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REVIEW

A Critical Insight into the Breeding for Resistance to Bacterial Diseases in Pepper (*Capsicum* spp.)

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Abstract

Pepper (*Capsicum* spp.) is widely cultivated throughout the globe due to its diversified use in food (vegetable, spice, paprika, oleoresin) as well as non-food (industrial, pharmaceutical) sectors. Despite its economic value, pepper cultivation faces significant challenges due to bacterial diseases such as bacterial wilt, bacterial spot, bacterial canker, and bacterial soft rot globally. Existing chemical, and biological control strategies have numerous limitations such as the emergence of new resistant strains, negative environmental impact, and lack of user-friendly formulations. Hence, host plant resistance offers a sustainable solution restricting the use of harmful chemicals. Although significant progress has been achieved in the identification and utilization of bacterial wilt and bacterial spot-resistant genotypes, newly emerging threats in pepper like bacterial canker and bacterial soft rot require immediate attention. This article focuses on genetic resources, inheritance patterns, and molecular markers associated with resistance to bacterial diseases in pepper to develop resistant pepper varieties, hybrids, or rootstocks.

Keywords Bacterial wilt · Bacterial spot · Bacterial canker · Bacterial soft rot · *Capsicum* spp.

Introduction

Pepper (*Capsicum* spp.) is widely cultivated throughout the warm climatic areas of the globe due to its diversified use as a vegetable (green), spice (dry), colorant, and in pharmacy (Thampi 2004). Pepper also has a wide range of non-food (defense, spiritual, and ethnobotanical) and food (paprika oleoresin) applications (Kumar et al. 2006; Meghvansi et al. 2010). The capsaicinoids in pepper have significant clinical and pharmacological applications due to their strong biological activity in treating neurological and musculoskeletal complications, as well as oxidative and inflammatory diseases (Review: Barik et al. 2022). In response to these demands, approximately 36.29 mio. t of fresh pepper and 4.84 mio. t of dry peppers were produced globally in 2021 from an area of 3.66 mio. ha (FAOSTAT 2021). China, with a production of 16.75 mio. t, leads the way as the largest producer of fresh pepper, followed by Mexico (2.74 mio. t) and Indonesia (2.58 mio. t) (FAOSTAT 2021). India is the world's largest dry pepper producer with 1.28 mio. t annually followed by China with 0.25 mio. t (FAOSTAT 2021).

Pepper cultivation is constrained by several biotic stresses, among which bacterial pathogens also pose a significant threat globally. Currently, the primary bacterial diseases affecting pepper cultivation worldwide include bacterial wilt, bacterial spot, bacterial canker, and bacterial soft rot. Bacterial wilt, caused by the *Ralstonia solanacearum* species complex (RSSC), is widely prevalent in pepper-growing regions, leading to substantial yield losses of up to 100% (Denny 2006; Jyothi et al.

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2012; Thakur et al. 2021) (source: https://gd.eppo.int/taxon/RALSSL/distribution). Similarly, bacterial spot of pepper is caused by the Xanthomonads which include *Xanthomonas euvesicatoria, X. vesicatoria, X. perforans*, and *X. gardneri* (Jones et al. 2000; Obradović et al. 2004). Although initially reported as infecting only tomatoes, the disease has now spread widely to pepper (Potnis et al. 2015; Osdaghi et al. 2016; Soliman 2022; Jibrin et al. 2022). It is characterized by irregular yellow necrotic areas on pepper leaves and ultimately affects various parts of the plants, such as stems, leaves, and fruits (Osdaghi et al. 2021). The endemic nature of the pathogen, favourable climatic conditions, questionable seed quality, and limited control practices have contributed to an alarming bacterial spot infection ratio as high as 50–95% in pepper growing areas (Obradović et al. 2000, 2001; Aysan and Sahin 2003). Bacterial canker is another bacterial disease in pepper, caused by *Clavibacter michiganensis* spp. *michiganensis* (*Cmm*), which can result in yield losses ranging from 50 to 100% (Oh et al. 2016). It was first reported in pepper fields in Korea and later rapidly spread worldwide (Latin et al. 1995; Lewis Ivey and Miller 2000; Yim et al. 2012; Kumar et al. 2015). Bacterial soft rot is caused by soil-borne bacteria known as *Pectobacterium* spp. (formerly *Erwinia*), is the most devastating postharvest disease of peppers, in which light-colored, water-soaked spots appear on fruits leading to the softening of the infected tissue, subsequently, a mushy watery mass develops, accompanied by a foul odour in the fruit (Bhat Bhat et al. 2010).

Current management of bacterial diseases involves crop rotation, using healthy seeds and transplants, eliminating infected crop residues, and implementing phytosanitary measures (Benítez et al. 2007; Namisy et al. 2019). The chemical method of disease suppression includes the application of copper-based fungicides like copper oxychloride which is combined with ethylene bis-dithiocarbamates and antibiotics like streptomycin and tetracycline or their combination product. However, frequent use of these chemicals has led to the emergence of new resistant bacterial strains (Mirik et al. 2008; Vallad et al. 2010; Griffin et al. 2017). Alternative strategies for managing bacterial diseases involve the use of biological control agents such as bacteriophages and bacterial biocontrol agents like *Pseudomonas mallei, Bacillus amyloliquefaciens* and *Ralstonia pickettii* (Wei et al. 2013; Pajčin et al. 2020). However, the lack of user-friendly formulation preparations restricts their commercial-scale acceptance (Akira et al. 2009; Yuliar et al. 2015). Therefore, a sustainable method of host plant resistance is crucial for effectively controlling bacterial diseases in pepper. Significant progress has been made through conventional breeding as well as marker-assisted breeding (MAB) to combat bacterial diseases, particularly bacterial wilt and bacterial spot. However, there are not much reports on genetic studies for resistance to bacterial canker and bacterial soft rot in peppers. This review presents a comprehensive compilation of the latest information regarding genetic resources, genetic inheritance, and molecular markers that can be effectively harnessed in breeding pepper varieties, hybrids, or rootstocks to combat bacterial diseases.

Bacterial Wilt

R. solanacearum, the bacterium responsible for bacterial wilt, has gained recognition as one of the top 10 deadly plant pathogenic bacteria due to its extensive geographical distribution, genetic variability, and ability to infect a wide range of hosts (Mansfield et al. 2012). It poses a threat to over 200 plant species, resulting in various diseases such as bacterial wilt in Solanaceous plants and ornamentals, brown rot in potatoes, and Moko Disease in the Musaceae family (Hayward 1964; Elphinstone 2005; https://www.cabi.org/isc/datasheet/45009).

The plant pathogenic *R. solanacearum* is a gram-negative, aerobic, non-sporulating, rod-shaped, and motile soil bacterium with a polar flagellar tuft (Smith et al. 1995; Yabuuchi et al. 1995). *R. solanacearum* strains are categorized into three races (Race 1, 2 and 3) based on physiological properties, pathogenicity, geographical distribution, and host range (Buddenhagen et al. 1962). Later, He et al. (1983) reported two additional races (races 4 and 5). RFLP fingerprinting carried out by Hayward (2000) revealed two divisions viz., division I belonging to the biovars 3, 4, and 5 originated from Asia, and division II belonging to the biovars 1, 2A, and 2T originated from South America. The recent reclassification of *R. solanacearum* led to the identification of three distinct species, namely, *R. pseudosolanacearum* (phylotypes I and III), *R. solanacearum* (phylotype II), and *R. syzygii* (phylotype IV), that have different geographic origin/distribution and host ranges (Safni et al. 2014).

