__Review Article__

A Comprehensive Review of Advances in Semiochemical Exploitation for Insect Pest Management

Abstract

In recent years, semiochemical-based pest management strategies have gained significant attention as they offer sustainable alternatives to conventional pesticides. The integration of semiochemicals into pest management strategies presents innovative approaches to addressing agricultural challenges. One promising method involves combining pheromones with entomopathogenic fungi, utilizing a "lure and infect" technique that attracts pests to fungal pathogens, enhancing control efficacy. Another advancement is the auto-dissemination approach, which promotes the spread of microbial pathogens within insect populations, effectively targeting pests like the fall armyworm. Additionally, the induction of plant defences through "plant vaccination" by zoophytophagous predators offers a novel way to enhance plant resistance against herbivores. Research into the production of insect pheromones in plants further supports sustainable pest management by disrupting pest mating behaviours. Electroantennography has emerged as a valuable tool for understanding insect olfaction, aiding in the identification of effective semiochemicals. The push-pull strategy employs plant semiochemicals to manipulate pest behaviour, while pheromone dispensers provide efficient and long-lasting applications of these compounds. Collectively, these advancements highlight the potential of semiochemicals in revolutionizing pest management practices, aligning with the increasing demand for sustainable agricultural solutions. Continued research and innovation in these areas are crucial for optimizing the use of semiochemicals, ultimately contributing to more effective and environmentally friendly pest control methods.

Key Words: Auto-dissemination, Electroantennography, Pheromone dispensers, Plant vaccination, Push-pull strategy, Semiochemicals, Trapping techniques

Introduction

The 21st century is a time of great challenges for global agriculture, with the world population expected to reach about 10 billion by 2050 (United Nations, 2019). This demographic shift requires a significant increase in crop productivity; however, at the same time, there is growing pressure to reduce the use of conventional chemical pesticides due to environmental and health concerns (Popp *et al.,* 2013). Consumers are increasingly demanding safe, healthy food with minimal chemical residues, driving the need for sustainable agricultural practices (Reganold and Wachter, 2016). To address these complex challenges, innovative solutions are required to enhance crop yield and quality while managing pest resistance and minimizing environmental impact. In this context, semiochemicals have emerged as a promising alternative to conventional pesticides, offering a more targeted and environmentally friendly approach to pest management (Pickett and Khan, 2016). Semiochemicals are chemicals that mediate interactions between organisms (Nordlund and Lewis, 1976; Agelopoulos*et al.*, 1999), derived from the Greek word "semeion" meaning sign or signal. These compounds can be classified into two main categories: pheromones that facilitate communication within species and allelochemicals that mediate interactions between different species (Whittaker and Feeny, 1971). The application of semiochemicals in agriculture aligns with the principles of Integrated Pest Management (IPM), providing effective tools for pest control while reducing reliance on broad-spectrum insecticides (Witzgall *et al.*, 2010). While extensive research has been conducted on lepidopteran pheromones, recent studies have expanded to non-lepidopteran groups including Hymenoptera, Isoptera and Hemiptera (Zarbin *et al.,* 2009). This broadening scope of research reflects the growing recognition of semiochemicals' potential across diverse pest species. Advances in molecular research have greatly improved our understanding of the mechanisms underlying semiochemical action. Studies on Pheromone Receptors (PRs) have shed light on how insects recognize and decode pheromone signals, providing valuable insights for the development of more effective pest management strategies (Touhara and Vosshall, 2009). This molecular-level understanding is crucial for optimizing the use of semiochemicals in agricultural applications. In addition to basic research, practical innovations in semiochemical deployment are gaining attention. The exploration of meso- and mega-pheromone dispensers represents a potential breakthrough in pheromone-based pest control methods (Miller and Gut, 2015). These novel dispensing systems offer the promise of more efficient and long-lasting semiochemical applications, potentially enhancing the efficacy and economic viability of pheromone-based pest management strategies. Semiochemicals play diverse roles in insect ecology, influencing behaviours such as mate location, aggregation, host finding, and oviposition site selection (Baker, 2002). By manipulating these natural chemical signals, it is possible to disrupt pest behaviours, attract pests to traps or repel them from crops offering multiple avenues for pest control (Cook *et al.,* 2007; Agelopoulos*et al.,* 1999). Furthermore, semiochemicals can be used to influence the behaviour of natural enemies of pests offering opportunities for biological control within IPM frameworks (Vet and Dicke, 1992; Agelopoulos*et al.,* 1999). As we continue to face the dual challenges of increasing agricultural productivity and environmental sustainability, exploiting semiochemicals for insect pest management offers a promising way forward. This review article aims at exploring recent advances in semiochemical research and application highlighting their potential to revolutionize pest management practices in the 21st century and beyond.

Semiochemicals in IPM: Market Trends and Types

Semiochemicals are chemical substances that mediate communication between organisms, playing a crucial role in insect behaviour and ecology. These compounds convey information about various aspects of the environment, such as mate location, territory marking, danger signaling, and coordination of group activities (Cork, 2004). The global semiochemicals market was valued at $4.74 billion in 2022 and is expected to grow at a CAGR of 15.84 per cent from 2023 to 2030 to reach $15.36 billion by 2030 (Semiochemicals Market, 2022). Insect sex pheromones currently dominate the semiochemicals market with a share of 69 per cent, followed by aggregation pheromones at 25% (Rizvi *et al.,* 2021). These chemicals play a crucial role in managing lepidopteran pests which account for approximately 82 per cent of their use while dipteran pests constitute about 7 per cent (Rizvi *et al.,* 2021). The Asia Pacific region is expected to witness the fastest growth in the semiochemicals market due to factors such as increased government support, adoption of sustainable agricultural practices and rise in pest-related challenges. Semiochemicals also play an important role in pre-border biosecurity providing effective tools for detection and eradication of invasive species thereby contributing significantly towards global agricultural sustainability and pest management (Rizvi *et al.,* 2021).

