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CHEMICAL COMMUNICATION IN INSECTS: BACKGROUND AND APPLICATION

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Abstract - The ultimate practical goal of pheromone research on insect pests is to place the communication system on a molecular basis and to use the knowledge to detect, survey, trap, or disrupt the population. The ideal procedure is to identify quantitatively all of the components and to use all or some of them as synthesized chemicals in the emitting device in the field. Some of the problems and pitfalls are discussed.

Detection and survey traps are widely used. Several successful demonstrations of mass trapping and of disruption have been carried out. Given cooperation of government agencies and industry, pheromones will surely be used as one component of integrated pest management.

DECISIONS, PROCEDURES, PITFALLS, AND QUESTIONS

In 1967, after three years of working with bark beetle pheromones, my colleagues and I suggested that the following rigorous protocol be generally adopted:[1]

1. Understand the behavior of the target insect in the field and develop a laboratory bioassay to mimic the important facets of the attractant or aggregation behavior -- the key facet being attraction over a distance.

2. Produce enough starting material to permit chemical identification of the active components. We considered extraction of insect bodies or glands, excreta, or trapping of emitted volatiles.

3. Fractionate the material, following each step with a laboratory bioassay. Test combination of fractions for additive or synergistic effects.

4. Identify the individual active components by means of spectrometric and microchemical techniques.

5. Confirm postulated structures by comparison with authentic synthetic compounds.

6. Confirm the biological activity of the synthesized compounds in both the laboratory and the field.

This remains a generally sound protocol, but we recognized the serious deficiency of compromising on a laboratory instead of a field test to monitor the chemical fractionation. Field tests, we decided, would consume too much of the starting material and would take too much time. We were lucky; the laboratory response of walking insects led us to the compounds that evoked the aggregation response of flying insects in the field. In 1971, to reinforce point 6, I further made the deceptively simple statement that the synthesized and natural pheromone must have the same activity,[2] but how to insure this was discreetly not specified. Also added was this statement: "Finally the entomologist must learn to use the synthetic material to manipulate the insect's behavior and to develop survey and control procedures. The hazards involved in such a study -- contamination of a [supposedly] pure but inactive fraction with a minute amount of the extraordinarily active pheromone, complications caused by synergistic and masking effects, problems of interpreting complex and variable responses of insects [to mention a few problems] -- demand close collaboration at a sophisticated level between the entomologist and the chemist, both of whom are intrigued by the possibility of understanding behavior at a molecular level."

In practice, one is faced with a series of decisions, confronted with pitfalls, and forced into a series of compromises. Some of these problems and procedures were discussed in a review written in 1975.[3]

Most investigators agree that a quantitative laboratory bioassay is necessary in most cases; in fact, the first successful pheromone study [4] used a laboratory bioassay. However, the criterion of short-range sexual excitation -- suitable for the silkworm moth (Bombyx mori), a unique "domesticated" species -- was adopted uncritically by subsequent investigators to achieve the goal of isolating and identifying the attractants produced by female moths that were responsible for the spectacular long-range responses by the male. Thus, for example, Sekul and Sparks (1967) reported that the sex pheromone of the fall armyworm (Spodoptera frugiperda) was cis-9-tetradecen-1-ol acetate.[5] Chemical fractionation was monitored by wetting a medicine dropper with the sample, pointing the dropper at the antennae and squeezing the bulb. "A full copulatory attempt by males with the source of stimulus was interpreted as a positive response." Subsequent attempts in the field to attract males to the synthesized compound were unsuccessful. In 1976 Sekul and Sparks reported the presence of (Z)-9-dodecen-1-ol acetate in the extracts of abdominal tips[6], and this compound was active in field tests[7,8].

