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Understanding Insect Behaviors and Olfactory Signal Transduction

Suliman A.I.Ali[1], Mory Mandiana Diakite[1], Saqib Ali[1], and Man-Qun Wang*[1]

[1]Hubei Insect Resources Utilization and Sustainable Pest Management Key Laboratory, College of Plant Science and Technology, Huazhong Agricultural University, Wuhan 430070, People's Republic of China

*Corresponding author: Man-Qun Wang, Hubei Insect Resources Utilization and Sustainable Pest Management Key Laboratory, College of Plant Science and Technology, Huazhong Agricultural University, Wuhan 430070, People's Republic of China, E-mail: mqwang@mail.hzau.edu.cn

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Abstract

Olfaction is a molecular sense, in which information carried in airborne chemicals is transformed into patterns of brain activity that underlie odor perception. It is probably the most important sense for survival of most animal species ranging from insects to mammals. Detection and localization of food, avoidance of toxins and predators, and communication with cohorts and mating partners through volatile pheromones are examples of the range of olfaction dependent behavior. Olfaction in insect, both medical and agricultural fields, is well documented today. That wide knowledge of insect olfaction (behaviour), especially in agriculture, has contributed to the development of the Integrated Pest Management (IPM) strategies, especially the use of semiochemicals for luring, trapping and killing of insect pests. The present literature review addresses the following general subjects: notion of the pest, importance of the sensilla in insect life, general mechanism of chemical signals transduction, odor identification and discrimination in insects, chemical messengers (pheromones and allelochemicals), insect-plant interactions, ratio-specific odor recognition, and evolution in pest-control strategies and the use of plant extracts in protecting stored-products. The purpose is to contribute in helping beginners in the modern agricultural entomology field for rapid familiarization with these terms frequently used in IPM strategies.

Keywords: Sensilla Olfactory organs; Signal transduction; Predator and parasite

Introduction

Insect relies on chemosensory or chemoreceptor organs located on antennae, mouthparts, wings, legs and ovipositors to live. In general, the chemosensory includes gustatory receptors involved in sense of taste and olfactory receptors involved in sense of odor. In other words, the olfactory receptors are most abundant on the antennae, but may also be associated with the mouthparts or external genitalia (especially near the tip of the female's ovipositor); while the taste receptors are most abundant on the mouthparts, but may also be found on the antennae, tarsi, and genitalia. The gustatory receptors are commonly described as thick-walled hairs, pegs, or pits; whereas olfactory receptors are usually thin-walled pegs, cones, or plates with numerous pores. Anyway, in either case the odor molecules enter through the openings (pores) located on the cuticle where the dendrites of several (usually up to five) sensory neurons are exposed. In sensory neuron cells, there are receptor genes encoding proteins, which mediate odor signal transduction. These small soluble proteins called OBPs (Odorant Binding Proteins) are secreted in large quantities by support cells surrounding the Olfactory Sensory Neurons (OSNs) [1]. They bind odorant messages allowing therefore, an insect to locate food source, aggregate, and mate [2-4].

Notion of the Pest

In agriculture, an insect species is considered as Pest if it can cause important damage to the growing crops or stored-products or livestock production. Thus, because of the competition with human beings for staple food, hundreds of insect species are classified as pests. They feed on leaves or burrows in stems, fruits, roots and stored grains. Those who depend on growing crops (e.g. green leaves) to live are called phytophagous; whereas those who feed on grains, especially the stored-grains, are called stored-grain pests or post-harvest pests. In terms of preference for food (host), the phytophagous, in turn, can be categorized into three groups, of which: monophagous (feeding on plants within a single genus), oligophagous (having hosts in different genera within the same plant family) and polyphagous (attacking a large number of plants of different families) [5,6]. At a very specific level, the insects can be categorized as leaf feeders, stem feeders or grain feeders, etc. Additionally, some insect pests are aggressive only when instar (case of lepidopteran pests), while others are dangerous in both larval and imago stages. The second type of damages, which makes an insect species as pest, is the transmission of epidemic diseases (e.g., bacterial, viral, or fungal infection) to the crops or facilitation of plant infection by epidemic diseases.

