*Indian Journal of Agricultural Sciences* **87** (3): 373–8, March 2017/Article
https://doi.org/10.56093/ijas.v87i3.68751

# Herbivore induced plant volatiles represents a favorable host to onion thrips (*Thrips tabaci*)

N R PRASANNA KUMAR[1], P D KAMALA JAYANTHI[2], VIVEK KEMPRAJ[3], M A RAVINDRA[4], T K ROY[5] and A VERGHESE[6]

*Indian Institute of Horticultural Research, Hessaraghatta Lake PO, Bengaluru, Karnataka 560 089*

Received: 16 December 2015; Accepted: 13 October 2016

ABSTRACT

Onion thrips, *Thrips tabaci*s Lindeman (Thysanoptera: Thripidae) is an important pest of horticulture crops throughout the globe. However, there is a paucity of studies on its behavioral ecology in relation to herbivore induced plant volatiles (HIPVs). An attempt was made to study behaviour of *T. tabaci* towards HIPVs and healthy plant volatiles. Olfactometer bioassays revealed that *T. tabaci* significantly preferred HIPVs from conspecific infested onion to volatiles from healthy onion plants. Gas chromatography-Mass spectrometry (GC-MS) analysis of HIPVs and volatiles from healthy onion plants revealed substantial changes in their volatile profiles. Our study provides empirical data on signals HIPVs may provide herbivores and suggests that the role of HIPVs, mostly generalized as defense, may vary based on the interaction and must be studied closely to understand their ecological roles. It also provides basis for the development of kairomone based management strategies against this devastating pest.

**Key words:** Bioassay, Host preference, Olfactometer, Thrips, Volatiles

Insect-Plant interactions are mainly guided by the host plant chemistry and the response of herbivorous insects to the herbivore induced plant volatiles (Bruce *et al*. 2005). Herbivore induced plant volatiles (HIPVs) are specific volatile organic compounds that a plant produces in response to herbivory (Holopainen and Blande 2013). A large number of herbivore induced chemicals with important ecological roles have been identified and characterized in several insect-plant interactions (Demoraes *et al*. 1998, 2001, Pichersky *et al*. 2006, Penaflor and Bento 2013). Thus, during host location, herbivores mainly depend on olfactory cues and HIPVs are important mediators of insect-plant interactions (Demoraes *et al*. 2001, Bruce *et al*. 2005, Dicke and Baldwin 2010). Several studies confirmed the differential behavioral responses of insect pests to HIPVs and their multiple functions at different trophic levels (Rodriguez and Frost 2010). Further, these interactions can be manipulated to formulate effective pest management strategies like push–pull technology where semiochemicals are used to repel pests from crops (Push-using repellent or non-host stimuli) and at the same time attract them into trap crops (Pull-using attractant or host stimuli) (Samantha *et al*. 2007).

Onion thrips (*Thrips tabaci* L.) (Thysanoptera: Thripidae) is an economically important pest of onion. The management options to control this pest mainly involves the use of insecticides with fewer alternatives, emphasizing the need of novel management options that can help to tackle insecticide resistance and resurgence problems that are common among sucking pests (Shiberu and Mahammed 2014). In this context, exploitation of host plant volatiles or behaviour-modifying compounds such as anti-feedants, oviposition deterrents, attractants, repellents, and mating disruption is gaining attention as a valid pest management strategy worldwide in several crops as the these tactics reduce insect feeding or egg laying without killing pests has intuitive appeal, because, such compounds are safer to non-target organisms (Mensah and Moore 2011). Therefore, an attempt has been made to understand the behavioural responses of onion *T. tabaci* to its preferred host plant, Onion (*Allium cepa* L.).

## MATERIALS AND METHODS

Adults of *T. tabaci* were collected from onion fields (2012–13) at the Indian Institute of Horticultural Research (IIHR), Bengaluru (12°58'N; 77°35'E) and used in all the behavioral studies. Thrips were collected during early hours of the day using a glass aspirator.

