Eur J Plant Pathol (2021) 160:349–364
https://doi.org/10.1007/s10658-021-02248-1

Genetic analysis of bacterial wilt resistance in eggplant (*Solanum melongena* L.)

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Accepted: 23 February 2021 / Published online: 12 March 2021

Abstract Bacterial wilt triggered by *Ralstonia solanacearum* is one of the major devastating diseases causing significant yield reduction in eggplant. F_1 hybrids (18 CARI-1 based F1 hybrids and 12 publicly available hybrids/varieties) were evaluated for bacterial wilt resistance, yield, and yield attributing traits. CARI-1 based F_1 hybrids showed superiority in yields, however showed a varied level of resistance to bacterial wilt. Further, inheritance and gene action involved in resistance to *Ralstonia solanacearum* was studied. CARI-1 was crossed with two susceptible parents, Arka Neelachal Shyama and Pusa Purple Long to develop six generations for both the combinations. The genetic control of resistance to bacterial wilt was found to be polygenic in the case of the Arka Neelachal Shyama x CARI-1 derived population. While di-genic with complementary gene action in the case of Pusa Purple Long x CARI-1 F_2 population, however deviation in expected ratios was observed in back cross populations. Generation mean analysis revealed the presence of epistasis. For Arka Neelachal Shyama x CARI-1 derived population, owing to the prevalence of additive × additive non-allelic interaction with a negative sign, delaying of selection to later generations, otherwise inter mating between the selected segregates accompanied by selfing for one or more generation(s) is advised for the aggregation of favorable alleles for enhancement of resistance. Similarly, for Pusa Purple Long x CARI-1 population, the simple selection can be efficient due to the prevalence of additive gene action. The inheritance details accumulated in this study would facilitate the introgression of bacterial wilt resistance into elite commercial genotypes.

Keywords Eggplant · Bacterial wilt · Genetics · AUDPC

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Introduction

Eggplant (*Solanum melongena* L.), popularly designated as the poor man's vegetable is one of the cheapest sources of vitamins and minerals. Fruits consist of a high percentage of polyunsaturated fatty acids (65%) which are helpful for liver problems and controlling high blood cholesterol (Daunay and Hazra 2012). The extract of eggplant root and leaves also have medicinal properties against skin diseases, throat, and stomach problems (Mak 2013; Murray 2004; Sekara et al. 2007). Eggplant is cultivated in approximately 1.86 million hectares of area with productivity of 29.1 t/ha, globally (FAOSTAT 2018). However, biotic stresses especially bacterial wilt induced by a soil-borne pathogen *Ralstonia solanacearum* is one of the

critical diseases affecting yield drastically even up to 100% (Mansfield et al. 2012; Nishat et al. 2015). The pathogen is prevalent in tropical, subtropical as well as the temperate region of the world (Fegan and Prior 2005). The pathogen consisting of 54 families has a wide host coverage of approximately 450 plant species (Wicker et al. 2007). Mechanical wounds or secondary root infection acts as the entry point of the pathogen into the vascular system of the plant. The proliferation of the pathogen in the xylem leads to obstruction of water translocation channels which causes instant wilting of plants, followed by the death of the plant. (Vasse et al. 1995).

Preventive measures, such as crop rotation with non-host crops have been found to be ineffective due to the existence of VBNC (Viable But Not Culturable) state by *Ralstonia solanacearum*, (VanElsas et al. 2000; Saddler 2005). Besides soil, the pathogen is additionally disseminated through seeds, water channels, and machinery contact (Ramesh 2008; Tahat and Sijam 2010; Choudhary et al. 2018), which restricts the options to mitigate this disease. Besides, on account of localization and multiplication of the bacterium inside the xylem vessels, exogenous application of antibiotics like Penicillin, Streptomycin, also found to be not highly effective to mitigate the disease (Namisy et al. 2019). Biological approach through antagonistic bacteria like *Pseudomonas mallei*, *Bacillus amyloliquefaciens*, and *Ralstonia pickettii*, were able to reduce *Ralstonia solanacearum* population up to a significant extent. But non-availability of user-friendly formulation preparation restricts the acceptance on a commercial scale (Akira et al. 2009; Yuliar et al. 2015).

As there is no efficient management technique, the researchers aim towards the development of resistant cultivars (Huet 2014; Namisy et al. 2019), which is environmentally safe and efficient to combat the disease. The development of bacterial wilt resistant cultivars through wide hybridization has been restrained by the affiliation of disease resistance with horticultural undesirable traits due to linkage drag (Denny 2006). Also, the resistance level of the developed varieties are region specific according to the strains and thus unstable under different climatic conditions (Chattopadhyay et al. 2012).

Inheritance of resistance is a key factor to be analyzed before initiation of any resistance breeding program, as it helps to determine the suitable breeding strategy for the development of a resistant variety or hybrids. Various gene actions have been reported viz., monogenic, digenic, polygenic (Review; Satyaprakash et al. 2020), including non-additive gene action (Singh et al. 2014). As the inheritance of bacterial wilt resistance is the genotype, environment, and bacterial strain-specific, it is very much required to study the genetics in hot spot regions. Hence, the current experiment was performed to identify and evaluate eggplant F_1 hybrids for yield, yield attributing traits as well as disease reaction to bacteria wilt and to study the genetics of resistance to better understand the gene action which will help breeders to adopt a suitable breeding approach.

Materials and methods

Experimental site

The present investigation was undertaken at Central Horticultural Experiment Station (ICAR-IIHR), Aiginia, Bhubaneswar, India during the period from 2018 to 2020. The site is located at 20015' N latitude, 85,053′ E longitude and 25.5 m above mean sea level. The red laterite soil in which the experiment was conducted was highly acidic with pH 4.4 and contained a medium quantity of organic carbon. The available nitrogen (N), phosphorus (P), and potassium (K) content were 296, 3.92, and 157 kg/ha soil, respectively. Soil being highly acidic and the environment being hot and humid tropic (very congenial for bacterial wilt incidence), Bhubaneswar location is considered as a hot spot for screening varieties or populations for bacterial wilt resistance in India.

Plant materials

Highly bacterial wilt resistant cultivar CARI-1 released from ICAR-Central Island Agricultural Research Institute, Port Blair, Andaman and Nicober Islands, India which also exhibited high level of resistance under Bhubaneswar conditions (97.16% survivability) was used as resistant parent. Eighteen F_1 hybrids were produced using CARI-1 as a common parent (Table 1) and other germplasm [IIHR-B-NE-1, IIHR-B-NE-4, IIHR-B-NE-24, IIHR-B-NE-25, IIHR-B-NE-35, IIHR-B-NE- 41 (Local collection from North Eastern part of India), Arka Nidhi, SM 6–7, IIHR-555, Rampur Local, WCGR, BR-112, 2-BMG-1 (ICAR-IIHR, Bangalore, Karnataka), Arka Neelachal Shyama, IC0598430 (ICAR-IIHR-CHES, Bhubaneswar, Odisha), Pusa Purple Long (ICAR-Indian Agricultural Research Institute, New Delhi), Andaman (ICAR-CIARI,

