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INSECT ATTRACTANTS[1]

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INTRODUCTION

Insect pests reduce crop yields, destroy forests and wood products, carry diseases that affect plants, man and animals, and damage food and other stored products. Although synthetic organic pesticides appeared to provide a solution to the problems of insect control, it has become apparent that repeated application of insecticides can be an inadequate method of control. Excessive reliance on insecticide use has been accompanied by the development of insect resistance and problems of environmental pollution. To minimize these problems, pest control should be considered in its entirety; and by combining several elements into an integrated system, undesirable consequences of overreliance on a single technique, such as chemical treatment, may be obviated. The term "integrated pest management" (IPM) has been coined to describe a planned combination of individual disciplines and strategies that can be used to reduce the impact of pests. However, the effective application of an integrated system depends on the understanding of individual components, their potential applications, and their interactions.

Insect attractants have played and will continue to play an important part in the management of insect pests. However, their potential has not been fully exploited, and research efforts continue in order to provide a basis for their greater utilization.

The field has developed rapidly during the past decade as a result of analytical developments that have simplified the identification of minute quantities of unknown organic compounds that occur in nature. Knowledge of the chemical structures of natural attractants has been increasing rapidly, and as the behavioral effects of attractants become better understood many potential applications in insect pest management are emerging. With insects, many attractive stimuli are chemical, although other stimuli such as warmth, light, color, sound, etc., often come into play and are the primary stimuli in many cases. This review is restricted to the discussion of chemical attractants. A recent survey (1) found that effective attractants have been reported for over 600 insect species, including many important pest insects, and that these attractants involved over 300 chemical compounds.

An insect attractant has been defined (2) as "a chemical which causes insects to make oriented movements towards its source." Workers studying behavioral effects of chemicals have pointed out that such a designation focuses attention on the chemical stimulus alone and that it does not take into account the multiple behavioral components that lead to the observed end result (3–5). In light of such considerations, Barton Browne (6) has suggested that a better definition of an insect attractant might be "a chemical or mixture of chemicals which, acting in the vapor phase, causes an insect to behave in ways which result in its moving toward the source of the material or toward a zone of preferred concentration."

Much of the interest in insect attractants has centered on their use in trapping for survey or monitoring. Insect trap catch has long been used as a criterion of attractant activity, and this bioassay method has endowed the term "attractant" with a particular connotation that might properly be expressed by the more pragmatic terms "lure" or "bait." For trapping studies, an attractant is therefore a volatile substance that can, by its presence in a trap, bring about an increase in insect catch, compared with the catch in a similar unbaited trap.

It is important to distinguish between synthetic attractants and attractants that have been found among the numerous naturally occurring chemicals that are involved in the life of an insect, as in mating, oviposition, etc. The term "synthetic attractant" has been used to designate those materials, either single compounds or complex mixtures, that have been found to be effective lures by systematically screening a variety of candidate substances. By consideration of the structure-activity relationships in selecting compounds for screening, a number of compounds with selective attractant properties for specific insects have been discovered; some of these appear to be related to food attractants (7), whereas others have no known analogues in nature.

Compounds that act as attractants because of their role in the life of an insect are usually more selective in their action than the synthetic attractants and are effective at much lower concentrations. These substances have been described in terms of the behavior they elicit: a compound involved in bringing opposite sexes together for mating has been termed a sex attractant; one important in locating a suitable site for egg laying, an oviposition attractant, etc. The general term "semiochemicals" (8) has been proposed to include all natural chemicals that are involved in inter- or intraspecific communication. If a chemical stimulus emitted by one individual is perceived by another individual of the same species, it is termed a "pheromone" (Greek: "pherein" to carry and "horman" to stimulate or excite) (9). Pheromones may be described as "primers" or "releasers" (10). Primer pheromones initiate a series of physiological changes, and they have been recognized, for example, in mammals such as the mouse, where pheromones present in male mouse urine modulate ovulation in the female (11), or in insects, where pheromones may determine social castes. Releaser pheromones elicit immediate behavioral responses.

In insects, a wide variety of behavioral responses have been shown to be affected by releaser pheromones; these include mating and the sequence of behaviors that precedes copulation, trail-following, dispersion, recruitment, aggregation, brood tending, alarm, etc. The pheromones responsible are correspondingly described as sex pheromones (or, more specifically, sex attractant pheromones, if the behavior elicited by the pheromone results in insects flying from a distance to locate mates), trail-following pheromones, alarm pheromones, etc. The responses are complex and the observations are often biased by the technique that is used for study; consequently the precise response to a given chemical stimulus may be difficult to measure.

Some compounds that have not been shown to be present in an insect may elicit behavior very similar to that elicited by pheromones. Such "pheromone mimics" have been termed "parapheromones" (12).

A parasite may locate its host or a predator its prey by means of intraspecific semiochemicals, termed "kairomones" (13). These are materials that are advantageous to the species that respond, regardless of their function in the species from which they originate. (Intraspecific semiochemicals that benefit the originating species rather than the responding species are termed "allomones.") Some kairomones act by stimulating a parasite to intensified search in an area, while others may bring about direct orientation of parasite to host. Since either of these actions may produce increased trap catch in a kairomone-baited trap, these compounds may also serve as attractants in survey traps.

