The Role of Herbivore-Induced Plant Volatiles in Tri-trophic Interactions and Pest Management

ABSTRACT

In agricultural ecosystems, the tri trophic interactions between plants, herbivores and their natural enemies are crucial for maintaining ecological balance and crop health. Natural enemies of pests predominantly regulate herbivore populations, emphasizing the importance of these interactions. Plants exhibit both induced and constitutive defences, Plants use herbivore-induced plant volatiles (HIPVs) as a key mechanism to attract natural enemies that defend them against the herbivores. HIPVs are chemical signals emitted in response to herbivore damage and can attract predators and parasitoids, indirectly they protect the plants. This review explores the role of HIPVs in plant defense, focusing on their evolutionary, chemical and practical aspects. with HIPVs acting as indirect defenses by recruiting natural enemies. The interaction between physical traits, chemical signals and semiochemicals, including volatile organic compounds (VOCs), significantly influences these interactions. Olfactometers, such as the Y-tube and four-arm designs, have been proven to be pivotal in studying insect responses to these volatile compounds, providing insights into their behaviour and effectiveness in pest management. Despite advances in understanding HIPVs, research indicates variability in volatile emissions and their effectiveness across different herbivore species and developmental stages. Further studies are needed to improve the specificity of HIPV research, incorporating field-based analyses to capture natural environmental complexities. Future research should focus on optimizing HIPV applications in pest management, understanding spatial and temporal scales of HIPV interactions, and addressing the influence of environmental factors on HIPV efficacy.

***Keywords**: Chemical Signaling, Herbivore-Induced Plant Volatiles (HIPVs),Natural Enemies, Pest Management and Trophic Interactions.*

1. INTRODUCTION

[18] first demonstrated that the regulation of herbivore populations is largely dependent on natural enemies rather than food availability. This observation underscores the importance of understanding key role of natural enemies in controlling herbivore populations. One key mechanism is which plants interact with these natural enemies is through the emission of herbivore-induced plant volatiles (HIPVs).

The intrinsic and extrinsic defenses of plants reduce the colonization rate of the herbivores. The conflict between intrinsic and extrinsic defenses affects the evolution of plant allelochemistry.

The plants have three options:

(1) They become highly attractive to beneficial insects, thus reducing the herbivore population. (2) They become poisonous to herbivores; it may harm third trophic level (extrinsic defense). (3) They achieve some compromise which exploits both protective mechanisms.

HIPVs compounds can attract predators and parasitoids that prey on or parasitize the herbivores, thereby indirectly protecting the plants. [47] introduced the concept of 'induced synomones,' where plants emit a chemical 'cry for help' to attract natural enemies in response to herbivore presence.

2. Trophic Interactions in Agro-Ecosystems

2.1. Physically DéfenseSystem

Physical characters of plants, such as glandular trichomes and leaf thicknesses, can impact herbivore and predator activities. For instance, trichomes can trap aphid parasitoids, reducing their effectiveness [26][30]. Plant morphological structure, including height and leaf size, influences the distribution of herbivores and their natural enemies [29] [41]. These physical factors can alter micro-climates and herbivore densities, thereby affecting natural enemy generations[9].

2.2 Chemically Mediated Interactions

Plants produce secondary metabolites as a defense mechanism against herbivores. These chemicals can deter herbivores or be sequestered by them, affecting their predators [37]. Some herbivores have evolved detoxification abilities to handle these chemicals [43]. For example, the parasitoids *Adaliabipunctata* and *Episyrphusbalteatus* have developed mechanisms to detoxify compounds used by aphids for defense [10]. Chemical signals from plants also influence parasitoid behavior and effectiveness [16].

2.3 Semiochemical Mediated Interactions

Semiochemicals are natural chemical compounds emitted by animals or plants into the environment. These compounds can either be extracted from the organism or synthetically produced to mimic the natural compound. Plants release kairomones and other VOCs that attract herbivores and their natural enemies [45]. For example, the parasitoid, *Diadegmarapae* uses mustard oil as a cue to locate aphid hosts [33]. Certain plant compounds can also mask attractants, affecting parasitoid effectiveness [28][23].

3. The Role of HIPVs in Plant Defense:

3.1 Induced and Constitutive Defenses

Plants exhibits both induced and constitutive defenses against herbivores. Induced defenses, including the production of HIPVs, are activated in response to herbivore attacks, while constitutive defenses are always present. HIPVs serve as indirect defenses by recruiting natural enemies of herbivores, thereby enhancing plant health, [14][4]. The effectiveness of these defenses depends on factors such as herbivore type and environmental conditions [23].

