

Insect Sex Pheromone

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Contributor: Gadi VP Reddy

Insect pheromones are specific natural compounds that meet modern pest control requirements, i.e., species-specificity, lack of toxicity to mammals, environmentally benign, and a component for the Integrated Pest Management of agricultural pests. Mass trapping and mating disruption strategies using sex pheromones have significantly reduced the use of conventional insecticides, thereby providing sustainable and ecofriendly pest management in agricultural crops.

Keywords: sex pheromones ; integrated pest management ; biosynthesis ; pheromone perception ; resistance

1. Introduction

Sex pheromones are chemical signals emitted by an organism that elicit a sexual response in a member of the opposite sex of the same species ^{[1][2]}. Since the structural characterization of the first sex pheromone of the silkworm moth *Bombyx mori* in 1959 ^{[3][4]}, more than 600 species ^[5] of lepidopteran pheromones have been identified. Their main features, e.g., species-specificity, non-toxicity to mammals and other beneficial organisms, their activity in minute amounts, and rapid degradation in the environment were soon envisioned to be promising tools for controlling insect pests, estimating pest populations, detecting the entry and progress of invasive pests, and preserving endangered species ^{[6][7][8]}. In fact, in recent years the most successful practical applications of sex pheromones in integrated pest management (IPM) have been the monitoring of pest populations, mass trapping, mating disruption, and push-pull strategies ^{[7][9][10][11]}.

Sex pheromones are mainly produced by females and used as attractant compounds to show the presence of potential mating partners and their reproductive status ^{[8][11]}. Sex pheromones comprise sex attractant pheromones, which induce upwind oriented movements to the conspecific individual, and courtship pheromones, which elicit a variety of close-range responses in the insect partner ^{[12][13]}. Since the first pheromone discovery, the rapid progress of methodologies developed to identify new pheromones, mainly GC, GC-MS, NMR, electrophysiological techniques [electroantennography (EAG), gas chromatography coupled to electroantennography (GC-EAD), single sensillum recordings (SSR), and coupled GC-SSR], have allowed the identification of thousands of compounds as insect sex pheromones ^[14].

2. Sex Pheromone Biosynthesis

Sex pheromone components are C₁₀–C₁₈ straight chain unsaturated compounds with an oxygenated functional group ^[15]. In many Lepidoptera species, sex pheromone production is regulated by the pheromone biosynthesis-activating neuropeptide (PBAN), a neurohormone originated in the subesophageal ganglion and released into the hemolymph to operate directly on the pheromone gland (PG) ^[16], which in turn activates functional group modification enzymes ^[17] or acetyl-coenzyme A carboxylase (ACC) ^[18]. In the first step of pheromone biosynthesis, the carboxylation of acetyl-CoA to malonyl-CoA is catalyzed by ACC, followed by fatty acid synthase action which leads to production of saturated fatty acids (C18:0 and C16:0) ^[18]. Through a series of enzymatic reactions, i.e., desaturation, chain-shortening reaction, reduction, acetylation, and oxidation, the palmitic or stearic acids are then converted to the final pheromone components in a stepwise manner ^{[17][19]}.

3. Mechanisms of Insect Sex Pheromone Perception

Insects detect volatile odorants/pheromone molecules using olfactory receptor (OR) sensilla present on their antennae and maxillary palps ^[20]. Pheromones and other odorant molecules that are absorbed on the cuticular surface of an olfactory sensillum diffuse inside through olfactory pores and the pore tubule ^[21]. The sensillum lymph contains the pheromone binding proteins (PBPs) that bind with volatile pheromones and solubilize them to pass across the sensillum lymph to activate pheromone receptors ^[22]. The structure and arrangement of olfactory sensilla and olfactory sensory

neurons (OSNs) on the antennae and palps of insects are very specialized and optimized to detect odorants, especially sex pheromones in the case of male antennae. OSNs carry the olfactory information from the periphery to the antennal lobe in the insect brain.

The peripheral olfactory hairs or olfactory sensilla that house the OSNs play an essential role in odorants perception, especially sex pheromones. Different morphological types and distribution of olfactory sensilla have been reported in multiple insect species based on their ecological niches.

Many studies have been published to understand the role of odorant binding proteins (OBPs), pheromone binding proteins (PBPs), sensory neuron membrane proteins (SNMPs), and sex pheromone receptors that are involved in the transport and central processing of pheromone molecules in *Drosophila* and different moth species [22][23][24]. An insect's age and the physiological state also affect its responsiveness to sex pheromones and other host plant volatiles. Recent studies have shown a significant interest in understanding the neurophysiological mechanisms that regulate the interaction between female sex pheromone and behaviorally active host plant odorants by using functional imaging of the antennal lobe (AL) and intracellular recordings (IRs) of projection neurons (PNs) that transmit olfactory signals to higher centers of insect brain [25].