With the introduction of more sophisticated techniques of behavioral analysis, investigation of the behavioral effects of semiochemicals has intensified. Insect sex pheromones elicit a series of responses that culminate in mating. Until 15 years ago it had been thought that the pheromone of an insect species consisted of a single compound specific for that species. With the advent of improved analytical techniques that have made it possible to identify trace components, it has become clear that most sex pheromones are mixtures of several components and that pheromonal specificity is determined by the nature of the components present as well as by their relative concentrations. The message conveyed to a male moth from a female that has everted her pheromone gland and adopted the characteristic posture termed "calling" is usually more closely analogous to a complex sentence than to a simple command. Behavioral analysis suggests that different pheromone components may often be involved in individual sequences of the overall response (14).

Bartell (15) has summarized the sequence of behavior commonly observed with pheromone-stimulated male moths as activation, orientation, and male-female close-range behavior. Male behavior often observed in the "activation" stage includes antennal elevation, "restlessness," and wing vibration. Such behavior has sometimes been used as a criterion in pheromone bioassays; it should always be remembered that a compound eliciting this behavior is not necessarily one that will also be active in subsequent steps. In the orientation step, the male moves toward the pheromone source —the female, or the pheromone-baited trap. The mechanisms by which this is accomplished have not been entirely elucidated, but it appears that in many cases the pheromone stimulates the male to fly upwind. Since the wind is carrying the stimulus, this upwind flight (anemotaxis) results in the male approaching the source of the stimulus. At close range, changes in the concentration of the stimulus or the presence of other pheromone components cause the male to slow down and alight near the female (or bait) and continue the sequence of actions that lead to copulation. In all these steps, other factors, particularly visual cues, affect the response of the insect.

"Primary" sex pheromone components have been defined as those components that are responsible for long-distance (greater than 1 m) upwind anemotaxis; or, as an approximation, those that are obligatory for trap catch in field tests when they are emitted at rates that are similar to those used by the "calling" insect (16). The primary pheromone components are thus sex attractant pheromones. With some insects a single component may be sufficient to elicit the whole sequence that leads to mating, but usually the full repertory is not evoked except in the presence of additional "secondary" pheromone components.

In addition to chemical identification and behavioral analysis of semiochemicals, the analysis of the physiological responses involved when an insect responds to an attractant is a major area of investigation. Chemical stimuli interact with chemoreceptors present on various parts of the insect body. Contact chemoreceptors, such as the gustatory receptors, respond to some behavioral stimuli, but the receptors involved in the perception of volatile chemicals such as attractants are the olfactory chemoreceptors, which are usually located on the insect antennae. The interaction of a stimulus with the chemoreceptor generates an electrical signal that is transmitted through a neuron to the central nervous system. If electrodes are inserted into an insect antenna or attached to an individual sensillum, this electrical signal can be recorded.

METHODS OF STUDY

Bioassay Techniques

Attractants elicit behavioral reactions which can be observed in the field or, to a lesser extent, within the laboratory. Laboratory studies and studies of artificially isolated groups of insects are subject to the criticism that behavioral cues may not operate in artifically created environments in the same way as in the natural situation. The methods of bioassay used in the laboratory are primarily electrophysiological techniques or behavioral studies, such as olfactometry and wind tunnel observations; the method of choice depends on the insect involved.

FIELD STUDIES Traditionally, synthetic attractants have been screened to determine which material trapped most insects; thus bioassays have been conducted in the field in natural populations of insects through a series of replicated experiments. Generally, the number of insects trapped by a given quantity of the candidate attractant serves as a measure of its activity. Other factors, such as trap design, trap placement, or metereological conditions, affect the number of insects caught; therefore, experimental results require careful statistical analysis. When natural populations of insects are unavailable, tests may be performed in populations of released insects, in field cages, or in the laboratory environment. Each produces useful information, but deviations from the "natural" environment may give results that cannot be reproduced in the field.

BEHAVIORAL STUDIES In the laboratory, individual insects or groups may be exposed to stimuli in a variety of ways. Tests that indicate whether the compound elicits a behavioral response are particularly useful, but it may be necessary to conduct more elaborate, or at least different, experiments to establish that the chemical is truly an attractant. For example, fractions obtained from extracts of female gypsy moth [*Lymantria dispar* (L.)] abdominal tips containing the sex pheromone, disparlure, were originally assayed by using an array of male moths on mounting racks (17). Excitation of the restrained insects is evidence for the presence of an active substance in a particular fraction, but field bioassay by trapping is necessary to demonstrate whether the fraction or the pure pheromone is truly an attractant.

A wind tunnel equipped with a continuous moving belt painted with distinct transverse stripes on the tunnel floor has been used to study the response of flying insects to sex pheromones (18, 19). In this tunnel, the duration and persistence of prolonged anemotactic response to a pheromone plume can be measured. The insect flying into the pheromone plume may be held in a stationary position relative to the observer by regulating the speed of the belt, because the air speed of the male moth in anemotactic flight is influenced by the ground pattern.

The wind tunnel has been used in studies of insect sex pheromones to ensure that an extract contains compounds that elicit positive anemotaxis in contrast to those that elicit only sexual excitation. It may be particularly useful for the study of multicomponent pheromones because the absence of a necessary component in the pheromone may be recognized by the failure of the chemical stimulus to elicit sustained flight.

