

Pest Management with Insect Sex Attractants and Other Behavior-Controlling Chemicals

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FOREWORD

The ACS SYMPOSIUM SERIES was founded in 1974 to provide a medium for publishing symposia quickly in book form. The format of the SERIES parallels that of the continuing ADVANCES IN CHEMISTRY SERIES except that in order to save time the papers are not typeset but are reproduced as they are submitted by the authors in camera-ready form. As a further means of saving time, the papers are not edited or reviewed except by the symposium chairman, who becomes editor of the book. Papers published in the ACS SYMPOSIUM SERIES are original contributions not published elsewhere in whole or major part and include reports of research as well as reviews since symposia may embrace both types of presentation.

PREFACE

In the past few years, scientists have registered notable progress in demonstrating the existence of some fundamental mechanisms that govern the behavior—and in many cases the survival—of important insect species. We know now that an insect's behavior is not dictated solely by instinct, but most often by chemical cues; in fact, the antennae of many responding insects are specially structured (probably down to the molecular level) to receive such signals, which then educe stereotyped behavior. Like diminutive robots, members of an insect species are programmed to respond in a precise manner to the appropriate stimulus.

Progress in this area has resulted largely from the spectacular advances in chemical instrumentation and the development of specialized techniques and devices that have facilitated the isolation and characterization of compounds at the microgram level. Chemicals potentially useful for manipulating the behavior of hundreds of insect species, including many of great economic significance, are now available, and reports on identifications and syntheses of such chemicals are becoming commonplace.

Exciting prospects involving these chemicals include the expansion of our knowledge of chemoreception and its effect on insect behavior and physiology, clarification of interactions of insects with other elements of their environment, elucidation of the role of these chemicals in genetic or evolutionary trends.

But interest in this area is not limited to the academic. Perhaps more intriguing are the prospects of utilizing nontoxic behavior chemicals to reach in among the many species populating a given area and single out for attack only injurious species. It is to the exploration of these prospects that this Symposium is dedicated. Rachel Carson in her book "Silent Spring" (1962) alluded to the use of behavior chemicals as one of the "creative approaches to the problem of sharing our earth with other creatures" and incidentally of minimizing thereby the use of pesticides and their side effects on non-target biota and the environment. But to bring matters up-to-date, the need for effective, economical, and safer means of insect suppression is greater now than ever in the past because the world population, now at an all-time high, is steadily increasing, and demands for food, fiber, and lumber are increasing concomitantly.

Some key questions are: How practical is this approach? What pitfalls are connected with the use of behavior chemicals? Where have they succeeded, and where have they failed? For the future, where are they apt to succeed or fail? How shall these chemicals be used in concert with other insect control agents? What are the registration requirements of the Environmental Protection Agency that must be met before behavior chemicals can be used for direct insect control? Will these regulations retard or accelerate the development and use of these chemicals?

To shed light on some of these questions and hopefully to accelerate further progress in upgrading the behavior chemicals to practical pest-control tools, we assembled some of the country's leading authorities to describe their experiences and to detail their views on the prospects of using behavior-controlling chemicals for the management of insect pests. Participants were chosen to illuminate latest practices, developments, and trends in the field. Hopefully, the revelation of gaps in our knowledge as well as differences in approach or methods will clarify the needs and directions of future research efforts.

The plethora of potentially valuable behavior chemicals that has recently been made available presages considerable activity in many diverse areas. Thus, the contents of this volume may appeal not only to chemists, biochemists, biologists, and entomologists but to insect control workers of all kinds, physiologists, animal behaviorists, and other workers interested in natural products and in the life sciences.

As an added feature of this volume, a comprehensive listing of insect behavior-controlling chemicals, many of which may be useful in pest management, has been added after the presentations. It was felt that much of the material being accumulated is losing a great deal of its value by being scattered throughout many volumes under different headings, and this listing (as well as this Symposium) would help bring together many of these diverse elements in one place. The references given should be invaluable in helping both the new and the veteran researcher keep abreast of the fast-developing field of chemical communication among insects.

The papers published in this volume (other than the listing of compounds) were originally presented at the Symposium on Prospects for Pest Management with Sex Attractants and Other Behavior-Controlling Chemicals at the 170th National Meeting of the American Chemical Society in Chicago, Illinois on August 26, 1975, under the auspices of the Pesticide Chemistry Division.

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Insects Generally Use Multicomponent Pheromones

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In 1964, Wright (1) suggested that multicomponent pheromones would be widely used because they could convey more information than a single compound; evolutionary selectivity would favor the organisms that had the better communication systems. Wright had little compunction in overriding the evidence reported prior to 1964 for single compounds in two moth species (the silkworm moth and the gypsy moth). But, in general, this proposal was ignored, and throughout the 1960s, a number of moths were reported to use single component pheromones.

What happened to lead so many investigators astray? Why was the "magic bullet" concept -- one insect, one specific compound -- so firmly implanted?

The story goes back to the heroic achievement by Butenandt's group, reported in 1959 (2): the isolation and identification of the chemical compound that elicited the sexual excitation response from the male silkworm moth; the work was done without benefit of modern instrumentation -- not even gas chromatography. The short-range bioassay used was entirely appropriate for a unique domesticated animal that had no field population. Unfortunately the title of the paper was "Über den Sexuallockstoff des Seiden-spinners....". And the term, "Sexuallockstoff", immediately became synonymous with "sex attractant", the material responsible for the ability of female moths to attract males over spectacular distances. Subsequent investigators uncritically adopted Butenandt's bioassay and succeeded in identifying a single compound that elicited short-range excitation from each moth. In almost every case, field trials based on a single compound were disappointing. In 1971, Silverstein (3) influenced by findings of multicomponent pheromones in several beetle species and by the repeated failures of field tests based on single compounds, decided that Wright was probably right.

¹Contribution No. 877 from Chemistry and Biology Research Institute.

A seminal paper in the area of moth pheromones was the report by Klun *et al.* (4), who demonstrated that addition of a small amount of trans-11-tetradecen-1-ol acetate to cis-11-tetradecen-1-ol acetate was necessary to trap the redbanded leafroller and the European corn borer in the field. The latter compound had been reported as the sex attractant of both insects (5,6) on the basis of isolation, electroantennogram responses, and successful field tests with the synthetic compound. Apparently these reports were based on the failure to separate the isomers by glc, and on the presence of just the "right" amount of the trans compound as an impurity in the synthetic material. In a reinvestigation, Roelofs (7) showed that several percent of the trans isomer was indeed present in the redbanded leafroller; furthermore, dodecyl acetate, which had been found empirically to enhance field catches, was also identified.

The identification by Jacobson *et al.* in 1970 (8) of 2 components of the sex pheromone of the southern armyworm, Spodoptera eridania, seems to be the first reported example of a multicomponent pheromone in moths. The compounds were cis-9-tetradecen-1-ol acetate and cis-9-trans-12-tetradecadien-1-ol acetate; each elicited the short-range excitation response in the laboratory, but both together were necessary for attraction in the field. It is interesting to note how many moth pheromones have been described as multicomponent in the past five years (Table I). In fact, a recent paper (9) by Persoons and Ritter is entitled "Binary sex pheromones in Tortricidae. Role of positional and geometric isomers". These authors suggest, on the basis of six species studied, that "in this family of insects, the feature of binary sex pheromones may well turn out to be a general one". They further suggest that "several earlier reports may need reconsideration". Nesbitt *et al.* recently reported (10) that the sex pheromone of the red bollworm moth consists of five components. Hendry *et al.* described (11) the oak leafroller pheromone as a "complex mixture of chemical signals".

Beetle pheromones (see Table II), from the beginning, presented a more complex picture. The very first report (12) described the aggregating pheromone produced by the male bark beetle, Ips paraconfusus, as a mixture of three terpene alcohols. None of the compounds individually is effective in the field, but the ternary mixture attracts both males and females in the field, mimicking the effect of a beetle infested tree. The aggregating pheromone of the western pine beetle, Dendroctonus brevicornis, consists of two bicyclic ketals, one produced by the female and one by the male, and a terpene hydrocarbon component produced by the host tree (13-18). The aggregating pheromone of the smaller European elm bark beetle, Scolytus multistriatus, consists of a bicyclic ketal and an alcohol produced by the female, and a terpene hydrocarbon component produced by the host tree (19).

Interestingly, the insect-produced components are found in the hindguts of all species of Ips and Dendroctonus examined, whereas this does not seem to be the case for the single species in the genus Scolytus examined to date (19). The male boll weevil, Anthonomus grandis, produces a 4-component aggregating pheromone (20) consisting of two terpene alcohols and two terpene aldehydes. Again, the pheromone components were isolated from fecal pellets.

In the coleopteran family Dermestidae (which includes many serious pests of stored food products), we can cite several spectacular examples of multicomponent sex attractants. It has been shown that there is a great deal of cross attractiveness among several species of the genus Trogoderma (21,22). The chemical basis of cross attraction among four species (23) is shown in Table III. Of the six components shared by the four species, 14-methyl-8-hexadecenal is by far the most potent -- i.e., effective at lowest concentration. This compound was completely missed in previous isolation studies of T. inclusum (24) and T. glabrum (25), which were done on extracts of macerated beetles. Despite this cross attraction, each species can readily distinguish its own pheromone, and is reproductively isolated by this preference -- and presumably by other factors. For example, each species has a threshold response to its own geometric isomer of 14-methyl-8-hexadecenal that is about 1000 times more sensitive than its threshold response to the other isomer (26). Greenblatt et al. (26) carried out a detailed study of the mating behavior of T. glabrum and showed how the individual components mediated the various phases of the total behavior.

Some speculation might be in order on the reasons for the failure to identify the most important pheromone component in the earlier studies of T. inclusum (24) and T. glabrum (25). Two possibilities are suggested. In these studies, the whole insect was macerated with a solvent in a Waring blender; it is possible that tissue enzymes may have selectively destroyed one of the components. Alternatively and possibly more convincingly, one component may be produced continuously in very small amounts from a precursor; this component might not be detected in a direct extraction of the insect, but it would accumulate during the aeration process. At least four other similar examples have appeared in the literature: Shearer and Boch (27) observed citral in the Nassanoff gland pheromone only when a secretion was allowed to stand overnight at room temperature. Bierl et al. (28) detected only minute amounts of the active component (an epoxide) and much larger amounts of the apparent precursor (an olefin) in the extract of abdominal tips of the gypsy moth. Hill et al. (29) identified an aldehyde as a major pheromone component by aeration of female orange tortrix moths, but could detect only minute amounts in the extract of abdominal tips. Weatherston et al. (30) could not identify the sex attractant compound of the spruce

budworm by extraction of abdominal tips, but the compound did accumulate on the glass walls of the containers; this compound was also an aldehyde.

In the Hymenoptera, Boch *et al.* (31) have shown that the pheromone released by the queen honey bee to stabilize swarms of workers does not consist of (E)-9-oxodec-2-enoic acid alone. Methyl 4-hydroxybenzoate, isolated from queen extract, synergizes the swarm attraction of the oxo acid and there are yet other active components in the extract to be identified (Young *et al.*, unpublished). Mediterranean and Caribbean fruit flies use multi-component sex pheromones (32,33). There is no need here to document further the prevalence of multicomponent pheromones in the complex societies of ants and bees. Several excellent, recent reviews are available (34-36).

We now raise the question: "Are there really any single component pheromones?" We cannot say. A number have been reported, and in some cases, a conscious effort was made to search for other components, but, of course, it is difficult to show that something may be missing. The only satisfactory criterion is to show that the component elicits the same total response as does the test animal at the same concentration. But how does one compare concentrations? An extract, as mentioned above, does not necessarily contain detectable amounts of all of the active components. The *Trogoderma* studies (24,25) showed that the compounds identified from the extract were equivalent in activity to the total extract, but the most important component was, in fact, missing from the extract. Until recent studies based on aeration, we could be satisfied by a comparison with the extract of the whole insect or a portion thereof. No longer! A number of reinvestigations based on aeration would seem to be in order. But in some cases, there remain technical difficulties. For example, Sonenshine *et al.* (37,38) reported that the sex pheromone of two species of ticks (we include this non-insect) was 2,6-dichlorophenol. No other fraction of the extract elicited a response. The investigators, conscious of the pitfall, attempted aeration of the ticks feeding on the body of a rabbit, but they were defeated by the mechanical difficulties involved in aerating thousands of ticks, not to mention the overwhelming concentration of rabbit odor. One mitigating feature of this study might be cited: the complex ritual of the sex response elicited by a feeding female from a male that has been feeding on the same animal was reproduced precisely by very low concentrations of authentic 2,6-dichlorophenol.

The aeration technique is ideally suited to insects such as adult dermestid beetles and moths, which do not feed and which go through a periodic "calling" performance. It can be used on bark and ambrosia beetles, but the components of the aggregation pheromone must be isolated from the complex mixture of host

compounds. A good laboratory bioassay becomes the sine qua non, but one still runs the risk of discrepancies between the laboratory response and field behavior. One feature of absorption on Porapak should be noted: It is not a very good absorbent for small polar molecules, but, of course, it is this very feature that permits passage of water. Furthermore, the aerated insects, container and contents should be investigated for the presence of active components of low volatility.

We have talked about single components without further definition, but an additional refinement remains. Many natural products are chiral compounds, but until recently the question of enantiomeric purity has been generally ignored. In the first place, it is frequently difficult to isolate enough material to obtain an accurate optical rotation. Secondly, two tacit assumptions prevail: chiral natural products are either one enantiomer or the other, and it probably makes little difference in the communication system. The above difficulty has been overcome with the advent of chiral shift reagents and chiral derivatizing agents, and of pulsed NMR; determinations of optical purity are feasible in many cases at the level of about 50 micrograms (39,40). The tacit assumptions have been destroyed by several findings of the presence of both enantiomers in pheromones, and by reports that at least several insects can discriminate between enantiomers. Riley and Silverstein (41) showed that the leaf-cutting ants, Atta texana and A. cephalotes respond to a lower concentration of the naturally occurring alarm pheromone, (S)-(+)-4-methyl-3-heptanone, than of its enantiomer. Kafka et al. (42) and Lensky and Blum (43) conditioned honeybees to discriminate between enantiomers, which, however, were not part of the natural communication system of the test insect. Mori (44,45) synthesized the enantiomers of exo-brevicomin and frontalin, pheromone components of the western and southern pine beetles (13-18). A determination was made of the enantiomeric composition of these components produced by the boring insect (40). exo-Brevicomin is present in the western pine beetle, and only in the (R)-(+ form. Laboratory bioassays showed that the beetles responded more strongly to (R)-(+ exo-brevicomin than to its enantiomer when these enantiomers were tested in combination with myrcene (the host component) and racemic frontalin (D. L. Wood and L. E. Browne private communication). The frontalin present in the southern pine beetle is approximately 85% (S)-(-)/15% (R)-(+ (40). Ipsdienol from Ips paraconfusus is 90% (+)/10% (-). California and Idaho populations of Ips pini contain the (-) enantiomer, whereas the New York population contain a 65% (+)/35% (-) mixture. Seudenol from the Douglas fir beetle is a 50:50 mixture (39). 4-Methyl-3-heptanol from the elm bark beetle consists of a single enantiomer out of four possible enantiomeric

structures (39).

Thus a description of ipsenol, ipsdienol, sulcatol, trans-verbenol, seudenol, 4-methyl-3-heptanol, 4-methyl-3-heptanone, exo-brevicomín, frontalín, or multistriatin as a single compound would be valid only in a world devoid of chirality. A complete identification of a chiral pheromone should therefore include a statement of enantiomeric composition and a description of the absolute configuration of the chiral center(s).

In summary, communications in the insect world are a good deal more complex than was thought by the early investigators. This statement is probably true of most natural phenomena despite the common misconception that Occam's Razor demands simplistic answers.

