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ORIGINAL ARTICLE

The role of ornamental plants as hosts of *Tomato chlorotic spot virus* and its vector thrips affecting tomato production

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Abstract

The tomato industry in South Florida (USA) is seriously affected by recently emerging *Tomato chlorotic spot virus* (TCSV). Western flower thrips, *Frankliniella occidentalis* (Pergande), and common blossom thrips, *Frankliniella schultzei* (Trybom) (Thysanoptera: Thripidae), are the two known vectors of TCSV in Florida. In the present study, the presence of thrips vectors and TCSV in 24 flowering ornamental plant species was observed in South Florida. The two thrips vectors, as well as melon thrips, *Thrips palmi* Karny (Thysanoptera: Thripidae), were abundant in the area; they were observed with a range from high (83.1 per sample of 10 flowers) in *Hibiscus rosa-sinensis* L. to low (3.7 per sample of 10 flowers) in *Catharanthus roseus* (L.) G. Don in a nursery study. In a subsequent greenhouse study, we selected seven species of ornamentals, among which the species with the highest thrips abundance, and planted them next to tomato, to determine their effects on TCSV incidence and thrips abundance in tomatoes. Tomatoes with *Portulaca oleracea* L. next to them showed a higher number of TCSV-infected plants (4.25 plants per plot in 2017, and 3.25 plants per plot in 2018) compared to tomatoes with some of the other ornamentals next to them. We report the presence of TCSV through reverse transcriptase polymerase chain reaction (RT-PCR) analysis in *Lantana camara* L., *H. rosa-sinensis*, *Mandevilla* spec., *Gazania linearis* (Thunb.) Druce, *Hemerocallis* spec., *Agastache* spec., and *P. oleracea*. Identification of alternative hosts of TCSV and thrips vectors can be helpful to evaluate the ongoing management programs and develop future programs in local tomato-growing areas.

KEYWORDS

tomato, thrips, *Tomato chlorotic spot virus*, alternative hosts, ornamental plants, Thysanoptera, Thripidae, *Frankliniella occidentalis*, *Frankliniella schultzei*, *Thrips palmi*, *Portulaca oleracea*, *Solanum lycopersicum*

INTRODUCTION

In the USA, *Tomato chlorotic spot virus* (TCSV) (Bunyaviridae, Tospovirus) was first identified in 2012 in tomato (*Solanum lycopersicum* L.) and bell pepper (*Capsicum annuum* L.) (both Solanaceae) in South Florida (Londono et al., 2012). The virus was also detected in tomatoes in Ohio (Baysal-Gurel et al., 2015) and in New York in 2017 (Sui et al., 2018). Significant crop loss was recorded in the southern Florida tomato industry with the outbreak of TCSV in 2014, when 20–40% of tomato plants were infected in the Homestead area (Zhang et al., 2019). The local tomato growers were using various conventional and reduced-risk insecticides including spinetorum (Radiant), tolfenpyrad (Torac), cyantraniliprole (Exirel), and acetamiprid (Assail) to manage this vector-borne disease (RA Khan & DR Seal, unpubl.).

Initially, infection of TCSV in tomatoes causes necrotic lesions, bronzing, and chlorotic spots observed about

3 weeks after transplanting, which can lead to terminal stem and leaf death, wilting, and deformation of leaves (Polston et al., 2013; Zhang et al., 2019). Plants infected at an early development stage (first 6 weeks after being transplanted in the field) are more vulnerable to TCSV, whereas the later stage plants (7–12 weeks after being transplanted in the field) can have deformed or infected fruits with necrotic rings, leaving them unmarketable (Zhang et al., 2015; 2016). Structurally, TCSV is similar to *Tomato spotted wilt virus* (TSWV) and *Groundnut ringspot tospovirus* (GRSV) because they are in the same virus family (Whitfield et al., 2005). Western flower thrips, *Frankliniella occidentalis* (Pergande), and common blossom thrips, *Frankliniella schultzei* (Trybom) (Thysanoptera: Thripidae), have been confirmed as the vectors of TCSV in southern Florida (Webster et al., 2015). In the USA, the host range of TCSV includes jimsonweed, *Datura stramonium* L. (Solanaceae) (Webster et al., 2013), annual vinca, *Catharanthus roseus* (L.) G. Don (Warfield et al., 2015), wax plant, *Hoya wayetii* Kloppenb. (both Apocynaceae), crab cactus, *Schlumbergera truncata* (Haw.) Moran (Cactaceae) (Baker & Adkins, 2015), tomatillo, *Physalis philadelphica* Lam., tobacco, *Nicotiana benthamiana* Domin, petunia, *Petunia* × *hybrida* Hort. Ex Vilm. (all three Solanaceae), impatiens, *Impatiens walleriana* Hook. fil. (Balsaminaceae) (Webster et al., 2015), Madagascar jasmine, *Stephanotis floribunda* Brongn. (Apocynaceae) (Dey et al., 2017), sweet basil, *Ocimum basilicum* L. (Lamiaceae), purslane, *Portulaca oleracea* L. (Portulacaceae) (Raid et al., 2017), and snap bean, *Phaseolus vulgaris* L. (Fabaceae) (Poudel et al., 2018). Identifying new natural hosts of TCSV in Central and South Florida may help to improve management of TCSV and its vector thrips in tomatoes.

Wild plants, as well as cultivated crops, can be potential hosts of both viruses and virus vectors. Thus, alternative hosts are important to be considered in the epidemiology of plant viruses (Duffus, 1971). Wild host plants are important virus reservoirs from where pathogens can spread to susceptible cultivated crops (Jones, 2014). Because TCSV is an emerging tospovirus established in southern Florida, many new host plants, including ornamental crops, have been recently identified. In the present study, we observed the abundance of thrips in 24 ornamental plants in southern Florida in a nursery study. In a separate greenhouse study, we evaluated the role of selected ornamental plants influencing TCSV incidence and its thrips vectors in the main crop, tomato. We hypothesized that some of these ornamental plants would serve as a host of TCSV-vector thrips and thus the tomatoes with those ornamental plants next to them would have more infected plants. The objective of this study was to obtain a thorough view of occurrence, importance, and epidemiology of TCSV in ornamental crops through the identification of its hosts, identification of the thrips vectors involved, and exploring the role of ornamental plants in TCSV virus epidemiology in the tomato agro-ecosystem of South Florida. We also investigated the presence of TCSV in some of these ornamental plants.