Andaman and Nicober Islands, India)] maintained at ICAR-IIHR, Bangalore, India. These developed F_1 hybrids along with ten private sector hybrids [Brinjal No. 38, Brinjal No. 132 (Sungro Seeds Ltd., Kolkata), Utkal, VNR B5 (VNR seeds Pvt. Ltd.), Indam GB-4 (Indo-American Hybrid seeds), Tarini (Seminis Pvt. Ltd), JK 803 & JK 8035 (JK seeds Pvt. Ltd.), Soham (Known-you seed India Pvt. Ltd.), Hazari 10 (Debgiri seeds Pvt. Ltd.)] and two public sector varieties [Arka Unnathi & Arka Harshitha (ICAR- Indian Institute of Horticultural Research, Bengaluru, Karnataka, India)] were evaluated for yield, yield attributing traits, and bacterial wilt resistance. Pusa Purple Long being highly bacterial wilt susceptible, was utilized as 'susceptible check' during the bacterial wilt screening of F_1 hybrids. For genetics study, two segregating F_2 populations and Back cross populations were developed from the cross between Arka Neelachal Shyama (BW susceptible) x CARI-1 and Pusa Purple Long (BW susceptible) x CARI-1. Parents (resistant and susceptible), F_1s, and corresponding F_2 populations and backcrossed populations with resistant ($BC1_R$) and susceptible parents ($BC1_S$) were evaluated for bacterial wilt resistance.

Assessment of F_1 hybrids for plant vigor, yield and yield attributing traits

Agronomic practices for F_1 hybrids

For assessment of F_1 hybrids for yield and yield attributing traits, 30 days old seedlings were transplanted and grown from 15th November 2018 to 25th March 2019 in the main field. The experiment was planned out in Randomized Complete Block Design (RCBD) with 3 replications. The main field was prepared to a fine tilth and well-decomposed FYM was added @20 t/ha. Plants were carefully planted at a spacing of 75 cm × 60 cm for easy intercultural operations. All the recommended cultivation practices were carried out.

Screening of F_1 hybrids and segregating populations to bacterial wilt resistance

Bacterial isolate maintenance and inoculation preparation

Bacterial wilt infected eggplant sample was collected from the bacterial wilt sick plot, Bhubaneswar at CHES-IIHR. One cm length stem portion at the collar region of the plant was rinsed with distilled water and surface sterilized with the help of 1% Sodium Hypochlorite solution (NaOCl) accompanied by repeated rinsing with distilled water. Then by using mortar and pestle, the sample was macerated and streaked on to the nutrient agar (HiMedia) petri plates containing glucose (0.4 g/ 100 ml) and 1% TTC (2, 3, 5 Triphenyl Tetrazolium Chloride) (70 μl/ 100 ml) solution (Buyela et al. 2017). The incubation of Petri plates was done at room temperature (26 ± 2 °C) and waited for the visual confirmation of the proliferation of pathogen. The bacterial colonies appeared as creamy white growth with pointed pink color at the center of the colony within 48–72 DPI. *Ralstonia solanacearum* isolate of Bhubaneswar region belongs to Phylotype I (Kumar et al. 2019), race I and biovar 3 (Chandrashekara et al. 2012).

Two loops out of freshly cultured *Ralstonia solanacearum* colonies were taken and suspended into 150 ml of nutrient agar media followed by shaking in an incubator maintained at 28 °C and 150 rpm for 24 h. Then, bacterial cultures were centrifuged at 4000 rpm at 4 °C for 15 min and the supernatants were discarded. The bacterial pellets were re-suspended in the required volume of sterile distilled water to obtain a final concentration of 10^7 CFU/ml ($OD_{600} = 0.3$) with the help of a spectrophotometer (Singh et al. 2018).

Raising of seedlings and inoculation of bacterial culture

For assessment of bacterial wilt resistance in F1 hybrids and segregating populations (F2 and backcrossed populations) needed for genetics study were sown in portrays containing coco peat, farmyard manure, and vermicompost (2:1:1) media followed by light irrigation and kept inside the poly house. Before sowing, seeds were soaked for 24 h for quick and uniform germination. Drenching with fungicides was done at regular intervals to protect young seedlings from damping-off and other fungal diseases. Two sprays of liquid fertilizer (19:19:19 NPK) were done at fortnight intervals for the luxurious growth of seedlings. The same methods of seedling raising were practiced for the estimation of F_1 hybrids for yield and yield attributing traits.

To inquire the inheritance of bacterial wilt resistance, 50 plants of the resistant parent, 50 plants of the susceptible parent, 51 plants of F1 population, 308 plants of F2 segregating population, 51 plants of $BC1_R$ (F_1 x CARI-1) and BC1S (F1 x Arka Neelachal Shyama) population were used for Arka Neelachal Shyama x CARI-1

Table 1 Evaluation of F_1 hybrids for plant vigor, yield and yield attributing traits and bacterial wilt incidence

