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Review

Current and Future Prospects for Insect Behavior-modifying Chemicals in China

Jia-Wei Du

Shanghai Institute of Entomology, Chinese Academy of Sciences
Chongqin Rd. #225, 200025, China

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In this paper we will assess the feasibility of some insect behavior-modifying chemicals for insect control, such as male orientation inhibitor, female calling interrupter and female attractant of cotton bollworm *Helicoverpa armigera*. These behavior-modifying chemicals have advantages of simple chemical structure, easy to synthesize and low price of products. The effects of sub-lethal insecticides on insect chemical communication system and the differences of pheromone communication systems between the resistant and susceptible strain of *H. armigera* will also be discussed.

Key words: *male orientation inhibitor, female calling behavior interrupter, female attractant,* Helicoverpa armigera.

Insecticide research led to the first "complete" victories in combating pests almost 50 years ago using chlorinated hydrocarbons, organophosphates, methylcarbamates, and pyrethroids (all neuroactive chemicals, some of which are selective and degradable compounds) and current genetic engineering techniques.[1] Significant advances have also been made to improve pest management efforts while reducing chemical pesticide use, particularly by shifting to semiochemicals. The semiochemicals can be used to lure pest insects to traps and sample the populations. This monitoring information can then be combined with other observations to improve control programs through better targeting and timing. The semiochemicals, in addition to their use in traps for successful detection, monitoring, and survey, also can be used in several other ways for control or suppression of insect population: (a) mass trapping, (b) mating disruption, and (c) combination of baits with toxicants, pathogens, or chemosterilants.[2] Mass trapping is useful only in a very limited number of specialized cases. One such successful case in China is the control of detrimental forest pest, poplar clearwing moth *Paranthrene tabaniformis*, in Northeast China.[3,4] The success can be attributed to the fact that the male moth of this species only mates with a female once and the population is low enough to be suitable for mass trapping. Other successful cases have been reported with boll weevil,[5] and oriental fruit fly,[6] among others. Mating disruption has been successful in controlling a number of insect pests including pink bollworm *Pectinophora gossypiella*,[7,8] oriental fruit moth *Grapholita molesta*,[9] Codling moth *Cydia pomonella*,[10,11] European grape moth *Eupoecilia ambiguella*, Grapevine moth *Lobesia botrana*. More than 20% of the grape growers in Germany and Switzerland employ this technique to control the insect pest injuries to the grapes and produce their wine without using insecticides. An example of the combination of toxicant with a bait is the use of such a preparation in the screwworm control program.[12,13] Control of codling moth, *Cydia pomonella* through an attract and kill formulation[10] and a new technique involving pheromone/virus combination were reproted.[14,15]

Using pheromone for controlling of insect pests in China was not met favorably by the farmers because the technique of using mating disruption was too expensive with little practical benefits, particularly for crops with low economical values. More farmers in China prefer to use the mass trapping for control of insect pests since (1) it is easy to use, (2) it allows the actual number of insect pests to be seen in traps, and (3) it is not expensive. But, most results of mass trapping tests in China have been very discouraging during the past years. In fact, mass trapping is often deemed to be uneconomical or at least noncompetitive compared to other means of control.

Protection of resources from pests is usually achieved by poisoning the pests with a toxic pesticide, but it can also be achieved by manipulating behaviors of the pests.[16] Recently, there has been increased an interest in such manipulation in China, including insect growth regulators diacyl-hydrazines,[17] botanical anti-feedants,[18] Avermectins,[19] insect-resistant plant with bacillus thuringiensis crystal protein genes,[20,21] and application of plant-based attractant and insecticides.[22,23]

The manipulation of a pest's behavior to protect a resource is not a new concept.[16] For example, the practice of trap cropping using a sacrificial resource for the pest to attack, in order to protect a valued resource, has been known for

E-mail: dujwei@isdnnet.sta.net.cn

Abbreviation: PBAN, pheromone biosynthesis activating neuropeptide.

Table 1. Some male pheromones found in *Noctuidae*.

