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Inheritance for ToLCV and EB resistance in tomato using *S. habrochaites* and *S. pimpinellifolium*

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ABSTRACT

Two accessions of wild species of tomato, *viz*. EC-520060 *(Solanum habrochaites)* and EC-521080 *(Solanum pimpinellifolium)* have been utilized for introgression of ToLCV and EB resistant gene into 12 susceptible cultivars bearing good yield traits. Most of the crosses of EC-520060 exhibited 13 (resistant): 3 (susceptible) genetic ratio but 'Flora Dade × EC-520060' expressed 3:1 genetic ratio. The crosses of EC-521080 have diverse genetic ratio of 1:2:1, 3:1 and 1:3. In result of inheritance of EB, the crosses of EC-520060 revealed 3:1 genetic ratio, and the crosses of EC-521080 represented 1:3, 1:2:1 and 3:1 genetic ratio. The crosses of EC-520060 and EC-521080 showed additive, dominance × dominance and additive × additive genetic models for both ToLCV and EB diseases. The inheritance among crosses and genetics of variables can be utilized for improvement of resistant tomato.

Key Words: Tomato, Interspecific crosses, Resistance, ToLCV, EB, Genetics

Tomato leaf curl virus (ToLCV) and early blight (EB) are responsible for complete yield loss (Singh *et al.*, 2010, 2014a,b, 2015a, 2017; Kumar and Kumar, 2018; Subhasmita *et al.,* 2021). Limited resistant source had been identified in cultivated tomato against ToLCV and EB (Singh *et al.*, 2014a,b, 2015a,b, 2017, 2018; Adhikari *et al.*, 2017; Kumar and Kumar, 2018). Wild accessions had been utilized to develop new ToLCV and EB resistant breeding lines and hybrids due to presence of maximum level of resistance or complex genetics of resistance in wild species or wild derivatives (Singh *et al.,* 2017, 2018, 2019; Subhasmita *et al.,* 2021).

Earlier, three wild species had been utilized for identification of six tomato leaf curl virus resistant genes (Kumar and Kumar, 2018; Singh *et al.*, 2019). The utilization of DNA markers may be more appropriate (Singh *et al.*, 2010, 2015a). Many accessions of wild species had been used in ToLCV and EB resistant breeding programmes (Singh *et al.,* 2013, 2014a,b, 2015a,b 2017, 2018; Subhasmita *et al.*, 2021). Thus, new sources of ToLCV and EB resistance is needed to know the gene action using wild species for improvement in tomato.

MATERIALS AND METHODS

A total five crosses were developed by using a resistant accession 'EC-520060' (Table 1). While, twelve crosses developed by using another resistant accession 'EC-521080' were used (Table 1). The seeds of these 17 crosses were sown in field to produce F_1 hybrids. The 17 F_1 hybrids were selfed to produce F_2. The seeds of 17 F_2 were sown in field. All the individual plant of each F_2 population were selfed and seeds harvested by single plant selection method to produce F_3. The seeds of only five similar crosses of F_3 of each accession 'EC-520060' and 'EC-521080' were sown in field and transplanted for raising the population. Seeds of each generation F_1, F_2 and F_3 along with P_1 and P_2 were saved and divided into two sections for testing in field and glasshouse conditions. In field condition, the experiments were designed during most favourable season (September-March) for pathogens of ToLCV and EB, respectively. In glasshouse, it was tested in two sections for ToLCV and EB on the same time.

Thirty plants of each parent and F_1 were planted in three replications (10 plants in each). Two hundred forty plants of each F_2 were transplanted in field in three replications (80 plants in each) but some plants could not survive. The survived plants were in the ranges of 208 (Hissar Anmol × EC-520060) to 135 (Flora Dade × EC-521080) of (Table 1). Ten plants of each F_3 progeny (developed by single fruits of each separate plant of $5F_2$s of EC-520060 and $5F_2$s of EC-521080

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through SSD methods) were transplanted. The susceptible tomato variety Punjab Chhuhara was also transplanted after every 10 rows between the plant population of parents, F_1, F_2 and F_3 generation. Spread of the vector population was allowed by avoiding spray for whitefly control.

A total fifteen seedlings of each parent and F_1s as well as 60 seedlings of each F_2 were transplanted in earthen pots, and kept in three replications, and divided into two sections with similar strength of plants on the same time. For ToLCV incidence, each tomato seedling covered by insect-proof cages and inserts 15-20 viruliferous whiteflies for 48 hr. Plants were examined on weekly intervals till 12 weeks for looking ToLCV symptom and followed same procedure of Singh *et al.* (2015a). For EB appearance, pure culture of virulent A. solani used potato dextrose broth (PDB) and uniformly sprayed on tomato seedlings for looking EB symptom as earlier used by Singh *et al.* (2017). The inoculated plants were maintained in glasshouse at 28 ± 2°C for symptom development.