MATERIALS AND METHODS

Thrips in ornamental plants in the nursery

This study was conducted in a commercial nursery in Homestead, Florida, USA (25°34'49.6″N, 80°30'18.8″W, altitude 7 m). Ornamental plant samples were collected between February and April 2017 and March and May 2018. The whole nursery was about 405 000 m^2 (40.5 ha), which consisted of approximately 500 greenhouses, each 30.5 × 12.2 m. Each greenhouse contained one or multiple species of ornamental plants maintained in plastic pots of different sizes (1–4 L). Seeds were planted or seedlings were transplanted into potting soil in pots (Miracle-Gro Potting Soil Mix; Miracle-Gro, Marysville, OH, USA; see Supporting Information for maintenance of the plants). To determine the thrips abundance in ornamental plants, we selected 24 species of commonly grown flowering ornamental plants at their flowering stage for sampling thrips. A profile of these plant species showing their family, habitat, and distribution is presented in Table S1. Samples were collected from four nursery houses (3.1 m long, 91.5 cm wide) placed side by side (1.5 m apart) for each ornamental plant species. There were thus four replications (plots) for each ornamental species.

Collecting and processing of samples in the nursery study

All ornamental plant samples were collected at their full bloom flowering stage, between 10:00 and 12:00 hours EST, as this is a peak activity time for thrips (RA Khan, unpubl.). Ten flowers (one flower per plant) were randomly collected from each selected plot of an ornamental species. Each sample of 10 flowers from each ornamental species was placed in a 0.47-L plastic cup (Deli containers; Uline, Pleasant Prairie, WI, USA) marked with ornamental plant species and plot number. Thus, we had four plastic cups (one cup per plot for a sample of 10 flowers) for each species. Immediately after collection, the cups were closed with well-fitted lids to prevent the thrips escaping and were brought back to the Integrated Pest Management (IPM) Laboratory at the Tropical Research and Education Center (TREC), UF-IFAS, Homestead, FL, USA, for further processing. Flower samples were processed using 70% ethanol following the protocol of Seal & Baranowski (1992). Finally, the thrips species in ethanol were counted under a Leica Wild M3Z stereo microscope (Micro Optics of Florida, St. Petersburg, FL, USA) at 10–30× magnification. Thrips were slide mounted and identified under a VHX-6000 digital microscope (Keyence, Itasca, IL, USA) at 50–200× magnification. The thrips were identified to species by observing taxonomic characters including antennal segments, the position of post ocellar setae in the ocellar triangle, and the microtrichial comb on the eighth abdominal tergite (Nakahara, 1997). The presence of virus was not assessed in these plants.

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Greenhouse study to assess *Tomato chlorotic spot virus* and its thrips vectors

The study was performed in a greenhouse at the TREC, UF/IFAS to assess the effect of selected ornamental plants on TCSV prevalence and its thrips vectors on tomatoes. The temperature of the greenhouse ranged from 28 to 34 °C with an average of 31 °C, and the r.h. ranged from 51 to 75% with an average of 69%. This study was conducted in April–June 2017 and repeated in May–July 2018. Data were collected from the study over the 2 years.

Treatments and experimental design of greenhouse study

The greenhouse experiment was conducted using tomato (*S. lycopersicum* cv. Sanibel) as the main crop. Planting, irrigation, and crop management followed standard practices (Freeman et al., 2016). Tomato transplants (Mobley Plant World, Labelle, FL, USA) were planted in 3.8-L plastic pots (Black Thermoformed Nursery Pot, black/matte; Grower's solution, Cookeville, TN, USA) containing garden soil (PRO-MIX; Premier tech home and garden, Quakertown, PA, USA). The selected ornamental plants were also grown in 3.8-L plastic pots like the tomato crop. Plants in the greenhouse were irrigated twice a day (at 08:00 and 16:00 hours EST), delivering 0.6 cm of water each time using a sprinkler system set at 120 cm above the plants. Overgrowing parts of ornamental plants were clipped off once every 3 weeks to ensure normal growth and development of the main crop (tomato).

Seven ornamental species including *P. oleracea*, *Hibiscus rosa-sinensis* L. (Malvaceae), *Lantana camara* L. (Verbenaceae), *Mandevilla* spec. (Apocynaceae), *Gazania linearis* (Thunb.) Druce (Asteraceae), *Hemerocallis* spec. (Asphodelaceae), and *Agastache* spec. (Lamiaceae), were selected to plant in association with tomatoes in the same research plot and were referred to as treatments. The ornamental plants were selected based on the abundance of thrips in them as found in our earlier study (nursery study). There was an untreated plot (control) of tomatoes with no ornamental plants. All plants were placed on a bench, considered a research plot (2.44 × 1.83 m, 0.91 m from the ground). There were 3.05-m-long non-planted spaces between the treatments. Thus, there were eight such benches for seven treatments and an untreated plot, which constituted a block (Figure 1). The treatments were arranged in a randomized complete block design replicated 4× using 32 benches in four blocks in the same greenhouse. We placed the tomato plants as a center row on each bench with three potted ornamental plants, 0.6 m apart from each other in a parallel row spaced 0.30 m from the center on each side. In total, we had five potted tomato plants in each plot and six ornamental plants of one species.

Collecting and processing of samples in the greenhouse study

Five fully expanded young leaves from fifth/sixth nodes of a tomato plant and five fully expanded yellow flowers, one of each plant part from each tomato plant, were randomly collected from each research plot and placed separately in the collection cups (0.47 L). Five flowers and leaves of ornamental plants from each plot were also randomly collected following the same method and placed separately in the collection cups. The samples were collected every week starting from 4 weeks after planting up to 10 weeks. The collection and processing of all these samples followed the procedure outlined in the previous section 'Collecting and processing of samples in the nursery study'.

Tomato chlorotic spot virus infected tomato plants and marketable fruit yield

Tomato chlorotic spot virus infected tomato plants were confirmed by visual symptoms including necrosis on leaves, chlorotic and necrotic ring spots followed by dwarfing and wilting of a portion or the entire plant, and necrotic ring spots on fruits (Polston et al., 2013). The number of TCSV-symptomatic plants was counted in

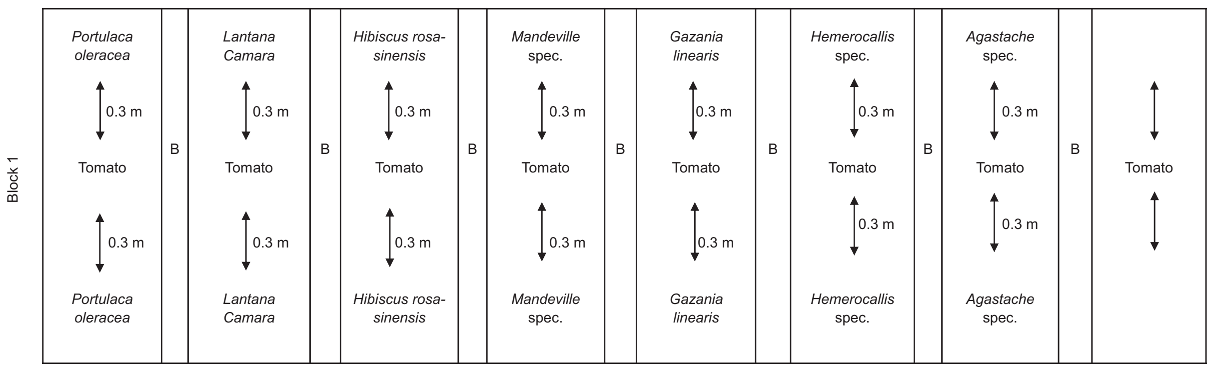

FIGURE 1 Experimental design of greenhouse study with tomatoes with ornamental plants next to them. Tomatoes (main crop) were placed in the middle row of the plot and ornamental plants were placed on each side of those tomatoes 0.3 m apart. B = unplanted buffer. This figure shows one block; the placement of treatments (ornamental plants) differed in the four blocks.

