

# Identification of tomato lines based on conventional and molecular tools for breeding

Jagesh Kumar Tiwari\*, Nagendra Rai, Manish K. Singh, Lokesh K. Mishra, Gaurav Mishra and T. K. Behera

ICAR-Indian Institute of Vegetable Research, Varanasi 221 305, India

**Identifying elite lines is a major research priority for developing new hybrids/varieties. A total of 153 tomato lines were characterized based on horticultural traits, total soluble solids (TSS) and tomato yellow leaf curl virus (ToLCV) resistance under natural field conditions. Molecular markers were applied for ToLCV (*Ty-2* and *Ty-3*), late blight (*Ph-3*) and root-knot nematode (*Mi-1.2*) resistance genes. Based on horticultural traits such as average fruit weight, fruit yield, TSS and ToLCV resistance, promising lines were identified belonging to improved lines, jointless tomato, cherry tomato, beta-carotene-rich lines, germplasm and varieties. An improved line VRT-02 possessing dwarf plant type was found suitable for pot culture, whereas H-88-78-2 had a delayed and partial fruit ripening. Thus, the present study identified elite lines using conventional and molecular tools for tomato breeding.**

**Keywords:** Breeding, elite lines, horticultural traits, tomato, virus.

TOMATO (*Solanum lycopersicum* L.) is an important vegetable crop for fresh consumption and processed products. It is a rich source of nutrients, vitamins A and C, antioxidants, mainly lycopene and several compounds with health benefits. Lycopene is a powerful antioxidant having anticancerous properties<sup>1</sup>. In 2022, the world tomato production was 189.13 million tonnes (mt) from an area of 5.16 million hectares (m ha) with average productivity of 36.60 t/ha (ref. 2). India ranks second (21.18 mt) after China (67.53 mt) in tomato production from an area of 0.84 m ha area with 25.06 t/ha productivity<sup>2</sup>.

Tomato crop production faces problems of several biotic stresses. First, tomato yellow leaf curl virus (ToLCV) is the most serious disease in the tropic and subtropic regions of the world. ToLCV, transmitted by whitefly (*Bemisia tabaci*), is the major virus under the genus *Begomovirus*, which includes more than 320 species<sup>3</sup>. Wild tomato species are the main source of ToLCV resistance; e.g. *Solanum hirsutum*-derived resistance was reported using embryo rescue methods<sup>4-6</sup>. Currently, ToLCV resistance genes (*Ty-1* to *Ty-6*) originating from the wild species have been introgressed into cultivated tomatoes<sup>5</sup>. These genes

are *Ty-1/3* (chr 6 from *Solanum chilense*), *Ty-2* (chr 11 from *Solanum habrochaites*), *Ty-4* (chr 3 from *S. chilense*), recessive gene *ty-5* (chr 4, cv. Tyking or *Solanum peruvianum*) and *Ty-6* (chr 10 from *S. chilense*). This has led to the development of resistant tomato varieties all over the world<sup>7,8</sup>. Second, late blight caused by the oomycetes *Phytophthora infestans* (Mont.) de Bary is another problem of tomatoes. The late blight resistance genes are *Ph-1* (chr 7, from *Solanum pimpinellifolium*), *Ph-2* (chr 10, from *S. pimpinellifolium*), *Ph-3* (chr 9, from *S. pimpinellifolium*/*S. habrochaites*), *Ph-4* (chr 2 from *S. habrochaites*), *Ph-5-1* (chr 1, from *S. pimpinellifolium*) and *Ph-5-2* (chr 10, from *S. pimpinellifolium*)<sup>9</sup>. Third, root-knot nematode (RKN, *Meloidogyne incognita*) is one of the major nematodes affecting tomato crops, which cause severe damage to the roots. Resistance breeding has been deployed in tomato breeding using resistance genes (*Mi-1* to *Mi-8*) originating from the wild species *S. peruvianum*. The known RKN resistance genes are *Mi-1* (chr 6), *Mi-2*, *Mi-3* (chr 12), *Mi-4*, *Mi-5* (chr 12), *Mi-6*, *Mi-7*, *Mi-8*, *Mi-9* (chr 6 from *S. arcanum*), and *Mi-HT* (chr 6), of which only five genes have been mapped<sup>10</sup>. *Mi-1* is the commercially available resistance source for breeding applications.

