Phytopathology Research

REVIEW

Open Access

Occurrence, distribution, and management of tomato yellow leaf curl virus in China

Fangfang Li[1†], Rui Qiao[1†], Xiuling Yang[1†], Pan Gong[1] and Xueping Zhou[1,2*]

Abstract

Tomato yellow leaf curl virus (TYLCV), belonging to the genus *Begomovirus* in the family *Geminiviridae*, is the most damaging virus for global tomato production. This virus has become one of the most studied plant viral pathogens because of its huge economic importance. Since it was firstly identified in Shanghai, China, in 2006, it has been spread to most parts of the country. The widespread occurrence, rapid spread to new regions, and enormous damage to tomato production, makes it an important agricultural pathogen in China. TYLCV has been characterized extensively at the molecular level. This review is focused on the occurrence and distribution of all TYLCV isolates in China, providing valuable information for further epidemiological studies. In addition, management strategies for TYLCV are also proposed, with the ultimate goal to prevent and control the further occurrence of this viral disease.

Keywords: Tomato yellow leaf curl virus, Occurrence, Distribution, Management, China

An introduction to geminiviruses and tomato yellow leaf curl virus (TYLCV)

Geminiviridae is the largest plant virus family. Geminiviruses are non-enveloped plant viruses with small circular single-stranded (ss) DNA genomes of 2.5 to 3.0 kilobases (kb) in a monopartite or bipartite arrangement encapsidated in twinned virions. Based on their genome features, insect vector, and host range, geminiviruses are divided into fourteen genera, and the genus *Begomovirus* is the largest genus, containing 445 virus species to date (Fiallo-Olivé et al. 2021). Begomoviruses have small genomes, composed of one (monopartite) or two (bipartite) DNA molecules of about 2.7 kb with similar genome structures and encoding 6–8 multifunctional typical proteins (Fiallo-Olivé et al. 2021; Devendran et al. 2022). TYLCV is a monopartite begomovirus and one of the most devastating plant pathogens worldwide. The symptoms of TYLCV in infected tomato plants include yellowing, chlorosis and leaf curling of young leaves, stunted growth, and marked reduction of leaf size (Fig. 1a, b), which causes up to 100% yield loss in tomato. The widespread occurrence and tremendous spread rate to new regions make it an important pathogen with enormous economic importance worldwide (Prasad et al. 2020).

The first report of tomato yellow leaf curl disease (TYLCD) came from the Jordan Valley of Israel in the 1950s, and it was first called 'tomato yellow top' (Cohen and Harpaz 1964). According to a study in 1986, the populations of whiteflies increased correlating with the occurrence of TYLCD (Cohen and Berlinger 1986). In 1988, the viral particles of TYLCV isolated from tomato and datura plants were observed with typical twinned structures, resembling those known for geminiviruses (Czosnek et al. 1988). In 1991, it was found that TYLCV has a circular ssDNA molecule as its genomic component (Navot et al. 1991). Since then, different strains of this virus have been identified around the globe (Cohen and Harpaz 1964; Lefeuvre et al. 2010; Oh et al. 2013; Hosseinzadeh et al. 2014; Mabvakure et al. 2016; Pérez-Padilla et al. 2020). With the outspread of TYLCV in

†Fangfang Li, Rui Qiao and Xiuling Yang contributed equally to this article

*Correspondence: zzhou@zju.edu.cn

[1] State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100193, China
Full list of author information is available at the end of the article

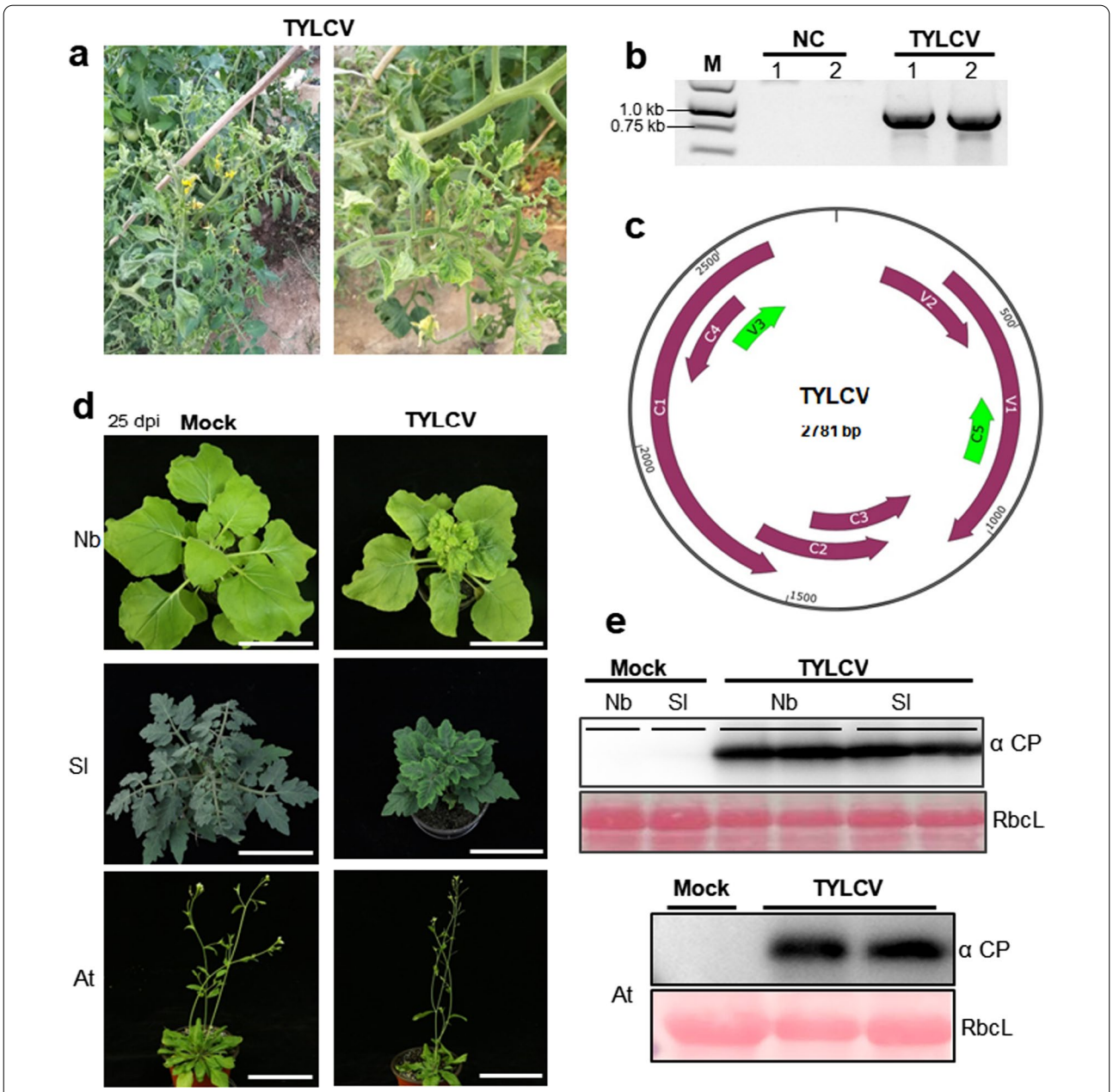

Fig. 1 Disease symptoms caused by tomato yellow leaf curl virus (TYLCV) and genome organization of TYLCV. **a** Disease symptoms induced by TYLCV in *Solanum lycopersicum* plants in the field. **b** Specific DNA bands detected in infected tomato plants by PCR using TYLCV-specific primers. Lanes 1 and 2 indicate DNA extracted from two independent TYLCV-infected *S. lycopersicum* plants. M: DNA ladder marker, NC: negative control using DNA extracted from uninfected tomato plants. **c** Schematic representation of TYLCV genomic organization. Open reading frames encoded on the virion-sense (V) strand and complementary-sense (c) strand are denoted (V1, V2, C1, C2, C3, and C4); the new ORFs V3 and C5 have been identified recently (Gong et al. 2021). **d** Disease symptoms induced in *Nicotiana benthamiana* (Nb), *S. lycopersicum* (Sl), and *Arabidopsis thaliana* (At) plants agroinoculated with mock (empty vector) or the infectious clones of TYLCV. Plants were photographed at 25 days post inoculation (dpi). Bars = 9 cm. **e** Western blot analysis of total proteins from (**d**) with anti-TYLCV-coat protein (CP) antibodies. Ponceau S staining of the large Rubisco subunit (RbcL) served as the loading control. *Note*: The TYLCV Beijing isolate (GenBank Accession No. MN432609) was used in this figure

Jordan, Lebanon, Sudan, Tunisian, and other countries, interest in this virus has increased for researchers. So far, more than 550 articles related to TYLCV can be found in PubMed (https://pubmed.ncbi.nlm.nih.gov/), demonstrating its scientific and economic importance.