The observations were recorded on plant height (PH), number of fruits / plant (NOFPP), fruit set per cent (FS%), average fruit weight (AFW) and fruit yield / plant (FYPP) in kilogram. The observation on disease incidence of ToLCV was recorded 15 days and 30 days after transplanting in glasshouse and field conditions, respectively. The disease incidence of EB was recorded 7 and 30 days after transplanting in glasshouse and field condition, respectively.

The disease was scored on a 0-5 scale for both ToLCV and EB incidence, where 0=0%-5% (highly resistant), 1=5.1%-12.0% (resistant), 2=12.1%-25.0% (moderately resistant), 3=25.1%-50.0% (moderately susceptible), 4=50.1%-75.0% (susceptible), and 5=75.1%-100% (highly susceptible). The per cent disease incidence (PDI) was calculated by using formula of Singh *et al.* (2015a, 2017).

$$PDI = \frac{\text{Score of individual plant} \times 100}{\text{No. of plant samples} \times \text{maximum rating scale}}$$

Genetic analysis

The chi-square analysis was studied for PDI of ToLCV and EB by using all the population of F_2 generation developed by 'EC-520060' and 'EC-521080'. Chi-square was calculated by following formula:

$$\chi^2 = \Sigma(O\text{-}E)^2 / E$$

where 'O' is observed frequency in each category; 'E' is the expected frequency in corresponding category.

For generation mean analysis (GMA) only five similar crosses of each parent 'EC-520060' and 'EC-521080' were used. In order to find differences among parents (P_1 and P_2) vs. F_1, F_2: F_3 the data obtained for each character (PDI of ToLCV and EB, PH, NOFPP, FS%, AFW and FYPP) were analysed by five parameter models (m, d, h, i and l) on the basis of previously used formula of Singh *et al.* (2015a).

RESULTS AND DISCUSSION

All female parents were susceptible to highly susceptible, while both male parents (EC-520060 and EC-521080) were highly resistant to ToLCV and EB diseases. All the cultivars were scored on '4-5' scale but two wild accessions, EC-520060 and EC-521080, were scored on '0-1' scale for both ToLCV and EB diseases during field and artificial screening. Resistance capacity in both wild accessions EC-520060 and EC-521080 were due to the background of *S. habrochaites* and *S. pimpinellifolium* (Singh *et al.*, 2010, 2012, 2015a, 2017, 2018, 2019; Subhasmita *et al.*, 2021). Total five and twelve crosses were developed by using the accessions, 'EC-520060' and 'EC-521080', respectively. These crosses were segregated to F_1:F_2:F_3 generations.

Mendelian inheritance for ToLCV and EB

Five F_1 crosses of EC-520060 were expressed highly resistant to ToLCV and EB diseases (Table 1). Total number of resistant plants were in the range of 100-160 for ToLCV. However, four F_2 were categorized into resistant (including highly resistant, resistant and moderately resistant): susceptible (including susceptible, moderately susceptible and highly susceptible) plants and showed 13 (resistant): 3 (susceptible) genetic ratio. While, one F_2 (Flora Dade × EC-520060) expressed 3 (resistant): 1 (susceptible) genetic ratio with chi-square value 0.144 and probability range 0.50-0.75 (Table 1). The inhibitory gene action and monogenic dominant gene action were reported by Singh *et al.* (2018). However, numbers of resistant plants were obtained in the range of 100-160 for EB. All the F_2s were expressed 3 resistant (highly resistant, resistant and moderately resistant): 1 susceptible (susceptible, moderately susceptible and highly susceptible) genetic ratio (Table 1) with chi-square value along with the probability range was 0.267 (0.50-0.75) to 1.297 (0.25-0.50). The crosses of EC-520060 *(S. habrochaites)* were expressed in 3:1 genetic ratio and monogenic dominant gene action for EB. The monogenic dominant gene effect for EB resistant has also been reported by Singh *et al.* (2017).

