A global invasion by the thrip, *Frankliniella occidentalis*: Current virus vector status and its management

Zhen He¹², Jing-Fei Guo¹, Stuart R. Reitz³, Zhong-Ren Lei¹ and Sheng-Yong Wu¹

¹State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing, China; ²School of Horticulture and Plant Protection, Yangzhou University, Yangzhou, Jiangsu Province, China and ³Malheur Experiment Station, Oregon State University, Ontario, OR, USA

Abstract Western flower thrip, *Frankliniella occidentalis* (Pergande), is among the most economically important agricultural pests globally, attacking a wide range of vegetable and horticultural crops. In addition to causing extensive crop damage, the species is notorious for vectoring destructive plant viruses, mainly belonging to the genera *Orthotospovirus*, *Ilarvirus*, *Alphacarmovirus* and *Machlomovirus*. Once infected by orthotospoviruses, thrips can remain virulent throughout their lifespan and continue transmitting viruses to host plants when and wherever they feed. These irruptive viral outbreaks in crops will permanently disrupt functional integrated pest management systems, and typically require a remedial treatment involving insecticides, contributing to further development of insecticide resistance. To mitigate against this continuing cycle, the most effective management is early and comprehensive surveillance of the pest species and recognition of plant viruses in the field. This review provides information on the pest status of *F. occidentalis*, discusses the current global status of the viruses vectored by this thrip species, examines the mechanisms involved in transmitting virus-induced diseases by thrips, and reviews different management strategies, highlighting the potential management tactics developed for various cropping systems. The early surveillance and the utilization of potential methods for control of both *F. occidentalis* and viruses are proposed.

Key words global distribution; integrated pest management; invasion; thrips; viruses transmission

Introduction

Thrips (order Thysanoptera) are minute insects only a few millimeters or less in length. Of the approximately 5500 described species of thrips in the world, scarcely 1% are considered to be serious pests of commercial crops (Morse & Hoddle, 2006; Healey et al., 2017). Among these pests, several species stand out as being among the most important global agricultural pests. These include four of the major thrip pests, the western flower thrip, *Frankliniella occidentalis* Pergande, the onion thrip, *Thrips tabaci* Lindeman, the melon thrip, *T. palmi* Karny and the yellow tea thrip (chili thrip), *Scirtothrips dorsalis* Hood (Mound, 2002; Riley et al., 2018). *F. occidentalis* is a polyphagous and ubiquitous invader of key agri- and horticultural crops in diverse field and greenhouse environments. This is due to the damage caused directly by its feeding and oviposition, and indirectly through transmission of plant viruses, of which tomato spotted wilt orthotospovirus (TSWV) is the most economically important (Schneweis et al., 2017). *F. occidentalis* was first described in 1895 in California, USA, and beginning in the late 1970s has since become a major global pest (Kirk & Terry, 2003). This species has been the most intensively studied member of the order Thysanoptera since 1980, accounting for over one-third of the publications based on this order (Reitz et al., 2011). *F. occidentalis* has continued its spread around the world...
and is now distributing in at least 57 countries (Fig. 1, Table S1). The spread of *F. occidentalis* and various vectored orthotospoviruses have frequently caused failure of established integrated pest management (IPM) systems for agricultural crops (Morse & Hoddle, 2006).

Phytophagous thrips have many traits that predispose them to be successful invaders, such as minute size, cryptic habits, high reproductive potential and high dispersal capability. *F. occidentalis* has superior or additional features, promoting their worldwide spread and sustained damage. The possible reasons for the start of the spread is intensive insecticide use in the 1970s and 1980s, which was reviewed by Kirk and Terry (2003). Biological factors facilitating invasion by thrips was reviewed by Morse and Hoddle (2006). Biological processes and molecular interactions involved in the virus acquisition and transmission by thrips was reviewed by Whitfield et al. (2005a). Over a decade after these reports, we aim to provide a summary of the extraordinary attributes that make for a successful invader with major economical damage potential. We have reconstructed in a chronological order the current global distribution of *F. occidentalis*, as well as several viruses transmitted. We have also summarized the control strategies based on IPM of *F. occidentalis*, stressing the recent progress in biological control.

**Biology and ecology**

*F. occidentalis* possesses several biological and ecological characteristics that enable it to become a dominant thrip species in many of the areas it has invaded. Its short generation time and high reproductive potential, often with a predisposition to parthenogenesis, enhances the likelihood of establishment (Kirk & Terry, 2003; Zhang et al., 2010); its cryptic behavior and high level of vagility enable it to disperse to a wide variety of crops (Cloyd, 2009; Reitz, 2009); its polyphagous nature likely supplements its predisposition to evolve resistance to many classes of insecticides through metabolic detoxification pathways (Demirozer et al., 2012); its widespread resistance to most major insecticides, in turn, makes it difficult to control (Bielza, 2010; Gao et al., 2012a); its highly efficient exploitation of food sources provides it with a competitive advantage over indigenous species and enables it to become successfully established in new regions (Morse & Hoddle, 2006; Demirozer et al., 2012). However, its propensity to transmit viruses often results in serious losses in a wide range of crops (Wijkamp et al., 2010; Ogada & Poehling, 2015). In most cases, combinations of these attributes contribute to its high invasion success, ultimately resulting in severe economic damage to crops throughout the world.

**Viruses transmitted by *F. occidentalis***

Thrips are the only known vectors of orthotospoviruses, but only 0.16% of the known species have been implicated in their transmission (Mound, 2004). Thrips transmit viruses belonging to at least four virus groups, including ilarviruses, machlomoviruses, alphacarmoviruses and
orthotospoviruses (Fig. 2, Table S2). (Jones, 2005; Morse & Hoddle, 2006). Using TSWV as an example, this particular virus, which is one of the most economically important members of the genus Orthotospovirus (Tospoviridae) (Mumford et al., 1996), has long been associated with F. occidentalis – one of the most important and efficient vector thrips (Wijkamp, 1995a; Arthurs et al., 2018a). TSWV acquisition by F. occidentalis is a developmental-stage dependent process, with the 1st instar larval stage considered as the most susceptible phase (Rotenberg et al., 2015). The interactions between TSWV and F. occidentalis and its dissemination route in thrips has been thoroughly reviewed by Whitfield et al. (2015a), Rotenberg et al. (2015) and Dietzgen et al. (2016). TSWV is acquired by the thrips’ stylets and travels across the alimentary canal to the anterior region of the midgut (MG), where the surface glycoproteins, Gn and Gc, facilitate its entrance into the thrips’ MG (Whitfield et al., 2004, 2005b). Subsequently, TSWV replicates and accumulates in the visceral muscles of the gut, later spreading back into the salivary glands through the connected ligaments, and is then transmitted to the plant by the stylets (Fig. 3). Abe et al. (2011) suggested that TSWV infection facilitates the production of thrips of the next generation, which will contribute to further spread of TSWV. Stafford et al. (2011) reported that TSWV infection directly influences the feeding behavior of thrips, and enhances the transmission efficiency of the virus, whereas, viruses such as ilarviruses are also thought to be transmitted very transiently by F. occidentalis (Aramburu et al., 2010), where the transmission starts when the thrips feed on virus-laden pollen and ends once the virus-laden pollen is gone.

**Current global status of the viruses transmitted by F. occidentalis**

Presently, a total of 11 viruses have been reported vectored by F. occidentalis. These include eight species in the genus Orthotospovirus (Tospoviridae): alstroemeria necrotic streak orthotospovirus (AlNSV), chrysanthemum stem necrosis orthotospovirus (CSNV), groundnut ringspot orthotospovirus (GRSV), impatiens necrotic spot orthotospovirus (INSV), tomato chlorotic spot orthotospovirus (TCSV), TSWV, tomato spotted wilt orthotospovirus (TSWV), tomato yellow ring virus (TYRV), and tomato zonate spot orthotospovirus (TZSV); parietaria mottle virus (PMoV) in the genus Ilarvirus (Bromoviridae); and pelargonium flower break virus (PFBV) in the genus Alphacarmovirus, and maize chlorotic mottle virus (MCMV) in the genus Machlomovirus (both in
A global invasion of Frankliniella occidentalis

Fig. 3 Virus localization sites in Frankliniella occidentalis. Viruses are initially acquired through the stylets. They then travel across the alimentary canal to the anterior region of the midgut (MG), where the surface glycoproteins, Gn and Gc, facilitate their entrance into the thrips’ MG. Subsequently, the viruses replicate, accumulate in the visceral muscles of the gut, and then spread to the salivary glands through the connective ligaments, where they are then transmitted back to the plants through the stylets.

Tombusviridae) (Fig. 2, Table S2). The global distributions, hosts, emergence and dissemination of these viruses are discussed below.

AINSV

AINSV was first described in Colombia, when it was found to cause necrotic streaks on the leaves of Peruvian lilies (Alstroemeria sp.) (Hassani-Mehraban et al., 2010). According to the nucleocapsid (N) protein gene sequence, phylogenetic analysis revealed that AINSV clustered with those orthotospoviruses from the American continent into a single lineage with a significantly close serological relationship (Hassani-Mehraban et al., 2010; Liu et al., 2017). Similar to other reference orthotospoviruses, AINSV is capable of infecting ornamentals as well as vegetables locally or systemically, and is transmitted by F. occidentalis under experimental conditions (Hassani-Mehraban et al., 2010).

CSNV

CSNV was first identified from chrysanthemums in Brazil in 1996 (Resende et al., 1996), followed by the Netherlands, Slovenia, UK, Japan and South Korea (Resende et al., 1996; Verhoeven et al., 1996; Mumford et al., 2003; Ravnikar et al., 2003; Okuda et al., 2013; Yoon et al., 2017a). In Brazil, CSNV also infects tomatoes with necrosis and necrotic spots on the stem and leaves, showing symptoms similar to those seen in chrysanthemums (Bezerra et al., 1999; Nagata et al., 2004). F. schultzei and F. intonsa have also been identified as vectors of CSNV although their efficiencies as vectors are much lower than F. occidentalis (Nagata et al., 2004; Okuda et al., 2013).

GRSV

GRSV was first described from South Africa and Brazil from peanuts and tomatoes, respectively
(Wijkamp, 1995b; Pappu et al., 2009). It was subsequently reported from Argentina, the USA, the Caribbean basin and Ghana from a relatively narrow host range compared to TSWV (Webster et al., 2010; Webster et al., 2011; Camelo-Garca et al., 2014; Spadotti et al., 2014; Leão et al., 2015; Webster et al., 2015; Appiah et al., 2016). In Brazil, GRSV was identified from several hosts including sweet peppers, coriander, cocucumbers, cubiu, peanuts and watermelons (Lima et al., 1999; Boari et al., 2002; Camelo-Garca et al., 2014; Spadotti et al., 2014; Leão et al., 2015). In North America, GRSV was initially reported from tomatoes in south Florida in 2009, subsequently from peppers, tomatillos and eggplants in peninsular Florida, and later in South Carolina and New York (Webster et al., 2010, 2011, 2015). Interestingly, a reassortant isolate GRSV-L_{G\text{M}_{1}S_{G}}, composed of the L and S RNAs from GRSV and the M RNA from TCSV, was reported from tomatoes in Florida in 2010 (Webster et al., 2011). The recent outbreaks of GRSV in Brazil and North America were probably driven by its major thrip vectors, *F. occidentalis*, *F. schultzei*, and *F. gemina* (Pappu et al., 2009; Gilbertson et al., 2015; Webster et al., 2015). Among the three species involved, *F. schultzei*, the local species from Brazil and North America, has a more efficient transmission than the other two thrip species (Nagata et al., 2004; Gilbertson et al., 2015; Webster et al., 2015).

