

# Development of high yield and tomato yellow leaf curl virus (TYLCV) resistance using conventional and molecular approaches: A review

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**Abstract:** Tomato (*Solanum lycopersicum* L.) belonging to the family Solanaceae is the second most consumed and cultivated vegetable globally. Since the ancient time of its domestication, thousands of cultivated tomato varieties have been developed targeting an array of aspects. Among which breeding for yield and yield-related traits are mostly focused. Cultivated tomato is extremely genetically poor and hence it is a victim for several biotic and abiotic stresses. Among the biotic stresses, the impact of viral diseases is critical all over tomato cultivating areas. Improvement of tomato still largely rely on conventional methods worldwide while molecular approaches, particularly Marker Assisted Selection (MAS) has become popular across the globe as a fast, low cost and precise tool which is essential in present day plant breeding. In this review paper, breeding tomato for high yield and viral disease resistance, particularly to tomato yellow leaf curl virus disease (TYLCVD) using conventional and molecular approaches will be discussed. Lining up of this set of information will be useful to those who are interested in tomato variety development with high yielding and TYLCVD resistance.

## Introduction

Tomato (*Solanum lycopersicum* L.) is an annual crop that is considered the second most consumed vegetable in the world, with production exceeding 180 million tons cultivated on over 4.8 million hectares (Food, 2018). It belongs to the Solanaceae family, which consists of about 3000–4000 species with approximately 96 genera across three subfamilies of economically important crops such as eggplant, tobacco, petunia, potato, and pepper. The global tomato industry is valued at more than fifty billion dollars (Mattoo and Handa, 2017). Tomato market comprises of fresh market and processing industries. Considering the volume consumed, tomato contributes significantly to the dietary intake of essential vitamins and minerals (Willcox *et al.*, 2003). Tomatoes, both processed and fresh market types, are a rich source of the dietary antioxidant lycopene, having the ability to protect cells from cancer (Giovannucci, 1999). The mountainous regions of the Andes, which comprise of

the current Chile, Ecuador, and Peru, were believed to be the origin of tomato (Dhaliwal *et al.*, 2020). The wild relatives and cultivated tomato had a similar karyotype and chromosome number of  $2n = 24$  (Foolad, 2007). With the domestication process started around 600 years ago (Rick, 1978) genetic variability of cultivated tomato is narrowed. This is because, during the domestication and evolution process, the cultivated tomato went through several genetic tailbacks as a result of extreme inbreeding and imposed selective breeding.

Hence, these events cause a reduction in genetic variation among the cultivated tomato. Therefore, it is estimated that the cultivated tomato contains approximately 5% less genome of the genetic variability of their wild relatives (Dhaliwal *et al.*, 2020).

At the end of the 19th century (late 1800's) farmers were used to the cultivation of open-pollinated cultivars (Heirlooms), while in the middle of the 20th century breeding of hybrid cultivars were initiated where 'Single Cross' being the first-ever tomato hybrid cultivar (Bai and Lindhout, 2007). After the invention of hybrid cultivars in mid of the 20th century, the whole tomato industry was dominated by various tomato hybrids. In 1994–1st

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transgenic cultivar 'Flavr-Savr'<sup>TM</sup> (Acquaah, 2012) was released. However, its popularity decreased within a few years of release due to unfavorable qualities. From the time of development of heirlooms up to transgenics, the tomato crop is highly affected by a number of diseases and environmental factors. Among these, viral diseases are considerably devastating. In particular, tomato yellow leaf curl disease (TYLCD) transmitted by *Bemisia tabaci* is a major viral disease across the world (Lapidot and Friedmann, 2002). Graphical plant-virus Interaction of TYLCV is reported by Prasad et al. (2020). TYLCD is a global limitation to tomato production and remains one of the most devastating viral diseases of tomato. Most of the cultivated tomato is susceptible to this disease showing symptoms such as flower abortion, severe stunting, leaves cupping, curling, and yellowing, which can result in up to 100% yield losses (Yan et al., 2018). However, many accessions of tomato wild relatives have been identified as TYLCV resistant sources (Yan et al., 2018). Meanwhile, Firdaus et al. (2012) has reported wild relatives of tomato with resistance to TYLCV vector (*S. pennellii* Correll, *S. habrochaites* S. Knapp, *S. habrochaites* f. *glabratum*, *S. pimpinellifolium* L., *S. chilense* (Dunal) Reiche). However, TYLCV has become difficult to control due to several reasons. One major reason is the polyphagous nature of TYLCV, where this virus-host range from many commercial crops viz., lisanthus (*Eustoma grandiflorum* (Raf.) Shinners), *Petunia* Juss., common bean (*Phaseolus vulgaris* L.), tobacco (*Nicotiana tabacum* L.), chili pepper (*C. chinense* Jacq.), sweet pepper (*Capsicum annuum* L.) and tomato (*S. lycopersicum*), and several common weeds (Diaz-Pendon et al., 2010). Up to now, introgression of TYLCV resistant genes from wild relatives to elite lines of cultivated tomato has paved way for the breeding of high-yielding tomato cultivars with TYLCV resistance (Vidavski et al., 2008).