Semiochemicals can be broadly classified into two main categories: pheromones that facilitate intraspecific communication; and allelochemicals that mediate interspecific interactions (Table 1). Pheromones are species-specific chemical signals that enable communication between individuals of the same species. These compounds can trigger behavioural or physiological changes in the recipient (Karlson and Luscher, 1959). Several types of pheromones have been identified based on their functions (El-Ghany, 2019).

Aggregation pheromones attract individuals of both sexes to food sources or reproductive habitats. For example, the hemiterpene 3-methylbut-3-en-1-ol serves as an aggregation pheromone for certain beetle pests (Bowers et al., 1991). Alarm pheromones alert conspecifics to potential threats. Sesquiterpenes like (E)-β-farnesene and germacrene A are common components of aphid alarm pheromones (Vandermoten*et al.,* 2012). Oviposition-deterrent pheromones discourage females from laying eggs in already occupied resources. This behaviour has been observed in fruit flies like *Rhagoletispomonella* (Prokopy *et al.,* 1982). Home recognition pheromones such as queen pheromones in social insects enable colony members to identify their nest and queen (Meer and Preston, 2008). Sex pheromones mediate mate attraction and are primarily produced by females to attract males. The first characterization of a sex pheromone was reported in the silk moth Bombyx mori (Butenandt *et al.,* 1959). Trail pheromones guide social insects to food sources exhibiting both recruitment and orientation effects (McPheron *et al.,* 1997). Recruitment pheromones induce nestmates to leave the nest and migrate to work sites. These are often discharged from specialized exocrine glands (Meer and Preston, 2008). Royal pheromones such as hydrocarbon heneicosane in termites enable workers recognize reproductive individuals and maintain caste division (Funaro *et al.*, 2018).

Allelochemicals facilitate communication between different species and can be further categorized based on benefits conferred to the emitter and receiver (El-Ghany, 2019). Allomones benefit the emitter the, often serving as defence mechanisms against predators or herbivores. For example, nicotine produced by tobacco plants acts as a deterrent to herbivorous insects (Vilela and Della Lucia, 2001). Kairomones benefit the receiver such as predators using prey pheromones to locate their targets.One example is the orientation of checkered beetles to bark beetle aggregation pheromones (Poland and Borden, 1997). Synomones are advantageous to both the emitter and receiver. Floral scents that attract pollinators and herbivore-induced plant volatiles that recruit natural enemies of insect pests are examples of synomones. Antimones are maladaptive for both the emitter and receiver, often eliciting repellent responses in interspecific interactions (Vilela and Della Lucia, 2001). Apneumones are emitted by non-living sources and elicit responses in receiving organisms that may be beneficial to some species but harmful to others (Dougherty *et al.*, 1995).

Table 1: Comprehensive Classification of Semiochemicals and Their Functions

Type	Subtype	Function	Example	Target

				Organism
Pheromones	Aggregation	Attract both sexes to food sources or habitats	3-methylbut-3-en-1-ol	Beetles
	Alarm	Alert conspecifics to threats	(E)-β-farnesene	Aphids
	Sex	Mediate mate attraction	Bombykol	Silk moths
	Trail	Guide social insects to food sources	(Z)-9-hexadecenal	Ants
	Oviposition-deterrent	Discourage egg-laying in occupied resources	Methyl eugenol	Fruit flies
	Home recognition	Enable colony members to identify nest	Cuticular hydrocarbons	Social insects
	Royal	Enable recognition of reproductive individuals	Heneicosane	Termites
Allelochemicals	Allomones	Benefit emitter (e.g., defense)	Nicotine	Tobacco plants
	Kairomones	Benefit receiver (e.g., prey location)	Bark beetle aggregation pheromones	Predatory beetles
	Synomones	Benefit both emitter and receiver	Floral scents	Plants and pollinators
	Antimones	Maladaptive for both emitter and receiver	Geosmin	Various organisms
	Apneumones	Emitted by non-living sources	Green leaf volatiles	Plants (post-damage)

The understanding of semiochemicals has led to their extensive use in integrated pest management (IPM) strategies. Pheromones, in particular, have found widespread applications. Pheromone traps are used to monitor and detect pest populations, allowing for timely interventions. Mass trapping through large-scale deployment of pheromone traps can significantly reduce pest populations. Mating disruption, which involves the release of synthetic sex pheromones, can interfere with mate location, reducing pest reproduction. The attract-and-kill strategy combines pheromones with insecticides to lure and eliminate pests (Reddy *et al.*, 2020). Other semiochemicals also play important roles in pest management.

Attractants and repellents derived from various allelochemicals can be used to manipulate pest behaviour. Kairomones are employed in stimulo-deterrent diversion strategies, where pests are lured away from crops and towards trap crops or other control measures (Reddy *et al.,* 2020).

