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REVIEW

Specificity of vectoring and non-vectoring flower thrips species to pathogen-induced plant volatiles

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Abstract

Insect-vectored plant pathogens are known to alter host-plant quality and associated cues, subsequently affecting the frequency of interactions with vectors and influencing pathogen transmission. It is unknown whether these changes deliver information highly specific to the vector and have evolved as a result of host manipulation or if they are more generalist indicator of plant status. In the current study, the responses of two thrips species, *Frankliniella occidentalis* Pergande, the vector of the tospovirus *Tomato spotted wilt virus* (TSWV) and a non-vectoring species, *F. tritici* Fitch, to pathogen-induced plant volatiles (PIPVs) in tomatoes were investigated. As the two species cohabit, and one is a vector of tospoviruses while the other is not, this system is perfectly suited to investigate the specificity of PIPVs to insect vectors. Both species were exposed to PIPVs of TSWV and the begomovirus *Tomato yellow leaf curl virus* (TYLCV) transmitted by the sweet potato whitefly, *Bemisia tabaci* Gennadius. *Frankliniella tritici* did not respond to PIPVs. *F. occidentalis* was attracted to both TSWV- and TYLCV-infected plants and showed no preference between plants infected by either virus. Volatiles from TSWV- and TYLCV-infected plants were collected and identified using GC–MS. Principal component analysis showed a clear differentiation between the volatiles of the uninfected and infected tomatoes. There was no differentiation between the volatile profiles of the two virus-infected tomatoes, suggesting that PIPVs may be a by-product of viral infection that elicit a generalist response in *F. occidentalis* and are likely not the result of host manipulation.

Keywords Plant–virus interactions · Pathogen-induced plant volatiles · Western flower thrips · Host manipulation

Key message

- The role of pathogen-induced plant volatiles (PIPVs) in vector attraction is controversial regarding if it is vector-specific manipulation or a by-product of infection.
- Western flower thrips (WFT) vectors *tomato spotted wilt virus* (TSWV), and Eastern flower thrips (EFT) does not.
- WFT was attracted to PIPVs from TSWV-infected plants, whereas EFT was not.
- WFT was attracted to PIPVs from plants infected with t*omato yellow leaf curl virus* (TYLCV), transmitted by whiteflies, and did not discriminate between TSWV and TYLCV volatiles.
- GC–MS analysis showed overlap of TSWV and TYLCV volatile profiles, indicating a lack of specificity of the signal mediated through PIPVs.

Introduction

Accumulating evidence provides support for the "Vector manipulation hypothesis," which proposes that pathogens are evolutionarily selected to induce changes in host and vector behaviors to enhance transmission (Ingwell et al. 2012; Carmo-Sousa et al. 2014). Following infection, pathogen-induced changes in the host plant may result in direct effects on the vector such as increased survivability, fecundity, dispersal, and altering feeding behaviors (Stafford et al. 2011; Shrestha et al. 2012; Martini et al. 2015) or indirect effects through host-mediated cues such as emitted volatiles, plant nutrients, and changes in plant morphology

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(Mauck et al. 2010, 2016; Mann et al. 2012; Mauck 2016; Eigenbrode et al. 2018). However, these effects vary and are inconsistent in their occurrence, and there remains a need for further information about these systems (Blanc and Michalakis 2016; Eigenbrode et al. 2018; Mauck 2016; Mauck et al. 2018; Mwando et al. 2018). Furthermore, it remains controversial if these indirect effects are genuine manipulation of the plant phenotype by the pathogen or a side effect of the infection (Blanc and Michalakis 2016; Mauck 2016; Mauck et al. 2018).

Viruses that share a particular transmission mechanism are likely to induce similar changes in host phenotype and vector behavior (Blanc and Michalakis 2016; Eigenbrode et al. 2018; Mauck 2016). For example, non-persistently transmitted viruses have less specific relationships with their vectors as many have multiple vectors (Carmo-Sousa et al. 2014), and prolonged feeding can reduce transmission efficiency (Carmo-Sousa et al. 2014; Mauck 2016; Mauck et al. 2010, 2016; Ng and Falk 2006). Mauck et al. (2010) concluded that plants infected with *Cucumber mosaic virus* were more attractive to the two aphid vectors, *Myzus persicae* and *Aphis gossypii,* due to changes in plant volatile blends, but the plants were poor hosts for the vectors, causing them to rapidly disperse after feeding to healthy plants, thus increasing virus transmission. Studies suggest that, for non-persistently transmitted viruses, vector behavior is influenced via indirect effects through the host plant (Carmo-Sousa et al. 2014; Mauck et al. 2010).