TYLCV encodes six canonical viral proteins (the virion-sense strand contains two ORFs, V1 and V2, and

the complementary-sense strand encompasses four ORFs, C1, C2, C3, and C4) (Fig. 1c). The coat protein (CP) encoded by the V1 ORF is required for the packaging of the viral DNA and the spread by insect vectors (Wei et al. 2017; Fondong et al. 2013). The V2 ORF encodes the V2 protein, which is an RNA silencing suppressor of transcriptional gene silencing (TGS) and post-transcriptional gene silencing (PTGS) (Glick et al. 2008; Wang et al. 2014, 2018, 2020). The replication-associated protein (Rep) encoded by the C1 ORF is essential for reprograming the cell cycle and mediating rolling circle replication (RCR) of the viral genome (Hanley-Bowdoin et al. 2013; Basak 2016). The C2 ORF encodes the transcription activator protein (TrAP) and can also suppress TGS, PTGS, protein ubiquitination, and jasmonic acid (JA) signaling (Lozano-Duran et al. 2011; Luna et al. 2012; Rosas-Diaz et al. 2016). The replication-enhancing protein (REn) is encoded by the C3 ORF and is vital for viral replication by interacting with POLA2, a subunit of DNA polymerase α, and POLD2, a subunit of DNA polymerase δ. The viral C3 protein may selectively mediate the effective recruitment of DNA polymerase δ over ε to enhance geminivirus replication (Wu et al. 2021). Geminivirus C4 displays a broad diversity of functions during the viral infection, both within and between geminiviruses (Medina-Puche et al. 2021). TYLCV C4 protein also has multiple roles in causing disease symptoms, participating in the viral movement, and repressing host DNA methylation and RNA silencing (Rojas et al. 2001; Kon et al. 2007; Luna et al. 2012; Guo et al. 2022). Recently, several studies have shown that geminiviruses, including TYLCV, encode additional small proteins with different subcellular localization patterns and virulence functions (Gong et al. 2021, 2022; Li et al. 2021a, b; Chiu et al. 2022; Zhao et al. 2022). Among these small proteins, the V3 protein of TYLCV is a Golgi- and partially endoplasmic reticulum (ER)-localized protein, which functions as an RNA silencing suppressor and a viral cellular movement protein (Gong et al. 2021, 2022). The TYLCV C5 protein is considered as a pathogenicity determinant and RNA silencing suppressor (Zhao et al. 2022).

TYLCV has a very diverse host range and it is reported to cause severe epidemics in *Phaseolus vulgaris* and solanaceous plants (Navas-Castillo et al. 1999). Notably, the infectious clone of TYLCV can effectively infect model plants *Nicotiana benthamiana* and *Arabidopsis thaliana* under laboratory conditions (Fig. 1d, e), which helps accelerate the studies of the biology of TYLCV and its interactions with both plant and vector.

TYLCV infection dramatically reduces plant productivity, resulting in substantial economic losses, and 20–100% yield loss depending on the plant growth stage at the time of infection (Levy and Lapidot 2008). Because of the economic importance of TYLCV and its devastating and widespread nature, efforts have been made to study TYLCV pathogenesis and develop tolerant or resistant plants.

Occurrence and distribution of TYLCV in China

Geographical distribution

Although TYLCV quickly became a devastating pathogen of tomato in the tropics, subtropics, and warm temperate regions shortly after it was first discovered, in China, however, there was no report on this virus before 2006. Wu et al. (2006) firstly observed that a yellow mosaic disease appeared on tomato plants with 90% disease incidence during March 2006 in fields of Sunqiao, Shanghai, China, and then confirmed that TYLCV isolate SH2 (GenBank Accession No. AM282874.1) caused this viral disease. Since then, multiple TYLCV isolates have been reported in China. Based on the published articles and annotated sequences, 99 species of geminiviruses with over 1600 isolates in total had been isolated, identified, and characterized in China by the end of 2021 (Li et al. 2022). Among them, TYLCV is the geminivirus with the highest number of isolates: 415 isolates with full-length nucleic acid sequences and distributed in most provinces of China have been identified so far (Table 1 and Additional file 1: Table S1), further demonstrating that this viral pathogen is a huge threat to agriculture because of its widespread incidence and tremendous rate of spread.

The top 5 provinces with the highest number of TYLCV isolates are Yunnan Province (119 isolates), Shandong Province (76 isolates), Henan Province (31 isolates), Beijing (29 isolates), and Hebei Province (21 isolates) (Additional file 2: Table S2). Of note, Yunnan, Shandong, and Henan are important provinces with the largest scale of tomato cultivation in China. Therefore, it is expected that most TYLCV isolates are isolated and identified in these provinces. TYLCV is also present in provinces where geminivirus species are rare (Li et al. 2022). For example, in Beijing, Shanxi, and Shaanxi, TYLCV is the dominant geminivirus species. In short, TYLCV has been spread over most provinces of China in recent 16 years (Table 1).

Host plants

A major challenge in controlling any pathogen is its maintenance in alternate hosts. TYLCV has a very diverse host range, and it has been detected in 49 species belonging to 16 families (Papayiannis et al. 2011). In China, TYLCV infects 25 species of plants, which include 14 species of cash crop plants and 11 species of non-cash plants (Additional file 3: Table S3). Fourteen species of cash crop plants include *Solanum lycopersicum* (tomato), *Capsicum annuum* (pepper), *Vigna unguiculata* (cowpea), *Capsicum frutescens* (millet pepper),

Table 1 Geographical distribution of TYLCV isolates in China

Provincial-level administrative region	Number of TYLCV isolates	Provincial-level administrative region	Number of TYLCV isolates
Yunnan	119	Hubei	4
Shandong	76	Sichuan	2
Henan	31	Hunan	1
Beijing	29	Chongqing	1
Hebei	21	Jilin	1
Jiangsu	14	Guizhou	1
Zhejiang	14	Tianjin	1
Liaoning	14	Taiwan	Symptom described
Fujian	13	Heilongjiang	Symptom described
Shanxi	12	Gansu	Symptom described
Guangdong	12	Ningxia	Symptom described
Xinjiang	11	Inner Mongolia	Symptom described
Gaungxi	9	Hong Kong	0
Anhui	8	Qinghai	0
Shanghai	8	Tibet	0
Shaanxi	7	Jiangxi	0
Hainan	6	Macao	0

The exact number of TYLCV isolates with the public full-length TYLCV nucleic acid sequences identified in each place is listed. 'Symptom described' represents the region where TYLCV-related disease symptoms have been described, but molecular confirmation of the presence of the virus is lacking. '0' represents no TYLCV disease or presence of TYLCV isolates, which might be due to limited sampling

Nicotiana tabacum (tobacco), *Phaseolus vulgaris* (kidney bean), *Cucurbita moschata* (pumpkin), *Malus domestica* (apple), *Abutilon theophrasti* (abutilon), *Gossypium hirsutum* (cotton), *Abelmoschus esculentus* (okra), *Agastache rugosa* (herba agastaches), and *Solanum melongena* (eggplant). Among these, the most affected plant is tomato, from which a total of 360 isolates of TYLCV have been identified, accounting for 85% of all isolates. Tomato, native to South America, belongs to the *Solanaceae* family and is one of the most important fruits and vegetable crops globally. There is a high tomato production in China. For example, in 2019, 62,869,500 tons of tomatoes were produced from tomato fields covering a total of 1,086,800 hm^2, accounting for 34.78% and 21.60% of the world's total harvested area and annual production, respectively (Zeng et al. 2021). Despite the high yield, demand far exceeds tomato production in China. One of the most important causes of yield loss affecting tomato is TYLCD, and TYLCV is one of the most important pathogens causing the disease. In addition, TYLCV can also combine with other viruses to form a disease complex, leading to enhanced symptoms on hosts. For example, the synergistic infection of TYLCV and tomato chlorosis virus (ToCV) results in a high disease severity index and causes dramatic losses (Li et al. 2022).

There are 9 isolates of TYLCV identified in pepper in three provinces in China, indicating that pepper is also a primary host of TYLCV in China. TYLCV also infects multiple weeds, including *Acalypha australis*, *Alcea rosea*, *Agastache rugosa*, *Abelmoschus esculentus*, and *Viola prionantha* (Additional file 3: Table S3). These weeds are considered alternate hosts, which provide a storehouse of inoculum during the growing season as well as crop-free periods, and must be taken into consideration when devising control strategies.