4. Sex Pheromone Autodetection

The phenomenon of a sex pheromone producer insect capable of detecting its conspecific sex pheromone components is termed autodetection [26]. One of the first cases recorded on autodetection was reported by Schneider et al. [27] in which electroantennographic responses to both pheromone components released by females of *Panaxia quadripunctaria* Poda (Lepidoptera, Arctiidae) were equally detected and with similar amplitude by both sexes. It revealed that not only males could detect the female-produced pheromones, but females were not 'anosmic' (unable to detect their conspecific sex pheromone) for their own attractant. In some cases, the pheromone only attracts males, thus acting as a sex pheromone, but may induce other behavioral effects on females, e.g., a repellent effect, an advance or delay in calling initiation, or an increase in calling frequency, among others [28]. Sex pheromones are secreted by one sex and cause an intraspecific attractant response and mating in individuals of the opposite sex, but in some rare cases, the pheromone attracts both sexes, functioning more like an aggregation pheromone. The aggregation pheromones are emitted by insects of one sex and cause individuals of both sexes to join for feeding and reproduction. In sex pheromone autodetection, female aggregation may increase the possibilities of mating success or induce dispersal at high population levels.

5. Resistance of Insects to Sex Pheromones

The continuous exposure or pre-exposure to high concentrations of sex pheromone as in mating disruption experiments can elicit habituation or desensitization [29]. This mechanism implies a reduction of response when pest species are treated with species-specific dispensers [30]. Adaptation of the peripheral neurons system to the sex pheromone has been shown to occur in most moths, but not in all cases where it has been examined, including *G. molesta* [29], *C. pomonella* [31], or *E. postvittana* [32].

6. Application of Insect Sex Pheromones

6.1. Interactions between Pheromones and Insects Biological Control Agents

It is believed that entomopathogenic fungi act slowly and take time to cause mortality in insects. On the other hand, the combined use of entomopathogenic fungi with chemical insecticides [33] or other entomopathogenic fungi [34] improves microbial control agents' efficacy. In the same approach, entomopathogenic fungi and pheromones can be used to increase the effectiveness (additive or synergistic) against the target insects. Thus, the simultaneous application of *Metarhizium anisopliae* var. *acridum* and the aggregation pheromone phenylacetone nitrile to *Schistocerca gregaria* Forsskal (Orthoptera: Acrididae) fifth-instar nymphs exhibited an additive interaction [35].

Sammani et al. [36] studied the effects of the sex pheromone components (Z,E)-9,12-tetradecadienyl acetate and (Z)-9-tetradecen-1-yl acetate of *Cadra cautella* (Walker) (Lepidoptera: Pyralidae) in the presence of botanical oils on insect mating, and the burrowing ability of *C. cautella* larvae in different types of flour treated with spinosad (*Saccharopolyspora spinosa*), a bacterial organism isolated from soil. The mating success was higher with botanical oils alone but declined with pheromone exposure either alone or combined with botanical oils [36].

6.2. Monitoring

One of the most widespread and successful applications of sex pheromones is in the detection and monitoring of pest populations [11]. Monitoring systems are based on the relationship between trap captures and the pest population or damage induced by the pest species. The number of male catches is used to establish thresholds for making decisions on when it is advisable to take treatment actions. Sex pheromones are very useful for evaluating trap catches because they are highly sensitive when detecting low insect population levels and are species-specific. These features also allow for the detection and survey of invasive species, and permit growers to perform timely insecticidal applications, thereby reducing economic and environmental costs [2].

6.3. Mass Trapping

Mass trapping is a direct control strategy that uses a large number of pheromone traps to reduce the population density of the target species and/or pest damage [37][38]. Compared to mating disruption, mass trapping is more efficient when both control methods have an equal number of pheromone sources [39].

6.4. Mating Disruption

Mating disruption (MD) is a strategy based on the permeation of the crop with synthetic sex pheromone to disrupt chemical communication between sexes and, thus, preventing mating. To date, MD is the most developed pheromone-based technology for the direct control of moth pests [40]. The species-specificity and low toxicity of pheromone applications have led to consider MD a reliable tool for use in area-wide programs to control insect pests and manage invasive species. Microencapsulation, hand application, aerial dispensers, and matrix formulations (SPLAT, Specialized Pheromone and Lure Application Technology), have been used for pheromone emission [41]. Ideally, the dispensers should release pheromones at a constant rate, should be mechanically applicable, completely biodegradable, and made from renewable and cheap organic materials, be economically cheap, and eco-toxicologically inert [42].

6.5. Push-Pull Strategy

The push-pull strategy, the simultaneous use of an attractant and repellent stimulus to divert pests, is an increasingly employed sustainable alternative to traditional pesticides. This strategy aims at reducing crop injury by modifying pest distribution using repellent stimuli to 'push' the insect pest away from the crop, and at the same time attractant stimuli to 'pull' the pest to other areas out of the crop. The development of push-pull strategies has been mainly directed to agricultural systems to manage insecticide resistance threats or diminish the use of insecticides. This strategy requires knowledge of insect biology, chemical ecology, and interaction between host plants and natural enemies [43].

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