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PLANT VOLATILE ORGANIC COMPOUNDS IN PLANT–PLANT AND PLANT–INSECT INTERACTIONS: ECOLOGICAL AND AGRICULTURAL SIGNIFICANCE

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ABSTRACT
Plant volatile organic compounds (VOCs) constitute a sophisticated chemical language that mediates critical ecological interactions between plants and their biotic environment. Up to one-third of assimilated carbon is released by plants in the form of VOCs, underscoring the substantial metabolic investment in these signaling molecules. This review synthesizes current knowledge on the ecological roles of plant VOCs in mediating plant–plant communication and plant–insect interactions, and evaluates their potential for sustainable agricultural applications. We examine the biosynthetic pathways, emission dynamics, and perception mechanisms of major VOC classes including terpenoids, phenylpropanoids/benzenoids, fatty acid derivatives, and amino acid derivatives. The review explores herbivore-induced plant volatiles (HIPVs) as signals that attract natural enemies, repel herbivores, and prime neighboring plants for enhanced defense. We also address recent advances in understanding volatile-mediated plant–plant interactions, including kin recognition, defense priming, and competitive signaling. The dual ecological functions of plant volatiles—simultaneously repelling insect herbivores while attracting their natural enemies are examined in detail. Finally, we discuss translational applications in integrated pest management, including push–pull strategies, synthetic biology approaches for engineering desirable VOC profiles, and the challenges of implementing VOC-based technologies in diverse agroecosystems.

KEYWORDS: Volatile Organic Compounds; Plant–Insect Interactions; Herbivore-Induced Plant Volatiles; Chemical Ecology; Sustainable Agriculture; Tritrophic Interactions.

1. INTRODUCTION

Plants are sessile organisms that have evolved an extraordinary repertoire of chemical defenses to cope with biotic and abiotic stressors. Among these, volatile organic compounds (VOCs) represent a diverse class of lipophilic, low-molecular-weight compounds with high vapor pressures that enable them to traverse atmospheric and soil environments [1,3]. The emission of VOCs constitutes a significant carbon cost for plants, with estimates suggesting that up to one-third of assimilated carbon can be released through this pathway [1]. This substantial metabolic investment implies that VOC emissions confer significant ecological advantages that have been preserved through evolutionary timescales. The ecological significance of plant VOCs extends across multiple trophic levels. These compounds serve as attractants for pollinators, repellents or toxins against herbivores, signals that recruit natural enemies of herbivores, and mediators of plant–plant communication [1,3,6]. In plant–plant interactions, VOCs can function as cues that alert neighboring plants to impending herbivore attack, allowing them to prime their own defense systems preemptively [6]. This volatile-mediated communication has been documented across numerous plant species and is now recognized as a fundamental component of plant chemical ecology.

The evolution of plant VOCs and insect olfactory systems has been deeply intertwined since the Angiosperm Terrestrial Revolution (100–50 million years ago), when the explosion of plant diversity stimulated diversification of insect lineages [5]. Insects have evolved sophisticated olfactory receptor systems to detect and discriminate among the complex VOC blends emitted by plants [5]. In moths, for example, receptors for benzenoids appear to be more ancient and conserved, whereas receptors for terpenes and aliphatic molecules show more recent diversification in response to plant evolution [5]. This co-evolutionary arms race has resulted in a remarkably nuanced chemical communication system. Figure 1 show Schematic representation of VOC-mediated interactions in a natural ecosystem. Arrows indicate the direction of volatile signal transmission. Panel A: Plant–plant

communication through airborne VOCs, including defense priming in neighboring plants. Panel B: Direct plant–herbivore interactions, showing herbivore-induced VOC emissions and herbivore repellence. Panel C: Tritrophic interactions, where HIPVs attract natural enemies (predators and parasitoids) of herbivores. Panel D: Plant–pollinator interactions mediated by floral VOCs.

From an agricultural perspective, understanding VOC-mediated interactions offers promising avenues for developing sustainable pest management strategies. The pressing demand for sustainable agriculture, coupled with advances in multi-omics technologies and precise gene editing tools, has accelerated research into the chemical conversation between plants and insects [1]. VOCs can be exploited to attract natural pest predators or deter herbivores, reducing the need for synthetic chemical pesticides [5]. However, despite decades of research, the translation of fundamental knowledge into practical agricultural applications remains limited [3]. This review aims to provide a comprehensive synthesis of the ecological roles of plant VOCs in plant–plant and plant–insect interactions, with particular emphasis on their significance for sustainable agriculture. We begin with an overview of VOC biosynthesis and diversity, followed by an examination of VOC-mediated plant–insect interactions, including herbivore defense, pollination, and tritrophic interactions. We then explore the mechanisms and ecological consequences of plant–plant communication through VOCs. Finally, we discuss current and emerging applications of VOC-based technologies in agricultural systems and identify key knowledge gaps and future research directions.