Of note, the damaging TYLCD is caused by many other begomoviruses in addition to TYLCV globally. In China, there are over 20 geminivirus species that can damage tomato in the field (Fig. 2) (Cui et al. 2004; Li et al. 2004, 2020, 2022; Xie et al. 2013a, b; Yan et al. 2021). Interestingly, tomato yellow leaf curl China virus (TYLCCNV) is a typical monopartite geminivirus associated with a tomato yellow leaf curl China betasatellite (TYLCCNB) in the field (Cui et al. 2004; Hu et al. 2020). Infection by TYLCCNV alone in tobacco or tomato plants fails to induce any apparent symptoms (Cui et al. 2004), while TYLCCNB is required for inducing dwarfing, leaf curling, yellow mosaic patterns, and stem distortion symptoms in tobacco or tomato plants infected by this virus complex. In most conditions, there is no satellite associated with the infection of TYLCV (Yan et al. 2021).

Transmission of TYLCV

TYLCV is transmitted between plants by an insect vector, *Bemisia tabaci* (commonly known as whitefly), in a persistent-circulative or persistent-propagative manner (Gottlieb et al. 2010; He et al. 2020). Whitefly is a cryptic species complex composed of 35 putative cryptic

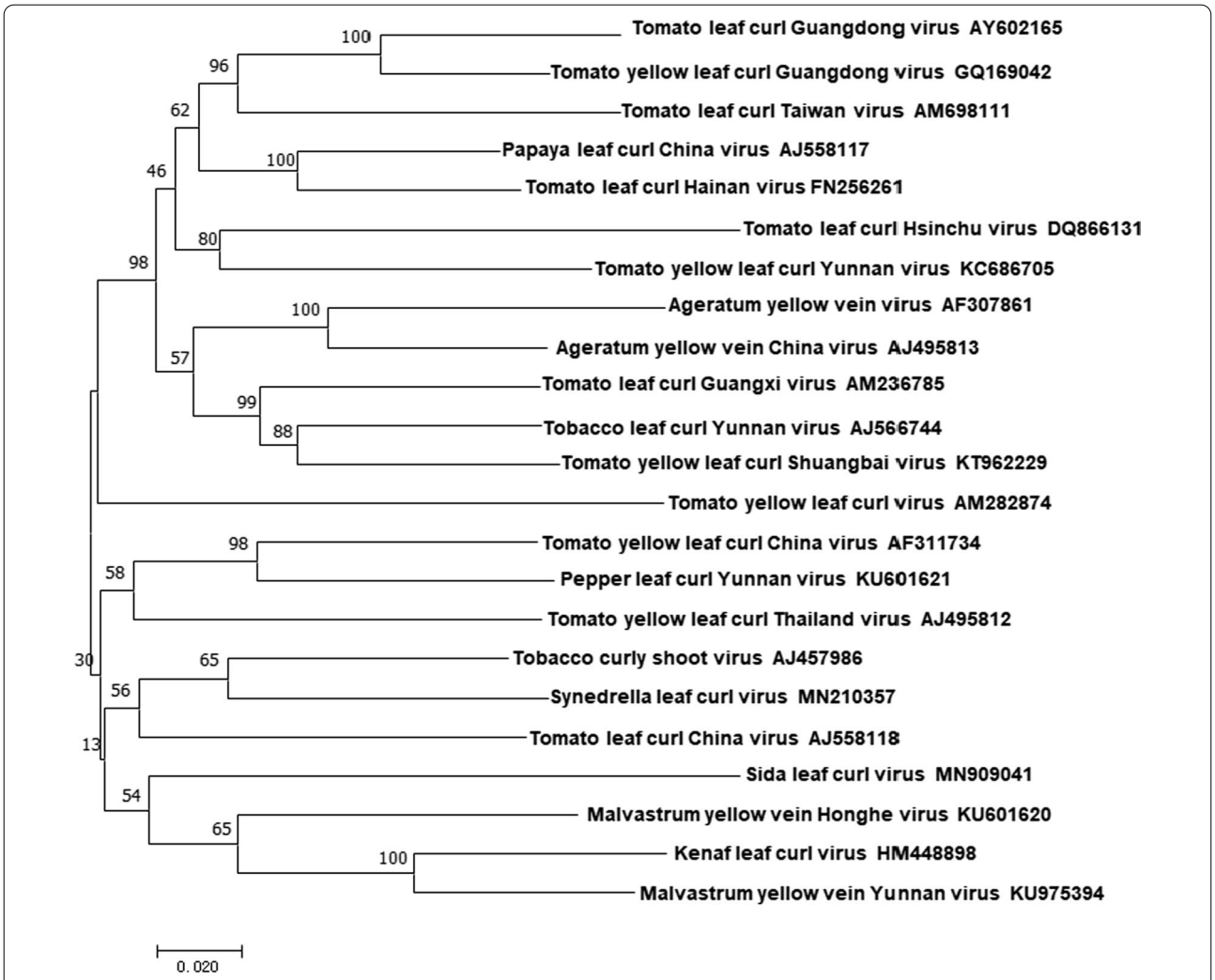

Fig. 2 Phylogenetic tree based on the full-length nucleic acid sequences of the geminivirus species from China that can infect tomato in the field. Numbers on the nodes suggest the percentage of bootstrap support from 1000 replicates

species (Luan et al. 2014). They attack more than 600 plant species and cause damage to plants through direct feeding and transmission of plant viruses (Boykin and De Barro 2014; Xia et al. 2021). Within this complex, the putative Middle East-Asia Minor 1 (MEAM1) and Mediterranean species (MED), known formerly as the 'B biotype' and 'Q biotype', respectively, are economically important pests that cause severe crop losses through direct feeding and transmission of plant viruses (Navas-Castillo et al. 2011). MED has a higher ability to develop insecticide resistance than other species, while MEAM1 is characterized by high fecundity and a broad host range (Ghanim et al. 2014). *B. tabaci* first appeared in China in the late 1940s. However, the first expansion of *B. tabaci* did not caused great harm until the appearance of the B biotype in the mid-1990s (Luo et al. 2002). A new biotype of whitefly with a higher ability to develop insecticide resistance, named the Q biotype, was first found in Yunnan Province of China in 2003 and rapidly expanded throughout China (Chu et al. 2007; Pan et al. 2011). Although B and Q biotype rapidly invaded the entire country, TYLCV was not identified until 2006 in China. Due to the almost simultaneous emergence of TYLCV and Q biotype, some studies hypothesized that the two exist in a stronger reciprocal relationship than TYLCV and B biotype and demonstrated that TYLCV was indirectly mutualistic to the Q biotype (Pan et al. 2013). In addition, there is a significant difference in the accumulation of viruses between viruliferous Q-infected leaves and viruliferous B-infected leaves at 7 days after the initial inoculation, with the former being higher than

the latter (Shi et al. 2014). Similarly, Q biotypes have been confirmed to be the predominant pathogenic vector of TYLCD in China and are responsible for TYLCD outbreaks in America (Gilbertson et al. 2015). These results offer an orientation for TYLCV management and TYLCD prevention.

During the last 20 years, the transovarial transmission of TYLCV has been reported in two invasive species of the *B. tabaci* complex (B and Q biotype whiteflies) (Fiallo-Olivé et al. 2020). However, the study of transovarial transmission of TYLCV by seven whitefly species indigenous to China showed that TYLCV virions were detected in eggs of all these species except one and in nymphs of two species but in none of the ensuing adults of all the species. These results suggest that these indigenous whiteflies cannot transmit TYLCV transovarially (Guo et al. 2019). Transovarial transmission is a feature of the circulative propagative plant virus. Many studies have also focused on the potential replication of TYLCV in its vector. Although there was controversy around this topic, He et al. recently provided evidence of the replication of TYLCV in the whitefly vector (He et al. 2020). Their findings revealed that TYLCV has evolved to induce and recruit insect DNA synthesis machinery to support its replication in vector salivary glands (He et al. 2020), which provides insights into how a plant virus may evolve to infect and replicate in an insect vector.