Semiochemicals in Insect-Plant Interactions: Mechanisms, Effects, and Applications in Pest Management

Insects are affected by semiochemicals that mediate different behaviors and physiological responses. Many active compounds have been isolated and identified from plant materials through phytochemical investigations, which have shown their various effects on insect pests (Hassan *et al.,* 2008; Salib*et al.,* 2014; Hassan *et al.,* 2015, 2016). These plant volatiles serve multiple functions for herbivorous insects such as food sources identification, mates' location, oviposition sites detection and hibernation locations (El-Ghany, 2019). Insects detect these compounds by stimulating chemoreceptor cells of taste sensilla present on antennae, tarsi and mouthparts (Miller and Strickler, 1984). The response of insects to plant volatiles can vary significantly from attraction to repulsion depending on the insect species and its adaptation to the host plant (El-Ghany, 2019). It is important to note that the classification of plant volatiles as attractants or repellents is not standardized because insect behavioral responses may fluctuate with concentration of these compounds (Reddy and Guerrero, 2004). Some insects have evolved to utilize host plant compounds as precursors for sex pheromones or as sex pheromones themselves. For example, male orchid bees collect terpenoid mixtures from orchids which they use as aggregation pheromones during mating (Dressler, 1982). Additionally, pyrrolizidine alkaloids are used by various insect species including moths butterflies, grasshoppers, beetles and aphids etc. as feeding deterrents against their natural enemies (Nishida, 2002).

The efficacy of semiochemicals in insect control strategies depends on several factors such as release rate and trap design. The release rate of semiochemicals is critical for trapping success because high levels of release may not necessarily result in increased insect captures and can even become repellent in the immediate vicinity of the trap. For example, studies on the red flour beetle, *Triboliumcastaneum*, have shown that high release rates of pheromones were neither attractive nor repellent to the beetles while older traps with lower release rates were more effective (Hussain *et al.,* 1994; Phillips, 1994). Trap design is another crucial factor affecting the efficacy of semiochemical-based control strategies. Different aspects of trap design such as shape, size, height, alignment with wind direction, position and timing can significantly affect catching efficacy (El-Ghany *et al.,* 2019). Common types of traps include sticky traps, water traps and inverted cone traps each having specific advantages for different monitoring or control purposes. Combining chemical and visual stimuli in trap design has been shown to enhance insect responses to lures (Singer, 1986).

Advances in Use of Semiochemicals in Insect Pest Management

1. New trapping technique by combining pheromones with entomopathogenic fungi

In recent years, the use of semiochemicals combined with entomopathogenic fungi has emerged as a promising strategy for pest management in agriculture. This method is often referred to as “lure and infect” and it utilizes natural dispersal mechanisms of pathogens while increasing their effectiveness through targeted application (Vega *et al.,* 2012). Entomopathogens are naturally dispersed through various means including aerial movement of spores, parasitoids, predators and insect vectors (Meyling and Eilenberg, 2007). However, the “lure and infect” strategy uses semiochemicals to attract pest insects to devices containing entomopathogenic fungi (Baverstock *et al.*, 2010). This allows target pests to be contaminated with the pathogen which they then spread to conspecifics leading to epizootic outbreaks in the pest population (Lacey *et al.,* 2015). The efficacy of this approach has been demonstrated in different pest management scenarios. Mfuti*et al.* (2017) investigated the combined use of Metarhizium anisopliae and the thrips attractant Lurem-TR for managing bean flower thrips on cowpea. Their field experiments compared spot and cover spray applications where spot application lure and infect was most effective. Thrips density was reduced by this approach from 67.4±10.30 thrips per plant in control to 30.5 ± 6.0 per plant. Importantly, this method required only 81.2 per cent less inoculum than cover sprays making it cost-effective for small-scale farmers. Hajjar *et al.* (2015) studied on red palm weevil used pheromone traps combined with the entomopathogenic fungus *Beauveria bassiana*. They designed a pheromone trap with internal surfaces coated with *B. bassiana*-treated fabric, which effectively attracted and infected both male and female weevils for up to 13 days after application. The study demonstrated high efficacy of B. bassiana at 1 x 10^9 spores per ml, with complete mortality observed even 13 days post-treatment. Kabaluk*et al.* (2015) did research on click beetles focused on an “attract and kill” strategy that combined a granular formulation of female sex pheromone with the entomopathogenic fungus *Metarhizium* *brunneum*. Banded applications of pheromone granules with *M. brunneum* conidia reduced beetle recapture by 98.2 per cent compared to *M. brunneum* alone. The pheromone bands significantly increased beetle attraction, allowing them to acquire lethal doses of fungal conidia rapidly. For example, successful applications have been reported for bark beetles (*Ips typographus*), weevils (*Cylas formicarius* and *Cosmopolites sordidus*), moths (*Plutellaxylostella*), stink bugs (*Plautia crossotastali*), thrips (*Megalurothripssjostedti*), and aphids (*Phorodonhumuli*) (Vega *et al*., 2009; Mfuti*et al*., 2016; Jaronski, 2010). However, despite these successes there are still challenges in optimizing the lure and infect strategy. In some cases, sex-specific semiochemicals that attract only one sex may limit its effectiveness (Witzgall *et al*., 2010). Additionally, applying this approach to soil-dwelling insects presents unique difficulties although promising developments have been made.

For instance, Agriculture and Agri-Food Canada has developed prototype granules that combine *Metarhizium brunneum* with pheromone compounds, which have potential for attracting Agriotes cutworms (Kabaluk and Ericsson, 2007). To make the "lure and infect" method more effective, it is necessary to consider carefully the physical separation between semiochemicals and entomopathogenic fungi in the delivery system (Pell *et al*., 2010). This spatial arrangement is critical for achieving optimal autoinoculation and ensuring successful infection of target pests. As research in this field advances, further refinements of the "lure and infect" strategy are likely to increase its applicability across a wider range of pest species and agricultural settings. The integration of entomopathogenic fungi with semiochemicals offers a promising avenue for future development of more sustainable and targeted pest management solutions.