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Table I. Lepidoptera reported having multicomponent pheromones

Species (Common name)	Pheromones (Ratio)	Bioassay ^a	References ^b
ARCTIIDAE			
<u>Utetheisa lotrix</u> (Cramer)	$\frac{1}{2} + \frac{2}{2}$ (?)	F ₀	1
DANAIDAE			
<u>Amauris niavius</u> Linnaeus	$\frac{3}{2} + \frac{4}{2}$ (?)	F ₀	2
<u>Danaus affinis affinis</u> Fabricius	$\frac{2}{2} + \frac{3}{2}$ (?)	F ₀	3
<u>D. a. albistriga</u>	$\frac{2}{2} + \frac{3}{2}$ (?)	F ₀	4
<u>D. chrysippus</u> Linnaeus (African monarch butterfly)	$\frac{3}{2} + \frac{5}{2}$ (?)	F ₀	5
<u>D. gilippus berenice</u> (Cramer) (queen butterfly)	$\frac{3}{2} + \frac{6}{2}$ (?)	F ₁	6
<u>D. hamatus hamatus</u> (MacL.)	$\frac{1}{2} + \frac{3}{2}$ (?)	F ₀	3
<u>D. h. moderatus</u> (Butler)	$\frac{1}{2} + \frac{3}{2}$ (?)	F ₀	4
<u>D. plexippus</u> Linnaeus (monarch butterfly)	$\frac{7}{2} + \frac{8}{2}$ (?)	F ₀	7,8
<u>Lycorea ceres ceres</u> Cramer	$\frac{1}{2} + C_{16}OAc + Z^{11}C_{18}OAc$ (?)	F ₀	9
GELECHIIDAE			
<u>Pectinophora gossypiella</u> (Saunders) (pink bollworm moth)	$Z^7Z^{11}C_{16}OAc + Z^7E^{11}C_{16}OAc$ (1:1)	F ₁	10
"	$Z^7Z^{11}C_{16}OAc + Z^7E^{11}C_{16}OAc$ (1:1)	F ₂	11
"	$\frac{9}{2} + \frac{10}{2} + Z^7C_{16}OH^e$ (?)	F ₁	12,13
NOCTUIDAE			
<u>Diparopsis castanea</u> Hmps. (red bollworm moth)	$C_{12}OAc + E^9C_{12}OAc + \Delta^{11}C_{12}OAc +$ $E^9\Delta^{11}C_{12}OAc + Z^9\Delta^{11}C_{12}OAc$ (?)	F ₁	14.
"	$\Delta^{11}C_{12}OAc + E^9\Delta^{11}C_{12}OAc + Z^9\Delta^{11}C_{12}OAc$ (?:4:1) plus $C_{12}OAc + E^9C_{12}OAc$ whose function is not clear.	F ₁	15

Table I. cont'd.

Species (Common name)	Pheromones (Ratio)	Bioassay ^a	References ^b
<u>Heliothis virescens</u> Fabricius (tobacco hornworm moth)	$Z^9C_{14}CHO + Z^9C_{16}CHO$ ($C_{14} < C_{16}$) ^f	F ₁	16
<u>Mamestra configurata</u> (Wlk.) (bertha armyworm moth)	$Z^{11}C_{16}OAc + E^{11}C_{16}OAc^g$ (85:15)	L	17
<u>Spodoptera eridania</u> (Cramer) (southern armyworm moth)	$Z^9C_{14}OAc + Z^9E^{12}C_{14}OAc$ (?)	L	18
"	" (1:1)	F ₁	19
<u>S. exempta</u> (Wlk.) (armyworm moth)	$Z^9C_{14}OAc + Z^9E^{12}C_{14}OAc$ (Z > ZE) ^f	L	20
<u>S. littoralis</u> Fabricius (cotton leafworm moth)	$Z^9E^{11}C_{14}OAc + Z^9E^{12}C_{14}OAc$ (~ 10:1)	L	21
"	$C_{14}OAc + Z^9C_{14}OAc + E^{11}C_{14}OAc +$ $Z^9E^{11}C_{14}OAc$ (?)	F ₁	14
"	$Z^9E^{11}C_{14}OAc$	F ₂	22,23
<u>S. litura</u> Fabricius	$Z^9E^{11}C_{14}OAc + Z^9E^{12}C_{14}OAc$ (?)	L	24
"	" (9:1)	F ₁	25
PYRALIDAE			
<u>Achroia grisella</u> (Fabricius) (lesser wax moth)	$C_{11}CHO + Z^{11}C_{13}CHO$ (10:1)	L	26

Table I. cont'd.

Species (Common name)	Pheromones (Ratio)	Bioassay ^a	References ^b
<u>Cadra cautella</u> (Walker) (almond moth)	Z ⁹ E ¹² C ₁₄ OAc + unident.	F ₁	27
"	Z ⁹ C ₁₄ OAc + Z ⁹ E ¹² C ₁₄ OAc + unident.	L	28
<u>Ephestia elutella</u> (Huebner) (tobacco moth)	Z ⁹ E ¹² C ₁₄ OAc + unident.	L	29
<u>Galleria mellonella</u> (Linnaeus) (greater wax moth)	C ₉ CHO + C ₁₀ CHO ^h (?)	L	30
<u>Ostrinia nubilalis</u> (Huebner) (France) (European cornborer moth)	Z ¹¹ C ₁₄ OAc + E ¹¹ C ₁₄ OAc (96:4)	F ₂	31
" (Iowa, Quebec)	" (96:4)	F ₂	32,33
" (New York)	" (~3:97)	F ₂	32,34,35
" (Pennsylvania)	" (97:3 and 2:98)	F ₂	36
<u>O. obumbratalis</u> (Lederer) (smartweed borer moth)	Z ¹¹ C ₁₄ OAc + E ¹¹ C ₁₄ OAc (1:1)	F ₂	32
<u>Plodia interpunctella</u> (Huebner) (Indian meal moth)	Z ⁹ E ¹² C ₁₄ OAc + unident.	L	37
<u>Pyrausta purpuralis</u> Linnaeus	Z ¹¹ C ₁₄ OAc + E ¹¹ C ₁₄ OAc (4:96)	F ₂	31
TORTRICIDAE			
<u>Adoxophyes fasciata</u> Walsingham (smaller tea tortrix moth)	Z ⁹ C ₁₄ OAc + Z ¹¹ C ₁₄ OAc ¹ (4:1)	F ₁	38
<u>A. orana</u> Fischer von Roeslerstamm (summerfruit tortrix moth)	Z ⁹ C ₁₄ OAc + Z ¹¹ C ₁₄ OAc (?)	F ₁	39,40

Table 1. cont'd.

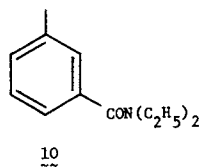
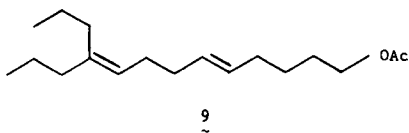
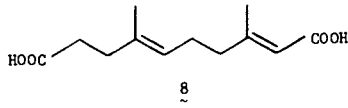
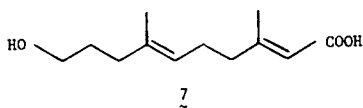
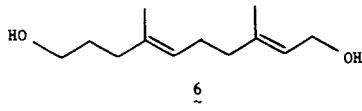
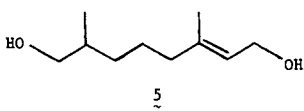
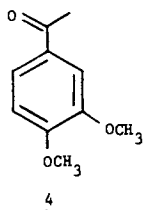
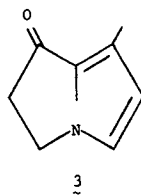
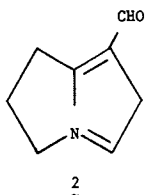
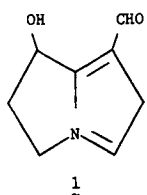
Species (Common name)	Pheromones (Ratio)	Bioassay ^a	References ^b
<u>A. orana</u> Fischer von Roeslerstamm (summerfruit tortrix moth)	Z ⁹ C ₁₄ OAc + Z ¹¹ C ₁₄ OAc (9:1)	F ₁	41
"	" (9:1)	F ₂	42,43
"	" (9:1)	F ₃	44-46
<u>Archips argyrospilus</u> (Walker) (fruit tree leafroller moth)	Z ¹¹ C ₁₄ OAc + C ₁₂ OAc ^e (1:4)	F ₂	47
"	Z ¹¹ C ₁₄ OAc + E ¹¹ C ₁₄ OAc (7:3) Z ¹¹ C ₁₄ OH + E ¹¹ C ₁₄ OH + C ₁₂ OAc also observed but not attractive	F ₂	48
<u>A. podana</u> (Scop.) (fruit tree tortrix moth)	Z ¹¹ C ₁₄ OAc + E ¹¹ C ₁₄ OAc (1:1)	F ₂	46,49
<u>A. rosanus</u> (Linnaeus)	Z ¹¹ C ₁₄ OAc + Z ¹¹ C ₁₄ OH ¹ (2:3)	F ₁	50
<u>A. semiferanus</u> Walker (oak leaf roller moth)	mixt. Δ ²⁻¹² C ₁₄ OAc all Z cmpds tested were attractive	F ₁	51
<u>Argyrotaenia velutinana</u> (Walker) (redbanded leafroller moth)	Z ¹¹ C ₁₄ OAc + E ¹¹ C ₁₄ OAc (92:8)	F ₂	32
"	" + C ₁₂ OAc ^e	F ₃	52,53
<u>Clepsia melaleucana</u>	Z ¹¹ C ₁₄ OAc + Z ¹¹ C ₁₄ OH ¹ (1:1)	F ₁	54,55

Table 1. cont'd.

Species (Common name)	Pheromones (Ratio)	Bioassay ^a	References ^b
<u>C. spectrana</u> (Treitschke)	Z ⁹ C ₁₄ OAc + Z ¹¹ C ₁₄ OAc (1:4)	F ₁	41,46
<u>Grapholitha moleata</u> (Busck) (oriental fruit moth)	Z ⁸ C ₁₂ OAc + E ⁸ C ₁₂ OAc + C ₁₂ OH (~97:3:?)	F ₂	56-59
<u>G. prunivora</u> (Walsh) (lesser appleworm moth)	Z ⁸ C ₁₂ OAc + E ⁸ C ₁₂ OAc ^e (98:2)	F ₂	58,59
<u>Gretchena bolliana</u> (Slingerland) (pecan bud moth)	Z ⁸ C ₁₂ OAc + E ⁸ C ₁₂ OAc + C ₁₂ OH (93:7:100)	F ₂	60
<u>Hedya chionosema</u> Zeller	E ⁸ C ₁₂ OAc + E ⁸ C ₁₂ OH ^j (?)	F ₁	54,55
<u>Laspeyresia pomonella</u> (Linnaeus) (codling moth)	7 unident. cmpds	L	61
<u>Platynota idaeusalis</u> Walker (tufted apple budworm moth)	E ¹¹ C ₁₄ OAc + E ¹¹ C ₁₄ OH (~1:1)	F ₂	62,63
<u>P. stultana</u> (Walsingham) (omnivorous leafroller)	Z ¹¹ C ₁₄ OAc + E ¹¹ C ₁₄ OAc (6:94) plus smaller amts Z ¹¹ C ₁₄ OH + E ¹¹ C ₁₄ OAc (~1:10). C ₁₄ OAc + C ₁₄ OH also present.	F ₂	64,65
<u>Rhyacionia frustana</u> Constock (Nantucket pine tip moth)	at least 2 unident. cmpds likely	F ₁	66

- a F_0 , F_1 , F_2 , and F_3 refer to no, preliminary, moderate, and extensive field testing, respectively, of pheromones or attractants. L refers to laboratory testing only.
- b References for Table I are listed at the end of this table.
- c Structures of numbered compounds are given in Figure 1.
- d Z or E refer to the \underline{Z} or \underline{E} configuration about a double bond, followed by the position number. C refers to the length of the straight carbon chain. OAc, OH, or CHO refer to an acetate, hydroxyl, or carboxaldehyde functionality, respectively, at carbon number one. Thus $Z^{11}C_{18}OAc$ means (\underline{Z})-11-octadecen-1-ol acetate.
- e This compound is not a natural component and acts as a synergist.
- f Optimum ratio not established.
- g This compound was not observed as a natural component; however, its presence was not excluded.
- h Both compounds act as excitants rather than attractants.
- i Interestingly, if the two components are presented sequentially (even within a few seconds), the male response is inhibited (67).
- j Both compounds observed to be attractants. They have not been identified from this insect.

Table I. cont'd.



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Table II. Coleoptera reported having multicomponent pheromones^a

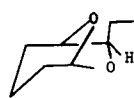
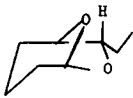
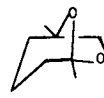
Species (Common name)	Compounds Isolated ^b	References ^c		
		Identification	Bioassay	
			Laboratory	Field
CURCULIONIDAE				
<u>Anthonomus grandis</u> Boheman (boll weevil)	Ga, Gb, Gc, Gd	1-3	1	4,5
<u>Curculio caryae</u> (Horn) (pecan weevil)	many volatiles ^d	6		6
<u>Rhabdoscelus obscurus</u> Boisduval	Ga, Gb, Gc, Gd ^e			7
DERMESTIDAE				
<u>Trogoderma</u> spp. see Table III				
ELATERIDAE				
<u>Limonium canus</u> LeConte (Pacific Coast wireworm beetle)	hexanoic acid + unsat branched C ₁₀ acid	8	8	
SCOLYTIIDAE				
<u>Dendroctonus brevicomis</u> LeConte (western pine beetle)	nB, xB, F, Mo, Pc, tP, V, cV, tV, 1, 2	9-15	16	11,17-23
<u>D. frontalis</u> Zimmerman (southern pine beetle)	nB, F, aH, bH, L, Ma, Mo, Pc, Pg, mP, tP, V, cV, tV ^d	10-13,15 24-29	27,30,31	10,11,24 27-29 32,33
<u>D. jeffreyi</u> Hopkins (Jeffrey pine beetle)	B, V, cV, tV	11		11
<u>D. ponderosa</u> Hopkins (mountain pine beetle)	nB, xB, F, Mc, V, cV, tV, 2	11,27,34	27	11,27,35-37
<u>D. pseudotsugae</u> Hopkins (Douglas fir beetle)	E, F, Mc, Sd, V, tV, 3, 4	38-42	38,39,43	39-41,43-53
<u>D. rufipennis</u> (Kirby) (spruce bark beetle)	Mc ^e			52,54
<u>D. valens</u> LeConte (red turpentine beetle)	Id, Mo, cP, tP, Pc ^d , cV, tV	13		
<u>Gnathotrichus sulcatus</u>	Sc	42,55		42,55
<u>Ips acuminatus</u> Gyll.	I, Id ^d	56		

Table II. cont'd.

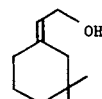
Species (Common name)	Compounds Isolated ^b	References ^c		
		Identification	Bioassay	
			Laboratory	Field
<u>I. avulsus</u> Eichhoff	Id, cV, tV	56-58		57
<u>I. bonansea</u> i Hopkins	Id, cV, tV ^d	56		
<u>I. calligraphus</u> Germar	I, Id, cV, tV	56-58		57
<u>I. confusus</u> LeConte	I, Id, V, cV, tV	59	59	
<u>I. cribricollis</u> Eichhoff	I, Id ^d	56		
<u>I. duplicatus</u> (Sahlberg)	Id	60		60
<u>I. grandicollis</u> Eichhoff	F, I, cV, tV, 2,6	56,58,61		61,62
<u>I. integer</u> Eichhoff	Id, cV, tV ^d	56		
<u>I. knausi</u> Swaine	Id, cV, tV ^d	56		
<u>I. latidens</u> LeConte	I, tV ^e			63
<u>I. paraconfusus</u> Lanier	I, Id, L, tV, cV, X	42,56,58 64,65	63	63,66
<u>I. pini</u> Say	Id, L, tV, cV	42,56,65		67
<u>I. sexdentatus</u> Boerner	I, Id	56		68
<u>I. typographus</u> Linnaeus	I, Id, cV, tV, 3-6	56		69
<u>Orthotomicus erosus</u> Woll.	c or tV, v ^e 1,2,4,5			70
<u>Scolytus multistriatus</u> Marsham (smaller European elm bark beetle)	Ms, Mh, 7	15,42,71		71
TENEBRIONIDAE				
<u>Tribolium confusum</u> Jacq. du Val (confused flour beetle)	1-pentadecene 1-heptadecene n-heptadecane	72	72	

- a In many cases, the beetles use some compounds to elicit a specific response at one stage of their life cycle and other compounds at another stage. In only a few instances have the responsible chemicals been correlated with their exact functions. Thus many of the references cited here give only fragmentary and sometimes conflicting views as to what is taking place in nature.
- b Lettered and numbered compounds have been identified from the insect and host, respectively. Structures are given in Figure 2 and Figure 3.
- c References for Table II are listed at the end of the table.
- d These compounds have been identified from the insect; however, their functions as pheromones have not been established.
- e Although these compounds are attractive, they have not been identified from this species.
- f Exists as a 65/35 mixture of the (S)-(+) and (R)-(-) enantiomers.

