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Pheromones and Chemical Communication in Insects

Nesreen M. Abd El-Ghany

Abstract

Chemical communication is an essential item for insects' survivals that qualify them to adapt their behavior depending on the surrounding environment. Semiochemicals defined as informative molecules (M) mainly play an important role that conveys specific chemical messages between insect and insect and plant and insect. Olfaction mechanism in insects is a key point of chemical communication between the same and different insect species. Discrimination of various odors through the olfaction system depends only on the evolutionary pressures of the molecules which stimulate the development of specific binding proteins (BPs) and specific receptor sites present on individual chemosensory neurons. Pheromones are defined as species-specific chemical signals which enable communication between life-forms of the same species. Recently, semiochemicals become as alternative or complementary components to insecticide approaches in integrated pest management (IPM) strategies. Pheromones are secreted by insects causing a specific reaction, for example, either a definite behavior or a developmental process. Pheromones have been classified into eight various types: aggregation pheromones, alarm pheromones, oviposition-deterrent pheromones, home recognition pheromones, sex pheromones, trail pheromones, recruitment pheromones, and royal pheromones. Pheromones are promising and can be used singly or in integration with other control strategies for monitoring and controlling insect pests in agricultural systems.

Keywords: chemical communication, semiochemicals, pheromones, insect olfactory

1. Introduction

Chemical communications in insects are exploited for many features as food seeking and preference, orientation, recruitment, defense, reproductive habitats, predator recognition, and mate attraction [1]. Chemical communication is distinguished by its effectiveness over long distances than others as mechanical and visual communications. Various active compounds were isolated and identified from different plant species that explore several activities toward other organisms [2–5]. The wide range of these compounds affects different insect pests in different ways. Herbivorous insects may use host plant volatiles for determination of food, mates, and/or oviposition and hibernation sites by stimulation of insect chemoreceptor cells in taste sensilla present on antennae, tarsi, and mouthparts [6]. The manipulation of insect behavior occurs by detection of the chemical stimuli known as semiochemicals [7] or infochemicals [8]. Semiochemicals are defined as informative molecules released from one organism that evokes either a behavioral

or physiological response between members of the same or different species. They are mainly used in plant-insect or insect-insect interactions as alternative or complementary components to insecticide approaches in different integrated pest management (IPM) strategies. Such compounds are mainly affecting the behavior of various insect pests via chemical signals which occur between insect and insect or plant and insect. Semiochemicals considered a promising component in IPM programs for controlling insect pests. They are involved in different control strategies such as monitoring, mass trapping, mating disruption, and attract-and-kill and push-pull strategies [1].

2. Insect-insect and plant-insect interactions

In insects, the interaction of chemical signals can either stimulate or inhibit the behavior of the pest and so change its response. The response of insects to plant volatiles differs and is either attractive (adapted herbivore) or repellent (non-adapted herbivore). The classification of plant volatiles as attractants and repellents is not standardized due to fluctuation of insect behavior responses to such volatiles depending on their concentration. Herbivorous insects develop host plant compounds and use them as sex pheromone precursors or sex pheromones [9]. For example, male orchid bees assemble terpenoid mixtures from orchids and transfer them as an aggregation pheromone to stimulate leakage in mating [10]. Furthermore, moths, butterflies, grasshoppers, beetles, and aphids utilize pyrrolizidine alkaloids as feeding deterrents against their parasites and/or predators [11]. The interactions which occur between different organisms are divided into two main categories, intraspecific and interspecific, depending on how the interactions occur. An intraspecific communication passes between individuals of the same species, while an interspecific communication involves an interaction between members of different species. Based on the communication signal and subsequently the relation between the receiver and the emitter, semiochemicals are classified into two main functional groups: pheromones and allelochemicals [1].

