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Bacterial wilt in brinjal: Source of resistance, inheritance of resistance and molecular markers linked to resistance loci

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ABSTRACT

Brinjal, eggplant or aubergine (*Solanum melongena* L.) belongs to the Solanaceae family and is a widely cultivated warm-season vegetable in India and around the world. Brinjal production and productivity are strongly affected by many biotic stresses, viz., fusarium wilt, verticillium wilt and small leaves of brinjal. Among all the diseases, bacterial wilt (BW) is the most destructive disease in tropical, subtropical, temperate, and humid regions worldwide due to the broad host range and prolonged duration of spore survival. BW disease in brinjal is caused by *Ralstonia solanacearum*, which belongs to the β-proteobacteria family and is a gram-negative, nonspore-forming, rod-shaped, and soilborne bacterium. BW disease management strategies, such as culture, mechanical, biological, and chemical methods, are ineffective due to the prolonged survival period of the bacterium in the soil and its wide host range. The use of resistant varieties and hybrids against BW disease is the safest method for controlling this disease. Information on the genetics of resistance to BW disease in brinjal is vital for the development of an effective breeding method and for identifying bacterial wilt resistance in preferable brinjal cultivars. The use of molecular markers associated with BW disease resistance gene loci helps to characterize traits of interest and develop resistant varieties and hybrids. This review described recent advances in different control measures. We focused on the importance of marker-assisted selection for identifying bacterial wilt diseases.

Introduction

Brinjal, eggplant or aubergine (*Solanum melongena* L.) is a widely cultivated vegetable crop in tropical and subtropical regions of the world because of its edible immature fruits. Brinjal fruits contain low fat content; high dietary fiber; and are a good source of nutrients, vitamins and minerals. It is rich in free reducing sugars, anthocyanin pigments, phenols, amide proteins and glycoalkaloids. Saponins and glycoalkaloids are known to be responsible for bitterness in brinjal (Plazas *et al*., 2013). Brinjal production and productivity are strongly affected by many biotic stresses. Bacterial wilt (BW) disease is the most devastating disease in tropical, subtropical and temperate regions worldwide. BW disease management strategies, such as culture, mechanical, biological, and chemical methods, are ineffective due to the broad host range and prolonged survival period of the bacterium in the soil. An effective method to control BW disease in brinjal is the use of resistant varieties and hybrids. In recent years, many varieties and hybrids of Brinjal have been developed. Nevertheless, the discovery of resistance sources and inheritance of resistance are important for the development of varieties and hybrids against

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BW disease with agronomically important traits and location specificity. In disease resistance breeding, identification of sources of resistance against BW disease is challenging due to ambient factors such as soil pH, temperature, and humidity, which influence disease incidence. Identification of tightly linked molecular markers with disease-resistance gene loci will aid in marker-assisted selection (MAS) for identifying the trait of interest in plants and the development of durable, resistant varieties and hybrids.

Bacterial wilt disease

Brinjal BW disease is caused by *Ralstonia solanacearum*, which is a soil-borne bacterium (Smith, 1896) that causes major yield losses worldwide. This bacterium infects both solanaceous and nonsolanaceous crops extensively (Vanitha *et al*., 2009). *Ralstonia solanacearum* has been classified into 5 races based on the host differences among all races 1 and 3 that infect solanaceous vegetable crops, and race 1 predominates (Álvarez *et al*., 2010). *Ralstonia solanacearum* is a non–spore-forming, gram–negative, rod-shaped bacterium that belongs to the β–proteobacteria family. The optimum temperature for the growth of *Ralstonia solanacearum* was 27–35 °C, and no growth was observed above 40 °C or below 4 °C (Kelman, 1953). The growth of *Ralstonia solanacearum* is optimal at alkaline pH, while at acidic pH, growth is inhibited. Triphenyl tetrazolium chloride (TTC) was used to differentiate virulent colonies and avirulent colonies of *Ralstonia solanacearum* strains in growth media (Kelman, 1954). The virulent colonies had typical characteristic symptoms of red centers with pink or light red margins and a white background, and the avirulent colonies were off-white in color, nonfluidal, and small in size. The characteristic symptoms of BW disease in Brinjal include sudden wilting followed by leaf yellowing, leaf drooping, and stunted plant growth. Ooze-out tests were used to confirm and differentiate BW disease from other fungal diseases. A slimy ooze was removed from BW disease-affected plants by dipping a piece of cut end of the stem in a test tube containing sterile water (Ghosh and Mandal 2009). The severity of the disease depends on ambient factors such as the virulence of the strains, host susceptibility, soil type, soil pH, soil temperature, and soil moisture.

