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Inheritance study in tomato (*Solanum lycopersicum*) for *Tomato leaf curl virus* (*ToLCV*) resistance

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ABSTRACT

A breeding programme was developed from an initial *S. lycopersicum* × *S. lycopersicum* (H 88-78-1) cross. The objective of this study was to determine the inheritance of resistant to leaf curl virus and yielding capacity in four crosses made within and between gene pools (TLBR 3 × H 88-78-1, PKM 1 × H 88-78-1, FLA 7421 × H 88-78-1 and Vaibhaw × H 88-78-1) using generation means analysis with five generations (P_1, P_2, F_1, F_2 and F_3) of each population under two environment (field and glasshouse). Results showed that the character of plants and fruits morphology was fit on 1:2:1 (P_1: intermediate: P_2) and ToLCV (PDI) value was fit on 3:1 (resistant: susceptible) Mendalian ratio in each four F_2 populations. In the present study, it was concluded that the generation mean analysis showed monogenic and partial recessiveness and incomplete penetrance. Each population displayed the additive and dominant gene action according to their heritability for using characters. The partial resistance derived from H 88-78-1 will be useful in homozygosis or may be combined with other resistance genes from other sources and can be grown in any climate challenging area.

Key words: Generation mean analysis, *S. lycopersicum, ToLCV* resistance, Yield traits

The most serious disease of tomato (*Solanum lycopersicum* L.) throughout the world is *tomato leaf curl virus* (*ToLCV*) disease caused by a gemenivirus transmitted by whitefly (*Bemisia tabaci* Genn.) (Singh *et al.* 2010). The disease directly affects tomato yield due to less production. It can be improved by introgression of resistant and high yielding tomato cultivars derivatives of wild background (Singh *et al.* 2014, 2015). Till date not many cultivars are reported as a resistant line except some wild lines, viz. *S. pimpinellifolium, S. peruvianum, S. chilense, S. habrochaites, S. chmielewskii* and *S. pinnellii* (Vidavski *et al.* 2008, Singh *et al.* 2014, 2015). It has already been reported that the disease resistant varieties can be obtained by breeding with wilds or wild derivative background and its inheritance was studied in F_2, BC_1, BC_2, F_3 generation of population (Banerjee and Kalloo 1987a, b; Momotaz *et al.* 2007). For developments of new resistant tomato cultivars (*Solanum lycopersicum* L.) have undoubtedly need to improve fruit quality, viz. fruit colour, shape and size, along with several other traits such as fruit number, fruit weight and fruit yield in tomato breeding programme (Coaker *et al.* 2002, Frary *et al.* 2003, Rodriguez *et al.* 2006). During the segregation in F_2 population, plants and fruit morphology also indicate to quantitatively inherited characters in tomato, which depend upon their parental morphology (Kabelka *et al.* 2004, Gonzalo and Knaap 2008, Zdravkovic *et al.* 2011).

The used resistant line H 88-78-1 in this study had developed from a homozygous genetic resource by the derivation of *S. lycopersicum* × *S. habrochaites f. glabratum* and developed by recombinant inbred lines (RILs) strategy (Banerjee and Kalloo 1987b). This line was also reported and used in the breeding programme as good combiners for developing high yielding as well as ToLCV resistant varieties (Singh *et al.* 2015). The scaling tests were performed for all the characters under investigation where using five and six parameter model for the study of generation mean analysis to know additive, dominance, additive × additive, dominance × dominance and additive × dominance inheritance model (Hayman 1958, Singh *et al.* 2015). Recently, an advanced RIL strategy has been used successfully to make practical use of this unexploited germplasm over other populations used for genetic mapping, and as because the lines are genetically homozygous they can be propagated without further segregation (Momotaz *et al.* 2007). The main objective of this work was to characterize the recombinant inbred lines (RILs) of tomato obtained by selection from intra-specific crossing (*S. lycopersicum* × *S. lycopersicum*) to develop expected resistant and high yielding varieties.

