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Research Article

Impact of Watermelon bud necrosis virus (WBNV) infected plants on the volatile emission pattern in cowpea plants

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Abstract
Pathogens, including tospoviruses, are known to manipulate the behaviour of vectors after virus acquisition by plants to enhance virus transmission. Furthermore, as recently proven in the maize chlorotic mottle virus pathosystem, the vector's choice for virus-infected plants can change to a preference for noninfected plants after virus uptake by the vector. A similar trend was observed in the cowpea - Watermelon Bud Necrosis Virus (WBNV) - *Thrips palmi* (Karny) pathosystem. Similarly, in the no-choice bioassay, viruliferous *T.palmi* (carrying WBNV) settled preferentially more on healthy cowpea plants (56%) compared to virus-infected plants (47.3%), whereas non-viruliferous *T.palmi* settled preferentially more on WBNV infected (58.67%) cowpea plants compared to healthy plants (44%). The changes in preference of thrips towards host plants before and after virus acquisition may be due to the change of volatile cues. This study looked at the headspace volatile composition of healthy and WBNV-infected cowpea plants that attract thrips. Furthermore, the volatile analysis revealed that 1, 2-Propanediamine (0.62%) and Tuaminoheptane (0.55%) from healthy cowpea plants, as well as Tetradecane (0.35%) from WBNV-infected cowpea plants, both have a higher area percent than other volatiles. The amine (53%) and hydrocarbon (69%) groups of volatile organic compounds make up the majority of host volatiles found in healthy and virus-infected plants. The increased contact rates of viruliferous and non-viruliferous *T.palmi* towards healthy and WBNV-infected host plants could enhance virus transmission if thrips feed on them and acquire the pathogen prior to dispersal and the recorded host volatiles might be useful in vector management in future.

Keywords: Thrips, Tritrophic interactions, WBNV, VOCs, Virus, Vector and Volatiles

INTRODUCTION

Cowpea (*Vigna unguiculata* (L); Family: Fabaceae), also known as black eye pea, is an annual herbaceous grain legume originating and domesticated in Southern Africa. It is an economically important food legume constituting a valuable source of protein in millions of people's diets. Root nodules of cowpea plants can fix atmospheric nitrogen and make it available to plants and are widely used for intercropping. Whole plants after harvest are used as cattle feed (Ehlers and hall, 1997; Timko and Singh, 2008). *Thrips palmi* Karny (Thripidae; Thysanoptera) was originally discovered on tobacco plants in Sumatra in 1925 and has since spread as an invasive pest to all tropical countries (Karny, 1925). It is a polyphagous pest that mostly infests plant groups such as Solanaceae, Cucurbitaceae, and Leguminosae in tropical countries. (Nakahara *et al*., 1984; Canon *et al*., 2007). It attacks agricultural and horticultural crops directly as well as indirectly. When

plants become infected with a virus, they emit Volatile Organic Compounds that attract the vectors and enable the virus to propagate effectively. The predilection of thrips for virus-infected plants is due to the release of volatiles by virus-infected plants after vector acquisition, which affects their behaviour and allows the virus to spread further.

Watermelon bud necrosis virus (WBNV) belongs to the genus Orthotospovirus, family Tospoviridae and order Bunyavirales. WBNV is an emerging and serious disease affecting watermelon and other cucurbitaceous crops in India (Mandal *et al.*, 2003; Jain *et al.*, 2007; Holkar *et al.*, 2019). *T. palmi* transmits the tospovirus WBNV in a persistent and propagative manner (Ghosh *et al.*, 2019). It was first reported in watermelon in Karnataka by Krishnareddy and Singh (1993) and later reported in all parts of India (Jain *et al.*, 2007; Kumar *et al.*, 2010; Rajasekharam, 2010; Priyanka *et al.*, 2019). The survival and multiplication of thrips increase with changes in weather conditions such as temperature, rainfall, and relative humidity (Aishwarya *et al.*, 2019; Holkar *et al.*, 2019). WBNV affected plants show leaf mottling, yellowing with necrotic spots on leaves, leaf crinkling, necrosis on veins, dieback of buds, shortened internodes, stunted growth, stem splitting, necrosis on tendrils, unopened flower buds and under severe conditions, necrotic spots on fruits and malformations (Kumar *et al.*, 2010; Rebijith *et al.*, 2014). This orthotospovirus was successfully transmitted by the vector *T. palmi* (Rajasekharam, 2010; Whitfield *et al.*, 2015). Mechanical transmission of the virus and not by seeds (Reddy *et al.*, 1983). The present study investigated the volatile emission patterns of healthy and WBNV infected cowpea plants to determine what factors might attract viruliferous thrips to healthy plants and nonviruliferous thrips to WBNV-infected plants.