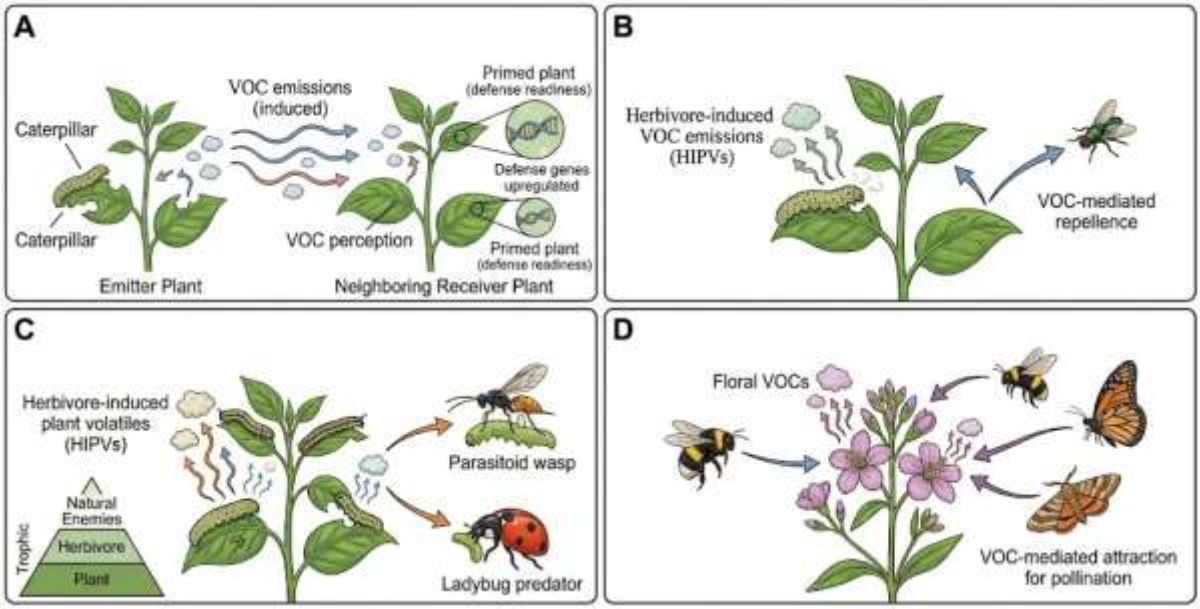

Figure 1. Schematic representation of VOC-mediated interactions in a natural ecosystem

2. Biosynthesis, Diversity, and Emission of Plant Volatile Organic Compounds

2.1 Major Biosynthetic Pathways

Plant VOCs are synthesized through four primary biosynthetic pathways: the terpenoid pathway, the phenylpropanoid/benzenoid pathway, the fatty acid derivative pathway, and the amino acid derivative pathway [3]. Each pathway generates distinct classes of volatile compounds with characteristic ecological functions.

Terpenoids constitute the largest and most chemically diverse class of plant VOCs. They are synthesized via the cytosolic mevalonic acid (MVA) pathway and the plastidial methylerythritol phosphate (MEP) pathway. Monoterpenes (C10) and sesquiterpenes (C15) are the most common volatile terpenoids, and they play critical roles in plant defense and pollinator attraction. The diversity of terpenoid structures arises from the activity of terpene synthases, which can produce multiple products from a single substrate.

Phenylpropanoids and benzenoids are derived from the amino acid phenylalanine through the shikimate pathway. These compounds, which include methyl salicylate, eugenol, and vanillin, are particularly important in floral scent production and plant defense signaling. Methyl salicylate, for instance, is a well-characterized systemic signal in plant defense responses.

Fatty acid derivatives are produced through the lipoxygenase pathway, yielding C6 aldehydes, alcohols, and esters commonly known as green leaf volatiles (GLVs). These compounds are rapidly emitted upon mechanical damage or herbivore attack and serve as early warning signals.

Amino acid derivatives include volatile compounds derived from branched-chain amino acids such as leucine, isoleucine, and valine, as well as sulfur-containing compounds from methionine. These compounds contribute to the characteristic odors of many flowers and fruits and play roles in both pollinator attraction and herbivore defense.

2.2 Constitutive versus Induced VOC Emissions

Plant VOC emissions can be broadly classified as constitutive (continuously produced) or induced (triggered by biotic or abiotic stimuli) [1,3]. Constitutive emissions are characteristic of reproductive tissues such as flowers and fruits, where they function in pollinator attraction and seed dispersal. Vegetative tissues typically emit VOCs at low constitutive levels but exhibit dramatic increases in emission rates upon herbivore attack or other stress conditions.

Herbivore-induced plant volatiles (HIPVs) are emitted in response to insect feeding and differ both quantitatively and qualitatively from constitutive emissions. The induction of HIPVs involves complex signaling cascades, including the jasmonic acid, salicylic acid, and ethylene pathways [7]. Plants can distinguish between mechanical damage and herbivore feeding through the recognition of herbivore-associated molecular patterns (HAMPs) present in insect oral secretions [1]. This specificity allows plants to mount appropriate defense responses tailored to the attacking herbivore species.