Improvement of yield in combination with disease resistance (e.g. ToLCV, late blight and RKN) are important breeding objectives in tomatoes. With the advent of molecular markers, there has been a voluminous increase in marker-assisted selection (MAS) in tomato breeding for *Ty-2/Ty-3* resistance genes against ToLCV<sup>11</sup>. Recently, we reviewed molecular markers for various diseases and insect pests in tomato breeding<sup>1</sup>. Gene pyramiding for ToLCV, late blight and RKN resistance genes showed elite tomato lines for northern Indian farmers<sup>12</sup>, and *Ty-2* and *Ty-3* genes in tomato breeding<sup>4,5</sup>. This study aimed to evaluate the available tomato lines for horticultural traits and screen them against ToLCV in natural open-field conditions. Additionally, linked molecular markers were used to find the host resistance genes against ToLCV, late blight and RKN.

## Materials and methods

### Plant materials and field experiment

A total of 153 tomato lines consisting of improved lines (15), jointless tomato (10), cherry tomato (5), beta carotene-rich

\*For correspondence. (e-mail: jageshtiwari@gmail.com)

**Table 1.** Selected tomato varieties/lines with fruit yield, total soluble solids (TSS) and *Ty-2/Ty-3* genes

Line	Average per fruit wt (g)	TSS (°Brix)	ToLCV	
			Class	Gene
VRT-01	81.60	3.79	MR	<i>Ty-3</i>
VRT-02	23.43	4.89	MS	<i>Ty-3(H)</i>
VRT-06	120.26	4.27	R	<i>Ty-3, Ty-2(H)</i>
VRT-16-1	54.35	4.26	MS	<i>Ty-3(H)</i>
VRT-19	112.37	4.12	HR	<i>Ty-3</i>
VRT-30	52.57	4.26	HR	<i>Ty-3</i>
VRT-34	65.75	4.71	HR	<i>Ty-3</i>
VRT-50	84.84	4.50	HR	<i>Ty-3(H)</i>
VRT-51	105.51	4.11	HR	<i>Ty-3</i>
VRT-67	29.95	5.36	R	<i>Ty-3(H)</i>
ToLCV-16	45.42	3.62	R	<i>Ty-3(H)</i>
ToLCV-28	68.67	4.04	R	<i>Ty-3</i>
ToLCV-32	75.82	4.22	HR	<i>Ty-3(H)</i>
H-88-78-1	39.20	4.07	HR	<i>Ty-2</i>
H-88-78-2	188.20	5.11	HR	<i>Ty-3</i>
Cheti tomato	12.8	8.32	R	<i>Ty-2</i>
Chikugrande	20.8	4.92	MR	<i>Ty-3(H)</i>
C-14-4	121.6	3.84	HR	<i>Ty-2(H), Ty-3(H)</i>
EC-520059	6.0	4.25	HR	<i>Ty-3</i>
EC-521047	44.6	5.29	HR	<i>Ty-3</i>
EC-538380	7.6	6.14	HR	<i>Ty-3(H)</i>
EC-620312	109.6	4.48	HR	<i>Ty-3</i>
EC-620402	86.6	4.56	R	<i>Ty-3</i>
EC-620419	128.4	3.84	HR	<i>Ty-2(H), Ty-3(H)</i>
EC-620435	50.6	4.34	R	<i>Ty-3, Ty-2(H)</i>
EC-620456	130.8	3.16	R	<i>Ty-3</i>
EC-620464	98.8	3.06	R	<i>Ty-2(H)</i>
EC-620465	87.6	4.78	R	<i>Ty-2, Ty-3</i>
EC-620474	104.4	3.42	R	<i>Ty-3</i>
EC-620494	89.6	3.82	HR	<i>Ty-3(H)</i>
EC-620533	164.8	3.23	R	<i>Ty-3, Ty-2(H)</i>
EC-625651	66.8	3.68	HR	<i>Ty-3</i>
EC-625652	53.6	4.20	R	<i>Ty-3</i>
EC-625660	57.6	3.92	R	<i>Ty-3</i>
EC-700936	94.4	4.07	R	<i>Ty-3, Ty-2(H)</i>
EC-715384	81.2	4.29	R	<i>Ty-2</i>
Indam 2103-6	72.5	3.68	MR	<i>Ty-3</i>
TLBR-3	49.2	4.19	S	<i>Ty-2</i>
Kashi Vishesh	107.0	3.48	HR	<i>Ty-3</i>
Kashi Abhay	121.0	3.27	S	<i>Ty-2, Ty-3(H)</i>
Kashi Aman	109.0	3.41	HR	<i>Ty-3</i>
Kashi Amul	119.0	4.25	HR	<i>Ty-3</i>
Kashi Chayan	120.2	3.64	HR	<i>Ty-3</i>
Pb. Barkha-1	144.4	3.76	HR	<i>Ty-3</i>
Sankranti	49.6	4.15	R	<i>Ty-2</i>
Vaibhav	45.6	4.72	HR	<i>Ty-2</i>
Mean	72.16	4.44	—	—
CD (5%)	7.49	2.22	—	—

