


Cucurbitaceous Vegetables' Gummy Stem Blight Research

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Abstract: Cucurbits are an important vegetable crop of the gourd family. Unfortunately, gummy stem blight (GSB) causes a major fungal disease on Cucurbitaceous vegetable crops. It is also known as black root when affecting fruits, and it is found all over the world. GSB is caused by the fungal pathogen *Didymella bryoniae*. Research efforts have investigated the different developmental stages and various parts of Cucurbits affected with this disease. In the present paper, we have completed a systematic review for the disease's symptomatic, pathogenic microbes, resistance resources, resistance inheritance regularity, molecular biology and genomic study of resistance gene and control method, etc., on Cucurbits. This review provides the background and rationale for future studies aiming to address the issues existing in gummy stem blight research and development.

Keywords: gummy stem blight; pathogenic fungus; resistance breeding; systematic review



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1. Introduction

Gummy stem blight (GSB), caused by the fungal pathogen *Didymella bryoniae*, is the most prevalent and devastating fungal disease on Cucurbitaceous vegetable crops [1]. Recent reports of this fungal pathogen have arisen from several countries including India [2,3], Thailand [4], China (including the Taiwan region) [5], the United States [6], Trinidad [7], Brazil [8], Egypt [9], Tanzania [10], Turkey [11], Tunisia [12], Iraq [13]. This pathogen has been reported on six continents with at least 12 genera and 23 species of Cucurbitaceae [14], including watermelon (*Citrullus lanatus*) [12], cucumber (*Cucumis sativus* L.) [15], pumpkins (*Cucurbita* spp.) [15,16], cantaloupe (*Cucumis melo* var. *saccharinus*) [4], muskmelon (*C. melo* L.) [17], and gourds (*Lagenaria siceraria* (Molina) Standl) [18]. The occurrence of GSB is intensified by warm, humid, semi-tropical, and tropical environments that are conducive to the germination of the spores and disease development [19,20]. Of particular interest is pathogenic development within vinyl house, heliogreenhouse facilities. The disease can occur in each growth stage of Cucurbits, and it can infect and damage different parts of Cucurbits, including leaves, petioles, vines, stems, tendrils, pedicels, flowers, peduncles, fruits, and seeds. This results in serious crop losses [21]. Meanwhile, the host of the pathogen is widely distributed, and its structure is complicated and diverse; therefore, it is not easy to control this disease [22]. To date, few studies have been conducted on the epidemiological aspects of *D. bryoniae* on Cucurbitaceous plants [23–26], which could help establish an efficient prevention and control method to reduce the incidence rate of GSB [27].

Despite limited research, GSB-resistant varieties of Cucurbitaceous vegetables have been found and documented [28,29]. Resistant genes and related genetic resistance mechanisms on various Cucurbitaceae crops have been reported, but the understanding of the molecular mechanisms of GSB is still lacking [30]. In this paper, the research achievements in this field from recent decades are examined and summarized. This review covers the bioinformatics, resistance research, and genetic resistance mechanisms of GSB on Cucurbits.

Future research directions and prospects for resistance to GSB of Cucurbit crops are also considered.

2. Pathogenic Fungus Profile

2.1. Acute Symptoms

The pycnidia and pseudothecia of the pathogen forms readily in leaf spots and lesions on other above-ground plant structures, including the petioles, vines, stems, tendrils, and pedicels of flowers and fruits. These have been exploited as diagnostic signs, so fruiting bodies form first in the center of lesions for *D. bryoniae* as a necrotrophic pathogen [31,32]. The pathogenic bacteria have different morphological characteristics in different parts of various Cucurbitaceous vegetable crops (such as color variability and symptoms of conidia) [33], as shown in Table 1. These characteristics of *D. bryoniae* may be similar to some other bacteria (such as *P. exigua*), and more attention should be given to distinguishing these symptoms [31].

Table 1. Morphological and cultural characters of pathogenic bacteria on Cucurbits.