Insect Pests	Male Pheromone
Pseudaletia unipuncta	2-phenyl ethanol[29]
Heliothis virescens	16:Ac, 16:OH, Z-11-16:Ac, 18:COOH 18:OH, 14:COOH,, 16:COOH, 18:COOH[30]
Helicoverpa armigera	14:OH, 16:OH, 18:OH, Z-11-16:OH, 14:Ac, 16:Ac, 18:Ac, 14:COOH, 16:COOH; 18:COOH[31,32]
Helicoverpa.subflexa	14:OH, 16:OH, 18:OH, 14:COOH, 18:Ac 16:COOH, 18:COOH, 16:Ac, Z-9-14:Ac[31]
Mythimna separata	benzaldehyde[33]
Peridroma saucia	benzaldahyde, benzyl alcohol, benzoic acid[34]
Spodoptera exigua	crude extracts[35]

centuries.[24]

Therefore, more time and efforts have been spent on the studies of insect chemical communication behavior and factors that mediate behavior in our laboratory and to explore new approaches of controlling pests using special behavior-modifying semiochemicals, such as male orientation inhibitor, female calling interrupter, and female attractant, among others.

Male Orientation Inhibitor

Disrupting behavior with stimuli that either elicit or inhibit orientation is also effective at long distances. Most works on the use of attractants to disrupt the finding behavior have focused on the mate location, particularly of moths, through the so-called mating disruption method. Large amounts of synthetic sex pheromone are distributed with the aim of preventing males from finding females. This so-called mating disruption method has been used successfully for the control of such herbivorous pests as the pink bollworm *Pectinophora gossypiella* on cotton, the Oriental fruit moth *Grapholita molesta* on stone fruits, the tomato pinworm *Keiferia lycopersicella* on tomatoes, and currant clearwing *Synanthedon tipuliformis* on blackcurrants.[25,26] However, this technique need high-quality pheromone and good formulation with prolonged release rates, which will lead to the increased technological problems and net cost of pheromone production. Furthermore, the technology to produce pheromones of high purity in multi-kilogram quantities has not yet been developed.[27]

It has been suspected for a long time that the brush-like organs found in the males of many lepidopterous species may store and disseminate pheromones during courtships.[28] Table 1 shows some male pheromones found in *Noctuidae*. Recently we identified 10 components from the extracts of cotton bollwom male hair-pencil (Table 1). The data of bioassay in the wind tunnel show that male moths of cotton bollworm produced the highest response to the binary components of Z-9-16:Ald and Z-11-16:Ald in a ratio of 5 : 95 at the dosage of 0.4 μg. When Z-11-16:OH was added to the binary blend, 5% of the alcohol completely inhibited the male orientation behavior. The results of inhibitory tests on field large-cage by spraying or coating the inhibitor on plastic tubes indicated that egg hatch rates were reduced to about 60-80% compared with the control (Table. 2). The research results show that the male orientation inhibitor is a very strong behavior-modifying chemical, which generally prevents males from finding their mates. Furthermore, its chemical structure is simple, easy to use, and does not need higher purity compound.

Table 2. Field-cage test of male orientation inhibitor of cotton bollworm *H. armigera*.

Field-cage test	Inhibitor	Hatching Rate of Egg (%)
Treatment	Z-11-16:OH	19.8±4.5
Control	-	100.0

*Sparying Z-11-16:OH formulation (10 mg/m^2)

Useful orientation inhibitor can be found from male hair-pencil or scales. Further researches will be conducted to synthesize a series of analogues and to screen for a simpler and more effective artificial inhibitor.

