STUDIES ON CHEMICAL ECOLOGY OF THRIPS, *Scirtothrips dorsalis* Hood (THYSANOPTERA: THRIPIDAE) ON *Capsicum annum* L.

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PALB 3115

DEPARTMENT OF AGRICULTURAL ENTOMOLOGY

UNIVERSITY OF AGRICULTURAL SCIENCES

BENGALURU-560 065

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In partial fulfillment of the requirements

For the award of the Degree of

MASTER OF SCIENCE *(Agriculture)*

IN

AGRICULTURAL ENTOMOLOGY

BENGALURU **JULY, 2015**

Affectionately Dedicated to
My Beloved Parents
Latha Srinivas & Sukanya Shivarmu,
My Family Members
and My Beloved Teachers

DEPARTMENT OF AGRICULTURAL ENTOMOLOGY
UNIVERSITY OF AGRICULTURAL SCIENCES
GKVK, BENGALURU-560065

CERTIFICATE

This is to certify that the thesis entitled "**STUDIES ON CHEMICAL ECOLOGY OF THRIPS, *Scirtothrips dorsalis* Hood (THYSANOPTERA: THRIPIDAE) ON *Capsicum annum* L.**" submitted by **Mr. SUBHASH, S., I.D. No. PALB 3115** in partial fulfillment of the requirement for the degree of **MASTER OF SCIENCE (Agriculture)** in **AGRICULTURAL ENTOMOLOGY**, to the University of Agricultural Sciences, Bengaluru is a *bonafide* record of research work done by him during the period of his study in this University under my guidance and supervision and the thesis has not previously formed the basis for the award of any degree, diploma, associate-ship, fellowship or other similar titles.

Bengaluru
July, 2015

(P. D. KAMALA JAYANTHI)
Major Advisor

APPROVED BY:

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(T. B. PUTTARAJU)

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Bengaluru *(Subhash, S.)*
July, 2015

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THESIS ABSTRACT

The chilli thrips, *Scirtothrips dorsalis* Hood, is an important pest on various commercially important vegetable, ornamental and fruit crops. The objective of our study was to understand its interaction with the host plant, *Capsicum annum* L. *cv. Indra*. Headspace samples were collected from different growth stages (pre-flowering, flowering and fruiting) of host plants as well as from healthy and thrips infested (herbivore induced) plant of *C. annum* and were subjected to olfactometer bioassays, GC-MS and GC-EAD with adult *S. dorsalis*. A positive behavioural response was observed when adults of *S. dorsalis* were exposed to fruiting stage volatiles and herbivore induced plant volatiles in olfactometer bioassays. GC-EAD with adult *S. dorsalis* revealed eight EAD-active compounds from 'fruiting stage host plant volatiles' and six EAD-active fractions from 'herbivore induced host plant volatiles'. The EAD-active fractions from 'fruiting stage' were identified as *o*-Cymene, 4-methyl-2-undecane, 3,6-Dimethyl decane, *β*-Elemene, *n*-Dodecane, Dodecyl iodide, 2,3,5-Trimethyl decane and *n*-Docosane and from herbivore induced host plant volatiles were identified as *δ*-3-Carene, Octadecane, *n*-Docosane, 4-Methyl-2-undecane, Dodecyl iodide and Tricosane. Synthetic samples of all these compounds were tested individually and were significantly attractive to thrips except *n*-Dodecane, Dodecyl iodide and Tricosane. Furthermore, synthetic blends with the same concentration and ratio as in the natural headspace samples were also found to be highly attractive (P = 0.002 for fruiting plant volatile & P = 0.003 for herbivore induced plant volatile). In a dual choice test, thrips shows equal preference for the natural samples and the synthetic blends.

July, 2015
Department of Agricultural Entomology
UAS, GKVK, Bengaluru-65

(P. D. Kamala Jayanthi)
Major Advisor

ದೊಣ್ಣೆಮೆಣಸಿನಕಾಯಿ (*ಕ್ಯಾಪ್ಸಿಕಮ್ ಆ್ಯನಮ್* ಎಲ್.) ಯಲ್ಲಿ ಕಂಡು ಬರುವ ಥ್ರಿಪ್ಸ್, *ಸಿಟ್ರೊಥ್ರಿಪ್ಸ್ ಡಾರ್ಸಾಲಿಸ್* ಹುಡ್ (ತೈಸನೊಪ್ಟೆರಾ: ಥ್ರಿಪಿಡೆ) ಕೀಟದ ರಾಸಾಯನಿಕ ಪರಿಸರದ ಅಧ್ಯಯನ

ಸುಭಾಷ್, ಎಸ್.

ಪ್ರಬಂಧದ ಸಾರಾಂಶ

ಮೆಣಸಿನಕಾಯಿ ಥ್ರಿಪ್ಸ್ ಕೀಟವೆಂದೆ ಪ್ರಖ್ಯಾತವಾಗಿರುವ, *ಸಿಟ್ರೊಥ್ರಿಪ್ಸ್ ಡಾರ್ಸಾಲಿಸ್* ಹುಡ್ ವಿವಿಧ ವಾಣಿಜ್ಯ ಬೆಳೆಗಳಾದ ತರಕಾರಿ, ಅಲಂಕಾರಿಕ ಮತ್ತು ಹಣ್ಣಿನ ಬೆಳೆಗಳಲ್ಲಿ ಪ್ರಮುಖ ಕೀಟವಾಗಿರುತ್ತದೆ. ಆದ್ದರಿಂದ ಈ ಕೀಟದ ಪರಸ್ಪರ ಪ್ರತಿಕ್ರಿಯೆಗಳನ್ನು ಅದರ ಮುಖ್ಯ ಸಸ್ಯವಾದ ದೊಣ್ಣೆಮೆಣಸಿನಕಾಯಿಯ ಇಂದ್ರ ತಳಿಯನ್ನು ಬಳಸಿಕೊಂಡು ಅರ್ಥಮಾಡಿಕೊಳ್ಳುವುದು ಈ ಅಧ್ಯಯನದ ಮುಖ್ಯ ಉದ್ದೇಶವಾಗಿತ್ತು. ಹೆಡ್‌ಸ್ಪೆಸ್ ಮಾದರಿಗಳನ್ನು ಮುಖ್ಯ ಸಸ್ಯಗಳ ವಿಭಿನ್ನ ಬೆಳವಣಿಗೆ ಹಂತಗಳಲ್ಲಿ (ಪೂರ್ವ ಹೂ ಬಿಡುವ, ಹೂ ಬಿಟ್ಟಿರುವ ಮತ್ತು ಕಾಯಿ ಬಿಟ್ಟಿರುವ) ಹಾಗೂ ಆರೋಗ್ಯಕರ ಮತ್ತು ಥ್ರಿಪ್ಸ್ ಬಾಧಿತ (ಶಾಖಾಹಾರಿ ಪ್ರೇರಿತ) ಸಸ್ಯಗಳಿಂದ ಸಂಗ್ರಹಿಸಲಾಯಿತು. ಈ ಹೆಡ್‌ಸ್ಪೆಸ್ ಮಾದರಿಗಳನ್ನು ವಯಸ್ಕ ಥ್ರಿಪ್ಸ್‌ನ ಜೊತೆ ಆಲ್‌ಫ್ಯಾಕ್ಟೊಮೀಟರ್ ಬಯೋಅಸ್ಸೆ, ಜಿಸಿ–ಎಂಎಸ್ ಮತ್ತು ಜಿಸಿ–ಇ.ಎ.ಡಿ ಪರೀಕ್ಷೆಗಳಿಗೆ ಒಳಪಡಿಸಲಾಯಿತು. ವಯಸ್ಕ *ಸಿಟ್ರೊಥ್ರಿಪ್ಸ್ ಡಾರ್ಸಾಲಿಸ್* ಕೀಟಗಳನ್ನು ಆಲ್‌ಫ್ಯಾಕ್ಟೊಮೀಟರ್ ಬಯೋ ಅಸ್ಸೆಯಲ್ಲಿ ಕಾಯಿಬಿಟ್ಟಿರುವ ಮತ್ತು ಶಾಖಾಹಾರಿ ಪ್ರೇರಿತ ಸಸ್ಯಗಳ ಬಾಷ್ಪ ಶೀಲಗಳಿಗೆ ಒಡ್ಡಿದಾಗ ಧನಾತ್ಮಕ ವರ್ತನೆಯನ್ನು ಅವುಗಳ ಪ್ರತಿಕ್ರಿಯೆ ಮೂಲಕ ಗಮನಿಸಲಾಯಿತು. ವಯಸ್ಕ *ಸಿಟ್ರೊಥ್ರಿಪ್ಸ್ ಡಾರ್ಸಾಲಿಸ್* ಕೀಟಗಳ ಜೊತೆ ಜಿ.ಸಿ.–ಇ.ಎ.ಡಿ. ಪರೀಕ್ಷೆ ಮಾಡಿದಾಗ, ಎಂಟು ಇ.ಎ.ಡಿ ಸಂಯುಕ್ತಗಳು ಕಾಯಿಬಿಟ್ಟಿರುವ ಮುಖ್ಯ ಸಸಿಗಳ ಬಾಷ್ಪ ಶೀಲ ಮಾದರಿಗಳಲ್ಲಿ ಹಾಗೂ ಆರು ಇ.ಎ.ಡಿ ಸಕ್ರಿಯ ಸಂಯುಕ್ತಗಳು ಶಾಖಾಹಾರಿ ಪ್ರೇರಿತ ಸಸಿಗಳ ಬಾಷ್ಪಶೀಲ ಮಾದರಿಗಳಲ್ಲಿ ಕಂಡು ಬಂದಿರುತ್ತವೆ. ಕಾಯಿಬಿಟ್ಟಿರುವ ಸಸ್ಯಗಳ ಬಾಷ್ಪಶೀಲ ಮಾದರಿಗಳಲ್ಲಿ ಕಂಡುಬಂದ ಜಿ.ಸಿ.–ಇ.ಎ.ಡಿ ಸಕ್ರಿಯ ಸಂಯುಕ್ತಗಳೆಂದರೆ ಒ–ಸೈಮಿನ್, ೪–ಮೀಥೈಲ್–೨–ಅನ್‌ಡೆಕನ್, ೩,೬–ಡೈ ಮೀಥೈಲ್ ಡೆಕನ್, *ಬೀಟಾ*–ಎಲಿಮಿನ್, *ಎನ್*–ಡೊಡೆಕೆನ್, ಡೊಡೆಕೈಲ್ ಐಯೋಡೈಡ್, ೨,೩,೫–ಟ್ರೈ ಮೀಥೈಲ್ ಡೆಕನ್ ಮತ್ತು *ಎನ್*–ಡೋಕೊಸೆನ್ ಹಾಗೂ ಶಾಖಾಹಾರಿ ಪ್ರೇರಿತ ಸಸ್ಯಗಳ ಬಾಷ್ಪಶೀಲ ಮಾದರಿಗಳಲ್ಲಿ ಕಂಡುಬಂದ ಜಿ.ಸಿ.–ಇ.ಎ.ಡಿ ಸಕ್ರಿಯ ಸಂಯುಕ್ತಗಳೆಂದರೆ *ಡೆಲ್ಟಾ*–೩–ಕ್ಯಾರಿನ್, ಆಕ್ಟಡೆಕನ್, *ಎನ್*–ಡೊಕೊಸೆನ್, ೪–ಮೀಥೈಲ್–೨–ಅನ್‌ಡೆಕನ್, ಡೊಡೆಕೈಲ್ ಅಯೊಡೈಡ್ ಮತ್ತು ಟ್ರೈಕೊಸೆನ್. ಎಲ್ಲಾ ಈ ಸಂಯುಕ್ತಗಳ ಕೃತಕ ಮಾದರಿಗಳನ್ನು ಪ್ರತ್ಯೇಕವಾಗಿ ಮತ್ತು ಅವುಗಳ ಮಿಶ್ರಣವನ್ನು ಪರೀಕ್ಷಿಸಲಾಗಿ, *ಎನ್*–ಡೊಡೆಕನ್, ಡೊಡೆಕೈಲ್ ಅಯೋಡೈಡ್ ಮತ್ತು ಟ್ರೈಕೊಸೆನ್ ಹೊರತುಪಡಿಸಿ ಉಳಿದ ಸಂಯುಕ್ತಗಳಿಗೆ ಥ್ರಿಪ್ಸ್ ಕೀಟವು ಗಮನಾರ್ಹವಾಗಿ ಆಕರ್ಷಣೆಗೊಂಡಿತು. ಇದಲ್ಲದೆ, ನೈಸರ್ಗಿಕ ಹೆಡ್‌ಸ್ಪೆಸ್ ಮಾದರಿಯಲ್ಲಿನ ಸಂಯುಕ್ತಗಳ ಕೇಂದ್ರೀಕರಣ ಮತ್ತು ಅನುಪಾತದ ಪ್ರಕಾರ ತಯಾರಿಸಿದ ಕೃತಕ ಸಂಯುಕ್ತಗಳ ಮಿಶ್ರಣವು ಕೂಡ ಅತ್ಯಂತ ಆಕರ್ಷಕವಾಗಿ ಕಂಡುಬಂದಿದೆ (ಪಿ=೦.೦೦೨ ಮತ್ತು ಪಿ=೦೦೩ ಕ್ರಮವಾಗಿ ಕಾಯಿ ಬಿಟ್ಟಿರುವ ಮತ್ತು ಶಾಖಾಹಾರಿ ಪ್ರೇರಿತ ಸಸ್ಯಗಳ ಬಾಷ್ಪಶೀಲ). ಉಭಯ ಆಯ್ಕೆ ಪರೀಕ್ಷೆಯಲ್ಲಿ ಥ್ರಿಪ್ಸ್ ಕೀಟವು, ಕೃತಕ ಸಂಯುಕ್ತಗಳ ಮಿಶ್ರಣ ಮತ್ತು ನೈಸರ್ಗಿಕ ಸಂಯುಕ್ತಗಳ ಮಿಶ್ರಣಕ್ಕೆ ಸಮಾನವಾದ ಆಕರ್ಷಣೆಯನ್ನು ತೋರಿಸಿರುತ್ತದೆ.

(ಪಿ. ಡಿ. ಕಮಲ ಜಯಂತಿ)
ಪ್ರಧಾನ ಮಾರ್ಗದರ್ಶಕರು

ಜುಲೈ, ೨೦೧೫
ಕೃಷಿ ಕೀಟಶಾಸ್ತ್ರ ವಿಭಾಗ
ಕೃಷಿ ವಿಶ್ವವಿದ್ಯಾನಿಲಯ, ಜಿ.ಕೆ.ವಿ.ಕೆ., ಬೆಂಗಳೂರು–೬೫

Olfactory Responses of Thrips, *Scirtothrips dorsalis* Hood, to Stage Specific Host Plant Volatiles of *Capsicum annum* L.

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Introduction

Insects detect and discriminate between multicomponent volatile organic compounds (VOCs) from host plants. They rely on olfaction for feeding, mating and oviposition and are guided by volatile signals from host plant and conspecifics. Host plants produce volatiles that can provide significant information about its suitability. The host plant VOCs are made up of multicomponent odour and change according to their physiology namely pre-flowering, flowering and fruiting stages. However, physiological stage of host plant and the corresponding volatile cues responsible for the insect attraction provides valuable information for formulating kairomone blends to strengthen our current IPM programs. Therefore, using the interaction between the thrips, *Scirtothrips dorsalis* and its host plant, *Capsicum annum* as a model system we show that the physiological stages of host plant is important in insect-plant interactions.

Objective

- To assess the attractiveness of volatile plumes of different physiological stages of host plant to thrips.
- To elucidate chemical composition of the volatile plumes produced by different physiological stages of Capsicum.
- To identify electrophysiologically active VOC's that instigate olfactory responses in thrips.

Materials and Methods

Insects, Host Plant & Volatile Collection. Adults of *S. dorsalis* were reared on Capsicum plants placed in glass cages were collected and starved for an hour before bioassay. Capsicum plants (cv. Indra) at different growth stages (pre-flowering, flowering and fruiting) were used for volatile collection. Headspace volatiles of plants were collected by air entrainment using Porapak Q.

Olfactometer Bioassays. Perspex four-arm olfactometer was used. A total of 20 replications were carried out and each replication was observed for 10 mins for time spent and entries.

GC-MS & GC-EAD. Porapak Q elutes were analysed by GC equipped with coupled MS/MS. GC coupled with Syntech EAG and IDAC-2 system with stimulus controller CS-55 was used.

Statistical Analysis. Paired t-test and one-way ANOVA followed by Tukey's multiple Comparison test were done for all bioassays.

Results

Figure 1. Volatile profile of pre-flowering (PF), flowering (FL) and fruiting (FR) capsicum plants identified by GC-MS. Colour Legend: 0 1 2 3 4 5 6 7 8 9 10 11 PPM

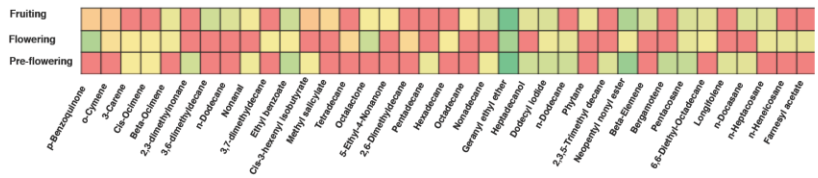

Figure 2. Fruiting plant volatiles are attractive to thrips, *S. dorsalis.*

Figure 3. Multiple choice assay between PF, FL and FR headspace volatiles to thrips, *S. dorsalis*.

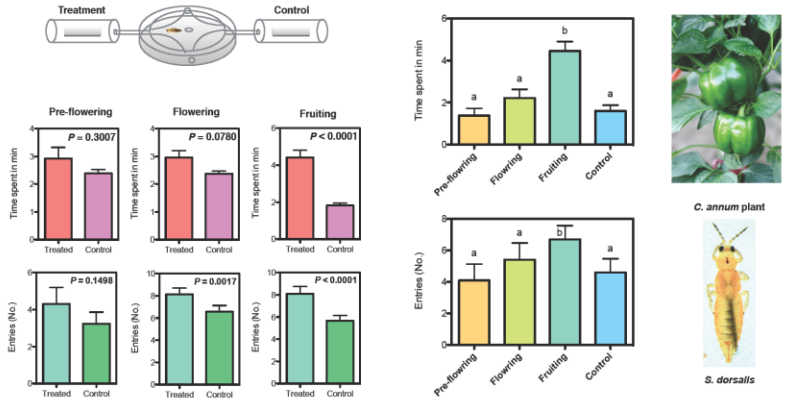

Figure 4. Electroantennogram detector (EAD) active compounds attractive to thrips, *S. dorsalis.*

- Volatile profile of each stage changed drastically and their attraction to thrips also differed (**Fig 1 & 2**).
- Olfactometer assays proved that time spent and entries were significant in the arm containing fruiting volatile plumes ($P < 0.0001$) (**Fig 2**).
- Multiple choice assay also proved that fruiting stage volatiles were significantly attractive to thrips more than pre-flowering ($q = 7.693$, $P < 0.0001$) and flowering ($q = 5.604$, $P < 0.001$) (**Fig 3**).
- GC-EAD assays reported 5 active compounds from the fruiting stage volatile (**Fig 4**).

Discussion

Insect-plant interaction is guided by host plant chemistry (Bruce *et al*., 2005). Our study revealed that fruiting stage is highly attractive to *S. dorsalis*. GC-EAD studies proved that specific compounds were active. These volatiles have been implicated in the host finding behaviour. Thrips being a devastating pest world wide, a novel, alternative, eco-friendly approach is the need of the hour.

Summary

- Stark difference in volatile profiles were noticed.
- Fruiting stage volatiles were attractive to thrips.
- Five specific VOCs are implicated as attractive.

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Reference

BRUCE, T. J. A., WADHAMS, L. J. AND WOODCOCK, C. M., 2005. *Trends in plant science,* **10** (6): 269 - 274.

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I INTRODUCTION

Capsicum (*Capsicum annum* L.) is a highly remunerative vegetable crop in the world. India's contribution is estimated to be 1,66,880 metric tons from an area of 29,730 hectares. India is one of the leading producers of Capsicum globally and contributes to 36 per cent (0.45 million tons) of the world's annual production (Anon., 2014). In India, the state of Karnataka has the highest area for Capsicum cultivation (3,190 hectares) with an annual production of 49,080 metric tons (Anon., 2014). Capsicum is grown for its fruits and is widely used in both cooked and raw form. It is highly nutritious and is rich in vitamin A and C. Every 100 g of Capsicum provides 24 Kcal of energy, 1.3 g of protein, 4.3 g of carbohydrate and 0.3 g of fat (Anon., 1997).

Although India is one of the largest producers of Capsicum, its contribution is lessened due to various factors. One major factor causing economic losses is insects. It is estimated that insects alone affect the production by 68 per cent (Mandi and Senapati, 2009). A recent survey conducted by the Asian Vegetable Research and Development Centre (AVRDC) noted thrips, *Scirtothrips dorsalis* Hood (Thysanoptera: Thripidae) as the most important factor limiting Capsicum production in India followed by aphids (*Myzus persicae* (Sulzer), *Aphis gossypii* Glover) and mites (*Polyphagotarsonemus latus* (Banks)) (Hosamani, 2007). *S. dorsalis* is also commonly known as "Chilli thrips" as it majorly attacks and damages Chillies.

Chilli thrips, *S. dorsalis* is an economically important pest, native to the Indian subcontinent. It is polyphagous in nature and has a pest status in more than 100 hosts belonging to 40 different families of plants (Mound and Palmer, 1981). It is majorly found infesting vegetables, ornamentals and fruit crops throughout the Oriental region, Oceania and parts of Africa (Ananthakrishnan, 1993).

This pest causes a characteristic leaf curl in Chillies, following death of the plant popularly known as "Murda disease" (Murda = dead body in hindi) (Kulkarni, 1922). The symptoms start with the upward curling followed by wrinkling and distortion of leaves. Apart, the thrips, *S. dorsalis*, also feeds on the meristems, buds, flowers and young fruits causing brittleness of the infested plant. This results in complete defoliation and loss in yield there by affecting the farmers economically (Amin, 1979). In addition to the above damage, *S. dorsalis* also serves as a minacious vector to plant viruses namely Chilli leaf curl virus (CLC) and Capsicum chlorosis virus (CaCV).

Development of effective management practices for *S. dorsalis* is still in its infancy. AVRDC has come out with several recommendations that serve as a basic management practice template for the control of this pest. The template involves recommendations for crop rotation, removal of weeds, insecticide rotation and using natural enemies such as predators and parasitoids. In the present scenario, farmers are finding it difficult to manage thrips even with the use of chemical insecticides. Generally, farmers are known to spray chemical insecticides heavily (approx. 25-40 times) for single harvest of crop. Despite heavy chemical insecticide sprays, losses have become inevitable and the insects are fast developing resistance (Kumar *et al*., 2013). Therefore, there is a

tenacious need for developing novel management strategies to curb this menacing insect pest. One strategy that holds promise is the use of semiochemicals like host-plant volatiles (kairomones) and pheromones from conspecifics. However, Insect-Plant interactions are extremely complex and thorough understanding of these interactions (Chemical ecology) will aid in developing semiochemical based strategies to strengthen the current IPM programs.

Insect-plant association has been guided to a large extent by the plant's bio-chemistry and plant volatiles play crucial role in host-location process of phytophagous insects (Jaenike, 1990; Bruce *et al*., 2005). The insects through years of co-evolution with its host may have developed preference for specific host plant volatiles to fulfill its nutritional requirements and to find suitable oviposition sites and this preference has led to specialization by herbivorous insects (Jan de Kogel, 2001; Jayanthi *et al*., 2014). Such specialization can be utilized for pest control and an example of utilization of specific cues to which insects have developed an innate preference is well studied in Oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Jayanthi *et al*., 2014). However, not all insects develop such preference to specific cues, but, specificity may be achieved either by species-specific compounds or particular ratios of host plant volatiles (Bruce *et al*., 2005). Similarly, studies related to Onion thrips have been implicated the involvement of host plant volatiles in host finding behaviour (Kirk, 1985). Therefore, we would like to study more specifically how healthy plant volatiles, herbivore-induced plant volatiles (HIPVs) and body odours of thrips affect the behaviour of Chilli thrips, *S. dorsalis*. This study will help us to elucidate volatile fractions responsible for attraction of Chilli thrips. Taken together, our study will provide empirical data on volatile compounds underpinning thrips attraction and the objectives below are framed accordingly.

1. To evaluate attractiveness of host plant volatiles of *Capsicum annum* L. to adult *Scirtothrips dorsalis* Hood.
2. To study the differential response of adult *S. dorsalis* and co-occurring sap sucking insects to healthy and infested plant volatiles.
3. To determine the influence of conspecific body odours to adult *S. dorsalis*.

II REVIEW OF LITERATURE

'Certainly insects cannot think, but they can react'- chemical cues (semiochemicals/phytochemicals) are used by insects to orient, survive and reproduce in their specific environments (Jayanthi *et al*., 2015). This reliance of insects on chemical cues offers a number of opportunities for insect control. Recently, semiochemicals are being increasingly used as important components in integrated pest management as push-pull strategies for a number of insect species.

Push-pull strategies or stimulo-deterrent diversionary strategies are behavioural manipulation methods that use repellent or deterrent (push) and attractive or stimulant (pull) compounds to direct the movement of pest or beneficial insects for pest management. However, their potential is under exploited particularly in horticultural crop pests. This may be due to lack of thorough understanding of chemical mediated processess that manipulate trophic interactions. Thus, development of reliable, robust and sustainable push-pull strategies requires a clear scientific understanding of the behavioural or chemical ecology of interactions involving hosts, conspecifics and natural enemies at different trophic levels to underpin key process that can be exploited as weak links (Jayanthi *et al*., 2015).

Usually, we are aware of the many odours surrounding us in nature and enjoy the pleasant smell of flowers or culinary herbs. Nevertheless, many of us may not be aware of the important role of olfaction in insects. To further elaborate, the perception of a flower fragrance in humans may be limited to "the plant smells good", but herbivore insects are able to smell not only the plant species but also the physiological state of the plant, as locating suitable host plant is indispensable for their survival (Ulland, 2007).

Plants release numerous volatiles that are important for interactions with other organisms, like herbivorous insects, natural enemies, microorganisms and even neighbouring plants. These volatiles are products of complex biosynthetic pathways, constituting the secondary metabolism of the plants, which are considered to play role either in host-plant defense or advantageous interspecific interactions.

Fraenkel (1959) suggested a defensive role of these secondary compounds against herbivory. Later, Ehrlich and Raven (1964) proposed that the plant produced secondary compounds are evolved in a co-evolutionary arm race of plant-defenses and herbivore responses. Today, plant produced secondary compounds are considered to be an essential part of the plant's biochemical armour to cope with factors such as herbivore and pathogen attack (Pare and Tumlinson, 1999; Gouinguene and Turlings, 2002).

Plants are known to emit more than 1000 different volatile compounds (Dudareva *et al.*, 2004). Some of them may act directly on the herbivores, for instance deterring oviposition by lepidopterans (De Moraes *et al.*, 2001; Kessler and Baldwin, 2001). Others may act indirectly by attracting natural enemies of the herbivores (Turlings *et al.*, 1990).

Plant defense can be either “constitutive” or “induced”, meaning that constitutive defenses are the compounds that are continuously produced, stored in specialized structures and released upon attack. Whereas, induced defenses on the other hand are triggered by herbivore or pathogen attack (Gouinguene and Turlings, 2002). The advantage of induced defense is a low physiological cost, *i.e*. production of volatiles occurs only during the attack (Gershenzon, 1994). Absence of an attacking organism does not necessarily mean that the compounds are not produced, rather the production is low and then increases upon attack.

Interestingly, recent studies have demonstrated that plants can emit specific volatile blends that differ depending on the attacking species, even closely related herbivore species (De Moraes *et al.*, 1998; Arimura *et al.*, 2004). Induction and release of volatile compounds can also be triggered by abiotic factors, such as UV radiation, ozone and temperature (Jonsson and Anderson, 1999; Pichersky and Gershenzon, 2002; De Moraes *et al.*, 2004).

Altogether, the vast amounts of relevant and non-relevant volatile components released by plants constitute a major challenge for insect species in their search for a suitable host plant. The challenge is met by the use of an extremely sensitive and specialized olfactory system in insects.

Thrips are believed to have descended from a mycetophilic ancestor during the Mesozoic era (Grimaldi *et al*., 2004) and many groups still feed upon and inadvertently redistribute fungal spores, but most research has been focused on those species that are usually feed on or in association with economically significant crops. Family Thripidae is particularly notorious for members with broad host ranges and the majority of pest thrips come from this family (Bailey, 1940; Ananthakrishnan, 1993). Some thrips are predatory, but the majorities are phytophagous insects feeding on pollen or the chloroplasts from the outer layer of plant epidermal as well as mesophyll cells (Heming, 1993; Kirk, 1995). These species are small cryptophilic organisms that prefer to feed within the tightly packed apical buds of new growth.

Of several phytophagous thrips, the chilli thrips or yellow tea thrips, *Scirtothrips dorsalis* Hood, is an extremely successful invasive species of pest-thrips which has expanded rapidly from Asia and is gradually achieving a global distribution (Morse and Hoddle, 2006). It is an important pest of various vegetables, ornamental and fruit crops. Feeding by *S. dorsalis*, has been reported on more than100 species of plants representing more than 40 different families. Chilli thrips appear to feed preferentially on new growth. Feeding usually occurs along the main vein or ribs of leaves and petals (Lewis, 1973). The feeding damage of *S. dorsalis* is distinctive and in some cases may be considered diagnostic of the pest (Anon., 2005). Infested plants usually develop characteristic wrinkled leaves with distinctive brown scarring along with veins of leaves, buds and calyx of fruit (Ali *et al*., 1973; Tatara and Furuhashi, 1992; Shibao, 1996; Chandrasekaran, 2005). Feeding damage can reduce the market value of farm produce and severe thrips incidence in the presence of environmental stress can kill the plants.

The objective of the present study is to investigate and document the role of chemical cues involved in the insect-plant interactions between chilli thrips, *S. dorsalis* that are otherwise hard to manage and its host plant *Capsicum annum* L. to explore the feasibility of isolating and identifying the potential host cues involved in behaviour modification of *S. dorsalis.* As the phyto-semiochemicals are proved to be useful behaviour manipulators in several insects, identification of such potent host cues may serve as potential components in designing push-pull strategies for managing this notorious pest.

Although there are limited studies available for understanding the chemical ecology of insect-plant interactions for thrips, innumerable studies on this aspect do exist in other groups of insects.

2.1 Volatile chemical cues from host plant guide host location and selection in insects

In general, the host plant selection behaviour of insects has been divided into several sequential steps comprising habitat finding, host plant finding, host plant recognition and acceptance which are in turn connected to host plant suitability (Prokopy and Owens, 1983; Jones, 1991). Herbivores use both chemical and visual cues to locate host plants and to discriminate host from non-host plants in diverse habitats (Bernays and Chapman, 1994; Fernandez and Hilker, 2007). It is assumed that phytophagous insects employ a specific 'host plant search image' during host plant location which is based on representative chemical and visual characteristics of their host plants (Stadler, 2002). Plant volatiles are usually derived from complex biochemical processes and some of these compounds appear to be common to different plant species. However, there are also compounds that are species-specific and are elicited during herbivory as herbivore-specific cues (Halitschke *et al*., 2001). Plant volatiles provide important information to insects in their search for host plants on which to feed or lay eggs and in the avoidance of plants that are unsuitable as hosts (Dicke and Van Loon, 2000).

Finding potential hosts in a complex environment is an essential component in the life history of many insects. Phytophagous, parasitic and parasitoid insects have evolved to do this efficiently and effectively. Insects may use a variety of host or habitat-derived cues to identify appropriate search arenas in a diverse habitat (Prokopy and Bush, 1973; Vinson, 1981, 1984).

Many studies show that typical volatile compounds emitted by host plants guide herbivores while searching and play an important role in host plant recognition (Visser, 1986; Honda, 1995; Bruce *et al*., 2005). Many leaf and flower-feeding insects have been reported to depend on visual cues (Lewis and Taylor, 1964) with a species-specific response to lighting stimuli of various wavelengths (Lewis, 1973). Chilli thrips, *S. dorsalis* is no exception and there is considerable evidence demonstrating that it does rely upon visual stimuli to identify hosts. Studies with chilli peppers demonstrated that morphological characters of plants including height, leaf size, petiole and leaf internode distance can have an impact on populations of *S. dorsalis* (Pramanick and Mohasin, 2004).

While host selection is usually dependent on many stimuli, the host cues that are responsible to thrips attraction to their host plant are poorly understood and such responses are frequently species-specific (Jan de Kogel and Koschier, 2002). For instance, it has been reported that host plant odour signals attract herbivores over distances of up to 100 meters (Schoonhoven *et al*., 2005). However, within habitats, olfactory and visual plant cues always occur in combination and the relative importance of either cue for herbivores during host location is sometimes difficult to assess. The relevance of different types of host plant cues seems to depend largely on the investigated species (Finch *et al*., 2003; Couty *et al*., 2006).

For odour recognition of a host plant, insect relies on specific volatiles in that particular host, termed "token stimuli", which are not present in unrelated plant species as reported by Fraenkel (1959).

Many phytophagous insects use odours as cues for orientation to food resources, either for their own nutrition or to deposit their offspring. Foliar, floral and fruit odours comprise hundreds of compounds, but studies of insect olfaction reveal that only a minority of the components in the complex odour blend are detected by the antenna (Jonsson and Anderson, 1999). Among the detected compounds, even fewer seem to be involved in eliciting behavioural responses from the insect (Rojas, 1999). Therefore, identifying the range of host-associated volatile cues that insects can detect is an important step towards understanding the role of olfaction in modulating insect behaviour.

Bruce *et al.* (2005) studied the importance of single odourants and odour blends in host plant recognition and proposed two major hypotheses. One hypothesis is that host recognition is based on detecting specific blend of volatiles generally produced in many plant species, implying that the ratio of concentrations of the many volatiles constitutes as the odour cue of a particular host plant and the other hypothesis is that use of ubiquitous plant volatiles as the most prevalent mechanism in mediating host-plant recognition.

Thus, it is well understood that insect herbivores use plant volatiles not only to recognize but to efficiently locate their host plants. Insects perceive these signals via specialized olfactory receptor neurons and use them to discriminate food sources, ovipositing sites or larval food plants from the background chemical environment (Dethier, 1982; Bernays, 2001). Therefore, the components used in host selection are probably not exclusively visual. Similarly, in case of *S. dorsalis*, the scent of rose petals as well as colour and volatile chemical compounds may be of greater importance in local dispersal. Several studies have directed towards understanding the colour attraction of *S. dorsalis* and evaluating different colour traps (Chu *et al*., 2006; Mannion *et al*., 2014). Nevertheless, host plant chemical communication, which is believed to be important, is poorly documented not only for *S. dorsalis* but for the whole of Thysanoptera. However, few studies reported that floral scents may play a role in host identification in some thrips (Blum, 1991).

Koschier *et al.* (2000) investigated the responses of adult female western flower thrips, *Frankliniella occidentalis* (Pergande) to plant volatiles at several concentrations in a Y-shaped glass tube olfactometer. They found that western flower thrips were attracted by the benzenoids: benzaldehyde and *p*- and *o*-anisaldehyde, the monoterpenes: geraniol, nerol, linalool and (+)-citronellol, the sesquiterpenes: (*E*)-*β*-farnesene, eugenol and 3-phenylpropionaldehyde, two phenylpropanoids and the non floral odour ethyl nicotinate, *p*-anisaldehyde, nerol, ethyl nicotinate. Of all these, (*E*)-*β*-farnesene elicited positive response at several concentrations. Whereas, all other volatiles were attractive at a specific concentration. Salicylaldehyde and a benzenoid elicited negative responses at two concentrations. The attractive volatile components for *F. occidentalis* were found among the monoterpenes.

Bruce *et al*. (2005) concluded that host plant location is crucial for a phytophagous insect to fulfill its nutritional requirements and to find suitable oviposition sites. Insects can locate their hosts even though the host plants are often hidden among an array of other plants and usually plant volatiles play important role in this host-location process. The recognition of a host plant by these olfactory signals could occur by using either species-specific compounds or specific ratios of ubiquitous compounds as mentioned earlier. Currently, most studies favour the second scenario, with strong evidence that plant discrimination is due to central processing of olfactory signals by the insect, rather than their initial detection.

Bruce and Pickett (2011) reported that volatile plant secondary metabolites are detected by the highly sensitive olfactory system employed by insects to locate suitable plants as hosts and to avoid unsuitable hosts. Perception of blends of plant volatiles plays a pivotal role in host recognition, non-host avoidance and ensuing behavioural responses can differ to a whole blend compared to individual components. Further, the emergent properties of blend perception because of certain components of the host blend may not be recognized as host when perceived outside the context of that blend. Often there is redundancy in the composition of blends recognized as host because certain compounds can be substituted by others.

Tasin *et al*. (2006a) reported that host plant odours attract gravid females of European grapevine moth, *Lobesia botrana* (Denis & Schiffer muller) (Lepidoptera: Tortricidae) for oviposition. They further opined that the identification of these plant volatile compounds is essential for understanding insect-plant relationships as this information contributes in breeding improved resistant cultivars against target insects. Chemical analysis of grape headspace and subsequent behavioural studies in the wind tunnel showed that host finding in grapevine moth, *L. botrana* is encoded by a ratio-specific blend of three ubiquitous plant volatiles. The odour signal that attracts mated females to grape consists of the terpenoids: (*E*)-*β*-caryophyllene, (*E*)-*β*-farnesene and (*E*)-4,8-dimethyl-1,3,7-nonatriene. These compounds represent only a fraction of the volatiles released by grapes and they are widespread compounds known throughout the plant kingdom. Therefore, the specificity may be achieved by the blend ratio, which was 100:78:9 in grape headspace. This blend elicited anemotactic behaviour in moths at remarkably small amounts.

Webster *et al*. (2010) reported that herbivorous insects recognize and locate their hosts by detecting characteristic blends of volatile compounds that these plants emit. They hypothesized that insects might show a positive response to host volatile compounds when encountered together in a blend but avoid the same volatiles when encountered individually. They further examined the behavioural responses of the black bean aphid, *Aphis fabae* Scopoli (Hemiptera: Aphididae) to physiologically relevant doses of volatile compounds emitted by its host, *Vicia faba L*., which had been previously implicated in host recognition. Of 15 volatiles tested for behavioural activity, 10 caused aphids to respond negatively, suggesting they were repellent and they made a blend comprising each of these compounds at the concentration at which they elicited the most negative behavioural response. The resultant blend elicited a positive response, suggesting it was attractive. This demonstrated that the same volatile compounds can function as both host and non-host cues depending upon the context in which they are perceived. The finding that odourants are perceived differently when combined suggests an emergent property of odour perception where discrimination of odour quality can occur according to blend properties.

Behavioural and EAG bioassays showed that adults of swallowtail, *Battus polydamas archidamas* (Boisduval) (Lepidoptera: Papilionidae) respond from a distance to volatile chemicals emitted by their host-plant, *Aristolochia chilensis* Bridges ex Lindl. Larvae of *B. polydamas archidamas* disperse in the field at the end of the third instar or beginning of the fourth instar and solitary-feeding fourth instar larvae also respond to the volatile chemicals emitted by their host plant. The fact that adults use olfactory cues to find their host plant in the laboratory suggests that when searching for host-plants in nature, they are able to find their hosts even in the presence of volatiles emitted by other plants. In other words, the mixture of volatiles present in the environment does not mask the cue emitted by their host plant (Pinto *et al*., 2009).

Alagarmalai *et al*. (2009) conducted a study aimed to identify host attractants for the lesser pumpkin fly (Ethiopian fruit fly), *Dacus ciliatus* (Loew) (Diptera: Tephritidae) through series of behavioural and electrophysiological bioassays. They tested volatile compounds from the fruits of a host plant, ripe and unripe Galia melon, *Cucumis melo* L. var. *reticulates*. Both sexes were attracted to ripe melon volatiles. Gas chromatography electroantennographic detection analysis of the behaviorally active ripe melon volatiles consistently showed that 14 compounds elicited similar antennal responses from both sexes. Twelve compounds were identified by gas chromatography mass spectrometry (GC-MS) using GC-MS libraries, retention indices (RI) and authentic standards. The electrophysiological activities of the compounds that were present at sufficient levels for identification are benzyl acetate, hexanyl acetate, (*Z*)-3-hexenyl acetate, (*Z*)-3-octenyl acetate, octanyl acetate, (*Z*)-3-decenyl acetate and (*E*)-*β*-farnesene. These compounds were further evaluated at six different dosage levels using electroantennography (EAG). The dose response in terms of attractiveness to synthetic compounds within the active range (as determined by EAG) also evaluated in the behavioural bioassay. Synthetic acetates were attractive to both sexes when tested individually. Blends of compounds in equal proportions were also found attractive to the insects. The most attractive blend was

a mixture of four or five identified acetates. The addition of an equal proportion of (*E*)-*β*-farnesene to this mixture had a deterrent effect.

Dattilo *et al*. (2009) tested the hypothesis that Amazonian ant-plant specialist, *Pheidole minutula* Mayr (Hymenoptera: Myrmicidae) queens use volatiles to distinguish their host *Maieta guianensis* L. (Melastomataceae) from other sympatric myrmecophytes. To do so, they used a Y-tube olfactometer to quantify the preference for volatiles of different plant species and results indicated that *P. minutula* queens discriminate the chemical volatiles produced by its host-plant from those of other sympatric ant-plant species. However, queens failed to distinguish the volatiles of *Maieta* from those of the ant-plant *Tococa bullifera* (Melastomataceae), with which *P. minutula* is not mutualistically associated.

