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Pheromones: Background and Potential for Use in Insect Pest Control

Robert M. Silverstein

The biosphere has been drenched with insecticides, but effective, environmentally acceptable control of insect pests has not been achieved.

Because of its extraordinary toxicity in insects and relative safety in mammals, DDT was formerly hailed as the agricultural analog of penicillin, the modern miracle of medicine—and justly so. DDT killed insects that destroyed crops and were vectors of disease; crops flourished and millions of human lives were saved in the era including and following World War II. But in response to continual, excessive applications of the insecticide, the major insect pests developed resistance. Furthermore, populations of the natural enemies of major and minor pests were often reduced to ineffective levels. Thus the major pest population rebounded, and minor pests became major pests. The inevitable response of the farmer, under the urging of the insecticide salesman, was to further increase the dosage (*1*). Finally, the problems of environmental contamination by nonbiodegradable insecticides were brought home to the public by the appearance in 1962 of *Silent Spring* (*2*). Because of resistance and environmental problems, industry produced new insecticides, many of which were biodegradable but much more toxic to nontarget organisms. The honey bee and other beneficial insects, birds and other wildlife, and humans continue to be at risk, and the ratchet effect of increased resistance leading to increased dosage goes on.

Summary. Pesticides have not been a satisfactory solution to the control of insect pests. Pheromones show promise as a component of integrated pest management.

This is by no means a plea for a total ban on insecticides. It would be as foolish to discard DDT and its analogs as to discard penicillin and its analogs simply because of the abuses committed in agriculture and in medicine. Retrospectively, the abuses are understandable. Both materials are extraordinarily effective and easy to apply, are manufactured cheaply in large quantities, and are made available in convenient form through defined channels: through insecticide salesmen directly to farmers; through pharmaceutical salesmen and practicing physicians to patients. Ideally, physicians prescribe the appropriate drug, but since they may lack time for continued training in pharmacology, they often find it convenient to accept the advertising literature and the urgings of the salesmen. Physicians may also accede to the demands of patients who have been conditioned to expect instant cures with miracle drugs. Farmers frequently have no buffer between themselves and the salesmen, and larger dosages mean larger returns to the salesmen and the manufacturers. In both cases, a sound concept is perverted to dubious use; the scientist proposes and the salesman disposes. In some instances, however, the farmer is well served by the local distributor whose interests are tied to those of the community. For example, Wilbur-Ellis Co. has effectively promoted integrated pest management programs and, in fact, helped carry out some of the programs that resulted in decreased insecticide use. The merits and limitations of conventional insecticides have been summarized and recommendations made for their use in systems of integrated pest management [see (*3*)].

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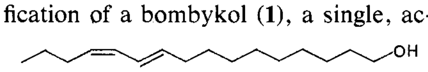
Under the rubric of integrated pest management are the following: (i) sound agricultural practices; (ii) use of resistant plants; (iii) selective use of pesticides; (iv) biological control through the introduction or manipulation of predators, parasites, and pathogenic organisms; (v) reproductive suppression by radiation or chemical sterilization; (vi) introduction of reproductively incompatible strains of pest insects; (vii) release of sterile insects; (viii) use of hormones or hormone analogs; (ix) use of pheromones and other behavioral chemicals; and (x) combinations of these. One may note that widespread use of toxic chemicals is incompatible with the use of beneficial organisms.

The Pheromone Story

I discuss here pheromones, compounds used in intraspecific communication to regulate the behavior of animals (insects in particular) in such activities as attraction to the opposite sex, aggregation of both sexes, sexual stimulation, and trail following. These responses are brought about by remarkably low concentrations of the pheromone components. Pheromones constitute only one category under the general term "semiochemicals" (semeion = signal), which includes both inter- and intraspecific signals.

Observations that male moths are attracted over considerable distances to females of the same species have been made during the last century, but it was not until 1959 that an active compound from a female moth was chemically identified by Butenandt *et al.* (*4*). Karlson and Lüscher coined the term pheromone for such intraspecific chemical signals (*5*).

