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Review

Research progress on tomato spotted wilt virus transmitted by Thrips

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Thrip is a collective name for Thysanoptera, an agricultural pest that is widely distributed around the world and transmits viruses, in addition, to directly eating crops, causing extremely serious economic losses. Tomato spotted wilt virus (TSWV) is one of the main viruses transmitted by thrips. Since the discovery of TSWV in 1919, much progress and achievements have been made in its characteristics, mechanism of transmission, comprehensive prevention and control of TSWV in the past hundred years. This article summarizes the characteristics, propagation mechanism and control measures of TSWV transmission in thrips, and looks forward to future research directions.

Key words: Tomato spotted wilts virus, thrips species, quarantine inspection, integrated control.

INTRODUCTION

Thrips are widely distributed all over the world and were first discovered by De Geer in 1744, at present more than 7,000 thrips insects have been discovered, and over 500 species have been recorded in China (Majid et al., 2011). Thrips can harm flower buds, leaves, branches and fruits, causing wilting of branches and leaves, falling flowers, spotting on the surface of the fruit, fruit deformity, and fruit falling in severe cases. Thrips not only cause direct harm by eating plants, but also carry and transmit plant viral diseases during feeding, indirectly causing harm to crops, such as tomato spotted wilt virus (TSWV).

TSWV can result in severe production or the unmarketability of many cash crops. For example, Tomato crops in the Nakuru District in Kenya were affected by TSWV infection during the November 1999 to March 2000 tomato-growing season, as much as 80% of its potential production is lost (Wang et al., 2001). In 2019, disease outbreaks were observed in South Sardinia, TSWV was detected in more than 80% of tomato plants (Parrella et al., 2020). In June 2019, TSWV was isolated in cucumber greenhouses in İzmir (western Turkey), disease incidence was estimated as 30%,

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resulting in a decline in cucumber production (Erilmez et al., 2022).

The suitable areas for TSWV are tropical, subtropical, temperate, etc. This is the same living environment as its vector, the thrips (Accotto et al., 2000). Global warming has led to the spread and harm of thrips, and further accelerated the spread of TSWV. This paper summarizes the characteristics of thrips and the way of virus transmission, the pathogenic morphology and pathogenic mechanism of TSWV, and the prevention and control methods of TSWV, and finally makes corresponding prospects for the future research direction of the virus.

The main vector - thrips

TSWV is mainly transmitted by thrips in circulative propagative transmission between different host plants (Whitfield et al., 2005). A small number of viruses are transmitted by mechanical friction, grafting, etc. Once a thrips is infected, it can carry the virus for life. Because thrips have a wide range of hosts and spread quickly, once the virus breaks out, it can cause a large reduction in the yield of agricultural and forestry crops.

Thrips species that spread TSWV

The literature was consulted and found that there are 12 thrips that have been reported to transmit the virus; however, 10 species of thrips have been proved to transmit TSWV effectively. They were *Frankliniella occidentalis*, *Thrips palmi* Karny, *Frankliniella schultzei* Trybom, *Thrips tabaci*, *Frankliniella fusca*, *Frankliniella bispinosa*, *Frankliniella intonsa*, *Frankliniella cephalica*, *Thrips setosus* and *Frankliniella tenuicornis* (Xie et al., 2013; Yang et al., 2011). Among them, *F. occidentalis*, *F. schultzei* Trybom, *F. fusca*, *F. bispinosa*, *F. intonsa*, *F. cephalica* and *F. tenuicornis* belong to *Frankliniella* Karny; *T. palmi* Karny, *T. tabaci* and *T. setosus* belong to *Thrips* Linnaeus.