Varietal improvement program of tomato during the last century is based on several standard breeding techniques such as hybridization followed by pedigree selection and backcrossing of preferred characters from one parent into another that resulted in the generation of improvement tomato hybrids and varieties with high yield and quality. Improvement in tomato occurred as a result of continuous exploitation of germplasm and incorporation of desirable genes into the genetic background of elite cultivars. Traditional breeding has not only developed genotypes with dominant and monogenic resistance for controlling certain plant pathogens or a combination of resistance F1 hybrids but has also aided the acquisition of good agronomic traits such as increase shelf-life and firmness suitable for long distant shipping, well-adapted genotypes, uniform ripening, earliness, fruit setting, and high fertility rate. Hence, the objectives of this review are to describe the recent methods of developing a durable high yielding tomato genotype with resistance to tomato yellow leaf curl virus (TYLCV) through conventional and molecular approaches and to comprehensively review the available information on TYLCV and yield genes, marker-assisted selection, gene transformation, and QTL analysis.

## Breeding Goals of Tomato across the Time

The tomato industry has two main categories, viz. fresh market and processing tomatoes (Arah et al., 2015), which makes the breeding objectives to be dynamic and varied across time. For example, tomato breeding in the 1970s mainly focused on yield; however, this scenario changed in the 1980s, where the major goal was focused mainly on shelf life. During the 1990s, the trend of tomato breeding was focused on taste, and in the 2000s, much attention has focused on the nutritional qualities and development of resistant varieties against pests and diseases (Osei et al., 2018). Apart from the variability along the time, there is a considerable variation in tomato breeding goals depend on the location, need of the community, and available resources (Acquaah, 2012; Rick, 1988).

The earliest approach in tomato breeding was achieved along with the domestication process, where farmers selected tomato cultivars with larger fruit size, lesser rates of dormancy, and higher rates of self-pollination. With the characteristic of self-pollination, earlier tomato cultivars were open-pollinated, and the selection was based on the uniform fruit shape, color, and size. Hence, these selected genotypes are referred to as "heirlooms" which were more or less similar to their parents (Watson, 1996; Bai and Lindhout, 2007). Towards the mid of the twentieth century, the new era of tomato breeding was commenced with the development of hybrid tomato cultivars, over leading the popularity of heirlooms. Hybrids are cultivars with combinations of commercially desirable characteristics or traits. The phenomenon called hybrid vigor or heterosis is generally associated with an increased yield (Bradshaw, 2016). Apart from hybrid vigor, hybrids are preferred to be developed by the breeders for uniformity, protection from unauthorized reproduction, and better resistance to pests and diseases (Fentik, 2017; Acquaah, 2012). With the development of the first hybrid tomato cultivar "Single Cross" (Bai and Lindhout, 2007) in 1946; breeders, producers, and growers were plagued by the benefits associated with the hybrid cultivars, and since both the fresh market and processing tomato industries were dominated by hybrid varieties (Fufa et al., 2009).

## Conventional Methods of Tomato Breeding

Before the development of molecular markers and genetic engineering tools, tomato breeding mostly depended on conventional methods. With the domestication, which began in South America, breeding methods such as selection (Mass selection) of better cultivars and introduction to the rest of the world was accomplished by the local farmers (Lin et al., 2014). The pedigree method is another method used in tomato breeding where controlled crossing and selection of superior plants from early generations (F2 generation), and continued until genetic purity is reached (Kaloo, 2012). Also, hybridization followed by pedigree selection is one of the most common methods used in tomato breeding, while back cross-breeding is used to transfer traits such as disease resistance to cultivated tomato (Fentik, 2017). Generally, most of the early conventional breeding programs were

practiced as combinations of backcross followed by the pedigree selection, which resulted in more successful cultivars. Casali and Tigchelaar (1975) proposed the single seed descendant method specially focused on low heritable traits. However, these findings showed that a single seed descendant method was not efficient as compared with the pedigree selection method.