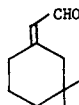
TABLE II. COMPOUNDS IDENTIFIED

nB
endo-BrevicomminxB
exo-BrevicomminE
EthanolF
Frontalin

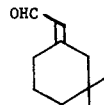
Ga



Gb



Gc



Gd

Ga-d constitute Grandlure

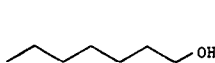
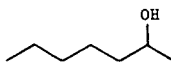
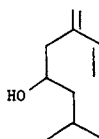
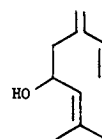
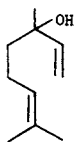
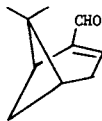
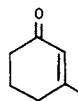
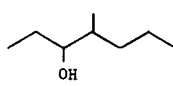
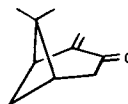
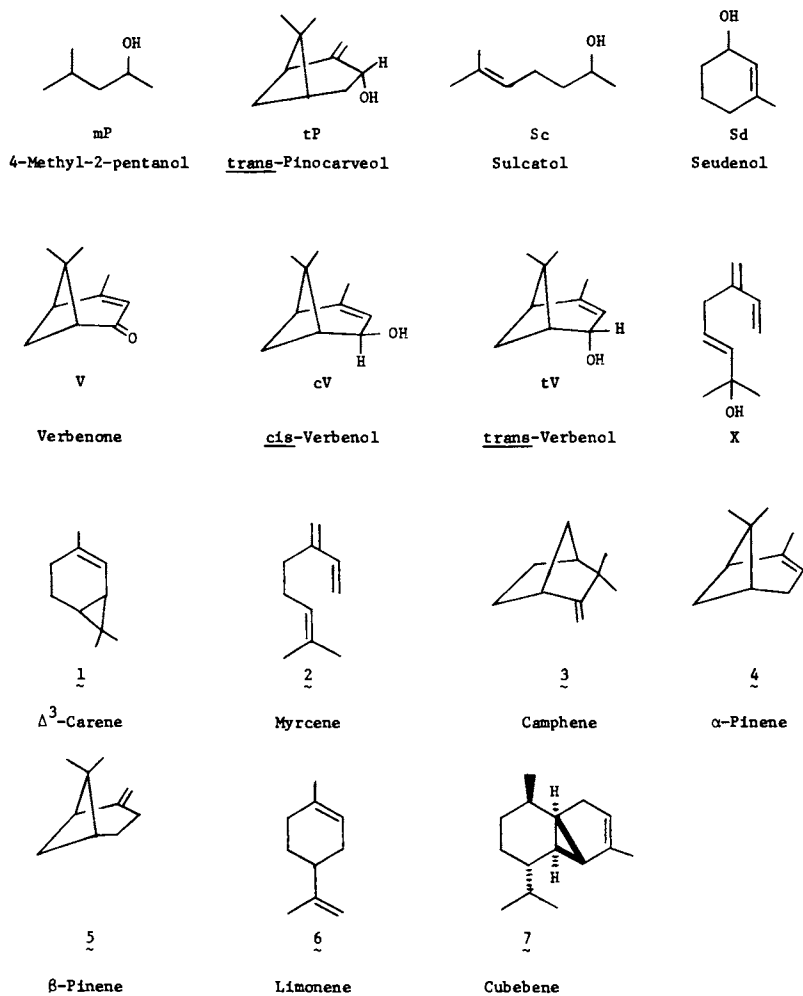
aH
1-HeptanolbH
2-HeptanolI
IpsenolId
IpsdienolL
LinaloolMa
MyrtenalMc
3-Methyl-2-cyclohexenoneMo
MyrtenolMs
MultistriatinMh
4-Methyl-3-heptanolPc
PinocarvonePe
1-Phenylethanol

Table II. cont'd.



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TABLE III
 PHEROMONE COMPONENTS OF TRIGGODERMA SPECIES (NG/BEETLE/DAY)
 (AERATION)

COMPONENT SPECIES	CAPROIC ACID	γ -CAPROLACTONE	14-ME-8- HEXADECENAL	ME 7-HEXA- DECENOATE	ME 14-ME- 8-HEXADECENOATE	14-ME-8- HEXADECENOL
I. <u>VARIABLE</u>	ABSENT	15.1	35.66 (Z)	MINUTE AMOUNT	< .03	< .04 (Z)
I. <u>INCLUSUM</u>	ABSENT	ABSENT	1.65, 2.35 (Z)	MINUTE AMOUNT?	0.39 (Z)	< .03 (Z)
I. <u>GLABRUM</u>	9.32	7.74	28.3 (E)	< 0.031 (Z)	< .02 (E)	< .02 (E)
I. <u>GRANARIUM</u> ^A	2.98	1.83	0.42, 1.64 2.34 (Z)	< 0.01	0.02	\leq 0.01

A. ADDITIONAL COMPONENT: P-1,8-MENTHADIENE

2

Utilization of the Boll Weevil Pheromone for Insect Control

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USDA, BWRL, ARS, So. Region, Miss. State, Ms. 39762

The boll weevil, Anthonomus grandis Boheman, was introduced from Mexico into the United States (near Brownsville, Texas) about 1892 (1). "Figure 1". By 1922 the pest had spread into cotton-growing areas of the United States from the eastern two-thirds of Texas and Oklahoma to the Atlantic Ocean. Its recent extension into west Texas now threatens cotton in New Mexico, Northwestern Mexico, Arizona and California. As early as 1895, recognition of the tremendous damage caused by this insect was noted, and Townsend (2) suggested that cotton growing be terminated in the region then infested and that a cotton-free zone be maintained along the Rio Grande River bordering Mexico. Several other entomologists studied and suggested ways to control the boll weevil. Howard (3) reported on the use of and lack of response to light traps. Malley (4) studied the use of poisons for weevil control as well as the use of cotton as trap plants. An act was passed by the Texas legislature in 1903 offering \$50,000 as a cash reward for a practical way to control the boll weevil. Sanderson (5) reported that hand picking of infested squares had been tried and was meeting with little success. "Figure 2".

Hunter (6) made the following statement: "It is concluded that there is not even a remote possibility that the boll weevil will be eradicated." Since that time, numerous methods of control have been tested and reported, 71 years have elapsed, and the boll weevil still has not been eradicated. From 1917 until the late 1940's the most effective method of control was dusting with calcium arsenate (7)(8). The development of DDT and other chlorinated hydrocarbons during World War II made a completely new group of insecticides available for controlling many insect pests including the boll weevil (9). However, in 1954 scientists in Louisiana reported that boll weevils were becoming resistant to the chlorinated hydrocarbons (10), and within two years resistance was widespread throughout the Cotton Belt.

The organophosphate insecticides have been successfully used since then to control boll weevils without resistance problems. However, \$70 million is spent annually for boll weevil control,

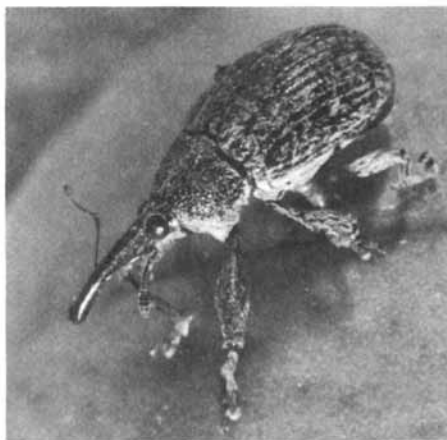


Figure 1.

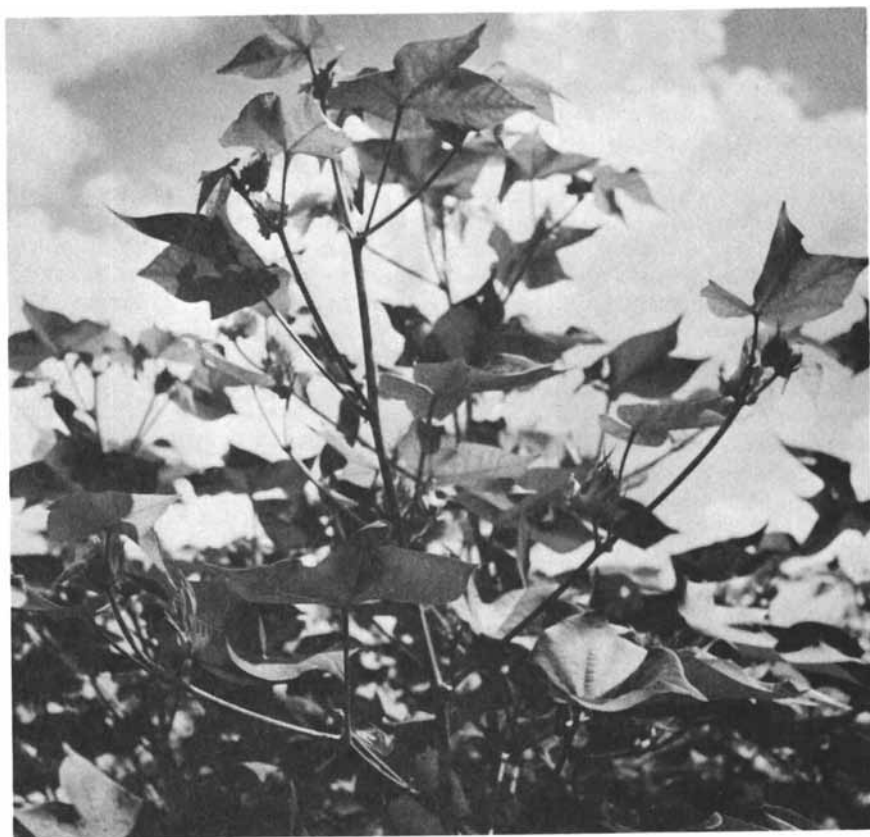


Figure 2.

and the pest still causes an estimated \$200 million in crop losses each year (11)(12). In recent years, these figures may have increased by 50% because of inflation, even with 10-20% less cotton grown.

More than three-fourths of all insect losses to cotton in the United States have been attributed to the boll weevil. It is generally agreed that cotton cannot be profitably grown in areas where the insect cannot be controlled.

Coker (13) estimated that 64,877,000 bales of cotton and 27,917,000 tons of cottonseed valued at \$7,680,000,000 were destroyed by the weevil from 1909 to 1954. Approximately one-third of the insecticide used for agriculture in the United States is required for boll weevil control (14).

In recent years, the cotton industry has been confronted with major competition from the synthetic fiber industry, which has penetrated markets that historically have belonged to American cotton producers. Competition is also felt from foreign cottons. In order to maintain cotton in a competitive position, the United States Congress has provided relief in two areas. (1) From the early 1950's until 1973, growers were subsidized to the extent of approximately \$0.10 per pound, which allowed them to compete with foreign cotton that sold for approximately \$0.20 per pound until 1970-2. However, Congress no longer provides price supports, and the current domestic price of about \$0.45 per pound (June 1975) is also the world price. (2) Research was intensified approximately 15 years ago to improve yields of cotton and to decrease costs of production. One part of this program has been an effort to control the boll weevil while decreasing the dependence on insecticides. Another part has involved eradicating the insect from the United States. Funds were provided to intensify research at existing facilities and for the construction and staffing of a larger central laboratory at State College (now Miss. State), Mississippi. Since then, the technology for an integrated effort to eliminate the boll weevil has been developed by scientists at this and other laboratories. This report describes work leading to the identification, synthesis, and utilization of the boll weevil pheromone (common name: grandlure for *A. grandis* Boh.) as an integral part of an attempt to eliminate the boll weevil from the Cotton Belt.

Biology of the Boll Weevil Pheromone:

In the earliest record of boll weevil mating, Hunter and Hinds (1) concluded that females were not attractive to males and that ". . . instead of seeking widely for the females, the males are content to wait for them to come their way." It was not until 1962 that Cross and Mitchell (15), confirmed by Keller et al. (16), showed conclusively that the male boll weevil produces a wind-borne sex attractant (pheromone) that is attractive to females.

In 1967 Cross and Hardee (17) demonstrated for the first time, Bradley et al. (18) confirmed, and Hardee et al. (19) showed in de-

tail that the pheromone of the male boll weevil is not only a sex pheromone for females but also acts as an aggregating pheromone for both sexes, primarily in the spring and fall and to a lesser degree in mid-season. In 1968, Hardee et al. (20) confirmed the aggregating characteristic of the pheromone and studied in the field the influence of diet on the production of the pheromone.

Isolation and Identification

The first isolation (16) of the sex attractant was accomplished by drawing air from caged males through a column of activated charcoal. A chloroform extract of the charcoal left a residue to which female weevils quickly responded in a laboratory test. Other isolation methods (21) investigated included aeration, solvent extraction, column chromatography of solvent-extracts, and steam distillation of dichloromethane extracts. The latter was the most suitable.

Extractions and further purifications from fecal material and insects were carried out in identical fashion. Each step was monitored by laboratory bioassay (22) of individual fractions and combinations of various fractions. "Figure 3". Insects (67,000 males and 4,500,000 weevils of mixed sexes) or fecal material (54.7 kg) were extracted with dichloromethane; the extract was steam distilled, the distillate was extracted with dichloromethane, and the solvent was again removed under vacuum.

The extract of the steam distillate from weevils and their feces was fractionated by column chromatography on Carbowax 20M coated silica gel. None of the individual fractions from this column were attractive to females, but the combination of two of the fractions was as active as the original distillate. Each of these two fractions was then separately fractionated on a column containing Adsorbosil-CABN (25% AgNO₃ on silica gel).

Various recombinations of all the fractions from both AgNO₃-silica gel columns yielded two fractions, one from each column, that were attractive together but almost totally unattractive separately. Each of these latter two active fractions was then fractionated by glc on Carbowax 4000 and SE-30. Three components were collected that were attractive when all three were combined but that were unattractive individually or in pairs. Rechromatography on Carbowax 4000, SE-30, and a 50-ft support-coated open tubular (SCOT) column showed two of these components to be pure I and II and the third to consist of two compounds, III, and IV. Concentrations of compounds I, II, III, and IV in fecal material, determined by glc, were 0.76, 0.57, 0.06 and 0.06 ppm. Concentrations in weevils were about tenfold less. Compound I was identified as (+)-*cis*-2-isopropenyl-1-methylcyclobutaneethanol on the basis of mass, ir, and nmr spectra. The configuration was assigned by comparison with the nmr spectrum of the synthetic *cis* isomer. The structure of compound II (*Z*)-3,3-dimethyl $\Delta^{1,\beta}$ -cyclohexaneethanol was elucidated on the basis of its mass, nmr, and ir spectra and

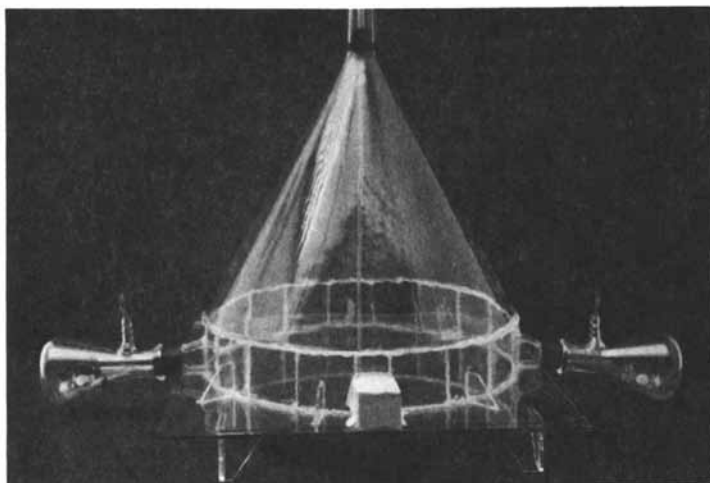


Figure 3.

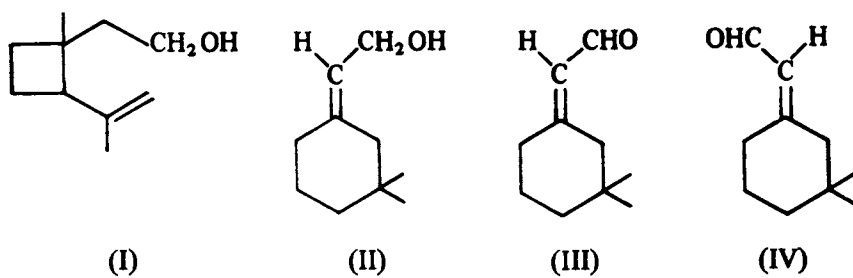


Figure 4.

with further evidence obtained from its palladium catalyst reduction and ozonolysis.

The structures of compounds III (*Z*)-3,3-dimethyl- Δ^1, α -cyclohexaneacetaldehyde) and IV (*E*)-3,3-dimethyl- Δ^1, α -cyclohexaneacetaldehyde) were deduced from the following information. When compounds III and IV were eluted as a single peak from a glc column into 2,4-dinitrophenylhydrazine reagent on a TLC plate, a derivative was produced that had an R_f similar to that of standard terpene carbonyls. The mass spectra of compounds III and IV were nearly identical with each other and similar to compound II. The parent peak had a m/e of 152 in both cases, appropriate for a monocyclic terpene aldehyde or ketone with one unsaturation. Reduction of compounds III and IV at the inlet of a gas chromatograph produced only one peak with a parent mass of 154, which confirmed the single unsaturation. The base peak in the spectrum of saturated III and IV, m/e 110, suggested a facile loss of the elements of acetaldehyde. The details of the structural elucidations were given in the reports by Tumlinson et al. (23,24), "Figure 4."