However, beyond the damages they cause on crops and stored-products, the insects also play many important roles in the nature. For instance, they aid bacteria, fungi, and other organisms in the decomposition of organic matter, in soil formation as well as plant pollination [7-10]. Certain insects provide sources of commercially important products such as honey, silk, wax, dyes, or pigments, all of which can be of direct benefit to man. Other species like grasshopper plagues, termite swarms, large palm weevil grubs, etc are still sources of protein in some countries. In the biological control of the insect pest, many insect species are used as predators or parasites. Briefly, the word "Pest" is a variable notion. A species becomes a pest if it appears where it's unwished or competes with human beings for staple foods.

Sensilla in Insect Survivorship

The sensilla are usually small hairs within which are housed olfactory organs adapted for perception of specific stimuli (e.g., touch, smell, taste, heat, cold) [11-15]. In most insects, Odorant receptors (ORs), gustatory receptors (GRs) and ionotrophic receptors (IRs) are olfactory organs (Figure 1c) mediating the binding of external odor molecules. Although these small sense organs occur all over the body surface, they are particularly abundant in antennae, palps, and cerci (cerci are sometimes called pincers). Antennae are the main organs bearing olfactory receptors [6,16,17]. They play the dominant role in insect's olfaction because they are more exposed to air currents as insects move upwind toward an odor source [18-20]. Depending on the external morphology, the antennae can be classified into different types and subtypes. Sensilla trichodea, sensilla placodea, sensilla basiconica, sensilla chaetica, sensilla coeleoconica, sensilla styloconica and sensilla campaniformia are among of the well-characterized sense receptor types [21]. The sensilla can be hairs, pegs, plugged or open grooves. They can be on the surface, or they can be located within a depression or a pit with a restricted opening [22,23]. The same sensilla type can be found in different species with the same characteristics. But in some cases, it can have some difference between sensilla in different species even being the same type. For example, a sinsillum can have smooth surface in a given species, while in other species, it can be grooved or striate or pitted [24-26]. The sensillum types present on moth antennae can be classified into six different groups. These are the sensilla trichodea, sensilla basiconica, sensilla auricillica, sensilla chaetica, sensilla styloconica and sensilla coeloconica. Sensilla trichodea are very long, thin, porous hair-like structures with sharp pointed tips. Sensilla can be categorized according to their putative function as well, of which some are mechanoreceptors (campaniformia and sensilla chaetica) or chemoreceptors (sensilla basiconica) or hygro or thermosensitive. A same type can even be mechano and chemoreceptors at the same time (sensilla digitiformia). Sensilla digitiformia is also thought to be hygroreceptor because of their abundance on the mouthparts of some hygrophilous species that depend on damp or wet patchy biotopes/seasons [27]. S. trichodea are known to play a major role in sensing mechanical stimuli and in detecting chemical stimuli in insects [25,26,28,29], and are thought to be innervated by 1–3 sensory cells [30], while sensilla coeloconica are thermosensitive and innervated by 1–5 sensory cells [31-33]. S. basiconica are considered to be olfactory receptors in phytophagous insects [25,34]. The morphology of this sensilla suggests that they are sensitive to many kinds of chemical stimulus [20,35-37]. Additionally, S. cavity is thought to be involved in perception of humidity and temperature [23] and might play a role in preventing desiccation [38]. Both olfaction and contact chemoreception are involved in host-plant selection, as well as in the integrity of insect societies, especially in nestmate recognition [25]. In sensilla characterization, it can have sexual dimorphism [20,39]. The ability of recognizing and discriminating thousands of odorant molecules in insects as in mammals (Figure 2) relies on specialized chemosensitive neural cells to express olfactory receptor proteins, which reside within segregated compartments called sensilla [40-42]. Lots of sensilla are located on the surface of the insect antennae with olfactory neurons being protected inside the binding of a ligand to a receptor protein is the key event in olfactory transduction, as it converts a chemical signal in the environment into an electrical signal that can be interpreted by the insect nervous system.