lines (22), germplasm (78) and varieties (23) were used in this study ([Supplementary Table 1](#)). Experiments were conducted in the field of randomized block design (RBD) for two years (2021–22 and 2022–23) in the main (*rabi* or winter) crop season at the research farm of the ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh under subtropical plain conditions (25.18°N and 82.83°E). The seeds were sown during September (second week), and 25-day-old seedlings were transplanted during October (first week) in both years. Twenty seedlings of

each line were transplanted and grown on the raised bed in paired-row at 60 × 45 cm<sup>2</sup> spacing in three replications following standard cultural practices.

#### *Evaluation for horticultural traits*

Plant phenotype, yield and its component traits were recorded in all lines for each trait for two years. Data were collected from 10 randomly selected plants. The measurable traits under observation were days to first fruit picking

**Table 2.** Key traits of elite tomato lines recorded over four years (2019–20, 2020–21, 2021–22 and 2022–23)

Line	Key traits
VRT-02	Determinate, dwarf plant, small fruit size (20–25 g), round fruit shape, suitable for pot culture and kitchen garden.
VRT-06	Semi-determinate, large fruit size (115–120 g), oval fruit shape, medium firmness, resistant to ToLCV.
VRT-19	Semi-determinate, large fruit size (110–115 g) with green shoulder, flat-round shape, highly resistant to ToLCV.
VRT-30	Determinate, medium fruit size (50–55 g), round shape, highly resistant to ToLCV.
VRT-34	Semi-determinate, medium fruit size (60–65 g), oval shape, medium firmness, highly resistant to ToLCV, drought stress tolerant.
VRT-50	Semi-determinate, large fruit size (80–85 g), round shape, medium firmness, highly resistant to ToLCV.
VRT-51	Semi-determinate, medium fruit size (100–105 g), round shape, medium firmness, highly resistant to ToLCV.
ToLCV-28	Semi-determinate, medium fruit size (65–70 g), flat fruit shape, resistant to ToLCV, highly serrated leaf.
ToLCV-32	Semi-determinate, large fruit size (75–80 g), oval fruit shape, highly resistant to ToLCV.
H-88-78-1	Semi-determinate, small fruit size (35–40 g), round fruit shape, medium firmness, highly resistant to ToLCV.
H-88-78-2	Semi-determinate, very large fruit size (185–190 g), flat-round fruit shape, medium firmness, yellow-green fruit colour, highly resistant to ToLCV, delayed/partial ripening.

