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SEMIOCHEMICALS MEDIATED INSECT PLANT INTERACTIONS: CHEMICAL SIGNALS, TRANSDUCTION MECHANISMS AND BEHAVIORAL ECOLOGY

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ABSTRACT

The interaction between insects and plants via their use of semiochemicals represents a complex relationship that is ecologically important throughout nature. Semiochemical mediated interactions determine many aspects of an insect's biology such as selecting a host plant for feeding, selecting mates for reproduction, identifying sites for egg-laying (oviposition) and defense against predators. In this review, we will examine the complexity of all the chemical signals used by insects when interacting with plants. Specifically, we will discuss volatile organic compounds (VOCs), herbivore-induced VOCs (HI-VOCs) and pheromones as they relate to these interactions. We will also discuss the molecular mechanisms involved in the transduction of chemical signals into behaviors and describe how insects interact chemically with plants and how plants defend themselves using secondary metabolites (constitutive and induced defenses). Additionally, we will focus on the biosynthesis of terpenoids, phenolics, alkaloids and green leaf volatiles (GLVs) as well as their ecological significance. Lastly, we will provide examples of how to integrate chemical ecology with agricultural practices. We will highlight several applications of semiochemicals as part of sustainable pest management including push-pull systems, mating disruption, and the development of attractants and repellents. Ultimately, understanding these chemical communication systems can aid in the development of environmentally friendly methods of crop protection and lead to enhanced agricultural sustainability in response to increased food demand and environmental stressors globally.
***Keywords*:** Semiochemicals, volatile organic compounds, odorant-binding proteins, olfactory receptors, herbivore-induced plant volatiles, terpenoids, behavioral ecology, host plant selection, plant defense mechanisms, integrated pest management.

Introduction

The chemical warfare between plants and insects has taken place for over 350 million years, producing complex communication systems that help determine how each interacts ecologically. Volatile Organic Compounds (VOCs) and Secondary Metabolites (SMs) serve as the primary means for mediating ecological/evolutionary relationships (J.S. *et al.*, 2024).

Because plants cannot move and therefore cannot fight off insects and attract beneficial insects like predators and pollinators, they use VOCs to alert them to danger and SMs to attract beneficial insects; whereas insects use VOCs and SMs to identify and understand these warning signals, ultimately affecting their behavior and survival strategies (J.S. *et al*., 2024). Semiochemicals represent a wide array of chemical signals that mediate interactions between organisms, e.g. pheromones for intra-specific communication and allelochemicals for inter-specific interactions (Kumar, 2016). Semiochemicals enable the exchange of information from one organism to another, leading to specific behavioral or physiological changes (Kumar, 2016). Olfactory cues play an important role in many biological functions of insects such as foraging, oviposition, and mate selection, thereby representing a critical component for creating species barriers and promoting speciation (Schooten *et al*., 2020).

Plants produce volatile organic compounds (VOCs), which are key components of plant-insect interactions and have a significant impact on herbivy, pollination and tritrophic interactions (Ashrith *et al*., 2025). Floral VOCs can also affect the foraging behavior of insects, because insects can detect the plant's secondary metabolites (including semiochemicals) to locate nectar, carbohydrates, prey, mates and other required resources (Rodriguez-Flores *et al*., 2025). Studying the VOCs of plants used by specific insect species, can lead to developing targeted pest management strategies and will allow us to gain a better understanding of the relationship between plants and insects (Rodriguez-Flores *et al*., 2025). Significant advancements in the fields of molecular biology, chemical ecology and neuroscience, have provided a much greater insight into the molecular basis of how chemical signals are generated, received and processed. The identification of olfactory genes, including odorant receptors, odorant-binding proteins and chemosensory proteins, has revolutionized the understanding of insect olfaction (Kordaczuk & Wojda, 2026). Odorant-binding proteins (OBPs) and chemosensory proteins (CSPs) are essential components of the extremely sensitive olfactory systems of insects, which bind and transport environmental odorants and pheromones to odorant receptors (Yang *et al*., 2025).

Semiochemical-mediated interactions in an ecological context extend to agroecological systems, where an understanding of these mechanisms could provide a significant opportunity for the development of sustainable pest management strategies. A large body of evidence exists describing different types of chemical cues that have been detected in various insect species, with a focus on relevant fruit fly pest species, highlighting the importance of chemical communication in integrated pest management (Scolari *et al*., 2021). Many aromatic compounds, including semiochemicals and pheromones, have been identified as effective defense compounds against harmful insects in crops and animals, allowing for increased crop production through the use of phytochemical lures for sustainable agriculture (Jaffar *et al*., 2024). This review is an attempt to synthesize the current state of knowledge on semiochemical-mediated insect-plant interactions, including chemical signals, transduction mechanisms and behavioral ecology. We address the diversity of chemical signals present, the molecular mechanisms of signal reception and processing, the behavioral responses induced and the practical applications of this knowledge in sustainable agriculture. Through combining biochemical, molecular, ecological and evolutionary approaches, we strive to provide a holistic understanding of the fascinating interactions between plants and insects that structure terrestrial ecosystems.

Classification and Diversity of Semiochemicals in Insect-Plant Interactions

Overview of Semiochemical Classification

Pheromones are secreted and released by an organism to stimulate specific reactions in the receiving members of the same species. Allelochemicals include those semiochemicals produced by one species that cause behavioral or physiological responses in another species (Field *et al*., 2000). There are several subcategories of allelochemicals based on their adaptive significance to the producer or receiver; kairomones induce a beneficial response in the receiver, allomones induce a response that is advantageous to the emitter, and synomones result in a mutually beneficial response (Kumar, 2016). Semiochemicals from the rice-plants and rice-insects vary greatly in chemical composition among the different rice-insect systems. Eight semiochemicals were identified from rice varieties, and the effects of these on rice pests were tested both individually and in a physiologically relevant blend (Zhang *et al*., 2021). Rice semiochemicals serve as the modifiers of rice pest behavior and act on the insect's olfactory system to find host and prey. Pest-susceptible varieties of rice expressed higher amounts of total rice semiochemicals and the expression of their biosynthesis genes compared to resistant varieties of rice, illustrating the close relationship between rice plant chemistry and the performance of rice pests (Zhang *et al*., 2021).