Laboratory study on host preference was conducted in

[1]Scientists (e mail: prassannaent@gmail.com), [2]Principal Scientist and National fellow (e mail: jaiinsect@gmail.com), [3,4]Research Associate (e mail: vivek.kempraj@gmail.com, ravindra.aurade@gmail.com), Division of Entomology and Nematology, [5]Chief Technical Officer (e mail: tkr@iihr.res.in), Division of Plant Physiology and Biochemistry, IIHR, Hessaraghatta Lake PO, Bengaluru 560 089, [6]Director (e mail: Abraham.avergis@gmail.com), National Bureau of Agriculturally Insect Resources, Hebbal Farm Post, Bengaluru, Karnataka 560 024.

rectangular plastic boxes (50 cm L × 30 cm W and 15 cm H) that served as behavioral arenas with different hosts. Two layers of filter paper were provided at the bottom of each plastic box to absorb excess moisture from different host plant parts as well as for traction. Different plant parts of common hosts of *T. tabaci* like pods of french bean (*Phaseolus vulgaris* L.), leaves of onion (*Allium cepa* L.), and fruits of capsicum (*Capsicum annum* L.) were randomly placed inside the arena at a distance of 10 cm to each other. Twenty field-collected thrips were randomly checked for any admixtures under a stereomicroscope (Leica M205A) and after confirmation they were released in the centre of the arena. A total of 50 replications were carried out in a complete randomized design (CRD). Observations on number of thrips settled on each host were recorded 24 h post-release of thrips. The data were subjected to one-way ANOVA (SPSS version 16). Means were separated using Fisher's LSD test with α set at 0.05.

Onion seedlings of 35-40 days old were transplanted into plastic pots (27 cm H × 27 cm top W × 22 cm base width) and placed in a glass house at IIHR experimental farm. Forty days after transplantation, the plants were artificially infested with thrips (150-200 thrips/ plant/ pot) collected from the field continuously for 10 days and placed in plant cages having a aluminum sheet base covered with glass on all the three sides as well as top and with fine muslin cloth on one side (0.55 m L x 0.55 m W x 0.55 m H) to prevent thrips escape. For comparison, the healthy onion plants were also maintained in thrips proof plant cages as described above. Daily, healthy plants were sprayed with water using pressurized hand sprayer to prevent settling of thrips if any entered the cage accidentally. Ten days after releasing the thrips, both the plants (viz. artificially infested, healthy) along with the pots were brought to the laboratory for volatile collection using air-entertainment. Before volatile collection, all the necessary glassware and aluminum plates were washed with aqueous teepol detergent, rinsed with distilled water followed by acetone, and then dried in a hot air oven at 120°C for 2 h. The Porapak Q tubes (50 mg, 60/80 mesh) of 5 mm diameter and 5 cm length are used for collection of volatiles. These tubes were eluted with redistilled diethyl ether and heated at 120°C for 2 h in hot air oven to remove contaminants. Autoclaved polythene bags were used to cover the onion plants. The polybag was inserted upside down to enclose the whole plant and made completely air proof by tying at the base of the plant with rubber band and the gaps were sealed using glass wool. Both inlet and outlet of the volatile collecting tubes were inserted in to the bag. Air purified by passage through an activated charcoal filter, was pumped into the bag at 600 ml/min through the inlet port and the air was drawn out at 800 ml/min through Porapak Q glass tube. All connections were made with polytetrafluoroethylene (PTFE) tubing with brass ferrules and fittings. The volatiles from onion plants were entrained for 48 h and the Porapak Q filters were eluted with 750 µl of redistilled diethyl ether, providing a solution which contained the isolated volatile compounds served as test sample. Sample was stored in glass vial in a freezer (-20°C) until further use.