**INSV**

INSV, which is considered to be an important pathogen of ornamental crops, was initially characterized and distinguished from New Guinea impatiens in the Netherlands in the late 1980s (Avila et al., 1992). It is now widespread throughout much of the world (Vaira et al., 1993; Peters et al., 1996; Lebas & Ochoa-Corona, 2007; Pappu et al., 2009). In northern Africa, the Middle East, Southeast Asia, southern New Zealand, the Caribbean and Central America, INSV has been reported from numerous field and greenhouse-grown ornamentals, including freesia, impatiens, lobelia, primula, ranunculus, begonia, chrysanthemum, and so on, (Lebas et al., 2004; Jones, 2005; Lebas & Ochoa-Corona, 2007; Pappu et al., 2009), as well as a number of weed species (Okuda et al., 2010). Traditionally, INSV was also believed to be a pathogen on some vegetable crops, although it is only capable of causing limited local symptoms or is symptomless on sweet peppers, pepinos, spinach, tomatoes and cucumbers (Verhoeven & Roenhorst, 1998; Vicchi et al., 1999; Sialer & Gallitelli, 2000; Mavric & Ravnikar, 2001). However, INSV has recently emerged as an important pathogen of lettuce caused by *F. occidentalis* transferring from ornamental hosts in coastal regions of California (Pappu et al., 2009; Kuo et al., 2014; Gilbertson et al., 2015). In addition to *F. occidentalis*, INSV can also be transmitted by *F. intonsa* and *F. fusca*, but with a lower efficiency (Naidu et al., 2001; Sakurai et al., 2004).

**TSVV**

In 1990, TCSV was first characterized as a distinct serotype of TSWV from tomatoes in Brazil (De Avila et al., 1990, 1993). Subsequently, TCSV was isolated from sweet peppers, potatoes, endives, celery, lisianthus and various weeds with mosaic, necrosis, chlorotic or stumpning symptoms in Argentina and Brazil (Boiteux et al., 1993; Gracia et al., 1999; Colariccio et al., 2001a; Dal Bio et al., 2001; Eiras et al., 2002), and from outbreaks on lettuce and gilo in Brazil (Colariccio et al., 2001b; Rabelo et al., 2002). In the USA, TCSV was first detected from tomatoes in south Florida in 2012 (Londoño et al., 2012), and then from lettuce, impatiens and peppers (Webster et al., 2015). In Puerto Rico, TCSV was also found from tomatoes, peppers, jimsonweed (*Datura stramonium*), and lettuce in 2013 (Estévez de Jensen et al., 2013; Estévez de Jensen & Adkins, 2014). More recently, TCSV was identified from tomatoes in the Dominican Republic (Batuman et al., 2014).
TSWV-infecting crops was evident when effective controls successfully managed this vector. When *F. occidentalis* extended its range to Europe, TSWV began to be a major threat to European horticultural crops (Jones, 2005). Today, TSWV is well established in almost all European countries, including Albania (Cota & Merkuri, 2004), Bulgaria (Dikova et al., 2013), Bosnia and Herzegovina (Trkulja et al., 2013), France (Marchoux et al., 1991), Greece (Chatzivassiliou et al., 1996; Chatzivassiliou et al., 2000b), Hungary (Salamon et al., 2012), Montenegro (Zindovic et al., 2011), Spain (Jorda, 1993; Aramburu et al., 1997), Portugal (Louro, 1996), and Slovenia (Mavric & Ravnikar, 2001). In Serbia, TSWV was isolated from *Gerbera hybrida* in 2009 (Stankovic et al., 2011), onions, garlic and chrysanthemums in 2011 (Stankovic et al., 2012, 2013), and *Brugmansia* sp. in 2012 (Nikolic et al., 2013).

In Africa, TSWV was first described from a wilt disease of tobacco in South Africa as early as 1905 (Moore, 1933), and later found in several provinces of the country infecting tobacco, tomatoes, peppers and potato crops (Moore & Andessen, 1939). After *F. occidentalis* was introduced into Africa, TSWV became widespread in other African countries (Moussa et al., 2000; Ben Moussa et al., 2005). Recently, TSWV has been found from *Amaranthus thunbergii* in South Africa (Kisten et al., 2016), butternut squash (*Cucurbita moschata*) and peppers in Zimbabwe in 2015 (Karavina et al., 2016a,b).

In Asia, TSWV was first recorded in the Middle Eastern countries. In July 1998, TSWV was identified from *Pittosporum tobira* shrubs with foliar ring spots, mild mosaic, and tip necrosis symptoms in a nursery in the Sharon Valley of Israel (Gera et al., 2000a), and later from several vegetables (Gera et al., 2000b). Similarly, the virus was also detected from potatoes in 1998 in Iran (Pourrahim et al., 2001), and subsequently from soybeans, tomatoes, and cucurbits (Golnaraghi et al., 2001; Massumi et al., 2007, 2009). TSWV has also been isolated from many important vegetable crops in Jordan and Lebanon (Anfoka et al., 2006; Abou-Jawdah et al., 2006). More recently, TSWV was reported from lettuce showing necrotic lesions, necrosis of the lamina of the younger leaves, and leaf curling symptoms in March 2014 from the Al-Uaynah area, in the central region of Saudi Arabia. In eastern Asia, TSWV is now widely distributed in China, Korea, and Japan in a number of vegetable and horticultural crops such as celery, peppers, cowpeas, lettuce, *Bidens pilosa*, tomatoes, potatoes, *Brugmansia suaveolens*, *Eustoma grandiflorum*, and miscellaneous other wild plant species (Choi et al., 2004; Zheng et al., 2010; Reitz et al., 2011; Okazaki et al., 2007, 2011; Choi & Choi, 2015; Li et al., 2015; Xiao et al., 2016; Yoon et al., 2017b). In India, TSWV was found on sunflowers exhibiting severe mosaic, systemic necrosis, leaf distortion, and ringspot symptoms in Tirupati in January 1998 (Subbaiah et al., 2000), and more recently from chrysanthemums grown in the Nilgiris district of Tamil Nadu State in August 2013 (Renukadevi et al., 2015).

In America and the Caribbean, TSWV was first discovered from pineapples causing yellow spot disease as early as 1926 in Hawaii (Kucherek et al., 2000). In the 1970s, the virus was reported from peanuts in Texas (Halilwell & Philley, 1974), and then from peppers, tobacco and tomatoes in Georgia and other areas of the southeastern USA in the mid-1990s (Culbreath et al., 1991). In the latest 20 years, TSWV has become widespread throughout most of the states in the USA (Groves et al., 1998; Holcomb et al., 1999; Diaz-Perez & Pappu, 2000; Holcomb & Valverde, 2000; Momol et al., 2000; Adkins et al., 2003; Whitfield et al., 2003; Mullis et al., 2004; Yang et al., 2004; Adkins & Baker, 2005; Mullis et al., 2006; Nischwitz et al., 2006a,b; Baker et al., 2007; Baker et al., 2009; Barkley et al., 2009; Crosslin et al., 2009) causing significant economic losses (Pearce, 2005). More recently, TSWV was isolated from *Stevia rebaudiana* and tomatoes with the *Sw-5* orthopoxvirus-resistance gene in Carolina (Koehler et al., 2016; Batuman et al., 2017). TSWV was found in a commercial chrysanthemum field of Mexico infesting several weeds including *Taraxacum officinale*, *Bidens sp.*, *Reseda luteola*, *Mirabilis jalapa* being transmitted by *F. occidentalis* (Martinez et al., 1999). In 2005 to 2006, tomatoes showing chlorosis, malformation of apical leaves, stunting, and ringspot lesions caused by TSWV were first noticed in the Baja California peninsula of Mexico (Holguin-Peña & Rueda-Puente, 2007). In the Dominican Republic, TSWV transmitted by *F. occidentalis* was found to be widely distributed in commercial peppers and tomatoes growing under protected greenhouse conditions (Martinez et al., 2014). In South America, tomato, pepper, and lettuce crops infected by TSWV were reported from Argentina, Brazil, Chile, and Venezuela causing a significant threat to the vegetable industry (Maluf et al., 1991; Gracia et al., 1999; EPPO, 2004; Lebas & Ochoa-Corona, 2007; Rosales et al., 2007; Marys et al., 2014; Pérez-Colmenares et al., 2015).

The first recognition that tomato spotted wilt disease was caused by TSWV occurred in Australia as early as 1915, although it was considered as an introduction from elsewhere following European colonization (Brittlebank, 1919; Pittman, 1927; Samuel et al., 1930; Smith, 1932).

In Australia, TSWV was mainly transmitted by *T. tabaci* and *F. shultzei* on several vegetables with limited spread occurring over a span of many decades. When *F. occidentalis* was detected in southwestern Australia in 1993, an...
outbreak of TSWV was being reported in eastern and southeastern Australia (Latham & Jones, 1997; Wilson et al., 2000; Pappu et al., 2009). Similarly, TSWV was detected from tomatoes and other vegetables in New Zealand soon after its discovery on the Australian continent, and, at the time, was also transmitted by T. tabaci (Chamberlain & Taylor, 1936, 1938). More recently, a serious epidemic of TSWV on ornamental plants grown in greenhouses on the North Island was caused by F. occidentalis rather than T. tabaci (Fletcher et al., 2005; Pappu et al., 2009).

**TYRV**

TYRV, a tentative orthotospovirus species, is closely related to iris yellow spot virus. The virus was first identified from tomatoes in Teheran Province, Iran (Hassani-Mehraban et al., 2005). Subsequently, TYRV was isolated from chrysanthemums, gazanias, potatoes, soybeans, and cineraria with high diversity in the N gene in Iran (Hassani-Mehraban et al., 2005, 2007; Rasoulpour & Izaadpanah, 2007). In 2012, TYRV was isolated from tomatoes with chlorotic ring spots on fruits and necrosis of stems and leaves in Kenya (Birithia et al., 2012). TYRV has now been found in Europe in tomato plants having symptoms of necrosis on leaves and stalks, and chlorotic and necrotic ringspots on fruits in Kujawsko-Pomorskie Province, Poland (Zarzyńska-Nowak et al., 2016).

**TZSV**

TZSV was first reported to naturally infect tomatoes, causing zoned ring spots on fruits in Yunnan Province, China (Dong et al., 2008). In Yunnan Province, TZSV was subsequently isolated from chili peppers (Capsicum annuum), peppers, tobacco, Iris tectorum, potatoes and several weeds, including Bidens pilosa and Rumex dentatus (Dong et al., 2010; Zheng et al., 2014; Huang et al., 2015; Liu et al., 2015; Wu et al., 2016a). During a survey from 2008 to 2010 in Guangxi Province, China, TZSV was also detected from tobacco. Infection symptoms included dwarfing, midrib browning, distorted apical buds, and concentric ringspot (Cai et al., 2011).

**PMoV**

PMoV, a member of the genus Iiarvirus, was originally isolated from the weed Parietaria officinalis in 1989 (Caciagli et al., 1989), and afterwards from tomato, Mirabilis jalapa, Capsicum annuum, Diplotaxis tenuifo- lia in Italy (Roggero et al., 2000; Parrella, 2002; Parrella et al., 2016, 2017). Besides Italy, PMoV has also been detected from tomatoes in France, Spain and Greece, and from Capsicum annuum in Spain (Ramasso et al., 1997; Roggero et al., 2000; Aramburu, 2001; Galipienso et al., 2005; Janssen et al., 2005).

**PFBV**

PFBV is a member of the genus Alphacarmovirus, affecting Pelargonium spp. which causes white flower streaking, chlorotic spotting of leaves and stunting on some cultivars. It was originally identified in Europe and has now spread throughout much of the world (Stone & Hollings, 1973; Bouwen & Maat, 1992; Blystad et al., 1995; Ivars et al., 2004; Rico et al., 2004; Rico & Hernández, 2006; Rico et al., 2006; Wei et al., 2015). It is primarily known for its detrimental effects on the production and quality of some Pelargonium spp. cultivars (Bouwen & Maat, 1992; Blystad et al., 1995; Krčzal et al., 1995; Ivars et al., 2004; Wei et al., 2015). PFBV is frequently transmitted and dispersed by vegetative propagation and irrigation systems as well as by the western flower thrip, F. occidentalis (Krčzal et al., 1995).