Chemical fractionations have been monitored by electroantennograms which have provided quick access to potential pheromone components in a number of moth species with closely related pheromone components.[9]

In recent years, laboratory bioassays have progressed to the use of a wind tunnel with a movable floor, which was first used by Kennedy and Marsh in sophisticated studies of flight behavior[10] and is now used widely to monitor chemical fractionation and to study responses to individual pheromone components and combinations.[11]

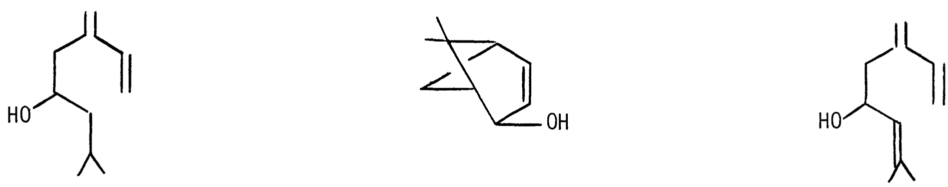
Another critical decision involves the choice of the source of the pheromone. Most investigators of moth pheromones have used extracts or rinses of abdominal tips. One of the early polemical exchanges in the field involved the use of hindguts versus frass as the source of the aggregation of bark beetles.[12] The problem is that the material present in the insect may not represent the actual material emitted by the sender (of the message) and perceived by the receiver. Aeration of the emitting insects and cold-trapping[13] or absorbent-trapping[14] of the volatiles have been used to overcome the problem. In a number of cases, the proportion of components in the aeration material has been found to be different from that in the gland extract. In several cases, the most important component was found only in the aeration material. Thus, for example, the major component, 14-methyl-8-hexadecenal, of the sex attractant of four species of Trogoderma beetles was found in the aeration material trapped on Porapak Q, but not in the extract of macerated beetles. Apparently, the major component is produced "on demand" only during the "calling" period of the female.[15] Aeration only during the calling period alleviates the possible problems of "breakthrough" or air oxidation. (Z)-11-Tetradecenal was identified as the major component of the sex pheromone of the orange tortrix moth, Argyrotaenia citrana, whereas it was barely detectable in the gland extract.[16] Although in earlier studies with bark beetles,[17,18] the components of the aggregation pheromone were identified from frass, this approach was not successful with the elm bark beetle, Scolytus multistriatus. Aeration of virgin females while they were boring in elm logs and collection of the volatiles on Porapak-Q lead to the identification of three components -- two produced by the female and one by the host tissues -- acting synergistically as the aggregation pheromone.[19] In a recent study, aeration of the female Comstock mealy bug, Pseudococcus comstocki, (on potato sprouts or Japanese pumpkin) over a 2-3 year period (about 5 x 10^6 female-day-equivalents), yielded approximately 30 mg of the pheromone for identification.[20] It would seem advisable to use the aeration procedure, wherever possible, to decipher the actual chemical message perceived by the receiver. Certainly where the synthetic pheromone based on analysis of gland extracts does not reproduce the responses elicited by the emitter under field conditions, reevaluation by means of the aeration procedure is strongly indicated.

Still other questions obtrude: Is the pheromone produced by laboratory-reared insects identical with that produced in the natural population? Will a laboratory-reared insect give a "natural" response? What is the effect of crowding on pheromone production? How much variation is present in a given geographic area? What are the factors involved in disruption by permeation of an area by the pheromone? What are the effects of concentration of the synthetic pheromone emitted from various formulations? What part do the individual components contribute to the total attraction process? What are the biosynthetic pathways to pheromone production? What are the contributions of the host plant? What are the visual and auditory inputs? Many of these questions can be lumped under the heading of "context". These issues and others are discussed in reviews by Tumlinson et al.[21], Chararas[22], Carde[23], and Roelofs[11].