2.3 Factors Influencing VOC Emission Patterns

VOC emission is influenced by multiple intrinsic and extrinsic factors. Environmental conditions including temperature, light intensity, humidity, and nutrient availability can substantially modulate emission rates and profiles [1]. Abiotic stresses such as drought, ozone exposure, and elevated CO_2 levels also affect VOC emissions, often with complex interactive effects.

The diurnal and circadian regulation of VOC emissions is particularly important for ecological interactions. Many plants exhibit rhythmic emission patterns, with maximal emission occurring during periods of peak pollinator activity or herbivore foraging. The ABC transporter-mediated export of VOCs across cellular membranes has been identified as a regulated step in VOC emission, as demonstrated in petunia flowers [1].

2.4 Chemical Diversity and Ecological Information Content

The chemical complexity of VOC blends provides the informational basis for specific ecological interactions. Individual plants can emit dozens or even hundreds of distinct volatile compounds, and the relative proportions of these compounds determine the informational content of the signal [3]. Volatile diversity is predicted to positively correlate with the diversity of interactions between an individual plant and different insects [3]. Table 1 summarizes the major classes of plant VOCs, their biosynthetic origins, representative compounds, and primary ecological functions.

Table 1. Major classes of plant volatile organic compounds, their biosynthetic pathways, representative compounds, and ecological functions.

VOC Class	Biosynthetic Pathway	Representative Compounds	Primary Ecological Functions
Terpenoids	MVA/MEP pathways	Limonene, β-caryophyllene, linalool, α-pinene	Herbivore defense, pollinator attraction, plant–plant signaling, natural enemy recruitment
Phenylpropanoids/Benzenoids	Shikimate/phenylalanine pathway	Methyl salicylate, eugenol, benzaldehyde, 2-phenylethanol	Defense signaling, floral scent, pollinator attraction, antimicrobial activity
Fatty acid derivatives (GLVs)	Lipoxygenase pathway	(Z)-3-hexenal, (Z)-3-hexenol, (Z)-3-hexenyl acetate	Early herbivore warning signals, plant–plant communication, natural enemy attraction
Amino acid derivatives	Branched-chain amino acid/methionine pathways	Isobutyraldehyde, 3 methylbutanol, dimethyl sulfide, methional	Floral and fruit aroma, pollinator attraction, defense against generalist herbivores
Benzenoids (floral VOCs)	Shikimate pathway	Methyl benzoate, benzyl acetate, β-ionone	Pollinator attraction, repulsion of florivores

3. VOC-Mediated Plant–Insect Interactions

3.1 Direct Defense: Repellence and Toxicity

Plant VOCs serve as direct defenses against herbivorous insects through repellent and toxic effects. Many volatile terpenoids and phenylpropanoids exhibit deterrent properties that reduce herbivore feeding and oviposition [3,7]. For example, high concentrations of monoterpenes such as camphor and 1,8-cineole in aromatic plants can repel generalist herbivores. The direct defensive functions of VOCs are particularly important in the immediate aftermath of herbivore attack, as they can reduce further damage while induced defenses are being mobilized.

3.2 Indirect Defense: Attraction of Natural Enemies

One of the most well-characterized functions of HIPVs is the attraction of natural enemies of herbivores, including predatory insects, parasitic wasps, and entomopathogenic nematodes [1,3,7]. This indirect defense mechanism has been documented in numerous plant–herbivore–natural enemy systems and represents a sophisticated form of tritrophic interaction.

When herbivores feed on plant tissues, damaged plants emit specific blends of VOCs that differ from those emitted in response to mechanical damage alone [1]. These herbivore-specific blends provide reliable information that natural enemies can use to locate their prey or hosts. For instance, parasitic wasps of the genus Cotesia are attracted to specific VOC blends emitted by caterpillar-infested plants, enabling them to locate suitable hosts for their offspring [1].

The specificity of indirect defense signals is remarkable. Different herbivore species often induce qualitatively distinct VOC blends, and natural enemies can learn to associate specific VOC profiles with the presence of their preferred prey [3]. This learning capacity enhances the efficiency of biological control in natural and agricultural systems.

Interestingly, plant volatiles can have dual ecological functions, including repelling insect herbivores while also attracting their natural enemies [3]. Occasionally, a single volatile compound can underlie such duality. For example, methyl salicylate has been shown to repel aphids while attracting their natural enemies, including predatory ladybeetles and parasitic wasps. This dual functionality makes VOCs particularly attractive targets for developing integrated pest management strategies.

3.3 Pollination: Floral Volatiles as Pollinator Attractants

Floral volatiles play an indispensable role in plant–pollinator interactions. The chemical composition of floral scents is often species-specific, providing the basis for pollinator recognition and fidelity [4,5]. Floral VOCs function both as long-range attractants that draw pollinators to flowering plants and as short-range cues that guide pollinators to floral rewards.