**MCMV**

MCMV, a member the genus Machlomovirus in the family Tombusviridae, was first identified from maize in the Americas including plants from Peru and the USA (Castillo-Loayza, 1977; Niblett & Clafin, 1978; Jiang et al., 1990). In maize, MCMV is among the important pathogens that characteristically induce typical symptoms in the plants such as mosaicism, stunting and necrosis (Niblett & Clafin, 1978; Mahuku et al., 2015; Chen et al., 2017). MCMV, together with other maize-infecting potyviruses, are responsible for inducing corn lethal necrosis disease, which was first described in Peru in 1974 and has since spread worldwide (Castillo-Loayza, 1977; Niblett & Clafin, 1978; Morales et al., 1999; Adams et al., 2014; Deng et al., 2014; Lukanda et al., 2014; Gowda et al., 2015; Mahuku et al., 2015; Quito-Avila et al., 2016; Chen et al., 2017). In addition to maize, MCMV also can infect sorghum, Coix seed and finger millet in several Asia and Africa regions, probably due to its diverse transmission methods including by seeds, mechanical inoculation, and insects including thrips and beetles (Jiang et al., 1990; Cabanas et al., 2013; Deng et al., 2014; Kusia et al., 2015; Achon et al., 2017; Chen et al., 2017).

In conclusion, from the emergence and dissemination of F. occidentalis and its transmitting viruses, we speculate that the western flower thrip has spread from its original distribution in western North America to...
tropical, subtropical, temperate and cold temperate zones of the world by the movement of horticultural material, such as cuttings, seedlings and potted plants, while the spread of F. occidentalis-transmitting viruses is shared along with the migration pattern (or trends) of its vector, especially TSWV and INSV. F. occidentalis was rarely reported in cold zones especially in areas with temperature dropping to −10 °C in winter which is 100% lethal to F. occidentalis attempting to overwinter outdoors.

Management of F. occidentalis

Because of their small size and the difficulty involved in detection and identification, successful invasions of thrips often occur unnoticed. As a result, F. occidentalis has become a major global pest with immense damage potential in only 30 years. In addition, adults are capable of migrating long distances to new host plants and are able to quickly transmit their viruses (Kliot et al., 2016). With these risks in mind, the most effective means of dealing with this potentially invasive and pestiferous thrip species is to prevent its entry and establishment into nonendemic regions. For example, methyl bromide was used for post-harvest fumigation of a number of commodities either by the exporting or importing country (provinces) after a thrip infestation is noticed (Morse & Hoddle, 2006). However, because of its ozone depletion effect, methyl bromide is being phased out worldwide (Deewatthana-C, 2016). The alternatives to methyl bromide include irradiation, sulfuryl fluoride, phosphine, ethane-dinitrile, low oxygen treatments, heat and cold treatments (Cox, 2017). A number of sustainable tactics have been developed in IPM programs for managing F. occidentalis and to inhibit its persistent spread worldwide with ever increasing damage to its many host crops.

Chemical control

Management of F. occidentalis has been a difficult task. Use of insecticides has traditionally been the primary strategy for control of F. occidentalis, especially in virus-sensitive crops (Bielza, 2008). The insecticides that are normally applied can be separated into two major groups: broad-spectrum insecticides, which include pyrethroids, neonicitinooids, organophosphates and carbamates, and narrow-spectrum insecticides, which include pyridalyl and lufenuron (Mouden et al., 2017). However, frequent applications of insecticides, especially those containing pyrethroids, organophosphates, neonicitinooids and carbamates have also decimated large percentages of natural enemies and led to the rapid development of insecticide resistance in F. occidentalis (Mouden et al., 2017). This propensity of F. occidentalis for developing insecticide resistance has been a primary factor in promoting its pest status.

Spinosad and the related spinetoram, which tend to be compatible with natural enemies, are now being extensively used and currently provide the most effective chemical control of F. occidentalis (Gao et al., 2012a; Li et al., 2016). However, the applications of any insecticide will eventually contribute to resistance development in a given pest species. Evidence has shown that Spinosad resistance is now present in some populations of F. occidentalis in the USA (Weiss et al., 2009), Australia (Herron et al., 2014) and China (Li et al., 2016). If deemed necessary, insecticide use should be accurate, precise and complement other compatible control approaches.

Agricultural practices

Thrips often overwinter in patches of uncultivated plants and migrate into cropping systems in the spring (Pearsall & Myers, 2000), with cropping systems often serving as a sink, with sources of insect populations occurring in field margins and fencerows. F. occidentalis, which is a highly polyphagous pest of many cultivated as well as wild plants, has been shown to feed on more than 240 host plants (Tommasini & Maini, 1995), including many weed species. In France, the weed, gallant soldier (Galinsoga parviflora Cav.), has been reported by Nyasani et al. (2013) as an excellent host of F. occidentalis for both feeding and reproduction under field conditions, and serves as a potential source of thrip outbreaks in French bean fields. In instances such as this, where alternative hosts are identified and known to be present, sound agricultural practices such as seasonal mowing of these weeds will likely decrease the number of thrips migrating into the cropping systems (Northfield et al., 2008).

Additional practices for managing F. occidentalis include creating a less favorable environment by irrigation to reduce numbers of F. occidentalis adults (Schuch et al., 1998), by decreasing the levels of nitrogen fertilization to reduce populations of F. occidentalis in ornamentals (Brodebeck et al., 2001; Chow et al., 2012), and by growing trap plants to draw F. occidentalis away from susceptible crops, thereby reducing the number of thrips on the target crop (Cook et al., 2006).

Physical control

Because of their small size, fine mesh screens have been widely used to cover greenhouse openings such as vents
to help physically prevent thrips from immigrating onto protected crops (Arthurs et al., 2018b). It was reported by Tinoco et al. (2014) that using appropriate mesh size screens on greenhouse windows would reduce the incidence of *F. occidentalis* by 20% in protected tomatoes. Because thrips find suitable host plants by utilizing different cues, including visual cues in the ultraviolet (UV) spectrum (Terry, 1997), using materials that reflect UV radiation can obscure their host-locating cues. Several researchers have found that using UV-reflective mulch significantly reduced early season abundance of adult thrips and disease incidence (Stavisky et al., 2002; Kigathi & Poehling, 2012).

Another conventional measure, sticky cards, are widely used by growers for monitoring thrip populations in greenhouses (Ren et al., 2008). It was reported that blue cards are highly attractive to *F. occidentalis* (Otiendo et al., 2018). Because adult thrips explore their host range in part through volatiles, the commercially available *F. occidentalis* semiochemicals are frequently used as lures in conjunction with sticky card traps (Broughton et al., 2015) to attract and monitor or eliminate thrips.

**Biological control**

There has been considerable interest in the use of biological control agents to reduce thrip populations, especially in protected crops. An effective use of agents has been shown to improve thrip management. Inoculative release of agents, beginning at crop initiation before the resident thrips approach economically damaging levels, is recommended (Reitz et al., 2011). The large number of biological control agents that have been reported to attack *F. occidentalis* can be separated into two groups: macrobials (predators and parasitoids) and microbials (fungal pathogens and entomopathogenic nematodes) (Mouden et al., 2017). The macrobials currently being widely and effectively used are anthocorid bugs (*Orius* spp.) (Mo et al., 2013; Aragón-Sánchez et al., 2018), green lacewing species (Sarkar et al., 2019) and predatory phytoseiid mites (Messelink et al., 2006; Ahmed & Lou, 2018), which predominantly attack 1st instar thrips on foliage, and soil-dwelling predaceous laelapid mites (Berndt et al., 2004; Wu et al., 2016b), which consume thrip pupae in soil.

Fungal pathogens used as biocontrol agents of *F. occidentalis* are *Beauveria bassiana* (Gao et al., 2012b; Lee et al., 2017), *Metarhizium anisopliae* (Maniania et al., 2003; Toledo-Hernández et al., 2017) and *Leconanicillum lecanii* (Gouli et al., 2009; Wang et al., 2013). The various nematode species used against soil-inhabiting pu-

© 2019 The Authors. *Insect Science* published by John Wiley & Sons Australia, Ltd on behalf of Institute of Zoology, Chinese Academy of Sciences, 27, 626–645

**Concluding remarks**

With the continuing increase in global trade in ornamental greenhouse plants, it is likely that *F. occidentalis* will continue its rapid spread into, as yet, uninfested areas around the world, causing substantial amounts of damage from feeding and virus transmission. Another consideration is that *F. occidentalis* may also be capable of expanding its range to new areas as a consequence of global climate warming (Wu et al., 2018). Considering the economic importance of *F. occidentalis* both as a pest and a vector of several notorious plant viruses, it is essential to establish early surveillance systems of the species and to encourage the rapid recognition of plant virus symptoms while keeping a constant vigil on further spread of the species, especially in cold zones where *F. occidentalis* has not been reported.

Aggregation pheromones of *F. occidentalis* have been identified and shown to be cost-effective for monitoring detection of this thrip species in the field (Kirk, 2017). Huang et al. (2010) and Zhang et al. (2012) provided a diagnostic polymerase chain reaction detection system, which can quickly and accurately identify *F. occidentalis* from thrip larvae to complement the traditional morphological identification. This method can also be used for on-site testing of samples at ports-of-entry in the future. Standard area diagrams (SADs) have been used as a tool to improve the accuracy and reliability of visual estimates of leaf spotting diseases. More than 100 diseases with a range of plant organs were validated by SAD (Del Ponte et al., 2017). Presently, enhanced accessibility of cameras and image analysis software has accelerated the development of more realistic, stylized color representations or diagrams based on photographs of diseased plant organs (Del Ponte et al., 2019). Hence, we consider that it is a potential method for rapid recognition of
F. occidentalis-transmitting virus symptoms in the near future.

Most of the vector thrip species have high fecundity, short reproductive cycles and extensive plant host ranges (Whitfield et al., 2005a). F. occidentalis populations tend to be efficient vectors of multiple orthotospovirus species. Although the research on biological processes involved in the transmission of orthotospoviruses and their thrip vectors has made progress during the last decade (Hogenhout et al., 2008; Rotenberg et al., 2015), there is still a lack of effective measures for management of F. occidentalis and its transmitted viruses. At present, there is still a heavy reliance on insecticides, which will continue to play an important role in thrip management in the foreseeable future. The increased incidence of F. occidentalis throughout the world that we are currently witnessing, could be a consequence of increased insecticide applications over the past 30 years. There is mounting evidence that synthetic pyrethroids can stimulate reproduction of F. occidentalis (Funderburk, 2009) and promote insecticide resistance (Gao et al., 2012a). Further studies, including the virus-vector relationship of F. occidentalis with insecticide resistance are needed to improve our understanding of basic biological concepts and develop alternative measures for thrip control.

Although significant research progress in control of F. occidentalis has been made after using alternative measures, this thrip species continues to threaten the production of many crops worldwide because of the severity of viruses and difficulty in preventing thrip transmission. Therefore, both the thrips and plant virus diseases transmitted should be taken into account in control tactics. First, because immature F. occidentalis can be found consistently in tomato blossoms (Beaudoin, 2011) and have been shown to acquire TSWV from infected tomato and then transmit to susceptible plants (Szostek et al., 2017), it was suggested that management of F. occidentalis infestations during the blooming season may be important for effective control of TSWV in susceptible tomato cultivars (Houle & Kennedy, 2017). Second, because adult thrips oviposit in plant tissue and prefer tight spaces, contact insecticides are often not effective against thrips. Induced systemic resistance (ISR) has recently gained more interest and might be an important option for management of thrips and transmitted virus (Mouden et al., 2017). It was reported that Pseudomonas strains induced resistance against virus diseases (Vasanthi et al., 2010); the combination of ISR by Pseudomonas and Neem oil, would be a best alternative in the future (Vasanthi et al., 2017). In addition, integration of new biotechnology-based strategies, as well as advances in computational systems will provide a powerful tool to drive innovation in reducing virus transmission and vector populations.

Acknowledgments

We wish to thank Dr. Cecil L. Smith (University of Georgia, USA) for help with the language editing of the manuscript. This work was supported by National Key Research & Developments (R&D) plan (Grant No. 2016YFD0201002), Key project at central government level: The ability establishment of sustainable use for valuable Chinese medicine resources (2060302) and the National Natural Science Foundation of China (No. 31601604).

Disclosure

The authors declare no competing interests.