Tang *et al*. (2009) revealed that maize weevil, *Sitophilus zeamais* Motsch (Coleoptera: Curculionidae) adults responded positively to volatiles emitted from stored rice with LOX-3 (Lipoxygenase) in choice between stored rice with LOX-3 and rice without LOX-3. Rice grain's volatiles produced by LOX-3 during storage are attractant to maize weevils, if LOX-3 is absent, that would affect the tropism of these weevils.

Jayanthi *et al*. (2012) isolated and identified potential host cues that are attractive to gravid oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) from overripe mango fruits. Headspace samples were collected from two cultivars of mango, *Alphonso* and *Chausa* and a strong positive behavioural response was observed when female *B. dorsalis* was exposed to these volatiles in olfactometer bioassays. Coupled GC-EAG with female *B. dorsalis* revealed 7 compounds from Alphonso headspace and 15 compounds from Chausa headspace that elicited an EAG response. The EAG active compounds from *cv. Alphonso* were identified using GC-MS as heptane, myrcene, (*Z*)-ocimene, (*E*)-ocimene, alloocimene, (*Z*)-myroxide and *γ*-octalactone with the two ocimene isomers being the dominant compounds. The EAG active compounds from *cv. Chausa* were 3-hydroxy-2-butanone, 3-methyl-1-butanol, ethyl butanoate, ethyl methacrylate, ethyl crotonate, ethyl tiglate, 1-octen-3-ol, ethyl hexanoate, 3- carene, *p*-cymene, ethyl sorbate, *α*-terpinolene, phenyl ethyl alcohol, ethyl octanoate and benzothiazole. Individual compounds were significantly attractive when a standard dose (1 µg on filter paper) was tested in the olfactometer. Furthermore, synthetic blends with the same concentration and ratio of compounds as in the natural headspace samples were highly attractive ($P < 0.001$) and in a choice test fruit flies did not show any preference for the natural samples over the synthetic blends.

Dormont *et al*. (2010) suspected that resource selection in coprophagous insects may be based on innate olfactory preferences. They analyzed the composition of different mammal dung volatiles and showed that adult beetles were more attracted to cattle as well as sheep dung odours. They further showed that the presence of other insects inside the dung resource affects the process of dung selection by adults. They identified 64 chemical compounds from dung emissions and showed that dung volatiles clearly differed among different mammal species, allowing olfactory discrimination by dung beetles.

Cabbage moth, *Mamestra brassicae* L. (Lepidoptera: Noctuidae) is equipped with a specific receptor neurons (RNs) that mainly detects odourants produced by many plant species, suggesting that recognition of host plants is mainly based on the odour blend or ratio of the volatiles released by a plant (Ulland, 2007).

Visser and Ave (1978) exposed colarado beetles to plant volatiles alone and in combination thereby confirming that stronger behavioural responses are obtained with appropriate blends or combinations of volatiles than with single compound. One of the earliest studies was that potato odour was shown to be attractive to colorado beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) but none of the individual components were found attractive [(*E*)-3-hexen-1-ol, (*Z*)-2-hexen-1-ol, (*E*)-2-hexen-1-ol or (*E*)-2-hexenal]. Further, enhancing levels of certain components, disrupted attraction to the host plant suggesting that even the ratio of volatiles played a role in host odour recognition. There are numerous other studies where insect behavioural responses to host volatile blends have been shown to exceed the responses to individual components. The number of components used for host recognition by an insect is usually in the range of 3-10 compounds which are vital for host recognition.

Heisswolf *et al.* (2007) investigated the importance of olfactory versus contact cues for host plant recognition in tortoise beetle, *Cassida canaliculata* Laich. (Coleoptera: Chrysomelidae), which is strictly monophagous on meadow sage. The reaction of adult beetles to olfactory and contact host cues was tested using three bioassays (locomotion compensator, six-chamber-olfactometer, stem arena) to account for different behavioural contexts. Bioassay-guided fractionation of plant extracts was elaborated to characterize the nature of contact stimuli. The beetles were only slightly attracted to odours from small amounts of leaf material. However, when contact cues were provided additionally, the beetles showed strong preferences for samples of their host plant over controls. Bioassay guided fractionation led to isolation of at least two non-polar contact stimuli acting in concert that are sufficient for host plant identification in *C. canaliculata*.

Tasin *et al*. (2010) reported that in case of herbivorous insects with more than one host plant, attraction to host odour could conceptually be mediated by common compounds or by specific compounds released by each plant or by combinations of common and specific compounds. They investigated by comparing the attraction of female grapevine moth, *L. botrana*, with specific and common (shared) odours from 2 different plants: a wild host (*Daphne gnidium* L.) and a recently colonized host (*Vitis vinifera* L.). Odour blends eliciting female attraction to *V. vinifera* have previously been identified. In this study, olfactory cues from *D. gnidium* were identified by electroantennographic detection and chemical analysis. The attraction of mated females to synthetic odour blends was then tested in a wind tunnel bioassay. Female attraction was elicited by a blend of compounds released by both from *D. gnidium* and *V. vinifera* and by 2 blends with the compounds released specifically from each host. However, complete odour blends of the both plants elicited stronger attraction. The common compounds in combination with the specific compounds of *D. gnidium* was the most attractive blend. This blend was tested with the common compounds presented both in

the ratio emitted by *D. gnidium* and by *V. vinifera*, but there was no difference in female attraction.

Rodriguez *et al*. (2010) revealed that ratios of compounds in host plant odours fluctuate with the phenological stage of the plant. They investigated the effect of changing ratios of host plant volatile constituents on herbivore insect attraction. They tested a synthetic mixture of bioactive peach shoot volatiles with different concentrations of one of the mixture constituents *viz*., benzonitrile, on oriental fruit moth, *Cydia (Grapholita) molesta* (Busck) (Lepidoptera: Tortricidae) females. Y-tube olfactometer bioassays showed that female attraction to the mixture was maintained while increasing the benzonitrile level up to 100 times. Nevertheless, further increases led to behaviourally ineffective mixtures.

Plant volatiles are important cues for many herbivorous insects when choosing a suitable host plant and finding a mating partner. An appropriate behavioural response to sensory cues from plants and other insects is crucial for their survival and fitness. As the natural environment can show both large spatial and temporal variability, herbivores may need to show behavioural plasticity to the available cues (Anderson and Anton, 2014).

Liu *et al*. (2010) reported that most adult lepidoptera feed on nectar, whereas caterpillars consume mainly structural tissue such as leaves, stems, flowers and/or fruits. This may result in behavioural trade-offs in which search time for high-quality oviposition sites suitable for larval food is restricted by adult foraging needs. In this study, they reported the preference and performance on flowering and non-flowering host plants of the generalist herbivore *Helicoverpa armigera* (Hubner) (Lepidotera: Noctuidae) to explore whether there are such behavioural trade-offs between moth and their offspring. They found that the adult moths have a strong oviposition preference for flowering tobacco and sunflower plants. Young caterpillars preferred to feed on the inflorescences.

Addesso and McAuslane (2009) suspected that the location of wild and cultivated host plants by pepper weevil (*Anthonomus eugenii* Cano) may be aided by visual cues, the male-produced aggregation pheromone and herbivore-induced/constitutive host plant volatiles. The attractiveness of constitutive plant volatiles to pepper weevils is important in understanding and perhaps controlling, dispersal of this insect between wild and cultivated hosts. Ten-day-old male and 2- and 10-day-old female weevils were tested in short-range Y-tube assays. Ten-day-old male and female weevils were attracted to the volatiles released by whole plants of three known oviposition hosts, 'Jalapeno' pepper, American black nightshade and eggplant, as well as tomato, a congener, which supports feeding but not oviposition. Two-day-old females were attracted to all plants tested, including lima bean, an unrelated non-host plant. Fruit volatiles from all three hosts and flower volatiles from nightshade and eggplant were also attractive. In choice tests, weevils showed different preferences for the oviposition hosts, depending on age and sex. Upwind response of 10-day-old male and female weevils to host plant volatiles was also tested in long-range wind tunnel assays. Weevils responded to pepper, nightshade and eggplant volatiles by moving upwind. There was no difference in the observed upwind

response of the weevils to the three host plants under no-choice conditions. Reproductively mature pepper weevils can detect, orient to and discriminate between the volatile plumes of host plants in the absence of visual cues, conspecific feeding damage or the presence of their aggregation pheromone.

Hori *et al*. (2006) investigated the behavioural responses of strawberry leaf beetle to host and non-host plant volatiles. Strawberry leaf beetle, *Galerucella vittaticollis* Baly, is an oligophagous insect that feeds on strawberry and polygonaceous plants. Beetles were attracted to the odours of their host, rosaceous plant, *Fragaria ananassa* Duchn. and polygonaceous plants, *Rumex obtusifolius* L., *Fagopyrum esculentum* Moench, *Polygonum thunbergii* Sieb. & Zucc., *Polygonum cuspidatum* Sieb. & Zucc. and *Polygonum blumei* Meisn. They were not attracted to non-host plants, *Raphanus sativus* L. (Brassicaceae), *Lycium chinense* Mill. (Solanaceae), *Artemisia princeps* Pampan. (Compositae) and *Triticum aestivum* L. (Gramineae). The main component of the headspace of all host plants tested was one of the green leaf volatiles, *cis*-3-hexenyl acetate.

It has been proven that many insect species use host plant odours as olfactory cues in finding hosts (Visser, 1986). Regarding the behavioural responses of Chrysomelidae to host plant odours, it is known that *Leptinotarsa decemlineata* (Say) are attracted to a specific combination of green leaf volatiles, *trans*-2-hexenal, *cis*-3-hexenyl acetate, *cis*-3-hexenol and *trans*-2-hexenol, from potato (Bernays and Chapman, 1994). Isothiocyanates, components of brassica volatile, attract *Phyllotreta cruciferae* (Goeze) and *Phyllotreta striolata* (Fabricius) (Feeny *et al*., 1970).

Bengtsson *et al*. (2001) reported that plant volatiles mediate host finding in insect herbivores and lead to host fidelity and habitat-specific mating. Chemical analysis and antennal recordings of apple fruit sucking moth, *Argyresthia conjugella* Zeller showed that 11 out of 15 rowan volatiles eliciting an antennal response in *A. conjugella* females co-occur in rowan and apple headspace, in a different proportion. In the field, *A. conjugella* was attracted to several of these plant volatiles, especially to 2-phenyl ethanol, methyl salicylate and decanal. Addition of anethole to 2-phenyl ethanol had a strong synergistic effect, the 1:1 blend is a powerful attractant for *A. conjugella* males and females. These results confirm that volatiles common to both plants may account for a host switch in *A. conjugella* from rowan to apple.

Bento *et al*. (2008) revealed that plant volatiles are important cues for the orientation of herbivorous insects. It is possible that these compounds indicate whether the plant is suitable for feeding and larval development or for mating aggregation. *Vernonia condensata L.* (Asteraceae) is known to attract species of leaf hoppers, most of them important vectors of the citrus variegated chlorosis (CVC). They evaluated the role of volatiles of *V. condensata* on the orientation of *Bucephalogonia xanthophis* (Berg.) (Hemiptera: Cicadellidae) using four-arm olfactometer bioassays and showed that only males were attracted to the volatiles of the host-plants *Citrus* sp. and *V. condensata*. Furthermore, fresh leaves of *V. condensata* induced a stronger response than volatiles from hexane-extracted leaves.

Johnson and Nielsen (2012) reported that root-feeding insects are key components in many terrestrial ecosystems. Like shoot-feeding insect herbivores, they exploit a range of chemical cues to locate host plants. They revealed that at least 74 other compounds elicit behavioural responses in root-feeding insects, with the majority (> 80 %) causing attraction. Low molecular weight compounds (e.g., alcohols, esters and aldehydes) underpin attraction, whereas hydrocarbons tend to have repellent properties. In contrast, they also reported that some secondary metabolites usually regarded as plant defenses (e.g., dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA)) can be exploited by some root-feeding insects for host location. While a range of plant-derived chemicals can affect the behaviour of root-feeding insects, limited attempts have been made to exploit these in pest management, though this may become a more viable option with diminishing control options.

In their quest for locating important resources such as mates, nutrients, oviposition and resting sites, insects rely on their chemical senses to a large extent. While gustatory neurons signal the quality of food or mates after contact, it is the information encoded by olfactory neurons that provides cues where to look in the first place (De Bruyne and Baker, 2008).

Responses of olfactory receptor neurons seem to indicate that host plant discrimination by herbivore insects must be mediated by the ratio of the compounds in the volatile blend (Bichao *et al*., 2003). Such strict ratio specificity, however, would question successful chemically mediated host-location behaviour by insects active across extended phenological stages of their host plants. In fruit orchards, quantitative composition of volatile blends emitted from trees varies with progressing plant development (Dotterl *et al*., 2005; Vallat *et al*., 2005), while attraction of fruit moths is maintained over several weeks (Vallat and Dorn, 2005). Given the variable nature of the chemical signal emitted by the same plant species, the question arises whether insect herbivores have evolved a certain degree of olfactory plasticity to locate their hosts within distinct threshold ratios of volatile blend constituents (Rodriguez *et al*., 2010).

Nishida (2014) concluded that plants produce a diverse array of secondary metabolites as chemical barriers against herbivores. Many phytophagous insects are highly adapted to these allelochemicals and use such unique substances as the specific host-finding cues, defensive substances of their own and even as sex pheromones or their precursors by selectively sensing, incorporating and/or processing these phytochemicals.

In insect-plant interactions, specificity might originate from the maintenance of a specific ratio in the plant-released volatile blends (Bruce *et al*., 2005). Studies on insect attraction to plants have largely focused on the use of affixed natural ratio of compounds in synthetic mixtures to mimic a given host plant blend (Natale *et al*., 2003; Webster *et al*., 2008). Insect attraction disappeared when the ratios of the key compounds as identified in the headspace of the host plant were replaced by the ratios of the same compounds emitted by a non-host plant (Tasin *et al*., 2006b).

Insect herbivores use plant volatiles to recognize and efficiently locate their host plants. Adult females perceive these odours via specialized olfactory receptor neurons and use the volatiles as chemical cues to identify suitable plants for feeding and/or oviposition (Anton *et al*., 2007; Carde and Willis, 2008). Volatile blends differ between plant species both qualitatively and quantitatively (Baldwin *et al*., 2006). The specific combination of compounds in these blends, many of which are ubiquitous as well as their ratios are assumed to drive host plant location in insects (De Moraes *et al*., 1998). Even minor constituents in a blend might contribute to the attraction of an insect species to its host plant (Birkett *et al*., 2004; Dalessandro *et al*., 2009; Tasin *et al*., 2007) and they may interact synergistically with major constituents at the behavioural and neurophysiological level as recently demonstrated for a fruit moth (Pinero and Dorn, 2007; Pinero *et al*., 2008).

Fraser *et al*. (2003) conducted an experiment using coupled gas chromatography with electroantennographic detection (GC-EAD) using antennae of adult female tobacco hornworm, *Manduca sexta* (Lin.) (Lepidoptera: Sphingidae) to screen for olfactory stimulants present in headspace collections from four species of larval host plants belonging to two families: Solanaceae-*Lycopersicon esculentum* L. (tomato), *Capiscum annuum* L. (bell pepper) and *Datura wrightii* L. and Martyniaceae-*Proboscidea parviflora* L. Headspace volatiles were collected from undamaged foliage of potted, living plants. GC–EAD revealed 23 EAD-active compounds, of which 15 were identified by GC-mass spectrometry. Nine EAD-active compounds were common to all four host plant species: (*Z*)-3-hexenyl acetate, nonanal, decanal, phenyl acetaldehyde, methyl salicylate, benzyl alcohol, geranyl acetone, (*E*)-nerolidol and one unidentified compound. Behavioural responses of female moths to an eight component synthetic blend of selected tomato headspace volatiles were tested in a laboratory wind tunnel. Females were attracted to the blend. A comparison of responses from antennae of males and females to bell pepper headspace volatiles revealed that males responded to the same suite of volatiles as females, except for (*Z*)-3-hexenyl benzoate. EAD responses of males also were lower for (*Z*)- and (*E*)-nerolidol and one unidentified compound.

Responses of female antennae to cotton odours were investigated in the Egyptian cotton leaf worm or African cotton leaf worm, *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae), is a polyphagous herbivore and an important pest of cotton using two different techniques. High sensitivity to different types of cotton odours were observed, among these several compounds known to be specifically induced by larval feeding. The effects of volatiles of plants infested by conspecific larvae were tested in two types of bioassay. The results indicated that odours from infested plants deterred oviposition, but females needed to perceive other plant stimuli for this discrimination. These studies showed that plant volatiles affect insects on several trophic levels and confirm that odours often interact with other plant stimuli in shaping insect behaviour (Jonsson, 2005).

Olfactory cues are likely to be signals that are more reliable. They may allow for host plant location even in a complex environment and the insect central nervous system receives the volatile information at a fine-scale spatio-temporal resolution (Held *et al*.,

2003). Nevertheless, certain semiochemicals can also be unreliable when they are emitted by both a host and a non-host (Eisner and Grant, 1981). Host odour specificity might be achieved through qualitative (Blight *et al*., 1995; Bartlet *et al*., 1997) or quantitative (Barata *et al*., 2000; Van Tol and Visser, 2002) blends of host volatiles and/or through the relative variability of compounds among hosts and non-hosts (Wright and Smith, 2004). Strictly monophagous herbivores may develop a great sensitivity to one or a few host-specific chemicals (Ferguson *et al*., 1983; Pereyra and Bowers, 1988).

Volatile cues emitted by plants guide insect host-finding and acceptance behaviour. Thus, traps releasing plant volatiles are used to repel herbivorous pests (Szendrei and Saona, 2010) or to attract and kill them (Gregg *et al*., 2010). Plants damaged by herbivore feeding emit an altered spectrum of volatiles that attracts parasitoids and predators. Herbivores may also avoid ovipositing on these plants (Das *et al*., 2013). Crop volatile emission can be manipulated by silencing existing volatile biosynthesis genes or by inserting them from other organisms. (*E*)-*β*-farnesene is emitted by many aphids when attacked by predators. *Arabidopsis thaliana* (L.) Heynh., tobacco and wheat have been transformed with genes for the biosynthesis of (*E*)-*β*- farnesene to discourage settlement by aphids (Yu *et al*., 2012).

The association of insect herbivores with their host plants is influenced by behaviours governing acceptance of those plants for feeding and oviposition. Behavioural changes accompany and may even precede host range expansion. Characterization and quantification of specific behaviours often form the basis of studies on host plant adaptation and chemical ecology. Behavioural assays of insects are usually designed to measure attraction for feeding or oviposition in relation to their host plants or specific chemistry. While carrying out behavioural assays of insect herbivores with host plants or the volatiles they emit, a special consideration should be given to design, analysis and interpretation to maximize ecological relevance. A tool kit of robust assays that can help to address fundamental issues at the intersection of ecology and evolution, such as the underpinnings of plant-insect interactions and the identification of genes involved in host race formation are reported by Knolhoff and Heckel (2014).

Pickett *et al*. (2012) reported that empirical exploitation of insect reception and detection at the peripheral neurosensory level has been extremely valuable for identifying pheromones and other semiochemicals mainly by electroantennogram or single cell preparations coupled with capillary gas chromatography. Differential sensitivity to semiochemicals at the single cell level has allowed the identification of some of the most active semiochemicals relating to host location and more importantly to the avoidance of non-hosts. Nevertheless, from electrophysiological studies to the most advanced molecular techniques, it has been possible to identify semiochemicals for the deception of pests in their quest to find plant and animal hosts, as well as mates. Even the deception of insects antagonistic to pests, particularly parasitoids, can now be exploited for managing pests in more sustainable systems.

Affixed natural ratio between different constituents of a blend is considered crucial in chemical communication between organisms including insect-mammal

(Takken *et al*., 1997), insect-human (Silva *et al*., 2005), predator-prey (Steullet *et al*., 2002), male-female insect (Carde and Minks, 1995; Linn *et al*., 1988; Witzgall *et al*., 2008) and insect-plant interactions (Visser, 1986). Meiners (2015) suggested that gaining a better understanding of infochemical-mediated host plant or host location behaviour of herbivores and their natural enemies in complex and heterogeneous chemical environments provides a multitrophic perspective to the chemical ecology and evolution of plant-insect interactions.

Use of plant volatiles technology as an additional tool in integrated pest management programs would offer a new and environmentally sound approach to crop protection. This technique involves the development of kairomones to attract insect pests, formulation of baits that attract beneficial organisms and the manipulation of biochemical processes that induce and regulate plant defenses as key factors in the improvement of current management programs against economically important pests (Arab and Bento, 2006).

2.2 Impact of herbivore induced plant volatiles (HIPVs) on herbivory

Plants under attack by a herbivore may emit characteristic volatiles that are implicated in the attraction of the natural enemies of the herbivore. The signal cascade between leaf damage and the volatile production is stimulated by high or low molecular weight elicitors from the secretions of the herbivore as reported by Boland *et al*. (1999).

In response to feeding damage, many plants release herbivore-induced plant volatiles (HIPVs), which are generally assumed to attract predators or parasitoids and thus, have the potential to act as an indirect defense. However, HIPVs are likely to affect the herbivores behaviour too. HIPVs released by herbivore-infested plants may deter further herbivores and thereby act as a direct defense (Dicke and Van Loon, 2000) but HIPV may also attract herbivores and thereby incur ecological costs (Bolter *et al*., 1997; Kalberer *et al*., 2001; Horiuchi *et al*., 2003). Thus, the ecological role of HIPVs may differ among plant and herbivore species.

The release of volatiles from vegetative organs following herbivore damage seems to be a general property of plant species. Examples are herbivore induced volatiles from cabbage (*Brassica oleracea* L.; Vuorinen *et al*., 2004), cucumber (*Cucumis sativus* L.; Mercke *et al*., 2004), wild legume (*Lotus japonicus* L.; Arimura *et al*., 2004) and maize (*Zea mays* L.; Degen *et al*., 2004). These substances serve as indirect plant defenses by attracting arthropods that prey upon or parasitize herbivores, thus minimizing further damage to plant tissue. In some cases herbivore-induced volatiles may also act as direct defenses by repelling (De Moraes *et al*., 2001) or intoxicating (Vancanneyt *et al*., 2001) herbivores and pathogens (Andersen *et al*., 1994).

Volatile compounds released by plants during thrips feeding have been documented to act both as an aggregation kairomone (Ananthakrishnan, 1993) and as a deterrent (Delphia *et al*., 2007).

Delphia *et al*. (2007) provided the first direct evidence that thrips feeding induces volatile responses and indicated that simultaneous herbivory by insects with different feeding habits can alter volatile emissions and in addition the findings demonstrated that induced plant responses influence host-plant selection by western flower thrips and suggested that the induction of volatile nicotine may play a role in this process.

Jordan *et al.* (2009) found that moths recognize a wide range of volatile compounds which they use to locate mates, food sources and oviposition sites. They identified 3 genes encoding olfactory receptors (ORs) from the tortricid moth, *Epiphyas postvittana* Walker (Lepidoptera: Tortricidae), a pest of horticultural crops. EpOR1 and EpOR3 both recognize a range of terpenoids and benzoates produced by plants. Of the compounds tested, EpOR1 shows the best sensitivity to methyl salicylate, a common constituent of floral scents and an important signaling compound produced by plants when under attack from insects and pathogens. EpOR3 best recognizes the monoterpene citral to low concentrations. Citral produces the largest amplitude electrophysiological responses in *E. postvittana* antennae and elicits repellent activity against ovipositing female moths.

Some plant species when attacked by herbivorous insects or mites call on other arthropods for help by emitting mixtures of volatile compounds dominated by terpenes to attract carnivorous arthropods that prey on or parasitize herbivores and so reduce further damage (Degenhardt *et al*., 2003).

Frati *et al*. (2008) conducted wind tunnel and vertical open Y-shaped olfactometer studies to test whether volatile cues from the host plant (*Vicia faba* L.), from conspecific bugs and from a plant-conspecifics combination, would elicit behavioural responses in mated males and females of the European tarnished plant bug, *Lygus rugulipennis* Popp (Hemiptera: Miridae). In the olfactometer, females moved towards volatiles from healthy plants but they do not respond to volatiles released by oviposition and/or feeding damaged plants without conspecifics, nor to conspecifics alone. Both in the wind tunnel and olfactometer, females responded to volatiles emitted by the plant-insect complex. By contrast, in the wind tunnel, both sexes moved significantly towards damaged host plants. Even the presence of conspecifics on these plants enhanced response only in the females. However, the presence of eggs from conspecifics on host plants reduced the responses of both sexes in the wind tunnel. Finally, males as well as females were less responsive to conspecifics alone compared with damaged plants especially when conspecifics were present on the host plants.

Robert *et al*. (2012) revealed that in response to herbivore attack, plants mobilize chemical defenses and release distinct bouquets of volatiles. Above ground herbivores are known to use changes in leaf volatile patterns to make foraging decisions, but it remains unclear whether below ground herbivores also use volatiles to select suitable host plants. They investigated how above and below ground infestation affects the performance of the root feeder western corn root worm, *Diabrotica virgifera* Leconte (Coleoptera: Chrysomelidae) and whether the larvae of this specialized beetle are able to use volatile cues to assess from a distance whether a potential host plant is already under herbivore

attack. Fittingly, *D. virgifera* larvae were attracted to plants that were infested with conspecifics, whereas they avoided plants that were attacked by *S. littoralis*. They identified (*E*)-*β*-caryophyllene, which is induced by *D. virgifera* and ethylene, which is suppressed by *S. littoralis*, are two signals used by *D. virgifera* larvae to locate plants that are most suitable for their development.

Pare and Tumlinson (1999) reported that in response to insect leaf feeding, the cotton (*Gossypium hirsutum* L.) plants release elevated levels of volatiles which can serve as a chemical signal that attracts natural enemies of the herbivore to the damaged plant.

Kessler and Baldwin (2001) found that herbivore attack increases the emission of volatiles, which attract predators to herbivore-damaged plants in the laboratory and agricultural systems. They quantified volatile emissions from *Nicotiana attenuata* plants growing in natural populations during attack by three species of leaf-feeding herbivores and mimicked the release of five commonly emitted volatiles individually. Three compounds *cis*-3-hexen-1-ol, linalool and *cis*-a-bergamotene increased egg predation rates by a generalist predator, linalool and the complete blend decreased lepidopteran oviposition rates. As a consequence, a plant could reduce the number of herbivores by more than 90 % by releasing volatiles.

Turlings and Ton (2006) revealed that plants actively and systemically emit herbivore induced plant volatiles (HIPVs) in response to feeding by arthropods and can be exploited in agricultural pest control because they might repel herbivores and serve as attractants for the enemies of the herbivores. Indeed, recent studies with transgenic plants confirm that odour emissions can be manipulated in order to enhance the plants attractiveness to beneficial arthropods. An additional advantage of manipulating HIPV emissions could be their effects on neighbouring plants, as a rapidly increasing number of studies show that exposure to HIPVs prime's plants for augmented defense expression. Targeting the right volatiles for enhanced emission should lead to ecologically and economically sound ways of combating important pests.

Herbivore damage to leaves and other vegetative tissues often stimulates the emission of volatile compounds, suggesting that these substances have a role in plant defense. In fact, ample evidence has accumulated in the last few years indicating that volatiles from vegetative plant parts can directly repel herbivores, such as ovipositing butterflies and host-seeking aphids. Volatiles have also been demonstrated to protect plants by attracting herbivore enemies, such as parasitic wasps, predatory arthropods and possibly even insectivorous birds. Even below ground herbivory results in the release of volatiles that attract herbivore enemies. However, plant volatiles are also known to attract enemies of plants. Hence, to determine the true value of these substances in defense more research is needed especially in natural communities with non agricultural species as reported by Unsicker *et al*. (2009).

McCormick *et al*. (2012) found that plants respond to herbivore attack by emitting complex mixtures of volatile compounds that attract herbivore enemies, both predators

and parasitoids. They explored that whether these mixtures provide significant value as information cues in herbivore enemy attraction and survey indicated that blends of volatiles released from damaged plants are frequently specific depending on the type of herbivore and its age, abundance and feeding guild. The sensory perception of plant volatiles by herbivore enemies is also specific according to the latest evidence from studies of insect olfaction. Thus, enemies do exploit the detailed information provided by plant volatile mixtures in searching for their prey or hosts but this varies with the diet breadth of the enemy.

Shulaev *et al*. (1997) and Park *et al*. (2007) reported that methyl salicylate is a common plant stress signal elicited in response to abiotic and biotic factors such as damage by insect herbivores and pathogens and is also the airborne version of salicylic acid, used by plants as a signal to propagate systemic acquired resistance.

Ulland *et al*. (2008) found that in the cabbage moth, *M. brassicae*, methyl salicylate is a strong deterrent of oviposition, likely acting as a signal to warn females that a plant has already been colonized and that the plant's defenses have been primed.

Tinzaara *et al*. (2005) reported that predators of the banana weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae) such as *Dactylosternum abdominale* (Fabricius) (Coleoptera: Hydrophilidae) and *Pheidole megacephala* (Fabricius) (Hymenoptera: Formicidae) are normally found in association with weevil-infested rotten pseudostems and harvested stumps. They investigated whether these predators are attracted to such environments in response to volatiles produced by the host plant, by the weevil or by the weevil-plant complex. They evaluated predator responses towards volatiles from banana pseudostem tissue (synomones) and the synthetic banana weevil aggregation pheromone Cosmolure+ in a two-choice olfactometer. The beetle *D. abdominale* was attracted to fermenting banana pseudostem tissue and Cosmolure+, whereas the ant *P. megacephala* was attracted only to fermented pseudostem tissue. Both predators were attracted to banana pseudostem tissue that had been damaged by weevil larvae irrespective of weevil presence.

Cardoza and Tumlinson (2006) found that pepper plant volatile profiles can be differentially induced by compatible and incompatible bacterial infection and beet armyworm (BAW) damage when applied alone or in combination upon the same host. They also found that plants under simultaneous compatible bacterial and BAW attack are able to produce volatiles in quantities greater than those produced by healthy plants in response to BAW feeding. In contrast, plants exposed to the incompatible pathogen challenge showed a total volatile release below the level of healthy plants exposed to BAW damage.

Despite the fact that volatiles are induced in response to caterpillar attack, their reciprocal effects on the host location behaviours of the same foraging herbivores are poorly understood. Orientation responses of sixth instar fall armyworm [FAW; *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae)] to odours from herbivore-damaged and undamaged maize seedlings (*Zea mays* var. Golden Queen) was examined

in Y-tube olfactometer bioassays. The results revealed that both damaged and undamaged maize seedlings were attractive compared with air, sixth instars preferred odours from damaged maize seedlings over odours from undamaged maize seedlings (Carroll *et al*., 2006)

Reisenman *et al*. (2013) studied the oviposition preference of female tobacco hornworm, *Manduca sexta* (Linnaeus) towards intact and damaged host plants of three species, *Datura wright* Regel, *Datura discolor* Bernh. (a less preferred feeding resource used by females for oviposition) and *Solanum lycopersicum* L. (tomato, used by moths as preferred oviposition resource). Damage was inflicted to the plants either by larval feeding or artificial damage. Mated females were exposed to an intact plant and a damaged plant and allowed to lay eggs for 10 min. Oviposition preferences of females were highly heterogeneous in all cases, but a larger proportion of moths laid significantly fewer eggs on feeding-damaged and artificially damaged plants of *S. lycopersicum*. Chemical analyses showed a significant increase in the total amount of VOCs released by vegetative tissues of feeding-damaged plants, as well as species specific increases in emission of certain VOCs.

Detailed studies involving chemical and behavioural assays by De Moraes *et al*. (2001) revealed that tobacco plants (*Nicotiana tabacum* L.) release herbivore-induced volatiles during both night and day. They found that several volatile compounds are released exclusively at night and are highly repellent to female tobacco budworm moths [*Heliothis virescens* (Fab.) (Lepidoptera: Noctuidae)]. They demonstrated that tobacco plants release temporally different volatile blends and the lepidopteran herbivores use induced plant signals released during the dark phase to choose sites for oviposition adds a new dimension to understanding of the role of chemical cues in mediating tritrophic interactions.

Arimura *et al*. (2009) revealed that HIPVs mediate sizable arrays of interactions between plants and arthropods, microorganisms, undamaged neighboring plants or undamaged sites within the plant in various ecosystems. HIPV profiles vary according to the plant and herbivore species and the developmental stages and conditions of the live plants and herbivores.

Saona *et al*. (2005) conducted an experiment to study whether herbivore-induced plant responses can affect the preference and performance of herbivores and their natural enemies. This study involved tomato plants damaged either by the caterpillar of beet armyworm/small mottled willow moth, *Spodoptera exigua* (Hubner) (Lepidoptera: Noctuidae) or the potato aphid, *Macrosiphum euphorbiae* (Thomas) (Homoptera: Aphididae) or damaged by both herbivores and undamaged controls. They measured the preference and performance of *S. exigua* and its parasitoid *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) and the activity of proteinase inhibitors (PIs) as an indicator of induced resistance. Compared to undamaged plants, caterpillar damage not only reduced the number of eggs laid by *S. exigua* adults but also reduced growth and consumption/survival of *S. exigua* larvae/*C. marginiventris* respectively. It further increased the activity of PIs by 43 %, but did not increase the attraction of

C. marginiventris. However, the pupal mass of *S. exigua* was not affected, but the pupal mass of *C. marginiventris* decreased on caterpillar-damaged plants compared to controls. In contrast, plants damaged by aphids were preferred for oviposition by *S. exigua* and had increased larval consumption and survival compared to controls. Aphid feeding did not affect the preference or performance of *C. marginiventris* or PI activity compared to controls.

Neveu *et al*. (2002) conducted an experiment using a four-arm olfactometer and investigated the attraction of naive females of *Trybliographa rapae* Westwood (Hymenoptera: Figitidae) (a specific larval endoparasitoid of *Delia* species) toward uninfested and infested turnip plants. The *T. rapae* females were not attracted to volatiles emanating from uninfested plants, whether presented as whole plants, roots or leaves. In contrast, they were highly attracted to volatiles emitted by roots infested with cabbage root fly, *Delia radicum* L. larvae, by undamaged parts of infested roots and by undamaged leaves of infested plants.

Tumlinson *et al*. (1999) reported that an increase in the release of volatile compounds by plants in response to insect feeding is triggered by interaction of elicitors in the oral secretions of insect herbivores with damaged plant tissues. This herbivore damage triggers *de novo* biosynthesis of volatile plant metabolites derived from several different biochemical pathways. Natural enemies of herbivores use these volatile semiochemicals to locate their hosts. Although some volatile compounds are released from storage in plants immediately whenever damage to cells or glands occurs, the induced compounds are only synthesized and released during the light period. This often results in a delay between feeding damage and release of volatiles. Plants release the induced compounds from undamaged as well as damaged leaves. Thus, damage to only a few leaves results in a systemic response and release of volatiles by the entire plant. They proposed that plants respond differently to individual herbivore species at least in part due to the composition of insect elicitors that come in contact with the plant. Specialist parasitoids can differentiate the volatile blends released due to damage by hosts from those resulting from non-host damage as well as from mechanical damage, thereby facilitating host location for the parasitoid.

Plants are commonly attacked by more than one species of herbivore, potentially causing the induction of multiple and possibly competing plant defense systems. Interaction between feeding by the phloem feeder silverleaf whitefly (SWF), *Bemisia tabaci* Gennadius (B-biotype = *B. argentifolii* Bellows and Perring) and the leaf-chewing beet armyworm (BAW), *S. exigua*, with regard to the induction of volatile compounds from cotton plants was studied in detail. Compared to undamaged control plants, infestation with SWF did not induce volatile emissions or affect the number and density of pigment glands that store volatile and nonvolatile terpenoid compounds, whereas infestation by BAW strongly induced plant volatile emission (Saona *et al*., 2003).

Volatiles are also serve as important cues for insect herbivores to assess host plant quality. It has been established in female moths of the Egyptian cotton leafworm, *S. littoralis* that they avoid oviposition on damaged cotton, *Gossypium hirsutum* L., which may mediated by herbivore-induced plant volatiles (HIPVs). Among the HIPVs,

some volatiles are released following any type of damage while others are synthesized *de novo* and released by the plants only in response to herbivore damage. In behavioural experiments oviposition by *S. littoralis* on undamaged cotton plants was reduced by adding volatiles collected from plants with ongoing herbivory. Gas chromatography-electroantennographic detection (GC-EAD) recordings revealed that antennae of mated *S. littoralis* females responded to 18 compounds from a collection of headspace volatiles of damaged cotton plants. Among these compounds, a blend of the seven *de novo* synthesized volatile compounds was found to reduce oviposition in *S. littoralis* on undamaged plants under both laboratory and ambient (field) conditions in Egypt. Volatile compounds that are not produced *de novo* by the plants did not affect oviposition (Zakir *et al*., 2013).

De Moraes *et al*. (1998) found that in response to insect herbivory plants synthesize and emit blends of volatile compounds from their damaged and undamaged tissues, which act as important host-location cues for parasitic insects. They used both chemical and behavioural assays to show that these plant emissions can transmit herbivore-specific information that is detectable by parasitic wasps (parasitoids). Tobacco, cotton and maize plants each produced distinct volatile blends in response to damage by two closely related herbivore species, tobacco budworm, *Helicoverpa virescens* and corn earworm, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae). The specialist parasitic wasp, *Cardiochiles nigriceps* Viereck (Hymenoptera: Braconidae) exploits these differences to distinguish the infestation by its host, *H. virescens*, from that by *H. zea*. The distinct volatile production by phylogenetically diverse plant species and the exploitation by parasitoids of highly specific chemical signals keyed to individual herbivore species indicate that the interaction between plants and the natural enemies of the herbivores that attack them is more sophisticated than previously realized.

Heil (2004) found that in response to feeding damage, lima bean releases HIPVs which are generally assumed to attract carnivorous arthropods as an indirect defense. While many studies have focused on such tritrophic interactions, he investigated effects of HIPVs on herbivores and conducted an experiment by using natural herbivores of wild lima bean and studied their responses to jasmonic acid-induced plants in an olfactometer and in feeding trials. Both, *Cerotoma ruficornis* (Olivier) and *Gynandrobrotica guerreroensis* (Jacoby) (Coleoptera: Chrysomelidae) significantly preferred control plants to induced ones in the olfactometer and they avoided feeding on induced plants. In contrast, Curculionidae significantly preferred HIPVs of the induced plant to those of the control in one plant pair and did not choose in the case of a second pair. In feeding trials, no choice occurred in the first plant pair, while control leaves were preferred in the second. Release of HIPVs deterred the chrysomelid herbivores and thus acted as a direct defense. This may be an important addition to indirect defensive effects. Whether or not HIPVs released by induced plants attracted herbivorous Curculionidae. Such incurring ecological costs varied among the plants. Such differences could be related to various HIPVs blends released by individual plants.

As semiochemicals induced volatiles may alter the recruitment of herbivores to the damaged host plant, not only by providing chemical cues for host plant location, but

also information on the damage status of the host plant (Bernasconi *et al*., 1998). Behavioural responses of foraging lepidopterans to these cues have been examined primarily in adults because selection of an appropriate host plant for offspring is largely a consequence of female oviposition preferences rather than the consumer (caterpillar) itself (Thompson and Pellmyr, 1991).

Alternatively, some adult coleopterans exploit the relatively greater volatile output of induced plants to locate hosts and conspecifics (Harari *et al*., 1994; Lougrin *et al*., 1995; Landolt *et al*., 1999). In both cases, the greater mobility of adults allows for expanded search capabilities for suitable host plants with reduced search time, minimal search costs and limited exposure to mortality factors (Stamps and Krishnan, 2005; Stamps *et al*., 2005).

Some herbivorous arthropods can detect their hosts using volatile compounds released by healthy plants, which can also stimulate oviposition and courtship behaviours in these organisms (Rojas *et al*., 2003). The Colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae) is attracted to damaged *Solanum tuberosum* L. (Solanaceae) plants (Dickens, 2002). Consequently, for herbivores, plant volatiles represent a complex message that is interpreted according to their biological context.

Dicke and Baldwin (2010) reported that herbivores, pathogens, pollinators and competitors also respond to HIPVs and in addition, neighbouring plants in native populations also emit volatiles that provide a background odour. These considerations enrich the evolutionary context of HIPVs and complicate predictions about their adaptive value.

2.3 Role of conspecific body odours in herbivores

Reddy and Guerrero (2004) reported that plant semiochemicals are known to produce a wide range of behavioural responses in insects. Some insects sequester or acquire host plant compounds and use them as sex pheromones or sex pheromone precursors. Other insects produce or release sex pheromones in response to specific host plant cues and chemicals from host plants often synergistically enhance the response of an insect to sex pheromones. Plant volatiles can also have inhibitory or repellent effects that interrupt insect responses to pheromones and attract predators and parasitoids to the attacking species after herbivore injury. They reviewed different interactions between plant semiochemicals and insect pheromones and concluded that paying attention to those can result in the development of more efficient and reliable programs for pest control.

Siciliano *et al*. (2014) concluded that olfaction plays a key role in the invasive potential of Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) and they did isolation of chemicals emitted by sexually mature individuals during the “calling” period and the electrophysiological responses revealed that these compounds elicit response on the antennae of male and female flies. This study aimed towards the creation of new powerful attractants or repellents applicable in the actual control strategies.

Terpenes such as citral, make up a large proportion of all volatile compounds produced by plants (Dudareva *et al*., 2004) and have been implicated as important oviposition cue in a number of moth species, including the codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) and *H. armigera* (Jallow *et al*., 1999; Witzgall *et al*., 2005). In adult light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), citral elicits the greatest electrophysiological responses by EAG in both males and females and in behavioural studies it is an oviposition repellent to females (Suckling *et al.*, 1996).