Among crosses of EC-521080 *(S. pimpinellifolium)*, all the F_1 were resistant to ToLCV and EB diseases (Table 1). In F_2 crosses, infected plants were categorized into highly resistant, moderately resistant and susceptible in the range of 30-160, 0-100 and 30-160, respectively. A total six F_2 were segregated in a 1:2:1 genetic ratio as resistant (including highly resistant): moderately resistant (including resistant and moderately resistant): susceptible (including susceptible,

Table 1. Performance of F_1s and F_2 populations of *S. lycopersicum* × *S. habrochaites* 'EC-520060' and *S. lycopersicum* × *S. pimpinellifolium* 'EC-521080' and χ^2 value for ToLCV and EB reaction

Character	F_2 populations									
	P_1 (HS)	P_2 (HR)	F_1	HR =0	R+MR =1+2	MS+S+HS =3+4+5	Genetic ratio	Degrees of freedom	Chi-square (χ^2)	Probability range
Tomato leaf curl virus (ToLCV)	Punjab Chhuhara	EC-520060	HR	140	0	40	13:3	1	1.425	0.10-0.25
	Pusa Ruby	EC-520060	HR	134	0	34	13:3	1	0.244	0.50-0.75
	Hissar Anmol	EC-520060	HR	160	0	48	13:3	1	0.410	0.50-0.75
	Hissar Arun	EC-520060	HR	120	0	34	13:3	1	1.123	0.25-0.50
	Flora Dade	EC-520060	HR	113	0	35	3:1	1	0.144	0.50-0.75
	Punjab Chhuhara	EC-521080	R	49	84	53	1:2:1	2	1.914	0.25-0.50
	Pusa Ruby	EC-521080	R	44	78	42	1:2:1	2	0.439	0.50-0.75
	Flora Dade	EC-521080	R	30	69	36	1:2:1	2	0.610	0.25-0.50
	Vaibhaw	EC-521080	R	36	88	38	1:2:1	2	1.259	0.25-0.50
	Arka Vikash	EC-521080	R	39	71	44	1:2:1	2	1.260	0.25-0.50
	Hissar Arun	EC-521080	R	51	93	53	1:2:1	2	0.655	0.25-0.50
	Kashi Vishesh	EC-521080	R	124	0	43	3:1	1	0.050	0.75-0.90
	TLBR-3	EC-521080	R	142	0	51	3:1	1	0.209	0.50-0.75
	IIHR-2200	EC-521080	R	121	0	54	3:1	1	3.202	0.05-0.10
	Hissar Anmol	EC-521080	R	129	0	59	3:1	1	4.085	0.25-0.50
	Meghalaya Local	EC-521080	R	48	0	136	1:3	1	0.116	0.75-0.90
	Sikkim Local	EC-521080	R	41	0	103	1:3	1	0.926	0.25-0.50
Early blight (EB)	Punjab Chhuhara	EC-520060	HR	132	0	48	3:1	1	0.267	0.50-0.75
	Pusa Ruby	EC-520060	HR	123	0	45	3:1	1	0.286	0.50-0.75
	Hissar Anmol	EC-520060	HR	151	0	57	3:1	1	0.641	0.25-0.50
	Hissar Arun	EC-520060	HR	119	0	35	3:1	1	0.424	0.50-0.75
	Flora Dade	EC-520060	HR	117	0	31	3:1	1	1.297	0.25-0.50
	Punjab Chhuhara	EC-521080	R	42	95	48	1:2:1	2	0.524	0.75-0.90
	Pusa Ruby	EC-521080	R	42	0	122	1:3	1	0.036	0.75-0.90
	Flora Dade	EC-521080	R	34	69	32	1:2:1	2	0.126	0.75-0.90
	Vaibhaw	EC-521080	R	37	86	39	1:2:1	2	0.556	0.25-0.50
	Arka Vikash	EC-521080	R	119	0	35	3:1	1	0.424	0.50-0.75
	Hissar Arun	EC-521080	R	39	111	48	1:2:1	2	4.457	0.10-0.25
	Kashi Vishesh	EC-521080	R	34	94	39	1:2:1	2	2.608	0.05-0.10
	TLBR-3	EC-521080	R	48	99	46	1:2:1	2	0.171	0.75-0.90
	IIHR-2200	EC-521080	R	134	0	41	3:1	1	0.231	0.50-0.75
	Hissar Anmol	EC-521080	R	42	97	49	1:2:1	2	0.713	0.25-0.50
	Meghalaya Local	EC-521080	R	48	89	47	1:2:1	2	0.203	0.50-0.75
	Sikkim Local	EC-521080	R	33	77	34	1:2:1	2	0.486	0.50-0.75

HR= Highly resistant; R= resistant; MR= moderately resistant; MS= moderately susceptible; S= susceptible; HS= highly Susceptible

moderately susceptible and highly susceptible). While, four F_2 expressed 3 (resistant): 1 (susceptible) genetic ratio and remaining two F_2 (Meghalaya Local × EC-521080 and Sikkim Local × EC-521080) were segregated as 1 (resistant): 3 (susceptible) with the chi-square value 0.1159 and 0.9259 and probability range 0.75-0.90 and 0.25-0.50 (Table 1).