Among the conventional techniques, hybrid breeding is the most intensively used technique in the development of new tomato varieties, hence, almost all commercial cultivated tomato cultivars are hybrids (van de Wiel et al., 2010). This hybrid development was achieved using complementary inbred lines as two parental lines. Hybrid vigor or heterosis is the phenomenon that adds value to the hybrids. Generally, due to the hybrid vigor, hybrids are more superior in many qualities than their parents. Though the percentage of contribution is not fully defined, over-dominance and additive effects are attributed to the hybrid vigor (Birchler et al., 2010; Chen, 2013). These hybrids are popular and accepted by many growers around the world for the fact that they allow an easy combination of many economically important traits such as disease-resistant genes that are dominant in gene action.

In hybrid production, the removal of anthers from the female plant (emasculation) is done manually. This tedious and laborious procedure has been replaced by the discovery of different techniques. As a solution, a set of nuclear recessive genes responsible for male sterility has been studied by Kaul (1991). However, this technique was not fully practiced or commercialized due to the nonheritable nature of the male-sterile character. In hybrid production, combining ability analysis is important for the selection of the best hybrids derived from crosses between selected inbred lines and the elite lines (Peralta et al., 2006). Kaushik and Dhaliwal (2018) reported the screening of best cross combinations based on multiple trait performance, including fruit yield and resistance to tomato yellow leaf curl virus (TYLCV), using diallele analysis. The selected hybrids can be further evaluated in multi-location replicated trials to short-list the broadly adapted crosses with lower genotype  $\times$  environment interaction. Peirce (1991) revealed that  $G \times E$  interaction is strongly significant to the marketable yield. The effect of  $G \times E$  for different fruit quality and plant characteristics have not given consistent results in all attempts. Even with many advancements of conventional breeding methods, it is obvious the difficulty of combining many desirable characteristics together into a single variety. On the other hand, the gene action of a quantitative trait is difficult to predict because the ultimate output or level of expression of traits are governed by multiple genes and are highly influenced by the environment (Osei et al., 2018).

Embryo rescue is another method where callus is raised from the excised embryos and regenerating plants. This method was reported as the only successful method for the cross between Tomato (*Solanum lycopersicum*) and *Solanum peruvianum* L. (Poysa, 1990). Similarly, Acquah (2012) reported the use of embryo rescue between crosses of the cultivated tomato and wild species *S. peruvianum* and *S. chilense* to use in gene transfer from wild relatives to the

cultivated tomato. The monosomic line is another method used in tomato breeding where the production of aneuploid plants with extra chromosomes from donor species with desirable genes (Pertuzé et al., 2003). Mutagenesis also plays a considerable role in tomato breeding, and yet the method is being used in many countries. Mutations are induced by exposing plant parts to ionizing radiation viz., X-rays and gamma-rays or mutagenesis by chemicals viz., EMS (Ethyl Methyl Sulfonate) and sodium azide (Oladosu et al., 2016). Rick et al. (1996) found that mutations of some monogenic traits of tomato were induced by mutagens. Most of the fruit mutants originated from the early cultivars/lines of *S. lycopersicum* out of which major mutations were used in the improvement of tomato fruit quality (Peralta et al., 2006). There is a continuous rise in the number of developed mutant tomatoes (IAEA, 2020).

Although desirable mutants could be transferred to the elite cultivars by successive backcrosses after about 10 generations, however, most mutants were not used due to the association of unfavorable traits linked with the gene of interest (pleiotropic effect) (Young and Tanksley, 1989). TILLING (Targeting Induced Local Lesions) in genomes has facilitated the way to identify an array of new mutants in tomatoes with still unrevealed gene actions (Comai and Henikoff, 2006).

Grafting is one of the most focused breeding techniques practiced in many countries in recent times. Rivard and Louws (2008) have reported the cultivation of high-quality heirloom varieties by grafting without the burden of soil-borne pathogens viz., bacterial wilt. Apart from the well-known benefit of grafting as a method to control soil-borne diseases, there are many other benefits viz., tolerance to drought, heat, and salinity stresses (Singh et al., 2017). Also, Rouphael et al. (2018) discussed the efficiency of water, nutrient uptake, photosynthesis, and powerful defense mechanisms in grafted tomatoes. Flores et al. (2010) investigated that the rootstock (cv. Radja) was able to induce both tomato fruit yield and fruit quality traits of the scion.

