibitor [70]. The quantification of secondary metabolites produced during the interaction between the resistant *C. annuum* accessions GBUEL104 and *C. siamense* revealed that high concentrations of caffeic and chlorogenic acid were produced, and their differential expression depended on the fruit development stage and the time that had elapsed post-inoculation [55].

7. Conclusions

Anthracnose fruit rot disease is caused by a complex of *Colletotrichum* species. It causes significant yield losses and has become a constraint for *Capsicum* production. The ultimate means of achieving the sustainable control of anthracnose is to breed for anthracnose resistance. Worldwide screenings have mostly identified resistant accessions in *C. baccatum* and *C. chinense*. In this study, we summarized information on *Capsicum* accessions that have been tested and shown to be either resistant or susceptible to *Colletotrichum* spp. Generally, *C. annuum* lacks anthracnose resistance, but the introgression of resistance from resistant *C. chinense* and *C. baccatum* accessions has resulted in multiple breeding lines. A

large number of genes and QTLs conferring anthracnose resistance that were anchored to the *C. chinense* and *C. baccatum* genomes were identified in various sources in the present study using an in silico mapping approach. Our results may be useful and informative for clarifying the locations of genes/QTLs from different sources for resistance to anthracnose rot disease in pepper, as well as for the introgression of resistance from donor accessions into elite cultivars.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy13051434/s1, Table S1: Published data on *Capsicum* accessions resistant to *Colletotrichum* species; Table S2: Published data on *Capsicum* accessions susceptible to *Colletotrichum* species; Table S3: Sequences from primer pairs, genes, proteins, or cDNA clones used in the in silico mapping of anthracnose resistance genes/QTLs [96–103].

Author Contributions: Conceptualization, Y.B. and R.E.V.; data curation, L.C. and M.C.v.d.M.; visualization and writing—original draft preparation, L.C.; writing—review and editing, L.C., M.C.v.d.M., Y.B. and R.E.V. All authors have read and agreed to the published version of the manuscript.

Funding: L.C. acknowledges financial support from the China Scholarship Council (201908140029).

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

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