ELECTROPHYSIOLOGICAL TECHNIQUES Olfactory receptors for perceiving pheromone signals are generally located on insect antennae. Male moths, for example, possess feathery antennae that contain an array of such receptors. When biologically active compounds interact with the receptors, electrical signals are generated that can be measured by connecting the antenna to an amplifier. There is a change in potential between the base and the tip of the antenna when an active chemical is perceived, and the change in potential can be amplified and recorded on a potentiometric recorder or an oscilloscope to give an electroantennogram (EAG). This technique has been used to identify materials that are biologically active in extracts obtained from insects. Its extension is the use of insect antennae as very specific detectors for monitoring the presence of pheromone components among the compounds eluted from a gas chromatograph (20).

The antennal receptors are located on numerous hair-like sensilla. For example, the giant silkworm [*Antherea polyphemus* (Cramer)] has over 60,000 sensilla with 150,000 receptor cells located on its antenna (21). Electrophysiological studies can be conducted on whole antennae or on single sensilla. Measurements with single sensilla are useful for studying the interaction of pheromone components because different sensilla may respond to different compounds, and even when the antenna is saturated with respect to one component (i.e. there is no further response to increased quantities of volatilized material), a second pheromone component may still elicit an electrical response (22).

Electroantennography has proved extremely useful for the identification of pheromones and for the study of behavioral effects elicited by chemicals. Lepidopteran female sex pheromones often contain long-chain unsaturated acetates, aldehydes, or alcohols; identification of the various components used by a given insect may be aided by EAG studies with series of synthetic chemicals of appropriate types. By studying EAG responses to a variety of compounds, Priesner et al (23) were able to predict the pheromone components of a variety of noctuid moths. The intensity of the response induced by individual positional and geometrical isomers was used to identify an attractant for *Phyllonorycter (Lithocolletis) blancardella* (F.) (24). Male response to a series of synthetic acetates showed that the greatest activity lay in (*E*)-10-dodecen-1-ol acetate, and this compound was found to be attractive in field tests. However, since insufficient material was available to demonstrate its presence in the insect, this synthetic material must be classified as a sex attractant or "parapheromone" until further study can show whether it is actually a pheromone. The chemical is now in use for monitoring infestations in orchards. The codling moth [*Cydia pomonella* (L.)] pheromone, (*E,E*)-8,10-dodecadien-1-ol, was initially recognized as a sex attractant through a similar EAG examination of synthetic compounds, and its presence in the natural pheromone was confirmed by subsequent chemical identification (25, 26).

The structure of the antennal receptors, their morphology, and function are receiving much attention (27, 28). EAG measurements and single cell measurements have been used singly and in combination to elucidate aspects of chemical communication in bark beetles (29). Bark beetles have segmented club-shaped antennae. Scanning electron microscopy shows the shape of the receptor structures and reveals that in the sensilla of the southern pine beetle [*Dendroctonus frontalis* (Zimmerman)], for example, approximately 2.9×10^6 minute pore tubules conduct odors from the air to the receptors, which respond to pheromones and to a variety of host odors. It appears that there are greater numbers of receptors for pheromones than for host odors, and individual cells appear to possess different degrees of specificity. Perception of pheromones and host odors is of critical importance for the survival of the bark beetles, because tree host selection, colonization of the host, and sexual behavior are regulated by host phytochemicals and insect pheromones.

The concentration of odorous substances that can be perceived by the olfactory system of the insect is extremely low. Only one molecule of the silkworm moth [*Bombyx mori* (L.)] pheromone, bombykol [(*E,Z*)-10,12-hexadecadien-1-ol], is necessary to trigger an electrical response at the receptor (30). The threshold concentration needed to elicit behavioral responses depends on the receptor type. Receptors may be regarded as generalized or specialized, depending on the specificity of their response. The specialist receptors respond only to a single compound and their sensitivity is much greater than that of the generalized type, which respond to a wider range of chemical stimuli.

The sequence of events that occurs at the receptor is considered to be the reversible attachment of the pheromone to an acceptor molecule, followed by a change in conformation of the acceptor molecule. This change increases the flow of ions through the dendritic membrane, and a signal is then transmitted as a nerve impulse (31).

Little is known of the fate of the pheromone and the deactivation process at the receptor, although a few investigations have been reported. *cis*-7,8-Epoxy-2-methyloctadecane (disparlure), the pheromone of the gypsy moth, is converted to two unidentified products (32), and (*Z*)-7-dodecenol acetate, the pheromone of the cabbage looper [*Trichoplusia ni* (Hübner)], is hydrolyzed to the alcohol (33). Three proteins that play a role in pheromone deactivation have been identified from the antennae of *Antheraea polyphemus* (34).

Chemical Investigations of Attractant Pheromones

Recent progress in the identification of naturally occurring insect attractants reflects progress in chemical techniques. Instrumentation and separation techniques introduced during the last decade have made it possible to elucidate the structure of compounds using microgram or submicrogram quantities for study. In 1959, Butenandt identified the first pheromone after a 20-year study in which 12 mg of a pheromone derivative was obtained by an extraction procedure that required about 500,000 virgin female silkworm moths (35). In recent years, such techniques as the combination of gas chromatography (GC) with mass spectrometry (MS) have reduced the amount of material needed for investigation, and the identification of many pheromones has led to increasing recognition of the types and classes of chemical that are likely to be encountered as pheromone components. More recently the application of wall-coated open tubular glass capillary GC, Fourier-transform nuclear magnetic resonance (NMR), and infrared (IR) spectroscopy have increased the amount of information that can be obtained from microsamples. Particularly noteworthy are developments in NMR, such as the use of shift reagents, that have made it possible to recognize the configuration of optically active pheromones with very small quantities of material (36).