Synthesis of the Boll Weevil Pheromone Compounds

The first synthesis of compound I that confirmed the proposed structure was reported by Tumlinson et al. in 1969 (23). A slightly modified procedure is illustrated in Scheme I ("Figure 5"), the details of which are reported by Tumlinson et al. (24). Since these syntheses were reported, several others have been devised by workers in this country and in Europe. Until 1973, an improved synthesis by Gueldner et al. (25) was employed to prepare approximately 1 kg. for field studies. This method has been replaced by a 2-step synthesis of Billups et al. (26) in which an isoprene dimerization gives several products, one of which is converted to the desired product when subjected to hydroboration.

The syntheses of Compounds II, III and IV are summarized in Scheme II ("Figure 6"). Further details are included in the reports of Tumlinson et al. (23,24). Initially, approximately 300g of each of these components were prepared for field studies by this procedure. However, the procedures have now been substantially revised by each of several vendors who prepare these compounds for field tests. As with compound I, a number of new syntheses have been published by chemists in this country and elsewhere.

Biosynthesis of the Boll Weevil Pheromone Compounds

Before the pheromones had been identified, it was established that males needed to feed, preferably on cotton, to become attractive. Hardee et al. (22), Bartlett et al. (27), and Hardee et al. (28) reported that the peak sexual activity of both males

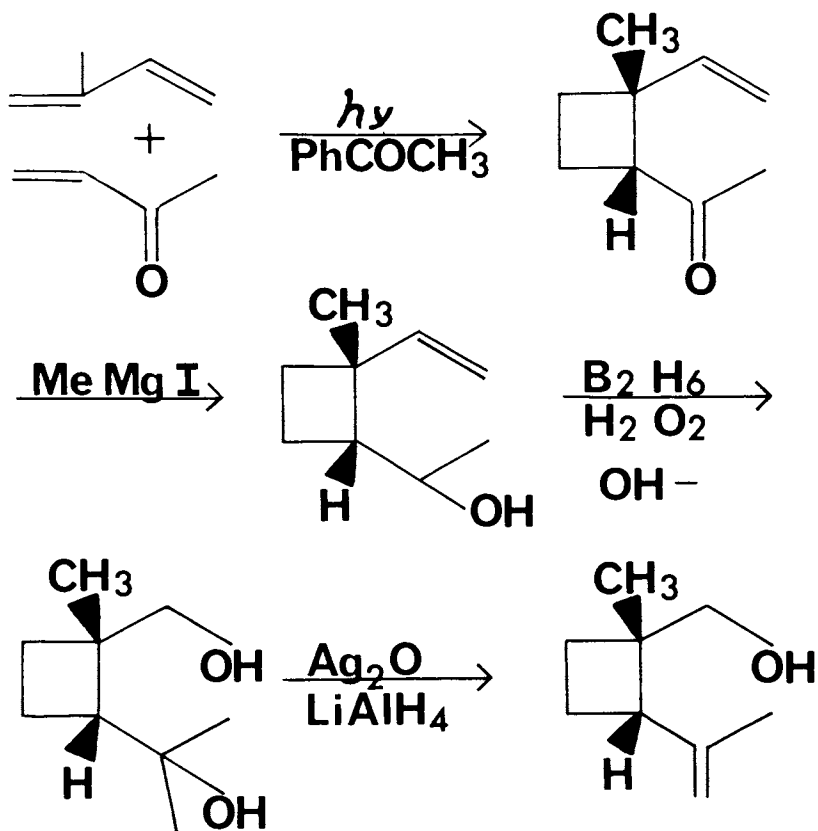


Figure 5.

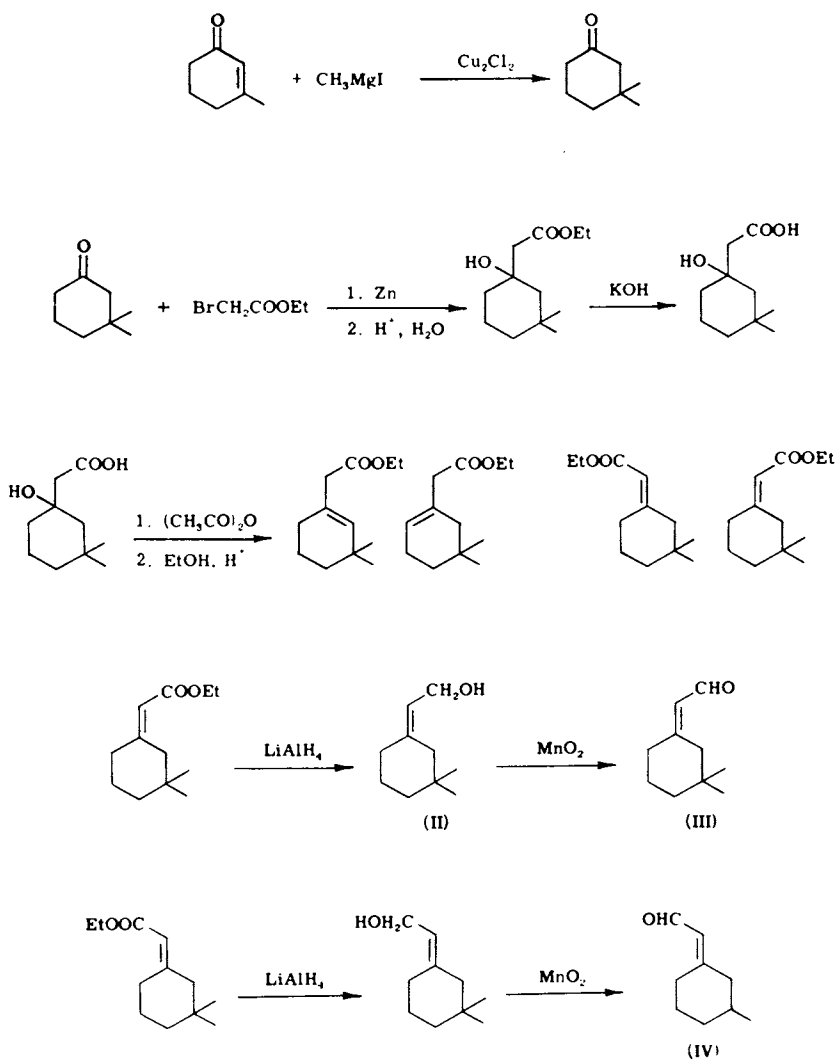


Figure 6.

and females did not occur until the weevils were 4 to 6 days old, and comparisons between laboratory-reared and native weevils indicated food to be of greater importance than culture in determining female response. Additional diet studies in the laboratory and field in 1966-69 by Hardee (29) showed that: (1) Males fed cotton squares, bolls, and blooms were considerably more attractive than males fed terminals, cotyledons, and leaves; (2) pheromone production by males was reduced by about 50 percent one hour and over 90 percent twenty-four hours after food was removed; (3) males survived well and produced pheromone in laboratory bioassays on a variety of foods (50-70 percent as much as on cotton squares) such as apples, bananas, okra, peaches, and string beans, but the most favorable diet was cotton squares; and (4) overwintered male boll weevils survived longer without food than laboratory-reared males, but both needed some food before pheromone production began. In field tests however, Cross et al. (unpublished data) were not able to show response to male boll weevils fed on any diet except cotton. The results indicated that a constant supply of adequate food, preferably cotton squares or small cotton bolls, is essential to continued production of a high level of pheromone by males.

Tumlinson et al. (23) calculated that compounds I, II, III, and IV were present in feces of mixed sexes at concentrations of 0.76, 0.57, 0.06 and 0.06 ppm (13:9:1:1) respectively. Hedin et al. (30) found that the total content of the components in males is 200 ng or less but that the average content in the frass produced during 1 day is 1268 ng; the lifetime production may be 40,000 ng. The ratio of the four components in male frass was 6:6:2:1/I:II:III:IV. None of the four components was found in females, but female frass contained traces in three instances, probably because of contamination with males. The biosynthesis is negligible immediately after adult emergence and increases to a maximum rate by day 8, which is essentially maintained for the remainder of the lifetime of the insects.

Even though males must feed, preferably on cotton, to attract females, Mitlin and Hedin (31) showed that the biosynthesis of the pheromone components was de novo: When the steam-distilled feces of adult males that had been injected with acetate- 1^{14}C , acetate- 2^{14}C , or glucose $^{14}\text{C}(\text{U})$ was fractionated by column and gas chromatography, approximately 0.02% of the administered radioactivity was incorporated into the volatile fraction, a typical percent incorporation of these precursors into monoterpenes by plants. The 4 components comprised 57 to 80% of the radioactivity of the volatiles but only 39% of the total content of the volatiles. Although the boll weevil is essentially an obligate insect of cotton, this insect does not appear to require any specific component in cotton for biosynthesis of the pheromone.

Nevertheless, some constituent in cotton may be efficiently converted to the pheromones. Tumlinson et al. (32) has devised a hypothetical scheme in which a myrcene precursor such as geraniol

could be converted into all four active components. ("Figure 7"). Myrcene and β -ocimene are major constituents of the cotton bud essential oil (33). Ten other monoterpene hydrocarbons (33) several monoterpene alcohols (34), and myrtenal (35) have also been found in cotton buds. For resolution of this question of precursors, the administration of ^{14}C -monoterpenoids seems indicated.

In recent work, Hedin et al. (36) showed that cotton buds promoted a higher level of pheromone biosynthesis by the insects than did the laboratory diet, mostly because weevils fed the laboratory diet produced lesser amounts of the aldehydes (III and IV). Unpublished work with P. P. Sikerowski (Miss. State Entomology Dept.) appeared to show that for a period in the late fall of 1974 germ-free insects fed the laboratory diet produced as much pheromone as insects fed buds and far more than bacterially contaminated insects (5,000 colonies per insect) fed the laboratory diet. However, during January through April 1975, very little pheromone was biosynthesized by insects on buds or any diet. In May and June, pheromone biosynthesis returned to the higher levels of previous summers. Although the laboratory strain employed here does not attain firm diapause as do field-collected insects, laboratory bioassays have always proved erratic each winter, and the apparent seasonal fluctuations of pheromone biosynthesis may have a real basis.

The matter of bacterial gut contamination is also of interest because R. McLaughlin (BWRL, private communication) has shown that larvae residing in fallen cotton squares (buds) are free of microorganisms. Adults that emerge from squares and feed on squares as adults generally have little contamination, but adults fed squares after having been reared on a contaminated laboratory diet remain contaminated (P. P. Sikerowski, MSU Ent. Dept., private communication). While the pheromone biosynthesis of insects maintained on these various regimens has not been analyzed in direct comparisons, the expectation is that the optimum biosynthesis would be achieved by microbially sterile males that were reared from buds and subsequently fed on buds.

On the assumption that the cotton plant contained some bacterial suppressants that acted to maintain the native insect free of gut bacteria, cotton bud extracts were prepared that did totally suppress the growth of *Bacillus thuringiensis* Berliner in petri plate tests. However, these extracts when added to boll weevil larval and adult diets were only marginal in their ability to suppress insect gut bacterial flora (P. A. Hedin, P. P. Sikerowski, O. H. Lindig, unpublished data). Cotton bud constituents, therefore, do not appear to directly control either pheromone biosynthesis or the gut microbiological population, and the effect of the gut flora on pheromone biosynthesis seems to be secondary and related to general insect health. Alternatively, the cotton bud constituents may mediate the establishment of a

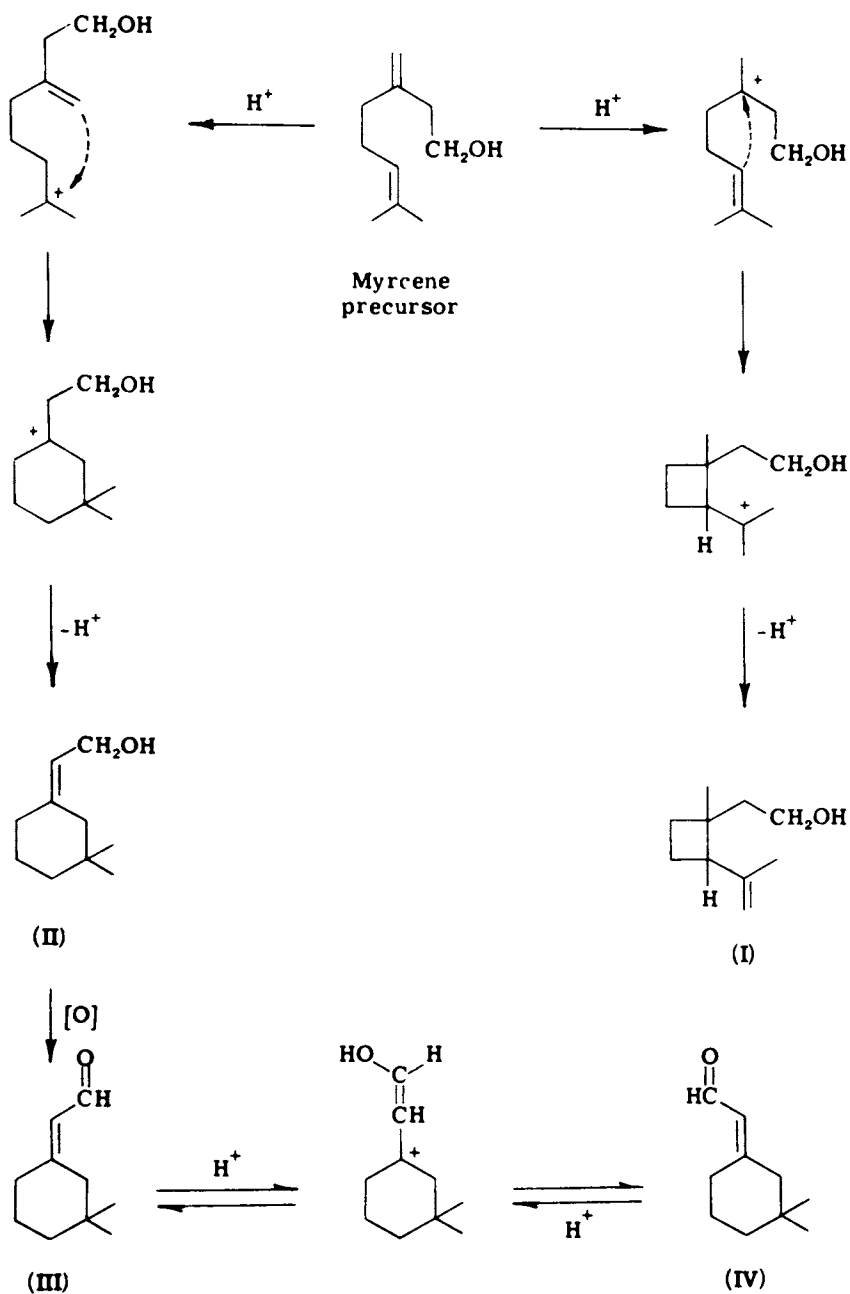


Figure 7.

microbial population favorable to pheromone biosynthesis. The overall indication that germ-free insects produce more pheromone is in apparent contrast to the work of Brand et al. (37) who reported that they had isolated a number of microorganisms from the gut of males of *Ips paraconfusus* Lanier and found that some are able to convert alpha-pinene to the pheromones, cis and trans-verbenol.

It has also been of interest to determine whether insects that have been sterilized biosynthesize as much pheromone as do normal males. Bartlett et al. (27) showed that males sterilized with apholate or gamma irradiation were as attractive as untreated males when both were fed cotton buds. Klassen and Earle (38) showed with field trap tests that the treatment of male boll weevils with the chemosterilant, busulfan, did not reduce pheromone production. However, in extensive field tests where males that had been chemosterilized in the mass rearing facility were released for the purpose of mating with untreated females, they were not competitive with untreated males (39) and experienced rapid mortality. Recently, however, insects of both sexes have been sterilized successfully as pupae by exposing them to a series of 25 doses of gamma radiation at 4 hour intervals of 250 rads each. These treated weevils have an acceptable level of mortality, and they appear to be competitive with untreated males. Presumably they therefore produce as much pheromone (Mitlin and Haynes BWRL, private communication)

There are, therefore, many factors that may modify pheromone production. The diet appears to be the main factor, but bacterial contamination of the gut, age, presence of females, season of the year, and treatment with drugs are some of the other contributing factors.