Volatile Organic Compounds as Primary Chemical Signaling Agents

Volatiles from plants also act as primary chemical signaling agents for the plant-rice pest system, providing multiple functional activities in plant defense and modifying rice pest behavior (Zhou & Jander, 2021). Single VOCs may have direct toxicity or deterrent activity and serve as signal molecules to attract predators of rice pests, or they may be detected by remote plant tissues and act as priming signals to prepare for anticipated herbivory (Zhou & Jander, 2021). As such, the complexity of plant-insect chemical communication in rice using VOCs is increased by the sophisticated molecular detection mechanisms of rice pests, where rice pests can detect single or multiple VOCs and therefore modulate rice pest behavior in ways that remain unexplored (Zhou & Jander, 2021). Research on volatile organic compounds in plant-insect systems have found that plants communicate with insects and other organisms through the emission of VOCs, with Boolean operator searches indicating a large body of research focusing on herbivore-induced plant VOCs (Niu *et al*., 2024). Herbivore-induced plant VOCs (HIPVs) activate the antennae of insects, attract adult insects and females of insects, and recruit natural enemies of herbivores. Terpenoids like α-pinene and β-myrcene affect rice pest behavior by attracting natural enemies, while β-ocimene and β-caryophyllene regulate aboveground and belowground rice-insect interactions (Niu *et al*., 2024). The variability of VOCs emitted by different plant species was shown in studies evaluating plant species visited by certain insects. A study of 18 plant species frequently visited by the invasive hornet Vespa velutina indicated 110 VOCs in the study samples, with 21 VOCs common to the samples, with terpenes being the largest group of VOCs (Rodriguez-Flores *et al*., 2025). Multivariate analysis of 33 VOCs that had variable importance scores greater than 1 showed that the most important VOCs included methylanthranilate, (Z)-β-ocimene, 1-octen-3-ol, and a variety of acetate and phenolic compounds. These VOCs contribute to our understanding of the functions of plant VOCs in mediating insect behavior and highlight the utility of VOCs as environmentally friendly approaches to pest management (Rodriguez-Flores *et al*., 2025).

Herbivore-Induced Plant Volatiles: Formation and Function

Herbivore-induced plant volatiles are a specialized type of chemical signal that plants produce when attacked by insects. Plants produce unique blends of herbivore-induced plant volatiles (HIPVs) that facilitate extensive interaction between plants and arthropods, microorganisms, undamaged adjacent plants, or other parts of the plant in various ecosystems (Arimura *et al*., 2009). The composition of HIPV blends varies depending on the insect species attacking the plants, the developmental stage of the insect, and the environment in which the plants and insects coexist, indicating the specificity and flexibility of these plant responses to insect attacks (Arimura *et al*., 2009). The synthesis of HIPVs requires the operation of complex biochemical pathways. The two major classes of HIPV biochemistry involve the synthesis of volatile terpenoids and green leaf volatiles. Additionally, the activation of plant responses by feeding herbivores and subsequent signal transduction pathways also operate in the biosynthesis of HIPVs (Arimura *et al*., 2009). Wild tobacco studies have shown that light suppresses the emission of terpenoids but increases the emission of green leaf volatiles after a delay, illustrating the environmental regulation of HIPV production (He *et al*., 2021). The promoters of HIPV biosynthetic genes contain various types of cis-acting regulatory elements involved in light, stress, phytohormone, and circadian regulation (He *et al*., 2021). Cotton plant studies have illustrated that many volatiles emitted by cotton in response to insect feeding, including acyclic terpenes like (E,E)-α-farnesene, (E)-β-farnesene, (E)-β-ocimene, linalool, (E)-4,8-dimethyl-1,3,7-nonatriene, and (E/E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene, as well as products of the shikimate pathway (indole), are synthesized de novo upon herbivore damage (Par & Tumlinson, 1997). Application of caterpillar oral secretions to damaged or undamaged control plants stimulated both the production of volatiles and the attractiveness of plants to parasitoids of herbivores, indicating that the plant participates in a dynamic and active way in mediating the interaction between herbivores and natural enemies of herbivores (Par & Tumlinson, 1997).

Molecular Mechanisms of Olfactory Signal Transduction

Odorant-Binding Proteins: Structure and Function

The olfactory systems of insects utilize a variety of different proteins associated with odor perception in order to achieve high precision in both detecting odors and transmitting signals about those odors (Kordaczuk & Wojda, 2026). Once an odorant molecule binds to an odorant-binding protein (OBP) it will be transported to an odorant receptor (OR), located on the surface of a sensory neuron, and initiate very specific signal transmission (Kordaczuk & Wojda, 2026). To help maintain the ability to detect odors, the signal transduction process initiated by the interaction between an odorant molecule and an odorant receptor is terminated rapidly and efficiently by odorant degrading enzymes (ODDE) preventing odorant receptors from becoming saturated (Kordaczuk & Wojda, 2026). Both odorant-binding proteins and odorant receptors are shaped by evolutionary forces, and thus are designed to meet the unique chemical detection requirements of each insect species; however, the olfactory sensitivity of each species may be altered based upon external environmental factors including temperature, nutrient levels, and circadian rhythms (Kordaczuk & Wojda, 2026). In addition to chemosensitizing an insect's sense of smell, the olfactory system plays a role in aiding insect immunity by controlling the way in which pathogens are recognized and how they elicit an immune response (Kordaczuk & Wojda, 2026). Some studies have shown that certain OBPs interact directly with Toll-like receptors, affecting an insect's antimicrobial responses and overall gut microbiota balance, while other research suggests that symbiotic bacteria can regulate OBP expression, creating a connection between olfaction and systemic immunity (Kordaczuk & Wojda, 2026). Furthermore, some OBPs and chemosensory proteins have been shown to exhibit direct antimicrobial properties, illustrating the multiple functional roles these molecules play in the biology of an insect (Kordaczuk & Wojda, 2026). Generally, odorant-binding proteins are structurally characterized as forming small, stable, globular structures composed of α-helices and/or β-sheets that allow them to perform a wide range of physiological functions and adapt to many environments (Yang *et al.*, 2025). There are two major theories regarding the mechanisms of action of OBPs: ligand-induced conformational changes and pH-dependent regulation. pH-dependent regulation is particularly significant, given that the environment surrounding the odorant-binding site in the sensillum lymph has a much higher pH than the dendritic membrane where the odorant-binding protein resides, and that these physiological conditions are necessary for promoting pheromone binding and selective ligand release from the odorant-binding protein at the target cell membrane, respectively (Mohanty *et al.*, 2008). The binding specificity of odorant-binding proteins has been investigated using a number of techniques including fluorescence competitive binding assays and molecular docking studies. In the parasitic wasp Baryscapus dioryctriae, for example, the odorant-binding protein BdioOBP50 exhibited strong binding affinity towards the repellent compound 1-octen-3-ol, and several residues including Arg47 and Tyr99 were identified as being essential for this interaction (Zhu *et al.*, 2025). In another example, the odorant-binding protein RpedOBP38 of the plant bug Riptortus pedestris was found to exhibit the greatest binding affinity to trans-2-decenal and trans-2-nonenal, and that polar residues such as His94 and Glu97, as well as non-polar residues like Leu29 and Ile59, played critical roles in determining its ligand-binding characteristics (Guo *et al.*, 2025). The structural information provided by these studies provides valuable insight into the mechanisms underlying the recognition of odors by insects, and ultimately informs the development of environmentally-friendly strategies for managing pests.

Olfactory Receptors and Signal Transduction Cascades

A very recent study indicates that insects have developed a unique mechanism of olfactory signal transduction using inositol trisphosphate (IP3), and this contrasts significantly with the G-protein coupled receptor-based signaling systems used by vertebrates (Yang *et al.*, 2025). When locusts sense the aggregation pheromone 4-vinylanisole, the pheromone is carried to the OR35/Orco receptor complex via OBPs (Olfactory Binding Proteins) OBP10 and OBP13, and the pheromone activates the downstream signaling cascades within the antennae (Yang *et al.*, 2025). One important component of these downstream cascades is the lipid-binding protein Clvs2, which is able to facilitate the transport of phosphatidylinositol 4,5-bisphosphate across the cytolemma; thus, it provides additional substrate for the production of IP3 (Yang *et al.*, 2025). Finally, the increased level of IP3 in the antennal lobe of the brain is due to the activity of PLCε1, an enzyme involved in the biosynthesis of IP3, and it is responsible for converting chemical signals from the antennae into electrical signals; therefore, it confirms IP3's role as a secondary messenger in olfaction (Yang *et al.*, 2025).