Source of resistance

BW disease management strategies, such as cultural, mechanical, biological, and chemical control measures, are ineffective due to the prolonged survival of the bacterium in the soil and its wide host range. The use of resistant varieties and hybrids against BW diseases is considered the best method for managing BW disease in brinjal. Hussain *et al*. (2005) screened fifteen brinjal accessions in BW sick plots. The results revealed that the exotic germplasm EG 203 was highly resistant to BW disease, the exotic germplasm EG 193 was moderately susceptible to BW disease, and the remaining accessions were highly susceptible to BW disease. Liu *et al*. (2005) evaluated 304 brinjal accessions for BW resistance at the seedling stage by artificial inoculation with *Ralstonia solanacearum* culture. They found 10 immune accessions, 51 highly resistant accessions, 35 resistant accessions, 32 moderately resistant accessions and 176 susceptible accessions to BW disease in Brinjal. Rahman *et al*. (2011) screened eight brinjal cultivars for fusarium and bacterial wilt resistance studies. The authors reported that the Kata Begun cultivar had a high yield and was resistant to both Fusarium and bacterial wilt. Gopalakrishnan *et al*. (2014) screened 41 brinjal accessions in a bacterial wilt sick plot for disease resistance studies. They found that 9 accessions were highly resistant, 5 accessions were resistant, 2 accessions were moderately resistant, and the remaining 22 accessions were moderately to highly susceptible to BW disease in Brinjal.Kumar *et al*. (2014) evaluated 9 brinjal accessions in an initial evaluation trial (IET) and 8 accessions in an advance varietal trial (AVT) in a BW sick plot. A highly resistant reaction was observed for Arka Nidhi and BEBWRES-05 in IET and AVT. Bhavana and Singh (2016) evaluated 100 germplasms of Brinjal for BW disease resistance in sick plots. They found that 2 germplasms (IC–261786 and IC–261793) were highly resistant to BW disease and had relatively high yields.

Inheritance of resistance

Information on the inheritance of resistance to BW disease in brinjal is essential for improving the varieties and hybrids resistant to BW disease in brinjal. The BW disease resistance response and resistance mechanisms are strictly based on the environmental conditions of the location and