(from the date of transplanting, i.e. DAT), days to last fruit picking, fruit length (cm, i.e. polar diameter), fruit diameter (cm, i.e. equatorial diameter), locule number, pericarp thickness (cm, measured using a Vernier calliper), average per fruit weight (g, measured based on the average of ten fruits), fruit yield/plant (kg), total soluble solid (TSS, °Brix, measured by a hand refractometer) and plant growth habit (determinate, indeterminate and semi-determinate). Besides, qualitative traits were recorded based on physical appearance, such as fruit shape, fruit colour, fruit firmness and special traits associated with the lines. Pooled data from two years of horticultural traits data were statistically analysed using pooled analysis using the OPSTAT software<sup>13</sup>. Test for homogeneity of variance and Tukey's honestly significant difference (HSD test) ( $P < 0.05$ ) were performed using XLSTAT (<https://www.xlstat.com/>).

#### Field screening for tomato yellow leaf curl virus resistance

All lines were evaluated for ToLCV resistance under natural field conditions for two years using control varieties like Punjab Chuhara (susceptible), Kashi Aman (resistant) and Kashi Chayan (resistant). Viral infection was recorded based on per cent disease infection on all plants at 45 and 90 days after transplanting. Disease severity scores were calculated using a six-point scale (0–5) method – score 0 (0–5%, HR = highly resistant), 1 (5.1–12.0%, R = resistant), 2 (12.1–25%, MR = moderately resistant), 3 (25.1–50.0% MS = moderately susceptible), 4 (50.1–75%, S = susceptible) and 5 (75.1–100%, HS = highly susceptible)<sup>14</sup>.

#### Molecular marker assays

All lines (153 nos) were tested for disease resistance against ToLCV, late blight and RKN using gene-based sequence characterized amplified region (SCAR) markers ([Supplementary Table 2](#)). Leaf tissues were used for DNA analysis employing the method as described earlier<sup>4</sup>. The polymerase chain reaction (PCR) was performed in a total volume of 25 µl containing 2 µl DNA (100 ng), 1× PCR buffer

consisting of 2.5 mM/l  $MgCl_2$ , 200 µM/l dNTP, 0.5 µM/l of primer and 1 U of *Taq* polymerase (Genei Laboratories Pvt Ltd, Bengaluru, India). The PCR cycle was run for denaturation at 94°C for 4 min, 36 cycles (denaturation at 94°C for 1 min, annealing at 55°C for 1 min, and extension at 72°C for 1 min) and extension at 72°C for 10 min in a thermal cycler (BIO-RAD, CA, USA). PCR products were resolved on 1.5% agarose gel and documented using the Gel-Doc system (Alpha Innotech, CA, USA).

## Results and discussion

### Horticultural traits performance

A total of 153 tomato genotypes were evaluated during the winter (main/*rabi*) crop season under field conditions for two years. Observations were recorded for 12 different horticultural traits, TSS and ToLCV resistance. Significant statistical differences ( $P < 0.05$ ) were observed amongst the genotypes for all quantitative traits (Table 1 and [Supplementary Table 1](#)). Among the improved lines, early genotypes based on days to first picking were VRT-67 (70.33 DAT), followed by VRT-30 or VRT-34 (70.67 DAT). On the contrary, H-88-78-2 was very late and highly delayed with partial fruit ripening. In other categories, days to first fruiting were shortest in KB-Jointless (71.67 DAT), VRCRT-9 (60.67 DAT, cherry tomato), KB-9 (beta-carotene), EC-625660 (germplasm) and Uttakal Pragya (variety). A few elite tomato lines were identified for key traits with consistent performance over the years (Table 2). Studies showed that genetic analysis based on yield and its component traits identified good combinations for tomato breeding<sup>15,16</sup>.