2.1 Pheromones

Pheromones are defined as species-specific chemical signals which enable communication between life-forms of the same species. Pheromones are secreted by insects which caused a specific reaction, for example, either a definite behavior (immediate effect on the behavior of the receiver) which is called a releaser pheromone or a developmental process (physiological effects on the receiver) which is called a primer pheromone [12]. Pheromones have been classified into eight various types: aggregation pheromones, alarm pheromones, oviposition-deterrent pheromones, home recognition pheromones, sex pheromones, trail pheromones, recruitment pheromones, and royal pheromones. Primer pheromones stimulate the olfactory sensory neurons that emit signals to the insect's brain which stimulate hormones released by the endocrine system [13]. Caste determination in social insects (bees, wasps, ants, termites, locusts) resembles the most famous example for primer pheromone in **Figure 1** [14]. Releaser pheromones are divided by function into sex pheromones, trail pheromones, alarm pheromones, etc. Sex pheromone is the most commonly known which species specific that attract opposite sexes for mating is highly. Concerning trail pheromones, these are commonly known in social insects for orientation and also for recruit nest mates toward a suitable food source. For example, ants and termites deposit these pheromones as they navigate their territory, thus promoting extensive nets of chemical routes [15].

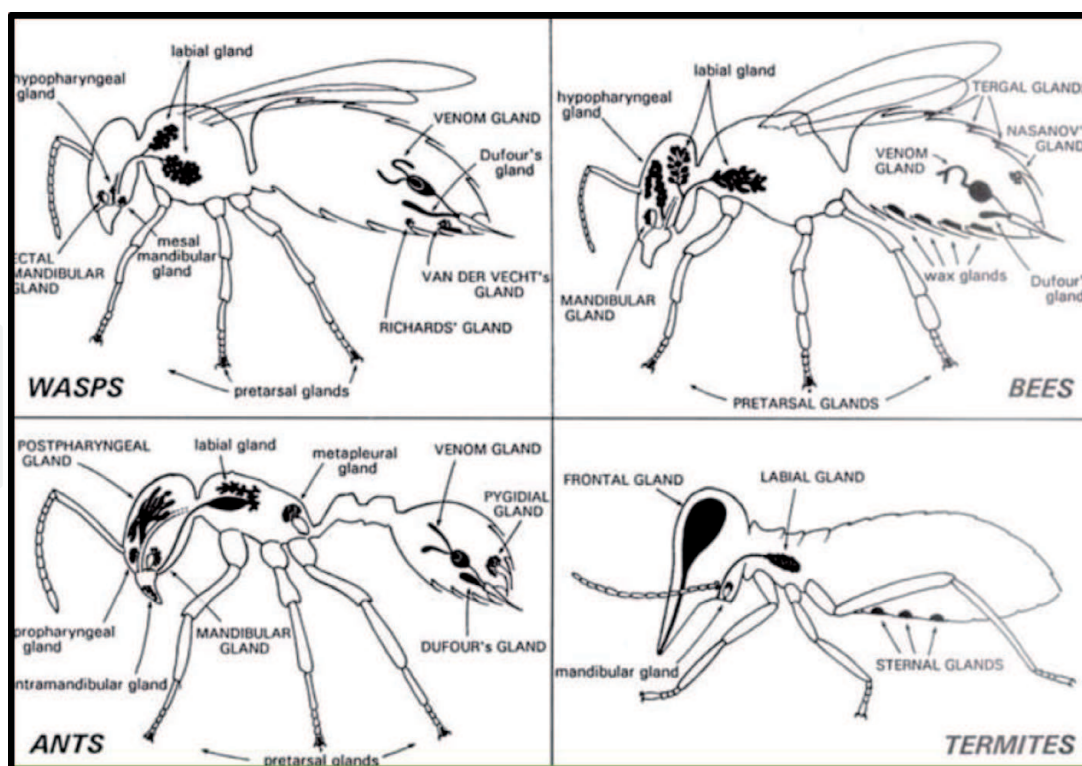


Figure 1.
 Schematic profile drawings for exocrine glands of some social insects with a pheromonal function (capital lettering) [14].

On the other hand, bees release airborne orientation pheromones including forage marking, nest entrance finding, and swarming from the Nasonov gland. These pheromones are composed of mixtures of geraniol, farnesol, citral, and other minor compounds [16]. Alarm pheromones are well-developed pheromones in social insects for defensive function and are composed of multicomponent volatiles as mono- and sesquiterpenes and acetates [16–18]. The aggregation pheromones attract conspecifics of both sexes, e.g., bark beetles. The beetles start digging up into the bark of the host tree, thus releasing a mixture of terpenoids which are long-range aggregation pheromones that synthesized *de novo*, and others produced terpenoids via gut symbiotic bacteria or sequestered from the host tree. Depending on evoke aggregation pheromones, a great number of beetles attack, leading to killing of the host tree [14, 19].