A Perspex four-arm olfactometer was used to determine the behavioural responses of adult *T. tabaci* to headspace samples of host plant volatiles (Pettersson 1970). Prior to each experiment, all glassware was washed with teepol, rinsed with acetone and distilled water, and baked in an oven overnight at 160ºC. Perspex components were washed with teepol solution, rinsed with 80% ethanol solution and distilled water, and left to air-dry. Experiments were conducted in an isolated room (25 ± 2°C, 60% RH) to avoid contaminant odours. The olfactometer had four glass side arms leading into a central arena, which was divided into four odor fields. The central area was fitted with a filter-paper base (Whatman No. 1, 12 cm diameter) to provide traction for the walking insect. The olfactometer was illuminated from above with uniform lighting using a white fluorescent light bulb (10 watts) covered with opaque dome to make it diffuse and was surrounded by a black wall cage (60 × 60 × 60 cm) to remove any external visual stimuli.

The field collected individual adult *T. tabaci* starved for 2 h was introduced through a hole in the top of the olfactometer. After introducing the thrips into the olfactometer arena, each test insect was given 2 min to acclimatize in the olfactometer, thereafter the experiment was run for 15 min continuously. If the test insect is not responding with in 2 min, it was discarded. A total of 10 such replications were carried out. For each replication a fresh, sterilized olfactometer was used. The olfactometer was rotated at 90º for every 2 min to eliminate any directional bias in the room. Air was drawn through the central hole at the rate of 900 ml/min. The central arena of the olfactometer was divided into four discrete odor fields corresponding to each of four glass inlet arms. Olfactory bioassays (both single choice and dual choice) were carried out to understand the response of adult *T. tabaci* to the host plant volatiles (collected from healthy as well as thrips infested onion plants) as per the procedures described by Kamala Jayanthi *et al*. (2012). The first series of assays were carried out with both healthy and infested onion plant volatiles separately, with one treated arm and three solvent control arms in each replicate. In the second series, dual choice assays were carried out to study the thrips response to both healthy and infested onion plant volatiles together. Here, each replicate involved two treated arms (healthy and infested onion plant volatiles) and two control arms (solvent blank). Test samples (10µl) were pipetted onto the filter paper strips and the solvent was allowed to evaporate prior to their placement in the treatment arm. The filter paper strips with solvent (diethyl ether) served as controls.

Observations on time spent in the each olfactometer arm and number of entries made in to each olfactometer arm were recorded with Olfa software (F. Nazzi, Udine, Italy). The mean time spent and also mean number of entries made in treated/ control regions were compared using a paired *t*-test (single choice) and analysis of variance (ANOVA) after conversion of the data into proportions and a log-ratio

transformation using Fisher's LSD test with $\alpha$ set at 0.05 (SPSS version 16).

Chemical composition of Porapak Q elutes were analyzed by GC-MS/MS using Varian 3800 apparatus equipped with coupled MS/MS [Saturn 4000]. A capillary column (DB-5ms) of 30 m length and 0.25 mm ID and 0.25 mm film thickness was used to examine samples. Oven temperature was programmed at 50-200°C with ramping at 3°C/min for 60 min. Helium was used as carrier gas at a flow rate of 1/mL. MS was in full scan mode (70 eV) and AMU ranged from 50 to 350. Two micro liter sample were injected in split mode (1:20) with injection temperature at 270°C. Compounds were identified by GC retention time, mass spectrum and KOVATS index using NIST 2007 and Wiley library as reference.

## RESULTS AND DISCUSSION

*Host preference*

Studies to understand the host preference of *T. tabaci* revealed that of three common hosts, viz. French bean, onion, bell pepper, thrips exhibited significant preference for onion ($P < 0.0001$; $F = 128.15$; df = 147). The number of thrips settled on onion (7.08 ±0.38) was significantly more compared to bell pepper (3.94 ±0.33) and French beans (0.44 ±0.90) (Fig.1).