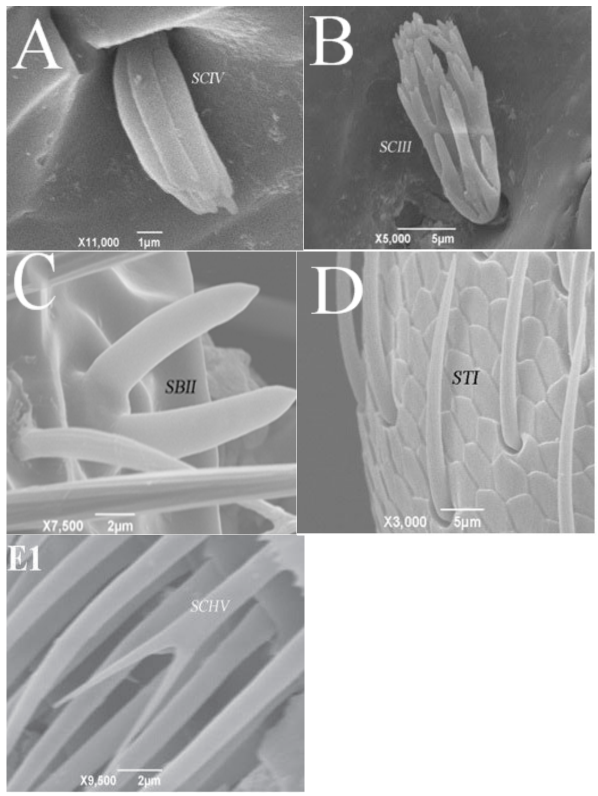


Figure 1: sensilla types A and B are sensilla from *Sitophilus granarious* which are classified as *Sensilla coeloconica*, while C, D and E are of *Tribolium castaneum*, and classified as *Sensisilla basiconica*, *S. trichodea* and *Sensilla chaetica.*

Mechanism of Chemical Signals Transduction

The mechanism starts by trapping chemical molecules dispersed in the air by special chemoreceptors or olfactory receptors expressed in the cell membranes of olfactory receptor neurons. Activated olfactory receptors initiate a signal transduction cascade which ultimately produces a nerve impulse (or action potential or spike). The neurons (electrically excitable cells) then processed and use neurotransmitter (an endogenous chemical stored in synaptic vesicle) to transmit signals from one neuron to the next, usually from the axon terminal till the signals reach central nervous system. In other words, axon terminals (distal terminations of the branches of an axon) are separated from neighboring neurons by a small gap called a synapse [43,44], across which impulses or signals are sent before being received by postsynaptic receptor and in a pattern neuron-to-neuron via synapses, the external signals converted into internal electrical signals or impulses by sensory neurons (Figure 3b), ultimately reach the spinal cord and brain (the two constitutive components of the central nervous system). Multipolar neurons play an important role in this complex neural communication or cell-to-cell communication. They allow for the integration of a great deal of information from other neurons. They include motor neurons and interneurons, and constitute the majority of neurons in the brain. We have to remember that second messengers intervene in this process by relaying signals, causing some kind of change in the activity of the cell and amplifying the strength of the signals that will be sent to the brain through glomeruli. They are a component of signal transduction cascades. In humans as well as most vertebrates, the sense of smell is mediated by specialized sensory cells of the nasal cavity (Figure 2), which can be considered analogous to sensory cells of the antennae of invertebrates (Figure 3) [45].

Figure 2 : Odorant Receptors and the Organization of the Olfactory System [125].