Butenandt's achievement—the identification of a bombykol (**1**), a single, ac-



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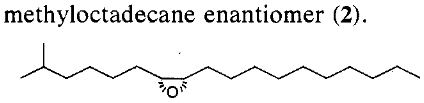
tive compound from hundreds of thousands of female silkworm moths (*Bombyx mori*) over a 25-year period without benefit of modern instrumentation—misled a number of subsequent investigators who uncritically adopted his bioassay, which elicited short-range sexual excitation. This was the appropriate response to measure in an insect that had been domesticated for silk production and no longer occurred in field populations, but it was later misused in monitoring chemical fractionation in the search for long-range attractants.

Furthermore, investigators of female moth pheromones through the 1960's searched for the single unique compound that would elicit a particular response. In most instances, the compound isolated through laboratory bioassays did not effectively attract male moths in field populations. In 1969, Moorhouse *et al.* (*6*) reported that the male red bollworm (*Diparopsis castanea*) responded in a laboratory bioassay to five substances isolated from the female, and that three fractions separated by gas chromatography (GC) produced an electroantennogram (EAG) response from male antennae. They suggested that failure to obtain a good field response for several species of moths was a consequence of failure to identify other active components of the pheromone; they proposed EAG recording of GC fractions, which has also been extensively exploited by Roelofs (*7*). As early as 1964, Wright (*8*) suggested that multicomponent pheromones would be expected to convey more information than single compounds and that such multicomponent communication systems would have evolved in nature. During the 1970's, most of the moth pheromones described were multicomponent, and reinvestigation of those identified earlier usually resulted in the identification of additional components with a conspicuous improvement in field responses. The "missing" component in several cases was found to be a small amount of the geometric isomer of the unsaturated component originally identified.

Typically, but with some exceptions, moth pheromone components are long-chain, unsaturated acetates, alcohols, and aldehydes. The pheromone may be a mixture of positional isomers, functional group isomers, geometric isomers, or structurally similar nonisomers; in a number of cases, a precise ratio of geometric isomers determines which of several closely related species is attracted in the field. An occasional epoxide, ketone, or hydrocarbon has been reported. Several moths respond to a single compound; the sex attractant of the gypsy moth, *Lymantria dispar*, for example, is a chiral molecule, and the moth responds only to the (7*R*, 8*S*)-(+)-*cis*-7,8-epoxy-2-methyloctadecane enantiomer (**2**).



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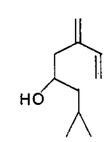
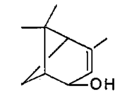
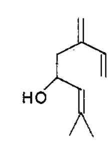
Investigations of pheromones of beetles and weevils (Coleoptera) took a different tack from the start (*9*). The bark beetle *Ips paraconfusus* Lanier [formerly *Ips confusus* (Le Conte)] attacks ponderosa pines, killing pole-size trees and the tops of mature trees in the Sierra Nevada range of California. D. L. Wood at the University of California, Berkeley, had worked out the behavior: The males bore into the trunk and, in the process of constructing the mating chamber, push frass (a mixture of wood borings and fecal pellets) out of the entrance tunnel. The aggregation pheromone in the fecal pellets attracts large numbers of males and females which overwhelm the tree by inoculating it with fungal spores, and the fungus kills the tree. Mating and egg-laying take place under the bark, and the broods emerge and repeat the cycle.

Wood's group collected frass and developed a laboratory bioassay that induced the beetles to walk upwind in an airstream that carried the volatile, attractive pheromone. My group at Stanford Research Institute extracted the frass, and obtained an active fraction by sequential short-path, high-vacuum distillation, liquid chromatography, and GC on a nonpolar column. The next step, GC of the active fraction on a polar column, yielded inactive fractions, but recombination of two of these fractions restored the activity. Eventually, three compounds, ipsenol (**3**), *cis*-verbenol (**4**), and ipsdienol (**5**) were isolated and identified from these fractions.



