



RESEARCH ARTICLE

# Explicating genetic inheritance of tomato leaf curl New Delhi virus resistance in cucumber

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Received: 02 November 2025; Accepted: 01 April 2026; Available online: Version 1.0: 31 May 2026

**Cite this article:** Naveena E, Rameshkumar D, Sneha LG, Lakshmi S, Rajasree V, Mohanasundram D, Deepamale N. Explicating genetic inheritance of tomato leaf curl New Delhi virus resistance in cucumber. Plant Science Today. 2026; 13(sp2): 1-8. <https://doi.org/10.14719/pst.12552>

## Abstract

Viral disease, especially tomato leaf curl New Delhi virus (ToLCNDV), pose a serious threat to cucumber cultivation in India and many other countries worldwide. Under natural epiphytotic screening conditions, this study elucidates the genetics of inheritance pattern of resistance to ToLCNDV in the crosses DC 773 × DC 70 and DC 769 × DC 70. To investigate the inheritance of resistance to ToLCNDV, we employed the F<sub>1</sub>, F<sub>2</sub>, BC<sub>1</sub> and BC<sub>2</sub> generations derived from the P<sub>1</sub> × P<sub>2</sub> and P<sub>3</sub> × P<sub>2</sub> crosses. The results indicated that resistance to ToLCNDV is governed by a monogenic recessive gene, with both parents contributing recessive alleles. Based on these results, it is possible to assume that a monogenic recessive gene for ToLCNDV disease resistance exists in the genetic background of the cucumber genotype (P<sub>2</sub>). These findings are crucial for the development of resistant cultivars in cucumber that resist the disease caused by ToLCNDV.

**Keywords:** cucumber; generation mean analysis; inheritance; monogenic recessive; natural screening; resistant; tomato leaf curl New Delhi virus

## Introduction

Cucumber (*Cucumis sativus* L., 2n = 2x = 14) is an important crop in the family Cucurbitaceae, which also includes squash (*Cucurbita* spp.), watermelon (*Citrullus lanatus* L.) and melon (*Cucumis melo* L.), along with several other cucurbits cultivated worldwide. Cucumbers are unique to Asia and comprises approximately 90 genera and 750 species. During 2023–24, India recorded cucumber production surpassing 2050.13 thousand metric tonnes and with a productivity of 14.70 metric tonnes per hectare over an area of 139.49 thousand hectares (1). Cucumbers are widely regarded as an excellent vegetable for fresh consumption.

Viral diseases pose a significant challenge to cucumber production, with tomato leaf curl New Delhi virus (ToLCNDV) being one of the most critical factors affecting yield. Tomato leaf curl New Delhi virus presents a substantial threat to cucumber cultivation. This virus is classified as a member of the bipartite begomovirus species within the family Geminiviridae. It is naturally transmitted in a persistent manner by the whitefly *Bemisia tabaci*. This virus has a broad host range, infecting various cucurbit species such as cucumbers, squash, melons and tomatoes. In India, the first reported crop affected by ToLCNDV was tomato (*Solanum lycopersicum* L.) (2). The manifestations of ToLCNDV symptoms in a number of hosts include curled leaves, thicker

veins, darkened leaf margins, decreased leaf area, short internodes and severely stunted plants (3). Tomato leaf curl New Delhi virus has caused substantial damage to various crops, particularly cucurbits such as melons. In central Spain, its impact on open-field melon production has been particularly severe with yield losses reported to reach up to 20 % (4). It has also been associated with immense economic losses, especially reduced yield and cracked, unmarketable fruits in Spain and other major cucurbit-growing regions (5).

Natural, chemical, physical and cultural techniques are frequently incorporated into vector control plans. However, continual fluctuations in whitefly populations and the development of insect vector insensitivity to various pesticides pose significant challenges in the control of viral infections (6). In addition, there are numerous health and environmental hazards associated to pesticide use, which makes it undesirable to utilise pesticides continuously to prevent viral diseases. The most effective way to mitigate yield losses in epiphytotic circumstances is to choose resistant cultivars. Multiple factors contribute to the spread of begomoviruses and the losses they have caused, including the presence of a large population of insect vectors, a wide host range, the formation of novel viral strains and species as a result of recombination and their diffusion (7).

Research on the inheritance pattern of begomovirus-

induced leaf curl diseases specifically, ToLCNDV is quite scarce. Studies have shown that sponge gourd inbred lines ‘DSG-6’ and ‘DSG-7’ possess a single dominant gene conferring resistance (8), while the melon accession ‘IC-274014’ carries a single recessive gene for resistance (9). Similarly, wild *Cucumis melo* var. *agrestis* group (WM-7) has one major gene and two minor genes governing resistance (4). For the resistance to tomato yellow leaf curl virus in tomatoes, one recessive gene containing one additional allele (10) and one dominant gene for the resistance to chilli leaf curl virus in chilli pepper (11). Furthermore, polygenic inheritance possibly contributed to tomato leaf curl virus resistance through additive or epistatic effects between genes (12). The inheritance of resistance is often complex and may be influenced by several factors, including experimental conditions, genetic background of the material, viral isolates, inoculation period and screening methods. Therefore, understanding the genetic basis of resistance to this complex pathogen is essential for developing effective breeding strategies. This study will eventually help in breeding ToLCNDV resistant lines and highlights the importance of virus specific resistance breeding. Cucumber tomato leaf curl virus disease caused by whiteflies is a reported disease; however, information on the genetics of resistance to ToLCNDV in cucumber remains scarce. The primary objective of the present study was to determine the inheritance pattern of ToLCNDV resistance in DC 773 × DC 70 and DC 769 × DC 70.