On the other hand, persistently transmitted viruses have highly specific relationships with their vectors and require longer acquisition time, and vectors of these viruses may exhibit behaviors of both direct and indirect effects including preference for infected plants over healthy plants associated with changes in plant volatiles, longer feeding times, and increased performance (Carmo-Sousa et al. 2014; Mauck et al. 2010). For example, Chen et al. (2017) demonstrated that *Tomato yellow leaf curl virus* (TYLCV) increased body size, longevity, and fecundity of its vector, the silverleaf whitefly, *Bemisia tabaci* Gennadius. In addition, several aphid species are vectors of persistently transmitted viruses that have been shown to increase vector growth, reproduction, and survival (Castle and Berger 1993; Jiménez-Martínez et al. 2004; Mauck et al. 2010).

There has been a recent focus toward understanding these complex interactions between plant pathogens and their hosts and vectors via host odor cues, or pathogen-induced plant volatiles (PIPVs), emitted by virus-infected plants on vector behavior. Infection with a pathogen can increase the overall amount of volatiles released by an infected plant or change the composition of volatiles released by up-regulating the release of specific compounds (Eigenbrode et al. 2018; Mann et al. 2012; Martini et al. 2014; Mauck et al. 2010, 2016, 2018). This change in volatile composition leads most of the time to a change in the host selection of the vector such as increasing attraction of an uninfected vector to an infected host. These types of interactions have been described for all types of pathogens including viruses, bacteria, fungi, and phytoplasma (Mann et al. 2012; Martini et al. 2017; Mauck et al. 2012; Mayer et al. 2008).

Information on these tritrophic interactions between the tospovirus *Tomato spotted wilt virus* (TSWV) and its flower thrips vector the western flower thrips (WFT), *Frankliniella occidentalis* Pergande, is limited (Maris et al. 2004; Tomitaka et al. 2015; Shalileh et al. 2016; Mwando et al. 2018). WFT and the eastern flower thrips (EFT), *Frankliniella tritici* Fitch, are two of the most abundant thrips species in the southeastern USA (Reitz et al. 2020). While both species are pestiferous and can cause damage of fruit and vegetable crops through feeding and oviposition, the WFT is most notable for the transmission of tospoviruses (Funderburk 2009; Mouden et al. 2017; Reitz et al. 2020). Although not a vector of tospoviruses, EFT often occurs concurrently with, and is more abundant than WFT in field settings and remains a concern for growers (Reitz et al. 2020; Wu et al. 2021).

Previous studies primarily investigated direct effects of TSWV infection on WFT behavior including changes in feeding, oviposition, longevity, and attraction (Abe et al. 2012; Maris et al. 2004; Ogada et al. 2013; Shalileh et al. 2016). Maris et al. (2004) reported that TSWV infection increases WFT oviposition and longevity and reduces larval development time. In addition, WFT adults exposed to TSWV as larvae preferentially fed on healthy, uninfected pepper leaf discs, and WFT adults not exposed to TSWV as larvae preferred infected pepper leaf discs (Ogada et al. 2013). In a study by Mwando et al. (2018), two vectors of *maize chlorotic mottle virus*, the maize thrips, *Frankliniella williamsi,* and onion thrips, *Thrips tabaci*, were more attracted to PIPVs from infected maize plants than healthy plants. Volatile analysis identified significant increases in (*E*)-4,8-dimethyl-1,3,7-nonatriene, methyl salicylate and (*E,E*)-4,8,12-trimethyltrideca-1,3,7,11-tetraene associated with the increase in attractiveness.