Formulation of the Boll Weevil Pheromone For Field Utilization

In initial laboratory bioassays during 1967-9 of fractions and synthetic materials, the components in pentane solution were impregnated on firebrick (23) in a ratio of approximately 1:1:1:1/I:II:III:IV. Hardee et al. (40) found that there was actually quite a latitude in ratios that were attractive and that in field tests, increased percentages of the alcohols relative to the aldehydes significantly improved performance. Combinations consisting of 2:6:1:1, 3:5:1:1, and 40:30:15:15/I:II:III:IV were the most promising. It is therefore possible to select a ratio of components based on least cost. After synthesis, the aldehydes are diluted with pentane for storage. The alcohols can be stored as the neat liquids. As a precaution, which is not completely necessary, all the components are refrigerated until formulated. Also, the formulations are refrigerated until they are used in the field.

Approximately 75 grams of each component was synthesized in-house initially. Since then, the pheromones have been procured

from contractors. The specifications call for 95% purity, and the components are analyzed on receipt by glc with a 250 ft X 0.03 in. capillary column coated with OV-17 prepared by Gueldner (unpublished data). Compound I as presently prepared by the Billups (26) procedure is a 1:1 mixture of optical isomers plus minor positional isomers. The predominant impurity of compound II is the E isomer. Three major impurities all resulting from oxidation of compounds III and IV, are 3,3-dimethylcyclohexanecarboxaldehyde, (Z)-3,3-dimethyl- $\Delta^{1,\alpha}$ -cyclohexanecarboxylic acid (and the E isomer); and (Z)-3,3-dimethyl- $\Delta^{1,\alpha}$ -cyclohexanemethanol formate (and the E isomer) (R. D. Henson, unpublished data).

In 1969-70, grandlure was compared in 6 formulations in traps in the field with males as follows: 1) dissolved in dichloromethane in polyethylene caps, 2) impregnated on firebrick in perforated cardboard pillboxes, with and without water added to saturation; 3) formulated in nylon resin or polyethylene glycol-1000 tablets (41); 4) formulated with glycerol, water, methanol, and polyethylene glycol 1000 at various concentrations and absorbed in cotton dental wicks (42). Initial results with the various formulations were positive only when water was added to firebrick or when the cotton dental wick formulation was used. In these formulations, grandlure was competitive with males at fairly high dosages but for only 2 days or less, indication of the need for a slow-release formulation.

Other formulations that had shown promise in laboratory bioassays were evaluated further in the field in 1970 by comparing the response of released, laboratory-reared females to square-fed males or to formulated grandlure in traps. The formulations were as follows: grandlure impregnated on a dental roll dipped in melted paraffin; grandlure + Tenox^R, an antioxidant, added to a nylon resin-clay slurry, and pressed into pellets; same as previous but without Tenox; grandlure added to a vaseline-clay slurry and pressed into pellets similar to the previous. All of the formulations tested except the vaseline-clay mixture were competitive with males the first day, but only the nylon resin-clay tablet plus antioxidant was active after the 3rd day. However, when the latter formulation was compared with males by releasing females in the field in south Florida, it was not at all competitive with males. Also a polyethylene glycol tablet formulation that was very effective in laboratory bioassays was ineffective in field tests in south Mississippi when the dry tablet was used but was nearly competitive with males when water was added to the tablet (42).

The increased activity obtained by adding water to the firebrick impregnated with grandlure and antioxidant to the nylon resin formulation suggested that the water prevented the oxidation of the aldehydes in grandlure to acids and consequently prolonged the activity of grandlure in the field. This then stimulated the development of a water-containing formulation with a slow-release agent (polyethylene glycol-1000), a humectant (gly-

cerol), and a diluent (methanol) in the following proportions: water 12.5, polyethylene glycol 12.5, glycerol 25, and methanol 50. Grandlure was incorporated into this mixture at a concentration of about 1.6 mg per ml, and then 0.5 ml of the total mixture was delivered to a preformed 5/16 in. X 3/4-in. wick prepared from a cotton dental roll (later changed to a cigarette filter). This formulation was very competitive with males fed squares in tests, but no more than 4 days activity was attainable (42).

Beginning in 1971, grandlure was provided to several private companies for formulation by their existing processes. An experimental gel-type formulation submitted by Zoecon Corporation, Palo Alto, Calif., was 90-100% as effective as males in field trials over a seven day period (43). In 1972 Bull et al. (44) improved the cigarette filter formulation of Hardee et al. (42) by placing the filters impregnated with grandlure inside a glass vial to provide a physical barrier to evaporation and physical breakdown. Because the open end of the vial was a restricted opening, a partial equilibrium existed within the vial in which the cigarette filter occupied nearly all the space, and the rate of loss over an extended period (2-3 weeks) was nearly linear as determined by glc (McKibben, unpublished data). In contrast, the rate of loss from a cigarette filter not placed in a vial was logarithmic. This formulation, known as the "BC" formulation, was used widely in 1973 and 1974 in 13 cotton-growing states and 5 foreign countries for survey and management of the boll weevil, as well as in the Pilot Boll Weevil Eradication Experiment (PBWEE) in south Mississippi (43).

In 1972 McKibben (this laboratory, unpublished data) developed 2 gel formulations that were effective in the field for at least 2 weeks and that compared favorably in numbers of boll weevils captured with 3 other formulations tested (44). The first contained a cottonseed oil base to which humectants, antifungal agents, emulsifying agents, gelling agents, and diluents were added. The second contained polyethylene glycol 400, gelling agents, and diluents. Both gels were dispensed into paper cups and the tops were sealed by aluminum foil. Approximately 100,000 of these gels, prepared by a commercial packer, were used during late 1972 and early 1973 in the PBWEE (43). However, the lower cost and greater ease of storing and handling PEG-impregnated cigarette filters mass-produced mechanically and enclosed in a 1-dram vial caused them to be chosen for use through the remainder of the 1973 season.

In 1974, several grandlure preparations were incorporated in a 3-layer laminated plastic dispenser (HERCON^R, Herculite Protective Fabrics Corp, N. Y., N. Y.), that had proved effective against the cabbage looper, *Trichoplusia ni* (Hubner), and the gypsy moth, *Porthetria dispar* (L.) by Beroza et al. (45). They were competitive with, or more effective than, the formulation of Bull et al. (44) throughout a 17-20 day period in 3 different tests (46). Presently (1975), the Herculite formulation,

formulations from several other private companies, and formulations prepared by USDA are being evaluated on the basis of cost, ease of storage and handling, shelf-life, and longevity in the field.

The Development Of Boll Weevil Traps

As the techniques for formulating grandlure improved, the designs of boll weevil field traps did also. After a variety of trap designs were tested beginning in 1966, a wing trap coated with Stikem^R and a Plexiglas^R oblique funnel trap (for live weevil capture) were selected for general use (17). Plywood wing traps painted dark green and metal traps painted yellow (47) were used extensively in large tests in Texas. Then paper wing traps were designed to reduce the cost of trapping programs; these and larger live traps incorporating the daylight fluorescent yellow colors (Saturn Yellow or Solar Yellow^R) were found most attractive to weevils (48). The Leggett trap was developed as a competitive non-sticky trap that utilized the behavior patterns of the boll weevil for most efficient capture (49). Although the daylight fluorescent yellow pigment alone is attractive to weevils, the proper display and handling of the pheromone is necessary for an effective trapping system (42). A subsequent modification of the Leggett trap has brought additional advantages. Mitchell and Hardee (50) reduced the size of this trap and stationed it closer to the ground and in the cotton rows; later in the season it can be placed on the tops of plants so as not to disturb cultivation. These were described as in-field traps and were found to aggregate both sexes in early and late season. Additionally, significant numbers of boll weevils, primarily females, were captured in mid-season whereas previous traps had failed to obtain this mid-season response. Currently, the Leggett and in-field traps are receiving the most extensive use. USDA and private companies are investigating modifications to lower the cost of their production. ("Figure 8").

Registration of Grandlure

The Code of Federal Regulations, Title 40, Chapter 1, Environmental Protective Agency, Subchapter E, Pesticide Programs, Part 162 provides regulations for the registration and classification of pesticides as required by the Federal Insecticide, Fungicide, and Rodenticide Act. Under 162.3(ff)*, attractants are defined as pesticides, if they themselves are used directly to suppress pest populations, and therefore when used as control agents are subject to the registration procedures of Part 162.6. The application for registration must contain complete labeling of printed matter which is to accompany the pesticide, supporting data of efficacy without causing unreasonable adverse effects on the environment, the complete formula, the manufacturing pro-

*Federal Register, July 3, 1975.



Figure 8.

cess, and the proposed classification. The critical considerations have to do with whether the product is hazardous based on the physical, chemical, and toxicological properties of the product itself and the use to which the product is put. Considerations of efficacy involve the minimum effective dosage and dosage range, application techniques, and compatibilities of the components of the formulated pesticide.

For outdoor terrestrial uses, data must be obtained about movement in the soil, soil persistence, laboratory scale leaching data on the parent pesticide, and the soil degradation products, laboratory scale runoff data, and rate of hydrolysis.

Henson et al. (unpublished data), in addressing these considerations, found that 98% of the 4 components of grandlure was lost from soil and water within 48 hours at constant temperatures of 21°C and 32°C. No evidence of the decomposition of alcohols I and II was detected; the aldehydes undergo moderately fast oxidation in storage solutions, but no products of decomposition were found in soil or water. The aldehyde and ester oxidation products of the pheromone aldehydes III and IV, 3,3-dimethylcyclohexanecarboxaldehyde and (E) and (Z)-3,3-(dimethylcyclohexylidene)methyl formate, were completely volatilized from soil within 24 hours; more than 90% of (E) and (Z)-(3,3-dimethylcyclohexylidene)acetic acid remained after 24 hours.

The following aspects of product hazard are to be considered: (1) human effects including oral, dermal, inhalation, and ocular, (2) sub-acute, chronic and delayed effects, (3) safety data including diagnostic and antidotal information, and precautions necessary for reentry into treated areas. For the investigation of the potential human hazards, grandlure was evaluated by several criteria under contract with Woodard Research Corporation, Herndon, Virginia. Grandlure (the 4 components as an equal weight mixture) was found to have the following toxicological properties:

1. Oral LD₅₀ in mice is in excess of 600 mg/kg.
2. Dermal LD₅₀ in rabbits is in excess of 500 mg/kg.
3. Intravenous LD₅₀ in mice is 100 mg/kg.
4. It is a mild skin irritant to rabbits.
5. It is moderately irritating to the eye of rabbits, and a warning label is indicated.
6. If grandlure is systemically absorbed, toxic and pharmacological signs occur at levels well below the lethal level and should serve as adequate warning signals indicating overexposure.
7. The 96-hour LC₅₀ for bluegill sunfish is 44 ppm.

A second product hazard, that of effects on the environment, requires that data on the hazard to fish and wildlife including mammalian toxicity, acute and subacute avian toxicity, acute aquatic organism toxicity, and subacute delayed or chronic effects hazards be obtained.

In contract with the Fish and Wildlife Service, U. S. Dept of the Interior, the toxicity of grandlure was studied in mallards and

bobwhite quail. Throughout the studies, a technical sample containing grandlure isomers I, II, III, and IV in the ratio of 30:40:15:15 was used. Grandlure was found to have the following toxicological properties:

1. The 8-day dietary LC_{50} for mallard ducklings is greater than 5000 ppm.
2. The 8-day dietary LC_{50} for bobwhite quail chicks is greater than 5000 ppm.
3. There were no mortalities in the five groups of mallard controls or in the five groups of bobwhite controls.
4. The concurrently determined 8-day LC_{50} values for diel-drin for mallard ducklings and bobwhite quail chicks are 91.0 and 31.8 ppm, respectively.

On the basis of the Woodard findings of 1972 and submission of a number of physical properties of the compounds, an experimental permit was issued for limited field studies with Grandlure in 1973 and 1974. After receipt of the soil, water, and bird studies and additional efficacy data obtained in 1973 and 1974, the USDA-APHIS prepared an application for registration for grandlure for submission to the EPA. However, it is the policy of the USDA-APHIS that the government should not become the registrant. Therefore, the petition has been re-submitted jointly by two private companies. Concurrently, the Zoecon Corporation is completing a study sponsored by a grant from EPA to determine what information should be necessary for registration of "New-Generation" pesticides such as attractants and hormones. It is expected that the guidelines, Part 162.40, 162.63 - 162.82 of the Federal Code will be revised on the basis of this report.

Utilization Of Grandlure In Integrated Insect Elimination Programs

The development of the boll weevil pheromone has been part of a broad research effort over the past 15 years to develop a multidisciplinary technology with which to eliminate the boll weevil as an economic pest. From 1970 to 1974 a number of field tests were carried out including the South Mississippi Pilot Boll Weevil Eradication Experiment (1971-1973). The literature on earlier field tests (1962-1970) was reviewed by Hedin et al. (51).

The 2-year Pilot Boll Weevil Eradication Experiment (PBWEE) that began in July 1971, was the fulfilment of plans made as long ago as 1958 by Federal, State, and industry researchers to develop technology capable of eliminating the boll weevil (E. P. Lloyd, BWRL unpublished data). In 1969, a site selection subcommittee determined that southern Mississippi was the portion of the country where it would be most difficult to eliminate the boll weevil. The experiment was therefore planned for southern Mississippi and adjoining areas in Louisiana and Alabama. The central core (eradication area) was encompassed by 3 buffer zones. The purpose of the experiment was to determine whether it was technically and operationally feasible to eliminate a boll weevil population from an

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In Pest Management with Insect Sex Attractants; Beroza, M.;
ACS Symposium Series; American Chemical Society: Washington, DC, 1976.

isolated area and to further develop suppression measures for use in an operational-sized program.

The suppression measures employed were as follows:

- I. In-season control of the boll weevil.
- II. Reproduction-diapause control of the boll weevil in late summer and fall.
- III. Pheromone trapping in the spring with:
 - a. Grandlure baited traps.
 - b. Grandlure baited trap crops.
- IV. Insecticide treatment at the pinhead square stage of cotton in the spring.
- V. Release of sterile male boll weevils.

During the first year of the Pilot Experiment, two major problems were encountered that resulted in larger than anticipated populations of boll weevils in the spring of 1972. These were (1) an ineffective volunteer in-season control program by growers in 1971, and (2) physical obstructions that prevented thorough coverage with insecticides applied by aircraft. In 1972, these problems were corrected by in-season insecticide treatments being supervised by program personnel and by supplemental application of insecticide with ground equipment. By mid-October 1972, weevils were not detected by field surveys or later by woods trash examinations.

In the spring of 1973, the capture of weevils in baited traps indicated that a substantial number of boll weevils had immigrated into the northern 1/3 of the core area that was presumed to be isolated. However, the movement of the boll weevils into this area from infested cotton less than 10 miles distant clearly showed that complete isolation did not exist. During the last month of the Pilot Experiment (terminated August 10), 33 of a total of 236 cotton fields, all located in the northern 1/3 of the eradication (core) area, received supplemental treatments with insecticide to eliminate low level infestations that were detected when cotton plants began fruiting. From several criteria, it was determined that the majority of these infestations may have developed from eggs laid by previously mated female weevils that had migrated up to 25 miles from moderately infested cotton. However, no infestations were detected in any of the 170 cotton fields located in the lower 2/3 of the eradication area, those that were isolated by 25 miles or more from infested cotton (E. P. Lloyd, BWRL unpublished data).

Upon completion of the Pilot Experiment, the Technical Guidance Committee for the Pilot Boll Weevil Eradication Experiment concluded that "it is technically and operationally feasible to eliminate the boll weevil as an economic pest from the United States" (52).

The specific contributions of the boll weevil pheromone to the PBWEE were as follows: Grandlure-baited Leggett traps were placed around cotton fields during the first year from mid-April until mid-July. They were baited twice weekly with the previously described PEG cigarette filter and Zoecon gel formulation.

During this period, 156,580 insects were captured with 5,418 traps in Zone 1 of the core area and 132,350 with 5,979 traps in Zone 2. Although the traps were not able to control the population build-up, they served in vital detection. Grandlure was also employed at bait stations in trap crops, early cotton plantings, four rows wide, with 3 bait stations, that were side-dressed with a systemic insecticide, aldicarb. Scott et al. (53) found that nearly all the emerging overwintered boll weevils moved into the trap crops and were killed before squaring (buds) in the normal plantings. Then, as squaring began in the normal plantings, the trap crops lost their attractiveness to later emerging insects. The pheromone traps (bait stations) improved the performance of the trap crop over unbaited trap crops.

In September 1972, trapping was resumed after cotton stalk destruction. During the fall, 559 weevils were trapped from 110 traps in Zone 1 of the core area and 1875 insects from 602 traps in Zone 2. While these numbers may appear low, this trapping occurred after a rigorous reproduction-diapause insecticide spray program that was designed to (and succeeded) sharply reduce the insect population that would otherwise enter diapause. The role of the traps in this phase was to assess the success of this control phase.