Milne *et al*. (2007) reported that in *Frankliniella schultzei* Trybom (Thysanoptera: Thripidae) most females responded to male presence before physical contact, suggesting that male pheromones may be involved.

Two major components have been detected in the headspace volatiles of adult male *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) that are not present in the headspace volatiles of adult females. The compounds were identified as (*R*)-lavandulyl acetate and neryl (*S*)-2-methylbutanoate by comparison with synthetic standards using gas chromatography (GC), GC mass spectrometry (MS) and chiral GC (Hamilton *et al*., 2005).

Kirk and Hamilton (2004) reported that olfactometer bioassays of walking adult western flower thrips, *F. occidentalis* showed that virgin females (1- to 3-d postemergence) were attracted to the odour of 25 adult males, but not to the odour of 25 adult females, providing behavioural evidence for a male-produced sex pheromone in this species. In contrast to earlier findings, mixed-age adult males were attracted to the odour of adult males. GC analysis of odours collected on SPME fibers revealed two major components and five minor components that were present in the male odour and not in the female odour. The compounds were not present in hexane extracts of males, indicating that these compounds are produced on demand and not stored.

Many insects use olfactory cues to find potential hosts, mates or oviposition sites to lay eggs. Over 1600 moth sex pheromones have been identified, along with smaller numbers of sex, aggregation and other types of pheromones for other insects. Kairomones (operating between species) include more generic cues used for host or habitat location and are also emerging as a potentially valuable monitoring tools for groups such as mosquitoes, bark beetles and other groups. Recent advances in the identification of behaviour-modifying chemicals (semiochemicals) have meant that their rate of identification has increased dramatically, along with the development of a new range of formulations for deploying them through slow release systems (Suckling and Karg, 2000).

Sexual communication in phytophagous insects is evidently strongly influenced by the host plant. Plant volatile compounds are known to act on the nervous and hormonal system of female moths to stimulate pheromone production and release and enhance attraction of male moths to female-produced sex pheromone (McNeil and Delisle, 1989; Raina *et al*., 1992; Landolt and Phillips, 1997). The interaction between sex pheromones and host plant volatiles enhances mate and host finding.

III MATERIAL AND METHODS

Capsicum (*Capsicum annum*) has attained the status of a high value crop in India during recent years but comprehensive studies on insect-plant interactions needs to be carried out to understand scientific basis of tri-trophic interactions that will in turn help to strengthen our current IPM programs. Of all insect pests that attack Capsicum, Thrips, *Scirtothrips dorsalis* Hood, is an important pest and it's interaction with the host plant is yet to be fully understood. Laboratory experiments were conducted to understand and identify the role of chemical cues involved in *S. dorsalis* and its host plant interaction. We also explored the feasibility of isolating/identifying the potential cues involved in behavioural modifications for use in push-pull strategies.

Studies were conducted at the Division of Entomology and Nematology, Indian Institute of Horticultural Research (IIHR), Hessaraghatta Lake PO, Bengaluru (located at latitude of 12^{o} 58' N, longitude of 77^{o} 35' E at an altitude of 890 m MSL) during 2014-2015. The details are presented under the following headings.

3.1 Insects

Adults of *S. dorsalis* collected from the *C. annum* fields at IIHR experimental farm were used for all the laboratory studies. Thrips were collected during early hours of the day using glass aspirator (10 cm length x 2 cm diameter) with rubber corks.

For conducting laboratory studies on co-occurring sap sucking insects and mites namely cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), silverleaf whitefly, *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) and spidermite, *Tetranychus macfarlanei* Baker & Pritchard (Acari: Tetranychidae) were selected. The adults of aphid, *A. gossypii* were collected from *C. annum* fields at IIHR experimental farm. Similarly, the adult whiteflies, *B. tabaci* were collected from french bean grown under glass house at GKVK experimental farm. The adult mite, *T. macfarlanei*, were collected from okra field at GKVK experimental farm. All the insects and mites were collected during early hours of the day (Plate 1).

3.2 Maintenance of host plants

Ready to transplant seedlings of *C. annum cv. Indra* (25-30 days old) were procured from Vegetable Nursery, (S. L. N. Nursery, Matkur cross, Shivakote, Hessaraghatta main road, Bengaluru-560089) and were transplanted into plastic pots (27 cm length × 27 cm top width × 22 cm base width) and placed in glass house at IIHR experimental farm. All regular cultural and agronomic practices were followed to maintain the plants (Plate 2).

3.3 Collection of Capsicum plant volatiles

3.2.1 Attractiveness of host plant volatiles of *Capsicum annum* to adult *S. dorsalis*

Host plant volatiles were collected at three different growth stages of the plant such as pre-flowering, flowering and fruiting using air entrainment systems to determine which growth stage of the crop is more attractive to thrips, *S. dorsalis* (Plate 4).

3.2.2 Attractiveness of herbivore induced plant volatiles (HIPVs) (thrips infested) to thrips, *S. dorsalis* and co-occurring sap sucking insects

Fifty to fifty five days after transplantation, the plants were artificially infested with thrips (250-300 thrips/plant/pot) collected from the field and placed in a glass cage having an aluminium 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 length x 0.55 m width x 0.55 m height) to prevent thrips escape from plants (Plate 3). For comparison, the healthy Capsicum plants were also maintained in thrips proof plant cages as described above. Daily the healthy plants were sprayed with water using pressurized hand sprayer to prevent settling of thrips if any on the plants. Ten days after releasing the thrips, both artificially infested as well as healthy Capsicum plants along with pots were brought to the laboratory for volatile collection.

Before volatile collection, all the necessary glasswares and aluminium plates were washed with aqueous teepol detergent, rinsed with distilled water followed by acetone and then dried in a hot air oven at 120^{o} C for 2 h. Porapak Q tubes (50 mg, 60/80 mesh; Supelco, Sigma Aldrich, India) of 5 mm diameter and 5 cm length were used for collection of volatiles. These tubes were washed with redistilled diethyl ether and heated at 120^{o} C for 2 h in a hot air oven to remove contaminants. Autoclaved polythene bags were used to cover the Capsicum plants. The poly bag 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 into 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 Capsicum plants were entrained for 48 hours and the porapak Q tubes containing the volatile compound were eluted with 750 µl of redistilled diethyl ether, providing a solution that contained the isolated volatile compounds that served as test sample. Sample was stored in glass vial in a freezer (-20^{o} C) until use.

3.3 Influence of conspecific body odours to adult *S. dorsalis*

3.3.1 Collection of thrips body odours through air entrainment

For collection of thrips body odours, a dome shaped glass vessel (6 cm length × 5 cm width; 50 ml volume) with inlet and outlet ports on either side of the dome was used. Before using, the vessel was sterilized with acetone and kept in hot air oven for 2 hrs at 120^{o} C. Later, the field collected thrips were placed in the vessel and made air tight. Later, the thrips contained vessel was connected to the volatile extraction machine

Scirtothrips dorsalis

Bemesia tabaci

Aphis gossypii

Tetranychus macfarlanei

Plate 1. Test insects used in experiment

Plate 2. Maintenance of host plants

Plate 3. Maintenance of host plants in cages

(Rothamsted Research, UK) through inlet and outlet connections using two suction tubes. The purified air as described in the section 3.2.2 was pumped into the glass vessel at 600 mL/min through the inlet port and was drawn out at 800 mL/min through Tenax glass tubes (50 mg, 60/80 mesh; Supelco, Sigma Aldrich, India) of 5 mm diameter and 5 cm length were used for collection of volatiles. All connections were made with polytetrafluroethylene (PTFE) tubing with brass ferrules and fittings. The volatiles from thrips body were entrained for 2 hrs and the Tenax filters were eluted with 600 µl of redistilled diethyl ether, providing a solution that contained the isolated volatile compounds that served as test sample. Sample was stored in glass vial in a freezer (-20^{o} C) until use (Plate 5).

3.3.2 Collection of thrips body wash in different solvents

For collection of thrips body wash, two solvents with varied polarity indices such as dichloromethane (polarity index is 3.1) and hexane (polarity index is 0.1) were used. The adult thrips collected from the field, permeated in dichloromethane and hexane solvents separately for 5 min. after which the solvent is filtered and concentrated. Sample was stored in glass vial in a freezer (-20^{o} C) until use.

3.4 Olfactometer bioassays

3.4.1 Four-arm olfactometer bioassays

A Perspex four-arm olfactometer (Pettersson, 1970) was used to determine the behavioural responses of adult *S. dorasalis* and also the co-occurring sap sucking insects namely aphids, whiteflies to head space samples of volatiles (Plate 6).

Prior to each experiment, all glasswares were washed with teepol, rinsed with acetone and distilled water and baked in an oven overnight at 160^{o} C. Perspex components were washed with teepol solution, rinsed with 80 per cent ethanol solution and distilled water and left to air dry. Experiments were conducted in an isolated room (25 ± 2^{o} C, 60 % RH) to avoid contaminant odours. The olfactometer had four glass side arms leading into a central area which was divided into four odour 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 by uniform lighting from white fluorescent bulb (10 watts) covered with opaque dome to make it diffuse and was surrounded by a black wall cage (0.62 m length × 0.62 m wide × 0.62 m height) to remove any extra visual stimuli. Olfactometer bioassay was conducted as described by Jayanthi *et al*. (2012).

3.4.2 Handling of test insects for olfactometer bioassays

The field collected adult *S. dorsalis* and other co-occurring sap sucking insects starved for 2 hours were introduced individually through a hole in the top of the olfactometer. After introducing the test insects in to the olfactometer arena, each insect was observed for 10 min. The olfactometer was rotated at 90^{o} for every two min. to eliminate any directional bias in the room. Air was drawn through the central hole at the rate of 900 mL min^{-1}. The central arena of the olfactometer was divided into four discrete odour fields corresponding to each of four glass inlet arms (Plate 6a). Of four glass arms,

one contained the treatment and the other three arms served as controls, unless a choice test was performed that used two different treated arms (opposite arms 1, 3) and two control arms (opposite arms 2, 4). Test samples (10 µl) 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 for head space volatile sample collection and dichloromethane and hexane for thrips body wash collection respectively) served as controls in the remaining three arms. Time spent in each olfactometer arm and also number of entries to each olfactometer arm was recorded with Olfa software (F. Nazzi, Udine, Italy).

3.4.3 Types of olfactometer bioassays carried out

Bioassays were carried out to understand the response of adult *S. dorsalis* to host plant volatiles (collected from preflowering, flowering, fruiting stages and from healthy as well as thrips infested Capsicum plants) and thrips body odours. Similarly, bioassays were also carried out to understand the response of healthy as well as thrips infested Capsicum plant volatiles to co-occurring sap sucking insects. Twenty replicates were carried out for each crop growth stage head space volatiles tested. Whereas, ten replicates were carried out for assays that involved healthy and herbivore induced host plant volatiles and also thrips body odour assays. Further, bioassays were also carried out to test the attraction of GC-EAD active compounds.

Five types of bioassays were carried out. The first and second series of bioassays (single test compound assay) had one treated arm and three solvent control arms in each replicate. In the first series of bioassays, responses of adult *S. dorsalis* to the natural air entrainment samples of Capsicum plant were studied. In the second series, responses to synthetic compounds were studied. Compounds were tested individually (10 µl dose) and as blends that contained identified compounds which elicited an EAD response at the same concentration and ratio as in the headspace sample.

In the third and fourth series (dual choice assays), choice tests between the healthy and infested plant volatiles and also natural sample and synthetic blends were conducted and each replicate had two treated arms (healthy/infested and natural sample/synthetic blend) and two control arms (solvent blank).

In the fifth series, multiple choice test between pre-flowering, flowering, fruiting plant volatiles and control were carried out simultaneously. Similarly, multiple choice assays were also carried out for healthy, infested, thrips body wash and control.

3.4.4 Statistical analyses

For the first and second series of bioassays, the mean time spent in treated and control regions and mean number of entries to treated and control regions were compared using a paired *t*-test (SPSS version 2006) after calculating the mean time spent and mean number of entries per control arm for each replicate.

In the third and fourth series involving dual choice assays, time spent in each odour field, (healthy *vs*. infested sample *vs*. solvent control and natural *vs*. synthetic blend

Plate 4. Collection of host plant headspace volatiles using air entrainment system

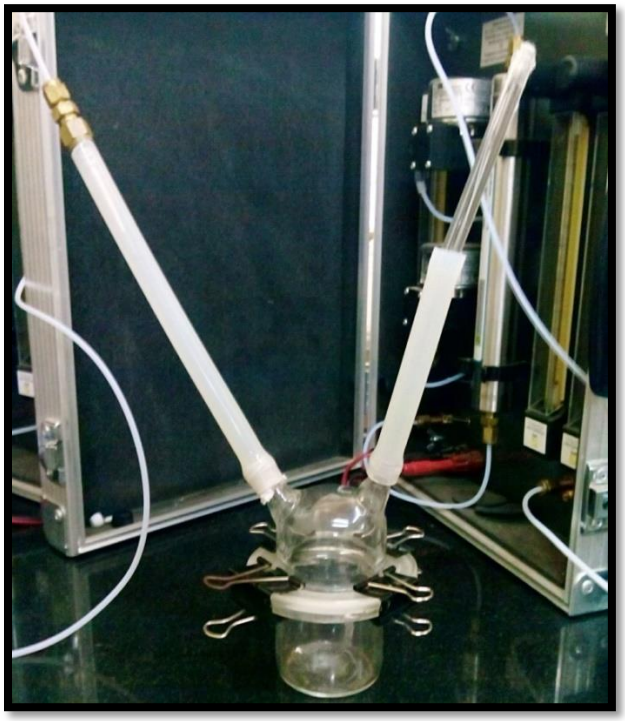


Plate 5. Collection of thrips body odour using air entrainment system

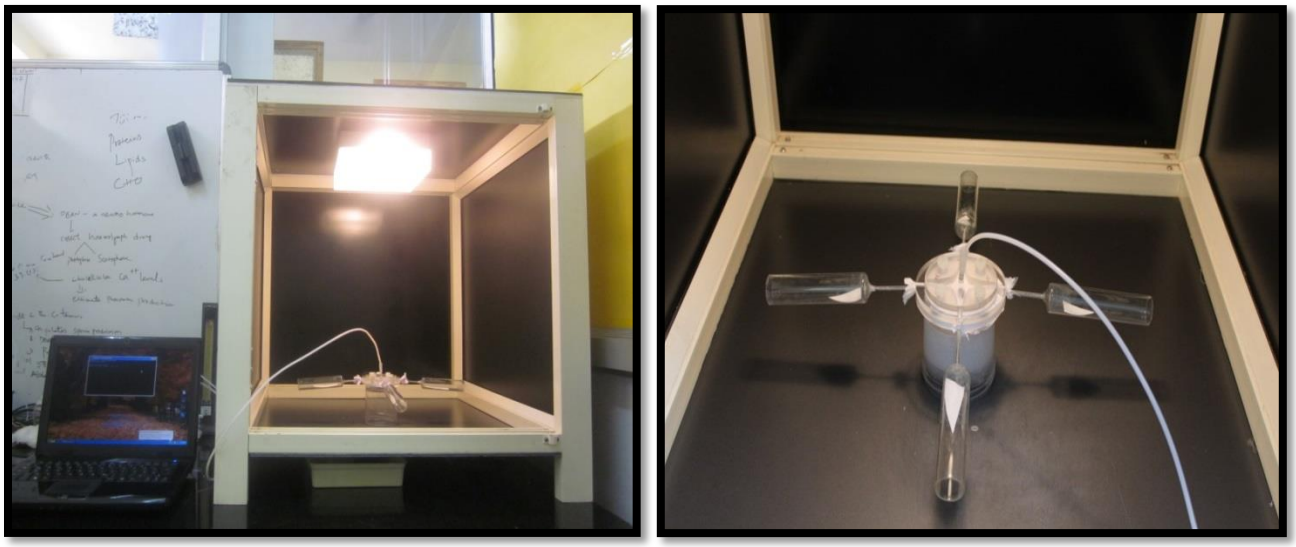


Plate 6. Perspex four-arm olfactometer (General view- left; closed view- right)

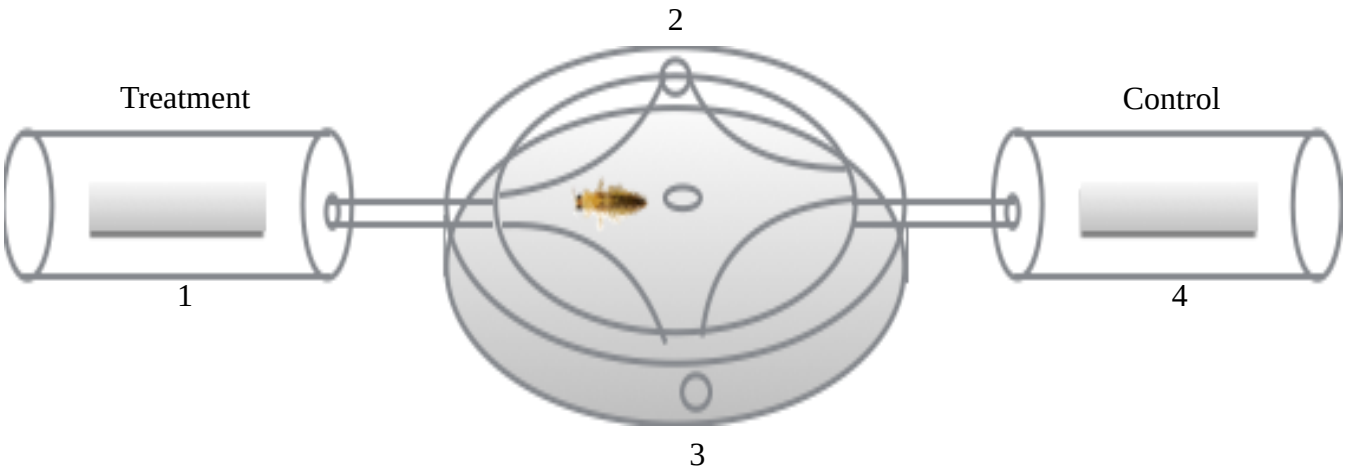


Plate 6a. Diagramatic representation of four-arm olfactometer

vs. solvent control) and mean number of entries to each treated arm and the control arm were compared by analysis of variance (ANOVA) after conversion of the data into proportions and a logratio transformation followed by post hoc analysis as Tukey's multiple mean comparision test. Means were separated using Fisher's LSD test with α set at 0.05 (Genstat version 12, VSN International)

In the fifth series, multiple choice tests involving pre-flowering, flowering, fruiting plant volatiles and control and also healthy, infested plant volatiles, thrips body wash and control, the bioassay data (time spent in each odour field, pre-flowering *vs*. flowering *vs*. fruiting *vs*. solvent control and healthy *vs*. infested *vs*. body wash *vs*. solvent control) were compared by analysis of variance (ANOVA) after conversion of the data into proportions and a logratio transformation followed by post hoc analysis as Tukey's multiple mean comparision test. Means were separated using Fisher's LSD test with α set at 0.05 (Genstat version 12, VSN International).

3.4.5 Y tube olfactometer bioassays

The behavioural responses of the adult mites, *T. macfarlanei* to healthy and thrips infested Capsicum plant volatiles of same age were tested in dual-choice Y-tube olfactometer bioassays. Olfactometer trials were carried out as described in Pinero and Dorn (2007) and Pinero *et al*. (2008). Briefly, the Y tube olfactometer consisted of a Y-shaped glass tube (1 cm diameter, 8 cm arm length and 16 cm common arm length) connected to two tubular glass chambers (6 cm long and 2.5 cm in diameter), where the odour sources were placed (one on each arm). Charcoal-filtered air was drawn into each of the two glass chambers and Y tube arms at a rate of 600 mL min^{-1} at the entrance. All parts of the olfactometer were washed in a detergent solution, rinsed with acetone and finally oven dried for at least 2 h at 120^{o} C before using for bio assay (Plate 7).

Bioassay experiments were conducted in an isolated dark room (25 ± 2^{o} C, 60 % RH) to avoid contaminant odour. Groups of adult mites (mixed sex) were brought into the experimental room 30 min. before the start of the experiments to allow acclimatization to the room conditions. A single mite was released at the entrance of the common arm of the Y-tube and exposed to healthy and infested plant odour combination, consisting of 10 µl test samples that were placed on filter paper strips and allowed them to evaporate before placing inside one of the two glass chambers that connected to one of the two arms of the Y-tube olfactometer. Once inside the Y tube, the behaviour of each mite was observed until it make choice upto10 min. White fluorescent (10 watts) light bulb was placed behind the olfactometer stand to allow observation of adult mite during 10 min. of observation period. A mite was considered to have made a choice if it entered either arm and crossed a score line drawn 2 cm from the intersection of the tube. By contrast, a mite was considered not having made a choice if it remained in the common arm of the Y-tube by the end of the observation period (Bertschy *et al*., 1997). A new pair of filter paper strip with odour was used for each individual mite tested. The sample size consisted of 30 adult mites.

Results of behavioral bioassays were analyzed for preference (percentage of adults that made a choice between healthy and infested plant volatiles) through Chi-

square test that was carried out to test the null hypothesis of no preference for a healthy and infested plant volatile odour combination.

3.5 Gas Chromatography Coupled Mass Spectrometry Analysis (GC-MS)

Chemical composition of porapak Q elutes and thrips body wash in solvents were analyzed by GC-MS/MS using Varian 3800 apparatus equipped with coupled MS/MS (Saturn 4000). A capillary column (DB-5 ms) 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^{o} C with rapping at 3^{o} C min^{-1} for 60 min. Helium was used as a carrier gas at a flow rate of 1 ml^{-1}. MS was in full scan mode (70 eV) and AMU ranged from 50 to 350. Two micro liter sample injected in split mode (1:20) with injection temperature at 270^{o} C. Compounds were identified by GC retention time, mass spectrum and KOVATS index using NIST 2007 and Wiley library as reference (Plate 8).

3.6 Electrophysiology Coupled Gas Chromatography-Electroantennodetector (GC-EAD)

Thrips response to extracts of porapak volatiles from Capsicum plants were studied by gas chromatography coupled electroantennographic detector (GC-EAD) GC model Agilent 7890A (Singapore) coupled with Syntech EAG Model IDAC-2 (Intelligent Data Acquisition Controller) system with GC-EAD interface temperature controller, TC-02 and with stimulus controller, CS-55. For separation of volatiles, the GC column having Agilent 19091J-413 HP-55 per cent Phenyl Methyl Siloxane capillary column (30 m x 320 µm x 0.25 µm) with maximum temperature of 325^{o} C and Helium (99.99 % purity) as the carrier gas (at a constant flow 2.0 mL/min) was used. The oven temperature maintained initially at 70^{o} C (2 min hold) to 260^{o} C with a ramp of 10^{o} C per minute. The transfer line (Syntech Laboratories, Germany) connects between the GC and EAD temperatures were maintained at 2^{o} C above the maximum temperature in order to avoid condensation. The electronic splitter with makeup gas was used to split the injected sample (1µl) in equal proportion with both EAD and FID. The EAG preparations were obtained using indifferent electrode being placed within the head capsule and the recording electrode was slipped over the one of the antennae and the electrodes are filled with 25 µl mM Nacl (Ringer solution). The purified fraction was eluted from the transfer line was carried out by a flow of humidified air with flow rate of 80 cm/s. The antennal responses against the GC peaks were recorded by Syntech GC-EAD software version 2010. Peaks eluting from the GC column were judged to be active if they elicited EAG activity in three or more of the coupled runs (Plate 9).

3.7 Chemicals

The GC-EAD active compounds are purchased from Sigma Aldrich to carry out futher behavioural bioassays. Authentic chemical standards of *n*-Dodecane (≥ 99 % purity), (99 % purity) of *n*-Docosane, *o*-Cymene, Octadecane and Tricosane, *β*-Elemene (≥ 98 %), Dodecyl iodide (98 %) and *δ*-3-Carene (90 %) were purchased from Sigma Aldrich (U.S.A, U.K and Netherlands).

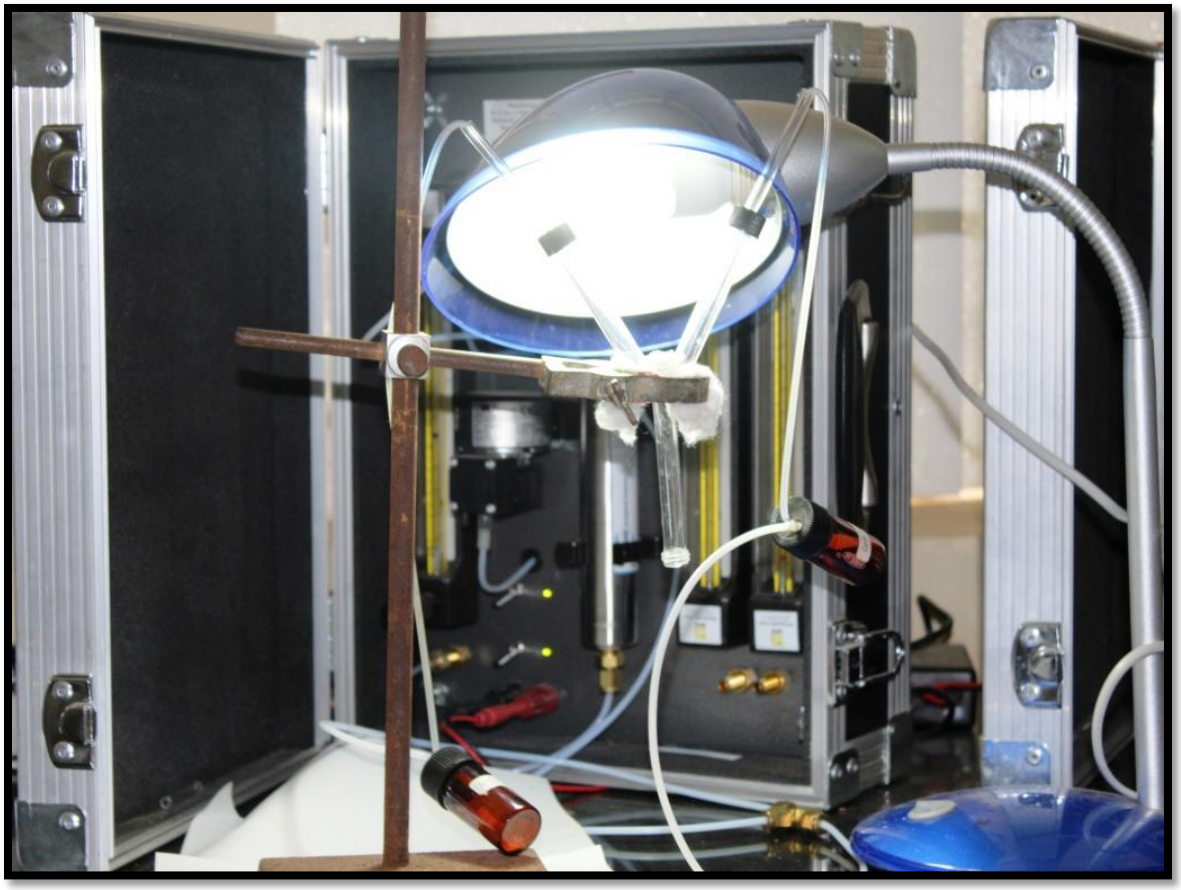


Plate 7. Y tube olfactometer

Plate 8. Gas Chromatography Coupled Mass Spectrometry

Plate 9. Electrophysiology Coupled Gas Chromatography - Electroantennodetector

IV EXPERIMENTAL RESULTS

Chilli thrips, *Scirtothrips dorsalis* Hood is one of the most wide spread and devastating pest in Chilli and Capsicum. Results of the investigations carried out during 2014-15 on "Chemical ecology of thrips, *Scirtothrips dorsalis* (Thysanoptera: Thripidae) and its host plant *Capsicum annum*" *i.e* attractiveness of thrips to different growth stages of host plant, differential response of thrips and other co-occuring sap sucking insects like aphids (*Aphis gossypii*), whiteflies (*Bemisia tabaci*) and mites (*Tetranychus macfarlanei*) to herbivore (thrips) induced (HIPVs) and healthy plant volatiles along with the influence of conspecific body odours on the thrips in behavioural assays are presented in this chapter.

4.1 Attractiveness of volatiles from different crop growth stages (*viz*., pre-flowering, flowering and fruiting) of host plant, *C. annum* to adult thrips, *S. dorsalis* in olfactometer assays

In order to know the behavioural response of thrips to different stages of host plant volatiles, olfactometer bioassays were carried out for each stage headspace samples individually along with solvent control. Further, multiple choice assay was carried out under controlled laboratory conditions to evaluate the attractiveness of different stages of *C. annum* host plant volatiles to *S. dorsalis.*

4.1.1 Behavioural responses of adult *S. dorsalis* to headspace samples of different growth stages of *C. annum*

In an olfactometer bioassay, responses of adult *S. dorsalis* to volatiles collected at different growth stages *viz*., pre-flowering, flowering and fruiting were investigated. There was no significant response when thrips were exposed to volatiles collected at pre-flowering and flowering stages of host plant, *C. annum* as the amount of time spent in treated and control regions did not differ significantly [pre-flowering: 2.92 ± 0.40 min (treatment); 2.39 ± 0.15 min (control); mean time spent ± S.E.; $t = 1.06$; $df = 19$; $P = 0.30$; flowering: 2.96 ± 0.25 min (treatment); 2.37 ± 0.09 min (control); mean time spent ± S.E.; $t = 1.86$; $df = 19$; $P = 0.08$]. However, thrips spent significantly more time [4.41 ± 0.39 min; mean time spent ± S.E.; $t = 4.93$; $df = 19$; $P < 0.0001$] in the treated region of the four arm olfactometer than in the control region [1.82 ± 0.13 min; mean time spent ± S.E.] when a 10 µl aliquot of *C. annum cv.'Indra'* headspace sample, collected at fruiting stage of *C. annum* was used (Table 1). In other words, headspace samples collected at fruiting stage were more attractive than other stages as thrips spent more time in the treated arm.

The mean number of entries by *S. dorsalis* to the treated region was significantly more when fruiting stage headspace volatiles were tested [8.10 ± 0.66; mean number of entries ± S.E.; $t = 5.29$; $df = 19$; $P < 0.0001$] compared to the mean number of entries made to the control region [5.65 ± 0.48; mean number of entries ± S.E.] (Fig. 3). Further, when the thrips *S. dorsalis* were exposed to flowering stage headspace volatiles also, they entered significantly more number of times to the treated region (8.15 ± 0.55; mean number of entries ± S.E.; $t = 3.64$; $df = 19$; $P = 0.002$] compared to the control [6.57 ±

Table 1. Response of adult *S. dorsalis* to different growth stages of *C. annum* headspace volatiles in olfactometer assay (N=20)

Growth stages	*df*	Paired *t*-test							
		Time spent (Minutes)				Entries (Numbers)			
		Treated (Mean ± S.E.)	Control (Mean ± S.E.)	P	*T*	Treated (Mean ± S.E.)	Control (Mean ± S.E.)	*P*	*t*
Pre-flowering	19	2.92 ± 0.40	2.39 ± 0.15	0.30	1.06	4.10 ± 0.64	3.78 ± 0.45	0.48	0.73
Flowering	19	2.96 ± 0.25	2.37 ± 0.09	0.08	1.86	8.15 ± 0.55	6.57 ± 0.56	0.002	3.64
Fruiting	19	4.41 ± 0.39	1.82 ± 0.13	< 0.0001	4.93	8.10 ± 0.66	5.65 ± 0.48	< 0.0001	5.29

0.56; mean number of entries ± S.E.] (Fig. 2). Nevertheless, no significant (t = 0.73; df = 19; P = 0.48) response was found in terms of mean number of entries made to treated [4.10 ± 0.64; mean number of entries ± S.E.] as well as control region [3.78 ± 0.45; mean number of entries ± S.E.] when thrips were exposed to headspace samples collected at pre-flowering stage (Fig. 1). These observations emphasize that the headspace volatiles of both flowering and fruiting stage were attractive to *S. dorsalis* compared to pre-flowering stage in terms of number of entries made in to the treated region compared to control region.

4.1.2 Behavioural responses of adult *S. dorsalis* to different growth stages of *C. annum* headspace samples in multiple choice assay

In four arm olfactometer bioassay, the responses of adult *S. dorsalis* to volatiles collected at different growth stages *viz*., pre-flowering, flowering and fruiting were investigated by providing multiple options of different headspace volatiles at a time i.e., multiple choice bioassay. The results are presented in the Table 2 and 2a. In this assay also headspace samples collected at fruiting stage of host plant elicited a positive behavioural response in terms of both time spent and number of entries made to the treated region. Adult *S. dorsalis* spent significantly [4.46 ± 0.44 min; mean time spent ± S.E.; F = 14.17; df = 3, 36; P < 0.0001] more time in the treated arm of four arm olfactometer containing fruiting stage headspace volatiles compared to the other three arms of the olfactometer containing headspace volatiles of pre-flowering [1.38 ± 0.33 min; mean time spent ± S.E.]/flowering stages [2.22 ± 0.41 min; mean time spent ± S.E.] and control [1.60 ± 0.27 min; mean time spent ± S.E.]. Further, thrips entered significantly (F = 6.58; df = 3, 36; P = 0.001) more number of times to the fruiting stage headspace volatiles treated region [6.70 ± 0.87; mean number of entries ± S.E.] compared to the flowering [5.40 ± 1.07; mean number of entries ± S.E.], pre-flowering headspace volatiles treated regions [4.10 ± 1.03; mean number of entries ± S.E.] and solvent control [4.60 ± 0.87; mean number of entries ± S.E.] (Fig. 4).

Given choice between different growth stages of *C. annum* headspace volatiles in multiple choice assay, thrips *S. dorsalis* preferred fruiting stage headspace volatiles by spending significantly (P < 0.0001) more amount of time and by making significantly (P = 0.001) more number of entries in to the treated region (Fig. 4).

The correlation analysis clearly indicated significant (P = 0.007) positive correlation between the growth stages of host plant, *C. annum* and behavioural responses of thrips *viz*., time spent and number of entries (Table 3 & 3a). In other words, as the growth stages progresses the thrips attraction to host plant increased which was evident by the significant positive correlation of amount of time spent (r = 0.36*) and number of entries (r = 0.50*) with the plant growth stages.

The regression analysis carried out to understand the per cent variability in the behavioural responses (*viz*., time spent and number of entries) that can be explained by host plant growth stages alone. The results revealed that up to 13 per cent ($y = 2.78 + 2x$; R^2 = 0.13; F = 8.60; df = 1, 58; P = 0.007) variability in the amount of time spent may be explained by the host plant growth stage differences alone. Similarly, in case of number

Table 2. Response of adult *S. dorsalis* to different growth stages of *C. annum* headspace volatiles in multiple choice assay (N=10)

Growth stages	*df*	ANOVA							
		Time spent (Minutes)				Entries (Numbers)			
		Mean ± S.E.	F_{cal}	F_{crit}	*P*	Mean ± S.E.	F_{cal}	F_{crit}	*P*
Pre-flowering	3, 36	1.38 ± 0.33	14.17	2.87	< 0.0001	4.10 ± 1.03	6.58	2.87	0.001
Flowering		2.22 ± 0.41				5.40 ± 1.07			
Fruiting		4.46 ± 0.44				6.70 ± 0.87			
Control		1.60 ± 0.27				4.60 ± 0.87			

Table 2a. Tukey's multiple comparison test: Response of adult *S. dorsalis* to different plant growth stages of *C. annum* in multiple choice assay

Treatments	*df*	*P*	
		Time spent (Minutes)	Entries (Numbers)
Pre-flowering vs. Flowering	3,36	Ns	ns
Pre-flowering vs. Fruiting		**	ns
Pre-flowering vs. Control		Ns	ns
Flowering vs. Fruiting		*	ns
Flowering vs. Control		Ns	ns
Fruiting vs. Control		**	ns

* = 0.01; ** = 0.001; *** = 0.0001; **** < 0.0001; ns - non significant

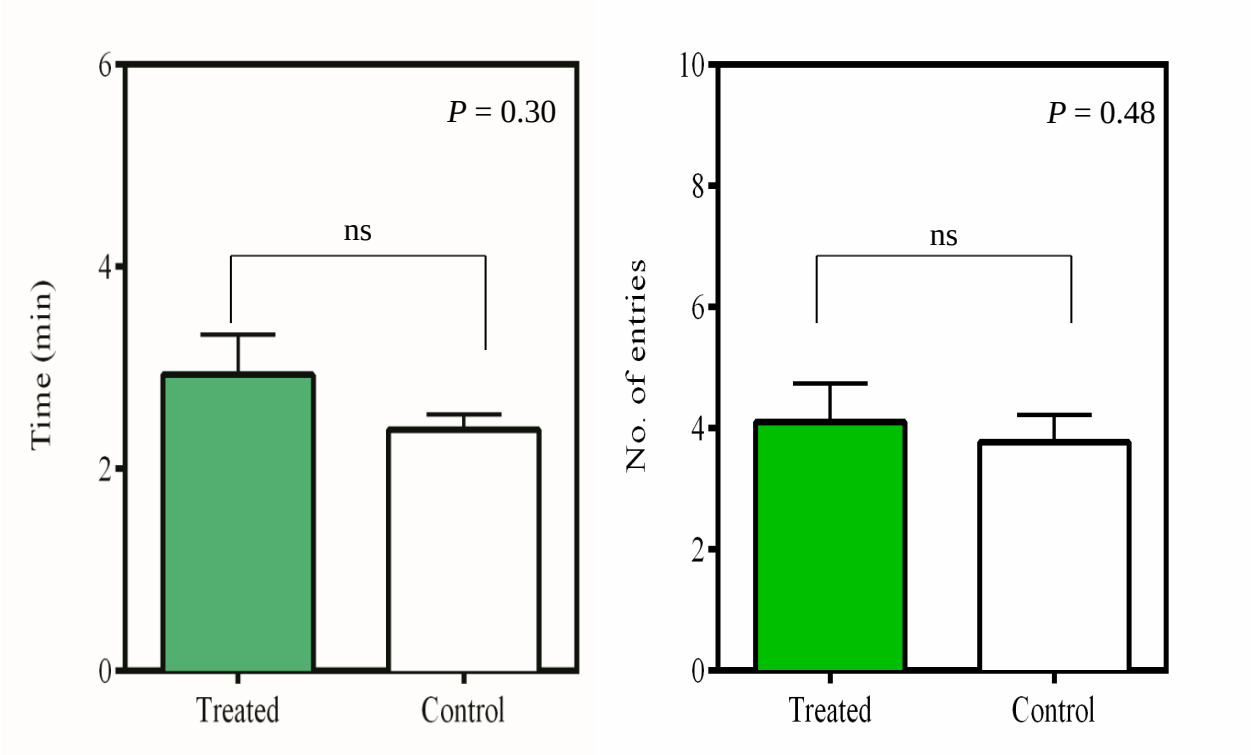
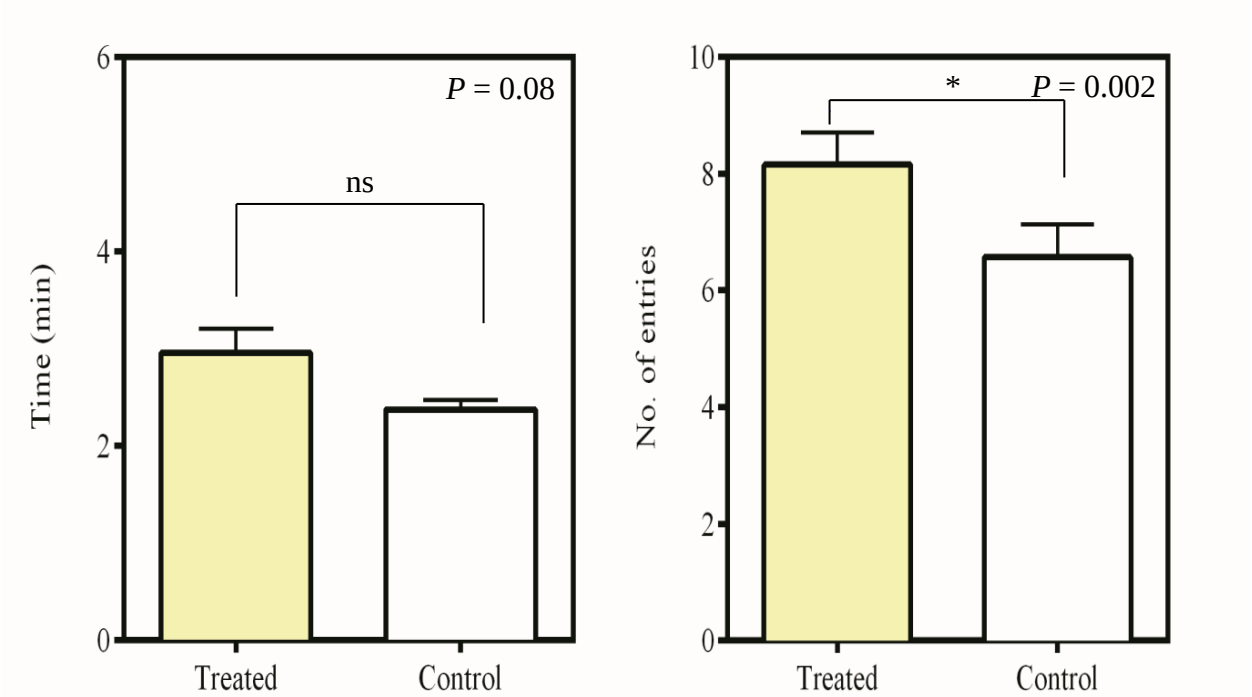