Interestingly, seed transmission has previously been reported in some RNA viruses, but geminiviruses have not previously been described as seed-borne viruses. In 2013 and 2014, TYLCV was detected in young tomato plants derived from fallen fruits of TYLCV-infected tomato plants in Korea (Kil et al. 2016), indicating TYLCV-IL could be transmitted via seeds, and tomato plants germinated from TYLCV-infected seeds might be an inoculum source of TYLCV. However, this finding was then revisited with a different result by a different laboratory in other tomato-growing areas. Pérez-Padilla et al. showed that TYLCV DNA was detected in tomato and *N. benthamiana* seeds collected from plants naturally or experimentally infected with TYLCV-IL, supporting its seed-borne nature (Pérez-Padilla et al. 2020). While the significant reduction in TYLCV DNA load after surface disinfection of tomato seeds suggests that the virus can be the contaminant of the seed coat, transmission assays carried out with seven tomato genotypes and more than 3,000 tomato plants revealed no evidence of seed transmission from "surface-disinfected" or untreated seed for two Mediterranean isolates of TYLCV-IL (Pérez-Padilla et al. 2020). Supporting this finding, Tabein et al. (2021) also found no evidence for the tomato seed transmissibility of tomato yellow leaf curl Sardinia virus (TYLCSV), one of the agents inducing the TYLCD. Therefore, TYLCV-IL is seed-borne but is not seed transmitted in tomato or *N. benthamiana*, suggesting that transmission through seed is not a general property of TYLCV.

Diagnosis of TYLCV

Early detection and precise diagnosis of TYLCV is a crucial step for preventing the possible spread of infectious disease and minimizing losses. The application of sensitive and specific detection methods is fundamental for managing TYLCV. The traditional method of identifying TYLCV is through visual observation of symptoms. This is often possible only after major damage has already been done to the crop, and a trained person can screen numbers of plants in the field by walking along the plant rows. However, symptom-based diagnosis of TYLCV is unreliable as asymptomatic infection often occurs at early stages, on one hand, and other plant viruses might cause similar symptoms, on the other hand. It is also crucial to accurately confirm the viral species infecting the plants. Currently, various methods have been developed to detect TYLCV, mainly by identifying the presence of viral protein such as the coat protein (CP) of TYLCV (protein-based detection) or by testing the presence of TYLCV DNA (nucleic acid-based detection) (Fig. 3).

Protein-based detection of TYLCV

Serological methods, such as enzyme-linked immunosorbent assay (ELISA), are based on the reliable detection of the CP of TYLCV using polyclonal or monoclonal antibodies. In the ELISA test, plant samples are immobilized to a solid surface. If TYLCV is present in the sample, the coat protein of TYLCV will interact with the primary antibody, which is then complexed into a secondary antibody conjugated with a reporter molecule, commonly an enzyme, to enable the detection of the virus by producing the chromogenic products (Fig. 3). In this approach, a high-quality TYLCV-specific antibody is a prerequisite for the sensitive and specific detection of TYLCV. Antibodies have been raised for TYLCV, and different types of ELISA such as dot-ELISA and direct tissue blot immunoassay have been developed to detect TYLCV from field tomato and whitefly samples. The developed dot-ELISA can be used to detect TYLCV from tissue crude extract diluted at 1:5,120 (w/v, g/mL) and viruliferous whitefly homogenate diluted at 1:128 (individual whitefly/μL) (Xie et al. 2013a, b). Due to their simplicity and low cost, ELISA is the most suitable method for the high-throughput analysis of samples in a short time.

Nucleic acid-based detection of TYLCV

Detection methods based on the nucleic acids of TYLCV can be classified into polymerase chain reaction (PCR)

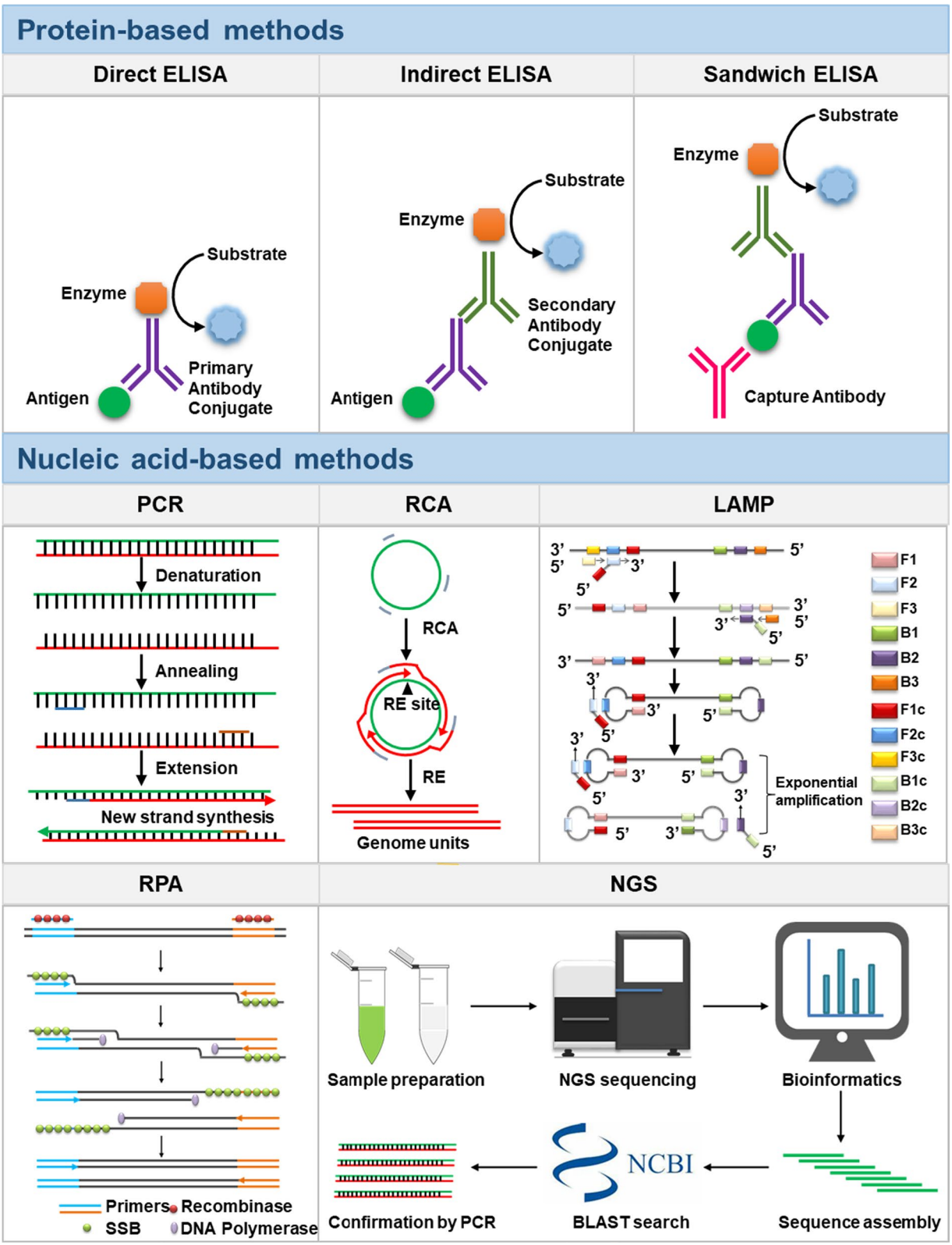

Fig. 3 Schematics of the protein- and nucleic acid-based diagnosis of geminiviruses, including TYLCV. ELISA, enzyme-linked immunosorbent assay; PCR, polymerase chain reaction; RCA, rolling circle amplification; LAMP, loop-mediated isothermal amplification; RPA, recombinase polymerase amplification; NGS, next-generation sequencing

and isothermal amplification, such as rolling circle amplification (RCA), loop-mediated isothermal amplification (LAMP), and recombinase polymerase amplification (RPA). In the past decade, high-throughput sequencing technologies, also known as next-generation sequencing (NGS), have revolutionized the discovery and characterization of geminiviruses (Fig. 3). A few of such methods are described here.

The PCR technique is the most popular technique used in the molecular characterization of TYLCV. After amplification of DNA regions in TYLCV using specific primers, subsequent DNA sequencing can be used to confirm TYLCV infection. The PCR method is highly sensitive and suitable for routine detection of TYLCV in laboratories. It can also be used to detect TYLCV from both tomato plants and whiteflies without extraction or purification of nucleic acids (Atzmon et al. 1998). However, using the PCR-based detection method for in-field diagnosis is a challenge as it requires expensive and specific equipment.