Fruit traits showed significant variations in the genotypes studied. The fruit length recorded significantly highest value in improved line VRT-06 (6.18 cm), jointless EC-605037 (6.73 cm), cherry tomato VRCRT-9 (3.19 cm), beta-carotene KB-33 (4.61 cm), germplasm Unique-1 (7.1 cm) and variety Kashi Abhay (6.4 cm). Fruit diameter was significantly highest in improved line H-88-78-2 (6.60 cm), jointless EC-538441-3 (5.38 cm), cherry tomato VRCRT-14

(2.08 cm), beta carotene line KB-32 (5.27 cm), germplasm EC-620419 (6.92 cm) and variety Uttkal Urvashi (6.16 cm). Locule number was found maximum in improved line H-88-78-2 (4.60), followed by VRT-19 (4.49), jointless EC-538441-3 (3.82), beta carotene line KB-1 (4.82), germplasm Unique-1 (13) and variety Hisar Arun (5.8). Likewise, pericarp thickness was observed maximum in H-88-78-2 (0.68 cm), followed by VRT-06 (0.55 cm), jointless EC-605094 (0.71 cm), cherry tomato VRCYT-3 (0.26 cm), beta carotene KB-20 (0.65 cm), germplasm EC-620419 (0.74 cm) and variety Uttkal Raja (0.74 cm) ([Supplementary Table 1](#)). Pericarp thickness and jointless traits are important criteria for processing tomatoes and nutrition-rich tomatoes that are essential for health benefits<sup>17</sup>.

Fruit yield is the most economically important trait. Average per fruit weight was observed maximum in H-88-78-2 (188.20 g), followed by VRT-06 (120.26 g), VRT-19 (112.37 g) and VRT-51 (105.51 g). VRT-02 was identified with the lowest average per fruit weight (23.43 g), had dwarf plant type and was therefore suitable for pot culture and kitchen gardens. In other categories, maximum average per fruit weight (g) was recorded in jointless EC-605037 (100.50 g), cherry tomato VRCRT-5 (9.59 g), beta-carotene KB-20 (97 g), germplasm Unique-1 (265.20 g) and variety Kashi Anupam (147.60 g). On the other hand, maximum fruit yield per plant was observed in improved lines ToLCV-28 (2.12 g), VRT-19 (2.09 g), VRT-34 (1.96 g), VRT-50 (1.94 g), VRT-51 (1.78 g), jointless EC-605037 (2.53 g), cherry tomato VRCRT-5 (1.33 g), beta-carotene line KB-3-1 (1.26 g), germplasm EC-620407 (5.51 g) and variety Uttkal Raja (4.9 g). TSS is the most important criterion for processing tomatoes. Maximum TSS was observed in improved line VRT-67 (5.36 °Brix), jointless EC-695037 (5.37 °Brix), cherry tomato VRCYT-3 (8.22 °Brix), beta-carotene line KB-6 (5.45 °Brix), germplasm Cheti tomato (8.32 °Brix) and variety Hisar Lalima (5.06 °Brix) ([Supplementary Table 1](#)). Similar findings have been reported earlier for processing and other yield traits in tomatoes<sup>17</sup>. Thus, we identified promising lines with high-yielding and high TSS suitable for processing tomatoes.

Regarding fruit shape, overall, most lines were a round shape, except VRT-19, H-88-78-2, EC-625651, EC-538408, EC-620486 and EC-625660, which were flat-round, and VRT-34, which was oval. Fruit firmness is one of the important parameters of tomatoes for long-duration storage and distant market transport<sup>18</sup>. The improved lines VRT-01, VRT-06, VRT-34, VRT-50, VRT-51, ToLCV-32 and H-88-78-1, and varieties Kashi Amul, Kashi Aman, Palam Pink and Uttkal Urvashi had medium fruit firmness, whereas the others were loose skin. Jointless VRT-69, EC-605037, EC-538441-2 and cherry tomato VRCRT-15 had tough firmness, while germplasm EC-620417, EC-620474 and EC-620533 had tough fruits. All the lines were red in colour, except H-88-78-2, which was green-yellow due to partial ripening and yellow/orange in beta-carotene-rich lines and