F_1 Hybrids	Days to 50% flowering	Plant Height (cm)	Number of Branches	Fruit yield per plant (g)	Number of fruits per plant	Fruit Length	Fruit Girth	Fruit Weight	Bacterial wilt in field (%)
IIHR-B-NE-35 x CARI-1	55.67^{bcd}	39.70^{no}	7.20^{ijkl}	873.58^{cdefg}	6.58^{abcd}	10.07^{ijkl}	18.58^{f}	135.03^{cdef}	16.67^{bcd}
Arka Nidhi x CARI-1	57.50^{abcd}	42.00^{lmno}	8.80^{ghij}	470.84^{ijklmn}	4.54^{cdefgh}	11.93^{h}	13.17^{lmn}	103.93^{def}	0.00^{h}
SM 6–7 x CARI-1	56.17^{abcd}	42.50^{lmno}	7.80^{hijkl}	946.17^{bcdef}	7.70^{ab}	10.68^{ij}	18.08^{fg}	123.39^{cdef}	3.33^{fgh}
IIHR-B-NE- 41 x CARI-1	57.00^{abcd}	47.20^{ghij}	10.70^{abcdef}	795.00^{cdefgh}	6.50^{abcd}	10.90^{i}	15.65^{ij}	123.17^{cdef}	10.00^{def}
IIHR-B-NE-4 x CARI-1	55.17^{cd}	58.70^{bcd}	8.20^{hijkl}	1237.50^{a}	9.05^{a}	9.20^{m}	17.83^{fgh}	136.55^{cdef}	3.33^{fgh}
IIHR-555 x CARI-1	55.67^{bcd}	62.10^{abc}	9.30^{defghi}	1000.00^{abcd}	$5.27^{bcdefgh}$	13.78^{f}	14.42^{jkl}	193.45^{abcd}	20.00^{bc}
IIHR-B-NE-24 x CARI-1	56.50^{abcd}	50.00^{fgh}	9.40^{cdefgh}	779.17^{cdefgh}	$4.93^{bcdefgh}$	9.28^{m}	22.93^{bc}	159.72^{abcdef}	20.00^{bc}
Arka Neelachal Shyama x CARI-1	57.50^{abcd}	54.30^{def}	9.20^{efghi}	957.67^{bcdef}	$5.08^{bcdefgh}$	9.49^{lm}	22.78^{c}	188.31^{abcd}	13.33^{cde}
IIHR-B-NE-25 x CARI-1	55.50^{bcd}	54.80^{de}	8.90^{fghij}	1023.33^{abc}	$4.92^{bcdefgh}$	9.20^{m}	24.55^{a}	208.16^{abc}	5.00^{fgh}
IC0598430 x CARI-1	57.00^{abcd}	49.30^{ghi}	8.60^{ghijk}	1180.84^{ab}	5.83^{bcdefg}	11.83^{h}	20.78^{e}	202.60^{abc}	0.00^{h}
Pusa Purple Long x CARI-1	54.83^{d}	46.40^{hijkl}	10.30^{bcdefg}	831.67^{cdefg}	$5.62^{bcdefgh}$	17.55^{b}	14.67^{jk}	147.92^{bcdef}	16.67^{bcd}
IIHR-B-NE-1 x CARI-1	56.67^{abcd}	51.50^{efg}	8.60^{ghijk}	825.00^{cdefg}	6.20^{abcdef}	14.68^{de}	16.60^{hi}	133.14^{cdef}	3.33^{fgh}
Rampur Local x CARI-1	57.00^{abcd}	62.70^{ab}	11.40^{ab}	703.75^{efghij}	$5.45^{bcdefgh}$	13.95^{ef}	17.00^{ghi}	128.69^{cdef}	5.00^{fgh}
CARI-1 x WCGR	57.75^{abcd}	59.70^{abc}	11.00^{abcde}	853.50^{cdefg}	4.53^{cdefgh}	10.25^{ijk}	22.48^{cd}	197.03^{abcd}	0.00^{h}
CARI-1 x Andaman	58.75^{ab}	55.10^{de}	11.20^{abc}	424.00^{klmn}	2.80^{hi}	10.03^{jkl}	22.52^{c}	160.63^{abcdef}	0.00^{h}
CARI-1 x BR-112	58.25^{abc}	63.20^{a}	11.10^{abcd}	534.00^{hijkl}	3.08^{ghi}	9.55^{klm}	20.20^{e}	187.62^{abcd}	0.00^{h}
2-BMG-1 x CARI-1	57.75^{abcd}	58.00^{cd}	12.30^{a}	977.50^{abcde}	4.00^{defgh}	10.38^{ij}	24.22^{ab}	244.42^{a}	0.00^{h}
Andaman x CARI-1	59.00^{a}	55.10^{de}	11.80^{ab}	420.50^{klmn}	3.60^{efghi}	9.05^{m}	23.20^{abc}	116.63^{cdef}	0.00^{h}
Brinjal No. 38	50.50^{e}	50.80^{efgh}	6.80^{kl}	651.67^{ghijk}	4.53^{cdefgh}	9.10^{m}	20.45^{e}	147.57^{bcdef}	1.67^{gh}
Hazari 10	50.17^{e}	47.70^{ghij}	8.20^{hijkl}	445.00^{jklmn}	$4.97^{bcdefgh}$	12.20^{gh}	10.65^{o}	91.28^{ef}	3.33^{fgh}
Utkal	44.67^{f}	41.50^{mno}	7.30^{ijkl}	524.67^{hijkl}	4.08^{cdefgh}	12.80^{g}	8.50^{p}	128.17^{cdef}	10.00^{def}
Indam GB-4	49.83^{e}	42.70^{klmno}	7.30^{ijkl}	531.67^{hijkl}	6.35^{abcdef}	14.65^{de}	14.20^{klm}	83.84^{ef}	1.67^{gh}
Tarini	50.00^{e}	47.00^{hijk}	7.80^{hijkl}	474.17^{ijklm}	$4.93^{bcdefgh}$	16.55^{c}	13.70^{klm}	105.47^{def}	8.33^{efg}
JK 8035	50.33^{e}	41.60^{mno}	7.60^{hijkl}	688.33^{fghijk}	$5.52^{bcdefgh}$	9.10^{m}	21.10^{de}	142.49^{cdef}	5.00^{fgh}
JK-8031	50.17^{e}	43.60^{jklmn}	7.50^{ijkl}	729.50^{defghi}	6.93^{abc}	14.70^{d}	12.95^{mn}	104.70^{def}	3.33^{fgh}
VNR-B5	49.67^{e}	38.80^{o}	7.50^{ijkl}	944.41^{bcdef}	$5.44^{bcdefgh}$	9.45^{lm}	22.35^{cd}	173.54^{abcde}	21.67^{b}
Soham	49.83^{e}	41.00^{mno}	6.60^{l}	198.33^{n}	0.85^{i}	7.23^{n}	14.85^{jk}	238.12^{ab}	85.00^{a}
Brinjal 132	49.50^{e}	43.40^{jklmn}	7.80^{hijkl}	548.33^{hijkl}	6.40^{abcde}	12.70^{g}	11.95^{no}	86.59^{ef}	10.00^{def}
Arka Unnathi (Variety)	46.00^{f}	50.30^{fgh}	8.90^{fghij}	287.50^{lmn}	3.50^{fghi}	20.45^{a}	8.20^{p}	79.76^{ef}	0.00^{h}
Arka Harshitha (Variety)	46.00^{f}	45.10^{ijklm}	8.20^{hijkl}	240.00^{mn}	3.55^{efghi}	20.90^{a}	8.25^{p}	68.15^{f}	0.00^{h}
Standard error of mean (±)	0.83	1.13	0.48	70.59	0.74	0.19	0.36	24.49	1.83

Table 1 (continued)

F_1 Hybrids	Days to 50% flowering	Plant Height (cm)	Number of Branches	Fruit yield per plant (g)	Number of fruits per plant	Fruit Length	Fruit Girth	Fruit Weight	Bacterial wilt in field (%)
Standard error of difference (±)	1.18	1.60	0.68	99.83	1.05	0.27	0.52	34.64	2.58
Critical difference ($p \leq 0.01$)	3.25**	4.42**	1.88**	275.16**	2.88**	0.74**	1.42**	95.48**	7.12**
Coefficient of variation (%)	2.20	3.24	7.65	14.19	20.54	2.22	2.99	23.94	29.05

Values accompanied by different letters suggest significant differences ($p \leq 0.05$); NS: Non-significant.; *- statistically significant differences ($p \leq 0.05$); **- statistically significant differences ($p \leq 0.01$) (Duncan's multiple range test)

derived population. Similarly, for Pusa Purple Long x CARI-1 derived population, 50 plants of the resistant parent, 50 plants of the susceptible parent, 51 plants of the F_1 hybrid, 210 plants of F_2 segregating population, 51 plants of backcross population with resistant ($BC1_R$) as well as susceptible ($BC1_S$) parents were screened for BW resistance.

The root dip inoculation method was followed for an artificial inoculation method as it is very effective (Du et al. 2017). 30 days old seedlings roots were dipped in bacterial suspension for 5–10 s and then seedlings were transplanted in the main sick plot for the quick buildup of the pathogen. The screening was done during April–June, 2018 synchronizing with the hot and humid conditions to provide optimum conditions for the rapid growth of the pathogen. The experiment was planned out in an augmented design consisting of three blocks consisting of $28F_1$ hybrids, two varieties/ and susceptible check (four rows in each block).