RCA is an isothermal amplification process that has led to a revolution in the diagnosis of TYLCV and related geminiviruses (Haible et al. 2006). It uses the DNA polymerase of bacteriophage phi29 to synthesize multiple copies of circular DNA molecules in a nonspecific manner. After annealing of primers to the single-stranded circular molecule, the polymerase reaches the primer binding site, displaces the newly synthesized strand, and goes on with DNA synthesis for several rounds at 30 °C (Johne et al. 2009). This mechanism produces a long concatemeric single-stranded DNA, which can be subsequently digested with the single-cutting restriction enzyme to yield fragments of full-genome length of TYLCV, cloned, and sequenced (Yang et al. 2014, 2017). As specific primer sequences are not required for this technique, RCA enables the detection of unknown geminiviruses. In addition, RCA has a higher sensitivity than PCR and can be used to detect geminivirus from dried plant samples (Shepherd et al. 2008).

LAMP is another isothermal amplification process conducted at a constant temperature of 60–65 °C. It uses the strand displacement and auto-cycling activity of *Bacillus stearothermophilus* (*Bst*) DNA polymerase. In the LAMP method, two inner primers and two outer primers are required to generate loops and displace newly generated strands. With the help of two different loop primers, more DNA products could be synthesized, and the resulting products can be visualized by agarose gel electrophoresis and/or a naked-eye system. LAMP has been used to detect TYLCV, maize streak virus, and several other begomoviruses, such as squash leaf curl virus, tomato leaf curl Bangalore virus, and tomato leaf curl New Delhi virus (Fukuta et al. 2003; Kuan et al. 2010; Tembo et al. 2020). The major limitation of the LAMP method is primer design.

RPA amplifies target DNA by using recombinase, DNA polymerase, and single-stranded DNA binding protein (SSB). In the RPA assay, SSB binds the primers and scans for the target sequences. The primers recombine with the target, and the polymerase extends the 3' end of the invading primer using the opposite strand as a template. Exponential amplification is achieved by the cyclic repetition of this process (Lobato and O'Sullivan 2018). RPA-based assays have been developed to detect TYLCV from crude extracts (Londono et al. 2016). Coupled to a portable lateral flow device, RPA can detect 0.5 pg of TYLCV DNA after 30 min at 37 °C without specialized equipment (Zhou et al. 2022).

NGS is a promising technique for identifying geminiviruses without prior knowledge or sequence information of the virus (Wu et al. 2010). In response to virus infection, the host plant employs the antiviral RNA silencing machinery to generate virus-derived small interfering RNAs, which can be assembled into contigs covering partial or complete virus genomes. Following further cloning and sequencing, NGS allows rapid and simultaneous detection of all known or unknown viral sequences present in a sample (Yang et al. 2021). In the past years, NGS has been successfully used to rapidly identify TYLCV and unknown geminiviruses from different hosts, including woody plants, such as mulberry mosaic dwarf-associated virus and apple geminivirus (Liang et al. 2015; Ma et al. 2015).

TYLCV management

Since TYLCV is an obligate intracellular parasite, the plant disease caused by this virus is incurable in field conditions, and management of TYLCV is a major concern worldwide (Rojas et al. 2018). Therefore, the success in management of TYLCV disease is dependent on good agricultural practices before, during, and after the growing season.

Before planting

Before planting or transplanting, it is critical to use virus-free and insect-free transplants and, if possible, resistant varieties. Growing resistant varieties is ideal and eco-friendly to control TYLCV disease. Six quantitative trait loci, namely *Ty-1/3*, *Ty-2*, *Ty-4*, *ty-5*, and *Ty-6*, have been identified from wild tomato species (Lapidot et al. 2014, 2015; Caro et al. 2015; Yan et al. 2021). These resistance genes/loci have been introduced into commercially acceptable cultivars during the past decades via traditional breeding methods and have played vital roles in rendering plant resistant to TYLCV and several

begomoviruses. However, they are ineffective against the entire suit of tomato-infecting begomoviruses, and resistance might be overcome by TYLCV-betasatellite disease complexes (Voorburg et al. 2020).

After selecting the variety and source of planting material, it is important to determine the planting dates and field location. In general, when viral infection of plants occurs at their early developmental stages, the disease symptoms caused by TYLCV will be more severe, and the yield loss will be higher. If the population information of whitefly and virus pressure of TYLCV is available, new planting can be established when the population of whitefly and sources of TYLCV inoculum are at the lowest levels. When possible, protected culture and row covers can be used to exclude whiteflies, especially for high-value vegetable crops grown in greenhouses. Furthermore, growing plants with adequate nutrition and water is helpful in improving soil health, plant immunity, and yield.

During the growing season

As the severity of the disease caused by TYLCV is correlated with the host, the titer of virus inoculum, and the population of whiteflies, it is vital to inspect the field frequently during the growing season. The population of whiteflies in protected cultures and the open field could be monitored using yellow sticky cards. At present, the application of insecticides is the most commonly used approach to control the population of insect vectors. However, one of the problems with using insecticides is the emergence of insect vector populations with insecticide resistance (Horowitz et al. 2004; Gilbertson et al. 2015). This is well documented for the supervector *B. tabaci* in China (Gilbertson et al. 2015). Thus, rotation of insecticides with different modes of action during a growing season is recommended to minimize the development of insecticide resistance in vector. An alternative approach for controlling insect vectors is to release biocontrol reagents such as predators, parasitoids, and fungi to reduce vector populations.

Roguing is a practice that involves the removal of TYLCV-infected plants during the growing season. This can reduce sources of virus inoculum and is most helpful in slowing down the spread of TYLCV if the incidence of the virus is low. To avoid releasing viruliferous whiteflies, rogued plants should be immediately sealed in whitefly-proof containers and destroyed.

After harvest

After harvest, it is critical to destroy infected plants properly. To eliminate or reduce the initial inoculum sources in a defined region, extensive sanitation should also be carried out to eliminate or reduce the initial inoculum sources. As weeds often serve as reservoir hosts of TYLCV, removing weeds in and around fields is critical. Crop rotation with non-host of TYLCV or whitefly can be used to combat TYLCV and whitefly pressure. A host-free period is advised to reduce virus inoculum or vector populations when possible. Host-free periods have successfully managed TYLCV in the Dominican Republic (Rojas et al. 2018).

In short, integrated pest management (IPM) is a general and valuable strategy to reduce economic losses and epidemics caused by TYLCV below an acceptable threshold. Therefore, the above TYLCV management is mainly based on two principles: one is to prevent TYLCV from entering the plants by using resistant plant varieties or using virus-free planting materials, and the other is to use prophylaxis practices to restrain TYLCV spread by eliminating reservoirs, surveillance, and control of whiteflies (Rubio et al. 2020).

Conclusion and future perspectives

TYLCV poses a serious threat to tomato production throughout the world's temperate regions. Because of the widespread distribution and the rapid global spread of this viral pathogen, TYLCD is expected to be a continuous challenge to tomato production in China and the rest of the globe. The largest number of TYLCV isolates identified in most provinces of China and many parts of the globe indicates that no region is immune to this pathogen, and stronger efforts to control its spread need to be made. Therefore, there is an urgent requirement for devising more efficient control measures based on the recent progress in the study of TYLCV. Future research must focus on developing plant resistance using cutting-edge techniques such as specific clustered regularly interspaced palindromic repeats (CRISPR)/Cas9 system and reliable RNA interference (RNAi) technology and applying and mining wild tomato resistance germplasm sources. With the development of CRISPR/Cas genome editing systems and the exploration and function identification of plant susceptibility genes to TYLCV, transgene-free resistant tomato plants generated by CRISPR/Cas in which susceptibility genes have been edited would offer a promising opportunity for the prevention and control of TYLCV in the field. At the same time, whiteflies are carriers of TYLCV, understanding of the tripartite interactions of plant-TYLCV-whitefly is important for effective field controlling method, and efforts to control the whitefly populations will be beneficial to control this disease and increase tomato yield. Like Bt crops, insecticidal proteins that are lethal to whiteflies can be expressed in plants using transgene technology, which would be a significant breakthrough. Controversially,

although transgenic plants have proved efficient against viral infection, concerns about transgenic food safety by consumers hamper their applicability. Therefore, the government should develop a comprehensive program to improve public understanding of transgene technology and promote acceptability of transgenic crops.

Abbreviations

At: *Arabidopsis thaliana*; *Bst*: *Bacillus stearothermophilus*; C: Complementary-sense; CP: Coat protein; ELISA: Enzyme-linked immunosorbent assay; ER: Endoplasmic reticulum; IPM: Integrated pest management; JA: Jasmonic acid; LAMP: Loop-mediated isothermal amplification; MEAM1: Middle East-Asia Minor 1; MED: Mediterranean species; Nb: *Nicotiana benthamiana*; NGS: Next-generation sequencing; ORF: Open reading frame; PCR: Polymerase chain reaction; PTGS: Post-transcriptional gene silencing; RbcL: Rubisco subunit; Rep: Replication associated protein; RCA: Rolling circle amplification; RCR: Rolling circle replication; REn: Replication enhancing protein; RNAi: RNA interference; RPA: Recombinase polymerase amplification; Sl: *Solanum lycopersicum*; SSB: Single-stranded DNA binding protein; TGS: Transcriptional gene silencing; ToCV: Tomato chlorosis virus; TrAP: Transcription activator protein; TYLCCNB: Tomato yellow leaf curl China betasatellite; TYLCCNV: Tomato yellow leaf curl China virus; TYLCD: Tomato yellow leaf curl disease; TYLCV: Tomato yellow leaf curl virus; V: Virion-sense.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42483-022-00133-1.