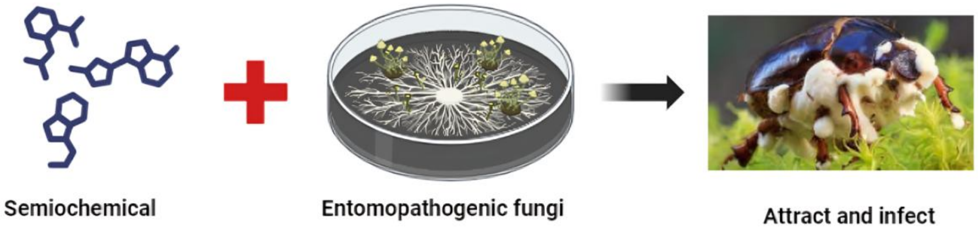

Figure 1: Lure and infect strategy for pest management. (Created with Biorender.com)

2. Auto-dissemination approach

Auto-dissemination is an innovative approach aimed at targeted application of microbials that promotes transmission of infective pathogen propagules within and between insect populations (Vega *et al.,* 2007). This technique has shown promise in managing *Spodoptera frugiperda* (fall armyworm) adults using certain entomopathogenic fungi such as *Beauveria bassiana* or *Metarhizium anisopliae* isolates (Akutse*et al.,* 2020; Meagher *et al.,* 2016). Cárcamo *et al.*(2020) conducted research and showed that *M. anisopliae* Ma-San Rafel-2 isolate combined with synthetic sex pheromone not only attracted but also killed male moths thus indicating its potential for fall armyworm control. In a related study, Akutse*et al.* (2019) identified *B. bassiana* ICIPE 621 and *M. anisopliae* ICIPE 7 as highly pathogenic to fall armyworm, causing 100 per cent mortality. These isolates were compatible with the FALLTRACT lure, thus further demonstrating their effectiveness in integrated pest management strategies against fall armyworm infestations (Akutse*et al.,* 2020; Mweke*et al.,* 2018). Therefore, auto-dissemination approach is a promising tool for improving the efficacy of microbial control agents in managing fall armyworm populations.

3. Plant vaccination by zoophytophagous predators beyond biocontrol

Plant vaccination by zoophytophagous predators is a promising approach to enhance plant resistance against insect pests and diseases (Pérez-Hedo *et al.,* 2022). These unique predators, which feed on both insects and plants, have been shown to induce plant defences through their phytophagy, resulting in complex plant responses that can enhance overall plant protection (Naselli *et al.,* 2016; Pappas *et al.,* 2015). The induced plant responses typically manifest as the emission of volatile organic compounds (VOCs) or the transcription of defence-related genes (Bouwmeester *et al.,* 2019; War *et al.,* 2012). These responses can exert plant protection effects through various mechanisms. For instance, they may repel arthropod pests directly or attract their natural enemies, thereby indirectly reducing pest populations (Dicke and Baldwin, 2010; Kessler and Baldwin, 2001). Additionally, these induced defences can activate defence mechanisms in neighbouring plants, preparing them against future attacks in a phenomenon known as plant priming (Mauch-Mani *et al.,* 2017; Conrath *et al.,* 2015). Among the various zoophytophagous predators studied, several groups have received extensive attention for their ability to induce plant defences. Pappas *et al.* (2020) explored innovative biological and molecular approaches for enhancing plant defence against pests and pathogens in agriculture. They highlighted the use of beneficial organisms such as zoophytophagous predators as “plant vaccination agents”. This concept may involve the induction of plant defences including production of volatile organic compounds that act as semiochemicals in interactions between plants and insects. De Puysseleyr (2014) examined interactions between two economically important zoophytophagous predators, *Nesidiocoris tenuis* and *Oriuslaevigatus*, and their host plants. The study revealed that both predators activate a jasmonic acid (JA)-mediated wound response in their host plants. Importantly, *N. tenuis* was found to induce the emission of volatile compounds like p-cymene, which can have repellent or toxic effects on herbivores. This finding directly relates to semiochemical-mediated interactions, as plant-derived volatiles can act as important signalling molecules in tritrophic systems. In a review of zoophytophagous mirid bugs as biological control agents, Pérez-Hedo *et al.* (2020) discussed the potential of harnessing mirid-induced plant defences for pest management. While not explicitly focused on semiochemicals, this approach likely involves changes in plant volatile profiles that could affect pest behaviour and plant-insect interactions. Predatory mites for example have been shown to elicit strong defensive responses in various plant species (Schimmel *et al.*, 2017; De Oliveira *et al.*, 2019). Anthocorid bugs particularly those belonging to the genus Orius have also been demonstrated to induce significant plant defences (Pérez-Hedo *et al.*, 2015; Bouagga*et al.*, 2018). Pappas *et al.* (2015) investigated the effects of the omnivorous predator *Macrolophus pygmaeus* on tomato plant resistance against two herbivore species. They found that prior exposure of tomato plants to *M. pygmaeus* reduced the performance of the two-spotted spider mite (*Tetranychusurticae*) but not the greenhouse whitefly (*Trialeurodesvaporariorum*). This induced resistance was associated with increased accumulation of proteinase inhibitor transcripts and activity, both locally and systemically in the plant. While not explicitly studying semiochemicals, this research demonstrates that zoophytophagous predators can induce plant defence responses that may involve changes in plant volatile emissions. The growing body of research on zoophytophagous predator-induced plant defences highlights the potential of these organisms as biological control agents and as tools for enhancing crop resistance.To fully understand the mechanisms behind these induced defences and to develop practical applications for agricultural systems, further studies are required (Messelink*et al.*, 2014; Pappas *et al.*, 2015).

