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Pheromones in lepidopteran insects: Types, production, reception and its application

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Abstract
The to semiochemicals that are released by one member of a species and evoke a specific reaction or reactions from members of the same species. Pheromones are known for both the specificity and the potency of their actions. Lepidopteran pheromones were the first to be widely studied and include a huge collection of mostly female based pheromones. Female typically produce long range, fatty acid derived molecules that function over long distances, where as male tend to produce close-range courtship compounds that are often very similar in structure to plant secondary metabolites. After knowing the nature of pheinsect's universe is filled with many odours. One of these odours is called pheromone, a term commonly applied romones and their potential for pest control along with the future prospective of pheromone technique in agriculture in India, it is highly recommended to enhance availability of pheromone in market, invest more in research and development and introduce newly identified pheromone for management of specific pests.

Keywords: sex pheromone, lepidoptera, ectohormone, attraction, behavior, management

Introduction
Pheromones are a naturally occurring chemical compounds found in all insects, animals, and humans. The term 'pheromone' was introduced by Karlson and Luscher (Karlson and Luscher, 1959) [9] and it derives from the Greek words 'pherein' (to carry) and 'hormon' (to excite). These are referred to as 'ecto-hormones' as they are chemical messengers that are emitted into the environment from the body where they can then activate specific physiological or behavioural responses in other individuals of the same species. These molecules are evolved signals, in defined ratios in the case of multiple component pheromones, which are emitted by an individual and received by a second individual of the same species, in which they cause effect on hormone levels or behavioural change or specific reaction (Thiel and Duffy, 2007) [20]. These are found in living things and are the most ancient form of animal communication (Karlson and Luscher, 1959) [9]. Pheromones are natural scents which play an important role in sexual communication. These Pheromone aromas convey signals relating to mood, status, drive and health to the subconscious awareness of the opposite sex. This philosophy holds well in the animal world, pheromones are consciously detected over considerable distances and serve at times in place of real communication. They help insects to mark territory, recognize mates, and signal sexual interest. These are produced by ectodermal glands on the abdomen and associated with mandibles of hymenopterans and wings of lepidopteran insects. Sex pheromone was first discovered by Butenandt in the silk worm (*Bombyx mori*) (David and Nesbitt, 1985). Unlike higher animals, the insects communicate between sex of their own species or with its sub-species or very rarely, with different species of a genus or family or species of a different order.

Classification of pheromones
Based on the responses elicited, pheromones can be classified into two groups.

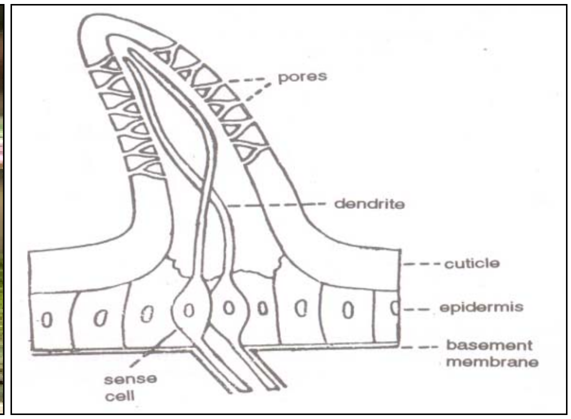
- **Primer pheromones:** They trigger off a chain of physiological changes in the recipient without any immediate change on the behaviour. They act through gustatory (taste) sensilla and are not found in Lepidopteron insects.
- **Releaser pheromones:** These pheromones produce an immediate change in the behaviour of the recipient. These act through olfactory (smell) sensilla and directly act on the central nervous system of the recipient and modify their behaviour. These are further subdivided into various types out of which only following three are known to occur in Lepidopteron insects.