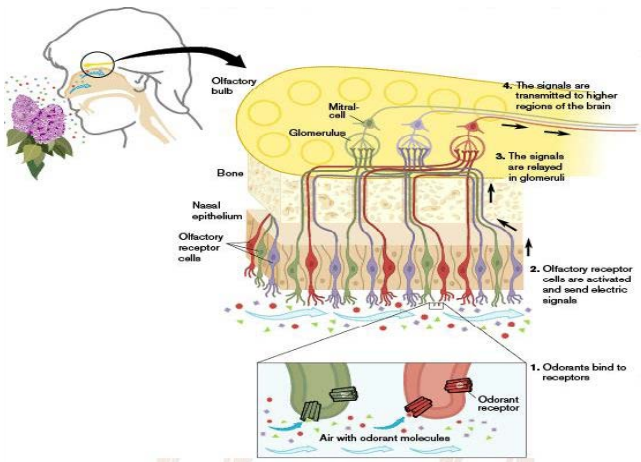
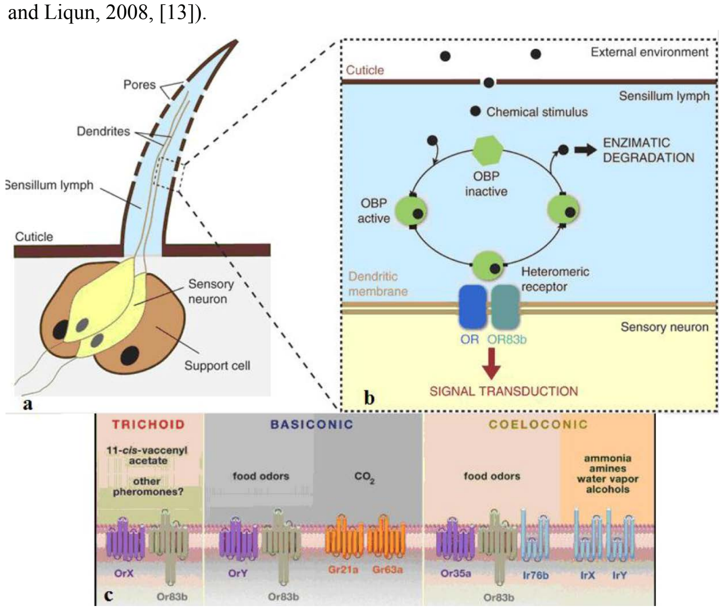


Figure 3: Anatomy of an olfactory sensillum [139] and Summary of odorant sensitivities and odorant receptor expression in different types of sensilla (Maria and Liqun, 2008, [13]).



Odor Identification and Discrimination in Insects

In insects, each sensillum (Figure 3a) possesses specialized sensory cells called ORNs that run chemical signals inward to the central nervous system. The individual ORNs express specific type of odorant receptor proteins called OBPs whose role is to bind external odorant (Figure 3b) and initiate transduction. After binding the odorant, the activated receptors send transduction signal (Figure 3b) to the glomeruli [46,47] via second messengers. We have to precise that each glomerulus receives signals from multiple receptors that detect similar odorant features. Because multiple receptor types are activated due to the different chemical features of the odorant, multiple glomeruli will be activated as well. All of the signals from the glomeruli will then be sent to the brain, where the combination of glomeruli activation will encode the different chemical features of the odorant. The brain will then essentially put the pieces of the activation pattern back together in order to identify and perceive the odorant [46,48,49]. Odorants that are alike in structure activate related patterns of glomeruli, which lead to a similar perception in the brain [46,50-53]. Within the glomerular array, the synaptic organization of afferent ORN axons and dendrites of antennal lobe interneurons forms the mechanism underlying odor identification and discrimination [54-56]. Generally, each OSN expresses one (or sometimes a few) OR and OSNs that express the same OR converge on a single glomerulus in each hemisphere [48,57-61]. Anyway, studies showed that OSNs may innervate the entire glomerulus, or just the glomerular periphery. In bees, OSNs from the distal antennal segments innervate the outer layer of the glomerular cap, and more proximal OSNs innervate the central layers [62]. The current dogma is that axons from all ORNs expressing the same receptor converge onto one or two glomeruli of a possible 1800 glomeruli in each olfactory bulb [63]. We have to remember that the glomeruli are located near the surface of the olfactory bulb (forebrain involved in odor perception). And, a glomerulus is the basic unit in the odor map of the olfactory bulb. The primary olfactory brain center of insects, the Antennal Lobe (AL), constitutes the first synaptic relay station of the antennal afferent pathways, as it receives input from antennal olfactory sensory neurons and sends the output to higher brain centers [64-67]. The building blocks of the AL found in most insect orders are the olfactory glomeruli, in which the interactions between antennal and deutocerebral neurons take place [68]. Additionally, the real difference between an insect's sense of smell and sense of taste lies in the form of the chemical it is collecting. Smelling is going with odor, while tasting occurs if the chemical substance is in solid or liquid status.