The current study aims to provide insight into how PIPVs of TSWV-infected tomatoes may affect the WFT vector and how specific these responses are when compared to those of the non-vector EFT. To further understand the specificity of these interactions, the responses of both species to tomato plants infected with a virus transmitted by whiteflies, TYLCV, were investigated. The volatile profiles of TSWV- and TYLCV-infected and healthy, uninfected tomatoes were compared by gas chromatography and mass spectrometry (GC–MS) to identify pathogen-induced changes in the volatile profiles that may elicit changes in thrips response.

Methods

Insect colonies

Thrips colonies were established with wild populations collected in Gadsden County and from the USDA-ARS in St. Lucie County, Florida. Adult thrips were reared in plastic containers (Rubbermaid, Atlanta, GA, USA) vented with thrips-proof mesh (BioQuip, Rancho Dominguez, CA, USA) and were provided with green beans for food and oviposition. Colonies were kept in an incubator at 25 °C, RH 60–70%, and 12L:12D photoperiod.

Plant inoculations

All tomato plants used in the described experiments were Florida-47 cultivar grown from untreated seed and planted in 10.2-cm nursery pots. After approximately one month, plants were mechanically inoculated with TSWV. Leaves from tomato plants in the field exhibiting symptoms of TSWV were collected and tested using ImmunoStrip® for tomato spotted wilt virus (Agdia, Elkhart, IN) to verify infection. The leaves were crushed in a chilled 5.2 mg/mL solution of sodium sulfite in distilled water to form a paste. The paste was applied to the top surface of three leaves of a healthy tomato using cheese cloth. Inoculated plants were kept in an incubator at 22 °C ± 2 °C and 12L:12D photoperiod. Plants that were visually symptomatic were tested for verification.

Tomatoes were inoculated with TYLCV by introducing 100 whiteflies collected from TYLCV-symptomatic tomatoes in the field onto healthy tomato plants. Whitefly adults and nymphs were mechanically removed from the infected tomatoes prior to use in experiments. Inoculated plants were kept in growth chambers. After an additional month past the initial date of inoculation, plants were tested for TYLCV by RT-PCR as described in Johnston and Martini (2020).

Thrips preference for virus-infected versus uninfected tomato

Differences in attraction between volatiles emitted by uninfected tomato and a TSWV- or TYLCV-infected tomato were evaluated in choice tests via Y-tube olfactometer assays. Choice tests were performed in the laboratory at 21 °C and 35% R.H. Volatile sources consisted of a single tomato plant infected with TSWV or TYLCV and uninfected tomato plants. Tomato plants were positioned within nylon oven bags (Reynolds Consumer Products, Louisville, KY, USA). One outlet of PTFE tubing connected the olfactometer to glass jars with distilled water. Charcoal-purified and humidified air were pushed at 0.2 L/min from a custom-made air delivery system (Sigma Scientific, Gainesville FL, USA) to another outlet connected to a single arm of the Y-tube glassware (10 cm × 9 cm arm length × 2 cm inner diameter). The Y-tube glassware was positioned vertically under a fluorescent light source mounted within a white fiberboard box for uniform light diffusion and the removal of any extraneous visual stimulus.

An individual adult female thrips was released at the base of the Y-tube. The thrips were given 15 min to exhibit a behavioral response. Three combinations for *F. occidentalis* were tested: (1) TSWV-infected versus uninfected tomatoes, (2) TYLCV-infected versus uninfected tomatoes, and (3) TSWV- versus TYLCV-infected tomatoes with 9, 8, and 6 trials of 20 thrips each, respectively. Two combinations were tested for *F. tritici*: (1) TSWV-infected versus uninfected tomatoes and (2) TYLCV-infected versus uninfected tomatoes with 8 and 4 trials of 20 thrips each, respectively. A trial consisted of measuring the preference of 20 thrips in succession. New tomato plants were used for each trial, and no thrips were used twice. The sides of the Y-tube were alternated after five thrips were tested to avoid directional bias. A positive response was recorded when an insect moved from the glass tube stem and up 5 cm into either arm of the Y-tube. If no choice was made after 15 min, the response was recorded as "no choice." Data from choice tests were analyzed using Chi-square tests from the pooled number of the different trials. Thrips that did not make a choice were excluded from the analyses.