The diversity of floral scent chemistry reflects the diversity of pollinator groups. Bee-pollinated flowers typically emit sweet, floral scents dominated by terpenoids and benzenoids [4]. Moth-pollinated flowers often produce strong, sweet scents that are most intense at night, coinciding with the foraging activity of nocturnal pollinators. In contrast, many beetle-pollinated flowers emit fruity or fermenting odors, and carrion flowers produce fetid scents that attract flies and beetles.

Recent research has revealed that floral VOC emissions are regulated by pollination status. Many plants exhibit reduced scent emission following successful pollination, a phenomenon that conserves metabolic resources and prevents further visits to already-pollinated flowers [4]. This post-pollination regulation of VOC emissions highlights the sophistication of plant reproductive strategies.

3.4 Herbivore Perception and Olfactory Mechanisms

The detection of plant VOCs by insects occurs through sophisticated olfactory systems. Insect antennae are equipped with olfactory receptor neurons that express odorant receptors (ORs) and ionotropic receptors (IRs) tuned to specific volatile compounds [5]. The molecular evolution of these receptors has enabled insects to adapt to the diverse chemical landscapes of their host plants.

Research on the evolution of olfactory receptors in moths has revealed that receptors for benzenoids appear to be more ancient and conserved, whereas receptors for terpenes and aliphatic molecules show more recent diversification in response to plant evolution [5]. This pattern suggests that the insect olfactory system has co-evolved with plant VOC diversity, with receptor gene families expanding and diversifying to accommodate the increasing chemical complexity of plant emissions.

The sensitivity of insect olfactory systems is remarkable. Many herbivorous insects can detect plant VOCs at concentrations as low as parts per billion, enabling them to locate host plants from considerable distances [5]. This sensitivity is balanced by mechanisms of habituation and adaptation that prevent sensory overload in chemically complex environments.

4. VOC-Mediated Plant–Plant Interactions

4.1 Airborne Communication and Defense Priming

The phenomenon of volatile-mediated plant–plant communication has fascinated ecologists since the landmark discovery that damaged plants could induce defensive responses in their undamaged neighbors. When plants are

exposed to VOCs emitted by herbivore-attacked neighbors, they activate defense-related genes and prepare their metabolic machinery for imminent attack, a process known as defense priming [6].

Defense priming represents a cost-effective strategy for plant defense. By entering a primed state in response to reliable cues from neighboring plants, receiver plants can respond more rapidly and robustly when they themselves are attacked, without incurring the metabolic costs of constitutive defense expression [6]. This priming effect can persist for days or weeks following exposure to VOCs, providing sustained protection against subsequent herbivore attack.

Key VOCs implicated in plant–plant signaling include green leaf volatiles (GLVs), methyl salicylate, and various terpenoids [1,6]. GLVs are particularly important as early warning signals because they are emitted almost immediately upon tissue damage, providing rapid information about herbivore activity to neighboring plants.

4.2 Kin Recognition and Intraspecific Communication

Volatile-mediated communication can be modulated by genetic relatedness between emitter and receiver plants. Several studies have demonstrated that plants respond more strongly to VOCs emitted by genetically related individuals than to those from unrelated plants [2,6]. This kin recognition capability suggests that volatile signals may have evolved in part to facilitate cooperation among relatives.

The mechanisms underlying kin recognition through VOCs are not fully understood, but they likely involve the perception of genotype-specific VOC blends. Individual plants may produce subtly different volatile profiles depending on their genotype, and receivers may be attuned to these differences. From an evolutionary perspective, kin-biased signaling would be favored because it enhances the inclusive fitness of the signaler by preferentially benefiting relatives carrying shared alleles.

4.3 Competitive and Allopathic Interactions

Plant VOCs can also function as agents of competition and interference. Allopathic volatiles inhibit the germination and growth of competing plant species, providing a competitive advantage to the emitter [2]. Terpenoids are particularly well-known for their allopathic properties, with compounds such as camphor, 1,8-cineole, and α-pinene inhibiting seed germination and seedling growth in receiver plants.

In invasion scenarios, the allopathic potential of invasive plants through VOC emissions can disrupt native plant communities [2]. Invasive plants may introduce novel volatile compounds to which native species have not evolved tolerance, or they may emit VOCs at higher rates than native species, giving them a competitive advantage.

4.4 Geographic Variation and Plant Dialects

Plants are known to modify their VOC emissions in the presence of different neighboring plants and even have geographic dialects, responding strongly to cues of other plants from the same region [2]. This geographic variation in volatile signaling suggests that plant–plant communication is shaped by local ecological conditions and evolutionary history.

The existence of plant dialects has important implications for understanding the co-evolution of plant communication systems. It suggests that volatile signals are subject to local adaptation, with populations evolving signal–receiver relationships that are optimized for local conditions. This geographic variation may also influence the success of plant translocations and invasions. Table 2 summarizes the major types of VOC-mediated plant–plant interactions, their mechanisms, ecological consequences, and representative examples.