Fig. 1. Olfactory response of adult *S. dorsalis* to pre-flowering stage headspace volatiles of *C. annum*



* - significant; ns - non significant

Fig. 2. Olfactory response of adult *S. dorsalis* to flowering stage headspace volatiles of *C. annum*

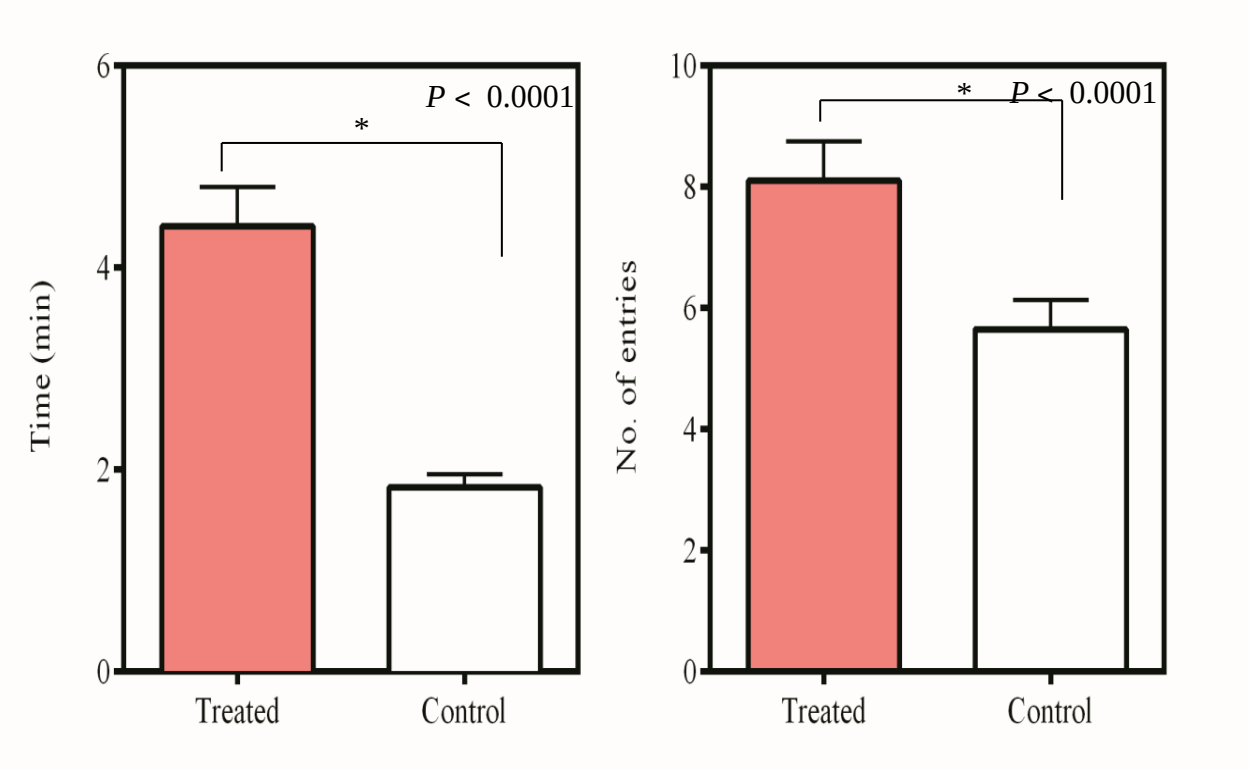


Fig. 3. Olfactory response of adult *S. dorsalis* to fruiting stage headspace volatiles of *C. annum*

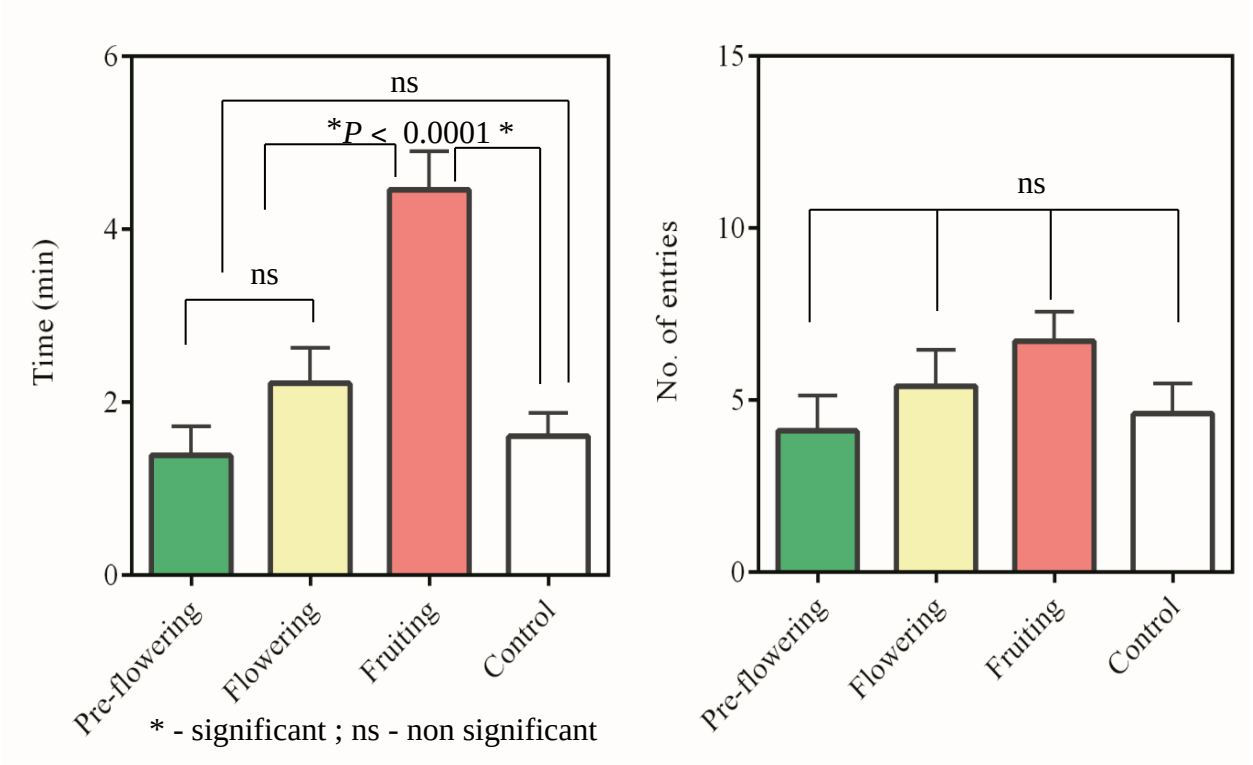


Fig. 4. Olfactory response of adult *S. dorsalis* to pre-flowering, flowering and fruiting stage headspace volatiles of *C. annum* in multiple choice assay

Table 3. Correlation matrix showing "*r*" between *S. dorsalis* response and different plant growth stages of *C. annum*

Variables	Growth stage	Time spent	Entries
Growth stage	1		
Time spent	0.36*	1	
Entries	0.50*	-0.02	1

* = Significant @ $P = 0.05$

Table 3a. Regression analysis: Response of adult *S. dorsalis* to different plant growth stages of *C. annum*

Dependent variables	Regression equation	*df*	F_{cal}	F_{crit}	R^2	*P*
Time spent	$y = 2.78 + 2x$	1,58	8.60	0.0048	0.13	0.007
Entries	$y = 1.95 + 0.74x$		19.01	< 0.0001	0.25	< 0.0001

of entries made by *S. dorsalis*, up to 25 per cent variability ($y = 1.95 + 0.74x$; $R^2 = 0.25$; $F = 19.01$; $df = 1, 58$; $P < 0.0001$) can be explained by the host plant *C. annum* growth stage differences.

4.1.3 Identification of compounds present in different growth stages of *C. annum* headspace volatiles through GC-MS

The compounds that are present in the different growth stages of *C. annum* plant headspace volatiles are identified using Gas Chromatography coupled to Mass Spectrometry (GC-MS) (Fig. 5, 6 and 7). The quantities of the compounds present in the *C. annum* headspace samples at different growth stages are listed in Table 4. There is a stark difference in the volatile profiles as well as in their abundance between different growth stages (Fig. 8). A total of 50 compounds were identified in the *C. annum* plant volatiles at different growth stages.

4.1.4 Identification of compounds that elicited an EAD response

Coupled GC-EAD (Gas Chromatography coupled to Electroanntenogram Detector) with adult *S. dorsalis* to *C. annum* fruiting stage plant volatiles elicited behavioural response to eight compounds through an EAD response (Table 5). The EAD-active compounds that elicited response were identified as *o*-Cymene, 4-methyl-2-undecane, 3,6-Dimethyl decane, *β*-Elemene, *n*-Dodecane, Dodecyl iodide, 2,3,5-Trimethyl decane and *n*-Docosane. A representative GC- EAD traces are shown in Fig. 9. The quantification of the EAD active compounds that are present in the *C. annum* plant fruiting stage natural headspace sample are listed in Table 5.

4.1.5 Behavioural responses of adult *S. dorsalis* to synthetic GC-EAD active compounds

Five compounds *viz*., *o*-Cymene, *β*-Elemene, *n*-Dodecane, Dodecyl iodide, *n*- Docosane out of eight compounds present in the fruiting stage volatiles that elicited an EAD response in *S. dorsalis* were tested in the olfactometer assay to know whether these compounds will instigate the behavioural response. The remaining three compounds were could not be tested due to their commercial unavailability. Among five compounds, *o*-Cymene, *β*-Elemene and *n*-Docosane were behaviourally active when presented individually at a standard dose (1 µg on filter paper), with adult *S. dorsalis.*

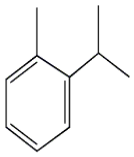
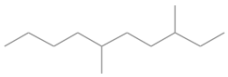
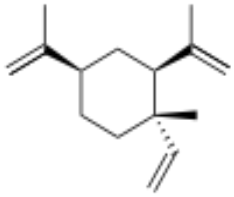
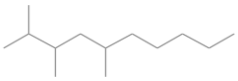
Adult thrips spent significantly longer time in the treated regions of *o*-Cymene [3.63 ± 0.19 min (treatment); 2.14 ± 0.09 min (control); mean amount of time spent ± S.E.; $t = 5.58$; $df = 9$; $P = 0.0003$], *β*-Elemene [2.56 ± 0.05 min (treatment); 2.20 ± 0.10 min (control); mean amount of time spent ± S.E.; $t = 2.70$; $df = 9$; $P = 0.02$], *n*-Docosane [3.31 ± 0.27 min (treatment); 2.05 ± 0.09 min (control) mean amount of time spent ±S.E.; $t = 3.60$; $df = 9$; $P = 0.006$] in the olfactometer and also entered significantly more number of times into the treated regions of *o*-Cymene [10.30 ±1.06 (treatment); 7.60 ± 0.86 (control); mean number of entries ± S.E.; $t = 3.92$; $df = 9$; $P = 0.004$], *β*-Elemene [7.50 ± 0.58 (treatment); 6.55 ± 0.64 (control); mean number of entries ± S.E.; $t = 2.71$; $df = 9$; $P = 0.02$], *n*-Docosane [8.00 ± 0.65 (treatment); 5.67 ± 0.71 (control); mean number of entries ± S.E.; $t = 6.52$; $df = 9$; $P = 0.0001$] in the olfactometer when

Table 4. GC-MS profile of different growth stages of *C. annum* headspace volatiles

CAS No.	Chemical Name	RT	Abundance (%)		
			PF	FL	FR
106-51-4	*p*-Benzoquinone	4.09	0.0	7.8	0.2
527-84-4	*o*-Cymene	5.70	0.0	0.7	0.2
13466-78-9	*δ*-3-Carene	5.80	0.2	0.8	0.0
3338-55-4	cis-Ocimene	5.90	0.1	0.8	0.0
13877-91-3	*β*-Ocimene	6.00	0.0	1.4	2.2
2884-06-2	2,3-dimethylnonane	6.10	4.4	0.0	0.0
17312-53-7	3,6-dimethyldecane	6.17	0.0	0.0	5.2
112-40-3	*n*-Dodecane	6.20	0.0	0.0	3.8
7045-71-8	2E- 4-methyl-2-undecane	6.50	1.1	0.0	1.0
124-19-6	Nonanal	6.80	0.0	1.0	0.0
17312-54-8	3,7-dimethyldecane	6.90	6.4	0.9	5.6
122332-13-2	2-methyl-1-phenyl-3-buten-1-ol	7.70	0.6	0.0	0.2
93-89-0	Ethyl benzoate	7.97	0.0	0.0	0.3
41519-23-7	cis-3-hexenyl isobutyrate	8.13	0.0	0.7	0.0
119-36-8	Methyl salicylate	8.37	0.0	5.5	0.6
698-76-0	*δ*-Octalactone	9.34	0.0	0.7	0.0
585-74-0	*m*-Methyl acetophenone	9.37	1.4	0.0	0.0
81534-55-6	5-ethyl-4-Nonanone	9.41	0.0	1.0	0.0
13150-81-7	2,6-dimethyldecane	9.42	0.0	0.0	1.0
629-59-4	Tetradecane	9.44	1.1	0.0	4.2
629-62-9	Pentadecane	9.52	13.0	8.8	15.0
544-76-3	Hexadecane	9.72	4.6	0.0	3.1
593-45-3	Octadecane	9.8	4.4	1.7	4.2
629-92-5	Nonadecane	9.82	4.6	2.6	0.0
40267-72-9	Geranyl ethyl ether	9.87	0.0	0.0	1.9
90388-00-4	Heptadecanol	9.88	3.2	0.0	0.0
4292-19-7	Dodecyl iodide	10.17	9.6	1.7	8.8
638-36-8	Phytane	10.30	5.7	0.0	0.0
112-95-8	Eicosane	10.40	5.5	2.6	4.2
62238-11-3	2,3,5-Trimethyl decane	10.51	0.0	1.6	3.1
Not Available	neopentyl nonyl ester	10.52	2.8	0.0	0.0
477735-90-3	4,7-dimethyl-2-benzofuran	10.70	2.3	0.0	3.8
515-13-9	*β*-Elemene	11.15	0.0	2.3	3.3
13474-59-4	trans-alpha-Bergamotene	11.70	0.0	2.5	0.0
78919-13-8	2,5-Cyclohexadiene-1,4-dione	12.12	0.0	2.5	0.0
629-99-2	Pentacosane	12.38	0.0	0.0	10
714275-45-3	6,6-diethyl-Octadecane	12.39	9.2	13.0	0.0
475-20-7	Longifolene	12.45	0.0	1.3	1.7
629-97-0	*n*-Docosane	12.50	2.5	3.9	3.3
96-76-4	2,4-Di-try-butylphenol	12.59	0.	1.3	0.0
97123-41-6	2,6-bis(1,1-dimethylethyl)-4-methyl-phenol	12.66	0.0	1.2	0.0
13287-23-5	8-methylheptadecane	12.71	0.0	2.0	0.0
593-49-7	*n*-Heptacosane	12.79	0.0	1.2	0.0
23676-09-7	4-Ethoxy ethylbenzoate	12.82	7.1	0.0	0.0
629-94-7	*n*-Heneicosane	12.91	0.0	8.5	4.2
646-31-1	Tetracosane	13.04	2.5	2.0	1.5
630-01-3	Hexacosane	13.16	2.1	1.3	0.8
629-94-7	*n*-Heneicosane	13.30	2.8	0.0	0.0
28290-41-7	Farnesyl Bromide	13.40	0.0	0.0	1.5
4128-17-0	Farnesyl acetate	13.44	2.1	9.5	0.0

*****RT - Retension time; PF - Pre-flowering; FL - Flowering; FR – Fruiting

Table 5. List of GC-EAD active compounds present in fruiting stage of *C. annum* plant headspace volatiles

CAS No.	Chemical name	RT	Abundance (%)	Structure
527-84-4	*o*-Cymene	5.70	0.2	
7045-71-8	4-methyl-2-undecane	6.60	1	
17312-53-7	3,6-Dimethyl decane	6.80	5.2	
515-13-9	*β*-Elemene	11.20	3.3	
112-40-3	*n*-Dodecane	6.30	3.8	
4292-19-7	Dodecyl iodide	10.10	8.8	
62238-11-3	2,3,5-Trimethyl decane	10.50	3.1	
629-97-0	*n*-Docosane	12.50	3.3	

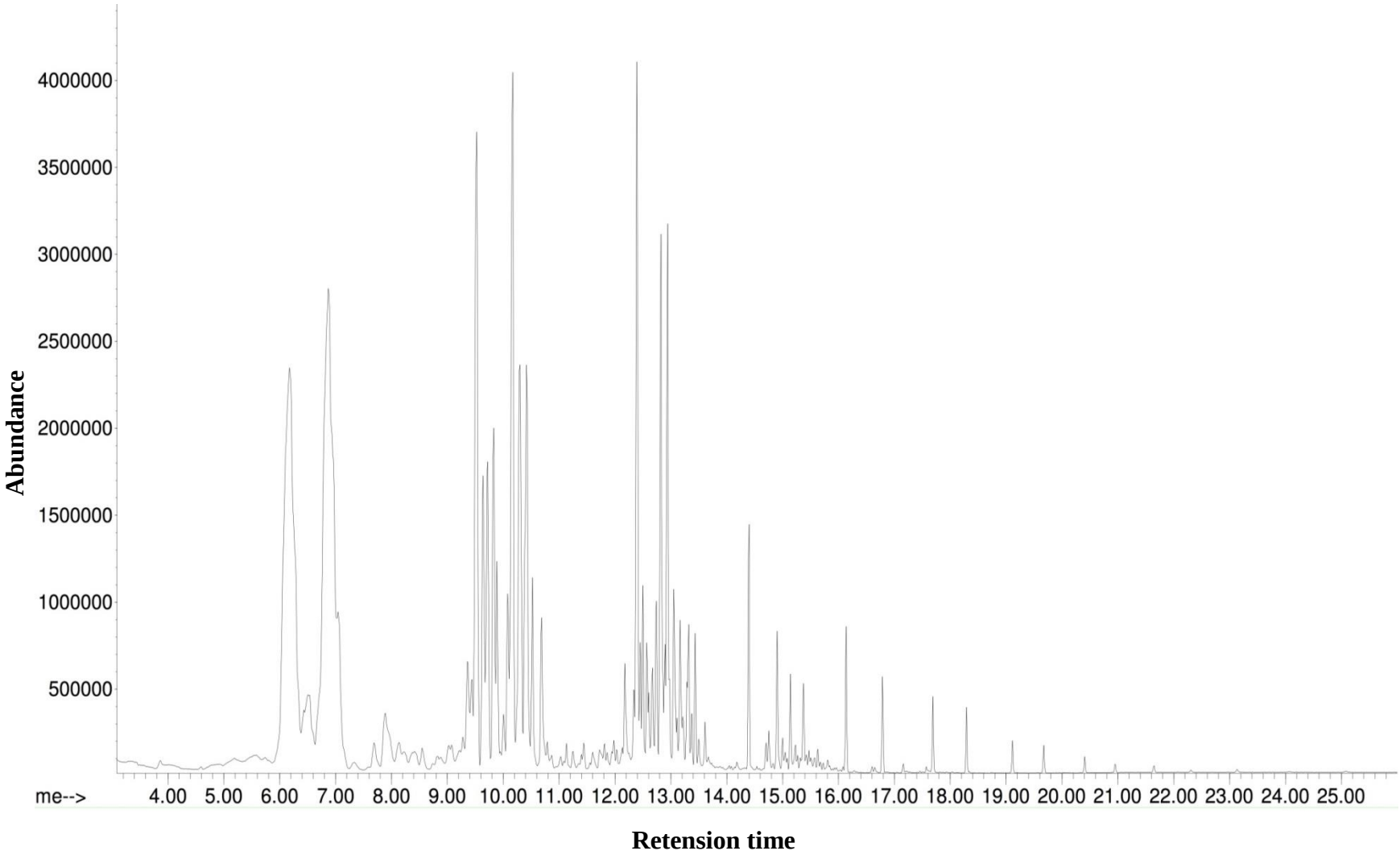


Fig. 5. GC-MS chromatogram of *C. annum* pre-flowering stage headspace volatiles

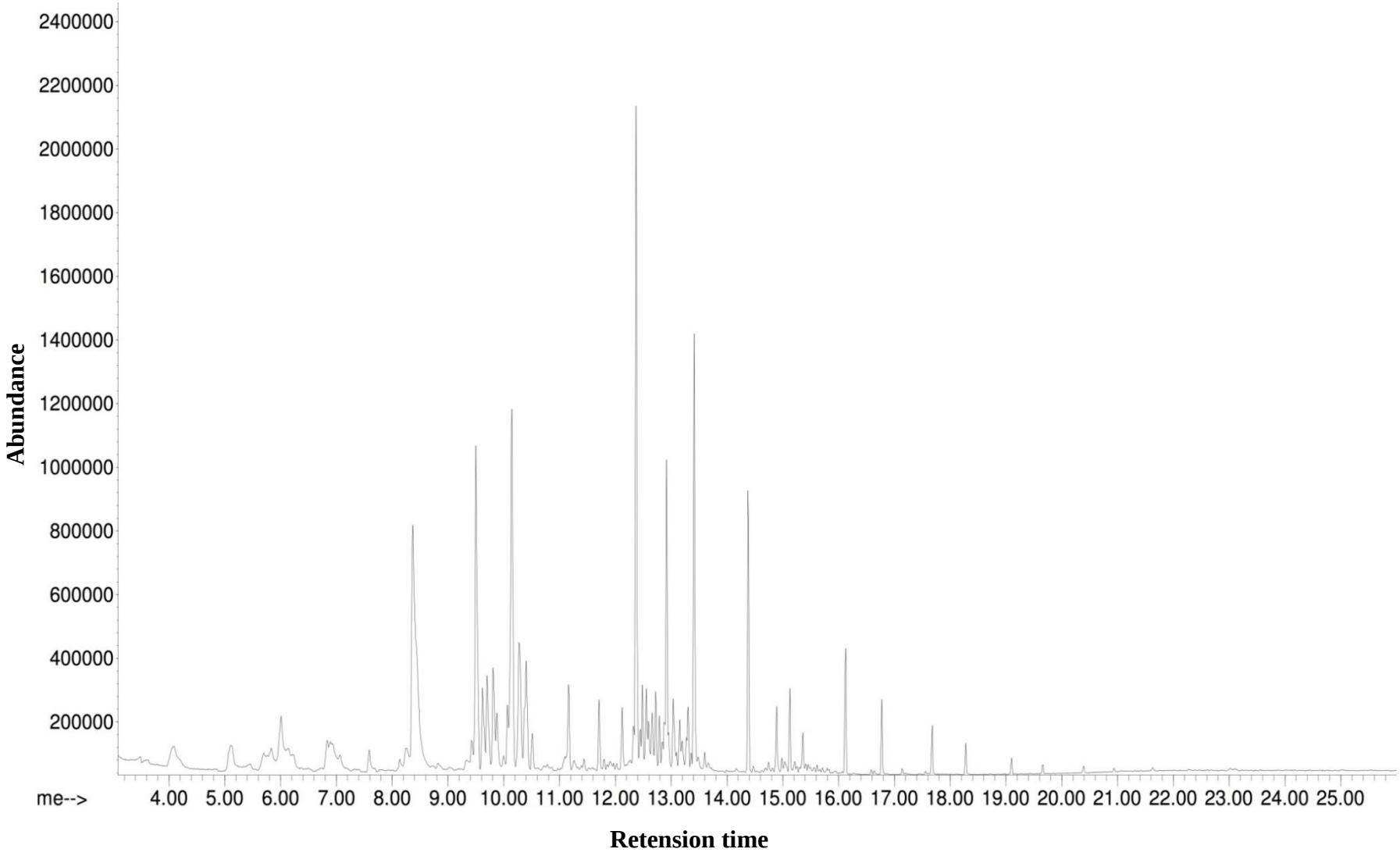


Fig. 6. GC-MS chromatogram of *C. annum* flowering stage headspace volatiles

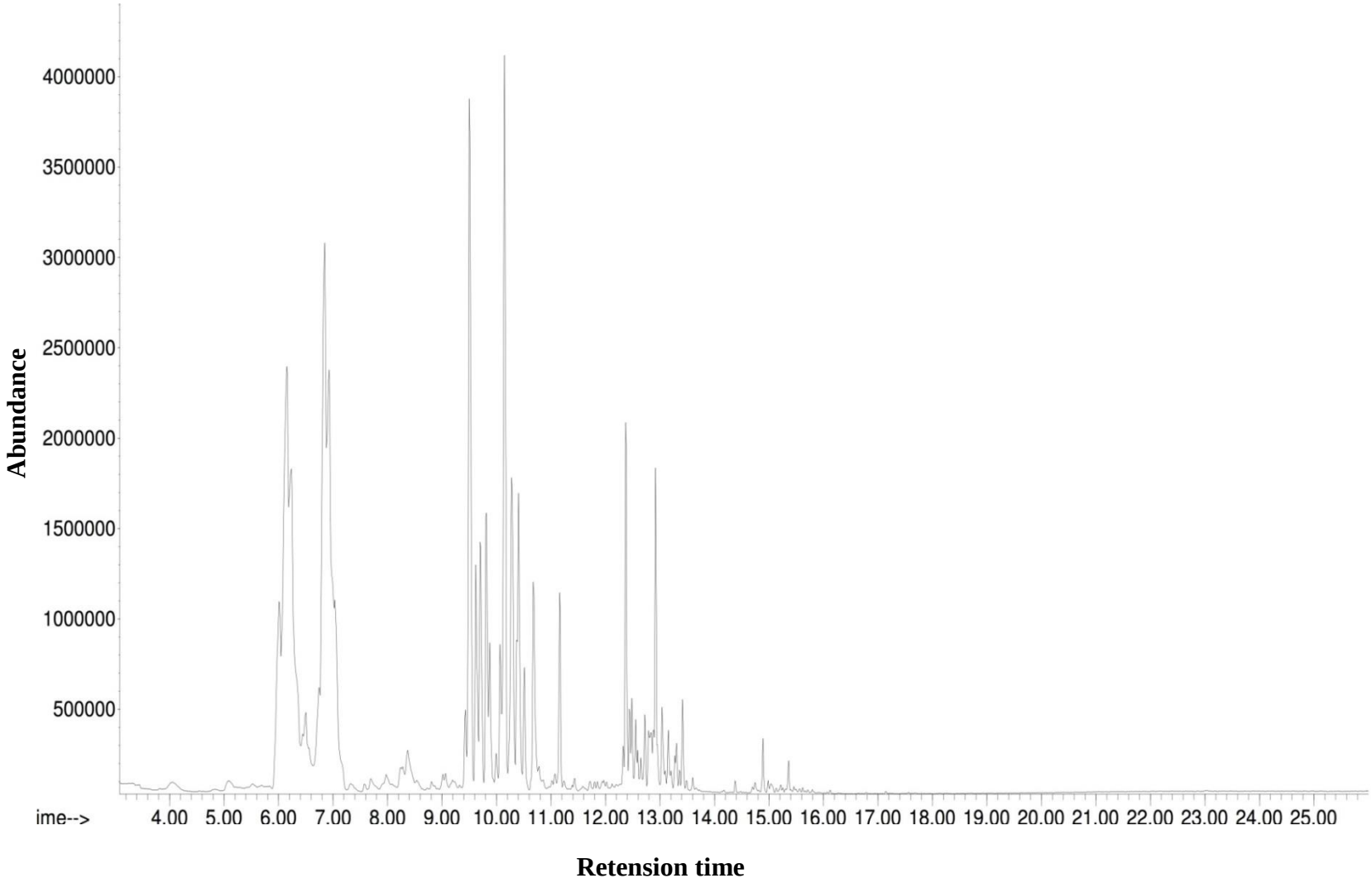
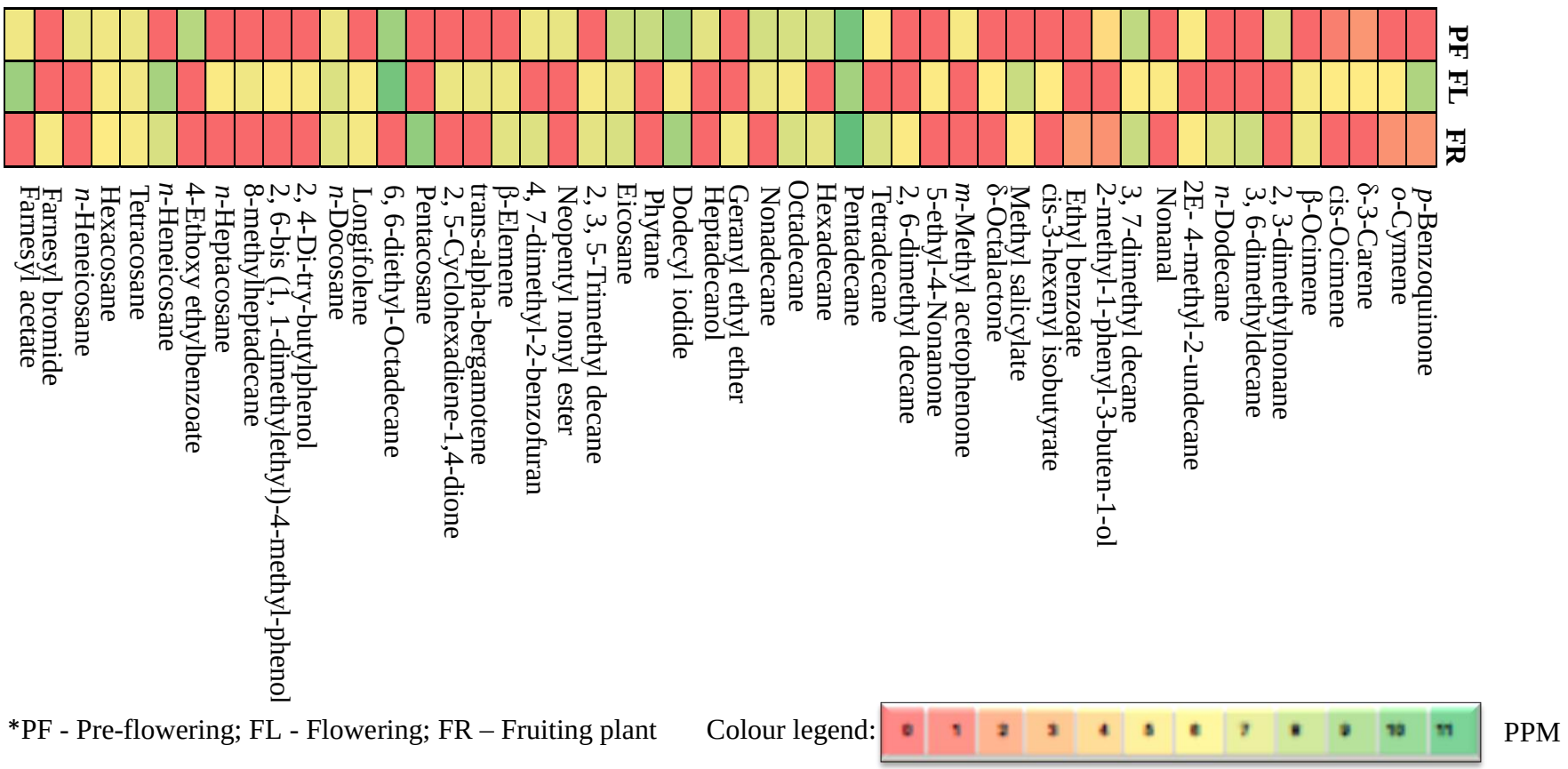


Fig. 7. GC-MS chromatogram of *C. annum* fruiting stage headspace volatiles



*PF - Pre-flowering; FL - Flowering; FR – Fruiting plant

Fig. 8. Heat map showing variation in the headspace volatiles abundance of *C. annum* pre-flowering, flowering and fruiting stage

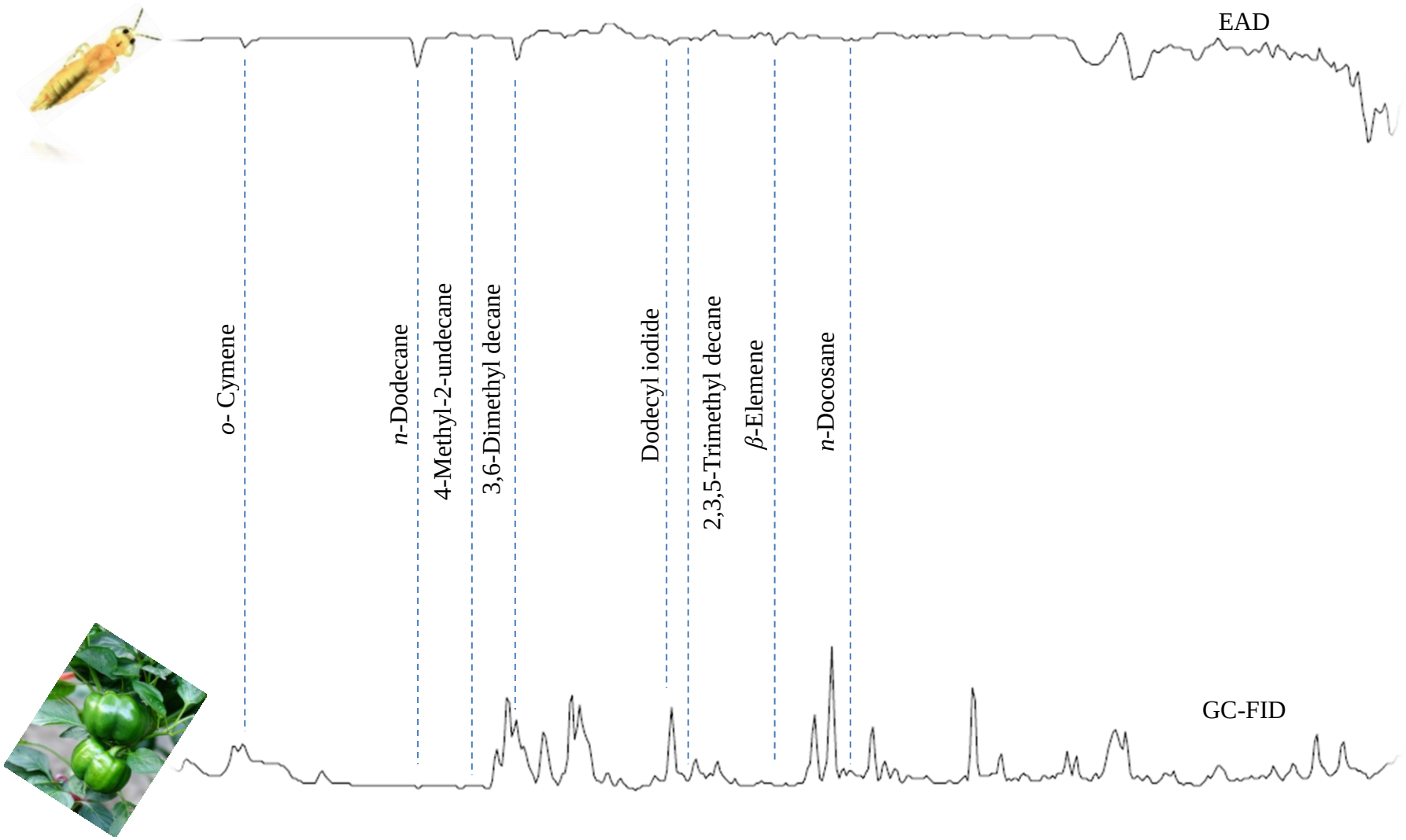


Fig. 9. GC-EAD traces showing the antennal response of adult *S. dorsalis* to fruiting stage *C. annum* headspace volatiles

presented individually. There was no significant difference for the amount of time spent between treated and control regions for the other two EAD active fractions *viz*., Dodecyl iodide [2.21 ± 0.17 min (treatment); 2.68 ± 0.08 min (control); mean amount of time spent ± S.E.; t = 1.96; df = 9; P = 0.08] and *n*-Dodecane [2.25 ± 0.14 min (treatment); 2.50 ± 0.06 min (control); mean amount of time spent ± S.E.; t = 1.31; df = 9; P = 0.22] when presented individually at a standard dose (1 µg on filter paper) (Table 6). However, there was significant difference for the number of entries into the treated region of the olfactometer compared to the control region (Dodecyl iodide, [7.90 ± 0.48 (treatment); 6.74 ± 0.49 (control); mean number of entries ± S.E.; t = 2.61; df = 9; P = 0.03] *n*-Dodecane, [7.40 ± 0.45 (treatment); 6.30 ± 0.56 (control) mean number of entries ± S.E.; t = 2.29; df = 9; P = 2.29]) (Fig. 10-14).

When presented together as a 5-component synthetic blend (formulated using the same ratio and concentration as in the natural sample), significant response both in terms of amount of time spent [4.26 ± 0.38 min (treatment); 2.02 ± 0.13 min (control); mean amount of time spent ± S.E.; t = 4.43; df = 9; P = 0.002] as well as number of entries [8.30 ± 0.54 (treatment); 6.03 ± 0.43 (control); mean number of entries ± S.E.; t = 4.27; df = 9; P = 0.002] was observed over control (Fig. 15).

Furthermore, in a dual choice test where thrips were offered both the natural sample and the synthetic blend simultaneously, there was no difference in behavioural response between these two treatments confirming a similar level of attraction to the synthetic blend [3.39 ± 0.15 min; mean amount of time spent ± S.E.; F = 29.12; df = 3, 36; P < 0.0001; 9.10 ± 0.66; mean number of entries ± S.E.; F = 9.70; df = 3, 36; P < 0.0001] as that observed with the natural sample [3.39 ± 0.19 min; mean amount of time spent ± S.E.; 9.00 ± 0.93; mean number of entries ± S.E.] compared to solvent controls [1.48 ± 0.13 and 1.85 ± 0.13 min; mean amount of time spent ± S.E.; 5.10 ± 0.40 and 6.50 ± 0.67; mean number of entries ± S.E.] (Table 7 & 7a and Fig. 16).

4.2 Response of adult *S. dorsalis* and co-occurring sap sucking insects to healthy and herbivore (= thrips) induced plant volatiles (HIPVs)

In order to know the response of thrips to healthy and herbivore (= thrips) induced host plant volatiles, olfactometer bioassays were carried out for both volatiles individually along with control solvent and also by dual choice assay under controlled laboratory conditions to evaluate their attractiveness to conspecifics (*S. dorsalis*) as well as heterospecifics (Cotton aphid, *Aphis gossypiii* Glover, silverleaf whitelfy, *Bemisia tabaci* (Gennadius) and spidermite, *Tetranychus macfarlanei* Baker and Pritchard). The response of other co-occurring sap sucking insects like aphids (*A. gossypii*), whiteflies (*B. tabaci*) and mites (*T. macfarlanei*) were also evaluated through dual choice assays under controlled laboratory condition to evaluate the attractiveness of healthy and herbivore induced volatiles.