Chemical Messengers

Pheromones

Pheromones are chemical signals that are secreted by an animal to the outside and cause a specific reaction in a receiving individual of the same species [69]. They consist in long carbon chains derived from the metabolism of fatty acids [70]. The pheromones usually wind borne, but may be placed on soil, vegetation or various items [71,72] as messengers. As reported earlier, the transport of the volatiles or pheromones from the external environment to the olfactory receptors is mediated by small proteins, called OBPs [73-75] with 135–220 amino acids long [75,76]. The bound odor molecules are then processed and conveyed to the central nervous system which produces all behavioral responses thereafter on receiving species [6,16,17]. The olfactory receptor genes encoding OBPs can be divided into Pheromone-Binding Proteins (PBPs) involved in the recognition of sex pheromones and General Odorant Binding Proteins (GOBPs) which are thought to participate in the recognition of general odorants [13]. Like OBPs, coding sequence of PBPs shows the six conserved cysteine residue's position linked by three disulfide bonds [77]. Chemosensory Proteins (CSP) constitute another class of small binding proteins. They are more conserved comparatively to OBPs, and are characterized by the presence of 4 conserved cysteines that form two disulfide bridges [78]. They may evolve from the OBPs in the early development of arthropods [79].

Types of Pheromones

There are different types of pheromones according to the response they induce in the Perceiving Individuals [80]. The most common pheromones are: Sex pheromones (usually emitted by females to induce mating behavior in males), Aggregation pheromones (usually secreted by males to induce host finding behavior, defense against predators or overcome host resistance by mass attack), Alarm pheromones (triggered once there is a threat), Trail pheromones (specific in social colonies to indicate the way leading to the discovered-food source), and lastly, Host marking pheromones (produced to reduce the competition between members of the same species) [70;81]. We have to precise that male-produced sex attractants have been called aggregation pheromones, because they usually result in the arrival of both sexes at a calling site; whereas most sex pheromones are produced by the females.

Allelochemicals

In chemical ecology field, pheromones and allelochemicals are both used, whence the reason to make the difference between the two terms. In other words, like pheromones, the allelochemicals are biochemical produced to influence the growth, survival, and reproduction of other organisms (Allelopathy). They can have beneficial (positive allelopathy) or detrimental effects (negative allelopathy) on the emitter or the attacker [82]. As shown in (Figure 4), the allelochemicals can be classified into two groups considering whether they act as intraspecific (pheromones) or interspecific (allelochemicals) mediators. Allelochemicals include allomones (emitter species benefits), kairomones (receptor species benefits) and synomones (both species benefit) [83]. Basically, the volatiles released by plants (Figure 5) can be categorized into four groups as followed [6]:

- Attractant: a chemical that causes an insect to make oriented movements toward the source of the stimulus.
- Repellent: a chemical that causes an insect to make oriented movements away from the source.
- Feeding or oviposition stimulant: a chemical that induces feeding or oviposition behavior.
- Deterrent or antifeeding stimulant: a chemical that inhibits feeding or oviposition.

However, a single chemical signal may act as both as pheromone and allelochemical, as attractant as repellent.