Disease Cycle

R. solanacearum can colonize non-host plants including a wide variety of symptomless weeds and can live in soil for up to 10 years without any host plant (Champoiseau et al. 2009). The pathogen enters the plant through roots or via secondary infection and multiplies quickly in the xylem, preventing the flow of water inside the plant and causing abrupt wilting that eventually kills the plant (Kabyashree et al. 2020). The initial symptom of wilt is the drooping of leaves, which is followed by whole plant wilting and discoloration of the vascular tissue (Nischay et al. 2021). The pathogen transmits from diseased plants to healthy

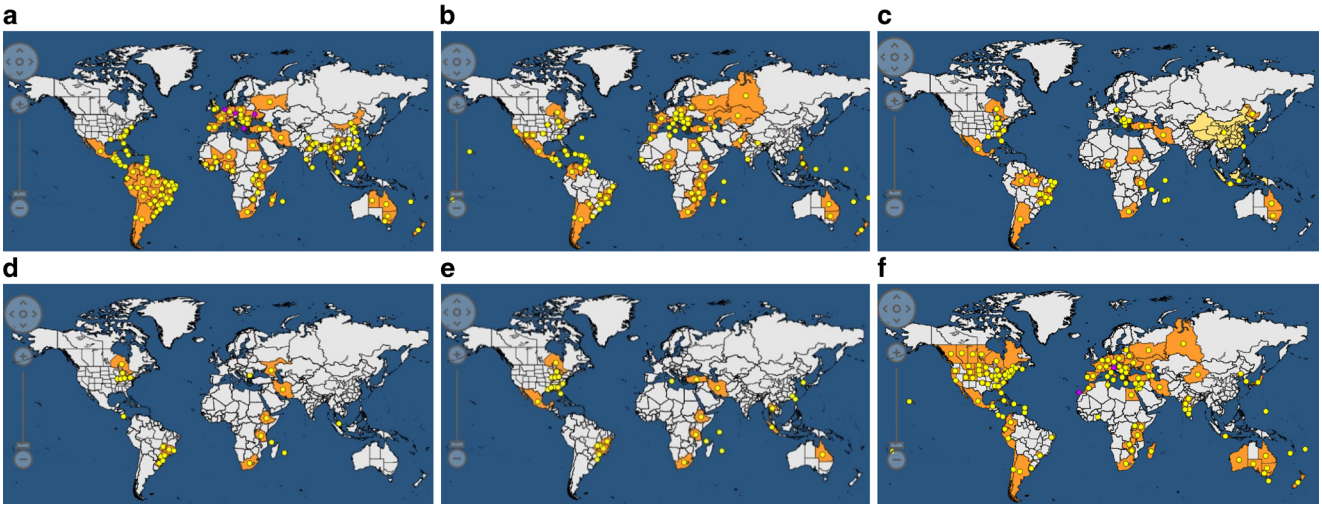

Fig. 1 Distribution of major bacterial pathogens around the world **a** *Ralstonia solanacearum*; **b** *Xanthomonas vesicatoria*; **c** *Xanthomonas euvesicatoria* pv. *euvesicatoria*; **d** *Xanthomonas hortorum* pv. *gardneri*; **e** *Xanthomonas euvesicatoria* pv. *perforans*; **f** *Clavibacter michiganensis* ssp. *michiganensis*] (EPPO 2024) (*Orange color* denotes the extent of bacterial disease occurrence in different countries; *yellow dots*-present and *purple dots*-transient)

plants through roots, water channels, and human or agro-machineries (Choudhary et al. 2018).

Epidemiology

Although *R. solanacearum* can grow in all types of soil, it prefers acidic soils and wet coastal locations (Li et al. 2017; Tafesse et al. 2021). Although alkaline soils are typically unfavourable for pathogen multiplication and disease development, the virulent pathogen can thrive in a pH range of 5.2–7.4 (VanElsas et al. 2000; Li et al. 2017). It is primarily found in hot and humid climates of tropical and subtropical countries, where rapid multiplication of this pathogen occurs (EPPO 2024) (Fig. 1). It can thrive in a wide range of temperatures (15–37 °C, with 35–37 °C being ideal), however, it cannot survive or multiply below 10 °C (VanElsas et al. 2000). The disease typically manifests when the average temperature is higher than 20 °C, and higher wilting is observed with temperatures of 30 °C or greater with increased soil moisture.

Screening for Bacterial Wilt Resistance

R. Solanacearum Inoculum Preparation

Bacterial wilt-infected plants can be identified by a high cell densities of *R. solanacearum* on vascular tissues, and a milky white bacterial slime/ooze that accumulates on the surface of recently cut stems (Denny 2006). In rare cases, when ooze does not form spontaneously due to the low cell density, the "stem-streaming" test can be a helpful diagnostic tool (Denny 2006). In this test, a newly cut stem segment is placed in a transparent vial of water for the stem-streaming test, also known as the "ooze test," to induce the release of a viscous, white-creamy slime specific to *R. solanacearum* (Champoiseau and Momol 2008; Barik et al. 2021). The bacterial suspension containing ooze diluted in distilled water. The diluted suspension is then cultured on Triphenyl tetrazolium chloride (TTC) medium in Petri plates and incubated at temperatures between 28 to 30 °C for 48 h. Following the incubation period, virulent colonies exhibiting irregular shapes, pink centers, and a mucoid appearance are carefully chosen and purified on nutrient agar medium (containing Peptone-5g, Beef extract-3g, and Distilled water). These selected colonies are preserved either in sterile distilled water at 37 or at –80 °C in a 30% glycerol solution for future use. To facilitate effective screening, the bacterial inoculum is prepared from the virulent solution and adjusted to an optical density (OD) of 0.3 at A_{600} nm using a spectrophotometer, corresponding to approximately 1.0×10^8 CFU/ml (Winstead and Kelman 1952; Gopalakrishnan et al. 2005). The bacterial population in the solution can also be quantified by employing serial dilution and spread plate techniques (Jett et al. 1997). Recently, Bhuyan et al. (2023) developed a rather simple and rapid method of counting bacterial colony-forming units using microliter spotting and micro-colony observation. They used a simple approach by spotting five to ten microliters of a diluted bacterial culture numerous times on a single Petri dish. Colony-forming units (CFU) were then counted using a phase-contrast microscope to identify micro-colonies. This method allows for the estimation of CFU in a culture of *R. solanacearum* within ten hours of spotting, with improved due to the increased colony size.

Inoculation Methods

To test for bacterial wilt resistance in genetic resources, an array of screening techniques can be used. Some of these techniques are given below.

a) Sick plot method: 20 to 30 days old seedlings can be transplanted in bacterial wilt sick plot (*R. solanacearum* bacteria population @ 10^6 to 10^8 CFU/gram of soil) after injury to the root by sterilized scissors for easy entry of the pathogen to the plant from the sick plot. Before transplanting, dipping in the bacterial wilt inoculum or even water containing bacterial ooze from infected plants reduces the bacterial wilt screening period (Artal et al. 2012).
b) Artificial inoculation: Artificial inoculation techniques are preferred for screening since the *R. solanacearum* population is not evenly distributed over the soil. After culturing the pathogen in suitable media (TTZ or CPG media) (Denny and Hayward 2001), bacterial suspension can be prepared and applied in the following ways.
   1. Soil drenching method: In this method, a bacterial suspension of 10 to 20 ml (1×10^8 CFU) will be used for soil drenching after root incisions approximately 1.0 cm away from the stem (Artal et al. 2012).
   2. Axil-puncturing method: The 2nd or 3rd leaf axils are pricked with *R. solanacearum* inoculum-dipped sterile needles. Precaution is taken to apply proper pressure so that the inoculum enters the vascular tissues (Artal et al. 2012).
   3. Leaf-clipping method: In this method, 3 to 5 leaves of the plant can be clipped by giving horizontal cuts using sterile scissors dipped in bacterial suspension (Artal et al. 2012; Kumbar et al. 2021). Recently, Kabyashree et al. (2020) through GUS staining showed that leaf inoculation was more efficient than root inoculation for bacterial wilt screening, as the pathogen directly accesses the xylem and reaches the adjacent apical meristem, while in the seedling inoculation method, the bacteria needed to migrate a long distance from the root to the apical regions to colonize and cause the disease.
   4. Hydroponically grown seedling inoculation: The seedlings are grown hydroponically in a nutrient solution inoculated with the bacterial inoculum maintained at a concentration of 10^8 CFU/mL (Hacisalihoglu et al. 2009).

Recently, the root inoculation method and leaf clipping method were followed for the *R. solanacearum* pathogenicity test in microfuge tubes in tomato and eggplant seedlings at the cotyledon stage that successfully displayed wilting symptoms within 48 h. As a result, the entire screening method could be completed in 2 weeks (Singh et al. 2018a; Phukan et al. 2019). Hence, this strategy can be replicated in pepper to speed up the bacterial wilt screening process.