Female Calling Behavior Interrupter

We know that Z-11-16:OH in *H. armigera* male hair-pencil plays an inhibitory role on the male orientation behavior. However, we do not know yet the biological function of saturated or unsaturated RCOOH in male hair-pencil on the female calling behavior. Hendricks *et al.*[36] reported that the emission of the female sex pheromone of tobacco budworm *Heliothis virescens* was effectively terminated when the females were exposed to 50 male equivalents of hair-pencil extracts or to untreated 2-day-old (virgin) male tobacco budworm. Extracts of hair-pencils made with ethyl ether were almost as effective as live males. We also found that odors of some unsaturated RCOOH and their analogues could interrupt the female calling behavior. Based on bioassay, the percentage of female calling behavior in scotophase through the treatment of RCOOH odors was reduced by 50-70% compared with the control. Therefore, we assumed that one of the biological functions of special fatty acids in *H. armigera* male hair-pencil would be to terminate the female calling behavior effectively. This means that some unsaturated RCOOH released by males can terminate the female calling behavior in order to guarantee successful mating.

Simulated field-cage tests also show that some unsaturated

Table 3. Field-cage test of female calling behavioral interrupter of cotton bollworm *H. armigera.*

Field-Cage Test	Interrupter	Hatching Rate of Egg (%)
Treatment	Z-9-18:COOH	18.8±15.4
Control	-	100.0

*Sparying Z-9-18:COOH formulation (20 mg/m^2)

RCOOH and their analogues could terminate the female calling behavior effectively. Large field-cage test by spraying Z-9-18 : COOH formulation shows egg hatch rate was decreased by about 70% compared with the control (Table 3). It is clear that unsaturated RCOOH could be a chemical signal to exert significant effects on the female calling behavior. The above results indicate that the female calling behavior interrupter is a valuable and promising behavior-modifying chemical for practical use.

In fact the female calling behavior interrupter released by males is an important communication signal between competing males and females choosing mates. It has influence on the male mating success and is very useful in pest management. In addition, its chemical structure is simple and easy to use.

Female Attractant

Trap-cropping is a plant stand grown to attract insects or other organisms to protect target crops from pest attacks. The principle of insect control through trap-cropping has been known for centuries and is still exploited in many traditional farming systems. Pest control ideas based on this principle have emerged through out this century, as documented in the entomological literature, but seldom have any of them led to practical uses.[24] The Chinese farmers have successfully used this trap-cropping in the cotton or other crop ecosystems for several decades. A typical example would be to trap cotton bollworm females and males using bundles of withered black poplar twigs *Populus nigra* or Chinese wing-nut tree *Pterocurya stenoptera* in the cotton fields.

There is a world wide effort to develop attractants for adult moths, especially females, in the family *Noctuidae* (which includes *Helicoverpa* spp.).[37] In recent years, works have been undertaken in the USA, Germany, UK, China, and India towards this goal. Our approach was to find an attractant for adult moths, which are particularly attractive to female moths, and to profile the volatile chemicals released by these plants through GC-MS. Blends of candidate compounds identified through this process are then formulated and tested in the olfactometer and field trials.

The gas chromatograms and GC-MS chemical identification of volatile from Chinese black poplar *Populus nigra* revealed the presences of 13 known compounds, 2-hexenal, 3-hexen-1-ol, benzaldehyde, hexanoic acid, 1,2-cyclohexanedione, 3-hexenol acetate, 2-cyclohexen-1-one, benzyl alcohol, 2-hydroxy-benzaldehyde, phenylethyl alcohol, eugenol, phytol, and hexadecanol. There are 11 known compounds in the volatile of withered leaves of Chinese wing-nut tree *Pterocurya stenoptera* (Table 4). The results of bioassay in wind tunnel show that blend C (5 components) and blend D (10 components) have strong attraction to cotton bollworm virgin female (Table 5). The formulation of such high volatile compounds and field works has been undertaken this year.

Such female attractant combined with insecticides could be used in an attract-and- kill strategy to reduce the population of next generation on an area-wide basis. Limitation of a sex pheromone attracting only males can be overcome by combining it with an attractant for females. Theoretically, such a combination should be more effective in the attract-annihilate method than with either attractant alone.[38] In cotton, the attract-and-kill approach using insect sex pheromone has led to a significant reduction in boll weevil population in the USA[39] and pink bollworm population.[40] An effective attractant for female moths would have obvious advantages over sex pheromones (which catch

Table 4. The volatile emitted from the withered leaves of Chinese black poplar and wing nut tree.