*Olfactometer bioassays*

Results of the four-arm olfactometer bioassay revealed that *T. tabaci* spent significantly more time (5.24 ± 0.76 min, $P = 0.01$) in arm treated with thrips infested onion plant volatiles (HIPV) compared to untreated control (2.37 ± 0.21 min). There was no significant difference between treated arm and untreated control with respect to time spent by *T. tabaci* for healthy onion plant volatiles (4.10 ± 0.68 min in treated arm and 2.93 ± 0.23 min in control arm). There was also no significant difference for the number of entries made by *T. tabaci* between treated arms (with healthy onion plant volatiles 10.00 ± 1.19; with HIPVs 7.50 ± 0.93) and control arms (9.13 ± 0.96 and 7.40 ± 0.93, respectively) (Table 1). The dual choice bioassays clearly indicated that *T. tabaci* spent significantly more time in arms treated with HIPVs (3.89 ± 0.49; $P$=0.01, $F = 6.24$; $df = 27$) compared to the arms treated with healthy onion plant volatiles (2.03 ± 0.39). Similar trend was exhibited with respect to number of entries where *T. tabaci* visited significantly (P=0.01, F = 5.28, df = 27) more times to the arm treated with HIPVs (10.50 ± 1.44) compared to the arm treated with healthy onion plant volatiles (3.85 ± 0.18) (Table 2). The GC-MS analysis exhibited stark difference in the profile of volatiles emitted by healthy and thrips infested onion plants (Table 3).

*Onion thrips, T. tabaci* is a devastating pest of vegetable crops all over world and understanding its host preference will certainly provide important clues about its ecology and management (Nault *et al*. 2014). Our host preference studies indicated that *T. tabaci* preferred onion to other hosts. Several studies earlier reported that although *T. tabaci* has a wide host range, its preferred association with host plants, viz. onion, leek and tobacco do exist (Nault *et al.* 2014, Brunner *et al.* 2004). Further, *T. tabaci* population tested in the present study was collected from onion fields only and the previous host feeding experience would have been reason for the observed host feeding preference on onion as the process of host selection also depends on internal state of insect like prior experience (Hansson 1999). Evidence of host association within different genetic lineages of *T. tabaci* populations with their cultivated hosts has been reported (Nault *et al*. 2014). Similarly, differences in host use patterns and differential responses to host plant quality were reported in several thrips species (Baez *et al*. 2011).

It is well understood that plants respond to insect herbivores by synthesizing and releasing specific volatile compounds (HIPVs), which provide important host-location cues for natural enemies of herbivores (De Moraes *et al.* 1998). Further, these HIPVs may repel conspecific individuals that may help them to prevent overcrowding (De Moraes *et al.* 2001). Present study investigated the response of onion thrips, *T. tabaci* to herbivore induced onion plant volatiles in comparison to healthy plants.

The behavioral and olfactometer assays revealed attraction of *T. tabaci* infested onion plant volatiles to conspecific thrips compared to volatiles from healthy plants as evidenced by amount of time spent and number of entries.

Table 2 Olfactory responses of *T. tabaci* to different host plant volatiles (Dual choice bioassays)

| Treatment | Plant volatiles | | Significance |
|---|---|---|---|
| | HIPVs | Healthy | |
| Time spent (Min + SE) | 3.89+ 0.49 | 2.03+ 0.39 | P = 0.01 ( N =10) |
| Visits (No. + SE) | 10.50+1.44 | 3.85 + 0.18 | P = 0.01 (N = 10) |

HIPVs: Herbivore induced plant volatiles.

Table 1 Olfactometer bioassays of *T. tabaci* showing preference for HIPVs

| Treatment | Time spent (Min + SE) | | Significance | No. of visits | | Significance |
|---|---|---|---|---|---|---|
| | Treatment | Control | | Treatment | Control | |
| Healthy onion plant volatiles | 4.10+ 0.68 | 2.93 + 0.23 | NS (N = 10) | 10.00+ 1.19 | 9.13 + 0.96 | NS (N= 10) |
| Infested onion plant volatiles (HIPVs) | 5.24+ 0.76 | 2.37 + 0.21 | P = 0.01 ( N =10) | 7.50 + 1.00 | 7.40 + 0.93 | NS ( N= 10) |

HIPVs: Herbivore induced plant volatiles.