Bacterial wilt scoring

Disease incidence in plants was monitored daily and observations were recorded at 3 days interval. Visible symptoms of the disease were observed 15 DPI. Plants showing wilt symptoms were confirmed to be caused by *Ralstonia solanacearum* through the ooze test by immersing the cut end of the stem in sterile water in test tubes. The bacterial wilt percentage disease incidence (PDI) of F1 hybrids was calculated as per Bainsla et al. (2016).

$$\text{Bacterial wilt PDI (\%)} = \frac{\text{Number of dead plants due to bacterial wilt disease x 100}}{\text{Total number of plants established}}$$

The test genotypes were categorized into 0–5 scale based on the PDI value (Gopalakrishnan et al. 2014), viz., [0-Immune (No wilt symptoms); 1- Highly Resistant/HR (1.00–20.00% plants wilted); 2- Resistant/ R (21.00–40.00% plants wilted); 3- Moderately Resistant/ MR (41.00–60.00% plants wilted); 4- Susceptible/ S (61.00–80.00% plants wilted); 5- Highly susceptible/ HS (More than 80% plants wilted).

Phenotypic assessment of the populations for their response to Ralstonia solanacearum

For genetics study, individual plants of parents, their respective F_1, F_2, and backcross derivatives were scored for bacterial wilt symptoms and confirmed through the ooze test. Individual plant mortality was recorded at 3 day intervals initiating from 3 to 35 days after inoculation. The surviving and 100% wilted plants were scored as 0 and 1, respectively. The area under disease progress curve (AUDPC) was worked out as per the survival percentage over 20, 23, 26, 29, 32, and 35 DPI (Campbell and Madden 1990)

$$AUDPC = \sum_{I=1}^{n-1} \left[\left\{ \frac{Xi + Xi + 1}{2} \right\} \times \{ti + 1 – ti\} \right]$$

Where

n	total number of observations
Xi	Survival percentage at i^{th} observation
$X_i + 1$	survival percentage at i + 1st observation
$t_i + 1 –$	number of days between subsequent
t_i	observations.

At 32 DPI for Pusa Purple Long x CARI-1 derived population and 35 DAP for Arka Neelachal Shyama x CARI-1 derived population, the bacterial wilt infestation reached the peak infection period after which no wilting was recorded. Hence, the data acquired at 32 and 35 DPI for the respective populations were utilized for elucidation of genetics of bacterial wilt resistance as well as gene action. The wilted and surviving plants in both parents, F_1, F_2 and backcross populations were calculated and were scored as 1 and 0, respectively.

Statistical analysis

Plant vigor, yield attributing traits and bacterial wilt resistance of F_1 hybrids were analyzed using R software (R Development Core Team 2012) using the agricolae package (de Mendiburu 2014). The data of segregating population of the two mentioned crosses was tested for goodness of fit against simple Mendelian ratios using $\chi 2$ analysis @ 5% level of significance (Panse and Sukhatme 1985))

$$\chi 2 = \sum \frac{(observed\ frequency - expected\ frequency)^2}{expected\ frequency}$$

The bacterial wilt disease reaction of each plant (0-surviving; 1- wilted/dead) at 32 and 35 DPI for respective mentioned population was further analyzed by joint scaling test (Cavalli 1952), scaling test (Mather 1949; Hayman and Mather 1955), and generation mean analysis utilizing six-parameter model involving mean (*m*), additive (*d*), dominance (*h*), additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*) (Hayman 1958; Jinks and Jones 1958). The magnitude of scales was estimated by the formulae: $A = 2BC1_R - P_1 - F_1 = 0$; $B = 2BC1_S - P_2 - F_1 = 0$; $C = 4F_2 - 2F_1 - P_1 - P_2 = 0$ and $D = 2F_2 - BC1_R - BC1_S = 0$. Six generation mean analysis was carried out in OP-STAT software (Sheoran et al. 1998).

Results

Evaluation of F_1 hybrids

Days to 50% flowering

The earliest F_1 hybrid to reach the 50% flowering stage was Utkal (44.67 days), while the most delayed flowering was observed in Andaman x CARI-1 F1 hybrid (59.00) (Table 1). Var. Arka Harshitha (46.00) and Var. Arka Unnathi (46.00) were statistically on par with Utkal.

Plant vigor

Significant differences existed among the F_1 hybrids for plant vigor (Table 1). The highest plant height was exhibited by CARI-1 x BR-112 (63.20 cm), while the plant height was observed to be the lowest in the case of VNR-B5 (38.80 cm). Rampur Local x CARI-1 (62.70 cm), IIHR-555 x CARI-1 (62.10 cm) and CARI-1 x WCGR (59.70 cm) were statistically on par with CARI-1 x BR-112 hybrid.

Similarly, the maximum and the minimum number of branches were recorded in 2-BMG-1 X CARI-1 (12.30) and Soham F_1 hybrid (6.60), respectively. Andaman x CARI-1 (11.80), Rampur Local X CARI-1 (11.40), CARI-1 x Andaman (11.20), CARI-1 x BR-112 (11.10), CARI-1 x WCGR (11.00), and IIHR-B-NE-41 x CARI-1 (10.70) were statistically on par with 2-BMG-1 x CARI-1 for the number of branches per plant.

Yield and yield attributing traits

Yield and yield attributing traits showed significant differences among the F_1 hybrids (Table 1). The highest yield per plant was found in IIHR-B-NE-4 x CARI-1 (1.27 kg), whereas, the lowest yield per plant was found in Soham (198.33 g) due to heavy infestation of bacterial wilt disease. IC0598430 x CARI-1 (1.18 kg), IIHR-B-NE-25 x CARI-1 (1.02 kg), IIHR-555 x CARI-1 (1.00 kg) and 2-BMG-1 x CARI-1 (0.98 kg) were statistically on par with IIHR-B-NE-4 x CARI-1 in terms of fruit yield per plant.

Statistical analysis suggested the prevalence of a significant difference among the hybrids for the number of fruits per plant. The highest number of fruits per plant was obtained from IIHR-B-NE- 4 x CARI-1 (9.05). The lowest number of fruits per plant was observed in Soham (0.85) owing to its high susceptibility reaction to bacterial wilt. SM 6–7 x CARI-1 (7.70), JK-8031 (6.93), IIHR-B-NE-35 x CARI-1 (6.58), IIHR-B-NE-41 x CARI-1 (6.50), Brinjal 132 (6.40), Indam GB-4 (6.35), IIHR-B-NE-1 x CARI-1 (6.20) were statistically on par with IIHR-B-NE-4 x CARI-1.

Fruit traits including fruit length, fruit girth, and individual fruit weight varied significantly among the hybrids. Var. Arka Harshitha produced the longest fruits (20.90 cm), whereas the lowest fruit length was recorded in Soham (7.23 cm). Var. Arka Unnathi (20.45 cm) was statistically on par with Var. Arka Harsitha for fruit length. Similarly, the highest fruit girth was observed in IIHR-B-NE-25 x CARI-1 (24.55 cm) and the lowest fruit girth was exhibited by Var. Arka Unnathi (8.20 cm). 2-BMG-1 X CARI-1 (24.22 cm), Andaman x CARI-1 (23.20 cm) were statistically on par with IIHR-B-NE-25 x CARI-1. The maximum and minimum average fruit weights were exhibited by 2-BMG-1 x CARI-1 (244.42 g) and Arka Harshitha (68.15 g), respectively. Soham (238.12 g), IIHR-B-NE-25 x CARI-1 (208.16 g), IC 0598430 x CARI-1 (202.60 g), CARI-1 x WCGR (197.03 g), CARI-1 x BR-112 (187.62 g), VNR-B5 (173.54 g) and CARI-1 x Andaman (160.63 g) were statistically on par with 2-BMG-1 x CARI-1 with respect to average fruit weight.