Variety	Signs of Plants	Symptom
Cucumber (<i>C. sativus</i>)	Irregular dark brown lesions at the leaf margin [11]	Aerial mycelium (white becoming gray with age), submerged mycelium (dark olive to black) [34]; Pycnidia (sporulation aparse), perithecia (black bodies) [11].
Muskmelon (<i>C. melo</i>)	Dry rot in stems (white) [34], leaf spots and dry rot in petioles (dark brown) [35].	Produced a conidial mass with a white aerial mycelium at The center of colony, few pycnidia were observed [34,35].
Watermelon (<i>C. lanatus</i>)	Angular water-soaked lesions, defoliation, dry, stem necrosis, gummy exudates, wilt and eventual death [11]; Leaf spots (dark brown) [35].	White aerial and olivaceous mycelium, and olive to dark green or black substrate mycelium [11]; The colony surface was rough and undulated, the conidia were round-ended, cylindrical, monoseptate, and hyaline [35].
Pumpkin (<i>Cucurbita maxima</i>)	-	Aerial mycelium (usually absent, very scanty), submerged mycelium (hyaline to brown), pycnidia (sporulation heavy), perithecia (no sporulation) [33]; Type I to type VII, type IV was the most predominant type (mostly white, a few for brown or yellow) [28].
Gherkin cucumber (<i>C. sativus</i>)	Leaf spots (tan to blackish-brown), dry rot in stems (brown gummy exudate), brown lesions in fruits (black rot) [36].	Conidia were hyaline, cylindrical with rounded ends, and non- or mono-septate; Ascospores were hyaline and monoseptate with two cells of differing sizes [36].
Squash (<i>Cucurbita digitata</i>)	Irregular dark brown lesions at the leaf margin [11].	-
Mellon (<i>C. melo</i>)	Leaf spots (brown), cankers (light brown to off-white) [11].	Angular water-soaked lesions; the fungal showed white aerial and olivaceous mycelium, and olive to dark green or black substrate mycelium; the conidia were round-ended, cylindrical, monoseptate, and hyaline [11].
Cantaloupe (<i>C. melo</i> var cantaloupe)	Black rot (black) and fruit decay [37].	A brown discoloration of the net; Pycnidia and pseudothecia were not produced in black rot lesions on cantaloupe fruit [37].

2.2. Biological Characteristics of Pathogenic Fungus

Gummy stem blight (GSB) is caused by the ascomycete fungus *D. bryoniae* (Auersw.) Rehm (the oldest name) and its anamorph *Phoma cucurbitacearum* (Fr.: Fr.) Sacc. are based on morphological similarities [38]. It has teleomorphic (sexually reproducing) and anamorphic (asexual) states [38,39]. Keinath (2014) determined the suitability of the hosts and various plant parts for the formation of sexual and asexual fruiting bodies of the pathogen for three years; it was found that fruiting bodies showed on high (86%) or low (28%) levels in different years [40].

It has since been established that GSB is caused by three *Stagonosporopsis* species: *S. cucurbitacearum* (syn. *D. bryoniae*) [35,41], *S. citrulli* [42], and *S. caricae* [36,43]. The pathogen of GSB in muskmelon was identified as *D. bryoniae* (Auersw.) Rehm., whose anamorph is *Ascochyta citrullina* Smith [44]. Although three *Stagonosporopsis* species had a similar morphology, they could be distinguished by using polymerase chain reaction-based microsatellite markers [25]. Jia et al. (2003) reported the naturally formed, perfect pathogen stage pseudoperithecium of GSB on gourd crops for the first time in Xingjiang, China. This was later named the *Mycosphaerella melonis* (Pass.) by Chiu et J. C. Walker [45]. Zhang et al. (2013) found the perfect stage of the pathogen of GSB in melons of Hainan, which was identified as ascomycete fungus *D. bryoniae* (Auersw.) Rehm. by measuring its pseudothecia, ascus, and ascospore [46]. Li et al. (2017) identified the mating-type loci (*MAT1*) in the three *Stagonosporopsis* species (*S. citrulli*, *S. cucurbitacearum*, and *S. caricae*) causing GSB in draft genome sequences. Both *MAT1-1-1* and *MAT1-2-1* were divergent, but all had the highly conserved and high mobility group (*MATA-HMG-box*) domain [47].

2.3. Genetic Diversity of Pathogenic Fungus

Corlett (1981) provided a detailed description and illustration of 15 species of *Didymella* and *Didymella*-like species, in which species of *Didymella* fall into two small but well-defined subgeneric groups and one large heterogeneous intermediate group [48]. There is less research regarding the molecular and phylogenetic relationships between *D. bryoniae* and these *Phoma* species, but many molecular techniques, such as AFLP: amplified fragment length polymorphism, RAPD: random amplified polymorphic DNA, SCAR: sequence characterized amplified regions, ELISA: enzyme linked immunosorbent assay, LAMP, and loop-mediated amplification have been well established for characterizing *D. bryoniae* and facilitating genetic fingerprinting of isolates from specific geographical locations [49–53].