Bacterial Wilt Disease Scoring

The following procedure can be used for bacterial wilt scoring to determine the degree of resistance displayed by the genotypes (Gopalakrishnan et al. 2005; Bainsla et al. 2016).

$$\text{Bacterial wilt severity}(\%) = \frac{\text{Number of bacterial wilt affected diseased plants}}{\text{Total number of plants inoculated}} \times 100$$

(No wilt symptom (0%)-Highly Resistant (HR) (0), 1.00–10.00% wilted plants-Resistant (R) (1), 10.01–20.00% wilted plants—Moderately Resistant (MR) (2), 20.01–30.00% wilted plant Moderately Susceptible (MS) (3), 30.01–40.00% wilted plants-Susceptible (S) (4), >40.01% wilted plants-Highly Susceptible (HS) (5)).

Besides bacterial wilt severity, percentage of disease index (PDI) can also be implemented for screening for bacterial wilt resistance based on a disease rating scale (0–5) (No symptoms = 0, partial wilting of 1 leaf = 1, wilting of 2 to 3 leaves = 2, wilting of all leaves except top 2 or 3 leaves = 3, wilting of all leaves = 4, died plant = 5 (Namisy et al. 2019)). The disease index (DI %) can be calculated using the formula: $DI = ((N_0 \times 0 + N_1 \times 1 + N_2 \times 2 + N_3 \times 3 + N_4 \times 4 + N_5 \times 5) / (Nt/5)) \times 100$, where N_0 to N_5 = number of plants with disease rating scale values from 0 to 5, and Nt = total number of plants.

The disease rating scale observations are recorded at 30 DPI (days post-inoculation). Another approach to score and identify bacterial wilt-resistant lines is to collect xylem exudates from the test genotypes and plate sap dilutions in TTC medium and calculate the colony-forming units. The resistant lines can be identified based on low colony-forming units as compared to the susceptible genotypes. Xylem exudates can be easily collected from the stem through capillary movement and root pressure (Buhtz et al. 2004) or through the negative pressure generated from handheld needleless syringes developed by Longchar et al. (2020).

Resistant Genetic Resources Against Bacterial Wilt

Resistant genetic resources are the prerequisites for exploring host plant resistance, which is the best-advocated strategy to mitigate bacterial wilt disease. The World Vegetable Centre (WVC), Taiwan holds a total of 8372 *Capsicum* accessions belonging to 15 species

Table 1 Genetic resources for bacterial wilt resistance in pepper

Accessions/Breeding Lines/F_1 hybrids	Reported country	Strain/Isolate	Reference
PBC631A, PBC66	France and Taiwan	MB1 and SM732	Subedi et al. 2024
Accession No. 5, Accession No. 4, Accession No. 11, and Accession No. 30	Indonesia	9 isolates	Ambarwati et al. 2023
BWT-PBC-631, BWT-49-AC, Kandaghat selection, BWT-48-AC, BWT-39-BR, BWT-39-DR, BWT-39, BWT-35, BWT-29, BWT-22-HY, BWT-22, BWT-7, BWT-6-1, BWT-5Y, BWT-3Y-3L, BWT-3Y-4L, BWT-3Y, BWT-2-16, BWT-1, BWT-Belle-1, BWT-CP, EC-464107, EC-464115	India	–	Sood et al. 2023a
DPCBWR-14-39, DPCBWR-14-36, DPCBWR-14-2, DPCBWR-14-35 and DPCBWR-14-29	India	–	Sood et al. 2023b
CA8 and MC4	United States	–	Lewis Ivey et al. 2021
Heiser 6240, LS 2390 (*C. frutescens*), LS1716, PBC385, PBC066, BC204, PBC1347, CNPH143 (MC4), CNPH14 (MC5), CNPH145 (HC10) (*C. baccatum*)	–	–	Parisi et al. 2020 (review)
CNPH 3800, Dedo-de-moca 1, 2, 3 (*C. baccatum*), Pimento-de-Bode red 2, Pimento-de-Bode red 4, Pimento-de-Bode yellow 1, Pimento-de-Cheiro 4 (*C. chinense*), Malagueta 1, Malagueta 4, Malagueta 5 (*C. frutescens*)	Brazil	CNPH-RS 380 (race 1, biovar 3, phylotype I, sequevar 18)	Rossato et al. 2018
PCWR-1-3-08, PCWR-Cap-7-08, PCWR-Cap-4-08, PCWR-33-1-3-08 and PCWR-33-3-1-08	India	–	Singh et al. 2018b
Hifly, Skyline II, Sanam	Pakistan	RsBd6 (Biovar 3)	Aslam et al. 2017
BVRC 1, PI 640435, PI 640444	China	Rs-SY 1 (phylotype-1)	Du et al. 2017
MC4	South Korea	KACC 10711	Hwang et al. 2017
Ujwala, Anugraha, VKC 2, VKC 11, VKC 76	India	–	James et al. 2017
Murasaki L4 Daisuke	Japan	–	Genda et al. 2017
YCM344	South Korea	–	Kang et al. 2016
YG4, YG5	South Korea	Rs010	Abebe et al. 2016
KokanKirti, CO-4, LCA-312, LCH-206, LCA-283, Pant-C-3, BC-24, Pb. Guchhedar, BC-28, BSS-273, LCA-33	India	–	Pawaskar et al. 2014
KC01263, KC01261, KC01260, KC01052, KC01051, KC00359, KC00355, and KC00121	South Korea	Rs005, Rs006, and Rs010	Wai et al. 2013
PBC66, PBC375, PBC535, PBC631A, PI 201234, AVPP0511, AVPP0307, AVPP0206, AVPP0205, AVPP0201, AVPP0104, AVPP0103, AVPP0102, AVPP9705, AVPP9703, AVPP9702	Italy	Pss71 (race 1, biovar 4)	Gniffke et al. 2013
Suketto C, Daisuke, and Dai-Power	Japan	KP9547 and KP0779	Matsunaga et al. 2013
BRS Garça	Brazil	–	Ribeiro et al. 2013
EC-464115, EC-464107, PBC-631, SKAU-SP-613-1, SKAU-SP-633-1	India	–	Sood and Kumar 2013
KC1055, KC1050, KC1045, KC1027, KC1021, KC1009, KC1006, KC999, KC995, KC981, KC980, KC126, KC350, KC351	South Korea	–	Tran and Kim 2012
PP0437-7506, PP97-7195-1, PP0237-7508, PP9848-4996, PP0537-7539, PP0337-7545, PP0337-7065, PP0007-2269, PP0337-7562, PP0337-7546, PBC 375, PBC 535, PP9852-173, PP0007-2247, PP0042-17, PP0237-7502, PP0537-7558, PP0537-7513, PP0537-7541, PP9955-15, PP0537-7528, PP0007-2259, PP9852-110	Uganda	–	Nsabiyera et al. 2012

Table 1 (Continued)

Accessions/Breeding Lines/F_1 hybrids	Reported country	Strain/Isolate	Reference
AC 30, AC 20 and AC17 (*C. chinense*)	Brazil	–	Demosthenes and Bentes 2011
Dai-Power	Japan	–	Saito et al. 2011
CM2M-54, SCM334, AC2258, No. 10	Myanmar	–	Matsunaga et al. 2011
KA2, CNPH145 (HC10), CNPH144 (MC5), CNPH143 (MC4), PBC1347, PBC204, PBC066, PBC385, LS1716, BGH 1761, LS 2390 (*C. baccatum*), Heiser 6240, Weonkyo 306 (*C. frutescens*), Tachi-Yatsubusa, Baramashi, Shin-Sakigake 2, LS1439, Kyo-Nami, Mie-Midori, Fushimi-Amanga, Ever Flavor Akashi, Avon Eg, Delicacy, Hot Beauty, Smatra, and Casali	India	–	Babu et al. 2011
Kyoto-Manganji No. 1	Japan	–	Mimura et al. 2010
MZC-180 and Shikou No. 3, Shikou No 4, Shikou No 5, Shikou No 6, 'Daisuke'	Japan	–	Semi et al. 2010
CM 334, BC3F5 (C annuum × C chinense), Perennial, CA8, PBC 384, MC 4, PBC 384	France	–	Lebeau et al. 2011
Manganji	Japan	–	Tsuro et al. 2007
KC897, KC939, KC936, KC126, KC350, KC351, KC353	Mexico and Nepal	–	Koh et al. 2005
PM 687	France	Biovar 1, race 1, phylotype II	Lafortune et al. 2005
MC-4', 'PBC 631', 'PBC 066', 'PBC 1347', and 'PBC 473	Brazil	–	Lopes and Boiteux 2004
IHR-546 and PBC 631	India	–	Yudhvir and Sonia 2004

