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REVIEW ARTICLE

Gummy stem blight in cucurbits: Pathogen biology, host range and management strategies

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Abstract

Gummy stem blight (GSB) is an emerging and serious disease affecting cucurbitaceous crops. It is caused by three closely related fungal pathogens: *Stagonosporopsis cucurbitacearum*, *S. citruli* and *S. caricae.* GSB has a wide host range among the cucurbitaceous family across the world. About 50-80 % yield losses were reported where the continuous cultivation of cucurbits is undertaken. Symptoms include water-soaked lesions on young leaves, chlorosis, splitting of cortical stem tissues and dark brown discoloration in mature fruits. The pathogen also forms chlamydospores-brown, unicellular and spherical in shape. Molecular techniques involving microsatellite markers and internal transcribed spacer (ITS) regions were used for molecular characterization of *Stagonosporopsis* spp. Management of GSB is still in a primitive stage; even when integrated methods are followed, they are still ineffective, specifically during rainy seasons. So, development of genetic resistance in the plants can be a good approach for minimal incidence. This review will provide insights on diversity, host range, life cycle and spread of *Stagonosporopsis* spp.; it also gives an emphasis on development of resistant cultivars. Genomic and molecular approaches (i.e., marker-assisted selection) will be the quick and accurate ways for selection and improvement of resistant lines.

Keywords: ascospores; conidia; Didymellaceae; integrated management; molecular characterization; resistant breeding; *Stagonosporopsis* spp.

Introduction

Cucurbitaceous crops represent a significant group of vegetable worldwide, which include cucumber, watermelon, muskmelon, pumpkin and various gourds (1, 2). About 95 genera with 1000 species are present in the cucurbitaceous family (3). According to FAO (2021), global production includes 101.6 million tonnes (Mt) of watermelon, 91.3 Mt of cucumber, 28.5 Mt of melons and 28 Mt of squashes and pumpkin (4).

Cucurbitaceous crops are nutritious because they provide beneficial vitamins and minerals (5). Beyond their nutritional value, cucurbit crops have long been used in traditional medicine due to their rich phytochemical content (6). Both cultivated and wild species exhibit therapeutic properties, including anti-inflammatory, anti-diabetic, anti-diarrheal and diuretic effects (7).

Cucurbit crops are susceptible to wide range of pathogens, including fungi, oomycetes, bacteria, phytoplasmas, viruses, viroids and nematodes (8). Among these, fungal infections cause significant economic losses due to yield and quality reduction (8, 9). Emerging fungal diseases in cucurbits include GSB, Downy mildew, Cercospora leaf spot, Anthracnose, Fusarium wilt and fruit rot (10). GSB is particularly severe and widespread and when it affects fruits, it is commonly referred to as black rot (1).

GSB is caused by three closely related species of *Stagonosporopsis*: *S. citruli*, *S. caricae* and *S. cucurbitacearum* formerly classified under *Didymella bryoniae* and later changed to *Stagonosporopsis* spp. (4, 11-13). The pathogen produces reproductive structures (pycnidia and pseudothecia) on infected leaves and other aerial plant parts, including petioles, vines, stems, tendrils and pedicels (14). Favourable environmental conditions, particularly high temperatures and rainfall, significantly promote GSB development and resulting in about a 17-43 % decrease in yield and fruit quality. The pathogen can survive in the absence of the host by persisting in soil, weeds and seeds (4, 15).

Contact fungicides such as mancozeb and chlorothalonil, along with other systemic fungicides, have been used to manage GSB (16). There are significant concerns about practicality of fungicides regarding environmental safety and acquired resistance of the pathogen to fungicides (17, 18). Sole reliance on chemical control, particularly during the rainy season, has proven insufficient (15). Under these circumstances, breeding for resistant cultivars presents a sustainable and effective alternative (19).