each plot at the end of the study. All marketable fruits were harvested from all tomato plants of each plot 12 weeks after transplanting. Marketable fruits (green stage) were weighed, using a scale of 31.8 kg capacity (CCI Scale, Ventura, CA, USA) and graded, representing USA no. 1, 2, and 3 comprising small (5.08 cm diameter), medium (5.72 cm diameter), and large (6.35 cm diameter) sizes following market standards (USDA, 2022).

Collection and processing of samples for detection of *Tomato chlorotic spot virus*

Five leaves and five flowers (one of each per plant) from each ornamental species planted next to tomatoes across all replicates in 2017 and 2018 were collected 8 weeks after transplanting the tomatoes and were placed in a Ziploc bag (SC Johnson & Son, Racine, WI, USA) and stored in a freezer (VIP series −86 °C; Sanyo North America, San Diego, CA, USA) at −80 °C in 2018. Five tomato leaves were also collected across all replicates in both years. The samples were tested for TCSV using reverse transcriptase polymerase chain reaction (RT-PCR) and sent for DNA sequencing, following the protocol mentioned by Poudel et al. (2018). Results are showing the positive results for the ornamental plant samples.

Statistical analysis

The mean number of thrips from each treatment was compared separately for each year. The number of thrips per ornamental species (for nursery studies) and the number of thrips per treatment (for greenhouse studies) were averaged to a single measure per block and treatment combination. Multiple sampling dates were averaged to remove the effects of repeated measures and the large number of zero counts. The resulting average was then subjected to square root transformation before statistical analysis to meet the assumption of normality. Marketable yield and TCSV (for greenhouse studies) were only measured once per year and therefore were not averaged but were still square root transformed. Non-transformed means are reported in the tables. All responses were analyzed using a linear mixed model (randomized complete block design) with the fixed effect treatment, and the random effect block (Proc GLIMMIX model). Degrees of freedom were estimated using the Kenward-Roger's method. If the F-value for the overall treatment effect was significant, differences of means among treatments (least square means) were separated using Tukey's multiple comparisons procedure. Pearson's correlation coefficient analysis was conducted to explore the correlation between the thrips population and the TCSV infected tomatoes for the greenhouse study (Benesty et al., 2009). The Wilcoxon two-sample test was applied to measure the t-approximation of the number of thrips. All analyses ($\alpha = 0.05$) were done using SAS v.9.3 (SAS Institute, Cary, NC, USA).

RESULTS

Thrips in ornamental plants in the nursery

Frankliniella occidentalis, *F. schultzei*, melon thrips (*Thrips palmi* Karny), chilli thrips (*Scirtothrips dorsalis* Hood), and onion thrips (*Thrips tabaci* Lindeman; all Thysanoptera: Thripidae) were observed in the flowers collected from 24 ornamental flowering plants. The numbers of *S. dorsalis* and *T. tabaci* were very low and they were only observed in a few plant species in an inconsistent pattern. Only *F. occidentalis*, *F. schultzei*, and *T. palmi* were considered for result interpretation.

Frankliniella occidentalis (ca. 75% of the total adult thrips population) was the dominant species on the 24 ornamental plants in the nursery during 2 years of sampling (Tables 1 and 2). In 2017, the number of *F. occidentalis* in flowers differed among the ornamental plants ($F_{23,72} = 59.74$, $P < 0.001$). The highest number was recorded in *H. rosa-sinensis* (mean ± SE = 59.08 ± 13.22 per sample of 10 flowers), followed by *G. linearis* (47.16 ± 4.18) (Table 1). The abundance of *F. schultzei* differed among the ornamental flowers ($F_{23,72} = 54.25$, $P < 0.001$). The numbers of *F. schultzei* were highest in *Helianthus annuus* L. and the numbers of *T. palmi* were highest in *Hibiscus* spec. More thrips larvae were recorded in *Agastache* spec. than in other ornamental flowers (Table 1). Similar thrips population trends were found in both years for *F. occidentalis*, *F. schultzei*, *T. palmi*, total adult thrips, and the thrips larvae (Table 2).

Thrips in ornamental plants in the greenhouse

A higher number of *F. occidentalis* was recorded in *H. rosa-sinensis* (mean ± SE = 27.75 ± 6.05 per sample of five flowers) than in other ornamental flowers in 2017 (Table 3). The number of *F. schultzei* was higher in *H. rosa-sinensis* (1.00 ± 0.45 per five flowers) than in *Hemerocallis* spec. and *Agastache* spec.; the number of *T. palmi* was higher in *H. rosa-sinensis* (1.75 ± 0.66 per five flowers) than in *P. oleracea* and *Hemerocallis* spec. (Table 3). More thrips adults were recorded in *H. rosa-sinensis* (31.14 ± 6.21) than in other ornamental flowers. Also more thrips larvae were found in *H. rosa-sinensis* (52.14 ± 12.90) than in other ornamental plants, except *Agastache* spec. (Table 3).

In 2018, numbers of *F. occidentalis* were higher than those of *F. schultzei* and *T. palmi*. Higher numbers of *F. occidentalis* (35.75 ± 8.45 per five flowers) and total adult thrips (38.85 ± 8.74) were recorded in *H. rosa-sinensis* than in other ornamental flowers (Table 3). More *F. schultzei* were recorded in *G. linearis* flowers (1.03 ± 0.35 per five flowers) than in *L. camara*, *Hemerocallis* spec., and *Agastache* spec. flowers; more *T. palmi* were found in *H. rosa-sinensis* (3.21 ± 1.20 per five flowers) than in *Hemerocallis* spec. (Table 3). The number of thrips larvae was highest in *H. rosa-sinensis*, followed by *Agastache* spec. and *G. linearis* (Table 3). Overall, very few ornamental leaf samples had thrips (data not shown).

TABLE 1 Mean (± SE) number of thrips per sample of 10 flowers of ornamental plants in a nursery study in 2017.

