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THE PLANT'S CRY FOR HELP: TRANSLATING VOLATILE SIGNALLING INTO SUSTAINABLE PEST CONTROL

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ABSTRACT

Plants naturally defend themselves against insect pests by releasing specific airborne chemical signals known as Herbivore-Induced Plant Volatiles (HIPVs). These dynamic emissions play a critical ecological role by repelling herbivores, warning neighbouring plants, and attracting beneficial predators and parasitoids. Because of these natural functions, HIPVs are increasingly recognized as a powerful, eco-friendly tool for sustainable pest management, offering an alternative to broad-spectrum synthetic insecticides. However, the practical application of HIPVs in agriculture is currently limited by a persistent research gap between controlled laboratory experiments and the unpredictable reality of field environments. Most foundational research relies on simplified models that fail to account for how environmental variables such as climate change, shifting microclimates, and atmospheric pollution (like ozone) rapidly degrade volatile plumes and disrupt chemical communication in the open field. Furthermore, there is a critical lack of understanding regarding how these volatile signals operate within structurally complex, perennial agroecosystems (such as tree crops), particularly concerning concealed, internal-feeding pests where traditional visual monitoring fails. Beyond ecological and biological unknowns, a major socio-economic gap remains where advanced synthetic delivery systems are often too expensive or technologically impractical for smallholder farmers. To successfully translate chemical ecology into reliable crop protection, future research must shift away from reductionist laboratory studies. Priorities must include field-based testing to understand signal stability under climate stress, the integration of belowground and aboveground volatile dynamics, and the development of cost-effective, scalable technologies that are accessible to diverse agricultural communities.

Keywords **:** Herbivore -induce plant volatiles, sustainable pest management, volatile signals, volatile dynamics.

Evolutionary context of plant herbivore interactions

The remarkable diversity of plant defensive traits observed in modern ecosystems is largely the result of long-term reciprocal adaptation between plants and herbivorous insects. Because plants are sessile and unable to escape from the herbivore attack, natural selection has favoured the evolution of defensive strategies that minimize tissue damage while maintaining physiological functionality. These strategies include both structural deterrents, such as lignified tissues, trichomes, and spines and an extensive repertoire of specialized metabolites that influence herbivore feeding behaviour and survival (Howe and Jander, 2008).

Chemical defences, in particular, have played a pivotal role in shaping plant-insect evolutionary dynamics. Secondary metabolites such as alkaloids, phenolics, and glucosinolates function as toxicants, digestibility reducers, or repellents that restrict herbivore exploitation of plant tissues (Schoonhoven *et al*., 2005). However, the adaptation is not one-sided where herbivorous insects also have evolved a diverse array of counter measures that enable them to tolerate or circumvent plant defences. These include enzymatic detoxification mechanisms, sequestration of plant

toxins for defensive purposes, and behavioural strategies that avoid highly defended tissues. Such reciprocal adaptations have generated a continuous evolutionary feedback loop that promotes diversification of both plant defence chemistry and insect herbivore specialization (Chen *et al*., 2015).

Increasingly, research has revealed that plant defence systems operate not only through direct chemical toxicity but also through complex ecological signalling networks. Among these networks, volatile-mediated communication has emerged as a critical mechanism through which plants interact with herbivores, natural enemies, and neighbouring vegetation. Plants continuously emit a wide range of volatile organic compounds (VOCs) into the surrounding atmosphere. Many of these compounds serve essential physiological functions unrelated to herbivore defence, including pollinator attraction, thermoregulation, and responses to abiotic stress. These baseline emissions, commonly referred to as constitutive VOCs, form part of the plant's routine metabolic activity.

In contrast, herbivore-induced plant volatiles represent a specialized category of inducible defence signals produced in response to biotic attack. When plant tissues are damaged by herbivore feeding or oviposition, biochemical signalling pathways are activated that lead to the synthesis or enhanced release of specific volatile compounds (Hilker and Fatouros, 2015; Paré and Tumlinson, 1999). These emissions are not merely by-products of cellular disruption; rather, they result from highly regulated metabolic processes coordinated through phytohormonal signalling networks involving jasmonic acid, salicylic acid, and ethylene.

The resulting volatile blends often contain complex mixtures of terpenoids, green leaf volatiles, and aromatic compounds whose relative proportions depend on the identity of the attacking herbivore. Such chemical signatures function as airborne signals that recruit predators and parasitoids capable of suppressing herbivore populations, thereby establishing an indirect defence strategy mediated through higher trophic levels (Dicke and Sabelis, 1988). By deploying these signals only when herbivore attack occurs, plants conserve metabolic resources while maintaining the capacity for rapid defensive activation.

Understanding the ecological and biochemical basis of HIPV production has therefore become a central focus of plant chemical ecology. Insights into the mechanisms governing volatile synthesis and perception provide a foundation for developing innovative pest management strategies that align with the principles of sustainable agriculture.

Since Integrated Pest Management (IPM) represents a paradigmatic shift in the direction, that advocates the coordinated use of biological control, habitat manipulation, and cultural practices to maintain pest populations below economically damaging thresholds, the exploitation of plant-mediated defence systems has a promising avenue. Herbivore-induced plant volatiles (HIPVs), which function as key mediators of multitrophic communication, offer a mechanistically sophisticated means of enhancing indirect plant defence by recruiting and modulating the activity of natural enemies (Mutyambai *et al*., 2022).

HIPV-based management is particularly relevant for endophagous pests such as stem borers and pod feeders which are beyond the reach of insecticide spray and conventional biological control agents. HIPVs provide an opportunity to target these concealed herbivores through repulsion or attracting their natural enemies.

Nevertheless, the integration of HIPV-mediated strategies into operational pest management remains an evolving frontier. Critical knowledge gaps persist regarding the consistency of volatile-mediated interactions across diverse cropping systems, the influence of environmental variability on signal reliability, and the scalability of such approaches in resource-limited agricultural contexts. Addressing these challenges will require a more holistic understanding of plant–insect–environment interactions, as well as the development of context-specific deployment strategies that align ecological functionality with agronomic feasibility.

A major research gap lies in applying current evolutionary and ecological understanding of HIPVs to complex perennial agroecosystems. Most foundational studies on herbivore-induced plant volatiles have been conducted in simplified annual cropping systems, where plants are attacked mainly by exposed leaf-feeding insects. As a result, the functioning and evolution of volatile-mediated interactions in multilayered environments, such as tree crop canopies, remain poorly understood. This review therefore synthesises current knowledge on HIPV biosynthesis, spatiotemporal emission dynamics, ecological functions across trophic levels, and applied pest management strategies, with specific attention to endophagous pests in perennial agroecosystems where these interactions remain critically understudied

Biosynthesis and regulatory mechanisms of HIPVs

The emission of herbivore-induced plant volatiles is the outcome of complex metabolic reprogramming triggered by herbivore attack. Unlike passive chemical leakage from damaged tissues, HIPV production reflects a coordinated biochemical response requiring substantial metabolic investment. Plants must therefore regulate the biosynthesis of these compounds with considerable precision to ensure that defensive signalling is deployed only under genuine herbivore pressure. Such regulation allows plants to balance defensive functions with essential physiological processes such as growth, reproduction, and nutrient allocation.

Metabolic origins and chemical diversity of HIPVs

The volatile blends emitted during herbivore attack consist of numerous chemically distinct compounds generated through several interconnected metabolic pathways (Arimura *et al*., 2005). The diversity of these compounds allows plants to produce highly specific chemical signatures capable of conveying information about the nature of the attack to surrounding organisms (De Moraes, *et al*. 1998).(year is different in reference list. Check it and add correct reference)

Among the most prominent components of HIPV mixtures are terpenoids, a group of compounds derived from isoprenoid biosynthesis. These metabolites include monoterpenes, sesquiterpenes, and homoterpenes that possess strong olfactory activity and high atmospheric diffusibility. Terpenoid biosynthesis is mediated by two compartmentalized metabolic routes that generate the precursor isopentenyl diphosphate. The cytosolic mevalonate pathway primarily produces sesquiterpenes, whereas the plastid-localized methylerythritol phosphate pathway contributes mainly to monoterpene and diterpene formation (Arimura *et al*., 2005). Because of their volatility and ecological signalling capacity, these compounds play a crucial role in attracting parasitoids and predators capable of locating herbivore hosts.