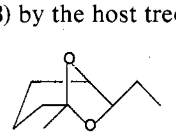




3 4 5

In the laboratory bioassay, two binary mixtures were active, but in the field, a mixture of three compounds was necessary to trap beetles—males and females. This was the first demonstration of a multicomponent pheromone and of the phenomenon of synergism in a pheromone. The specificity of synergistic effects was demonstrated by the fact that a related, sympatric species, *Ips latidens*, responded in the field to a mixture of **3** and **4** but not to the ternary mixture; the blocking effect of compound **5** was confirmed in the laboratory bioassay. Furthermore, the ternary mixture also attracted the predator *Enocleris lecontei*. Thus, the compounds that regulate intraspecific behavior also regulate interspecific behavior to prevent mating attempts between different *Ips* species and to enable predators to find the prey. The general term allelochemics is applied to interspecific agents: kairomones specifically when the benefit accrues to the receiver (as above), and allomones specifically when to the emitter.

The aggregation pheromone of the western pine beetle, *Dendroctonus brevicomis*, furnished a significant variation on the theme of multicomponent pheromones (*10*). The pheromone consists of three synergistic components: *exo*-brevicomin (**6**) contributed by the female, frontalin (**7**) by the male, and myrcene (**8**) by the host tree. Compound **8** can be



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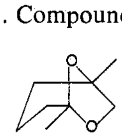

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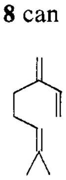

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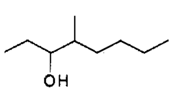
regarded as a pheromone component or as an allelochemic component—in the latter sense, the tree affecting the behavior of the attacking insect. The predator, *Temnochila chlorodia*, was attracted to compound **6**.

The European elm bark beetle, *Scolytus multistriatus*, is the principal vector of the Dutch elm disease pathogen, *Ceratocystis ulmi*. Declining elm trees are weakly attractive, but when the female beetles bore into the phloem-cambium region, they produce a potent aggregation pheromone that attracts males and females. This pheromone consists of two components, 4-methyl-3-heptanol (**9**) and α-multistriatin (**10**), secreted by the female, and one component, α-cubebene (**11**), produced by the tree (*11*); the three



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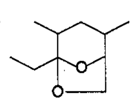

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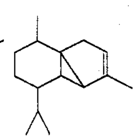

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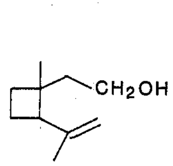
components constitute a synergistic pheromone.

The male cotton boll weevil, *Anthonomus grandis*, produces a four-component (**12** to **15**) synergistic pheromone,



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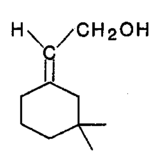

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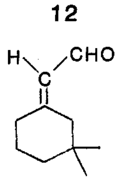

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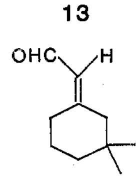

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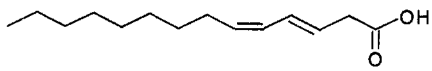
which aggregates males and females in the field (*12*).

Not all beetles use multicomponent pheromones. The sex excitant and attractant pheromone emitted by the female black carpet beetle, *Attagenus megatoma*, apparently consists of a single compound, megatomoic acid (**16**) (*13*).



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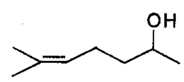
An ambrosia beetle in the Pacific Northwest (*Gnathotrichus sulcatus*) degrades logs and lumber by boring directly into the xylem. In this process the male releases sulcatol (**17**), which aggre-



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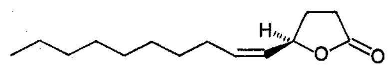
gates both sexes. However, neither enantiomer of **17** is attractive by itself; rather, a synergistic mixture of both enantiomers (over a rather broad range of ratios) is required. A closely related, sympatric species, *Gnathotrichus retusus*, produces and responds to only a single enantiomer of the same compound; the response is inhibited by the other enantiomer. We are thus furnished with an example of enantiomer-based interruption of attraction between sympatric species (*14*).