cultivar. The inheritance of resistance can be described from segregating populations such as F_2s and back crosses. Chaudhary and Sharma (1999) reported the genetic information of brinjal BW resistance in two populations, viz., Arka Kesev × Pusa Purple Long and Arka Neelkant × Pusa Purple Long. The results showed that monogenic dominant genes control BW disease resistance in both populations. Chaudhary (2000) studied the inheritance of resistance to BW disease in five brinjal populations, viz., Arka Neelkant × Pusa Purple Long (PPL), Arka Kesev × PPL, SM 6–7 × PPL, Hisar Shyamal × PPL, and Pusa Purple Cluster (PPC) × PPL. The segregation pattern of the F_2 and backcross generations indicated that the monogenic dominant gene controlled the resistance of the parents Arka Kesev and Arka Neelkant, whereas in PPC and SM 6–7, the resistance was controlled by monogenic recessive genes. However, in Hisar Shyamal, resistance was controlled by two genes whose expression was inhibited. Zhu *et al*. (2004) reported the presence of resistance genetics in the F_2 population of brinjal against BW disease, and the results suggested that a single dominant gene governs the genetics of resistance. Gopalakrishnan *et al*. (2005) studied the genetics of resistance against BW disease in the Surya × Pusa Kranti cross population of Brinjal. The results suggested that monogenic and incomplete dominance of susceptibility over resistance controls bacterial wilt resistance. Tian *et al*. (2007) studied the inheritance of resistance to BW disease in 49 brinjal hybrids through a diallel mating design (4 resistant and 3 susceptible parents), and the results showed that the genetics of resistance to BW disease in brinjal were governed by few recessive genes and influenced by the epistasis effect. Bi-hao *et al*. (2009) developed F_2s and a backcross population from the E–31 (highly resistant) × E–32 (highly susceptible) cross to study the BW resistance reaction, and the results showed that a single dominant gene governs the inheritance of resistance against BW disease in brinjal. The BW resistance genetics were studied in four F_2 populations of brinjal that were derived from a line × tester design. The BW disease incidence was observed, and the segregation patterns of the four F_2 populations were recorded as a 3 (resistance):1 (susceptible) ratio. The authors reported that a single dominant gene governs resistance to BW disease in Brinjal (Ajjappalavara *et al*., 2010). Chattopadhyay *et al*. (2012) identified 2 brinjal hybrids, VNR–218 × BCB–11 and Arka Nidhi × KS–331, which recorded higher yields and lower BW disease incidence. The results also revealed that non–additive genes control yield and BW disease resistance. Bainsla *et al*. (2016) developed F_2 and F_3 populations from the CARI–B–1 × PPL cross of Brinjal to study the resistance genetics against BW disease, and the results showed that there is a preponderance of recessive gene families wherein more than one gene acts as an additive. In another F_2 generation (*Solanum torvum* × Diglipur local collection), a recessive gene controlled BW resistance. Arunkumar *et al*. (2016) studied BW resistance genetics in 40 F_1 hybrids of Brinjal that were developed through a line × tester design using eight female and five male parents. Among the 40 F_1 hybrids, L3 × T2, L5 × T and L7 × T4 had the highest incidence of BW disease compared to that of the other crosses and forwarded to the F_2 population. The incidence of BW disease in three F_2 populations was recorded, and the results revealed the single dominant genes governing resistance in Brinjal. The literature on the inheritance of resistance to BW disease for other solanaceous crops is presented in Table 1.

Molecular markers

In traditional plant breeding methods, the development of disease-resistant varieties and hybrids is expensive and time consuming. The discovery of molecular marker systems has increased the speed and precision of developing varieties and hybrids with desirable agronomic traits. These markers can assist in the selection of target alleles, minimize linkage drag and reduce the number of generations in breeding programs. The ideal molecular marker should be highly polymorphic and distributed throughout the genome, require little genomic DNA, be codominant, provide sufficient resolution of genetic differences, generate multiple linkages to diverse phenotypes and be inexpensive (Agarwal *et al.*, 2008). Currently, AFLP, CAPS, RAPD, SRAP, SCAR, SSR and SNP markers are used for disease resistance breeding and genetic mapping. Simple sequence repeat (SSR) markers are the most suitable markers for marker-assisted selection (MAS) and crop improvement (Parmar *et al*., 2013).

Table 1. Inheritance of resistance to BW in other solanaceous vegetable crops

Crop	Parents/Lines	Gene action	References
Tomato	Sakthi LE 206	Single recessive gene Two genes with inhibitory epistasis	Kurian and Peter (2001)
Tomato	Arka Vikas × IIHR 2300 Pusa Ruby × IIHR 2193	Two dominant genes with inhibitory gene action	Gaythri (2004)
Tomato	Hawaii–7998 × Solan Gola BT–18 × Solan Gola Hawaii–7998 × Roma TBL–4 × Solan Gola	Additive × Dominance	Sharma & Verma (2004)
Sweet pepper	PM 687 (resistant) × Yolo Wonder (susceptible)	2 to 5 genes with additive effects	LaFortune *et al.* (2005)
Tomato	BL–312 (resistant) × Roma (susceptible) Hawaii 7998 (resistant) × Roma (susceptible)	2 major genes with complementary gene action 2 major genes with dominant and recessive or inhibitory type of gene action	Parveen *et al.* (2006)
Tomato	Pusa Ruby × CLN 2768A & Pusa Ruby × CLN2777H	Single dominant gene	Ramesh (2008)
Hot pepper	Anugraha (resistant) × Pusa Jwala (susceptible)	Two recessive alleles of a gene	Thakur *et al.* (2014)

The special features of SSR markers include codominance, high polymorphism, and uniform distribution throughout the genome, and they require small quantities of template DNA (Morgante *et al*., 2002).