The specific functions and the importance of ORs have been demonstrated through functional studies on the specificity and function of the ORs in insect behavioral responses. The mutagenesis of the Orco gene in Helicoverpa armigera was shown to cause significant olfactory dysfunction with many odors present in both host plant volatiles and sex pheromone components producing no measurable electrophysiological responses in the antennae of Orco mutants (Fan *et al.*, 2022). Wind tunnel experiments showed that the ability of Orco mutant males to fly upwind towards sex pheromones was greatly diminished. Additionally, the ability of Orco mutant females to choose among different host plants where they would lay eggs was lost entirely. Therefore, these results suggest that the OR-dependent olfactory response is necessary for pheromone communication, host-plant choice for oviposition, and chemotaxis during larval development, and that disrupting or eliminating the OR-dependent olfactory response may provide a strategy to inhibit or disrupt the mate-finding and host-finding behaviors of pest moths (Fan *et al.*, 2022).

Chemosensory Proteins and Their Roles

Chemosensory proteins (CSPs) represent a very important class of olfactory proteins which enable the recognition and binding of odorous molecules to odorant receptors, and subsequently allow for the modulation of numerous behaviors related to insects' responses to chemical stimuli (Yang *et al.*, 2025). Bradysia odoriphaga is an example of a pest species; BodoCSP3 has been identified as being significantly up-regulated in the antennae of adult B. odoriphaga, suggesting it may have a role in the sense of smell. Competitive fluorescence binding assays indicated that BodoCSP3 can bind two host plant volatiles, dimethyl trisulfide and ethyl dodecanoate, at high affinities (Yang *et al.*, 2025).

Further, site directed mutagenesis using fluorescence binding assays confirmed that five amino acid residues, Ile73, Leu69, Tyr120, Lys117, and Tyr116, are essential for the binding of BodoCSP3 to both dimethyl trisulfide and ethyl dodecanoate. Finally, RNA interference, along with behavioral assays, have shown that Bradysia odoriphaga exhibits dose dependent attraction to dimethyl trisulfide and ethyl dodecanoate, demonstrating that BodoCSP3 plays a crucial role in the recognition of host plant volatiles (Yang *et al.*, 2025).

Tissue-specific expression of CSPs provides valuable insight into their functional specialization. For example, PxylCSP18 from Plutella xylostella was observed to be highly expressed in both antennal and head tissues; however, males exhibited higher expression levels in their antennae compared to females (Qie *et al.*, 2024). PxylCSP18 was capable of binding with 14 different plant volatiles that are either repulsive or attractive to P. xylostella, but demonstrated little to no binding to pheromone components. Knock-down of PxylCSP18 via RNA interference resulted in reduced attractiveness of certain volatile compounds, as well as reduced repellence of other volatile compounds; these results indicate that PxylCSP18 likely plays a significant role in detecting host plants, avoiding undesirable host plants, and selecting appropriate oviposition locations, but does not contribute to mate-finding behaviors (Qie *et al.*, 2024).

Table 1: Major Classes of Olfactory Proteins and Their Functions in Insect-Plant Interactions

Protein Class	Primary Function	Key Characteristics	Representative Examples	Reference
Odorant-Binding Proteins (OBPs)	Transport volatile compounds across sensillum lymph to olfactory receptors	Small (15-20 kDa), soluble, acidic isoelectric points, six conserved cysteines	BdioOBP50 (1-octen-3-ol binding), RpedOBP38 (trans-2-decenal binding), BminOBP3 (undecanol binding)	(Guo *et al.*, 2025; Kordaczuk & Wojda, 2026; Zhu *et al.*, 2025)
Odorant Receptors (ORs)	Form ligand-gated ion channels for odorant detection	Heteromultimeric complexes with Orco, species-specific ligand selectivity	HarmOrco (pheromone detection), CpomOR3 (pear ester detection), CpomOR6a (codlemone acetate detection)	(Cattaneo *et al.*, 2017; Fan *et al.*, 2022)
Chemosensory Proteins (CSPs)	Facilitate odorant recognition and transport	Broadly expressed across tissues, diverse binding spectrum	BodoCSP3 (dimethyl trisulfide binding), PxylCSP18 (host plant volatile binding)	(Qie *et al.*, 2024; Y. Yang *et al.*, 2025)
Sensory Neuron Membrane Proteins (SNMPs)	Support pheromone detection and receptor function	Membrane-associated, critical for pheromone sensitivity	OBP/SNMP complexes in moth antennae	(Kordaczuk and Wojda, 2026)
Ionotropic Receptors (IRs)	Detect various chemical stimuli including acids and amines	Ancient chemosensory receptor family, divergent from ORs	Multiple IRs in fruit flies and moths	(Jaffar *et al.*, 2024)

Herbivore-Induced Plant Volatiles: Biosynthesis and Ecological Significance

Terpenoid Biosynthesis and Regulation

Secondary metabolites of the plant kingdom can be divided into three main categories: alkaloids, phenolics and terpenoids, which are further subdivided based on their chemical structure. Terpenoids have the highest diversity among these metabolite types due to the fact that plants produce more than 25,000 different terpenoid structures, illustrating a large potential for plant evolution and defense mechanisms (Navya *et al*., 2025). Plant terpenoid production is largely dependent on biosynthetic pathways that use isopentenyl diphosphate (IPP) and its allylic isomer dimethylallyl diphosphate (DMAPP) as initial substrates and terpene synthases play an important role in producing volatile terpenoids (Cheng *et al*., 2007).

Studies have demonstrated that when tea plants are exposed to aphid infestation, it stimulates the production of elemene, which enhances resistance to aphid infestation by stimulating jasmonic acid-mediated pathways (Luo *et al*., 2025). Aphid feeding stimulated the production of elemene in tea plants; furthermore, the authors were able to identify aphid-stimulated CsELE as a terpene synthase enzyme responsible for the last step of elemene biosynthesis from farnesyl pyrophosphate. In addition, transient overexpression and gene silencing of CsELE resulted in changes to elemene levels in tea plants, and thus influenced the resistance of tea plants to aphid feeding (Luo *et al*., 2025). Dual-luciferase and yeast one-hybrid assays also showed that CsELE expression was regulated by MYC2a, a core transcriptional regulator in the JA signaling pathway (Luo *et al*., 2025).

Terpenoid biosynthesis regulation includes interaction of multiple environmental cues with endogenous signaling pathways. Herbivores stimulate mechanical perception by the long trichomes of tomato plants, which transduce the stimulus via an intra-trichome communication network, probably involving calcium waves (Sun *et al*., 2024). Upon activation of the JA signaling pathway in the short glandular trichomes of the plants, they upregulate the Woolly-SlMYC1 regulatory module for terpene biosynthesis providing plants with an early warning signal against herbivore invasion (Sun *et al*., 2024).