Severity of bacterial wilt on F_1 hybrids under field condition

There were significant differences existing among the F1 hybrids for bacterial wilt resistance in the normal field condition with low bacterium load. F1 hybrids such as Arka Nidhi x CARI-1, IC0598430 x CARI-1, CARI-1 x WCGR, CARI-1 x Andaman, CARI-1 x BR-112, 2-BMG-1 x CARI-1, Andaman x CARI-1, and two varieties i.e Arka Unnathi, and Arka Harshitha exhibited a high degree of resistance to bacterial wilt disease showing no wilting symptom. Hybrid Soham showed the highest susceptible reaction towards bacterial wilt disease (85.00%).

Severity of bacterial wilt on F_1 hybrids through artificial inoculation

The resistance reaction of thirty (28 F_1 hybrids and two varieties) of eggplant along with the susceptible check against *Ralstonia solanacearum* is presented in Table 2. The susceptible check (Pusa Purple Long) displayed the expected reactions of high susceptibility (94.62%) to bacterial wilt disease. None of the F_1 hybrids showed an immune reaction to bacterial wilt disease in our experimental material. Statistical analysis revealed the existence of a high degree of variability concerning bacterial wilt resistance in the F1 hybrids. The highest bacterial wilt resistance was manifested in Var. Arka Harshitha and F1 hybrid JK 8035 showing only 3.63% bacterial wilt symptoms. Arka Nidhi x CARI-1, IC0598430 x CARI-1, CARI-1 x WCGR, CARI-1 x Andaman, CARI-1 x BR-112, Andaman x CARI-1, Indam GB-4, JK 8031 hybrids were categorized as highly resistant hybrids, where only up to 20% of plants showed wilting symptoms. Besides susceptible check, Soham, Pusa Purple Long x CARI-1, and VNR B5 showed a highly susceptible reaction towards bacterial wilt in which >80% of plants succumbed to bacterial wilt disease.

Disease incidence and progression of bacterial wilt in Arka Neelachal Shyama x CARI-1 and Pusa purple long x CARI-1 derived populations

All the generations of both the crosses including susceptible check (Pusa Purple Long) started showing bacterial wilt symptoms after 20 days of planting. Disease progression continued up to 32 days in Pusa Purple Long x CARI-1 derived population, while for Arka Neelachal Shyama x CARI-1 population, bacterial wilt symptoms continued up to 35 DAP (Fig. 1). The number of days taken for completion of wilting exhibited a significant difference among the generation means in

both the crosses (Fig. 1). The delayed occurrence of bacterial wilt symptoms was recorded when resistant parent CARI-1 was backcrossed with its corresponding hybrids. The AUDPC of various generations fluctuated among the two cross combinations and also varied significantly between the resistant as well as the susceptible populations (Fig. 2). In the present study, resistant parent CARI-1 (12.00) exhibited very low value of AUDPC, while significantly high AUDPC values were observed for susceptible parents, F_2, and backcross populations.

Inheritance pattern of bacterial wilt disease resistance

The disease reaction of parents, F_1, F_2, and backcross populations with the resistant parent as well as the susceptible parent are given in Table 3. The resistant parent CARI-1 exhibited 96.00% survivability, while susceptible parents, Arka Neelachal Shyama, and Pusa Purple Long, showed an average survival percentage of 20% and 4%, respectively. The F1 generation of both the crosses showed a lower survival percentage (37.25% in Arka Neelachal Shyama x CARI-1 and 9.8% in Pusa Purple Long x CARI-1 exhibiting high susceptibility towards bacterial wilt. The F_2 population had a mean survival percentage of 37.99 in Arka Neelachal Shyama x CARI-1, whereas the F_2 population of Pusa Purple Long x CARI-1 showed a mean survival of 4.35%.

F_1s in both the crosses were recorded to be highly susceptible indicating the bacterial wilt resistance in both the combinations to be under the control of a recessive gene (s). The inheritance pattern of bacterial wilt disease resistance was further tested for the goodness of fit using the chi-square test. Phenotypic scoring revealed that 191 plants of 308 were susceptible, while the remaining 117 plants showed resistant reaction in Arka Neelachal Shyama x CARI-1 derived F_2 population. This susceptible and resistant proportion was tested against 3:1 as well as 9:7 ratio. Chi-square value was found to be significant for both of these ratios indicating that the expected and the observed values were not comparable with the segregation pattern. As the segregation ratio neither followed monogenic nor di-genic ratio, indicating polygenic control of the disease resistance.

Similarly, in Pusa Purple Long x CARI-1 derived F_2 population, out of 207 plants, 198 plants were susceptible and nine plants were resistant. The susceptible resistant ration was tested against 1:1, for which chi-square value was significant. Observed phenotypic values were again subjected to expected ratio of 15:1. As the observed ratio was found to be segregated in 15.3:0.7 ratio, for which non-significant chi-square value was observed, indicating the resistance is regulated by two recessive genes with duplicate dominant epistasis.

Similarly, the disease reaction of the backcross population to bacterial wilt was analyzed to fit with the expected ratio of 1:0 (backcross with bacterial wilt resistant parent) as well as 1:3 (backcross with bacterial wilt susceptible parent). However, none of the backcrosses to susceptible parents as well as to resistant parent exhibited a suitable fit with the expected ratio.

The inheritance pattern of bacterial wilt resistance could not be concluded entirely from the bacterial wilt disease reaction of the populations, due to the marginal probability as well as unpredicted segregation pattern of the backcross progenies. Hence, populations were developed using CARI-1, a highly resistant bacterial wilt genotype, and two susceptible genotypes, Arka Neelachal Shyama and Pusa Purple Long, followed by six-generation mean analysis to elucidate the gene effects governing bacterial wilt resistance.

Gene action of bacterial wilt resistance

Generation mean analysis was carried out utilizing the individual plant ratings for Arka Neelachal Shyama x CARI-1 and Pusa Purple Long x CARI-1 derived populations at 35 DPI and 32 DPI, respectively. The findings of the scaling test along with the estimates of various genetic components {mean (*m*), additive (*d*), additive × additive (*i*), dominance (*h*), additive × dominance (*j*) and dominance × dominance (*l*)} for both Arka Neelachal Shyama x CARI-1 and Pusa Purple Long x CARI-1, crosses are presented in Table 4. The ABCD scaling test implies towards the absence or presence of gene interactions (Mather and Jinks 1982). Significance of any one of these scaling tests indicates the presence of genes interaction, suggesting the inadequacy of the additive-dominance model. Hence, the significant value of A, D′ and 'A, C, D' components in the scaling test of the Arka Neelachal Shyama x CARI-1 and Pusa Purple Long x CARI-1 crosses respectively, revealed the presence of epistasis (Table 4).