3.2 Volatile Organic Compounds and Their Role

Volatile Organic Compounds (VOCs) are released by plants that mediates plant-plant interactions above ground, roots can detect the chemical signals originating from their neighbors and roots release VOCs involved in biotic interactions Below the ground [8].

Certain volatile organic compounds (VOCs) can be considered as Damage-associated molecular patterns (DAMPs). Due to their chemical nature, VOCs are supposed to act not only locally and systemically in the same plant but also between plants. The possibility to use such airborne DAMPs as eco-friendly compounds which stimulate natural defense in agriculture in order to avoid pesticides [5].

VOCs are low molecular weight compounds mostly belong to terpenoids, alcohol, aldehyde fatty acid and amino acid derivative. They are synthesized by different metabolic pathway [46].Common HIPVs include sesquiterpenes like (E)-caryophyllene and (E, E)-farnesene, homoterpene DMNT and green leaf volatiles (GLVs) such as (Z)-3-hexen-1-ol [6][35]. These compounds also provide an information about herbivore presence, developmental stages and damage symptoms and levels, influencing natural enemy behavior[14][15](Fig. 1).

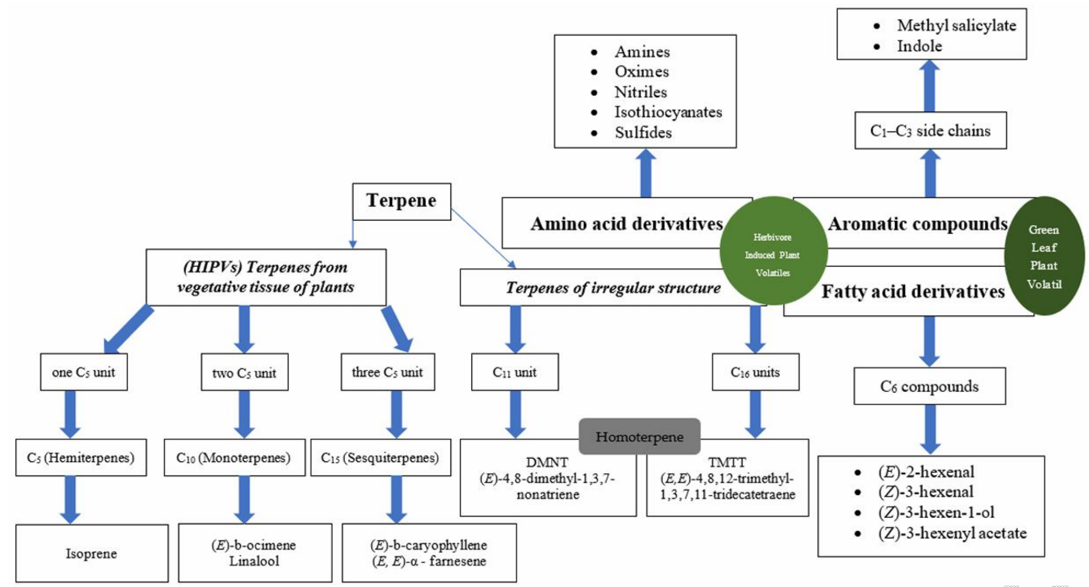

Fig. 1. Plant volatile organic compounds (VOCs) consist of chemicals from different chemical classes, which have been identified in blends after herbivore damage, [3].

Research studies on volatile emissions, odour trapping and insect behaviour has become highly relevant, with olfactometers emerging as crucial tools in these studies. [27,They investigated beetle responses to host-plant odours using a Y-shaped glass tube[27]. This device allowed the researchers to intrude odours through the arms of the tube and observe which arm the beetles preferred, based on their attraction to the odours.

Y-tube and T-tube olfactometers are still widely used for assessing the olfactory responses of various arthropods, including predatory spider mites (*Phytoseiulus persimilis*) [34],parasitoid wasps (*Cotesia glomerate*) [39], cabbage seed weevils *(Ceutorhynchusassimilis)*[7] and other pests. The four-arm olfactometer, introduced by Pettersson in 1970 and later refined by [44], allows for the testing of multiple odour sources simultaneously [40][11]. In this setup, odour sources are placed at the centre of the olfactometer and insects are released into a chamber with four distinct odour fields. This design facilitates studies involving several treatments and provides insights into insect behaviour in response to multiple odours. (Fig.2 and Fig.3).