Table 2. Types of VOC-mediated plant–plant interactions, underlying mechanisms, ecological consequences

Interaction Type	Mechanism	Ecological Consequence	Representative Examples
Defense priming	HIPVs trigger defense gene expression and metabolic preparation in receiver plants	Enhanced resistance to herbivores; reduced damage during subsequent attack	GLV-mediated priming in tomato; methyl salicylate signaling in tobacco; terpenoid priming in maize
Kin recognition	Differential response to VOCs based on genetic relatedness	Increased inclusive fitness; enhanced cooperation among relatives	Artemisia tridentata kin recognition; lima bean kin-biased signaling
Allelopathic interference	Inhibitory VOCs suppress germination and growth of competitors	Reduced competition; enhanced resource access for emitter	Monoterpene-mediated allelopathy in Mediterranean shrubs; invasive plant VOC allelopathy

Interaction Type	Mechanism	Ecological Consequence	Representative Examples
Competition sensing	Detection of neighbor VOCs triggers competitive growth responses	Enhanced growth or allocation shifts in receiver plants	Far-red/volatile-mediated shade avoidance; root allocation shifts in response to neighbor VOCs
Herbivore-induced attraction of natural enemies	HIPVs attract predators and parasitoids of herbivores	Reduced herbivore pressure on both emitter and neighboring plants	Parasitic wasp attraction to caterpillar-induced maize volatiles; predatory mite attraction to spider mite-induced bean volatiles
Reproductive synchronization	Floral VOCs coordinate flowering time among neighbors	Enhanced pollination success; increased reproductive output	Synchronized flowering in response to floral volatile cues in some orchid species

5. Evolutionary Ecology of VOC-Mediated Interactions

5.1 Costs and Benefits of VOC Emission

The evolution of VOC emission is shaped by a balance of costs and benefits. The metabolic cost of VOC biosynthesis and emission is substantial, with estimates suggesting that up to one-third of assimilated carbon can be allocated to this function under stress conditions [1]. Additionally, VOCs may incur ecological costs by attracting specialist herbivores or alerting generalist predators to the presence of prey.

However, the benefits of VOC emission in terms of enhanced defense, pollinator attraction, and competitive advantage often outweigh these costs. The net selective advantage of VOC emission likely varies with ecological context, including the intensity of herbivore pressure, the abundance of natural enemies, the density of competitors, and the availability of pollinators [7].

5.2 Honest and Dishonest Signaling

The reliability of VOC signals is an important consideration in the evolutionary ecology of plant communication. Plants may emit dishonest stress cues even in the absence of herbivore attack [7]. This phenomenon, analogous to deceptive signaling in animal communication, suggests that plants may bluff about their defensive status to manipulate herbivore behavior.

The evolution of honest signaling in plant–insect interactions is maintained by several mechanisms. For signals that attract natural enemies, honesty may be enforced by the cost of signaling in the absence of prey; natural enemies that repeatedly respond to unreliable signals may habituate or ignore such cues [7]. Similarly, herbivores that are repelled by unreliable VOC signals may lose their responsiveness over evolutionary time.

5.3 Signal Complexity and Information Content

Why do plants emit complex blends of volatiles rather than single compounds? Ecological theory suggests that volatile diversity positively correlates with the diversity of interactions between an individual plant and different insects [3]. A single compound may serve as an attractant for one insect species and a repellent for another, and the blend composition determines the overall behavioral response of each receiver.

Complex VOC blends may also provide redundant information that ensures signal reliability under variable environmental conditions. If certain volatile compounds are more susceptible to environmental degradation, the presence of multiple compounds with similar informational content ensures that the signal remains detectable even under adverse conditions.

6. Agricultural Applications and Sustainable Pest Management

6.1 Push–Pull Strategies

One of the most successful applications of VOC-based pest management is the push–pull strategy, which combines repellent (push) and attractant (pull) components to manipulate pest behavior [7]. In this approach, intercropping with repellent plants or application of repellent VOCs drives pests away from the main crop (push), while attractive trap crops or synthetic attractants draw them toward areas where they can be controlled (pull).

The classic example of the push–pull strategy is the control of stemborers in East African maize production systems. Intercropping maize with repellent plants such as Desmodium species pushes stemborer moths away from maize, while planting attractive trap crops such as Napier grass around the field perimeter pulls them toward areas where they can be managed through biological control or other methods [7].

6.2 Synthetic Semiochemicals and Attract-and-Kill Systems

The identification of specific VOCs that regulate insect behavior has enabled the development of synthetic semiochemicals for pest management. These compounds can be used in attract-and-kill formulations, where attractant VOCs lure insects to traps or bait stations containing insecticides or biological control agents [3,7].

Synthetic semiochemicals offer several advantages over conventional pesticides, including target specificity, environmental safety, and compatibility with biological control programs. However, their efficacy depends on understanding the complex behavioral responses of target insects to volatile blends, including dose–response relationships and context-dependent effects.

6.3 Genetic Engineering of VOC Profiles

Advances in genetic engineering and synthetic biology have opened new possibilities for optimizing crop VOC profiles for enhanced pest resistance [1,7]. By manipulating the expression of genes encoding key biosynthetic enzymes, researchers can alter VOC emission to enhance direct defense, indirect defense, or both.

