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New Bioactive Products: Growth Regulators, Antifeedants, Pheromones and Other Attractants (***)

ABSTRACT — Recognition of the problems associated with the large-scale use of broad-spectrum insecticides has dictated the need for effective, biodegradable chemicals with greater selectivity. Consequently, chemicals which disturb insect growth processes or affect behavior are increasingly being deployed for ecologically sound pest management. This paper reviews the status and potential of insect growth regulators, antifeedants, pheromones, and other attractants.

More than one-third of world crops is destroyed by insects, pathogens and weeds (Cramer, 1967). Pesticide use has, therefore, become indispensable to modern crop protection technology. Without pesticides, crop losses may escalate to 50%, and even higher in developing countries. Since the advent of DDT, most insecticides used commonly have been synthetic, non-selective, poisonous chemicals. While they have effectively controlled some insect pest species, their extensive use has led to serious social and environmental repercussions. The poisoning of livestock, fish, wildlife, and other beneficial organisms has been linked with pesticide use. Likewise, there has been a disturbing increase in human poisoning, particularly in developing countries. Pest resurgence associated with pesticidal destruction of natural enemies, and the development of pesticide resistance in pests have necessitated increased doses or more powerful pesticides, ending in a pesticide treadmill. That not only is uneconomical but exacerbates the problem.

The continued need for insect control in crop protection would not permit

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complete elimination of insecticides, but new bioactive products will be needed which are pest-specific, nontoxic to man and beneficial organisms, biodegradable, less prone to pest resistance, and less expensive. The alternative insect control agents developed as a result of rational leads from basic research in entomology include metabolic disruptors and inhibitors and behavior modifiers of insects. Since the target sites of action for these chemicals are known, they have less deleterious effects on nontarget species. This paper reviews the status and potential of insect growth regulators, antifeedants, pheromones, and other attractants.

Insect Growth Regulators

Insect growth regulators (IGRs) have become an important class of insect-based pesticides over the past several years (Saxena, 1983). These chemicals selectively and specifically affect the growth and development of insects. IGRs are slow-acting chemicals which adversely interfere with the normal growth and development of insects. In addition to their short environmental persistence (Quistad *et al.*, 1974) and generally low toxicity to vertebrates (Siddall, 1976), IGRs have several characteristics that make them potentially successful alternatives to standard insecticides. However, IGRs effectiveness depends on synchrony with certain events in the insect's life in which the absence or presence of the growth regulator is critical for normal development. Four groups of IGRs based on hormonal processes are known: 1) molting hormones, 2) anti-molting hormones, 3) juvenile hormones, and 4) anti-juvenile hormones.

Molting Hormones

Molting hormones are a group of steroid hormones found in insects and crustaceans which are responsible for maintenance of the normal molting, growth and maturation pattern (Watkinson and Clarke, 1973). Any disruption in the metabolism of these might possibly uncouple the insect's control over its own hormonal system. The molting hormones are represented by ecdysone, ecdysterone and other ecdysteroids. These are biochemically derived from cholesterol, still retaining its C_{27} carbon skeleton. These compounds cannot be economically synthesized. Although certain plant sources are rich in phytoecdysones, their extraction for insect control would be economical only if they are highly effective. But generally they are effective only through injection. Also, the use of any chemical resembling steroid hormones, which play important roles in man and higher animals, would require careful testing to eliminate the possibility of side effects. The molting hormones have also a regulatory function in crustaceans and, therefore, would be less selective. So the potential for these compounds as insect control agents will be low. Although a number of ecdysone-like compounds show their effectiveness against various insects, the studies of Watkinson and Clarke (1973) have shown that the complexity of the ecdysone detoxification system makes it an unlikely candidate as their site of action.

Anti-Molting Hormones

Some chemicals are known to be antagonists for insect molting hormones, but their use for insect control is still experimental (Staal, 1976; Saxena, 1983). For example, certain azosterols, or even non-steroidal secondary and tertiary amines, are reported to disturb growth and development of phytophagous insects. However, the mode of action depends on the conversion of dietary sterol for insects' cholesterol requirement because most insects require a dietary sterol for normal growth and development (Clayton, 1964), and plant feeding insects must be able to convert the major phytosterols of their host to cholesterol (Walker and Svoboda, 1973). The anti-molting hormones inhibit insect growth when incorporated into its diet by causing a marked reduction in the cholesterol content of the insects and an accumulation of certain intermediates involved in the conversion of these phytosterols to cholesterol (Svoboda and Robbins, 1967, 1968, 1971; Svoboda *et al*., 1969).