Cytochrome P450 enzymes also are involved in the diversification of terpenoids by acting as catalysts for oxidation reactions, and in some instances, backbone rearrangement, methyl group migration, and carbon-carbon cleavage (Frey *et al*., 2025). Oxidation and other modifications by cytochrome P450 enzymes are involved in the metabolism of monoterpenes, sesquiterpenes, diterpenes, and triterpenes, and are also involved in the biosynthesis of plant hormones, volatiles and defense compounds (Frey *et al*., 2025). For example, many commercially important terpenoids require such enzymatic reactions in their biosynthesis, including terpenoids involved in the development of pesticides and drugs (Frey *et al*., 2025).

Green Leaf Volatiles and Their Multifunctional Roles

Green leaf volatiles, a class of saturated and unsaturated six carbon aldehydes, alcohols and esters produced by plants as a response to mechanical damage (Scala *et al*., 2013) represent one of the quickest defense reactions of plants. GLVs are important for indirect defense mechanisms such as recruitment of natural predators and enemies of insects and additionally exhibit direct toxicological activity toward insects (Scala *et al*., 2013) and are able to stimulate and condition plant defense responses (Scala *et al*., 2013). Furthermore, GLVs can interact with plant hormones, primarily jasmonic acid, and thereby affect the plant's ability to defend against pathogens and thus serve as co-protagonists of the interaction between plants and different types of biotic stressors (Scala *et al*., 2013).

GLV biosynthesis occurs through the lipoxygenase pathway. For example, in cowpeas infested with Megalurothrips usitatus, two major C8 VOCs produced during the initial phases of thrip infestation were identified as 1-octen-3-ol and 2-ethyl-1-hexanol (He *et al*., 2025). The concomitant increase of the glycoside forms of these VOCs along with increases in lipoxygenase and hydroperoxide lyase transcript levels, suggest that an increase in production of these VOCs results from increased regulation of de novo synthesis of these VOCs through the induction of jasmonate by herbivores. Additionally, it was determined that 1-octen-3-ol displayed strong repellent activity toward the thrip and attracted its natural predator at low concentration, whereas 2-ethyl-1-hexanol displayed repellent activity towards the thrip but did not demonstrate a significant attractant effect towards the predator (He *et al*., 2025). In addition to the multi-functionality of GLVs in mediating insect-plant interactions, there is evidence that intact plants can communicate through the release of GLV. The literature suggests that plants exposed to GLVs produce defense-related VOCs indicative of herbivory, and therefore suggest that GLVs are involved in plant-plant communication (Ruther &

Frstenau, 2005). Maize plants exposed to naturally occurring GLVs [(Z)-3-,(E)-2- and saturated derivatives] stimulated the release of VOC blends typical of those released in response to herbivory. The position or configuration of a double bond, but not the functional group, affected the intensity of the VOC releases, with (Z)-3-configured compounds producing significantly greater VOC releases than (E)-2- and saturated derivatives (Ruther & Frstenau, 2005).

Phenylpropanoids and Aromatic Compounds

Phenylpropanoids comprise one other group of significant defense compounds in plant-insect interactions. Tea plants contain (Z)-3-hexenyl acetate which is recognized as a compound that is associated with resistance to herbivores, where a defensive pathway that begins from the transcription factor NAC and TCP for the BAHD acyl transferase catalyzing its synthesis (Gu *et al.*, 2024). Enzyme CsCHAT1 converts (Z)-3-hexenol into 3-HAC and suppression of CsCHAT1 reduces the amount of 3-HAC produced and the resistance of tea plants to geometrid caterpillars. Transcription factors CsNAC30 and CsTCP11 are co-expressed with CsCHAT1 and regulate its expression (Gu *et al.*, 2024).

Phenylpropanoid pathways were identified through integrated analyses of transcriptome and metabolome information as key secondary metabolism pathways in S. habrochaites. Plants secreted higher concentrations of phenylpropanoids and flavonoids than cultivated tomatoes by up-regulating expression of relevant genes within the phenylpropanoid pathway (Wang *et al.*, 2024) contributing to increased resistance to phytophagous insects. Notably, virus induced silencing of Sl4CLL6 resulted in both a reduction in gene expression of genes downstream of the phenylpropanoid biosynthesis pathway and also a decrease in resistance to mites in tomato (Wang *et al.*, 2024).

The dynamic modulation of phenylpropanoid pathway metabolites have important functions in regulating plant defenses. Herbivorous feeding of the fall armyworm down-regulated the expression of genes involved in monolignol biosynthetic pathway and their associated phenolic intermediate metabolites at 10 days post-infestation in sorghum challenged by fall armyworm (Grover *et al.*, 2022). However, resistant genotypes showed elevated levels of flavonoid compounds after feeding indicating a shift of precursor utilization from the lignin biosynthesis pathway to the flavonoid pathway. Bioassay studies using sorghum lines exhibiting altered levels of flavonoids supported genetic evidence that flavonoids provide critical resistance against fall armyworm (Grover *et al.*, 2022).

Plant-Plant Communication via HIPVs

Herbivore-induced plant volatiles are not only useful for attracting natural enemies but also for communicating with other plants to create defensive responses within their immediate area. Plants attacked by insects will release chemical signals that help neighboring plants to accumulate jasmonic acid, reducing the chances of being attacked by herbivores (Jing *et al.*, 2020). Six chemicals were shown to be produced by geometrid caterpillar attack on tea plants. The most effective compound at producing JA in neighboring intact plants is (E)-4,8-dimethyl-1,3,7-nonatriene (DMNT), which results in higher resistance to insects attacking those intact plants. Jing *et al.* (2020) reported that CsCYP82D47 was determined to be a P450 enzyme that converts (E)-nerolidol to DMNT.

Guava plants, when grown in close proximity to citrus plants in an intercropped system, increase jasmonate-dependent herbivore resistance in citrus plants through volatile organic compounds (VOCs) that prime the defense signaling pathway (Ling *et al.*, 2022). Guava plants produce large amounts of (E)-β-caryophyllene and (E)-4,8-dimethyl-1,3,7-nonatriene (compounds similar to those that produce JA in neighboring plants), thereby increasing resistance to Asian citrus psyllid (ACP) feeding on citrus plants. Additionally, exposure to VOCs emitted by guava plants increases indirect defense in citrus plants through attraction of the parasitic wasp Tamarixia radiata (Ling *et al.*, 2022).

Herbivores damaging plants below ground can cause significant releases of volatile organic compounds (VOCs) above ground that will provide increased resistance to neighboring plants (Thompson *et al.*, 2023). Damaged plants released more (E)-β-ocimene, a key VOC in the systemic HIPV blend, than non-damaged control plants; however, exposure to systemic HIPVs was shown to increase the resistance of neighboring plants to above ground squash bug attacks. Additional research indicated that β-ocimene alone is capable of eliciting plant resistance to squash bug attacks, providing evidence of another type of volatile-mediated interaction between plants that spans the entire spectrum of the soil/plant/above ground ecosystems (Thompson *et al.*, 2023).