The pheromone of the Japanese beetle, *Popillia japonica*, consists of a single enantiomer, japonilure (**18**), and the ad-



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dition of even a few percent of the antipode diminishes the response (*15*).

In the case of other insects mentioned above that produce chiral compounds, the response is to only one of the enantiomers; the other isomer appears to be inert and does not interfere. Interpopulational differences and interspecific interactions have been demonstrated at the level of enantiomers (*14, 16*).

These few examples of pheromones provide evidence of the diversity, complexity, sensitivity, and specificity of such behavioral chemicals (*17*). One further problem in studying them is that the extract of a pheromone-emitting gland may not represent the actual airborne message perceived by the recipient, in which case collection of the airborne material may be the best procedure (*18*). Chemical communication in insects may be described as a language in which complex statements can be made with combinations of chemicals. The language has a vocabulary and syntax, and the message depends on the context: insects call and respond only at particular times under particular circumstances. A study of the languages forms the basis of a branch of taxonomy, chemosystematics (*19*).

Chemists and biologists have studied the molecular basis of many of the behavioral responses to pheromones. They have identified the compounds that evoke responses and have furnished remarkable tools for studying insect behavior. Let us now ask to what further uses these tools can be put. The communication code broken, it should be possible to mimic the original message in a false context and pervert normal behavior to self-destructive responses.

Pest Control with Pheromones

The concept of integrated pest management is beginning to take hold, but full implementation is conditional upon the values and thrust of society and on user acceptance. Can we forgo the desire for the quick fix and the need for short-term returns on investment? Can marketing strategies be devised? Will we support the basic studies needed? What values do we assign to environmental quality?

It is exciting to consider the part that pheromones (or semiochemicals in general) may play in integrated pest management, but it is sobering to assay the obstacles. Most of the participants in the effort to develop practical applications agree that the potential is there, and, in fact, small-scale, demonstrably successful applications are in use.

The first requirement is that the behavior of a particular insect pest be understood; unfortunately, the study of insect behavior languished for years while many applied entomologists sprayed and counted. Next, the chemist must define the chemical message at least completely enough for practical purposes. Third, the chemical compounds and an effective delivery system must be furnished, and detailed field studies must be carried out. Fourth, the delivery system must be approved (registered) by the Environmental Protection Agency. Fifth, industry must be furnished an incentive to become involved. Sixth, professionals must be educated in chemical ecology and technicians trained. Properly trained county agriculture extension agents could play an important role in the United States.

Can we decrease the use of a profitable, convenient though partially discredited tool for an approach that requires a sophisticated understanding of the target insect, that demands precise timing and uses small dosages, that may promise only partial success rather than the illusions of widespread extermination, and that cannot guarantee large concentrated profits? Will strategies be decided by competent professionals who are free of conflicts of interests and of the concept of panaceas? To repeat, insecticides probably cannot be abolished, at least for the near future, but rather should be relegated to an appropriate role within holistic programs despite their inherent incompatibility with the use of beneficial organisms. The difficult transition will make severe demands on administrators in governmental mission and regulatory agencies, and in industry.

Fig. 1. A pink bollworm (*Pectinophora gossypiella*) male moth is attracted to the synthetic female sex attractant (pheromone) evaporating from the open end of a hollow fiber dispenser. The response of the male moth to the pheromone often includes attempts to copulate with the dispenser. [Photo copyright, Albany International Corp. Taken by J. Running, Flagstaff, Arizona]

One of the encouraging developments is the recent tacit acknowledgment by the Environmental Protection Agency that, operationally, there is a vast difference between spraying kilograms per hectare of a liquid or solid, toxic, persistent, broad-spectrum pesticide to kill insects, and releasing minute amounts of a biodegradable, species-specific, natural product in the vapor phase to lure an insect to a trap or to disorient the mate-finding process. The agency proposes to consider pheromones as "biorational pesticides" and now has more realistic registration requirements. The purist may still argue that pheromones are behavioral compounds and that they are not pesticides (toxicants), sweetened though the term may be by "biorational."