Great strides have also been made in pheromone synthesis. The synthesis of many optically active pheromones of known configuration has played an important role in structure-activity studies, and the application of ylide synthesis has provided the scientist with a battery of compounds for evaluation and for confirmation of structures inferred from instrumental data (37, 38). Application of new synthetic techniques has made available geometrical isomers of long-chain unsaturated compounds in high purity. At the same time, refinements in separation technology such as the use of silver nitrate-treated columns in high pressure liquid chromatography (39) and the application of molten liquid crystal phases in GC (40, 41) have simplified some of the problems of separation of geometrical isomers.

No general description (42, 43) of techniques for isolation, separation, and identification of pheromone components is adequate, since each study brings up new problems that must be resolved. The greater the quantity of interfering material, the greater is the problem of identification. Techniques of isolation which involve collecting the active stimulus from the vapor phase or selective dissection of the biological structures containing the stimuli before extraction are preferable to extraction of whole insects. It is most important that all stages of the separation be monitored by adequate bioassays and the chemical integrity of the stimulus should be assured by protecting all materials from the effects of light and oxidation. It is also important to ensure that the materials originate from sexually mature, attractive insects.

Fractionation of extracts is an essential part of the purification procedure. The active materials must be obtained as free from inactive contaminants as possible. GC-MS analysis of simple or relatively complex mixtures may indicate identity or further procedures for separation.

Conventional techniques of preparative organic chemistry are difficult to apply at the microgram level, and special techniques must be designed for use at the submicrogram level. Selective chemical reactions in the gas chromatograph can be used to demonstrate the presence or absence of functional groups, and the hydrocarbon skeleton of the molecule can be deduced from GC data after on-column or pre-column reduction. Retention time data from GC afford useful indications of functionality and double-bond position. The position of the latter within a long chain may be inferred from microozonolysis. Further indications are provided by epoxidation and the preparation of derivatives that give characteristic mass spectra (44).

Throughout such studies, there is a constant need to be aware of the possible presence of artifacts and contaminants. It is also important to have available authentic samples of related analogues so that valid correlations may be drawn from the data and structural inferences can rest on a substantial basis. Useful extensions of biological and instrumental data can often be obtained if closely related analogues are available for study as model compounds.

COMPOUNDS IDENTIFIED AS INSECT ATTRACTANT PHEROMONES

Lepidoptera

Among insects for which attractants have been identified, Lepidoptera far outnumber other Orders. Attractant pheromones have been identified for nearly 150 lepidopteran species (mostly moths), and parapheromones have been found for over 300 others (45). Many of the latter may yet prove to be pheromones, but at the present time, they have not been shown to be produced by the insect. The majority of the lepidopteran attractant pheromones are mixtures of C_{12} to C_{18} unsaturated unbranched primary alcohols, acetates, and aldehydes.

The composition of the pheromone blend appears to remain relatively constant during development and maturity of a given insect. For example, the female redbanded leafroller [*Argyrotaenia velutinana* (Walker)] produces a pheromone that consists of a mixture of (*Z*)- and (*E*)-11-tetradecen-1-ol acetate (91:9) in a 2:3 ratio with dodecyl acetate. The ratio of *Z:E* components remained constant throughout pupal and adult stages of the insect (46).

The specificity of the pheromone blend produced by the female must be matched by the ability of the male to perceive the signal. EAG and biological studies confirm the importance of the precise blend (47). The best attractant for a male moth in the field often appears to be the mixture of compounds in the ratio approximating that emitted by the female. A highly specific and selective communication system that involves several structurally related components in ratios that vary from species to species reduces the necessity for gross differences in the physiology of pheromone synthesis or perception. The structural requirements are quite specific. EAG measurements of the response of 16 noctuid species to about 100 pheromone analogues showed that there was a rapid reduction in response when the double bond was shifted by one carbon atom from the optimum or the chain length was increased or decreased by one or two methylene groups (23).

Conclusions concerning the general types of chemical structure present in lepidopteran pheromones have been reinforced by studies of synthetic attractants. In a screening test for attractants, about 100 unsaturated alcohols or acetates with chain lengths from C_{10} to C_{16} were synthesized and placed in traps. Male moths of 93 species belonging to 15 lepidopteran families were caught. Although more complex blends would be expected in nature, the observations with single compounds provide a useful starting point for more detailed study of pheromone composition (48). Similar experiments have provided attractants for practical use and information for pheromone studies.

Components or blends of components play different roles in eliciting stages of precopulatory behavior. The pheromone blend of the oriental fruit moth [*Grapholita molesta* (Busck)] contains (*Z*)-8-dodecen-1-ol acetate. About 7% of the (*E*)-isomer is required for attractancy. Although another component, dodecanol, did not elicit upwind anemotaxis when used alone, its presence in the lure mixture led to increased trap captures. Behavioral studies (14) showed that inclusion of dodecanol in the attractant mixture elicited close-range precopulatory behavior (landing near the source of the chemical, wing fanning, etc.); these close-range effects may have contributed to the observed increase in lure efficiency. However, it was subsequently shown (49) that a fourth component, (*Z*)-8-dodecen-1-ol, played a more important role than dodecanol in the male response sequence.