A second major class of HIPVs consists of green leaf volatiles (GLVs), which arise rapidly following tissue injury. These compounds are predominantly six-carbon aldehydes, alcohols, and esters formed through the lipoxygenase-mediated oxidation of polyunsaturated fatty acids released from damaged membranes (Matsui, 2006). The rapid generation of GLVs allows plants to emit an immediate signal within seconds of herbivore feeding, functioning as an early warning system that can prime nearby tissues or neighbouring plants for enhanced defensive readiness (Heil and Kost, 2006).

Table 1: Key Herbivore-Induced Plant Volatiles (HIPVs): Chemical Classification, Crop Sources, and Ecological Signalling Functions

Chemical Class	Volatile Organic Compound (VOC)	Plant Species (Crop)	Ecological Context / Eliciting Herbivore	Reference
Terpenoids (Mono-, Sesqui-, & Homoterpenes) Terpenoids (Mono-, Sesqui-, & Homoterpenes)	(E)-β-caryophyllene	Maize (*Zea mays*)	Systemic belowground emission induced by rootworm feeding to attract entomopathogenic nematodes.	(Holopainen & Blande, 2013)
	(E)-4,8-dimethyl-1,3,7-nonatriene (DMNT)	Cotton (*Gossypium hirsutum*)	Key volatile that suppresses host-location and mate-finding behaviours in *Spodoptera littoralis*.	(Hatano *et al*., 2015)
	(E)-β-ocimene	Lima Bean (*Phaseolus lunatus*)	A dominant monoterpene functioning as a critical info chemical for carnivorous natural enemies.	(Mumm & Dicke, 2010)
	(E,E)-α-farnesene	Lima Bean (*Phaseolus lunatus*)	Specialized sesquiterpene involved in indirect plant defence and bodyguard attraction.	(Mumm & Dicke, 2010)
	Isoprene	Maize (*Zea mays*)	Rapidly emitted transient volatile released during early mechanical stress and contact.	(Markovic *et al*., 2018)
	Linalool	Assorted crops (Cotton, Rice)	Synthesized via the plastidic methyl erythritol phosphate pathway; deters feeding and oviposition.	(Zhou & Jander, 2021)
	Gossypol	Cotton (*Gossypium* spp.)	A heavily defensive sesquiterpene associated with direct toxicity to piercing-sucking herbivores.	(Zhou & Jander, 2021)

Green Leaf Volatiles (GLVs)	(Z)-3-hexenal	Maize (*Zea mays*)	Emitted immediately following structural damage and exposure to *Spodoptera exigua* regurgitant; primes defences.	(Engelberth *et al*., 2004)
	(Z)-3-hexen-1-ol	Maize (*Zea mays*)	Functions as an early airborne signal priming neighbour plants against impending attack.	(Engelberth *et al*., 2004)
	(Z)-3-hexenyl acetate	Maize (*Zea mays*)	Enhances jasmonic acid synthesis and primes systemic defences.	(Engelberth *et al*., 2004)
	1-hexanol	Sweet Pepper (*Capsicum annuum*)	Induced by zoo phytophagous mirid feeding; acts in intra- and inter-plant signalling.	(Riahi *et al*., 2022)
	(Z)-3-hexenyl propanoate	Sweet Pepper (*Capsicum annuum*)	Functions as a direct repellent to pests like *Frankliniella occidentalis*.	(Riahi *et al*., 2022)
	(Z)-3-hexenyl butanoate	Sweet Pepper (*Capsicum annuum*)	Highly attractive to the predatory bug *Orius laevigatus*.	(Riahi *et al*., 2022)
	Hexyl butanoate	Sweet Pepper (*Capsicum annuum*)	Contributes to the upregulation of SA and JA defensive pathways in receiver plants.	(Riahi *et al*., 2022)
	Hexanal	Lima Bean (*Phaseolus lunatus*)	Common constituent of the rapid-response GLV defensive bouquet.	(Mumm & Dicke, 2010)
Aromatic & Phenylpropanoid Compounds	Methyl salicylate	Sweet Pepper (*Capsicum annuum*)	Induces broad defence responses and serves as a strong repellent to whiteflies and thrips.	(Riahi *et al*., 2022)
	Methyl jasmonate	Sweet Pepper (*Capsicum annuum*)	Volatile phytohormone derivative that upregulates proteinase inhibitors and defensive genes.	(Riahi *et al*., 2022)
	Indole	Maize (*Zea mays*)	A nitrogen-containing aromatic compound frequently utilized by specialist parasitoids for host location.	(Mumm & Dicke, 2010)
Other Diverse Metabolites	Isothiocyanates (general)	Crucifers (*Brassicaceae*)	Breakdown products of glucosinolates triggered by mechanical disruption and herbivore feeding.	(Mumm & Dicke, 2010)
	Methanol	Maize (*Zea mays*)	Elicited in response to continuous mechanical contact and stress, persisting in the volatile plume.	(Markovic *et al*., 2018)
	Soluble Glycosides (derived from (Z)-3-hexenol)	Tomato (*Solanum lycopersicum*)	Volatiles taken up by receiver plants and converted into toxic glycosides to suppress *Spodoptera litura* growth.	(Zhou & Jander, 2021)
Terpenoids	α-farnesene	Apple (*Malus domestica*)	Repels aphids and attracts aphid parasitoids such as *Aphidius* spp.	(Bruce & Pickett, 2011)
	TMTT ((E,E)-4,8,12-trimethyltrideca-1,3,7,11-tetraene)	Maize (*Zea mays*)	Homoterpene strongly involved in the attraction of parasitoids and predatory mites.	(Mumm & Dicke, 2010)
	cis-α-bergamotene	Wild Tobacco (*Nicotiana attenuata*)	Key volatile that repels *Manduca sexta* moths and attracts *Geocoris* predators.	(Kessler & Baldwin, 2001)
	α-pinene	Conifers (*Pinus* spp.)	Modulated by abiotic stress and herbivory; contributes to broad volatile defense signalling.	(Holopainen & Gershenzon, 2010)
	Terpinolene	Tomato (*Solanum lycopersicum*)	Repels whiteflies and contributes to indirect defense networks.	(Zhou & Jander, 2021)
	α-terpineol	Rice (*Oryza*	Possesses antifungal and	(Loreto &