F. occidentalis, the leading spreader of TSWV, is one of the important quarantine pests in the world. Adults are yellow in color and have wings less than 2 mm in length. *F. occidentalis* was first discovered in the western United States (Mound, 1996). Because of its host abundance, omnivorous, strong survival and other characteristics, it quickly spread to all over the world after 1980s. In 1996, *F. occidentalis* was listed as quarantine pests by the Ministry of Agriculture of the People's Republic of China (Dai et al., 2004), and has been reported in Beijing, Xinjiang, Yunnan, Shandong, Ningxia, Inner Mongolia, Guizhou, Jilin and other places (Peng et al., 2022; Zhang et al., 2018; Yuan et al., 2010).

T. palmi Karny, the adult worm color is yellow-brown or black, body length 1 to 2 mm, like to eat nightshade and melons. It was first discovered on tobacco grown in Sumatra (Waterhouse et al., 1987). In 1976, *T. palmi* Karny was found on vegetable crops in Guangdong, and are currently distributed in Guangdong, Guangxi, Hainan, Hunan, Yunnan, Zhejiang, Sichuan and other places (Yuan et al., 2021).

F. schultzei Trybom, the adult worm color is brown or yellow, with a body length of about 1.2 mm, and the virus transmission efficiency of brown species is higher than that of yellow species. It feeds on crops such as cotton, tomatoes, peas, soybeans, sorghum, peppers, onions, etc. It was first reported in 1991 (Vierbergen and Mantel, 1991) and first recorded in 2011 in Guangxi in our country (Xie et al., 2011). In 2019, it was recorded on pomegranates in Shaanxi Province, and it has not been reported in other provinces in China (Ning et al., 2019).

T. tabaci, the adult worm color is light yellow to dark brown, body length 1.0 to 1.5 mm, and it was feed on more than 150 crops such as onions, tobacco, cotton, grapes, apples, green onions, garlic, etc. It was first documented on Russian Bessarabian tobacco in 1889. It is distributed in most provinces in China, but the adults found are all females, and no male insects have been reported in our country. Male *T. tabaci* have been reported in a few areas such as New Zealand and New York (Liu et al., 2008; Wang et al., 2016).

F. intonsa, the females are light brown, the males are yellowish-white, about 1.3 mm long, and it showed obvious tendency to flowers. In 1997, *F. intonsa* was first found on navel oranges in China, and is now widely distributed in various provinces (Zhu, 2012). *F. fusca*, the adult worm color is dark to light brown with yellow legs and brown markings on the femur, and are 1.2 to 1.8 mm long (Nakao et al., 2011). *F. cephalica*, the adult worm color is yellow-brown, and is native to the Caribbean region of Central America. It feed during the flowering period of plants such as Compositae, Solanaceae, Poaceae, and Rutaceae. Chinese scholar Tong found it on Guangdong *Bidens pilosa* L. in 2008 (Tong et al., 2013).

The process of obtaining and transmitting poison

The metamorphosis type of thrips was hyperpaurometamorphosis. It had five stages (egg, nymph, pseudopupa, pupa, and adult). The egg and pupal stages do not infect and transmits the virus. At the 1 to 2 instar nymphs, thrips acquire the virus by feeding on plants that have been infected with the virus through rasping-mouthparts for more than 15 min. The virus enters the digestive system through the mouth of thrips, and the glycoprotein on the surface of TSWV protects the virus from digestive juices and replicates and proliferates in the midgut, and then expands to midgut muscle cells and salivary glands, and the completion time of proliferation needs to last more than 72 h (Jones, 2005; Nagata et al., 2002). The peritrophic matrix on the midgut of thrips extends beyond the cardiac valve with nymph growth and gradually thickens, isolating the virus. As a result, thrips are infected only in the nymph stage, and the adult stage transmits virus. The route of transmission of thrips in the adult stage is the same as the route of infection, and it is also transmitted by feeding. The mobility of thrips in adult stage is stronger than that in nymph stage, by flying and bouncing onto plants that are not infected with the virus, and invading host plant tissues while feeding, adults release virus-containing saliva to transmit poison. According to the literature, thrips can maintain their virulence for 22 to 30 days, almost throughout their adult life history, but the virus does not spread vertically through eggs (Ullman et al., 1997).