Based on the available sequence data, *Didymellaceae* can be segregated into at least 18 distinct clusters (including the taxonomic description of eight species and two varieties); four of these clusters were defined well enough by means of phylogeny and morphology [54]. Many isolates of *D. bryoniae* were placed into four phylogenetic groups (RG I, RG II, and RG IV) through RAPD analysis. Meanwhile, *phoma* spp. clustered into a separate group, RG III [35,49,55]. Shim et al. (2006) isolated *D. bryoniae* clusters and divided them into two major genotypes, the RG I (I-a, I-b, I-c, and I-d) and RG II (II-a, II-b, and II-c) [51]. The isolates were grouped into cluster DB Ia (RG I group), DB Ib (RG II group), DB II, and DB III [56,57]. Workneh (2014) identified the presence of two isolates (DB-05 and DB-33) based on their biological and molecular diversity, which had a higher similarity to *D. bryoniae* isolated from China, with internal transcribed spacer (ITS) region analysis [58].

2.4. Differentiation of Physiological Race

The understanding of the pathogenesis and virulence factors of *D. Bryoniae* may provide new information to develop effective methods of controlling *D. bryoniae* on Cucurbit crops [59]. Isolates from the RG I group were the most predominant and highly virulent, while RG III was slightly virulent [55]. Virulence of the RG I isolates was stronger than RG IV in cucumber [51]. Hu et al. (2012) found that the pathogenicity of 19 strains of *D. bryoniae* was significantly different with disease indexes of 85.11–4.58 on watermelon and melon [60].

Fungal isolates produced polygalacturonase (PG) activity, while PG played an important role in the pathogenesis of *D. bryoniae* in Cucurbitaceous decayed tissue [37]. Furthermore, the virulence factors of *D. bryoniae* have been studied regarding fungal growth and the production of cell wall-degrading enzymes, pectate lyase (PL), polygalacturonase (PG), β -galactosidase (β -Gal), pectin lyase (PNL), and cellulase (Cx); the results suggest that these enzymes appeared to be virulence factors of *D. bryoniae* in cantaloupe decay with PG and β -Gal as the most predominant fruit decay enzymes [61]. Three kinds of defense enzymes (PAL: phenylalanine ammonia-lyase, PPO: polyphenol oxidase, and POD: peroxidase) were closely related to the resistance of GSB on melons [62]. At the same time, the activities POD, SOD (superoxide dismutase), CAT (catalase), and PPO were also positively correlated with resistance of GSB in melons [63,64].

2.5. Genomic Characteristics

To better understand the pathogenicity of the fungus GSB, research on the genomic characteristics of *D. bryoniae* on selected Cucurbitaceous vegetables, including Cucurbits, muskmelons, watermelon, pumpkin, and melon, has been performed, and the results are summarized in Table 2.

Table 2. Genetic characteristics of the fungus of GSB in various Cucurbitaceous vegetables.

Variety	Genetic Characteristics	References
Cucurbits	Two to four amplified fragments were unique to all 27 isolated bacterium, 13 additional fragments were present in all <i>D. bryoniae</i> ;	[31]
	RG I group with a single band of 650 bp fragment while RG II group with about a 1.4 kb fragment.	[51]
Muskmelon (<i>C. melo</i>)	The similarity in sequence identity between the rDNA ITS region was 100% and 95.0%; Nucleotide sequences of the rDNA ITS reform BLAST search from pure culture ranged from 98.2% to 99.8%;	[34]
	Two isolates possessed a single nucleotide substitution of A to G at position 131 of the ITS 1 region.	[35]
Watermelon (<i>C. lanatus</i>)	The isolates produced fragment sizes of approximately 120, 780, and 560 bp;	[11]
	Two isolates possessed a single nucleotide substitution of A to G at position 131 of the ITS 1 region.	[35,57]
Pumpkin (<i>C. maxima</i>)	Two motifs contained sequence variations unique to two groups: Type A (exhibited high similarity with one another, a typical dominant physiological Cucurbita GSB fungal group) and Type B (variant genotypic offshoots with the farthest genetic distance).	[28]
Melon (<i>C. melo</i>)	Ace 2 of <i>Sphaerorheeafuliginea</i> in <i>C. melo</i> PI 124111 conferred by an incompletely dominant gene.	[65]

3. Resistance Breeding and Resistance Mechanism

3.1. Identification of Germplasm Resistant to Disease

Selecting and producing disease-resistant varieties is the goal of every breeder [66–69]. Selection of different varieties and genera of Cucurbitaceous crops with GSB resistance, as well as foliar blight, downy mildew, and crown canker [70–72], has been carried out and reported with various Cucurbitaceous vegetables, including muskmelon [73] and watermelon [72,74], in recent decades. These are summarized in Table 3.