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MATERIALS AND METHODS

Parents (P_1 and P_2) include four susceptible (TLBR 3, PKM 1, FLA 7421 and Vaibhaw) tomato genotypes and one resistant (H-88-78-1) genotype (Table 1) of ToLCV disease (Singh *et al.* 2015). The crosses TLBR 3 × H 88-78-1, PKM 1 × H 88-78-1, FLA 7421 × H 88-78-1 and Vaibhaw × H 88-78-1 were made between some diverse vegetative traits by emasculation and pollen transfer in *rabi* (October–February) season of 2008. A total of 50 pollination were made per cross and F_1 were confirmed to be hybrid based on fruit shape and size. F_1 plants were used as seed sources for the F_2 generation in *kharif* (July–October) season of 2009 and subsequently in *rabi* season of 2009, the crosses were proceeds to F_2 to F_3 generation. In *kharif* season of 2010, seeds of F_1 and F_2 were sown along with F_3 generation. These five treatments were grown in field and glasshouse conditions with equal seed numbers to represent to two different environments. During the data observation, observed values were used as average of both field and glasshouse conditions. Thus a total of 5 treatments were obtained, corresponding to the two parents (P_1 and P_2) and the F_1, F_2 and F_3 generations for study of genetics.

The five treatments (P_1, P_2, F_1, F_2 and F_3) for each population were planted in *kharif* season of 2010 (obtained by practices of crosses made, F_1 generation advancement and F_2 generation advancement during 2006/07-2008/09) at a field site in Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India (83^{0}00'00"E longitude and 25^{0}19'59"N latitude at an elevation of 128.93m from MSL annual mean rainfall approximately 1113.3 mm with average number of 47 rainy days; average annual temperature 28±4^{0}C) and in glasshouse maintained at temperature 26±2^{0}C. This region is characterized by sandy-loam soil of loam texture with a pH of 7.5. The four populations were planted in separate experiments each in randomized complete block design with four replications at spacing of 45 cm (plant to plant) and 60 cm (row to row). Standard cultural practices and plant protection measures were adapted to raise healthy crops. Measurements were recorded of 20 plants of each 5 parental lines and 4 F_1's, while 150 plants of each F_2 and F_3 generation with 5 variables severity grade (SG), percent disease incidence (PDI), number of fruits per plant (NOFPP), average fruit weight (AFW) and fruit yield per plant (FYPP).

The severity grade (SG) and percent disease incidence (PDI) was scored on 0-5 point scale and PDI value was calculated by using formula of Singh *et al.* (2015). However, the numbers of fruits per plant (NOFPP), average fruit weight (AFW) and fruit yield/plant (FYPP) was observed as per standard procedure of horticultural parameters (Singh *et al.* 2015).

The chi-square analysis was studied for PDI of ToLCV along with plants and fruits morphology by using four population of F_2 generation. Chi-square formula was calculated by following formula-

$$\chi^2 = \Sigma\, (O–E)^2 / E$$

where, 'O'= observed frequency in each category; 'E'= expected frequency in the corresponding category; 'χ^2' = chi-square.

Generation mean analysis was analyzed by using five generations, viz. P_1, P_2, F_1, F_2 and F_3 in RCBD and five parameter models, viz. m, d, h, i and l (Hayman 1958, Singh *et al.* 2015) with some minor modifications.

RESULTS AND DISCUSSION

Mendalian ratio for ToLCV disease, plants and fruit morphology

Out of 150 plants of F_2 and F_3 that were evaluated in field only 118, 131, 110 and 145 plants survived of TLBR 3 × H 88-78-1, PKM 1 × H 88-78-1, FLA 7421 × H 88-78-1 and