TSWV

TSWV, Bunyavirales: Tospoviridae: Orthotospovirus: It is one of the plant negative stranded RNA viruses, a systemic infection disease, ranking second among the top ten dangerous plant viruses. In 2007, China listed it in the List of Quarantine Pests in Imported Plants of the People's Republic of China.

Viral distribution

In 1919, Australian scholar Brillelebank found a new type of victimization symptom on tomatoes, but did not identify the specific cause and named it spotted wilt (Brittlebank, 1915). Samuel et al. (1930) confirmed that it was caused by a viral infection and conducted corresponding research. Subsequently, TSWV was reported around the world, and the virus was found to be widely distributed in many countries and regions such as the United States, South Korea, Japan, the United Kingdom and Hungary (Srinivasan et al., 2017; Asano et al., 2017; András et al., 2006). Its hosts include more than 1,000 plants in more than 80 families such as bellflower, pepper, potato, chrysanthemum, peanut and so on (Yoon et al., 2017; Chung et al., 2012; Sivaprasad et al., 2018; Culbreath et al., 2003).

In 1984, TSWV was first discovered in the investigation of southern peanut disease in China. In 1986, the virus was isolated on peanut bud wilt plants in the experimental site of the Guangdong Academy of Agricultural Sciences (Xu et al., 1989). TSWV has been reported on tobacco in Sichuan in 1992, potato disease strains cultivated in Kunming in 2004, Phalaenopsis orchids planted in Yunnan in 2008, chili peppers planted in Guangzhou in 2010, chili peppers and eggplants planted in Beijing in 2012, and kiwifruit grown in Guizhou in 2015 (Yao, 1992; Li et al., 2012).

Viral morphology

TSWV consists of 5% nucleic acids, 70% protein, 5% carbohydrates and 20% lipids. It has the shape of a spherical coated particle with a diameter of 80 to 110 nm, the outer layer of the particle is bounded by a membrane and wrapped in a membrane surface containing two glycoproteins Gn and Gc. The genome contains 3 negative single-stranded ssRNAs, SRNA (2916 nucleotides), MRNA (about 5000 nucleotides), and LRNA (about 8000 nucleotides). SRNA arrangement: encoding non-structural NSs proteins and N proteins; MRNA arrangement encodes non-structural NSm proteins and G1 and G2 glycoproteins; LRNA arrangement encodes the RNA-dependent polymerase RdRp (Peter et al., 1991).

Pathogenic mechanism

TSWV enters host cells while thrips feeding replicates and transcribes in the cytoplasm, and genomic RNA and N proteins synthesize a large number of invasive ribonucleoprotein granule RNPs. The non-structural protein NSm is a mobile protein of TSWV, which promotes the spread of the virus in the host, modifies the intercellular filaments Plasmodesmata (PD) in adjacent cells, induces the formation of ducts to connect adjacent cells, helps RNPs transport to the Golgi apparatus, and the virus particles assemble in the Golgi apparatus, and then form double-enveloped viruses (DEVs). DEVs enter the endoplasmic reticulum containing mature monoencapsulated virus accumulation, resulting in systemic disease of the whole crop (Qian, 2019; Xiang, 2019).

Hazard symptoms

The symptoms of TSWV are various in different hosts. On peanuts, TSWV infection is symptomatic as the top shoots shrinking and chlorisis. The young leaves on the top have yellowing ring spots on the front and tan spots on the back, and the petioles and stems are brown, whole plant are partly twisted. The old lower leaves show yellow spots, and the root system withers and further decomposed, causing the whole plant to dwarf and die. Peanuts gradually develop resistance to TSWV along with their own growth and development, and infection at the seedling stage can easily lead to dwarfing death of plants, and in the later stage infection will hardly cause plant dwarfing death, but the yield of infected single plant is lower than the normal yield (Dong and Li, 2022).