The resistant lines have been identified in melon PI 12411 in 1986 [65], while in watermelon PI 271778 was achieved in 1998 [75]. Five resistance lines (PI 157082, PI 482398, PI 511890, PI 482399, and PI 140471) of melon were identified in 2004, which had five independent loci that each control monogenic resistance to GSB [76]. The lines PI 420145

were reported in melons repeatedly [77,78], as well as PI 200818 in cucumber [79–81]. However, many disease-resistance resources have not been fully utilized (such as chocho and white gourd) (Figure 1); subsequent and thorough research would be beneficial to the development of GSB resistance in Cucurbitaceous vegetables.

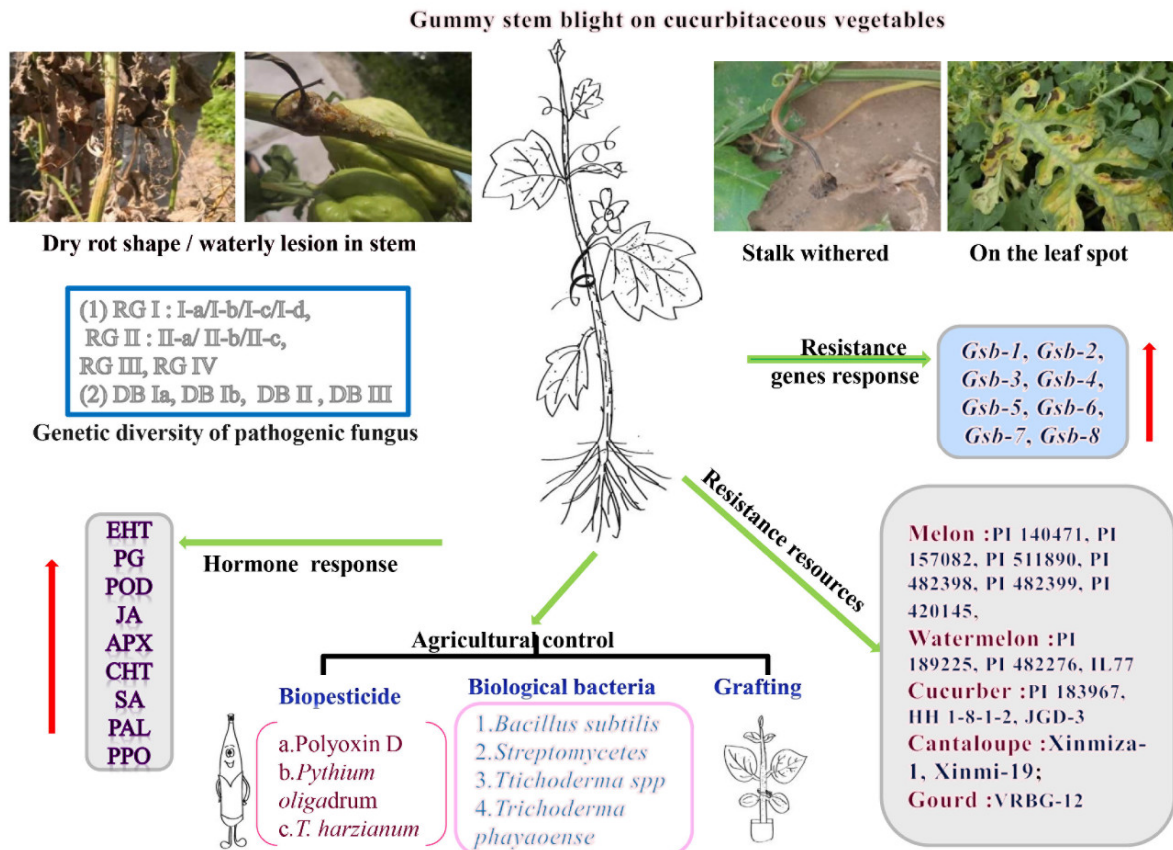


Figure 1. GSB on Cucurbitaceous vegetables and resistance mechanism.

Table 3. Resistance resources of Cucurbits to GSB.