Additional file 1: Table S1. Information of all tomato yellow leaf curl virus isolates in China

Additional file 2: Table S2. Distribution of all tomato yellow leaf curl virus isolates in China

Additional file 3: Table S3. The host plants of all tomato yellow leaf curl virus isolates in China

Acknowledgements

We thank our colleagues in China who work on TYLCV research for their input in proofreading the detailed information of each TYLCV isolate. We thank Dr. Rosa Lozano-Durán for her valuable suggestions and English editing of the manuscript. We apologize that, due to space constraints, we have not been able to cite all published works that underlie the development of this field.

Author contributions

XZ and FL designed the research; FL, RQ, XY and PG analysed the data; FL, RQ, XY and XZ wrote the paper. All authors read and approved the final manuscript.

Funding

This work was supported by grants from the National Key Research and Development Program of China (2021YFD1400400) to Fangfang Li, and the National Natural Science Foundation of China (31720103914) to Xueping Zhou.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethical approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

[1]State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100193, China. [2]State Key Laboratory of Rice Biology, Institute of Biotechnology, Zhejiang University, Hangzhou 310058, Zhejiang, China.

Received: 5 May 2022 Accepted: 4 July 2022
Published online: 25 July 2022

References

Atzmon G, van Oss H, Czosnek H. PCR-amplification of tomato yellow leaf curl virus (TYLCV) DNA from squashes of plants and whitefly vectors: application to the study of TYLCV acquisition and transmission. Eur J Plant Pathol. 1998;104:189–94. https://doi.org/10.1023/A:1008699603559.

Basak J. Tomato yellow leaf curl virus: a serious threat to tomato plants world wide. J Plant Pathol Microbiol. 2016;7:346. https://doi.org/10.4172/2157-7471.1000346.

Boykin LM, De Barro PJ. A practical guide to identifying members of the *Bemisia tabaci* species complex: and other morphologically identical species. Front Ecol Evol. 2014;2:45. https://doi.org/10.3389/fevo.2014.00045.

Caro M, Verlaan MG, Julian O, Finkers R, Wolters AA, Hutton SF, et al. Assessing the genetic variation of *Ty-1* and *Ty-3* alleles conferring resistance to tomato yellow leaf curl virus in a broad tomato germplasm. Mol Breed. 2015;35:132. https://doi.org/10.1007/s11032-015-0329-y.

Chiu CW, Li YR, Lin CY, Yeh HH, Liu MJ. Translation initiation landscape profiling reveals hidden open-reading frames required for the pathogenesis of tomato yellow leaf curl Thailand virus. Plant Cell. 2022;34:1804–21. https://doi.org/10.1093/plcell/koac019.

Chu D, Jiang T, Liu GX, Jiang DF, Tao YL, Fan ZX, et al. Biotype status and distribution of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in Shandong Province of China based on mitochondrial DNA markers. Environ Entomol. 2007;36:1290–5. https://doi.org/10.1093/ee/36.5.1290.

Cohen S, Berlinger MJ. Transmission and cultural control of whitefly-borne viruses. Agric Ecosyst Environ. 1986;17:89–97. https://doi.org/10.1016/0167-8809(86)90030-7.

Cohen S, Harpaz I. Periodic, rather than continual acquisition of a new tomato virus by its vector, the tobacco whitefly (*Bemisia tabaci* Gennadius). Entomol Exp Appl. 1964;7:155–66. https://doi.org/10.1111/j.1570-7458.1964.tb02435.x.

Cui X, Tao X, Xie Y, Fauquet C, Zhou X. A DNAβ associated with tomato yellow leaf curl China virus is required for symptom induction. J Virol. 2004;78:13966–74. https://doi.org/10.1128/JVI.78.24.13966-13974.2004.

Czosnek H, Ber R, Antignus Y, Cohen S, Navot N, Zamir D. Isolation of tomato yellow leaf curl virus, a geminivirus. Phytopathology. 1988;78:508–12. https://doi.org/10.1094/phyto-78-508.

Devendran R, Namgial T, Reddy KK, Kumar M, Zarreen F, Chakraborty S. Insights into the multifunctional roles of geminivirus-encoded proteins in pathogenesis. Arch Virol. 2022;167:307–26. https://doi.org/10.1007/s00705-021-05338-x.

Fiallo-Olivé E, Pan LL, Liu SS, Navas-Castillo J. Transmission of begomoviruses and other whitefly-borne viruses: dependence on the vector species. Phytopathology. 2020;110:10–7. https://doi.org/10.1094/PHYTO-07-19-0273-FI.

Fiallo-Olivé E, Lett JM, Martin DP, Roumagnac P, Varsani A, Zerbini FM, et al. ICTV virus taxonomy profile: *Geminiviridae* 2021. J Gen Virol. 2021;102:001696. https://doi.org/10.1099/jgv.0.001696.

Fondong VN. Geminivirus protein structure and function. Mol Plant Pathol. 2013;14:635–49. https://doi.org/10.1111/mpp.12032.

Fukuta S, Kato S, Yoshida K, Mizukami Y, Ishida A, Ueda J, et al. Detection of tomato yellow leaf curl virus by loop-mediated isothermal amplification reaction. J Virol Methods. 2003;112:35–40. https://doi.org/10.1016/s0166-0934(03)00187-3.

Ghanim M. A review of the mechanisms and components that determine the transmission efficiency of tomato yellow leaf curl virus (*Geminiviridae*; *Begomovirus*) by its whitefly vector. Virus Res. 2014;186:47–54. https://doi.org/10.1016/j.virusres.2014.01.022.

Gilbertson RL, Batuman O, Webster CG, Adkins S. Role of the insect supervectors *Bemisia tabaci* and *Frankliniella* occidentalis in the emergence and global spread of plant viruses. Annu Rev Virol. 2015;2:67–93. https://doi.org/10.1146/annurev-virology-031413-085410.

Glick E, Zrachya A, Levy Y, Mett A, Gidoni D, Belausov E, et al. Interaction with host SGS3 is required for suppression of RNA silencing by tomato yellow leaf curl virus V2 protein. Proc Natl Acad Sci U S A. 2008;105:157–61. https://doi.org/10.1073/pnas.0709036105.

Gong P, Tan H, Zhao S, Li H, Liu H, Ma Y, et al. Geminiviruses encode additional small proteins with specific subcellular localizations and virulence function. Nat Commun. 2021;12:4278. https://doi.org/10.1038/s41467-021-24617-4.

Gong P, Zhao S, Liu H, Chang Z, Li F, Zhou X. Tomato yellow leaf curl virus V3 protein traffics along microfilaments to plasmodesmata to promote virus cell-to-cell movement. Sci China Life Sci. 2022;65:1046–9. https://doi.org/10.1007/s11427-021-2063-4.

Gottlieb Y, Zchori-Fein E, Mozes-Daube N, Kontsedalov S, Skaljac M, Brumin M, et al. The transmission efficiency of tomato yellow leaf curl virus by the whitefly *Bemisia tabaci* is correlated with the presence of a specific symbiotic bacterium species. J Virol. 2010;84:9310–7. https://doi.org/10.1128/JVI.00423-10.

Guo Q, Shu YN, Liu C, Chi Y, Liu YQ, Wang XW. Transovarial transmission of tomato yellow leaf curl virus by seven species of the *Bemisia tabaci* complex indigenous to China: not all whiteflies are the same. Virology. 2019;531:240–7. https://doi.org/10.1016/j.virol.2019.03.009.

Guo Y, Jia M, Li S, Li F. Geminiviruses boost active DNA demethylation for counter-defense. Trends Microbiol. 2022. https://doi.org/10.1016/j.tim.2022.02.002.

Haible D, Kober S, Jeske H. Rolling circle amplification revolutionizes diagnosis and genomics of geminiviruses. J Virol Methods. 2006;135:9–16. https://doi.org/10.1016/j.jviromet.2006.01.017.