## Materials and Methods

### Plant material

The genotypes DC 773 ( $P_1$ ) and DC 769 ( $P_3$ ) were susceptible to ToLCNDV were employed in the study, whereas the genotype DC 70 ( $P_2$ ) was resistant to ToLCNDV.  $P_1$  and  $P_3$  were long-fruited monoecious genotypes whereas  $P_2$  is an Indian type of monoecious cucumber which were obtained from Indian Agricultural Research Institute (IARI), New Delhi. The experimental material comprised parental genotypes along with  $F_1$ ,  $F_2$ ,  $BC_1$  and  $BC_2$  populations obtained from two crosses. In our earlier two years of natural epiphytic screening and artificial screening,  $P_2$  exhibited a high level of resistance to ToLCNDV. To develop the  $F_1$  generation, the susceptible genotypes  $P_1$  and  $P_3$  were crossed with the resistant genotype  $P_2$  during the kharif season of 2023 (July–October). During the crop growing period (November to February) of 2023–2024, the resultant  $F_1$  progenies have been backcrossed with the resistant parent  $P_2$  to generate  $BC_1$  and  $BC_2$  (backcrossed with susceptible parents  $P_1$  and  $P_3$  and self-pollinated to create  $F_2$ ). These six generations were used to investigate the genetics of ToLCNDV resistance in natural epiphytic conditions from March to June 2024. Weather data for the crop growing period were provided in Annexure I.

### Tomato leaf curl New Delhi virus screening under natural epiphytic conditions

In March 2024, a field experiment was conducted at the Department of Vegetable Science, College Orchard, Tamil Nadu Agricultural University (TNAU), Coimbatore. Geographically, the experimental site has emerged at 426.6 m above mean sea level and situated at latitudes 11° N and longitudes 77° E. During the rabi season, the primary pathogen ToLCNDV which is transmitted by the insect vector whitefly is more prevalent in the natural epiphytic condition. Due to this, infection develops in the genotypes that are susceptible as soon as the insects visit the plants. An unreplicated trial was adopted for this experiment. The experiment focused on inheritance patterns of ToLCNDV resistance, where replication is statistically less critical. Conclusions were based on large population sizes and segregation ratios analysed using Chi-square ( $\chi^2$ ) tests under uniform epiphytic conditions ensured by susceptible checks. Thus, the unreplicated design was statistically adequate for inheritance analysis. Seeds of all six populations were sown in raised beds wrapped with plastic mulch, with 1.5 m between each plant and 1.5 m between rows. To promote infection and prevent any possibility of disease escape, susceptible checks were planted on a regular basis. All recommended agronomic practices for raising a healthy crop were followed, with the exception of the use of pesticides, to maintain sufficient populations of the vector, for effective ToLCNDV transmission.

### Tomato leaf curl New Delhi virus disease scoring

To develop the  $F_1$  generations in the field, controlled crossings were established between the resistant ( $P_2$ ) genotype (used as the male parent) and the susceptible parents ( $P_1$ ) and ( $P_3$ ), which were utilised as female parents. Two  $F_1$  populations were self-pollinated to create  $F_2$  populations as well as backcrossed to develop  $BC_1$  and  $BC_2$  populations during the rabi season. In the cross ( $P_1 \times P_2$ ), 40 plants of each  $P_1$  and  $P_2$ , along with 50 plants of  $F_1$  were employed for screening, while 191 plants of  $F_2$  population and 63 plants of  $BC_1P_1$  ( $F_1 \times P_1$ ) and 60  $BC_1P_2$  ( $F_1 \times P_2$ ) plant populations were employed. In another cross of  $P_3 \times P_2$ , 29 plants of susceptible parents ( $P_3$ ), 28 plants of resistant parent ( $P_2$ ), 38  $F_1$  plants, 146  $F_2$  individuals, 45 susceptible backcross progenies ( $F_1 \times P_3$ ) and 43 resistant backcross progenies. Individual plants have been evaluated using a standardised 6-point interaction phenotypic measure (8) for ToLCNDV disease under the natural epiphytic screening approach (Table 1). Totally four scorings were taken at 15-day intervals starting from 30 days after sowing and categorised into resistant (R) (score of 0, 1 and 2) and susceptible (S) (score of 3, 4 and 5) classifications. Plants were classified on the basis of disease reaction and the data was analysed using  $\chi^2$  test to investigate the inheritance of disease resistance.

**Table 1.** Disease reaction scale in cucumber for tomato leaf curl New Delhi virus (ToLCNDV) disease

| Severity grade | Symptoms                                                                                             | Rating scale                | Severity range |
|----------------|------------------------------------------------------------------------------------------------------|-----------------------------|----------------|
| 0              | No symptoms                                                                                          | Highly resistant (HR)       | 0 %            |
| 1              | Young leaves with mild mosaic that covers <10 % of the leaf surface                                  | Resistant (R)               | 1–10 %         |
| 2              | Young leaves with mosaic accounting <25 % of the surface                                             | Moderately resistant (MR)   | 11–25 %        |
| 3              | Young leaves exhibit blistering and puckering occupies <50 % of the surface in a mosaic              | Moderately susceptible (MS) | 26–50 %        |
| 4              | Severe leaf deformation and a mosaic of young leaves occupying <75 % of the surface                  | Susceptible (S)             | 51–75 %        |
| 5              | Serious leaf deformation, stunting and a mosaic of immature leaves encompassing >75 % of the surface | Highly susceptible (HS)     | 76–100 %       |

## Chi-square analysis

The segregation ratios of resistant (R) and susceptible (S) plants in the  $F_2$  and backcross populations were analysed using the  $\chi^2$  test, based on the expected phenotypic ratios (13). The  $\chi^2$  test determines the goodness of fit between expected and observed segregation ratios. The variations from these were computed by applying the  $\chi^2$  test formula.

$$\chi^2 = \sum \frac{(O - E)^2}{E}$$

Where,

$O$  indicates the observed ratio.