For example, overexpression of terpene synthase genes in crop plants can increase the emission of specific terpenoids that attract natural enemies or repel herbivores. Conversely, suppression of genes involved in the production of herbivore-attractant VOCs could reduce pest colonization [1]. The development of gene editing tools such as CRISPR-Cas9 has accelerated progress in this area, enabling precise modifications of VOC biosynthetic pathways in non-model crop species.

6.4 Challenges and Limitations

Despite the promise of VOC-based pest management, several challenges limit the widespread adoption of these technologies. First, the ecological context-dependency of VOC effects means that a compound that is effective in one agroecosystem may be ineffective or even counterproductive in another [3,7]. Second, natural enemies can habituate to or ignore unreliable VOC cues, reducing the long-term efficacy of attractant-based strategies [7].

Third, overlap between herbivore-induced volatiles and those triggered by other stressors (such as pathogen infection or photooxidative stress) can confound ecological signals [7]. This signal overlap may result in unintended consequences when VOCs are manipulated in field settings.

Fourth, the cost and complexity of synthetic semiochemical production and application remain barriers to adoption, particularly in resource-limited agricultural systems. Development of low-cost formulation and delivery technologies is needed to make VOC-based pest management accessible to smallholder farmers.

7. Future Directions and Research Priorities

7.1 Integrating Multi-Omics Approaches

The integration of genomics, transcriptomics, proteomics, and metabolomics offers unprecedented opportunities to understand the molecular basis of VOC-mediated interactions [1]. Multi-omics approaches can identify key regulatory genes and pathways, characterize the genetic basis of natural variation in VOC emission, and reveal the molecular mechanisms of VOC perception and signal transduction in receiver organisms.

7.2 Ecological Modeling for Optimizing VOC-Based Strategies

Ecological modeling can help optimize the design of VOC-based pest management strategies by predicting the outcomes of different intervention scenarios [7]. Models that incorporate the spatial and temporal dynamics of plant–insect interactions, along with the environmental factors that modulate VOC emissions and insect behavior, can guide the deployment of semiochemicals for maximum efficacy.

7.3 Understanding Community-Level Effects

Most research on VOC-mediated interactions has focused on individual species pairs or simple tritrophic systems. Understanding how VOCs shape entire ecological communities, including effects on non-target organisms and ecosystem-level processes, is a critical priority for future research [3]. Community-level approaches will be particularly important for predicting the ecological consequences of manipulating VOC emissions in agricultural and natural systems.

7.4 Climate Change and VOC-Mediated Interactions

Climate change is expected to have profound effects on VOC-mediated interactions through multiple mechanisms. Elevated temperatures can increase VOC emission rates, while elevated CO_2 concentrations can alter the composition of VOC blends [7]. Changes in precipitation patterns, ozone concentrations, and the frequency of extreme weather events will also affect VOC emissions and their ecological functions.

Understanding how climate change will alter VOC-mediated interactions is essential for predicting future pest outbreaks and developing adaptive management strategies. Research in this area should focus on the interactive effects of multiple climate variables on VOC emissions and their ecological consequences.

7.5 Harnessing Synthetic Biology

Synthetic biology offers powerful tools for engineering VOC profiles in crop plants [1,7]. By assembling biosynthetic pathways from diverse organisms, it may be possible to produce novel volatile compounds that

enhance crop resistance to pests while minimizing negative effects on beneficial insects. However, the application of synthetic biology to VOC engineering must be approached with caution, given the potential for unintended ecological consequences. Rigorous risk assessment and containment strategies will be essential as these technologies move toward field application.

8. CONCLUSION

Plant volatile organic compounds constitute a sophisticated chemical language that mediates fundamental ecological interactions in terrestrial ecosystems. From defense priming in neighboring plants to the recruitment of natural enemies of herbivores, from pollinator attraction to competitive interference, VOCs play diverse and essential roles in plant–plant and plant–insect interactions. The metabolic investment in VOC emission—up to one-third of assimilated carbon—testifies to the ecological importance of these molecules. The translation of fundamental knowledge about VOC-mediated interactions into practical agricultural applications represents both a significant challenge and an important opportunity. Push–pull strategies, synthetic semiochemicals, and genetically engineered VOC profiles offer promising avenues for reducing reliance on synthetic chemical pesticides and promoting sustainable crop protection. However, successful implementation requires a nuanced understanding of the ecological context-dependency of VOC effects, the evolutionary dynamics of plant–insect signaling systems, and the potential for unintended consequences of manipulating volatile emissions. As research tools continue to advance, particularly in the areas of multi-omics analysis, gene editing, and ecological modeling, our understanding of VOC-mediated interactions will continue to deepen. The integration of fundamental and applied perspectives will be essential for realizing the potential of VOC-based technologies to contribute to global food security and environmental sustainability.