The olfactory system of insects involves odorant receptors (ORs) and odorant-binding proteins (OBPs). ORs are responsible for triggering the olfactory signalling cascade, while OBPs aid in the solubilization and transport of odorants [11][31]. Despite this understanding, some studies have found that herbivore-induced volatile emissions do not significantly change across different herbivore species or developmental stages [19][25]. For example, volatiles from coyote tobacco induced by various herbivores-such as the five-spotted hawk moth, tobacco flea beetle and a sucking fly-showed similar compounds, albeit in varying proportions, influencing predator behaviour [25].

Improving the specificity of herbivore-induced volatile research requires more extensive chemical analysis of plant volatile blends and advanced statistical methods to account for compositional and abundance changes [42]. Field samples are essential to understanding how natural variables affect volatile blends, as laboratory studies often fail to capture the complexity of natural environments. The specificity of herbivore-induced plant volatiles (HIPVs) is ultimately determined by the blend of volatiles and their proportions, influencing the behaviour of natural enemies like predators and parasitoids.

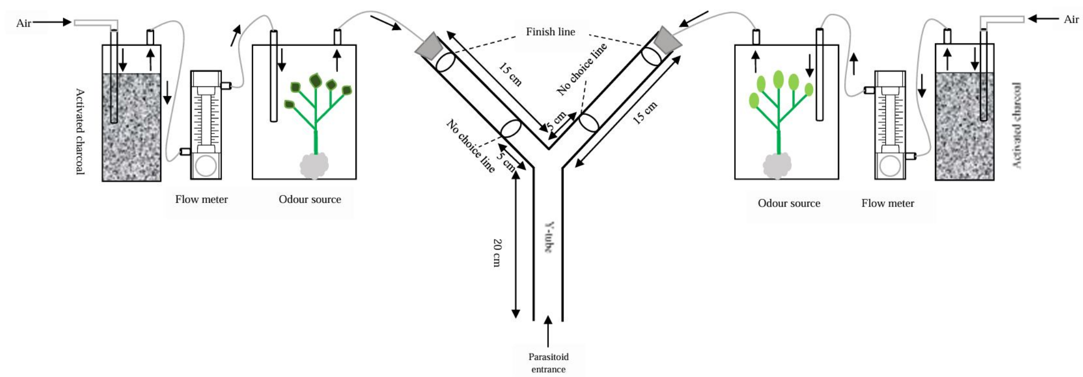

Fig. 2. Schematic diagram of the Y-tube olfactometer, [4]

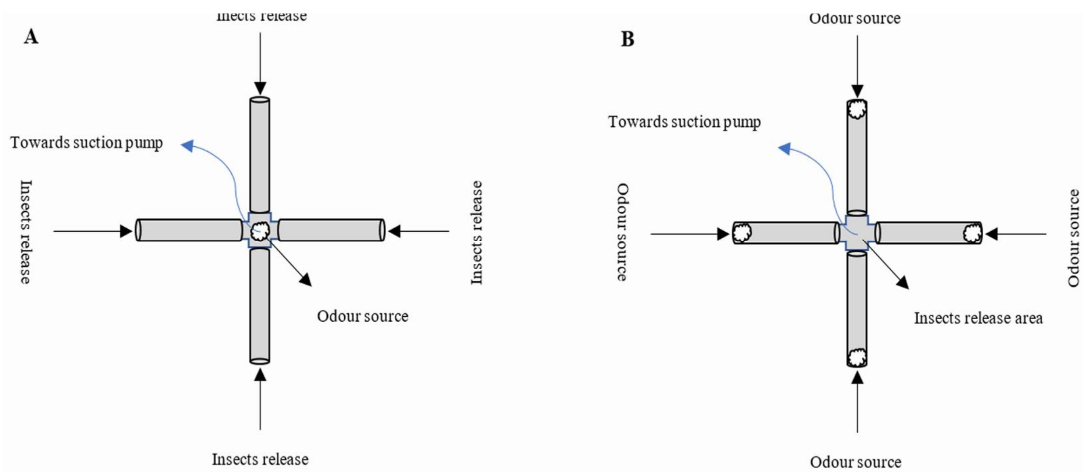

Fig. 3. Schematic Diagram of the four- arm olfactometers, (A): Odour source testing with 4 different insects release area, (B): Four Separate odour sources testing with same insect

3.3 Examples of HIPV-Mediated Interactions

Studies have shown that specific VOCs can attract natural enemies effectively. For example, the parasitoid *Cotesiamarginiventris* responds to compounds such as (E)-2-hexenal, (Z)-3-hexenyl acetate, linalool and geranyl acetate after herbivore damage [48].Similarly, the mite *Phytoseiulus persimilis* is attracted to a mixture of compounds including (E)- and (Z)-β-ocimene and DMNT [22]. These interactions demonstrate the specificity of VOCs in mediating plant defense.