Ornamental plant species	*Frankliniella occidentalis*	*Frankliniella schultzei*	*Thrips palmi*	Total adult thrips	Total thrips larvae
Torenia spec.	21.00 ± 3.04efgh	5.16 ± 2.33abcd	6.16 ± 1.05bc	32.33 ± 4.26cdefg	40.66 ± 11.60bc
Hibiscus spec.	59.08 ± 13.22a	0.66 ± 0.28 h	17.25 ± 4.47a	77.00 ± 16.59a	59.41 ± 12.09b
Fuchsia spec.	14.83 ± 3.23ghij	0i	6.00 ± 1.66bcd	20.83 ± 4.62ghi	9.00 ± 1.88fghijk
Ericameria arborescens (A. Gray) Greene	3.00 ± 1.10mn	1.50 ± 0.41efgh	0h	4.50 ± 1.14kl	3.83 ± 1.06ijk
Petunia spec.	11.91 ± 1.58hijk	0i	7.00 ± 0.92bc	18.91 ± 1.99hi	6.75 ± 1.14hijk
Cosmos spec.	19.58 ± 1.59fgh	0i	7.66 ± 0.94b	28.08 ± 2.23efgh	7.75 ± 1.01ghijk
Tagetes erecta L.	13.50 ± 1.92hij	2.83 ± 1.11cdef	3.58 ± 1.54bcde	19.91 ± 3.50ghi	14.75 ± 1.21defgh
Pentas lanceolata (Forssk.) Deflers	1.83 ± 0.74n	1.00 ± 0.42 h	7.25 ± 1.81b	10.75 ± 2.21ijk	1.83 ± 0.71 k
Gerbera spec.	8.83 ± 1.08ijkl	0i	4.00 ± 0.96bcde	12.83 ± 1.26ij	14.58 ± 1.31defghi
Portulaca oleracea	36.16 ± 5.99bcd	4.83 ± 0.75abcd	4.66 ± 1.66bcde	45.16 ± 7.27cb	33.91 ± 5.60bcd
Gazania linearis	47.16 ± 4.18ab	5.33 ± 0.90abc	19.58 ± 2.36a	71.33 ± 4.81a	17.33 ± 1.74defgh
Lantana camara	4.50 ± 1.22lmn	1.33 ± 0.56fgh	6.00 ± 0.63bc	13.66 ± 2.39ij	13.66 ± 0.63efghij
Impatiens walleriana	5.83 ± 1.73klmn	2.83 ± 0.69defg	0.66 ± 0.44fgh	9.33 ± 1.71jkl	3.08 ± 1.06jk
Begonia semperflorens Link. et Otto	6.83 ± 1.07jklm	5.91 ± 2.35ab	5.25 ± 2.77bcde	18.00 ± 3.29hij	4.66 ± 1.49hijk
Kalanchoe blossfeldiana v. Poelln.	33.41 ± 3.11bcde	1.08 ± 0.46gh	6.91 ± 0.91bc	41.41 ± 3.43bcde	9.08 ± 1.00fghijk
Lilium 'Matrix'	36.25 ± 2.61bcd	0.83 ± 0.57 h	0h	37.08 ± 2.62bcdef	10.66 ± 1.34efghij
Helianthus annuus	39.25 ± 6.83bc	6.66 ± 2.79a	2.41 ± 1.04cdef	48.33 ± 9.94b	26.58 ± 2.65cde
Catharanthus roseus	3.66 ± 0.39lmn	0i	0h	3.66 ± 0.39l	2.83 ± 0.98jk
Canna spec.	17.25 ± 2.13ghi	1.33 ± 0.37fgh	0.33 ± 0.22gh	18.91 ± 2.24hi	15.41 ± 1.88defghi
Celosia argentea L.	21.16 ± 1.79efgh	0i	5.58 ± 0.92bcd	26.25 ± 2.19fgh	11.91 ± 1.09efghij
Plumbago auriculata Lam.	24.50 ± 2.59defg	3.08 ± 0.62cdef	1.25 ± 0.41efgh	28.83 ± 3.22defgh	22.00 ± 2.11cdefg
Agastache spec.	37.91 ± 2.82bcd	3.75 ± 0.61abcd	1.83 ± 0.56defg	43.50 ± 2.69bcd	143.25 ± 32.52a
Mandevilla spec.	30.33 ± 3.70cdef	3.08 ± 0.55cdef	3.16 ± 1.06bcde	36.58 ± 4.69bcdef	26.33 ± 2.96cde
Hemerocallis spec.	45.50 ± 7.07abc	3.41 ± 0.48bcde	0h	48.91 ± 6.90b	23.75 ± 2.32cdef
$F_{23,72}$	59.74	54.25	34.76	56.42	34.30
P	<0.001	<0.001	<0.001	<0.001	<0.001

Means within a column followed by the same letter are not significantly different (Tukey's test: $P > 0.05$).

Thrips in tomatoes in the greenhouse

Thrips numbers were low in tomato flowers (mean ± SE = 0.50 ± 0.21 to 2.16 ± 1.01 adult thrips per sample of five flowers; Table 4) as well as on tomato leaves (<1.0 per five leaves; Table 5) in both 2017 and 2018. The numbers of *F. schultzei* in tomato flowers were almost zero. In both years, there were no significant differences between tomatoes without (control) vs. with ornamental plants next to them in the abundance of *F. occidentalis*, *F. schultzei*, *T. palmi*, total adult thrips, and thrips larvae, both in tomato flowers (Table 4) and on tomato leaves (Table 5).

On average, in tomato the numbers of adult and larval thrips were lower than in the ornamental plants (adults: 1.33 ± 2.25 vs. 9.91 ± 18.78 per five flowers, t-approximation of the Wilcoxon two-sample test: $t = 6.28$; larvae: 0.43 ± 1.27 vs. 18.41 ± 35.71, $t = 6.97$, both $P < 0.001$).

Marketable yield and *Tomato chlorotic spot virus* infected tomato plants

In both years the yield differed among treatments (2017: $F_{7,24} = 8.14$; 2018: $F_{7,24} = 7.90$, both $P < 0.001$) – the yield in tomatoes with *P. oleracea* next to them was lower than in tomatoes with any of the other ornamentals next to them or than in tomatoes without plants nearby (control) (Figure 2). Also TCSV prevalence differed among treatments (2017: $F_{7,24} = 3.24$, $P = 0.015$; 2018: $F_{7,24} = 4.46$, $P = 0.0035$) – on tomato plants with *P. oleracea* next to them TCSV prevalence was significantly higher than on tomatoes with *L. camara* or *Hemerocallis* spec. next to them (2017) or than on tomatoes with *Hemerocallis* spec. next to them (2018) (Figure 3). In both years, we observed TCSV symptoms in tomatoes without (control) and with ornamental plants next to them in the study area.

TABLE 2 Mean (± SE) number of thrips per sample of 10 flowers of ornamental plants in a nursery study in 2018.