2.2 Allelochemicals

The second subclass of semiochemicals is allelochemicals which includes substances that transmit chemical messages between different species. Fundamentally, these substances resemble an interspecific communication which are emitted by individuals of one species and are understood by individuals of a different species. Allelochemicals are divided depending on the benefits and costs to the signaler and receiver. They have been divided into five categories according to [1, 20] as follows.

2.2.1 Allomones

Allomones (from Greek “allos + hormone” = excite others): released from one organism that stimulate a response in an individual of another species. The response is beneficial to the emitter, e.g., poisonous allelochemicals. They can also be seen

as a deterrent emitted by insects against their predators as a defense mechanism. Granular trichomes which cover plant leaves and stems release herbivore-deterrent allomones under stress conditions as a defense process. These allomones are toxic for the herbivorous insect pests, e.g., nicotine from a tobacco plant. Moreover, bolas spiders can deceit, lure, and capture male moths by synthesizing and mimicking moth pheromones [14].

2.2.2 Kairomones

Kairomones (from a Greek word “kairos” = opportunistic or exploitative): emitted by one organism that stimulate a response in an individual of another species. The response is beneficial to the recipient, e.g., orientation of predaceous checkered beetles (Coleoptera, Cleridae) toward the aggregation pheromone of their prey and bark beetle (Coleoptera, Curculionidae, Scolytinae) [14, 21]. Kairomones may be allomones or pheromones depending on the circumstances. For example, American bolas spiders attract their prey (male moths) by releasing attractant allomones which serve as sex pheromones emitted by female moths. Also, exudates of warm-blooded animals that pull blood-sucking insects toward their hosts serve as kairomones.

2.2.3 Synomones

Synomones: beneficial to both the releaser and receiver. Examples include scents used by flowers to attract pollinating insects. Moreover, herbivore-induced plant volatiles are considered to be active synomones which recruit natural enemies of insect pests toward the affected plants [22]. Also, synomones play an essential role in mate-finding communication. This role relies on the reduction of competition in the olfaction communication channel between closely related species with overlapping pheromone components. This advisable action is important in preventing exhaustion from the time and energy required for orientation toward heterospecifics [23]. In termites, hydroquinone is a phagostimulant compound secreted by labial glands distinguished as pheromones and synomones when different species are partaking the same foraging territory. It acts as a pheromone when recognized by nest mates of the same species and as a synomone when perceived by another termite species [24].

2.2.4 Antimones

Antimones: maladaptive for both the releaser and receiver. These substances are produced or acquired by an organism that, when encountered by another individual of a different species in the natural environment, activate in the receiving individual a repellent response to the emitting and receiving individuals [1].

2.2.5 Apneumones

Apneumones (from a Greek word “a-pneum” = breathless or lifeless): emitted by a non-living source, causing a favorable behavioral or physiological reaction to a receiving organism, but harmful to other species that may be found either in or on the non-living material. Apneumones were suggested by [7]. Rare cases of these allelochemicals have been found later in the literature, e.g., hexanal and 2-methyl-2-butanol released from rabbit stools attract sandfly females for oviposition [25].

3. Mechanisms of chemical communication in insects

Chemical communication is an essential item for insects' survivals that qualify them to adapt their behavior depending on the surrounding environment [1]. In insects, chemical communication is based on a mixture of one or several semiochemical substances which stimulate various receptor organs. The efficiency of semiochemicals in chemical communication is mainly based on various physical properties such as chemical nature, solubility volatility, and its lifetime in the environment. Also, the stability of such volatiles affects their efficiency in IPM programs [1]. Dispersal is a natural activity of insect where the movement is directed (taxes) or random (kineses) which is motivated by chemical or visual stimuli. There are three mechanisms of insect behavioral responses for finding an odor source. In the first mechanism called true chemotaxis, the insects align their body directly toward the odor source due to sensing the gradient of odor molecules. For the second mechanism, the insect does not discover the odor direction but becomes stimulated either for moving at different rates which is called orthokinesis or turning at various frequencies depending on changes in odor concentration (klinokinesis). The third mechanism depends on the odor of molecules impulse insect toward some other stimulus. Anemotaxis is the most common example for this mechanism where the molecules of an attractive chemical stimulate the receptive insects to fly upwind [26].