In 1973, Leggett traps were placed around all cotton fields in Zones 1 and 2 at the rate of 1 trap/acre. The grandlure formulation used as bait contained 3 mg of grandlure in PEG impregnated filters that were placed in a vial (44). With the improved formulation, traps were rebaited only weekly. From April 16 to August 3, 1973, 1436 weevils were captured in the core area and 40,173 weevils (100 per trap) in the buffer areas. Only 28 weevils were collected in the eradication (core) area from May until August 1973, all but one in the northern half of the eradication area (the south half included 80% of the total acreage). Grandlure-baited trap crops were also used in 1973; results were similar to those obtained in 1972 (E. P. Lloyd, BWRL, unpublished data).

Since the PBWEE, a less extensive population suppression program has been carried out in Arkansas. In 1974, in-field traps (pheromone) plus insecticides prevented reproduction of emerging over-wintered weevils from June 13 to July 6. In-field traps alone captured 76% of the emerging weevils from planting time to pin-head squares and 95-96% from July 6 to July 31. Clumping of eggs (a number found in a small area) by females was obvious and prevented the traps alone from being more effective in capturing females emerging within the clumps (E. B. Mitchell, BWRL, unpublished data).

The Farm Bill for 1973 directs the Secretary of Agriculture to undertake a beltwide boll weevil eradication program. A conceptual plan for a beltwide program was developed by a committee of scientists under the auspices of the National Cotton Council. However, this plan was not endorsed by the USDA. In October 1974,

the State Agricultural Experiment Station Directors, the Commissioners of Agriculture and the Heads of the Entomology Departments of the Land Grant Universities of the involved States, officials of the USDA, and representatives of the cotton industry unanimously agreed that a beltwide eradication program should be preceded by an eradication trial on roughly 100,000 acres. This trial if successful might lead directly to a beltwide program. Funds for the trial program have not yet been requested by the Administration nor appropriated. On the other hand, the Extension Service has requested additional funds for managing boll weevil populations.

Abstract

In 1969, four terpenoid compounds were demonstrated by identification and synthesis to comprise the boll weevil pheromone. Since then the pheromone has been utilized successfully for monitoring and population reduction and has been a component in several integrated pest management and elimination programs. In the course of these tests, it was necessary to develop a long-lasting formulation, to determine the best ratio of components, to improve the methods of syntheses to reduce costs, to commence registration with EPA, and to develop efficient traps and trapping procedures. The pheromone was effectively utilized in the recent South Mississippi tests to monitor and reduce the insect population. Plans for future tests are discussed. Recent studies showed that gut microflora, deficient diets, and sterilization decrease pheromone biosynthesis.

Disclaimer

The use of trade or proprietary names does not necessarily imply the endorsement of these products by the U. S. Department of Agriculture.

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Manipulating Complexes of Insect Pests with Various Combinations of Behavior-Modifying Chemicals

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An important advantage of pheromones for insect control is their specificity for the target species. In some cases several closely related species may respond to the same compound and, through its use the environmental pollution, ecological disruption, and the destruction of beneficial insects brought about by the use of insecticides may be avoided. Unfortunately, we seldom find a situation wherein only one economically important insect pest occurs in a particular crop or area. Thus, for practical pest management purposes, this specificity of pheromones could be almost as great a disadvantage as an advantage.

In survey programs the specificity of pheromones is an obvious advantage, and traps baited with synthetic pheromones have been used extensively to monitor for insect pests. Monitoring of specific pest populations is now incorporated into several pest management programs to allow more timely application of insecticides (1,2,3).

Mass trapping, wherein a sufficient number of traps are deployed to reduce the numbers of the attracted sex in an area, has enjoyed limited success (3). In one experiment redbanded leafroller, *Argyrotaenia velutinana* (Walker), populations were reduced to an economically acceptable level over a 3-year period by placing 100 traps/ha in a 25-ha apple orchard (4). However, since at least 5 other major lepidopteran pests exist in New York apple orchards, mass trapping does not appear to be a practical solution for that pest complex (3).

In a technique equivalent to mass trapping, attractants mixed with a small amount of toxicant have been used to remove the attracted insects from a population. An example is the use of methyl eugenol, a potent attractant for males of a tephritid pest, the oriental fruit fly, *Dacus dorsalis* Hendel. Methyl eugenol mixed with about 5% technical naled can be distributed at discrete spots to which the male flies are attracted and killed; the result is virtually total removal of the males from the population and, thus, no fertilization of the females. The technique was successfully employed in the Marianas Islands by

Steiner *et al.* (5), who coined the term "male annihilation" for this logistically simplified form of mass trapping. Chambers *et al.* (6) reviewed improvements in the technique and their impact on introductions of tephritid pests to the mainland U.S. Later Chambers (7) reviewed other male annihilation programs. Admixture of acceptable toxicants with pheromones has considerable promise in pest management, particularly when logistical or biological considerations make one of the other potential management techniques using pheromones less feasible.

Impressive results have recently been achieved by permeating the atmosphere with small amounts of a pheromone or other behavior-modifying chemical and thus disrupting the insect's mating process. Shorey and co-workers demonstrated reduction in pink bollworm, *Pectinophora gossypiella* (Saunders), infestations comparable to that provided by commercial insecticide applications by continuously evaporating hexalure, (*Z*)-7-hexadecen-1-ol acetate (Z7-16:Ac), into the air of cotton fields (8). In Australia, the orientation of the male oriental fruit moth, *Grapholitha molesta* (Busck), to traps was reduced 95% by atmospheric permeation with its pheromone, (*Z*)-8-dodecen-1-ol acetate (Z8-12:Ac) (3). Similarly, mating and orientation of male gypsy moths, *Porthetria dispar* (L.), to lure and to their females was suppressed by applying microencapsulated disparlure, (*cis*)-7,8-epoxy-2-methyloctadecane, to forest plots (9,10).

Although considerable potential for success has been demonstrated in suppressing populations of a few insect pests by disrupting their mating process or by annihilative trapping, the problem of controlling several important pests within a given pest management area still exists. Complexes of insect pests probably cannot be simultaneously mass-trapped efficiently because of cross-interference of the attractants, different trap requirements, etc. We must also consider that in most instances an atmospheric permeation or trapping program may have to be applied over a large area to ensure success. It would be much more practical and economical if several species could be controlled simultaneously in a given area. If we are ever to succeed in the practical use of pheromones to control insect pests we must design systems to take advantage of all the knowledge gained in the last 15 years about insect behavior and the chemistry of insect pheromones. Insect pest management schemes must be devised that utilize behavior modifying chemicals in combination with other methods to manipulate all key pestiferous insects in any given complex, and possibly the beneficial insects as well, to achieve the desired results.

Interspecific Reactions to Pheromones and Inhibitors

We now have numerous examples of two or more species of insects that utilize the same compound for their pheromone or have it as a component of their pheromone. Sex attraction

specificity and reproductive isolation in the family Tortricidae have been studied extensively by Roelofs and co-workers (11,12). They report several instances where two species utilize the same compound in their pheromones but achieve species isolation through the use of mixtures or blends of several compounds. However, the mechanism of species isolation is more complex than it appeared when this area was first investigated. Not only do most insect species respond only to a very specific blend of certain compounds, but they may actually be inhibited by one or more components of that blend in the absence of the proper amount of the other components. Some insects also appear to be inhibited by the pheromones of other species that coexist in the same area.

The cabbage looper, Trichoplusia ni (Hübner), and the soybean looper, Pseudoplusia includens (Walker), both utilize (Z)-7-dodecen-1-ol acetate (Z7-12:Ac) as their pheromone, and males of both species respond to the synthetic compound in the field (13). However, male soybean loopers will not respond to their own females or to the synthetic pheromone when female cabbage loopers are in the same trap. Thus, the female cabbage looper inhibits the response of male soybean loopers, probably by chemical means. The male cabbage looper is uninhibited by the presence of female soybean loopers, although he seems to prefer his own females (14).

Similarly, when electric grid traps were baited with a combination of tobacco budworm, Heliothis virescens (F.), and corn earworm, H. zea (Boddie), virgin females, the number of captured males of both species was reduced by 24.2 and 77.5%, respectively, compared with traps baited with the 2 species individually (15). The complete pheromone of the corn earworm has not been elucidated although (Z)-11-hexadecenal (Z11-16:ALD) has been isolated from the female and is thought to be a constituent (16,17). A mixture of (Z11-16:ALD) and (Z)-9-tetradecenal (Z9-14:ALD) was identified as the pheromone of the tobacco budworm (17,18).

Males of the Indian meal moth, Plodia interpunctella (Hübner), and the almond moth, Cadra cautella (Walker), both respond to the same pheromone (Z,E)-9,12-tetradecadien-1-ol acetate (Z9E12-14:Ac) (19), but Indian meal moth females release a volatile substance that inhibits the response of almond moth males to the pheromone or to their own females (20). A compound, (Z,E)-9,12-tetradecadien-1-ol (Z9E12-14:OH), produced by Indian meal moth females and inhibitory to almond moth male pheromone response was isolated and identified by Sower *et al.* (21). Additionally, almond moth females were found to produce (Z)-9-tetradecen-1-ol acetate (Z9-14:Ac) (22) which inhibits the response of Indian meal moth males to the pheromone (23). In one study Indian meal moths appeared to suppress populations of the almond moth and of another related species, the raisin moth, Cadra figulilella (Gregson), when all three were competing

for the same food source (24). Although the evidence was not conclusive it seems possible that this could be the result of a stronger inhibitor produced by the Indian meal moth disrupting communication in the other two species. However, Sower (25) found that greater than 75% of Indian meal moths and almond moths were mated in concurrent populations when the density was 1-10 insects per m² of wall surface and the population ratios were 1:10, 1:1, or 10:1, respectively.

A somewhat different mechanism appears to operate in peach orchards and other areas occupied by the peachtree borer, Sanninoidea exitiosa (Say), and the lesser peachtree borer, Synanthedon pictipes (Grote & Robinson). The pheromones of these two species were isolated and identified as (Z,Z)- and (E,Z)-3,13-octadecadien-1-ol acetate, (Z3Z13- and E3Z13-18:Ac), respectively (26). In the course of this investigation it was discovered that as little as 1% of Z3Z13-18:Ac mixed with the (E,Z) isomer, completely inhibited the response of the lesser peachtree borer to its synthesized pheromone. Coincidentally, it was noted that an orchard containing large numbers of the lesser borer did not usually have many peachtree borers so that bioassays for the different species usually were run in different orchards (27). Subsequent studies with these pheromones indicate that one or more of the isomeric forms of 3,13-octadecadien-1-ol acetate may be the essential component of the pheromone for several members of the family Sesiidae and that the (Z,Z) isomer is attractive to more species than the other isomers (28).

(Z,E)-9,12-Tetradecadien-1-ol acetate and (Z)-9-tetradecen-1-ol acetate are the reported sex pheromones of the beet armyworm, Spodoptera exigua (Hübner), and fall armyworm, S. frugiperda (J. E. Smith), respectively (29,30). Z-9-Dodecen-1-ol acetate (Z9-12:Ac) is also a pheromone of the latter (31). In addition, the pheromone of the southern armyworm, S. eridania (Cramer), is reportedly a mixture of Z9E12-14:Ac and Z9-14:Ac (32), and males of the armyworm, Spodoptera dolichos (F.) are attracted by Z9E12-14:Ac (33). In field tests Mitchell et al. (34) found that Z9E12-14:Ac, dispensed from the same trap, reduced attraction of male fall armyworms to their females 90-100% or to Z9-12:Ac 93-95%.

The two bark beetle species, Ips pini (Say), and I. paraconfusus Lanier, occur in the same forest stands and infest the same portions of their common host. Both species attack at the same time of the day and year, but the two species are seldom found in the same piece of host material. The male I. paraconfusus and a component of its aggregating pheromone, ipsenol, ((-)-2-methyl-6-methylene-7-octen-4-ol), both inhibit the response of I. pini to male I. pini. Similarly, linalool (3,7-dimethyl-1,6-octadien-3-ol) a component of male I. pini aggregating pheromone reduces the response of I. paraconfusus to male I. paraconfusus. Thus, the first species to arrive obtains exclusive use of the host (35).

In the examples discussed so far inhibitors play a vital role in isolating closely related species. However, there is substantial evidence that insect pheromones also act as inhibitors of other species that are not closely related but that may be competing for the same food source or ovipositional sites. The cabbage looper and soybean looper pheromone, Z7-12:Ac, also attracts the related alfalfa looper, *Autographa californica* (Speyer) (36), and *Trichoplusia oxygramma* (Geyer) (37), but when dispensed from the same trap, it inhibits the response of male fall armyworms (34) and *Spodoptera dolichos* (33) to their own attractants. Similarly, the fall armyworm pheromone, Z9-12:Ac, which is very attractive to fall armyworm males in the field (31), inhibits the response of cabbage looper males to their pheromone. Still another example is Z9E12-14:Ac which has been identified as a component of the pheromones of the Indian meal moth, almond moth (19), southern armyworm (32), beet armyworm (29), and as a sex attractant for *S. dolichos* (33). It inhibits the response of the cabbage looper and soybean looper to their own respective pheromones (unpublished data and 33).

Thus, we see that interspecific inhibitors are components of the natural environment that help regulate species isolation and also probably regulate populations of competitive species to some extent. With adequate knowledge of the chemistry of this complex environment and insect behavior, and proper utilization of disruptive techniques, we should be able to manipulate these chemical communication systems to achieve the desired control of economically important insect pests.

Disruption of Intraspecific Communication with Pheromones and Inhibitors

Experiments designed to identify compounds that are effective disruptants of intraspecific pheromonal communication have been conducted with several species at the Insect Attractants, Behavior, and Basic Biology Research Laboratory in Gainesville, Florida. The experimental methods have been described in detail by Mitchell and coworkers (34,38,39).

Briefly, selected chemicals were evaporated into the atmosphere of an 81-m² plot from 16 small polyethylene vial dispensers attached to wooden stakes arranged at intervals of 3 m in a 4 x 4 checkerboard pattern (Figure 1). Each dispenser contained 25 mg of the test chemical. A cylindrical electric grid trap (40) baited with either synthetic pheromone or virgin females was positioned in the center of each test plot. On several occasions, two or three attractants (virgin females and/or synthetic pheromone) were used in the same plot but always in separate traps to avoid any unnecessary complications. The effectiveness of each chemical in disrupting pheromonal communication was then evaluated by comparing the number of male moths captured in the treated plots with the number of males

captured in an untreated control. This procedure established the ability of a male to locate a source of pheromone and also can be equated to actual reduction in mating (41,42).

Recent experiments have shown that the above experimental method is valid for identifying compounds that will disrupt pheromonal communication within a species. In addition tests have shown that some potent inhibitors that drastically reduce trap captures do not disrupt communication when they are dispersed throughout a given area surrounding a trap. For example, disruption of pheromone communication in cabbage loopers with their pheromone, Z7-12:Ac, has been studied extensively for several years by Shorey and his co-workers (41,43,44), and they have demonstrated conclusively that this is an effective method of disrupting mating in this species. Meanwhile, a potent inhibitor, (Z)-7-dodecen-1-ol, (Z7-12:OH), of male cabbage looper response to their pheromone was discovered in a synthetic batch of pheromone (45), and it was hoped that this compound would be useful in disrupting pheromonal communication in cabbage loopers. However, Kaae et al. (46) and McLaughlin et al. (47), using the atmospheric permeation technique, discovered that when Z7-12:OH was evaporated into the air around female- or pheromone-baited traps at rates of less than 200 ng/min per m², no disruption occurred, and, in fact, a slight but statistically insignificant increase in trap capture was noted in some instances. Additionally, permeation with Z7-12:OH did not interfere with disruption by permeation with Z7-12:Ac.

Similar results were achieved in tests with the fall armyworm. As we noted earlier, the cabbage looper pheromone, Z7-12:Ac, inhibited the response of male fall armyworms to traps baited with their own females or their sex attractant, Z9-12:Ac, as did Z9E12-14:Ac, a pheromone of several armyworm species, including *S. exigua* and *S. eridania*. In atmospheric permeation experiments, Z9-12:Ac and Z9E12-14:Ac effected a greater than 85% disruption of communication between male and female fall armyworms (33), and in a subsequent field test, attraction of male beet armyworms to their females was reduced by more than 90% by atmospheric permeation with Z9E12-14:Ac (38). However, permeation of the air with Z7-12:Ac actually doubled the capture of male fall armyworms by traps baited with their females (30).

It is also possible to disrupt pheromonal communication in a species with a compound that is not a pheromone (46). For example, hexalure, (Z)-7-hexadecen-1-ol acetate, (Z7-16:Ac) a sex attractant but not a pheromone of the pink bollworm, is very effective as a disruptant in that species (48).