4.The Evolution and Application of HIPVs
4.1 Evolutionary Perspectives

The evolution of HIPVs is always debated, with some researchers questioning whether these compounds evolved primarily to attract natural enemies. While there is evidence that HIPVs can attract natural enemies and reduce plant damage [12] [25], it is also possible that HIPVs serve other functions, such as signaling within and between plants or providing direct defences against herbivores and pathogens [20] [21].

4.2 Practical Applications in Pest Management

The practicability of HIPVs for biological control involves optimizing their application in agricultural systems. Synthetic HIPV lures, such as those based on methyl salicylate, are used to attract natural enemies [20] [24]. However, interference from natural plant volatiles can affect lure effectiveness, suggesting the need for optimized blends and concentrations [17]. These includeinvestigating the spatial and temporal scales of HIPV-mediated interactions, including how these compounds influence parasitoid movement on a landscape scale [38].Exploring the effects of environmental factors and other odors on HIPV effectiveness [49][2] and improving field studies to better understand the practical implications of HIPVs in pest management [42] [36].

5. CONCLUSION

Herbivore-induced plant volatiles (HIPVs) play a crucial role in mediating trophic interactions within agricultural ecosystems by attracting natural enemies that help control herbivore populations. This review highlights the complex interplay between HIPVs, plant defenses and their evolutionary and practical implications. While advances in understanding the chemical and ecological functions of HIPVs have been significant, variability in volatile emissions and their effectiveness across different herbivore species and developmental stages persists. Future research should focus on refining our knowledge of HIPV specificity, improving field studies to capture natural environmental complexities, and optimizing the application of synthetic HIPVs in pest management. By addressing these areas, we can enhance the practical utility of HIPVs in sustainable agriculture, leveraging their potential to reduce reliance on chemical pesticides and promote ecological balance. Enhanced understanding and application of HIPVs will contribute to more effective and environmentally friendly pest management strategies.

ETHICAL APPROVAL: This article does not contain any studies with human participants or animals performed by any of the authors.

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REFERENCES

1. Aartsma Y, Pappagallo S, van der Werf W, Dicke M, Bianchi F J J A, Poelman E H. Spatial Scale, Neighbouring Plants and Variation in Plant Volatiles Interactively Determine the Strength of Host-Parasitoid Relationships. *Oikos*. 2020; 1429-1439.
2. Ali M Y, Naseem T, Arshad M, Ashraf I, Rizwan M, Tahir M, Rizwan M, Sayed S, Ullah M I, Khan R R. (2021). Host-Plant Variations Affect the Biotic Potential, Survival, and Population Projection of *MyzusPersicae* (Hemiptera: Aphididae). *Insects. 2021;* 375.