cherry tomato. Plant growth habit was observed determinate in improved lines (VRT-02, VRT-16-1 and VRT-30), cherry tomato (VRCRT-15) and beta-carotene lines (KB-1, KB-2 and KB-32), and indeterminate type in cherry tomato (VRCYT-3, VRCRT-5, VRCRT-9 and VRCRT-14) and germplasm (EC-521047, EC-538440, EC-520059 and EC-538380), and cv. Uttkal Pragya, whereas the other lines were semi-determinate ([Supplementary Table 1](#)). Some unique traits were noticed in a few lines, e.g. VRT-02 was dwarf plant-type and, therefore, suitable for pot culture and kitchen gardens or vertical farming. VRT-06 had a large fruit size, VRT-19 also had a large fruit size with a green shoulder on the fruit, VRT-34 was moisture stress-tolerant, ToLCV-28 had highly serrated leaves, and, most importantly, H-88-78-2 had delayed partial fruit ripening. Horticultural traits have been studied for yield and its component traits, including processing attributes in tomato<sup>18</sup>.

#### *Field screening for tomato yellow leaf curl virus resistance*

All the lines were screened for ToLCV resistance under natural field conditions for two years, and significant variations were recorded ( $P < 0.05$ ) (Table 1 and [Supplementary Table 1](#)). Virus infection was measured based on whole plant symptoms (%). A few improved lines were categorized into highly resistant (HR: 0–5% infection; VRT-19, VRT-30, VRT-34, VRT-50, VRT-51, ToLCV-32, H-88-78-1 and H-88-78-2) and resistant category (R: 5.1–12% infection; VRT-06, VRT-67, ToLCV-16, ToLCV-28). In addition, other highly resistant lines in different groups were jointless (EC-695037, EC-605037, EC-538441-2, EC-605094, and New-Jointless), cherry tomato (VRCYT-3, VRCRT-5, VRCRT-9 and VRCRT-15) and beta-carotene lines (KB-2, KB-3-1, KB-3-2, KB-5, KB-10, KB-17 and KB-20). A good number of germplasm (HR: 24, R: 42, MR: 8) and varieties (HR: 12, R: 4, MR: 3) were also identified ([Supplementary Table 1](#)). Similar results were reported in tomatoes against ToLCV resistance by field screening, and resistant sources were identified for breeding applications<sup>4,5</sup>.

#### *Molecular marker assays for ToLCV, late blight and root-knot nematode resistance genes*

All lines were tested for host resistance genes using molecular markers for ToLCV (*Ty-2* and *Ty-3*), late blight (*Ph-3*) and RKN resistance (*Mi-1.2*) (Table 1 and [Supplementary Table 1](#)). Some of the improved lines, such as VRT-01, VRT-06, VRT-19, VRT-30, VRT-34, VRT-51, ToLCV-28 and H-88-78-2 showed the presence of the *Ty-3* resistance gene, while the *Ty-2* gene was found in delayed and partial-ripening genotype H-88-78-1. Our findings are consistent with studies on molecular markers-based gene pyramiding of *Ty-2* and *Ty-3* genes for ToLCV resistance in tomato