This review discusses emerging GSB disease in cucurbits. It is one of the most devastating diseases affecting cucurbits worldwide, causing significant yield losses and quality reduction. Despite numerous studies, the complex interactions between different *Stagonosporopsis* species and cucurbit hosts, as well as recent advances in molecular characterization and disease management, are scattered across various publications. Therefore, a comprehensive review is needed to consolidate the current understanding of the pathogen biology, host range, molecular identification, resistance mechanisms and management practices. To conduct this review, a comprehensive literature search was performed using Google Scholar. Keywords such as "gummy stem blight," "cucurbits resistance," specific cucurbit crop names, "Stagonosporopsis," and "molecular characterization" were used to retrieve relevant articles. Studies were selected that focused on the pathogen's biology, host range, disease resistance and management strategies. Priority was given to recent research to ensure up-to-date coverage of the topic. Duplicate and irrelevant articles were excluded. This approach enabled a focused and thorough review of the existing knowledge on gummy stem blight in cucurbits.

Impact of the GSB on production

Gummy stem blight (GSB) affects cucurbitaceous crops globally and has been documented in India across several species, including wax gourd, bitter gourd, chayote, cucumber, muskmelon and ridge gourd (20). In watermelon it was first reported at IIHR Bengaluru, India, where the year-round cultivation of watermelon (*Citrullus lanatus*) is being done. Previously it has not been documented in this location, but in recent days GSB has become a hazard to watermelon production (20). Since evolving seed-borne diseases are major limiting factors in the seed production system of vegetables, GSB is a major problem in cucurbit seed production as it is transmitted through seeds and increasing the cost of production in terms of control measures (10, 21). Severe disease outbreaks cause plant drying, which leads to sudden death of the plants results significant decrease in production (22) (Table 1).

Table 1. Yield/economic losses due to GSB in cucurbits

Crop	Economic/yield loss (%)	References
Watermelon	40 %	(23)
Musk melon	30-60 %	(24)
Cucumber	80 %	(25)

The incidence of GSB was more prevalent than that of other foliar diseases in the field. It was also stated that between 2013 and 2016, the Percent Disease Index nearly reached 75 % during the wet season. The dry season reached around 68 %, which is less than the rainy season (22).

Geographical distribution and economic importance

Gummy stem blight (GSB) is a globally distributed and economically significant disease of cucurbits (11). It was first recorded in 1823 on an unidentified cucurbit in Sweden and later reported in India on chayote in Mysore (26). Since then, it has spread to other cucurbit crops such as cucumber, bitter gourd, ash gourd, muskmelon and ridge gourd, which collectively contribute significantly to the country's vegetable production (13). Table 2 lists initial country - level reports of GSB on various cucurbit hosts. At present the disease (GSB) is said to be noticed in 37 different species of cucurbits with 21 different genera on every continent where cucurbits are grown (27). *S. citrulli* was the most common species with broad geographic distribution and *S. caricae* was also similarly widespread. However, *S. cucurbitacearum* has only been noticed in temperate areas (28).

Table 2. Incidence of GSB in different countries

Country	Year	Name of the crop	References
Germany	1869	White bryony	(29)
Italy	1885	Musk melon	(29)
Usa (Delaware)	1891	Watermelon	(29)
France	1891	Cucumber	(29)
India	1967	Chayote	(26)

Host range

Stagonosporopsis spp. occurs across the world and infects 21 genera with 37 species of the Cucurbitaceae (27). But, as per 2011 report by Keinath the host range was about 12 genera with 23 species, this indicates the significant extension in host range of the pathogen to 14 new species (27, 30). Among all cucurbit hosts disease severity was found to be highest in watermelon than cucumber, musk melon and squash (21) and watermelon and musk melon are most susceptible (27).

While bottle gourd was historically considered resistant or unaffected, recent outbreaks have been reported in India from Uttar Pradesh, Karnataka and Andhra Pradesh, indicating an emerging threat to this crop (18, 20, 30, 31).