On peppers, TSWV causes the leaves on the plant to show chlorotic or yellow spots, the petioles and foliar vascular bundles are brown, and necrosis in the newborn leaves. The dwarf and yellowing of the plants infected by the virus are obvious, some petals fall off, and the fruits are deformed (Wang et al., 2019; Zhu et al., 2019).

On tobacco, TSWV causes lace-like necrosis of leaf veins, necrotic mottled curl along the leaf veins, and the overall plant shape becomes smaller, with necrotic spots and concentric ring patterns, after 4~5 weeks of infection, tobacco leaves wither and die (Liu et al., 2009).

In summary, the common symptoms of plant infection are young shoots withering, yellowing of the leaf surface, brown markings on petioles and rhizomes, dwarf and wilting of plants, and finally death.

Quarantine inspection methods

The existing detection methods of TSWV are biological observation, serological identification, electron micro scope and molecular biology testing. The biological observation method is to isolate the virus from the plant that has been infected with the virus and inoculate it to the indicator plant, and observe the symptom of the indicator plant to confirm its virus species. However, this method is time-consuming and inefficient. Just observing the symptoms of the disease is not a way to distinguish between the same virus and whether there are symptoms of multiviral complex infection. This method should only be used as an initial test for the virus and is currently less commonly used. Serological identification is a test method based on the interaction between pathogenic proteins and antibodies, and the test result is positive. The Enzyme Linked Immuno Sor-bent Assay (ELISA) method is one of the main methods used in serological identification. ELISA can be used for asymptomatic plant testing, taking the leaves and roots of plants for testing. This method is sensitive and fast, and antibodies can be stored for a long time. However, the close serological relationship of the virus may lead to false positive cross-reaction (Yu et al., 2018). Therefore, these methods alone do not provide 100% confirmation of the virus and need to be combined with other methods (Elliott et al., 1996). Electron micro scope can observe TSWV granular morphology and subcellular structure in host plants through ultrathin sectioning, negative stain, immunosorbent electron microscopy (IEM), etc (Qin et al., 2017). This method is simple and intuitive, high in sensitivity, but the cost of electron microscopy equipment is high, the instrument is larger, and it is less used in field inspections. Molecular biology methods identify viruses based on nucleic acids, common methods are reverse transcription-PCR (RT-PCR) detection and realtime fluorescence PCR (RF-PCR) detection. With rapid detection, high sensitivity, little environmental impact, simple operation and easy repetition, it is the most widely used method for testing TSWV at present. It is considered to be a revolutionary method for plant pathogen identification and plant disease diagnosis (Yu et al., 2020; Wu et al., 2020).

The current quarantine standard of China customs is GB/T 31802-2015, and the quarantine methods are ELISA detection method, RT-PCR detection method, RF-PCR detection method and biological determination method. The positive determination criterion is that the ELISA test is positive, and there was one positive in both RT-PCR and RF-PCR (GB/T 31802-2015).

WAYS TO PREVENT *THRIPS* FROM SPREADING VIRUS

Insect control is an important control strategy for many insect-borne plant virus diseases. As the main vector of TSWV, thrips are mainly controlled to reduce the transmission of the virus through agricultural, physical, chemical and biological control measures. The following are techniques to prevent *Thrips* from spreading virus.

Agricultural control

Agricultural prevention and control are the basis for comprehensive management. Breeding virus-resistant plant varieties is the most effective means of TSWV controlling, and breeding thrips-free seedlings stops the spread of the virus at the source. Zhu et al. (2019) vaccinated 40 domestic pepper cultivars with TSWV and screened out the breed white millet pepper No. 2 for effective disease resistance. Mo et al. (2016) artificially inoculated independently bred and introduced tomato breed (lines) for 3 years, discovered the tomato inbred line ‘YNAU335' was immune to TSWV. Insect-free seedlings address the source of thrips in the planting area. Thrips eggs were tested before transplanting, and seedlings with thrips eggs were cleaned up. This can prevent and control thrips from the source.