Cucurbits Species	Resistant Strains	References
Melon (<i>C. melo</i>)	PI 140471, PI 266935, PI 296345, PI 436533;	[82]
	PI 124111;	[65]
	PI 266935, PI 266934;	[83]
	PI 157084, PI 482399, PI 157082, PI 157080, PI 482393, PI 482402,	[84]
	PI 157076, PI 482408, PI 482403, PI 255478, PI 511890;	[85]
	MEX-2, KOR-33, JMu-15.	[76]
	PI 157082, PI 482398, PI 511890, PI 482399, PI 140471;	[77]
	PI 157076, PI 420145, PI 323498, PI 255478, PI 420147, PI 618834,	
	PI 200819, PI 482409, PI 482402, PI 164797, PI 436534, PI 200819,	
	PI 321004, PI 470253, PI 185111, PI 511890, PI 435345, Ames 26707;	
Perlita Busle S1, Valenciano Elíptico, Glaver, MR1, 2526;	[86]	
Charentais From 1, AC-29, C160, PI420145, PI482398, PI532830;	[78]	
Baipicui.	[87]	

Table 3. Cont.

Cucurbits Species	Resistant Strains	References
Watermelon (<i>C. lanatus</i>)	PI 271778;	[75]
	All-golden producer, All-sweet scarlet, A56, H25;	[88]
	PI 279461, PI 482379, PI 254744, PI 526233, PI 482276, PI 271771,	[89]
	PI 164248, PI 244019, PI 296322, PI 490383;	
	PI 279461, PI 254744, PI 482379, PI 244019, PI 526233, PI 482276,	[90]
	PI 164248, PI 482284, PI 296332, PI 490383, PI 271771, PI 379243;	
	Au-producer, All- sweet scarlet, Au-Jubilant, Sugarlee, SSDL;	[91]
	Smokylee, Summit, Sugarlee, Calhoun Gray, Dixie lee, Texa W5,	[92]
Conqueror;		
M2K, L8K, M3SK, L3K;	[77]	
Swmx-001E-PL#13-01, WMX-001E-PL#04-01,	[93]	
WMX-001E-PL#02-02.		
Cucumber (<i>C. sativus</i>)	Leningradsky, Wjarnikovsky, Rheinische Vorgebirge, PI 200818,	[79]
	PI 339241;	
	Homegreen #2, PI 200818;	[80]
	PI 164433, PI 390264, Slice, M12, M17;	[67]
	Transamerica, Homegreen#2, Poinsett76, AR79-75, PI 390243,	[81]
PI200815, PI 432855, PI 279469, LJ 90430;		
Sour cucumber, Chaoyou-3, HH1-8-57, HH1-8-2;	[94]	
HH1-8-1-2, HH1-8-5, HH1-8-1-16.	[95]	
Cantaloupe (<i>C. melo</i> var. <i>saccharinus</i>)	Xinmiza-1, Xinmi-19.	[96]
Gourd (<i>Lagenaria siceraria</i> (Mol.) Standl.)	BARI Lau-1, BARI Lau-2;	[18]
	VRBG-12.	[97]

3.2. Molecular Technique on Resistance of Breeding

Molecular diagnostic techniques have been used in the resistance breeding of GSB in Cucurbitaceous crops [98–100]. Babu et al. (2015) studied the genetic characterization and made a genetic profile of *D. bryoniae* isolates infecting watermelon and other Cucurbits in Florida and Georgia through internal transcribed spacer (ITS), RFLP, and RAPD analysis [57]. To detect resistance and susceptibility of melons to GSB, in vitro leaf inoculation combined with molecular marker-assisted selection was used [29]. MAS-based (Marker-assisted selection) pyramiding multiple GSB resistance genes into Cucurbit cultivars (such as melons) has been reported as an effective strategy to develop a broad resistance spectrum and to increase the duration of GSB resistance for breeding Cucurbitaceous vegetable crops [101].

3.3. The Inheritance of Resistance

Knowledge of the genetic basis and heritability of resistance to *D. bryoniae* is essential for the efficient development of resistant cultivars [79]. Wyszogrodzka et al. (1986) reported that 'Homegreen #2' and PI 200818 were resistant ($r = 0.424$) types [80]. A useful germplasm screening method to determine cucumber resistance to GSB had a high correlation ($r = 0.82$ to 0.96) with field ratings [68]. Phenotypic correlations between leaf and stem ratings in cucumber were moderate ($r = 0.52$ to 0.72) with generation means analysis of leaf and stem resistance to GSB [102]. Gusmini et al. (2017) developed four families of six progenies (Pr, Ps, F1, F2, BC1Pr, and BC1Ps) from four crosses of resistant PI accessions with susceptible cultivars; the results suggest that resistance to GSB of PI 482283 and PI 526233 might be under the control of a more complex genetic system due to the partial failure of the data to fit the single gene inheritance [103]. Rivera-Burgos et al. (2021) produced three hundred recombinant inbred lines (RILs) in a population, which carried resistance genes to GSB and evaluated these lines for disease severity ratings ($r = 0.67\sim 0.98$) [104].