It is not within the scope of this paper to delve deeply into mechanisms of olfaction or pheromonal disruption. However, it is important to note that several mechanisms are possible and one or more may be occurring in any given instance. Thus a compound may modify or block responses to pheromones by acting at the peripheral site of pheromone perception or at another

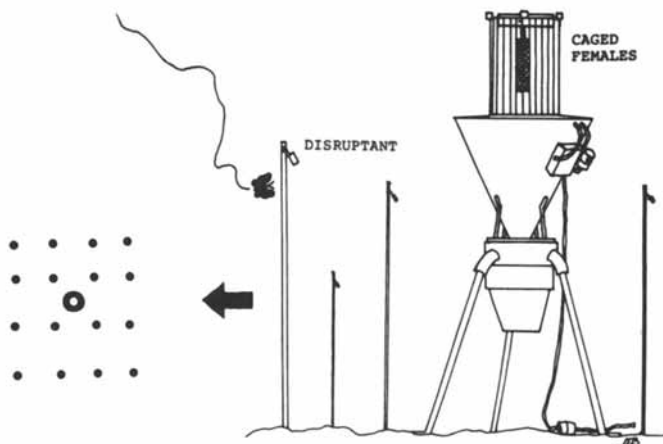


Figure 1. Candidate chemicals are tested as possible disruptants of pheromonal communication by evaporating the compounds from polyethylene vials or caps surrounding an electrical grid trap baited with virgin females or synthetic sex pheromone

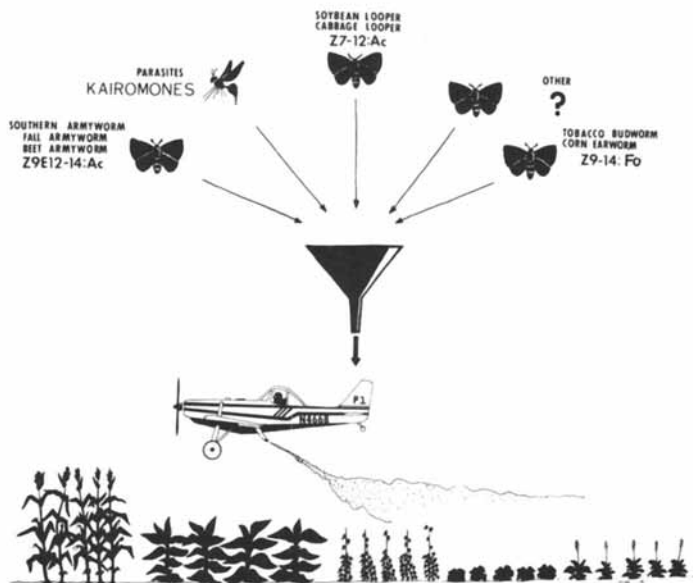


Figure 2. It is theoretically possible to develop broad-spectrum insect control programs by using the atmospheric permeation technique to treat large areas with several chemicals simultaneously. The combination of chemicals could be varied to manipulate different insects, both major and minor pests, and beneficial species depending on the host crops and/or geographical areas.

Finally, it should be noted that the effectiveness of atmospheric permeation in reducing mating is highly dependent on population density and the concentration of the disrupting chemical in the atmosphere. Sower *et al.* (51) demonstrated that Indian meal moths could probably be controlled by permeation of the atmosphere in a closed environment with greater than 5×10^{-4} mg/m³ of Z9E12-14:Ac at a population density of less than 0.1 pairs of insects/m² of wall surface.

Multi-species Disruption

It would be very desirable to disrupt communication in two or more species simultaneously in the same area, a simple matter when two species utilize the same pheromone. For example cabbage loopers and soybean loopers can both be controlled with Z7-12:Ac. Additionally, corn earworms and tobacco budworms are both disrupted by Z9-14:Fo, a compound not known to be a pheromone.

Communication can sometimes be disrupted simultaneously in two species that use different pheromones. Male and female pheromonal communication was disrupted in both peachtree borers and lesser peachtree borers by permeation of the atmosphere with either Z3Z13-18:Ac or E3Z13-18:Ac (52). In this instance it should be possible to control both species with only one compound. This concept is strengthened by the observation (53) that females of these species oviposit immediately after mating. Thus, invasion by gravid females may not be a problem. Additionally, this technique may be feasible for control of other Sesiidae species that are pests of woody ornamentals.

Mitchell *et al.* (38) recently disrupted pheromonal communication in corn earworms, tobacco budworms, cabbage loopers, soybean loopers, and *T. oxygramma* by simultaneously evaporating Z9-14:Fo and Z7-12:Ac in the same field plot. Moreover, they achieved the same degree of disruption (86-93%) by evaporating the compounds from separate dispensers or by mixing them. Similarly, 90% of pheromonal communication was disrupted between males and females of cabbage loopers, soybean loopers, fall armyworms, and beet armyworms by simultaneously evaporating Z7-12:Ac and Z9-14:Ac in the same test plot. Thus Z9-14:Fo, Z7-12:Ac, and Z9-14:Ac can probably be evaporated simultaneously in a given area to achieve a high degree of disruption in several economically important species. The multichemical approach to disruption of mating communication in insects and its possible use for controlling several insect pests simultaneously in a wide variety of agroecosystems is discussed in a recent paper by Mitchell (39).

Formulations

The success of simultaneous multi-chemical disruption of several species will depend to a great extent on our ability to

formulate these chemicals and dispense them at the proper rates to achieve maximum effectiveness. Presently, rapid progress is being made in formulating pheromones and similar materials in controlled release matrices (10). Microcapsules, laminated plastic strips, and hollow fibers show considerable promise as dispensers and allow a variety of applications. Thus a disruptant may be applied aerially in microcapsules or confetti-like strips, or (at the other extreme) dispensers may be placed in orchard trees by hand. In certain instances where the chemical nature of several compounds may preclude mixing them, they may be formulated separately and then dispensed simultaneously. Additionally, it is now possible to prepare formulations that are effective in the field for several months, thus eliminating the high cost of repeated applications throughout a season.

There is still considerable research to be done in the area of formulation and application of behavior-modifying chemicals for trapping, disruption, or other techniques. Optimum release rates, absorption of pheromones by plants, ultimate fate of pheromones in the environment, and other similar studies need to be carried out. Undoubtedly, new formulations or new variations of existing formulations will be required for new and unique applications in the future. For example, pesticides or microbial agents might be incorporated with a pheromone for a male annihilation program.

Projected Experiments

Our ability to combine several chemicals and techniques based on our knowledge of insect behavior and pheromone chemistry to achieve control of almost any pest complex should be limited only by our imagination. Certainly many techniques still require much refinement, and more knowledge is needed in certain areas to facilitate our task; nevertheless, the basic concepts are available and have been proved. For example, we should be able to combine biological control using parasites or predators with a disruption experiment. The advantage of spraying kairomones on a crop to encourage searching of parasites for their prey and to keep released parasites in a given area has been demonstrated (54). Thus, one or more kairomones might be formulated with several disruptants in a pest management system. This system has the added advantage that by augmenting the parasites with pheromones or other behavior-modifying chemicals we are eliminating pesticides that are detrimental to the parasites. This type of system could be utilized in a large multicrop area or in a monoculture.

Chemists and entomologists at the Insect Attractants, Behavior, and Basic Biology Laboratory, Gainesville, Florida, have been cooperating with entomologists at the USDA, ARS, Fruit and Tree Nut Research Laboratory, Byron, Georgia, in studies designed to elucidate the pheromone chemistry, behavior, ecology,

and population dynamics of the insect pest complex in peach orchards. As part of this program, a long-range disruption experiment has been initiated based on information already obtained. New information, including newly elucidated pheromones or other behavior-modifying chemicals, will be incorporated in this experiment as it progresses.

This experiment was begun in early spring 1975, in two orchards of about 0.8 ha each. These orchards are planted with peach trees that are 2 years old and have relatively little insect damage. During the 1975 season, disruption will be conducted against peachtree borers, lesser peachtree borers, and oriental fruit moths by permeating the atmosphere with Z3Z13-18:Ac and Z8-12:Ac. The orchards will be monitored with pheromone-baited traps, and trees will be inspected periodically for damage. When the pheromones of the white peach scale, Pseudaulacaspis pentagona (Targioni-Tozzetti), and the plum curculio, Conotrachelus nenuphar (Herbst), have been identified and synthesized, these compounds will be added to the system. Eventually we plan to test the hypothesis that insects in the complex of pests on peaches can be controlled with an integrated program based primarily on disruption of chemical communication.

A similar experiment is planned in Florida to investigate the possibility of controlling the corn earworm, tobacco budworm, cabbage looper, soybean looper, and several armyworm species by simultaneously disrupting their communication systems by atmospheric permeation with Z9-14:Fo, Z7-12:Ac, and Z9E12-14:Ac. This experiment will be conducted in a multicrop area and may be expanded to include other species and to utilize parasites and predators (Fig. 2).

Preliminary experiments conducted in Florida in 1975 indicate that the communication system of the boll weevil, Anthonomus grandis Boheman, may be disrupted with either grandlure, the 4-component synthetic boll weevil pheromone or a mixture of (Z)- and (E)-3,3-dimethyl- Δ^1, α -cyclohexaneacetaldehyde, two of the components of grandlure (55). Thus it may be possible to control the four most important pests of cotton, the boll weevil, the corn earworm (bollworm), the tobacco budworm, and the pink bollworm (56), simultaneously by atmospheric permeation with a mixture of only three or four compounds: one of the boll weevil pheromone components, Z9-14:Fo, and the pink bollworm pheromone.

Conclusions

Experiments conducted in small field plots have already proved that a high degree of disruption of chemical communication in three or more species of insects can be achieved by evaporation of a multicomponent pheromone-inhibitor complex into the atmosphere. This technique will allow us to tailor our attack to exactly the specificity required to control several

pest species in a given area. It may even be expanded to include the use of kairomones to enhance parasite searching. Of course, these methods will probably be integrated with other techniques in a pest management system. Thus, a high degree of control may be possible without concomitant environmental pollution.

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Air-Permeation with Gossyplure for Control of the Pink Bollworm

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The pink bollworm, Pectinophora gossypiella (Saunders), (Gelechiidae) is a devastating pest of cotton in many areas of the world. Because the damaging larval stage is usually secluded within cotton fruiting bodies--buds (squares), flowers, and immature bolls--pest-control efforts directed against this stage are ineffective. Conventional insecticides are applied mainly for control of the adult moths, necessitating frequently repeated applications and creating a number of actual or potential problems. The problems include the high cost of the insecticide treatments, toxicity of many insecticides to man and other non-target organisms including biological control agents, and the development of resistance to the insecticides by the pink bollworm and other cotton pests. These problems make a selective, environmentally compatible pest-control technique desirable.

In common with a number of other lepidopterous pests, the pink bollworm utilizes a female-produced sex pheromone for distance communication between the sexes (1,2). The pheromone is released by a female which is ready for mating and not only induces male moths to orient from a distance toward her but also at high concentration stimulates them to attempt to copulate with her.

Assuming that this communication between the sexes is absolutely dependent on the pheromone message, then man should be able to disrupt the communication process and thus mating by "jamming" the message. The jamming is based on permeation of the atmosphere with synthetic pheromone, or perhaps a chemical closely related to the pheromone, so that the males sense the presence of the chemical everywhere in the environment and therefore cannot obtain the necessary directional odorous cues to enable them to find the females. Several factors probably interact to bring about this disruption of communication. When the males are continuously exposed to the odor, sensory adaptation and/or habituation in their nervous systems cause their threshold for perception of--or reaction to--the odor to increase greatly. Also, if the synthetic pheromone sources release more of the chemical than do the natural females in the field, then those

males that are still capable of orienting to odor sources at all probably tend to orient most often to the synthetic sources.

The pink bollworm appears to be an excellent model insect for development of the concepts and practical details involved in a pheromone-communication disruption scheme (3). First, the pink bollworm has few host crops other than cotton. Thus, control measures can be directed almost exclusively toward that crop. Second, although the extent of within-field and between-field movements by the moths has not been determined, their relatively weak flight behavior may restrict the normal wanderings of many moths to within the bounds of a single cotton field. Third, a potent sex pheromone, gossyplure, consisting of the cis,cis and cis,trans isomers of 7,11 hexadecadienyl acetate has been identified (4) and is available commercially. And fourth, the economic importance of cotton and of the pink bollworm stimulate federal, state, and corporate organizations to provide funding for the necessary research.

Before the identification of gossyplure, a related chemical had been discovered by empirical screening in the field to be an attractant for males of the pink bollworm (5,6). This chemical, hexalure, cis-7-hexadecenyl acetate, does not occur naturally in the females. Although it is approximately 100-fold less active biologically than gossyplure (4,7,8), hexalure was used in early experimentation to establish many of the principles upon which later programs using gossyplure for disruption of pink bollworm presexual communication were based.

Development of the Communication Disruption Strategy

Although the communication disruption concept appears intuitively sound, a number of variables have to be considered to determine whether the concept is practically workable. The pre-mating behavior of the target insect species must be well understood so that the synthetic pheromone can be employed at a time and in a location that will allow it to achieve maximum effectiveness. Pheromone evaporators must be engineered and means must be developed for placing them in the field. Especially if the pheromone is highly expensive, the evaporators must be designed in such a way that they release most of the chemical into the air at the time when normal moth pheromone communication occurs. The optimum separation between evaporators and the optimum release rate of pheromone from each evaporator must be determined. Finally, chemicals other than the true pheromone should be evaluated to determine which chemical produces the best disruptive effect per unit cost.

Experiments to evaluate the above variables were conducted in cotton fields in southern California. The experimental procedure was based on the use of evaporators that released the disruptive chemicals at known rates, previously determined in the laboratory under conditions of controlled temperature and air

flow. The basic evaporator design was an open reservoir having a constant surface area of the neat, liquid chemical exposed to the air. Evaporative surface areas ranged from as small as 0.1 mm^2 (the tip of a teflon capillary into which the chemical had been drawn) to as large as 810 cm^2 (an aluminum-foil backing lined with nylon cloth, which held the chemical by capillarity between the meshes). By deploying various sizes of evaporators at various densities in the field, the amount of chemical released into the air per unit time over a given surface area of cotton could be related directly to the efficiency of communication disruption. The degree of disruption was evaluated by determining the ability of male moths to orient toward (and thus become captured in) traps containing pheromone-releasing females that were placed in the centers of the chemical-permeated plots, as compared with male orientation to similar traps in non-permeated areas.

Vertical Location of Evaporators in the Field. During the middle of the growing season, a cotton field is a 3-dimensional foliar system, extending from ground level to 1.5 or more meters above ground. Air movement through the foliage is greatly impeded, and the vertical location of evaporators is critical. Hexalure evaporators placed at the level of the top of the foliage canopy gave 82% and 97% better disruption of male:female communication than did those placed midway between the top of the foliage and the ground surface or those placed on the ground, respectively (9). Correspondingly, most males and females of the pink bollworm appear to aggregate near the top of the canopy prior to the time of natural pheromone communication (10,11).

However, environmental variables and related behavioral characteristics of the moths may complicate the situation. The moths apparently sense the prevailing wind velocities, and on windy nights they move down in the plant canopy, sometimes to ground level, before engaging in pheromone communication (11). Presumably, they select a location at which the air movement is optimal for odor dispersion from the females and for responses by the males. Under windy conditions, then, we might expect that evaporators would have to be located at low levels in the foliage canopy to be maximally effective.

Spacing of Evaporators and Release Rate of the Disruptant Chemical. When evaporators giving various hexalure release rates were placed at various separations in the field, ranging from 1 to 30 m, neither the separation nor the release rate seemed to be the critical factor determining the degree of communication disruption (9). Rather, the critical factor was the interaction between these two variables, giving the total amount of chemical released over a given area per unit time. A greater than 90% disruption was achieved when the array of evaporators released in excess of 10 mg of hexalure per ha during each 10-hr night.

However, there must be some upper limit to the distance between substrates, beyond which the atmosphere in all critical zones of the cotton would not be uniformly permeated with the chemical. More recent experimentation with gossypure indicates that this upper limit is ca 70 m (12). The need for evaporators to be placed relatively close together gives considerable impetus to research on microdispersible (perhaps microencapsulated) formulations that can be dispensed by conventional insecticide-application equipment. However, research workers should be aware that there also may be a lower limit to the effective separation between substrates. Many miniature substrates, each releasing pheromone at a lower rate than that released by female moths in the field, might not be able to outcompete the female moths in attracting males.

Comparison of the Disruptive Effect of Various Chemicals.