- **Sex pheromones:** These are usually released by one sex to lure the opposite sex from a distance to excite it sexually. Though most commonly released by females, they may be released by either sex. Over 150 species of insects are known in which the females produce sex pheromones and about 50 species in which the males do so. The male and female sex pheromones differ in their property and action. The female sex pheromone acts at a longer range, excites males to copulate and by and large is species specific. The male sex pheromones on the other hand act at short range and only lower the female's resistance to mating.
- **Trail pheromone:** These pheromones are laid in form of intermittent or continuous lines on a soil substrate which trial followers perceive by their antennae to reach the destination which could be mating site or a food source. Trail pheromones help in finding mates and food source. Trail pheromones are known from larvae of some Lepidoptera e.g. tent caterpillar (*Malacosoma americanum)*. It is possible to manipulate trail following and recruitment of tent caterpillar e.g. *Malacosoma americanum* (Fitzerald, 1993) that is a serious defoliator in North American forests.
- **Host marking Pheromone:** Host marking and host discrimination are an expected result of evolution in some lepidopterous insects. In order to survive and develop properly, they use a chemical signal, that is, a host marking pheromone (HMP), for communication to avoid laying eggs by other females of same species at the same site. This phenomenon was noted 140 years ago, but it was studied and described for the first time in the 1970's. Since then, the purposes and functions of host marking have been determined, as well as the strategies and methods of host marking and discrimination. e. g. Arctiid Moth *Amsacta albistriga.*

Pheromone producing glands: The glands that produce pheromones are ectodermal in origin; they open and release their products outside the body. They are therefore called exocrine glands as distinct from the endocrine glands which release their products (hormones) inside the body. These glands can be present on any part of the body i.e. head, thorax, abdomen, legs or wings-depending on the species. However, in Lepidopteron insects these appear as eversible sacs located in the inter-segmental membrane behind the eighth abdominal sternite. Aphrodisiac glands take the form of pair of extrusible hair pencil (brush organs or scent brushes) located at the end of the abdomen in some male butterfly e.g. *Danaus* spp. or glandular scales called androconia on the wings in males of other lepidoptera.

Pheromone secreting glands in insects.

Pheromone reception: Pheromone communication system consists of three components: pheromone production (exocrine glands), medium (air or water) through which the pheromones travel from the point of emission to the point of reception and pheromone receptors. Pheromone receptors could be olfactory (smell) or gustatory (taste) sense organs, though in majority of the cases they are of the former type. The olfactory sensilla are present mainly on the antennae. Pheromone molecules make their entry into the sensillum through their numerous pores. These pores lead into the lumen of the sensillum which is filled with a fluid called the sensillum liquor that baths the dendrites. The pheromone molecules are possibly absorbed by the liquor and then move by diffusion to combine with the acceptor (receptor) site on the dendrites to initiate transduction (transformation of the stimuli into electrical impulses that reach the brain). It should, however be mentioned that the mechanism of pheromone perception (reception and transduction) is still not well understood. But what is well known is that the insect olfaction is by far more sensitive than any man made electronic detection system. For instance, it has been estimated that 30 g of disparlure, a synthetic sex attractant will be enough to bait some sixty thousand traps per year for the next 50 years (Jacobson, 1972).



Pheromone reception in insects.

How a male smells its way through: It is necessary to know which way the male has to fly to find the source of tinting (i.e. its female). Theory of positive anemotaxis propounded by Schwinck of the University of Munich (Germany) says that when the male moth is activated by the pheromone, it simply flies upwind and thus inevitably moves towards the female. If by accident, it passes out of the active zone (odour corridor); it either abandons the search or flies about at random to pick up the scent again. Eventually, as it approaches the female, there is slight but gradual increase in the concentration of the chemical attractant and this serves as a guide for the rest of distance.

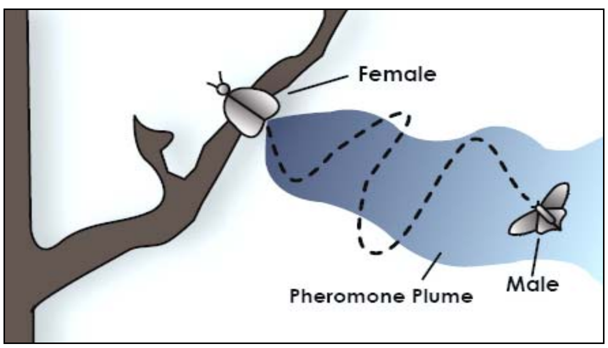


Fig : Attraction of male towards source of tinting (female moth).