4. Chemosensory stimulation in insects

In insects, chemosensory stimulation occurs in various receptor organs via constant bombardment of chemical signals which improved the insect's ability to detect, discriminate, and distinguish innumerable different molecules as different odors. The insect receptor organs include antennae, mouthparts, and ovipositors. These receptors are very sensitive even for a few molecules of specific semiochemicals. Attraction (directed movement toward stimuli) and repulsion (directed movement away from stimuli) are the main insect responses to various odors. For field traps, insect catches not only occur via taxes but also via kineses (random movement). The insect can detect any odor by olfactory receptors located in the sensory organs including antennae, mouthparts, and ovipositors [27]. Various types of sensilla are recorded including trichodea, basiconica, styloconica, chaetica, etc. Knowledge of the types of sensilla on the antennae and mouthparts provides a foundation for understanding the olfaction and feeding preferences of herbivorous insect pests and subsequently can be useful for improving new control strategies for the target pests [28, 29]. The basic structure of sensillum is explored by [30] in **Figure 2**. The sensillum formed from the sensory neuron attached to branched cuticular pores (P) which allows odor passage. Sensillum pores act to filter molecules received from the airstream and concentrated it in the lumen of the sensillum and passed to branched neurons which convey impulses from and to the central nervous system.

In insects, the ability to discriminate different odors depends only on the evolutionary pressures of the molecules which stimulate the development of specific binding proteins (BPs) and specific receptor sites present on individual chemosensory neurons. This selectivity bestowed upon chemosensory neurons by the receptor types expressed represents one level of signal filtering in the insect's olfactory system. The olfaction mechanism in insects is summarized by [14] in **Figure 3**. In brief, a chemical signal crosses the sensillum lymph (SL) through a pore and then binds to highly specific binding proteins: pheromone binding proteins/

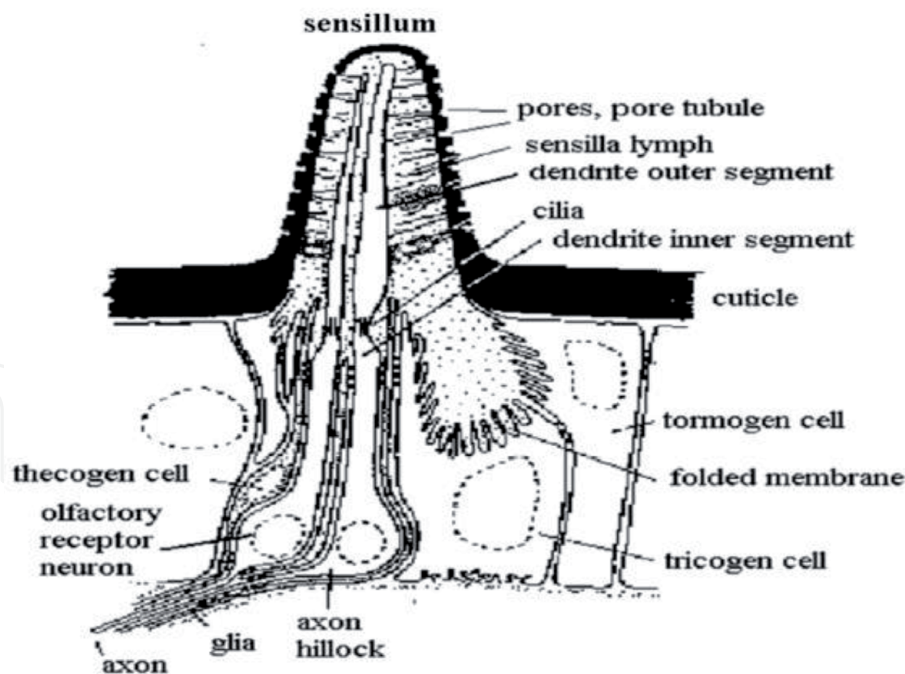


Figure 2.
Basic structure of sensillum [30].