The anti-molting hormones may also interfere with steroid hormonal regulation in higher animals and, therefore, the use of such chemicals for insect control may not be an easy proposition. The high cost of azosterols limits any agricultural use but simpler antagonists may have some potential against phytophagous insects that do not have access to cholesterol in their diet. Also, it may be possible to find other types of non-steroid antagonists affecting synthesis, transport, storage or recognition by endogenous hormones (Staal, 1976).

Juvenile Hormones

Insect juvenile hormone (JH) was first described by Sir V.B. Wigglesworth in 1935 as a metamorphosis preventing secretion of corpus allatum. After extensive studies on its various physiological aspects, C.M. Williams in 1956 suggested the possibility of using JH to upset normal growth of insect pests. After the discovery that the abdomen of the male *Cercopia* moth was a rich source of JH, Williams (1967) proposed JH-active substances as powerful "third generation pesticides" to which the pest species may be unable to develop resistance. The concept, that upsetting the titer of JH at certain periods during the insect's life history will adversely affect its metamorphosis, evoked considerable interest in its use for pest control. This can be gleaned from numerous publications (Novak, 1966; Wigglesworth, 1970; Slama *et al*., 1973; Staal, 1975; Bowers, 1984; Retnakaran *et al*., 1985). One of the main reasons for JH being attractive as an insect control agent is its terpenoid nature which enables it to penetrate the cuticle with great ease and exert its effect on the target tissue, whereas the steroid hormones have little topical effect and face the risk of degradation upon ingestion (Retnakaran *et al*., 1985).

Four different naturally occurring juvenile hormones (JH-0, I, II and III) have been identified occurring singly or in combination in different insect species (Richards, 1981). The number of carbon atoms ranges from 19 for JH-0, 18 for

JH I and 16 for JH II-III. However, the use of natural JH as an insecticide is not feasible because of its instability and difficulties in synthesis. Bowers (1969) made a breakthrough by synthesizing several hundred-fold more active substituted aromatic terpenoid esters, which began the era of juvenile hormone analogs (JHA). Synthesis and evaluation of thousands of such synthetic analogs have yielded compounds with higher specific activity, greater stability, lower manufacturing costs, and enhanced selectivity for several insect orders (Staal, 1976). The basic mode of action of JHA appears identical to that of exogenously applied natural JHs, but many of the analogs escape the normal degradation route of the natural hormone and exert agonistic function. A representative list of pests of field crops and stored grain on which control with JH analogs was tried is presented in Table 1.

Anti-Juvenile Hormones

After the discovery and deployment of various JHAs as mimics of natural juvenile hormone, W.S. Bowers (1976) discovered two anti-juvenile hormone compounds (AJH) (7-methoxy and 6,7-dimethoxy-2, 2-dimethyl-chromene named precocenes 1 and 2) from extracts of the bedding plant, *Ageratun houstonianum*. The insect species on which the activity was first detected was *Oncopeltus fasciatus*, the milkweed bug. Contact with precocenes induced immature bugs to skip succeeding nymphal instars by premature metamorphosis which developed into tiny sterile female or male "adultoids" with varying degree of viability. Some other group of compounds such as ethyl 4-2-(tert-butylcarbonyloxy) butoxybenzoate, ethyl-3-methyl-2-dodecenoate, and piperonyl butoxide (Staal, 1976) also show characteristics of JH-antagonists against tobacco hornworm, *Manduca sexta* and tobacco cutworm, *Heliothis virescens*. Because these chemicals interfere with the activity of JHs they can be explored to complement the use of JHAs and may be more useful in circumstances where larval damage after treatments is not acceptable (Staal, 1976). The precocenes can readily penetrate into the insect system, migrate to and penetrate the corpora allata and destroy the natural oxidizing enzymes which are essential in the final epoxidation step in the biosynthesis of JH hormones (Staal, 1986). Although AJH research is very fascinating and innovative, and has produced much interest for physiological and biochemical research, the practical application of AJH and its analogs is limited because of the high and narrow dose requirement and their hepatotoxic and nephrotoxic effects on vertebrates.