Chinese black poplar *Populus nigra*	Chinese wing-nut tree *Pterocurya stenoptera*
2-hexenal	3,5,5-trimethyl 2-cyclohexen-1-on
2-hexen-1-ol	4,5-dihydro-5,5-dimethyl-1H-pyrazole
benzaldehyde	γ-cubebene
hexanoic acid	1-ethenyl-1-methyl-2,4-bis(1-methylethenyl)-cyclohexane
1,2-cyclohexanedione	caryophyllene
3-hexenol acetate	4,11,11-trimethyl-8-methylene bicyclo-(7,2,0)-undec-4-ene
2-cyclohexen-1-one	1,1,4,8-tetramethyl-cis4,cis7,cis10-cycloundecatriene
benzyl alcohol	α-caryophellene
2-hydroxy-benzaldehyde	1-methyl-4-(5-methyl)-cyclohexene
phenylethyl alcohol	1.2.3.5.6.7.8.8a-octahydro-1,8a-dimethyl-7-(1-methylethnynal)-naphtanlene
eugenol	caryophyllene oxide
phytol	
hexadecanol	

Table 5. Attraction of blend A, B, C and D to cotton bollworm females in wind tunnel.

Blend	A	B	C	D
% of testing female attracted in test sample	51.2	51.6	63.3	85.8
Control (%)	31.0	31.0	28.3	31.8

N = 60-110
A = eugenol(2.2%) + benzyl alcohol(0.8%) in 1 m*l* of vegetable oil(V/V)
B = phenyl alcohol(1.7%) + benzyl alcohol(0.8 %) + benzaldehyde(0.3 %) in 1 m*l* of vegetable oil(V/V)
C = phenyl alcohol(5.0%) + eugenol(2.2%) + phenylethyl alcohol(1.7%) + benzyl alcohol(0.8%) + benzaldehyde(0.3%) in 1 m*l* of vegetable oil(V/V)
D = phenyl acetaldehyde(30.0%) + eugenol(10.0%) + phenylethyl alcohol(2.0%) + benzyl alcohol(2.0%) + benzaldehyde(1.0%) + linalool(2.0%) + methyl eugenol(2.0%) + geraniol(1.0%) + Z3-hexanol(1.0%) + cineole(2.0%) in 1 m*l* of vegetable oil(V/V)

Table 6. Effects of sub-lethal insecticides and eserine on female calling behavior, pheromone production and PBAN-like activity in *O. furnacalis* and *H. armigera.*

Test Idem	Malathrion	Deltamethrin	λ Cyhalothrin*	Eserine
calling behavior activity	low	low	low	low
recovery of calling behavior	yes	no	no	no
titer of sex pheromone	low	low	low	low
shifting of E/Z ratio	no	no	no	yes
orientation ability	low	low	low	low
PBAN activity	-	low	-	low

only males). This technique using female attractant will reduce the levels of insecticides used, and has the ability to selectively place them and avoid drift, offering significant environmental advantages over current methods. Another potential use for female attractant would be to assist in the dissemination of selective pathogens of *Helicoverpa* spp., particularly vertically transmitted ones.[14] In this role, female moths would be lured to a trap, contaminated with the pathogen, sent back to the field, then allowed to mate with native males, resulting in the transmission of pathogen to the offspring.

This method might be particularly valuable with the new generation of genetically modified pathogen, which kill their hosts quickly, without causing an epidemic.

Effects of Sub-lethal Insecticides on Insect Chemical Communication System

In recent years, there have been only few detailed studies concerning the potential behavioral effects of sub-lethal doses of insecticides. For example, sub-lethal doses of insecticides have been shown to adversely affect the calling in pink wollworm *Pectinophora gossypiell*,[41] the wing fanning response of males to pheromones,[42] and the pheromone-mediated flight behavior of oriental fruit moth *Grapholita molesta* (Busck).[43] The potential for control of behavior with sub-lethal neurotoxicants is just beginning to be realized.