Table 2 Gene action studies for bacterial wilt resistance in pepper

Gene action	Population	Genotypes used	Reference
Digenic	F_2	MC4 (R) X Subicho (S)	Kwon et al. 2021
Digenic	F_2	IIHR-B-HP-130 (R) and CM334 (S)	Naveena et al. 2020
Single dominant gene	F_2	EC 464107 × Sweet Happy I	Devi et al. 2015
Two genes with dominant epistasis		EC 464107 × Kandaghat Selection	
Two genes with recessive epistasis		EC 464115 × Kandaghat Selection	
Monogenic Recessive	F_2	Anugraha (R) × Pusa Jwala (S)	Thakur et al. 2014
Single dominant gene	F_2 and backcross populations	PBC-631 (R) × California Wonder (S), PBC-631 (R) × Yellow Wonder (S) and IHR-546 (R) × California Wonder (S)	Sharma et al. 2013
Oligogenic to polygenic	F_2 and backcross populations	KC350-3-4-2, KC351-2-2-2-4, KC980-3-1, KC995-2-1, KC9999-3-1 and KC1009-3-2 (R), Chilbok-1, Chilbok-4, KC201-1, KC201-7 and KC256 (S)	Tran and Kim 2010
Polygenic	Double haploid (DH)	California Wonder' × 'LS2341'	Mimura et al. 2009
Digenic interaction/Polygenic (2–5 genes involvement)	Double haploid progeny	PM 687 (R) × Yolo Wonder (S)	Lafortune et al. 2005
Digenic, Incomplete dominance	F_2	Mie-Midori (R) X AC2258 (S)	Matsunaga et al. 1998
Digenic recessive	F_2	PI 257069 (R), PI 201234 (R), California Wonder (S), and Yolo Wonder (S)	Thakur 1990

collected from 104 countries (http://www.avrdc.org; accessed on 20.04.2024). They have identified breeding lines such as AVPP0511, AVPP0307, AVPP0206, AVPP0205, AVPP0104, AVPP0103, AVPP0102, AVPP9705, AVPP9703, AVPP9702, PBC473, PBC385, PBC384, R1-26 (17), Chinda 23, CA8, IR, Paris Minyak, Chili Langkap, MC5, MC4, AVPP0201, PBC066, PBC375, PBC535, PBC631A, PI 201234, and exhibiting high bacterial wilt resistance against *R. solanacearum* strain Pss71 (race 1, biovar 4) (Wang and Berke 1997; Gniffke et al. 2013) In India, several genotypes such as Utkal Ava (BC 14-2), Utkal Rasmi (BC 21-2), Anugraha, Konkan Kirti, Punjab Gucchedar, CA219 (Ujawala), CA33 (Manjari), Pant-C-3, KA2, etc have been released for commercial cultivation in bacterial wilt prone areas (Gopalakrishnan and Peter 1991; Jyothi 1992; KAU 2002; ICAR 2006; Pawaskar et al. 2014). The identified bacterial wilt-resistant genotypes can be either directly introduced into bacterial wilt-prone areas for cultivation or can be utilized to transfer disease resistance into commercial high-yielding cultivars through conventional or marker-assisted backcross breeding (MABB). Some of the identified bacterial wilt-resistant pepper genotypes/breeding lines/HYVs/hybrids around the globe of immense importance are given in Table 1.

Genetics of Bacterial Wilt Resistance

The inheritance of bacterial wilt disease resistance is influenced by numerous factors such as race, biovar, strain, environment, and genotype. Consequently, there has been a growing emphasis on comprehending the genetic aspects and inheritance patterns associated with bacterial wilt resistance. Multiple reports indicate that resistance to bacterial wilt in pepper is controlled by digenic with complementary gene action with other minor genes, polygenic recessive gene action, as well as monogenic dominant or recessive gene action (Sharma et al. 2013; Tran and Kim 2010; Thakur et al. 2014; Naveena et al. 2020; Kwon et al. 2021) (Table 2).

Molecular Markers Associated with Bacterial Wilt Disease Resistance

In resistance breeding, choosing the most reliable markers is highly rewarding during a MAB program. In recent years, the rapid progress in next-generation sequencing (NGS) technologies has spearheaded notable advancements in pepper genetics and genomics (Lozada et al. 2022). Multiple NGS-based genetic maps of pepper have facilitated the mapping of diverse agricultural traits, encompassing disease resistance (Han et al. 2018; Lee et al. 2020; Siddique et al. 2019; Solomon et al. 2021). The substantial size of

Table 3 Molecular marker/mapping studies for bacterial wilt resistance in pepper

QTL	Marker	Marker type	Mapping	Population	Parents used	Chromosome location	Strain	Reference
QTL.Bw5	–	Single Nucleotide Polymorphism (SNP)	Combined bi-parental QTL mapping and GWAS	$F_{5:7}$ recombinant inbred lines	*C. annuum* accession 3501 (R) and *C. annuum* accession 3509 (S)	Chr. 5	–	Lee et al. 2024
GWAS.Bw.4						Chr. 4		
GWAS.Bw.5						Chr. 5		
GWAS.Bw.8.1, GWAS.Bw.8.2						Chr. 8		
Bwr6w-7.2	C07_224926788-HRM, C08_134064617-HRM, C09_3486004-HRM, C10_232244800-HRM, C05_224016474-HRM, and C07_115436147-HRM	High-Resolution Melting (HRM)	QTL Mapping, Genotyping by Sequencing (GBS)	F_2	Konesian Hot (R) & Geonchowang (S)	Chr. 7	'HS' isolate (group III, race 1, & biovar 4)	Lee et al. 2022
Bwr6w-8.1						Chr. 8		
Bwr6w-9.1, Bwr6w-9.2						Chr. 9		
Bwr6w-10.1						Chr. 10		
Bwr6w-5.1						Chr. 5	'HWA' isolate (group I, race 1, & biovar 4)	
Bwr6w-6.1						Chr. 6		
Bwr6w-7.1						Chr. 7		
pBWR-1	–	SNP	QTL Mapping	F_2	KC352 (R) & 14F6002-14 (S)	Chr. 1	WR-1 strain (race 1, biovar 3)	Chae et al. 2022
Bw1	CAMS451 marker	Simple Sequence Repeats (SSR)	QTL Mapping	Accessions	Byadagi Dabbi, California Wonder and Kt-Pl-19 (S) and White Kandari, Ujwala and Anugraha (R)	–	–	Mathew 2020
CA04g02500	–	Cleaved amplified polymorphic sequences (CAPS)	–	Recombinant Inbred Lines (RILs)	YCM334 (R) & Taean (S)	–	–	Ha et al. 2019
qRRs-10.1	ID10-194305124	SNP	QTL Mapping	F_2 and back-cross population	BVRC1 (R) & BVRC25 (S)	Chr. 10	Rs-SY1	Du et al. 2019
Rr (Bacterial wilt resistant recessive allele)	EcoACT + MseCAC	Amplified Fragment Length Polymorphism (AFLP)	Bulked segregant Analysis (BSA)	F_2	Anugraha (R) & Pusa Jwala (S)	Not mapped	–	Thakur et al. 2014
Rs_P4a_3	TG 132	AFLP	BSA	Double haploid (DH)	PM687 (PI322719) (R) & Yolo Wonder (S)	P4	Phylotype I *R. solanacearum* strain, CMR 143 (RUN 224)	Mahbou-Somo-Toukam 2010
Rs_P4a_4	E38/M61_158y					P4		
Rs_P9_1	E38M61_320c					P9		
Rs_P10a_2	E41/M61_266y					P10a		
Rs_P11a_1	E32/M55_079c					P11a		
Rs_Lg22_2	E41/M54_351c					Lg22		
Bw1	CAMS451 marker	SSR	QTL Mapping	Double haploid (DH)	California Wonder (S) & LS2341 (R)	LG 11/Chr 1	KP9547	Mimura et al. 2009