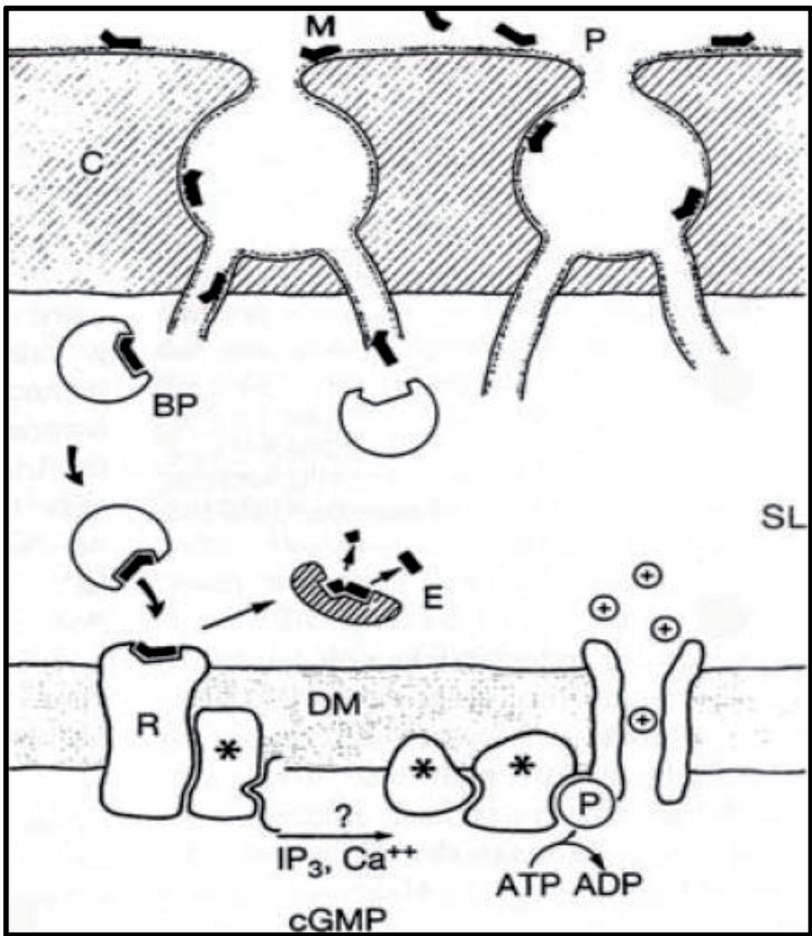


Figure 3.
Simplified schematic concept of perireceptor events in the insect's chemosensory sensilla. Absorbed stimulus molecules diffuse from the sensillum surface through pores in the cuticle (C) into the sensillum lymph. There, they are taken up by odorant- or pheromone-binding proteins and are transported through the aqueous lymph until they reach a specific receptor molecule (R) on the outer dendritic membrane (DM). This activates dendritic ion channels via membrane-bound proteins (*) and intracellular second messenger cascades such as cyclic guanosine monophosphate (cGMP), inositol trisphosphate (IP₃), and Ca⁺⁺ ions. Also, the stimulus molecule could degrade in the sensory lymphatic room by specific enzymes (E) into inactive metabolites so that it can no longer activate the receptor [35].