4.2.1 Behavioural responses of adult *S. dorsalis* to healthy and herbivore (thrips) induced plant volatiles

In an olfactometer bioassay, responses of adult *S. dorsalis* to volatiles collected from healthy and artificially thrips infested *C. annum* plants were investigated. There was

Table 6. Response of adult *S. dorsalis* to fruiting stage EAD active synthetic fractions and their blend in olfactometer assay (N=10)

Synthetic fractions	*df*	Paired *t* test							
		Time spent (Minutes)				Entries (Numbers)			
		Treated (Mean ± S.E.)	Control (Mean ± S.E.)	*P*	*t*	Treated (Mean ± S.E.)	Control (Mean ± S.E.)	*P*	*t*
o-Cymene	9	3.63 ± 0.19	2.14 ± 0.09	0.0003	5.58	10.30 ±1.06	7.60 ± 0.86	0.004	3.92
β-Elemene	9	2.56 ± 0.05	2.20 ± 0.10	0.02	2.70	7.50 ± 0.58	6.55 ± 0.64	0.02	2.71
n-Dodecane	9	2.25 ± 0.14	2.50 ± 0.06	0.22	1.31	7.40 ± 0.45	6.30 ± 0.56	0.05	2.29
n-Dodecyl iodide	9	2.21 ± 0.17	2.68 ± 0.08	0.08	1.96	7.90 ± 0.48	6.74 ± 0.49	0.03	2.61
n-Docosane	9	3.31 ± 0.27	2.05 ± 0.09	0.006	3.60	8.00 ± 0.65	5.67 ± 0.71	0.0001	6.52
Synthetic blend	9	4.26 ± 0.38	2.02 ± 0.13	0.002	4.43	8.30 ± 0.54	6.03 ± 0.43	0.002	4.27

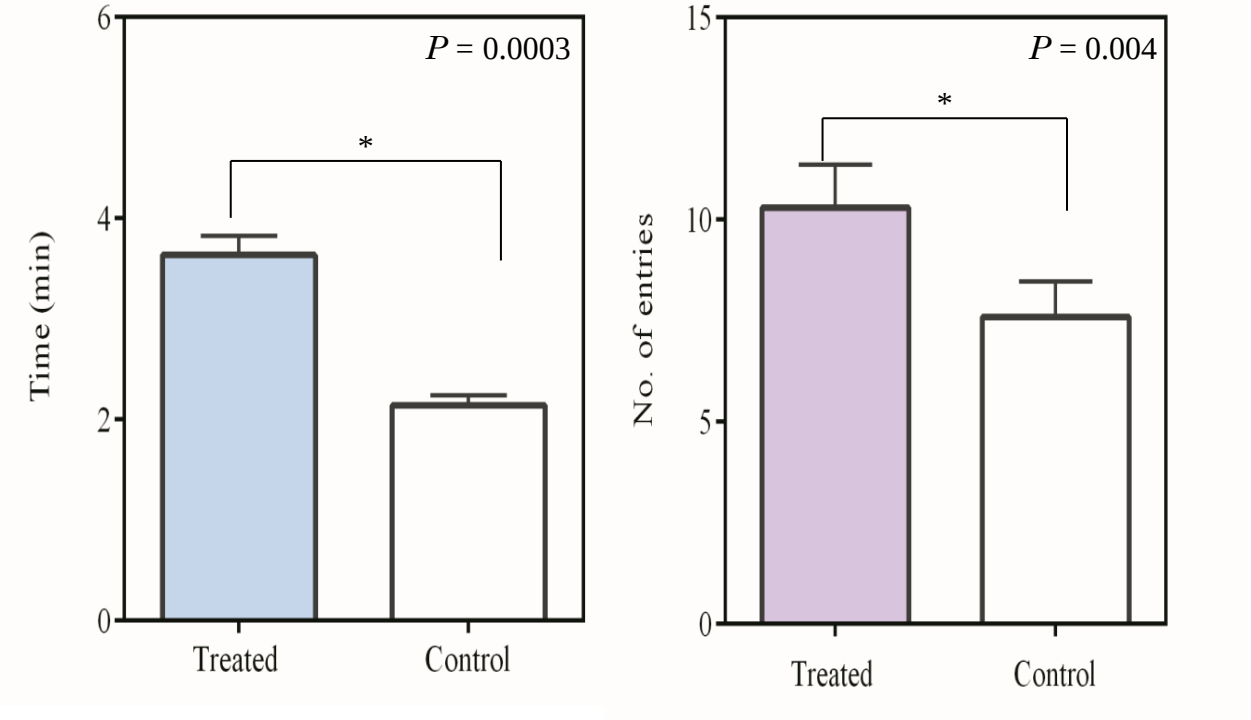
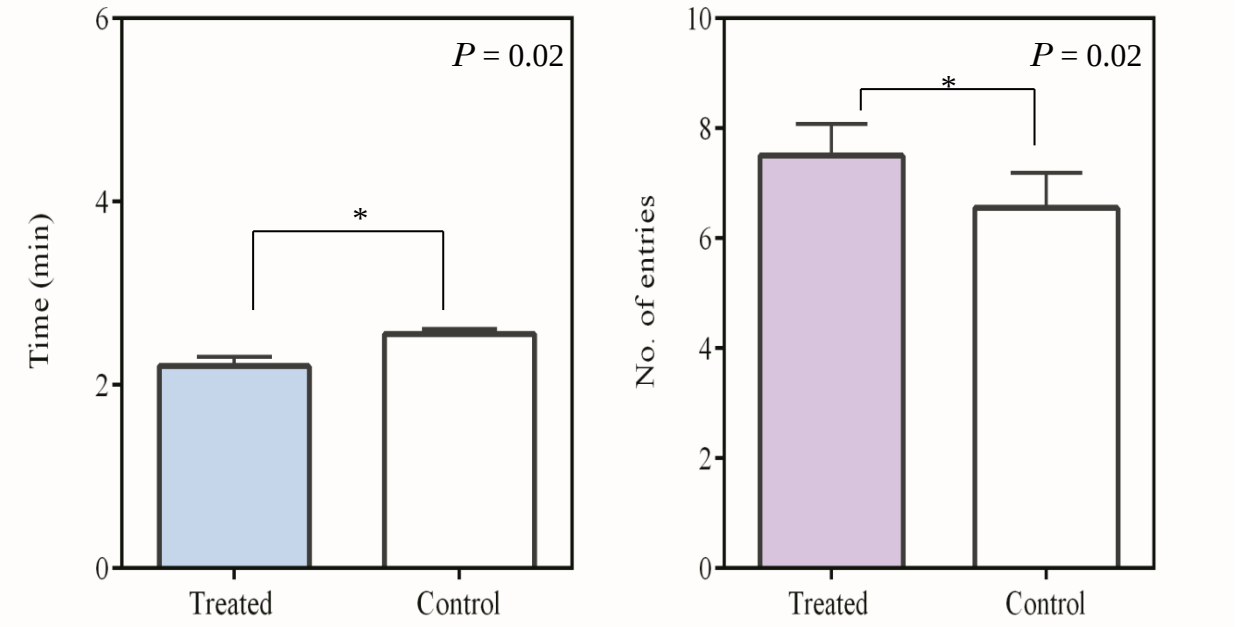


Fig. 10. Olfactory response of adult *S. dorsalis* to *o*-Cymene



* - significant; ns - non significant

Fig. 11. Olfactory response of adult *S. dorsalis* to *β*-Elemene

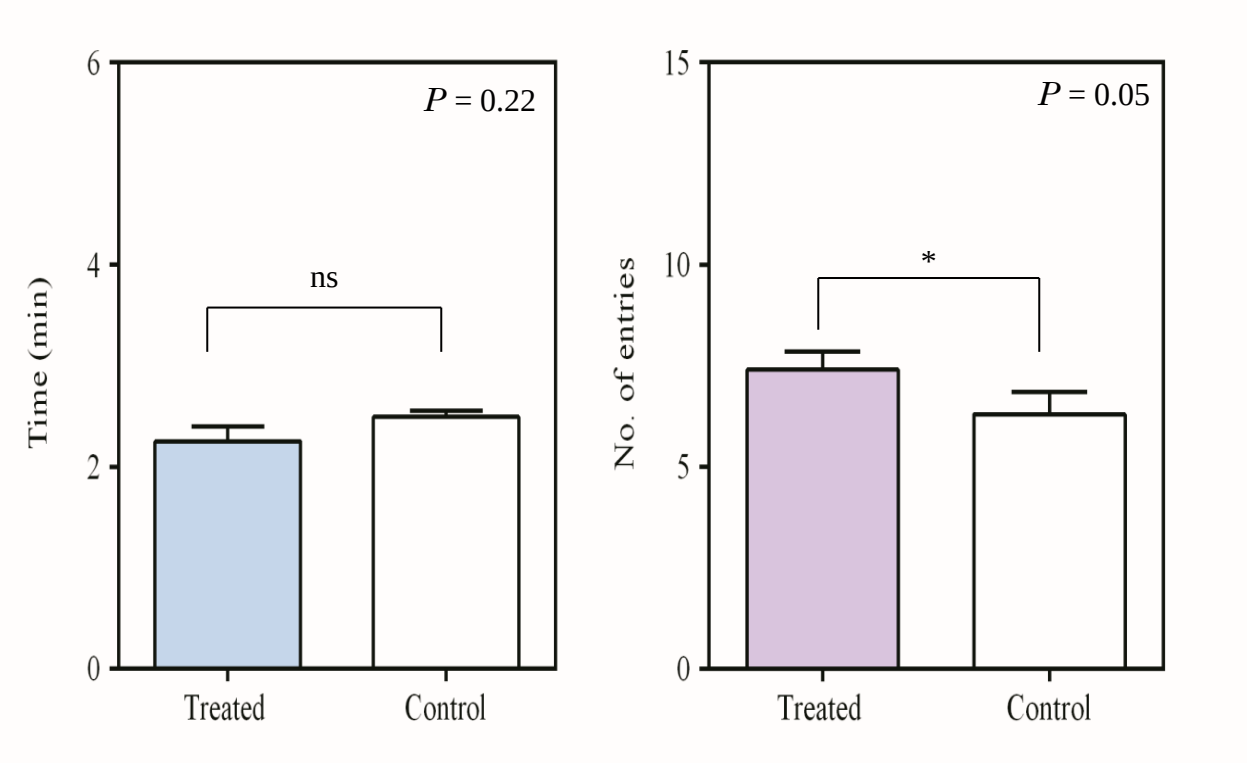
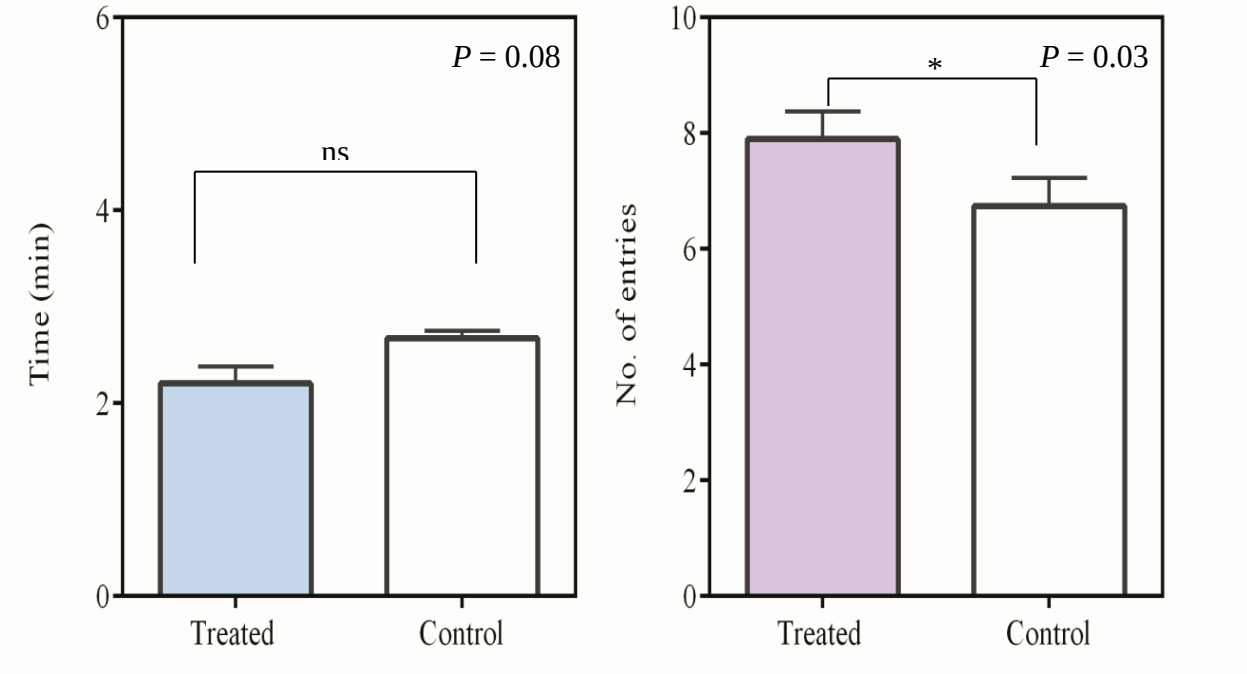


Fig. 12. Olfactory response of adult *S. dorsalis* to *n*-Dodecane



* - significant; ns - non significant

Fig. 13. Olfactory response of adult *S. dorsalis* to Dodecyl iodide

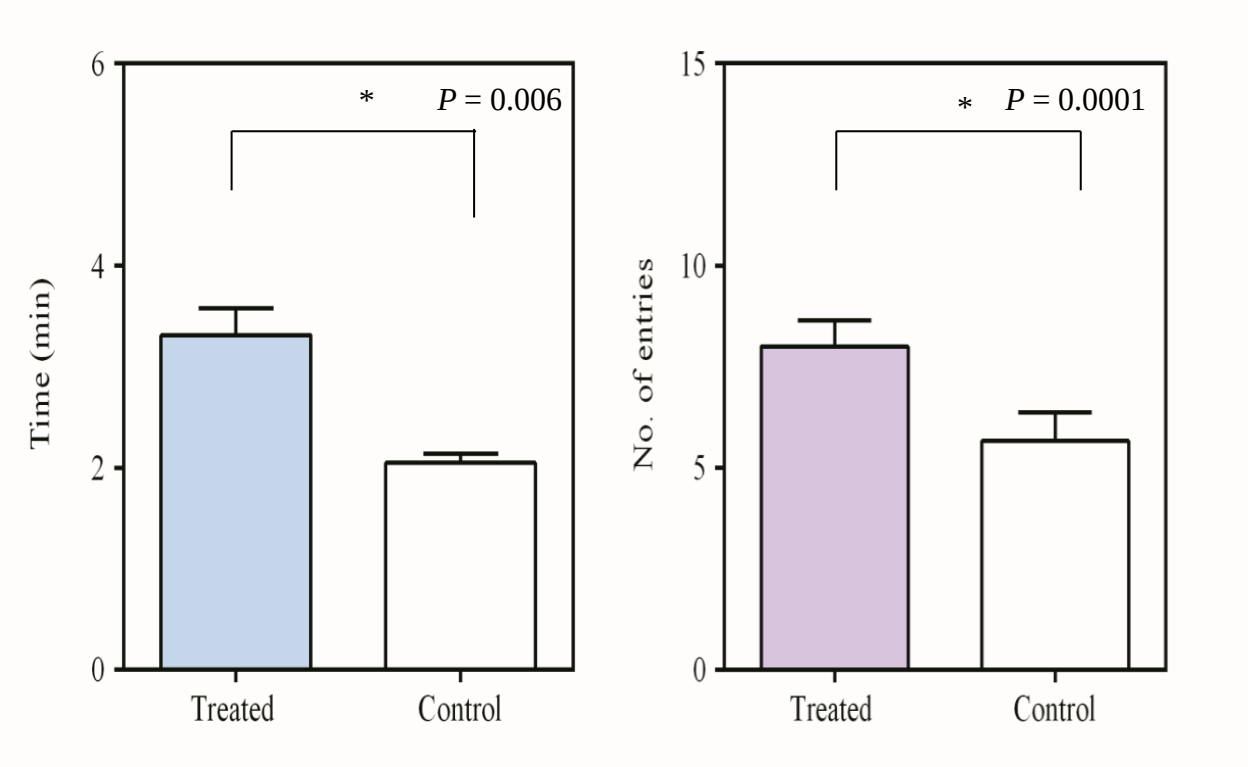
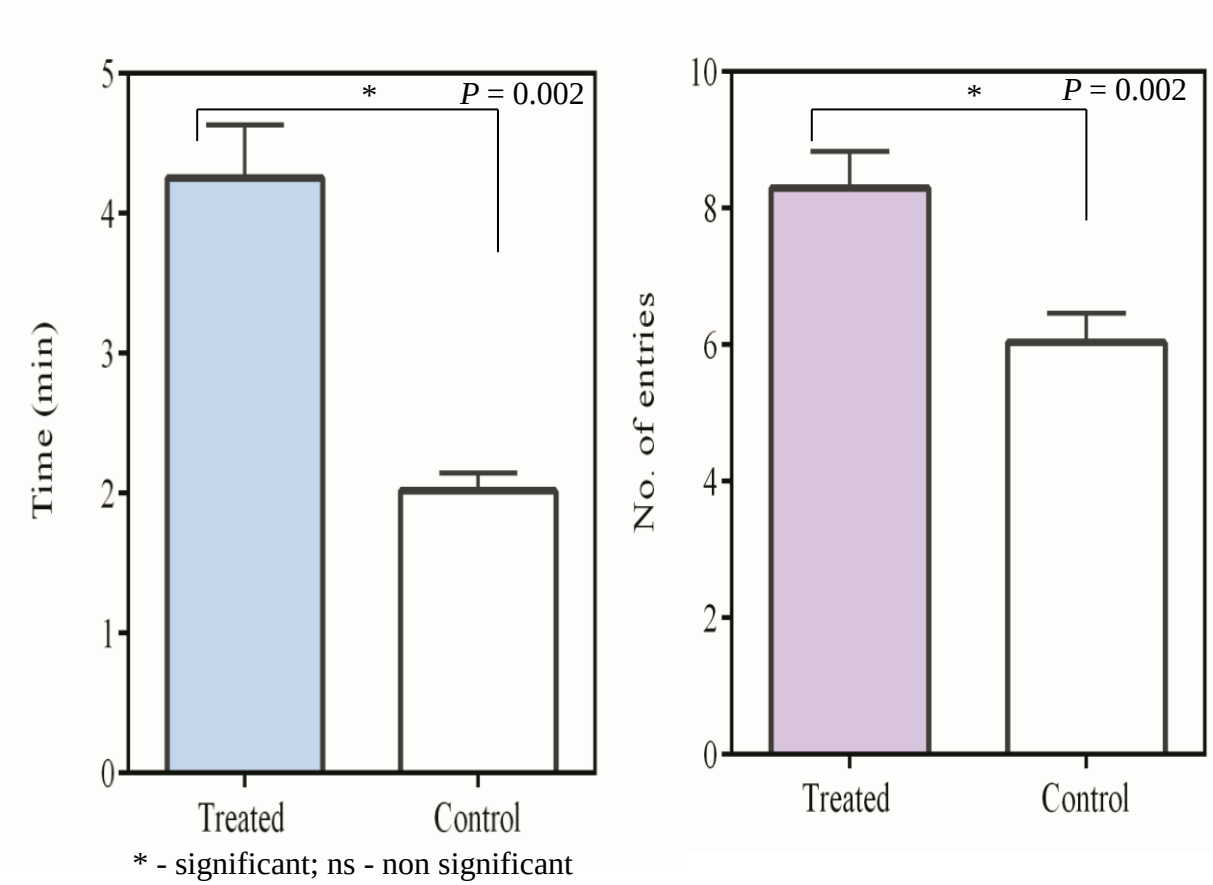


Fig. 14. Olfactory response of adult *S. dorsalis* to *n*-Docosane



* - significant; ns - non significant

Fig. 15. Olfactory response of adult *S. dorsalis* to five component synthetic blend of fruiting stage headspace volatiles

Table 7. Response of adult *S. dorsalis* to fruiting stage EAD active synthetic fractions blend and natural blend in dual choice assay (N=10)

Treatments	*df*	ANOVA							
		Time spent (Minutes)				Entries (Numbers)			
		Mean ± S.E.	F_{cal}	F_{crit}	P	Mean ± S. E.	F_{cal}	F_{crit}	P
Synthetic blend	3, 36	3.39 ± 0.15	29.12	2.87	< 0.0001	9.10 ± 0.66	9.70	2.87	< 0.0001
Natural blend		3.39 ± 0.19				9.00 ± 0.93			
Control 1		1.48 ± 0.13				5.10 ± 0.40			
Control 2		1.85 ± 0.13				6.50 ± 0.67			

Table 7a. Tukey's multiple comparison test: Response of adult *S. dorsalis* to fruiting stage EAD active synthetic fractions blend and natural blend in dual choice assay (N=10)

Treatments	*Df*	*P*	
		Time spent (Minutes)	Entries (Numbers)
Synthetic Blend vs. Natural Blend	3, 36	ns	ns
Synthetic Blend vs. Control 1		****	**
Synthetic Blend vs. Control 2		****	ns
Natural Blend vs. Control 1		****	**
Natural Blend vs. Control 2		****	ns
Control 1 vs. Control 2		ns	ns

* = 0.01; ** = 0.001; *** = 0.0001; **** < 0.0001; ns - non significant

a significant response when thrips were exposed to headspace volatiles collected from healthy and infested Capsicum plants individually along with the control solvent (Table 8).

When thrips were exposed to healthy plant volatiles, they spent significantly more time (t = 3.73; df = 9; P = 0.005) in the treated region of the olfactometer [4.16 ± 0.45 min; mean time spent ± S.E.] than in the control region [1.91 ± 0.15 min; mean time spent ± S.E.] and the mean number of entries to the treated region [7.30 ± 0.63; mean number of entries ± S.E.] of the olfactometer was also found to be significant than to control region [5.03 ± 0.51; mean number of entries ± S.E.; t = 3.62; df = 9; P = 0.006] when a 10 µl aliquot of *C. annum cv.'Indra'* headspace sample, collected from healthy plant was used (Fig. 17). Similarly, thrips spent significantly more time (t = 2.74; df = 9; P = 0.02) in the treated region of the olfactometer [3.47 ± 0.39 min; mean time spent ± S.E.] than in the control regions [2.03 ± 0.14 min; mean time spent ± S.E.] and they entered significantly more number of times to the treated region of the olfactometer compared to the control (t = 3.22; df = 9; P = 0.01) when a 10 µl aliquot of *C. annum cv.'Indra'* headspace sample, collected from artificially infested Capsicum plant was used (Fig. 18).

In dual choice assay, thrips spent significantly more time (F = 7.05; df = 3, 36; P = 0.001) in the infested Capsicum plant volatile treated region of the olfactometer [4.14 ± 0.22 min; mean time spent ± S.E.] than in the healthy plant volatile treated region [2.12 ± 0.28 min; mean time spent ± S.E.] and solvent controls in the olfactometer [1.80 ± 0.33 and 1.60 ± 0.32 min; mean time spent ± S.E.] respectively, when a 10 µl aliquot of *C. annum cv.'Indra'* headspace sample, collected from healthy and thrips infested plant was used (Table 9 & 9a). The thrips entered significantly (F = 9.15; df = 3, 36; P = 0.0001) more number of times to the infested plant volatile treated region [7.30 ± 0.73; mean number of entries ± S.E.] compared to the healthy plant volatile treated region [5.10 ± 0.71; mean number of entries ± S.E.] and the solvent control treated regions [5.10 ± 1.04 and 4.00 ± 0.65; mean number of entries ± S.E.] respectively (Fig. 19).

In order to confirm whether the exhibited behavioural response is due to the effect of herbivore induced plant volatiles or due to the host plant volatiles alone, behavioural response of adult *S. dorsalis* was evaluated in dual choice assay with fruiting stage *C. annum* plant volatiles and artificially infested *C. annum* (with thrips) plant volatiles along with the solvent control. When the thrips were given dual choice, they spent significantly more time in the infested plant volatiles treated region [3.45 ± 0.20 min; mean time spent ± S.E.] than in fruiting stage plant volatile treated region [2.59 ± 0.25 min; mean time spent ± S.E.] and solvent control treated regions [1.77 ± 0.24 and 1.77 ± 0.18 min; mean time spent ± S.E.] respectively (Table 10 & 10a). There is a significant response (F = 7.70; df = 3, 36; P = 0.0004) to herbivore induced plant volatiles in a dual choice assay over fruiting stage as thrips spent significantly more amount of time in herbivore induced plant volatiles treated region. Further, thrips entered significantly (F = 3.93; df = 3, 36; P = 0.02) more number of times to the herbivore induced volatile treated region [6.20 ± 0.68; mean number of entries ± S.E.] compared to the fruiting stage

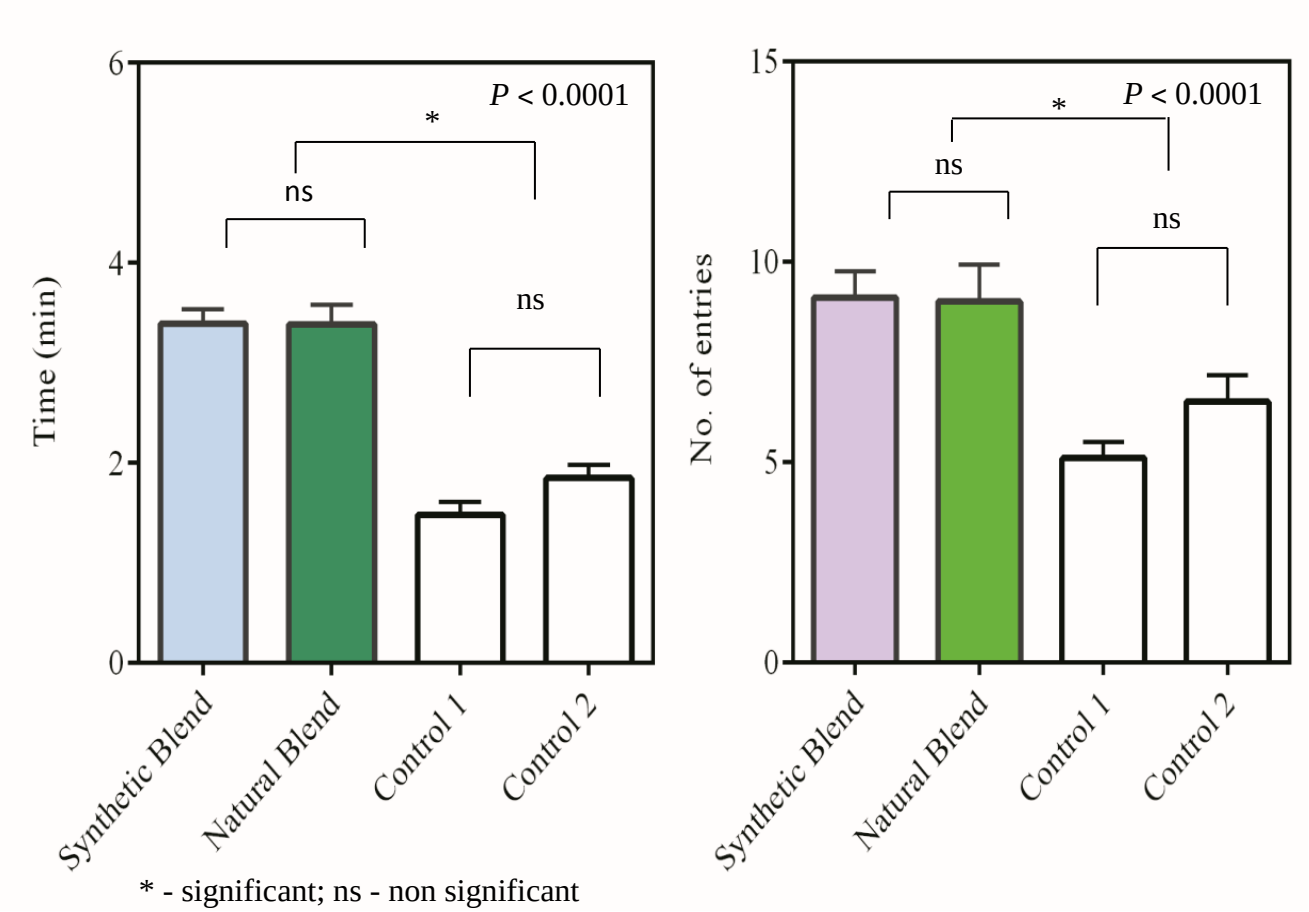


Fig. 16. Olfactory response of adult *S.dorsalis* to synthetic *v/s* natural blend of fruiting stage headspace volatiles in dual choice assay

Table 8. Response of adult *S. dorsalis* to healthy and herbivore induced (thrips) *C. annum* volatiles in olfactometer assay (N=10)

Treatments	*df*	Paired '*t*' test							
		Time spent (Minutes)				Entries (Numbers)			
		Treated (Mean ± S.E.)	Control (Mean ± S.E.)	*P*	*t*	Treated (Mean ± S.E.)	Control (Mean ± S.E.)	*P*	*t*
Healthy	9	4.16 ± 0.45	1.91 ± 0.15	0.005	3.73	7.30 ± 0.63	5.03 ± 0.51	0.006	3.62
Infested	9	3.47 ± 0.39	2.03 ± 0.14	0.02	2.74	8.50 ± 0.64	6.67 ± 0.38	0.01	3.22

Table 9. Response of adult *S. dorsalis* to HIPVs and healthy *C. annum* plant volatiles in dual choice assay (N=10)

Treatments	*df*	ANOVA							
		Time spent (Minutes)				Entries (Numbers)			
		Mean ± S. E.	F_{cal}	F_{crit}	*P*	Mean ± S. E.	F_{cal}	F_{crit}	*P*
Infested	3, 36	4.14 ± 0.22	7.05	2.87	0.001	7.30 ± 0.73	9.15	2.87	0.0001
Healthy		2.12 ± 0.28				5.10 ± 0.71			
Control 1		1.80 ± 0.33				5.10 ± 1.04			
Control 2		1.60 ± 0.32				4.00 ± 0.65			

Table 9a. Tukey's multiple comparison test: Response of adult *S. dorsalis* to HIPVs and healthy *C. annum* plant volatiles in dual choice assay (N=10)

Treatments	*Df*	*P*	
		Time spent (Minutes)	Entries (Numbers)
Infested vs. Healthy	3, 36	***	ns
Infested vs. Control 1		****	ns
Infested vs. Control 2		****	*
Healthy vs. Control 1		ns	ns
Healthy vs. Control 2		ns	ns
Control 1 vs. Control 2		ns	ns

* = 0.01; ** = 0.001; *** = 0.0001; **** < 0.0001; ns - non significant

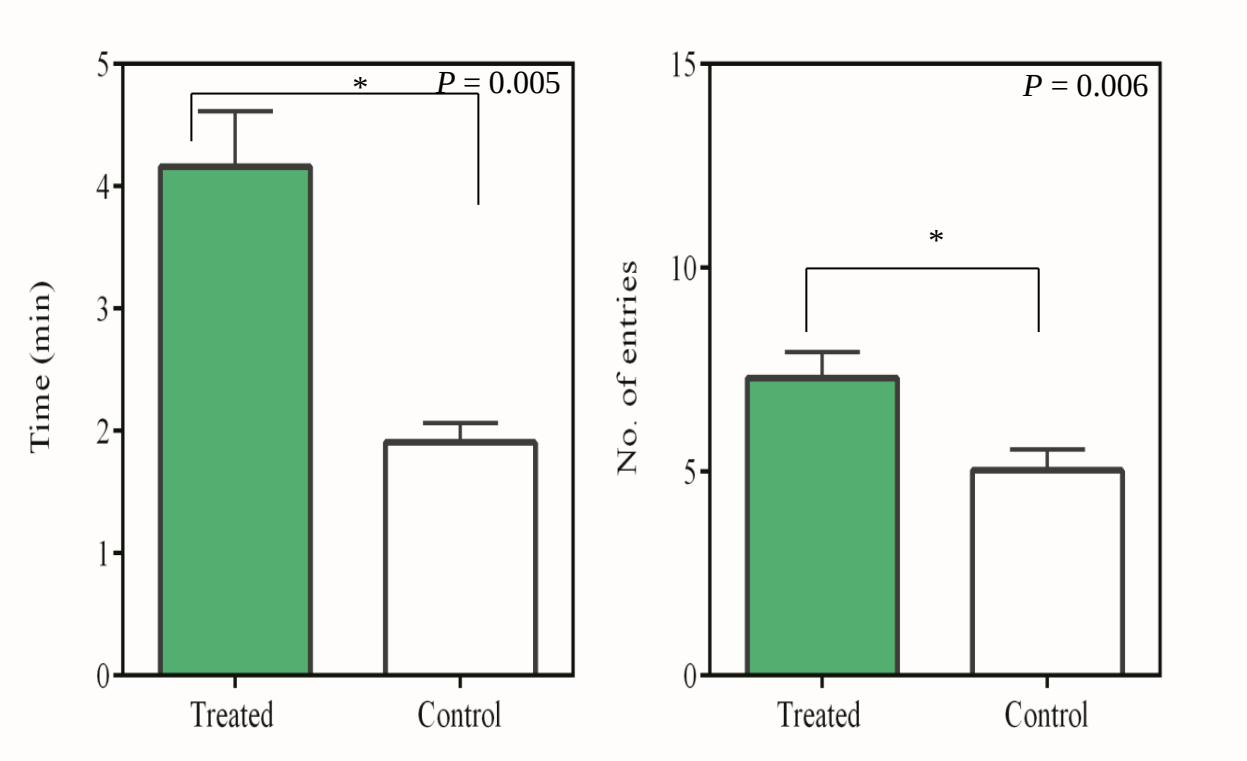
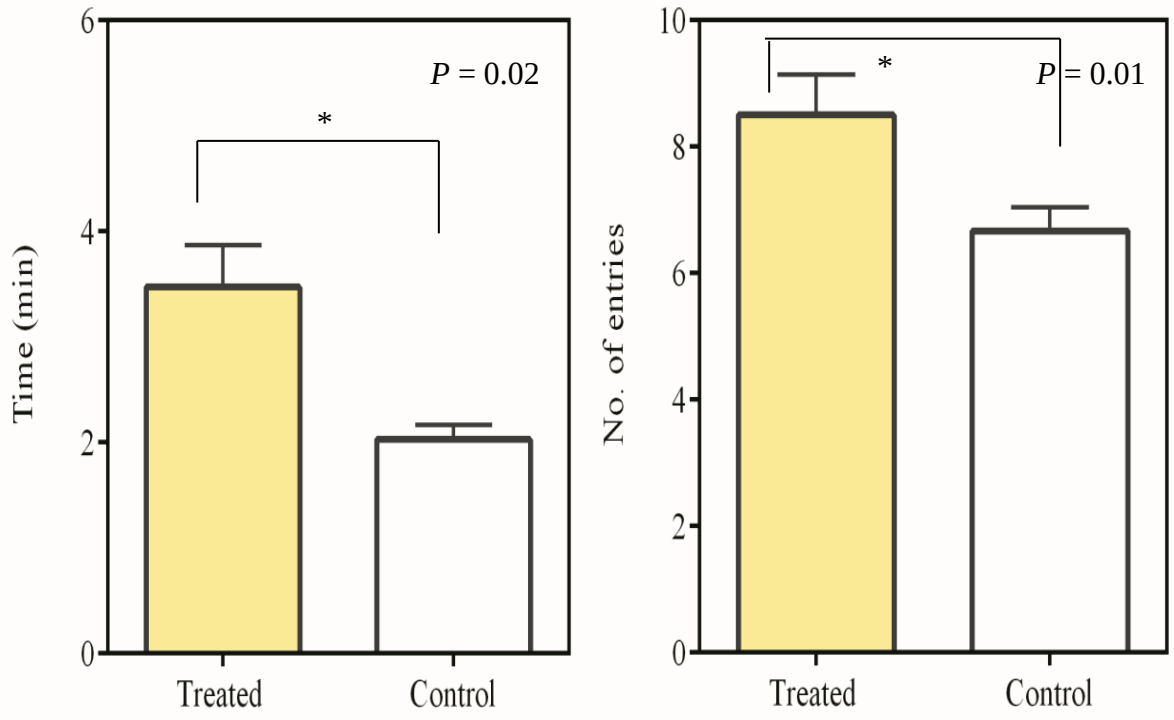


Fig. 17. Olfactory response of adult *S. dorsalis* to healthy *C. annum* plant volatiles



* - significant; ns - non significant

Fig. 18. Olfactory response of adult *S. dorsalis* to herbivore (Thrips) induced *C. annum* plant volatiles

Table 10. Response of adult *S. dorsalis* to HIPVs and fruiting stage *C. annum* plant volatiles in dual choice assay (N=10)

Treatments	*df*	ANOVA							
		Time spent (Minutes)				Entries (Numbers)			
		Mean ± S.E.	F_{cal}	F_{crit}	*P*	Mean ± S.E.	F_{cal}	F_{crit}	*P*
Infested	3, 36	3.45 ± 0.20	7.70	2.87	0.0004	6.20 ± 0.68	3.93	2.87	0.02
Fruiting		2.59 ± 0.25				5.60 ± 0.72			
Control 1		1.77 ± 0.24				4.40 ± 0.56			
Control 2		1.77 ± 0.18				4.30 ± 0.77			

Table 10a. Tukey's multiple comparison test: Response of adult *S. dorsalis* to HIPVs and fruiting stage *C. annum* plant volatiles in dual choice assay (N=10)

Treatments	*Df*	*P*	
		Time spent (Minutes)	Entries (Numbers)
Infested vs. Fruiting	3, 36	*	ns
Infested vs. Control 1		****	ns
Infested vs. Control 2		****	ns
Fruiting vs. Control 1		ns	ns
Fruiting vs. Control 2		ns	ns
Control 1 vs. Control 2		ns	ns

* = 0.01; ** = 0.001; *** = 0.0001; **** < 0.0001; ns - non significant

host plant volatile [5.60 ± 0.72; mean number of entries ± S.E.] and solvent controls [4.40 ± 0.56 and 4.30 ± 0.77; mean number of entries ± S.E.] respectively (Fig. 20).

4.2.2 Behavioural responses of co-occurring sap sucking adult insects *viz*., cotton aphid, *Aphis gossypii* Glover, silverleaf whitelfy, *Bemisia tabaci* (Gennadius) *and* spidermite, *Tetranychus macfarlanei* Baker and Pritchard to healthy and herbivore (thrips) induced plant volatiles

In four arm olfactometer bioassay, responses of adult cotton aphid, *A. gossypii* (Homoptera: Aphididae) and adult silverleaf whitefly, *B. tabaci* (Homoptera: Aleyrodidae) to volatiles collected from healthy and artificially thrips infested *C. annum* plants were investigated. The responses of adult spidermite, *T. macfarlanei* (Acari: Tetranychidae) to volatiles collected from healthy and artificially thrips infested *C. annum* plants were also investigated in Y-tube olfactometer bioassay, by giving a dual choice between healthy and thrips infested plant volatiles.

There was a significant response when aphids, *A. gossypii* were exposed to volatiles collected from healthy and infested *C. annum* plants in a dual choice assay along with the control solvent. Aphids spent significantly more time (F = 4.73; df = 3, 36; P = 0.007) in the infested plant volatile treated region of the olfactometer [3.39 ± 0.39 min; mean time spent ± S.E.] than in the regions treated with healthy plant headspace volatiles [1.51 ± 0.29 min; mean time spent ± S.E.] and control solvents [1.96 ± 0.34 and 2.52 ± 0.31 min; mean time spent ± S.E.] respectively (Table 11 & 11a) in a dual choice assay. In dual choice, aphids entered significantly (F = 2.99; df = 3, 36; P = 0.04) more number of times to the infested plant volatile treated region [2.60 ± 0.37; mean number of entries ± S.E.] compared to the healthy plant volatile treated region [2.00 ± 0.45; mean number of entries ± S.E.] and solvent control treated region [1.60 ± 0.45 and 2.20 ± 0.42; mean number of entries ± S.E.] respectively (Fig. 21).

Similar results were also observed in case of silverleaf whitefly, *B. tabaci* in dual choice bioassays. There was a significant response when whiteflies were exposed to volatiles collected from healthy and infested Capsicum plants in dual choice assay along with the control solvents. Whiteflies spent significantly more time (F = 25.73; df = 3, 36; P < 0.0001) in the thrips infested *C. annum* plant volatiles treated region of the olfactometer [4.38 ± 0.15 min; mean time spent ± S.E.] than in the healthy plant volatile treated region [1.51 ± 0.29 min; mean time spent ± S.E.] and solvent control arms [1.96 ± 0.34 and 2.52 ± 0.31 min; mean time spent ± S.E.] (Table 12 & 12a). In dual choice, whiteflies entered significantly (F = 8.74; df = 3, 36; P = 0.0002) more number of times to the infested plant volatile treated region [4.30 ± 0.30; mean number of entries ± S.E.] compared to the healthy plant volatile treated region [3.40 ± 0.48; mean number of entries ± S.E.] and solvent control treated regions [3.20 ± 0.36 and 2.00 ± 0.29; mean number of entries ± S.E.] respectively (Fig. 22).