		sativa)	antibacterial properties; involved in stress signalling.	Schnitzler, 2010)
Green Leaf Volatiles (GLVs)	(E)-2-hexenal	Tomato (*Solanum lycopersicum*)	Strong antimicrobial volatile; deters feeding and oviposition by herbivores.	(Scala *et al*., 2013)
	(E)-2-hexenol	Bean (*Phaseolus vulgaris*)	Functions in airborne defense priming and predator attraction.	(Arimura *et al*., 2009)
	cis-3-hexenyl isobutyrate	Maize (*Zea mays*)	Attracts parasitoids and predatory insects during early herbivore attack.	(Dicke & Baldwin, 2010)
	cis-3-hexenyl valerate	Cotton (*Gossypium* spp.)	Enhances indirect defense through rapid natural enemy recruitment.	(Heil & Karban, 2010)
Aromatic / Phenylpropanoid VOCs	Benzyl alcohol	Tobacco (*Nicotiana attenuata*)	Attracts predatory insects and may suppress microbial pathogens.	(Kessler & Baldwin, 2001)
	Eugenol	Basil (*Ocimum basilicum*)	Potent antimicrobial and insect-repellent compound.	(Pichersky & Gershenzon, 2002)
	Linalool	Rice (*Oryza sativa*)	Key defensive volatile that repels brown planthoppers and attracts parasitoids.	(Zhou & Jander, 2021)
	Salicylaldehyde	Willow (*Salix* spp.)	Defense-associated aromatic compound involved in anti-herbivore signalling.	(Bruce *et al*., 2005)
	(Z)-3-hexenyl butyrate	Wild Tobacco (*Nicotiana attenuata*)	Functions as a direct repellent to ovipositing moths and acts in tritrophic signalling.	(Kessler & Baldwin, 2001)
Nitrogen-Containing VOCs	Benzoxazinoids (volatile derivatives)	Maize (*Zea mays*)	Defensive metabolites toxic to herbivores and involved in belowground signalling.	(Erb *et al*., 2015)
	Methyl anthranilate	Citrus (*Citrus* spp.)	Repellent to insect pests and antimicrobial against select pathogens.	(Pichersky & Gershenzon, 2002)
	Phenylacetonitrile	Cabbage (*Brassica oleracea*)	Attracts parasitoids while simultaneously altering herbivore foraging behaviour.	(Bruce & Pickett, 2011)
Sulfur-Containing VOCs	Allyl isothiocyanate	Mustard (*Brassica juncea*)	Strong fumigant-like defense compound repelling insects and inhibiting fungi/bacteria.	(Hopkins *et al*., 2009)
	Carbon disulfide	*Brassica* roots	Acts in localized soil defense and influences belowground herbivore interactions.	(Holopainen & Blande, 2013)
Oxylipin-Related VOCs	Jasmonic acid derivatives	Tomato (*Solanum lycopersicum*)	Trigger systemic acquired resistance and induce anti-herbivore proteins.	(Wasternack & Hause, 2013)
	Traumatic acid derivatives	Bean (*Phaseolus lunatus*)	Wound-induced signalling compounds involved in immediate defense activation.	(Arimura *et al*., 2009)
Other Bioactive VOCs	Acetaldehyde	Poplar (*Populus* spp.)	Released during stress; contributes to localized signalling and antimicrobial defense.	(Loreto & Schnitzler, 2010)
	Ethyl acetate	Strawberry (*Fragaria* × *ananassa*)	Influences insect orientation and exhibits generalized antimicrobial effects.	(Dudareva *et al*., 2006)
	2-phenylethanol	Rose (*Rosa* spp.)	Attracts beneficial insects while repelling certain specialized herbivores.	(Pichersky & Gershenzon, 2002)
	Nonanal	Rice (*Oryza sativa*)	Attracts parasitoids and functions heavily in herbivore-induced signalling cascades.	(Bruce *et al*., 2005)

	Decanal	Citrus (*Citrus* spp.)	Possesses antimicrobial activity and modulates insect host-location behaviour.	(Dudareva *et al*., 2006)

In addition to terpenoids and GLVs, plants release aromatic compounds derived from phenylpropanoid metabolism. These metabolites originate from phenylalanine via the shikimate pathway and include volatile benzenoids such as methyl salicylate that participate in systemic acquired resistance and long-distance signalling (Dudareva *et al*., 2013). Amino-acid-derived volatiles further increase the complexity of HIPV mixtures. For example, indole, produced from tryptophan metabolism, has been identified as an important component of the defensive volatile bouquet in crops such as maize, where it enhances the attraction of parasitoid wasps when combined with other volatile compounds (Frey *et al*., 2000).

The simultaneous activation of these metabolic pathways generates complex volatile blends whose composition varies depending on plant species, herbivore identity, and environmental conditions. The major classes of HIPVs and the volatile blends that belongs to respective classes reported to different crops are compiled and given in table no 1.

Signal Perception and Hormonal Regulation

For HIPV emission to occur, plants must first detect the presence of herbivores and distinguish this form of damage from mechanical injury. This discrimination is achieved through the perception of herbivore-associated molecular patterns (HAMPs), which are bioactive compounds present in insect saliva, regurgitant, oviposition fluids, or frass. When herbivores feed on plant tissues, these molecules interact with receptors in plant cells, initiating signalling cascades that activate defence pathways.

One of the most widely studied elicitors is volicitin, a fatty acid-amino acid conjugate found in the oral secretions of caterpillars. In maize, this compound strongly stimulates the production of terpenoid volatiles following feeding by beet armyworm larvae (Alborn *et al*., 1997). Such elicitors enable plants to mount highly specific responses that reflect the identity of the attacking herbivore.

Early stages of signal perception are characterized by rapid cellular responses, including calcium ion influx and the generation of reactive oxygen species (Maffei *et al*., 2007). These events subsequently activate phytohormonal signalling networks that regulate downstream defence responses. Among these hormonal regulators, jasmonic acid plays a dominant role in coordinating plant responses to chewing herbivores by inducing the expression of genes involved in volatile biosynthesis and defensive metabolism (Thaler *et al*., 2012).

While jasmonate signalling dominates the response to chewing herbivores, it does not operate in isolation. The salicylic acid (SA) pathway typically elicited by biotrophic pathogens and piercing-sucking insects exerts strong antagonistic crosstalk upon JA-dependent defences. Mediated by transcriptional regulators such as WRKY70, this SA-JA antagonism allows the plant to fine-tune its defensive phenotype, prioritizing responses based on the most immediate threat. However, this regulatory node also represents an ecological vulnerability, as certain herbivores and opportunistic microbes can exploit this crosstalk, artificially inducing SA pathways to suppress the JA-mediated synthesis of defensive volatiles (Fig 1; Pieterse *et al*., 2012; Thaler *et al*., 2012). Concurrently, ethylene (ET) and abscisic acid (ABA) function as critical modulators, integrating abiotic stress signals to optimize the allocation of metabolic resources toward HIPV emission (Brosset & Blande, 2022).

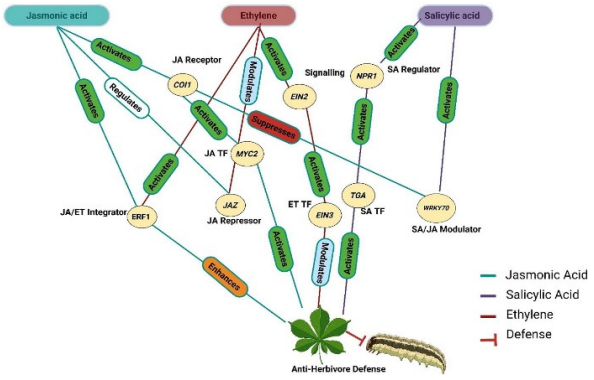

Fig 1: Phytohormone signalling network mediating anti-herbivore defence. The jasmonic acid (JA) receptor COI1 degrades JAZ repressors, releasing MYC2 and ERF1 transcription factors. Ethylene (ET) activates JA/ET integration via ERF1 while suppressing MYC2. The salicylic acid (SA) pathway antagonises JA-dependent defences through WRKY70, enabling herbivore guild-specific immune fine-tuning (Vasantha-sreenivasan *et al*. 2025).

HIPV emission may occur through two principal mechanisms. In many cases, volatile compounds are synthesized de novo following transcriptional activation of biosynthetic enzymes, resulting in a relatively delayed but highly specific response. Alternatively, some plants store volatile precursors in inactive forms such as glycosides. When cellular compartments are disrupted during herbivore feeding, enzymatic cleavage rapidly releases active volatile

molecules, producing an immediate chemical signal (Maffei, 2010).