4. Production of insect pheromone in plants

In the past few years, research has revealed new insights into the intricate interplay between plant semiochemicals and insect sex pheromones, which have important implications for pest management strategies. Plant volatiles have been shown to significantly affect the attractiveness of herbivore sex pheromones to conspecifics (Rodriguez-Saona and Stelinski, 2009). For example, studies on cotton leaf worms have demonstrated that certain combinations of host volatiles are necessary for sex pheromones to effectively attract individuals to mating sites (Zakir *et al.,* 2013). Conversely, specific plant defence compounds such as 4,8-dimethylnona-1,3,7-triene can strongly suppress pheromone signals (Hatano *et al.,* 2015). These findings provide new opportunities for crop breeders to manipulate plants' volatile profiles so that crop fields may become unsuitable as mating sites for pests or improve the effectiveness of mass trapping using pheromone traps (Bruce and Pickett, 2011). The interaction between plant volatiles and pheromone signals offers both possibilities and challenges in pest management. Landolt and Phillips (1997) stressed the importance of host plants in sexual behavior of phytophagous insects. Many insects acquire compounds from host plants to use as sex pheromones or pheromone precursors while others produce them in response to specific plant cues. Understanding these relationships is crucial for developing effective pest management strategies based on natural plant-insect interactions. Recent advances in biotechnology have allowed production of insect pheromones in heterologous hosts like plants and yeasts. These organisms can express enzymes crucial for pheromone biosynthesis including desaturases, reductases and esterase (Petkevicius*et al.,* 2020). This approach offers a promising alternative to traditional chemical synthesis methods, potentially providing a more sustainable and cost-effective means of pheromone production. The biosynthesis of lepidopteran sex pheromones typically involves modifications of palmitoyl-CoA by fatty acid desaturases (FADs), chain shortening or elongation, and subsequent transformations by fatty acid reductases (FARs), acetyltransferases, or fatty alcohol oxidases (Jurenka, 2004). The diversity of these Type I pheromones, which constitute approximately 75 per cent of all known moth pheromones, arises from the varying specificity of these enzymes and their combinations (Petkevicius*et al.,* 2020). Ding *et al.* (2014) pioneered the production of moth sex pheromones using Nicotiana benthamiana as a plant factory. By transiently expressing multiple genes responsible for consecutive biosynthetic steps, they successfully synthesized multicomponent sex pheromones for two small ermine moth species, *Yponomeutaevonymella* and *Y. padella*. The plant-derived pheromones exhibited high efficiency and specificity in trapping male moths, comparable to conventionally produced pheromones. This semisynthetic approach presents a novel and cost-effective method for generating large quantities of high-purity pheromones while minimizing hazardous waste, highlighting the potential of genetically modified plants in pest management strategies. Building on this innovative concept, Wang *et al.* (2022) demonstrated the feasibility of utilizing genetically modified oilseed crops for pheromone production. They engineered Camelina sativa to express (Z)-11-hexadecenoic acid, a precursor for several moth species' sex pheromones. Field trials revealed that the pheromone derived from the engineered plant oil was equally effective as synthetic pheromones in monitoring the diamondback moth (*Plutellaxylostella*) and disrupting mating of the cotton bollworm (*Helicoverpaarmigera*). This study underscores the potential for large-scale, economically viable production of pheromones using plant factories. In a groundbreaking study, Bruce *et al.* (2015) reported the first crop plant genetically engineered to release an insect pheromone for defence.

They genetically modified hexaploid wheat to produce (E)-β-farnesene (Eβf), an alarm pheromone for various pest aphids. Laboratory tests showed that the transgenic wheat plants were effective in repelling three species of cereal aphids and increasing the foraging activity of a parasitic natural enemy. Although field trials had mixed results, possibly due to low insect populations and erratic climatic conditions, this study demonstrates the potential for engineering crops to autonomously produce pest-repelling pheromones. The use of plant semiochemicals and insect pheromones in pest management strategies is gaining momentum. Reddy and Guerrero (2004) reviewed the intricate interplay between plant volatiles and insect pheromones, observing that plant semiochemicals can either enhance or inhibit insect responses to pheromones. This dynamic relationship can be exploited strategically to improve the efficacy of pheromone-based pest control methods as well as attract natural enemies of pests. In addition, Schlaeger *et al.* (2018) discussed the possibility of manipulating whitefly behaviour using volatile organic compounds derived from plants as an alternative to chemical pesticides in controlling these important agricultural pests. This growing body of research underscores the importance of incorporating plant-based solutions into pest management practices. Future studies should aim at better understanding these interactions through collaboration between crop breeders and insect chemical ecologists. Furthermore, attempts to engineer crops that release alarm signals for pests must take into account overall profiles of both pheromones and plant volatiles because they may ultimately determine how pests behave (Szendrei and Rodriguez-Saona 2010). As research advances in this area, it becomes increasingly clear that tailor-made production systems for different moth pheromone components could be developed using genetically modified plants. This approach provides a new environmentally friendly way of producing moderate to large amounts of high purity pheromones with minimal hazardous waste (Hagström *et al.*, 2013).