Several recent reviews discuss the practical applications of pheromones (*20*), which can be categorized as follows:

1) Pheromones used in trapping insects for monitoring and survey. Insect populations can thus be estimated and new areas of infestation can be detected at a very early stage. Such applications of pheromones allow the use of insecticides only when needed.

2) Pheromones used as lures in circumscribed areas that are treated with insecticides, hormone analogs, or pathogens. Insects lured to the areas become coated or infected with the harmful substances that they then spread to the rest of the population.

3) Pheromones used in the mass trapping of insects for population suppression.

4) Pheromones used to permeate the air to disrupt mate-finding or aggregation, the end result being population suppression. Parapheromones (chemicals that mimic pheromones) or antipheromones (chemicals that interrupt responses) may also be used.

The use of pheromones would seem to be a remarkably safe procedure even under the most misguided management; at worst, no benefits would result and the effort would simply be wasted. However, since several pheromone components are also interspecific behavioral compounds (allelochemics), mass trapping in some cases may also trap predators or parasites. This undesirable possibility was circumvented in the *Ips typographus* trapping program by making the holes in the traps too small to admit the attracted predators. Sticky traps might be screened with a (nonsticky) mesh of the appropriate size. The selectivity of these devices would result in a beneficial increase in the local predator population.

The insecticide industry has been slow to embrace detection and control procedures that reduce sales of insecticides. In fact, the small amounts and diversity of compounds individually tailored for each insect species and the need for sophisticated techniques of application all mitigate against involvement in pheromones by the agrichemical industry as it is now structured. But when industry can no longer create demand, it will respond to the demands of an enlightened market. Attempts to commercialize pheromones have been undertaken by several small organizations and by small groups within larger companies with the result that the cost of pheromones is no longer a serious bar to large-scale tests. With the public sector carrying most of the burden of research, with increasing awareness by the public, and with increasing involvement by industry, momentum is slowly building. The caveat most often voiced by scientists is that exploitation of pheromones by industry may outrun the still primitive understanding of insect behavior, and a backlash by disillusioned users may result. Several industrial concerns are projecting a complete crop protection service.

Several companies are now producing pheromones. Albany International, for example, formulates the pheromone of the pink bollworm in hollow plastic fibers and has demonstrated mating disruption of this insect in cotton fields in the United States and South America (Fig. 1). The company also produces pheromones for controlling the western pine shoot borer and the European elm bark beetle. The Hercon Division of Health-Chem Corporation provides pheromone formulations in laminated dispensers that can be used for mass trapping of the gypsy moth and the Japanese beetle or disruption of the western pine shoot borer and the gypsy moth. This company also manufactures pheromones for mass trapping of the European elm bark beetle and for disruption of the pink bollworm.

Marketing to the general public was started recently by the J. T. Baker Chemical Co. with the introduction of baited traps for the Japanese beetle and baited traps for the gypsy moth to be used in conjunction with a spray of *Bacillus thuringiensis* spores to control the larvae. The bait in each case consists largely of a single enantiomer; in both cases, the antipode decreases trap catch.

Zoecon Corporation produces traps for use as survey and monitoring devices for a number of moth species, as well as a short-range attractant of the house fly which is marketed with a mixture of sugar and insecticide to control the insect in nonresidential areas. The company also produces traps for monitoring California red scale and San Jose scale in citrus orchards. Zoecon has impressive synthetic capabilities and is developing large-scale syntheses for several pheromones, in particular that of the Indian meal moth, *Plodia interpunctella*.