3. Ali M Y, Naseem T, Holopainen J K, Liu T, Zhang J, Zhang F. Tritrophic Interactions among Arthropod Natural Enemies, Herbivores and Plants Considering Volatile Blends at Different Scale Levels. *Cells. 2023;* 12, 251.
4. Ali M Y, Naseem T, Zhang J, Pan M, Zhang F, Liu T. Plant Volatiles and Herbivore Induced Plant Volatiles from Chili Pepper Act as Attractant of the Aphid Parasitoid. *Plants. 2022;* 11, 1350.
5. Anja Katharina Meents, Axel Mithöfer. Plant-Plant Communication: Is There a Role for Volatile Damage Associated Molecular Patterns? *Frontiers in plant Sciences*. 2020. 11. https://doi.org/10.3389/fpls.2020. 583275.
6. Arimura G I, Kopke S, Kunert M, Volpe V, David A, Brand P, Dabrowska P, Maffei M E, Boland W. Effects of Feeding *Spodoptera Littoralis* on Lima Bean Leaves: IV. Diurnal and Nocturnal Damage Differentially Initiate Plant Volatile Emission. *Plant Physiology. 2008;*146, 965-973.
7. Bartlet E, Blight M M, Hick A J, Williams I H. The Responses of the Cabbage Seed Weevil (*Ceutorhynchusassimilis*) to the Odour of Oilseed Rape (*Brassica napus*) and to Some Volatile Isothiocyanates. *EntomologiaExperimentalis et Applicata.*1993; 68, 295-302.
8. Benjamin M, Delory PD, Delaplace M-L, Fauconnier M-L, du Jardin P. Root-emitted volatile organic compounds: can they mediate belowground plant-plant interactions? *Plant and Soil*. 2016; 402, 1-26.
9. Bezemer TM, Wagenaar R, van Dam NM, Wackers FL. Interactions between above and belowground insect herbivores as mediated by the plant defence system. *Oikos.* 2003; 101, 555-562.
10. Bhatt N, Singh R. Bionomics of an aphidiid parasitoid Trioxys indicus (Subba Rao and Sharma). Effect of host plants on reproductive and developmental factors. *Biology and Agriculture Horticulture. 1989*; 6, 149-157.
11. Conchou L, Lucas P, Meslin C, Proffit M, Staudt M, Renou M. Insect odorscapes: From plant volatiles to natural olfactory scenes. *Frontiers in Physiology.* 2019; 10, 972.
12. Degenhardt J, Kollner TG, Gershenzon J. Monoterpene and sesquiterpene synthases and the origin of terpene skeletal diversity in plants. *Phytochemistry.* 2009; 70, 1621-37.
13. Dicke M, Loon JJAA. Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. *EntomologiaExperimentalis et Applicata.* 2000; 97, 237-249.
14. Dicke M. Behavioural and community ecology of plants that cry for help. *Plant, Cell & Environment.* 2009; 32, 654-665.
15. Dudareva N, Klempien A, Muhlemann JK, Kaplan I. Biosynthesis, function and metabolic engineering of plant volatile organic compounds. *New Phytologist.* 2013; 198, 16-32.
16. Ferran J, Godfray HC. Resistance to a fungal pathogen and host plant specialization in the pea aphid. *Ecology Letters.* 2003; 6, 111.
17. Flint MH, Salter SS, Walters S. Caryophyllene: an attractant for the green lacewing. *Environmental Entomology.* 1979; 8, 1123-1125.
18. Hairstone NG, Smith FE, Slobodkin LB. Community structure, population control and competition. *American Naturalist.* 1960; 94, 421-425.
19. Hare JD, Sun JJ. Production of induced volatiles by Datura wrightii in response to damage by insects: Effect of herbivore species and time. *Journal of Chemical Ecology.* 2011; 37, 751-764.
20. Hare JD. Ecological role of volatiles produced by plants in response to damage by herbivorous insects. *Annual Review of Entomology.* 2011; 56, 161-180.
21. Heil M. Herbivore-induced plant volatiles: targets, perception and unanswered questions. *New Phytologist.* 2014; 204, 297-306.