### Marker-Assisted Selection (MAS) as a Tool of Tomato Breeding

Marker-assisted selection is a DNA based marker used in plant breeding for three major purposes viz., (i) Accumulation of favorable alleles by through generations tracing of either recessive or dominant desirable alleles (ii) Identification of desirable individuals genotype from segregated breeding population/lines based on either part of allelic composition or entire genome (iii) Introgression of favorable alleles from a donor parent into elite cultivar by breaking the undesirable linkage loci. The general terms used in modern molecular breeding techniques include genome-wide selection (GWS) or genomic selection (GS), marker-assisted pedigree selection (MAPS), marker-assisted selection (MAS), marker-assisted backcrossing (MABC) and marker-assisted recurrent selection (MARS). Among the solanaceous crops, tomato is one of the most studied based on genomic and genetic studies. MAS is an indirect method of selection for the trait based on the genotype of an associated marker instead of the trait of interest (Osei et al.,

2018). For the past few decades, MAS is the most popularly used technique by breeders to develop new cultivars (Banga and Banga, 1998). Also, MAS is a constructive way for gene pyramiding or identification of quantitative trait loci (QTL), especially for low heritability traits (Jacob *et al.*, 2016).

Different categories of linked markers have been identified in the tomato breeding program following the simple Mendelian inheritance. These markers were useful to select the plants or lines with traits of interest. There are over 1300 markers that have been identified in tomatoes (Osei *et al.*, 2018). They include morphological (*viz.*, leaf shape, seedling anthocyanin, and fruit shape), physiological (*viz.*, days to flowering, self-incompatibility/male sterility), pest and disease-resistant traits. However, the setback associated with the genetic markers such as dominance, epistasis, pleiotropic effects, penetrance, and expressivity leads to the lowering of selection efficiency of breeding programs (Peralta *et al.*, 2006). After genetic markers in 1970–1980, a set of isozyme markers was developed as second-generation markers. These isozyme markers were low in diversity and hence could not identify closely related genotypes (Foolad *et al.*, 1993).

### Molecular Markers

Molecular MAS has become an essential tool for crop improvement over the phenotypic selection. MAS is useful to select genes of interest from the donor or wild relative (foreground selection) to the recurrent parent and at the same time can recover the recurrent genome (background selection) by breaking the linkage drag (Osei *et al.*, 2018). In this technique, tightly linked molecular markers are used to select the gene of interest (Usman *et al.*, 2018; Usman *et al.*, 2017).

With the invention of DNA markers such as RFLPs (Restricted Fragment Length Polymorphism) and AFLPs (Amplified Fragment Length Polymorphism), a lot of constraints associated with genetic linkage maps were successfully overcome (Foolad, 2007). Then, PCR (Polymerase Chain Reaction) based markers such as CAPS (Cleaved Amplified Polymorphic Sequence) and SCAR (Sequence Characterized Amplified Region) were used as DNA markers in the marker-assisted selection in molecular breeding (Bai *et al.*, 2004). Recently developed high-resolution molecular markers such as SNP (Single Nucleotide Polymorphism) and InDels (Insertion Deletions) (Yang *et al.*, 2004; Foolad, 2007) have allowed breeders to distinguish the differences within and among closely related species. The latest updates of the newest molecular markers of tomato can be obtained from the SOL Genomics Network, 2020 (SGN) website ([https://solgenomics.net/community/links/related\\_sites.pl](https://solgenomics.net/community/links/related_sites.pl), retrieved June 15, 2020).

### Linkage maps

Bernatzky and Tanksley (1986) published the first linkage map of tomato, and since then, several improvements have been affiliated to the map bringing more usefulness to the breeders. The density of the tomato molecular linkage map is being gradually expanded across time with the untiring effort of scientists in several related disciplines all over the

world. Most of the genes and QTLs responsible for commercially desirable traits (*viz.*, fruit quality, yield, and disease resistance) are found in wild relatives, and MAS is a supporting tool to transfer those genes and QTLs to cultivated tomato (Tanksley and McCouch, 1997). However, earlier developed molecular markers such as RFLPs, CAPS, or AFLPs have not been able to distinguish between closely related cultivars and close wild relatives. The discovery of SNP markers would be helpful to mitigate the limitations associated with such molecular markers. Major QTL identification of high-resolution fine maps will facilitate the use of MAS in breeding new cultivars in the future (Foolad, 2007).