the pepper genome (>3 Gb) has necessitated the utilization of genotyping by sequencing (GBS), restriction site-associated DNA sequencing, and the Illumina Pepper SNP 16 K array, for cost-effective genome-wide genetic variation detection and target loci mapping (Mohan and Paran 2019; Simko et al. 2021). Quantitative Trait Loci (QTLs) associated with bacterial wilt resistance in pepper have been identified on chromosomes 1, 4, 5, 6, 7, 8, 9, and 10 (Mimura et al. 2009; Du et al. 2019; Lee et al. 2022; Chae et al. 2022; Lee et al. 2024). Lee et al. (2022) identified three QTLs (*Bwr6w-5.1, Bwr6w-6.1,* and *Bwr6w-7.1*) and 5 QTLs (*Bwr6w-7.2, Bwr6w-8.1, Bwr6w-9.1, Bwr6w-9.2,* and *Bwr6w-10.1*) conferring resistance to two bacterial isolates (HWA: highly pathogenic and HS: moderately pathogenic) of *R. solanacearum*, respectively in F_2 populations derived from Konesian Hot (R) × Geonchowang (S) population and developed six high-resolution melting (HRM) markers closely associated with resistance to bacterial wilt. Similarly, Chae et al. (2022) identified QTL '*pBWR-1*' on chromosome 1 conferring resistance to WR-1 strain (race 1, biovar 3) of *R. solanacearum* in F_2 populations originated from KC352 (R) and 14F6002-14 (S). Through Genome Wide Association Study (GWAS), marker-trait associations (MTAs) for bacterial wilt resistance in peppers on the G2PSol Capsicum core collection from the World Vegetable Center and additional accessions from the Gene bank in Taiwan was carried out (Brindisi 2022). They identified significant MTAs on chromosomes 4, 7, and 11 against the Pss2074 (phylotype I, biovar 3, sequevar 34) strain. Combination of bi-parental QTL mapping and a GWAS were explored to identify loci associated with BW resistance in $F_{5:7}$ recombinant inbred lines derived from the cross between *C. annuum* accession 3501 (R) and *C. annuum* accession 3509 (S) which led to identification of a significant QTL (*QTL.Bw5*) on chromosome 5's telomeric region and four BW resistance-associated loci (*GWAS.Bw.4, GWAS.Bw.5, GWAS.Bw.8.1*, and *GWAS.Bw.8.2*) on chromosomes 4, 5, and 8 through GWAS analysis (Lee et al. 2024) Furthermore, they identified 13 candidate genes within QTL regions and near GWAS single-nucleotide polymorphisms (SNPs), primarily associated with plant stress, defense, or hormone signalling pathways. A detailed list of molecular marker studies in pepper on resistance to bacterial wilt is given in Table 3.

Rootstock Breeding

Pepper, especially bell peppers, is highly susceptible to bacterial wilt, which is a major constraint for growing bell peppers in bacterial wilt endemic areas and protected cultivation (Devi et al. 2015). Chemical treatment frequently causes hazardous residues to appear in the fruits, raising food safety concerns and lowering the export potential of pepper, which is one of the most important crops exported outside India (Pimentel 2005; Radwan et al. 2005; WHO Pesticide Poisoning and Public Health. 2017). Hence, grafting is an environment-friendly substitute to minimize disease that occurs due to soil-borne pathogens and to elevate the tolerance of susceptible cultivars against biotic stresses (Rouphael et al. 2018). To avoid soil-borne diseases in uninterrupted cropping in peppers, the rootstocks of the same species are generally used for grafting purposes. Several rootstocks have been identified for bacterial wilt disease in peppers (Table 4) (Jang et al. 2012; Wu et al. 2010; Rana et al. 2015; Nischay et al. 2021). The World Vegetable Center, Taiwan has identified genotypes viz., AVPP0205 (PP0237-7502), VI037556 (PBC535), and VI014995 (PI201232) as potential rootstocks in peppers for managing bacterial wilt (http://www.avrdc.org).

Table 4 Grafting studies to manage bacterial wilt in pepper

Rootstock	Scion	Reference
CRS-1 (*C. annuum*), CR-8 (*C. frutescens*)	Massilia RZ F_1	Naik et al. 2024
Weishi	Xinfeng 2	Duan et al. 2022
BRS Acará, Fortaleza, AF-8253	Margarita, Pampa	Ragassi et al. 2022
IIHR-B-HP-130	Pasarella, Bachata, Inspiration, Arka Mohini	Nischay et al. 2021
PI-201232	Indra	Rana et al. 2015
YG5, YG4, YG3, YG2	Gilsang	Abebe et al. 2016
Dai-Power and Daisuke	Kyo-suzu	Matsunaga et al. 2013
PR 920, PR 921, PR 922	Nokkwang	Jang et al. 2012
PP0237-7502 and PP0237-7065	Andalus, Blue Star, Hazera	Wu et al. 2012

Bacterial Spot of Pepper

Bacterial spot or bacterial leaf spot disease of pepper, caused by the *Xanthomonas* spp. viz., *X. euvesicatoria* pv. *euvesicatoria, X. euvesicatoria* pv. *perforans, X. hortorum* pv. *gardneri* and *X. vesicatoria*, have been reported worldwide (EPPO 2024; https://gd.eppo.int/search?k=Xanthomonas) (Fig. 1). The gram-negative, motile, aerobic, short rod-shaped bacteria can infect leaves, fruits, and stems, causing necrotic lesions and defoliation (Utami et al. 2023). Four physiological races of the Xanthomonads (P1, P3, P7, P8) have been identified so far, with P8 being the most widespread (Ignjatov et al. 2012). The host range of the bacterial spot expands over a large number

of species of pepper including *C. annuum, C. pubescens, C. chinense, C. anomalum, C. baccatum,* and *C. frutescens* (Stall et al. 2009; Potnis et al. 2015; Osdaghi et al. 2021; Soliman 2022). However, during the past several years, the incidence of the bacterial spot has been reported in other Solanaceous (*Physalis* spp., *Nicotiana rustica, Lycium* spp., *Hyoscyamus* spp., *Datura* spp., etc.) as well as non-Solanaceous plant species (*Emilia fosbergii, Sida glomerata, Amaranthus lividus*, and *Aeollanthus suaveolens*) (Santos et al. 2020; Osdaghi et al. 2021).

Disease Cycle

The Xanthomonads are seed-borne in nature (Giovanardi et al. 2018). They can survive on a volunteer (pepper/tomato) plant, undecomposed crop residue, and also epiphytically on non-host species in the field (Potnis et al. 2015; Soliman 2022). The bacteria spread through water droplets (dew or rainfall) and aerosols (McAvoy et al. 2021). The bacteria enter the plant system through natural openings (lenticels/stomata) and wounds, after which they move to the center veins for multiplication. When the bacteria inside the host achieve optimum population, they invade the mesophyll tissues leading to the characteristics of leaf spot symptoms (Chatterjee et al. 2008).

Epidemiology

The most favorable conditions for the multiplication and colonization of the bacteria are warm weather, especially day temperatures of 30 to 35 °C and night temperatures above 20 °C coupled with high humidity above 85% (Zhang et al. 2009).

Screening for Bacterial Spot Resistance

Xanthomonas spp. Inoculum Preparation

The bacteria can be isolated from the affected plant parts (stems, fruits and leaves). A small cut across a young lesion can be made and crushed in sterile distilled water or a sterile inoculation needle can be used to pierce through a leaf lesion (Schaad et al. 2001; Osdaghi et al. 2016; Klein-Gordon et al. 2021). A loopful of the suspension can be streaked for individual colonies on a YDC (yeast extract-dextrose-CaCO3) medium followed by incubation at 25 to 28 °C for 48 to 72 h (Osdaghi et al. 2016; Burlakoti et al. 2018).

Inoculation Method

The bacterial suspension (1×10^6 CFU/ml to 1×10^7 CFU/ml) can be prepared from a 48-hour-old culture grown on the YDC medium. The test plants can be inoculated by swabbing bacterial suspension amended with carborundum onto the stems, petioles, and fully expanded leaves using a cotton applicator (Jones et al. 2000). After being inoculated, the plants have to be covered for 24 h with clear polythene bags to maintain high relative humidity, which encourages bacterial multiplication and penetration (Lamichhane 2015). An optimum temperature of 27 to 30 °C and relative humidity of 85 to 95% is maintained for rapid and efficient screening (Jones et al. 2000). The symptoms normally appear as water-soaked patches on the lower epidermis of leaves 5–10 days after inoculation under optimum screening conditions.