MATERIALS AND METHODS

Emigration bioassay for preference studies of *T. palmi*

Nonviruliferous thrips colony- collection and maintenance

A healthy adult *T. palmi* population maintained under controlled conditions in alternate host (Bhatti, 1980) cow pea (*Vigna ungiculata* L.) (cv. CO-5) seedlings. Four to five seedlings were grown in 4-inch pots containing a 1:2:1 pot mixture of sand, compost, and loamy soil and kept in a plant development chamber (Percival Inc., USA) at 250°C, 80% relative humidity, and a 12:12 h L:D photoperiod. Adult thrips were collected from cowpea and watermelon plants from the field by tapping the terminal bud and flowers on a black background sheet and sucked by the aspirator. First, these adults were released inside the insect-proof bug dorm (Megaview, Taiwan) cages kept in a glasshouse using a 50 ml aspirator tube. Then, adults from greenhouse populations were transferred inside the insect-proof bug dorm kept inside the plant growth chamber.

Viruliferous thrips colony- collection and maintenance

To obtain viruliferous thrips, adult thrips collected from healthy colonies werereared inside the cowpea seedlings that were mechanically inoculated with WBNV. Older plants were periodically removed with newer mechanically inoculated WBNV plants at weekly intervals. Viruliferous thrips colonies were maintained inside the insect-proof bug dorm placed in plant growth chamber (Percival Inc., USA) at 250C with 80% RH and a 12:12 h L:D photoperiod. The purity of the viruliferous colony was monitored by RNA isolation for the presence or absence of WBNV in adult thrips samples from the plant growth chamber.

No choice test for settling preference of *T. palmi*

Viruliferous and non-viruliferous *T.palmi* were used in preference studies that permitted contact and volatile cues to be combined with recorded thrips emigration rates. T. palmi viruliferous (raised on virus-infected plants) and nonviruliferous (raised on virus-free plants) settling preferences were studied in connection to WBNV. Healthy insects were collected from pure mother culture and virus infected insects were collected from cowpea plants maintained in screen house by proper inoculation with virus. To begin the experiment, test insects were starved for 1 hour before bioassay, and 10 adults were introduced on cowpea leaf disc placed adaxial side upwards in a plastic petridish with the moistened filter paper (Whatman No. 46) (35 mm diameter x 3.5 cm ht) lined with plaster of paris and activated charcoal at 9:1 ratio. For ventilation, the covering lid was removed and fixed with nylon mesh (diameter, 34 mm; mesh size, 63 µm). Then the arena was covered with a lid, sealed with parafilm and kept inside the environmental plant growth chamber (Percival, USA) (25ºC temperature, a photoperiod of 12 L:12 D and 80% RH). Each treatment was replicated 15 times. At 1, 2, 3, 6, 20, and 24 hours after release, the number of adults settling on infected and noninfected leaves was measured.

Plants to evaluate for volatile collection

Healthy cowpea plants

Cowpea seedlings were grown in insect-proof bugdorm -enclosed tiny pots with a 1:2:1 mixture of sand, compost, and loamy soil in a growth chamber at 25 ± 1^0C. Two-week-old robust cowpea plants were chosen for volatile collection.