### Introgression lines (ILs)

ILs are interspecific lines with a single ‘exotic’ chromosome segment introgressed from wild relatives and the rest of the genome of the recipient (Eshed and Zamir, 1995). ILs have high potential in QTL identification than those interspecific crosses used in the early days of MAS. So far, several ILs have developed, including *S. habrochaites* (Monforte and Tanksley, 2000), *S. lycopersicoides* Dunal–Peruvian wolfpeach, and *S. sitiens* I.M.Johnst (Canady *et al.*, 2006) and *S. pennellii* (Eshed and Zamir, 1995; Tomato Genetics Resource Center, 2020). These ILs or pre-breeding lines facilitate plant breeders to pyramid many commercially important traits such as high yield, resistance to pests, diseases, and abiotic stresses together into a single cultivar (Fridman *et al.*, 2004). Among the mapping populations, ILs may be useful for developing NILs (Near Isogenic Lines) for fine mapping and cloning of genes and QTLs controlling traits like fruit weight (Frary *et al.*, 2000). Apart from this, IL populations were found to be used for marker-assisted selection of QTLs responsible for the yield of tomato (Foolad, 2007; Gur and Zamir, 2004).

### Use of in molecular markers in advancement of yield components of tomato

Fruit size is a highly heritable character that can be achieved through conventional breeding or phenotypic selection (Kemble and Gardner, 1992). Besides the high heritability, tomato fruit size is controlled by multiple genes and highly influence environmental conditions to greater proportions (Causse *et al.*, 2004). Molecular markers allow the dissection of such quantitative traits into discrete QTL which can be located on a genetic map. Recombinants of QTLs may have led to big-fruited heirlooms (fruit weight ~1000 g) while QTLs fw1.1, fw2.1, fw 2.2, fw 3.1 and fw 3.2 and fw 11.3 may have led to medium-sized tomatoes which do not affect locule number (Foolad, 2007; Grandillo *et al.*, 1999). Cultivated tomato bears large fruits while the wild relatives bear small berries (Bauchet and Causse, 2012). The first-ever map-based cloning of a QTL for fruit size fw2.2 was conducted on tomato (Frary *et al.*, 2000), and this particular locus is responsible for most of the variation in fruit size (Lippman and Tanksley, 2001) (Tab. 1). Very limited studies have been done on QTL of fruit yield in tomatoes due to low heritability and the complexity of the character. In addition, it is difficult to measure or predict fruit yield which is affected by various complex genetic and environmental factors (Foolad, 2007).

TABLE 1

Summary of markers associated with important yield-related parameters

QTL/gene	Chr	Markers	Gene action
fw 1.1	01	TG125	Partially Additive
fw 1.2	01	TG273	More recessive
fw 2.1	02	TG337	Partially Additive
fw 2.2	02	TG167-TG151	More recessive
fw 3.1	03	TG 246	More additive
fw 11.3	11	TG384-TG36-TG393	Additive
fl 1.1	01	TG 125	Additive
fl 1.2	01	TG 273-TG 59	Recessive
fl 2.1	02	TG 337-TG 167-TG 151	Recessive
fl 3.1	03	TG 129-TG 246- TG214	More Additive
fl 4.1	04	TG 178	Over dominant
fl 9.1	09	TG 20A	Recessive
fl 11.1	11	TG 314 -12 TG 396	More Additive
fd 1.1	01	TG 273	Largely recessive
fd 1.2	01	TG 125	Dominant
fd 2.1	02	TG337-TG167-TG151	Largely recessive
fd 3.1	03	TG129-TG246	Additive
fd 4.1	04	CT 178	Over dominant
fd 7.1	07	TG 20A	Largely additive
fd 11.1	11	TG 384-12-TG 393	Additive
Lcn 2.1	02	TG 337	Partially additive
Lcn 2.2	02	TG 167	Partially recessive
Lcn 11.1	11	TG 384-12-TG 393	Partially recessive

Source: Lippman and Tanksley (2001)

*Conventional approaches in controlling viral diseases*

To date, breeding resistance varieties seem the best approach for controlling viral diseases. At present, there are many commercial varieties available with partial resistance to viruses (Glick *et al.*, 2009). Pico *et al.* (1999) developed several tomato advanced breeding lines using the backcrossing method with *S. chilense* as the donor parent. In general, tropics and subtropics are good breeding grounds for viruses to outbreak. To control the viral outbreak from growing beyond the economic threshold level, combinations of management practices and the development of resistant varieties are a prerequisite. Among these, modified cultural practices such as crop rotation, use of virus-free planting materials, use of virus-host resistance and their insect-vectors, cross-protection, and application of insecticides to physical and chemical control of vector are important (Tripathi and Verma, 2017). An efficient environmental and user-friendly approach of resistant breeding for tomato is the combination of vector control (by conventional and chemical methods) and breeding resistant varieties.