Table 2: Production of Insect Pheromones in Plants and Their Role in Pest Management

Pheromone/ Compound	**Plant Source**	**Insect Target**	**Mechanism/Effect**	**Reference**
Host volatiles	Various plants	General	Enhance attractiveness of sex pheromones to conspecifics	Rodriguez-Saona and Stelinski (2009)
4,8-dimethylnona-1,3,7-triene	Not specified	General	Suppress pheromone signals	Hatano *et al.* (2015)
Pheromone biosynthesis enzymes	Genetically modified plants and yeasts	Various moth species	Biosynthesis involving desaturases, reductases, and esterases	Petkevicius *et al.* (2020)
Multicomponent sex pheromones	Nicotiana benthamiana	*Yponomeutaevonymella, Y. padella*	High efficiency and specificity in trapping male moths	Ding *et al.* (2014)
(Z)-11-hexadecenoic acid	Genetically modified Camelina sativa	*Plutellaxylostella, Helicoverpaarmigera*)	Equally effective as synthetic pheromones in monitoring and disrupting mating	Wang *et al.* (2022)
(E)-β-farnesene (Eβf)	Genetically modified hexaploid wheat	Various pest aphids	Repels cereal aphids and enhances foraging activity of parasitic natural enemies	Bruce *et al.* (2015)
Plant volatiles	Various plants	General	Can enhance or inhibit insect responses to pheromones; potential to attract natural enemies	Reddy and Guerrero (2004)
Plant-derived volatile organic compounds	Various plants	Whiteflies	Potential alternative to chemical pesticides	Schlaeger *et al.* (2018)
Pheromone and plant volatile profiles	Not specified	General	Influence on pest behavior and effectiveness of pest alarm pheromones	Szendrei and Rodriguez-Saona (2010)
Type I pheromones	Not specified	Moths	Biosynthesis involving modifications of palmitoyl-CoA	Jurenka (2004)

			by FADs, chain shortening or elongation, transformations by FARs, acetyltransferases, or fatty alcohol oxidases	
General plant-insect interactions	Various plants	Phytophagous insects	Critical role in sexual behavior; insects use plant compounds as sex pheromones or precursors	Landolt and Phillips (1997)
Pheromone production systems	Genetically modified plants	Various moth species	Potential for tailor-made production systems for high-purity pheromones with minimal hazardous waste	Hagström *et al.* (2013)

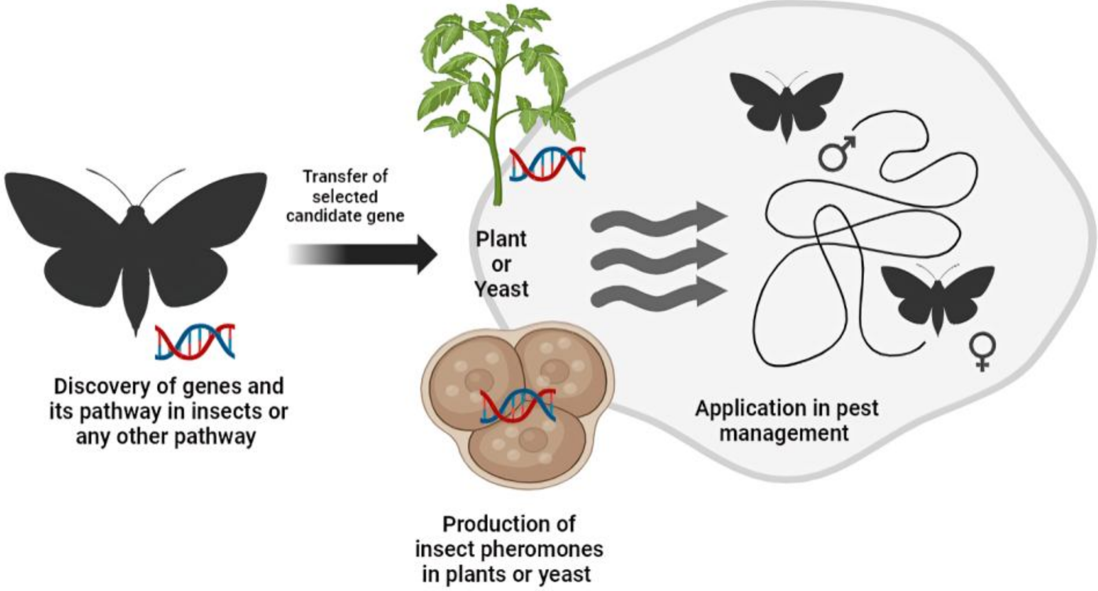

Figure 2: Production of insect pheromone in plants/yeast. (Created with Biorender.com)