3.4. Physiology and Biochemistry of GSB Resistance

Currently, the regulatory resistance mechanisms of GSB in Cucurbitaceae vegetables are largely unknown. The greatest polygalacturonase (PG) may play an important role in the pathogenesis of *D. bryoniae* during cantaloupe fruit decay [37]. Ren et al. (2012) were probably the first group to study the relationship between the ascorbate peroxidase gene (APX) and plant disease resistance at the transcriptional level. They indicated that APX might play roles in melon resistance to GSB, but the roles in different varieties were not the same [105]. Xu et al. (2014) researched the expression analysis of defense genes (*PAL*, *APX*, and *CHT*), and found that pyramided gene materials could enhance their resistance to GSB [106]. A study by Lu et al. (2018) suggested that (1) high concentration of JA (jasmonic acid) and SA (salicylic acid) and low concentration of ETH (ethylene) in PI 420145 enhanced their resistance to GSB; and (2) the high expression levels of EIN2, PDF1.2, EDS5, and NPR1 in PI420145 in the early days of inoculation resulted in an earlier reaction than ‘Baipicui’ to the infection of *D. bryoniae* [107].

4. Gene(s)/Genome Information of Resistance Mechanism

4.1. Resistance Genes

Inheritance and segregation analysis demonstrated that several independent GSB-resistant and monogenetic dominant-resistant loci were associated in many GSB-resistant Cucurbit varieties by the pathogen fungal of *D. bryoniae*. Genetic maps with hundreds to thousands of single nucleotide polymorphism makers were recently released [108]. At present, the studies have mainly focused on three Cucurbitaceous vegetables (melon, watermelon, and cucumber), within-depth research on resistance genes and genetic diversity (Table 4).

Table 4. Genetic diversity and resistance genes in some Cucurbitaceous vegetables.

Resistant Variety	Gene(s)/QTLs/Cucurbits Species	Genetic Diversity	
Melon (<i>C. melo</i>)	<i>Gsb-1</i> (from PI 140471) [76,87,109]; <i>Gsb-2</i> (from PI 157082) [76,110]; <i>Gsb-3</i> (from PI 511890) [76,111];	A linkage distance of 5.2 cM to <i>Gsb-1</i> [109]; the linkage distance was 11.3 cM [110]; The gene distance between ISSR-100 and <i>Gsb-3</i> is 8.3 cM [111];	
	<i>Gsb-4</i> (from PI 482398) [76,85,112,113]; <i>gsb-5</i> (from PI 482399) [76]; <i>Gsb-6</i> (from PI 420145) [87,113,114]; <i>NBS-LRR</i> (from PI 482399) [115];	the genetic distance between CMTA170a and <i>Gsb-4</i> was 5.14 cM [112]; - GSB resistance gene at a distance of 2.0cM [114]; ch 9, the first intron of MELO3C022157 linked to GSB resistance [115];	
	<i>Sb-x</i> (from 4G21) [116]; <i>edr2</i> [117];	linkage group LG1, the genetic distances were 2 cM and 3 cM respectively [116]; T-DNA inserted in its genome [117];	
	<i>PAL</i> (from PI 420145 × PI 140471) [106,118]; <i>CHT</i> [106]; <i>Mc</i> (from PI 140471) [119]; <i>APX</i> [105,106].	- - - -	
	Cucurber (<i>C. sativus</i>)	<i>HH1-8-1-2</i> (susceptible 8419) [95];	11 cM covering 1.299 Mbp; 12 cM spanning 3.569 Mbp with phenotypic variations of 8.7 [95];
		<i>gsb-s1.1</i> , <i>gsbs2.1</i> , <i>gsb-s6.1</i> , <i>gsb-s6.2</i> , <i>gsb-s6.3</i> [101];	<i>gsb-s6.2</i> accounted for the highest phenotypic variation [101];
		<i>gsb3.1</i> , <i>gsb3.2</i> , <i>gsb3.3</i> , <i>gsb4.1</i> , <i>gsb5.1</i> , <i>gsb6.1</i> (From PI 183967) [120];	Chr3, Chr4, Chr5, Chr6; Locus <i>gsb5.1</i> accounted for the highest phenotypic variation (17.9%) [120];
		<i>GSB4-1</i> , <i>GSB4-2</i> , <i>GSB4-3</i> (PH1-8-1-2) [121];	Chr4; The physical distance between the two markers for 375.89 kb [121];
	<i>gsb1.1</i> , <i>gsb2.1</i> , <i>gsb3.1</i> , <i>gsb5.1</i> , <i>gsb6.1</i> (JGD-3) [122]; Csa1G65487 (‘IL77’) [123].	Chr1, Chr2, Chr3, Chr5, Chr6; characteristic of quantitative character inheritance, controlling by the poly-genes [122]; Located in the 24.6-27.1 Mb [123].	