Bacterial Spot Disease Scoring

Pepper bacterial spot severity can be evaluated by estimating the percentage of the leaf surface covered with necrotic spots using a visual disease severity scale of 0 to 9, as with 0 = no lesions, 1 = less than 1% of leaf area covered with lesions, 2 = 1 to 10% of leaf area covered with lesions, 3 = 11 to 20% of leaf area covered with lesions or defoliated, 4 = 21 to 35% leaf area covered with lesions or defoliated, 5 = 36 to 50% of leaf area covered with lesions or defoliated, 6 = 51 to 65% of leaf area covered with lesions or defoliated, 7 = 66 to 80% of leaf area covered with lesions or defoliated, 8 = 81 to 99% of leaf area covered with lesions or defoliated, and 9 = complete defoliation (Horsfall and Barratt 1945; Jones et al. 2002).

Resistant Genetic Resources Against Bacterial Spot

Resistant genetic resources are instrumental in enhancing crop improvement programs, especially in combatting diseases like bacterial spots. Incorporating resistant genes from diverse pepper species into cultivated varieties enhances genetic diversity, which is crucial for creating crops capable of withstanding various environmental stresses, including evolving pathogens. Owing to the severity of the disease and widespread occurrence, numerous accessions resistant to bacterial spot from cultivated pepper species and closely related wild species have been identified (Table 5). Bacterial spot-resistant genotypes belonging to *C. annuum* (Early California Wonder-30 R, PI 640513, PI 432818, KC01617, KC01760, KC01779, KC01137, KC01704, and KC01777, KC00939, and Chilbok No. 2), *C. chinense* as well as *C. chacoense* (Romero et al. 2002; Byeon et al. 2016; Srivastava et al. 2018; Potnis et al. 2019) are potential donors.

Genetics of Bacterial Spot Resistance

The understanding of genetic mechanisms controlling bacterial spot resistance in peppers has advanced significantly with the identification of several dominant and recessive

Table 5 Genetic resources for bacterial spot resistance in pepper

Genotypes	*Xanthomonas* spp	Reported country	Strain/isolate	Reference
Cbp1, Cbp2, Cbp3, and Cbp4	*X. hortorum* pv. *Gardneri*	Hungary	LMG962, SRB, Xg51, Xg152, Xg153, Xg156, Xg177	Tóth et al. 2023
PI 163192	*X. gardneri*	India	Xg444	Sharma et al. 2022
Capsicum chacoense	*X. gardneri*	United States	USVLXG1	Potnis et al. 2019
Capsicum chinense	–	India	–	Srivastava et al. 2018
UENF 1381, UENF 1490, UENF 1770, UENF 1624, UENF 1626, UENF 1629, UENF 1635, UENF 1703, H4, H5, UENF 1718, H7, H8, H9, 'Criolo de Morellos', 'UENF Campista','UENF Carioquinha', 'UENF Carioca', UENF 1750	*X. euvesicatoria*	Brazil	ENA 4135	Bento et al. 2017
Globál (Cherry type)	–	Hungary	–	Palotás 2016
KC01617, KC01760, KC01779, KC01137, KC01704, and KC01777, KC00939 and Chilbok No. 2	*X. euvesicatoria*	South Korea	Xcv072, Xcv015, Xcv046, Xcv076	Byeon et al. 2016
UENF 1381	–	Brazil	–	Moreira et al. 2013
Early California Wonder-30R, PI 640513, PI 432818	–	Germany	–	Römer et al. 2010
KC00043, KC00047, KC00079, KC00995-3, KC01006-1, KC01006-2, KC01006-3, KC01327, KC01328	–	South Korea	–	Ahn and Kim 2010
ECW12346	*X. euvesicatoria*	United States	Strain XV157 of Race 6	Vallejos et al. 2010
PI 163192, PI 260435, PI 271322, PI 235047, PI 163192, PI 271322, PI 163192, PI 271322	*X. euvesicatoria*	United States	–	Stall et al. 2009
KC01327, KC01328, KC00897, KC00177, KC00046, KC00079, KC00127, KC00995, KC00997, and KC01006	*X. axonopodis* pv. *vesicatoria*	Laos, Nepal and South Korea	–	Kim et al. 2009
KC995, KC997, KC1006, KC1015, and KC1027	*X. axonopodis* pv. *vesicatoria*	Vietnam	–	Ngoc Hung and Byung-Soo 2006
Fla. XVR 3-25 and 25-11-3-2	*X. axonopodis* pv. *vesicatoria*	South Korea	–	Kim et al. 2007
5776, 7141, 8302	*X. axonopodis* pv. *vesicatoria*	United states	–	Nagata et al. 2005
BGH 3071 and BGH 1772	*X. axonopodis* pv. *vesicatoria*	Brazil	ENA 4135	Costa and Rodrigues 2002
ECW-123R, ECW-13R, ECW-20R, X3R-Camelot	*X. axonopodis* pv. *vesicatoria*	United States	Xcv 135, Xcv 293, Xcv 314, or Xcv 259	Romero et al. 2002

genes (Table 6). Resistance to bacterial spot in pepper has been reported to be governed by digenic, polygenic recessive, and additive gene action as well as monogenic dominant or recessive gene action (Jones et al. 2002; Costa and Rodrigues 2002; Riva et al. 2004; Silva et al. 2017). Several dominant genes such as *Bs1* (*C. annuum* 'PI163192'), *Bs2* (*C. chacoense* 'PI260435'), *Bs3* (*C. annuum* 'PI271322'), *Bs4* (*C. pubescens* 'PI235047'), *Bs7* (*Capsicum baccatum* var. *pendulum* 'UENF1556'), *BsT* (*Capsicum pubescens* 'PI235047A') and 3 recessive genes i.e. *bs5* (*C. annuum* 'PI271322' and 'PI163192' and), *bs6* (C. annuum 'PI271322' and 'PI163192') and *bs8* (*C. annuum* 'PI 163192') governing bacterial spot resistance have been identified (Hibberd et al. 1988; Tai et al. 1999a; 1999b; Jones et al. 2002; Römer et al. 2007; Stall et al. 2009; Potnis et al. 2012; Strauß et al. 2012; Sharma et al. 2022). Additionally, the interaction of resistance genes with races of Xanthomonads: *Bs1*-races 0, 2, and 5; *Bs2*-races 0, 1, 2, 3, 7, and 8; *Bs3*-races 0, 1, 4, 7, and 9; *Bs4* races 0, 1, 3, 4, and 6 further enriches the understanding

Table 6 Genetic inheritance studies for bacterial spot resistance in pepper

Gene action	Population	Genotypes used	Reference
Monogenic recessive	F_2 population	PI 163192 (R) × Early CalWonder (S)	Sharma et al. 2022
Polygenic recessive (> 5 genes)	$F_{2:3}$ populations	UENF2285(S) × UENF1381 (R)	da Graça et al. 2020
Polygenic recessive gene action with additive effect	F_2 and Backcross populations	UENF 2285 (S) × UENF 1381 (R)	Silva et al. 2017
Polygenic recessive (> 3)	Six-generation mean analysis (Hercules, UENF 1381, F_1, F_2, BC_1, and BC_2)	Hercules (S) × UENF 1381 (R)	Riva et al. 2004
Additive gene action	Diallel population	Five *Capsicum annuum* L. genotypes, three susceptible (UENF 1420, UENF 1421, and UENF 1422) and two resistant (BGH 3071 and BGH 1772) to bacterial spot	Costa and Rodrigues 2002
Digenic recessive	F_2 and Backcross populations	ECW12346 (R) × ECW123 (S)	Jones et al. 2002
Polygenic recessive	F_2 and Backcross populations	PI1271322 (R) × PI123464 (S)	Kim et al. 1991
Single dominant gene	F_1, F_2, and Backcross populations	PI201234, PI271322 and PI163192 accessions	Kim and Hur 1990

of the genetic basis of bacterial spot resistance in peppers. (Stall et al. 2009). Jones et al. (2002) identified two recessive genes, '*bs5*' and '*bs6*', resistant to *X. campestris* pv. *vesicatoria* (*Xcv*) race 6 strains. Similarly, the recessively inherited '*bs8*' gene was identified as exhibiting resistance to *X. gardneri* (Sharma et al. 2022). A detailed list of inheritance studies performed by various researchers is mentioned in Table 7.

