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Analysis of Generation Means for Resistance of Tomato Leaf Curl Virus in Two Interspecific Crosses of Tomato (*Lycopersicon* sp.)

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ABSTRACT. *To understand the inheritance of resistance of tomato leaf curl virus (TLCV) and to investigate the types of gene action involved in several architectural traits and fruit yield, crosses were made between Lycopersicon esculentum cultivars (Arka Saurabh and Arka Vikas) and a TLCV tolerant L. pimpinellifolium. Individual plant data from five generations (P_1, P_2, F_1, F_2 and F_3) were subjected to joint scaling test to determine the importance of gene effects for fruit yield and its component traits viz., plant height, days to fruit maturity, average fruit weight and TLCV related traits viz., days to TLCV symptoms expression and symptoms severity. A simple additive-dominance model adequately explained variation for days to fruit maturity in the Arka Vikas x L. pimpinellifolium cross and days to TLCV symptoms expression in both the crosses. For all the other traits, it was necessary to add one or more digenic epistatic effects to the model. Heterosis of the F_1 over both mid-and better-parent was highly significant for all the traits in both the crosses.*

INTRODUCTION

Tomato leaf curl virus (TLCV) disease transmitted by the whitefly (*Bemisia tabaci* Gen.) is the most serious disease of tomato (*Lycopersicon esculentum* L.) in India, and causes substantial yield loss and deterioration of fruit quality. Efforts were made to explore the possibility of protecting tomato crops from TLCV by means of crop resistance (Banerjee and Kalloo, 1987). Resistance to the disease was identified in wild species *viz., L. hirsutum, L. peruvianum* and *L. pimpinellifolium* (Banerjee and Kalloo, 1987; Muniyappa *et al.*, 1991). The resistant genotypes should also possess other desirable economic traits to make them viable at a commercial level. A programme was, therefore, undertaken with the objective of investigating the types of gene action involved in several architectural traits, fruit yield and their association with disease resistance in order to propose strategic methods of tomato improvement.

MATERIALS AND METHODS

Considering the popularity, local adaptability, yield and fruit quality of the variety, Arka Saurabh and Arka Vikas cultivars of *L. esculentum* L. were selected as one set of parents. To complement the drawback of TLCV susceptibility of these two cultivars, a local line of *L. pimpinellifolium*, resistant to TLCV was identified for interspecific hybridization and other studies. To generate F_1, crossing was undertaken during *Kharif* season, 1992. Arka Saurabh and Arka Vikas were used as female parents and *L. pimpinellifolium* was used as pollen parent. A part of the seeds collected from F_1 plants from each cross involving *L. esculentum* and *L. pimpinellifolium* was sown to produce F_2 generation. A random sample was drawn from the F_2 bulk seed to raise the F_3 generation. Both F_2 and F_3 generations were obtained by controlled pollination. Seeds of parental F_1, F_2 and F_3 generations for each of the two interspecific crosses were planted during *Kharif* season (June 1993) at the University of Agricultural Sciences, Bangalore, India. The experimental design was randomized block design with three replications. Separate blocks were assigned for all the crosses. Generations were randomized within crosses and crosses were randomized within blocks. The 30 days old seedlings were transplanted with a spacing of 30cm between each plant and 60cm between each row in 3m rows. Standard cultural practices were followed, including supplemented irrigation and fertilizer application. Populations maintained during the field test in each replication were as follows; parents and F_1s represented by 15 plants and F_2 and F_3 generations by 150 and 100 plants, respectively. Data were recorded on individual plants at maturity for the following traits: plant height, days to fruit maturity, average fruit weight, fruit yield and TLCV related traits *viz.*, days to TLCV symptoms expression and symptoms severity percentage. The TLCV symptom severity was visually graded as per the scale of Banerjee and Kalloo (1987).

Generation means for those traits for which genetic variation among five generations (P_1, P_2, F_1, F_2 and F_3) was detected were subjected to estimate gene effects *viz.*, mean (m), additive ([d]), dominance ([h]), additive x additive ([i]), and dominance x dominance ([l]) using joint scaling test (Cavalli, 1952), as described by Mather and Jinks (1983). Simultaneously, the adequacy of additive-dominance model was determined by the significance of chi-square test.

Heterosis over both mid and better-parents was calculated as percentage increase or decrease of mean of F_1 performance by the methods of Turner (1953).

RESULTS AND DISCUSSION

Heterosis of the F_1 over both the mid parent and better-parent was significant for all the traits in the *L. esculentum* (Arka Saurabh and Arka Vikas) X *L. pimpinellifolium* crosses, except mid parent heterosis of days to fruit maturity in Arka Saurabh x *L. pimpinellifolium*, indicating complete dominance to over dominance (Tables 1 and 2). However, the effects of over dominance cannot be separated from the effects of linkage and epistasis. Therefore, the actual degree of dominance of the individual genes for these traits may only be in the range of partial to complete dominance.