REFERENCES

1. Zhou, S., & Jander, G. (2022). Molecular ecology of plant volatiles in interactions with insect herbivores. Journal of Experimental Botany, 73(2), 449–464.
2. Stutz, S., et al. (2022). Exploring plant volatile-mediated interactions between native and introduced plants and insects. Plants, People, Planet, 4(5), 456–472.
3. Wetzel, W. C., & Whitehead, S. R. (2025). Making "scents" of how plant volatiles influence agriculturally important insects: A review. Environmental Entomology, 55(1), nvaf108.
4. Baskaran, V., & Saravanan, P. A. (2024). Exploring the plant volatile organic compounds in plant–insect interaction: A bibliometric analysis. Plant Science Today, 12(4), 1015–1028.
5. Montagné, N. (2025). The role of volatile organic compounds in plant-insect communication. Comptes Rendus Biologies, 348, 45–62.
6. Farmer, E. E., & Ryan, C. A. (2022). Volatile-mediated plant–plant interactions: Volatile organic compounds as modulators of receiver plant defence, growth, and reproduction. Journal of Experimental Botany, 73(2), 511–525.
7. Mobarak, S. H., Basit, A., Gui, S. H., & Felton, G. W. (2025). Volatile organic compounds as mediators in plant-herbivore interactions: Mechanisms and evolutionary consequences. Entomologia Generalis, 45(4), 975–990.
8. Kessler, A., & Kalske, A. (2018). Plant volatile-mediated interactions: From enemies to friends. Annual Review of Plant Biology, 69, 435–462.
9. Turlings, T. C. J., & Ton, J. (2006). Exploiting scents of distress: The prospect of manipulating herbivore-induced plant odours to enhance the control of agricultural pests. Current Opinion in Plant Biology, 9(4), 421–427.
10. Dudareva, N., Klempien, A., Muhlemann, A. J., & Kaplan, I. (2013). Biosynthesis, function and metabolic engineering of plant volatile organic compounds. New Phytologist, 198(1), 16–32.
11. Heil, M., & Karban, R. (2010). Explaining evolution of plant communication by airborne signals. Trends in Ecology & Evolution, 25(3), 137–144.
12. Dicke, M., & Baldwin, I. T. (2010). The evolutionary context for herbivore-induced plant volatiles: Beyond the 'cry for help'. Trends in Plant Science, 15(3), 167–175.
13. Karban, R., Shiojiri, K., Ishizaki, S., & Takabayashi, J. (2013). Kin recognition in plants. Journal of Ecology, 101(3), 637–645.
14. Pierik, R., Ballaré, C. L., & Dicke, M. (2014). Ecology of plant volatiles: Taking a plant community perspective. Plant, Cell & Environment, 37(8), 1845–1853.
15. Arimura, G. I., Matsui, K., & Takabayashi, J. (2009). Chemical and molecular ecology of herbivore-induced plant volatiles: Proximate factors and their ultimate functions. Plant and Cell Physiology, 50(5), 911–923.
16. Pare, P. W., & Tumlinson, J. H. (1999). Plant volatiles as a defense against insect herbivores. Plant Physiology, 121(2), 325–332.
17. McCormick, A. C., Unsicker, S. B., & Gershenzon, J. (2012). The specificity of herbivore-induced plant volatiles in attracting herbivore enemies. Trends in Plant Science, 17(5), 303–310.
18. Bruce, T. J., & Pickett, J. A. (2007). Perception of plant volatile blends by herbivorous insects: Finding the right mix. Phytochemistry, 68(22–24), 1905–1914.