Ornamental plant species	*Frankliniella occidentalis*	*Frankliniella schultzei*	*Thrips palmi*	Total adult thrips	Total thrips larvae
Torenia spec.	24.33 ± 3.31efgh	5.16 ± 2.33abc	6.33 ± 1.42bc	35.83 ± 5.15de	38.66 ± 13.30bc
Hibiscus spec.	67.58 ± 15.55a	0.66 ± 0.28i	14.83 ± 3.63a	83.08 ± 18.32a	61.58 ± 13.96b
Fuchsia spec.	12.75 ± 3.09ijkl	0j	4.83 ± 0.90bcde	18.41 ± 3.99fghi	6.58 ± 0.96fghi
Ericameria arborescens	3.66 ± 0.87no	1.50 ± 0.59efghi	0i	5.16 ± 1.07kl	3.83 ± 0.87ghi
Petunia spec.	12.33 ± 2.15jklm	0j	5.41 ± 0.73bcd	17.75 ± 2.38fghi	5.33 ± 1.14fghi
Cosmos spec.	22.91 ± 1.95fghij	0j	6.00 ± 0.65bcd	28.91 ± 2.27ef	7.75 ± 1.35fghi
Tagetes erecta	13.08 ± 2.04ijkl	2.83 ± 1.11cdefg	2.41 ± 1.05defg	18.33 ± 3.29fghi	15.58 ± 1.92cdefgh
Pentas lanceolata	1.33 ± 0.46o	1.00 ± 0.42hi	4.91 ± 1.20bcde	7.25 ± 1.21jkl	1.16 ± 0.45i
Gerbera spec.	7.90 ± 1.07klmn	0j	4.00 ± 0.83bcdef	11.90 ± 1.31hijk	16.36 ± 1.70cdefg
Portulaca oleracea	40.50 ± 7.23bcde	4.83 ± 0.75abc	4.41 ± 1.51bcdef	49.75 ± 8.75 cd	34.91 ± 5.75bcd
Gazania linearis	49.61 ± 6.44abc	4.92 ± 0.92abc	20.15 ± 3.11a	74.69 ± 8.14ab	15.61 ± 1.38cdefgh
Lantana camara	3.16 ± 0.82no	1.33 ± 0.56fghi	4.50 ± 0.84bcdef	9.00 ± 1.21ijkl	10.83 ± 1.52efgh
Impatiens walleriana	5.83 ± 1.74lmno	2.83 ± 0.69cdefgh	0.66 ± 0.44hi	9.33 ± 1.89ijkl	2.91 ± 1.00 hi
Begonia semperflorens	5.66 ± 0.58lmno	5.91 ± 2.35ab	4.25 ± 2.36cdefg	15.83 ± 3.00ghij	6.16 ± 2.51fghi
Kalanchoe blossfeldiana	37.41 ± 3.53bcdef	1.08 ± 0.46ghi	7.91 ± 0.85b	46.41 ± 4.14 cd	6.75 ± 1.65fghi
Lilium 'Matrix'	34.75 ± 2.21cdef	0.83 ± 0.57i	0i	35.58 ± 2.08de	8.41 ± 1.23fghi
Helianthus annuus	38.75 ± 5.81bcdef	6.66 ± 2.79a	1.25 ± 0.68gh	46.66 ± 8.48 cd	28.91 ± 2.42cde
Catharanthus roseus	4.50 ± 0.57mno	0j	0i	4.50 ± 0.57l	1.25 ± 0.62i
Canna spec.	16.58 ± 2.27hijk	1.33 ± 0.37defghi	1.66 ± 0.73efgh	19.58 ± 2.87fgh	14.33 ± 2.04defgh
Celosia argentea	25.66 ± 2.50defgh	0j	3.58 ± 0.63bcdefg	29.25 ± 2.34ef	11.58 ± 1.48efgh
Plumbago auriculata	19.66 ± 2.63ghij	2.58 ± 0.43cdefgh	1.41 ± 0.25fgh	23.66 ± 2.75efg	20.50 ± 2.15cdef
Agastache spec.	40.91 ± 2.34bcd	3.25 ± 0.46bcde	1.83 ± 0.32efgh	46.00 ± 2.41cd	165.75 ± 37.64a
Mandevilla spec.	32.50 ± 3.75cdefg	3.08 ± 0.55cdef	3.08 ± 0.80cdefg	38.66 ± 4.50de	27.66 ± 3.79cde
Hemerocallis spec.	54.33 ± 10.17ab	3.33 ± 0.52bcd	0i	57.66 ± 9.98bc	19.41 ± 1.70cdef
$F_{23,72}$	54.86	47.25	41.70	61.23	33.92
P	<0.001	<0.001	<0.001	<0.001	<0.001

Means within a column followed by the same letter are not significantly different (Tukey's test: P > 0.05).

TABLE 3 Mean (± SE) number of thrips per sample of five flowers of selected ornamental plants in the greenhouse study in 2017 and 2018.

Ornamental treatments		*Frankliniella occidentalis*	*Frankliniella schultzei*	*Thrips palmi*	Total adult thrips	Total thrips larvae
2017	*Portulaca oleracea*	3.64 ± 0.83b	0.46 ± 0.21abc	0.11 ± 0.05bc	4.28 ± 0.81b	8.50 ± 2.24c
	Lantana camara	4.82 ± 1.14b	0.07 ± 0.07abc	0.25 ± 0.19abc	5.21 ± 1.12b	5.92 ± 1.37c
	Hibiscus rosa-sinensis	27.75 ± 6.05a	1.00 ± 0.45ab	1.75 ± 0.66ab	31.14 ± 6.21a	52.14 ± 12.90a
	Mandevilla spec.	7.39 ± 1.82b	0.32 ± 0.15abc	0.71 ± 0.26abc	8.82 ± 1.81b	5.17 ± 1.33c
	Gazania linearis	6.35 ± 1.41b	0.89 ± 0.30a	1.42 ± 0.51a	8.57 ± 1.36b	17.85 ± 3.37bc
	Hemerocallis spec.	5.64 ± 1.08b	0c	0.07 ± 0.07c	5.17 ± 1.07b	5.00 ± 0.98c
	Agastache spec.	3.25 ± 0.81b	0.03 ± 0.03bc	0.42 ± 0.19abc	3.75 ± 0.83b	28.46 ± 6.03ab
	$F_{6,21}$	24.71	4.34	4.33	22.03	16.56
	P	<0.001	0.0053	0.0071	<0.001	<0.001
2018	*Portulaca oleracea*	3.28 ± 1.02b	0.46 ± 0.21ab	0.25 ± 0.15ab	3.92 ± 0.1.01b	8.21 ± 2.68c
	Lantana camara	4.89 ± 1.43b	0b	0.42 ± 0.21ab	5.28 ± 1.43b	5.75 ± 1.54c
	Hibiscus rosa-sinensis	35.75 ± 8.45a	0.50 ± 0.18ab	3.21 ± 1.20a	38.85 ± 8.74a	59.35 ± 14.28a
	Mandevilla spec.	5.10 ± 1.62b	0.46 ± 0.21ab	1.32 ± 0.50ab	6.53 ± 1.62b	5.17 ± 1.49c
	Gazania linearis	7.00 ± 1.53b	1.03 ± 0.35a	1.07 ± 0.35ab	9.21 ± 1.47b	19.92 ± 4.13bc
	Hemerocallis spec.	5.10 ± 1.07b	0b	0.07 ± 0.07b	5.17 ± 1.06b	4.35 ± 0.74c
	Agastache spec.	2.17 ± 0.56b	0.11 ± 0.07b	0.42 ± 0.16ab	2.67 ± 0.60b	31.78 ± 6.90ab
	$F_{6,21}$	25.09	5.85	3.81	20.83	14.05
	P	<0.001	0.0016	0.013	<0.001	<0.001

Means within a column and within a year followed by the same letter are not significantly different (Tukey's test: P > 0.05).