Table 2: Major Classes of Herbivore-Induced Plant Volatiles and Their Ecological Functions

Compound Class	Representative Compounds	Biosynthetic Pathway	Ecological Functions	Refrences
Plant Species	Reference	Monoterpenes	Linalool, β-ocimene, α-pinene, β-myrcene	
Mevalonate/MEP pathway	Attract natural enemies, prime neighboring plants, direct toxicity	Cotton, maize, tobacco		(Niu *et al.*, 2024; Par & Tumlinson, 1997)
Sesquiterpenes	(E)-β-caryophyllene, (E)-β-farnesene, α-farnesene, DMNT	Mevalonate pathway	Belowground-aboveground signaling, attract parasitoids, induce plant defenses	
Tea, guava, citrus		Green Leaf Volatiles (GLVs)	(Z)-3-hexenal, (Z)-3-hexenol, (Z)-3-hexenyl acetate	
Lipoxygenase pathway	Plant-plant communication, direct repellence, prime defenses	Tea, cowpea, maize		(Gu *et al.*, 2024; Y. He *et al.*, 2025; Scala *et al.*, 2013)
Aromatic Compounds	Indole, methyl salicylate, methyl anthranilate	Shikimate pathway	Systemic signaling, attract predators, antimicrobial activity	
Cotton, pomegranate, rice		Homoterpenes	(E)-4,8-dimethyl-1,3,7-nonatriene (DMNT)	(sakni *et al.*, 2025; Par & Tumlinson, 1997)
Terpene degradation	Long-distance signaling, induce neighboring plant defenses	Tea, citrus, Arabidopsis		(Jing *et al.*, 2020; Ling *et al.*, 2022)

Behavioral Ecology of Insect-Plant Interactions

Host Plant Selection and Recognition

Beginning with the selection of host plants, the decision to select a host plant can be one of the most important behavioral choices that phytophagous insects make; it will directly influence their survival, their reproductive success, and overall fitness. Odorant binding proteins (OBPs) are key features of chemoreception in host plant selection by phytophagous insects, since OBPs facilitate chemical communication between insects and vertebrates (Zhou *et al.*, 2015). The process of selecting a host plant is composed of several steps that include long distance orientation towards a host plant using volatile cues, contact evaluation during landing, and eventually accepting or rejecting a host plant based on an integration of all available sensory information (Bruce, 2014).

Glycaspis brimblecombei, the psyllid, selects the eucalyptus tree (Eucalyptus camaldulensis), and in this selection the psyllid recognizes the host plant's volatiles using odorant-binding proteins. As well as being part of many behaviors, such as intersexual communication, oviposition and interaction with the host plant (Abla *et al.*, 2025), the OBP plays a critical role in many behaviors exhibited by insects. The essential oils collected from the leaves of the eucalyptus trees that were infested by G. brimblecombei were analyzed using gas chromatography-mass spectrometry and found to contain 66 compounds. Among the identified compounds, the three major components included p-cymene, α-phellandrene, and cryptone. Of the identified compounds, nine compounds (farnesol, nerolidol, several farnesals, and several linalool derivatives) had the lowest Gibbs free energy values, indicating favorable interactions with the hydrophobic cavity of the OBP CcapOBP22 (Abla *et al.*, 2025). Functional studies of olfactory genes have made possible the understanding of the molecular basis of host plant recognition. The study of Diorhabda tarsalis demonstrated how interfering with the expression of the olfactory receptor co-receptor (Orco) affected host recognition. After RNAi treatment of D. tarsalis that targeted the Orco gene, the beetles lost their ability to find hosts (Chen *et al*., 2022). In addition, DtarORco, DtarOR7, and DtarOR26 were specifically expressed in the antennae of D. tarsalis, and after the RNAi treatment, the relative expression level of DtarORco in the antennae significantly decreased, and electrophysiological responses to host location odor signals significantly decreased (Chen *et al*., 2022).

Oviposition Site Selection and Pheromone Communication

Oviposition in female insects is one of the most important activities for them to perform and it will have a significant impact on her fitness and the success of her offspring (Zhang & Wang, 2025). A female's choice of an appropriate place for laying her eggs is necessary for the continued growth of her offspring and to minimize competition for resources among members of the same or other species (Zhang & Wang, 2025). While this process is based upon multiple sensory modalities (e.g. visual, mechanical), chemosensory information is one of the primary sources of information for females during oviposition. Oviposition deterring pheromones are examples of chemical signals which have been shown to influence oviposition behaviors and thus provide an additional form of communication among both intra- and interspecific individuals (Zhang & Wang, 2025).

Chemical signals including volatile organic compounds (VOCs) play an important role in the identification of potential oviposition sites. Many studies have demonstrated the role of VOCs in selecting oviposition sites for various insect plant associations. For example, seventeen electoantennogram active compounds were identified from the floral VOCs of cowpea from which the legume pod borer Maruca vitrata was attracted. Two new general odorant-binding proteins (MvitGOBP1 and MvitGOBP2) were identified from the antennae of M. vitrata and were purified and studied using fluorescence binding assays (J. Zhou *et al*., 2015). The binding affinities for each protein were determined for 17 individual volatile odorants. Using field trapping methods, the authors demonstrated that 6 floral VOCs were capable of attracting female moths to the traps. The combination of data obtained from the bioassays indicated that MvitGOBPs and the identified floral VOCs are likely to be involved in the olfactory response behavior of female moths and therefore may be of importance in the selection of oviposition sites (Zhou *et al*., 2015).

Pheromone mediated communication is essential in both locating mates and in the reproductive behavior of the individual communicating the pheromone. In the case of tephritid fruit flies, the intra-specific communication system is comprised of a complex series of sensory cues that are both species and sex specific (Scolari *et al*., 2021). There are three types of chemical signals used in communication among tephritid fruit flies: long distance pheromones produced by either sex, cuticular hydrocarbons having low volatility and therefore acting at medium to short distances as well as being deposited onto surfaces or bodies of insects and host marking compounds which are deposited on fruit after oviposition. Each type of chemical cue provides essential information regarding multiple aspects of a fruit fly's life history including the location of a suitable mate or suitable host for oviposition (Scolari *et al*., 2021).

Insects use pheromones not only for communication with other insects but also to elicit responses from plants, resulting in fascinating feed back mechanisms within chemical ecology. Pine exposed to the sex pheromones of the pine sawfly Diprion pini exhibited enhanced defenses against the eggs laid by the sawfly and the survival rate of the eggs laid on pheromone treated pine needles was lower than those on untreated pine (Rahman-Soad *et al*., 2024). Sawfly females were unable to distinguish between the odors of pheromone-treated and untreated pine using olfactory tests alone; however, when given the opportunity to contact the trees, more untreated than treated trees received eggs, suggesting that sawflies have evolved counteradaptation to the pine responses (Rahman-Soad *et al*., 2024).

Mate Recognition and Sexual Communication

Insects recognize their mates and communicate sexually using species specific pheromone blends which are recognized by specialized olfactory receptors. Sex pheromone communication in Lepidoptera moths is one of the best studied models where males detect the signals emitted by females for large distance (Ray & Mohanty, 2025). Pheromone binding proteins central to this process bind to and transport hydrophobic pheromones into the sensillar lymph toward the olfactory receptors, providing the ability to specifically receive the signal (Ray & Mohanty, 2025).