The ability to distinguish between optically active enantiomers of the same compound is common to many species and is an important factor in pheromone studies. The gypsy moth responds to (7*R*, 8*S*)-(+)-disparlure; this response is inhibited by the antipode at higher concentrations, whereas the racemic form and the (+) enantiomer are equivalent as male moth attractants at low concentrations (50). Single sensillum studies indicated that only one receptor type is present on the gypsy moth antenna (51). However, saturation studies in which the antenna was exposed continuously to the (+) enantiomer or the racemic compound gave evidence for the presence of one receptor type with a greater affinity for (+)-disparlure and another type having greater affinity for the antipode (52). The relationship of biological activity to the enantiomeric composition of chiral pheromones has been discussed in detail by Silverstein (53).

If we assume that biological receptors discriminate between enantiomers because the stereochemistry of one enantiomer permits maximal interaction with the active sites on the receptor, interaction between an achiral molecule and a receptor will probably be favored when the former adopts a conformation which fits most closely the contours of the active sites. Although long-chain compounds can adopt many possible conformations, Chapman et al (54) suggested that preferred conformations might be identified by synthesis of closely related analogues containing an asymmetric carbon atom. Analogues of a nonchiral lepidopteran pheromone into which an optically active center had been introduced were synthesized and a comparison of biological activity of the enantiomeric pair of pheromone analogues thus obtained provided an indirect method for probing the stereochemistry of the receptor site.

In general, lepidopteran pheromones identified as long-distance attractants have been emitted by female moths. Two species of wax moth provide exceptions to this generalization. Undecanal and nonanal have been identified from the male greater wax moth [*Galleria mellonella* (L.)] and have been shown to elicit behavioral responses in the female similar to those elicited in females exposed to the male pheromone (55). Similarly, undecanal and (*Z*)-11-octadecenal have been obtained from male lesser wax moths [*Achroia grisella* (F.)], and the combination is attractive to females (56). In the latter insect, an auditory stimulus aids in attracting the females.

With many lepidopteran species, a variety of compounds have been identified in male-specific secretions; some of these appear to function as "aphrodisiacs" and elicit close-range precopulatory responses from the females.

Coleoptera

The relatively complex structures of the beetle pheromones have provided an interesting and diverse range of problems in identification and synthesis. With the bark beetles, aggregation pheromones may be released by one or both species when a habitat favorable to survival has been located. Survival depends on identification of a suitable host, host-attack, mating, colonization, and dispersal. From studies with some chiral bark beetle pheromones, it has been shown that biological activity depends on the proportions of enantiomers present in the stimulus (53). Clearly there is a differential response to the enantiomers, and a change in proportion may block or synergize an observed response.

The first multicomponent pheromone was identified from the frass of the male bark beetle *Ips paraconfusus* (Lanier). It attracts both males and females and contains 3 compounds: ipsenol [(–)-2-methyl-6-methylene-7-octen-4-ol], (+)-*cis*-verbenol [(1*S*,2*S*,5*S*)-4,6,6-trimethylbicyclo[3.1.1] hept-3-en-2-ol], and ipsdienol [(+)-2-methyl-6-methylene-2,7-octadien-4-ol] (57). A mixture of all three compounds was required for effective attraction in the field. One or more of these terpene alcohols occurs in a number of *Ips* species, and cross attraction responses among members of this genus has been investigated in much detail.

The western pine beetle [*Dendroctonus brevicomis*] (LeConte) also employs a 3-component aggregation pheromone. One component, *exo*-brevicomin (*exo*-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane), is provided by the female; a second component, frontalin (1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane), comes from the male; and the third, myrcene (7-methyl-3-methylene-1,6-octadiene) is found in the insect but is considered to originate from the host tree (58).

The biosynthesis of some bark beetle pheromone components has been studied, particularly the route by which monooxygenated terpenes are formed (59). Verbenol, ipsenol, and ipsdienol can be formed by the allylic hydroxylation of α-pinene and myrcene. Both compounds occur in host pine trees.

The pheromone of a major cotton pest, the boll weevil [*Anthononmus grandis* (Boheman)] provides an example of a complex pheromone secreted by the male. The pheromone contains four components, all of which are needed for attraction: (+)-*cis*-2-isopropenyl-1-methylcyclobutaneethanol, (*Z*)-3,3-dimethyl-$\Delta^{1,\beta}$-cyclohexaneethanol, (*Z*)-3,3-dimethyl-$\Delta^{1,\alpha}$-cyclohexaneacetaldehyde and (*E*)-3,3-dimethyl-$\Delta^{1,\alpha}$-cyclohexaneacetaldehyde (60).

The sex attractant pheromone of the Japanese beetle [*Popilla japonica* (Newman)], which females release to attract males, has been identified as

(*Z*)-5-(1-decenyl)dihydro-2(3*H*)-furanone. The (*R*) enantiomer was synthesized and found to elicit the complete male response (61). However, the racemic form was inactive and the (*S*)-enantiomer was inhibitory.