Table 1 Description about used 5 parental lines of tomato

Entry	Species	Characteristics	Source
TLBR 3	*Solanum lycopersicum*	Indeterminate plant growth, medium and round fruit size and shape, susceptible for *Tomato leaf curl virus* and tolerant for bacterial diseases	UAS, Bangalore, India
PKM 1	*Solanum lycopersicum*	Determinate plant growth, medium and flat fruit size and shape, useful for transportation, susceptible for *Tomato leaf curl virus* and fungal diseases	TNAU, Coimbatore, India
FLA 7421	*Solanum lycopersicum*	Indeterminate plant growth, fruit size is medium and round in shape, maximum flash thickness and susceptible for *Tomato leaf curl virus* and resistance to early blight disease	FAU, Florida, USA
Vaibhaw	*Solanum lycopersicum*	Indeterminate plant growth, long fruit shape and medium in fruit size, susceptible for *Tomato leaf curl virus* disease	UAS, Banglore, India
H 88-78-1	*Solanum lycopersicum* derivatives of *S. habrochaites f. glaboratum*	Intermediate plant growth with climbing in nature, round and small fruit shape and size and resistant capacity for some common diseases e.g., *Tomato leaf curl virus* and early blight diseases	IIVR, Varanasi, India

UAS refers to University of Agricultural Sciences, Bangalore; TNAU refers to Tamil Nadu Agricultural University, Coimbatore; FAU refers to Florida Agricultural University, Florida; IIVR refers to Indian Institute of Vegetable Research, Varanasi.

Table 2 Number of plants in six classes (score) for tomato leaf curl virus symptom and three classes (score) for tomato plants and fruits morphology and chi- square (χ^2) test value in four F_2 populations

F_2 populations	Total plants	Number of resistant and susceptible plants			Chi-square	P- value
		Resistant	Moderate	Susceptible	3: 1	*DF=1
Tomato leaf curl virus						
TLBR 3 × H 88-78-1	118	92	0	26	0.731	0.25–0.50
PKM 1 × H 88-78-1	131	98	0	33	0.003	0.90–0.95
FLA 7421 × H 88-78-1	110	73	0	27	1.103	0.25–0.50
Vaibhaw × H 88-78-1	145	114	0	31	1.014	0.25–0.50
Type of plants and fruits morphology		*$^*P_1$*	*Intermediate (P_1&P_2)*	*$^*P_2$*	*1:2:1*	**DF=2*
TLBR 3 × H 88-78-1	118	23	67	28	2.593	0.25–0.50
PKM 1 × H 88-78-1	131	38	61	32	1.168	050–0.75
FLA 7421 × H 88-78-1	110	28	53	29	0.164	0.90–0.95
Vaibhaw × H 88-78-1	145	38	75	32	0.669	050–0.75

$^*P_1$= Parent 1 (female), P_2= Parent 2 (male), *DF = Degrees of freedom.

Vaibhaw × H 88-78-1 populations, respectively. Due to variation in number of plants surviving in field, similar size of population was used from glasshouse for study of PDI. Tomato leaf curl disease of individual plant was scaled on 0-5 point for every four population of F_2 generation. These F_2 Mendelian populations were fit on 3:1 genetic ratio (Table 2). For TLBR 3 × H 88-78-1 population, F_2 generation was categorized with 92 plant resistant and 26 plants susceptible with chi-square value of 0.731, p value range of 0.25-0.50. In population of PKM 1 × H 88-78-1, out of 131 plants, 98 were resistant and 33 plants susceptible in F_2 generation with chi-square value of 0.003 and p value range of 0.90-0.95. For the population of FLA 7421 × H 88-78-1, the chi-square value was 1.103, p value range was 0.25-0.50, whereas, plant ratio of 73 (resistant): 27 (susceptible) in F_2 generation was observed. Out of 145 plants, 114 plants were resistant and 31 susceptible in F_2 generation with chi-square value of 1.014, p value range of 0.25 – 0.50 in the cross of Vaibhaw × H 88-78-1.

The plants and fruit morphology of F_2 generation were fit on 1:2:1 genetic ratio (P_1: intermediate: P_2) of each population in comparison to both parents (Table 2). In TLBR 3 × H 88-78-1 population, 23 plants of P_1 (TLBR 3), 28 plants of P_2 (H 88-78-1) and remaining 67 plants as intermediate type with the chi-square value of 2.593 and p value range of 0.25-0.50 was observed. For the PKM 1 × H 88-78-1 population, the chi-square value was 1.168, p value in range of 050-0.75 and 38 plants indicated to P_1 (PKM 1), 32 plants to P_2 and 61 plants were intermediate of both P_1 and P_2 types. In the case of FLA 7421 × H 88-78-1 population, 28, 29 and 53 plants and fruit morphology indicated to P_1, P_2 and intermediate type, respectively while the chi-square value was 0.164 and p value range from 0.90-0.95. In, Vaibhaw × H 88-78-1 population, the plant and fruit morphology showed 38:75:32 genetic ratio where, 75 plants was intermediate type with the chi-square value and p value range were 0.669 and 050-0.75, respectively.