breeding<sup>4,5</sup>. In this study, *Ty-3* gene was recorded in many germplasm and varieties (Table 2). This gene was found in germplasm Cheti tomato, EC-620465, EC-715384, TLBR-3, and varieties Kashi Abhay, Sankranti and Vaibhav. On the other hand, the late blight resistance gene (*Ph-3*) was observed in only two genotypes, viz. VRT-01 and VRT-16-1. RKN resistance gene *Mi-1.2* was found in only four germplasms. In other genotypes, no amplification or some heterozygous forms were noticed. A study showed the identification of virus resistance sources by screening local and foreign tomato varieties in Kazakhstan using genetic markers<sup>18</sup>. Recently, gene-based markers for the tomato yellow leaf curl virus resistance gene *Ty-3* have been developed<sup>19</sup>. A co-dominant SCAR marker was developed to detect the begomovirus-resistance *Ty-2* locus derived from *S. habrochaites* in tomato germplasm<sup>20,21</sup>. A study showed that the *Ph-3* gene from *S. pimpinellifolium* encoded CC-NBS-LRR protein, conferring late blight resistance<sup>22</sup>. Notably, gene pyramiding in tomatoes with ToLCV, late blight and RKN resistance has been employed to develop elite lines with multiple disease-pest resistance<sup>12</sup>. Overall, the present study has identified potential tomato lines for gene pyramiding using molecular and conventional approaches.

## Conclusion

We identified a group of elite tomato genotypes with high yielding and other horticultural traits, high TSS and ToLCV resistance; a few lines had late blight and RKN resistance. Based on fruit yield, promising genotypes were improved lines (VRT-06, VRT-19, VRT-34 and VRT-51), jointless (EC-605037 and EC-695037), cherry tomato (VRCYT-3, VRCRT-5, VRCRT-14 and VRCRT-15), beta-carotene line (KB-3-1, KB-3-2, KB-20, KB-32), and many germplasm and varieties. The genotypes containing high TSS (>5 °Brix) were improved line (VRT-67), jointless (EC-695037), cherry tomato (VRCYT-3) and germplasm (Cheti tomato, EC-521047, EC-538380, EC-620362, and EC-620510). Importantly, we identified ToLCV-resistant improved lines (VRT-06, VRT-19, VRT-30, VRT-34, VRT-50, VRT-51 and VRT-67), and others. A few lines were identified for special features, such as VRT-02 for pot culture. The line H-88-78-2 is known for delayed and partial fruit ripening, which is a good line for introgression of non-ripening genes to extend the shelf-life in tomatoes.

1. Tiwari, J. K. *et al.*, Progress in marker-assisted selection to genomics-assisted breeding in tomato. *Crit. Rev. Plant Sci.*, 2022, **41**(5), 321–350.
2. <https://www.fao.org/faostat/en/#data> (accessed on 17 June 2023).
3. Prasad, A., Sharma, N., Hari-Gowthem, G., Muthamilarasan, M. and Prasad, M., Tomato yellow leaf curl virus: impact, challenges, and management. *Trends Plant Sci.*, 2020, **25**(9), 897–911.
4. Prasanna, H. C., Kashyap, S. P., Krishna, R., Sinha, D. P., Reddy, S. and Malathi, V. G., Marker assisted selection of *Ty-2* and *Ty-3* carrying tomato lines and their implications in breeding tomato leaf curl disease resistant hybrids. *Euphytica*, 2015, **204**, 407–418.