Table 3 GC-MS profiling of volatile chemicals from healthy/thrips infested onion plants

| Retention time (RT- min.) | CAS No. | Compounds | Area % | |
|---|---|---|---|---|
| | | | Healthy | Infested |
| 4.196 | 111-27-3 | 1-Hexanol | 1.33 | 0.00 |
| 4.476 | 15870-10-7 | 2-Methyl-1-heptene | 1.78 | 0.00 |
| 6.024 | 95-47-6 | o-Xylene | 0.44 | 0.78 |
| 6.899 | 106-42-3 | p-Xylene | 0.52 | 1.11 |
| 7.414 | 638-02-8 | 2,5-Dimethylthiophene | 0.00 | 3.44 |
| 8.694 | 106-51-4 | p-Benzoquinone | 1.52 | 0.00 |
| 8.683 | 75-08-1 | Methyl hydsosulfide | 0.00 | 3.43 |
| 9.033 | 505-23-7 | 1,3-Dithiane | 0.00 | 2.40 |
| 11.441 | 3387-41-5 | Sabinene | 0.69 | 0.24 |
| 11.715 | 1585-17-7 | 1,2,3-Trimethylbenzene | 0.00 | 0.35 |
| 12.131 | 108-95-2 | Phenol | 0.00 | 0.67 |
| 13.258 | 99-87-6 | Cymene | 0.00 | 0.38 |
| 14.177 | 124-18-5 | Decane | 0.81 | 0.00 |
| 14.396 | 20664-46-4 | Octenal | 1.36 | 0.00 |
| 14.871 | 39130-02-8 | 2-Butyloctanol | 5.97 | 0.27 |
| 15.708 | 4057-42-5 | (4E)-2-6-Dimethyl-4-octene | 2.18 | 0.00 |
| 15.698 | 1955-39-1 | 2-Phenylbutenolide | 0.00 | 0.48 |
| 16.507 | 112-40-3 | Dodecane | 2.00 | 0.17 |
| 16.791 | 41884-28-0 | 2-Isopropyl-5-methyl-1-hexanol | 1.38 | 0.26 |
| 16.924 | 818-81-5 | 2-Methyl-1-octanol | 9.94 | 0.72 |
| 17.195 | 112-53-8 | Dodecanol | 4.38 | 0.49 |
| 17.525 | 72437-68-4 | Methyl pentyl disulfide | 0.23 | 6.38 |
| 18.505 | 624-48-6 | Dimethyl (2Z)-2-butenedioate | 0.00 | 1.08 |
| 20.833 | 93-89-0 | Ethyl benzoate | 0.26 | 0.00 |
| 24.952 | 629-62-9 | Pentadecane | 0.61 | 0.28 |
| 26.443 | 68526-86-3 | Isotridecyl alcohol | 1.30 | 25.70 |
| 27.174 | 108-46-3 | Resorcinol | 4.59 | 2.76 |
| 27.371 | 19780-79-1 | 2-Hexyl-1-octanol | 6.53 | 5.40 |
| 27.785 | 112-70-9 | 1-Tridecanol | 3.04 | 1.65 |
| 28.189 | 39130-02-8 | 2-Butyloctanol | 1.89 | 0.88 |
| 29.492 | no CAS# | 6,7-Dimethyl-2-benzofuran-1(3H)-one | 2.01 | 0.00 |
| 31.161 | 88-84-6 | β-Guaiene | 0.00 | 0.70 |
| 31.38 | 93-15-2 | Methyl eugenol | 0.00 | 0.96 |
| 32.88 | 33922-66-6 | 2-Hexyl-5-methyl-3(2H)-furanone | 0.00 | 2.81 |
| 34.693 | 18252-46-5 | (Z)-CIS-α-BERGAMOTENE | 0.69 | 1.82 |
| 35.437 | 28387-44-2 | Germacrene-B | 0.91 | 0.9 |
| 36.303 | 23676-09-7 | Ethyl para-ethoxy benzoate | 4.16 | 0.71 |
| 36.531 | 112-39-0 | Methyl palmitate | 1.44 | 4.27 |
| 51.297 | 22770-28-3 | α-Glyceryllinoleate | 1.86 | 4.788 |