Use of pheromones in Lepidopteran pest management
Sex pheromones are being used in lepidopteron pest management in following different ways:

1. Pheromones in indirect control: Indirectly the pheromones are used for pest management in various ways as follows.

i. Use of monitoring systems in pest detection: In monitoring system pheromones are used for three purposes.

a. Early warning of pest incidence
Pheromone traps are used to detect the arrival of dispersing or migrating insect pests. A net work of traps is used over the whole region of East Africa to monitor movements of the African army worm, *Spodoptera exempta*. Information on pest appearance is collected from traps and fed back to a coordination centre at the desert locust control organization for East Africa, from where timely warnings are transmitted to areas about to experience an attack from the pest (McVeigh and Bettany, 1986) [13].

b. Survey to define infested areas
The pheromones are used for this purpose in monitoring the spread of Gypsy moth, *Lymantria dispar*, an introduced pest of broad leaf forests in North America (Schwallbe, 1979) [13]. Large number of traps baited with the pheromone for this pest i.e. disparlure are now used annually by the US Department of Agriculture to survey the areas infested by this insect.

c. Arrival of quarantine pests in pest-free areas
The pheromone based detection system is now also being used to monitor the potentially very damaging race of *Lymantria dispar*, the Asian gypsy moth, in those countries where it is regarded as a major quarantine pest.

ii. Use of monitoring systems in timing of control measures
a. Timing of spray treatments
This approach is applied to both immigrant pest populations of insects such as the pea moth, *Cydia nigricana* (Macaulay *et al.*, 1985) [12] and emergent but resident populations such as those of the codling moth, *Cydia pomonella* (Glen and Brain, 1982) [7]. A threshold catch is usually established for any trapping system before any spray treatment is justified.

b. Timing of other sampling methods
Trap catch information is often not sufficient by itself to take pest management decisions. In bollworm pests of cotton, a threshold catch in a pheromone trap triggers the taking of a sample of cotton bolls for inspection for eggs or young larvae. If the eggs are ready to hatch or larvae were found, then a spray application is made (Lopez *et al.*, 1990; Campion, 1994) [11, 1].

iii. Use of monitoring system in population density estimates
a. Population trends
One of the objectives of monitoring *Choristoneura fumiferana* is to identify population trends over many generations. Sanders (1990) [16] has shown that trap catches obtained since 1973 so broadly reflect trends to be cyclical in importance (outbreaks lasting 5-10 years in cycles of 35-40 years) then the pheromone-baited trapping system can be used to provide a very good indication of population trends over a long period.

Table 1: Present status of pheromone research in India.