Volatile collection and GC–MS analysis

A volatile collection system was used to identify the profile of uninfected, TSWV- and TYLCV-infected tomato plant volatile odors. The top half of the main stem was enclosed within an oven bag (40.6 cm × 44.4 cm) (Reynolds, Lake Forest, IL, USA) and tied at the top and bottom with zip ties. A volatile collection trap (7.5 cm long) with 30 mg of HayeSep Q adsorbent (Volatile Assay Systems, Rensselaer, NY, USA) was connected to the bottom of the bag with a PTFE fitting. Incoming air was purified via charcoal filter and pushed in at the top of the plant at a rate of 1.0 L/min. The volatiles were forced to the bottom of the bag by pulling air at 0.5 L/min through volatile collection traps with a controlled vacuum from the automated volatile collection system for 24-h collection period.

Collected volatile samples were extracted in vials with 150 µl of dichloromethane, and 1.0 µL of 1 µg/µL nonyl acetate as an internal standard (Sigma-Aldrich, St. Louis, MO, USA) was added to the samples. One microliter of each sample was injected into GC–MS (Thermo Scientific ISQ) using an autosampler. Helium was used for the carrier gas at a linear flow velocity of 2 mL/min. All samples

were analyzed on a TG-5MS column (5% Phenyl Methyl polysiloxane) (Thermo Fisher Scientific, Waltham MA) 30 min × 0.25 mm ID. The column oven temperature was maintained at 40 °C for 1 min and increased at a rate of 7 °C/min to a final temperature of 300 °C and maintained at 300 °C for 6 min. The injector temperature was set at 270 °C with the detector set at 200 °C. Compounds were tentatively identified by comparison of mass spectra with available mass spectra libraries. Identification of the compounds was confirmed by comparison with external standards, when available. Quantitation was assigned by comparing peak areas of known amounts of internal standard with the area under the peaks of compounds extracted from the treatments. Data were log-transformed, and ANOVA was used to determine significant differences in concentrations of individual compounds among treatments (PROC GLM, SAS 9.4, SAS Institute Inc., Cary. NC). Principal component analysis (PCA) was conducted on transformed data to identify key compounds of the three treatments according to their volatiles (JMP®, Version JMP Pro 16.1. SAS Institute Inc., Cary, NC).

Results

Thrips preference for virus-infected versus uninfected tomato

The non-vectoring species, *F. tritici*, showed no preference for either TSWV- or TYLCV-infected tomatoes over healthy, uninfected tomatoes ($\chi^2 = 4.0461$; $d.f. = 1$; $p = 0.2565$ and $\chi^2 = 10.4959$; $d.f. = 1$; $p = 0.1622$, respectively) (Fig. 1).

The vectoring species, *F. occidentalis,* was attracted to both TSWV- and TYLCV-infected tomatoes over uninfected tomatoes ($\chi^2 = 20.2092$; $d.f. = 1$; $p = 0.0096$ and $\chi^2 = 14.4327$; $d.f. = 1$; $p = 0.0439$, respectively) (Fig. 2). When given a