WBNV infected cowpea plants

Symptoms of WBNV virus-infected watermelon including stunted growth, chlorosis, bud necrosis, stem pitting, stem necrosis, leaf mottling, bronzing, and leaf drying (Holkar *et al*., 2019; Rajabaskar *et al*., 2019; Arunkumar *et al*., 2020) were transmitted by *T.palmi*, which was collected from the field and employed as a source of virus inoculum. After collecting the samples in resealable plastic bags, mechanical inoculation was performed for virus maintenance in two-leaf stage healthy cowpea plants. One gram of WBNV-infected leaf sample was macerated in 0.1 M phosphate buffer set to pH 7 under refrigeration. Buffer was made by mixing 6.15 ml and 3.85 ml of KH_2PO4 and K_2HPO4 to make up to 100 ml. Then, 0.01 M 2-mercaptoethanol and 0.3 g sodium sulphate (Na_2SO4) were added. Mechanical inoculation was performed by swabbing the virus inoculum on two leaf stage cowpea plants early in the morning or late in the evening. Prior to swabbing the inoculum to the leaves, a small amount of abrasives, specifically 1% celite 545 and Carborundum 320 grit, were utilised to injure the leaves (Fisher Scientific, USA). After swabbing the inoculum to the leaves, wash the leaves with distilled water for 2-3 minutes. Swabbing was done with care to prevent damaging the leaves, and the inoculated plants were then housed within an insect-proof bugdorm with a label to provide the best conditions for virus establishment. Plants will show symptoms of virus infection 7-10 days following inoculation. Plants that had been injected with the virus for two weeks were chosen for volatile collection.

VOC analysis and quantification

For the extraction of VOCs, HPLC grade dichloromethane was utilised. The volatile collecting chamber was cleaned with dichloromethane (DCM) before collection. To prevent volatiles from exiting the soil, the plant pot was covered with an aluminum foil sheet. The covered cowpea plant was then placed within the volatile collection chamber, which was connected to a push and pull motor via tubes on both sides of the chamber and a light source at the top. At a flow rate of 300 cm^3 per minute, 300 cm^3 of compressed air filtered with activated carbon was delivered to the chamber through the inert tube during volatile collection. Air was confined inside the Porapak Q sorbent tube connected to the chamber outlet. The trapped air was then eluted from porapak with 500 l of HPLC grade DCM. For volatile profile analysis, eluted samples were analysed using GCMS equipment. Gas chromatography-mass spectrometry (Agilent Technologies- 7890B GC interfaced with Agilent 5977B mass selective detector) was utilised for injection of the sample using autosampler and detection of VOCs. An autosampler was used to inject approximately 500 µl of eluent (plant volatile extracts) into the GC intake port. A 30 m long DB-5MS fused silica capillary with a 0.25 mm internal diameter served as the GC column. Helium (99.999 per cent purity) was employed as the carrier gas, with a 1 ml/min flow rate and a column head pressure of 12.445 psi. At a volume of 500 µl, the sample was injected at 2500°C with a split mode of 5:1 at a temperature of 2800°C transfer line, 230°C ion source, and 1500°C quadrapole. Each sample took a total of 42 minutes to run. The oven temperature was set to 60°C for 2 minutes, increased to 230°C at 5°C/min for 5 minutes, and then to 280°C at 20°C/min for 21 minutes. Peaks of plant extract ingredients were detected by comparing retention data to spectrum matches in the NIST mass spectra library database and published Kovats indices.

Data analysis

The data collected under the lab experiments recorded for preference studies under changes in the infected and noninfected plants were analysed with student's t test by using SPSS Statistics ver.17.0. The peak area of each replication was proportional to the total peak area of each component when analysing the volatiles. R software version 3.6.1 was used to perform principal component analysis (PCA) and heatmap analysis for VOCs. Score plots were used to show the results, which were then compared.

RESULTS AND DISCUSSION

No choice test for settling preference of *T. palmi*:

Preference of nonvirulifeous *T. palmi* to infected and healthy cowpea plants

The percent preference of nonviruliferous *T. palmi* for WBNV infected and healthy cowpea plants is given in Fig. 1. The results stated that the percent settling of nonviruliferous thrips was 58.67% on infected and 44% on healthy plants at 6-hour after release. The mean settling percent of nonviruliferous thrips on infected leaf discs was 58.66% at 6-hour and 48% at 24-hour intervals respectively. The preference was significant at 1 hr ($t = 4.75$, $df = 14$, $P=0.001$), 2 hr ($t = 4.17$, $df = 14$, $P=0.001$), 3 hr ($t = 2.73$, $df = 14$, $P=0.01$), 6 hr ($t = 3.77$, $df = 14$, $P=0.006$), 20 hr ($t = 7.43$, $df = 14$, $P=0.000$) and 24 hr ($t = 6.12$, $df = 28$, $P=0.0002$) after the release of nonviruliferous thrips on infected and healthy leaves.