Diptera

The sex pheromones of flies are not powerful long-distance attractants, as are many lepidopteran pheromones, but are generally short-range attractants or sex-recognition pheromones. The major component of the sex pheromone of the housefly (*Musca domestica* L.), (*Z*)-9-tricosene, is present in the cuticular wax (62). Mediterranean fruit fly [*Ceratitis capitata* (Wiedemann)] males secrete several compounds, including methyl (*Z*)-6-nonenoate and (*Z*)-6-nonen-1-ol (63). The Caribbean fruit fly [*Anastrepha suspensa* (Loew)] male pheromone contains mono- and diunsaturated 9-carbon alcohols and two lactone esters (64).

Stimuli that attract mosquitoes and biting flies have been extensively studied. Carbon dioxide is an important factor in orientation of mosquitoes to human skin, but its role is considered to be that of a locomotor stimulant rather than a true attractant (65). Host odors play a significant role as long-range attractants, but little is known of the specific components responsible.

Hymenoptera

Bees and ants secrete complex mixtures of fatty acid derivatives, esters, alcohols, ketones, hydrocarbons, terpenes, nitrogenous compounds, etc. The array of pheromonal components and the variety of behavioral responses elicited by individual components or blends show the potential of chemical communication systems and their adaptation to insect sociality (66–68).

Some hymenopteran sex attractant pheromones have been identified. For example, (*E*)-9-oxo-2-decenoic acid (Queen substance) is an attractant for flying drones that occurs in the mandibular gland of the queen honey bee (*Apis mellifera* L.) (69) and has been identified in several *Apis* species (70).

The potent attractant pheromones emitted by females of several diprionid sawflies are acetate and propanoate esters of 3,7-dimethylpentadecan-2-ol (71). When four of the eight possible stereoisomers of these esters were tested against the white pine sawfly [*Neodiprion pinetum* (Norton)], one of the acetate isomers proved to be a potent attractant, while the other compounds tested had negligible activity (72).

Other Orders

Relatively few attractant pheromones have been identified from insects in other Orders. In part, this is because some insects rely less on chemical cues than on other stimuli for locating mates.

Attractant pheromones have recently been reported for several scale insects (Homoptera). These include the California red scale [*Aonidiella aurantii* (Maskell)] (73), the yellow scale [*Aonidiella citrina* (Coquillett)] (74), the San Jose scale [*Quadraspidiotus perniciosus* (Comstock)] (75), the white peach scale [*Pseudaulascaspis pentagona* (Targioni-Tozzetti)] (76), the Comstock mealybug [*Pseudococcus comstocki* (Kuwana)] (77), and the citrus mealybug, [*Planococcus citri* (Risso)] (78). Many of these pheromones have chiral centers and their biological activity is related to enantiomeric composition. The availability of synthetic pheromones to replace live females as lures in survey traps will aid greatly in combating these insects, which are serious pests of a variety of fruits.

In the Orthoptera, studies are under way with several cockroach species. Sex pheromones have been identified for the American cockroach [*Periplaneta americana* (L.)] (79) and the German cockroach [*Blatella germanica* (L.)] (80), but they appear to act more as stimulants than as attractants.

Various phenols have been identified from females of several species of ixodid ticks (Acari) (81, 82). These compounds appear to be short-range male attractants.

SYNTHETIC ATTRACTANTS

It was pointed out in the Introduction that there are two major routes by which new insect attractants may be discovered. The first involves analysis of the insect or its habitat to discover cues that occur naturally. The second requires systematic screening of potential baits that might be used in traps. The former approach requires a combination of analytical expertise and sensitive instrumentation. The latter requires intuition combined with a facility for systematic experimentation and observation. Systematic screening of this sort has provided a number of insect attractants, and many of these have been used in pest management.

Promising leads were obtained by screening chemicals, botanical extracts, food substances, and other likely candidates. Early discoveries were based on random screening and, as structural leads were revealed, synthesis of analogues was undertaken. Between 1950 and 1955 over 5000 materials were screened as attractants for the melon fly [*Dacus cucurbitae* (Coquillett)] or Mediterranean fruit fly in Hawaii and over 8000 materials as attractants for the Mexican fruit fly [*Anastrepha ludens* (Loew)] in Mexico.

A number of attractants for fruit flies have been developed, and the history of some of these efforts has been reviewed by Chambers (83). From the early years of the present century, many mixtures derived by fermentation and decomposition of sugar or proteins have been tested and found to attract several species. In addition, several synthetic lures have been discovered by screening and are used in large-scale programs to prevent the establishment of fruit fly infestations within the continental United States. However, some of these synthetics attract only males of a limited number of species, whereas food attractants such as protein hydrolysates attract both sexes of most tephritids and of many other insects.

The Mediterranean fruit fly is the primary tropical fruit fly species of concern to growers in the southern and western United States. A potent attractant for males, *tert*-butyl 4-(or 5)-chloro-*trans*-2-methylcyclohexanecarboxylate (trimedlure) (84) is now extensively used throughout the world; it also attracts males of the Natal fruit fly [*Ceratitis rosa* (Karsch)] (83). The oriental fruit fly [*Dacus dorsalis* (Hendel)] is a major pest in many areas in the Pacific; methyl eugenol (4-allyl-1,2-dimethoxybenzene) is a powerful attractant for males of this species and has been used in combination with insecticides in campaigns to eradicate the insect on infested islands (85). An attractant for male melon flies and Queensland fruit flies [*Dacus tryoni* (Froggatt)] is cue-lure [4-(*p*-hydroxyphenyl)-2-butanone acetate] (86); it has also been used in male annihilation programs to eradicate isolated infestations.