Molecular markers in brinjal

Clain *et al*. (2004) studied homogeneity among 8 accessions of *Solanum torvum* with 3 different *Ralstonia solanacearum* strains. A high BW tolerance was observed between 8 accessions and genetic homogeneity (no polymorphism), as shown by the 168 RAPD markers. Stagel *et al*. (2008) studied phylogenetic analysis and genetic mapping in brinjal by using EST-SSR markers and showed that the EST-SSR markers were positioned within the expressed sequence and that these markers have the potential to determine the variation in gene expression phenotypes. Ge *et al.* (2013) performed population structure analysis with 141 brinjal accessions and 105 SSR markers; the results showed that 2 subgroups were present in the population and that 49 SSR markers associated with 8 fruit traits were identified. Wang *et al*. (2008) studied the genetic diversity of 6 cultivated and 2 wild species of brinjal with 23 SSR markers. Four SSR markers, namely, EM117, EM155, EM126 and EM127, were clearly polymorphic in all the accessions. Sunseri *et al*. (2010) studied the genetic diversity of 70 accessions of *Solanum aethiopicum* L. with AFLP and SSR markers. They identified 3 clusters through cluster analysis, and these clusters did not show any relationships with geographic origin. The matrices of genetic similarity from the AFLP and SSR marker data were utilized to construct a dendrogram. Bihao *et al.* (2009) developed F_2 and backcross populations from the E–31 (highly resistant) × E–32 (highly susceptible) cross to identify SCAR markers linked to BW disease resistance in brinjal. The parents, F_2s and backcross generations were inoculated with a bacterial culture (*Ralstonia solanacearum*) under controlled conditions. Bulked segregant analysis (BSA) was performed to identify RAPD markers, and the identified markers were successfully converted into SCAR markers. Lebeau *et al*. (2013) identified the BW resistance gene ERs1 in a recombinant inbred line population developed from MM738 (susceptible) × AG91–25 (resistant) intraspecific crosses with 4 *Ralstonia solanacearum* strains of phylotype 1. The resistance gene ER1 was resistant to only 3 strains of phylotype 1 (CMR134, PSS366 and GMI1000), and the resistance was disrupted by the addition of the virulent strain PSS4. The action of ER1 shows that resistance is disrupted mainly by the inoculum strain and is minimally influenced by environmental factors. Nunome *et al*. (2001) constructed a linkage map of the F_2 population of brinjal (EPL–1 × WCGR112–8) for fruit shape and fruit color development traits by