S. No.	Pest species	Pheromone components	use
1	Yellow stem borer (*Sciphophaga incertulas*)	Hexadecenal, (Z)-9-Hexadecenal.	MN, MT,MD
2	Leaf folder (*Cnaphalocrocis medinalis*)	Hexadecyl acetate, (Z)-11-Hexadecenyl acetate.	MN
3	Leaf folder (*Marasmia patnalis*)	(Z)-13-Octadecenyl acetate.	MN
4	Maize stalk borer (*Chilo partellus*)	(Z)-11-Hexadecenal, (Z)-9-Hexadecenal.	MN
5	Striped stem borer (*Chilo suppressalis*)	Hexadecenal (Z)-9-Hexadecenal.	MN
6	Climbing cutworm (*Mythimna separata*)	(Z)-11-Hexadecenal, (Z)-11-Hexadecen-1-ol	MN
7	Purple stem borer (*Sesamia inferens*)	(Z)-11-Hexadecenyl acetate.	MN
8	Rice green caterpillar (*Naranga aenescens)*	9-Tetradecenyl acetate, (Z)-9-Hexadecenyl acetate.	MN
9	Pink bollworm (*Pectinophora gossypiella)*	(Z,Z)-7, 11-Hexadecadienyl acetate	MN, MT,MD
10	Spotted bollworm (*Earias vittella)*	(E,E)-10, 12-Hexadecadienal -10, 12-Hexadecen-1-o1	MN, MT,MD
11	Spiny bollworm (*Earias insulana)*	(E,E)-10, 12-Hexadecadienal	MN, MT,MD
12	Gram pod borer (*Helicoverpa armigera)*	(Z)-9-Hexadecenal, (Z)-11-Hexadenal, Hexadecenal	MN,MT
13	Oriental tobacco budworm (*Helicoverpa assulta*)	Hexadenal, (Z)-9-Hexadecenal.	MN,MT
14	Tobacco caterpillar (*Spodoptera litura)*	(Z)-9(E)-11-Tetradecadienyl acetate	MN,MT
15	Castor semi looper *(Achaea janata)*	9-Heneicosadiene, (Z,Z,Z)-3,6,9-Heneicosatriene	CI
16	Red hairy caterpillar (*Amsacta albistriga)*	Octadecanal (Z,Z)-9,12-Octadecadienal	CI
17	Bihar hairy caterpillar (*Spilosoma obliqua*)	3, 5-cis-9, 10-Epoxy-1, 3, 6-heneicosatriene.	CI
18	Tobacco caterpillar (*Spodoptera litura*)	(Z)-9(E)-11-Tetradecadienyl acetate.	MN,MT
19	Diamond-back moth (*Plutella xylostella)*	(Z)-11-Hexadecenal, (Z)-11-Hexadecenyl acetate.	MN,MT
20	Cabbage stem borer (*Hellula undalis)*	(E,E)-11, 13-Hexadecadienal.	MN
21	Brinjal borer (*Leucinodes orbonalis)*	(Z)-11-Hexadecenyl acetate, (E)-11-Hexaden-1-0l.	MN,MT
22	Cutworm (*Spodoptera exigua*)	Tetradecyl acetate, (Z)-9-Tetradecenyl acetate.	MN,MT
23	Potato tuber moth (*Phthorimoaea operculella*)	4, 7, 10-Tridecatrienyl acetate.	MN
24	Sugarcane stalk borer (*Chilo auricilius*)	Tetradecenyl acetate (Z)-10-Pentadecenyl acetate.	MN
25	Early shoot borer (*Chilo infuscatellus)*	(Z)-11-Octadecen-1-ol.	MN,MT
26	Internode borer (*Chilo sacchariphagus*)	(Z)-13-Octadecenyl acetate (Z)-13-Octadecen-1-ol.	MT
27	Armyworm *(Mythimna separata*)	(Z)-11-Hexadecenal (Z)-11-Hexadecen-1-ol	MN
28	Purple stem borer *(Sesamia inferens*)	(Z)-11-Hexadecenyl acetate (Z)-11-Hexadecen-1-ol	MN
29	Leafroller (*Archips pomivora*)	E-11-Tetradecenyl acetate	MN
30	Codling moth (*Cydia pomonella*)	Codlure	MN
31	Gypsy moth (*Lymantria obfuscata*)	10 acetoxycis-7-hexa-decnol (Gyplure)	MN

MN= Monitoring, MT= Mass trapping, MD = Matting disruption, CI = Chemical identified.

a. Population density correlations

Obtaining quantitative information about pest populations from trap catch data has proved difficult in many cases, especially in strong flying, highly mobile insects such as *Heliothis spp*. (Srivastava *et al.*, 1992) [19]. In some cases, species have been trapped successfully in the field, but their presence in traps has not correlated well with subsequent sampling of eggs or larvae or with damage. This may be due to the fact that sex pheromones in Lepidoptera at least, usually attract the males and a correlation between male and female numbers in the field does not always exist. Indeed, the females may not be present, or are in a migratory phase and not laying eggs, or have already oviposited elsewhere before the males moved to the site being monitored.

b. Effects of control measures

Pheromones can be used to monitor the effects of control measures e.g. Catches of *Ephestia kuhniella* (storage moth pest) in the funnel traps in a flour mill over a period of eight months clearly demonstrated the effects of total fumigation of the mill in June of that year (Spinelli and Arsura, 1984) [18].

iv. Use of pheromones in monitoring resistance

Repeated application of insecticides can result in an increase in insecticide resistance and dispersion in the population. Traditional methods to monitor the presence and distribution of insecticide resistant insects are often laborious, mainly because of the difficulties involving population sampling. A more elegant method for extracting independent samples of genotypes from the population is based on the use of pheromones. This approach is based on attracting large number of insects for collection to traps (Riedl *et al.*, 1985) [15].

2. Pheromones in direct control of lepidopteron pests.

Direct control methods using pheromones against insects are as follows.

i. Mass trapping

In mass trapping, a very high proportion of the pest is caught before mating or oviposition to reduce the pest population. For Lepidopteron insects, it is essential that males are trapped before mating and it is most likely to succeed with insects that mate only once.