$E$  represents the expected ratio.

## Detection of gene effects

The data were used to determine the mean value of ToLCNDV response in the parents ( $P_1$  and  $P_2$ ),  $F_1$  ( $P_1 \times P_2$ ),  $F_2$  ( $F_1$  selfed) and their first-generation backcrosses ( $BC_1$ :  $F_1 \times P_1$  and  $BC_2$ :  $F_1 \times P_2$ ) for both the crosses. These estimates served as the fundamental element for calculating different statistics. A scaling test was performed to identify the existence of epistasis before assessing the various parameters (14). For non-interacting crosses, the three parameters have been determined by employing the formula in previous study (15).

## Results

### Inheritance pattern of cross 1 and 2 under natural epiphytotic conditions for tomato leaf curl New Delhi virus resistance

#### Chi-square analysis to determine the goodness of fit to the classical Mendelian ratio

In cross 1 the inheritance of ToLCNDV resistance was investigated. A total of 40 plants from the  $F_1$  generation were assessed, out of which 11 were found to be resistant while remaining 39 were found to be susceptible which indicates susceptible outnumbered resistant. A total of 191  $F_2$  plants of cross 1 were assessed for disease response of which 47 plants showed resistance and 144 plants displayed susceptible reaction. When 60  $F_1$  was backcrossed with ( $P_2$ ) resistant parent ( $BC_2$ ) generation produced 28 susceptible and 32 resistant plants. The backcross population ( $BC_2$ ) adhered to the mendelian segregation pattern (1:1). Four plants were found to be resistant and 59 plants were susceptible to the disease in a ratio of 1:0 when 63  $F_1$  was backcrossed with ( $P_1$ ) susceptible parent ( $BC_1$ ) generation. The hypothesis of monogenic control of ToLCNDV resistance was

assessed using a  $\chi^2$  test for goodness of fit. A probability ( $p$ ) value  $>0.05$  was feasible for the genetic model. As a result, only the monogenic segregation ratio was satisfied when the  $F_2$  population data was analysed by  $\chi^2$  analysis and expressed segregation pattern ratio of 3:1 (susceptible: resistant) with the calculated  $\chi^2$  value of 0.015;  $p = 0.902$ . [The  $BC_2$  computed  $\chi^2$  value 0.266;  $p = 0.606$ . These calculated  $\chi^2$  value was lesser than the tabulated value of 3.84]. The observed and expected frequencies are in close conformity because the computed  $\chi^2$  value was non-significant. Based on these results, it is possible to assume that a single major recessive gene for ToLCNDV disease resistance exists in the genetic background of the cucumber genotype ( $P_2$ ) (Table 2).

In cross 2 the inheritance pattern of ToLCNDV resistance was investigated. The male parent ( $P_2$ ) was highly resistant, except for two plants, whereas the female parent ( $P_3$ ) was susceptible. In the  $F_1$  generation, 38 plants were assessed, of which 29 were susceptible and 9 were resistant, with majority of the plants exhibiting a susceptible reaction signifying the dominance of susceptible over resistant reactions. A total of 146  $F_2$  plants produced from the cross 2 were assessed for disease response, out of which 35 resistant plants and 111 susceptible plants were identified. Thereafter  $F_1$  was backcrossed with a resistant parent ( $BC_1$ ) yielded a ratio of 1:10 in  $F_2$  and led to the segregation of most of the susceptible plants 38 and the persisting 7 were resistant. Furthermore, when 43  $F_1$  plants were backcrossed with a resistant parent ( $BC_2$ ) segregated into 25 resistant plants and 18 susceptible plant groups fitted under 1:1 ratio. Using a  $\chi^2$  test for goodness of fit, the monogenic regulation of ToLCNDV resistance theory was explored. For the genetic model, a probability ( $p$ ) value of  $> 0.05$  was optimal. The  $F_2$  population displayed a 3:1 (susceptible:resistant) segregation pattern ( $\chi^2 = 0.08$ ;  $p = 0.774$ ). The backcross population ( $BC_2$ ) was employed to verify the inheritance pattern results ( $\chi^2 = 1.139$ ;  $p = 0.285$ ). The calculated  $\chi^2$  values of  $F_2$  and  $BC_2$  were lower than the tabulated value of 3.84 hence it is non-significant. The non-significance of calculated  $\chi^2$  values suggests that the observed and expected frequencies are closely related. Based on the results, it was confirmed again that a monogenic recessive gene is responsible for the inheritance of ToLCNDV resistance in the genetic background of 'DC 70' (Table 2).

#### Generation mean analysis for tomato leaf curl New Delhi virus resistance in cucumber

Generation mean analysis was employed in the present study to estimate gene effects and evaluate their relative significance in the inheritance pattern of ToLCNDV resistant genes comprising two crosses. The adequacy of the additive-dominance model was tested using the basic scaling tests (A, B, C and D). In addition, a