Insect Antifeedants

Insect damage to plants results from direct feeding or from indirect transmission of disease organisms during feeding. Therefore, antifeedants which reduce pest injury by rendering plants unattractive or unpalatable offer a novel approach in vector and disease management and can be considered as a potential substitute

TABLE 1 - Selected examples of control of some tropical insect pests of field crop and stored grain by juvenile hormone analogs.

Host	Insect pest	JHA used	Mode of action
Field crops			
Cabbage	Cabbage aphid (*Brevicoryne brassicae*)	ZR-619	Prevention of pupal diapause
Citrus	Citrus mealybug (*Pseudococcus citri*)	several	Sterility and adult mortality
Cotton	Cotton stainer (*Dysdercus cingulatus*)	Amino acid-type analogs	Embryonic effect
Mustard	Mustard aphid (*Lipaphis erysimi*)	ZR-512	Morphogenetic and embryocidal effects
Potato	Potato aphid (*Macrosiphum euphorbiae*)	ZR-512	Sterility
Stored grain			
Corn and wheat	Confused flour beetle (*Tribolium confusum*)	several	Morphogenetic effects
	Indian meal moth (*Plodia interpunctella*)	ZR-512 ZR-515	Prevention of metamorphosis
	Lesser grain moth (*Rhyzopertha dominica*)	ZR-512 ZR-515	Mortality
Wheat flour	Almond moth (*Cadra cautella*)	Pyridyl and Phenyl ether analogs	not known

Adapted from Retnakaran *et al.* (1985).

for insecticides (Mariappan and Saxena, 1983). Antifeedants are not necessarily toxic to insects but when perceived prevent or reduce their feeding (Saxena *et al.*, 1981a). Consequently, insect growth, development, survival, and reproduction are adversely affected (Norris, 1986).

Unlike insecticides that kill outright both pests and predators, the antifeedants obtained from plants are relatively safe for natural enemies that subsist on pests rather than on plants (Saxena *et al.*, 1981b). Also, the high cost of synthetic insecticides limits their use by the average farmer, particularly in developing countries. Moreover, the use of a 'wrong' insecticide may cause greater harm and more economic loss than if no insecticide had been used (Heinrichs *et al.*, 1979). In this perspective, antifeedants derived from locally available and widely distributed plants represent a relatively more safe, cheap and novel approach to plant protection than do conventional pesticides.

Natural defenses of plants against insects involve several defense chemicals including antifeedants. The chemistry of antifeedants is highly variable including small molecular weight organosoluble compounds and high molecular weight glycosides and proteins (Bowers, 1984). The greater diversity of antifeedants is found in higher plants as compared to primitive plants, and is attributed to a vast array of secondary compounds (Norris, 1986). Several classes of secondary plant compounds possessing antifeedant activity are listed in Table 2. Because the antifeedants are the messengers in chemical ecology which reduce or prevent organismal ingestion, they determine which substrates are consumed by insects (Norris, 1986).

The use of antifeedants in pest management programs may have enormous advantages, because it satisfies the need to protect the crop while avoiding damage to non-target organisms (Bernays, 1983). Because of the biodegradable nature and relative safety for beneficial organisms in the environment, research on the biological activity and chemistry of antifeedants is being emphasized (Kubo and Nakanishi, 1977). Many plants are presently being investigated for the presence of feeding inhibiting compounds and many crude plant extracts have been tested against a variety of insect pests (Jacobson, 1986; Jacobson *et al.*, 1978; Saxena *et al.*, 1981 a,b, 1984 a,b). Programs have been launched in several countries to utilize the feeding deterrents known to occur naturally in some plants.

Although the current use of antifeedants as dependable crop protectants under field conditions is still limited, research on the mode of action of insect antifeedants is today an important front in scientific investigations. Perhaps the most widely known and used phytochemical with antifeedant activities to numerous insects

TABLE 2 - Secondary products which have antifeedant activity against one or more species of insects.