*Pest resistant traits of tomato as an approach to control virus transmitting vectors*

A study conducted by Mutschler *et al.* (1996) showed that *L. pennellii* accession LA716 secretes acyl sugars by type-IV

glandular trichomes on the leaf surface, which act as oviposition deterrents for Silverleaf whitefly (i.e., TYLCV vector). Similarly, retardation in oviposition and the number of nymphs of whitefly have been observed in tomato genotypes with high acyl sugar content (Neiva *et al.*, 2019). Oliveira *et al.* (2020) have recently reported a repellence effect and non-preference to oviposition by whiteflies in tomato genotypes with high zingiberene content obtained at F<sub>2</sub>BC<sub>2</sub> from an interspecific cross between *S. lycopersicum* × *S. habrochaites* var. *hirsutum*. In another study, Lawson *et al.* (1997) included a pest-resistant gene into cultivated tomatoes; however, this attempt failed due to linkage drag showing the complex gene function. At present, farmers control pests by applying pesticides, however, more pest-resistant gene incorporation to tomato cultivars is expected with the advancement of MAS together with the potential and applicable conventional breeding approaches (Foolad, 2007).

*Disease resistant traits of tomato as an approach to control virus transmitting vectors*

Viral diseases are limiting factors affecting crop productivity, especially in tomatoes, due to the unavailability of antiviral control measures (Hanson *et al.*, 2000). Among the top viral diseases affecting tomato, TBSV (tomato bushy stunt virus),

TSWV (tomato spotted wilt virus), and TYLCV (Tomato Yellow Leaf Curl Virus) were considered the most destructive (Scholthof *et al.*, 2011). PCR-based markers are available only for few disease-resistant traits due to the low polymorphism, which is a limiting factor in exploiting MAS for resistant breeding in tomatoes. However, the discovery of SNP markers seems to be helpful to mitigate this constraint. Major QTL identification using fine maps with high resolution will facilitate the use of MAS in breeding new cultivars ahead (Foolad, 2007). Schuch *et al.* (1991) showed that breeding of virus and insect-resistant cultivars is difficult solely by the traditional approach. Agrama and Scott (2006) have identified resistant genes responsible for TYLCV and ToMV (tomato mosaic virus) and the tightly linked markers with the resistant genes.

Apart from the conventional breeding approach, MAS, transgenic approach, and pathogen-induced resistance is common attempts of resistant variety development (Saidi and Warade, 2008). Hamilton *et al.* (1999) reported the identification of resistant genes (*Cmr*) for cucumber mosaic virus (CMV) in tomato and Patil *et al.* (2002) identified the resistant gene (*Pot 1*) for potyviruses, Bruening and Lyons (2000) identified three resistant genes ToMV *Tm-1*, *Tm-2*, and *Tm-2<sup>2</sup>* while Martin *et al.* (1993) reported *Sw 5* spotted wilt virus (TSWV) resistant gene in tomato. However, the use of these resistant genes and QTLs in the development of virus-resistant tomato cultivars are rarely reported (Foolad, 2007). Apart from the nematode resistance, the *Mi* gene in the tomato genome has been reported with the resistant action against two biotypes of whitefly (*B. tabaci*) (Osei *et al.*, 2018). There are many records on R genes and QTLs for the tomato yellow leaf curl virus, such as qTy 4.1, 6.1, 10.1, and 11.1 (Prasanna *et al.*, 2015; Kadirvel *et al.*, 2013).

#### TYLCV—resistant traits

Lapidot and Friedmann (2002) stated that none of the chemical and physical barriers would help-in controlling whitefly during a severe outbreak, and the best approach would be the development of resistant varieties using classical or genetic engineering to control TYLCV in tomato. Up to now, there are six *Ty* genes that act independently (Gorovits *et al.*, 2017; Dhaliwal *et al.*, 2020) and have been incorporated into commercial cultivated tomato by introgression from its wild relatives (Singh *et al.*, 2019). Kumar *et al.* (2014) reported the successful pyramiding of the *Ty-2* gene to two TYLCV susceptible cultivars and the production of crosses with TYLCV resistance throughout the lifecycle.