Bend Research, Inc., provides attractants for monitoring and survey for the codling moth, corn earworm, European corn borer, fruit flies, gypsy moth, and pink bollworm. Borregard Industries Ltd. (Norway), furnishes traps and pheromone components for trapping the spruce bark beetle, as well as pheromones for the codling moth, tobacco budworm, pink bollworm, and an ambrosia beetle, *Trypodendron lineatum*.

Other companies manufacturing pheromones include Plant Protection Division of ICI, Wolfson Unit of Chemical Ecology, and Oecos Ltd. Monitoring and Control Development, England; Celamerck, Hoechst, and Bayer, West Germany; TNO, Holland; Shin-Etsu Chemical Co. and Takeda Chemical Ind., Ltd., Japan.

Case Histories

Cotton. If insect pests on cotton crops could be controlled by alternatives to insecticides, a large proportion of the "insecticide problem" would vanish. Cotton is afflicted by several major primary pests and by secondary pests whose populations have increased as a result of massive applications of insecticides; approximately one-third of the insecticides produced worldwide are applied to cotton crops. The cost of sprays against the boll weevil *Anthonomus grandis* in the United States alone was estimated at $50 million in 1974.

Beginning in 1958, intensive efforts were directed against the boll weevil whose resistance to insecticides threatened the entire cotton industry. In 1962, the Boll Weevil Research Laboratory was built and a series of studies were begun that included more effective use of insecticides, mass rearing and sterilization of males for subsequent release, host-plant resistance, and pheromones. In 1968, it was concluded that the state-of-the-art with respect to integrated pest management justified a large-scale program of eradication experiments. As recounted by Perkins (*21*), the program apparently degenerated into a series of futile attempts to prove or disprove that "eradication" was not only theoretically possible but actually feasible with present technology. Nevertheless, the boll weevil pheromone was shown to be a valuable monitoring component of integrated control efforts, with trapping and disruption being feasible in populations of low density. The potential exists for a 60 to 70 percent reduction in insecticide use on a countywide basis if the concepts of integrated pest management, including the use of pheromones, are applied.

Of all attempts at population control with pheromones, several large-scale efforts directed against the pink bollworm *Pectinophora gossypiella* offer the most impressive documentation and economic justification. In 1980, Albany International treated a total of 35,000 hectares of cotton in the southwestern United States and South America. 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 . . ." (*22*). 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.

Forest and shade trees. Where valuable shade trees are affected by insects in populated areas, there is usually economic justification for intensive pest control. The gypsy moth, *Lymantria dispar*, because of its highly visible defoliation of trees in populated areas and its rapidity of spread, has been the target of intensive control efforts mainly by the U.S. Department of Agriculture. Survey and detection traps are useful for defining infested areas and especially for detecting new areas of infestation in early stages. For example, a recent gypsy moth infestation in the San Francisco Bay area was successfully controlled after early detection with pheromone traps. In the last year or two, improved formulations and a better understanding of insect behavior have resulted in effective mating reduction in low populations. Commercial availability of a pheromone formulation will permit mass trapping by the general public, but results may be difficult to interpret. The nun moth, *L. monacha*, in Europe is also susceptible to disruption by the same pheromone.

In 1970, an experiment was conducted to suppress a western pine beetle (*Dendroctonus brevicomis*) population within a moderately infested area of 65 km^2 at Bass Lake, California. Large, baited, sticky traps in a grid pattern captured approximately 750,000 beetles of both sexes, essentially the total population estimated for the area, and tree mortality dropped from 283 before the experiment to 83 in the following year. Tree mortality remained low for the next 4 years. However, on a larger scale in a heavily infested area (McCloud Flats, California), tree mortality was not apparently affected despite the trapping of 7 million beetles. The successful demonstration at Bass Lake notwithstanding, the economics of forest management probably will not justify use of pheromones for control of the western pine beetle. However, survey and detection traps may find use.

The larvae of the western pine shoot borer, *Eucosma sonomana*, mine the terminal shoot of ponderosa pine causing loss of tree growth. Disruption by pheromone formulation resulted in damage reduction by 76 to 88 percent in areas of 8 to 600 hectares. Economic factors may be favorable for use of the pheromone because extensive damage is caused by low populations over the well-defined areas of pine plantations.