In single choice olfactometer bioassays the adult *T. tabaci* spent significantly more time in arm treated with HIPVs compared to healthy onion plant volatiles. Nevertheless, there is no significant difference for the number of entries made by *T. tabaci* between treated arms (with healthy onion plant volatiles/ with HIPVs) and control arms. Further, the dual choice assays indicated that *T. tabaci* clearly preferred arm with HIPVs compared to healthy onion plant

volatiles which was evident by more time spent (P=0.01, df=9) and maximum entries (P=0.02, df=9) in HIPVs treated arms. This clearly reveals that thrips infested onion plants attracts conspecifics and this is in contrary to the widely accepted view that HIPVs repel the conspecifics. Nevertheless, (conspecific attraction to HIPVs) have been observed in very few cases whereby mixture of major HIPVs are highly attractive to host seeking oligophagous female moths, *Helicoverpa assulta* (Guenee) (Lepidoptera: Noctuidae) (Sun *et al*. 2012). In earlier studies, volatile chemicals induced due to herbivore damage in onion have been implicated in host finding behavior of thrips (Kirk 1997). Similarly, spider mites, *Tetranychus urticae* Koch (Acari: Tetranychidae) preferred odors of cucumber plants infested with conspecifics insects, but strongly avoided plants infested by thrips, *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) (Pallini *et al.* 1997). In a well-studied interaction between lima bean plants (*Phaseolus lunatus* L.) and spider mites *T. urticae*, it was found that mites avoided odors of conspecific infested plants (Dicke 1986, Harrison and Karbon 1986).

Thus, HIPVs could serve as foraging cues for *T. tabaci* over long distances indicating presence of suitable host plants and/or presence of conspecifics in the immediate vicinity. However, final decision to reject or accept the host by phytophagous insects may involve a series of steps viz., host habitat location, host location, host recognition, host acceptance, host suitability and host consumption that is similar to classical foraging model of parasitoids (Stuwart and Cunningham 2012). Recent studies proved that western flower thrips, *Frankliniella occidentalis* (Pergande) depends on olfactory cues from host plants to assess host suitability (Yu Cao *et al*. 2014).

The GC-MS volatile profiling revealed significant differences between healthy onion plant volatiles and HIPVs indicating change in the volatile blends following thrips infestation. Herbivore induced changes in plant odors that were specific to particular herbivore damage have been documented in several plants and terpenoid compounds are usually found to be major constituents (Gosset *et al.* 2009).

Generally, these herbivore-induced plant volatiles (HIPVs) are highly attractive to parasitoids and predators of herbivores playing crucial role in multi-trophic interactions. Several previous studies have correlated the HIPVs as potent attractants for natural enemies of crop pests (Kesseler and Baldwin 2001, Degenhardt *et al*. 2003, Schnee *et al*. 2006, Shiojiri *et al*. 2006, Kaplan, 2012) and as feeding deterrents and/or oviposition deterrents to crop pests (Abdul Rashid *et al*. 2011). However, in the present study, the HIPVs in onion enhanced conspecific *T. tabaci* attraction. Reports do exist on HIPVs affecting the herbivores themselves in host seeking behaviors viz., oviposition site preference, attraction to host plant, aggregation on host plants. Attraction of *T. tabaci* to volatiles of cotton seedlings with foliar damaged inflicted by conspecifics was observed in dual-choice olfactometer assays and seedlings damaged by higher densities of *T. tabaci* were more attractive than seedling damaged by lower densities (Silva *et al*. 2014). Further studies to understand the influence of density of conspecific incidence on attraction/ repulsion of *T. tabaci,* natural enemies and the underlying phytochemical basis will help us to develop push-pull strategies against this devastating pest. Phytophagous insects that are outside the habitat of their host plants must first locate the area where host plant occurs for which they usually depend on either olfactory stimulus from host plant or combination of visual and olfactory cues. In the present study, onion thrips *T. tabaci* exhibited attraction to volatiles of onion plant infested by conspecifics indicating the HIPVs serves as olfactory cues to locate host plants.