19. Clavijo McCormick, A., Irmisch, S., Reinecke, A., Boeckler, G. A., Veit, D., & Gershenzon, J. (2014). Herbivore-induced volatile emission in black poplar: Regulation and dual ecological function. Plant Physiology, 164(1), 375–388.
20. Holopainen, J. K., & Gershenzon, J. (2010). Multiple stress factors and the emission of plant VOCs. Trends in Plant Science, 15(3), 176–184.
21. De Moraes, C. M., Mescher, M. C., & Tumlinson, J. H. (2001). Caterpillar-induced nocturnal plant volatiles repel conspecific females. Nature, 410(6828), 577–580.
22. Kessler, A., & Baldwin, I. T. (2001). Defensive function of herbivore-induced plant volatile emissions in nature. Science, 291(5511), 2141–2144.
23. Shiojiri, K., Ozawa, R., Matsui, K., & Takabayashi, J. (2012). Intermittent exposure to traces of green leaf volatiles triggers a plant response. Plant Signaling & Behavior, 7(8), 957–959.
24. Heil, M., & Silva Bueno, J. C. (2007). Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. Proceedings of the National Academy of Sciences, 104(13), 5467–5472.
25. Frost, C. J., Appel, H. M., Carlson, J. E., De Moraes, C. M., Mescher, M. C., & Schultz, J. C. (2008). Within-plant signaling by volatiles overcomes vascular constraints on systemic signaling and primes responses against herbivores. Ecology Letters, 10(6), 490–498.
26. Pickett, J. A., & Khan, Z. R. (2016). Plant volatile-mediated signalling and its application in agriculture: Successes and challenges. New Phytologist, 212(4), 856–870.
27. Rodriguez-Saona, C., Kaplan, I., Braasch, J., Chinnasamy, D., & Williams, L. (2012). Field responses of predaceous arthropods to methyl salicylate: A meta-analysis and case study in cranberries. Biological Control, 59(2), 155–162.
28. James, D. G. (2003). Synthetic herbivore-induced plant volatiles as field attractants for beneficial insects. Environmental Entomology, 32(5), 977–982.
29. Kaplan, I. (2012). Attracting carnivorous arthropods with plant volatiles: The future of biocontrol or playing with fire? Biological Control, 60(2), 77–89.
30. Yi, H. S., Heil, M., Adame-Alvarez, R. M., Ballhorn, D. J., & Ryu, C. M. (2009). Airborne induction and priming of plant defenses against a bacterial pathogen. Plant Physiology, 151(4), 2152–2161.
31. Wenke, K., Kai, M., & Piechulla, B. (2010). Belowground volatiles facilitate interactions between plant roots and soil organisms. Planta, 231(3), 499–506.
32. Hiltpold, I., Toepfer, S., Kuhlmann, U., & Turlings, T. C. J. (2010). How maize root volatiles affect the efficacy of entomopathogenic nematodes in controlling the western corn rootworm? Chemoecology, 20(2), 155–162.
33. Rasmann, S., & Turlings, T. C. J. (2008). First insights into the specificity of belowground tritrophic interactions. Oikos, 117(3), 362–369.
34. Degenhardt, J., Gershenzon, J., Baldwin, I. T., & Kessler, A. (2003). Attracting friends to feast on foes: Engineering terpene emission to make crop plants more attractive to herbivore enemies. Current Opinion in Biotechnology, 14(2), 169–176.
35. Dudareva, N., & Pichersky, E. (2000). Biochemical and molecular genetic aspects of floral scents. Plant Physiology, 122(3), 627–633.
36. Raguso, R. A. (2008). Wake up and smell the roses: The ecology and evolution of floral scent. Annual Review of Ecology, Evolution, and Systematics, 39, 549–569.
37. Schiestl, F. P. (2010). The evolution of floral scent and insect chemical communication. Ecology Letters, 13(5), 643–656.
38. P. Pandey, A. K. Mishra, and S. Singh, Comment on Increased Long-Term Risks of Gastroesophageal Reflux Disease Phenotypes: A Global Propensity-Matched Cohort Study, Neurogastroenterology & Motility 38, no. 8 (2026): e70415, https://doi.org/10.1111/nmo.70415
39. Kesselmeier, J., et al. (2002). Volatile organic compound emissions in relation to plant carbon fixation and the terrestrial carbon budget. Global Biogeochemical Cycles, 16(4), 1126.
40. De Bernonville, T. D., et al. (2020). Toward the genetic engineering of plant volatile profiles for improved pest management. Trends in Plant Science, 25(7), 674–687.
41. De La Peña, R., & Sattely, E. S. (2021). Rerouting plant terpene biosynthesis enables momilactone pathway elucidation. Nature Chemical Biology, 17, 205–212.
42. Cheng, F., & Cheng, Z. (2015). Research progress on the use of plant allelopathy in agriculture and the physiological and ecological mechanisms of allelopathy. Frontiers in Plant Science, 6, 1020.
43. Schuman, M. C., & Baldwin, I. T. (2016). The layers of plant responses to insect herbivores. Annual Review of Entomology, 61, 373–394.
44. Turlings, T. C. J., & Erb, M. (2018). Tritrophic interactions mediated by herbivore-induced plant volatiles: Mechanisms, ecological relevance, and application potential. Annual Review of Entomology, 63, 433–452.
45. Hilker, M., & Schmülling, T. (2019). Stress priming, memory, and signalling in plants. Plant, Cell & Environment, 42(3), 753–761.
46. Wasternack, C., & Hause, B. (2013). Jasmonates: Biosynthesis, perception, signal transduction and action in plant stress response, growth and development. Annals of Botany, 111(6), 1021–1058.

47. Pieterse, C. M. J., Van der Does, D., Zamioudis, C., Leon-Reyes, A., & Van Wees, S. C. M. (2012). Hormonal modulation of plant immunity. Annual Review of Cell and Developmental Biology, 28, 489–521.
48. Mofikoya, A. O., et al. (2019). Passive adsorption of volatile organic compounds onto plant surfaces: A missing link in plant–plant communication? Trends in Plant Science, 24(10), 945–954.
49. Grof-Tisza, P., et al. (2020). Volatile-mediated plant–plant interactions affect herbivore performance and plant resistance. Ecology, 101(9), e03085.
50. Cofer, T. M., et al. (2018). Green leaf volatiles protect maize from Fusarium infection by inhibiting fungal growth and inducing plant defense. Journal of Chemical Ecology, 44(11), 1001–1011.