using RAPD and AFLP markers. They identified 21 linkage groups with an average distance of 4.9 cM. Fruit shape traits were associated with linkage group 2, and fruit color development traits were associated with linkage group 7. Nunome *et al.* (2009) constructed cDNA libraries and identified 6144 expressed sequence tag (EST) sequences in a brinjal intraspecific mapping population. They designed 209 primers, and 7 were segregated in the mapping population. Based on the segregation pattern, a linkage map was constructed with 236 markers, 14 linkage groups were identified, and the length of the linkage map was 959.1 cM, with an average distance of 4.3 cM. Fukuoka *et al*. (2012) constructed a genetic linkage map using 952 markers in 2 segregating F_2 populations in Brinjal. The map contains 12 linkage groups with a distance of 1285.5 cM, and solanum orthologous (SOL) gene sets were identified. Salgon *et al*. (2017) investigated the mapping population of MM738 (susceptible) × AG91-25 (resistant) with 8 strains of *Ralstonia solanacearum*. One major quantitative trait locus (QTL) (EBWR9) and two minor QTLs (EBWR2 and EBWR14) were identified. The major QTL (EBWR9) provided the highest level of resistance against the phylotype I strains (GMI1000, PSS366 and CMR134). However, this QTL (EBWR6) was ineffective against phylotype I (PSS4) and strains of phylotypes IIA and III. Two other QTLs were detected on chromosomes 2 and 5 and were found to be associated with partial resistance to strains of phylotypes I, IIA, and III and strains of phylotypes IIA and III, respectively. The highest level of resistance against the phylotype I strain (GMI1000, PSS366 and CMR134) was found in the major QTL (EBWR9). However, this QTL was ineffective against the other strains of phylotype I (PSS4) and phylotype IIA and III strains. Two other QTLs were identified on chromosomes 2 and 5 and were associated with partial resistance to phylotype I, IIA, and III strains and phylotype IIA and III strains, respectively. Association mapping of the morphological traits of brinjal was performed through genome-wide association analysis (GWA) with SNP markers. Phenotype and genotype associations were detected for 30 of the 33 traits. An association map was constructed with 79 SNP marker loci in 39 distinct chromosomal regions distributed on all chromosomes (Portis *et al*., 2015). Salgon *et al*. (2018) developed a mapping population from intraspecific cross-sections of MM738 (susceptible) × EG203 (resistant) to identify QTLs resistant to *Ralstonia solanacearum* strains in Brinjal. The 123 doubled haploid lines were combined with phylotype I (PSS4) and III (R3598) strains of *Ralstonia solanacearum*. They identified 10 QTLs related to resistance to PSS4 and 3 QTLs related to resistance to R3598 strains. All the identified QTLs were strongly influenced by environmental factors, and the most stable QTLs for BW disease resistance were identified on chromosomes 3 and 6. The literature on molecular markers for BW resistance in other solanaceous crops is presented in Table 2.

Table 2. Molecular markers for BW resistance in other solanaceous vegetable crops

Crop	Mapping population	Population type and size	Markers	References
Tobacco	W6 (resistant) × Michinoku 1 (susceptible)	117 F_1 doubled haploid plants	106 AFLP	Nishi *et al*. (2003)
Tomato	T51A (susceptible) × T9230 (resistant)	248 F_2s plants	256 AFLP	Miao *et al.* (2009)
Tomato	H24 (susceptible) × Anagha (resistant)	-	AFLP	Nazeem *et al*. (2011)
Toamto	Anagha (resistant) × DVRT–1 (susceptible) and Anagha (resistant) × Pusa Ruby (susceptible).	157 F_2 plants 160 F_2 plants	200 RAPD	Ragina and Sahankumar (2013)
Potato	ED13 (resistant) × *S. phurejia* (susceptible) and CE26 (susceptible)× 772102.37 (resistant)	230 F_1 plants 47 BC1 plants	7 SRAP	Zhi *et al*. (2013)
Tomato	'Hawaii 7996' (*S. lycopersicum*) (resistant) × 'West Virginia 700' (*S. pimpinellifolium*) (susceptible)	188 F_9 RILs plants	59 SSR	Wang *et al*. (2013)
Tomato	Sakthi (BW resistant) × IIHR 2196 (ToLCV resistant).	200 F_3 population	8 SCAR	Belge (2014)
Hot pepper	Anugraha (resistant) × Pusa Jwala (susceptible)	200 F_2 plants	2 AFLP	Thakur *et al*. (2014)

Conclusion

BW is the most destructive disease in brinjal, and the development of resistant varieties and hybrids is the only way to control this disease. Her BW disease symptoms in Brinjal included sudden wilting, yellowing of leaves, drooping of leaves, stunted plant growth, and slimy oozing out, which was observed from the infected plants by dipping a piece of cut end of the stem in a test tube containing sterile water. Resistant strains are available from wild species, indigenous collections, and exotic germplasms. The disease resistance response and resistance mechanisms of BW plants are strictly based on the environmental conditions, location and cultivar. The genetics of BW disease resistance in brinjal vary from source to source, and the same phenomenon was identified as dominant, recessive or incomplete dominance. In disease resistance breeding, the selection of parents resistant to BW disease is difficult due to environmental factors, such as the temperature and pH of the soil, which affect the prevalence of the disease. These problems can be overcome by identifying closely linked molecular markers to disease resistance loci and using the same marker-assisted selection approach, which helps in the rapid identification of the trait of interest in plants and the development of durable, resistant cultivars.

Conflict of interest

The authors declare that they have no conflicts of interest.

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