References

Abe, H., Tomitaka, Y., Shimoda, T., Seo, S., Sakurai, T., Kugimiyas, S. et al. (2011) Antagonistic plant defense system regulated by phytohormones assists interactions among vector insect, thrips and a tospovirus. Plant Cell Physiology, 53(1), 204–212.
Abou-Jawdah, Y., El Mohtari, C., Sobh, H. and Nakhla, M.K. (2006) First report of Tomato spotted wilt virus on tomatoes in Lebanon. Plant Disease, 90, 376.
Achon, M.A., Serrano, L., Clemente-Orta, G. and Sossai, S. (2017) First report of Maize chlorotic mottle virus on a perennial host, Sorgo halepense, and maize in Spain. Plant Disease, 101, 393.
Adams, I.P., Harju, V., Hodges, T., Hany, U., Skelton, A., Rai, S. et al. (2014) First report of maize lethal necrosis disease in Rwanda. New Disease Reports, 29, 22.
Adkins, S. and Baker, C.A. (2005) Tomato spotted wilt virus identified in desert rose in Florida. Plant Disease, 89, 526.
Adkins, S., Breman, L., Baker, C.A. and Wilson, S. (2003) First report of Tomato spotted wilt virus in blackberry lily in North America. Plant Disease, 87, 102.
Ahmed, N. and Lou, M. (2018) Efficacy of two predatory phytoseid mites in controlling the western flower thrips, Frankliniella occidentalis (Pergande) (Thysanoptera: Thripidae) on cherry tomato grown in a hydroponic system. Egyptian Journal Biological Pest Control, 28, 15.
Anfoka, G.H., Abhary, M. and Stevens, M.R. (2006) Occurrence of tomato spotted wilt virus (TSWV) in Jordan. EPPO Bulletin, 36, 517–522.
Appiah, A.S., Ofie, S.K., Tegg, R.S. and Wilson, C.R. (2016) Varietal response to groundnut rosette disease and the first
report of groundnut ringspot virus in Ghana. *Plant Disease*, 100, 946–952.

Aragón-Sánchez, M., Román-Fernández, L.R., Martinez-García, H., Aragón-García, A., Pérez-Moreno, I. and Marco-Mancebón, V.S. (2018) Rate of consumption, biological parameters, and population growth capacity of *Orius laevigatus* fed on *Spodoptera exigua*. *BioControl*, 63, 785–794.

Aramburu, J. (2001) First report of *Parietaria mottle virus* on tomato in Spain. *Plant Disease*, 85, 1210.

Aramburu, J., Galipienso, L., Aparicio, F., Soler, S. and López, C. (2010) Mode of transmission of *Parietaria mottle virus*. *Journal of Plant Pathology*, 92, 679–684.

Aramburu, J., Laviña, A., Moriones, E., Riudavets, J. and Arnó, J. (1997) The proportion of viruliferous individuals in field populations of *Frankliniella occidentalis*: Implications for tomato spotted wilt virus epidemics in tomato. *European Journal of Plant Pathology*, 103, 623–629.

Arthurs, S.P., Heinz, K.M. and Mitchell, F.L. (2018a) Comparison of *Frankliniella fusca* and *Frankliniella occidentalis* (Thysanoptera: Thripidae) as vectors for a peanut strain of tomato spotted wilt orthotospovirus. *Environmental Entomology*, 47, 623–628.

Arthurs, S.P., Krauter, P.C., Gilder, K. and Heinz, K.M. (2018b) Evaluation of deltamethrin-impregnated nets as a protective barrier against Western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae) under laboratory and greenhouse conditions. *Crop Protection*, 112, 227–231.

Ávila, A.C., Haan, P. De, Kitajima, E.W., Kormelink, R., Resende, R.D.O., Goldbach, R.W. *et al.* (1992) Characterization of a distinct isolate of *Tomato spotted wilt virus* (TSWV) from *Impatiens* sp. in the Netherlands. *Journal of Phytopathology*, 134, 133–151.

Baker, C.A., Davison, D. and Jones, L. (2007) *Impatiens nécrotic spot virus* and *Tomato spotted wilt virus* diagnosed in *Phalaenopsis* orchids from two Florida nurseries. *Plant Disease*, 91, 1515.

Baker, C.A., Jones, L., Leahy, R.M. and Soltis, D.E. (2009) *Tomato spotted wilt virus* found in five species of the genus *Tragopogon* in a Florida greenhouse. *Plant Disease*, 93, 546.

Barkley, N.A., Pinnow, D.L., Wang, M.L. and Pederson, G.A. (2009) First report of *Tomato spotted wilt virus* infecting African clover (*Trifolium tembense*) in Georgia. *Plant Disease*, 93, 202.

Batuman, O., Rojas, M., Almanzar, A. and Gilbertson, R. (2014) First report of *Tomato chlorotic spot virus* in processing tomatoes in the Dominican Republic. *Plant Disease*, 98, 286.

Batuman, O., Turini, T.A., Oliveira, P.V., Rojas, M.R., Macedo, M., Mellinger, H.C. *et al.* (2017) First report of a resistance-breaking strain of *Tomato spotted wilt virus* infecting tomatoes with the Sw-5 tospovirus-resistance gene in California. *Plant Disease*, 101, 637.

Beaudoin, A.P.L. (2011) Temporal and spatial patterns of thrips dispersal in relation to the epidemiology of tomato spotted wilt virus. PhD Dissertation, Order No. 3497228, North Carolina State University.

Ben Moussa, A., Marrakchi, M. and Makni, M. (2005) Characterisation of tospovirus in vegetable crops in Tunisia. *Infection Genetics and Evolution*, 5, 312–322.

Berndt, O., Meyhofer, R. and Poehling, H.M. (2004) The edaphic phase in the ontogenesis of *Frankliniella occidentalis* and comparison of *Hypoaspis miles* and *Hypoaspis aculeifer* as predators of soil-dwelling thrips stages. *Biological Control*, 30, 17–24.

Bezerra, I.C., Resende, R., Pozzer, L., Nagata, T., Kormelink, R. and De Ávila, A.C. (1999) Increase of tospoviral diversity in Brazil with the identification of two new tospovirus species, one from chrysanthemum and one from zucchini. *Phytopathology*, 89, 823–830.

Bielza, P. (2008) Insecticide resistance management strategies against the western flower thrips, *Frankliniella occidentalis*. *Pest Management Science*, 64, 1131–1138.

Bielza, P. (2010) Insecticide resistance management strategies against the western flower thrips, *Frankliniella occidentalis*. *Pest Management Science*, 64, 1131–1138.

Biritiha, R., Subramanian, S., Villinger, J., Muthomi, J.W., Narla, R.D. and Pappu, H.R. (2012) First report of *Tomato yellow ring virus* (*Tospovirus, Bunyaviridae*) infecting tomato in Kenya. *Plant Disease*, 96, 1384.

Blystad, D.R., Naess, V. and Haugslien, S. (1995) Optimizing immunosorbent electron microscopy for detection of pelargonium flower-break Carmovirus in pelargonium. *EPPO Bulletin*, 25, 239–245.

Boari, A.J., Maciel-zambolim, E., Lau, D.D., Lima, G.S.A., Kitajima, E.W., Brommonschenkel, S.S.H. *et al.* (2002) Detection and partial characterization of an isolate of *Groundnut ringspot virus* in *Solamum sessiliflorum*. *Fitopatologia Brasileira*, 27, 249–253.

Boiteux, L., Nagata, T., Dusi, A. and de Avila, A. (1993) Natural occurrence of the two tospovirus species infecting *Capsicum* spp. in Brazil. *Capsicum Eggplant Newsletter*, 12, 75.

Bouwen, I. and Maat, D.Z. (1992) Pelargonium flower-break and nut ringspot virus *Plant Pathology*, 98, 141–156.

Boiteux, L., Nagata, T., Dusi, A. and de Avila, A. (1993) Natural occurrence of the two tospovirus species infecting *Capsicum* spp. in Brazil. *Capsicum Eggplant Newsletter*, 12, 75.

Bouwen, I. and Maat, D.Z. (1992) Pelargonium flower-break and nut ringspot virus. *Plant Disease*, 98, 141–156.

Britebank, C. (1919) Tomato diseases. *Journal of Agricultural Victoria*, 27, 231–235.

Brodebeck, B.V., Stavisky, J., Funderburk, J.E., Andersen, P.C. and Olson, S.M. (2001) Flower nitrogen status and populations of *Frankliniella occidentalis* feeding on *Lycopersicon esculentum*. *Entomologia Experimentalis et Applicata*, 99, 165–172.
Broughton, S., Cousins, D.A. and Rahman, T. (2015) Evaluation of semiochemicals for their potential application in mass trapping of Frankliniella occidentalis (Pergande) in roses. Crop Protection, 67, 130–135.

Buitenhuis, R. and Shipp, I.L. (2005) Efficacy of entomopathogenic nematode Steinernemafeltiae (Rhabditida: Steinernematidae) as influenced by Frankliniella occidentalis (Thysanoptera: Thripidae) developmental stage and host plant stage. Journal of Economic Entomology, 98, 1480–1485.

Cabanás, D., Watanabe, S., Higashi, C.H.V. and Bressan, A. (2013) Dissecting the mode of maize chlorotic mottle virus transmission (Tombusviridae: Machlomovirus) by Frankliniella williamsi (Thysanoptera: Thripidae). Journal of Economic Entomology, 106, 16–24.

Caciagli, P., Boccardo, G. and Lovisolo, O. (1989) Parietaria mottle virus, a possible new ilarvirus from Parietaria officinalis (Urticaceae). Plant Pathology Journal, 38, 577–584.

Cai, J.H., Qin, B.X., Wei, X.P., Huang, J., Zhou, W.L., Lin, B.S. et al. (2011) Molecular identification and characterization of Tomato zonate spot virus in tobacco in Guangxi, China. Plant Disease, 95, 1483.

Camelo-Garca, V.M., Lima, E.F.B., Mansilla-Crdova, P.J., Rezende, J.A.M., Kitajima, E.W. and Barreto, M. (2014) Occurrence of Groundnut ringspot virus on Brazilian peanut crops. Journal of General Plant Pathology, 80, 282–286.

Castillo-Loayza, J. (1977) Maize virus and virus-like diseases in Peru. Proceedings of International Maize Virus Disease Colloquium Workshop (eds. L.E. Williams, D.T. Gordon & L.R. Nault) pp. 40–44.

Chamberlain, E. and Taylor, G. (1936) The occurrence of spotted-wilt on tomatoes in New Zealand. New Zealand Journal of Agriculture, 52, 9–17.

Chamberlain, E. and Taylor, G. (1938) Spotted wilt. Host range and transmission by thrips. New Zealand Journal of Science and Technology, Section A., 20, 133–142.

Chatzivassiliou, E.K., Weekes, R., Morris, J., Wood, K.R., Barker, I. and Katis, N.I. (2000a) Tomato spotted wilt virus (TSWV) in Greece: its incidence following the expansion of Frankliniella occidentalis, and characterisation of isolates collected from various hosts. Annual of Applied Biology, 137, 127–134.

Chatzivassiliou, E.K., Livieratos, I., Jensen, G. and Katis, N. (2000b) Ornamental plants and thrips populations associated with tomato spotted wilt virus in Greece. Phytoparasitica, 28, 257–264.

Chatzivassiliou, E.K., Livieratos, I., Katis, N., Avegelis, A. and Lykouressis, D. (1996) Occurrence of tomato spotted wilt virus in vegetables and ornamentals in Greece. Acta Horticulturae, 431, 44–50.

Chen, L., Jiao, Z., Liu, D., Liu, X., Xia, Z., Deng, C. et al. (2017) One-step reverse transcription loop-mediated isothermal amplification for the detection of Maize chlorotic mottle virus in maize. Journal of Virological Methods, 240, 49–53.

Choi, G.S., Kim, J.S., Choi, J.K. and Kim, J.H. (2004) Characterization of Tomato spotted wilt virus from paprika in Korea. Plant Pathology Journal, 20, 297–301.

Choi, S.K. and Choi, G.S. (2015) First report of Tomato spotted wilt virus in Solanum tuberosum in Korea. Plant Disease, 99, 1657.

Chow, A., Chau, A. and Heinz, K.M. (2012) Reducing fertilization: a management tactic against western flower thrips on roses. Journal of Applied Entomology, 136, 520–529.

Cloyd, R.A. (2009) Western flower thrips (Frankliniella occidentalis) management on ornamental crops grown in greenhouses: have we reached an impasse? Pest Technology, 3, 1–9.

Colariccio, A., Chaves, A., Eiras, M. and Chagas, C. (2001a) Identification of the tomato chlorotic spot virus in endemic (Cichorium endiva L.). Summa Phytopathology, 27, 325–327.