Three species of *Stagonosporopsis*: *S. citruli*, *S. caricae* and *S. cucurbitacearum* overlaps in host range and geographical distribution (4). *S. cucurbitacearum* and *S. citruli* were more aggressive on cucurbits, but *S. caricae pathogenic to cucurbits but* aggressively infects the papaya (32).

Symptoms

Stagonosporopsis spp. infects cucurbit crops at all growth stages, with visible symptoms typically 3 to 12 days after infection (14, 16). Symptoms may appear before and after transplantation in the field. Early symptoms on seedlings include discoloration to yellow with tissue decay on the seed leaves (cotyledons) and prior to the development of chlorosis or necrosis, the tissue may appear as water-soaked lesions on leaves (16). The disease spread from the leaf margin to inside the leaf lamina and invaded the entire leaf (20). On stem initial symptoms appeared as brown to dark brown spots that grew about 1 to 20 (mm) in length with an oval to elongated shape (33). GSB infections produce a wide range of symptoms and it is referred to as black rot on cucurbit fruits. Infections occur both on the internal and external surfaces of the fruit. Rotting of fruit starts from the inside of the blossom end and becomes more pronounced as it moves to the fruit exterior, in some cases, malformed tapering at the fruit tip is observed (34) (Fig. 1).

Fig. 1. Symptoms of GSB on different plant parts.

In muskmelon, symptoms start as water-soaked lesions that turn into brown or greenish yellow; eventually forming blighted patches as spots merge. In watermelon, angular water-soaked lesions are typical on leaves, while necrosis and gummy exudates may be observed on stems (21) (Table 3).

Pathogen

Gummy stem blight (GSB) is caused by a complex of three phylogenetically distinct fungal species: *S. cucurbitacearum*, *S. citrulli* and *S. caricae*. These species belong to the phylum Ascomycota, class Dothideomycetes and family Didymellaceae. Despite their genetic differences, all three exhibit indistinguishable morphological features (11).

Historically, the pathogen was classified under the genus *Didymella*, that established by Pier Andrea Saccardo in 1880, with the species later named *Didymella bryoniae* by Heinrich Rehm in 1881 (4). This name is now considered as a synonym for the current *Stagonosporopsis* classification. Among the three, *S. citrulli* is the most widespread and aggressive species (30) (Table 4).

Molecular characterization

Pathogen profiling and molecular tests have become crucial for developing effective management strategies (35). Also, *Stagonosporopsis* spp. have undistinguishable morphology but are genetically distinct, thus, employing microsatellite markers based on polymerase chain reaction can be an accurate way for identification of the pathogen (11). Microsatellite markers of Db01, Db05 and Db06 DNA regions, ITS-1, ITS-4 primers and TUB_T1_F, TUB_T22_R primers of β-tubulin (TUB) DNA region; DNA sequence data help to distinguish *Stagonosporopsis* spp. ITS-1, ITS-4 primers are of widely used and considered to be universal primers (28, 33, 38) (Table 5).

Life cycle

Stagonosporopsis spp. endures high temperatures by growing on crop residues (18). The species of *Stagonosporopsis* yield both asexual fruiting bodies called pycnidia and sexual fruiting bodies called pseudothecia (8). Asexual spores (conidia) move short distances by rain and runoff, while sexual spores (ascospores) are airborne and may move far (36). Ascospores have the ability to travel about 366 m. Thus, ascospores are considered to be the primary inoculum for diseases and rapidly spread to the other fields (37). Large masses of conidia are released by black pycnidia (33). Upon

Table 3. Symptoms of GSB on different plant parts

Plant part	Symptoms	References
Leaf	Dark discolouration on leaf margin Water-soaked lesions Development of necrosis	(16, 20)
Stem	Initial symptoms brown to dark brown spots on stem Waxy water-soaked lesions on cortical tissue Gummy exudates and presence of fruiting bodies on lesions	(33)
Fruit	Fruit rot at blossom end with brown discolouration and moves towards fruit tip exterior Development of fruiting bodies Dried and blackened tissue	(34)

Table 4. Morphological characterization of *Stagonosporopsis* spp.