**Table 2.** Estimates of chi square values and their probability for classical Mendelian ratio for tomato leaf curl New Delhi virus (ToLCNDV) resistance in the crosses of DC 773  $\times$  DC 70 and DC 769  $\times$  DC 70 under natural epiphytotic condition

| Crosses | Generations | Description           | Total | S   | R  | Genetic ratio | Chi square | P value |
|---------|-------------|-----------------------|-------|-----|----|---------------|------------|---------|
| Cross 1 | $P_1$       | DC 773                | 40    | 39  | 1  |               |            |         |
|         | $P_2$       | DC 70                 | 40    | 0   | 40 |               |            |         |
|         | $F_1$       | DC 773 $\times$ DC 70 | 50    | 39  | 11 |               |            |         |
|         | $F_2$       | DC 773 $\times$ DC 70 | 191   | 144 | 47 | 3:1           | 0.015      | 0.902   |
|         | $BC_1$      | $F_1 \times$ DC 773   | 63    | 59  | 4  | 1:0           | –          | –       |
|         | $BC_2$      | $F_1 \times$ DC 70    | 60    | 28  | 32 | 1:1           | 0.266      | 0.606   |
| Cross 2 | $P_3$       | DC 769                | 29    | 27  | 2  |               |            |         |
|         | $P_2$       | DC 70                 | 28    | 0   | 28 |               |            |         |
|         | $F_1$       | DC 769 $\times$ DC 70 | 38    | 29  | 9  |               |            |         |
|         | $F_2$       | DC 769 $\times$ DC 70 | 146   | 111 | 35 | 03:01         | 0.082      | 0.774   |
|         | $BC_1$      | $F_1 \times$ DC 769   | 45    | 38  | 7  | 01:00         | –          | –       |
|         | $BC_2$      | $F_1 \times$ DC 70    | 43    | 18  | 25 | 01:01         | 1.139      | 0.285   |

$\chi^2$  at 0.05 with 1df = 3.84. S: susceptible plants; R: resistant plants.

joint scaling test (15) was performed to estimate genetic effects using a three-parameter model.

#### Mean performance, variance and standard error of various generations in both crosses

In cross 1, the mean, variance and standard errors were estimated for all six generations of individuals ( $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$  and  $BC_2$ ) were examined primarily to compare the means of populations with each other. The mean of  $F_2$  (2.047),  $BC_1$  (3.603) and  $BC_2$  (1.133) generation disease score value lower than (4.000) ( $P_1$ ) the parental mean (Table 3). The mean of the  $BC_2$  generation (1.133) was lower than the mean of  $F_1$  generation (2.700). The mean of susceptible parent ( $P_1$ ) (4.000) was higher than  $BC_1$  population (3.603). The variance of non-segregating generations  $P_1$  (1.025),  $P_2$  (0.025) and  $F_1$  (1.316) possessed relatively lower values than segregating generations of  $F_2$  (3.108) and  $BC_1$  (1.469).

For cross 2,  $F_2$  disease score mean (1.968) was higher than (1.279)  $BC_2$  generation but it was lower than the  $F_1$  (2.894) and  $BC_1$  (3.133) generations. The mean disease score of the  $F_2$  (1.968),  $BC_1$  (3.133) and  $BC_2$  (1.279) generation values were lower than ( $P_1$ ) the parental mean (3.413) and the mean of  $F_1$  (2.894) but higher than (1.279) the  $BC_2$  population. The  $BC_1$  population (3.133) recorded lower mean disease score than the susceptible parent ( $P_1$ ) value of 3.413. Variance of non-segregating generations  $P_1$  (2.322),  $P_2$  (0.068) and  $F_1$  (2.096) exhibited comparatively lower than segregating generations  $F_2$  (2.936) and  $BC_2$  (2.872). The mean disease score, standard error and variance of parents,  $F_1$ ,  $F_2$  and backcross generations of the cross 1 and 2 are given in Table 3.

#### Scaling test of two crosses for tomato leaf curl New Delhi virus resistance

The results of cross 1, obtained under natural epiphytotic conditions, were subjected to scaling tests to determine the presence or absence of epistasis through A, B, C and D scales and parameters m, d and h were estimated for ToLCNDV disease resistant trait. The individual scaling tests revealed that A (0.506), B (−0.458), C (−1.236) and D (−0.642) scales for cross 1 were non-

significant, indicating the absence of inter-allelic interactions or epistasis for inheritance of the trait. The scaling test results for this cross unveiled that ToLCNDV disease resistance follows a classical Mendelian inheritance pattern.

The scaling test estimates of cross 2 demonstrated non-significant of the A (−0.041), B (−0.408), C (−1.439) and D (−0.494) scales for cross 2 confirmed the absence of epistasis (non-allelic interactions) in that trait inheritance and results were conformity with  $X^2$  analysis are shown in Table 3.

#### Confirmation of tomato leaf curl New Delhi virus resistance gene effects by adopting three parameter model

The results of the gene effect for crosses 1 and 2 are provided in Table 3. In cross I, the mean effect ( $m = 0.728$ ) was non-significant and positive. Highly significant and positive magnitude values were observed in additive (1.987) and dominance (3.304) effects. Therefore, the cross was non-interacting type and in close conformity with the  $X^2$  analysis results suggesting that additive and dominance effects were present.

In cross II, the three-parameter model revealed that the mean effect (0.753) and dominance effect (2.680) were positive but non-significant. Highly significant and positive magnitude value was observed only in additive effect (1.671) by cross 2. The results demonstrated that the resistance to the ToLCNDV disease occurred due to presence of additive effect, which is considered to have a major role in the trait expression in this cross.