There was an interaction effect due to the infection status of the leaves (healthy and infected) on the vector thrips (Table 1). The interaction between duration and thrips was statistically significant, but the duration of release was on par with the infection status of the leaves and no significant difference was found.

Table 1. Interaction of nonviruliferous *T. palmi* with infected and healthy cowpea

Factors	SEm	SEd	CD	Significance
Time (hr)	1.64	2.31	4.57	**
Infection (%)	0.94	1.34	2.64	**
Interaction	2.31	3.27	6.46	**
				NS

Table 2. Interaction of viruliferous *T. palmi* with infected and healthy cowpea

Factors	SEm	SEd	CD	Significance
Time (hr)	1.44	2.04	4.02	**
Infection (%)	0.83	1.18	2.32	**
Interaction	2.04	2.88	5.69	**
				NS

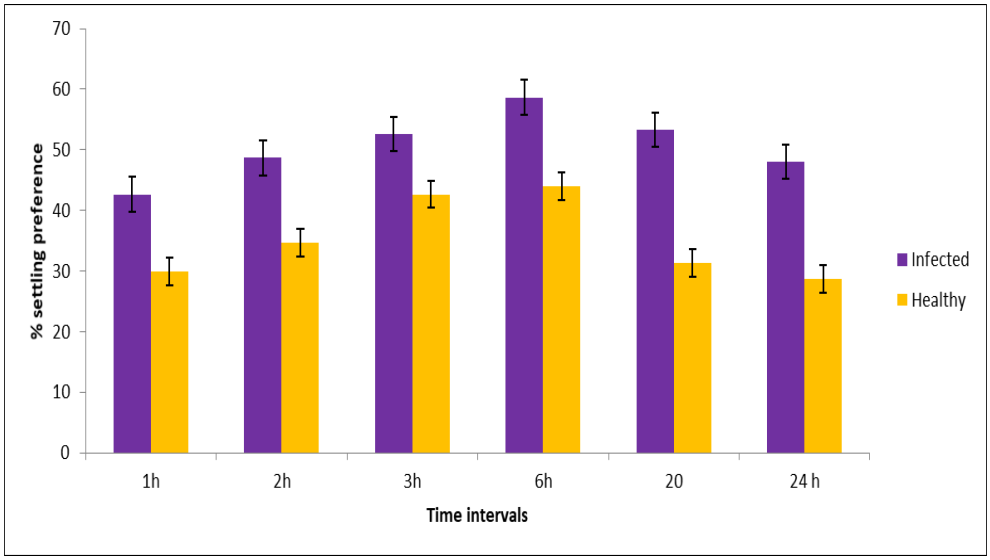

Fig. 1. *Preference of nonviruliferous T. palmi to infected and healthy cowpea hosts*

Preference of viruliferous *T. palmi* to infected and healthy cowpea plants

The preference of viruliferous *T. palmi* for healthy and infected cowpea plants were listed in Fig. 2. The results indicated that the settling percent of viruliferous thrips was 47.3% on infected leaves and 56% on healthy leaves at 6 hr after release. At 3 hr (t = 2.08, df = 14, P=0.05), 6 hr (t = 3.38, df = 14, P=0.04) and 20 hr (t = 2.32, df = 14, P=0.03). There was a significant difference in the settling percent of the thrips in between healthy and infected leaves. There was an interaction effect due to the infection status of the leaves (healthy and infected) on the vector thrips (Table 2). The interaction between duration and thrips was statistically significant, but the duration of release was on par with the infection status of the leaves and no significant difference was found.

The results showed that healthy (nonviruliferous) thrips preference was greater on WBNV infected hosts and reversed after virus acquisition, whereas the viruliferous thrips preferred healthy hosts. These findings are in line with earlier works on different pathosystems viz., aphids and luteoviruses (Eigenbrode *et al*., 2002; Jimenez-Martinez *et al*., 2004; Moritz *et al*., 2004; Werner *et al*., 2009; Rajabaskar *et al*., 2013a; 2013b; 2013c; Rajabaskar *et al*., 2014; Eigenbrode *et al*., 2018), thrips-tospoviruses (Maris *et al*., 2004; Stafford *et al*., 2011; Shrestha *et al*., 2012; Ogada and Poehling, 2015; Shalileh *et al*., 2016; Daimei *et al*., 2017), whiteflies and begomoviruses (Moreno-Delafuente *et al*., 2013; Fereres, 2016; Ranjithkumar *et al*., 2019) where they reported that viruses influenced feeding preferences after manipulating the host physiology and behaviour might be reversed after acquiring the virus from host plants by vector manipulation. This phenomenon helps the virus spread further in addition to supporting vector fitness for effective survival (Eigenbrode *et al*., 2018; Mauck *et al*., 2019).