In the Arka Neelachal Shyama x CARI-1 population, the mean (0.380), dominance (negative), additive x additive (negative), additive × dominance (negative), dominance × dominance (positive) were observed to be significant. Additive component (*d*) was not

Table 2 Reaction of F_1 hybrids to bacterial wilt disease (Artificial inoculation)

F_1 Hybrids/varieties	Bacterial wilt (%)*	Disease reaction
IIHR-B-NE-35 (S) x CARI-1 (R)	55.57^{defghj}	Moderately Resistant
Arka Nidhi (R) x CARI-1 (R)	6.55^{o}	Highly Resistant
SM 6–7 (R) x CARI-1 (R)	$22.23^{iklmnop}$	Resistant
IIHR-B-NE-41 (S) x CARI-1 (R)	$39.88^{ghijklm}$	Resistant
IIHR-B-NE-4 (R) x CARI-1 (R)	20.27^{klmno}	Resistant
IIHR-555 (R) x CARI-1 (R)	49.68^{fghijk}	Moderately Resistant
IIHR-B-NE-24 (S) x CARI-1 (R)	65.37^{cdefg}	Susceptible
Arka Neelachal Shyama (S) x CARI-1 (R)	67.33^{bcdefg}	Susceptible
IIHR-B-NE-25 (R) x CARI-1 (R)	$37.92^{ghijklmn}$	Resistant
IC0598430 (R) x CARI-1 (R)	19.63^{klmno}	Highly Resistant
Pusa Purple Long (S) x CARI-1 (R)	87.86^{abcde}	Highly Susceptible
IIHR-B-NE-1 (R) x CARI-1 (R)	$29.04^{hijklmno}$	Resistant
Rampur Local (S) x CARI-1 (R)	78.06^{abcdef}	Susceptible
CARI-1 (S) x WCGR (R)	19.23^{klmno}	Highly Resistant
CARI-1 (R) x ANDAMAN (R)	13.35^{lmno}	Highly Resistant
CARI-1 (R) x BR-112 (R)	9.43^{mno}	Highly Resistant
2- BMG-1 (R) x CARI-1 (R)	$21.19^{iklmnop}$	Resistant
Andaman (R) x CARI-1 (R)	13.35^{lmno}	Highly Resistant
Brinjal No. 38	$36.88^{ghijklmno}$	Resistant
Hazari 10	$25.12^{hijklmno}$	Resistant
Utkal	$44.81^{fghijkl}$	Moderately Resistant
Indam GB-4	5.59^{mno}	Highly Resistant
Tarini	56.57^{efghi}	Moderately Resistant
JK 8035	3.63^{no}	Highly Resistant
JK-8031	7.55^{mno}	Highly Resistant
VNR-B5	87.95^{abcd}	Highly Susceptible
Soham	95.79^{abc}	Highly Susceptible
Brinjal 132	5.59^{mno}	Highly Resistant
Arka Unnathi (Variety)	5.59^{mno}	Highly Resistant
Arka Harshitha (Variety)	3.63^{no}	Highly Resistant
Susceptible Check-1 (Pusa Purple Long)	94.17^{ab}	Highly Susceptible
Susceptible Check-2 (Pusa Purple Long)	95.00^{a}	Highly Susceptible
Susceptible Check-3 (Pusa Purple Long)	94.33^{a}	Highly Susceptible
Susceptible Check-4 (Pusa Purple Long)	95.00^{a}	Highly Susceptible
CV (%)	5.21	

*Values accompanied by different letters exhibit significant differences ($p \leq 0.05$)

significant in the tested population indicating the prevalence of non-additive interactions. The scaling test pointed towards existence of additive × additive type of epistasis due to the significant value of 'D' component. The contrasting signs of dominance *(h)* and dominance x dominance *(l)* suggested the epistasis to be of duplicate type. The magnitude of dominance x dominance (*l*) was found to be higher than additive × additive (*i*), additive × dominance (*j*), and dominance (*h*). The potency ratio of −0.579 also indicated partial dominance (recessive) in the inheritance of resistance to bacterial wilt.

Similarly, in the Pusa Purple Long x CARI-1 derived population, all the components except dominance (*h*)

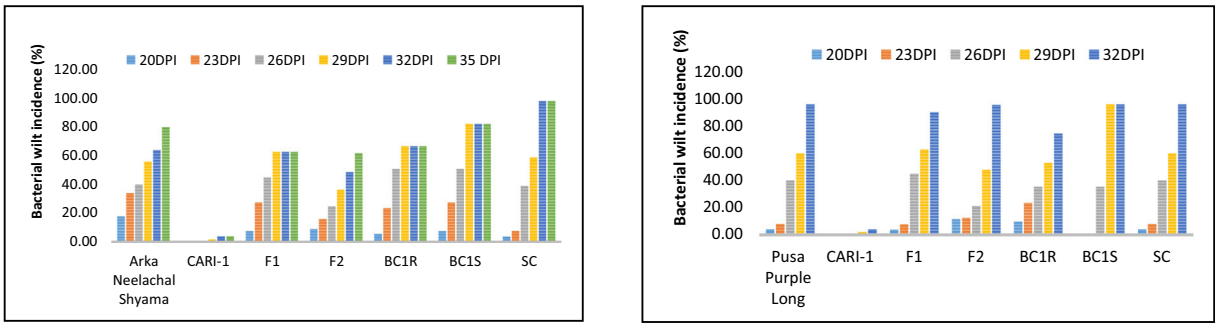

Fig. 1 Disease progression rate in the six generations along with susceptible check (SC) of two different cross combinations

were observed to be significant. The significant value of 'A', 'C' and 'D' components of the scaling test suggested existence of additive x additive and dominance x dominance type of epistasis, and the alike signs of dominance *(h)* and dominance x dominance *(l)* pointed towards the complementary type of epistasis. The magnitude of additive × additive (*i*) was recorded to be the highest followed by additive (*d*) and additive x dominance (*j*). The high potence ratio of −0.874 implied to involvement of the recessive gene (s) in the inheritance of this trait.

Discussion

Bacterial wilt, triggered by *Ralstonia solanacearum*, infesting eggplant all over the world, usually regarded as the second most disastrous among the bacterial diseases causing significant economic loss to the growers (Mansfield et al. 2012; Huet 2014). Integrated crop protection strategies involving crop rotation, chemical, and biological methods of control cultural practices have not yielded any accomplishment to control bacterial wilt disease (VanElsas et al. 2000; Yuliar et al. 2015; Namisy et al. 2019). Hence, the cultivation of resistant cultivars/hybrids is the best economically feasible option.

CARI-1 is one of the best bacteria wilt resistant genotype identified maintaining its resistance property even in diverse climatic conditions (Krishna et al. 2012; Bainsla et al. 2016; Khapte et al. 2018). It was found to be highly resistant in our screening experiment during the earlier stage of the research. High bacterial wilt resistance, tall stature, and large round type of fruits in CARI-1 made it unique to be exploited for the eggplant improvement programs.

In the current experiment, all the F_1 hybrids developed using CARI-1 as one of the parents (male parent), flowered very late i.e. nearly two months after transplanting in the main field. All the remaining private and public sector hybrids used in this study flowered comparatively early than CARI-1 derived hybrids. It may be due to the dominance of CARI-1 over the female parent for late flowering, as the CARI-1 genotype generally took more than 60 days for 50% flowering in the initial evaluation of our experiment.