Factors that make mass trapping non-viable on large scale:

- Lack of attraction of females by the attractant source.
- Lack of highly efficient traps.
- Problem of high insect populations and trap saturation.
- Need for a high density of traps per unit of surface area which in turn renders the technique too costly.

ii. Lure and kill technique: Also referred as "attracticide", "attract and kill", "attraction-annihilation", or "male annihilation" it is a modification of mass trapping in which the moth lured by a synthetic pheromone is not only caught in the trap, but also subjected tactics combine pheromones with insecticides. McVeigh and Bettany (1986) [13] reported a lure and kill technique against the Egyptian cotton leaf worm (*Spodoptera littoralis*), that used treated filter paper as the substrate. More recently, lure and kill has been reported to work against codling moth, *Cydia pomonella* (Charmillot and Hofer, 1997) [4] and commercial product "Sirene" Novartis is now registered in Switzerland.

iii. Lure and infect technique: A more elegant development of this general approach is called auto-dissemination and combines insect pathogens with pheromones. The aim of this tactics is not to kill the insects' right way, but rather to use them as vectors of the disease into the wider population. Different pathogens could be used, with slightly different pathways from virus e.g. baculo-virus or grannulosis virus, fungus e.g. *Zoopthora radicans* (Pell *et al.*, 1993), or a bacterium e.g. *Serratia entomophilla* or even entomopathogenic nematodes This approach has been explored with nucleopolyhydrosis virus against Tobacco budworm, *Spodoptera littura* (Jackson *et al.*, 1992) and a granulosis virus against codling moth, *Cydia pomonella* (Hrdy *et al.*, 1996) [8].

iv. Mating disruption: Another direct control tactics using pheromones for the control of insects is called mating disruption. Here, the aim is to prevent mating and hence reduce the incidence of larvae in the next generation. This is normally done by releasing a large amount of sex pheromone in the treated area. The behaviour of male insects is disturbed by their exposure to synthetic pheromone released by dispensers (Carde and Minks, 1995) [3].

v. Auto-confusion: It is a pest management strategy that differs from the traditional mating disruption in that it uses males as mobile dispensers. The relevance of this technique lies in that limited quantities of pheromone and a small number of dispensers per hectare (25-30/ha) are needed, resulting in important benefits for farmers in terms of deployment time and for the environment since less waste material is produced.
Mechanism of auto-confusion

- It inhibits mating by attracting males in an outer, where a dispenser containing an electrostatic powder carrying the female pest sex pheromone is placed.
- The powder gets stuck to the body of the males overwhelming their pheromone receptors and preventing them from locating females for mating.
- In this way males become themselves carriers of the pest pheromone throughout the orchard.
- Contact between males ensures that the powder and the confusion effect are automatically passed on.

Methods of pheromone application

Different methods have been devised for the application of pheromones in the field.

a. Micro-encapsulation method: The pheromone is enclosed in small (Ca.50 µm) plastic capsules which are dispensed with conventional spray equipments to provide their uniform distribution.

b. Hollow fibre method: Here the pheromone is kept in hollow plastic fibres (capillaries) which are cut in small pieces and scattered by the help of an aircraft. The fibres may also be fashioned into hoops (coils) and tied to upper part of stems.

c. Pheromone baited traps: These are specially devised structures of various shapes and sizes which could be suspended from trees or elevated objects. Many types of traps are now available commercially of which the Pherocon R, Sector XC-26 and Sector 1 traps are more popular.

d. Pheromone dispensers: These are the latest devices that can release the pheromone at precisely calculated rates. A commonly used dispenser has been patented as Pherocon controlled release dispenser. It is made up of the plastic laminates, the middle layer acting as a reservoir in which the pheromone (or any lure) is embedded and the outer layer as a barrier that regulate the rate of pheromone release. These dispensers come in shapes of square (0.5-2.5 cm) ribbons and flakes. Flakes are scattered (with a sticker to stick the particles to the crops foliage) by an aircraft over dense vegetation (forests, orchards) while squares and ribbons can be placed manually. Some 10000-20000 sex pheromone flakes can mask the odour of a "calling" female in one acre area thereby causing mating disruption.