Strengthen field management in planting areas and remove infected plants on time (Zhang et al., 2021), clean the planting area before transplanting, remove weeds and dead leaves from burning fields and plough the soil to eliminate thrips. Reduce thrips populations and prevent them from migrating into the fields. Strengthen water and fertilizer management to promote plant growth and robustness. Remove infected plants on time to reduce the source of infection and prevents field thrips from feeding to spread the virus. Weeds and crops around the planting area can affect the thrips population. Crop rotation and intercropping also affect thrips numbers. If weeds around crops are infested with TSWV, thrips can roost and multiply between weeds and crops. In this way, the source of the virus is not easy to detect and difficult to kill when the disease occurs. TSWV will occur in the planting area for a long time.

Physical control

Color preference of thrips is used to control the spread of TSWV. Dong et al. (2018) studied the trapping effect of 6 different color sticky board on *F. occidentalis*. The trapping effect is yellow> blue> white> green> red> black = white (Dong et al., 2018). Chen et al. (2017) based on the quantitative function relationship between Dan Bruton virtual wavelength and RGB value on the color tendency of *F. intonsa*, concluded that thrips have the strongest tendency to blue and white. Combining the insect pheromone with the tendency, Li et al. (2021) reported that the use of 3750 times solution of 1.5% VDAL solution mixed with thrips pheromone sticky card increased the control efficacy by 4.92% in the field test in mango orchards, and the mango single fruit increased weight by 50.91%, achieving control and yield increase.

Plant essential oils were used against thrips. Guo et al. (2021) reported that citrus oil, nutmeg essential oil, citronella oil, garlic essential oil and camphor oil have an avoidance effect on thrips. Guo et al. (2021) concluded that 20% rosemary essential oil micro-emulsion × 500 times liquid can control thrips at the early stage. Lu et al. (2018) found that wintergreen oil, oregano oil, cinnamon oil, thyme oil, citral, sassafras oil, perilla leaf oil, garlic oil, dipentene, and terpineol had high fumigation activity against both the 2nd instar nymphs and adults of *Anaphothrips obscurus*.

With the aim of wintering habit of thrips, mulching the mulch film in the planting area in winter reduces the population of thrips in the following year. Yang et al. (2022) reported that silver-black and silver-grey mulching films both can reduce TSWV morbidity and disease index in tobacco field effectively and have the obvious deterrent effect on thrips. Among them, the silver-black mulch film has the best control effect on thrips.

Chemical control

Chemical control is the main method at present, which has the characteristics of fast effect, high broad-spectrum and easy operation. There are many options for pesticides, such as chlorfenapyr, imidacloprid, acetamiprid, avermectin, beta-cypermethrin and spinetoram (Chen et al., 2020; Zhao et al., 2018). However, long-term use of the same or type of pesticide can make thrips develop resistance. Li et al. (2022) and Pan et al. (2021) reported that alfalfa thrips in Yinchuan had developed moderate resistance to neonicotinoids, pyrethroids and benzoamides. Wan et al. (2016) investigated *F. occidentalis* in Beijing and Kunming. The results showed that the spinosad resistance of thrips in the two places was 150 and 305 times, the resistance of Beijing to spinetoram has increased to 7,730 times, and the LC_{50} value to spinetoram had increased by a maximum of 258 times, the initial value in five years. Song et al. (2021) found that pesticides such as avermectin and spinetoram were used in large areas, and the control effect on thrips was significantly reduced. Thrips developed moderate levels of resistance to acetamiprid and low levels of resistance to avermectin. The broad spectrum of pesticides is high, and the lethality of natural enemies of thrips is also very large, and the compatibility of pesticide and natural enemies is highly controversial in pesticide use. Lin et al. (2022) tested the toxicity of 7 new insecticides to *Orius strigicollis* (the natural enemy of *Thrips hawaiiensis*). Results showed that 4 insecticides were equally effective against *O. strigicollis* and *T. hawaiiensis*, causing the death of natural enemies (Lin et al., 2022).