Environmental and Biological Modulators of HIPV Expression

Although HIPV production is genetically encoded, its expression is strongly influenced by both intrinsic plant characteristics and external environmental factors. Genetic variation among plant species and cultivars represents one of the most important determinants of volatile emission patterns. Comparative studies have revealed that wild plant relatives frequently exhibit more diverse and intense HIPV emissions than domesticated crop varieties. Selective breeding for yield and agronomic traits may inadvertently reduce the production of secondary metabolites involved in indirect defence (Chen *et al*., 2015).

Plant developmental stage also influences the intensity of volatile responses. Young tissues and reproductive structures often produce stronger HIPV signals because their protection is essential for plant fitness and reproductive success.

Environmental stress conditions further modify volatile biosynthesis. Abiotic factors such as drought, salinity, ultraviolet radiation, and temperature extremes can alter phytohormonal balance within plant tissues, thereby influencing both the quantity and composition of emitted volatiles. For example, specific green leaf volatiles such as (Z)-3-hexenyl butyrate have been associated with physiological responses related to stomatal regulation and water stress adaptation (Payá *et al*., 2024). Temperature fluctuations may also influence the atmospheric stability of volatile signals, with high temperatures increasing volatilization but potentially degrading reactive terpenoids that function as olfactory cues for natural enemies (Holopainen and Gershenzon, 2010).

Another emerging dimension of HIPV regulation involves interactions with soil microbial communities. Beneficial microorganisms, including plant growth-promoting rhizobacteria and arbuscular mycorrhizal fungi, can prime plant defence responses, enabling faster and more intense HIPV emission following herbivore attack. These findings highlight the importance of belowground ecological interactions in shaping aboveground chemical signalling.

The Role of Common Mycorrhizal Networks (CMNs) in Signal Transduction

The conceptual framework of plant communication has expanded beyond intra-organismic signalling to encompass complex inter-plant networks mediated by both aboveground and belowground pathways. While the role of phytohormones in coordinating systemic defense responses within individual plants is well established, increasing attention has been directed toward the contribution of rhizosphere-associated symbioses in facilitating information exchange between neighbouring plants. In particular, common mycorrhizal networks (CMNs), established by arbuscular mycorrhizal fungi linking the root systems of adjacent hosts, have been proposed as subterranean channels through which defense-related signals may be transmitted (Babikova *et al*., 2013). Within this framework, herbivore-induced cues generated in an attacked plant can be conveyed via fungal hyphae to connected neighbours, potentially enabling a more rapid and targeted transmission of information than diffusion-based airborne signalling (Fig 2; Song *et al*., 2010).

Functionally, such belowground connectivity may enable receiver plants to enter a primed defensive state prior to direct herbivore exposure. This includes the upregulation of defense-associated gene expression and the anticipatory activation of metabolic pathways responsible for volatile emission (Song *et al*., 2014). From an ecological perspective, this form of symbiotically mediated signalling represents a significant extension of plant defense strategies, integrating microbial partners into the regulation of plant–plant communication and potentially increasing the spatial scale and efficiency of induced resistance. The implications for agroecosystem management are considerable, particularly in the context of sustainable crop protection, where leveraging naturally occurring biological networks could reduce dependence on external inputs and enhance system-level resilience.

However, despite the conceptual appeal of CMN-mediated signalling, its ecological relevance under field conditions remains a subject of ongoing debate. Much of the supporting evidence originates from controlled experimental systems characterized by simplified biotic interactions and reduced environmental variability. In contrast, natural soils are highly heterogeneous, containing diverse microbial communities, complex chemical gradients, and multiple competing signalling pathways that may interfere with or obscure CMN-based communication. Recent critical assessments have questioned whether the strength and specificity of signal transmission observed in laboratory microcosms can be maintained under such conditions, highlighting the potential for signal dilution, degradation, or misinterpretation within complex soil matrices (Karst *et al*., 2023).

This discrepancy underscores a broader challenge in translating mechanistic discoveries into agronomic applications. To determine the functional significance of CMNs in crop systems, future research must prioritize field-based investigations that account for soil biodiversity, environmental variability, and crop management practices. Such studies should aim to quantify the reliability, speed, and ecological consequences of belowground signalling relative to established aboveground pathways such as HIPVs. Ultimately, clarifying the role of CMNs in plant communication will be essential for assessing their potential contribution to climate-resilient and ecologically grounded pest management strategies.

Spatiotemporal Dynamics of Herbivore-Induced Plant Volatile Emissions

The ecological functionality of herbivore-induced plant volatiles (HIPVs) extends beyond their biochemical synthesis; their effectiveness largely depends on how these signals are deployed across space and time within complex agro-ecosystems. Volatile release is not a static phenomenon but rather a tightly coordinated process shaped by circadian regulation, herbivore activity, plant tissue specialization, and environmental conditions. Understanding these spatial and temporal patterns is critical because the ecological success of HIPV-mediated signalling particularly in attracting natural enemies relies on precise synchronization between volatile emission and the behavioural ecology of interacting organisms.

Temporal Regulation of Volatile Signalling

Plants regulate HIPV production in a temporally structured manner that often mirrors daily biological rhythms within ecological communities. Numerous plant species exhibit pronounced diurnal fluctuations in volatile emission (Arimura *et al*., 2008), suggesting that the timing of signal release has evolved to coincide with the peak activity periods of beneficial arthropods. For example, many parasitoids and predatory insects rely on visual orientation during daylight hours; consequently, volatile signals that peak during the day enhance the probability of successful detection and host location.

The temporal sequence of HIPV emission is also influenced by the progression of herbivore attack. Immediately after tissue disruption, plants rapidly release green leaf volatiles (GLVs) derived from membrane lipids, generating an early chemical alarm that spreads quickly through the surrounding environment. These compounds typically function as short-lived warning signals. As herbivory persists, plants activate more complex metabolic pathways responsible for synthesizing terpenoids and aromatic volatiles that persist longer and disperse over greater distances, thereby reinforcing defensive signalling across the plant canopy (Pinto-Zevallos *et al*., 2013). This phased emission pattern suggests that HIPV signalling represents a hierarchical defence system in which rapid preliminary cues are followed by metabolically costly but ecologically robust signals.

Spatial Compartmentalization: Aboveground and Belowground Volatile Networks

While research on HIPVs has historically focused on aerial emissions, plants also communicate chemically belowground. The root system represents a dynamic interface where plants interact with herbivores, soil microbes, and beneficial organisms. Consequently, volatile signalling in the rhizosphere forms an important but often underexplored dimension of plant defence ecology.

Aboveground HIPVs primarily guide flying predators and parasitoids through the aerial environment, helping them locate herbivore-infested plants within complex vegetation structures. In contrast, roots can emit volatile compounds directly into the soil matrix, where they diffuse through pore spaces and create chemical gradients detectable by subterranean organisms. In response to root herbivory, maize synthesizes the sesquiterpene (E)-β-caryophyllene, which spreads through the soil and attracts entomopathogenic nematodes capable of infecting the rootworm larvae (Rasmann *et al*., 2005; Degenhardt *et al*., 2009). This interaction illustrates how plants can indirectly mobilize biological control agents even within belowground environments, effectively extending defensive signalling into multiple ecological compartments.

Environmental Fate and Transformation of Volatile Signals

Once emitted, HIPVs enter a dynamic atmospheric environment where their ecological function can be influenced by physical transport and chemical transformation. Wind currents, turbulence, and thermal gradients determine the dispersion pattern of volatile plumes, influencing how far and how accurately natural enemies can trace these signals to their source.

In structurally complex environments, such as the dense, multilayered canopies of tropical cocoa agroforests, these physical factors create highly heterogeneous microclimates. The reduced wind velocity and high humidity within these dense canopies restrict broad atmospheric diffusion, meaning that

volatile signals often remain highly localized. Consequently, managing pests in such systems particularly concealed borers requires an understanding of highly precise, localized chemical signalling rather than reliance on the broad, field-wide attractant plumes that are typically effective in monocultural row crops.