Hanley-Bowdoin L, Bejarano ER, Robertson D, Mansoor S. Geminiviruses: masters at redirecting and reprogramming plant processes. Nat Rev Microbiol. 2013;11:777–88. https://doi.org/10.1038/nrmicro3117.

He YZ, Wang YM, Yin TY, Fiallo-Olivé E, Liu YQ, Hanley-Bowdoin L, et al. A plant DNA virus replicates in the salivary glands of its insect vector via recruitment of host DNA synthesis machinery. Proc Natl Acad Sci USA. 2020;117:16928–37. https://doi.org/10.1073/pnas.1820132117.

Horowitz AR, Kontsedalov S, Ishaaya I. Dynamics of resistance to the neonicotinoids acetamiprid and thiamethoxam in *Bemisia tabaci* (Homoptera: Aleyrodidae). J Econ Entomol. 2004;97:2051–6. https://doi.org/10.1093/jee/97.6.2051.

Hosseinzadeh MR, Shams-Bakhsh M, Osaloo SK, Brown JK. Phylogenetic relationships, recombination analysis, and genetic variability among diverse variants of tomato yellow leaf curl virus in Iran and the Arabian Peninsula: further support for a TYLCV center of diversity. Arch Virol. 2014;159:485–97. https://doi.org/10.1007/s00705-013-1851-z.

Hu T, Song Y, Wang Y, Zhou X. Functional analysis of a novel βV1 gene identified in a geminivirus betasatellite. Sci China Life Sci. 2020;63:688–96. https://doi.org/10.1007/s11427-020-1654-x.

Johne R, Muller H, Rector A, van Ranst M, Stevens H. Rolling-circle amplification of viral DNA genomes using phi29 polymerase. Trends Microbiol. 2009;17:205–11. https://doi.org/10.1016/j.tim.2009.02.004.

Kil EJ, Kim S, Lee YJ, Byun HS, Park J, Seo H, et al. Tomato yellow leaf curl virus (TYLCV-IL): a seed-transmissible geminivirus in tomatoes. Sci Rep. 2016;6:19013. https://doi.org/10.1038/srep19013.

Kon T, Sharma P, Ikegami M. Suppressor of RNA silencing encoded by the monopartite tomato leaf curl Java begomovirus. Arch Virol. 2007;152:1273–82. https://doi.org/10.1007/s00705-007-0957-6.

Kuan CP, Wu MT, Lu YL, Huang HC. Rapid detection of squash leaf curl virus by loop-mediated isothermal amplification. J Virol Methods. 2010;169:61–5. https://doi.org/10.1016/j.jviromet.2010.06.017.

Lapidot M, Legg JP, Wintermantel WM, Polston JE. Management of whitefly-transmitted viruses in open-field production systems. Adv Virus Res. 2014;90:147–206. https://doi.org/10.1016/B978-0-12-801246-8.00003-2.

Lapidot M, Karniel U, Gelbart D, Fogel D, Evenor D, Kutsher Y, et al. A novel route controlling begomovirus resistance by the messenger RNA surveillance factor Pelota. PLoS Genet. 2015;11: e1005538. https://doi.org/10.1371/journal.pgen.1005538.

Lefeuvre P, Martin DP, Harkins G, Lemey P, Gray AJ, Meredith S, et al. The spread of tomato yellow leaf curl virus from the Middle East to the world. PLoS Pathog. 2010;6:e1001164. https://doi.org/10.1371/journal.ppat.1001164.

Levy D, Lapidot M. Effect of plant age at inoculation on expression of genetic resistance to tomato yellow leaf curl virus. Arch Virol. 2008;153:171–9. https://doi.org/10.1007/s00705-007-1086-y.

Li ZH, Zhou XP, Zhang X, Xie Y. Molecular characterization of tomato-infecting begomoviruses in Yunnan, China. Arch Virol. 2004;149:1721–32. https://doi.org/10.1007/s00705-004-0334-7.

Li Z, Du Z, Tang Y, She X, Wang X, Zhu Y, et al. C4, the pathogenic determinant of tomato leaf curl Guangdong virus, may suppress post-transcriptional gene silencing by interacting with BAM1 protein. Front Microbiol. 2020;11:851. https://doi.org/10.3389/fmicb.2020.00851.

Li J, Wang J, Ding T, Chu D. Synergistic Effects of a Tomato chlorosis virus and tomato yellow leaf curl virus mixed infection on host tomato plants and the whitefly vector. Front Plant Sci. 2021a;12:672400. https://doi.org/10.3389/fpls.2021.672400.

Li P, Su F, Meng Q, Yu H, Wu G, Li M, et al. The C5 protein encoded by Ageratum leaf curl Sichuan virus is a virulence factor and contributes to the virus infection. Mol Plant Pathol. 2021b;22:1149–58. https://doi.org/10.1111/mpp.13103.

Li F, Qiao R, Wang Z, Yang X, Zhou X. Occurrence and distribution of geminiviruses in China. Sci China Life Sci. 2022. https://doi.org/10.1007/s11427-022-2125-2.

Liang P, Navarro B, Zhang Z, Wang H, Lu M, Xiao H, et al. Identification and characterization of a novel geminivirus with a monopartite genome infecting apple trees. J Gen Virol. 2015;96:2411–20. https://doi.org/10.1099/vir.0.000173.

Lobato IM, O'Sullivan CK. Recombinase polymerase amplification: basics, applications and recent advances. Trends Anal Chem. 2018;98:19–35. https://doi.org/10.1016/j.trac.2017.10.015.

Londono MA, Harmon CL, Polston JE. Evaluation of recombinase polymerase amplification for detection of begomoviruses by plant diagnostic clinics. Virol J. 2016;13:48. https://doi.org/10.1186/s12985-016-0504-8.

Lozano-Duran R, Rosas-Diaz T, Gusmaroli G, Luna AP, Taconnat L, Deng XW, et al. Geminiviruses subvert ubiquitination by altering CSN-mediated derubylation of SCF E3 ligase complexes and inhibit jasmonate signaling in *Arabidopsis thaliana*. Plant Cell. 2011;23:1014–32. https://doi.org/10.1105/tpc.110.080267.

Luan JB, Wang XW, Colvin J, Liu SS. Plant-mediated whitefly-begomovirus interactions: research progress and future prospects. Bull Entomol Res. 2014;104:1–10. https://doi.org/10.1017/S000748531400011X.

Luna AP, Morilla G, Voinnet O, Bejarano ER. Functional analysis of gene silencing suppressors from tomato yellow leaf curl disease viruses. Mol Plant Microbe Interact. 2012;25:1294–306. https://doi.org/10.1094/MPMI-04-12-0094-R.

Luo C, Yao Y, Wang RJ, Yan FM, Hu DX, et al. The use of mitochondrial cytochrome oxidase mtCOI gene sequences for the identification of biotypes of *Bemisia tabaci* (Gennadius) in China. Acta Entomol Sin. 2002;45:759–63. https://doi.org/10.16380/j.kcxb.2002.06.011.

Ma Y, Navarro B, Zhang Z, Lu M, Zhou X, Chi S, et al. Identification and molecular characterization of a novel monopartite geminivirus associated with mulberry mosaic dwarf disease. J Gen Virol. 2015;96:2421–34. https://doi.org/10.1099/vir.0.000175.

Mabvakure B, Martin DP, Kraberger S, Cloete L, van Brunschot S, Geering ADW, et al. Ongoing geographical spread of tomato yellow leaf curl virus. Virology. 2016;498:257–64. https://doi.org/10.1016/j.virol.2016.08.033.

Medina-Puche L, Orílio AF, Zerbini FM, Lozano-Durán R. Small but mighty: functional landscape of the versatile geminivirus-encoded C4 protein. PLoS Pathog. 2021;17:e1009915. https://doi.org/10.1371/journal.ppat.1009915.

Navas-Castillo J, Sánchez-Campos S, Díaz JA, Sáez-Alonso E, Moriones E. Tomato yellow leaf curl virus-Is causes a novel disease of common bean and severe epidemics in tomato in Spain. Plant Dis. 1999;83:29–32. https://doi.org/10.1094/pdis.1999.83.1.29.

Navas-Castillo J, Fiallo-Olivé E, Sánchez-Campos S. Emerging virus diseases transmitted by whiteflies. Annu Rev Phytopathol. 2011;49:219–48. https://doi.org/10.1146/annurev-phyto-072910-095235.