That specificity of pheromone reception was demonstrated by characterizing the function of pheromone receptors. The candidate pheromone receptors CpomOR1, CpomOR3, and CpomOR6a from the codling moth *Cydia pomonella*, belong to the pheromone receptor lineage (Cattaneo *et al*., 2017). These receptors were expressed heterologously in Drosophila olfactory sensory neurons and human embryonic kidney cells; electrophysiology and calcium imaging studies demonstrated that each of the receptors formed a functional ionotropic receptor channel. CpomOR3 responded to the plant volatile compound pear ester ethyl-(E,Z)-2,4-decadienoate, and CpomOR6a responded to the strong pheromone antagonist codlemone acetate showing the complexity of the interaction of pheromones and host volatiles (Cattaneo *et al*., 2017).

Host shift may alter mating behavior due to changed chemical signaling. For example, when males of the seed predator *Acanthoscelides obtectus* underwent artificial host shifts onto bean or chickpea, the composition of male sex pheromone blends differed among host lines (Vuts *et al*., 2018). Females of the bean host line did not differentiate between the pheromone blends, but those of the chickpea and chickpea/bean host lines preferred the chickpea pheromone blend. However, electrophysiological responses of the antennal tissues of the three female host lines to male odor were similar, and all of the females preferred the males that had been reared on beans, demonstrating that host shifts leading to the development of divergent chemical signaling systems does not always lead to the formation of host races (Vuts *et al*., 2018).

Chemosensory Divergence and Speciation

Chemosensory communication plays an incredibly vital role in the lives of insects and contributes to many biological processes, such as mate finding, foraging, and oviposition behaviors. These traits also play a crucial role during the process of speciation; in which, chemical perception can act as a barrier for the formation of new species (Schooten *et al*., 2020).

The genetic architecture of chemoperception and the role of chemosensing during speciation was examined through both genomic and transcriptomic methods in Heliconius butterflies. The research provided an accurate and complete representation of how chemosensory gene expression relates to sensory tissue, sex, and life-stage in Heliconius butterflies (Schooten *et al*., 2020).

Out of the 252 chemosensory genes found in Heliconius butterflies, HmOBP20 (involved in detecting volatile) and HmGr56 (a putative synephrine-related receptor), were among the strongest candidate genes for chemosensory divergence due to differences in detecting pheromones and host plants, respectively (Schooten *et al*., 2020). Neither of these genes are physically linked to wing color-pattern loci or other genomic areas that are directly related to visually mediated mate preference and therefore provide evidence for chemosensory divergence between rarely hybridizing butterflies that have similar mate and host plant preferences and support a polygenic model of the species boundary (Schooten *et al*., 2020).

An additional example of species-specific chemically-mediated mutualistic species interactions influencing trait evolution and lineage diversification are those between the cycad and the weevil pollinator (Salzman *et al*., 2021). In addition to being significantly more different than other characteristics of closely related species of Zamia cycads, the volatile compounds produced by the Zamia cycads are also more strikingly different than other phenotypic characters. Two distantly related pollinating weevil species have specialized responses only to volatile compounds from their respective host Zamia species. Furthermore, approximately a fifth of genes related to volatile compound production in plant transcriptomes are experiencing positive selection, thus emphasizing that chemical signaling acts as a major driver of co-evolutionary processes occurring between cycads and their weevil pollinators (Salzman *et al*., 2021).

Plant Defense Mechanisms: Secondary Metabolites and Resistance

Classification of Plant Secondary Metabolites

Agricultural scientists have studied the effects of many types of chemical compounds that can affect insect herbivore populations through a number of mechanisms. Alkaloids, Terpenoids, Phenolic Compounds, Sulfur-, and Nitrogen-containing Metabolites represent classes of plant secondary metabolites that are used for their potential anti-feedant properties, as well as their potential to kill insects, such as aphids; disrupt normal physiological processes leading to increased mortality among herbivorous insects; and increase the attractiveness of the herbivorous insects to natural enemies (Farhan *et al*., 2024).

Secondary metabolites from plants have shown promise as biopesticides in agricultural settings because they offer many of the same benefits as traditional synthetic pesticides with fewer negative environmental impacts (Farhan *et al*., 2024). Secondary metabolites have evolved to serve a variety of roles within the plant, including the ability to defend against pathogens and herbivores, as well as play roles in regulating various defense-related signaling pathways (Divekar *et al*., 2022).

Upon herbivore injury, a series of events occur that ultimately result in the production and accumulation of secondary metabolites (Divekar *et al*., 2022). The process of producing these metabolites is regulated by the interaction of various signaling molecules, including phytohormones and plant volatile metabolites produced by plants upon injury by herbivores, which have the ability to either induce or prime the plant's defense signaling pathway(s) via hormone-mediated signaling (Divekar *et al*., 2022).

In addition to providing a means of understanding the potential for plants to resist insect herbivory in general, research on secondary metabolites has provided significant insights into how these compounds function in specific agricultural systems. For example, in Kenya, secondary metabolites present in common food crops such as maize, beans, and tomatoes have been shown to serve as both toxic compounds and chemical deterrents that alter the behavior and physiology of herbivorous insects (Mwaura, 2024). These secondary metabolites are essential to developing sustainable methods for controlling insect herbivores in agricultural ecosystems by providing native alternatives to the use of synthetic pesticides and maintaining ecological balance (Mwaura, 2024).

Alkaloids and Nitrogen-Containing Compounds

Wild species generally show higher levels of secondary metabolites than cultivated species, which can contribute to an important role for wild species in providing high-quality traits for agricultural purposes (Dilish *et al*., 2025). The ability of a plant to produce alkaloids varies greatly among different species and cultivars, as well as the types of environmental stresses and agronomic practices a plant is exposed to (Wu *et al*., 2025). Secondary metabolite production can be influenced by numerous factors including light quality, soil condition, and water availability; as a result, factors like these can also influence the biosynthesis of alkaloids (Wu *et al*., 2025). Pyrrolizidine alkaloids are used as a defense mechanism by Chromolaena odorata; these alkaloids act as chemical defense agents against natural predators, which contributes to the invasive potential of this species in new habitats (KatoNoguchi & Kato, 2023). Alkaloids are produced in response to biotic stresses by storing the alkaloids within specialized structures, and they can be used as a direct defense against herbivores through toxic or repellent properties or indirectly by attracting the natural enemies of the herbivore (Khayri *et al*., 2023).

Phenolic Compounds and Flavonoids

Phenolic compounds and Flavonoids are a key group of metabolites that play an important role in plant defense metabolism. They have demonstrated potential for use as chemical signals in biotic and abiotic stress responses. In the absence of environmental stressors, flavonoids play a variety of roles in seed development and longevity, seed maturation, and pollen tube development; under environmental stressors, they participate in plant defense mechanisms through the production of secondary metabolites.

The antifungal and anti-insect activities of phenylpropanoids have been well-documented. In particular, phenylpropanoids exhibit antifungal activity against three species of fungi, Fusarium oxysporum, Rhizoctonia solani, and Alternaria alternata (Kumar *et al*., 2023). Increased concentrations of flavonoids in plants infested with insects will result in reduced populations of insects that can cause damage to plants and facilitate virus transmission. In addition, studies have shown that activation of the PAL gene in the early stages of the phenylpropanoid biosynthetic pathway occurs post-infection; other genes involved in the phenylpropanoid biosynthesis process are activated at a later stage of the infection response (Kumar *et al*., 2023).