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TABLE 4 Mean (± SE) number of thrips per sample of five flowers of tomatoes with selected ornamental plants next to them, in the greenhouse study.

Main crop + ornamental treatments		*Frankliniella occidentalis*	*Frankliniella schultzei*	*Thrips palmi*	Total adult thrips	Total thrips larvae
2017	Tomato + *Portulaca oleracea*	1.00 ± 0.46	0	0.16 ± 0.11	1.16 ± 0.48	0.58 ± 0.35
	Tomato + *Lantana camara*	1.20 ± 0.41	0	0.37 ± 0.16	1.58 ± 0.45	0.75 ± 0.34
	Tomato + *Hibiscus rosa-sinensis*	0.41 ± 0.20	0	0.08 ± 0.08	0.50 ± 0.21	0
	Tomato + *Mandevilla* spec.	1.20 ± 0.38	0.08 ± 0.08	0.33 ± 0.16	1.62 ± 0.42	0.41 ± 0.23
	Tomato + *Gazania linearis*	1.50 ± 0.67	0	0.29 ± 0.16	1.79 ± 0.68	0.45 ± 0.37
	Tomato + *Hemerocallis* spec.	0.95 ± 0.51	0	0.25 ± 0.12	1.21 ± 0.51	0.20 ± 0.10
	Tomato + *Agastache* spec.	1.20 ± 0.56	0	0.33 ± 0.14	1.54 ± 0.59	0.12 ± 0.09
	Tomato	0.62 ± 0.26	0	0.20 ± 0.10	0.83 ± 0.26	0.25 ± 0.17
	$F_{7,24}$	0.90	1.00	1.71	1.25	1.44
	P	0.52	0.46	0.16	0.32	0.26
2018	Tomato + *Portulaca oleracea*	1.54 ± 0.58	0	0.16 ± 0.11	1.70 ± 0.59	0.75 ± 0.35
	Tomato + *Lantana camara*	0.95 ± 0.36	0	0.41 ± 0.19	1.37 ± 0.44	0.50 ± 0.24
	Tomato + *Hibiscus rosa-sinensis*	0.83 ± 0.41	0	0.33 ± 0.15	1.16 ± 0.42	0.50 ± 0.22
	Tomato + *Mandevilla* spec.	1.04 ± 0.40	0	0.33 ± 0.16	1.37 ± 0.41	0.66 ± 0.41
	Tomato + *Gazania linearis*	1.50 ± 0.97	0	0.66 ± 0.39	2.16 ± 1.01	0.95 ± 0.57
	Tomato + *Hemerocallis* spec.	1.37 ± 0.44	0	0.33 ± 0.20	1.70 ± 0.44	0.45 ± 0.19
	Tomato + *Agastache* spec.	0.54 ± 0.27	0	0.33 ± 0.16	0.87 ± 0.29	0.20 ± 0.12
	Tomato	0.79 ± 0.32	0.08 ± 0.08	0.29 ± 0.12	1.16 ± 0.32	0.25 ± 0.15
	$F_{7,24}$	0.94	1.00	0.48	0.46	0.71
	P	0.50	0.46	0.84	0.85	0.66

TABLE 5 Mean (± SE) number of thrips per sample of five leaves of tomatoes with selected ornamental plants next to them, in the greenhouse study.

Main crop + ornamental treatments		*Frankliniella occidentalis*	*Frankliniella schultzei*	*Thrips palmi*	Total adult thrips	Total thrips larvae
2017	Tomato + *Portulaca oleracea*	0.20 ± 0.13	0.15 ± 0.11	0	0.35 ± 0.16	0.10 ± 0.10
	Tomato + *Lantana camara*	0	0	0.00 ± 0.10	0	0
	Tomato + *Hibiscus rosa-sinensis*	0.10 ± 0.10	0.10 ± 0.10	0.10 ± 0.10	0.30 ± 0.16	0.05 ± 0.05
	Tomato + *Mandevilla* spec.	0.20 ± 0.13	0	0	0.20 ± 0.13	0
	Tomato + *Gazania linearis*	0.10 ± 0.10	0	0	0.10 ± 0.10	0
	Tomato + *Hemerocallis* spec.	0	0.10 ± 0.10	0	0.10 ± 0.10	0.05 ± 0.05
	Tomato + *Agastache* spec.	0.30 ± 0.16	0	0.15 ± 0.11	0.45 ± 0.18	0
	Tomato	0	0	0.20 ± 0.13	0.20 ± 0.13	0
	$F_{7,24}$	1.22	1.21	1.75	1.98	0.73
	P	0.33	0.34	0.14	0.11	0.65
2018	Tomato + *Portulaca oleracea*	0.10 ± 0.10	0.15 ± 0.11	0.15 ± 0.15	0.40 ± 0.26	0.30 ± 0.21
	Tomato + *Lantana camara*	0	0	0.10 ± 0.10	0	0
	Tomato + *Hibiscus rosa-sinensis*	0.05 ± 0.05	0	0	0.05 ± 0.05	0.05 ± 0.05
	Tomato + *Mandevilla* spec.	0.25 ± 0.20	0	0	0.25 ± 0.20	0
	Tomato + *Gazania linearis*	0.10 ± 0.10	0	0	0.10 ± 0.10	0
	Tomato + *Hemerocallis* spec.	0	0.20 ± 0.20	0	0.20 ± 0.20	0.15 ± 0.15
	Tomato + *Agastache* spec.	0.10 ± 0.10	0	0.10 ± 0.10	0.20 ± 0.13	0
	Tomato	0	0	0.20 ± 0.13	0.20 ± 0.13	0
	$F_{7,24}$	0.85	1.39	1.05	0.39	1.54
	P	0.56	0.25	0.43	0.90	0.20