The production of sex pheromone in a number of moth species follows diel rhythm, which may be regulated by neural,[44] neuroendocrine[45] or hormonal factors.[46] The production of sex pheromone in Asian corn borer *O. furnacalis* appears to be under the control of a neuroendocrine regulation factor, pheromone biosynthesis-activating neuropeptide (PBAN).[47] It is not clear if and how the sub-lethal pesticides affect this process.

We found that topically applied sub-lethal doses of malathrion, deltamethrin, and eserine affect the female calling, sex pheromone production, and PBAN activities in *O. furnacalis* (Table 6). The sub-lethal doses of α-cyhalothrin also affect the female calling, pheromone production, and male orientation ability of cotton bollworm.

Since PBAN controls the production of pheromone, PBAN-like activity might be expected from deltamethrin, which affects the production of pheromone. The present results show injecting 1, 1/2, 1/4, and 1/8 FE of Br-SOG homogenate of normal female into decapitated females induced the pheromone production by 90.3, 85.5, 81.2, and 44.6% of the normal *O. furnacalis* female production, respectively. On the other hand, injecting 1, 1/2, 1/4, and 1/8 FE of 1ng-deltamethrin-treated female Br-SOG homogenate into the decapitated females only induced 64, 31, 30.7, and 8.1% of the normal female pheromone production, respectively. The observed decrease in the dose-response curve of Br-SOG could be due to the differences in the PBAN-like activities of the *O. furnacalis* females.

Effect of sub-lethal deltamethrin on the female sex pheromone biosynthesis has not been documented before this study. Sex pheromone biosynthesis in insects involves a complex coordination of physiological activities. Pheromone emission by *O. furnacalis* is controlled by interrelated physiological and behavioral factors. It was suggested that calling behavior and transport of pheromone to the gland surface are synchronized in time. These activities are under

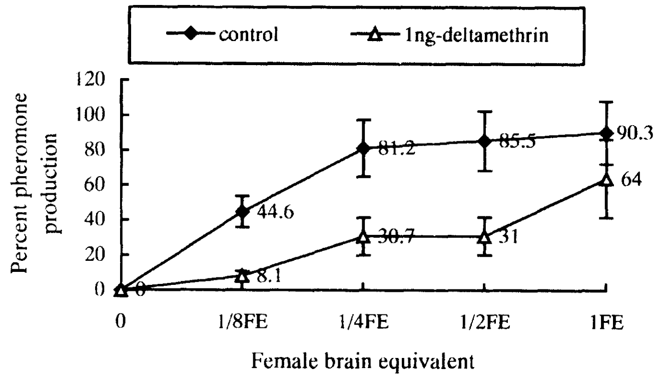

Fig. 1. Comparison of PBAN-like activity between normal females and sub-lethal deltamethrin-treated females.

hormonal and neuronal controls.

Our study indicated that sub-lethal deltamethrin affected not only the pheromone production but also the activity of PBAN-like factor. Certainly, decreasing the PBAN-like factor activity will also cause a decrease in the pheromone production. These effects could be expected to interfere with the female reproductive capacity and cause a decrease in the mating rate, which it could result in a decreasing population density. Therefore, our research works in this area may help to provide a basic knowledge to develop new behavior-modifying chemicals. The most important aspect of our research, and of all previous studies on the sub-lethal effects of insecticides, is the emphasis on screening for an ideal insect behavior-modifying candidate for controlling pests.

Differences in Pheromone Communication Systems Between the Resistant and Susceptible Strains of Cotton Bollworm *H. armigera*

Communication system of insects can be influenced by many factors, including chemical insecticides.

So far, no comparative studies on the pheromone communication systems of the resistant and susceptible insect strains had bee done, though some studies showed temporary behavior changes with sub-lethal dose treatments of chemical insecticides. Recently we have systematically studied the pheromone communication systems of resistant and susceptible strains of cotton bollworm *H. armigera* through GLC analysis of pheromone titer and ratio as well as male orientation behavior in the wind tunnel.

Table 7. Sex pheromone titer of the susceptible and resistant strain of cotton Bollworm *H. armigera.*

Test Insect	Titer (ng/ ♀)	CV %
Susceptible strain (N = 60)	26.07.3a	27.8
Resistant strain (N = 70)	161.037.9b	23.5

Duncans Test (P<0.05), N = 20.