Navot N, Pichersky E, Zeidan M, Zamir D, Czosnek H. Tomato yellow leaf curl virus: a whitefly-transmitted geminivirus with a single genomic

component. Virology. 1991;185:131–61. https://doi.org/10.1016/0042-6822(91)90763-2.
Oh S, Kim S, Vinod N, Koo JM, Jang KM, Choi CW, et al. PCR-RFLP-based typing for differentiation of tomato yellow leaf curl virus (TYLCV) genotypes from infected host plants in Korea. Virus Genes. 2013;47:579–83. https://doi.org/10.1007/s11262-013-0959-2.
Pan HP, Chu D, Ge DQ, Wang SL, Wu QJ, Xie W, et al. Further spread of and domination by *Bemisia tabaci* biotype Q on field crops in China. J Econ Entomol. 2011;104:978–85. https://doi.org/10.1603/EC11009.
Pan H, Chu D, Liu B, Shi X, Guo L, Xie W, et al. Differential effects of an exotic plant virus on its two closely related vectors. Sci Rep. 2013;3:2230. https://doi.org/10.1038/srep02230.
Papayiannis LC, Katis NI, Idris AM, Brown JK. Identification of weed hosts of Tomato yellow leaf curl virus in Cyprus. Plant Dis. 2011;95:120–5. https://doi.org/10.1094/PDIS-05-10-0346.
Pérez-Padilla V, Fortes IM, Romero-Rodríguez B, Arroyo-Mateos M, Castillo AG, Moyano C, et al. Revisiting seed transmission of the type strain of tomato yellow leaf curl virus in tomato plants. Phytopathology. 2020;110:121–9. https://doi.org/10.1094/PHYTO-07-19-0232-FI.
Prasad A, Sharma N, Hari-Gowthem G, Muthamilarasan M, Prasad M. Tomato yellow leaf curl virus: impact, challenges, and management. Trends Plant Sci. 2020;25:897–911. https://doi.org/10.1016/j.tplants.2020.03.015.
Rojas MR, Jiang H, Salati R, Xoconostle-Cazares B, Sudarshana MR, Lucas WJ, et al. Functional analysis of proteins involved in movement of the monopartite begomovirus, tomato yellow leaf curl virus. Virology. 2001;291:110–25. https://doi.org/10.1006/viro.2001.1194.
Rosas-Diaz T, Macho AP, Beuzon CR, Lozano-Duran R, Bejarano ER. The C2 protein from the geminivirus tomato yellow leaf curl Sardinia virus decreases sensitivity to jasmonates and suppresses jasmonate-mediated defences. Plants (basel). 2016;5:8. https://doi.org/10.3390/plants5010008.
Rubio L, Galipienso L, Ferriol I. Detection of plant viruses and disease management: relevance of genetic diversity and evolution. Front Plant Sci. 2020;11:1092. https://doi.org/10.3389/fpls.2020.01092.
Shepherd DN, Martin DP, Lefeuvre P, Monjane AL, Owor BE, Rybicki EP, et al. A protocol for the rapid isolation of full geminivirus genomes from dried plant tissue. J Virol Methods. 2008;149:97–102. https://doi.org/10.1016/j.jviromet.2007.12.014.
Shi X, Pan H, Zhang H, Jiao X, Xie W, Wu Q, et al. *Bemisia tabaci* Q carrying tomato yellow leaf curl virus strongly suppresses host plant defenses. Sci Rep. 2014;4:5230. https://doi.org/10.1038/srep05230.
Tabein S, Miozzi L, Matić S, Accotto GP, Noris E. No evidence for seed transmission of tomato yellow leaf curl Sardinia virus in tomato. Cells. 2021;10:1673. https://doi.org/10.3390/cells10071673.
Tembo M, Adediji AO, Bouvaine S, Chikoti PC, Seal SE, Silva G. A quick and sensitive diagnostic tool for detection of maize streak virus. Sci Rep. 2020;10:19633. https://doi.org/10.1038/s41598-020-76612-2.
Voorburg CM, Yan Z, Bergua-Vidal M, Wolters AA, Bai Y, Kormelink R. *Ty-1*, a universal resistance gene against geminiviruses that is compromised by co-replication of a betasatellite. Mol Plant Pathol. 2020;21:160–72. https://doi.org/10.1111/mpp.12885.
Wang B, Li F, Huang C, Yang X, Qian Y, Xie Y, et al. V2 of tomato yellow leaf curl virus can suppress methylation-mediated transcriptional gene silencing in plants. J Gen Virol. 2014;95:225–30. https://doi.org/10.1099/vir.0.055798-0.
Wang B, Yang X, Wang Y, Xie Y, Zhou X. Tomato yellow leaf curl virus V2 interacts with host histone deacetylase 6 to suppress methylation-mediated transcriptional gene silencing in plants. J Virol. 2018;92:e00036-e118. https://doi.org/10.1128/JVI.00036-18.
Wang L, Ding Y, He L, Zhang G, Zhu JK, Lozano-Duran R. A virus-encoded protein suppresses methylation of the viral genome through its interaction with AGO4 in the Cajal body. Elife. 2020;9:e55542. https://doi.org/10.7554/eLife.55542.
Wei J, He YZ, Guo Q, Guo T, Liu YQ, Zhou XP, et al. Vector development and vitellogenin determine the transovarial transmission of begomoviruses. Proc Natl Acad Sci USA. 2017;114:6746–51. https://doi.org/10.1073/pnas.1701720114.
Wu JB, Dai FM, Zhou XP. First report of tomato yellow leaf curl virus in China. Plant Dis. 2006;90:1359. https://doi.org/10.1094/pd-90-1359c.
Wu Q, Luo Y, Lu R, Lau N, Lai EC, Li WX, et al. Virus discovery by deep sequencing and assembly of virus-derived small silencing RNAs. Proc Natl Acad Sci USA. 2010;107:1606–11. https://doi.org/10.1073/pnas.0911353107.
Wu M, Wei H, Tan H, Pan S, Liu Q, Bejarano ER, et al. Plant DNA polymerases alpha and delta mediate replication of geminiviruses. Nat Commun. 2021;12:2780. https://doi.org/10.1038/s41467-021-23013-2.
Xia J, Guo Z, Yang Z, Han H, Wang S, Xu H, et al. Whitefly hijacks a plant detoxification gene that neutralizes plant toxins. Cell. 2021;184:1693–705. https://doi.org/10.1016/j.cell.2021.02.014.
Xie Y, Jiao X, Zhou X, Liu H, Ni Y, Wu J. Highly sensitive serological methods for detecting tomato yellow leaf curl virus in tomato plants and whiteflies. Virol J. 2013a;10:142. https://doi.org/10.1186/1743-422x-10-142.
Xie Y, Zhao L, Jiao X, Jiang T, Gong H, Wang B, et al. A recombinant begomovirus resulting from exchange of the C4 gene. J Gen Virol. 2013b;94:1896–907. https://doi.org/10.1099/vir.0.053181-0.
Yan Z, Wolters AA, Navas-Castillo J, Bai Y. The global dimension of tomato yellow leaf curl disease: current status and breeding perspectives. Microorganisms. 2021;9:740. https://doi.org/10.3390/microorganisms9040740.
Yang X, Zhou M, Qian Y, Xie Y, Zhou X. Molecular variability and evolution of a natural population of tomato yellow leaf curl virus in Shanghai, China. J Zhejiang Univ Sci B. 2014;15:133–42. https://doi.org/10.1631/jzus.B1300110.
Yang X, Wang B, Luan J, Xie Y, Liu S, Zhou X. Molecular variation of tomato yellow leaf curl virus in the insect vector *Bemisia tabaci*. Sci Rep. 2017;7:16427. https://doi.org/10.1038/s41598-017-16330-4.
Yang X, Du M, Li S, Zhou X. Coinfection of cotton plants with watermelon mosaic virus and a novel polerovirus in China. Viruses. 2021;13:2210. https://doi.org/10.3390/v13112210.
Zeng XJ, Zhang C, He Y, Zhou Q, Li D, Zheng L, et al. Analysis of world tomato production based on FAO data from 1980 to 2019. Hunan Agric Sci. 2021;11:104–8. https://doi.org/10.16498/j.cnki.hnnykx.2021.011.026. (In Chinese)
Zhao S, Gong P, Ren Y, Liu H, Li H, Li F, et al. The novel C5 protein from tomato yellow leaf curl virus is a virulence factor and suppressor of gene silencing. Stress Biol. 2022. https://doi.org/10.1007/s44154-022-00044-3.
Zhou Y, Zheng HY, Jiang DM, Liu M, Zhang W, Yan JY. A rapid detection of tomato yellow leaf curl virus using recombinase polymerase amplification-lateral flow dipstick assay. Lett Appl Microbiol. 2022;74:640–6. https://doi.org/10.1111/lam.13611.