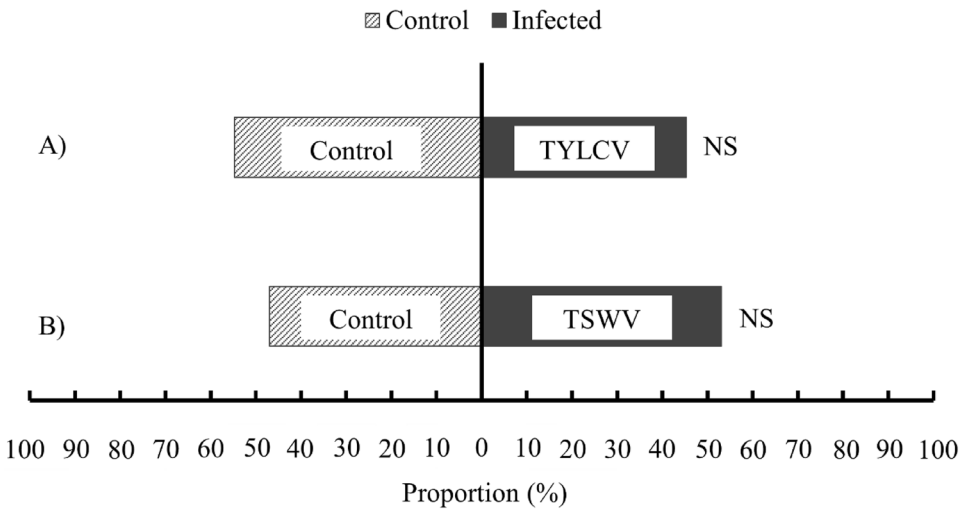

Fig. 1 Response of *Frankliniella tritici* to **A** *Tomato yellow leaf curl virus* (TYLCV)- and **B** *Tomato spotted wilt virus* (TSWV)-infected tomatoes versus healthy, uninfected tomatoes ($n = 137$ and 66, respectively). NS = non-significant

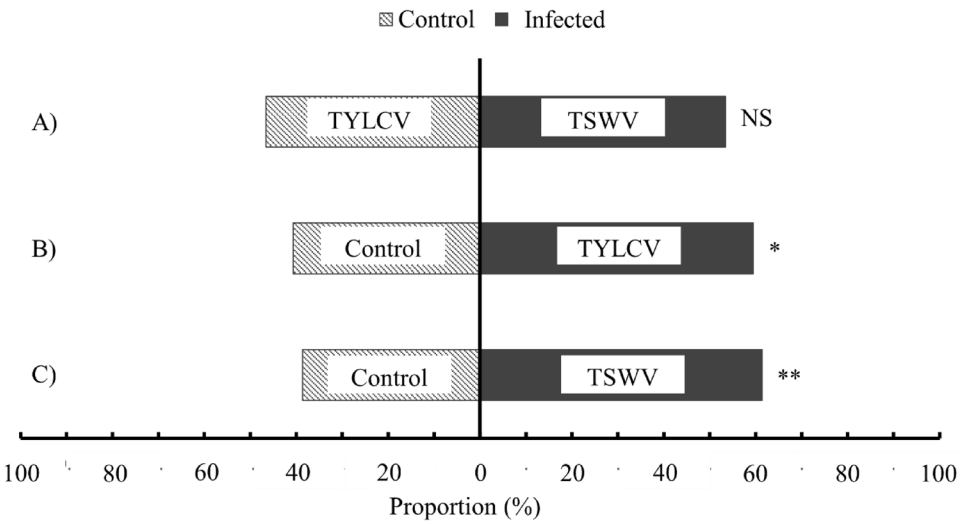

Fig. 2 Response of *Frankliniella occidentalis* to **A** *Tomato yellow leaf curl virus* (TYLCV)-infected versus *Tomato spotted wilt virus* (TSWV)-infected tomato, **B** *Tomato yellow leaf curl virus*-infected versus healthy, uninfected tomatoes, and **C** *Tomato spotted wilt virus*-infected versus healthy, uninfected tomatoes ($n = 118$, 155, and 142, respectively). NS = non-significant. * indicates p-value < 0.05 and ** indicates p-value < 0.01

choice between the tomato plants infected by either TYLCV or TSWV, *F. occidentalis* did not differentiate between the two, and there was no significant attraction to one or the other (and $\chi^2 = 1.6225$; $d.f. = 1$; $p = 0.8985$) (Fig. 2).

Volatile collection and GC–MS analysis

Chromatograms and spectrum profiles of each tentatively identified compounds are in the supplement materials. A total of 15 volatile compounds were tentatively identified and quantified in the three treatments of uninfected, TSWV-infected, and TYLCV-infected tomatoes, including 5 monoterpenes, 7 sesquiterpenes, 1 sesquiterpenoid oxide, 1 ester, and 1 phenol (Table 1). Methyl salicylate and α-copaene were released in higher concentrations in both TSWV- and TYLCV-infected tomatoes than in uninfected tomatoes ($F = 23.29$; $d.f. = 2,13$; $p = < 0.0001$ and $F = 230.45$; $d.f. = 2,13$; $p = < 0.0001$, respectively). The concentrations of γ-elemene and β-copaene were higher in TSWV-infected plants than in TYLCV-infected and uninfected plants ($F = 308.21$; $d.f. = 2,13$; $p = < 0.0001$ and $F = 8.03$; $d.f. = 2,13$; $p = 0.0054$, respectively). *Cis*-calamenene and butylated hydroxytoluene were significantly lower in TSWV-infected tomatoes than in TYLCV-infected and uninfected tomatoes ($F = 26.11$; $d.f = 2,13$; $p = < 0.0001$; $F = 4.81$; $d.f. = 2,13$; $p = 0.0273$, respectively). Caryophyllene oxide concentrations were higher in TYLCV-infected tomatoes than in TSWV-infected and uninfected ($F = 9.88$; $d.f = 2,13$; $p = 0.0025$) (Table 1).