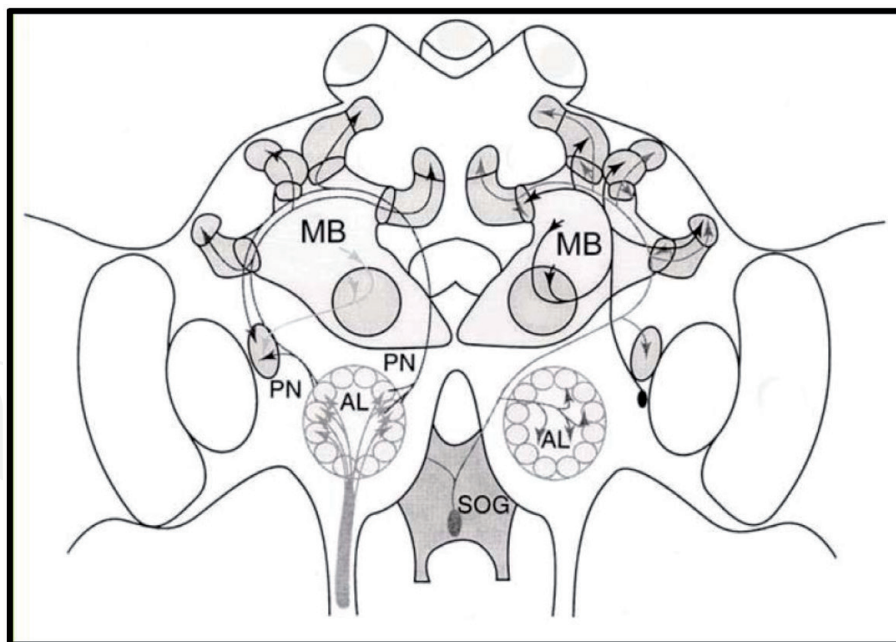


Figure 4.
Schematic view of the central brain area of the honeybee showing the antennal lobes with their specific glomeruli (small circles). From the AL projection neurons (PN) send olfactory information into the mushroom bodies. The MBs are higher-order integration centers of olfactory, visual, and mechanosensory information and are believed to play a role in the control of complex behaviors as well as learning and memory. SOG: Sub-esophageal ganglion [36].

odorant binding proteins (PBPs/OBPs). The signal-PBP/OBP-complex passes or is transported to the chemosensory neuron, where it binds to a specific olfactory receptor protein (OR or R) in the neuron membrane. These receptor proteins were identified in 1999 by [31, 32]. They all belong to the same “seven-transmembrane-domain” protein family; however, they differ between taxa a great deal [33]. From a molecular perspective, binding to the OR activates so-called G-proteins, which are also located in the neuron membrane and part of a phosphorylation-dependent energy exchange, triggering a cascade of signaling reactions. These eventually lead to electrical impulses being sent down from the axon of the neuron to the antennal lobe (AL) (**Figure 4**). The AL is structured into a number of neuron groups (glomeruli) that are innervated separately and only in response to specific individual odors or classes of chemically similar ones [34]. Filtering of these signals is accomplished after reaching the AL glomeruli depending on their quality, quantity, and temporal and spatial characteristics. From the AL, specific patterns of neural activity are processed to higher integrative centers of the brain, such as the mushroom bodies (MBs; **Figure 4**), which are believed to be involved in the control of complex behaviors.

5. Utilization of olfactory communication in IPM

Olfactory/chemical signals represent essential components in different insect management strategies including monitoring, mass trapping, luring and killing, mating disruption, and push-pull strategy (stimulo-deterrent diversion). Also, host plant volatiles play an important role in IPM strategies as the main olfactory response of insect pests for determination of food, mates, and/or oviposition and hibernation sites [1]. Host plant volatiles are often induced by different environmental factors. For instance, the feeding process of herbivore may increase emission of volatiles in plants; these volatiles are referred to as herbivore-induced plant volatiles that stimulate natural enemies to find their prey as illustrated in **Figure 5** [37].