## Discussion

#### Disease response in DC 773 × DC 70 and DC 769 × DC 70 crosses

The resistant parent ( $P_2$ ) remained highly resistant over the growing period and did not show any disease symptoms when screened and crossed with the susceptible parents,  $P_1$  and  $P_3$ . Similarly, it has been demonstrated that five accessions of the *Cucurbita moschata* plant expressed genetic resistance to the

**Table 3.** Generation mean, variance, standard error, scaling tests and estimates of genetic parameters for tomato leaf curl New Delhi virus (ToLCNDV) disease scoring

|                        |           | Cross 1         | Cross 2         |
|------------------------|-----------|-----------------|-----------------|
| <b>Generation mean</b> |           |                 |                 |
| $P_1$                  | Mean ± SE | 4.000 ± 0.160   | 3.413 ± 0.283   |
|                        | Variance  | 1.025           | 2.322           |
| $P_2$                  | Mean ± SE | 0.025 ± 0.025   | 0.071 ± 0.049   |
|                        | Variance  | 0.025           | 0.068           |
| $F_1$                  | Mean ± SE | 2.700 ± 0.162   | 2.894 ± 0.234   |
|                        | Variance  | 1.316           | 2.096           |
| $F_2$                  | Mean ± SE | 2.047 ± 0.127   | 1.958 ± 0.141   |
|                        | Variance  | 3.108           | 2.9362          |
| $BC_1$                 | Mean ± SE | 3.603 ± 0.152   | 3.133 ± 0.217   |
|                        | Variance  | 1.469           | 2.118           |
| $BC_2$                 | Mean ± SE | 1.133 ± 0.141   | 1.279 ± 0.258   |
|                        | Variance  | 1.202           | 2.872           |
| <b>Scales</b>          |           |                 |                 |
| A                      | Mean ± SE | 0.506 ± 0.381   | −0.041 ± 0.568  |
| B                      | Mean ± SE | −0.4583 ± 0.327 | −0.408 ± 0.570  |
| C                      | Mean ± SE | −1.236 ± 0.626  | −1.439 ± 0.790  |
| D                      | Mean ± SE | −0.642 ± 0.329  | −0.494 ± 0.440  |
| <b>Parameters</b>      |           |                 |                 |
| m                      | Mean ± SE | 0.728 ± 0.663   | 0.753 ± 0.893   |
| d                      | Mean ± SE | 1.987** ± 0.081 | 1.671** ± 0.143 |
| h                      | Mean ± SE | 3.304** ± 1.639 | 2.680 ± 2.372   |

\*\*Significant at 5 % and 1 % level.