Generation mean analysis

In Turkey's multiple means comparison test both parents P_1 and P_2 were more diverse with each trait in every population for five treatments. For the cross TLBR 3 × H 88-78-1 population, the traits SG and PDI showed a better fit to an additive inheritance model (m+d) than to dominance, additive × additive and dominance × dominance model, while PDI also showed significant for additive × additive model (Table 3). Meanwhile, for NOFPP the additive, dominance, dominance × dominance model (m+d+h+l) had significant and higher fit than the additive × additive model. For AFW and FYPP, only additive inheritance model was highly significant (m+d) than other dominant, additive × additive and dominance × dominance, inheritance model. The chi-square value was goodness of fit for each trait (Table 3).

In the PKM 1 × H 88-78-1 population, additive, dominant and additive × additive model exhibited (m+d+h+i) higher significance than dominance × dominance model for SG and PDI. For NOFPP additive, additive × additive and dominance × dominance (m+d+i+l) inheritance models were significant while dominance model was non-significant. For AFW, additive, dominance and additive × additive were highly significant but dominance × dominance (m+l) model was non-significant. In case of FYPP it manifested non-significance for additive, dominance, additive × additive and dominance × dominance (m+d+h+i+l) inheritance model.

For the cross FLA 7421 × H 88-78-1 population, additive, dominance and additive × additive (m+d+h+i) model was significant for SG and PDI but dominance × dominance model was non-significant. For NOFPP and AFW, additive, dominance, additive × additive and dominance × dominance (m+d+h+i+l) inheritance models were significant and highly goodness fit on chi-square (χ^2). For FYPP, only additive model was significant but other three were non-significant.

For population of Vaibhaw × H 88-78-1, additive inheritance model (m+d) was more significant than dominance, additive × additive and dominance × dominance (m+h+i+l) inheritance model for SG and PDI. For NOFPP additive, additive × additive and dominance × dominance (m+d+i+l) model were significant as compared to dominant model (m+h). For AFW only additive model was significant

Table 3 Estimates of five quantitative genetic parameters with their standard errors in four populations