Chemical class	Estimated number of known structures	Example
Acetylenes	750	Dihydromatricaria
Alkaloids	4,500	Nicotine
Amino acids	250	Canavanine
Carotenoids	300	Fucoxanthin
Coumarins	150	Coumarin
Cyanogenic glycosides	50	p-Hydroxymandelonitrile glucoside
Flavonoids	1,200	Quercetin
Glucosinolates	80	Sinigrin
Lignins	50	Excelsin
Phenolic acids	100	p-Hydroxybenzoic acid
Quinones	200	Juglone
Terpenes	1,100	Glaucolide-A
Steroids	600	Ecdysteroids
Proteins	?	Lectins

After Norris (1986).

is the triterpenoiod azadirachtin. It is present in the leaves and seeds of the Indian neem tree, *Azadiractha indica*.

Centuries before synthetic insecticides became available, farmers in the Indian subcontinent protected crops with natural repellents and feeding deterrents found in the fruits and leaves of the neem tree (Saxena, 1983). Three International Neem Conferences held in 1980, 1983, and in 1986 indicate the importance of developing natural insecticides from plants, such as neem. Scientists in many countries are investigating the insect-repellent, antifeedant, and growth-disrupting properties of neem derivatives.

Experimental trials indicate useful control of pests of several field crops and stored products using neem derivatives. Neem oil and neem cake were found to be highly effective in reducing rice tungro virus transmission by the green leafhopper, *Nephotettix virescens* (Mariappan and Saxena, 1983; Saxena and Khan, 1985 a; Saxena and Justo Jr., 1986; Saxena and Khan, 1986) and ragged stunt and grassy stunt transmission by the brown planthopper, *Nilaparvata lugens* (Saxena *et al.*, 1981; Saxena and Khan, 1985 b). Application of neem oil on brown planthopper females disrupted their mating behavior (Saxena and Khan, unpublished data). The complex structure of azadirachtin ($C_{35}H_{44}O_{16}$) prevents its synthesis in commercial quantities. However, its abundance in neem seed and the ease of neem tree cultivation in Asia and Africa encourage the use of crude extracts from the tree and as a commercial source of azadirachtin. Neem is widely distributed in most of the rice producing countries in Asia and Africa and its seed oil and cake can be easily obtained at low cost by the average farmer. In India alone there are about 14 million neem trees (Ketkar, 1976). In one season a single tree produces 30-50 kg neem fruits; 30 kg of neem seeds yield; 6 kg of neem oil and 24 kg of neem cake.

The potential of neem and other tropical plants with antifeedant properties has not been fully exploited for pest management because of the advent and acceptance of highly effective broad-spectrum synthetic insecticides. However, the growing awareness of hazards associated with the use of synthetic insecticides has recently evoked a worldwide interest in pest control agents of plant origin.

Insect Pheromones

Pheromones are defined as chemicals secreted by one organism that affect the behavior of other individuals of the same species. Chemical modes of communication through pheromones are now known to occur in most groups of animals, but they play a dominant role in insects. Pheromones, like other communication means, imply a social relationship between individuals (Shorey, 1976). Although pheromones can evoke many types of behavioral responses, the sex attractant pheromones are the ones most frequently used for insect control programs. During the last two decades remarkable progress has been made in the identification and use of sex and aggregation pheromones, particularly those of lepidopterans and coleopterans, but alarm, dispersal, social and trail pheromones have also been investigated (Beevor *et al.*, 1983).

Pheromones can be used as a successful means to reduce our dependence upon conventional broad-spectrum insecticides. At least three approaches to the use of pheromones in pest management programs have been explored, one of which, the monitoring of insect population by using traps baited with sex attractants, has already proved valuable in several crops (Anonymous, 1979; Raman, 1982; Nakasuji and Kiritani, 1976). Pheromone-baited traps are relatively inexpensive and simple to construct and maintain, and provide a highly sensitive means of detecting the insect pests with many advantages over conventional methods such as light traps and scouting programs (Beevor *et al.*, 1983). The two other strategies for pheromone use in pest management are the mass trapping and "male confusion" techniques. Both these methods ultimately prevent reproduction of the target insects.