However, the atmospheric stability of many HIPV compounds is limited. Terpenoids and other reactive volatile organic compounds readily interact with atmospheric oxidants such as ozone and hydroxyl radicals. These reactions can rapidly alter the chemical composition of volatile plumes, thereby reduce their detectability or altering their behavioural effects on insects (Pinto-Zevallos *et al*., 2013). Anthropogenic pollution further exacerbates this problem by accelerating oxidative degradation. Such transformations may disrupt the reliability of volatile cues that predators and parasitoids depend upon, raising important questions regarding the resilience of HIPV-mediated ecological interactions in increasingly polluted agricultural landscapes.

Impacts of Climate Change and Atmospheric Pollution on HIPV Efficacy

The reliability of HIPVs as ecological info-chemicals is increasingly threatened by global climate change and anthropogenic atmospheric pollution. Elevated atmospheric carbon dioxide (CO_2) and rising global temperatures alter plant carbon-to-nutrient ratios, which can shift metabolic allocation away from secondary defensive metabolites, consequently altering the composition and intensity of HIPV blends (Jamieson *et al*., 2012).

More critically, reactive atmospheric pollutants, particularly tropospheric ozone (O_3) and nitrogen oxides (NO_x), rapidly degrade specific volatile compounds especially reactive sesquiterpenes as they diffuse through the air (Blande *et al*., 2014). This oxidative degradation effectively shortens the "active radius" of the volatile plume, making it significantly harder for parasitoids and predators to locate herbivore-infested host plants (Pinto *et al*., 2007). Understanding how climate-altered environments quench or distort chemical signals is currently one of the most pressing priorities in chemical ecology, as it directly impacts the future viability of biological control in agroecosystems (Holopainen and Blande, 2013).

Methodological Frameworks for Investigating HIPVs

Advancing knowledge of HIPV biology requires interdisciplinary approaches that integrate plant physiology, analytical chemistry, and insect behavioural ecology.

Behavioural and Olfactory Bioassays

Understanding the ecological relevance of HIPVs first requires determining how insects perceive and respond to these volatile cues. Laboratory bioassays such as Y-tube olfactometers and multi-arm olfactometer systems are commonly used to quantify insect orientation toward specific odour sources (Fig 4; Tholl *et al*., 2006). These assays enable researchers to assess attraction, avoidance, or neutral behavioural responses to individual compounds or complex volatile blends.

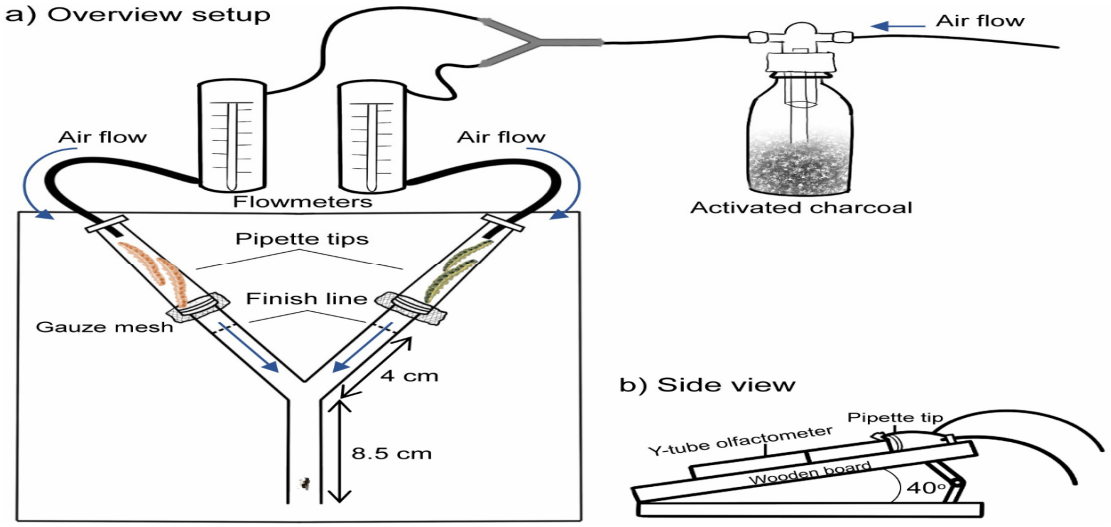

Fig. 2 : Design and components of a dual-choice Y-tube olfactometer. **(a)** The top-down overview displays the air purification system (activated charcoal), airflow regulation (flowmeters), and the odour source chambers (pipette tips containing distinct biological samples) connected to the Y-tube via gauze mesh. **(b)** The side view demonstrates the spatial orientation of the behavioural assay, highlighting the 40° incline of the wooden support board designed to facilitate directional movement of the test insect from the 8.5 cm stem toward the 4 cm choice arms (Bourne *et al*., 2023).

To complement laboratory experiments, wind-tunnel tests and semi-field cage experiments are often conducted to evaluate insect host-location behaviour under conditions that more closely resemble natural agricultural environments. Such experimental frameworks provide valuable insights into how volatile cues guide insect foraging behaviour within complex odour landscapes.

Chemical Profiling and Omics Approaches

Identification of HIPV compounds relies primarily on advanced analytical chemistry techniques. Gas chromatography coupled with mass spectrometry (GC-MS) remains the standard method for characterizing volatile profiles emitted by plants (Tholl *et al*., 2006). Volatile compounds are typically collected using dynamic headspace sampling techniques such as solid-phase microextraction (SPME), which allow sensitive detection of trace compounds.

In recent years, systems biology approaches have significantly enhanced understanding of HIPV biosynthesis. Transcriptomic and metabolomic analyses enable researchers to trace the sequence of molecular events linking herbivore perception to the activation of volatile biosynthetic pathways (Arimura *et al*., 2005). These approaches have revealed intricate networks of gene regulation, enzyme activity, and metabolite accumulation that collectively determine the composition of volatile emissions.

Real-Time Volatile Monitoring and Electrophysiological Techniques

Historically, the collection of HIPVs required time-intensive headspace trapping on porous adsorbents followed by thermal desorption, which provided only a "snapshot" of volatile emissions (Tholl *et al*., 2006). Today, advances in mass spectrometry, specifically Proton-Transfer-Reaction Time-of-Flight Mass Spectrometry (PTR-TOF-MS), allow researchers to monitor the emission of specific volatile compounds in real-time (Brilli *et al*., 2011). This technique provides high-resolution temporal data, revealing the exact kinetics of volatile release immediately following herbivory.

Furthermore, to confirm the ecological relevance of identified compounds, chemical profiling is now routinely coupled with electrophysiology. Gas Chromatography-Electroantennographic Detection (GC-EAD) and single-sensillum recordings allow researchers to measure the neurological action potentials of insect antennae as they are exposed to fractionated HIPV blends (D'Alessandro and Turlings, 2006). This ensures that researchers focus only on the specific volatile constituents that actually elicit sensory responses in target herbivores or natural enemies (Bruce *et al*., 2005).

Statistical and Computational Analysis of Complex Volatile Blends

The vast amounts of high-dimensional data generated by GC-MS, PTR-TOF-MS, and transcriptomic profiling necessitate robust statistical and computational frameworks to decode complex chemical signals. Since herbivore-induced volatile blends often consist of dozens to hundreds of individual compounds, identifying the specific ecologically active constituents the defensive "signal" amidst the background metabolic "noise" remains a significant analytical challenge (Ranganathan and Borges, 2010).

