

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

## ABSTRACT

In agricultural ecosystems, the ~~three~~ trophic level interactions between plants, herbivores and their natural enemies are crucial for maintaining ecological balance and crop health. Natural enemies ~~of pests~~ are predominantly regulating 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~~ and 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. ~~Plants exhibit both induced and constitutive defences,~~ 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.

Comment [PC1]: tritrophic interaction

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Comment [PC3]: the abstract doesn't say anything about ecological implications of behavioural pest management

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

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## 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 colonisation 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 ~~the~~ third trophic level

Comment [PC5]: what are intrinsic and extrinsic plant defenses?

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(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.

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## 2. Trophic Interactions in Agro-Ecosystems

### 2.1. Physically Mediated Interactions

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].

Comment [PC9]: "physical defense system" would be a better term

### 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 *Episyrphus balteatus* 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 Semiochemically Mediated Interactions

Semiochemicals, which includes mainly volatile organic compounds (VOCs), plays an important role in mediating interactions between plants, herbivores and their natural enemies. Plants release kairomones and other VOCs that attract herbivores and their natural enemies [45]. For example, the parasitoid, *Diadegmarapae* uses mustard oil as a chemical cue to locate aphid hosts[33]. Certain plant compounds can also mask attractants, affecting parasitoid effectiveness [28][23].

Comment [PC10]: define semiochemicals

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## 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].

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### 3.2 Volatile Organic Compounds and Their Role

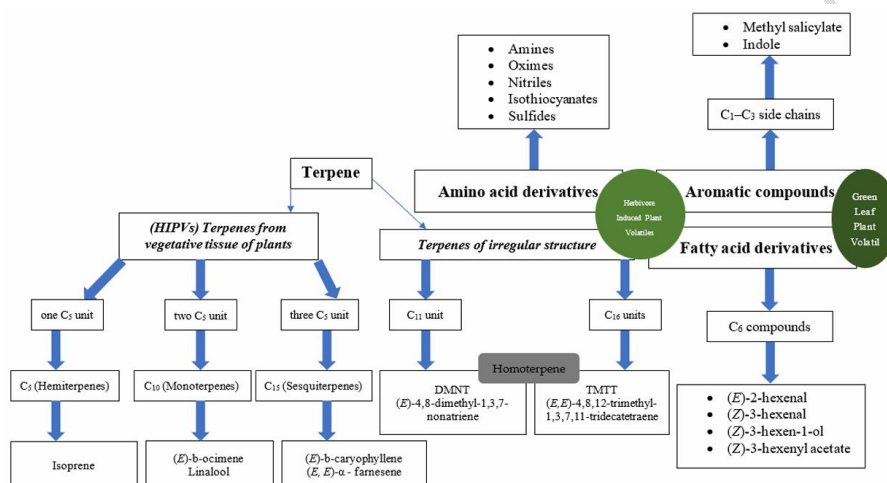
Volatile Organic Compounds (VOCs) are released by plants that mediates plant-plant interactions above ground, roots can detect the chemical signals originating from their neighbors and roots release VOCs involved in biotic interactions Below the ground [8].

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

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use such airborne DAMPs as eco-friendly compounds which stimulate natural defense in agriculture in order to avoid pesticides [5].

Chemically, 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 relevantly, 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 (*Ceutorhynchus assimilis*) [7] and other pests. The four-arm olfactometer, introduced by Petterson 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].

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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 or greenhouse 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.

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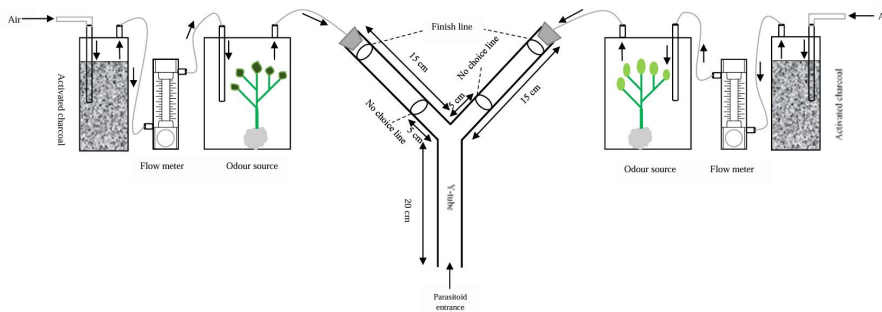


Fig. 2. Schematic diagram of the Y-tube olfactometer, [4]

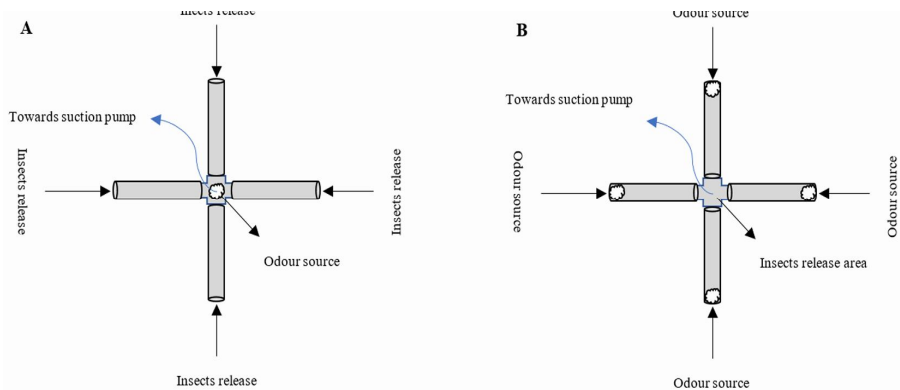


Fig. 3. Schematic Diagram of the four- arm olfactometers, (A): Odour source testing with 4 different insects release area, (B): Four Separate odour sources testing with same insect

### 3.3 Examples of HIPV-Mediated Interactions

Studies have shown that specific VOCs can attract natural enemies effectively. For example, the parasitoid *Cotesia marginiventris* responds to compounds such as (E)-2-hexenal, (Z)-3-hexenyl acetate, linalool and geranyl acetate after herbivore damage [48]. ~~For example, the parasitoid *Cotesia marginiventris* 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)- $\beta$ -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 an 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].

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### 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 include investigating 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].

Comment [PC20]: Briefly discuss why such behavioral pest management tactics are environment friendly

## 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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