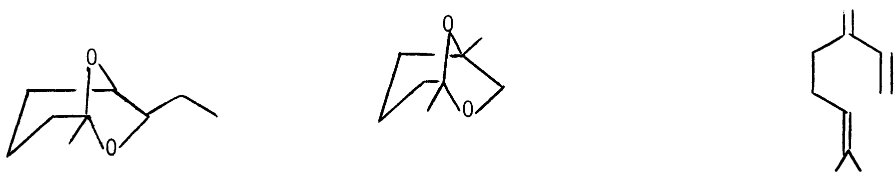
CHEMICAL DIVERSITY AND COMPLEXITY

In earlier reviews[2,3,17-19,24-29] the theme of multicomponent pheromones has been developed as contrasted with the earlier "magic bullet" concept of a single unique chemical compound for each insect. Retrospection induces some humility when I recall the time wasted in looking for the magic bullet in the frass of the bark beetle *Ips paraconfusus* (then called *Ips confusus*), but the experience was remarkably instructive.[30] In the first place, it was the first pheromone study carried out with modern instrumentation for elucidation of structure. Furthermore, it formed the basis for the concept of multicomponent pheromones (three compounds produced by the male), for the synergistic effect of a combination of three, male-produced components that show little or no individual activity, for the concept of multifunctionality of the components (i.e., kairomonal activity to predators), and for species isolation based on a difference in pheromonal blend. The optical properties of the components were carefully noted, and at a later date, the concept of enantiomeric effects was developed. A three component aggregation pheromone is produced by the western pine beetle, *Dendroctonus breviocomis*.[31] One of the compounds is produced by the female, one by the male, and one by the host tree. Two of the components are representative of a novel class of natural products, bicyclic ketals. Again the concepts of synergism, pheromonal and kairomonal activity, and speciation were delineated. In collaboration with Dr. G.N. Lanier and Dr. J.W. Peacock[19], we demonstrated a three-component synergistic pheromone for the elm bark beetle, *Scolytus multistriatus*, two produced by the female and one by the host tree. A landmark investigation by Tumlinson et al.[32] in 1969 showed that the male cotton boll weevil produces a four-component, synergistic aggregation pheromone.

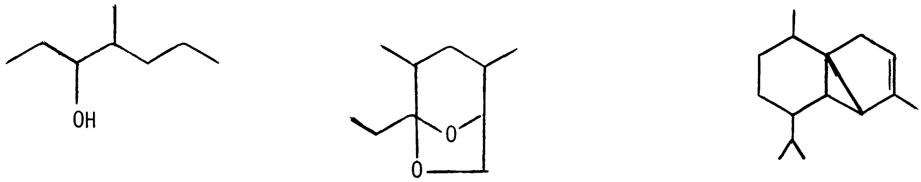
Ips paraconfus components



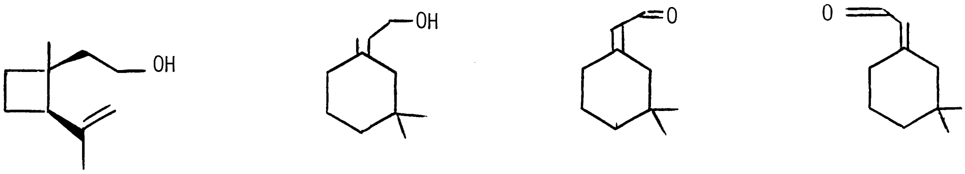
Dendroctonus brevicomis components



Scolytus multistriatus components

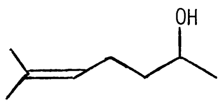


Cotton boll weevil components



The magic bullet concept engendered by the early work on moth pheromone disappeared by the early 1970's when it had become evident that several of the single components identified were not effective in the field. Awareness, improved isolation techniques, and more relevant bioassays of all fractions and combinations thereof quickly led to the discovery of multicomponent pheromones in most of the moths studied. In general the more important components were closely related unsaturated straight chain acetates, alcohols, and aldehydes. Homologs, functional group isomers, positional isomers, and geometric stereoisomers were commonly found and in many cases the ratios were critical. An up-to-date, comprehensive list of moth pheromones is provided by Tamaki[33]. We note examples throughout the Orders of insects in which a pheromone consists of a single active compound, two or more active compounds whose combined activity is the sum of the parts, and two or more compounds whose combined activity is greater than the sum of the parts (synergism).