Morphological parameter	Characteristics	References
Mycelium	• White and hairy aerial mycelium	(35)
Pycnidia	• Black in colour • Globose to sub globose in shape • Ostiolate • 120-180 µm in diameter	(33, 35)
Conidia	• Smooth, round ended and cylindrical in shape • Aseptate/septate (mono or di septate) with slight constriction • Average length and width of conidia was 8 × 3 µm	(21, 35, 33)
Chlamydospores	• Unicellular • Spherical or ellipsoid in shape • Light brown in colour • 7.7-13 × 6-12 µm in size • Single or 5-10 in chain	(33)

Table 5. Different primers used for molecular characterization

Primers			DNA sequence	References
Microsatellite marker primers	Db01 (DNA regions)	Db01_F	CGGTCCGGTCAACCTACTAC	(28)
		Db01_R	CACGCCAGCAAATCTCACTA	
	Db05 (DNA regions)	Db05_F	TATGACGTTGGGCAAGTGAG	
		Db05_R	TTTGCTGGGATGGTGTTGTA	
	Db06 (DNA regions)	Db06_F	GGTGACATCTTGCGTGAATG	
		Db06_R	TGGTTGTTTGGTTGTTTGGA	
ITS primers		ITS-1 ITS-4	5'-TCC GTA GGT GAA CCT GCG G-3' 5'-TCC TCC GCT TAT TGA TAT GC-3'	(33, 38)
(TUB)		TUB_T1_F TUB_T22_R	5'-TCTGGATGTTGTTGGGAATCC-3' 5'-ACCCGCTGAACTTAAGC-3'	(28, 33)

infection, pseudothecia may grow before pycnidia and within the 7 days, ascospores were released from pseudothecia (37). Germination of the spores forms the appressoria; help to penetrate the host plant through the intact leaf surface (cuticle); later the pathogen spreads in the host plants and damages the plant tissue (38).

Survival and spread

GSB spreads via air, soil and seed, with wind and splashing water facilitating rapid transmission in cucurbit-growing regions (18, 31). Ascospores, the primary inoculum, are airborne and capable of traveling long distances, while conidia, embedded in sticky matrices, are suited for short-range dissemination through rain splash (16) (Fig. 2).

In India, *D. bryoniae* was discovered in muskmelon crops as a seed-borne disease that spreads from seed to seedling; again, inoculum gets transmitted from plant to seed (39). With the advent of the free trade regime during the last two decades, there is an increased movement and exchange of seed material. This has probably led to the arrival of this new disease in Bengaluru, India, where the vegetable seed business is active (20). Field-grown cucurbits were also infected by GSB from grafted cucurbits. Both the scion and the rootstock are infected by GSB, as the wounds would encourage the growth of GSB, as the grafted plants are frequently misted or maintained at high humidity levels to encourage graft union repair (40).

Management

Effective management of GSB requires an integrated approach that combines cultural, biological and chemical practices to minimize disease incidence and severity (15) (Fig. 3).

Cultural methods

Collection and destruction of diseased material from the fields immediately after noticing the disease incidence was the first most important measure to control the disease spread (22). Soil amendments, such as chicken litter and mustard oilcake applied during the early growth stages, have been shown to reduce GSB incidence (41). Since, it can spread through seeds, purchasing seeds from trustworthy companies with a track record of producing GSB-free seeds was advisable. Also, seed treatment is a mandatory measure to limiting the source of inoculum through seed (16).

Biological methods

Biological control, involving the use of beneficial microorganisms, presents a sustainable and cost-effective alternative to synthetic pesticides, offering environmental safety along with disease suppression (42).