Similarly, the growth attributes including plant height (63.20 cm) and the number of branches (12.30) were found maximum in the CARI-1 based F_1 hybrids surpassing the existing private and public sector F1 hybrids, owing to the vigorous growth habit of CARI-1. Moreover, the yield and yield attributing traits except for fruit length viz., number of fruits per plant (9.05), yield per plant (1.27 kg), and individual fruit weight

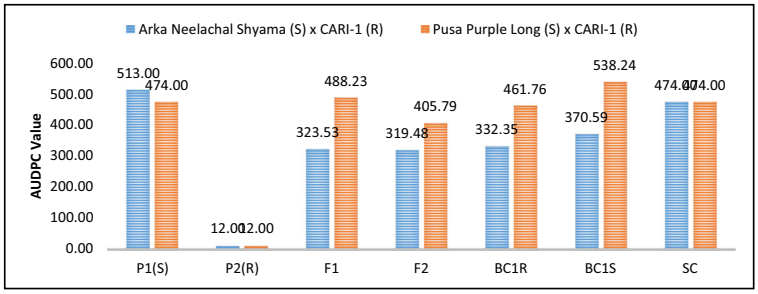

Fig. 2 Comparative analysis on bacterial wilt disease development in six generations of Arka Neelachal Shyama x CARI-1 and Pusa Purple Long x CARI-1 cross combinations [with susceptible check]

Table 3 Reaction of the parents, F_1 and segregating progenies of Arka Neelachal Shyama x CARI-1 and Pusa Purple Long x CARI-1 crosses towards bacterial wilt

Cross combination	Generation	Number of plants				Observed ratio (S:R)	Expected ratio (S:R)	$\chi 2$ value (Calculated)	$\chi 2$ value (reference)
		Total number of plants screened	Susceptible	Resistant	Survival percentage (%)				
Arka Neelachal Shyama x CARI-1	P_1	50	40	10	20.00	0.80:0.20	All S	–	–
	P_2	50	2	48	96.00	0.04:0.96	All R	–	–
	F_1	51	32	19	37.25	2.50:1.50	–	–	–
	F_2	308	191	117	37.99	2.48:1.52	3:1 (Monogenic)	27.71*	3.84
						9.92:6.08	9:7 (Di-genic)	4.16*	3.84
	$BC1_R$	51	34	17	33.33	1.33:0.67	1:1	5.67	3.84
	$BC1_S$	51	42	9	17.65	0.82:0.18	1:0	144.35	3.84
Pusa Purple Long x CARI-1	P_1	50	48	2	4.00	0.96:0.04	All S	–	–
	P_2	50	2	48	96.00	0.04:0.96	All R	–	–
	F_1	50	45	5	9.80	3.60:0.40	–	–	–
	F_2	207	198	9	4.35	3.82:0.18	3:1 (Monogenic)	47.09*	3.84
						15.3:0.7	15:1 (Di-genic)	1.28 ^{NS}	3.84
	$BC1_R$	51	38	13	25.49	1.49:0.51	1:1	12.25	3.84
	$BC1_S$	51	49	2	3.92	0.96:0.04	1:0	4.40	3.84

*If $\chi 2$ ($P = 0.05$, df = 1) calculated is less than the reference $\chi 2$, then null hypothesis is accepted, *i. e* the observed ratio does not differ from the tested ratio. If $\chi 2$ calculated is greater than the reference $\chi 2$, then null hypothesis is rejected i.e. the observed ratio differs from the ratio tested

(244.42 g) were observed to be maximum in F_1 hybrids with CARI-1 as one of the parents exceeding the private and public sector hybrids. This high yielding imparting factor may be credited to CARI-1, owing to its high yielding nature and larger size fruit traits (Krishna et al. 2012).

In the bacterial wilt resistance survey of F_1 hybrids, tested F_1 hybrids under study viz., Arka Nidhi x CARI-1, IC0598430 x CARI-1, CARI-1 x WCGR, CARI-1 x Andaman, CARI-1 x BR-112, Andaman x CARI-1, public sector $_{Hybrids}$ varieties viz., Arka Unnathi, Arka Harshitha, and private sector hybrids viz., JK 8031, Indam GB-4, JK 8031 showed high bacterial wilt resistant reaction. Besides high resistant reaction, resistant, moderately resistant, susceptible as well as highly susceptible disease reactions were observed in CARI-1 based F_1 hybrids. High variability in disease reaction in the F_1 may be due to a discrepancy in the number of genes governing bacterial wilt resistance and mode of gene action (Thakur et al. 2004; Ishihara et al. 2012). It was observed that hybrids generated from crossing between parents both possessing bacterial wilt-resistance led to the production of resistant F_1 hybrids. However, F_1 hybrids developed due to hybridization between parents exhibiting a significantly varied level of disease reaction to bacterial wilt led to the production of bacterial wilt susceptible hybrids.

The inheritance of resistance to bacterial wilt varies according to genotypes, prevailed environmental conditions, race, and strain as well as biovar of *Ralstonia solanacearum*. The comprehension of inheritance pattern of a specific character is of utmost importance as selection of suitable and efficient breeding strategy and mating pattern are fully relied on it. AUDPC utilizes multiple evaluations and does not depend upon transformations, which leads to more simple and precise phenotypic assessment (Campbell and Madden 1990) and it also indicates the progression of the disease throughout its growth cycle (Roy et al. 2009). The lowest AUDPC value exhibited by CARI-1 confirmed the high resistance reaction of the genotype to bacterial wilt. The susceptible parents and segregating populations of both the crosses showed a significantly higher AUDPC value owing to their high susceptible reaction

Table 4 Six generation mean analysis (P_1, P_2, F_1, F_2, $BC1_R$ and $BC1_S$) for bacterial wilt resistance as assessed in two susceptible × resistant crosses using six-parameter model

Parameters	Arka Neelachal Shyama x CARI-1[§]	Pusa Purple Long x CARI-1[§]
A	0.653 (0.153)**	0.548 (0.133) **
B	0.207 (0.140)	0.060 (0.075)
C	0.361 (0.187)	1.022 (0.109) **
D	0.250 (0.102)*	−0.207 (0.073) **
mean (*m*)	0.380 (0.028) **	0.043 (0.014) **
additive (*d*)	0.157 (0.086)	0.216 (0.067) **
dominance (*h*)	−0.720 (0.218) **	0.012 (0.154)
additive × additive (*i*)	−0.500 (0.204) *	0.414 (0.146) **
additive × dominance (*j*)	−0.446 (0.183) *	−0.489 (0.141) **
dominance × dominance (*l*)	1.360 (0.391) **	0.194 (0.291)
d+ *h*	−0.563	0.228
l+ *i*+*j*	0.414	0.119
Magnitude of Gene Effect	l>j>i>h	i>d>j
Epistasis	Duplicate	Complementary
Potence ratio (F_1)	−0.579	−0.874
Potence ratio (F_2)	−1.053	−1.985

[§] Values in the parenthesis are standard errors (SE) **Significant ($p \leq 0.01$); *Significant ($p \leq 0.05$)

to bacterial wilt. However, AUDPC values among the susceptible parents as well as the segregating populations of both the crosses varied a little, due to difference in time taken to exhibit the symptoms of bacterial wilt. As Pusa Purple Long was more susceptible to bacterial wilt as compared to Arka Neelachal Shyama, the segregating population viz., F_2, $BC1_R$, and $BC1_S$ of Pusa Purple Long x CARI-1 showed high AUDPC value than the segregating population derived from Arka Neelachal Shyama x CARI-1.