Attractants have been developed for other economically important species. A mixture of phenethyl propanoate and eugenol (4-allyl-2-methoxyphenol) was found to be attractive to both sexes of the Japanese bettle (87). Combination of the 3:7 phenethyl propionate-eugenol mixture with the natural pheromone gives a mixture 2–8 times as attractive as either attractant alone (88).

A serious pest of coconut plantations in the Pacific Islands is the coconut rhinoceros beetle [*Oryctes rhinoceros* (L.)]; attractants have been used to trap these beetles. The beetles can be inoculated with a virus and released to spread the virus; this technique has substantially controlled infestations in Samoa, Tonga, and Fiji (89). Ethyl dihydrochrysanthemumate (chrislure) and ethyl chrysanthemumate (rhinolure) are attractants for the beetle (90, 91).

Some species of yellowjacket wasps [primarily *Vespula pensylvanica* (Saussure)] are attracted by 2,4-hexadienyl butyrate, heptyl butyrate, or octyl butyrate (92). However, predominant East Coast species *V. squamosa* (Drury) and *V. maculifrons* (Buysson) are only weakly attracted by these compounds (93).

European chafers [*Amphimallon majalis* (Razoumowski)] are attracted by butyl sorbate. A more effective attractant is propyl 1,4-benzodioxan-2-carboxylate (amlure) (94).

INSECT ATTRACTANTS IN PEST MANAGEMENT

In devising strategies for insect pest management, it is necessary to understand the ecology and distribution of the target insect. Studies of population dynamics are needed to determine the influence of natural factors on the economic effects of a pest infestation and the success of control measures. It is also important to know whether control measures may adversely affect beneficial species and other insects. This information can often be obtained by using traps containing attractants.

Attractant traps are also valuable for detection and survey of many major pest insects. Information from arrays of traps, combined with meteorological data, can be used in computer-based systems to predict the future spread of an infestation. Trapping data may be used to follow movements of insects and changes in the infested area. Another major use is in the correct timing of insecticide applications; this is important to the grower because routine application of insecticides hastens the onset of insecticide resistance and represents a waste of expensive chemicals. For the pink bollworm, [*Pectinophora gossypiella* (Saunders)], it was claimed that with the use of traps baited with a parapheromone, costs of insecticide treatment were reduced by half (95).

Traps containing chemical lures have long been used for detecting insects and surveying insect populations. The use of attractants of various sorts to detect major insect pests such as the oriental fruit fly, the Mediterranean fruit fly, the Japanese beetle, the gypsy moth, the pink bollworm, the boll weevil, and the screwworm [*Cochliomyia hominivorax* (Coquerel)] by government agencies in the United States is a well-established practice. Such use is essential to maintain quarantines and to control the movement of produce from infested areas.

Attractant traps are also valuable in monitoring for stored-product pests (96). For example, traps consisting of four squares of hairy cloth stitched together and impregnated with (*Z*)-trogodermal [(*Z*)-14-methyl-8-hexadecenal], the pheromone of the khapra beetle [*Trogoderma granarium* (Everts)], attracted and retained the beetle, as well as its larvae, over a 6-week period. Paper strips covered with adhesive to which a capsule containing pheromone was attached trapped phyticid moths in infested granaries. Food baits were effective for detecting infestations of some coleopterous species. A combination of these techniques to monitor the build-up of an insect population, with partial or complete fumigation when needed, may provide more desirable systems for control of stored-product pests than those currently in use.

Specific attractants are highly advantageous in monitoring and survey traps, as trap catches are not limited to single species and highly trained personnel are not required for identification of insect specimens as is necessary with less selective traps. Chemically baited traps are more suited to routine monitoring than are light traps because light traps are more expensive, require an electrical power supply, and are less selective. However, sex attractant pheromone traps are only capable of monitoring the adult reproductive stage of the insect, and direct observation of insects in the field may be needed to obtain information on early stages of an infestation.

In addition to their use in traps for detection, monitoring, and survey, attractants may be used in several ways for control or suppression of insect populations: (*a*) combination of baits with toxicants, pathogens, or sterilants; (*b*) mass-trapping; (*c*) interference with, or disruption of, mating. These techniques may be used as the sole method of control, or several techniques may be used in combination. Knipling (97) has recently surveyed the basic principles of insect suppression and management and has predicted the effects of pheromone applications on population decline.

A recent example of the combination of toxicant with a bait is the use of such a preparation in the screwworm control program. The female screwworm fly lays its eggs in or near wounds of warm-blooded animals, and the development of larvae causes death or disabling of the animal. Infestations occurred extensively throughout southern United States, Central America, and the Caribbean area. Populations of this insect can be reduced or eliminated by successive releases of sterile males; however, the success of the sterile male release technique depends on the ability of the released males to compete effectively with native males, and a means of reducing native populations is needed to increase the effectiveness of subsequent sterile male releases (98).

Before the discovery of a chemical attractant, the standard attractant for the screwworm had been decomposing beef liver, which was an inconvenient standard for routine use. A search for a chemical replacement resulted in an unpleasant-smelling but reproducible mixture of chemicals (swormlure-2) that effectively attracted flies to traps. This attractant was formulated in a wax pellet that also contained a feeding bait and an insecticide (99). Area-wide distribution of the resultant device effectively reduced screwworm populations.