To address this, multivariate statistical techniques, particularly Principal Component Analysis (PCA) and Partial Least Squares-Discriminant Analysis (PLS-DA), have become essential tools in modern chemical ecology. These dimensionality-reduction approaches allow researchers to visualize variations in complex volatile profiles and statistically differentiate the emissions of healthy, mechanically damaged, and herbivore-infested plants (Gromski *et al*., 2015). Furthermore, emerging computational methods utilizing machine learning algorithms, such as Random Forests, and open-source metabolomic platforms are increasingly being applied to predict insect behavioural responses based on specific volatile signatures (Chong *et al*., 2018). These advanced statistical analyses are crucial for filtering out non-essential metabolites and isolating the key semiochemical biomarkers required to develop synthetic blends for targeted pest management.

Ecological Roles of HIPVs Across Trophic Levels

HIPVs function as info-chemicals that mediate interactions among plants, herbivores, and natural enemies within ecological communities. Their ecological significance extends far beyond individual plant defence influencing population dynamics and trophic relationships across entire agroecosystems (Mutyambai *et al*., 2022).

Direct Impacts on Herbivorous Insects

Plant defence against herbivory is increasingly understood as a multilayered system in which volatile and non-volatile metabolites operate in a coordinated yet functionally distinct manner. While classical secondary metabolites such as alkaloids and glucosinolates primarily exert toxicity through direct

physiological disruption, herbivore-induced plant volatiles (HIPVs) contribute a more dynamic dimension of defence by modulating herbivore behaviour and, under certain conditions, exerting sublethal physiological effects. Rather than functioning solely as airborne signals, some HIPVs or their immediate precursors can accumulate in damaged tissues and participate in oxidative processes that impose metabolic stress on feeding insects, ultimately constraining growth, development, and reproductive potential (Reitz *et al*., 2020). This dual functionality challenges the traditional dichotomy between direct and indirect plant defences, suggesting a more integrated defensive continuum mediated by chemical plasticity.

A particularly significant role of HIPVs lies in their capacity to alter herbivore decision-making processes, especially in relation to host selection and oviposition. Adult female insects frequently rely on volatile cues to assess host plant suitability, balancing nutritional quality against potential risks to offspring. Plants emitting strong, herbivore-induced volatile blends may signal prior infestation, increased competition, or elevated likelihood of natural enemy presence, thereby deterring oviposition (De Moraes *et al*., 1998). This behaviourally mediated avoidance effectively reduces future herbivore load, representing a pre-emptive defensive strategy that operates before direct damage occurs. Such mechanisms are especially relevant in agroecosystems, where manipulating volatile profiles could influence pest colonization patterns and reduce initial infestation pressure.

Beyond these immediate effects, the interaction between plant chemical defences and herbivore physiology introduces important trade-offs that further enhance plant protection. The metabolic burden associated with detoxifying plant-derived compounds can divert resources from other vital functions in herbivores, including immune defence. As a consequence, individuals feeding on chemically defended plants may exhibit reduced resistance to pathogens and entomopathogenic organisms, increasing their susceptibility to infection (Cory and Hoover, 2006). This interaction represents a form of indirect defence amplification, wherein plant chemistry not only affects herbivores directly but also enhances the efficacy of natural biological control agents.

Collectively, these processes highlight the multifaceted role of HIPVs within the broader context of plant defence strategies, extending beyond their established function in Tri trophic signalling. By simultaneously influencing herbivore physiology, behaviour, and susceptibility to natural enemies, HIPVs contribute to a highly integrated defence network that is particularly relevant for sustainable pest management. However, the extent to which these mechanisms operate consistently under field conditions, especially in diverse and climate-variable agroecosystems, remains insufficiently resolved. Future research should therefore focus on quantifying these interactions across ecological gradients and exploring how they can be harnessed to develop resilient, low-input crop protection systems.

Indirect defence through natural enemy recruitment

Perhaps the most widely recognized ecological function of HIPVs is the attraction of predators and parasitoids that attack herbivorous insects. This tri trophic interaction was first demonstrated when herbivore-infested plants were shown to emit volatile compounds that attracted predatory mites (Dicke and Sabelis, 1988).

Since this discovery, numerous studies have documented similar interactions across diverse plant insect systems. Parasitoid wasps, predatory beetles, and even entomopathogenic nematodes use HIPV signals to locate herbivore hosts. These interactions create a mutualistic relationship in which plants benefit from reduced herbivore damage while natural enemies gain access to prey resources (Dicke and Baldwin, 2010).

Importantly, the effectiveness of this signalling system often depends on complex mixtures of volatiles rather than individual compounds. Specialized parasitoids can discriminate among subtle variations in volatile blends to identify plants attacked by specific herbivore species. HIPVs also function as signals that facilitate communication between plants. When neighbouring plants detect volatile emissions from damaged individuals, they may undergo physiological priming that prepares their defence systems for potential attack (Engelberth *et al*., 2004).

Primed plants exhibit faster and stronger defensive responses upon subsequent herbivore attack. Recent studies suggest that such priming may involve epigenetic modifications that alter chromatin structure and enable rapid activation of defence genes such as *PR1* (Pérez-Pérez *et al*., 2024). Field studies indicate that plants exposed to HIPV signals often experience reduced herbivore damage due to enhanced defensive capacity or early recruitment of natural enemies (Heil and Kost, 2006).

Community-level chemical landscapes

When multiple plants in an ecosystem emit HIPVs simultaneously, the resulting chemical environment

become more complex than any single plant emission study. A natural enemy under real pest pressure must be able to locate its prey within the overlapping, dynamic and sometimes contradictory volatile signals. (Piesik *et al*., 2022). How insects manage this volatile noise remain poorly understood and studies addressing this concern are still rare.

Moreover, the aboveground volatile signalling cannot be fully understood in isolation from belowground ecological processes. Plant–soil feedback mechanisms, mediated through the rhizosphere microbial communities, exert a significant influence on plant defensive phenotypes and associated volatile outputs. Agricultural practices such as intercropping and the incorporation of companion species can restructure soil microbial assemblages, thereby modulating phytohormonal signalling pathways and altering the qualitative and quantitative composition of HIPVs. These changes can cascade upward, influencing herbivore performance and reshaping arthropod community structure across cropping cycles (Lang *et al*., 2024). This integration of belowground and aboveground processes highlights the need to consider HIPV dynamics within a holistic, system-level framework that captures feedback loops between soil biology, plant metabolism, and insect ecology.

Ultimately, the ecological realization of HIPV-mediated interactions is governed by the physical environment through which these signals disperse. Atmospheric turbulence, temperature gradients, humidity, and radiation regimes collectively determine the dispersion, dilution, and chemical stability of volatile compounds. These factors introduce significant spatiotemporal variability in signal transmission, affecting both the range and fidelity of information conveyed to target organisms. In this regard, a critical research frontier lies in quantifying the aerodynamics and persistence of HIPV plumes under realistic field conditions, particularly in structurally complex agroecosystems where canopy architecture and microclimatic stratification further complicate signal movement. Advancing this understanding will be essential for integrating HIPVs into predictive models of pest dynamics and for designing robust, climate-resilient pest management strategies that operate effectively at ecosystem scales.

Exploiting HIPV signalling for sustainable pest management

The growing recognition of HIPVs as mediators of multitrophic interactions has stimulated considerable interest in their potential use within sustainable crop protection strategies. Conventional reliance on broad-spectrum insecticides has generated ecological and economic challenges, including resistance development, non-target toxicity, and disruption of beneficial arthropod communities. In this context, leveraging plant-derived chemical signals offers a biologically grounded alternative capable of strengthening ecological pest regulation.

Chemical elicitors and induced plant defences

One approach to utilizing HIPV signalling involves artificially stimulating plants to emit defensive volatiles before pest populations reach damaging levels. Application of signalling molecules such as jasmonic acid or methyl jasmonate can activate the plant's defensive pathways (Thaler, 1999), triggering widespread HIPV production across crop fields. By inducing these responses prophylactically, crops may become more attractive to predators and parasitoids early in the season, thereby reinforcing natural biological control mechanisms.