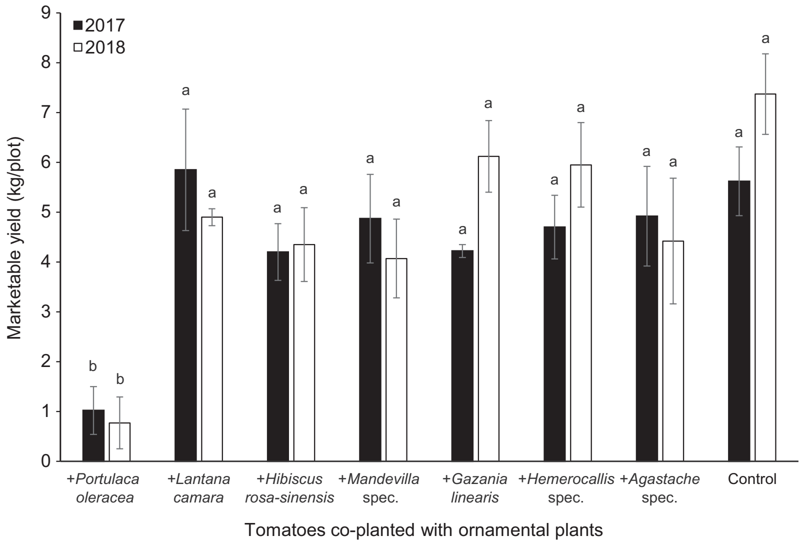

FIGURE 2 Mean (± SE) marketable yield per plot (kg) in tomatoes with selected ornamental plants next to them in 2017 and 2018. The ornamental plants, and therefore the tomatoes, varied in thrips densities (see Tables 3–5). Control: no plant next to the tomato plants. Means within a year capped with the same letter are not significantly different (Tukey's test: $P > 0.05$).

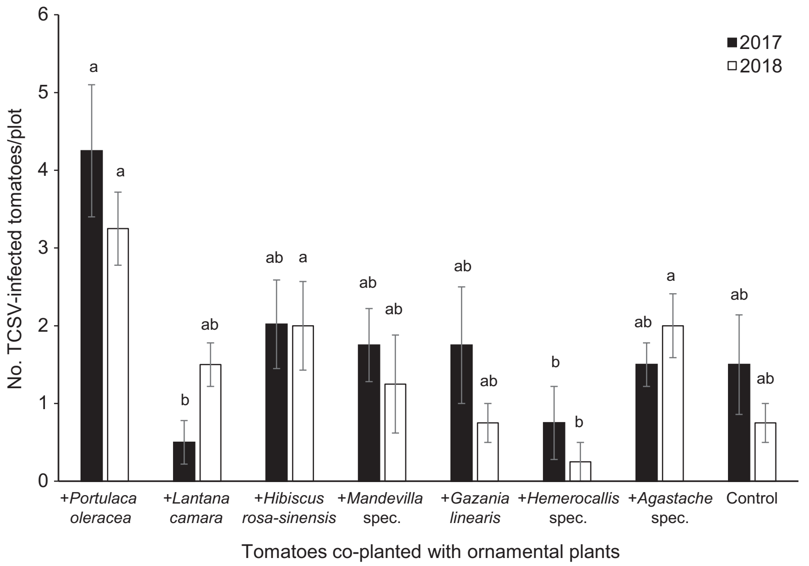

FIGURE 3 Mean (± SE) incidence of *Tomato chlorotic spot virus* (TCSV) in tomatoes with selected ornamental plants next to them in 2017 and 2018. The ornamental plants, and therefore the tomatoes, varied in densities of the thrips, vectors of the virus (see Tables 3–5). Control: no plant next to the tomato plants. Means within a year capped with the same letter are not significantly different (Tukey's test: $P > 0.05$).

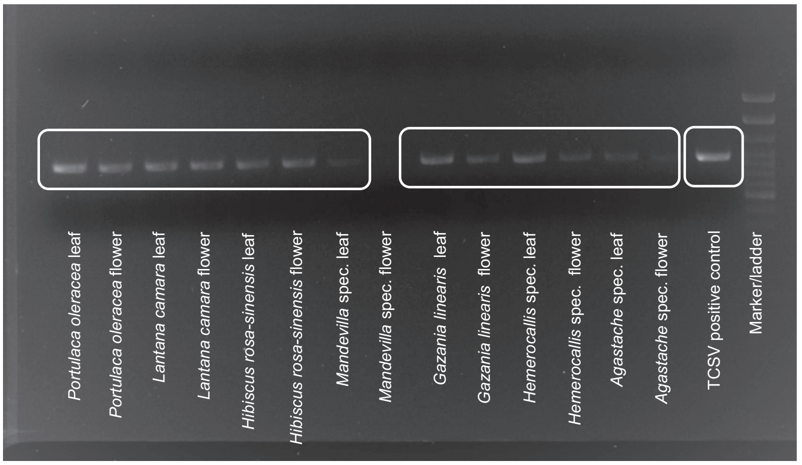

FIGURE 4 Electrophoresis gel of RT-PCR products showing ornamental leaf and flower samples positive for *Tomato chlorotic spot virus* (TCSV). Samples from symptomatic and non-symptomatic plants were not distinguished in this figure.

The numbers of adult and larval thrips in tomato leaves were positively correlated with the prevalence of TCSV disease (i.e., the number of plants with visible symptoms) in both years (2017, adults: Pearson's $r = 0.09$, larvae: $r = 0.12$; 2018, adults: $r = 0.03$, larvae: $r = 0.11$). Also, the numbers of adult and larval thrips in tomato flowers were positively correlated with the prevalence of TCSV disease (2017, for adults: $r = 0.10$, larvae: $r = 0.15$, 2018, adults: $r = 0.14$, larvae: $r = 0.15$).

Ornamental plants as reservoir of *Tomato chlorotic spot virus* in the greenhouse

The RT-PCR analysis showed that both leaf and flower samples of six out of the seven tested ornamental species were positive for TCSV in both 2017 and 2018: *P. oleracea*, *H. rosa-sinensis*, *L. camara*, *G. linearis*, *Hemerocallis* spec., and *Agastache* spec. For *Mandevilla* spec., only the flowers were positive, but not the leaves (Figure 4). The results were not separated for symptomatic and non-symptomatic plants.

DISCUSSION

In the nursery study, various species such as *F. occidentalis*, *F. schultzei*, *T. palmi*, *S. dorsalis*, *T. tabaci*, and thrips larvae were recorded from 24 ornamental plants. The highest numbers of both adult thrips and larvae were recorded in *H. rosa-sinensis* among all tested ornamentals. These thrips species are commonly found in ornamental plants in Florida and are known to transmit different species of tospoviruses (Rotenberg, 2015; Cluever & Smith, 2017). The current study on thrips abundance in ornamental plants was conducted during late spring to early summer when the vegetable growing season was nearly over. A high number of both adult and larval thrips, as we determined from the present study, indicated that the thrips migrated to flowers of ornamental plants from the nearby vegetable growing area (Ramachandran et al., 2001). *Frankliniella occidentalis* was the dominant thrips species in the nursery study; this is a vector of tospoviruses including TSWV and TCSV (Riley et al., 2011; Wijkamp et al., 1995). The second dominant thrips species in ornamental plants was *T. palmi*, which was reported to be the vector of some tospoviruses (Riley et al., 2011). Besides their role in transmitting tospoviruses, both *F. occidentalis* and *T. palmi* are known to feed and reproduce on the terminal growth of some ornamental plants (Funderburk et al., 2007). The numbers of *F. schultzei*, another confirmed vector of TCSV in Florida, were comparatively low in ornamental flowers. However, a small number of viruliferous thrips can play a significant role in transmitting tospoviruses (Boonham et al., 2002).