In the mass trapping technique, traps are usually baited with sex pheromones that lure the male insects to the trap rather than to the females. The method has been most successful in situations where the pest population is localised by artificial barriers such as in warehouses and orchards (Burkholder, 1985; Maclellan, 1976; Negishi *et al.*, 1980).

"Male confusion" or male disruption is achieved by permeating the atmosphere with female sex pheromones. Permeation of the atmosphere with synthetic pheromones has been shown to disrupt pheromone-based communication, although the exact biological mechanism is not clear and may indeed vary in different species. Mating disruption has been explored as a control technique for pests of food crop, but mostly in relatively small scale trials (Anonymous, 1981; Tatsuki and Kanno, 1981; Lee *et al.*, 1981). Considerable success has also been achieved in large scale programs using gossyplure, a sex pheromone, against the pink boll worm, *Pectinophora gossypiella*, in cotton (Shorey *et al.*, 1976; Gaston *et al.*, 1977).

Pheromones undoubtedly have an important role to play in pest management but fundamental changes in their manufacturing and distribution strategies are needed to ensure that such chemicals are available for field use. These behavior modifying chemicals when intelligently integrated with other tools will be helpful to make the environment less suitable for survival or reproduction of agricultural pests.

Other Attractants

An attractant is defined as a stimulus to which an insect responds by orienting its movement towards the apparent source. Attractants play a dominant role in many vital aspects of insect behavior and govern various activities of the insect, such as finding the food, the opposite sex and a place to lay their eggs (Jacobson, 1966; Beroza, 1970; Städler, 1983). The use of food and oviposition attractants in insect population suppression is discussed here.

Food Attractants

The use of food attractants is widespread in trapping of insects for detecting infestation or determining population and in devices that capture, kill or snare insects when they respond to the bait. Although at present sex pheromones are popular and are more extensively used for determining insect population, they are sex-specific, attracting only the males and therefore sometimes it is difficult to correlate the number of trapped insects with pest population density and crop damage (Städler, 1983). Therefore, traps using food attractants (synthetic or originating from host plant) may hold more promise for population monitoring.

The concept of using food attractants to control insects is not new and several food attractants for control of various major pests have been identified (Table 3).

Among the food attractants, methyl eugenol is probably the most powerful synthetic insect attractant. It has been investigated more extensively for control of insect pests than any other synthetic attractant (Steiner, 1952). Methyl eugenol in combination with a fast-acting insecticide was used to eradicate the oriental fruit fly from Rota, a small island in the Pacific Ocean (Steiner *et al.*, 1965). The advantage of this approach was that only the offending insect was killed whereas non-target organisms were unaffected. The successful control of the oriental fruit fly population by the use of methyl eugenol also indicated the potential of food lures for control of isolated populations of insects.

The investigations and use of host plant volatiles acting as attractants seem to hold maximum scope for future applied research for improving or designing

TABLE 3 - Selected examples of host-plant derived and synthetic chemicals identified as food attractants for some tropical insect pests.

Chemical(s)	Insect species
Host-plant derived	
Isothiocyanates	Pests of crucifers
Phenyl acetaldehyde	Lepidopterans
Carbonyl compounds	Saw-toothed grain beetle (*Oryzaephilus surinamensis*)
Hexanoic acid	Saw-toothed grain beetle (*Oryzaephilus surinamensis*)
Triglycerides	Saw-toothed grain beetle (*Oryzaephilus surinamensis*)
Wheat germ extracts	Red flour beetle (*Tribolium castaneum*)
Oryzanone	Rice stemborer (*Chilo suppressalis*)
Synthetic	
Cuelure	Melon fly (*Dacus cucurbitae*)
Methyl eugenol	Oriental fruitfly (*Dacus dorsalis*)

Modified after Beroza (1970) and Städler (1983).

traps and baits for estimation of population and control of pests in integrated pest management.

Despite limitations of working with attractants, i.e., the time and expense involved in finding a truly effective chemical, insect attractants can be increasingly deployed in insect suppression strategies in the future as more powerful attractants and methods of effectively dispensing them are discovered.