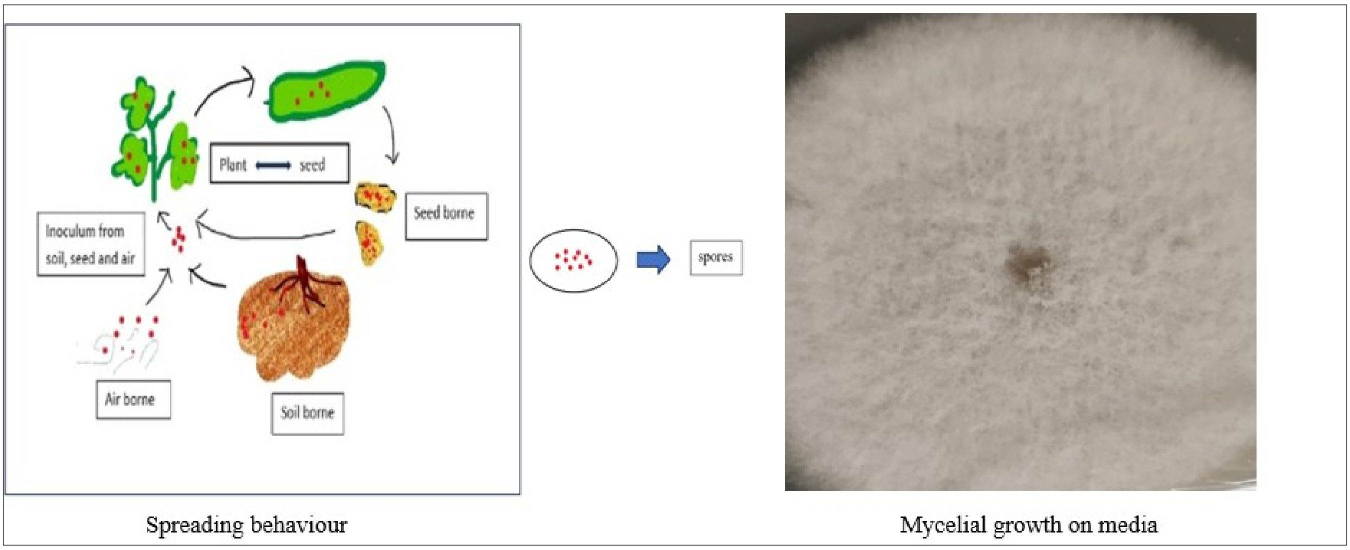

Fig. 2. Growth and spread of *Stagonosporopsis* spp.