Table 4. Cont.

Resistant Variety	Gene(s)/QTLs/Cucurbits Species	Genetic Diversity
Watermelon (<i>C. lanatus</i>)	<i>Qgsb8.1</i> locus (from PI 189225) [124]; <i>CIGSB3.1</i> , <i>CIGSB5.1</i> , <i>CIGSB7.1</i> (PI 482276) [125]; <i>qLL8.1</i> , <i>qSB8.1</i> , <i>qSB6.1</i> [126]; <i>NBS-encoding R</i> [Cla001821(Chr1), Cla019863 (Chr2), Cla020705 (Chr5), Cla012430, Cla012433 and Cla012439 (Chr8), Cla001017 and Cla001019 (Chr8)] [127].	One associated region spanning 5.7 Mb (Chr8: 10,358,659–16,101,517) [124]; explaining between 6.4 and 21.1% of the phenotypic variation, <i>CIGSB5.1</i> includes an NBS-LRR gene, Locus <i>CIGSB7.1</i> accounted for the highest phenotypic variation [125]; Chr8 and Chr6, explaining 10.5, 10.0% and 9.7% of the phenotypic variations [126];
		-

APX: Ascorbate peroxidase gene; NBS-LRR: Nucleotide-binding site leucine-rich repeat genes; NBS: Nucleotide binding site; CHT: Chitinase gene; APX: Ascorbic acid oxidase; PAL: Phenylalanine ammonia-lyase.

4.2. Genome

Fully mining and utilizing genomic data will provide a more effective theoretical basis for research on GSB on Cucurbitaceous vegetables crops [128], such as watermelon [129,130] and pumpkin [131]. Branham et al. (2018,2019) identified the novel source of resistance to Fusarium wilt race 1 and bacterial fruit blotch in *Citrullus amarus* by QTL mapping [132,133]. Wang et al. (2021) first presented the draft whole genome sequence, gene prediction, and annotation of *S. cucurbitacearums* train DBTL4, which was isolated from diseased watermelon plants [134]. These examples provide insight and knowhow for GSB-caused *D. Bryoniae* genome research.

4.3. circRNA

Through the study of circRNA and screening of large genes before and after the inoculation of *D. bryoniae*, to investigate the role of circRNA involved in the resistance of GSB on Cucurbitaceous vegetables, Chen et al. (2020) screened out 4 and 3 differentially expressed circRNA in PI 420145 and 'Baipicui', respectively, of which one was differentially expressed in both materials. The result showed that the genes of *MELO3C022310*, *MELO3C002560*, and *MELO3C010763* had relations to the resistance of GSB on melons, so the circRNA was involved in the defense response of melon source PI 420145 to the invasion of *D. bryoniae* [135].

5. Prevention Methods

Due to the agricultural importance of preventing and controlling GSB, numerous studies from conventional management (such as soil amendment) to integrated management (such as chemical) and organic production (such as biological control) have been conducted for several decades [136–141].

5.1. Grafting

Grafting has been widely used for controlling soil pathogen inhabitants of many fruits and vegetables, and the utilization of resistant rootstocks to adverse conditions is an alternative for disease control [142–144]. Ito et al. (2009) selected the resistance rootstocks to *D. bryoniae* that utilized 17 Cucurbit genotypes of lancewok melon by grafting under-resistant genotypes 'Bonus No 2'; it was found that the Benicia hispid rootstock was the most associated with melons [145]. Gasparotto et al. (2016) grafted four muskmelon hybrids (Bonus II, Sunrise, Louis, and Princehakusho) onto the squash hybrid Shelper, which is immune to *D. bryoniae*; this significantly reduced the severity of *D. bryoniae* by 54.3%, 57.3%, 54.1%, and 44.6%, respectively [146]. An et al. (2020) studied the rootstocks and grafting interaction for GSB and horticultural traits in parthenocarpic cucumber, finding that the splice grafting technique, in combination with bottle gourd rootstock, has been

most relevant for resistance against GSB under protected conditions and for attaining maximum production [144].