Plant height

The full five-parameter model (m, [d], [h], [i] and [l]) was necessary to explain the variation among generation means for plant height (Tables 3 and 4), leaving no degrees of freedom to test the model. Both the digenic interaction effects were significant, indicating that plant height is complexly inherited with complementary type of epistasis.

Days to fruit maturity

It appeared that different genetic systems control days to fruit maturity in the two crosses. A simple additive-dominance model adequately explained the data for Arka Vikas X *L. pimpinellifolium* cross, but it was necessary to extend the model to include additive x additive form of epistasis for the Arka Saurabh X *L. pimpinellifolium* cross (Tables 3 and 4). Khattra *et al.* (1990), and Peter and Rai (1990) arrived at a similar conclusion on inter-varietal crosses of tomato.

Table 1 . **Generation means (Mean±SE), and heterosis estimates for several traits in the cross Arka Saurabh x *L. pimpinellifolium*.**

Generation	Fruit yield and its component traits				TLCV related traits	
	Plant height (cm)	Days to fruit maturity	Average fruit weight (g)	Fruit yield (kg/plant)	Days to symptoms appearance	Symptoms severity percentage
P_1	47.40±1.44	91.20±0.56	53.29±2.95	1.22±0.10	57.90±1.30	84.30±1.62
P_2	78.77±3.25	86.13±0.57	1.42±0.09	0.44±0.02	79.09±2.78	14.83±0.72
F_1	84.64±1.61	89.07±0.55	14.67±0.42	0.94±0.08	70.24±1.28	23.77±1.41
F_2	57.81±0.93	91.64±0.24	20.19±0.78	0.82±0.02	72.78±1.12	44.73±1.78
F_3	52.57±0.84	89.85±0.65	24.91±0.77	0.79±0.03	77.40±1.71	52.29±2.05
(MP)	34.17**	0.46ns	-46.38**	38.11**	8.91**	-52.04**
(BP)	7.45**	2.34**	-72.45**	-22.89**	-11.19**	60.28**

P_1 = Arka Saurabh P_2 = *L. pimpinellifolium*
MP = Mid parent Heterosis; BP = Better parent Heterosis
** = Significant at 1% level ns = non significant

Table 2. **Generation means (Mean±SE), and heterosis estimates for several traits in the cross Arka Vikas x *L. pimpinellifolium*.**

Generation			Fruit yield and its component traits		TLCV related traits	
	Plant height (cm)	Days to fruit maturity	Average fruit weight (g)	Fruit yield (kg/plant)	Days to symptoms apearance	Symptoms severity percentage
P_1	54.73±2.67	89.45±0.86	56.73±1.29	1.55±0.13	59.65±1.67	82.63±1.61
P_2	74.67±3.22	84.34±0.67	1.40±0.08	0.45±0.01	79.65±2.66	14.73±0.68
F_1	97.20±2.83	88.17±0.93	11.82±0.54	1.06±0.06	73.33±2.33	23.20±1.34
F_2	49.72±0.98	90.67±0.34	19.33±0.91	0.97±0.02	68.68±2.98	44.88±1.78
F_3	53.00±1.27	89.85±0.78	26.65±1.17	1.01±0.03	78.60±2.30	51.89±2.08
(MP)	53.79**	1.47**	-59.35**	24.35**	5.28**	-52.34**
(BP)	35.63**	-1.43**	-79.16**	-31.97**	-7.93**	-71.92**

P_1 = Arka Vikas; P_2 = *L. pimpinellifolium*
MP = Mid parent Heterosis; BP = Better parent Heterosis
** = Significant at 1% level

Table 3. **Joint scaling test and estimates of gene effects for several traits in the cross Arka Saurabh x *L. pimpinellifolium*.**

Generation	Fruit yield and its component traits				TLCV related traits	
	Plant height (cm)	Days to fruit maturity	Average fruit weight (g)	Fruit yield (kg/plant)	Days to symptoms appearance	Symptoms severity percentage
m	57.81±0.94**	91.64±0.06**	17.19±0.78**	0.316±0.02**	72.41±1.17NS	44.73±1.79**
[d]	-15.68±1.80**	-2.47±0.16**	25.93±1.47**	0.541±0.05**	13.10±1.40**	34.73±0.89**
[h]	22.27±3.10**	3.07±3.35NS	4.39±2.89NS	0.499±0.09**	-1.90±0.89NS	-34.14±6.61**
[i]	-16.25±3.56**	-2.73±0.40**	68.94±2.80**	1.321±0.14**	–	61:13±6.24**
[l]	115.14±9.34**	-16.43±9.53ns	-18.86±7.50*	1.013±0.31**	–	15.59±18.46NS
Chi-sqaure value	58.48**	17.28**	47.23**	98.18**	9.17NS	30.43**
Type of epistaris	C	–	–	C	–	–