Colariccio, A., Eiras, M., Alexandre, L., Chaves, R. and Chagas, C. (2001b) Characterization of tomato chlorotic spot virus from hydroponic grown lettuce in Brazil. Thrips and Tospoviruses: Proceedings of the 7th International Symposium on Thysanoptera (eds. R. Marullo & L. Mound), pp. 99–104. Reggio Calabria, Italy: ANIC.

Cook, S.M., Khan, Z.R. and Pickett, J.A. (2006) The use of push-pull strategies in integrated pest management. Annual Review of Entomology, 52, 375–400.

Cota, E. and Merkuri, J. (2004) Introduction of Frankliniella occidentalis and occurrence of Tomato spotted wilt tospovirus in Albania. EPPO Bulletin, 34, 421–422.

Cox, D. (2017) Quarantine and pre-shipment uses of methyl bromide 2013–2016 and the potential for its replacement. Report to the Australian Government Department of the Environment and Energy.

Crosslin, J.M., Mallik, I. and Gudmestad, N.C. (2009) First report of Tomato spotted wilt virus causing potato tuber necrosis in Texas. Plant Disease, 93, 845.

Culbreath, A.K., Csinos, A.S., Bertrand, P.F. and Demski, J.W. (1991) Tomato spotted wilt virus epidemic in flue-cured tobacco in Georgia. Plant Disease, 75, 483–485.

Dal Bio, E., Chiaronne, G., Rolleri, J. and Ronc, L. (2001) New tospoviruses found in La Plata. Revista de la Facultad Agronomia (La Plata), 104, 35–40.

De Avila, A.C., De Haan, P., Kormelink, R., De Resende, O.R., Goldbach, R.W. and Peters, D. (1993) Classification of tospoviruses based on phylogeny of nucleoprotein gene sequences. Journal of General Virology, 74, 153–159.

Diaz-Pérez, J.C. and Pappu, H.R. (2000) First report of Tomato spotted wilt virus infection of tomatillo in Georgia. Plant Disease, 84, 1155.
Dietzgen, R., Mann, K. and Johnson, K. (2016) Plant virus–insect vector interactions: current and potential future research directions. *Viruses*, 8, 303.

De Avila, A.C., Huguenot, C., De Resende, O.R., Kitajima, E.W., Goldbach, R.W. and Peters, D. (1990) Serological differentiation of 20 isolates of tomato spotted wilt virus. *Journal of General Virology*, 71, 2801–2807.

Deewathanawong, A., Chanapan, S. and Suwanagul, A. (2016) Evaluation of methyl bromide alternatives to control thrips in orchid cut-flowers. *I International Symposium on Tropical and Subtropical Ornamentals* 1167, pp. 393–398.

Del Ponte, E.M., Pethybridge, S.J., Bock, C.H., Michereff, S.J., Machado, F.J. and Spolti, P. (2017) Standard area diagram aids for aiding severity estimation: Scientometrics, pathosystems and methodological trends in the last 25 years. *Phytopathology*, 107, 1161–1174.

Del Ponte, E.M., Nelson, S.C. and Pethybridge, S.J. (2019) Evaluation of app-embedded disease scales for aiding visual severity estimation of cercospora leaf spot of Table Beet. *Plant Disease*, 103, 1347–1356.

Demirozer, O., Tyler-Julian, K., Funderburk, J., Norm, L. and Stuart, R. (2012) *Frankliniella occidentalis* (Pergande) integrated pest management programs for fruiting vegetables in Florida. *Pest Management Science*, 68, 1537–1545.

Deng, T.C., Chou, C.M., Chen, C.T., Tsai, C.H. and Lin, F.C. (2014) First report of *Maize chlorotic mottle virus* on sweet corn in Taiwan. *Plant Disease*, 98, 1748.

Dikova, B., Petrov, N., Djourmaniska, A. and Lambev, H. (2013) First report of *Tomato spotted wilt virus* on a new host *Leuzia carthamoides* in Bulgaria and the World. *Plant Disease*, 97, 1258.

Dong, J., Zhang, Z., Yin, Y., Cheng, X., Ding, M. and Fang, Q. (2010) Natural host ranges of *Tomato zonate spot virus* in Yunnan. *Journal of Insect Science*, 10, 12–13.

Dong, J.H., Cheng, X.F., Yin, Y.Y., Fang, Q., Ding, M., Li, T.T. et al. (2008) Characterization of tomato zonate spot virus, a new tospovirus in China. *Archives of Virology*, 153, 855–864.

Ebssa, L., Borgemeister, C. and Poehling, H.M. (2004) Effectiveness of different species/strains of entomopathogenic nematodes for control of western flower thrips (*Frankliniella occidentalis*) at various concentrations, host densities and temperatures. *Biological Control*, 29, 145–154.

Eiras, M., Chaves, A., Colariccio, A., Harakava, R., de Araujo, J. and Chagas, C. (2002) Characterization of a *Tomato chlorotic spot virus* isolated from gilo in Peraiba Valley, Sao Paulo, Brazil. *Fitopatologia Brasileira*, 27, 285–291.

EPPO (2004) Data sheets on quarantine pests: *Tomato spotted wilt tospovirus*. *Data Sheets Quar. Pests* (revision Orig. 1997c data sheet).

Estévez de Jensen, C. and Adkins, S. (2014) First report of *Tomato chlorotic spot virus* in lettuce in Puerto Rico. *Plant Disease*, 98, 1015.

Estévez de Jensen, C., Rivera-Vargas, L.I., Rodrigues, J.C.V., Mercado, W., Frantz, G., Mellinger, H.C. et al. (2013) First report of *Tomato chlorotic spot virus* (TCSV) in tomato, pepper, and jimsonweed in Puerto Rico. *Plant Health Progress*, https://doi.org/10.1094/PHP-2013-0812-01-BR

Fletcher, J., France, C. and Butler, R. (2005) Virus surveys of lettuce crops and management of lettuce big-vein disease in New Zealand. *New Zealand Plant Protection*, 58, 239–244.

Funderburk, J. (2009) Management of the western flower thrips (*Thysanoptera: Thripidae*) in fruiting vegetables. *Florida Entomologist*, 92, 1–6.

Galipienso, L., Herranz, M.C., Pallás, V. and Aramburu, J. (2005) Detection of a tomato strain of *Parietaria motile virus* (PMoV-T) by molecular hybridization RT-PCR in field samples from north-eastern Spain. *Plant Pathology*, 54, 29–35.

Gao, Y., Lei, Z. and Reitz, S.R. (2012a) Western flower thrips resistance to insecticides: detection, mechanisms and management strategies. *Pest Management Science*, 68, 1111–1121.

Gao, Y.L., Reitz, S.R., Wang, J., Tamez-Guerra, P., Wang, E.D., Xu, X.N. et al. (2012b) Potential use of the fungus *Beaverva bassigna* against the western flower thrips *Frankliniella occidentalis* without reducing the effectiveness of its natural predator *Orius sauteri* (Hemiptera: Anthocoridae). *Biocontrol Science and Technology*, 22, 803–812.

Gera, A., Kritzman, A. and Cohen, J. (2000a) *Pittosporum toboira*: a new host for *Tomato spotted wilt virus*. *Plant Disease*, 84, 491.

Gera, A., Kritzman, A., Cohen, J., Raccach, B. and Antignus, Y. (2000b) Tospoviruses infecting vegetable crops in Israel. *EPPO Bulletin*, 30, 289–292.

Gilbertson, R.L., Batuman, O., Webster, C.G. and Adkins, S. (2015) Role of the insect supervecutors *Bemisia tabaci* and *Frankliniella occidentalis* in the emergence and global spread of plant viruses. *Annual Review of Virology*, 2, 67–93.

Golnaraghi, A.R., Shahraeen, N., Pourrahim, R., Ghorbani, S. and Farzadfar, S. (2001) First report of *Tomato spotted wilt virus* on soybean in Iran. *Plant Disease*, 85, 1290.

Gouli, V.V., Gouli, S.Y., Skinner, M. and Shternshis, M.V. (2009) Effect of the entomopathogenic fungi on mortality and injury level of western flower thrips, *Frankliniella occidentalis*. *Archives of Phytopathology and Plant Protection*, 42(2), 118–123.

Gowda, M., Das, B., Makumbi, D., Babu, R., Semagn, K., Mahuku, G. et al. (2015) Genome-wide association and genomic prediction of resistance to maize lethal necrosis disease in tropical maize germplasm. *Theoretical and Applied Genetics*, 128, 1957–1968.

Gracia, O., De Borbon, C.M., Granval De Millan, N. and Cuesta, G.V. (1999) Occurrence of different tospoviruses in vegetable crops in Argentina. *Journal of Phytopathology*, 147, 223–227.
Groves, R.L., Kennedy, G.G., Walgenbach, J.F. and Moyer, J.W. (1998) Inoculation of Tomato spotted wilt virus into Cotton. Plant Disease, 82, 959.

Haliwell, R. and Philley, G. (1974) Spotted wilt of peanut in Texas. Plant Disease Report, 58, 23–25.

Hassani-Mehraban, A., Botermans, M., Verhoeven, J.T.J., Meekes, E., Saaijer, J., Peters, D. et al. (2010) A distinct tospovirus causing necrotic streak on Alstroemeria sp. in Colombia. Archives of Virology, 155, 423–428.

Hassani-Mehraban, A., Saaijer, J., Peters, D., Goldbach, R. and Kormelink, R. (2005) A new tomato-infecting Tospovirus from Iran. Phytopathology, 95, 852–858.

Hassani-Mehraban, A., Saaijer, J., Peters, D., Goldbach, R. and Kormelink, R. (2007) Molecular and biological comparison of two tomato yellow ring virus (TYRV) isolates: challenging the tospovirus species concept. Archives of Virology, 152, 85–96.

Healey, M.A., Senior, L.J., Brown, P.H. and Duff, J. (2017) Relative abundance and temporal distribution of adult Frankliniella occidentalis (Pergande) and Frankliniella schultzei (Trybom) on French bean, lettuce, tomato and zucchini crops in relation to crop age. Journal of Asia-Pacific Entomology, 20, 859–865.

Herron, G.A., Gunning, R.V., Cottage, E.L., Borzatta, V. and Gobbi, C. (2014) Spinosad resistance, esterase isoenzymes and temporal synergism in Frankliniella occidentalis (Pergande) in Australia. Pesticide Biochemistry and Physiology, 114, 32–37.

Hogenhout, S.A., Ammar, E.D., Whitfield, A.E. and Redinbaugh, M.G. (2008) Insect vector interactions with persistently transmitted viruses. Annual Review of Phytopathology, 46, 327–359.

Holcomb, G.E. and Valverde, R.A. (2000) First report of Oidium sp. powdery mildew and Tomato spotted wilt virus on Melampodium divaricatum. Plant Disease, 84, 1152–1152.

Holcomb, G.E., Valverde, R.A., Sim, J. and Nuss, J. (1999) First report on natural occurrence of Tomato spotted wilt tospovirus in Basil (Ocimum basilicum). Plant Disease, 83, 966.

Holguin-Peña, R.J. and Rueda-Puente, E.O. (2007) Detection of Tomato spotted wilt virus in tomato in the Baja California Peninsula of Mexico. Plant Disease, 91, 1682.

Houle, J.L. and Kennedy, G.G. (2017) Tomato spotted wilt virus can infect resistant tomato when western flower thrips inoculate blossoms. Plant Disease, 101, 1666–1670.

Huang, C.J., Liu, Y., Yu, H.Q. and Li, B.L. (2015) Occurrence of Tomato zonate spot virus on potato in China. Plant Disease, 99, 733.

Huang, K.S., Lee, S.E., Yeh, Y., Shen, G.S., Mei, E. and Chang, C.M. (2010) Taqman real-time quantitative PCR for identification of western flower thrips (Frankliniella occidentalis) for plant quarantine. Biology letters, 6(4), 555–557.

Ivars, P., Alonso, M., Borja, M. and Hernández, C. (2004) Development of a non-radioactive dot-blot hybridisation assay for the detection of Pelargonium flower break virus and Pelargonium line pattern virus. European Journal of Plant Pathology, 110, 275–283.

Janssen, D., Saez, E., Segundo, E., Martin, G., Gil, F. and Cuadrado, I.M. (2005) Capsicum annuum – a new host of Parietaria mottle virus in Spain. Plant Pathology, 54, 567.