Semiochemical technologies and attract-and-kill strategies

The translation of semiochemical ecology into operational pest management has progressively shifted from simple attractant-based interventions toward integrative strategies that actively restructure trophic interactions within agroecosystems. Central to this transition is the capacity to synthetically replicate herbivore-induced plant volatiles (HIPVs), thereby enabling precise manipulation of insect behaviour across multiple functional guilds (Pickett & Khan, 2016). Early applications primarily focused on deploying individual compounds, such as methyl salicylate, to enhance the recruitment of predatory arthropods into crop systems (Khan *et al*., 1997). However, contemporary approaches have moved beyond single-compound lures toward the formulation of complex volatile blends that more accurately emulate natural emission profiles, thereby improving ecological realism and behavioural efficacy. These advances have underpinned the development of attract-and-kill systems, wherein pest populations are behaviourally aggregated into localized zones for targeted suppression, significantly enhancing the spatial efficiency of control measures while reducing reliance on broad-spectrum insecticides (Weber *et al*., 2023).

Despite these advances, a critical limitation of purely attraction-based systems lies in their inability to ensure the persistence of recruited natural enemies under conditions of low prey availability. This constraint has catalysed the emergence of attract-and-reward strategies, which represent a conceptual

convergence between chemical signalling and habitat manipulation. In this framework, synthetic HIPVs function not merely as transient cues but as components of a broader ecological infrastructure, wherein companion plantings provide essential nutritional resources such as nectar and pollen. By coupling olfactory attraction with resource provisioning, these systems enhance the retention, longevity, and reproductive performance of parasitoids and predators, thereby stabilizing biological control services even in the absence of immediate pest outbreaks (Fig 5; Razo-Belman and Ozuna, 2023). Such integration reflects a shift toward sustaining functional enemy populations rather than episodically recruiting them, aligning with principles of conservation biological control and agroecological intensification.

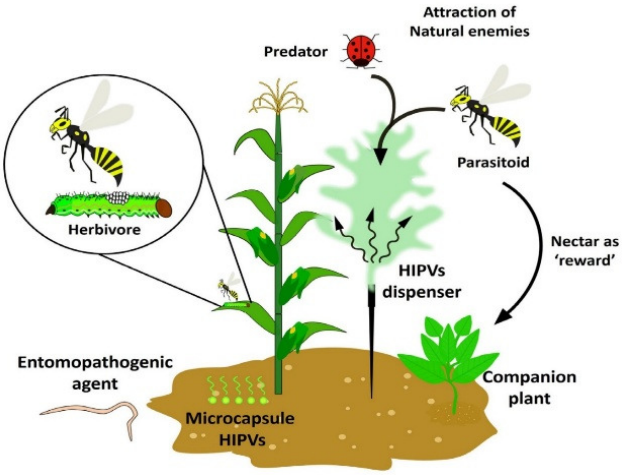

Figure 3. The "attract and reward" method is a pest control strategy that enhances the efficiency and survival periods of natural enemies (parasitoids and predators), which allows the establishment of stable populations **(Razo-Belman and Ozuna, 2023)**.

Recent innovations further extend this paradigm into the belowground domain, where microencapsulated HIPVs have been utilized to modulate soil biota, particularly entomopathogenic nematodes targeting cryptic pest life stages. This vertical integration of semiochemical signalling across above- and belowground compartments exemplify a systems-level approach to pest regulation, bridging chemical ecology with soil ecology and microbial-mediated control processes (Razo-Belman and Ozuna, 2023). Collectively, these developments underscore a broader transformation in crop protection strategies, wherein the objective is not solely pest suppression but the deliberate engineering of resilient agroecosystems capable of self-regulation.

Nevertheless, several knowledge gaps remain. The context dependency of HIPV responses under variable climatic conditions, the potential for non-target effects, and the scalability of such systems in diverse cropping environments require further investigation. Additionally, optimizing the temporal dynamics and release kinetics of synthetic volatiles to synchronize with pest phenology represents a critical research frontier. Addressing these challenges will be essential for advancing semiochemical technologies as cornerstone components of sustainable, climate-resilient pest management frameworks**.**

Plant Improvement and Genetic Manipulation

A more systemic strategy for enhancing HIPV-mediated pest suppression involves improving the volatile signalling capacity of crop plants themselves. Domestication and modern breeding have frequently prioritized yield and agronomic performance at the expense of defensive traits, including volatile production. As a result, many commercial cultivars exhibit weaker indirect defense responses compared with their wild relatives.

Breeding programs can exploit the genetic diversity present in wild germplasm to restore or enhance volatile emission profiles associated with natural enemy recruitment (Rogge and Meyhöfer, 2021). In parallel, biotechnology offers opportunities to directly manipulate biosynthetic pathways responsible for volatile production. A notable example is the reintroduction of the (E)-β-caryophyllene synthase gene into North American maize lines that had lost the ability to produce this compound. Restoring this pathway successfully re-established the plant's capacity to attract entomopathogenic nematodes that attack rootworm larvae (Degenhardt *et al*., 2009). Such interventions demonstrate how targeted genetic modifications can revive ancestral ecological defences in modern crops.

Ecological Engineering and Intercropping Systems

Among the most successful field applications of HIPV-based ecological principles is the push pull cropping system developed in sub-Saharan Africa for the management of maize stem borers. In this system, maize is intercropped with repellent plants such as *Desmodium*, which emit volatiles that deter ovipositing moths, thereby "pushing" pests away from the crop. Simultaneously, trap crops such as Napier grass are planted around field margins to attract the pests and "pull" them away from the maize crop (Cook *et al*., 2007).

This strategy not only suppresses pest populations but also enhances biodiversity and soil fertility. Subsequent innovations have expanded push -pull technology to address emerging threats such as the invasive fall armyworm (*Spodoptera frugiperda*) and have adapted similar volatile-mediated cropping systems for vegetables and cotton (Cheruiyot *et al*., 2021; Chi *et al*., 2021; Chidawanyika *et al*., 2023; Mutua *et al*., 2024). These developments illustrate how ecological insights from chemical signalling can be translated into scalable agricultural practices.

Integration with Integrated Pest Management

The success of conventional pest management strategies in perennial tropical agroecosystems is limited. In such agroecosystems (eg. Shaded cocoa agroecosystem), the conventional management strategies face structural problems like the dense multilayered canopy that traps the sprays, humic microclimate which accelerates insecticide degradation and the nature of endophagous pests that extends beyond the reach of sprays. These makes the management strategies narrow and limit the chemical access. These limitations have catalysed a paradigm shift toward ecologically sound pest management strategies that prioritize system-level resilience over input intensification.

Within this evolving framework, herbivore-induced plant volatiles (HIPVs) have emerged as pivotal mediators of multitrophic interactions, offering a mechanistically sophisticated alternative to conventional control tactics. Rather than acting as direct toxicants, HIPVs function as dynamic information carriers that influence insect behaviour across trophic hierarchies, thereby restructuring pest–natural enemy networks in situ. Their compatibility with Integrated Pest Management (IPM) strategies lies in their transient nature, specificity, and minimal non-target effects, aligning with the broader objective of maintaining ecological integrity while ensuring crop productivity. Importantly, the deployment of HIPV-based strategies necessitates their integration into holistic management systems that exploit endogenous plant signalling pathways, rather than treating them as isolated technological solutions.

The interaction between plants and endophagous pests exemplifies the intricate coupling between herbivore behaviour and host plant physiology in tropical agroforestry contexts (Srikumar *et al*., 2018). A defining feature of this system is the insect's oviposition preference for vascularized tissues, enabling larvae to establish within concealed niches shortly after hatching, effectively bypassing external control measures. This rapid internalization is accompanied by a cascade of plant defence responses initiated by herbivore-associated molecular patterns, which activate jasmonate-regulated signalling pathways during early herbivory. As infestation progresses and tissue damage intensifies, often involving secondary microbial associations salicylate-mediated responses become increasingly prominent, resulting in complex phytohormonal crosstalk. These temporally and spatially differentiated signalling events generate distinct HIPV emission profiles that reflect the stage of infestation, tissue specificity, and physiological state of the host plant.