There was a significant response when mites were exposed to volatiles collected from healthy and infested *C. annum* plants in dual choice assay using Y-tube olfactometer. During the assay, majority of the mites made their choice towards herbivore induced Capsicum plant volatiles than healthy plant volatiles. There was a significant

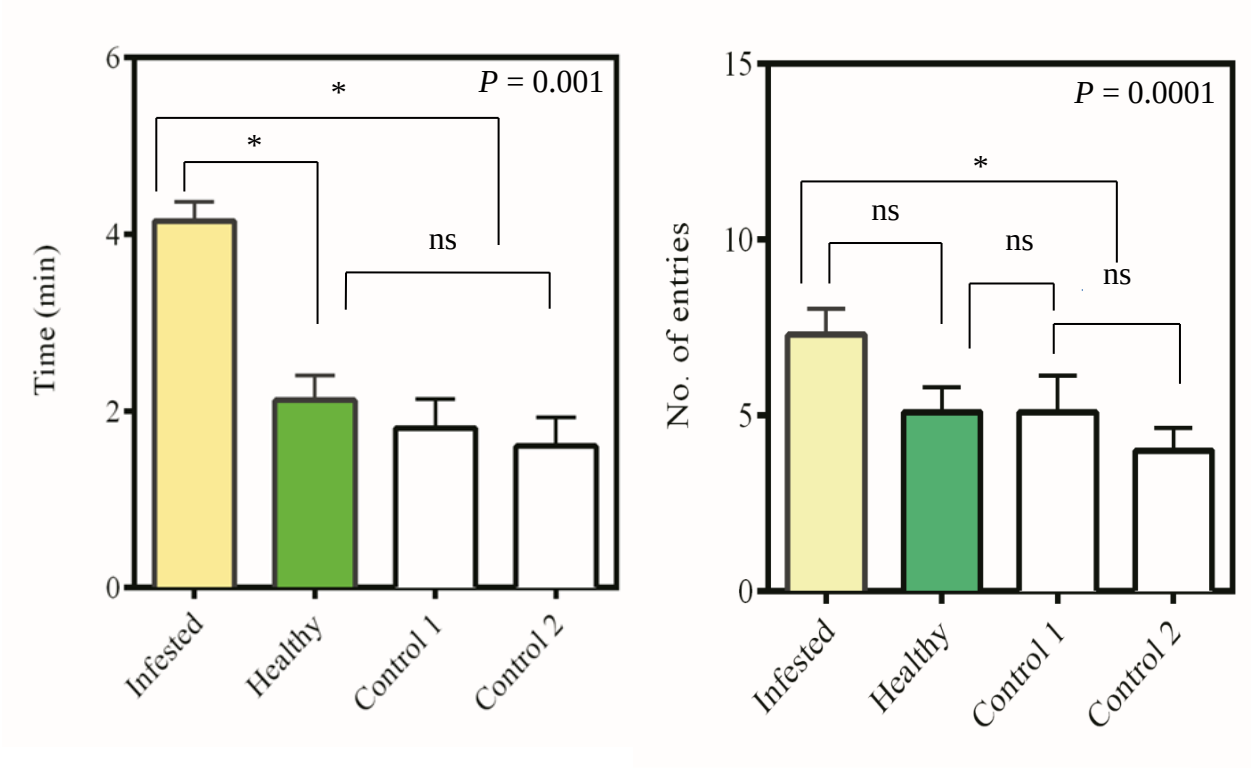
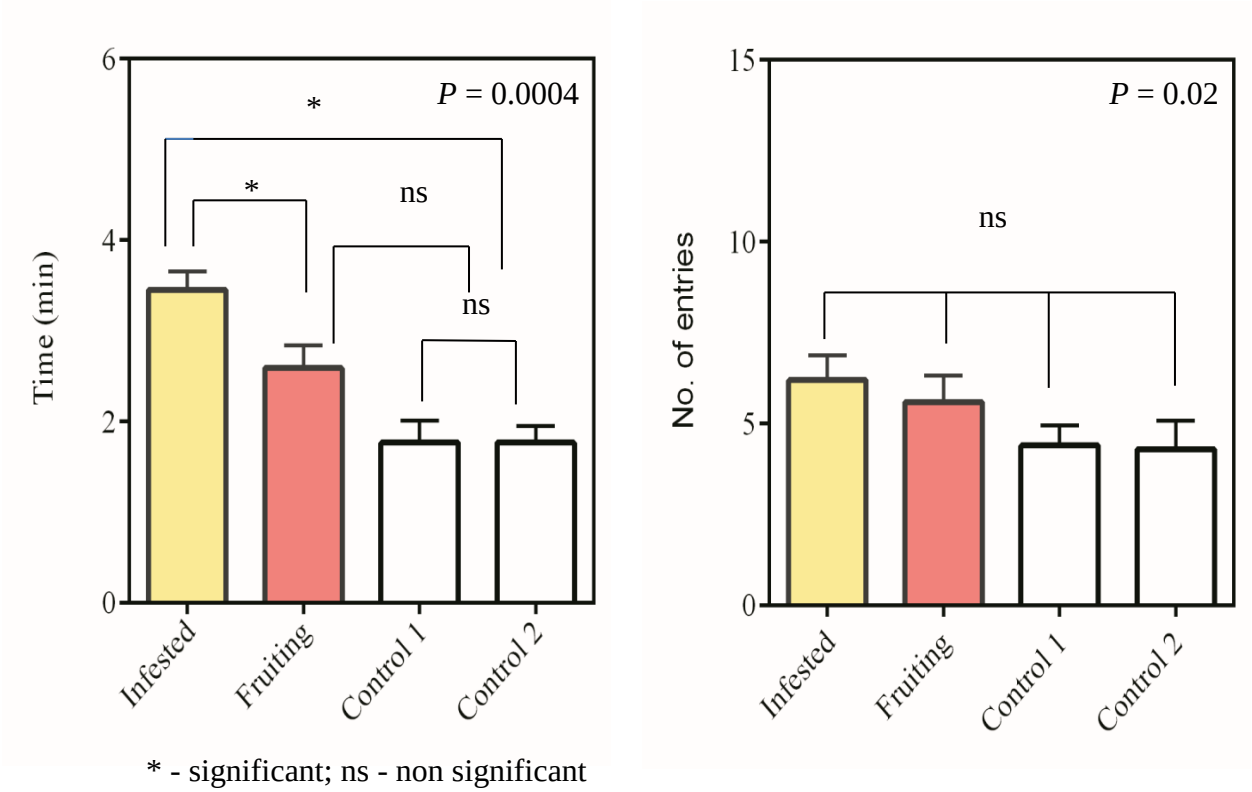


Fig. 19. Olfactory response of adult *S. dorsalis* to HIPVs and healthy *C. annum* plant volatiles in dual choice assay



* - significant; ns - non significant

Fig. 20. Olfactory response of adult *S. dorsalis* to HIPVs and fruiting *C. annum* plant volatile in dual choice assay

Table 11. Response of adult *A. gossypii* to HIPVs and *C. annum* healthy plant volatiles in dual choice assay (N=10)

Treatments	*df*	ANOVA							
		Time spent (Minutes)				Entries (Numbers)			
		Mean ± S.E.	F_{cal}	F_{crit}	*P*	Mean ± S. E.	F_{cal}	F_{crit}	*P*
Infested	3, 36	3.39 ± 0.39	4.73	2.87	0.007	2.60 ± 0.37	2.99	2.87	0.04
Healthy		1.51 ± 0.29				2.00 ± 0.45			
Control 1		1.96 ± 0.34				1.60 ± 0.45			
Control 2		2.52 ± 0.31				2.20 ± 0.42			

Table 11a. Tukey's multiple comparison test: Response of adult *A. gossypii* to HIPVs and *C. annum* healthy plant volatiles in dual choice assay (N=10)

Treatments	*Df*	*P*	
		Time spent (Minutes)	Entries (Numbers)
Infested vs. Healthy	3, 36	**	ns
Infested vs. Control 1		*	ns
Infested vs. Control 2		ns	ns
Healthy vs. Control 1		ns	ns
Healthy vs. Control 2		ns	ns
Control 1 vs. Control 2		ns	ns

* = 0.01; ** = 0.001; *** = 0.0001; **** < 0.0001; ns - non significant

Table 12. Response of adult *B. tabaci* to HIPVs and healthy *C. annum* plant volatiles in dual choice assay (N=10)

Treatments	*df*	ANOVA							
		Time spent (Minutes)				Entries (Numbers)			
		Mean ± S. E.	F_{cal}	F_{crit}	*P*	Mean ± S. E.	F_{cal}	F_{crit}	*P*
Infested	3, 36	4.38 ± 0.15	25.73	2.87	< 0.0001	4.30 ± 0.30	8.74	2.87	0.0002
Healthy		1.96 ± 0.11				3.40 ± 0.48			
Control 1		2.25 ± 0.25				3.20 ± 0.36			
Control 2		1.38 ± 0.21				2.00 ± 0.29			

Table 12a. Tukey's multiple comparison test: Response of adult *B. tabaci* to HIPVs and healthy *C. annum* plant volatiles in dual choice assay (N=10)

Treatments	*Df*	*P*	
		Time spent (Minutes)	Entries (Numbers)
Infested vs. Healthy	3, 36	****	ns
Infested vs. Control 1		****	ns
Infested vs. Control 2		****	***
Healthy vs. Control 1		ns	ns
Healthy vs. Control 2		ns	*
Control 1 vs. Control 2		*	ns

* = 0.01; ** = 0.001; *** = 0.0001; **** < 0.0001; ns - non significant

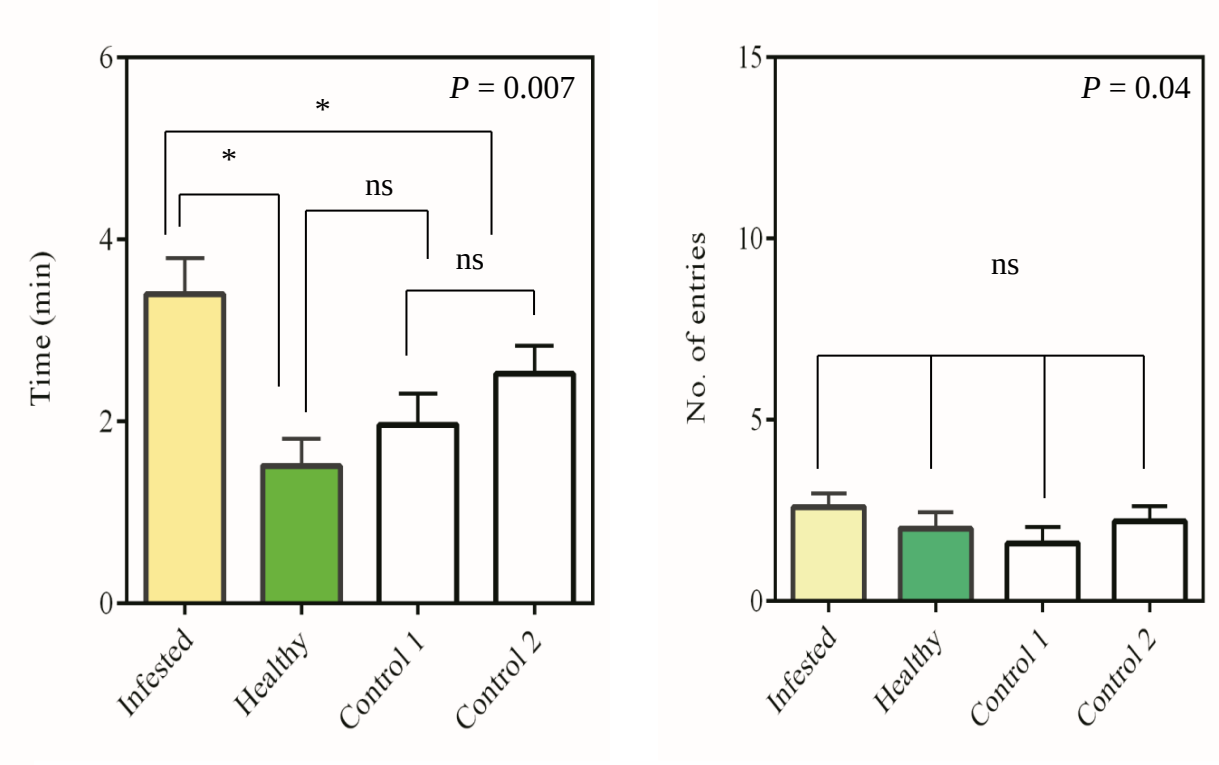
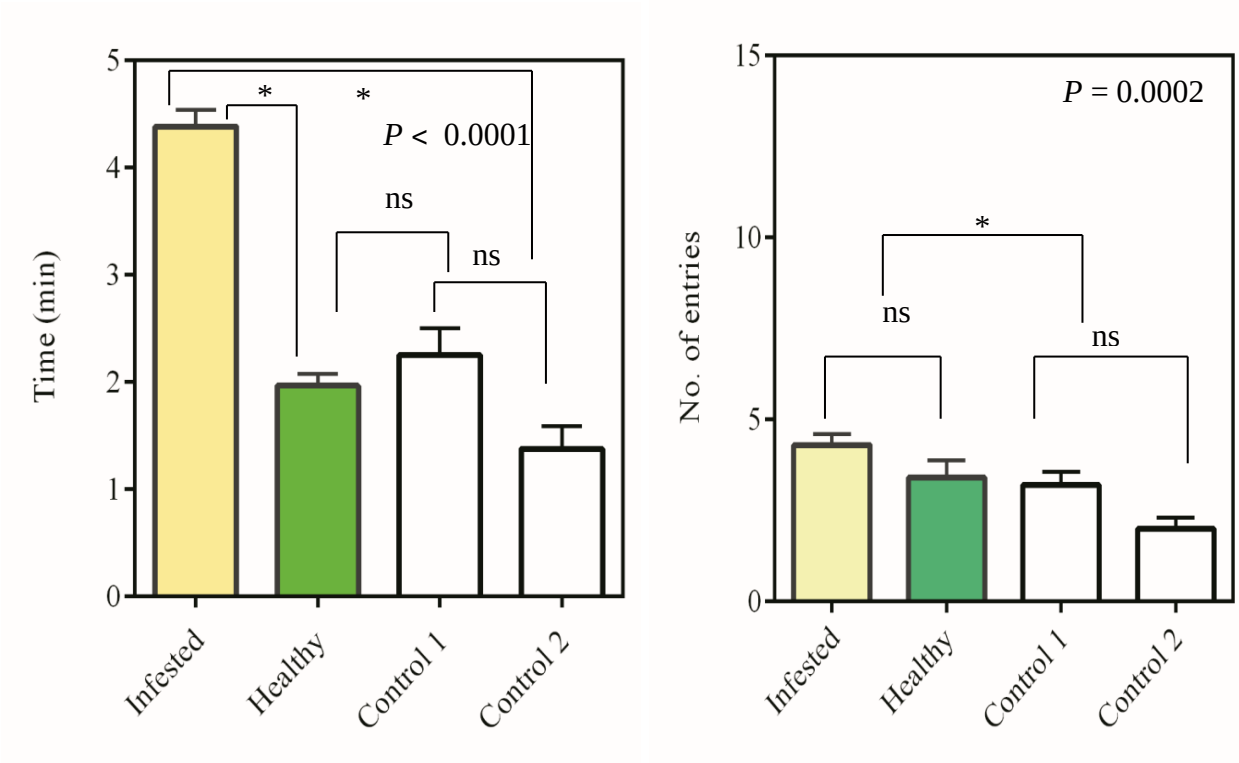


Fig. 21. Olfactory response of adult cotton aphid, *A. gossypii* to HIPVs and healthy *C. annum* plant volatiles in dual choice assay



* - significant; ns - non significant

Fig. 22. Olfactory response of adult silverleaf whitefly, *B. tabaci* to HIPVs and healthy *C. annum* plant volatiles in dual choice assay

difference in their choice towards healthy and herbivore induced plant volatiles (P = 0.01) (Fig. 23).

4.2.3 Identification of compounds present in healthy and herbivore (thrips) induced *C. annum* plant volatiles

The compounds that are present in the healthy and herbivore (thrips) induced Capsicum plant volatiles are identified using Gas chromatography coupled to mass spectrometry (Fig. 24 & 25). The quantities of the compounds present in the healthy and artificially thrips infested Capsicum headspace samples are listed in Table 13. There is a stark difference in the abundance of various volatile compounds in both healthy and infested plants (Fig. 26). A total of 19 compounds were identified in the both Capsicum volatiles collected from healthy and infested plants.

Table 13. GC-MS profile of infested and healthy *C. annum* plant headspace volatiles

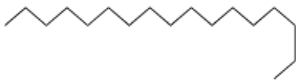
CAS	Chemical name	RT	Abundance	
			Healthy	Infested
13466-78-9	δ-3-Carene	5.8	0.3	0.4
3338-55-4	cis-Ocimene	5.9	0.3	0.2
3779-61-1	trans-Ocimene	6.0	3.5	0.0
2884-06-2	2,3-dimethylnonane	6.1	3.8	0.0
7045-71-8	2E- 4-methyl-2-undecane	6.5	5.0	0.0
17312-54-8	3,7-dimethyldecane	6.8	18	2.6
53398-83-7	trans-3-Hexenyl butyrate	8.13	2.0	0.0
106-32-1	Ethyl caprylate	8.27	0.4	1.6
1560-97-0	Methyldodecane	9.43	3.5	0.0
629-59-4	Tetradecane	9.47	2.5	39
629-62-9	Pentadecane	9.6	2.5	8.7
544-76-3	Hexadecane	9.71	13	16
593-45-3	Octadecane	9.8	8.8	17
629-92-5	Nonadecane	9.92	7.6	0.9
Not Available	2-ethylhexyl pentyl oxalate	10.0	1.3	0.0
629-78-7	Heptadecane	10.1	23	0.0
4292-19-7	Dodecyl iodide	10.2	0.3	0.0
629-97-0	*n*-Docosane	12.5	5.0	13
638-67-5	Tricosane	15.6	0.3	0.0

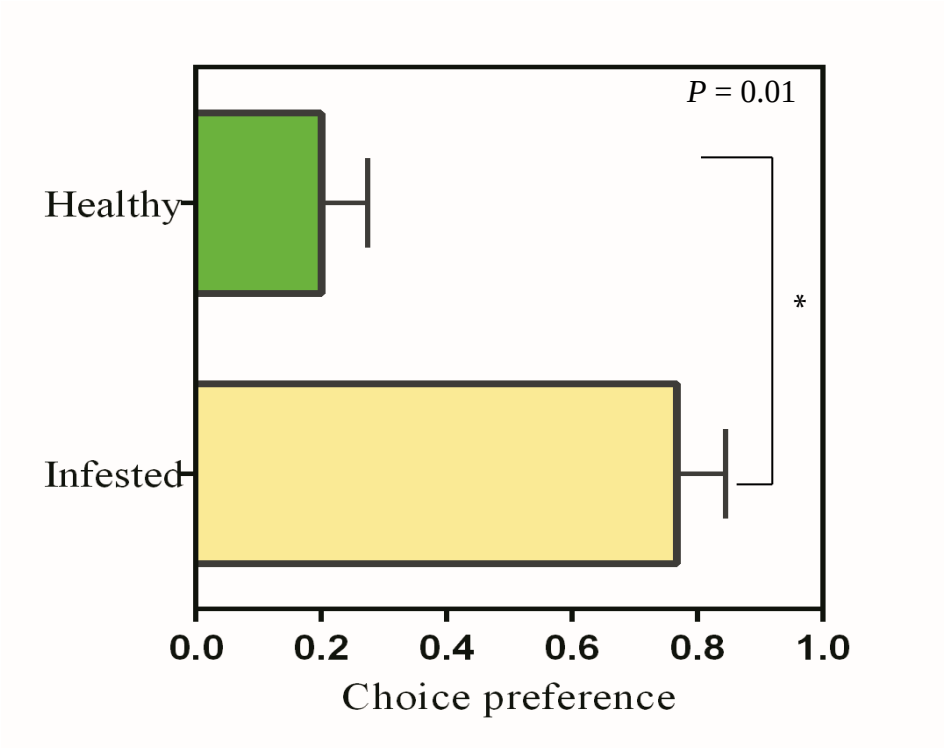
*****RT - Retension Time

4.2.4 Identification of compounds in herbivore induced *C. annum* plant volatiles that elicited an EAD Response

Coupled GC-EAD with adult *S. dorsalis* to herbivore (thrips) induced Capsicum plant volatiles revealed six compounds that could elicit an EAD response (Table 14). These EAD-active compounds were identified as *δ*-3-Carene, Octadecane, Dodecyl iodide, *n*-Docosane, Tricosane and 4-methyl-2-undecane. A representative GC- EAD trace is shown in Fig. 27. The quantities of the EAD active compounds that are present in the artificial thrips infested Capsicum plant headspace sample that served as basis for synthetic blends are listed in Table 14.

Table 14. List of GC-EAD active compounds present in thrips infested *C. annum* plant volatiles

CAS No.	Chemical name	RT	Abundance (%)	Structure
13466-78-9	*δ*-3-Carene	5.70	0.4	
7045-71-8	4-methyl-2-undecane	6.60	0.05	
593-45-3	Octadecane	9.80	17	
4292-19-7	Dodecyl iodide	10.30	0.05	
629-97-0	*n*-Docosane	12.70	13	
638-67-5	Tricosane	15.50	0.05	



* - significant; ns - non significant

Fig. 23. Olfactory response of adult mite, *T. macfarlanei* to HIPVs and healthy *C. annum* plant volatiles in dual choice assay in Y-tube olfactometer

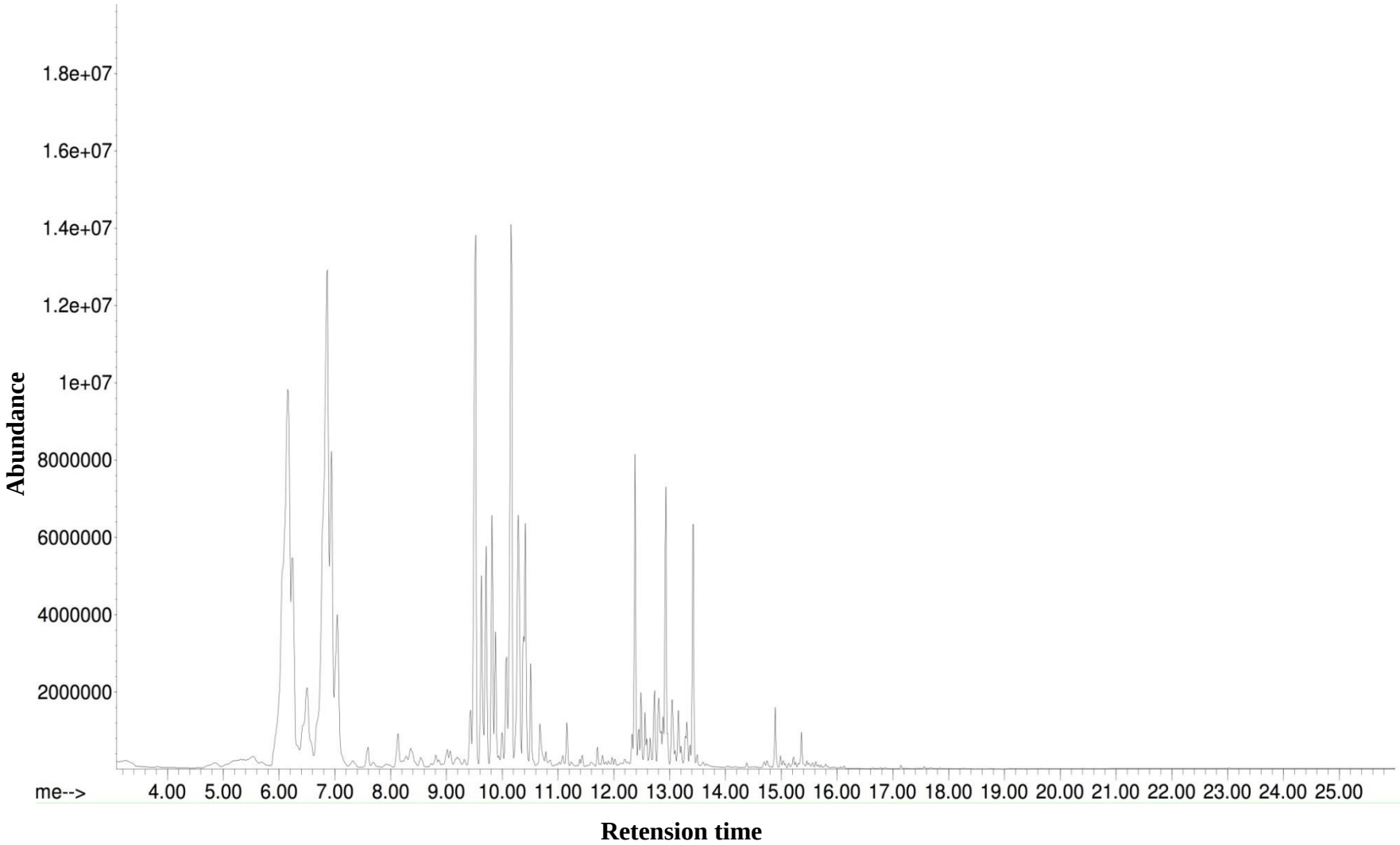


Fig. 24. GC-MS chromatogram of *C. annum* healthy plant volatiles

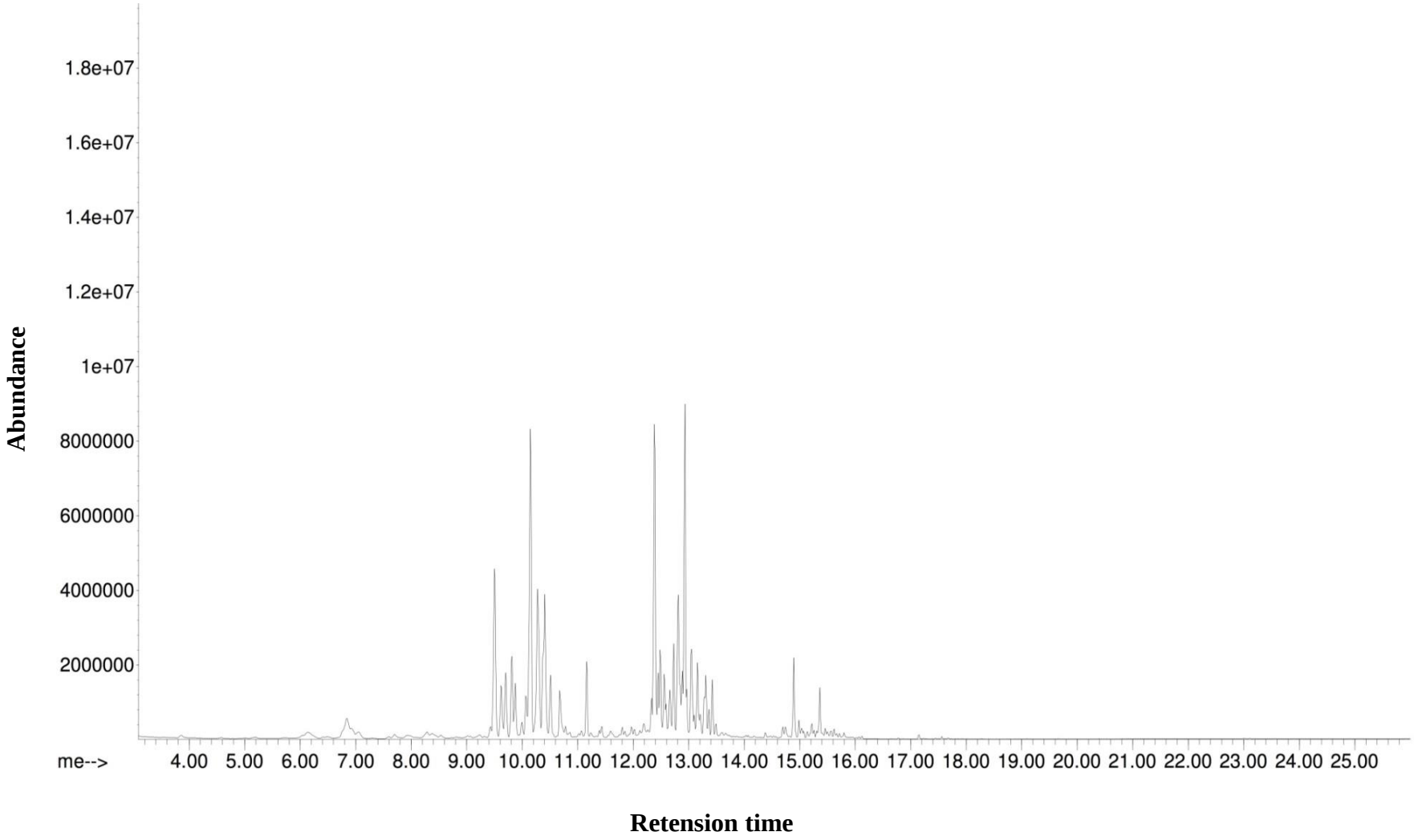
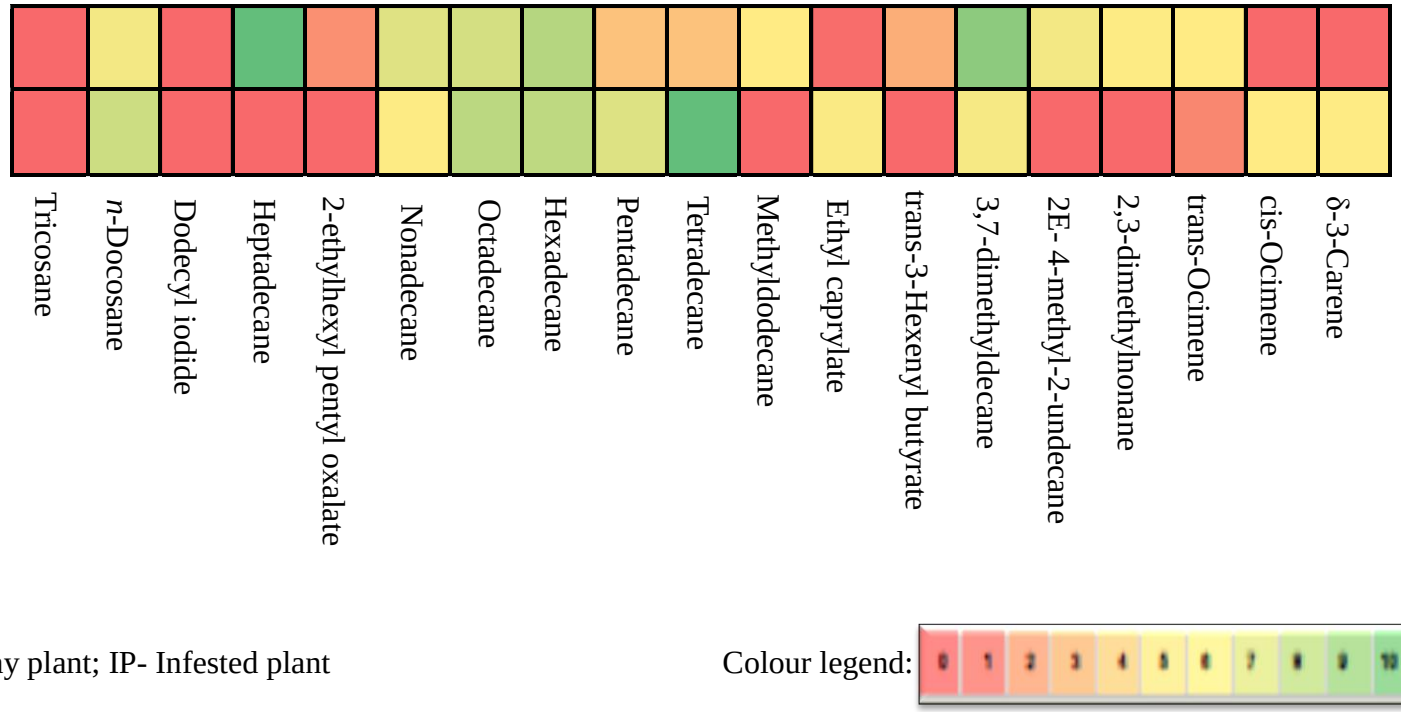


Fig. 25. GC-MS chromatogram of herbivore induced *C. annum* plant volatiles



*HP- Healthy plant; IP- Infested plant

Colour legend: 0 1 2 3 4 5 6 7 8 9 10 11 PPM

Fig. 26. Heat map showing variation in the headspace volatiles abundance of *C. annum* infested and healthy plant

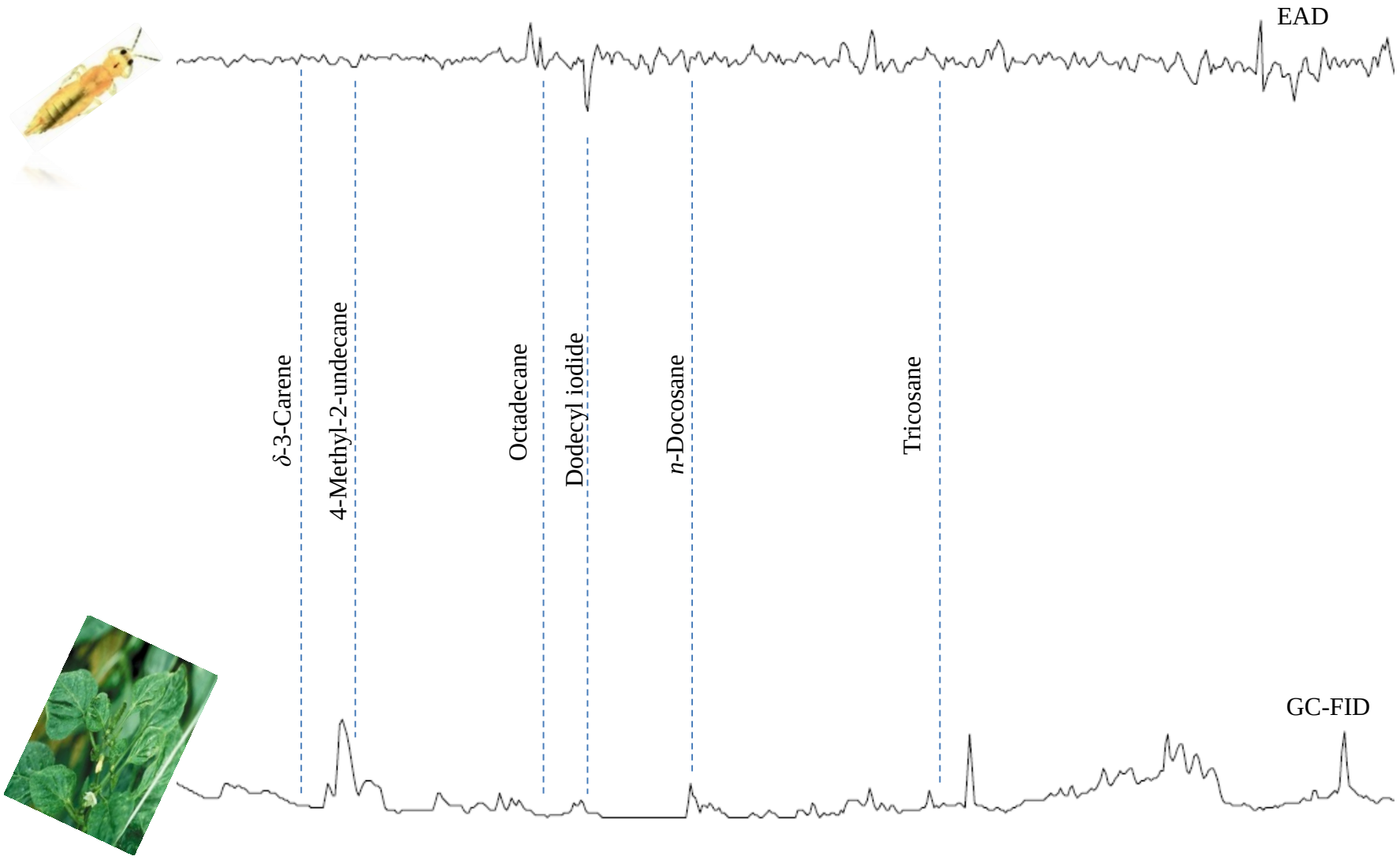


Fig. 27. GC-EAD traces showing the response of adult *S. dorsalis* to infested *C. annum* plant volatiles

4.2.5 Behavioural responses of adult *S. dorsalis* to synthetic fractions of herbivore induced plant volatiles in *C. annum*

Five compounds *viz*., *δ*-3-Carene, Octadecane, Dodecyl iodide, *n*-Docosane, Tricosane out of six that elicited an EAD response in the herbivore (thrips) induced volatiles were tested in the olfactometer assay to know their behavioural response. Due to the commercial unavailability of 4-methyl-2-undecane, we could not assay this compound. Among five compounds tested, *δ*-3-Carene, Octadecane, *n*-Docosane were behaviourally active whereas Dodecyl iodide and Tricosane were not behaviourally active when presented individually at a standard dose (1 µg on filter paper) to adult, *S. dorsalis.*

Thrips spent significantly longer time in the treated regions *viz*., *δ*-3-Carene [2.58 ± 0.08 min (treatment); 1.99 ± 0.09 min (control); mean time spent ± S.E.; $t = 5.71$; $df = 9$; $P = 0.0003$]; Octadecane [3.68 ± 0.26 min (treatment); 2.03 ± 0.09 min (control); mean time spent ± S.E.; $t = 4.64$; $df = 9$; $P = 0.001$]; *n*-Docosane [4.11 ± 0.53 min (treatment); 1.86 ± 0.16 min (control); mean time spent ± S.E.; $t = 3.28$; $df = 9$; $P = 0.0096$] of the olfactometer and also entered significantly more number of times in to the treated region *viz*., *δ*-3-Carene [9.60 ± 1.12 (treatment); 7.13 ± 0.82 (control); mean number of entries ± S.E.; $t = 3.45$; $df = 9$; $P = 0.007$]; Octadecane [9.00 ± 0.86 (treatment); 6.26 ± 0.77 (control); mean number of entries ± S.E.; $t = 3.86$; $df = 9$; $P = 0.004$]; *n*-Docosane [6.70 ± 0.79 (treatment); 4.43 ± 0.82 (control); mean number of entries ± S.E.; $t = 6.48$; $df = 9$; $P = 0.0001$] of the olfactometer.

In case of Dodecyl iodide and Tricosane, there is no significant difference between the mean time spent (Dodecyl iodide [2.30 ± 0.15 min (treatment); 2.58 ± 0.08 min (control); mean time spent ± S.E.; $t = 2.07$; $df = 9$; $P = 0.06$]; Tricosane [2.81 ± 0.26 min (treatment); min (control); 2.38 ± 0.07 mean time spent ± S.E.; $t = 1.45$; $df = 9$; $P = 0.18$]) while there is a significant difference in the mean number of entries in treated region and the control solvent (Dodecyl iodide [7.60 ± 0.54 (treatment); 6.30 ± 0.67 (control); mean number of entries ± S.E.; $t = 2.83$; $df = 9$; $P = 0.02$]; Tricosane [7.90 ± 0.74 (treatment); 6.47 ± 0.72 (control); mean number of entries ± S.E.; $t = 4.20$; $df = 9$; $P = 0.002$]) when presented alone at a standard dose (1 µg on filter paper) (Table 15 and Fig. 28-32).