5. Electroantennography

Electroantennography (EAG) is a technique that has become valuable in the field of insect olfactory research, giving insight into the average output of an insect antenna to its brain in response to specific odours (Schneider, 1957; Roelofs, 1984). This method has been widely used in electrophysiology studies to understand how the olfactory pathway works in different species of insects (Kaissling, 1986; Park *et al.,* 2002). The use of EAG has been particularly important for understanding the olfactory responses of agricultural pests and thus contributing to better pest management strategies. *Conotrachelus nenuphar* (Herbst), commonly known as plum curculio, is a major pest in commercial fruit orchards and research has focused on identifying attractive odor sources through EAG. Leskey*et al.* (2009) developed a reliable EAG technique utilizing a whole-body mount with glass electrodes. Their findings showed that female plum curculios had significantly higher EAG response amplitudes than males across various odor stimuli. This finding highlights the potential for developing sex-specific attractants which could lead to more targeted pest management strategies. In another study Kumar *et al.* (2021) investigated the EAG responses of shoot and fruit borer, *Eariasvittella* (Fabricius), towards host plant volatiles and green leaf volatiles. Their results showed sexual dimorphism in olfactory responses with green leaf volatiles eliciting stronger reactions compared to host plant extracts. This information is crucial for designing novel semiochemicals aimed at integrated pest management for *E.vittella* in cotton and okra crops. Optimization of pheromone blends has been emphasized by studies on *Chilo partellus* spotted stem borer. Guleria*et al.*(2023) found that a specific ratio of the major pheromone component (Z)-11-hexadecenal and the minor component (Z)-11-hexadecenol was most effective in attracting male moths. This research emphasizes the critical role that minor pheromone components play in enhancing the overall attractiveness of synthetic lures. Synergistic effects between pheromones and other volatile compounds have also been explored. Basana*et al.*(2015) found that addition of 1-Octen-3-ol to sex pheromone blend of legume pod borer, *Maruca vitrata* significantly enhanced its attractiveness. This finding highlights the potential for identifying synergistic compounds that can improve the efficacy of pheromone-based trapping systems. Red Palm Weevil (*Rhynchophorusferrugineus*), a notorious insect pest affecting palm trees that has garnered considerable attention worldwide (Giblin-Davis *et al.*, 2013). The management of this pest poses significant challenges due to its concealed nature within the palm tissue, often evading detection until severe damage has occurred (Faleiro, 2006; El-Shafie, 2012). In recent years, researchers have focused on developing innovative approaches to combat this pest, with a particular emphasis on exploiting its olfactory system. Pheromone traps have emerged as a crucial component in the integrated management of the Red Palm Weevil (Hallett *et al.*, 1999; Oehlschlager, 2016). These traps use synthetic versions of the insect's aggregation pheromone to attract and capture adult weevils. However, recent studies suggest that combining them with food baits may enhance their efficacy as pheromone-based traps (Vacas *et al.,* 2013). Vibina and Kesavan (2019) used EAG to evaluate insects' responses towards different food baits. Their study showed that combining banana volatiles with aggregation pheromones resulted in the highest attraction of adult weevils during field trials. This research demonstrates the potential for integrating food-based attractants with pheromones to improve pest monitoring and management strategies.These methods synergistically combine the chemical communication system and feeding behavior of pests to develop more effective monitoring and control strategies.

6. Push-pull strategy

The push-pull strategy has become a major innovative approach in IPM that combines repellent and attractive stimuli for insect pest control. This method, which was first conceived in Australia in 1987, uses a combination of behavior modifying stimuli to manipulate the distribution and abundance of pests thereby reducing reliance on chemical insecticides (Miller and Cowles, 1990; Khan and Pickett, 2004). The success of this strategy depends on an understanding of insect biology, chemical ecology, plant-insect interactions that can be used to tailor applications for maximum pest control (El-Ghany, 2019). The push-pull strategy is based on using repellent "push" stimuli to keep pests away from valuable resources while employing attractive "pull" stimuli to attract them into traps or trap crops for targeted elimination. This dual approach has been successfully implemented in various agricultural contexts. For instance, it has been effectively used to manage stemborers and *Striga hermonthica* in maize-based farming systems through intercropping techniques that utilize repellent plants and attractive trap crops emitting green leaf volatiles (Zhang *et al.,* 2013). Semiochemicals have been found to enhance the push-pull strategy as shown by research findings. Alarm pheromones from aphids have been explored as repellents making protected resources less attractive to pests (Cook *et al.,* 2007). Furthermore, orientation disruption tactics for bark beetles combined with deployment of attractive semiochemicals have shown promise in pest management (Borden *et al.,* 2008). Recent advancements also include applying push-pull tactics to suppress oviposition in *Drosophila suzukii* Matsumura where combining attract-and-kill tactics with oviposition deterrents resulted in significant reductions in pest populations (Wallingford *et al.,* 2017). The push-pull strategy has also demonstrated effectiveness in controlling the Asian citrus psyllid (*Diaphorinacitri*Kuwayama), a vector of the devastating citrus huanglongbing disease. Research has focused on identifying effective repellent and attractant chemicals from plant sources to manage psyllid populations and mitigate disease spread (Yan *et al.*, 2014). In greenhouse settings, adaptations of the push-pull strategy have been employed to manage the western flower thrips (*Frankliniella occidentalis*) on hot pepper crops. This non-chemical approach integrates alarm pheromones as a "push" component to deter thrips from entering greenhouses, while aggregation pheromones serve as a "pull" component to attract thrips to traps, demonstrating significant reductions in thrips density (Kim *et al.*, 2023). Furthermore, the lesser mealworm (*Alphitobiusdiaperinus*), a pest in poultry production, has been targeted using push-pull systems. Hassemer *et al.* (2018) identified several alarm and aggregation pheromones that effectively manipulate pest behaviour, showcasing the superior results of the push-pull approach compared to using aggregation pheromones alone. Overall, this is an example of how transformative approaches can be applied in pest management by manipulating behavior through semiochemicals for increased agricultural productivity with reduced reliance on chemical insecticides. This integrated framework not only addresses pest control challenges but also promotes sustainable agricultural practices making it a valuable tool in modern IPM programs.