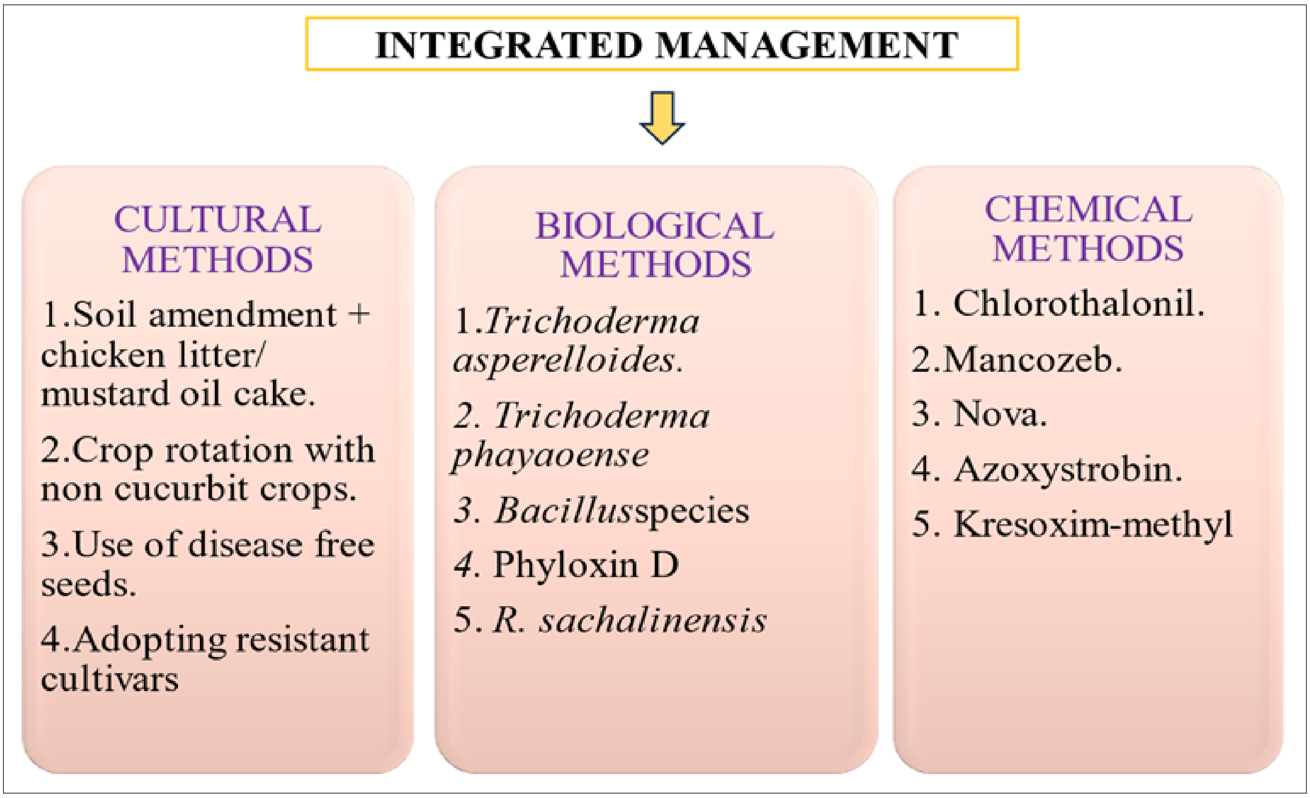

Fig. 3. Integrated management methods to control the gummy stem blight disease in cucurbits.

Trichoderma

Trichoderma asperelloides PSU-P1 is a biological control agent (BCA) that has higher antifungal properties against *S. cucurbitacearum.* It also showed the lowest disease severity during the seedling stage. A novel *Trichoderma phayaoense* species was found to effectively control GSB and promote plant growth in muskmelon (43), by inhibiting the mycelial growth of *S. cucurbitacearum* (44). Formulations of *Trichoderma* are used as seed treatments or soil applications in solid and liquid forms (45). Dry powder formulations are better for seed coating and effective methods against soil-borne fungi (46). Powder formulation @ 3-10 g/kg of seed used for treating the seeds (47). For soil treatment, *Trichoderma* can be added in the soil before sowing (48).

Bacillus

As bio-control agents, *Bacillus* species have their prime role in managing plant diseases. *Bacillus* species were found to have antagonistic effects against *D. bryoniae* as they inhibit the hyphal growth of *D. bryoniae* (49).

Bio-pesticides

Bio-pesticides such as polyoxin D and *Reynoutria sachalinensis* extracts have demonstrated effectiveness as alternatives to chemical fungicides like chlorothalonil in managing GSB (42).

Chemical methods

Non-systemic fungicides such as chlorothalonil and mancozeb are commonly used for GSB control. Foliar application of mancozeb @ 0.2 % effectively suppressing disease development (41, 50). In addition, silicon applications not only help reduce disease severity but also enhance fruit quality and yield (51). Three foliar sprays of Nativo 75 WG @

0.1 %, Aimstar Top 325 SC @ 0.1 % and Bordeaux combination (1:1:100) @ 0.1 %, with a 10-day interval, were observed to lower Percent Disease Index (PDI) by 8.50-9.0 % and improving yield by 14.72-17.89 t/ha (52). Cyprodinil 0.37 kg/ha + Fludioxonil 0.25 kg/ha and Cyprodinil 0.29 kg/ha + 0.10 kg/ha difenoconazole have been reported to decrease disease severity. It was also reported that interaction result of these chemicals, more effective in reducing severity than application alone (53).