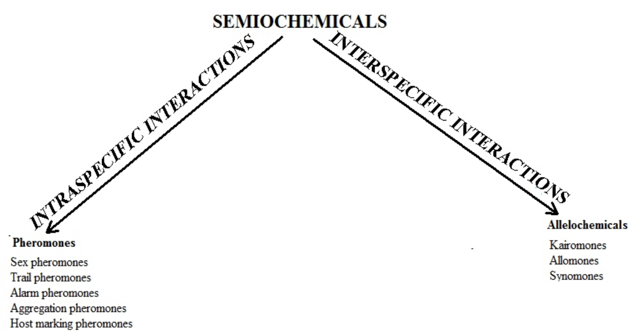


Figure 4:Types of semiochemicals

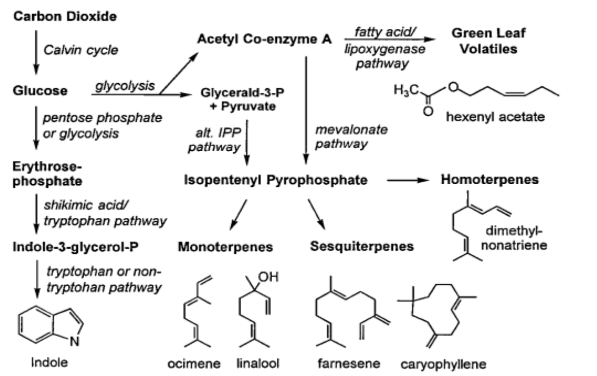


Figure 5:Biosynthetic pathways leading to the release of plant volatiles.

Insect-Plant Interactions

Interactions between plants and insects can be both antagonistic and mutualistic [84,85]. The plant volatiles are signals used by insects to locate hosts, find mates, prey and select oviposition sites [86]. The majority of volatiles collected from plants, and grains are: terpenoids, fatty acid derivatives, benzenoids and nitrogen-containing compounds. Some of the volatiles are specific to certain species, while others are general and found in many species [87,88]. Once released by a source (Figure 5), the volatiles are dispersed (Figure 6), mixed, and diluted by the ambient motion of air to form a shifting and filamentous plume [89]. The relationship between insects and plants is largely influenced by the ambient air that disperses odor molecules. The olfactory world is characterized by constant movement and flux. Gradients of plant odors do not concentrate a few centimeters distant from a plant due to air turbulence [6]. Explicitly, host odors exist in the form of pockets blowing downwind along with the non-odorous air creating an odor gradient. As the wind swings about, the order is broken into a series of pockets (Figure 6). And, by positive anemotaxis the insects will identify and reach a food source [90]. Indole, a product of the shikimic acid pathway, is formed from indole-3-glycerol-P either as an intermediate in Trp biosynthesis or by a Trp-independent pathway leading to a family of nitrogen-containing defense compounds (e.g. 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) [91]. Sesquiterpenes are synthesized via the isopentenyl pyrophosphate (IPP) intermediate following the classical mevalonate pathway, whereas monoterpenes and diterpenes are synthesized via an alternative IPP pathway with glyceraldehyde-3-P and pyruvate identified as the direct precursors of IPP [92]. The mevalonate pathway is localized in the cytosol and reactions to the non-mevalonate pathway are localized in plastids. The homoterpene (E) -4,8-dimethyl-1,3,7-nonatriene and (E, E) -4,8,12-trimethyl-1,3,7,11-tridecatetraene are derived from their 15 and 20 carbon precursors, farnesyl- and geranylgeranyl-pyrophosphate, respectively, by a series of enzymatic steps with the overall loss of four carbon units [93]. The green-leaf volatiles derive from linolenic acid via a 13-hydroperoxylinolenic acid intermediate [94]. This oxidized linolenic acid, instead of losing water and committing the molecule down the defense signaling jasmonic acid pathway, is cleaved to form two fragments of 12 and six carbon units (Figure 3). The variety of green-leaf volatiles are formed from this second pathway by multiple rearrangement steps of the six-carbon (Z) -3-hexenal [95].

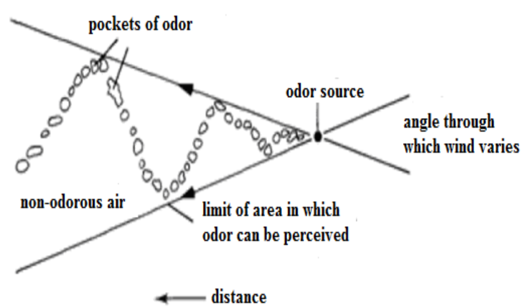


Figure6: Dispersal of odour source [6].