In case of EB, F_2s infected plants in range of 30-140, 0-120 and 30-140 as highly resistant, moderately resistant and susceptible, respectively. One F_2 (Pusa Ruby × EC-521080) was segregated into 1 resistant (highly resistant, resistant and moderately resistant): 3 susceptible (susceptible, moderately susceptible and highly susceptible) genetic ratio with the 0.0325 and 0.75-0.90 chi-square value and probability range (Table 1). Nine F_2 were categorized into three categories of resistant (including highly resistant): moderately resistant (including resistant and moderately resistant): susceptible (including susceptible, moderately susceptible and highly susceptible) plants and segregated as 1:2:1 genetic ratio along with chi-square value and probability range were 0.1259 (0.75-0.90) to 2.6083 (0.05-0.10).

Remaining two F_2s (Arka Vikash × EC-521080 and IIHR-2200 × EC-521080) were expressed 3 (resistant): 1 (susceptible) genetic ratio along with the chi-square value 0.1159 and 0.9259 and probability range 0.50-0.75 and 0.50-0.75, respectively (Table 1). The crosses of 'EC-521080 *(S. pimpinellifolium)*' indicated partial dominant gene effects, monogenic dominant gene effects and monogenic recessive gene effects for both ToLCV and EB diseases (Singh *et al.*, 2017, 2018; Oladokun *et al.*, 2022).

Generation mean analysis

Among the crosses of EC-520060, all the crosses showed 'additive (m+d)' genetic models for resistant to ToLCV and EB, while a population 'Hissar Arun × EC-520060' showed 'additive and 'dominance × dominance (m+d+l)' for the resistant to EB (Table 2). Earlier, 'additive' and 'dominant' gene action for ToLCV and EB were also reported by Singh *et al.* (2015b, 2017, 2018, 2019) in the population of *S. habrochaites*.

For PH, Punjab Chhuhara × EC-520060, Pusa Ruby × EC-520060 and Hissar Anmol × EC-520060 exhibited dominance genetic models (m+h), while, the Hissar Arun × EC-520060 and Flora Dade × EC-520060 showed dominance × dominance (m+l) and dominant (m+l) and dominance × dominance (m+h+l) genetic models. The dominant genetic characters of plant height may be possible due to the luxurious plant growth habit of *S. habrochaites* (Singh *et al.,* 2014a,b, 2018, 2019). For NOFPP, the crosses of Punjab Chhuhara × EC-520060, Pusa Ruby × EC-520060 and Hissar Anmol × EC-520060 showed dominant and additive × additive (m+h+i) inheritance models while, crosses Hissar Arun × EC-520060 and Flora Dade × EC-520060 indicated additive × additive and dominant × dominant (m+i+l) inheritance models.

For FS%, Punjab Chhuhara × EC-520060 and Pusa Ruby × EC-520060 showed dominant (m+h) gene effects. The crosses Hissar Anmol × EC-520060 and Hissar Arun × EC-520060 exhibited dominance and additive × additive (m+h+i) genetic models, and Flora Dade × EC-520060 was indicated dominance × dominance genetic models (m+l). For AFW, only Hissar Arun × EC-520060 exhibited additive and additive × additive genetic model (m+d+i) but remaining four crosses showed additive genetic model (m+d). Two crosses, Hissar Anmol × EC-520060 and Hissar Arun × EC-520060 exhibited additive (m+d) and dominance (m+h) genetic effects and remaining crosses showed additive and dominant × dominant (m+d+l) inheritance model for FYPP (Table 2).

The number of fruits, fruit set per cent, fruit weight and fruit yield per plant of the crosses showed 'dominant' and 'additive' genetic models, while the crosses of 'Hissar Anmol × EC-520060', 'Hissar Arun × EC-520060', and 'Flora Dade × EC-520060' indicated either 'additive' or 'dominant' inheritance models for these traits. This may be due to the presence of either *S. habrochaites* in pedigree background of 'Hissar Anmol', 'Hissar Arun' and 'Flora Dade' or presence of any other close pedigree of wild species (Zdravkovic *et al.,* 2011; Singh *et al.,* 2014a, b, 2018).