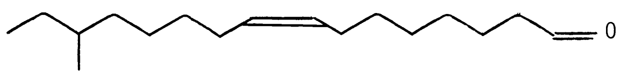
There are indeed single-component pheromones, although it is interesting to note that even the cabbage looper, Trichoplusia ni, was graced with an additional component after serving as a single-component bastion for about 14 years[34]. By following our own precepts, we isolated from the ambrosia beetle, Gnathotrichus sulcatus, what appeared to be a single-component pheromone, 6-methyl-5-hepten-2-ol (sulcatol)[35].



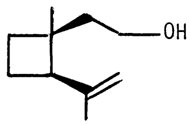
But this, of course, is a chiral compound, and we promptly set out to determine which enantiomer was present, having recently found that the naturally occurring enantiomer, (S)-(+)-4-methyl-3-heptanone, -- the alarm pheromone of the leaf-cutting ant, Atta Texana -- produced a threshold response at a lower concentration than did the antipode. To our surprise, we found a 65% (+)/35% (-) mixture in the ambrosia beetle. Neither enantiomer by itself evokes an appreciable response. Obviously then, we have a two-component, synergistic system at the enantiomeric level.

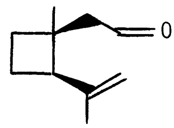
A complete identification of a pheromone component must therefore include a statement of enantiomeric composition and, if possible, a description of the absolute configuration of chiral elements. This, in fact, has been done in a number of cases (see ref. 27, pp. 133-146 and ref. 28). In most examples, a single enantiomer is present, and it is more active than the other enantiomer, which is an artifact. In several cases, addition of the unnatural enantiomer decreases or even blocks the activity (pheromone of the Japanese beetle, Popillia japonica[36], the gypsy moth, Lymantria dispar[37], and the California population of Ips pini[38]). In the second example, the racemic synthetic can be used despite its diminished activity; in the first and third examples, an expensive resolution or highly specific synthesis to produce the active enantiomer is required.

Enantiomeric composition is determined by measuring the optical rotation, by using a chiral derivatizing reagent and comparing the peaks of the diastereomers by chromatography, or by using a chiral shift reagent with NMR[39,40]. Such determinations can sometimes be extremely difficult for the following reasons: 1) It may not be possible to separate the diastereomeric derivatives or to separate the corresponding atoms by NMR, usually because of the distance between the chiral center and the functional groups; thus, we have not been successful with the compound from several Trogoderma species[15],



or with the compounds from several Pissodes species[41].



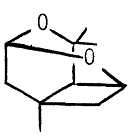


2) The optical rotation and the amount of material available may both be very small. Such is the case with the Trogoderma compound. 3) Suitable functional groups may not be available. 4) Chemical manipulation to provide a suitable functional group close to, or part of, a chiral center may not be feasible on the small amounts available. Under these circumstances, the only recourse is to challenge the responding insect against synthesized pure enantiomers and mixtures thereof on the not-unreasonable assumption that the most effective sample represents the natural composition. This last-resort approach should not be taken as a concession to a general screening of "likely" compounds as the initial approach to determining the chemical communication system[42] despite the useful information sometimes obtained.

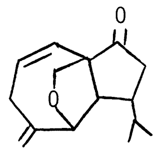
Only a few attempts have been made to elucidate the function of individual components in a complex blend. Following the initial identification of (Z)-8-dodecenyl acetate as the major component of the pheromone of female Oriental fruit moth, Grapholitha molesta, a series of studies with empirical mixtures implicated three other closely related compounds, and these compounds were subsequently shown to be present in the pheromone.[43] The sequence of events exhibited by the male in the presence of this four-component blend included pre-flight wing fanning, upwind flight, landing, post-flight walking with wing-fanning, and hair-pencil display.[44] Individual components produced individual effects but some of them were effective only in the presence of the other components (synergism).