Jiang, X., Wilkinson, D. and Berry, J. (1990) An outbreak of maize chlorotic mottle virus in Hawaii and possible association with thrips. Phytopathology, 80, 1060.

Jones, D.R. (2005) Plant viruses transmitted by thrips. European Journal Plant Pathology, 113, 119–157.

Jorda, C. (1993) Nuevas virosis de mayor incidencia en cultivos hortícolas. Phytopama Espana, 30, 7–13.

Karavina, C., Ibaba, J.D. and Gubb, A. (2016a) First report of Tomato spotted wilt virus infecting butternut squash (Cucurbita moschata) in Zimbabwe. Plant Disease, 100, 870.

Karavina, C., Ximba, S., Ibaba, J.D. and Gubb, A. (2016b) First report of a mixed infection of Potato virus Y and Tomato spotted wilt virus on pepper (Capsicum annuum) in Zimbabwe. Plant Disease, 100, 1513.

Kigathi, R. and Poehling, H.M. (2012) UV-absorbing films and nets affected the dispersal of western flower thrips, Frankliniella occidentalis (Thysanoptera: Thripidae). Journal of Applied Entomology, 136, 761–771.

Kirk, W.D. and Terry, L.I. (2003) The spread of the western flower thrips Frankliniella occidentalis (Pergande). Agricultural and Forest Entomology, 5, 301–310.

Kirk, W.D. (2017) The aggregation pheromones of thrips (Thysanoptera) and their potential for pest management. International Journal of Tropical Insect Science, 37, 41–49.

Kisten, L., Moodley, V., Gubb, A. and Mafongoya, P.L. (2016) First detection of Tomato spotted wilt virus (TSWV) on Amaranthus thunbergii in South Africa. Plant Disease, 100, 2176.

Kliot, A., Kontsedalov, S., Lebedev, G. and Ghanim, M. (2016) Advances in whiteflies and thrips management. Advances in Insect Control and Resistance Management, pp. 205–218. Springer, Cham.

Koehler, A.M., Brown, J.A., Huber, B., Wehner, T.C. and Shew, H.D. (2016) First report of Tomato spotted wilt virus in Stevia rebaudiana in North Carolina. Plant Disease, 100, 1251.

Krczal, G., Albov, J., Dany, I., Kusiak, C., Deogratias, J.M., Moreau, J.P. et al. (1995) Transmission of pelargonium flower break virus (PFBV) in irrigation systems and by thrips. Plant Disease, 79, 163–166.

Kucharek, T., Brown, L., Johnson, F. and Funderburk, J. (2000) Tomato spotted wilt virus of agronomic, vegetable, and ornamental crops. Plant Pathology Fact Sheet Circ-914., pp. 13. Florida Cooperative Extension Service/Institute of Food and Agricultural Sciences/University of Florida.

© 2019 The Authors. Insect Science published by John Wiley & Sons Australia, Ltd on behalf of Institute of Zoology, Chinese Academy of Sciences, 27, 626–645
Kuo, Y.W., Gilberston, R.L., Turini, T., Brennan, E.B., Smith, R.F. and Koike, S.T. (2014) Characterization and epidemiology of outbreaks of Impatiens necrotic spot virus on lettuce in coastal California. Plant Disease, 98, 1050–1059.

Kusia, E.S., Subramanian, S., Nyasani, I.O., Khamis, F., Villinger, J., Ateka, E.M. et al. (2015) First report of lethal necrosis disease associated with co-infection of finger millet with Maize chlorotic mottle virus and Sugarcane mosaic virus in Kenya. Plant Disease, 99, 899.

Latham, L.J. and Jones, R.A.C. (1997) Occurrence of tomato spotted wilt tospovirus in native flora, weeds, and horticultural crops. Australian Journal of Agricultural Research, 48, 359.

Leão, E.U., de Almeida Spadotti, D.M., Rocha, K.C.G., de Fátima da CunhaPantoja, K., Rezende, J.A.M., Pavan, M.A. et al. (2015) Citrullus lanatus is a new natural host of Groundnut ring spot virus in Brazil. Journal of Phytopathology, 163, 1014–1018.

Lebas, B.S. and Ochoa-Corona, F. (2007) Impatiens necrotic spot virus. Characterization, Diagnosis and Management of Plant Viruses. Vol. 4: Grain Crops and Ornamentals (eds. G.P. Rao, C. Bragard & B.S.M Lebas), pp. 221–243. Texas: Stadium Press LLC.

Lebas, B.S., Ochoa-Corona, F., Elliott, D., Tang, Z., Alexander, B.J. and Froud, K.J. (2004) An investigation of an outbreak of Impatiens necrotic spot virus in New Zealand. Phytopathology, 94, S57–S58.

Lee, S.J., Kim, S., Kim, J.C., Lee, M.R., Hossain, M., Shin, T.S. et al. (2017) Entomopathogenic Beauveria bassiana granules to control soil-dwelling stage of western flower thrips, Frankliniella occidentalis (Thysanoptera: Thripidae). BioControl, 62, 639–648.

Li, D.G., Reitz, S.R., Nauen, R., Lei, Z.R., Lee, S.H. et al. (2016) Field resistance to spinosad in western flower thrips Frankliniella occidentalis (Thysanoptera: Thripidae). Journal of Integrative Agriculture, 15, 2803–2808.

Li, Y.Y., Xiao, L., Tan, G.L., Fu, X.P., Li, R.H. and Li, F. (2015) First report of Tomato spotted wilt virus on celery in China. Plant Disease, 99, 734.

Lima, M.F., de Ávila, A.C., da G Wanderley, L.J., Nagata, T. and da Gama, L.J.W. (1999) Coriander: a new natural host of Groundnut ring spot virus in Brazil. Plant Disease, 83, 878.

Liu, L.Y., Ye, H.Y., Chen, T.H. and Chen, T.C. (2017) Development of a microarray for simultaneous detection and differentiation of different tospoviruses that are serologically related to Tomato spotted wilt virus. Journal of Virology, 14, 1.

Liu, Y., Huang, C.J., Tao, X.R. and Yu, H.Q. (2015) First report of Tomato zonate spot virus in Iris tectorum in China. Plant Disease, 99, 164.

Londoño, A., Capobianco, H., Zhang, S. and Polston, J.E. (2012) First record of Tomato chlorotic spot virus in the USA. Tropical Plant of Pathology, 37, 333–338.

Louro, D. (1996) Detection and identification of tomato spotted wilt virus and impatiens necrotic spot virus in Portugal. Acta Horticulturae, 431, 99–105.

Lukanda, M., Owati, A., Ogunsanya, P., Valimunzigha, K., Katsongo, K., Ndeme, H. et al. (2014) First report of Maize chlorotic mottle virus infecting maize in the Democratic Republic of the Congo. Plant Disease, 98, 1448.

Mahuku, G., Lockhart, B.E., Wanjala, B., Jones, M.W., Kimunye, J.N., Stewart, L.R. et al. (2015) Maize lethal necrosis (MLN), an emerging threat to maize-based food security in Sub-Saharan Africa. Phytopathology, 105, 956–965.

Maluf, W., Toma-Brahini, M. and Corte, R.D. (1991) Progress in breeding tomatoes for resistance to tomato spotted wilt. Brazilian Journal of Genetics, 14, 509–525.

Maniania, N.K., Ekesi, S., Löhr, B. and Mwangi, F. (2003) Prospects for biological control of the western flower thrips, Frankliniella occidentalis, with the entomopathogenic fungus, Metarhizium anisopliae, on chrysanthemum. Mycopathologia, 155, 229–235.

Marchoux, G., Gebre-selassie, K. and Villevieille, M. (1991) Detection of tomato spotted wilt virus and transmission by Frankliniella occidentalis in France. Plant Pathology, 40, 347–351.

Martínez, R.T., Poojadi, S., Tolín, S.A., Cayetano, X. and Naidú, R.A. (2014) First report of Tomato spotted wilt virus in peppers and tomato in the Dominican Republic. Plant Disease, 98, 163.

Martínez, D.L.O., Zavaleta-Mejía, E., Mora-Aguilera, G. and Johansen N.R.M. (1999) Implications of weed composition and thrips species for the epidemiology of tomato spotted wilt in chrysanthemum (Dendranthema grandiflora). Plant Pathology, 48, 707–717.

Marys, E., Mejías, A., Rodríguez-Román, E., Avilán, D., Hurtado, T., Fernández, A. et al. (2014) The first report of Tomato spotted wilt virus on gerbera and chrysanthemum in Venezuela. Plant Disease, 98, 1161.

Massumil, H., Samei, A., Pour, A.H., Shaabanian, M. and Rahimian, H. (2007) Occurrence, distribution, and relative incidence of seven viruses infecting greenhouse-grown cucurbits in Iran. Plant Disease, 91, 159–163.

Massumil, H., Shaabanian, M., Pour, A.H., Heydarnejad, J. and Rahimian, H. (2009) Incidence of viruses infecting tomato and their natural hosts in the southeast and central regions of Iran. Plant Disease, 93, 67–72.

Mavric, I. and Ravnikar, M. (2001) First report of Tomato spotted wilt virus and Impatiens necrotic spot virus in Slovenia. Plant Disease, 85, 1288.

Messelink, G.J. and Janssen, A. (2014) Increased control of thrips and aphids in greenhouses with two species of generalist predatory bugs involved in intraguild predation. Biological Control, 79, 1–7.
Messelink, G.J., van Steenpaal, S.E.F. and Ramakers, P.M.J. (2006) Evaluation of phytoseiid predators for control of western flower thrips on greenhouse cucumber. *BioControl*, 51, 753–768.

Mo, L.F., Zhi, J.R. and Tian, T. (2013) Biological control efficiency of *Orius similis* Zheng (Hemiptera: Anthocoridae) on *Frankliniella occidentalis* (Pergande) under different spatial and caged conditions. *Acta Ecologica Sinica*, 33, 7132–7139.

Momol, M.T., Pappu, H.R., Dankers, W., Rich, J.R. and Olson, S.M. (2000) First report of *Tomato spotted wilt virus* in habanero and tabasco peppers in Florida. *Plant Disease*, 84, 1154.

Moore, E. (1933) The kromnek or kat river diease of tobacco and tomato in the east province (South Africa). Deptment of Agriculture, Union of South Africa. *Science Bulletin*, 123, 5–28.

Moore, E. and Andessen, E.E. (1939) Notes on plant virus diseases in South Africa. the kromnek disease of tobacco and tomato. Department of Agriculture, Union of South Africa. *Science Bulletin*, 182, 1–36.

Morales, F., Arroyave, J.A., Castillo, J. and Leon, C.D. (1999) Cytopathology of *Mazie chlorotic mottle virus* in *Zea mays L.* *Maydica*, 44, 231–235.

Morse, J.G. and Hoddle, M.S. (2006) Invasion biology of thrips. *Annual Review of Entomology*, 51, 67–89.

Mouden, S., Sarmiento, K.F., Klinkhamer, P.G. and Leiss, K.A. (2017) Integrated pest management in western flower thrips: past, present and future. *Pest Management Science*, 73, 813–822.

Mound, L.A. (2002) So many thrips—are so few tospoviruses//Thrips and tospoviruses. *Proceedings of the 7th International Symposium on Thysanoptera*. Australian National Insect Collection, Canberra, 15–18.

Mound, L.A. (2004) *Thysanoptera*: diversity and interactions. *Annual Review of Entomology*, 50, 247–269.

Moussa, A. Ben, Makni, M. and Marrakchi, M. (2000) Identification of the principal viruses infecting tomato crops in Tunisia. *EPPO Bulletin*, 30, 293–296.

Mullis, S.W., Csinos, A.S., Gitaitis, R.D. and Martinez-Ochoa, N. (2006) First report of pinaceae in Georgia naturally infected with *Tomato spotted wilt virus*. *Plant Disease*, 90, 376.

Mullis, S.W., Langston, D.B., Gitaitis, R.D., Sherwood, J.L., Csinos, A.C., Riley, D.G. et al. (2004) First report of vidual onion (*Allium cepa*) naturally infected with *Tomato spotted wilt virus* and *Iris yellow spot virus* (family Bunyaviridae, genus Tospovirus) in Georgia. *Plant Disease*, 88, 1285.