Generation	Tomato leaf curl virus		Yield components		
	SG	PDI	NOFPP	AFW	FYPP
TLBR 3 × H 88-78-1					
m	1.57** ±0.08	5.81** ±0.62	35.80** ±3.39	50.25** ±3.62	1.72** ±0.16
d	0.43** ± 0.02	3.45** ± 0.12	–17.50** ± 1.59	33.98** ± 2.09	0.58** ± 0.13
h	–0.49 ±0.25	–3.59 ±1.91	21.33* ±9.42	–13.27 ±12.53	0. 51 ±0.45
i	–0.48 ± 0.25	–3.78* ± 1.89	3.28 ± 9.81	6.96 ± 12.21	0.17 ± 0.51
l	0.34 ±0.78	2.51 ±5.94	78.93** ±30.50	–18.67 ±35.62	2.45 ±1.43
Chi-square (χ2)	1729.17	1056.68	2035.25	1705.85	799.59
PKM 1 × H 88-78-1					
m	1.76** ±0.05	7.27** ±0.31	43.80** ±3.77	49.50** ±2.50	2.23 ±0.23
d	0.45** ± 0.03	3.57** ± 0.17	–21.55** ± 1.69	14.80** ± 1.27	–0.21 ± 0.10
h	–0.36* ±0.16	–2.60* ±1.04	12.17 ±16.21	–23.13* ±9.40	–1.38 ±0.78
i	–0.37* ± 0.18	–2.90** ± 1.11	–29.62* ± 14.02	–25.53** ± 8.57	–2.51 ± 0.74
l	–0.49 ±0.52	–4.42 ±3.38	95.33* ±42.06	17.87 ±25.78	4.17 ±2.26
Chi-square (χ2)	2296.42	1038.86	1358.51	2939.24	880.59
FLA 7421 × H 88-78-1					
m	1.73** ±0.05	7.12** ±0.29	30.30** ±2.43	64.70** ±4.16	1.94** ±0.18
d	0.37** ± 0.04	2.97** ± 0.32	-14.40** ± 1.71	32.45** ± 1.80	0.84** ± 0.13
h	–0.50**±0.15	–3.36** ±0.91	–30.43** ±8.17	32.30** ±9.69	–0.61 ±0.47
i	–0.58** ± 0.17	–4.36** ± 1.18	–43.63** ± 8.21	55.00** ± 11.32	–0.35 ± 0.56
l	–0.10 ±0.48	–1.86 ±3.09	197.47** ±24.77	–183.60** ±34.79	2.44 ±1.60
Chi-square (χ2)	2376.78	766.80	1074.41	2441.25	816.47
Vaibhaw × H 88-78-1					
m	1.63** ±0.09	6.20** ±0.63	56.00** ±5.99	44.45** ±4.18	2.29** ±0.26
d	0.47** ± 0.03	3.64** ± 0.18	–10.75** ± 2.71	10.90** ± 1.72	0.20 ± 0.14
h	–0.16 ±0.27	–1.46 ±2.01	–49.67 ±25.80	–17.33 ±11.30	–3.93** ±1.33
i	0.06 ± 0.27	–0.07 ± 1.97	–83.87** ±22.61	–10.08 ± 12.04	–4.64** ± 1.11
l	–1.20 ±0.83	–8.87 ±6.09	231.73** ± 66.95	–27.73 ±36.92	9.01** ±3.25
Chi-square (χ2)	1679.98	568.27	1037.30	869.09	446.27

*P < 0.05, **P < 0.01, m = Mean effect, d = Pooled additive effects, h = Pooled dominance effect, i = Pooled additive × additive epistatic effects and l = pooled dominance × dominance epistatic effects.

but dominance, additive × additive and dominance × dominance (m+h+i+l) inheritance models were non-significant. For FYPP, dominance, additive × additive and dominance × dominance (m+h+i+l) inheritance models were more significant than additive model (m+d) and chi-square value was also goodness of fit for these traits (Table 3).

PDI of tomato leaf curl virus of each population were fit on the 3:1 Mendelian ratio. This was an indication of monogenic dominant genetic character of male parent (H 88-78-1) which is a derivative of *S. habrochaites* f. *glabratum*. As discussed earlier that *S. habrochaites* is resistant for multi diseases and a good combiner for developing to resistant variety (Banerjee and Kalloo 1987a, b, Vidavski *et al.* 2008, Singh *et al.* 2015). In present investigation, while phenotypic screening of F_2 plant population were categorized in resistant ('0' scale) and susceptible ('1-5' scale) and obtained 3:1 Mendelian genetic ratio, indicating involvement of dominant epistatic gene action for the expression of ToLCV in each four population was evident. Singh *et al.* (2015) also observed a similar genetic ratio (3:1) when the crosses of *S. habrochaites* were used which is in conformity with our findings. In present finding, it was also observed that phenotypically resistant dominance of H 88-78-1 had been transferred in F_2 individual plant population which may be due to the *S. habrochaites* f. *glabratum* background known for possessing tight gene linkage for ToLCV resistance. Momotaz *et al.* (2007) also observed more than 85% coverage of *S. habrochaites* genome in a cross between the cultivated tomato *L. esculentum* (E. 6206) and *S. habrochaites* (LA 1777).