One last aspect of complexity may be mentioned -- complexity of the structure of the individual molecule. From the standpoint of practical applications, it is fortunate that most of these compounds can be quite readily synthesized, unless a high degree of optical purity is demanded. However, lineatin, the aggregation pheromone of the ambrosia beetle, Trypodendron lineatum,[45] and, in particular, the periplanone pheromone of the American cockroach, Periplaneta americana,[46] stand as challenges to the synthetic chemist.

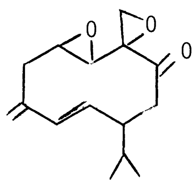
4,6,6-lineatin



Periplanone A



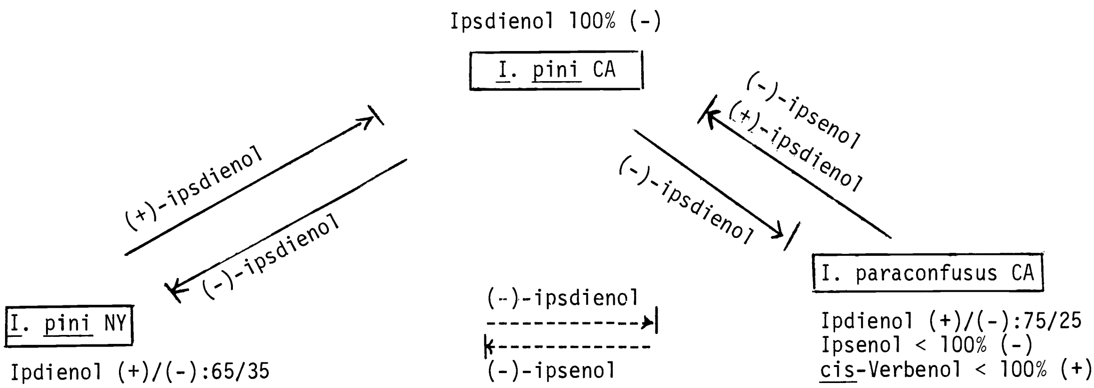
Periplanone B



INTERSPECIFIC AND INTERPOPULATIONAL EFFECTS

Semiochemicals play an important role in speciation (evolution of species) and in the maintenance of species integrity in sympatric populations. Thus, for example, two distinct populations of the European corn borer, Ostrinia nubilalis have been identified in Europe and North America on the basis of pheromone composition; one population uses a 96:4 mixture of the E:Z isomers of 11-tetradecen-1-ol acetate[47] and the other a 3:97 mixture of the E:Z isomers[48].

In an extensive study of the pine engraver beetle, Ips pini, Lanier et al.[49] showed that the morphological variability from the west coast to the east coast correlated with variability in responses to their pheromones. Ips pini beetles from California and Idaho produce and respond to (-)-ipsdienol. The (+) enantiomer strongly inhibits the response; that is, the beetles do not respond to synthetic racemic ipsdienol. Ips pini beetles from New York produce a 65:35 mixture of (+):(-) enantiomers, respond to the synthetic racemic compound and respond much more strongly to the (+) than to the (-) enantiomer. Birch et al.[48] showed that as little as 5% of the (+) enantiomer interrupted the response of the California population of Ips pini to the (-) enantiomer. Since the (+)-enantiomer is a component of the pheromone of the competing species, Ips paraconfusus, the previously observed interruption of the attraction of Ips pini to its conspecifics in California by the presence of boring Ips paraconfusus males is at least partially explained; some of this interruption is also caused by the presence of (-)-ipsenol, another component of the Ips paraconfusus attractant.[51] Converse inhibition of the pheromone response of Ips paraconfusus is caused by the (-)-ipsdienol pheromone of Ips pini in California.[52] This complex interrelationship can be depicted as follows:



Whereas, as described above, the ambrosia beetle Gnathotrichus sulcatus produces a 65%:35% mixture of the (+):(-) enantiomers, a sympatric species, G. retusus produces only the (+) enantiomer. Since G. sulcatus requires the presence of both enantiomers, it does not respond to G. retusus. Nor does the converse response of G. retusus to G. sulcatus occur, being interrupted by the (-) enantiomer.[53]

Several other examples of interspecific effects of components of several moth pheromones are cited by Tamaki (See Ref. 42, pp. 169-180).