Mumford, R.A., Barker, I. and Wood, K.R. (1996) The biology of the tospoviruses. *Annals of Applied Biology*, 128, 159–183.

Mumford, R.A., Jarvis, B., Morris, J. and Blockley, A. (2003) First report of *Chrysanthemum stem necrosis virus* (CSNV) in the UK. *Plant Pathology*, 52, 779.

Nagata, T., Almeida, A.C.L., Resende, R.O. and de Avila, A.C. (2004) The competence of four thrips species to transmit and replicate four tospoviruses. *Plant Pathology*, 53, 136–140.

Naidu, R.A., Deom, C.M. and Sherwood, J.L. (2001) First report of *Frankliniella fusca* as a vector of *Impatiens necrotic spot tospovirus*. *Plant Disease*, 85, 1211.

Niblett, C. and Clafin, L. (1978) Maize lethal necrosis—a new virus disease of maize in Kansas. *Plant Disease Report*, 62, 15–19.

Nikolić, D., Stanković, I., Vučurović, A., Ristić, D., Milojević, K., Bulajić, A. et al. (2013) First report of *Tomato spotted wilt virus* on *Brugmansia* sp. in Serbia. *Plant Disease*, 97, 850.

Nischwitz, C., Mullis, S.W., Gitaitis, R.D. and Csinos, A.S. (2006a) First report of *Tomato spotted wilt virus* in Soybean (*Glycine max*) in Georgia. *Plant Disease*, 90, 524.

Nischwitz, C., Mullis, S.W., Gitaitis, R.D., Csinos, A.S. and Olson, S.M. (2006b) First report of *Tomato spotted wilt virus* in leek (*Allium porrum*) in the United States. *Plant Disease*, 90, 525.

Northfield, T.D., Paim, D.R., Funderburk, J.E. and Reitz, S.R. (2008) Annual cycles of *Frankliniella* spp. (*Thysanoptera: Thripidae*) thrips abundance on North Florida uncultivated reproductive hosts: predicting possible sources of pest outbreaks. *Annals of the Entomological Society of America*, 101, 769–778.

Nyasani, J.O., Meyhöfer, R., Subramanian, S. and Poehling, H.M. (2013) Feeding and oviposition preference of *Frankliniella occidentalis* for crops and weeds in Kenyan French bean fields. *Journal of Applied Entomology*, 137, 204–213.

Ogada, P.A. and Poehling, H.M. (2015) Sex-specific influences of *Frankliniella occidentalis* (western flower thrips) in the transmission of *Tomato spotted wilt virus* (*Tospovirus*). *Journal of Plant Disease Protection*, 122, 264–274.

Okazaki, S., Okuda, M., Komi, K., Yamasaki, S., Okuda, S., Sakurai, T. et al. (2011) The effect of virus titre on acquisition efficiency of *Tomato spotted wilt virus* by *Frankliniella occidentalis* and the effect of temperature on detectable period of the virus in dead bodies. *Australas Plant Pathology*, 40, 120–125.

Okazaki, S., Okuda, M., Komi, K., Yoshimatsu, H. and Iwamani, T. (2007) Overwintering viruliferous *Frankliniella occidentalis* (*Thysanoptera: Thripidae*) as an infection source of *Tomato spotted wilt virus* in green pepper fields. *Plant Disease*, 91, 842–846.

Okuda, M., Fuji, S., Okuda, S., Sako, K. and Iwamani, T. (2010) Evaluation of the potential of thirty two weed species as infection sources of *Impatiens necrotic spot virus*. *Journal of Plant Pathology*, 92, 357–361.

Okuda, S., Okuda, M., Matsuura, S., Okazaki, S. and Iwai, H. (2013) Competence of *Frankliniella occidentalis* and *Frankliniella intonsa* strains as vectors for *Chrysanthemum*
stem necrosis virus. European Journal of Plant Pathology, 136, 355–362.

Otiendo, J.A., Stukenberg, N., Weller, J. and Poehling, H.M. (2018) Efficacy of LED-enhanced blue sticky traps combined with the synthetic lure Lurem-TR for trapping of western flower thrips (Frankliniella occidentalis). Journal of Pest Science, 91, 1301–1314.

Pérez-Colmenares, Y., Mejías, A., Rodríguez-Román, E., Avilán, D., Gómez, J.C., Marys, E. et al. (2015) Identification of Tomato spotted wilt virus associated with fruit damage during a recent virus outbreak in pepper in Venezuela. Plant Disease, 99, 896.

Pappu, H.R., Jones, R.A.C. and Jain, R.K. (2009) Global status of tospovirus epidemics in diverse cropping systems: successes achieved and challenges ahead. Virus Research, 141, 219–236.

Parrella, G. (2002) First report of Parietaria mottle virus in Mirabilis jalapa. Plant Pathology, 51, 401.

Parrella, G., Greco, B. and Troiano, E. (2016) Severe symptoms of mosaic and necrosis in bell pepper associated with Parietaria mottle virus in Italy. Plant Disease, 100, 1514.

Parrella, G., Greco, B. and Troiano, E. (2017) First report of Parietaria mottle virus associated with yellowing disease in Diplotaxis tenuifolia in Italy. Plant Disease, 101, 850.

Pearce, M. (2005) 2004 Georgia plant disease loss estimates. University of Georgia, Cooperative Extension Service, 24.

Pearsall, I.A., and Myers, J.H. (2000) Population dynamics of western Bower thrips (Thysanoptera: Thripidae) in nectarine orchards in British Columbia. Journal of Economic Entomology, 93, 264–275.

Peters, D., Wijkamp, I., van De Wetering, F. and Goldbach, R. (1996) Vector relations in the transmission and epidemiology of tospoviruses. Acta Horticulturae, 431, 29–43.

Pittman, H. (1927) Spotted wilt of tomatoes. preliminary note concerning the transmission of the spotted wilt of tomatoes by an insect vector (Thrips tabaci Lind.). Australian Council for Scientific and Industrial Research Bulletin, 1, 74–77.

Pourrahim, R., Farzadfar, S., Moini, A.A., Shahraeen, N. and Ahoonmanesh, A. (2001) First report of tomato spotted wilt virus on potatoes in Iran. Plant Disease, 85, 442.

Quito-Avila, D.F., Alvarez, R.A. and Mendoza, A.A. (2016) Occurrence of maize lethal necrosis in Ecuador: a disease without boundaries. European Journal of Plant Pathology, 146, 705–710.

Rabelo, L., Pedrazzoli, D., Novaes, Q., Nagata, T., Rezende, E. and Kitajima, J. (2002) High incidence of tomato chlorotic spot virus in the state of Sao Paulo, Brazil. Fitopatologia Brasileira, 27, 105–112.

Ramasso, E., Roggero, P., Dellavalle, G. and Lisa, V. (1997) Necrosc apicale del pomodoro causata da un Ilarvirus. Mikologiya I Fitopatologiya, 1, 71–77.

Rasoulpour, R. and Ezzadpanah, K. (2007) Characterisation of cineraria strain of Tomato yellow ring virus from Iran. Australas. Plant Pathology, 36, 286–294.

Ravnikar, M., Vozelj, N., Mavrič, I., Svijgelj, S., Zupančič, M. and Petrović, N. (2003) Detection of Chrysanthemum stem necrosis virus and Tomato spotted wilt virus in chrysanthemum. Abstracts 8th International Congress of Plant Pathology ICPP, Christchurch (NZ).

Reitz S.R. (2009) Biology and ecology of the western flower thrips (Thysanoptera: Thripidae): the making of a pest. Florida Entomology, 92, 7–13.

Reitz, S.R., Gao, Y.L. and Lei, Z.R. (2011) Thrips: Pests of concern to China and the United States. Journal of Integrative Agriculture, 10, 867–892.

Ren, J., Lei, Z.R. and Hua, L. (2008) The study on trapping effects of colorful card on Frankliniella occidentalis (Pergande). Chinese Plant Protection, 28, 34–35.

Renukadevi, P., Nagendran, K., Nakkeeran, S., Karthikeyan, G., Jawaharlal, M., Alice D. et al. (2015) First report of Tomato spotted wilt virus infection of chrysanthemum in India. Plant Disease, 99, 1190.

Resende, R., Pozzer, L., Nagata, T., Bezerra, I., Lima, M., Giordano, L. et al. (1996) New tospoviruses found in Brazil. Acta Horticulturae, 431, 78–89.

Rico, P. and Hernández, C. (2006) Infectivity of in vitro transcripts from a full-length cDNA clone of pelargonium flower break virus in an experimental and a natural host. Journal of Plant Pathology, 88, 103–106.

Rico, P., Herméndez, C. and Hernández, C. (2004) Complete nucleotide sequence and genome organization of Pelargonium flower break virus. Archives Virology, 149, 641–651.

Rico, P., Ivars, P., Elena, S.F. and Hernandez, C. (2006) Insights into the selective pressures restricting Pelargonium flower break virus genome variability: evidence for host adaptation. Journal of Virology, 80, 8124–8132.

Riley, D., Sparks Jr, A., Srinivasan, R., Kennedy, G., Fonsah, G., Scott, J. et al. (2018) Thrips: Biology, ecology, and management. Sustainable Management of Arthropod Pests of Tomato, pp. 49–71. Academic Press.

Roggero, P., Ciuffo, M., Katis, N., Alioto, D., Crescenzi, A., Parrella, G. et al. (2000) Necrotic disease in tomatoes in greece and southern Italy caused by the tomato strain of Parietaria mottle virus. Journal of Plant Pathology, 82, 159.

Rosales, M., Pappu, H., Arayam, C. and Aljaro, A. (2007) Characterization of Tomato spotted wilt virus (Tospovirus, Bunyaviridae) from lettuce (Lactuca sativa) in Chile. Phytopathology, 97, S101.

Rotenberg, D., Jacobson, A.L., Schneweis, D.J. and Whitfield, A.E. (2015) Thrips transmission of tospoviruses. Current Opinion of Virology, 15, 80–89.
Saito, T. and Brownbridge, M. (2016) Compatibility of soil-dwelling predators and microbial agents and their efficacy in controlling soil-dwelling stages of western flower thrips Frankliniella occidentalis. Biological Control, 92, 92–100.

Sakurai, T., Inoue, T. and Tsuda, S. (2004) Distinct efficiencies of Impatiens necrotic spot virus transmission by five thrips vector species (Thysanoptera: Thripidae) of tospoviruses in Japan. Applied Entomology and Zoology, 39, 71–78.

Salamon, P., Nemes, K., Salánki, K. and Palkovics, L. (2012) First report of natural infection of pea (Pisum sativum) by Tomato spotted wilt virus in Hungary. Plant Disease, 96, 295.

Samuel, G., Bald, J. and Pittman, H. (1930) Investigations on “spotted wilt” of tomatoes. Australian Council for Scientific and Industrial Research, 44, 1–64.

Sarkar, S.C., Wang, E.D., Zhang, Z.K., Wu, S.Y. and Lei, Z.R. (2019) Laboratory and glasshouse evaluation of the green lacewing, Chrysopa pallens (Neuroptera: Chrysopidae) against the western flower thrips, Frankliniella occidentalis (Thysanoptera: Thripidae). Applied Entomology and Zoology, https://doi.org/10.1007/s13355-018-0601-9

Schneweis, D.J., Whitfield, A.E. and Rotenberg, D. (2017) Thrips developmental stage-specific transcriptome response to tomato spotted wilt virus during the virus infection cycle in Frankliniella occidentalis, the primary vector. Virology, 500, 226–237.

Schuch, U.K., Rdak, R.A. and Behlke, J.A. (1998) Cultivar, fertilizer and irrigation effect vegetative growth and susceptibility of chrysanthemum to western flower thrips. Journal of America Society Horticulture Science, 123, 727–733.

Sialer, M.M.F. and Gallitelli, D. (2000) The occurrence of Impatiens necrotic spot virus and Tomato spotted wilt virus in mixed infection in tomato. Journal of Plant Pathology, 82, 244.

Smith, K. (1932) Studies on plant virus diseases XI. Further experiments with a ringspot virus: its identification with spotted wilt of tomato. Annals of Applied Biology, 19, 305–320.

Spadotti, D., Leão, E. and Rocha, K. (2014) First report of Groundnut ringspot virus in cucumber fruits in Brazil. New Disease Reports, 5197.