In the current experiment, a significant difference was observed in disease reaction between the resistant and the susceptible accessions, making them desirable to be used in population development to better-understand the inheritance and gene action of bacterial wilt resistance. F_1 plants from Arka Neelachal Shyama x CARI-1 and Pusa Purple Long x CARI-1 crosses showed high susceptibility reaction to bacterial wilt disease, indicating that bacterial wilt resistance to be governed by recessive gene (s) (Uttamrao 2012; Bainsla et al. 2016). The overall frequency of bacterial wilt occurrence was skewed toward the subsequent susceptible parents, indicating dominance of susceptibility over resistance (Mensah et al. 2005).

F_1s were susceptible indicated that resistance is recessive in nature Chi-square test in both Arka Neelachal Shyama x CARI-1 and Pusa Purple Long x CARI-1 populations revealed the absence of a monogenic nature which is contradictory to the study conducted by Ajjappalavara et al. (2008), Cao et al. (2009), Lebeau et al. (2013), Xi'ou et al. (2015), Kurhade et al. (2017) who recorded bacterial wilt resistant to be governed by single dominant gene in their respected studied populations. Pandiyaraj et al. (2019) at Bengaluru, Karnataka conditions reported that F2 population derived from CARI-1 (R) x Rampur Local (S) segregated in 3 (R):1 (S) ratio indicating single dominant gene action, this clearly showed that resistance mechanism is highly strain and environment-specific. The same CARI-1 resistance gene action differed across Bengaluru and Bhubaneswar. Bhubaneswar, Odisha is considered as one of the hot spots for bacterial wilt disease mainly due to the hot and humid climate and acidic soils (Sarkar and Chaudhuri 2016).

The segregating F_2 population of Arka Neelachal Shyama and CARI-1 was further tested for the digenic ratio. However, the chi-square value was significant, which indicated the involvement of polygenes as the segregation of susceptible and resistant plants fitted neither the monogenic nor digenic ratio indicating the polygenic recessive nature of inheritance (Chaudhary 2000. Bainsla et al. 2016). In the case of Pusa Purple

Long x CARI-1 cross, the F_2 population segregated in a ratio which was a fit with the expected 15:1 susceptible/resistant ratio. This suggested bacterial wilt resistance to be governed by two recessive genes with duplicate dominant epistasis, contradicting results concluded by Bainsla et al. (2016) in same cross combination at Andaman and Nicobar islands, India location. However, back cross populations deviated from expected ratios which indicated the presence of epistasis and modifier genes.

To confirm the existence of non-allelic interaction, scaling test along with generation mean analysis for six parameter model were carried out in both the crosses, to assess the gene actions for resistance to bacterial wilt. The scaling test was observed to be significant (A and D for Arka Neelachal Shyama x CARI-1 and A, C, and D for Pusa Purple Long x CARI-1) for bacterial wilt resistance in both the crosses, which led to realization of existence of a higher order of epistasis for the manifestation of bacterial wilt resistance (Parihar et al. 2016).

Additionally, six parameter model was utilized to determine the gene action for bacterial wilt resistance in the subsequent crosses. The additive x dominance [*j*] component was found to be significant with a negative sign in both the crosses, which indicated that the contributing genes involved in the manifestation of the resistance trait in both the parents were somehow countering the effect of each other leading to decline in the resistance in the subsequent generations. A similar kind of result was observed for prolificacy traits in maize by Prakash et al. (2019) and by Rai et al. (2020) for bud necrosis disease resistance in tomato. In the case of the Arka Neelachal Shyama x CARI-1 population, the effects of epistasis (cumulated $i + j + l$) were significantly higher than the combined main effects ($d + h$) for bacterial wilt resistance. Mean effects (*m*) were highly significant suggesting quantitative inheritance of bacterial wilt resistance.

Again, high dominance (*h*) in a negative direction, suggested towards significant involvement of recessive genes. Additive × additive type (*i*) non-allelic interaction was observed to be significant for this trait, however negative sign suggested the inadequacy of simple selection approach for improvement in resistance. Meanwhile, the magnitude of dominance × dominance (*l*) was higher in comparison with additive × additive (*i*) as well as additive × dominance (*j*). This suggested pedigree method of breeding accompanied by an acute selection of desirable segregates in a later generation would be efficient for the incorporation of disease resistance (Bhutia et al. 2015; Acharya et al. 2018). In such a scenario, it is also advised for the delaying of selection in later generations. Alternatively, inter-mating among the selected segregates accompanied by selfing for one or more generations can be done. These strategies will be useful to discard undesirable linkage for the congregation of suitable alleles for enhancement of resistance to bacterial wilt. Furthermore, negative additive × additive (*i*) type gene action along with duplicate epistasis indicated a low probability of acquiring transgressive segregates in the later generation from this cross.

Similarly, in the case of Pusa Purple Long x CARI-1 derived population, the inheritance of bacterial wilt indicated that they are digenically controlled by complementary action of two recessive genes, which can be exploited through allele pyramiding. A significant mean effect (*m*) suggested the presence of epistasis interaction. The combined main effects ($d + h$) were significantly higher than the effects of epistasis (cumulated $i + j + l$) for bacterial wilt resistance. Dominance (*h*) effects were non-significant, whereas additive x additive [*i*] component was found to be significant in the cross. This indicated the predominance of additive gene action. Hence, it's fixable in nature and selection method can be highly efficient in the enhancement of this trait (Rai et al. 2020).

Complementary type of interaction is reported to be operating as indicated by positive signs of both dominance (*h*) as well as dominance x dominance (*l*) components (Acharya et al. 2018). This led to realization that selected parents for the experiment were diverse in nature and hence, it is feasible to expect a significant amount of heterosis as well as genetic gain in the breeding program. Positive additive × additive (*i*) type gene action and complementary epistasis indicated a high probability of acquiring transgressive segregates in the later generations. Kurhade et al. (2017) also found the presence of complementary gene action for bacterial wilt resistance in eggplant by studying F_2 populations derived from BR 14 x Pusa Purple Cluster and Manjarigota X BB54.

In conclusion, CARI-1 was found to be highly bacterial wilt resistant. F1 hybrids developed using CARI-1 as one of the parents have shown a varied level of resistance. Genetic analysis through six-

generation mean analysis in the populations derived from two crosses viz., Arka Neelachal Shyama x CARI-1 cross and Pusa Purple Long x CARI-1 indicated bacterial wilt is polygenically controlled and the existence of epistasis. High significant additive × additive type non-allelic interaction in Arka Neelachal Shyama x CARI-1 cross suggested for the delaying of selection in later generations for the accumulation of favorable alleles for improvement of bacterial wilt resistance. In the case of Pusa Purple Long x CARI-1 derived population, additive gene action is predominant indicating simple selection will be highly effective for bacterial wilt resistance.

Declarations

Conflict of interest The authors declare that they have no conflict of interest. The study presented in the manuscript does not involve human or animal subjects. All authors have reviewed the final version of the manuscript and agree to its submission to your journal.

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