Among the TYLCV resistant loci so far identified, Prasanna *et al.* (2015) explained that TYLCV disease-resistant gene *Ty-3* contributed a vital role for broad-spectrum resistance after gene pyramiding, and this would be utilized in TYLCV prevalence areas as a potential genetic resource for tomato hybrid breeding programs. Research done in Guatemala reported that tomato inbred lines with both *Ty-3* and *Ty-4* genes had a higher level of resistance to TYLCVD compared with lines with only *Ty-3* (Nakhla *et al.*, 2004; Vidavski, 2007). Nevame *et al.* (2018) reported a new molecular marker for the *Ty-3* gene and stated that tomato hybrid carrying *Ty-2* and *Ty-3* resistance genes can

mitigate the effect of the virus as compared to a single gene. Dhaliwal *et al.* (2020) have reviewed the importance of possessing TYLCV resistant genes in both parents when developing an effective resistance in tomato hybrids since *Ty* genes contribute partial dominance.

According to Gill *et al.* (2019), the resistance incurred by *Ty 6* major gene located on chromosome 10 thrives with the presence of the TYLCV resistant gene *Ty 3* and *Ty 5*. In a comprehensive study by Yan *et al.* (2018), 138 out of 708 wild tomato accessions tested using two different inoculation methods were resistant to TYLCD. In addition, they identified allelic polymorphism in *Ty1/Ty3* gene using VIGS (virus-induced gene silencing) and allele mining in few *S. chilense* accessions. Their findings will pave the way for tomato breeders to develop new tomato cultivars with TYLCV resistance. Ammara *et al.* (2015) developed transgenic tomato plants with RNAi (RNA interference) based resistance against TYLCV Oman strain and the associated beta satellite. Though the developed transgenic plants were not immune to TYLCD, they conferred the reduction of disease symptom severity.

Similar efforts of producing TYLCD resistant transgenic tomato plants expressing TYLCV capsid protein have been reported by Singh *et al.* (2019). It has been reported that the association of TYLCV with the beta satellites of other plant viruses altering the gene action of already identified resistant (*Ty*) genes. A recent finding by Gelbart *et al.* (2020) has revealed such association of cotton leaf curl Gezira Beta satellite with TYLCV, which compromises the gene action of resistance covered by *Ty-1* gene in tomato. In addition to the major genes and QTLs presented in Tab. 2, Zamir *et al.* (1994) mapped two modifier genes in chromosomes 3 and 7, respectively, associated with the action of the *Ty-1* gene. Similarly, Kadirvel *et al.* (2013) reported that the QTLs 4.1 and 10.1 in chromosomes 4 and 10 contain virus-resistant candidate genes such as *CTV 22* and eukaryotic translation initiation factor 4E. The majority of findings on the usage of molecular markers are based on TYLCV resistant markers as summarized in Tab. 2.

#### Future direction of tomato cultivar development for high yield and viral disease—resistant traits

In addition to unexploited knowledge on gene function, repulsion linkages between clustered resistance loci (Scott, 2004), linkage drag, and low resolution of the linkage maps are major constraints in TYLCV resistance breeding (Foolad, 2007). In the future, a combination of traditional or conventional knowledge together with a re-sequenced genetic map with high-resolution markers like SNPs and InDels will be helpful to minimize the present-day constraints in tomato breeding (Foolad, 2007). More disease-resistant genes in tomato wild relatives will unveil in the future, and breeders will be able to develop new cultivars with multiple disease resistance and higher fruit quality through breeding by design (Bai *et al.*, 2004). The transition of tomato breeding from traditional breeding techniques to the new “omics” era will allow breeders to expand their knowledge on gene expression and metabolism of each gene efficiently and effectively (Peleman and van der Voort, 2003).