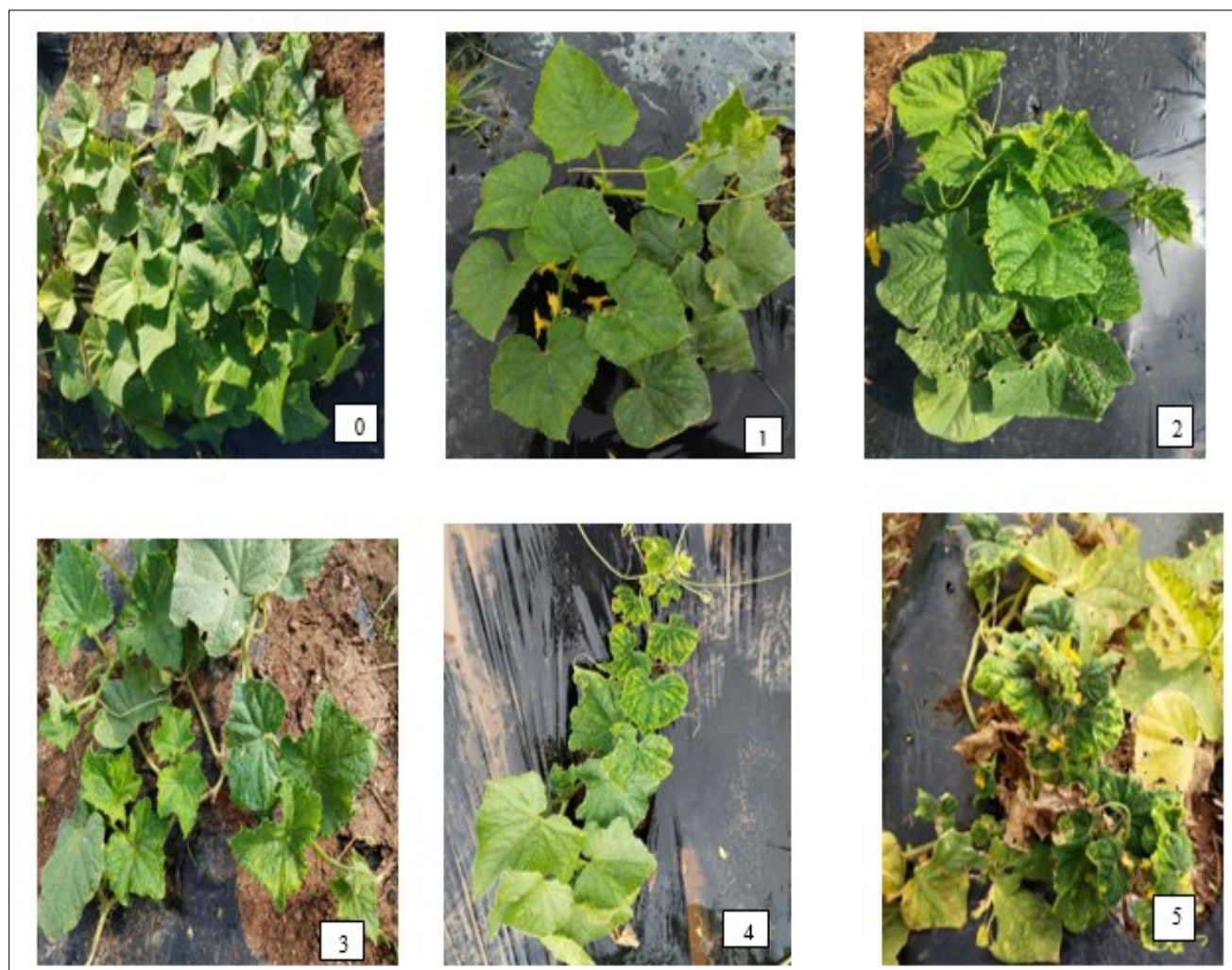


**Fig. 1.** Scoring scale (0–5) for ToLCNDV screening in cucumber.

ToLCNDV without any symptoms (4). It may be possible that many ToLCNDV resistant cucurbit accessions from India, could be pertinent to the co-evolution of host and pathogen in this region of the world where ToLCNDV became apparent in infecting cucurbits many years ago. In both crosses, individuals from the  $F_1$ ,  $F_2$ ,  $BC_1$  and  $BC_2$  populations exhibited a wide range of disease reactions, varying from no visible symptoms to severe leaf curling, mosaic, yellowing and plant stunting, which are characteristic symptoms of ToLCNDV infection (Fig. 1).

#### **Inheritance pattern of tomato leaf curl New Delhi virus resistance in DC 773 × DC 70 and DC 769 × DC 70 crosses**

The present study was designed to understand more about the nature and degree of generation means and gene effects for ToLCNDV in cucumber. The  $\chi^2$  analysis for both crosses, resistance found in the DC 769 × DC 70 and DC 773 × DC 70 crosses were recessive. Under natural screening conditions, a clear distinction between susceptible and resistant plants was the preliminary basis for the inheritance of resistance against ToLCNDV. The results indicated that resistance was inherited as a recessive trait as nearly all  $F_1$  plants in both crosses exhibited susceptible reactions.  $P_2$  was proved to be resistant in both crosses. The phenotypic data of the  $F_2$  population in the crosses DC 773 × DC 70 and DC 769 × DC 70 confirms the recessive nature of the segregation of resistant and susceptible plants, with the number of susceptible plants exceeded the resistant ones. The segregation of  $F_2$  populations into susceptible and resistant plants fitted in a 3:1 ratio, representing that susceptible plants were again greater than

resistant ones and results further support the recessive nature of resistance. In addition, a study of  $BC_1$  population produced through backcrossing with susceptible parents revealed all plants of the population depicted susceptible reactions (Fig. 2 and 3). Based on the disease incidence of the  $F_1$ ,  $F_2$  and backcross populations obtained by the two crosses, it was proven the fact that the major recessive gene in the genetic background of the  $P_2$  genotype governed resistance to ToLCNDV. In these crosses, ToLCNDV resistance was inherited from a monogenic recessive trait whereas susceptibility was dominant over resistance. This could be attributed to the recessive gene “r” holds the role of expressing the resistance gene while dominant gene producing susceptibility impeded the function of dominant gene generating resistance. Interestingly, a number of virus resistance systems frequently exhibit recessive regulation of resistance, since recessive resistance genes disrupt several phases of the viral life cycle by targeting specific cells and cell-to-cell movement (16). Notably, recessive gene regulation of resistance is a common strategy exploited by several viral resistance mechanisms. Similar findings were reported (17), where resistant CGN23089 accession crossed with the susceptible accession BGV011742, which exhibited resistance to ToLCNDV, integrated with recessive monogenic inheritance model for genetic control in cucumber. The present results are also consistent with earlier reports on the genetic regulation of ToLCNDV resistance in various cucurbits in loofah (18) and in musk melon (19). However, contrasting evidence has been reported in *Luffa cylindrica*, where resistance to ToLCNDV is inherited by a single dominant gene (20). Different types of