Ratio-Specific Odor Recognition

Numerous electrophysiological studies on a wide range of phytophagous insects have demonstrated that peripheral receptors are tuned to the detection of ubiquitous plant volatiles. Because phytophagous insects generally recognize the host odor by using ratios of common plant volatiles, and recognition is thus not restricted to species-specific compounds, it would appear that the central processing of peripheral signals is extremely important [88]. Many insect studies have suggested that generalist olfactory receptors are responsible for host plant odor perception, but there is some evidence for the presence of specialist olfactory receptors for the detection of plant odor in insects such as *Spodoptera littoralis*. Pheromone detectors usually are very sensitive and selective to their specific key compounds. The neurons are likely to function as labeled lines, with each type of neuron carrying information about a single odorant compound [96]. Chemical cues released into the air can guide moths (nocturnal flyers) to food sources or mating sites over long distances [97], even at very low concentrations (a few molecules of pheromone or plant odors). Different flower species often share many volatile components [88,98], but their combination and concentration are unique to each species, forming an "odour code" [99] that specialist insect may use to identify their hosts. Ratorderf compounds are assumed to drive host plant location in insects [16,88,100]. Even the lowest level of a compound in a blend might contribute to the attraction of an insect species to its host plant [101,102].

Evolution in Pest-Control Strategies

The primary objective for pest control was to avoid the spread of diseases by insects through land managing, improved housing or sanitation of food facilitation before storing. Indeed, the continuous effort for controlling pest led early to the production of DDT, a remarkable compound that is highly toxic to most insects and long-lasting in effect. Widely used in agriculture for many years, DDT is not anymore an ideal insecticide because of environmental concerns. Similar ecological problems were encountered with many successors to DDT like Dieldrin or Endrin. In other words, the continuous use of synthetic insecticides, in particular, has not only caused death through poisoning, accumulated in man, concentrated in food chains, but also caused resistance in pest populations and destroyed parasites, predators and pollinators. Thus, biological methods as well as the use of semiochemicals becomes increasingly important with the increase of the restriction on the use of undesirable insecticides [103]. We have to remember that, the biological methods include introducing pest strains that carry lethal genes or parasitoids, while semiochemicals consist of the use of pheromones to trap and disrupt mating behavior of the insect pests. The role of feeding-induced plant volatiles in host habitat location by natural enemies is well documented [85,104-107]. Exploitation of plant volatiles that attract natural enemies has been potential for enhancing biological control in agroecosystems [108]. For instance, synthetic herbivore-induced plant volatiles (HIPVs) have been used to attract and retain beneficial insects into vineyards and hopyards [109,110]. However, a successfully pest management requires combined strategies for an adequate long-term solution [111]. And, the presence of some insect pests in the field does not automatically result in damage or yield loss. Therefore, there is a threshold that should be reached before deciding treatment.

Pheromones and Semiochemicals in Pest Control

The characterization of the first insect sex pheromone was established by [112], and was isolated from female *Bombyx mori* (Lepidoptera). This discovery led to the development of commercial activities in the synthesis of semiochemicals previously identified as potential agents for controlling pests. Since then we have assisted the replacement of synthetic insecticides with pheromone products [81,97], and the emergence of a new scientific discipline: the chemical ecology or Chemical communication. In parallel, the gas chromatography appeared in chemistry and brought simplicity in identification of volatile molecules. Rapidly, the economic interest for using pheromone compounds in pest controls was updated and included in Integrated Pest Management (IPM) programs [70], which imply various strategies depending the goals and scopes to achieve. Monitoring of insect populations, trapping by using traps lured with synthetic attractant associated with a killing substance [113], Push-pull strategy, which consists of pushing away crop enemies while luring them to the pheromone dispensers containing killing substances, is among of the current IPM strategies [114-118]. We have to precise that the aggregation pheromones are one of the most ecologically selective pest suppression methods. They are nontoxic and effective at very low concentrations [119]. An Additionally, crop rotations, field sanitation (crop residue management), seed quality, weed management, tillage, healthy soil, crop and variety selection, intercropping etc, are also part of integrated pest management strategies, especially in organic crop systems.

Conclusion

Understanding the technical terms relevant to insect behavior and chemical messenger's transduction could be of paramount importance for beginners in the entomology field. All these terms addressed to here have been already previously reported in different sources. However, the effort provided here to collect and define and differentiate the similar terms in an easy way could be very useful for many people in the modern agricultural entomology field in which the terms such as semiochemicals, are frequently used.

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