Possibly the first commercial application of pheromone traps for pest control was initiated in 1975 by the Chemainus sawmill, British Columbia, Canada, to protect its timber and sawed lumber from the ambrosia beetle *Gnathotrichus sulcatus*. The traps are placed around the perimeter to trap beetles emerging within, and to intercept beetles from without. The procedure is justified on the basis of the prior investment in growing, surveying, harvesting, and sawing timber.

The smaller European elm bark beetle, *Scolytus multistriatus*, the vector of a phytotoxic fungus, has virtually eliminated the American elm as a shade tree throughout most of the United States. Pheromone traps have been widely used to determine the areas and extent of infestations and have been investigated as a population suppression device. They are very effective on perimeters of lightly or moderately infested groves, particularly if there are no heavily infested woodlots nearby and if infested wood is removed. To reduce woodlot infestations, low-value trees (trap trees) are killed with a sylvicide and baited; thereby, large numbers of beetles are attracted, but the broods do not survive. Results from large-scale attempts to reduce populations in heavily infested areas were inconclusive, however, despite the trapping of several million beetles. Nevertheless, an integrated approach using traps, trap trees, and removal of infested wood may succeed even in heavy infestations.

The spruce budworms *Choristoneura fumiferana* and *Choristoneura occidentalis* defoliate the coniferous forests of eastern and western Canada and the United States. Massive outbreaks have been countered with massive insecticide sprays, but the apparent need to continue such treatment for the indefinite future is not acceptable. Early warning systems of pheromone traps are in use, but control by trapping or disruption on a large scale is still in the future.

Undoubtedly the largest single attempt to control a pest by mass trapping was the joint Norway-Sweden project launched in 1979. After 3 years of drought that killed or weakened the trees, about 7 million spruce trees were killed by the spruce bark beetle, *Ips typographus*, in southern Norway in 1978–1979. Although biologists had misgivings that basic behavioral and population studies were incomplete, it was apparent that a catastrophic explosion in beetle population was at hand and drastic measures were needed. Therefore, Norway and Sweden involved more than 40,000 forest owners in the distribution and monitoring of about 1 million pheromone-baited traps throughout the infested forests. The total trap catch for 1979 was 2.9 billion beetles, and the estimated direct costs, not including manpower, was $23 million. In 1980, the program was repeated with some modifications, and the total number of beetles trapped in Norway alone was estimated at 4.5 billion. Tree mortality was still heavy, but even though the anticipated catastrophic outbreak did not occur, cause and effect cannot be assumed. As with other efforts, the best results were achieved in areas of low to moderate populations. Mass trapping does not afford protection in overmature stands after a heavy outbreak is under way, and recourse to harvesting may be the only choice.

Orchards and vineyards. In New York State, pheromone monitoring is an important component of the farm advisory pest management system. Savings in insecticide costs are reported to range up to 50 percent of the costs under the previously used spray regime. Direct population control with pheromones is not yet possible because of the large variety of insect pests on fruits in this region.

Throughout the apple and pear orchards of western Canada and the northwestern United States, only a few major pests need be contained. Sprays against the codling moth *Laspeyresia pomonella* are timed with the widespread use of pheromone traps. Mass trapping and mating disruption have also effected population control and reduced crop damage. Similar results for a variety of moths are reported throughout Europe, Japan, Australia, and New Zealand. In most cases, investigators caution that these procedures succeed best in areas of low insect population, but improved technology may give better results with denser populations.