22. Hodge S, Ward JL, Galster AM, Beale MH, Powell G. The effects of a plant defence priming compound—aminobutyric acid—on multitrophic interactions with an insect herbivore and a hymenopterous parasitoid. *Biocontrol.* 2011; 56, 699-711.
23. Horn DJ. Vegetational complexity and parasitism of green peach aphids (Myzuspersicae (Sulzer) (Homoptera, Aphididae) on collards. *Journal of the New York Entomological Society.* 1984; 92, 19-26.
24. James DG. Synthetic herbivore-induced plant volatiles as field attractants for beneficial insects. *Environmental Entomology.* 2003; 32, 977-982.
25. Kessler A, Baldwin IT. Defensive function of herbivore-induced plant volatile emissions in nature. *Science*. 2001; 291, 2141-2144.
26. Marcovitch S. Experimental evidence on the value of strip farming as a method for the natural control of injurious insects with special reference to plant lice. *Journal of Economic Entomology.* 1935; 28, 62-70.
27. McIndoo NE. An insect olfactometer. *Journal of Economic Entomology.* 1926; 19, 545-571.
28. Monteith LG. Influence of plants other than the food plants of their host on host finding by tachinid parasites. *Canadian Entomologist.* 1960; 92, 641-652.
29. Moreno DS, Gregory WA, Tanigoshi LK. Flight response of Aphytismelinus (Hymenoptera: Aphelinidae) and *Scirtothripscitri* (Thysanoptera,Thripidae) to trap colour, size, and shape. *Environmental Entomology.* 1984; 13, 935-940.
30. Obrycki JJ, Tauber MJ. Natural enemy activity on glandular pubescent potato plants in the greenhouse: An unreliable predictor of effects in the field. *Environmental Entomology.* 1984; 13, 679-683.
31. Pelosi P, Iovinella I, Zhu J, Wang G, Dani FR. Beyond chemoreception: Diverse tasks of soluble olfactory proteins in insects. *Biological Reviews.* 2018; 93, 184-200.
32. Pettersson J. Studies on Rhopalosiphumpadi (L.) I. Laboratory studies of olfactometric responses to the winter host Prunus padus (L.). *LantbrukshogskolansAnnaler*. 1970; 36, 381-399.
33. Read DP, Feeny PP, Root RB. Habitat selection by the aphid parasite, Diaeretiellarapae (Hymenoptera: Braconidae), and hyperparasite, Charipsbrassicae (Hymenoptera: Cynipidae). *Canadian Entomologist.* 1970; 102, 1567-1578.
34. Sabelis MW, van de Baan HE. Location of distant spider mite colonies by phytoseiid predators: Demonstration of specific kairomones emitted by Tetranychusurticae and Panonychusulmi. *EntomologiaExperimentalis et Applicata.* 1983; 33, 303-314.
35. Schaub A, Blande JD, Graus M, Oksanen E, Holopainen JK, Hansel A. Real-time monitoring of herbivore induced volatile emissions in the field. *Physiologia Plantarum.* 2010; 138, 123-133.
36. Schuman MC, Barthel K, Baldwin IT. Herbivory-induced volatiles function as defenses increasing fitness of the native plant Nicotiana attenuata in nature. *eLife Sciences.* 2012; 1, e00007.
37. Shorey HH, McKelvey JJ. Chemical control of insect behaviour: Theory and application. John Wiley & Sons; New York; 1977.
38. Simpson M, Gurr GM, Simmons AT, Wratten SD, James DG, Leeson G, Nicol HI, Orre-Gordon GUS. Attract and reward: Combining chemical ecology and habitat manipulation to enhance biological control in field crops. *Journal of Applied Ecology*. 2011; 48, 580-590.

39. Steinberg S, Dicke M, Vet LEM, Wanningen R. Response of the braconid parasitoid Cotesia (Apanteles) glomerata to volatile infochemicals: Effects of bioassay set-up, parasitoid age and experience and barometric flux. *EntomologiaExperimentalis et Applicata.* 1992; 63, 163-175.
40. Sullivan BT, Pettersson EM, Seltmann KC, Berisford CW. Attraction of the bark beetle parasitoid Roptrocerusxylophagorum (Hymenoptera: Pteromalidae) to host-associated olfactory cues. *Environmental Entomology.* 2000; 29, 1138-1151.
41. Tripathi SK, Singh R. Effect of host-food plant transfer on the life-table of LysiphlebiamirzaiShuja-Uddin, an aphid parasitoid of cereal aphids. *Malaysian Journal of Applied Biology.* 1997; 26, 5-55.
42. Van Dam NM, Poppy GM. Why plant volatile analysis needs bioinformatics—detecting signal from noise in increasingly complex profiles. *Plant Biology.* 2008; 10, 29-37.
43. Vanhalen N, Haubruge E, Gaspar C, Francis F. Adaptations of aphidophagous predators to the chemical defence of their prey. In: Proceedings of the International Symposium on Insect Evolutionary Ecology and Entomology. The Royal Entomological Society; University of Reading; UK; 2003.
44. Vet LEM, Dicke M. Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology.* 1992; 37, 141-172.
45. Vinson SB. Chemical signals used by parasitoids. Redia. 1991; 74, 15-42.
46. War Rashid Abdul, Sharma Chand Hari, Paulraj Gabriel Michael, War MohdYousf, IgnacimuthuSavarimuthu. Herbivore induced plant volatiles: Their role in plant defense for pest management. *Plant Signaling & Behavior.* 2011; 6(12), 1973-1978.
47. Wegener R, Schulz S, Meiners T, Hadwich K, Hilker M. Analysis of volatiles induced by oviposition of elm leaf beetle *Xanthogalerucaluteola* on *Ulmus minor*. *Journal of Chemical Ecology.* 2001; 27, 499-515.
48. Wei J, Wang L, Zhu J, Zhang S, Nandi OI, Kang L. Plants attract parasitic wasps to defend themselves against insect pests by releasing hexanol. *Public Library of Science ONE.* 2007; 2, e852.
49. Yuan JS, Himanen SJ, Holopainen JK, Chen F, Stewart CN. Smelling global climate change: Mitigation of function for plant volatile organic compounds. *Trends in Ecology & Evolution.* 2009; 24, 323-331.