The first and second principal components explained 37.0 and 21.8% of the variance, respectively. In the PCA score plot (Fig. 3A), the samples from TSWV- and TYLCV-infected plants were positively correlated to the first principal component. The distribution of samples from the uninfected tomatoes was negatively correlated to the second principal component. There was a separation ($\alpha < 0.05$) of the samples from the uninfected, control tomatoes and the samples from virus-infected tomatoes. There was, however, no separation of TSWV- and TYLCV-infected tomatoes. All samples were located within the 95% confidence interval.

The PCA loading plot (Fig. 3B) showed the volatiles corresponding to the groupings of samples in the score plot. Humulene, caryophyllene, δ-elemene, and β-copaene were the compounds with the largest absolute loadings for the first principal component. Components with the highest absolute loading values for the second principal component were α-pinene, 4-carene, m-cymene, and β-phellandrene. These loadings corresponded to TSWV- and TYLCV-infected samples in the score plot.

Table 1 Compounds detected in the volatile emissions in uninfected, *Tomato spotted wilt virus* (TSWV)-infected, and *Tomato yellow leaf curl virus* (TYLCV)-infected tomatoes

Retention time	Compound	Retention index	Ratio			*F*-value	*P*-value
			Uninfected	TSWV-infected	TYLCV-infected		
8.735	α-pinene*	942	0.23	0.33	0.19	0.15	0.8607
9.888	3,7,7-trimethyl-1,3,5-cycloheptatriene	982	1.58	1.69	1.83	0.04	0.9656
10.86	(+)-4-carene	1016	5.10	7.41	7.35	0.11	0.9002
10.959	α-terpinene	1019	1.29	2.76	1.37	1.31	0.3027
11.935	β-phellandrene	1052	15.67	19.89	18.71	0.10	0.9066
16.911	Methyl salicylate*	1224	0a	0.09b	0.75b	23.29	< 0.0001
21.176	δ-elemene	1382	0.60	2.13	1.12	0.83	0.4560
22.288	α-copaene*	1426	0a	0.12b	0.08b	230.45	< 0.0001
23.543	Caryophyllene*	1479	1.19	4.46	3.65	1.14	0.3491
23.781	γ-elemene	1488	0a	0.11b	0a	308.21	< 0.0001
24.346	Humulene	1492	0.33	1.25	0.95	1.31	0.3022
23.864	β-copaene	1515	0a	0.14b	0a	8.03	0.0054
24.458	Butylated hydroxytoluene	1521	0.16a	0.02b	0.15a	4.81	0.0273
24.697	*Cis*-calamenene	1534	0.06a	0b	0.11a	26.11	< 0.0001
25.836	Caryophyllene oxide	1596	0a	0.07a	0.12b	9.88	0.0025

Internal standard (IS) was calculated based on nonyl acetate (RT = 19.36) injected under the same conditions as samples. Ratio is the average ratio between the peak compound and the IS. Within each row, different letters indicate significant differences among treatments