Table 2: Mean (±SEM) cumulative oriental fruit moth *Grapholitha molesta* pheromone trap captures in unmanaged (abandoned), conventional insecticide treated and mating disruption orchards in Henderson country, North Carolina.

Year	Location	Treated	No.	Moths/traps
2000	Barnwell	Sprayable pheromone	16	8.8
		Isomate-M100	16	0.6
		Conventional	16	14.1
		Abandoned	16	29.1
		Total		52.6
	Henderson	Sprayable pheromone	16	2.7
		Isomate-M100	16	0.3
		Conventional	16	6.8
		Abandoned	16	28.9
	Total			38.7
	Staton	Sprayable pheromone	16	4.3
		Isomate-M100	16	2.6
		Conventional	16	10.9
		Abandoned	16	97.8
	Total			115.6
2001	Henderson	Sprayable pheromone	16	1.9
		Isomate-M100	16	0.3
		Conventional	16	22.2
		Abandoned	16	29.3
	Total			53.7

For isomate M100 with conventional and abandoned (F = 142.17, df = 3.49, P = 0.01)

In Henderson country, North Carolina, the Oriental fruit moth population varied considerably among study sites in both 2000 and 2001 with mean season trap capture in the conventional treatments ranging from 0.9 (Staton) to 64.1 (Barnwell) in 2000 and from 3.5 (Staton) to 22.2 (Henderson) in 2001 (Kovanci *et al.*, 2005). In 2000 there was a significant interaction between location and treatment (F=39.14, df = 6.109, p=0.01). Pheromone traps caught significantly fewer moths in mating disrupted blocks compared with conventional blocks at all locations except Staton, where Oriental fruit moth populations were low. A similar trend was observed at the Henderson orchard in 2001, where trap captures were signficiantly lower in mating disruption block as compared with conventional and abandoned blocks (F=142.17, df=3.49, p = 0.01). Thus isomate M100 proved highly effective by reducing the moth population significantly than microcapsule sprayable pheromone, conventional treatment and abandoned blocks.

Table 3: Mean number of predatory insect ha-1 in cotton sampled by D-vac suction apparatus following the application of pheromones and insecticides.

Genus	Stage	Insecticide treated		Pheromone treated	Ratio insecticide : pheromone	
		Area 1	Area 2	Area 3	1:3	2:3
Coccinells	Adult	33	250	3717	1:112.6	1:14.9
Paederus	Adult	417	17	1717	1:4.1	1:101
Scymnus	Adults	33	0	1184	1:35.9	-
Chrysoperla	Adults	17	0	200	1:11.8	-
Orius	Adults	0	0	583	-	-
Orius	Nymphs	0	0	183	-	-
Total		500	267	7584	1:15.2	1:28.4

In Egypt the results of comparison between pheromone and insecticide application indicated overwhelming benefit of mating disruption technique on beneficial insect populations possibly explaining the absence of any secure outbreaks of secondary pests in the areas treated with pheromones (Campion *et al.*, 1989) [2].

Conclusion
In attempting to summarise both the current role of pheromones in insect pest management and the prospects for future utilisation, a multiplicity of behavioural patterns that are under pheromone regulation and an ever expanding diversity of identified pheromone structures must be considered. The use of pheromone baited traps for precise monitoring of a pest density is underway worldwide. This population information allows conventional pesticides to be applied only as required and at times that exert maximum effect. Future applications of pheromone – based monitoring system seems widespread, since this use pattern will not require the lengthy and costly registration procedures necessary for economic poisons. Utilisation of pheromones for direct population control is clearly a future prospect. In the case of mass trapping the technique has been demonstrated feasible and efficacious for certain species but so far this method has remained economically impractical for the particular organisms, for which control could be achieved at lower cost using a conventional insecticide. In mating disruption, there is increasing evidence that a sprayable microdispersable formulation of disruptant is highly effective even in the suboptimal formulations currently available but to reduce the application rate of active ingredient to reasonably economical dosages and to allow season-long tests of efficacy, formulation matrics that volatilize much of the active ingredient at a relatively constant rate must be developed. During the next decade perhaps we can look forward for development and implementation of pheromones as major control agents.

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