ACKNOWLEDGEMENT

Authors are grateful to the Director, ICAR-Indian Institute of Horticultural Research, for the help and cooperation in carrying out the research. We acknowledge the ICAR-National Fellow Project awarded to the second author for its financial assistance.

REFERENCES

Abdul Rashid W, Sharma H C, Michael Gabriel P, Mohd Yousf War and Savarimuthu I. 2011. Herbivore induced plant volatiles: Their role in plant defense for pest management. *Plant Signal Behavior* **6**(12): 1 973–8.

Baez I, Stuart R Reitz, Joseph E Funderburk and Steve M Olson. 2011. Variation within and between *Frankliniella* species in host plant utilization thrips. *Journal of Insect Science* **11**: 41.

Bruce T J A, Wadhams L J and Woodcock C M. 2005. Insect host location: a volatile situation. *Trends in Plant Science* **10:** 269–74.

Brunner P C, Chatzivassiliou E K, Katis N I and Frey J E. 2004. Host-associated genetic differentiation in *Thrips tabaci* (Insecta; Thysanoptera), as determined from mtDNA sequence data. *Heredity* **93:** 364–70.

De Moraes C M, Lewis W J, Pare P W, Alborn H T and Tumlinson J H. 1998. Herbivore-infested plants selectively attract parasitoids. *Nature* **393:** 570–3.

De Moraes C M, Mescher M C and Tumlinson J H. 2001. Caterpillar-induced nocturnal plant volatiles repel conspecific females. *Nature* **410:** 577–80.

Dicke M. 1986. Volatile spider-mite pheromone and host-plant kairomone, involved in spaced-out gregariousness in the spider-mite *Tetranychus urticae*. *Physiological Entomology* **11:** 251–62.

Dicke M and Baldwin I T. 2010. The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help'. *Trends in Plant Science* **15**(3): 167–75.

Degenhardt J, Gershenzon J, Baldwin I T and Kessler A. 2003. Attracting friends to feast on foes: engineering terpene emission to make crop plants more attractive to herbivore enemies. *Current Opinean Biotechnology* **14:** 169–76.

Gosset V, Harmel N, Gobel C, Francis F, Haubruge E and Wathelet J. 2009. Attacks by a piercing-sucking insect (*Myzus persicae* Sultzer) or chewing insect (*Leptinotarsa decemlineata* Say) on potato plants (*Solanum tuberosum* L.) induce differential changes in volatile compound release and oxylipin synthesis. *Journal of Experimental Botany* **60:** 1 231–40.

Hansson B S. 1999. Insect Olfaction. Springer-Verlag Berlin Heidelberg Publication, Germany.

Harrison S and Karban R. 1986. Behavioral-response of spider-mites (*Tetranychus urticae*) to induced resistance of cotton plants. *Ecological Entomology* **11:** 181–8.

Holopainen J K and Blande J D. 2013. Where do herbivore-induced plant volatiles go? *Frontiers in Plant Science* **4**: 185.

Kamala Jayanthi P D, Christine M Woodcock, John Caulfield, Michael A Birkett, Toby J A Bruce. 2012. Isolation and identification of host cues from mango, *Mangifera indica*, that attract gravid female oriental fruit fly, *Bactrocera dorsalis*. *Journal of Chemical Ecology* **38:** 361–9.