5.2. Biocontrol Bacterium

Researchers have conducted in-depth studies on the characteristics of non-toxic, efficient, and stable biological bacteria usage in crops (vegetables) [147]. Dong et al. (2008) found and identified the strains G 8 and Sh 34 as *Bacillus subtilis* strains (an antagonistic bacteria) on the basis of their morphological and biochemical characteristics and analyzed the partial sequence of their 16S rDNA [148]. Three isolates of *Streptomyces* (MA1F4#2, WI1B#5, and MA2A4#2) appeared to be most effective for biological control of GSB in cantaloupe, especially when used in combination [149]. Nga et al. (2010) identified the rhizobacteria (endophytic bacterium *Ps. Aeruginosa* 231-1) from the Mekong Delta of Vietnam, which could control *D. bryoniae* in watermelon by antibiosis and induce resistance under greenhouse and field conditions [150]. Actinomycete strain C28, identified as *Streptomyces globisporus* subsp. *globisporus*, showed clear antagonistic effects with the diameters of inhibition zones of GSB on melons. Actinomycete strain C28 also demonstrated a promotion effect on melon seed germination and growth [151]. Bai et al. (2019) concluded that the *Ceriporia lacerate* HG2011 strain could inhibit hyphen growth of *M. melons*, and could also decompose lignin and cellulose, as well as grow rapidly in crop straw [152]. Lu et al. (2019) found that *Trichoderma* spp. strains [A3 (HL100), A7 (JY013), B7 (QH060) and B9 (*Trichoderma harzianum* DQ002)] could significantly accelerate the growth of melon seedlings, especially roots, and could clearly inhibit the growth of the pathogens of *mycospharellamelonis* strains [153]. A newly identified endophytic fungus-isolated UP-L1I3, as *Trichoderma phayaoense*, displayed the highest percentage in terms of inhibition of the mycelia growth of *S. cucurbitacearum* at 81.60%, which causes GSB in muskmelon seedlings. Researchers also found that *T. phayaoense* was effective in improving plant development and ability to tolerate a commonly applied fungicide (metalaxy) [154].

Currently, the control of GSB in Cucurbitaceous vegetables by using synthetic fungicides (biopesticide) is on the rise. The antagonistic effects of *Trichoderma* spp. (*T. harzianum*, *T. virid,i* and *T. longatum*) against GSB were studied, and results showed that *T. harzianum* had a higher antagonism than others [147]. Tiadinil and thymol-based formulations could be a potential biopesticide for use in watermelon production for effective GSB disease suppression [57]. The biocontrol effect of *Pythium oligandrum* broth (POB) could control GSB on cucumber seedlings, while also promoting plant growth, increased fruit yield, and improved plant qualities [155]. Polyoxin D could reduce the severity of GSB and be used to prevent outbreaks of GSB on watermelon and muskmelon seedlings grown for use as transplants [156].

6. Outlook

Gummy stem blight (GSB) is a significant fungal disease that damages Cucurbitaceous vegetables. Most of the current research focuses on the identification of the pathogens, simple genetic development of disease-resistance, screening of resistance materials, and control methods. There are relatively few studies on the lack of systematic screening of resistance resources to GSB, and the resistance sources of existing resistant varieties. Meanwhile, the results of previous research around the world are inconsistent and not in-depth; furthermore, the related research of molecular biology is relatively weak. Up to now, there has been an imbalance in the research on GSB among Cucurbitaceous vegetables. Melon and watermelon have made rapid progress while the progress of other Cucurbitaceous vegetables such as cucumber, gourd, and cantaloupe has seldom been reported. The GSB on Cucurbitaceous vegetables and resistance mechanisms are summarized in Figure 1.

In the future, GSB research on Cucurbitaceous vegetables should focus on the following aspects. First, explore the resistance mechanism of the host to pathogen of GSB. Second, establish stable and efficient identification methods and evaluation systems for resistance to GSB. Third, further clarify the genetic development of resistance of GSB via full usage

of screened resistant and susceptible materials. Fourth, strengthen molecular biological studies related to GSB on Cucurbits. Fifth, mine and make full use of genomic data to find more effective, efficient, stable, and non-toxic control measures to GSB. Last, the breeding materials with excellent comprehensive properties against GSB should be used to develop new disease-resistant varieties.

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