Oviposition Attractants

Ovipositing females are recognized as the crucial "agents" in most insect-plant relationship (Städler, 1983). Therefore, natural attractants that guide these insects to suitable oviposition sites are vital to survival of an insect species. Although no oviposition attractant is routinely used for the control of insect pests, these chemicals can nonetheless be deployed in insect pest management. The success of such chemicals in pest control would largely depend on identification and duplication of natural oviposition attractants of insects and their use at some strategic time or place where the competing natural attractant is greatly limited. For plant feeding insect pests, which lay their eggs on host plants, the natural oviposition sites are so vastly distributed that the oviposition attractants cannot compete to a degree of practical control unless an oviposition attractant is really powerful over the natural attractants by a factor of nine or more (Knipling, 1979). The ovipositional attractants could theoretically be used to attract the ovipositing females on non-host plants. Since the host crop or variety will not lose its attractancy for oviposition, care would have to be taken to reduce its suitability by delayed sowing or by using repellents or deterrents. Table 4 presents some examples of oviposition attractants.

TABLE 4 - Selected examples of insect oviposition attractants.

Chemical	Insect pest	Reference
Allyl isothiocyanate	Diamond-back moth (*Plutella maculipennis*)	Gupta and Thorsteinson (1960)
α-pinene β-pinene limonene eugenol	Desert locust (*Scistocerca gregaria*)	Carlisle *et al.* (1965)
	Pulse beetle (*Callosobruchus chinensis*)	Applebaum *et al.* (1965)
Ferulates, diglycerides free sterols	Grain weevil (*Sitophilus zeamis*)	Maeshima *et al.* (1985)
Resoro plant extract	Rice stemborer (*Chilo suppressalis*)	

More research on insect oviposition behavior, identification and synthesis of strong oviposition attractants and their mode of application will certainly be helpful in finding ways to use these chemicals in control of insect pests.

Future Considerations and Conclusions

Human survival largely depends upon the availability of food. The first green revolution and other advances in agricultural sciences have greatly helped in limiting the starvation in the tropics. Besides high yielding varieties, crop protection technology played a major role in increased food production. Until now the control of agricultural pests and disease vectors largely depends upon the use of toxic, non-selective, synthetic pesticides. While the use of such chemicals cannot be avoided to avert crop losses, naturally occurring bioactive pest control agents can be exploited to decrease our dependence on the synthetic pesticides. A large array of botanical and insect-based pesticides are available today to supplement and even supplant the use of persistent synthetic pesticides. The selectivity of these bioactive products makes them valuable in integrated pest control. Examples of their successful use against insect pests have demonstrated their potential for development as future generation insecticides. However, production methods, formulation, and method and timing of application are more critical to the development and use of natural pesticides than of conventional pesticides.

The insect-based pesticides will be directed against insect pests as growth disturbing agents. While a number of JHA have shown promise in control of various insect pests, their use in the field is still limited due to high cost. Also, the original speculations that insects may be unable to acquire resistance against compounds resembling their natural hormones has already been deflated by the facts. However, the continuous development of novel IGRs and further neuro-endocrinological research will be needed in order to stay ahead in the continuous struggle with insect pests.

The plant kingdom is the richest source of organic chemicals on this earth. Several of such chemicals possess antifeedant activity which would be highly valuable in pest control. Many potent chemicals have been discovered in plants which were not even thought of possessing defense chemicals. For instance, an effective rice stemborer oviposition deterrent was isolated at IRRI from a rice variety 'TKM6' and was identified as pentadecanal. Efforts are under way to synthesize and evaluate the novel chemical. On the other hand, Margosan-O and Margosan-D insecticides, based on neem antifeedants, are being developed in the USA.

Sex pheromones can play a major role in reducing the losses of food crops due to insect pests. Field workers and extension advisors will be required to exploit the use of these chemicals in conjunction with other techniques in integrated pest management and to select the most appropriate method and timing for their application.

Feeding and oviposition attractants in insect-plant relationship seem to hold most promise in insect pest management. Despite past disappointments or failures, these attractants can be made to play a prominent role in insect suppression strategies in the future as new powerful attractants and their effective application methods are discovered.

The future of pest control in the 21st century looks very promising as it will be supported by new bioactive products of known chemistry and physiology.

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