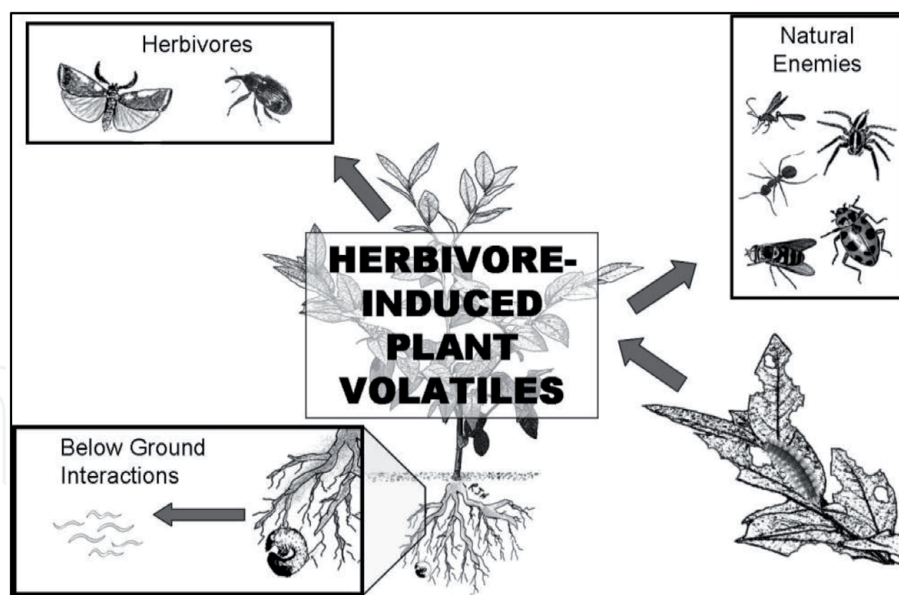


Figure 5.
Herbivore-induced volatile effects on herbivores and their natural enemies [37].

Moreover, isolation and identification of such molecules are essential for consideration as new substances involved in IPM programs.

Recently, the application of different semiochemicals has become an important category of integrated pest management. Various semiochemical compounds are widely applied not only for controlling insect pests [38–41] but also for conservation of rare and threatened insects [42]. Semiochemical substances provide prospective interest in IPM programs depending on the outcome advantages of using such substances. For instance, these substances are distinguished by high volatility that allows diffusion for long distances, application in low concentrations, and rapid dissipation that reduces health and environmental risks compared with chemical pesticides. The efficacy of such molecules mainly depends on their physical properties, i.e., molecular structure, volatility, solubility, and lifetime in the environment. Also, the environmental factors are an important parameter that affect the activity of semiochemical compounds. For example, temperature affects the stability of such compounds by increasing the diffusion of volatile compounds, leading to decreased molecule lifetime in the environment [1].

Control strategies of herbivorous insects are mainly based on semiochemicals which include monitoring, mass trapping, lure-and-kill (attract-annihilate), mating disruption, and push-pull strategy (stimulo-deterrent diversion) tactics. Pheromones are considered as a promising and important component in IPM programs. It can be applied singly or in integration with other control strategies in the agricultural system management for monitoring and controlling various insect pests [1]. The pheromone application is performed in two ways: indirect control and direct control strategies. The direct control involved mass trapping and area-wide dissemination which includes disruption, attractant, and attract-and-kill (lure-and-kill). However, the indirect control involves monitoring for quarantine and spray timing strategy. Pheromone traps are widely used commercially for different purposes in IPM strategies. For example, pheromone-baited traps are used as attract-and-kill or mating disruption techniques to prevent males from reproducing. Furthermore, pheromone can play an important role for detection of information about insect populations. It represents an overview for sex ratio and the mating status which are serious data for the detection of the population phase which is subject to cyclical changes in population density [43, 44]. Interestingly, strategies depending on pheromone application are useful for measuring the genetic diversity

of insect pests. For example, the genetic diversity of the Asian long-horned beetle in Asia, North America, and Europe is reported to be based on pheromone traps [45].

6. Combination of chemical and other communication signals in IPM


Combinations of different communication signals are extremely more efficient in attracting insects than a single stimulus for controlling insect pests. The most successful strategies for insect management were recorded for a combination between different communication signals as visual (color, shape, or size) and olfactory stimuli [1]. Lure-and-kill strategy is an important and widespread tactic which used sticky materials to prevent captured insect from escaping and/or baited with insecticide. Also, combining an insecticide and/or a food stimulant can further enhance the efficacy of visual-depending traps for field applications. The chemical and visual stimuli that attract insects to their host plants have been incorporated into a wide range of insect traps that work better than using a single stimulus [46–50]. Many examples exist where visual stimuli enhance insect responses to semiochemical-based traps [51–53]. Using spheres with red color attractant coated with a non-drying adhesive combined with attractants with odors resembling ripening apples results in an excellent control of the apple maggot fly, *Rhagoletis pomonella* (Walsh) [47]. Also, the choice for suitable places for female mosquitoes to lay eggs is a key factor for the survival of immature stages (eggs and larvae). This knowledge stands out in importance concerning the control of disease vectors. The selection of a place for oviposition requires a set of chemical, visual, olfactory, and tactile cues that interact with the female before laying eggs, helping the localization of adequate sites for oviposition [54].

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