Host-plant resistance

The increasing resistance of the pathogen to chemicals (4) and the presence of inoculum in the soil, makes it is difficult to prevent GSB disease through chemical control methods alone, specifically under open field conditions (18, 19, 54). In addition, pesticide application has hazardous effects on the environment.

Therefore, developing GSB-resistant varieties has become important approaches for the crops severely affected by GSB (25). So, the choice of the breeders is to select and create disease-resistant types (55). In recent decades, it has become possible to identify distinct kinds and genera of cucurbitaceous crops that are less susceptible to GSB (56). Although, genetic resistance mechanisms associated with resistant genes in Cucurbitaceae crops have been documented, the underlying molecular mechanisms need further attention (35).

Grafting through employing the rootstocks, which are enduring the hostile situations, also helps to manage GSB and it is extensively exploited for managing geophilic pathogens (14). Here is the example: squash hybrid Shelper, resistant to *D. bryoniae*, can be utilized as muskmelon rootstock (57).

Molecular breeding tools (i.e., marker-assisted selection) are more efficient than those of conventional breeding methods for developing the GSB-resistant cultivars because molecular breeding tools are accurate and take less time than conventional breeding methods (58). Transcriptome-based gene mining may assist in identifying host genes, infection-associated metabolic processes, signal transduction pathways and molecular control networks in plant-pathogen interplay; such knowledge would assist in understanding cucurbit molecular pathways that drive host resistance to *Stagonosporopsis* (59).

Metabolites such as oxalic acid and eriodictyol act as marker metabolites in melon resistance against GSB (60). BLAST analysis of the genomic areas carrying the significant QTLs of *gsb-s6.1* and *gsb-s6.2* identified 117 genes, 14 of which were disease resistance-related (25). Adding numerous GSB-resistant genes to cultivars improves resistance and longevity (61) (Table 6).

Conclusion

India has reported cases of this biotic stress in a number of cucurbits, including chayote, cucumber, muskmelon, ridge gourd, wax gourd and bitter gourd by *S. cucurbitacearum*, *S. citruli* and *S. caricae*. GSB leads to severe yield losses with increasing severity and in recent years GSB incidence has become severe in crops like bottle gourd to which this disease was initially negligible. The *Stagonosporopsis* spp. are morphologically indistinguishable but can be identified through molecular characterization. The major symptoms of the disease include irregular brown spots that coalesce and develop as blight and gummy exudates appear on the stem. On leaf symptoms appear as dark discolouration and necrosis of leaf margin. All cultural, biological and chemical methods are used to control the disease. Since the pathogen is air-borne, seed-borne and soil-borne, making it difficult to control the disease only through these methods. Hence, the host plant resistance plays a key role in minimizing the disease incidence. Genomic and molecular-based approaches offer the advantage of speed and accuracy in identifying resistance traits, which are essential in combating future outbreaks of GSB in cucurbit crops - one of India's major vegetable groups. Moving forward, enhancing research and development efforts in this area will be vital in safeguarding crop yields and ensuring the sustainability of cucurbit production in India.

Table 6. Resistant genes/QTLs of major cucurbits against *Stagonosporopsis*

Crop	Resistant genes	References
Muskmelon	*gsb-4* and *gsb-6*	(61)
Cucumber	*gsb-s1.1*, *gsbs2.1*, *gsb-s6.1*, *gsb-s6.2*, *gsb-s6.3*	(25)
Watermelon	*ClGSB3.1*, *ClGSB5.1* and *ClGSB7.1*, *Qgsb8.1 locus*	(58, 62)

Authors' contributions

GR and MK wrote the original draft and performed the tables. VS and SA performed the figures. TC, MN and IC reviewed and edited the manuscript. All authors have read and agreed to the published version of the manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

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