5. Prasanna, H. C. *et al.*, Pyramiding *Ty-2* and *Ty-3* genes for resistance to monopartite and bipartite tomato leaf curl viruses of India. *Plant Pathol.*, 2015, **64**, 256–264.
6. Vidavsky, F. and Czosnek, H., Tomato breeding lines resistant and tolerant to tomato yellow leaf curl virus issued from *Lycopersicon hirsutum*. *Phytopathology*, 1998, **88**(9), 910–914.
7. El-Sappah, H. A. *et al.*, Natural resistance of tomato plants to tomato yellow leaf curl virus. *Front. Plant Sci.*, 2022, **13**, 1081549.
8. Ren, Y., Tao, X., Li, D., Yang, X. and Zhou, X., *ty-5* confers broad-spectrum resistance to Geminiviruses. *Viruses*, 2022, **14**(8), 1804.
9. Mazumdar, P., Singh, P., Kethiravan, D., Ramathani, I. and Ramakrishnan N., Late blight in tomato: insights into the pathogenesis of the aggressive pathogen *Phytophthora infestans* and future research priorities. *Planta*, 2021, **253**(6), 119.
10. El-Sappah, A. H. *et al.*, Tomato natural resistance genes in controlling the root-knot nematode. *Genes (Basel)*, 2019, **10**(11), 925.
11. Foolad, M. R. and Panthee, D. R., Marker-assisted selection in tomato breeding. *Crit. Rev. Plant Sci.*, 2012, **31**, 93–123.
12. Kumar, A., Jindal, S. K., Dhaliwal, M. S., Sharma, A., Kaur, S. and Jain, S., Gene pyramiding for elite tomato genotypes against ToLCV (*Begomovirus* spp.), late blight (*Phytophthora infestans*) and RKN (*Meloidogyne* spp.) for northern India farmers. *Physiol. Mol. Biol. Plants*, 2019, **25**(5), 1197–1209.
13. Sheoran, O. P., Tonk, D. S., Kaushik, L. S., Hasija, R. C. and Pannu, R. S., Statistical software package for agricultural research workers. In *Recent Advances in Information Theory, Statistics & Computer Applications* (eds Hooda, D. S. and Hasija, R. C.), Department of Mathematics Statistics, Chaudhary Charan Singh Haryana Agricultural University, Hisar, 1998, pp. 139–143.
14. Banerjee, M. K. and Kalloo, G., Sources and inheritance of resistance to leaf curl virus in *Lycopersicon*. *Theor. Appl. Genet.*, 1987, **73**, 707–710.
15. Singh, R. K., Rai, N., Singh, M., Singh, S. N. and Srivastava, K., Genetic analysis to identify good combiners for ToLCV resistance and yield components in tomato using interspecific hybridization. *J. Genet.*, 2014, **93**(3), 623–629.
16. Singh, R. K., Rai, N., Lima, J. M., Singh, M., Singh, S. N. and Kumar, S., Genetic and molecular characterisations of tomato leaf curl virus resistance in tomato (*Solanum lycopersicum* L.). *J. Hortic. Sci. Biotechnol.*, 2015, **90**(5), 503–510.
17. Tiwari, J. K., Behera, T. K., Rai, N., Yerasu, S. R., Singh, M. K. and Singh, P. M., Tomato breeding for processing in India: current status and prospects. *Veg. Sci.*, 2022, **49**(2), 123–132.
18. Pozharskiy, A. *et al.*, Screening a collection of local and foreign varieties of *Solanum lycopersicum* L. in Kazakhstan for genetic markers of resistance against three tomato viruses. *Heliyon*, 2022, **8**(8), e10095.
19. Shen, X. *et al.*, The NLR protein encoded by the resistance gene *Ty-2* is triggered by the replication associated protein Rep/C1 of tomato yellow leaf curl virus. *Front. Plant Sci.*, 2020, **11**, 545306.
20. Dong, P., Han, K., Siddique, M. I., Kwon, J.-K., Zhao, M., Wang, F. and Kang, B.-C., Gene-based markers for the tomato yellow leaf curl virus resistance gene *Ty-3*. *Plant Breed. Biotechnol.*, 2016, **4**, 79–86.
21. Garcia, B. E., Graham, E., Jensen, K. S., Hanson, P., Mejia, L. and Maxwell, D. P., Co-dominant SCAR marker for detection of the begomovirus-resistance *Ty-2* locus derived from *Solanum habrochaites* in tomato germplasm. *Rep. Tomato Genet. Coop.*, 2007, **57**, 21–24.
22. Zhang, C. *et al.*, The *Ph-3* gene from *Solanum pimpinellifolium* encodes CC-NBS-LRR protein conferring resistance to *Phytophthora infestans*. *Theor. Appl. Genet.*, 2014, **127**, 1353–1364.

**ACKNOWLEDGEMENTS.** We thank the competent authority for necessary support under the ICAR CRP-Hybrid Technology (Tomato) project, and the ICAR-LBS Award project (to J.K.T.).

Received 23 July 2023; revised accepted 16 November 2023

doi: 10.18520/cs/v126/i5/569-573