Table 3. Headspace VOCs trapped from healthy and WBNV-infected cowpea plants

Healthy cowpea plants				WBNV infected cowpea plants			
Retention Time (min)	**Area%**	**Name of the compound**	**Group/ class**	**Retention Time (min)**	**Area%**	**Name of the compound**	**Group/ class**
4.3162	0.1174	2-Pentanamine	Amine	5.6769	0.0567	1-Pentanol	Alcohol
5.7346	0.1713	2-Octanamine		6.7808	0.2187	2-Ethyl-1-dodecanol	
6.5463	0.6209	1,2-Propanediamine		6.8588	0.0767	1-Hexanol	
6.7532	0.2966	1-Octanamine, N-methyl-		10.1977	0.0757	2-Coumaranone	Ketone
8.5171	0.0184	Octodrine		6.2131	0.0813	Dodecane	Hydrocarbon
29.6209	0.0048	Pterin-6-carboxylic acid	Acids	6.735	0.0585	Undecane	
5.8149	0.2792	Acetic acid		9.3184	0.1764	Octadecane	
4.6254	0.06	Cyclobutanol	Alcohol	9.5725	0.1075	Hexadecane	
29.3614	0.0342	Propanamide	Amide	10.9012	0.3599	Tetradecane	
8.0704	0.062	Acetaldehyde	Alde-hyde	14.6293	0.1521	Tetracosane	
10.1458	0.0992	2-Aminononadecane	Alkane	16.8705	0.0896	Eicosane	
5.5137	0.5571	Tuaminoheptane	Hydro-carbon	8.621	0.0347	4H-1,3-Benzodioxin	Phenyl pyrazole

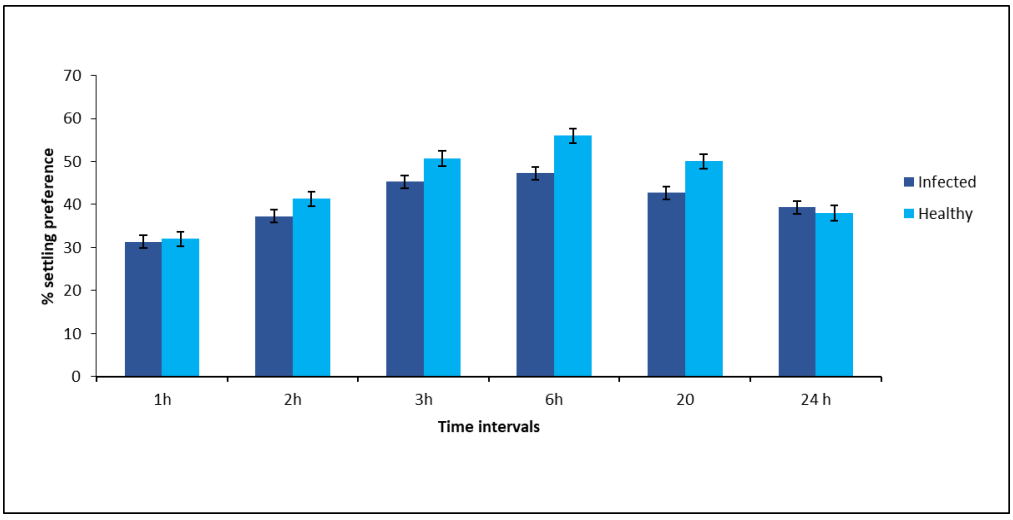

Fig. 2. *Preference of viruliferous T. palmi to infected and healthy cowpea hosts*

Identification of headspace volatiles emitted by healthy and WBNV-infected cowpea plants