Kaplan I. 2012. Trophic complexity and the adaptive value of damage-induced plant volatiles. *PLoS Biology* **10**(11): 1001437.

Kirk W D J. 1997. Distribution, abundance and population dynamics. (*In*) *Thrips as Crop Pests,* pp 217–57. Lewis T (ed.). United Kingdom, CAB, Oxon.

Kessler A and Baldwin I T. 2001. Defensive function of herbivore-induced plant volatile emissions in nature. *Science* **291**: 2 141–4.

Liu T X and Sparks A N. 2003. Injury and distribution of onion thrips (Thysanoptera: Thripidae) in red cabbage heads. *Southwestern Entomology* **28:** 77–79.

Mensah R K and Moore C. 2011. Exploitation of semiochemicals for the management of pest and beneficial insects with special emphasis on cotton cropping systems in Australia: A Review. *Journal of Biological Control* **25**(4): 253–269.

Nault B A, Kain W C and Wang P. 2014. Seasonal changes in *Thrips tabaci* population structure in two cultivated hosts. *PLoS ONE* **9**(7): 101791.

Pallini A, Janssen A and Sabelis M W. 1997. Odour mediated responses of phytophagous mites to conspecific and heterospecific competitors. *Oecologia* **110**: 179–85.

Pettersson J. 1970. An aphid sex attractant part 1 biological studies. *Entomologica Scandinavica* **1:** 63–73.

Penaflor M F G V and Bento. 2013 Herbivore-induced plant volatiles to enhance biological control in agriculture. *Neotropical Entomology* **42**(4): 331–43.

Pichersky E, Noel J P and Dudareva N. 2006. Biosynthesis of plant volatiles: nature's diversity and ingenuity. *Science* **311**: 808–11.

Rodriguez-Saona C R and Frost C J. 2010. New evidence for a multi-functional role of herbivore-induced plant volatiles in defense against herbivores. *Plant Signaling and Behaviour* **5**: 58–60.

Samantha M C, Zeyaur R K and John A Pickett. 2007. The use of push-pull strategies in integrated pest management. *Annual Review of Entomology* **52**: 375–400.

Schnee C, Kollner T G, Held M, Turlings T C, Gershenzon J and Degenhardt J. 2006. The products of a single maize sesquiterpene synthase form a volatile defense signal that attracts natural enemies of maize herbivores. *Proceedings of National Academy of Sciences USA* **103:** 1 129–34.

Shiberu T and Mahammed A. 2014. The Importance and Management Option of Onion thrips, *Thrips tabaci* (L.) (Thysanoptera: Thripidae) in Ethiopia. *A Review Journal of Horticulture* **1**: 107.

Shiojiri K, Kishimoto K, Ozawa R, Kugimiya S, Urashimo S, Arimura G, Horiuchi J, Nishioka T, Matsui K and Takabayashi J. 2006. Changing green leaf volatile biosynthesis in plants: an approach for improving plant resistance against both herbivores and pathogens. *Proceedings of National Academy of Sciences USA* **103**: 16 672–6.

Silva R, Gimme H Walter, Lewis J Wilson and Michael J. 2014. Furlong, Responses of *Thrips tabaci* to odours of herbivore-induced cotton seedlings. *Entomologia Experimentalis et applicata* **151**(3): 239–46.

Stuart A West and Cunningham J P. 2002. A general model for host plant selection in phytophagous insects. *Theoretical Biology* **214**: 499–513.

Sun J, Huang L and Wang C. 2012. Electrophysiological and behavioral responses of *Helicoverpa assulta* (Lepidoptera: Noctuidae) to tobacco volatiles. *Arthropods Plant Interactions* **6**: 375–84.

Yu Cao, Junrui Zhi and Chunlei Cong. 2014. Olfactory cues used in host selection by *Frankliniella occidentalis* (Thysanopatera: Thripidae) in relation to host suitability. *Journal Insect Behaviour* **27**: 41–56.