When presented together as a 5-component blend formulated using the same ratio and concentration as in the natural sample, significant level of attraction [3.53 ± 0.28 min (treatment); 2.18 ± 0.14 min (control); mean time spent ± S.E.; $t = 3.96$; $df = 9$; $P = 0.003$ and 8.90 ± 0.98 (treatment); 6.05 ± 0.79 (control); mean number of entries ± S.E.; $t = 4.61$; $df = 9$; $P = 0.001$] was observed (Fig. 33). Furthermore, in a dual choice test when thrips were offered both the natural sample and the synthetic blend, there was no significant difference in their behavioural response for both mean amount of time spent (synthetic blend [3.27 ± 0.41 min; mean time spent ± S.E.]; natural sample [3.27 ± 0.14 min; mean time spent ± S.E.] and solvent control treated regions [1.83 ± 0.18 and 1.69 ± 0.24 min; mean time spent ± S.E. respectively) ($F = 9.99$; $df = 3, 36$; $P < 0.0001$) and mean number of entries made to natural sample and synthetic blend treated region ($F = 8.27$; $df = 3, 36$; $P = 0.0003$; synthetic blend [9.70 ± 1.12; mean number of entries ± S.E.]; natural sample [9.40 ± 0.70; mean number of entries ± S.E.] compared to solvent

Table 15. Response of adult *S. dorsalis* to EAD active synthetic fractions of herbivore induced (thrips) *C. annum* plant volatiles and their blend in olfactometer assay (N=10)

Synthetic fractions	*df*	Paired '*t*' test							
		Time spent (Minutes)				Entries (Numbers)			
		Treated (Mean ± S.E.)	Control (Mean ± S.E.)	*P*	*t*	Treated (Mean ± S.E.)	Control (Mean ± S.E.)	*P*	*t*
δ-3-Carene	9	2.58 ± 0.08	1.99 ± 0.09	0.0003	5.71	9.60 ± 1.12	7.13 ± 0.82	0.007	3.45
Octadecane	9	3.68 ± 0.26	2.03 ± 0.09	0.001	4.64	9.00 ± 0.86	6.26 ± 0.77	0.004	3.86
Dodecyl iodide	9	2.30 ± 0.15	2.58 ± 0.08	0.06	2.07	7.60 ± 0.54	6.30 ± 0.67	0.02	2.83
n-Docosane	9	4.11 ± 0.53	1.86 ± 0.16	0.0096	3.28	6.70 ± 0.79	4.43 ± 0.82	0.0001	6.48
Tricosane	9	2.81 ± 0.26	2.38 ± 0.07	0.18	1.45	7.90 ± 0.74	6.47 ± 0.72	0.002	4.20
Synthetic blend	9	3.53 ± 0.28	2.18 ± 0.14	0.003	3.96	8.90 ± 0.98	6.05 ± 0.79	0.001	4.61

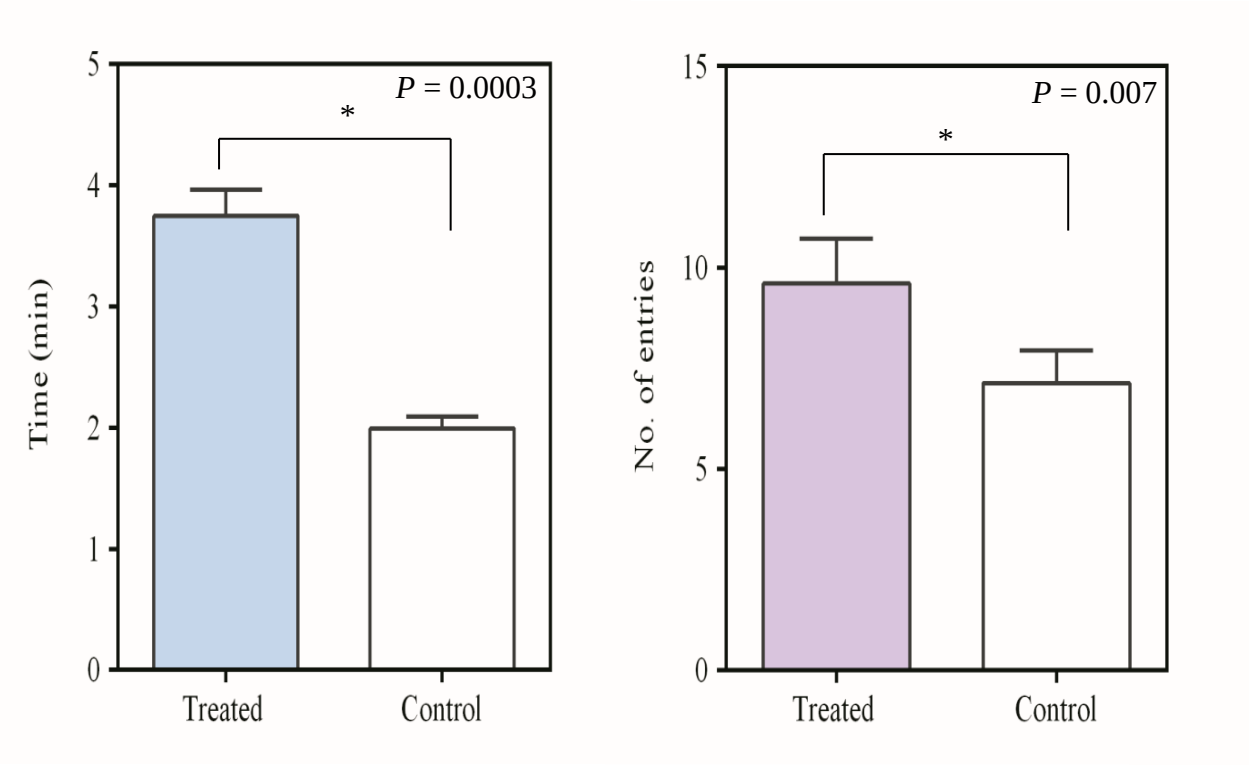
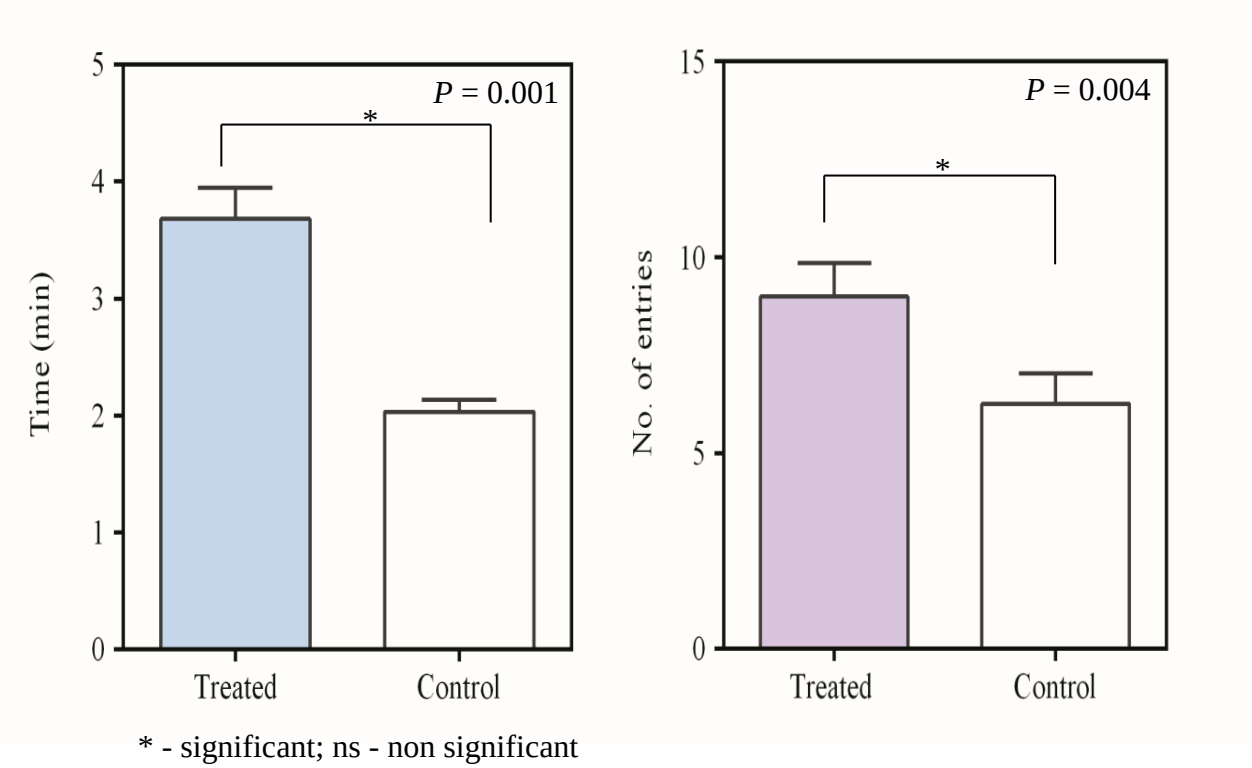


Fig. 28. Olfactory response of adult *S. dorsalis* to *δ*-3-Carene



* - significant; ns - non significant

Fig. 29. Olfactory response of adult *S. dorsalis* to Octadecane

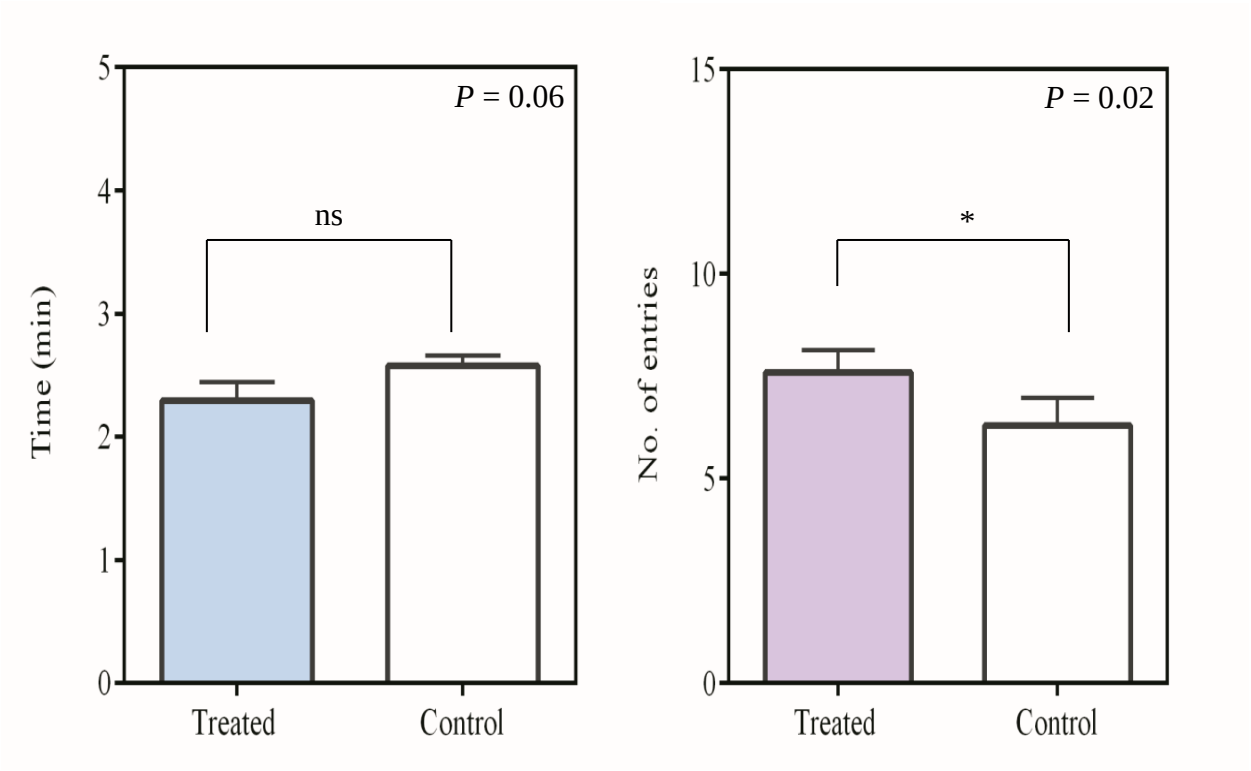
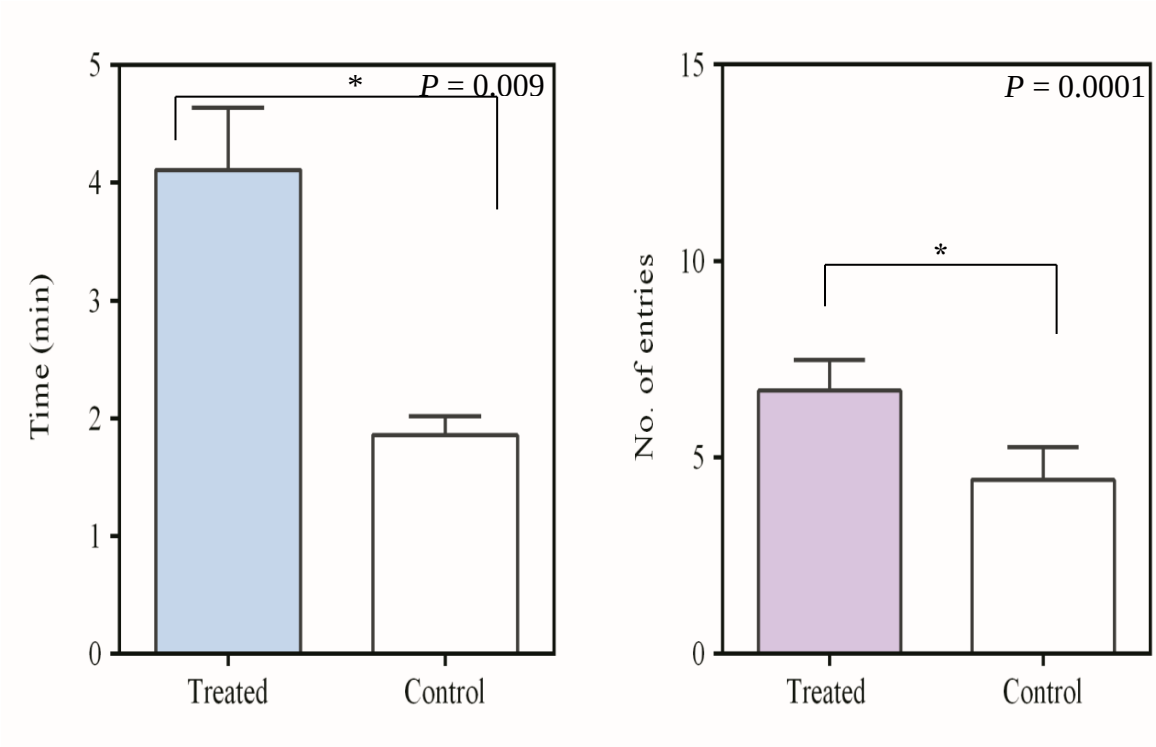


Fig. 30. Olfactory response of adult *S. dorsalis* to Dodecyl iodide



* - significant; ns - non significant

Fig. 31. Olfactory response of adult *S. dorsalis* to *n*-Docosane

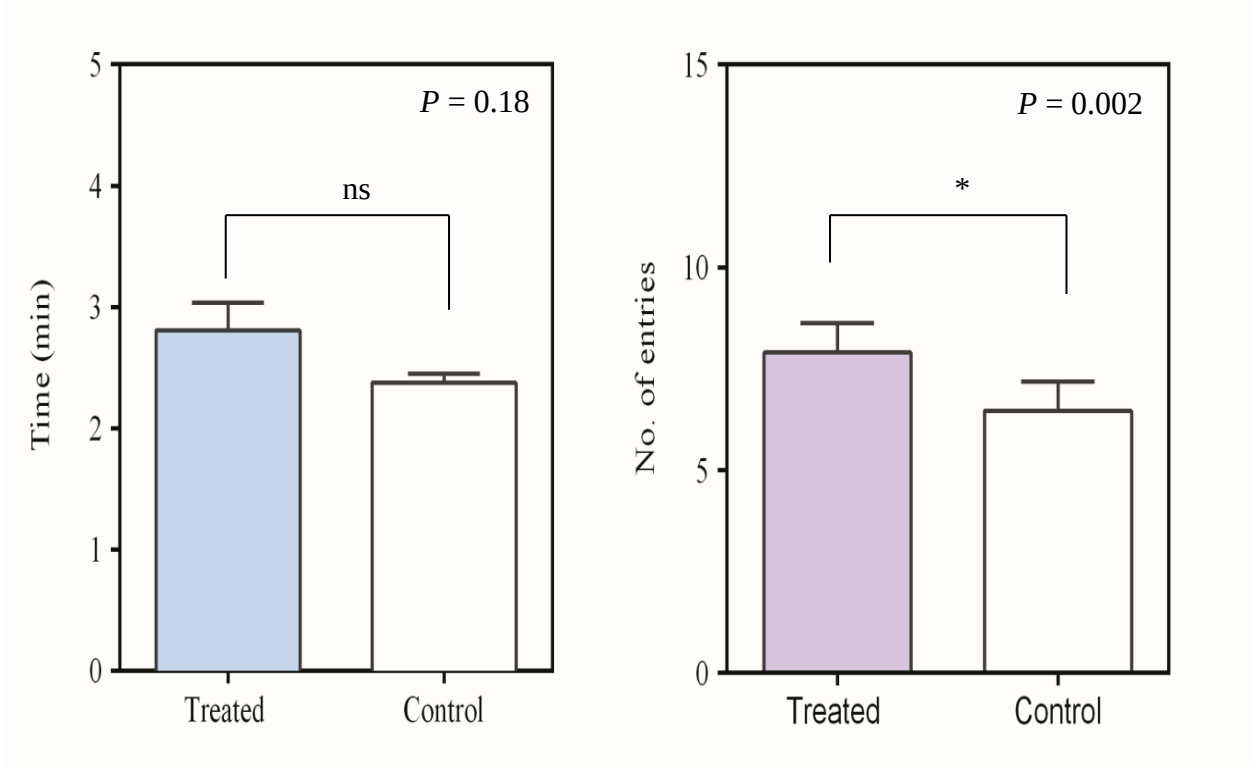
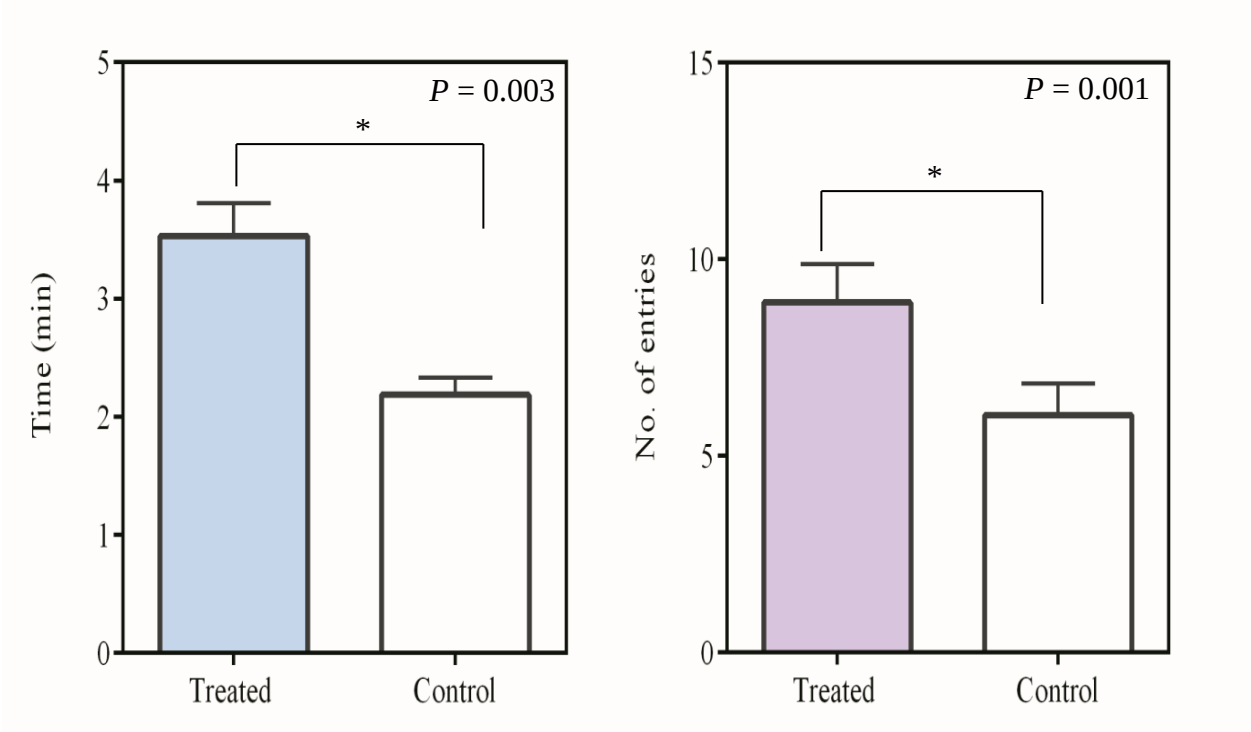


Fig. 32. Olfactory response of adult *S. dorsalis* to Tricosane



* - significant; ns - non significant

Fig. 33. Olfactory response of adult *S. dorsalis* to five component synthetic blend of HIPVs

control treated regions [6.10 ± 0.85 and 5.40 ± 0.78; mean number of entries ± S.E. respectively) (Table 16 & 16a and Fig. 34).

4.3 Influence of conspecific body odours and body wash to adult *S. dorsalis*

In an olfactometer bioassay, responses of adult *S. dorsalis* to body odours and body wash collected from conspecifics were investigated. In order to confirm the effect of herbivore induced plant volatile on adult *S. dorsalis* further multiple choice assay test was done in olfactometer using healthy plant volatiles, artificially thrips infested plant volatiles and their conspecific body wash along with control solvent.

4.3.1 Response of adult *S. dorsalis* to conspecific body odours and body wash

There was no significant difference between mean time spent when body wash collected using dichloromethane (t = 0.43; df = 9; P = 0.67) was tested. The mean time spent in the treated [2.61 ± 0.34 min; mean time spent ± S.E.] and in the control regions [2.40 ± 0.15 min; mean time spent ± S.E.] in olfactometer assay when a 10 µl aliquot was used reveals the same.

Similarly, when thrips were exposed to body wash collected using hexane also, there was no significant (t = 0.99; df = 9; P = 0.35) difference between the mean time spent in the treated [2.75 ± 0.39 min; mean time spent ± S.E.] and the control regions [2.26 ± 0.11 min; mean time spent ± S.E.] in olfactometer assay when a 10 µl aliquot was used (Table 17).

Further, there is no significant difference for number of entries also to the treated region [7.40 ± 0.95; mean number of entries ± S.E.] and the control region [6.00 ± 0.76; mean number of entries ± S.E.] in olfactometer assay when both body washes collected in dichloromethane (t = 2.18; df = 9; P = 0.06) and hexane [6.80 ± 0.94; mean number of entries ± S.E.; t = 0.93; df = 9; P = 0.09] along with control solvents [6.87 ± 0.73; mean number of entries ± S.E.] were tested (Fig. 35 & 36).

There was no significant response when thrips were exposed to body odour collected by air entrainment using diethyl ether solvent. However, there was no significant difference between mean time spent (t = 0.50; df = 9; P = 0.63) in the treated region of the olfactometer [2.52 ± 0.31 min; mean time spent ± S.E.] and in the control region [2.31 ± 0.12 min; mean time spent ± S.E.] when a 10 µl aliquot was used. The mean number of entries to the treated region [7.40 ± 0.97; mean number of entries ± S.E.] and control region [6.33 ± 0.50; mean number of entries ± S.E.] was also found to be non-significant (t = 1.49; df = 9; P = 0.17) (Fig. 37).

Thus, there was no significant response when thrips were exposed to body wash collected using two different solvents such as dichloromethane/hexane and also to body odour volatiles collected from their conspecifics using diethyl ether solvent. Further, none of the volatile compounds were identified from the thrips bodywash extract in dichloromethane solvent (Fig. 38).

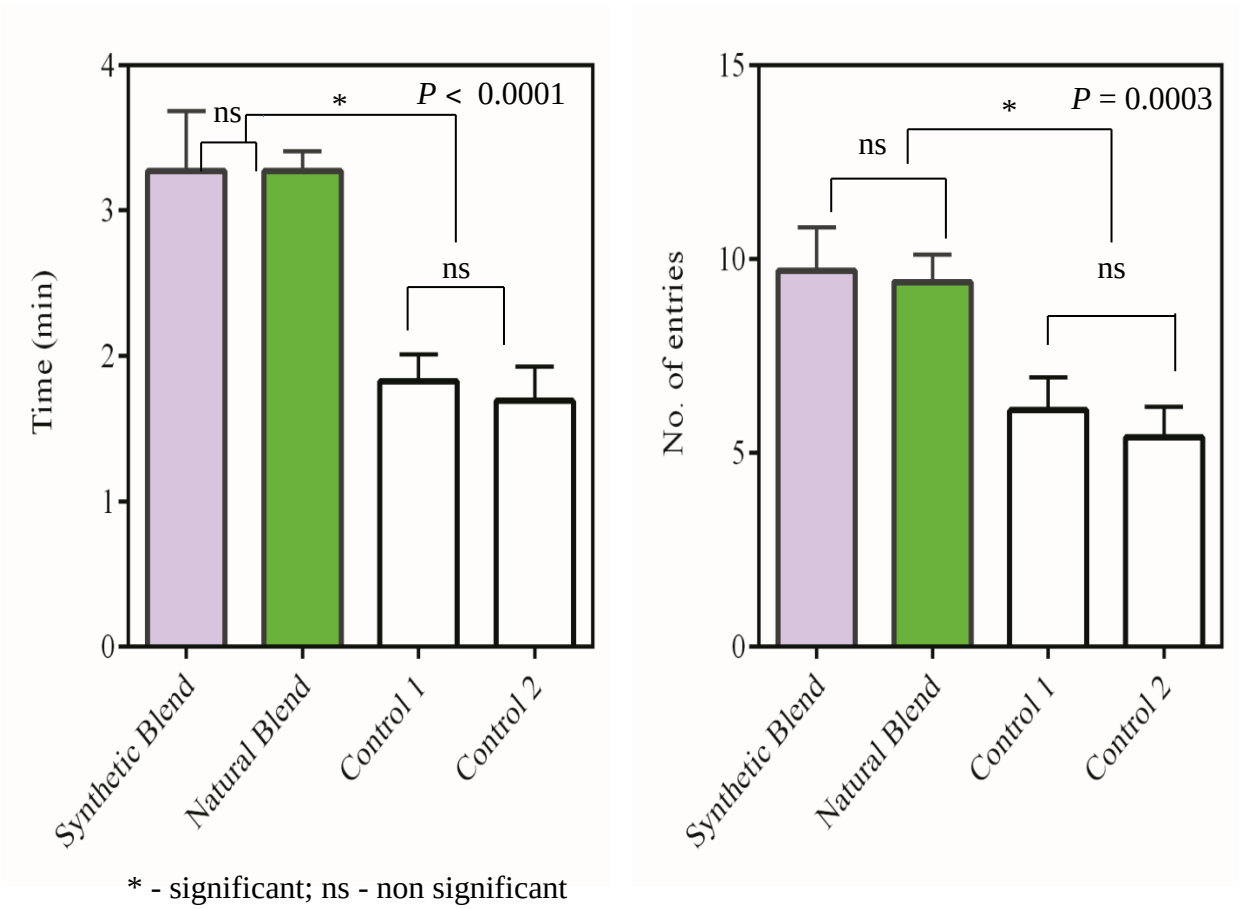
Table 16. Response of adult *S. dorsalis* to EAD active synthetic fractions of herbivore induced (thrips) *C. annum* plant volatiles and natural blend in dual choice assay (N=10)

Treatments	*df*	ANOVA							
		Time spent (Minutes)				Entries (Numbers)			
		Mean ± S.E.	F_{cal}	F_{crit}	*P*	Mean ± S.E.	F_{cal}	F_{crit}	*P*
Synthetic blend	3, 36	3.27 ± 0.41	9.99	2.87	< 0.0001	9.70 ± 1.12	8.27	2.87	0.0003
Natural blend		3.27 ± 0.14				9.40 ± 0.70			
Control 1		1.83 ± 0.18				6.10 ± 0.85			
Control 2		1.69 ± 0.24				5.40 ± 0.78			

Table 16a. Tukey's multiple comparison test: Response of adult *S. dorsalis* to EAD active synthetic fractions of herbivore induced (thrips) *C. annum* plant volatiles and natural blend in dual choice assay (N=10)

Treatments	*Df*	*P*	
		Time spent (Minutes)	Entries (Numbers)
Synthetic Blend vs. Natural Blend	3,36	ns	ns
Synthetic Blend vs. Control 1		**	**
Synthetic Blend vs. Control 2		***	ns
Natural Blend vs. Control 1		**	**
Natural Blend vs. Control 2		***	ns
Control 1 vs. Control 2		ns	ns

* = 0.01; ** = 0.001; *** = 0.0001; **** < 0.0001; ns - non significant



* - significant; ns - non significant

Fig. 34. Olfactory response of adult *S. dorsalis* to synthetic *v/s* natural blend of HIPVs in dual choice assay

Table 17. Response of adult *S.dorsalis* to thrips body wash and body odour in different solvents (N=10)

Treatments	*df*	Paired '*t*' test							
		Time spent (Minutes)				Entries (Numbers)			
		Treated (Mean ± S.E.)	Control (Mean ± S.E.)	*P*	*t*	Treated (Mean ± S.E.)	Control (Mean ± S.E.)	*P*	*t*
i. Body wash									
Dichloromethane	9	2.61 ± 0.34	2.40 ± 0.15	0.67	0.43	7.40 ± 0.95	6.00 ± 0.76	0.06	2.18
Hexane	9	2.75 ± 0.39	2.26 ± 0.11	0.35	0.99	6.80 ± 0.94	6.87 ± 0.73	0.09	0.93
ii. Body odour									
Diethyl ether	9	2.52 ± 0.31	2.31 ± 0.12	0.63	0.50	7.40 ± 0.97	6.33 ± 0.50	0.17	1.49

4.3.2 Olfactory response of adult *S. dorsalis* to conspecific body wash, healthy and infested *C. annum* plant volatiles in multiple choice assay

In olfactometer bioassay, responses of adult *S. dorsalis* to volatiles collected from healthy and artificially thrips infested Capsicum plant along with body wash collected in dichloromethane were investigated by giving multiple choice at a time to know the effect of healthy, herbivore (thrips) induced volatiles and their conspecifics body wash. In this assay sample collected from artificially thrips infested Capsicum plant elicited a positive behavioural response over others. Adult *S. dorsalis* spent significantly more time in the herbivore induced plant volatile treated region of the olfactometer compared to healthy plant volatile, body wash and control regions of the olfactometer ($F = 92.55$; $df = 3, 36$; $P < 0.0001$). Mean time spent in the herbivore induced plant volatile treated region was 4.13 ± 0.16 min [mean time spent ± S.E.], compared to healthy plant volatile [2.89 ± 0.12 min; mean time spent ± S.E.], body wash [1.60 ± 0.10 min; mean time spent ± S.E.] and in the control solvent [1.37 ± 0.13 min; mean time spent ± S.E.] regions of the olfactometer (Table 18 & 18a).

In multiple choice assay, when the thrips were exposed to herbivore induced plant volatiles, healthy plant volatiles and body wash, they entered significantly ($F = 66.63$; $df = 3, 36$; $P < 0.0001$) more number of times to the herbivore induced plant volatile treated region [10.20 ± 0.76; mean number of entries ± S.E.] compared to the healthy plant volatiles [8.70 ± 0.68; mean number of entries ± S.E.], body wash [5.30 ± 0.54; mean number of entries ± S.E.] and control solvent [5.20 ± 0.59; mean number of entries ± S.E.] treated regions (Fig. 39).

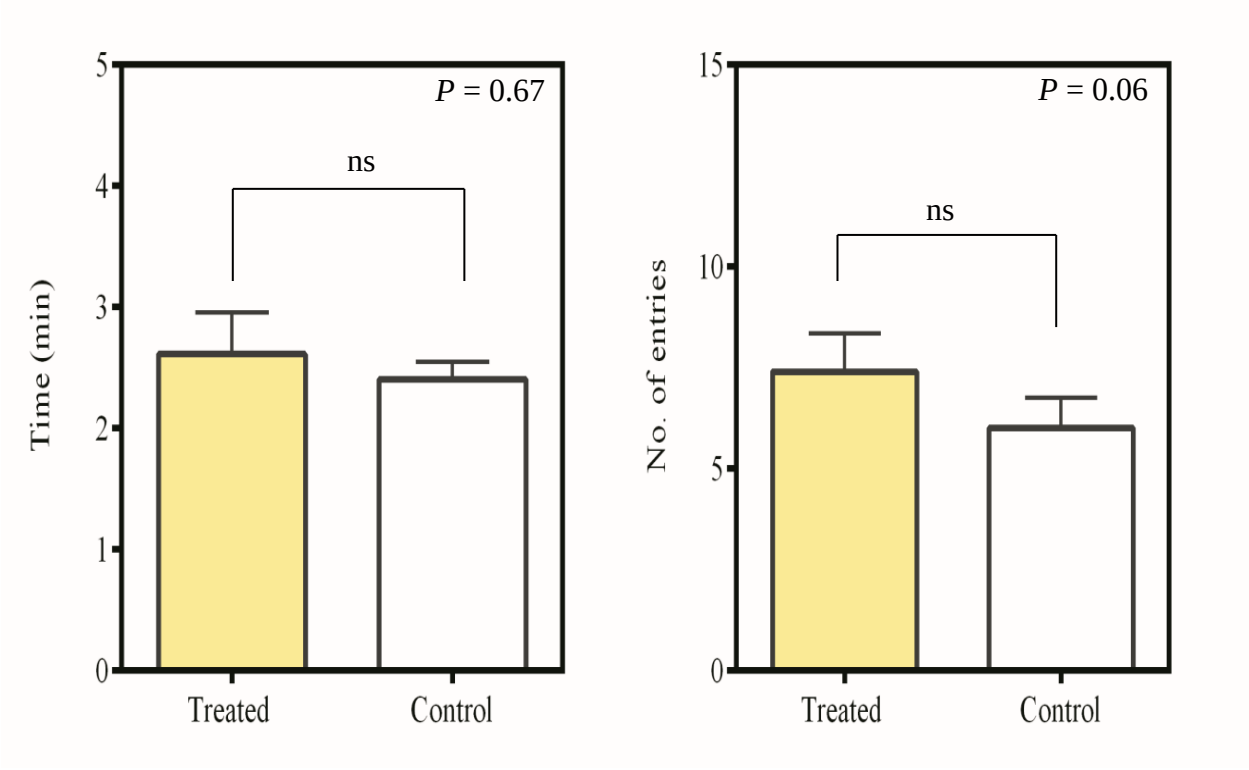
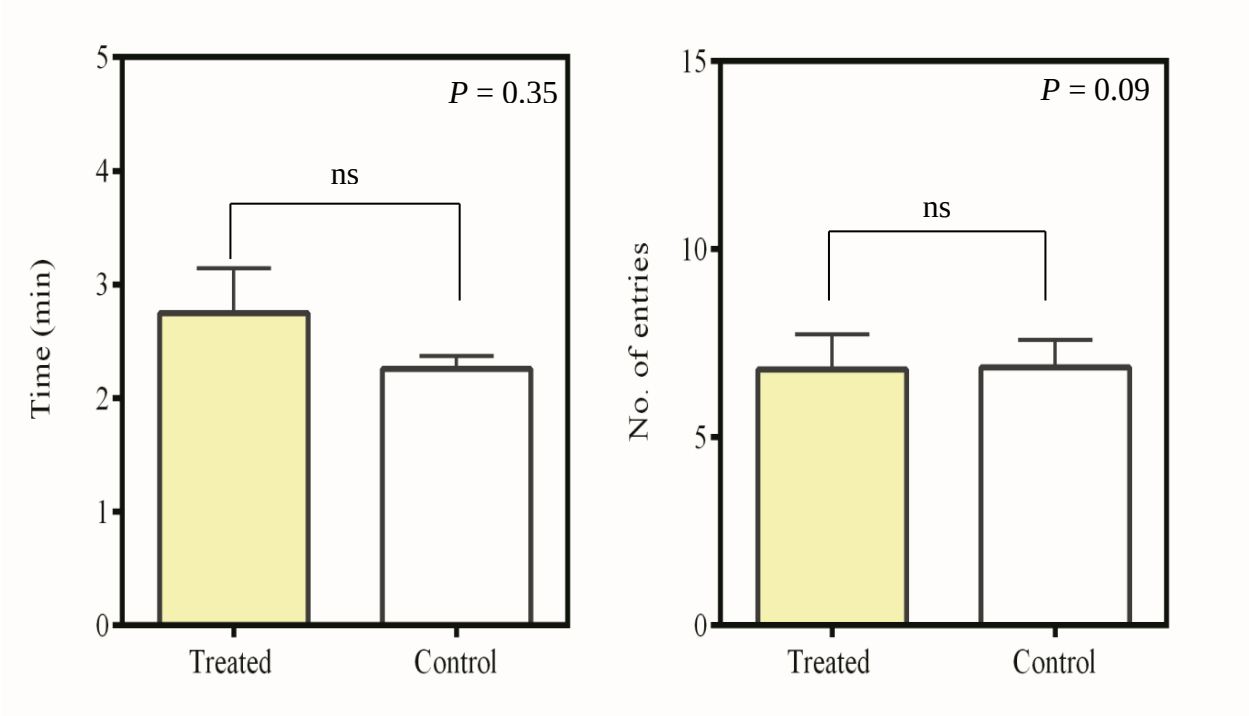


Fig. 35. Olfactory response of adult *S. dorsalis* to thrips body wash in dichloromethane



* - significant; ns - non significant

Fig. 36. Olfactory response of adult *S. dorsalis* to thrips body wash in hexane

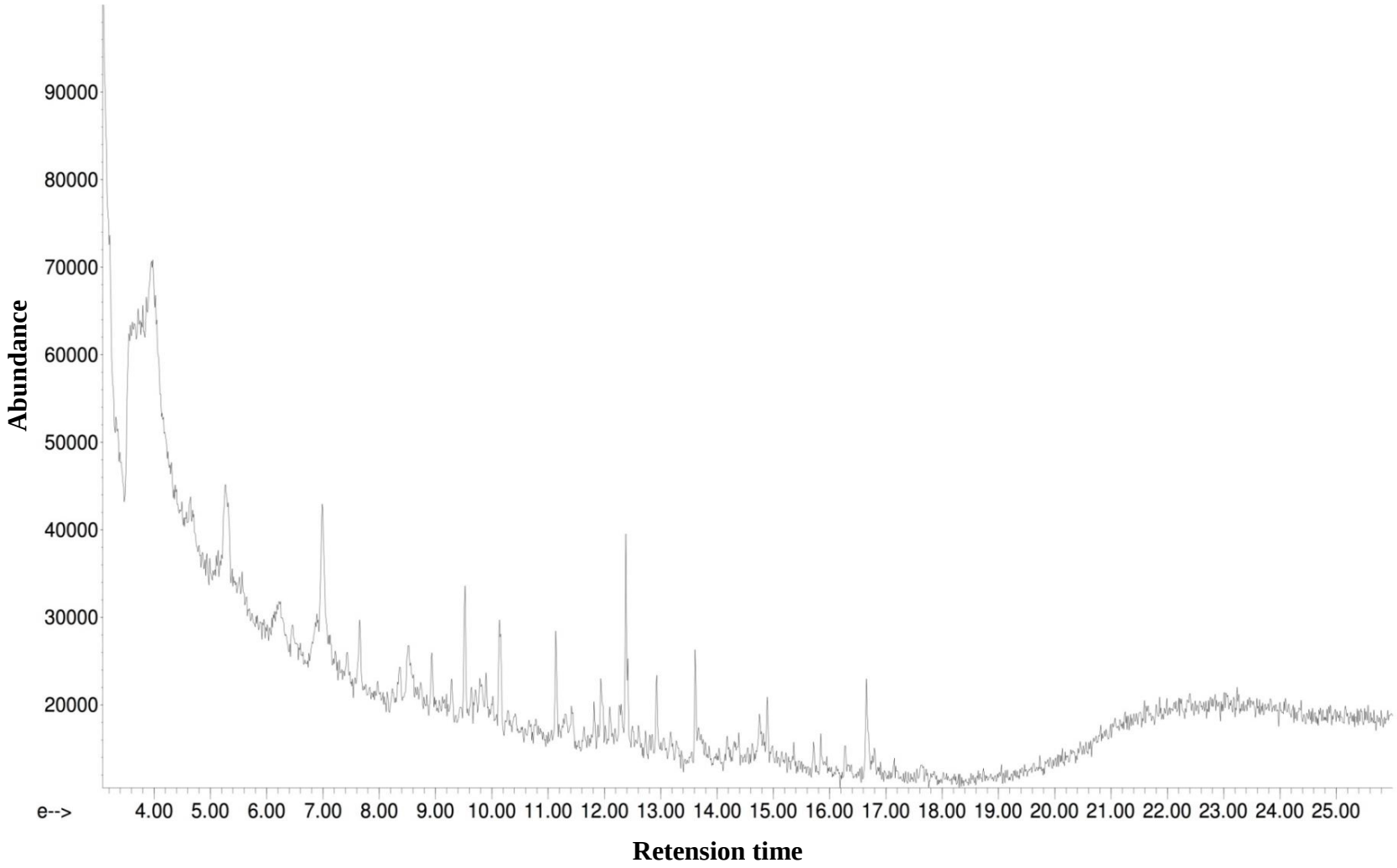
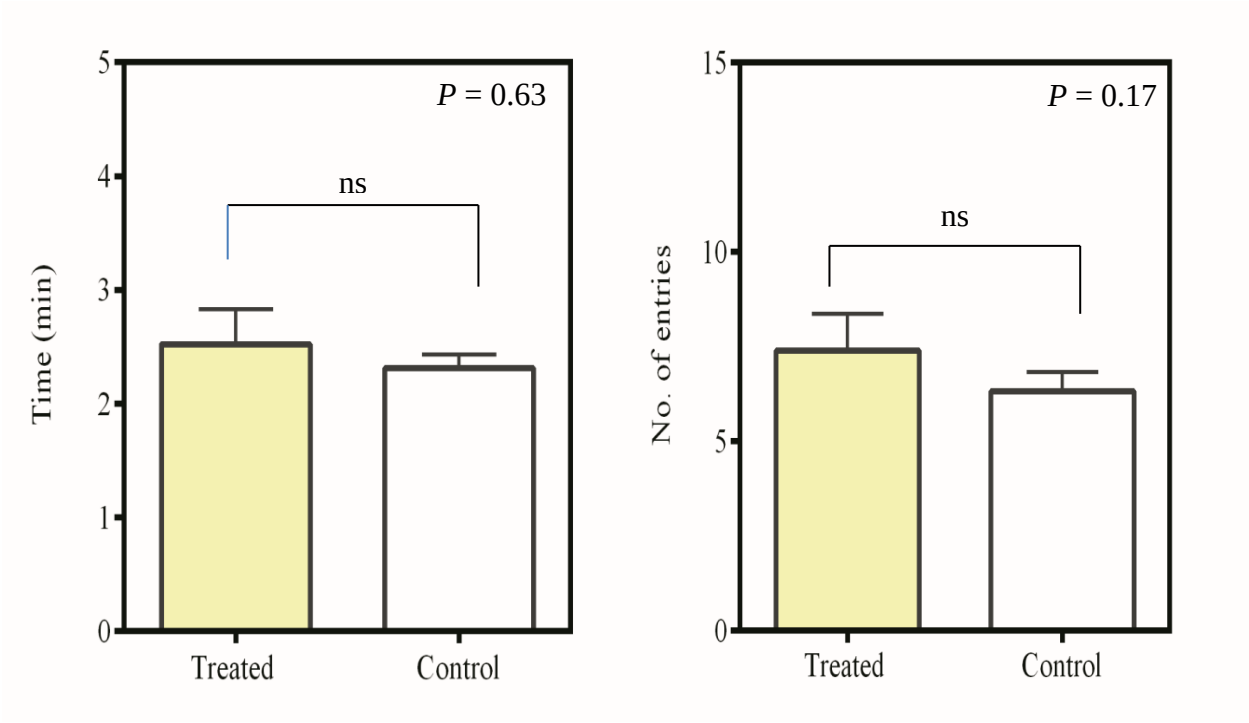


Fig. 38. GC-MS chromatogram of thrips body wash collected in dichloromethane solvent extract



* - significant; ns - non significant

Fig. 37. Olfactory response of adult *S. dorsalis* to thrips body odour in diethyl ether

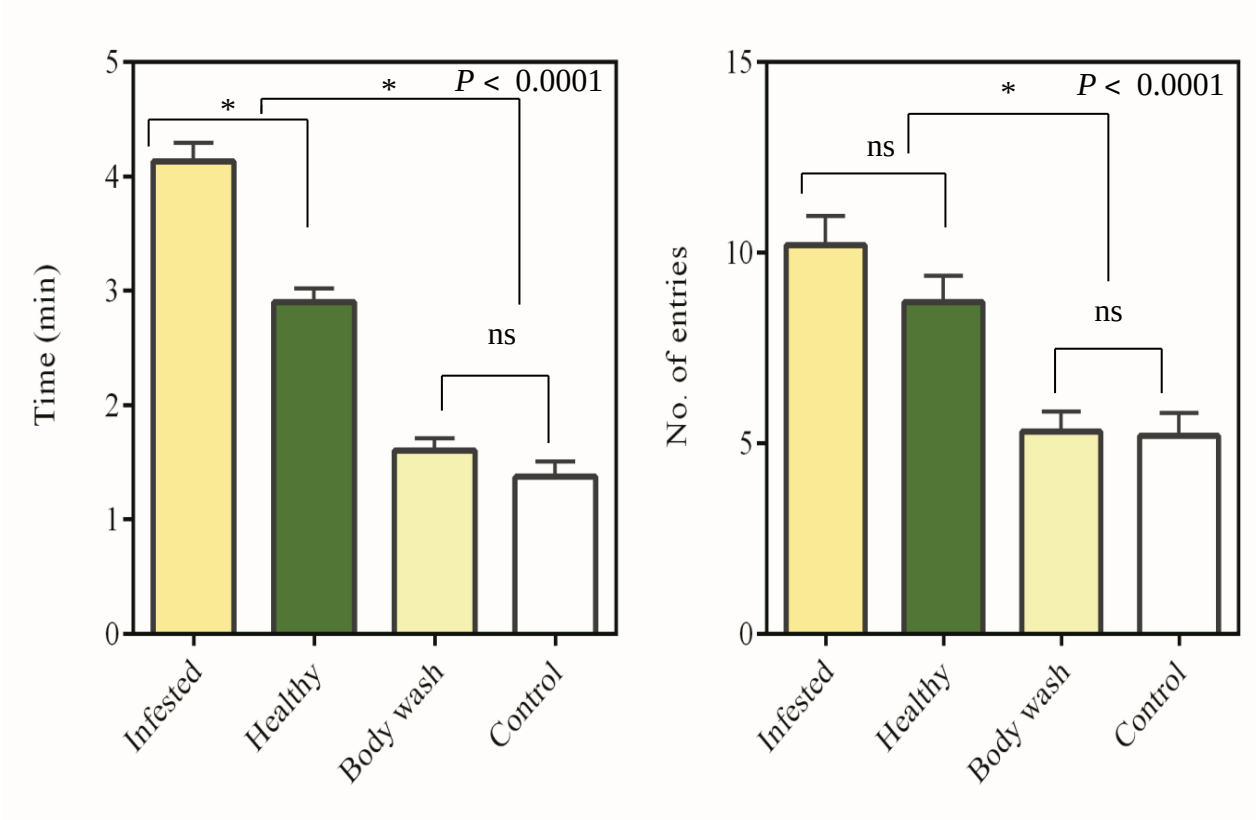
Table 18. Response of adult *S. dorsalis* to herbivore induced (thrips) and healthy *C. annum* plant volatiles and thrips body wash in multiple choice assay (N=10)

Treatment	*df*	ANOVA							
		Time spent (Minutes)				Entries (Numbers)			
		Mean ± S.E.	F_{cal}	F_{crit}	*P*	Mean ± S.E.	F_{cal}	F_{crit}	*P*
Infested	3, 36	4.13 ± 0.16	92.55	2.87	< 0.0001	10.20 ± 0.76	66.63	2.87	< 0.0001
Healthy		2.89 ± 0.12				8.70 ± 0.68			
Body wash		1.60 ± 0.10				5.30 ± 0.54			
Control		1.37 ± 0.13				5.20 ± 0.59			

Table 18a. Tukey's multiple comparison test: Response of adult *S. dorsalis* to herbivore induced (thrips) and healthy *C. annum* plant volatiles and thrips body wash in multiple choice assay (N=10)

Treatments	*Df*	*P*	
		Time spent (Minutes)	Entries (Numbers)
Infested vs. Healthy	3, 36	**	ns
Infested vs. Body wash		**	**
Infested vs. Control		**	**
Healthy vs. Body wash		**	*
Healthy vs. Control		**	*
Body wash vs. Control		ns	ns

* = 0.01; ** = 0.001; *** = 0.0001; **** < 0.0001; ns - non significant



* - significant; ns - non significant

Fig. 39. Olfactory response of adult *S. dorsalis* to HIPVs, healthy *C. annum* plant volatiles and thrips body wash in multiple choice assay

V DISCUSSION

Bell pepper (popularly called as Capsicum), *Capsicum annum* L. is one of the most popular and economic vegetable crop grown throughout the world. Bell pepper has attained the status of a high value crop in India during recent years. The high market price it fetches to farmers is usually attributed to the heavy demand from the urban consumers. Therefore, even a small blemish on the fruit will drastically reduce its market value. Under these circumstances the study of insect pests which not only reduce the fruit quality but also fruit yield is very important.