Stored products. Small detection traps containing the pheromone of the khapra beetle, *Trogoderma granarium*, and an insecticide are now in use in a number of storage facilities and on ships as part of the quarantine procedure. The very high level of response makes early detection in a sparse population much more feasible than previous procedures. The recent breaches of quarantine procedures by the khapra beetle lend urgency to further use of the pheromone for monitoring and to further development of control by trapping or mating disruption. Four other *Trogoderma* species respond to the same pheromone. These beetles have been lured to baited traps that contained a pathogen that can be transmitted by contact with other beetles. Several moths (Indian meal moth, almond moth, and Angoumois grain moth) can be monitored and disrupted, but no large-scale demonstration of efficacy has been made.

Several general conclusions may be drawn from attempts to use pheromones as a component of pest control.

1) Survey and monitoring traps are becoming widely used and are very successful even though correlations between trap catches and the size of insect populations are not readily determined. Large reductions in the use of conventional insecticides have been achieved by using the monitoring information to mediate the spray schedule.

2) Suppression by trapping or disruption has been demonstrated in a number of cases for low-density populations, but attempts to control high-density populations have often 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 formulations, improper distribution of traps or of 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.

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The Essential Trace Elements

Walter Mertz

Summary. Essential trace elements are required by man in amounts ranging from 50 micrograms to 18 milligrams per day. Acting as catalytic or structural components of larger molecules, they have specific functions and are indispensable for life. Research during the past quarter of a century has identified as essential six trace elements whose functions were previously unknown. In addition to the long-known deficiencies of iron and iodine, signs of deficiency for chromium, copper, zinc, and selenium have been identified in free-living populations. Four trace elements were proved to be essential for two or more animal species during the past decade alone. Marginal or severe trace element imbalances can be considered risk factors for several diseases of public health importance, but proof of cause and effect relationships will depend on a more complete understanding of basic mechanisms of action and on better analytical procedures and functional tests to determine marginal trace element status in man.

The bulk of living matter consists of hydrogen, carbon, nitrogen, oxygen, and sulfur. The concentrations of these elements in biological matter can be expressed in grams per kilogram; they are required in gram amounts per day in humans. The macrominerals sodium, magnesium, phosphorus, chlorine, potassium, and calcium serve as structural components of tissues, as constituents of the body fluids, and are essential for the function of all cells. Their concentrations in living tissue and the adult human requirement are somewhat lower than those of the bulk elements, but still can be expressed as grams per kilogram and grams or fractions of a gram per day. The remaining elements of the periodic system occur in the organism in much lower concentrations and are expressed in terms of milligrams or micrograms per kilogram of tissue. Such concentrations were not easily quantified by the early analytical methods, hence the name "trace" elements (*1*).

Trace elements, which include all the naturally occurring elements in the periodic system except the bulk elements and macrominerals, are best classified in two categories: those elements whose essentiality has been established by accepted scientific standards and those for which proof of essentiality does not exist. Research during the past three decades has added molybdenum, selenium, chromium, nickel, vanadium, silicon, and arsenic to the list of essential elements. This suggests that additional elements could be proved essential by future research and the number of elements now accepted as essential should not be considered final.

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Essentiality, Dose, and Response

By the simplest definition, an essential element is one required for maintenance of life; its absence results in death of the organism. Severe deficiencies of an element that result in death are difficult to produce, particularly if the element is required in very low concentrations. A broader definition of essential elements has therefore been proposed and is widely accepted: An element is essential when a deficient intake consistently results in an impairment of a function from optimal to suboptimal and when supplementation with physiological levels of this element, but not of others, prevents or cures this impairment (*2*). Essentiality is generally acknowledged when it has been demonstrated by more than one independent investigator and in more than one animal species. By these criteria, the following trace elements are now considered essential in animals: silicon, vanadium, chromium, manganese, iron, cobalt, nickel, copper, zinc, arsenic, selenium, molybdenum, and iodine. Growth depression resulting from deficiency of fluorine and tin and growth stimulation following supplementation with these elements have been reported (*3*), but not yet confirmed. Nevertheless, fluorine can be considered essential on the basis of its demonstrated effect on dental health (*4*) (Fig. 1).

The degree to which a function is impaired in an animal with a deficiency is not related to the criterion of essentiality but depends on the degree to which

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