The variations in volatile emissions in healthy and WBNV-infected cowpea plants were investigated. From both healthy and WBNV-infected cowpea plants, a total of nine groups/classes of volatile chemical compounds (amine, acids, alcohol, amide, aldehyde, alkane, hydrocarbon, ketone, phenyl pyrazole) were identified. (Table 3). The Amine group of compounds recorded the highest proportion (area wise) among healthy cowpea plants, whereas, the hydrocarbon group of compounds recorded the highest proportion (area wise) among WBNV infected cowpea plants. In the case of healthy cowpea plants, the VOCs identified were 2-pentanamine (0.11%), 2-octanamine (0.17%), 1,2-propanediamine (0.62%), 1-octanamine, N-methyl- (0.29%), octodrine (0.01%), pterin-6-carboxylic acid (0.0048%), acetic acid (0.27%), cyclobutanol (0.06%), propanamide (0.03%), acetaldehyde (0.06%), 2-aminononadecane (0.09%), tuaminoheptane (0.55%). Similarly, WBNV-induced VOCs emitted from cowpea plants were 1-pentanol (0.05%), 2-ethyl-1-dodecanol (0.21%), 1-hexanol (0.07%), 2-coumaranone (0.07%), dodecane (0.08%), undecane (0.05%), octadecane

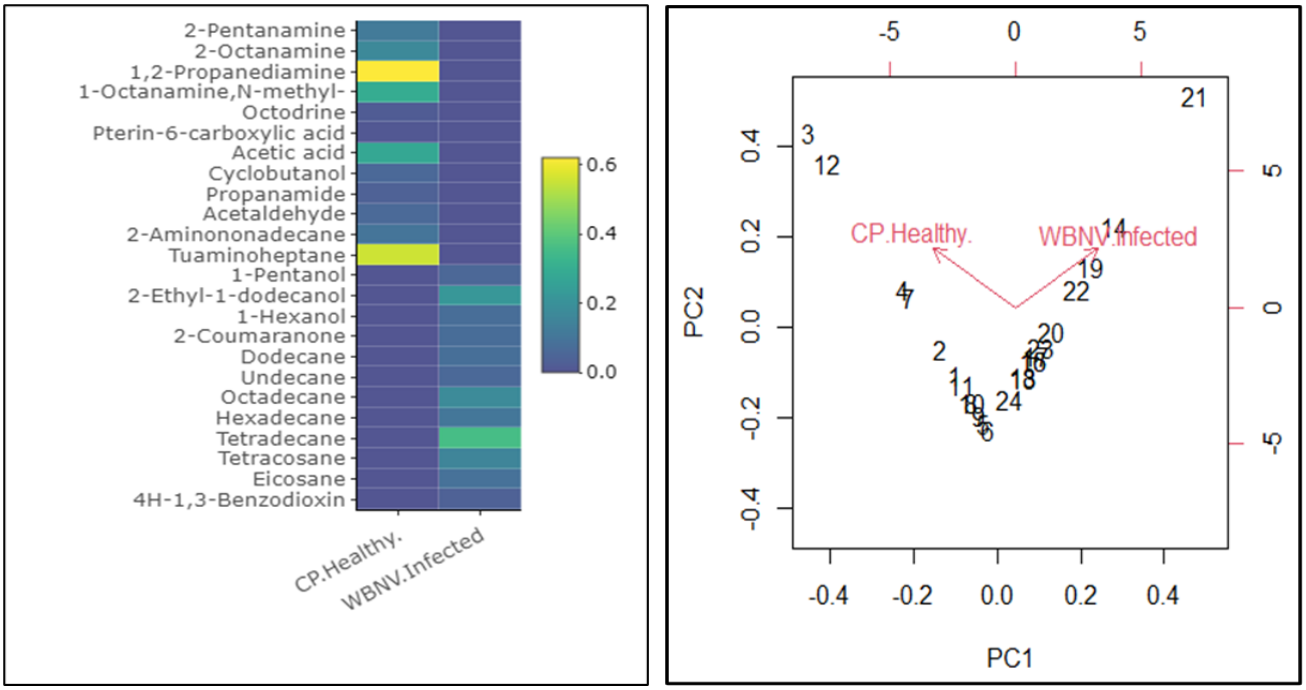

Fig. 3. *VOCs emitted from healthy and WBNV infected cowpea plants a. Heatmap and b. Principal component analysis 1. 2-Pentanamine, 2. 2-Octanamine, 3. 1,2-Propanediamine, 4. 1-Octanamine, N-methyl- 5.Octodrine, 6. Pterin-6-carboxylic acid, 7. Acetic acid, 8. Cyclobutanol 9. Propanamide, 10. Acetaldehyde, 11. 2-Amininononadecane, 12. Tuaminoheptane, 13. 1-Pentanol, 14.2-Ethyl-1-dodecanol, 15. 1-Hexanol, 16. 2-Coumaranone, 17. Dodecane, 18. Undecane, 19. Octadecane,20. Hexadecane, 21. Tetradecane, 22. Tetracosane, 23. Eicosane, 24. 4H-1,3-Benzodioxin*