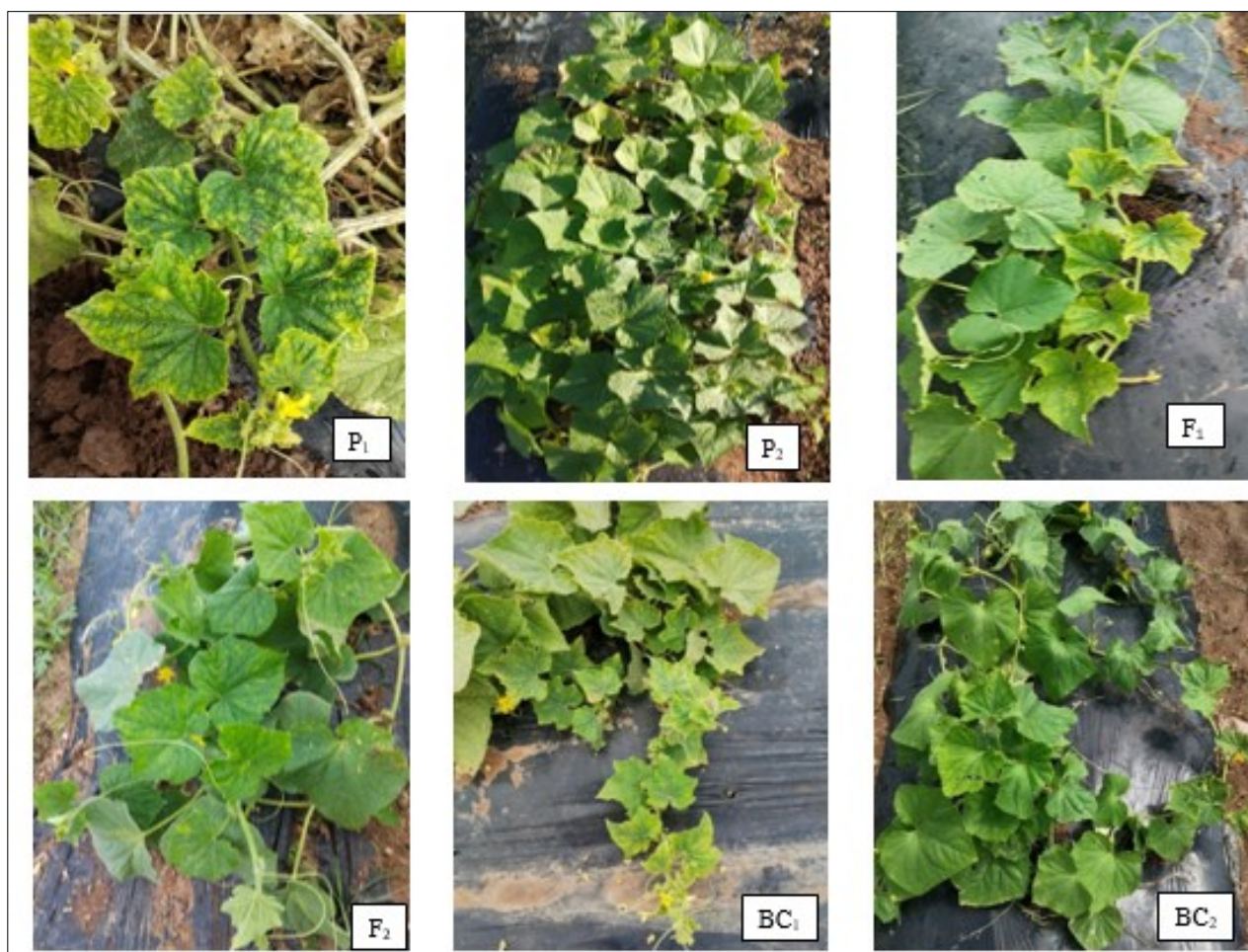


**Fig. 2.** Natural epiphytotic screening of parents and population produced from the cross of DC 773 × DC 70.

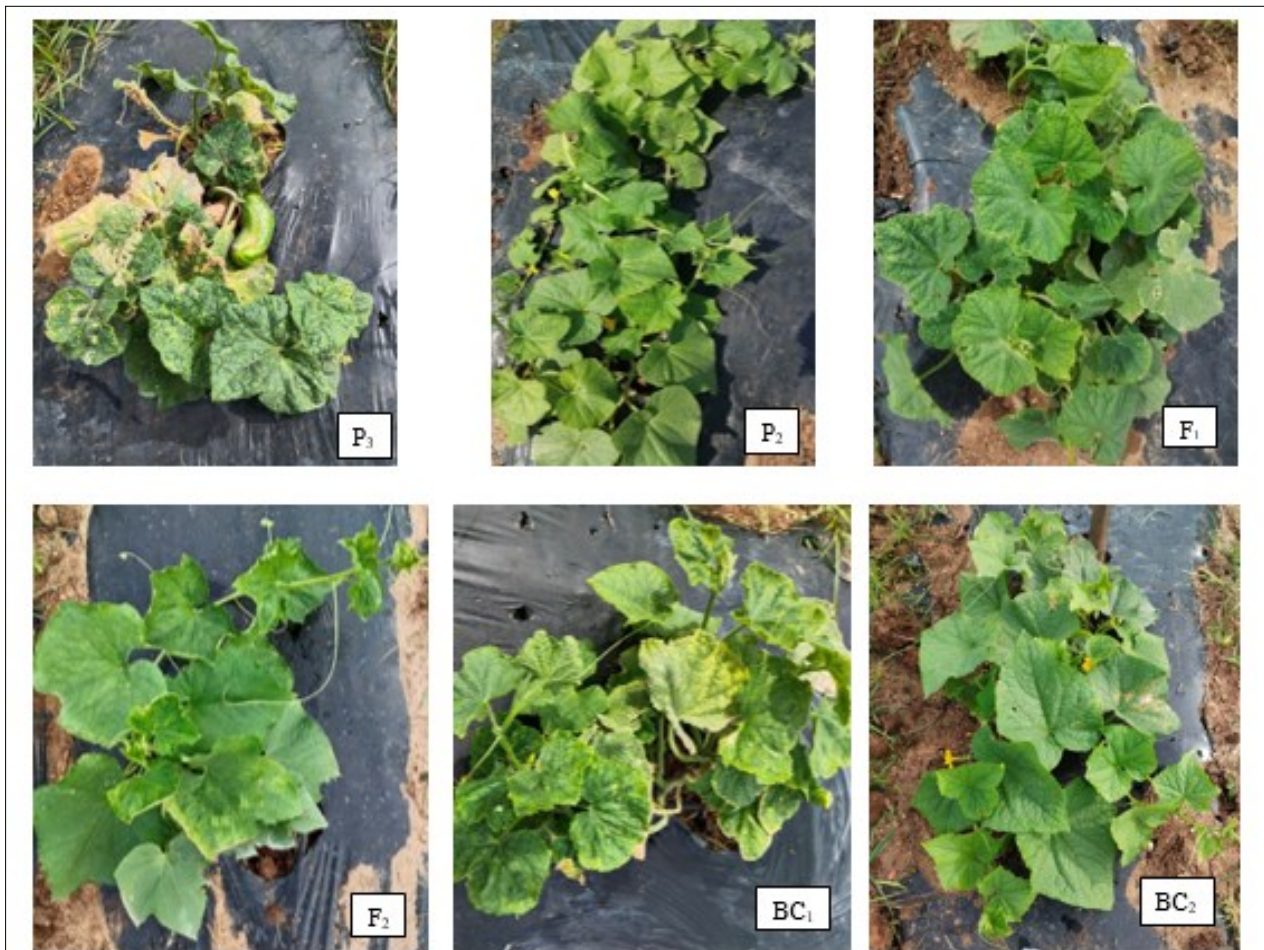


**Fig. 3.** Natural epiphytotic screening of parents and population produced from the cross of DC 769 × DC 70.

resistance for the disease pertaining to variations in the genetic makeup of resistance may result from the virus being examined together with different resistant sources under examination.