Such finely tuned volatile signatures represent an underutilized diagnostic dimension of plant defence with transformative implications for pest surveillance. Traditional monitoring methods, heavily reliant on visual inspection, are inherently inadequate for detecting early infestations of cryptic feeders, leading to delayed interventions and suboptimal control outcomes. In contrast, advances in analytical techniques, including dynamic headspace sampling coupled with high-resolution chromatographic and spectrometric platforms, now enable the real-time characterization of volatile emission dynamics associated with key biological events such as oviposition and initial larval penetration. This effectively reframes plant responses as quantifiable biochemical indicators, enabling the development of early-warning systems grounded in plant physiology.

The practical translation of these insights into field-applicable technologies represents a critical frontier in precision agriculture. Emerging innovations, such as portable electronic olfaction systems and cost-effective sensor arrays capable of detecting specific volatile classes, offer the potential to operationalize HIPV-based diagnostics at the farm level. These tools facilitate spatially explicit, real-time decision-making, allowing interventions to be synchronized with critical windows of pest vulnerability. Furthermore, identified semiochemicals can be strategically deployed in behavioural manipulation frameworks, including attract-and-kill systems targeting adult populations and kairomone-based enhancement of parasitoid foraging efficiency (Mutyambai *et al*., 2022; Weber *et al*., 2023).

Despite these advances, significant challenges remain in scaling HIPV-based approaches within complex agroecosystems. Environmental factors such as temperature fluctuations, humidity gradients, and airflow patterns can influence both the emission and dispersion of volatile compounds, potentially compromising signal reliability (Holopainen & Blande,

2013). Additionally, the chemically heterogeneous background of tropical canopies may interfere with signal detection by both natural enemies and sensor technologies (Ranganathan & Borges, 2010). Addressing these constraints will require interdisciplinary integration across chemical ecology, environmental physics, and sensor engineering, alongside rigorous field validation under diverse agroecological conditions. Ultimately, embedding HIPV-mediated strategies within IPM frameworks represents a transition toward anticipatory, knowledge-driven pest management systems that enhance ecological resilience, reduce chemical dependency, and contribute to the sustainability of tropical agricultural landscapes under changing climatic regimes (Reitz *et al*., 2020).

Emerging Challenges and Research Priorities

Notwithstanding substantial advances in elucidating the biochemical and ecological functions of herbivore-induced plant volatiles (HIPVs), their translation into reliable, field-deployable technologies remains constrained by a series of interrelated scientific and socio-economic challenges. A fundamental limitation arises from the context-dependent nature of volatile-mediated interactions. Individual compounds do not operate as invariant signals; rather, their ecological meaning is modulated by a matrix of factors including plant genotype, phenological stage, background odour complexity, and prevailing abiotic conditions. Consequently, the same volatile cue may elicit divergent behavioural responses across environments or target organisms, thereby complicating efforts to design broadly applicable semiochemical interventions (Dicke and Baldwin, 2010). This inherent plasticity underscores the need to reconceptualize HIPVs not as universal attractants or repellents, but as components of dynamic signalling networks embedded within specific ecological contexts.

Bridging the persistent gap between controlled experimentation and field-level performance represents an equally pressing research priority. While laboratory studies have been instrumental in identifying mechanistic pathways and behavioural responses, they often fail to capture the environmental heterogeneity characteristic of agricultural landscapes. Fluctuations in temperature, the presence of atmospheric oxidants, variability in soil microbial communities, and complex odour backgrounds can all influence both the emission and perception of HIPVs, thereby altering their functional outcomes (Hunter, 2001). Addressing this discrepancy will require coordinated, long-term field evaluations conducted across diverse agroecosystems, with particular emphasis on understanding how volatile-mediated interactions are reshaped under climate variability and landscape complexity (Mutyambai *et al*., 2022).

In parallel, technological constraints associated with the stabilization and delivery of synthetic volatiles continue to limit their practical applicability. Many HIPV compounds, particularly reactive terpenoids, exhibit rapid degradation under ultraviolet radiation and oxidative atmospheric conditions, reducing their effective lifespan in open-field environments. Advances in formulation science—including nano-encapsulation, controlled-release polymer matrices, and biodegradable dispensers (Bhagat *et al*., 2013; Oliveira *et al*., 2014) offer promising avenues for enhancing the temporal stability and spatial precision of volatile release (Weber *et al*., 2023). However, these innovations introduce additional layers of complexity, particularly in structurally heterogeneous systems such as tropical agroforestry. In cocoa-based landscapes, for instance, dense canopy architecture, elevated humidity, and reduced wind flow create highly variable microclimatic conditions that influence the dispersion, dilution, and persistence of volatile plumes. Despite the ecological importance of these factors, empirical data on HIPV aerodynamics under such conditions remain scarce, representing a critical knowledge gap for the optimization of semiochemical deployment strategies.

Beyond biophysical and technological considerations, cost is a real barrier. Expensive nano-encapsulated delivery systems may work in laboratories but may not be affordable to small holder farmers. This widens the gap between the technological innovations and their field adoption (Parsa *et al*., 2014). Therefore, research priorities must include low-cost and locally replicable alternatives. For example, the strategic use of companion plants capable of emitting behaviourally active volatiles can effectively modify pest and natural enemy dynamics. Similarly, the application of minimally processed botanical materials may offer low-cost means of inducing or mimicking HIPV emissions in situ.

Such approaches align with the principles underlying push–pull systems, which integrate semiochemical signalling with habitat management to achieve sustainable pest suppression (Khan *et al*., 2014). Nevertheless, their effectiveness is inherently context-specific, influenced by local environmental conditions, cropping practices, and socio-cultural factors. As such, scaling these interventions requires careful adaptation to regional agroecological conditions and active engagement with farming communities.

Future research must therefore pursue a dual trajectory that integrates mechanistic refinement with socio-economic feasibility. This includes advancing our understanding of HIPV biosynthesis, emission dynamics, and ecological function, while simultaneously developing cost-effective, user-friendly deployment strategies. Participatory research models, in which farmers contribute to the co-design and evaluation of interventions, will be essential for ensuring practical relevance and adoption. Ultimately, the long-term viability of HIPV-based pest management will depend not only on scientific innovation but also on the capacity to embed these technologies within equitable and resilient agricultural systems that support both productivity and biodiversity conservation.

Conclusions

Herbivore-induced plant volatiles represent one of the most sophisticated components of plant defence ecology, linking intracellular biochemical responses with community-level ecological interactions. Through highly regulated signalling pathways involving jasmonic acid, salicylic acid, and ethylene, plants can detect herbivore attack and respond by emitting complex volatile blends that influence the behaviour of organisms across multiple trophic levels.

These airborne signals perform diverse ecological functions, including direct deterrence of herbivores, recruitment of predators and parasitoids, and the priming of neighbouring plants for enhanced defence. Such capabilities highlight the potential of HIPV-mediated communication as a cornerstone of sustainable crop protection.

The successful application of these principles in agricultural systems particularly through breeding strategies, genetic engineering, and ecological engineering approaches such as push - pull cropping demonstrates the feasibility of harnessing plant chemical signals for practical pest management (Sobhy *et al*., 2022). Continued progress will depend on addressing key challenges related to environmental stability, context-dependent insect responses, and large-scale implementation across diverse farming systems.

By integrating advances from chemical ecology, molecular biology, and agro-ecosystem management, HIPV research offers a promising pathway toward resilient agricultural systems capable of reducing pesticide dependence while maintaining stable crop productivity.

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