*indicates compounds that were verified with external standards

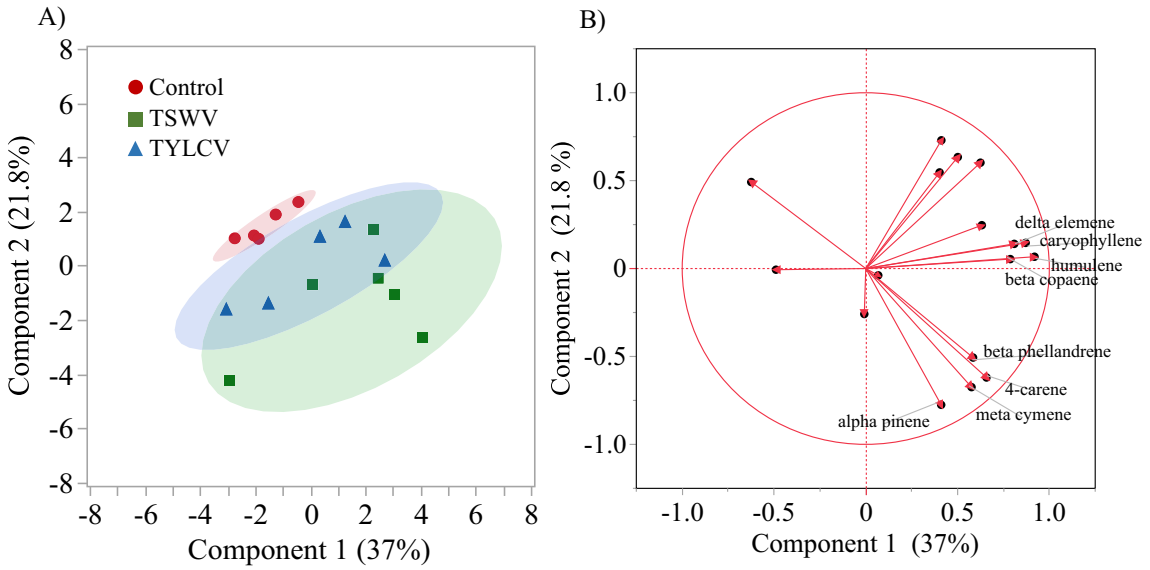

Fig. 3 Principal component analysis (PCA) showing main differences in volatiles of the *Tomato spotted wilt virus* (TSWV)-infected, *Tomato yellow leaf curl virus* (TYLCV)-infected, and uninfected tomatoes. **A** PCA score plot of all samples depicting separation *of Tomato spotted wilt virus* (green), *Tomato yellow leaf curl virus* (blue), and uninfected (red) tomato volatiles within 95% confidence ellipses. **B** Loading plot of variables associated with tomato volatiles

Discussion

Previous research has shown that pathogen infection can alter host-plant phenotype and, in turn, potentially influence vector behavior to maintain or enhance transmission. TSWV is a persistently transmitted virus that is only acquired by thrips during the larval stage (Maris et al. 2004; Mauck et al. 2012). Therefore, preference of WFT females and increased oviposition as well as decreased larval development time on TSWV-infected plants would likely increase the probability of pathogen acquisition and transmission (Maris et al. 2004; Mauck et al. 2012; Shalileh et al. 2016). The current study demonstrated that the TSWV-vector *F. occidentalis* was more attracted to virus-infected tomatoes than uninfected tomatoes. The non-vectoring species, *F. tritici*; however, showed no preference between uninfected and infected tomatoes, indicating that the attraction to PIPVs is a vector-specific response.

While this change in behavior observed only in the virus-vectoring thrips species may indicate genuine host-plant manipulation of the vector by PIPVs, it can be argued that this attraction should be specific to the pathogen-transmitted (Blanc and Michalakis 2016; Mauck et al. 2010, 2018; Mwando et al. 2018). However, the results of this study demonstrate a lack of specificity in WFT response to TSWV and TYLCV PIPVs infection. Indeed, WFT also showed a preference for TYLCV-infected plants, a virus it does not transmit, over uninfected tomatoes. In addition, when given a choice between plants infected with TSWV and TYLCV, WFT did not discriminate between the PIPVs from the two viruses. Both TSWV and TYLCV are persistently transmitted viruses and have been shown to elicit changes in behavior in their vectors (thrips and whiteflies, respectively) including increased attraction and probing on infected plants (Maris et al. 2004; Fang et al. 2013; Shalileh et al. 2016).