PRACTICAL APPLICATIONS

The communication codes of a number of insect pests have been broken, and the behaviorist now has some remarkable tools. It should therefore be possible to mimic the original message in a false context and pervert normal insect behavior to self-destructive responses, and to do so without the widely publicized hazards of pesticides. Where then do we stand? What are the prospects? These issues were addressed in a recent book.[54]

Practical applications of pheromones can be categorized as follows:

1. Trapping insects for monitoring and survey. New areas of infestation can be detected at an early stage, and pesticides can be applied only when warranted by population increases beyond economically accepted thresholds.

2. Luring insects to circumscribed areas treated with insecticides, hormone analogs, or pathogens.

3. Mass trapping for population suppression.

4. Permeating an area to disrupt mate-finding or aggregation, the end result being population reduction.

The present status can be summarized as follows:

1. Monitoring and survey traps are available from several commercial sources and are widely used throughout the

world. They are very useful even though correlations between trap catches and population size are not readily determined. Quarantine procedures are greatly augmented by these traps.[55]

2. Suppression by trapping or disruption has been demonstrated in a number of cases for low-to-moderate densities, but a number of attempts to reach an economical acceptable threshold have failed. A rigorous demonstration of efficacy is a difficult goal, demanding careful planning and a major investment, and very few, if any, efforts have satisfied all reviewers.

3. Failures to suppress populations and limit damage can be traced to such factors as inadequate understanding of insect behavior, high insect density, too small an effort, improper pheromone formulation, improper distribution of traps or release sources, invasion from outside the treated area, lack of chemical definition of the natural communication system, or poor timing.

4. Pheromones are becoming an important component of integrated pest management, but the transfer of technology to user groups must be accelerated.

Pheromones have been used to protect field crops (cotton in particular); forest trees, shade trees, and timber; orchards and vineyards; and stored food products. Impressive savings in pesticides applications have been realized by gearing such applications to information from population-monitoring traps. A successful application of mass trapping and one of permeation are given.

Probably the first commercial application of mass trapping to control population was initiated in 1975 by the Chemainus sawmill, British Columbia, Canada to protect its timber and sawed lumber from the ambrosia beetle, *Gnathotrichus sulcatus*.[56] These beetles attack logs within two weeks after felling. Degrade of lumber and veneer results from galleries bored into the outer 5-8 cm of logs. The direct loss to industry by degrade was estimated at about $7 million in British Columbia in 1975-1976. The following additional massive problems result: export restrictions, remanufacture and repacking, need for rapid inventory turnover, and cost of direct insect control. On a routine basis since 1975, pheromone-baited traps have been maintained around the perimeter of the sawmill to trap beetles emerging from within and to intercept beetles attempting to fly in from surrounding infestations. The procedure is justified on the basis of prior investment in growing, surveying, harvesting, and sawing timber. It should be noted from the discussion above that separate traps containing only the (+) enantiomer will have to be used, in a separate area, to trap the sympatric species, *G. retusus*.