(0.17%), hexadecane (0.10%), tetradecane (0.35%), tetracosane (0.15%), eicosane (0.08%), 4H-1,3-benzodioxin (0.03%).

According to headspace analysis of VOCs, the emission of VOCs differed between WBNV-infected and healthy cowpea plants. This could be due to the plant's altered physiology following virus infection, and VOC signals would aid the herbivore's host selection process. These volatiles have a very specific role that varies depending on the plant's age, phenotype, and genotype (Eigenbrode *et al.*, 2002; Dudareva and Pichersky, 2008). The amount and content of VOCs produced varied according to infection state and disease development. VOCs released by virus-infected plants differ from those emitted by healthy plants and are important mediators of insect vector attraction and decision-making when choosing a host plant (Eigenbrode *et al.*, 2002; Rajabaskar *et al.*, 2013). This was justified by the present findings of the preference of viruliferous *T. palmi* towards healthy and nonviruliferous *T. palmi* towards virus-infected cowpea plants. VOCs may influence vector preference, and higher levels of volatiles generated by diseased plants were found to be more effective than specific metabolites in attracting vectors (Eigenbrode *et al.*, 2002).

Kumar *et al*. (2017) conducted experiments on host volatiles of Brassica plants and concluded that heptadecane, dodecane, octadecane, tridecane compounds were released as host volatiles of hydrocarbon group of compounds. The present study also shows the same group of compounds from healthy cowpea plants that shows strong induction of host volatiles. Rice volatile compounds released due to BPH feeding, 4H-1,3-benzodioxin were reported in our present study from VOCs of WBNV infected cowpea plants. The VOCs emitted from host plants as a result of sucking pest infestations (mites, bugs, aphids, whiteflies) result in an analysis of wide range of compounds like eicosane, tetracosane, pentacosane, dodecane, pentadecane, nonaic acid, nonanal, octacosanal (Kumar *et al.*, 2017).

Heatmap analysis

The Volatile profiles of healthy and WBNV infected cowpea plants were compared by heatmap analysis (Fig. 3a). The results of heatmap analysis are represented in different colours (dark to light colour) according to area percent. Heatmap analysis of the area percent of healthy and WBNV infected cowpea plants shows that compounds 1,2-propanediamine and tuaminoheptane (yellow color) were recorded at higher levels in healthy cowpea plants. Tetradecane (light green color) was recorded to be higher in WBNV infected cowpea plants.

Principal component analysis

The volatile profiles of healthy and WBNV-infected cowpea plants were analysed by PCA (Fig. 3b). PCA of the area percent of 24 compounds shows a strong induction of 1,2-propanediamine and tuaminoheptane with the compound number (3 and 12) from healthy

cowpea plants. Tetradecane with compound number (21) was recorded to be the most abundant among WBNV infected cowpea plants.

Conclusion

The present study findings from WBNV-infected cowpea plants also show a similar range of compounds that may attract the vector for virus spread. The increased volatile chemicals in WBNV-infected cowpea plants compared to healthy cowpea plants could be related to the plant's altered physiology following virus infection, which attracts the vector to virus-infected plants for rapid virus dissemination. Viruliferous thrips preferred healthy plants, while nonviruliferous thrips preferred WBNV-infected plants due to the presence of VOCs *viz*., 1,2-propanediamine, tuaminoheptane from healthy cowpea plants and tetradecane from virus-infected cowpea plants, which could serve as an attractant for *T. palmi*. This information will help us better understand a pathogen that alters the physiology of plants and emits volatile cues for the efficient spread of the pathogen. The current study also paves the way for developing novel techniques in managing thrips through synthetic blends of VOCs emitted from both plants that could be used as cues that can be applied in yellow sticky traps for eco-friendly management thrips in respective cropping systems.

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Conflict of interest

The authors declare that they have no conflict of interest.

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