In the preliminary research and development process of pesticides for chemical control, the compatibility with natural enemies should be improved, and natural enemies and pesticides should cooperate to control pests. Growers need to apply the appropriate medicine, timely use, efficiently apply medicines by turns to avoid repeated use of single pesticide and slow down the development of resistance.

Biocontrol

In terms of biological control, thrips natural enemies are used to control thrips. Natural enemies have been reported to include predatory mites, orius, parasitic wasps, nematodes and fungal microorganisms. Sun et al. (2021) reported that the number of *Orius similis* preying on Thrips flavus nymphs was significantly higher than that of adults, and the population densities of *O. similis* were increased with the increase of Thrips flavus. Li et al. (2022) found that, in the range of 16 to 32°C, the predation of 5th instar *Orius maxidentex* nymph increases with the temperature rises and reaches a maximum at 32°C. Wang et al. (2022) reported that *Nesidiocoris poppiusi* preyed on *F. occidentalis*, and the number of prey by females is much greater than that by males. Li et al (2021) reported *Amblyseius eharai* Amitai et Swirski preys on *T. hawaiiensis*. Yu et al. (2022) found that *Propylea japonica* preyed on 2 to 3 instar nymphs of *Selenothrips rubrocinctus*. The prey on thrips of *Nesidiocoris poppiusi*, *A. eharai* Amitai et Swirski and *P. japonica* all belong to the Holling II type and have strong control potential. Xu et al. (2021) have also done experiments related to predatory mites. The experiment reported the simultaneous release of *Amblyseius cucumeris* Oudemans, *Amblyseius swirskii* and spraying Spirotetramat in the orchard. The control effect of Spirotetramat was better in the first 15 days, and the control effect of *A. cucumeris* Oudemans and *A. swirskii* after 30 days was better than that of Spirotetramat. After 45 days, the number of thrips in the Spirotetramat area showed a rebound and rose sharply. The area where predatory mites are released has good protection and a long effective period. This experiment also once again proved the advantages of biological control (Xu et al., 2021).

Pathogenic microorganisms can also control thrips well. At present, the fungi that have been reported include *Beauveria bassiana*, *Metarhizium anisopliae*, *Metarhizium flavoviride*, *Isaria fumosorosea*, *Lecanicillium lecanii*, and *Neozygites parvispora* (Ge et al., 2019, 2018). Zhang (2019) proved that the spores of *B. bassiana* can complete the attachment of pseudopupae of *F. occidentalis* within 60 h, and the strain GZGY-1-3 shows high virulence against *F. occidentalis*. Zeng et al. (2019) used *M. anisopliae* and *B. bassiana* against adults of *Gynaikothrips uzeli*, and the corrected mortality of the 2 strains against *G. uzeli* adults is over 80%. The increase in the concentration of infectants and the prolongation of infection time were positively correlated with the mortality rate of thrips (Zeng et al., 2019). The use of biological control technology can reduce the use of pesticides and improve the quality and safety of agricultural products.

PROSPECT

TSWV is a world virus that seriously harms agricultural production, ranking second among the top ten dangerous plant viruses, and its main vector is thrips. In this paper, the ways in which TSWV harms plants, the types of thrips that transmit TSWV are introduced, and the existing research on agricultural, physical, chemical and biological control is analyzed. At present, chemical insecticide is the main single control measure, which will bring irreversible damage to the agricultural ecological environment and seriously endanger the production safety of crops. Therefore, the prevention and treatment of TSWV must be comprehensively treated from multiple angles. Various measures combining agriculture, physics, chemistry, biology and other aspects should be adopted to form an all-round, multi-level and comprehensive control measures. The cooperation of multiple control methods can make up for shortcomings of diffferent ways, establish a stable, safe and sustainable pest control system to ensure the safety of food production.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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