Cotton is afflicted by several major primary pests and by secondary pests whose population has increased as a result of massive application of pesticides; approximately one-third of the insecticides produced worldwide is applied to cotton crops. The annual cost of sprays against the boll weevil in the United States alone was estimated at $50 million in 1974. Of all attempts thus far at population control with pheromones, several large-scale efforts directed against the pink bollworm, *Pectinophora gossypiella* offer the most impressive documentation and economic justification for the disruption methodology. In 1978, the U.S. Environmental Protection Agency granted the first registration for commercial use of a pheromone as a disruptant, following several demonstrations of efficacy. In 1980, Albany International treated a total of 35,000 hectares in southwestern United States, India, and South Ameica. These studies were particularly timely since the massive applications of pesticides on cotton had reached a point of no return in many areas because of resistance and increased buildup of otherwise unimportant species (*Heliothis* in particular).[57] On a 296-hectare farm in Bolivia, five aerial applications of the formulated pheromone (a total of 14.3 grams of active ingredients) were delivered at 21-day intervals during the growing season. In addition, six applications of insecticides (a total of 1.62 kilograms of active ingredients) were used to control aphids, cotton leafworm, and *Heliothis* species. On a 97-hectare check (control) farm, 12 applications of insecticides (total of 4.46 kg of active ingredients) were used. Pheromone traps were used to monitor both fields for moths; larvae were monitored by boll sampling. The results were summarized: "...an acceptable level of pink bollworm suppression [was achieved] while affording a 64 percent reduction in conventional chemical insecticide use and 13 percent lower insect control costs relative to the conventional-practice check farm. The demonstration farm outproduced the check farm by about 18 percent in fiber and 22 percent in seed..."[58] Pheromone formulations are now under development for *Heliothis* species, and studies in laboratories throughout cotton-growing areas indicate that further reductions in insecticide sprays may be realized.

Similar successful experiments have been carried out in cotton fields in Israel. The Centre for Overseas Pest Research in England has similar programs throughout the Mediterranean area and in India.[59] The Egyptian cotton leafworm, *Spodoptera littoralis* is a major pest of many crops in Israel. Mass trapping of this pest in cotton fields has resulted in a decrease in the amount of pesticide required.[60]

PROSPECTS FOR PHEROMONES

Pheromones will undoubtedly take their place as a component of integrated pest management. Prospects depend as much on societal values, industrial practices, support from governmental agencies, and user acceptances as on the scientific issues involved. The key issue may well come down to industrial responses to a methodology that is complex, that will reduce sales of profitable insecticides, and that will not return large, concentrated profits in the short term through established channels.

Formulation technology has been developing,[61] and three systems -- hollow fibers, laminated plastics, and microencapsulation are quite effective and will certainly be improved and tailored for particular application. But the basic question remains: What constitutes an effective, practical bait or disruptant? One might reasonably argue that replication of the entire pheromone system of the insect would be most effective. This information in all detail, however, is available for relatively few, if any, insects. But from the practical viewpoint, we should try to compromise and use the minimum number of components needed. The selection criteria would be: 1) effectiveness for target insect, 2) stability, 3) cost, 4) ability to trap or disrupt other pest insects, 5) lack of interference with trapping or disruption of other pest species, and 6) lack of the ability to trap or disrupt beneficial insects.

These are difficult decisions, and it is not likely that all of these criteria can be met. It was mentioned above, for example, that racemic sulcatol, the aggregation pheromone of *Gnathotrichus sulcatus* would interfere with trapping of *G. retusus*. Some of the *Ips paraconfusus* pheromone components would interfere with trapping of *Ips pini*. One of the components of the aggregation pheromone of *Dendroctonus brevicomis* or of *Ips typographus* would result in the trapping of beneficial insects unless the latter were prevented from entering the traps.[18,62] It may be necessary to formulate key components separately to provide the required ratio of release rates. It may be advisable to use a racemate or a parapheromone (pheromone mimic) even though it may be less effective, in place of an effective but unstable or very expensive component. Compromise can indeed be a high art form.

Despite large gaps in our understanding of insect behavior, incomplete chemical characterization of many pheromones, and the still primitive state of the technology, the use of pheromone traps for monitoring and survey is an accepted tool in pest management. Several companies have found acceptance for pheromone-baited traps for the gypsy moth and the Japanese beetle; these traps are marketed directly to the individual "home-owner". However to firmly establish systematic, supervised, large-scale use of pheromones for population reduction as part of integrated pest management programs will require cooperation of government and the evolution of special kinds of industry to overcome some inherent problems.

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