Molecular Markers Associated with Bacterial Spot Resistance

Amplified Fragment Length Polymorphism (AFLP) marker 'A2' associated with *Bs2* gene has been identified by Tai et al. (1999b), while two tetra-primer ARMS-PCR markers, 25-1 and 25-2, were developed associated with *Bs2* gene in 4 resistant lines (8NH1, 8NH2, 8NH3, and 8NH4) and 4 susceptible lines (8N1, 8N2, 8N3, and 8N4) (Truong et al. 2011). Similarly, AFLP markers associated with the *Bs3* gene (flanking markers, P23-70 and P22-3) governing AvrBs3 protein recognition against *Xanthomonas campestris* pv. *vesicatoria* have been identified at a genetic distance of 0.13 cM from the *Bs3* gene (Pierre et al. 2000). A codominant Sequence Characterized Amplified Region (SCAR) marker PR-Bs3 associated with the *Bs3* gene was also developed by Römer et al. (2010). Additionally, the KASP genotyping technology was used to provide user-friendly markers for the *Bs3* gene (Holdsworth and Mazourek 2015). A set of AFLP markers for *bs5* was discovered after the pepper genome was examined using restriction fragment length polymorphism and AFLP markers. Two recessive genes, *bs5* and *bs6* were reported to act complementary and provide high resistance to race 6 (Vallejos et al. 2010). Five AFLP markers (*PepA2, PepC2, PepF4, PepB7*, and *PepG 4*) associated with the *bs5* gene, localized to chromosome 6 were reported to confer resistance, and its related markers are available (Vallejos et al. 2010). However, *Xanthomonas gardneri*, another pathogenic bacterium, is unaffected by the resistance gene '*bs5*'. Sharma et al. (2022) identified resistance against *X gardneri* in a pepper accession 'PI 163192' and developed near-isogenic lines 'ECW80R', by crossing Early Calwonder (S) with PI 163192 (R) to characterize this novel resistance and to map the resistance gene(s) to the pepper genome. They reported the quantitative recessive nature of resistance against *X. gardneri* and major resistance locus on the subtelomeric region of chromosome 11 and designated it as '*bs8*'. Recently, Sharma et al. (2023) mapped the recessive *bs5* loci to a ~ 535 Kbp interval on chromosome 3, and *bs6* to a ~ 666 Kbp interval on chromosome 6 in the F_2 population of ECW50R (R) × ECW (S) and ECW60R (R) × ECW (S), respectively.

Bacterial Canker

Bacterial canker caused by *Clavibacter michiganensis* is a gram-positive, aerobic, non-spore-forming coryneform bacteria (Eichenlaub et al. 2006). The infiltration and rapid multiplication of the pathogen within xylem vessels result in the discoloration of internal vasculature, accompanied by the progressive deterioration of vascular tissues. This disruption hampers water transportation, ultimately culminating in wilting symptoms during the initial phases of infection (Eichenlaub and Gartemann 2011). The pathogen has a wide host range including potato, maize, beans, etc (Vidaver and Mandel 1974; Manzer and Genereux 1981; Gonzalez and Trapiello 2014). It is divided into five subspecies depending on host specificity (Gartemann et al. 2003; Eichenlaub and Gartemann 2011). *Clavibacter michi-*

Table 7 Molecular marker/mapping studies for resistance to bacterial spot in pepper

QTL	Marker	Marker type	Mapping/marker development method	Studied Population	Parents used	Chromosome location	*X.* spp. (strain)	Reference
bs5 *bs6*	3g_C0.26 6g_C175.02 & 6g_C180.10	SNP	QTL Mapping; GBS	F_2	ECW (S) & ECW50R (R)	Chr. 5 Chr. 6	*X. euvesicatoria* (race P6 strain Xv157)	Sharma et al. 2023
bs8	C3.80	HRM and CAPS	BSA; Whole genome SNP analysis	F_2	PI 163192 (R) & Early CalWonder (S)	Chr. 11	*X. gardneri* (strain Xg444)	Sharma et al. 2022
Bs3	KASP_Bs3	Kompetitive Allele-Specific PCR (KASP)	–	Accessions & F_1 hybrids	Early California Wonder (S), ECW10R (S). ECW20R (S), F_{1S}–A, B, C (S), ECW30R (R), ECW123R (R)	Chr. 1	–	Holdsworth and Mazourek 2015
Bs2	25-1/25-2 14F/14R	SNP	Tetra-primer amplification refractory mutation system-PCR	Resistant and susceptible accessions	8NH1, 8NH2, 8NH3, 8NH4 (R) & 8N1, 8N2, 8N3, 8N4 (S)	Chr. 9	*X. campestris* pv. *vesicatoria*	Truong et al. 2011
Bs3	PR-Bs3	Functional Nucleotide Polymorphism (FNP)	Linkage analysis	F_2	Early California Wonder (S) × ECW-30R (R)	Chr. 2	*X. campestris* pv.*vesicatoria*	Römer et al. 2010
Bs3	B104SP6, B103T7	AFLP (converted to CAPS)	High-resolution linkage mapping	Resistant and susceptible accessions	Yolo wonder, Vat, Vania, SC 81, PM 687, PI 197409, PI 195299, Perennial, HAD 160, HAD 103, H3, ECW-30R, CM 334, Ben Xi (*C. annuum*), PM 1156 (*C. frutescens*), and Chi 8, Chi 7 (*C. chinense*)	Chr. 2	*X. campestris* pv. *vesicatora* strain 85–10 pDS300F and 82–8	Jordan et al. 2006
Bs2	SCF10	Random Amplified Polymorphic DNA (RAPD)	BSA	F_1 and BC_1 F_1	3-25-27 (R) and Early California Wonder (S)	Chr. 9	*X. campestris* pv. *vesicatoria* (Race I)	Kim et al. 2001
Bs3	P23-70, P22-3	Amplified Fragment Length Polymorphism (AFLP)	AFLP Analysis; BSA	Resistant and susceptible accessions	Yolo wonder, Vat, Vania, SC 81, PM 687, PI 197409, PI 195299, Perennial, HAD 160, HAD 103, H3, ECW-30R, CM 334, Ben Xi (*C. annuum*), PM 1156 (*C. frutescens*), and Chi 8, Chi 7 (*C. chinense*)	Chr. 2	*X. campestris* pv. *vesicatoria* strain 85-10 and 85-10 (pD36)	Pierre et al. 2000
Bs2	A2, B3, F1	AFLP	High-resolution genetic and physical mapping	F_2 and backcrossed population	Early Calwoder (S) & Early Calwonder-123R (R)	Chr. 9	*X. campestris* pv. *vesicatoria*	Tai et al. 1999a

ganensis subsp. *michiganensis* (*Cmm*) is the only species of the genus *Clavibacter* that has been officially recognized to infect pepper (Lewis Ivey and Miller 2000; Yim et al. 2012; Oh et al. 2016). Bacterial canker disease infecting pepper has been reported in the USA (Latin et al. 1995; Ivy and Miller 2000), Korea (Oh et al. 2016; Kyeon et al. 2016), the Netherlands (Lee et al. 1999) and India (Kumar et al. 2015; Kumar 2016). Recently, Hwang et al. (2018) proposed to change the subspecies of *Clavibacter michiganensis* infecting pepper to *Clavibacter michiganensis* ssp. *capsici*.

Disease Cycle

Contaminated seed and contaminated transplants are the primary sources of inoculum for *Cmm* (De León et al. 2011). Epiphytic populations of *Cmm* can be established by plants either from a primary inoculum source or through the guttation of fluid containing high densities of *Cmm* from hydathodes. The severity of secondary spread is influenced by cultural practices such as grafting, as well as environmental factors (Chang et al. 1992; Carlton et al. 1998). Furthermore, entry sites for this bacterium have been identified as pruning wounds, damaged roots, fractured trichomes, and broken trichomes (Carlton et al. 1994). In addition to these means of entry, *Cmm* can infect seeds through the vascular route, as well as by penetrating the ovary wall or floral parts (Medina-Mora et al. 2001; Tancos et al. 2013).

Epidemiology

Strider (1969) provided information on the temperature ranges for the development and survival of *Cmm*, stating that the minimum, ideal, and maximum temperatures are 1 °C, 24 to 28 °C, and 35 °C, respectively. Additionally, several other factors contribute to the accelerated spread of the disease including high atmospheric relative humidity, soil with an 80% water-holding capacity (WHC), low light levels, high nutrient conditions, and sandy soils (in contrast to organic soils) (Xu et al. 2012).