C = Complementary   ns = non significant   * = Significant at 5%   ** = Significant at 1%

Table 4. **Joint scaling test and estimates of gene effects for several traits in the cross Arka Vikas x *L. pimpinellifolium*.**

Generation	Fruit yield and its component traits				TLCV related traits	
	Plant height (cm)	Days to fruit maturity	Average fruit weight (g)	Fruit yield (kg/plant)	Days to symptoms appearance	Symptoms severity percentage
m	49.73±0.98**	90.67±0.20**	19.33±0.91**	0.974±0.02**	70.23±2.93**	44.88±1.78**
[d]	-8.47±2.09**	0.40±0.47ns	27.66±2.15**	0.704±0.07**	11.57±1.68**	33.95±0.87**
[h]	30.89±4.35**	-2.68±0.45**	4.53±3.64ns	0.388±0.11**	-2.69±0.96*	-33.14±6.57**
[i]	-20.04±5.10**	–	68.04±3.89**	1.589±0.13**	–	60.24±6.17**
[l]	128.14±12.84**	–	-12.99±9.72ns	1.557±0.31**	–	20.41±18.28ns
Chi-sqaure value	229.59**	3.17ns	12.65**	88.58**	7.78ns	36.01**
Type of epistasis	C	–	–	C	–	–

C = Complementary ns = non significant; * = Significant at 5% ** = Significant at 1%

Average fruit weight

Variation for average fruit weight was not explained adequately by a three-parameter model (Tables 3 and 4). Therefore, the model was extended to include additive x additive epistatic effect for the Arka Vikas x *L. pimpinellifolium* cross, and additive x additive, and dominance x dominance effects for the Arka Saurabh x L. pimpinellifolium cross. Predominance of additive, and additive x additive gene effects were observed for the inheritance of average fruit weight. *L. esculentum* was increasing parent. The additive and additive x additive gene effects were significant and positive. It implies that *L. esculentum* carries a greater number of genes with additive effects for increased mean weight of fruits and suggests the effectiveness of simple selection even in early segregating generations in improving this trait.

Fruit yield

Variation among generation means for fruit yield was sufficiently explained by the five-parameter model. Both types of digenic effects were significant in a complentary manner, indicating that fruit yield is complexly inherited. Singh *et al.* (1976) arrived at a similar conclusion after studying the progeny of diallel crossing. In the present study, all types of gene effects were significant, but the magnitude of interaction effects was comparatively higher than the primary gene effects. Both intra-and inter-population selection methods could be effective in accumulating favourable gene combinations for improving fruit yield.

Days to TLCV symptoms expression

Variation for days to TLCV symptoms expression was explained adequately by additive-dominance model. In this, the effects of linkage were not detected, since linkage affects the epistatic terms in the model (Hayman, 1958). Linkage may not be important for this trait; however, the failure to detect linkage does not imply that it does not exist. Days to TLCV symptoms expression was predominantly governed by additive gene effects without non-allelic interactions. Hence, lines showing delayed expression of symptoms may be isolated from the segregating population derived from the crosses in which TLCV tolerant *L. pimpinellifolium* is involved.

Symptoms severity

Variation among generation means for TLCV symptom severity was not sufficiently explained by a simple additive-dominance model. Jalikop (1992) also reported that a six parameter model was necessary to explain the data. He showed the predominant role of additive gene effects in governing this trait in the crosses of *L. esculentum* x *L. pimpinellifolium*. In the present study, both additive, and additive x additive effects were predominant. Therefore, additive component of TLCV resistance can be salvaged from the segregating population by direct selection in these crosses.

CONCLUSIONS

Selection on the basis of selfed progeny exposes deleterious recessives, which are expected to be prevalent in crosses with exotic germplasm. In tomato, as in any other crop, the effectiveness of selection for any quantitative trait is primarily determined by the nature of the genetic effects controlling its inheritance. Once the relative importance of the contributions from various genetic effects is estimated for a particular trait in a given cross, the breeding objectives will dictate how the various effects will be exploited in the development of breeding lines or improved cultivars.

Thus, the aspects concerning TLCV resistance breeding (symptoms appearance and symptoms severity), apart from yield and other attributes of interest, are to be dealt with concurrently by a breeder. Since the traits in question are quantitative in nature, it is desirable to advance the progenies to F_2 and F_3 generations and alternated with progeny testing.

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