As mentioned above, specific attractants available for fruit flies are used routinely by public agencies in quarantine programs to prevent the establishment of these pests within the continental United States, and grids of traps are deployed in areas susceptible to rapid infestation. In these programs, baits combined with toxicants are also used to attract flies to discrete sites for trapping or killing (100, 101).

The combination of attractants with other materials that will control insect populations is another potential application. Attractants have been used to lure insects to sites where they are infected with bacteria or viruses (89). Feeding attractants provide ways of introducing cumulative toxicants or chemicals that affect development (juvenile hormone mimics) into populations of insects.

Theoretically, mass trapping can be used for control of insect populations, and mathematical models have been proposed (102, 103). Its value as a component of IPM systems for insects that affect stored products is being explored (96).

In Israel, attempts to control the Egyptian cotton leafworm [*Spodoptera littoralis* (Boisduval)] by mass trapping have employed synthetic (*Z,E*)-9,11-tetradecadien-1-ol acetate, the main component of the sex pheromone. In 1977 over 4 million male moths were caught by 1660 traps in 2½ months (104). It was reported that there was a 40% reduction in egg masses, compared with those in an untreated control area. During the 3-year duration of the experiment there was also a reduction in required pesticide treatments.

The use of mass trapping as a method for pest control depends on the availability of labor and the cooperation of the users in the infested area. It reduces pesticide use and may eventually become a valuable technique. However, it is difficult to obtain a measure of its effectiveness without studies over several crop seasons.

Another potential application of attractants is the use of pheromones for suppression of adult insect populations by techniques variously referred to as "disruption of communication," "confusion," or simply as "air permeation." In contrast to the mass-trapping techniques, in which the reproductive cycle is disrupted by removing a large fraction of a single sex from the population, the "air permeation" technique relies on maintaining an aerial concentration of sex attractant pheromone in the infested area throughout the period of adult flight and mating to achieve a similar objective.

Attraction of males for mating requires release of chemical stimuli by the females, and if large amounts of the same stimuli are released from artificial sources, natural orientation and mating behavior may be adversely affected. In recent years, the scale of efforts to interrupt the reproductive cycle by permeating the air with pheromone components or synthetic analogues (parapheromones) has intensified. A major advantage is that small quantities of generally innocuous, degradable compounds are used, and natural enemies of the pest and beneficial insects are unaffected. Combinations of components of pheromones may be useful for simultaneous control of several species (105).

A disadvantage of the technique is that it is probably of little value when a number of pests are present at the same time. If pheromone treatment results in control of only one or two pests and insecticides must still be used to control the remainder, the use of pheromones may be of little benefit.

There have been many experiments, some on a large scale, to demonstrate that pheromones will affect insect mating in treated areas (106). More recent studies have been directed towards an understanding of effects on behavior, mating success, and economic impact. Commercial interest in this technique has recently increased.

The practical problems of development are substantial. Pheromone application requires only a few grams of chemical per acre and the application is directed against a single major pest insect. Therefore, total amount of chemical needed is relatively small compared with that typically used in the application of broad-spectrum insecticides. Although this would have the advantage of reducing the environmental burden of synthetic toxicants, the economics associated with large-scale production are absent. Many pheromones are costly, and there is need for research into improved methods of manufacture and the discovery of less expensive analogues.

The high cost of pheromones and their analogues used in trapping or mating disruption and their relatively rapid environmental degradation are handicaps to their economical use. Their biological activity is also extremely high. The combination of these factors necessitates a delivery system or formulation that will release a predictable concentration over an extended period. The formulation should protect the active ingredient from environmental degradation and ensure that it is completely released within a predetermined period. Fluctuations in release rate must be minimized despite the effects of environmental variables. These are stringent requirements, but there has been sufficient development in the technology of controlled-release formulations to provide several workable alternatives for use in pest control programs (107).

Formulations for use in traps include rubber septa impregnated with pheromone, three-layer laminated polymeric dispensers, hollow fibers, and similar devices. For mating disruption, the formulation must be applied over a large area; therefore a formulation that is suitable for application by aircraft spray equipment is desirable. Types of formulation that have been used for aerial application include hollow fibers, microcapsules, and flakes (based on the three-layer laminated polymeric dispenser).

CONCLUSION

The chemist, with improved techniques of analysis, now has the capability to determine the composition (quantitative and qualitative) of chemical signals released by insects. In many cases, a single insect may be sufficient for complete analysis. The information thus obtained provides important clues to the understanding of insect behavior, reproductive isolation, and communication. Insect taxonomic and physiological studies will benefit by this knowledge.

The neurobiologist can identify individual receptors and study the electrical responses generated by the chemical stimulus. There has been progress in the techniques for studying insect behavioral responses elicited by pheromones, and there have been attempts to categorize observed behaviors more rigorously. However, many studies have been aimed at an immediate practical outcome, and this goal has often taken precedence over the systematic acquisition of behavioral information.

Although there has been a considerable amount of research into the effect of insecticides in the fields of neurochemistry and physiology, much remains to be learned of the effects of behavioral compounds. This is particularly true of the processes accompanying the generation of the neural signal and the resultant sequence of events.

The use of attractants in pest management has developed in response to special needs. Discovery and application have progressed through highly empirical phases. Attractants have proved extremely valuable as practical tools and promise to play an important role in the management of insect pests, but there is a need for greater basic understanding of their biological function and activity.

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