Screening for Bacterial Canker Resistance

Clavibacter Michiganensis ssp. capsici Inoculum Preparation

Cmm bacteria can be isolated from the disease affected plant part after surface sterilisation with 70% ethanol followed by rinsing with sterile distilled water. Sample has to be crushed and can be streaked onto yeast extract YDCA medium (Fatmi et al. 2017) or in King's B (KB) medium (0.15% K_2HPO_4, 0.15% $MgSO_4$, 1% glycerol, 2% protease peptone, and 2% Bacto agar at pH 7.0) (Hwang et al. 2018) to multiply further by incubating the plates at 26 °C for 24 to 48 h.

Inoculation Method

Pepper seedlings can be inoculated with approximately 10^8 CFU/ml *Cmm* bacterial suspension either through needle prick inoculation of the pedicel tip of small fruits with a droplet of bacterial suspension or inoculation of the stem with a droplet of bacterial suspension deposited at the insertions of first pair of permanent leaves or by clipping the petiole of the first true leaf of a seedling with scissors dipped in the bacterial suspensions (Francis et al. 2001; Bogo et al. 2002). Inoculation by spraying the flowers with the bacterial suspension can also be done which invades the seeds through the calyx and vascular bundle (Tancos et al. 2013).

Bacterial Canker Disease Scoring

Disease rating of symptoms scoring can be carried out on a 0–5 scale as: 0: Absence of any symptoms; 1: less than 5% leaf area affected; 2: 5–25% leaf area affected; 3: 25–50% leaf area affected; 4: 50–75% leaf area affected; 5: more than 75% leaf area affected and further PDI can be calculated to assign the resistance (Hwang et al. 2018).

Resistant Genetic Resources Against Bacterial Canker

Due to the recent emergence of bacterial canker as a significant threat to pepper crop, there remains a pressing need to identify and characterize resistant genetic resources. With limited work having been done thus far on this front, researchers are exploring the genetic diversity of pepper to identify resistant sources to bacterial canker. At The Ohio State University, Researchers screened 35 genotypes of *Capsicum* spp., in which the percentage of fruits with bacterial canker symptoms differed significantly among varieties, ranging from 0.7 to 13.1% infected fruits and they identified genotypes viz. Everman, Orizaba, 3108, Fury, Panuco, Playmaker, exhibiting resistance against *Clavibacter michiganensis* subsp. *michiganensis* strains C290 and A226 (https://bpb-us-w2.wpmucdn.com/u.osu.edu/dist/e/4539/files/2021/12/Plant-Pathology-Series-2022_Veg-Pathology-Research-Rpts-2021_final.pdf).

Bacterial Soft Rot

Soft rot disease caused by *Pectobacterium* spp. (specifically *Pectobacterium caratovorum*) poses a major challenge to pepper production (especially bell pepper) due to

its occurrence throughout the growth season, transit, and storage stages (Su et al. 2022). This disease inflicts substantial losses in both the production and market value of bell peppers (Hua et al. 2020). It is a gram-negative and non-spore-forming bacterium that produces numerous extracellular plant cell wall degrading enzymes such as protease, cyanoses, arabanases, hemicellulases, cellulase, and pectic enzymes (Islam et al. 2019). The *Pectobacterium* genus is presently categorized into six species, which include *P. cacticida* (Alcorn et al. 1991), *P. aroidearum* (Nabhan et al. 2013; Hua et al. 2020), *P. carotovorum, P. wasabiae, P. betavasculorum, P. atrosepticum* (Gardan et al. 2003). Notably, *P. carotovorum* exhibits significant diversity (Toth et al. 2003) and is further subdivided into six subspecies: *carotovorum, wasabiae, betavasculorum, odoriferum, atrosepticum* (Hauben et al. 1998), and *brasiliense* (Duarte et al. 2004; Hua et al. 2020). Bacterial soft rot disease infecting *Capsicum* spp. has been reported in the USA (Hua et al. 2020), China (Li et al. 2023), Venezuela (Gillis et al. 2017), and Egypt (El-Hendawy et al. 2002).

Disease Cycle

The most frequent causes of the spread of this bacterium are human activities, including pruning, the movement of soil and plant detritus by equipment or people, overhead watering, etc (Li et al. 2024). The primary source of infection is frequently the wounds left by broken peduncles both during growth and during harvest (Hua et al. 2020). Typically, pungent pepper cultivars possess a distinct abscission zone and are generally resilient against stem infections, unless they undergo damage during the harvesting process (Care 2003). The soft rot in the peduncle and calyx tissue spreads to the entire fruit within 2–6 days, turning it into a watery mass. Extracellular enzymes massively secreted by the bacterium can macerate plant cell walls to release nutrients for bacterial growth and colonization in pepper (Toth et al. 2003; Lagaert et al. 2009).

Epidemiology

The temperature range of 27 to 30 °C is considered optimal for the growth of bacterial soft rot. The bacterium can still grow at temperatures as low as 3 °C. Favourable conditions for the rapid growth and proliferation of the bacterium include low oxygen levels, high humidity, and temperatures around 27 to 30 °C (Perombelon 2002).

Screening for Bacterial Soft Rot Resistance

P. Caratovorum Inoculum Preparation

For bacteria isolation, the infested fruits and stems can be disinfected with 0.85% NaOCl for 2 min followed by thorough rinsing with sterile distilled water. After disinfection, the samples have to be homogenized by crushing the tissues with 5 ml of sterile 0.85% NaCl and allowed to sit for 30 min. Next, a loopful of each homogenate can be streaked onto a Luria-Bertani (LB) agar plate, which is then incubated at 28 °C for 48 h. Following this, single colonies from the newly sub-cultured plate has to be transferred to liquid LB medium and placed in a shaker at 150 rpm for 24 h at 28 °C for multiplication. The concentration of bacterial inoculum for inoculation can be adjusted to 1×10^7 CFU/ml by measuring concentration at OD_{600} through spectrophotometer ($OD_{600} = 0.1 \approx 1 \times 10^8$ CFU/ml) (Hua et al. 2020; Wasendorf et al. 2022).

Inoculation Methods

Two inoculation methods can be followed viz. seedling inoculation and fruit inoculation method. In seedling inoculation method, 3 to 4 weeks-old seedlings with 7 to 8 true leaves are subjected to bacterial inoculum suspension by spraying them with a hand-held sprayer until runoff. Inoculated seedlings are to be covered with misted plastic bags for 48 h by maintaining temperature range of 22/30 °C (night/day) and a photoperiod of 14 h. In fruit inoculation method, mature fruits will have to be disinfected with 0.85% NaOCl for 2 min, followed by rinsing with sterile distilled water and drying with sterile paper towels. Using sterile needle, 5 µl bacterial suspension can be inoculated into the hypodermic puncture made in the middle of the rind and fruits can be incubated at 25 °C (room temperature) in Petri dishes covering with polypropylene boxes lined with wet paper towels for symptoms expressions.

Bacterial Soft Rot Disease Scoring

The severity of the diseases can be scored at 1, 2, 3, 4, 5, and 6 dpi using a 1–10 scale, where 0: no decaying of fruit, 1: 1–10% of decaying of fruit, 2: 11–20% of decaying of fruit, etc., with 10 = 91–100% of decaying of fruit and PDI is calculated based on the score (Hua et al. 2020).

Future Thrust and Conclusion

Bacterial diseases pose a significant threat to pepper cultivation worldwide. Due to high strain diversity, the mentioned global resistant genetic resources can be screened

to identify durable resistance sources that can be utilized through breeding resistant varieties/hybrids. In case of bacterial wilt, resistance sources can also be directly used as rootstock that solves the problem of altering genetic backgrounds, as desirable scions can be grafted onto the resistant rootstocks. multifaceted strategy integrated with traditional breeding methods with cutting-edge biotechnological tools that include the utilization of diverse genetic resources (wild Capsicum species and landraces) coupled with advanced genomic techniques such as GWAS and marker-assisted selection (MAS) need to be implemented. Initially, the available public markers can be validated and utilized in individual marker-assisted backcross breeding programs to integrate into different genetic backgrounds. Furthermore, the integration of CRISPR-Cas gene editing holds immense potential for targeted manipulation of key genes conferring resistance to bacterial pathogens through targeting the candidate genes reported. Harnessing these tools and strategies will pave the way for developing robust, environmentally sustainable, and disease-resistant pepper cultivars, ensuring food security and agricultural sustainability.

Conflict of interest S. Barik, S. Kumar Sharma, P. Naresh, A. Kumar Karna, S. Ganesan, L. Kumar Acharya and G. Chandra Acharya declare that they have no competing interests.

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