TABLE 2

Summary of important markers associated with TYLCV resistant /QTLs genes

QTL/gene	Chr	Gene action	Markers	Marker	Reference	Remarks
qTy 4.1	04	Recessive	SINACI SLM 4-34	CAPS SSR	(Kadirvel <i>et al.</i> , 2013)	Derived resistance from <i>S. chilense</i> LA2779
qTy 6.1	06	Recessive	SLM 6-55/ TES 014	SSR SSR	(Kadirvel <i>et al.</i> , 2013)	Derived resistance from <i>S. chilense</i> LA2779
qTy 6.1	06	Recessive	TG 153 CT83	RFLP RFLP	(Chagué <i>et al.</i> , 1997)	Derived resistance from <i>S. pimpinellifolium</i> hirsute
qTy 10.1	10	Recessive	SLM 10-80 SLM 10-46	SSR SSR	(Kadirvel <i>et al.</i> , 2013)	Derived resistance from <i>S. chilense</i> LA2779
qTy 11.1	11	Recessive	SLM 11-2 SLM 11-17	SSR SSR	(Kadirvel <i>et al.</i> , 2013)	Derived resistance from <i>S. chilense</i> LA2779
Minor qTy	01	Semi dominant	C2_at4g34700	CAPS	(Anbinder <i>et al.</i> , 2009)	Derived resistance from <i>S. peruvianum</i>
Minor qTy	07	Minor additive	TG 174	CAPS	(Anbinder <i>et al.</i> , 2009)	Derived resistance from <i>S. peruvianum</i>
Minor qTy	09	Minor additive	SISUMO	CAPS	(Anbinder <i>et al.</i> , 2009)	Derived resistance from <i>S. peruvianum</i>
Minor qTy	11	Dominant	C2_at4g22260	CAPS	(Anbinder <i>et al.</i> , 2009)	Derived resistance from <i>S. peruvianum</i>
Ty-1 (close to Mi locus)	06	Partial dominant	TG 297 TG 97	RFLP RFLP	(Kadirvel <i>et al.</i> , 2013; Zamir <i>et al.</i> , 1994; Ji <i>et al.</i> , 2007a)	Derived resistance from <i>S. chilense</i> LA1969
Ty-2	11	Dominant	TG 393 TG 36 C2-At-1g07960 cLEN -11-F24	RFLP (PCR) RFLP CAPS	(Banerjee, 1990; Hanson <i>et al.</i> , 2000; Hanson <i>et al.</i> , 2006; Ji <i>et al.</i> , 2009a)	Derived resistance from from <i>S. habrochites</i>
Ty-3	06	Partial Dominant/ More Additive	cLEG-31-P16 C2_At5g41480/ T1079 ACY	CAPS Indel based	(Ji <i>et al.</i> , 2007a; Ji <i>et al.</i> , 2007b; Nevame <i>et al.</i> , 2018)	Derived resistance from <i>S. chilense</i> LA2779 Resistance from <i>S. pennellii</i>
Ty-4	03	Dominant	TO302 C2-At4g17300 C2-At5g60160	SCAR CAPS	(Kadirvel <i>et al.</i> , 2013; Ji <i>et al.</i> , 2009b)	Lesser resistant. Derived resistance from <i>S. chilense</i> (LA1932)
Ty-5	04	Partially Dominant	SINACI	CAPS	(Anbinder <i>et al.</i> , 2009)	Lesser resistant. Derived resistance from <i>S. peruvianum</i>
ty-5	04	Recessive	SINACI	CAPS	(Hutton <i>et al.</i> , 2012)	Derived from tomato variety LA1938/ Tyking (originated from <i>S. peruvianum</i> )
Ty-6	10	Partially Dominant	UF_10.61192		(Gill <i>et al.</i> , 2019)	Derived resistance from <i>S. chilense</i>

CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats) technology is a milestone in molecular breeding where the outcome is quite similar to that obtained from conventional breeding but with a very short time (Bortesi and Fischer, 2015). This is a cheap, fast, and reliable method. Changes in the regulatory region of genes responsible for tomato yield have been made with SDN-1 (site-directed nuclease-1) mutant using the use of CRISPR technology. This makes positive changes to increase the variation of the regulatory region of the gene of interest. This has boosted the tomato yield in a short time. Hence, CRISPR technology is expected to be a powerful tool to achieve goals in tomato breeding (Gao,

2018). Similar efforts on producing TYLCV resistant tomato cultivars using CRISPR/ Cas 9 technology have been made by Tashkandi *et al.* (2018). The advanced molecular technologies, tools, strategies, conventional approaches, and agronomic practices should go hand in hand to see the success of future tomato variety development programs irrespective of the breeding goals. Similarly, no exception for the development of high yielding and TYLCD resistant tomato varieties. Especially with the upcoming unpredictable environment conditions such as extreme climates, pest and disease outbreaks and their complex interactions could be addressed only by these integrated approaches.

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