Analysis of volatile profiles of TSWV- and TYLCV-infected tomatoes using GC–MS provides some key insights into specific emitted compounds that elicit an increased attractiveness of WFT to virus-infected tomatoes. Insights into the specificity of the vector–plant–pathogen relationship were further elucidated as PCA results showed a clear separation between the volatile profiles of the uninfected plants and the virus-infected plants, but there was no separation between the volatile profiles of the two viruses. Humulene, caryophyllene, δ-elemene, and β-copaene, α-pinene, 4-carene, m-cymene, and β-phellandrene were the compounds identified as having the largest influence on the principal components, and thus, changes in these compounds can be viewed as the main variables in the volatile profiles of virus-infected tomatoes. Several of the identified peaks such as α-pinene, α-copaene, γ-elemene and β-copaene, cymene, (+)-4-carene, caryophyllene, and γ-terpinene are terpenoids produced by tomato plants (Chen et al. 2017; Nishida et al. 2000; Picard et al. 2012; Ren 2020a). In addition, methyl salicylate is an ester produced by many plants in response to biotic stress. Methyl salicylate was absent in uninfected plants and was detected in higher amounts in both TSWV- and TYLCV-infected plants. Methyl salicylate, α-pinene, caryophyllene, and caryophyllene oxide are known repellents of WFT (Kirk et al. 2021).

Pathogen infection causes various physiological and biochemical responses in the host plant to adapt to or resist disease, and these responses are predominantly regulated by the phytohormone, salicylic acid (SA) (Abe et al. 2012; Nachappa et al. 2013, 2020; Wu et al. 2019). In response to insect herbivory, plants activate defense pathways that are regulated by the phytohormone, jasmonic acid (JA), a signaling molecule for the production of several metabolites contributing to herbivore resistance (Abe et al. 2012; Nachappa et al. 2013, 2020; Wu et al. 2019). A negative relationship, known as antagonistic crosstalk, between these two pathways has been reported for several plant-pathogen systems, and herbivores are known to take advantage of this interaction to avoid effective JA-related plant defenses (Abe et al. 2012; Nachappa et al. 2020). Infection with TSWV and/or TYLCV up-regulates SA-related gene expression, which, in turn, suppresses JA-regulated gene expression induced by herbivory (Abe et al. 2012; Nachappa et al. 2013, 2020; Shi et al. 2016; Wu et al. 2019). Furthermore, both TSWV and TYLCV infection results in inhibition of the JA pathway and, subsequently, terpene-mediated defense responses against their respective vectors by directly interacting with MYCs, key regulators of the JA signaling pathway (Li et al. 2014; Wu et al. 2019). WFT can detect not only specific compounds but can also discriminate changes in blends or ratios of volatiles in host plants, such as those that would occur from the above interactions, which could explain the increase in attractiveness to infected plants (Mwando et al. 2018).

WFT were more attracted to yellow flower shapes in combination with volatiles from flowering *Medicago sativa* L. than to volatiles alone but not compared to visual cues alone (Ren et al. 2020a, b). However, the presence of olfactory cues resulted in higher residence times by WFT than did the absence of olfactory cues (Ren et al. 2020a, 2020b). WFT also have been shown to be more attracted to plants infected with a non-transmissible strain of TSWV over wild-type TSWV (Tomitaka et al. 2015). These previous results combined with the findings from the current study indicate that, although PIPVs may play a role in vector-specific attraction, direct effects of pathogen infection such as changes in visual cues or nutritional imbalances may dominate selection behavior of WFT (Ren et al. 2020a, b; Ren et al. 2020a, b; Tomitaka et al. 2015).

Multi-trophic interactions between plant viruses, hosts, and insect vectors are complex. Our current findings established that, in the case of TSWV plant host and vector interactions, PIPVs may be a by-product of pathogen infection rather than evidence of host-plant manipulation of the vector. Infection with TSWV induces changes in volatile profiles of tomato plants that are attractive to the vector WFT but not to the non-vector EFT. The response of WFT to a non-thrips transmitted virus, however, was comparable to its response to TSWV, and the main volatile compounds mediating the interactions were found to be indiscernible for the two viruses. Examining the effects of individual volatile components and specific blends and ratios of compounds on not only WFT but also other vectoring thrips species behavior is an important focus for future research. The insights from these studies will provide further clarity on the TSWV–host–vector interactions and improve integrated pest management strategies for flower thrips.

Author contributions

All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by IS and XM. The first draft of the manuscript was written by IS, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval This article does not contain any studies with human participants and/or animals other than insects performed by any of the authors.

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