F_2 generations of four populations were found in 1:2:1 (resistant: intermediate: susceptible) Mendelian ratio for the plants and fruit morphology, it may be possible by the genetic inheritance pattern of two parent used in the breeding programme or heterozygous in nature of crosses. Development of intermediate type of plants showed the heterozygosis in segregating population, this may be depends upon their parental genotypes. Such type of study for the plant growth morphology and fruit quality had been defined by many workers in current decades (Coaker *et al.* 2002, Rodriguez *et al.* 2006) and the related study of inheritance for these characters in segregating population of interspecific and intervarietal crosses were reviewed in many different studies, viz. QTLs controlling stem morphology (Coaker *et al.* 2002), for improved fruit quality (Frary *et al.* 2003), improved fruit colour of tomato (Kabelka *et al.* 2004), evaluation of plant and fruit traits in RILs of tomato (Rodriguez *et al.* 2006, Zdravkovic *et al.* 2011) and genetic bases of morphology in tomato with fruit shape (Gonzalo & Knaap 2008).

In all four populations, the mean of the parents (P_1 and P_2) showed a tendency to be more extreme and contrasting than the means of the F_1 and F_2 generation for each trait understudy, viz. SG, PDI, NOFPP, AFW and FYPP. Generation mean analysis has been used in tomato to study inheritance of other complex traits such as a general method of additive, dominant and epistatic variation for traits and inheritance of earliness and fruit weight in interspecific crosses in tomato (Singh *et al.* 2014, 2015) and fruit yield and its components in tomato (Zdravkovic *et al.* 2011, Singh *et al.* 2015). For the cross TLBR 3 × H 88-78-1 population, additive gene action was most significant for SG and PDI than dominant genetic model because there were significant differences between F_1 and F_3 generation. Similar additive gene action (m+a) was exhibited for AFW and FYPP but NOFPP was found for additive, dominant and additive × additive inheritance model because there were no significant differences between P_1, F_1 and F_3 generation. In the cross of PKM 1 × H 88-78-1 population, additive, dominant and additive × additive gene model was observed for SG, PDI and AFW while for NOFPP was indicated to additive, additive × additive and dominance × dominance inheritance model as because there were significant difference between two parents (P_1 and P_2), F_1 and F_3 generation. The FYPP was static in this population and not found significant due to less diversity between P_2, F_1 and F_2 generation. In a study of Zdravkovic *et al.* (2011) the additive and dominance model was discussed for the various characters of yield and yield traits in P_1, P_2, F_1, F_2, BC_1 and BC_2 generation.

In the cross FLA 7421 × H 88-78-1 population, additive, dominant, additive × additive inheritance model for SG and PDI were observed because more significant difference existed between P_1 and P_2. NOFPP and AFW were significant for additive, dominant, additive × additive and dominance × dominance model due to dominance of male parents (H 88-78-2) for the studied traits. FYPP showed only additive gene action because both parents P_1 and P_2 were more diverse to each other for these traits. In the cross Vaibhaw × H 88-78-1, additive genetic model was found for SG, PDI and AFW because more significant difference between both parents P_1 and P_2 existed for these characters. NOFPP had additive, additive × additive and dominance × dominance genetic model but FYPP exhibited dominant, additive × additive and dominance × dominance model because no significant difference was present between the P_1, P_2, F_1, F_2 and F_3 generation. The dominant yield was may be due to more number of fruit with dominant character. This type of gene action had been earlier reported by Zdravkovic *et al.* (2011) and Singh *et al.* (2015).

The investigated traits SG, PDI, NOFPP, AFW and FYPP were diverse in both parents P_1 and P_2 in each cross. FYPP of PKM 1 × H 88-78-1 population was not significantly diverse for both parents. Hence, it was non-significant for additive and dominant genetic model. This study where generation mean analysis was used in diverse parental crosses for using characters, was supported by Singh *et al.* (2015). In earlier studied diverse traits of parents showed additive gene action in both interspecific and intervarietal crosses, respectively (Singh *et al.* 2014, 2015).

In the present study, it was concluded that the significance of the generation mean analysis performance was highly affected by the genetic background of parental genotypes and environments. Observed additive gene action from these four crosses were specific for the traits, viz. SG, PDI and FYPP and the generation mean analysis specify as a monogenic and partial recessiveness and incomplete penetrance. Each population displayed the additive and dominant gene action according to their heritability for using characters. It is remarkable that the considerable potential exists in these materials and a new resistant line H 88-78-1 can be used fluently in tomato breeding programme. The crosses can be utilized for developing high yielder and resistant variety in a challenging climate.

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