Stafford, C.A., Walker, G.P. and Ullman, D.E. (2011) Infection with a plant virus modified vector feeding behavior. Proceedings of the National Academy of Sciences USA, 108, 9350–9355.

Stanković, I., Bulajić, A., Vučurović, A., Ristić, D., Milojević, K., Nikolić, D. et al. (2013) First report of Tomato spotted wilt virus on chrysanthemum in Serbia. Plant Disease, 97, 150.

Stavisky, J., Funderburk, J.E., Brodbeck, B.V., Olson, S.M. and Andersen, P.C. (2002) Population dynamics of Frankliniella spp. and tomato spotted wilt incidence as influenced by cultural management tactics in tomato. Journal of Economic Entomology, 95, 1216–1221.

Stone, B.O.M. and Hollings, M. (1973) Some properties of pelargonium flower-break virus. Annual of Applied Biology, 75, 15–23.

Subbaiah, K.V., Sai Gopal, D.V.R. and Krishna Reddy, M. (2000) First report of a tospovirus on sunflower (Helianthus annuus L.) from India. Plant Disease, 84, 1343.

Szostek, S.A., Rodriguez, P., Sanchez, J., Adkins, S. and Naidu, R.A. (2017) Western flower thrips can transmit Tomato spotted wilt virus from virus-infected tomato fruits. Plant Health Prog, 18(1), 1–6.

Terry, L.I. (1997) Host selection, communication and reproductive behavior. Thrips as Crop Pests (ed. T. Lewis), pp. 65–118. CAB International, New York.

Tinoco, C.E., Gutiérrez, G.A.M., Bolaños, T.A. and Sánchez, D.M. (2014) Screen porosity and exclusion of pest in greenhouse tomatoes (Solanum lycopersicum L.). Southwest Entomology, 39, 625–634.

Toledo-Hernández, R.A., Ortiz-Girón, J.A. and Sánchez, D. (2017) Preliminary observations on pathogenicity of commercial formulations of Metarhizium anisopliae and Beauveria bassiana entomopathogenic fungi for control of Frankliniella insidiosum under laboratory conditions. Southwest Entomology, 42, 1035–1040.

Tommasini, M.G. and Maini, S. (1995) Frankliniella occidentalis and other thrips harmful to vegetable and ornamental crops in Europe. Biological Control of Thrips (eds. A.J.L. Loomans, J.C. van Lenteren, M.G. Tommasini, S. Maini & J. Riudavets), Papers 95.1, pp. 1–42. Wageningen Agricultural University, the Netherlands.

Trkulja, V., Salapura, J.M., Ćurković, B., Stanković, I., Bulajić, A., Vučurović, A. et al. (2013) First report of Impatiens necrotic spot virus on begonia in Bosnia and Herzegovina. Plant Disease, 97, 1004.

Vaira, A.M., Roggero, P., Lusoni, E., Masenga, V., Milne, R.G. and Lisa, V. (1993) Characterization of two tospoviruses in Italy: tomato spotted wilt and impatiens necrotic spot. Plant Pathology, 52, 530–542.

Vasanthi, V.J., Kandan, A., Raguchander, T., Ramanathan, A., Balasubramanian, P. and Samiyappan, R. (2010) Pseudomonas fluorescens-based formulations for management of tomato leaf curl gemini virus (TLCV) and enhanced yield in tomato. Archives of Phytopathology, 17, 553–569.

© 2019 The Authors. Insect Science published by John Wiley & Sons Australia, Ltd on behalf of Institute of Zoology, Chinese Academy of Sciences, 27, 626–645
Vasanthi, V.J., Samiyappan, R. and Vetivel, T. (2017) Management of tomato spotted wilt virus (TSWV) and its thrips vector in tomato using a new commercial formulation of *Pseudomonas fluorescens* strain and neem oil. *Journal of Entomol Zoology Studies*, 5, 1441–1445.

Verhoeven, J., Roenhorst, J., Cortes, I. and Peters, D. (1996) Detection of a novel tospovirus in chrysanthemum. *Acta horticulture*, 432, 44–51.

Verhoeven, T.J. and Roenhorst, J.W. (1998) Occurrence of tospoviruses in the Netherlands. *Fourth International Symposium on Tospoviruses and Thrips in Floral and Vegetable Crops* pp. 77. Wageningen, The Netherlands: Graduate Schools of Experimental Plant Sciences and Production Ecology.

Vicchi, V., Fini, P. and Cardoni, M. (1999) Presence of impatiens necrotic spot tospovirus (INSV) on vegetable crops in Emilia-Romagna region. *Mikologiya I Fitopatologiya*, 49, 52–55.

Wang, H., Lei, Z., Reitz, S., Li, Y. and Xu, X. (2013) Production of microsclerotia of the fungal entomopathogen *Lecanicillium lecanii* (Hypocreales: Cordycipitaceae) as a biological control agent against soil-dwelling stages of *Frankliniella occidentalis* (Thysanoptera: Thripidae). *Biocontrol Science and Technology*, 23, 234–238.

Webster, C.G., Frantz, G., Reitz, S.R., Funderburk, J.E., Mellinger, H.C., McAvoy, E. et al. (2015) Emergence of Groundnut ringspot virus and Tomato chlorotic spot virus in vegetables in Florida and the southeastern United States. *Phytopathology*, 105, 388–398.

Webster, C.G., Perry, K.L., Lu, X., Horsman, L., Frantz, G., Mellinger, H.C. et al. (2010) First report of *Groundnut ringspot virus* infecting tomato in South Florida. *Plant Health Progress*.

Webster, C.G., Reitz, S.R., Perry, K.L. and Adkins, S. (2011) A natural M RNA reassortant arising from two species of plant- and insect-infecting bunyaviruses and comparison of its sequence and biological properties to parental species. *Virology*, 413, 216–225.

Webster, C.G., Turechek, W.W., Mellinger, H.C., Frantz, G, Roe, N., Yonce, H. et al. (2011) Expansion of *Groundnut ringspot virus* host and geographic ranges in solanaceous vegetables in Peninsular Florida. *Plant Health Progress*.

Wei, M.S., Li, G.F., Ma, J. and Kong, J. (2015) First report of *Pelargonium flower break virus* infecting *Pelargonium* plants in China. *Plant Disease*, 99, 735.

Weiss, A., Dripps, J. and Funderburk, J. (2009) Assessment of implementation and sustainability of integrated pest management programs. *Florida Entomologist*, 92, 24–28.

Whitfield, A.E., Campbell, L.R., Sherwood, J.L. and Ullman, D.E. (2003) Tissue blot immunoassay for detection of *Tomato spotted wilt virus* in *Ranunculus asiaticus* and other ornamentals. *Plant Disease*, 87, 618–622.

Whitfield, A.E., Ullman, D.E., and German, T.L. (2004) Expression and characterization of a soluble form of tomato spotted wilt virus glycoprotein GN. *Journal of Virology*, 78(23), 13197.

Whitfield, A.E., Ullman, D.E. and German, T.L. (2005a) Tospovirus–thrips interactions. *Annual Review of Phytopathology*, 43, 459–489.

Whitfield, A.E., Ullman, D.E. and German, T.L. (2005b) *Tomato spotted wilt virus* glycoprotein GC is cleaved at acidic pH. *Virus Research*, 110, 183–186.

Whitfield, A.E., Falk, B.W. and Rotenberg, D. (2015) Insect vector-mediated transmission of plant viruses. *Virology*, 479, 278–289.

Wijkamp, I. (1995a) Distinct levels of specificity in thrips transmission of tospoviruses. *Phytopathology*, 85, 1069–1074.

Wijkamp, I., Fvande, W., Goldbach, R. and Peters, D. (2010) Transmission of tomato spotted wilt virus by *Frankliniella occidentalis*; median acquisition and inoculation access period. *Annual of Applied Biology*, 129, 303–313.

Wijkamp, I. (1995b) Virus-Vector Relationships in the Transmission of Tospoviruses. Ph.D. thesis, Wageningen, The Netherlands.

Wilson, C.R., Wilson, A.J. and Pethybridge, S.J. (2000) First report of *Tomato spotted wilt virus* in common agapanthus. *Plant Disease*, 84, 491.

Wu, K., Zheng, K.Y., Zhang, Z.K., McBeath, J.H. and Dong, J.H. (2016a) First report of *Crinum asiaticum* as a natural host of tomato zonate spot virus in China. *Journal of Plant Pathology*, 97, 76.

Wu, S.Y., Zhang, Z.K., Gao, Y.L., Xu, X.N. and Lei, Z.R. (2016b) Interactions between foliage- and soil-dwelling predatory mites and consequences for biological control of *Frankliniella occidentalis*. *BioControl*, 61, 717–727.

Wu, S.Y., Tang, L.D., Zhang, X.R., Xing, Z.L., Lei, Z.R. and Gao, Y.L. (2018) A decade of a thrips invasion in China: lessons learned. *Ecotoxicology*, 27, 1032–1038.

Wu, S.Y., He, Z., Wang, E.D., Xu, X.N. and Lei, Z.R. (2017) Application of *Beauveria bassiana* and *Neoseiulus barkieri* for improved control of *Frankliniella occidentalis* in greenhouse cucumber. *Crop Protection*, 96, 83–87.

Xiao, L., Li, Y.Y., Lan, P.X., Tan, G.L., Ding, M., Li, R.H. et al. (2016) First report of *Tomato spotted wilt virus* infecting cowpea in China. *Plant Disease*, 100, 233.

Yang, H., Ozias-Akins, P., Culbreath, A.K., Gorbet, D.W., Weeks, J.R., Mandal, B. et al. (2004) Field evaluation of *Tomato spotted wilt virus* resistance in transgenic peanut (*Arachis hypogaea*). *Plant Disease*, 88, 259–264.

Yoon, J.Y., Choi, G.S. and Choi, S.K. (2017a) First report of *Chrysanthemum stem necrosis virus* on *Chrysanthemum morifolium* in Korea. *Plant Disease*, 101, 264.
Yoon, J.Y., Choi, G.S. and Choi, S.K. (2017b) First report of Tomato spotted wilt virus in Eustoma grandiflorum in Korea. Plant Disease, 101, 515.
Zarzyńska-Nowak, A., Rymelska, N., Borodynko, N. and Hasiów-Jaroszewska, B. (2016) The occurrence of Tomato yellow ring virus on tomato in Poland. Plant Disease, 100, 234.
Zhang, X.R., Lei, Z.R., Reitz, S.R., Wu, S.Y. and Gao, Y.L. (2019) Laboratory and greenhouse evaluation of a granular formulation of Beauveria bassiana for control of western flower thrips, Frankliniella occidentalis. Insects, 10(2), 58.
Zhang, Z.J., Wu, Q.J., Li, X.F., Zhang, Y.J., Xu, B.Y. and Zhu, G.R. (2010) Life history of western flower thrips, Frankliniella occidentalis (Thysan., Thripae), on five different vegetable leaves. Journal of Applied Entomology, 131, 347–354.
Zhang, G.F., Meng, X.Q., Min, L., Qiao, W.N. and Wan, F.H. (2012) Rapid diagnosis of the invasive species, Frankliniella occidentalis (Pergande): a species-specific COI marker. Journal of Applied Entomology, 136, 410–420.
Zheng, X., Zhang, J., Chen, Y., Dong, J. and Zhang, Z. (2014) Effects of Tomato zonate spot virus infection on the development and reproduction of its vector Frankliniella occidentalis (Thysanoptera: Thripidae). Florida Entomology, 97, 549–554.
Zheng, Y.X., Huang, C.H., Cheng, Y.H., Kuo, F.Y. and Jan, F.J. (2010) First report of Tomato spotted wilt virus in sweet pepper in Taiwan. Plant Disease, 94, 920.
Zindović, J., Bulajić, A., Krstić, B., Ciuffo, M., Margaria, P. and Turina, M. (2011) First report of Tomato spotted wilt virus on pepper in Montenegro. Plant Disease, 95, 882.

Manuscript received April 7, 2019
Final version received July 30, 2019
Accepted August 10, 2019

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. The worldwide distribution of Frankliniella occidentalis.

Table S2. The worldwide distribution and host of viruses transmitted by Frankliniella occidentalis.