Seven ornamental plant species were selected in a greenhouse study to observe their effect on the incidence of TCSV and thrips vectors in tomatoes. We found a high number of thrips in the beginning of the study period. Thrips numbers in the ornamental flowers decreased as the study progressed. The experiment was started in late spring when thrips are usually found in higher numbers and numbers decrease with the approach of the summer, with heavy rain (RA Khan, unpubl.). Among several thrips species, *F. occidentalis* were found in higher numbers than other species in ornamental flowers in the present study. Thrips species recorded in this study are considered as pests of ornamental plants in Florida, where they inflict injury to these plants by feeding on flowers and terminal shoots. These thrips species were also found to aggregate on flowers (Funderburk et al., 2007). Whereas some plant species are only feeding hosts for thrips, the presence of both adults and larvae on ornamental flowers indicated that these plants are reproductive hosts for thrips. From these plants, thrips can migrate to the neighboring crop fields (Northfield et al., 2008).

The number of thrips in tomatoes, the main crop in the greenhouse study, was very low. *Frankliniella occidentalis* were found in comparatively higher numbers than *F. schultzei* and *T. palmi* in tomatoes, and this coincided with the higher abundance of *F. occidentalis* in the selected ornamental plants used in combination treatments with tomatoes. The presence of higher numbers of adult thrips and larvae in tomato flowers than in the leaves show their greater attraction to the flowers compared to the leaves. The lower number of adult thrips and larvae in tomatoes compared to the ornamental plants indicated that tomato is not a favored host for thrips. Hirano et al. (1994) identified the presence of α-tomatine, a steroidal glycoalkaloid in tomatoes, that acts as a strong antifeedant for thrips.

Although there was no significant difference between the numbers of thrips in tomatoes without (control) and with ornamental plants next to them, planting ornamentals had a significant effect on the disease incidence of TCSV (i.e., number of plants with visible symptoms) and marketable yield in tomatoes. Tomatoes with *P. oleracea* next to them showed a higher incidence of TCSV compared to other treatments. The RT-PCR analysis of leaf samples from symptomatic ornamental plants revealed that all samples were positive for TCSV. Leaf samples from TCSV infected tomato plants were also positive for TCSV (results not shown). *Portulaca oleracea* was already identified as a reservoir of TCSV (Raid et al., 2017), and this was confirmed in the present study. In a greenhouse study, Costa & Carvalho (1960) observed that the tissue of *P. oleracea* can maintain a high titer of TSWV for a long time. There is a possibility of *P. oleracea* tissues maintaining a high TCSV titer as well, which could lead to thrips infection with the virus. Our study showed a relatively high number of TCSV infected tomatoes with *P. oleracea* next to them, possibly indicating high virus titer in *P. oleracea*.

Plant hosts that support both vectors and viruses are important in disease epidemiology. In this study, we found that ornamental plants support the growth and development of thrips populations. The same ornamental plants were also observed to be reservoirs of TCSV. Although thrips numbers in tomatoes were low, tomatoes without (control) and with ornamental plants next to them were all infected with TCSV. These results indicated that thrips recorded on the tomatoes migrated from nearby ornamental plants, which can be considered as viruliferous. Coutts et al. (2004) revealed that tospovirus spread in crops was monocyclic, where the viruliferous thrips vectors were coming from outside sources and infecting the crops. Khan et al. (2020) observed the presence of thrips and the edge effect of

TCSV spread in infected tomato fields, which concurred with our present study. The geographical distribution of TCSV occurrence is still restricted in southern Florida. More potential hosts of TCSV can be expected from weeds, ornamental plants, or other cultivated crops in southern Florida. Considerable disease prevalence can be expected because TCSV is present in the region of southern Florida where growers produce vegetable crops, with ornamental nurseries, tropical fruits, and transplants in proximity (Zhang et al., 2019).

Results from the current study revealed the ornamental plants *P. oleracea*, *H. rosa-sinensis*, *L. camara*, *Mandevilla* spec., *G. linearis*, *Hemerocallis* spec., and *Agastache* spec. as TCSV reservoirs in southern Florida where the disease is most prevalent. Perennial ornamental crops can be natural reservoirs for plant viruses and help in virus circulation and transmission to other economically important crops (Mitrofanova et al., 2018). Ornamental flowering plants are mostly grown during late spring and summer, whereas most of the vegetable crops are grown in fall and spring in southern Florida. Various vegetable crops, ornamental nursery crops (both foliage and flowering plants), and fruits are grown side by side, as close as 9 m apart (Seal & RA Khan, unpubl). Thrips species with a polyphagous nature can migrate from the ornamentals to the vegetable plants. *Tomato chlorotic spot virus* detected in ornamental plants as found in this study revealed the fact that more alternative hosts of this virus may exist in the vicinity. In the future, other ornamental plants, weeds, and vegetable plants need to be examined for TCSV. Thrips abundance and seasonal cycles also need to be evaluated in those plants.

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AUTHOR CONTRIBUTIONS

Rafia Akhtar Khan: Conceptualization (supporting); data curation (lead); formal analysis (equal); investigation (equal); methodology (equal); project administration (supporting); resources (supporting); supervision (lead); validation (equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Dakshina R Seal:** Conceptualization (lead); data curation (equal); formal analysis (supporting); funding acquisition (lead); investigation (equal); methodology (lead); project administration (lead); resources (lead); software (supporting); supervision (equal); validation (lead); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Shouan Zhang:** Conceptualization (equal); data curation (supporting); formal analysis (supporting); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (equal); resources (lead); software (supporting); supervision (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Oscar Emanuel Liburd:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); funding acquisition (supporting); investigation (supporting); methodology (supporting); project administration (supporting); resources (supporting); software (supporting); supervision (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (supporting). **Rajagopalbabu Srinivasan:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); funding acquisition (supporting); investigation (supporting); methodology (supporting); project administration (supporting); resources (supporting); software (supporting); supervision (equal); validation (equal); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **James Colee:** Conceptualization (equal); data curation (equal); formal analysis (lead); investigation (supporting); methodology (equal); project administration (supporting); resources (supporting); software (supporting); supervision (supporting); validation (equal); visualization (supporting); writing – original draft (equal); writing – review and editing (equal).

DATA AVAILABILITY STATEMENT

Research data are not shared.

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SUPPORTING INFORMATION

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

Table S1 Profile of ornamental plants investigated in this study.

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