Butani (1976) reported over 20 insect species on Chillies (*Capsicum* spp.) from India. Recently, over 35 species of insect and mites are reported as pests of Chillies which include thrips, aphids, whiteflies, fruit borers, cutworms, plant bugs, mites and other minor pests (Sorensen, 2005). Of which, thrips (*Scirtothrips dorsalis* Hood) (Thysanoptera: Thripidae), aphids [*Aphis gossypii* Glover and *Aphis laburni* Koch (*Aphis craccivora* Koch) (Homoptera: Aphididae)] and silverleaf whiteflies, *Bemesia tabaci* (Gennadius) (Homoptera: Aleyrodidae) are among the most damaging insect pests.

Thrips may cause 30 to 50 per cent crop loss directly as pests and are also indirectly causes immeasurable yield losses by serving as vectors for viral diseases like leaf curl and capsicum chlorosis. The Chilli thrips, *S. dorsalis* is an economically important pest on bell pepper, *C. annum*. The management of this precarious pest is mainly done using synthetic insecticides. However, other alternate management strategies have been less explored for this pest. Therefore, there is a need to develop novel strategies to control this pest. Management practices from an ecological point of view must be environmental friendly but from a growers' viewpoint must be economical, fast acting as well as long lasting.

Recently, semiochemicals are being increasingly explored as important components of integrated pest management (IPM) as push-pull strategies for a number of insect species all over the world (Cook *et al*., 2007). However, development of reliable, robust and sustainable push-pull strategies requires a clear scientific understanding of the behavioural or chemical ecology of the insect pest and its interactions with its host, conspecifics and natural enemies (Jayanthi *et al*., 2015).

Chemo-behavioural strategies involving host kairomones and insect body odours are seen as a new, effective and sustainable form of management practice. This study involves the elucidation of the host kairomones and insect body odours that may have an influence on the Chilli thrips, *S. dorsalis*. Such elucidated kairomones/pheromones can play a vital role in the sustainable management of thrips.

Studies regarding the chemical ecology of thrips, *S. dorsalis* are meager and our study will be first of its kind to understand thrips and their host plant relationships. Since intensive research on interaction of thrips, *S. dorsalis* with its host plant *C. annum* was not done so far, the present study was carried out on various aspects *viz*., attractiveness of host plant volatiles of *C. annum* to adult *S. dorsalis*, differential response of adult

S. dorsalis/co-occurring sap sucking insects to healthy/infested plant volatiles and the influence of conspecific body odours on adult *S. dorsalis*. The results obtained on these aspects have been discussed briefly here under.

5.1 Attractiveness of host plant volatiles of *C. annum* to adult *S. dorsalis*

As *S. dorsalis* is regular and persistent pest on Capsicum, in order to understand the interaction between the pest insect, *S. dorsalis* and its host plant, *C. annum* behavioural assays were carried out to know whether there is any influence of host plant phenology on the host selection behaviour of this phytophagous insect. Three different growth stages *viz*., pre-flowering, flowering and fruiting of bell pepper, *C. annum* were chosen and evaluated for their attractiveness to thrips, *S. dorsalis* through headspace volatiles in four arm olfactometer assay. Among all the three plant growth stages tested, the volatiles from tender fruit forming stage was found to be significantly more attractive to *S. dorsalis*, as thrips spent more amount of time [4.41 ± 0.39 min; mean time spent ± S.E.; $t = 4.93$; $df = 19$; $P < 0.0001$] in the treated region of the olfactometer and also they entered significantly more number of times to the treated region of the olfactometer [8.10 ± 0.66; mean number of entries ± S.E.; $t = 5.29$; $df = 19$; $P < 0.0001$] (Fig. 1-3). In order to further confirm their attraction towards fruit forming stage of the host plant, we provided multiple choices among all growth stages of host plant volatiles along with the control solvent in the four arm olfactometer. Similar results were obtained in the multiple choice assays also as the thrips spent significantly more amount of time in the fruiting stage volatiles treated region [4.46 ± 0.44 min; mean time spent ± S.E., $F = 14.17$; $df = 3, 36$; $P < 0.0001$] of olfactometer compared to the pre-flowering [1.38 ± 0.33 min; mean time spent ± S.E.] and flowering stage [2.22 ± 0.41 min; mean time spent ± S.E.] plant volatiles treated regions. Even the number of entries was also found to be significantly different as the thrips entered more number of times to the fruiting plant volatile treated region [6.70 ± 0.87 numbers; mean number of entries ± S.E.; $F = 6.58$; $df = 3, 36$; $P = 0.001$] compared to flowering [5.40 ± 1.07; mean number of entries ± S.E.] and pre-flowering [4.10 ± 1.03; mean number of entries ± S.E.] plant volatiles treated regions of the olfactometer (Fig. 4). This is probably due to the variation in the volatile profile at different plant growth stages. As it is persistent pest on Capsicum, we would expect it to be attracted to a wider range of host cues than specific cues from a particular growth stage. However, for odour recognition of a host plant, insect relies on specific volatiles in that particular host, termed "token stimuli", which are not present in unrelated plant species as reported by Fraenkel (1959). In case of tephritid fruit flies also though gravid female fruit flies oviposit on physiologically mature green fruits, several reports suggested that fruit ripeness increases the attraction to tephritid fruit flies. Oriental fruit fly, *Bactrocera dorsalis* prefers to oviposit on overripe and rotten fruits (Jayanthi *et al*., 2012). Similarly, the lesser pumpkin fly, *Dacus ciliatus* prefers ripe melon over unripe (Alagarmalai *et al*., 2009). Thus, volatiles from host plant may play a major role in the orientation of insects to their host. Jan de Kogel and Koschier (2002) also opined that the host cues which are responsible for thrips attraction to their host plant are poorly understood.

Our further analysis of headspace volatiles of different plant growth stages through GC-MS revealed that, there is a stark difference in the volatile profiles and their

abundance among different plant growth stages of host plant *viz*., pre-flowering, flowering and fruiting (Fig. 8). Rodriguez *et al*. (2010) revealed that ratios of compounds in host plant odours fluctuate with the phenological stage of the plant.

However, in the present study, strong behavioural responses of *S. dorsalis* were obtained to headspace samples from fruiting stage of *C. annum* plant. Again we had a question that which specific volatile cues among an array of compounds present in the fruiting stage headspace sample are instigating the olfactory responses in case of thrips, *S. dorsalis* towards their host plant. So, further we used GC-EAD analysis to identify specific volatile compounds from *C. annum cv*. *Indra* that were responsible to elicit positive behavioural responses with *S. dorsalis.* Tasin *et al*. (2006b) also opined that the identification of the plant volatile compounds that attract gravid female European grapevine moth, *Lobesia botrana* to its host are essential for understanding insect-plant relationships as this information contributes in breeding improved resistant cultivars against target insects.

The fruiting stage plant emitted large number of volatile compounds, of which *o*-Cymene, 4-methyl-2-undecane, 3,6-Dimethyl decane, *β*-Elemene, *n*-Dodecane, Dodecyl iodide, 2,3,5-Trimethyl decane, *n*-Docosane were GC-EAD active compounds that elicited an EAD response in thrips, *S. dorsalis* (Fig. 9). Similary, Koschier *et al.* (2000) who investigated the responses of adult female western flower thrips, *F. occidentalis* to plant volatiles found that western flower thrips were attracted by the benzenoids: benzaldehyde and *p*- and *o*-anisaldehyde, the monoterpenes: geraniol, nerol, linalool and (+)-citronellol, the sesquiterpenes: (*E*)-*β*-farnesene, eugenol and 3-phenylpropionaldehyde, two phenylpropanoids and the non floral odour *p*-anisaldehyde, nerol, ethyl nicotinate. Of all these, (*E*)-*β*-farnesene elicited positive response at several concentrations. Whereas, all other volatiles were attractive at a specific concentration only. Salicylaldehyde and a benzenoid elicited negative responses at two concentrations. The more attractive volatile components for *F. occidentalis* were found among the monoterpenes.

Finding a suitable host on which to feed, survive and reproduce is crucial for phytophagous insects (Thompson and Pellmyr, 1991) and olfaction plays an important role in enabling the insect to recognize host plants at distance (Dethier, 1982; Visser, 1986, 1988; Bernays and Chapman,1994; Pickett *et al*., 1998). Furthermore, recent studies have suggested that host recognition depends on blends or ratios of volatiles emitted rather just the presence or absence of individual compounds (Bruce *et al*., 2005; Bruce and Pickett, 2011). We evaluated the attractiveness of individual EAD active synthetic fractions and their blend in four arm olfactometer assay to prove their attraction to thrips, *S. dorsalis*. However, in the current study, when individual synthetic fractions were offered as a choice against clean air, single compounds such as *o*-Cymene, *n*-Docosane and *β*-Elemene did elicit significant attraction in *S. dorsalis*. Whereas, the other two compounds such as *n*-Dodecane, *n*-Dodecyl iodide did not elicit significant attraction when they were tested individually (Fig. 10-14). Herbivore insects recognize and locate their hosts by recognizing characteristic blends of volatiles but avoid the same volatiles when encountered individually (Webster *et al*., 2010). Further, formulation of

synthetic blend using all five GC-EAD active compounds *viz*., *o*-Cymene, *β*-Elemene, *n*-Docosane, *n*-Dodecane, Dodecyl iodide in their natural concentration and ratio as observed in natural sample proved to be biologically active as the thrips spent significantly more time [4.26 ± 0.38 min; mean amount of time spent ± S.E.; $t = 4.43$; $df = 9$; $P = 0.002$] and entered significantly more number of times [8.30 ± 0.54; mean number of entries ± S.E.; $t = 4.27$; $df = 9$; $P = 0.002$] to the treated region of olfactometer (Fig. 15). This result agrees with previous studies carried out with *A. fabae* where blends were found crucial for obtaining positive behavioural responses than individual compounds (Webster *et al*., 2010).

Further, dual choice assays with synthetic blend of GC-EAD active fractions and natural headspace sample of fruiting stage *C. annum* revealed that there is no significant difference {synthetic blend [3.39 ± 0.15 min; mean amount of time spent ± S.E.; $F = 29.12$; $df = 3, 36$; $P < 0.0001$; 9.10 ± 0.66; mean number of entries ± S.E.; $F = 9.70$; $df = 3, 36$; $P < 0.0001$] and natural sample [3.39 ± 0.19 min; mean amount of time spent ± S.E.; 9.00 ± 0.93; mean number of entries ± S.E.]} between these two samples over solvent control and *S. dorsalis* preferred both equally (Fig. 16). This clearly indicates that sufficient synthetic compounds were identified to explain the activity of the natural headspace samples because there was no preference in a choice test between the natural sample and the synthetic blend as observed by Jayanthi *et al*. (2012) for *Bactrocera dorsalis*.

Therefore, it is concluded that physiological growth stages of host plant probably influences the olfactory response in case of phytophagous insects like *S. dorsalis* as observed in the present study. This finding is in agreement with results of Ulland (2007) who suggested that recognition of host plant is mainly based on the odour blend or ratio of the volatiles released by a plant as observed in *M. brassicae*.

Although thrips tends to cause damage on tender leaves, flower buds and tender fruits, our results revealed that tender fruit formation stage attracts significantly more number of thrips followed by flowering plants than pre-flowering plants. This is probably because of the change in the volatile profile of host plant at different plant growth stages. These results are similar to the results of responses of tephritid fruit flies to their host palnt volatiles and oviposition sites (Jayanthi *et al.*, 2012). Several reports have emphasized that fruit ripeness increases the attraction of tephritid fruit flies as over ripe and rotten fruit is being preferred. Syed *et al*. (1970) found that *B. dorsalis* adults remained in orchards when there were ripe fruits on the trees. This agrees with the observations of Andrei *et al*. (2000) who suggested that areas with plentiful ripe guava fruit attract females, searching for oviposition sites.

Therefore, adult *S. dorsalis* may use the odours of tender fruit forming stage of host plant as their long-distance orientation cues while searching for suitable sites feeding and oviposition. The present study suggested that olfactory cues may play role in attracting female *S. dorsalis* to host plant. In case of Chilli thrips, *S. dorsalis*, blends may be required to elicit attraction and to further confirm this outside in the field future studies to evaluate the present laboratory studies are indeed essentially needed.

A perusal of literature on chemical ecology of insect-plant interactions revealed that chemical cues from the host plant play major role in the orientation of adult phytophagous insects to their hosts from a distance and they determine the probability of alighting on a given host. After landing, the combination of contact chemoreception, visual and physical cues provide further sensory input leading to acceptance or rejection of the feeding habitats and oviposition sites (Ramaswamy, 1988; Renwick and Chew,1994). Host plant recognition and selection in insects is determined mainly by the adults since newly emerged nymphs are often limited in their dispersal abilities.

5.2 Differential response of adult thrips, *S. dorsalis* and co-occurring sap sucking insects to healthy and infested *C. annum* plant volatiles

There are several studies which emphasizes the role of herbivore induced host plant volatiles in indirect defense by host plant as these volatiles play a crucial role in attracting the herbivore natural enemies. *i.e* herbivore induced plant volatiles plays crucial role in tritrophic interactions (Degenhardt *et al*., 2003, Pare and Tumlinson, 1997, 1999; Turlings and Ton, 2006). Nevertheless, there are very few studies that emphasize the impact of herbivore induced plant volatiles on the attraction of phytophagous insects. So in our study we wanted to know the behavioural response of adult thrips, *S. dorsalis* along with co-occurring sap sucking adult insects like cotton aphid, *Aphis gossypii* Glover, silverleaf whitefly, *Bemisia tabaci* (Gennadius) and spidermite, *Tetranychus macfarlanei* Baker and Pritchard to herbivore (thrips) induced plant volatiles (HIPVs) and healthy plant volatiles in a dual choice olfactometer assays.

For thrips, *S. dorsalis*, we compared the attractiveness of healthy plant volatiles and herbivore (thrips) induced plant volatiles that are collected from the same aged plant in olfactometer assay. Our results revealed that both healthy and herbivore induced plant volatiles instigated the behavioural response in case of thrips when individual headspace samples were offered as a choice against clean air, in olfactometer. The thrips not only spent significantly more amount of time (healthy plant volatile [4.16 ± 0.45 min; mean time spent ± S.E.]; $t = 3.73$; $df = 9$; $P = 0.005$ and HIPVs [3.47 ± 0.39 min; mean time spent ± S.E.] $t = 2.74$; $df = 9$; $P = 0.02$) but made significantly more number of entries (healthy plant volatile [7.30 ± 0.63; mean number of entries ± S.E.]; $t = 3.62$; $df = 9$; $P = 0.006$ and HIPVs [8.50 ± 0.64; mean number of entries ± S.E.]; $t = 3.22$; $df = 9$; $P = 0.01$) to the treated region compared to the solvent control region of the olfactometer (Fig. 17 & 18). Further, in order to know the preference of *S. dorsalis* for both healthy and herbivore induced plant volatiles, we gave dual choice in the four arm olfactometer. Interestingly, we found that thrips, *S. dorsalis* spent significantly higher amount of time ([4.14 ± 0.22 min; mean time spent ± S.E.]; $F = 7.05$; $df = 3, 36$; $P = 0.001$) in the herbivore induced host plant volatiles treated region than in the healthy [2.12 ± 0.28 min; mean time spent ± S.E.] and solvent control region [1.80 ± 0.33 and 1.60 ± 0.32 min; mean time spent ± S.E.]. Even they entered significantly more number of times to the HIPVs treated region of the olfactometer ([7.30 ± 0.73; mean number of entries ± S.E.]; $F = 9.15$; $df = 3, 36$; $P = 0.0001$) than to the others in the olfactometer (Fig. 19). Again in order to confirm the role of HIPVs in attracting thrips, *S. dorsalis* to host plant, we gave dual choice between HIPVs and fruiting plant volatiles along with the solvent control in the four arm olfactometer. Here also we found that HIPVs are highly attractive to thrips,

S. dorsalis compared to the fruiting stage plant volatiles as they spent significantly higher amount of time and entered more number of times to HIPVs treated region of the olfactometer [3.45 ± 0.20 min; mean time spent ± S.E.; $F = 7.70$; $df = 3, 36$; $P = 0.0004$; 6.20 ± 0.68; mean number of entries ± S.E.; $F = 3.93$; $df = 3, 36$; $P = 0.02$] than fruiting plant volatiles treated region of the olfactometer [2.59 ± 0.25 min; mean time spent ± S.E.; 5.60 ± 0.72; mean number of entries ± S.E.] (Fig. 20). Our results clearly revealed that herbivore induced plant volatiles are implicated in the host finding behaviour of thrips, *S. dorsalis* which is in agreement with the results of Kirk (1985) who reported that infested onion plant volatiles plays an important role in the host finding behaviour of thrips, *Thrips tabaci* (Lindeman). This may be due to the volatile compounds that are released by plants during thrips feeding which may act as an aggregation kairomone as reported earlier (Ananthakrishnan, 1993).

In response to herbivore attack, plants mobilize chemical defenses and release distinct bouquets of volatiles. It is proven with the results of Robert *et al*. (2012) whose study revealed *Diabrotica virgifera* Leconte larval attraction to plants that were infested with conspecifics. Whereas they avoided plants that were attacked by *Spodoptera littoralis* and this is because (*E*)-*β*-caryophyllene, which is induced by *D. virgifera* and ethylene, which is suppressed by *S. littoralis.* Therefore, these two signals used by *D. virgifera* larvae to locate plants that are most suitable for their development.

Further our results agrees with Addesso and McAuslane (2009) who opined that the location of wild and cultivated host plants by pepper weevil (*Anthonomus eugenii* Cano) may be aided by herbivore-induced/constitutive host plant volatiles along with the visual cues and the male produced aggregation pheromone. Alternatively, some adult coleopterans exploit the relatively greater volatile output of HIPVs to locate hosts and conspecifics (Harari *et al*., 1994; Lougrin *et al*., 1995; Bolter *et al*., 1997; Landolt *et al*., 1999). The colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae) is attracted to damaged *Solanum tuberosum* L. (Solanaceae) plants (Dickens, 2002).

Interestingly, we noticed, Capsicum plant infested by thrips in the field was also found to be infested by other sap sucking insects like aphids, mites and in some cases whiteflies. So we evaluated the attractiveness of both healthy and herbivore induced plant volatiles in a dual choice assay along with the solvent control to these co-occurring sap sucking insects. Interestingly, we found that in case of aphids, *A. gossypii*, herbivore induced plant volatiles elicited a positive behavioural response compared to the healthy plant volatiles as the aphids spent significantly more amount of time ([3.39 ± 0.39 min; mean time spent ± S.E.]; $F = 4.73$; $df = 3, 36$; $P = 0.007$) in the HIPVs treated region of the olfactometer than healthy plant volatile treated region [1.51 ± 0.29 min; mean time spent ± S.E.]. Further, their entries to HIPVs treated region of the olfactometer are quite significant ([2.60 ± 0.37; mean number of entries ± S.E.]; $F = 2.99$; $df = 3, 36$; $P = 0.04$) than the healthy plant volatile treated region [2.00 ± 0.45; mean number of entries ± S.E.] (Fig. 2). From this result, it is concluded that for aphids, thrips infested *C. annum* plant was found to be quite attractive as olfactory responses were significant for HIPVs headspace sample.

Similarly, when we evaluated the attractiveness of both healthy and HIPVs to the silverleaf whiteflies, *B. tabaci* in a dual choice assay, again similar results were noticed as that of aphids. Whiteflies spent significantly more amount of time ([4.38 ± 0.15 min; mean time spent ± S.E.]; $F = 25.73$; $df = 3, 36$; $P < 0.0001$) and made significantly more number of entries to the HIPVs treated region ([4.30 ± 0.30; mean number of entries ± S.E.]; $F = 8.74$; $df = 3, 36$; $P = 0.0002$) than healthy plant volatile treated region [1.51 ± 0.29 min; mean time spent ± S.E.; 3.40 ± 0.48; mean number of entries ± S.E.] of the olfactometer (Fig. 22).

When we gave dual choice test between the HIPVs and healthy plant volatiles in Y-tube olfactometer to spidermites, *T. macfarlanei*, again it was found that mites used to make a choice towards the arm containing HIPVs plant volatiles ($P = 0.01$) (Fig. 23).

Earlier studies clearly indicated that HIPVs may alter the recruitment of herbivores to the damaged host plant not only by providing chemical cues for host plant location but also regarding the information on the damage status of the host plant (Bernasconi *et al*., 1998). However, generally HIPVs represent a complex message to array of herbivores that is interpreted according to their biological context. Some adult coleopterans are used to exploit the relatively greater volatile output of induced plants to locate hosts and conspecifics (Harari *et al*., 1994; Lougrin *et al*., 1995; Bolter *et al*., 1997; Landolt *et al*., 1999). However, in case of some lepidopterans the HIPVs may act as oviposition deterrents (De Moraes *et al.*, 2001; Kessler and Baldwin, 2001). Similarly, Delphia *et al*. (2007) provided the first direct evidence that thrips feeding induces volatile responses and highlighted that simultaneous herbivory by insects with different feeding habits can alter volatile emissions. Their findings further demonstrated that induced host plant responses influence the host-plant selection by western flower thrips and suggested that the induction of volatile, nicotine may play a role in this process.

In the cases where HIPVs are being used as cues by heterospecifics as observed in the present study, the volatile plumes of damaged plants may serve as potent cues for host location to the co-occurring herbivores as it results in reduced search time thereby minimal search costs and limited exposure to mortality factors which is in agreement with the report of Stamps and Krishnan (2005).

The reason for attraction of HIPVs to thrips, *S. dorsalis* may be due to certain specific plant volatile compounds that are present compared to that of healthy plant volatiles might have instigated the olfactory responses. Interestingly, volatile profiles of the healthy and infested Capsicum plant [herbivore (thrips) induced plant] were quite different (Fig. 25) and strong behavioural responses by *S. dorsalis* were obtained to headspace samples from herbivore (thrips) induced Capsicum plant volatiles. Again we had a question that among array of volatile compounds present in the HIPVs, which specific volatile compounds instigated the olfactory responses in case of thrips, *S. dorsalis* towards their conspecifics infested host plant. So, further we used GC-EAD analysis to identify specific volatile compounds from *C. annum cv. Indra* that were elicited positive behavioural responses with *S. dorsalis*.

The herbivore induced plant emitted quite large amount of *δ*-3-Carene, Octadecane, *n*-Docosane and very less or trace amounts of 4-methyl-2-undecane, Dodecyl iodide and Tricosane which were GC-EAD active compounds (Fig. 27).

Further we evaluated the attractiveness of individual EAD active synthetic fractions and their blend in four arm olfactometer assay to prove their effective attraction to *S. dorsalis*. However, in the current study, when individual volatiles were offered as a choice against clean air, compounds such as *δ*-3-Carene, Octadecane and *n*-Docosane were found to be highly attractive as the thrips spent significantly more amount of time (*δ*-3-Carene [2.58 ± 0.08 min; mean time spent ± S.E.; $t = 5.71$; $df = 9$; $P = 0.0003$]; Octadecane [3.68 ± 0.26 min (treatment); mean time spent ± S.E.; $t = 4.64$; $df = 9$; $P = 0.001$]; *n*-Docosane [4.11 ± 0.53 min (treatment); mean time spent ± S.E.; $t = 3.28$; $df = 9$; $P = 0.0096$]) in the treated region of the olfactometer. When presented as individual compounds, Dodecyl iodide and Tricosane were not attractive to *S. dorsalis*. Nevertheless, when synthetic blend made up of all GC-EAD active fractions (at a concentration as they presented in the natural sample) was tested in dual choice assay along with natural sample the mean time spent in both treated and control region of olfactometer is found to be on par (synthetic blend [3.27 ± 0.41 min; mean time spent ± S.E.]; natural sample [3.27 ± 0.14 min; mean time spent ± S.E.]; $F = 9.99$; $df = 3, 36$; $P < 0.0001$) (Fig. 28-33). This may be due to the fact that these two individual compounds *viz*., Dodecyl iodide and Tricosane may play role in forming behaviourally active blend as it is confirmed from our results that thrips entered significantly more number of times to the treated region of the olfactometer when presented with synthetic blend. It may be due to the fact that certain compounds that are elicited during herbivory may act as herbivore-specific cues or species specific cues (Halitschke *et al*., 2001).

Blend of attractants representing HIPVs was formulated based on the natural concentration and ratio of compounds in natural headspace sample. This elicited potent attraction to *S. dorsalis* during olfactometer bioassay. This clearly indicates that sufficient synthetic compounds were identified to explain the activity of the natural headspace sample because there was no preference in a choice test between the natural sample and the synthetic blend when offered together (Fig. 34). Therefore, it is concluded that conspecifics infested host plant probably attracts phytophagous insects like *S. dorsalis* which is in agreement with Stamps and Krishnan (2005) and Stamps *et al*. (2005).

5.3 Influence of conspecific body odours to adult *S. dorsalis*

When we looked at the differential response of thrips, *S. dorsalis* to the infested and healthy host plant, *C. annum* volatiles, we used to get a question that whether thrips are getting attracted towards the infested plant due to the presence of conspecific body odours rather than HIPVs alone. Thus, we further explored the role of conspecific body odours to thrips, *S. dorsalis*. So we designed one more objective to evaluate the attractiveness of conspecific body odours alone to thrips, *S. dorsalis*.

In this we used three solvents *viz*., dichloromethane, hexane and diethyl ether with different polarity and employed different methods *viz*., body wash, air entrainment of body odours to extract the volatile components that are present in the thrips, *S. dorsalis*.

Then we assessed the attractiveness of thrips, *S. dorsalis* towards their conspecific body odours using the above mentioned solvent extracts along with solvent control in the four arm olfactometer. Our results revealed that no solvent extract has attracted the thrips towards treated region significantly than the control solvent. Both the parameters like time spent and number of entries to the treated region of olfactometer and control solvent were found to be on par and there was no significant difference at all (Fig. 35-37). So this clearly indicates that there is no role of thrips body odour in instigating olfactory responses in thrips to the infested plant and HIPVs are the sole reason for thrips attraction, which is in agreement with the findings of Kirk and Hamilton (2004) who reported that the body volatile compounds which were present in thrips are produced on demand and are not stored. Even GC-MS analysis of body extracts also could not detect any volatile compounds in the extracts (Fig. 38).

Further in order to confirm the attractiveness of thrips towards HIPVs, we tried multiple choice assays with healthy plant volatiles, HIPVs and thrips body odour extract along with the control solvent in the four arm olfactometer assay. It was clearly found that thrips are attracted towards HIPVs over others as they spent significantly more amount of time in the HIPVs treated region of the olfactometer (4.13 ± 0.16 min [mean time spent ± S.E.]; F = 92.55; df = 3, 36; $P < 0.0001$) compared to the healthy plant volatiles [2.89 ± 0.12 min; mean time spent ± S.E.], the body odour extract [1.60 ± 0.10 min; mean time spent ± S.E.] and control solvent treated regions [1.37 ± 0.13 min; mean time spent ± S.E.]. Even they entered significantly more number of times to the HIPVs treated region ([10.20 ± 0.76; mean number of entries ± S.E.]; F = 66.63; df = 3, 36; $P < 0.0001$) compared to healthy plant volatiles [8.70 ± 0.68; mean number of entries ± S.E.], body odour extract [5.30 ± 0.54; mean number of entries ± S.E.] and solvent control regions [5.20 ± 0.59; mean number of entries ± S.E.] of the olfactometer (Fig. 39). Probably as mentioned earlier, presence of specific volatile plumes in HIPVs would have served as aggregation kairomones (Ananthakrishnan, 1993) not only to conspecific thrips, *S. dorsalis* but also to other co-occurring heterospecifics like aphids, *A. gossypii*, silverleaf whitely, *B. tabaci* and spidermite, *T. macfarlanei* as they found thrips infested *C. annum* plant more attractive over healthy plant. In nature over a period of time herbivores could have evolved to locate their host plants which are already infested by their conspecifics/heterospecifics so that they can incur lower physiological costs in finding their host plant. However, the herbivore density dependent shift in HIPVs emissions and their influence on conspecifics as well as heterospecifics may be an interesting future course of study and beyond the scope of present study.

5.4 Future line of investigation

The focal species of this study is *S. dorsalis* for their huge economic loss in Capsicum. The dominant features of thrips research have been a considerable preoccupation with chemical management and no serious efforts have been yet made in India about chemo-behavioural strategies involving host kairomones for *S. dorsalis*. Studies in other species revealed that the visual and chemical cues play an important role in the host-finding behaviour of thrips. However, such studies are limited in case of *S. dorsalis*.

The current study had clearly shown that Capsicum plant volatiles elicit attraction in adult *S. dorsalis* and the compounds responsible for attraction have been identified. This will make possible future studies where a lure for adult *S. dorsalis* may be developed for monitoring and mass trapping applications. Having an attractant for adults greatly increases the scope of using semiochemical based management options against this noxious pest. The next step will be to conduct trapping trials to evaluate the performance of the identified kairomones in the current study under field conditions. Further, as *S. dorsalis* is highly polyphagous, efforts to identify potent kairomones in other host crops is worth pursuing.

VI SUMMARY

Capsicum is an important highly remunerative vegetable crop grown in Karnataka. Among several pests of Capsicum, Chilli thrips, *Scirtothrips dorsalis* Hood (Thysanoptera: Thripidae) is one of the most widespread and destructive insect pest. The present study was carried out at Indian Institute of Horticultural Research, Hessaraghatta lake post, Bengaluru during 2014-15. The results of the study that focuses on the behavioural chemical ecology of thrips [*viz*., insect-host plant interaction by evaluating the attractiveness of host plant volatiles to adult *S. dorsalis*, effect of healthy and herbivore induced plant volatiles on the adult *S. dorsalis* and co-occurring sap sucking insects like aphids, *Aphis gossypii* Glover (Homoptera: Aphididae), silverleaf whitefly, *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) and spidermite, *Tetranychus macfarlanei* Baker & Pritchard (Acari: Tetranychidae) and also the influence of conspecifics body odour on adult *S. dorsalis*] are summarized below.

Among the three different growth stages of the host plant, *Capsicum annum* chosen for volatile collection, headspace sample of tender fruit forming stage is found to be highly attractive to thrips ($P < 0.0001$; $t = 1.06$ for time spent and $P < 0.0001$; $t = 0.73$ for entries) rather than flowering ($P = 0.08$; $t = 1.86$ for time spent and $P = 0.002$; $t = 3.64$ for entries) and pre-flowering plant volatiles ($P = 0.30$; $t = 4.93$ for time spent and $P = 0.48$; $t = 5.29$ for entries) when tested in the four arm olfactometer. Multiple choice assay among the different plant growth stage headspace samples also revealed that fruiting stage plant volatiles are highly attractive to thrips followed by flowering and pre-flowering stage plant volatiles ($P < 0.0001$; $F = 14.17$ for time spent and $P = 0.001$, $F = 6.58$ for entries).

Further, GC-MS analysis of different plant growth stages of host plant headspace samples revealed that there is a stark difference in the volatile profile of each plant growth stage. Further, there was also a drastic change in the abundance of volatile compounds that were present in different plant growth stages. A total of 50 compounds were identified among all the three headspace volatile samples which are collected at pre-flowering, flowering and fruiting stages of host plant.

Among the vast array of volatile compounds that are present in the fruiting stage volatile samples, GC-EAD analysis revealed the eight specific EAD active volatile compounds such as *o*-Cymene, 4-methyl-2-undecane, 3,6-Dimethyl decane, *β*-Elemene, *n*-Dodecane, Dodecyl iodide, 2,3,5-Trimethyl decane, *n*-Docosane instigated the olfactory responses in case of thrips, *S. dorsalis*. Further, the evaluation of attraction of synthetic fractions of these GC-EAD active compounds individually and in blends revealed that *o*-Cymene ($P = 0.0003$; $t = 5.58$ for time spent and $P = 0.004$; $t = 3.92$ for entries), *β*-Elemene ($P = 0.02$; $t = 2.70$ for time spent and $P = 0.02$; $t = 2.71$ for entries) and *n*-Docosane ($P = 0.006$; $t = 3.60$ for time spent and $P = 0.0001$; $t = 6.52$ for entries) were found to be highly attractive to thrips, *S. dorsalis*. Whereas, *n*-Dodecane and Dodecyl iodide were not biologically active when presented as individual compounds. Nevertheless, when all the five GC-EAD active compounds were formulated as synthetic

blend, it was found to be significantly attractive to *S. dorsalis* ($P = 0.002$; $t = 4.43$ for time spent and $P = 0.002$; $t = 4.27$ for entries).

Further the dual choice assay between natural sample and synthetic blend of GC-EAD active fractions of fruiting stage revealed that there is no significant difference in olfactory responses of thrips, *S. dorsalis* to the natural sample over the synthetic blend compared to solvent control ($P < 0.0001$; $F = 29.12$ for time spent and $P < 0.0001$; $F = 9.70$ for entries). First time we reported these five volatile compounds as attractant cues for *S. dorsalis* and in future we can utilize the formulated synthetic blend as base to develop the field attractant for thrips, *S. dorsalis* which will be useful for their sustainable management in an effective way.

Studies on the differential response of thrips, *S. dorsalis* and other co-occurring sap sucking insects like aphids, *A. gossypii*, silverleaf whitefly, *B. tabaci* and spidermites, *T. macfarlanei* to healthy and herbivore (thrips) induced plant volatiles (HIPVs) revealed that herbivore induced plant volatiles instigated olfactory responses in case of thrips and also other insects in the olfactometer assays. When we evaluated the attractiveness of both HIPVs and healthy plant volatiles individually, thrips responded to both of them but in dual choice assay it exhibited significant preference to HIPVs treated region of olfactometer ($P = 0.001$; $F = 7.05$ for time spent and $P = 0.0001$; $F = 9.15$ for entries) than healthy plant volatile treated region of olfactometer.

Further to confirm thrips, *S. dorsalis* attraction towards the HIPVs, a dual choice assay was carried out between HIPVs and fruiting stage plant volatiles. In this assay, thrips preferred HIPVs ($P = 0.0004$; $F = 7.70$ for time spent and $P = 0.02$; $F = 3.93$ for entries) than the fruiting plant volatile treated region of the olfactometer. The thrips, *S. dorsalis* feeding (herbivory) on host plant, *C. annum* could have induced a change in the volatile profile of host plant and the induced specific volatiles from such thrips infested plant would have acted as aggregation kairomones there by attracting more number of conspecifics (*S. dorsalis*) in olfactometer bioassays.

Similar results were obtained with other co-occurring sap sucking insects like aphids, *A. gossypii* as they significantly preferred HIPVs treated region of olfactometer ($P = 0.007$; $F = 4.73$ for time spent and $P = 0.04$; $F = 2.99$ for entries) than healthy plant volatile treated region. Silverleaf whitefly, *B. tabaci* also significantly attracted towards HIPVs treated region of the olfactometer ($P < 0.0001$; $F = 25.73$ for time spent and $P = 0.0002$; $F = 8.74$ for entries) than healthy plant volatile treated region in the four arm olfactometer. When spidermites, *T. macfarlanei* were given the choice between HIPVs and healthy plant volatiles in Y-tube olfactometer assay, similar results were obtained as they made choice towards the HIPVs treated arm of olfactometer ($P = 0.01$).

Further, GC-MS analysis of herbivore (thrips, *S. dorsalis*) induced and healthy host plant volatiles revealed that there is a stark difference and drastic change in the abundance of volatile compounds that are present between herbivore induced and healthy host plant headspace samples. A total of 19 compounds were identified among two head space volatile samples which are collected from herbivore induced and healthy host plant.

Among an array of these volatile compounds that are present in the herbivore induced host plant volatile samples, GC-EAD analysis revealed six specific active volatile compounds which instigated the olfactory responses in case of thrips, *S. dorsalis* such as *δ*-3-Carene, Octadecane, *n*-Docosane, 4-Methyl-2-undecane, Dodecyl iodide and Tricosane. Further evaluation of attraction of synthetic fractions of these GC-EAD active compounds individually and as blend in olfactometer assays revealed that *δ*-3-Carene ($P = 0.0003$; $t = 5.71$ for time spent and $P = 0.007$; $t = 3.45$ for entries), Octadecane ($P = 0.001$; $t = 4.64$ for time spent and $P = 0.004$; $t = 3.86$ for entries) and *n*-Docosane ($P = 0.0096$; $t = 3.28$ for time spent and $P = 0.0001$, $t = 6.48$ for entries) were highly attractive to thrips. Whereas, the fractions *viz*., Dodecyl iodide, Tricosane were not attractive to thrips in olfactometer bioassays when presented individually. However, when they were formulated as synthetic blend along with *δ*-3-Carene, Octadecane and *n*-Docosane as in natural sample, it was found significantly attractive ($P = 0.003$; $t = 3.96$ for time spent and $P = 0.001$; $t = 4.61$ for entries).

Further the dual choice assay between natural sample and synthetic blend revealed that there is no significant difference in olfactory responses of thrips to the natural sample over the synthetic blend but there is a significant response when compared over the control solvents ($P < 0.0001$, $F = 9.99$ for time spent and $P = 0.0003$, $F = 8.27$ for entries). First time, we reported these five volatile compounds *viz*., *δ*-3-Carene, Octadecane, *n*-Docosane, 4-Methyl-2-undecane, Dodecyl iodide and Tricosane from HIPVs as attractant cues for *S. dorsalis* and in future we can utilize the synthetic blend based on these cues to develop lures for thrips management to strengthen our current IPM programs.

Evaluation of the attractiveness of thrips body odours extracted in three different solvents such as dichloro methane, hexane and diethyl ether to conspecific adult *S. dorsalis* in four arm olfactometer revealed that thrips were not attracted towards any one of the body odour extracts. There is no significant difference between the treated region [dichloromethane ($P = 0.67$; $t = 0.43$ for time spent and $P = 0.06$, $t = 2.18$ for entries); hexane ($P = 0.35$, $t = 0.99$ for time spent and $P = 0.09$; $t = 0.93$ for entries) and diethyl ether ($P = 0.63$; $t = 0.50$ for time spent and $P = 0.17$; $t = 1.49$ for entries)] and the control in the olfactometer.

Further multiple choice assays were conducted between HIPVs, healthy plant volatiles and thrips body odours along with solvent control in four arm olfactometer. Thrips, *S. dorsalis* significantly preferred HIPVs treated region of the olfactometer ($P < 0.0001$; $F = 92.55$ for time spent and $P < 0.0001$; $F = 66.63$ for entries) followed by healthy plant volatile treated region of the olfactometer. Thus, the herbivory by thrips, *S. dorsalis* on host plant, *C. annum* altered the volatile emissions and thrips preferred conspecifics infested plant than the healthy plant.

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