The results showed obvious differences in pheromone communication systems between resistant and susceptible strains of *H. armigera*. The sex pheromone titer of the resistant female was much higher than that of the susceptible female (Table 7). It seems the resistant female released a large amount of sex pheromone and more chance to attract males than the susceptible females. Furthermore, the resistant male of *H. armigera* preferred resistant female to susceptible female in a wind tunnel (Table 8). But resistant moths could still communicate with susceptive ones and mate with each other since there were no significant differences in female sex pheromone components and their ratios, releasing rhythm of female sex pheromone, calling rhythm, and calling rate of females.

From our preliminary research, it seems the resistant strain of *H. armigera* has stronger competition ability than the susceptible strain in the chemical communication of mate findings. This is the most difficult problem in "resistance management."

In Future

Biological control of pests in agriculture and forests is becoming more important due to the limitations in pest management related to ecological issues such as pollution, food contamination, and development of pest resistance. Sex pheromones for monitoring, mass trapping, and mating disruption to control several agricultural and forest insect pests in China have been used for over three decades. A

Table 8. Behavioral responses of the susceptible and resistant strain of *H. armigera* in wind tunnel.

Test insect	Pheromone source	No. of test insect	Behavioral response (%)			
			Taking flight	Orientation	1/2 Orientation	Landing
	live S ♀	63	100.0	76.2a	38.1ab	19.0a
S ♂	live R ♀	58	100.0	86.2a	37.9ab	20.7a
	dispenser	70	100.0	88.6a	48.5bc	31.4a
	live S ♀	64	100.0	53.1b	21.9a	12.5a
R ♂	live R ♀	76	100.0	84.2a	78.9d	68.4b
	dispenser	66	100.0	90.9a	63.6cd	18.2a

S ♂ = Susceptible strain of male moths,
R ♂ = Resistant strain of male moths,
S ♀ = Resistant strain of female moths,
R ♀ = Susceptible strain of female moths.

recurring problem with using pheromone for control of insect pests is the cost of the product to the end-user.

At present, research institutes supply most of the pheromone products in China, not companies. In fact, laboratory synthesis of pheromones in China is too difficult and expensive to be practical. Most Chinese fine-chemical industries are not interested in pheromone production from a commercial viewpoint. Scientists in China are reluctant to put their efforts to technology transfer when the applied aspects grow more satisfying. These problems will be solve by Yunnan Xinlian Eco-Scientific & Technological Industry Co. LTD. found this year, which is organized and invested by Yunnan Xianlian Chemical Industries, Shanghai Institute of Entomology, Chinese Academy of Sciences, and Department of Chemistry, Yunnan University. There are still great many pheromone technologies they will have to learn. The company will supply low priced commercial pheromone products (5 dispensers/US$) and products of azadirachtin from seed oil of neem tree. Neem tree now grows in Yunna Provice on a large scale.

Up to now, manipulating insect behavior was an important component of pest control programs worldwide. However, pest management is currently dominated by broad-spectrum of toxic chemicals. The limited adoption of behavioral manipulation methods suggests that the perceived advantages such as specificity and low toxicity are generally not sufficient to overcome disadvantages such as cost and inability to control other pests, compared to the advantages and disadvantages of chemical pesticides.[16] However, due to health and environmental concerns, such as recent initiatives in Europe to reduce agricultural pesticide usage by 50%,[48] and pesticide resistance, the long-term future of such pesticides is somewhat uncertain, and opportunities for behavioral manipulation methods may increase. Our researches show that male orientation inhibitor, female calling behavior interrupter, and female attractant have advantages of simple chemical structure, easy to synthesize, and low product costs. Future application prospects of new technique is likely to depend on the amount of research on finding more male orientation inhibitor, female calling behavior interrupter, as well as female attractants, and the development of creative techniques for utilizing the results of researches. We believe that behavioral-modifying chemicals will play a more important role in the future integrated pest management programs than the pheromone has been doing up to now.

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