7. Advanced Pheromone Dispensers

Modern IPM strategies require the development and optimization of pheromone dispensers. These dispensers are used to deploy semiochemicals that play a vital role in pest control through attraction, repulsion, and mating disruption. A comprehensive review by Klassen *et al.* (2022) highlights various types of pheromone dispensers, including septum, membrane, solid matrix dispensers, and sprayable formulations. Each type has its own advantages in terms of pheromone release rates and application methods; however, ongoing research is aimed at improving their reusability and efficiency to enhance the sustainability of pheromonal pest control systems. The efficacy of these dispensers is heavily influenced by the emission of semiochemical blends which is crucial for optimizing their effectiveness against target insect pests. Controlled-release systems are essential for achieving release rates that mimic natural emission patterns (El-Ghany, 2019). Two primary types of devices have been identified for semiochemical application: retrievable and passive non-retrievable dispensers (EFSA, 2016; El-Ghany, 2019). Retrievable dispensers include passive types such as extruded or reservoir dispensers that continuously emit semiochemicals while active ones release them discontinuously (Baker *et al.*, 1997). Passive non-retrievable products encompass biodegradable dispensers, dosable matrix dispensers, capsule suspension products and granular products each offering distinct advantages depending on specific application requirements (Heuskin*et al.,* 2011; EFSA, 2016; El-Ghany, 2019). For example, biodegradable dispenses provide continuous emission with minimal environmental impact (Hummel *et al.,* 2002). Pheromone dispenser effectiveness in mating disruption strategies has been intensively studied. Baker *et al.* (2016) emphasizes optimizing point-source emission rates and geometries of pheromone mega-dispensers, suggesting that emission rates should be evaluated on a per-dispenser-per-minute basis for accurate performance assessment. They also highlight the critical role of plume strand concentrations in influencing moth behaviour, advocating for refined dispenser designs to achieve better behavioural outcomes while maintaining longevity and cost-effectiveness. In specific pest management contexts, Zahradník and Zahradníková (2024) evaluated various pheromone dispensers for attracting the spruce bark beetle, *Ips typographus*. Their findings revealed significant variations in dispenser efficacy and longevity, with some types, such as IT Ecolure Mega, demonstrating superior performance throughout the beetles' flight activity period. This underscores the importance of selecting appropriate dispensers based on both effectiveness and duration for successful pest management strategies. The application of pheromone-based mating disruption in urban environments has also yielded promising results. Ceballos *et al.* (2024) reported successful control of *Lobesiabotrana* in urban areas using meso-dispensers (MeD), which contain higher pheromone loads than standard types. These dispensers significantly reduced male moth captures and pest infestations in grape clusters, providing an effective alternative in areas where chemical sprays are restricted. Recent advancements in pheromone delivery systems include aerosol devices, which offer potential advantages over traditional passive dispensers. Benelli *et al.* (2019) discuss the benefits of aerosol systems such as lower application densities and the ability to time pheromone releases to coincide with pest activity; however, they note challenges remain in understanding the precise mechanisms of action and optimizing deployment strategies for these devices.The development and optimization of pheromone dispensers are crucial for advancing integrated pest management strategies.The diversity of dispenser types, their controlled release mechanisms, and ongoing research efforts to enhance their effectiveness and sustainability underscore their importance in modern pest control.In the process of development, new approaches like aerosol technologies and biodegradable dispensers can be used to find solutions for eco-friendly pest control.

Limitations

There are several limitations that hinder the effective use of semiochemicals in pest management. First, it is difficult to identify specific pheromones for different pests. This requires a lot of research and advanced techniques especially for non-lepidopteran pests such as Hymenoptera and Hemiptera. Moreover, these pheromones are not easily produced on a commercial scale because their synthesis or extraction requires specialized facilities and technology which may be too expensive. The extraction and characterization of semiochemicals are labour-intensive processes that involve meticulous methods and advanced analytical techniques. In addition, the use of semiochemicals can be more expensive than conventional pesticides due to difficulties in synthesizing stable formulations. Physical constraints also present significant challenges; the instability and volatility of pheromone compounds make their formulation and effective deployment problematic. Furthermore, some pest control strategies such as attract-and-kill methods may not work well because they depend on sex-specificity of some pheromones that only attract one sex of the pest. This limitation can reduce the overall effectiveness of control strategies. Despite some progress with prototype granules, applying semiochemicals to soil-dwelling insects has unique difficulties. To promote adoption of semiochemical-based pest control strategies in sustainable agriculture, several limitations must be addressed including improving identification processes, enhancing production efficiency, streamlining extraction methods, reducing deployment costs, and overcoming formulation challenges. Continued research and innovation are essential for optimizing the use of semiochemicals within IPM frameworks. By addressing these issues, we can improve feasibility and efficacy of semiochemical applications thus leading to more sustainable environmentally friendly pest management solutions.

Future Prospects

However, promising the future looks for semiochemical-based pest management there are still limitations that need to be recognized. One of the major challenges is that insect responses to semiochemicals are highly variable depending on concentration and environmental factors, which may result in inconsistent pest attraction or repulsion. Additionally, the effectiveness of semiochemical applications can be hindered by the specificity of certain semiochemicals, which may only attract one sex of a pest population, limiting their overall efficacy. It is important to optimize release rates and trap designs since high release levels can become repellent while various design factors significantly affect trapping success. Moreover, integrating semiochemicals into existing agricultural practices may face stability and compatibility issues that require further research and development. Lastly, although molecular techniques have advanced and formulation exploration is ongoing, practical implementation of these innovations in diverse agricultural contexts remains a challenge. These limitations must be addressed for successful adoption of semiochemical strategies as sustainable alternatives to conventional pesticides so that they work effectively in real-world applications.

Conclusion

Semiochemicals have become a vital part of sustainable pest control in 21st century agriculture, which is aimed at increasing food production and reducing environmental impact. This review demonstrates their versatility and potential in various applications ranging from mating disruption to push-pull strategies. The integration of semiochemicals with biological control agents such as entomopathogenic fungi and the development of auto-dissemination techniques are examples of innovative approaches to pest management. Of particular interest is the possibility for plants to produce insect pheromones that could change how they are delivered in agricultural settings. In addition, semiochemicals can induce plant defences, thereby enhancing crop resilience against pests. The rapid growth of the global semiochemicals market indicates their growing significance in shaping sustainable agricultural practices. As research continues to uncover new applications and refine existing techniques, semiochemicals are poised to play an ever more crucial role in integrated pest management. Semiochemicals provide a sophisticated, targeted approach to pest control that aligns with the goals of sustainable agriculture. Their continued development and implementation will be essential in creating more resilient and environmentally friendly food production systems worldwide.

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