The data indicated that population of Pusa Ruby × EC-521080 for ToLCV, EB, AFW and FYPP, the population of Flora Dade × EC-521080 for ToLCV and EB, and population of Hissar Arun × EC-521080 for AFW showed additive (m+d) genetic models (Table 2). The population of Pusa Ruby × EC-521080 exhibited additive × additive and dominant × dominant genetic models (m+i+l) for NOFPP; dominance and additive × additive genetic models (m+h+i) for FS%; additive (m+d) genetic effects for ToLCV, EB, AFW and FYPP; and dominance (m+h) and dominant × dominant (m+h+l) genetic model for PH and NOFPP. Whereas, population Hissar Anmol × EC-521080 exhibited additive and dominant × dominant genetic models (m+d+l) for ToLCV and FYPP; additive and additive × additive genetic models (m+d+i) for EB and AFW; and dominance and dominant × dominant (m+h+l) genetic model for PH, NOFPP and FS%.

The population of Hissar Arun × EC-521080 displayed additive and dominant × dominant genetic models (m+d+l) for ToLCV; additive and additive × additive genetic models (m+d+i) for EB and FYPP; dominance and dominant × dominant (m+h+l) genetic model for NOFPP. The population of Flora Dade × EC-

Table 2. Genetic effects of 5 parameters in 5 populations developed by *S. habrochaites* 'EC-520060' and *S. pimpinellifolium* 'EC-521080' for ToLCV and EB.

Generation	PDI (ToLCV)	PDI (EB)	PH	NOFPP	FS%	AFW	FYPP
Punjab Chhuhara × EC-520060	m+d	m+d	m+h	m+h+i	m+h	m+d	m+d+l
Pusa Ruby × EC-520060	m+d	m+d	m+h	m+h+i	m+h	m+d	m+d+l
Hissar Anmol × EC-520060	m+d	m+d	m+h	m+h+i	m+h+i	m+d	m+d
Hissar Arun × EC-520060	m+d	m+d+l	m+l	m+i+l	m+h+i	m+d+i	m+i
Flora Dade × EC-520060	m+d	m+d	m+h+l	m+i+l	m+l	m+d	m+d+l
Punjab Chhuhara × EC-521080	m+d+l	m+d+i	m+h+l	m+h+l	m+h+l	m+d+i	m+d+l
Pusa Ruby × EC-521080	m+d	m+d	m+h	m+i+l	m+h+i	m+d	m+d
Hissar Anmol × EC-521080	m+d+i	m+d+l	m+h+l	m+h+l	m+h+i	m+d+i	m+d+l
Hissar Arun × EC-521080	m+d+l	m+d+i	m+h	m+h+l	m+h	m+d	m+d+i
Flora Dade × EC-521080	m+d	m+d	m+h+i	m+i+l	m+h+l	m+d+l	m+i

m=Mean effect, d=pooled additive effects, h=pooled dominance effect, i=pooled additive × additive epistatic effects and l=pooled dominance × dominance epistatic effects, PDI=Percent Disease Incidence, ToLCV=tomato leaf curl virus; EB=early blight; PH= plant height; NOFPP= number of fruits per plant; FS%= fruit set percent; AFW= average fruit weight; FYPP= fruit yield per plant

521080 exhibited additive genetic models (m+d) for ToLCV and EB; dominance and additive × additive genetic models (m+h+i) for PH; additive × additive and dominant × dominant genetic models (m+i+l) for NOFPP; dominance and dominant × dominant (m+h+l) genetic model for FS%; additive and dominant × dominant genetic models (m+d+l) for AFW; and additive × additive genetic models (m+i) for FYPP (Table 2).

All the crosses of 'EC-521080' had shown additive (m+d), dominant × dominant genetic models (m+d+l) and additive × additive genetic models (m+d+i) for ToLCV and EB resistance due to presence of S. pimpinellifolium background (Singh *et al.*, 2017, 2018). Among the yield traits, all crosses showed either additive, dominant × dominant and additive × additive gene effect for AFW and FYPP or represented dominant, additive × additive and dominant × dominant genetic effects for PH, NOFPP and FS%. Earlier, many reports have been published for genetics of yield traits by using *S. pimpinellifolium* or any other background of tomato (Zdravkovic *et al.,* 2011; Singh *et al.,* 2018).

CONCLUSION

It was concluded that crosses of 'EC-520060' exhibited inhibitory gene action and monogenic dominant gene action, while crosses of 'EC-521080' showed partial dominant, monogenic dominant and monogenic recessive for both ToLCV and EB resistance. The accessions of *S. habrochaites* had a strong and fix genetic architecture in resistant breeding programmes but accessions of *S. pimpinellifolium* would be given flexible results of genetics in resistance breeding of tomato.

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