Metabolomics and Transcriptomics of Color-Dependent Resistance Mechanisms in Quinoa Plants Challenged with Spodoptera exigua Resistant quinoa varieties exhibited significantly increased concentrations of ferulic acids and lignins, which are structural components of cell walls, to increase resistance to insect attack. Significant increases were also observed in the expression of anthelmintic differential metabolites (e.g., indole-3-acetic acid, choline, ferulic acid, caffeic acid, and anthranilic acid) (Liu *et al*., 2025). Structural genes regulated by Kaempferol and Kaempferol-3-O-rhamnoside, along with MYB/MYB-related transcription factors, were expressed at high levels in resistant quinoa varieties challenged with S. exigua (Liu *et al*., 2025).

Induced Resistance and Hormonal Signaling

Induced Resistanc a dynamic defense strategy plants defend themselves after an attack, potentially reducing the amount of pesticides required in pest control (Gaddam *et al*., 2024). Elicitors cause a rise in Secondary Metabolism which creates resistance to insects and allows for manipulation of resistance in the host plant. Jasmonic Acid is an exogenous chemical that has been shown to induce insect resistance in many different plant species. In Daylily (Hemerocallis) that was under attack from Thrips palmi, treated leaves had much greater amounts of secondary metabolites than non-treated leaves. The secondary metabolites were tannins, flavonoids, and total phenols. There was also greater activity of the defense enzymes peroxidase, phenylalanine ammonia lyase, polyphenol oxidase, and protease inhibitor (Sun *et al.*, 2024).

The Molecular Mechanisms Involved in Induced Resistance are Complex Signaling Networks. Genes that were differentially expressed were involved in pathways such as lignin biosynthesis, cell wall thickening, antioxidant enzyme synthesis, and protease inhibitor and secondary metabolite biosynthesis (Sun *et al.*, 2024). Weighted Gene Co-Expression Network Analysis Identified Key Genes Involved in Stomatal Regulation, Lipid Barrier and Polymer Biosynthesis, Alkaloid Biosynthesis, and Salicylic Acid and Ethylene Biosynthesis Pathways. These Findings Provide a Scientific Basis for the Utilization of Antagonist Hormones in Pest Management (Sun *et al.*, 2024).

Table 3: Major Classes of Plant Secondary Metabolites and Their Defense Functions Against Insect Herbivores

Metabolite Class	Representative Compounds	Mode of Action	Target Insects	Plant Species	Reference
Alkaloids	Pyrrolizidine alkaloids, nicotine, caffeine	Toxicity, feeding deterrence, growth inhibition	Generalist herbivores, lepidopteran larvae	Chromolaena odorata, tobacco, coffee	(Khayri *et al.*, 2023; KatoNoguchi & Kato, 2023)
Phenolics	Chlorogenic acid, caffeic acid, ferulic acid, tannins	Antifeedant, protein precipitation, oxidative stress	Aphids, caterpillars, beetles	Quinoa, daylily, lentil	(Liu *et al.*, 2025; Sun *et al.*, 2024; Zafeiriou *et al.*, 2022)
Flavonoids	Kaempferol, quercetin, isoquercetin, rutin	Antioxidant, enzyme inhibition, antimicrobial	Aphids, thrips, mites	Quinoa, sorghum, tomato	(Grover *et al.*, 2022; Liu *et al.*, 2025; Wang *et al.*, 2024)
Terpenoids	Elemene, gossypol, DIMBOA	Direct toxicity, repellence, growth regulation	Aphids, lepidopteran larvae, hemipteran pests	Tea, cotton, maize	(Luo *et al.*, 2025; Navya *et al.*, 2025)
Glucosinolates	Indole glucosinolates, aliphatic glucosinolates	Isothiocyanate release, deterrence	Specialist and generalist herbivores	Brassica species, Arabidopsis	(Vos *et al.*, 2008)
Saponins	Triterpenoid saponins, steroidal saponins	Membrane disruption, deterrence, toxicity	Beetles, aphids, nematodes	Camellia, alfalfa, various legumes	(Shakeel *et al.*, 2025; S. Zhang *et al.*, 2020)

Applications in Sustainable Agriculture and Integrated Pest Management

Semiochemical-Based Pest Management Strategies

Semiochemicals are increasingly being used in a variety of ways that are useful for farmers who want to manage pests in their agricultural systems. Several methods have been found to be useful for integrated pest management. One new method is Specialized Pheromone and Lure Application Technology (SPLAT), which has been developed to decrease pest populations through interference with mating, attraction and elimination of insects, or repulsion of insects (Panigrahi *et al.*, 2025). The wax-based SPLAT formulation provides for slow and consistent release of pheromones over a period of time and will provide effectiveness for up to two weeks or up to six months based upon environmental conditions (Panigrahi *et al.*, 2025). SPLAT has been successfully applied in a number of different crops, including SPLAT-PBW, which reduced male moth catches and boll damage in cotton, and SPLAT-BSFB, which reduced damage to shoots and fruits of brinjal (Panigrahi *et al.*, 2025).

Another method is the "push-pull" strategy, which represents a second example of a successful application of chemical ecology principles for managing pests. The "push-pull" strategy includes the combination of repellent and attractive semiochemicals to modify the behavior of insects for protecting crops (Liu *et al.*, 2025). Approaches using chemical ecology for modifying insect behavior for managing pests have significant potential for developing sustainable approaches for managing pests. Odorant binding proteins represent key molecular targets for controlling the behavior of insects. Isoeugenol derivatives rationally engineered by identifying specific OBPs demonstrate outstanding bioactivity, including both high levels of pest repellency and attractiveness to beneficial insects (Liu *et al*., 2025).

Monitoring and Mass Trapping

The use of semiochemicals has been successful as tools to monitor pest populations, and to implement large-scale trapping techniques. There is considerable interest in the application of semio-chemicals to develop and utilize chemical cues for pest control. A number of compounds have been identified and utilized to detect both native and exotic species of insects and their impact on crops through mass trapping and/or annihilation, mating disruption, behavioral modification, or prevention of location of hosts. Due to specificity, high biodegradability, and low usage levels, the utilization of such compounds could be an ecologically friendly substitute for insecticides in the context of ecological pest management (Kumar, 2016).

Semio-chemical based attractants have shown practical effectiveness in the field. Six floral volatile compounds that were identified from cowpeas were effective at attracting female moths and there was a statistically significant difference when compared to blank lures (Zhou *et al*., 2015). Such compounds will likely contribute to further exploration of efficient methods for monitoring and developing integrated pest management strategies for this pest in the field. Developing mixtures of attractants that simulate the natural volatiles emitted by plants can lead to both monitoring populations of pests and reducing damage to crops through targeted trapping (Zhou *et al*., 2015).