### Generation mean analysis for tomato leaf curl New Delhi virus resistance in DC 773 × DC 70 and DC 769 × DC 70 crosses

Generation mean analysis represents a few genetic techniques used to predict different genetic effects. To determine the nature of gene interaction associated with ToLCNDV resistance under natural epiphytotic screening, generation mean analysis was performed on the DC 773 × DC 70 and DC 769 × DC 70 crosses. In cross 1,  $F_2$  mean disease score lower than  $BC_1$  and  $F_1$  generations but it was higher than  $BC_2$  generation. In cross 2,  $F_2$  mean disease score was higher than  $BC_2$  generation but it was lower than the  $F_1$  and  $BC_1$  generations. These results from two crosses revealed that  $F_1$  and  $BC_1$  were directed towards susceptible parent whereas  $F_2$  and  $BC_2$  were directed towards the resistant parent. In this study, individual scaling tests (A, B, C and D) were employed in cross 1 and 2 to assess the fitness of the three-parameter model (mean, additive and dominance) on ToLCNDV symptom severity grades. Based on the results of individual scaling tests, results showed that neither cross showed any statistically significant effects. The three-parameter model was found to be appropriate due to the absence of epistasis. Hence, these crosses were referred as non-interacting crosses adopted to additive-dominance model and were consistent with the  $X^2$  analysis results. Therefore, the gene action found in this specific trait can be adequately explained by a three-parameter model. The results are in agreement with previous reports (21). The results suggest that a specific gene effect exists in the pattern of inheritance of this trait implying that additive and dominance effects of genes are ideal for explaining the inheritance pattern of this particular trait. The resistance against ToLCNDV possibly could have evolved from basic autosomal inheritance, maternal effects or the absence of distinct epistatic interactions. Similar observations have been reported for vine decline resistance in melon (22).

With respect to the results of generation mean analysis, highly significant additive (d) and dominance (h) effects were involved and played a crucial role in determining the inheritance of ToLCNDV resistance for cross 1. The primary factor involved in controlling the inheritance of this trait in cross 2 was found to be controlled by additive gene action as indicated by the significant expression of additive (d). Highly significant additive (d) gene action among crosses suggests that additive gene action played a critical role in the trait inheritance, as a result selecting a resistant line will be effective in producing disease-free lines (23). In order to produce desirable progenies, parental material would progressively influence their favourable alleles. Therefore, it would be beneficial to select character controlled by additive gene effect at an early generation stage (24). The results of generation mean analysis in both crosses suggest that magnitude of additive or dominant gene action control was more important in determining disease resistance inheritance than non-fixable gene action types (epistatic). Similar findings have been reported in cucurbits, where resistant *C. moschata* accessions PI 604506 and PI 381814 (Indian landrace) crossed with a susceptible accession PI 419083 (25). Evaluation of symptoms and viral titers from all populations, both resistant accessions inherited the same monogenic recessive genetic control. From the results, it can be observed that ToLCNDV disease resistance is governed by a monogenic recessive gene in

the genetic background of ( $P_2$ ). The predominance of additive gene action and the monogenic recessive nature of ToLCNDV resistance suggest that this trait can be efficiently exploited in practical breeding programs through early-generation selection and integration into marker-assisted selection (MAS), once tightly linked markers are identified. The resistant parent ( $P_2$ ) can be effectively used as a donor in backcross or pedigree breeding to develop stable, disease-resistant lines. However, the present findings are based solely on phenotypic generation mean analysis and the absence of molecular validation limits precise gene introgression.

### Conclusion

The inheritance study in DC 773 × DC 70 and DC 769 × DC 70 crosses indicates that resistance is inherited as a recessive trait under natural epiphytotic conditions, where susceptible plants outnumbered resistant ones in the segregating population. In the  $F_2$  population, the ratio of susceptible and resistant plants was found to be 3:1. The calculated  $\chi^2$  value was lower than the tabulated value, confirming that the inheritance pattern of ToLCNDV resistance in DC 70 is monogenic recessive nature in both crosses. From the results, it can be concluded that DC 70 showed a durable resistant reaction and the resistant source identified is a good candidate for the resistant breeding programs for ToLCNDV in cucumber. In future, studies may focus on molecular characterisation of the ToLCNDV resistance gene in DC 70 to develop linked markers for marker-assisted selection. Multi-season and multi-location validation is needed to confirm the stability of the monogenic recessive resistance. Fine mapping and gene sequencing will further elucidate the genetic basis of resistance. Evaluation against diverse ToLCNDV strains will enhance its application in cucumber breeding programs.

### Acknowledgements

The authors acknowledge the support of the Department of Vegetable Science, Horticultural College and Research Institute, Tamil Nadu Agricultural University, for providing facilities, technical assistance and guidance for this study. The authors also gratefully acknowledge the financial support provided by the Indian Council of Agricultural Research (ICAR) under the NASF programme, Krishi Bhawan, New Delhi.

### Authors' contributions

NE conducted field visits, collected data and performed the research design and analysis. RD was involved in the literature review and drafting of the manuscript. SLG carried out the statistical analysis. LS participated in the design of the study. RV reviewed and approved the final manuscript. MD and DN assisted in fieldwork and data collection. All authors read and approved the final manuscript.

### Compliance with ethical standards

**Conflict of interest:** Authors do not have any conflict of interests to declare.

**Ethical issues:** None

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