Enhancing Biological Control

Herbivore-induced plant volatiles are critical to the tri-trophic interactions in that they attract natural enemy's of herbivores; thus, manipulation of the signal can enhance the efficacy of biological control (M. *et al*., 2024). The VOCs acting as indirect defense mechanisms recruit the natural enemy's and the interaction among physical attributes, chemical signals, and semi-chemicals will be significant in influencing the interaction of the three trophic levels. Although, there has been progress made in understanding HIPV's it appears that there is variability in volatile emission and effectiveness based on the various herbivore species and developmental stage of herbivores (M. *et al*., 2024).

Further enhancement of pest suppression may occur when beneficial microorganisms are integrated into the semiochemical signaling. For example, Trichoderma harzianum treatments have been shown to induce a "primed" state in tomato plants that upon aphid attacks results in increased attraction of parasitoids, and this was found to be mediated through an enhanced emission of VOCs that are known to elicit parasitoid flight responses (Coppola *et al*., 2017). Transcriptome sequencing of Trichoderma treated plants infested with aphids indicated a remarkable increase in the transcription of genes involved in terpenoid biosynthesis and salicylic acid pathways consistent with the observed parasitoid flight response (Coppola *et al*., 2017).

Breeding for Enhanced Chemical Defenses

Breeding plants with a greater level of natural defense against pests has the potential to result in higher yields by using genetic information regarding secondary metabolism. The discovery of critical genes and transcription factors for biosynthetic pathways for defensive compounds will provide a target for metabolic engineering (Luo *et al*., 2025). For example, MYC2a, a transcription factor, is known to activate the synthesis of terpene synthases that are important for elemene production; therefore, this research has increased our knowledge of how transcription factors regulate volatile compounds produced as an attack by a pest, and provided new evidence of the ecological significance of terpene volatiles when exposed to biotic stress (Luo *et al*., 2025). However, domestication and selective breeding have reduced the natural defensive capabilities of many crops, which has emphasized the need to utilize both wild relatives and recent advances in genetics for restoring and increasing crop defenses (B *et al*., 2025). Secondary metabolites occur at a higher rate in wild plant populations than in domesticated plant populations; therefore, it is recommended to maintain wild plant populations to preserve desirable traits and include secondary metabolite rich characteristics in future agricultural practices (Dilish *et al*., 2025). Marker assisted selection, and genomics can be used to introduce favorable alleles from wild relatives into cultivars (B *et al*., 2025).

Table 4: Semiochemical-Based Strategies for Sustainable Pest Management

Strategy	Mechanism of Action	Semiochemicals Used	Target Pests
Advantages	Reference	Mating Disruption	Interfere with mate finding by saturating environment with pheromones
Sex pheromones (SPLAT formulations)	Lepidopteran pests (cotton bollworm, brinjal shoot borer)	Long-lasting release, species-specific, low environmental impact	(Panigrahi *et al*., 2025)
Push-Pull Systems	Repel pests from crops while attracting to trap plants	Repellent and attractant volatiles (verbenone, nonhost volatiles)	Bark beetles, stem borers
Dual mechanism, enhances biodiversity	(Y. Liu *et al*., 2025)	Mass Trapping	Attract and capture large numbers of pests
Host plant volatiles, aggregation pheromones	Fruit flies, pod borers, weevils	Population suppression, monitoring capability	(Kumar, 2016; J. Zhou *et al*., 2015)
Attract Natural Enemies	Enhance biological control by recruiting predators/ parasitoids	HIPVs (DMNT, β-caryophyllene, methyl salicylate)	Aphids, caterpillars, whiteflies
Sustainable, enhances ecosystem services	(Coppola *et al*., 2017; Ling *et al*., 2022)	Behavioral Manipulation	Disrupt host-finding and oviposition
OBP-targeted compounds, non-host volatiles	Aphids, thrips, various herbivores	Target-specific, novel mode of action	(Liu *et al*., 2025; Wagner *et al*., 2024)

Conclusion

Semiochemical-mediated interactions between insects and plants represent a remarkable example of evolutionary adaptation and ecological complexity. The chemical dialogue between these organisms encompasses a vast array of volatile and non-volatile compounds that govern fundamental biological processes including host selection, mate recognition, defense activation, and tritrophic interactions. Our understanding of these systems has advanced substantially through the integration of chemical ecology, molecular biology, neuroscience, and behavioral ecology, revealing intricate mechanisms at multiple levels of biological organization.

The molecular architecture of insect olfaction, centered on odorant-binding proteins, olfactory receptors, and chemosensory proteins, demonstrates sophisticated specialization for detecting and discriminating among thousands of chemical signals. These proteins not only facilitate odor perception but also contribute to immune functions, highlighting their multifaceted roles in insect physiology. The discovery of novel signal transduction pathways, including the role of inositol trisphosphate as a second messenger, continues to reshape our understanding of how chemical signals are converted into behavioral responses.

Plant defense strategies mediated by secondary metabolites and herbivore-induced volatiles showcase the dynamic nature of plant responses to insect attack. The biosynthesis of terpenoids, phenolics, alkaloids, and green leaf volatiles involves complex regulatory networks integrating hormonal signaling, transcriptional control, and environmental inputs. These compounds serve multiple functions, acting as direct toxins, feeding deterrents, attractants for natural enemies, and signals for plant-plant communication. The induced nature of many defensive responses allows plants to allocate resources efficiently while maintaining flexibility in responding to diverse herbivore threats.

From a behavioral ecology perspective, insects have evolved remarkable abilities to navigate complex chemical landscapes, integrating information from multiple sources to make adaptive decisions about host selection, oviposition, and mate choice. The plasticity of these behaviors, modulated by learning and experience, enables insects to respond to spatial and temporal variation in their environment. Chemical communication also plays pivotal roles in speciation processes, with divergence in chemosensory genes and pheromone profiles contributing to reproductive isolation and the formation of host races.

The application of semiochemical knowledge to sustainable agriculture holds tremendous promise for reducing reliance on synthetic pesticides while maintaining crop productivity. Strategies including mating disruption, push-pull systems, and enhancement of biological control through volatile manipulation have demonstrated practical efficacy across diverse agricultural systems. The development of novel attractants and repellents based on understanding of olfactory protein function represents a frontier for innovation in pest management. Furthermore, breeding approaches that enhance natural chemical defenses while maintaining agronomic performance offer pathways toward more resilient cropping systems.

Looking forward, several research frontiers merit continued investigation. The integration of multi-omics approaches with field ecology will enhance understanding of how chemical interactions function in natural and agricultural ecosystems under varying environmental conditions. Climate change impacts on volatile emission, perception, and effectiveness require systematic study to predict and mitigate potential disruptions to chemical communication networks. Advances in genome editing and synthetic biology offer opportunities to engineer crops with optimized defensive chemistry, though such applications must be carefully evaluated for ecological and evolutionary consequences. Finally, translating laboratory findings into practical pest management tools requires continued collaboration among chemical ecologists, entomologists, plant scientists, and agricultural practitioners.

The study of semiochemical-mediated insect-plant interactions exemplifies how fundamental research in chemical ecology can yield both theoretical insights into evolutionary processes and practical solutions to applied challenges. As global agriculture faces mounting pressures from pest pressures, climate change, and environmental degradation, harnessing the power of chemical communication offers a sustainable path forward that works with natural processes rather than against them. Continued investment in understanding these fascinating systems will be essential for developing the next generation of environmentally sound pest management strategies and ensuring food security for growing human populations.

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