One might expect that a chemical would have to be an attractant for males of pink bollworms, or at least cause them to exhibit some behavioral activity, in order to be effective as a disruptant of male:female communication when used to permeate the atmosphere. Such is not necessarily the case. For example, looplure, cis-7-dodecenyl acetate, the sex pheromone of the cabbage looper moth, Trichoplusia ni (Hübner) (Noctuidae) does not attract male pink bollworm moths, although it does prevent them from orienting to their females when used to permeate the atmosphere (13,14). However, ca 10-fold more looplure than hexalure is needed to cause an equivalent disruption effect. In turn, hexalure is ca 100-fold less active as a disruptant than the natural pink bollworm pheromone, gossypure, although hexalure has an effect about equal to that of either of the two isomers of gossypure when they are displayed in the field separately (12).

A number of other chemicals have also been found to disrupt pink bollworm pre-mating communication although the degree of disruption seems to diminish as the chemicals are increasingly modified from the correct pheromone structure (14). Although tetradecyl acetate was reported to suppress the entry of pink bollworm males into traps baited with hexalure (15), tetradecyl acetate was later found to not reduce the response of males to traps containing natural pheromone-releasing females (16). However, the search to find one or more non-pheromone chemicals which, when released into the atmosphere, will effectively disrupt pre-mating communication should continue. Perhaps chemicals can be found that will disrupt communication between males and females of a complex of the pest species that infest cotton.

Development of Communication Disruption as a Pest-Management Technique

The pink bollworm has a rapid development time, progressing through several generations in a cotton field during a single

growing season. The adults resulting from one generation mate and give rise to the damaging larvae of the next generation. A variety of experiments was conducted to evaluate the effect of hexalure (and later gossyplure) evaporated into the atmosphere of whole cotton fields throughout the growing season on the ultimate, practical target of the disruption program--the development of infestations of the larval stage in cotton bolls.

Closely Spaced Evaporators Releasing Hexalure. A cotton field was treated with hexalure-impregnated cotton-string evaporators during a 16-week period in the summer of 1972 (17). Approximately 6250 evaporators per ha were distributed weekly in a 0.9 x 1.8-m grid. Each evaporator was innoculated with 10 μ l of hexalure, giving a total application of 848 g per ha-season. An estimated 750 mg of hexalure evaporated into the atmosphere of each ha per 10-hr night. Evaluation of the number of larvae in immature cotton bolls during mid-August, at the time of highest potential pink bollworm damage, indicated that the larval infestation was reduced 84% below that found in two nearby untreated fields. Although this degree of pink bollworm control may be adequate for a pest management system, the expenditure of such massive quantities of hexalure is economically impractical.

Widely Spaced Evaporators Releasing Hexalure. During the summer of 1973, six cotton fields were supplied weekly with large, non-adsorptive evaporators impregnated with hexalure (17). Each evaporator was constructed of an aluminum-foil cylinder covered with nylon cloth. The evaporators were positioned 20 to 40 m apart, throughout the fields. High release-rate evaporators (releasing ca 200 mg per ha-night) were placed in three of the fields and low release-rate evaporators (20 mg per ha-night) in the other three. Total hexalure expenditures were 350 g per ha-season (high release-rate fields) or 35 g per ha-season (low release-rate fields). Cotton boll inspections during mid-August indicated that numbers of pink bollworm larvae were reduced by 93% (high release-rate fields) and 83% (low release-rate fields), compared to untreated cotton fields in the area. Other comparison fields that were treated 4 to 8 times with commercial applications of the insecticide carbaryl achieved no better control of larval infestations in the cotton bolls than either the high or low release rates of hexalure. These experimental results, especially in fields receiving the low hexalure release rates, provide a system which is commercially feasible for economic pink bollworm control.

Widely Spaced Evaporators Releasing Gossyplure. With the identification of gossyplure during the summer of 1973 and the finding that this material was greatly superior to hexalure in either attracting pink bollworm males or in disrupting male:female premating communication, the way appeared open for a truly practical and effective pest-control program. To investigate this

potential, gossyplure was continuously evaporated into the air of all cotton fields (ca 1600 ha) in the Coachella Valley of California during the 1974 growing season (12). Evaporators were spaced 40 m apart in the fields, and fresh evaporators were placed in position biweekly for ca 16 weeks. The evaporators were positioned so that they were level with the top of the foliage canopy. A total of 9 g of gossyplure were distributed per ha-season, giving a gossyplure release rate of 5 mg per ha-night.

Because all cotton fields in the valley were treated with the single system, concurrent comparisons of the resulting insect control with untreated fields could not be made. However, through mid-August, the amount of larval boll infestation was comparable with that observed during the three previous seasons in fields that received conventional pest-control treatments. Also, there was a 3 to 4-week delay in the onset of larval infestations in the bolls in 1974 as compared to the previous years. Even as an experiment, the cost per ha-season (ca \$66) for the pheromonal pest-control technique was approximately equal to that normally expended for insecticidal control of the pink bollworm in the experimental area. The investigators concluded that the 40-m separation between evaporators was probably marginally wide for providing effective control, and it is likely that the development of efficient techniques for producing miniature evaporators such as microcapsules and for dispensing them onto the foliage will provide even more effective pest control.

Development of an Integrated Pest-Management System

The key to the development of a truly practical and effective pest-management system is the acquisition of such an intimate knowledge of the pest and its environment that vulnerable aspects of its life can be attacked by man. The need for the sexes of the pink bollworm to communicate by pheromones, as described above, is one such vulnerable aspect.

Another point of vulnerability is the necessity for pink bollworms to spend their winter, when their usual plant hosts are not available, in a dormant state as diapausing larvae in the soil. The larvae are triggered to enter diapause by sensing the reduced length of the daylight period during each 24-hour cycle that occurs around September 1 (18). This period of initiation of diapause is near the end of the cycle of production of the fruiting bodies that are susceptible to infestation by pink bollworms, although the exact pattern of fruiting by the plants varies somewhat according to the cotton variety, geographic area, climatic conditions, and cultural operations by growers. Thus, the nucleus of pink bollworms that is available to infest cotton plants at the beginning of each cotton growing season results from individuals that successfully overwintered as diapausing larvae, and those larvae developed in fruiting bodies during the end of the previous growing season. This gives rise to another pest-management

strategy, diapause control. The strategy is based on the removal of the susceptible fruiting bodies from the plants at the end of the cotton growing season by cultural or chemical means (19).

Still another useful pest-management method involves conventional insecticides, selectively timed and applied so as to operate advantageously in conjunction with the other strategies.

We visualize that a very effective pink bollworm control technique might be based on the three strategies: disruption of pre-mating communication, diapause control, and insecticide applications. The diapause control program would reduce the reservoir of overwintering larvae. The use of pheromones starting during the beginning of the next growing season would suppress and delay the buildup of pink bollworm populations during the growing season, and the insecticides would be used selectively to reduce populations if they approach damaging levels late in the season.

Abstract

Females of the pink bollworm release gossyplure, a mixture of the cis,cis- and cis,trans-isomers of 7,11-hexadecadienyl acetate, to attract males for mating. Hexalure, cis-7-hexadecenyl acetate, although not a natural pheromone of this species, is also attractive to the male moths. The atmosphere above extensive acreages of cotton was continuously permeated with gossyplure or hexalure for periods up to 20 weeks. The resulting disruption of pre-mating communication between males and females provided ca 75% reduction in the numbers of pink bollworm larvae infesting cotton bolls, compared with larval infestations in untreated cotton fields. An intimate knowledge of the normal pre-mating behavior of the moths is essential to the intelligent development of this technique for disruption of communication.

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Pheromone Research for the Control of Lepidopterous Pests in New York

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The numerous species of insects and mites that feed on apple trees in New York represent one of the most formidable pest complexes affecting any cultivated crop. The high quality insect-free fruit desired by the consumer has necessitated the use of a preventive chemical pesticide program that blankets the growing season from bud break in April practically until the fruit is harvested in the fall. The divergent concerns of economics, ecology and pesticide resistance, however, have increased pressure for the implementation of pest management programs that integrate a variety of techniques. The development of pheromone lures for the major lepidopterous pests has provided the capability of monitoring for the presence of these species for more accurate timing of insecticide sprays. A pest management research project in New York (1) has relied heavily on the use of pheromone monitoring traps for most of the species listed in Table I. The change from preventative spray programs to well-timed sprays applied only as required has resulted in a monetary savings to the growers, as well as in increased populations of beneficial parasites and predators.

Although at least 47 species of tortricid moths have been found to feed on apple in New York (2), only the ones listed are currently considered to be pests. On grapes, only two tortricid species, the grape berry moth and the redbanded leafroller moth, are major pests. Sex pheromone monitoring traps for these pest species can help reduce the amount of needless spray applications, but further reduction in the use of chemical insecticide will require an alternative method of controlling the target species. Sex pheromones have been proposed as a promising control agent and many research programs have been initiated to tap this potential (3). We have conducted experiments in both apple orchards and vineyards for control of several tortricid species by sex pheromone trapping and mating disruption, and we will summarize the results in this paper.

Mass trapping

Apple Orchard. Our first experiments with sex pheromone mass trapping were conducted with the redbanded leafroller moth (RBLR) in apple orchards. This species has been recorded to feed on over 65 host plants and can commonly be found throughout wooded areas surrounding orchards. It overwinters as a pupa and in New York this species has adult flight periods in April-May, in July-August, and a partial flight in September. It is not an ideal insect for mass trapping experiments because of the outside population pressures and its capacity to build up large infestations with each succeeding generation. It was chosen, however, for the first experiments because of the availability of a potent lure and because it had developed into a major pest of apple.

In 1968 an 8 ha orchard with a heavy infestation of RBLR was used during the summer flight period (4). A total of 1700 ice-cream carton traps lined with Stikem^R and baited with c-11:14:Ac (8% trans) were used. Although ca. 4000 RBLR males were captured, the larval damage became so extensive that insecticide sprays were required to salvage the fruit. The dodecyl acetate pheromone component was then found to enhance the lure potency many fold (5), and so the experiment was repeated in 1969 in the same heavily-infested orchard, as well as in an additional 6 ha orchard with a low initial pest population level such as is found in a commercial orchard (6). Sticky traps from the 3M Co. were baited with the 3-component pheromone blend (Table I). In the heavily infested orchard, 2400 traps (3/tree) captured over 17,000 RBLR males, but the resulting fruit injury averaged 32%. This experiment demonstrated that mass trapping is not practical at high population levels. Theoretical calculations (6) based on the competitiveness of traps, moth emergence patterns, survival rates and protandry indicated that an initial trap:female ratio of at least 5:1 was needed to obtain a 95% suppression of mating with RBLR. The ratio would have required the impractical number of 50 traps/tree in the heavily-infested orchard. In the other orchard, 1100 traps (2/tree) attracted 700 males in the spring flight and only 76 in the summer flight. The population was apparently kept at a low level, in spite of outside population pressures, and less than 0.1% fruit injury was recorded.

The latter mass trapping experiment was continued for another 3 years in the same orchard, although the test area was increased to a total of 24 ha of apple (7). It was found that a trap density of 1/tree was sufficient to maintain the RBLR population at a commercially acceptable level. A total annual moth catch of 2552, 4513, and 1153 was obtained in 1970, 1971, and 1972, respectively, with corresponding fruit injury of 0.5%, 2.3% and 0.1%. The majority of males were trapped in peripheral traps, as seen in Fig. 1, indicating that there were high populations in the surrounding areas and that the population within the orchard remained very low. A check plot of 6 ha located 800 m from the mass-trapped section was started in 1971 and the RBLR population developed rapidly, causing 12% fruit injury in the

Table I. Sex attractant lures used for monitoring tortricid populations in New York orchards and vineyards.

Species	Sex Attractant ¹	Reference
<u>Tortricidae: Olethreutinae</u>		
Codling moth (<u>Laspeyresia pomonella</u>)	t8,t10-12:OH	14
Lesser apple worm (<u>Grapholitha prunivora</u>)	c8-12:Ac(2% <u>trans</u>)	15,16
Oriental fruit moth (<u>Grapholitha molesta</u>)	c8-12:Ac(7% <u>trans</u>)	15,16,17
Eyespotted bud moth (<u>Spilonota ocellana</u>)	c8-14:Ac	18
Grape berry moth (<u>Paralobesia viteana</u>)	c9-12:Ac	19
<u>Tortricidae: Tortricinae</u>		
Redbanded leafroller moth (<u>Argyrotaenia velutinana</u>)	c11-14:Ac(7% <u>trans</u>) + 200% 12:Ac	20,21,22
Obliquebanded leafroller moth (<u>Choristoneura rosaceana</u>)	c11-14:Ac(7% <u>trans</u>)	23
Fruittree leafroller moth (<u>Archips argyrospilus</u>)	c11-14:Ac(30% <u>trans</u>) + 400% 12:Ac	24
Threelined leafroller moth (<u>Pandemis limitata</u>)	c11-14:Ac + 7% c9-14:Ac	unpub.
Tufted apple bud moth (<u>Platynota idaeusalis</u>)	t11-14:OH + t11-14:Ac (1:1)	25

¹

Attractant structures are abbreviated with cis and trans denoted by c and t, followed by the double bond position, the carbon chain length, and Ac or OH for acetate and alcohol moieties

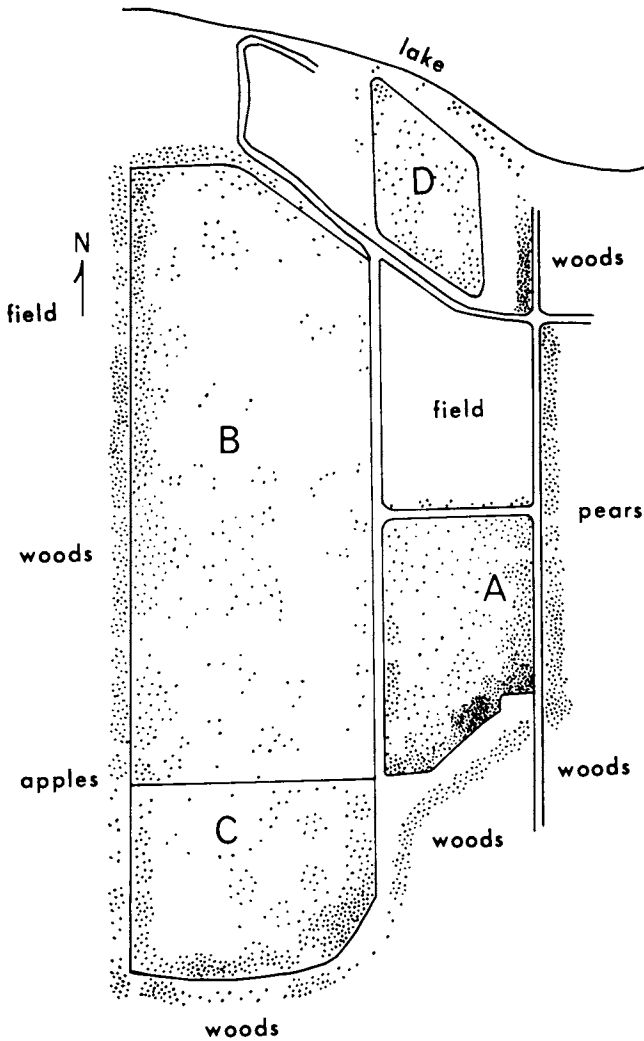


Figure 1. Distributional pattern of 2637 male redbanded leaf-roller captures in 2809 pheromone traps in blocks A-D of an apple orchard during the 1971 summer flight. Each dot represents one moth.

first year. The experiment showed that we could successfully control RBLR with sex pheromone traps at a density of 100/ha (1/tree), but the rapid build-up of obliquebanded leafroller (OBLR) and threelined leafroller (TLR) infestations in the test plot also demonstrated the futility of mass trapping when a complex of insect species is involved.

Efforts were then made (8) to mass trap at reduced trap densities of 43/ha and 10/ha for the control of codling moth, TLR, OBLR, RBLR, oriental fruit moth and lesser appleworm. None of the populations were suppressed at those trap densities, but the results did reveal that there is a relationship among trap catch, the apple foliage volume and trap density. The foliage volume, therefore, is a variable that must be considered when determining trap density for mass trapping experiments in different orchard environments.

Grape Vineyards. Insecticide sprays in New York vineyards are applied only for control of the RBLR and the grape berry moth (GBM) throughout much of the summer. This represents a less complex system than apple for the use of an alternative method of insect control. Although the pheromone mass trapping potential had been demonstrated with RBLR on apple, the technique was tried with RBLR in the vineyard in 1971 and 1972 (9). A total of 334 RBLR pheromone traps were placed in one vineyard section (rows 1-26, 1.1 ha), while the remaining rows, with the exception of the end check rows (48-52), were treated with insecticide. A large number (4700) of RBLR males were trapped in 1971, although 70% of these were captured in the border row traps, suggesting that the endemic vineyard population was much lower than indicated by the total catch. Even though the indicated population was high in the trapped area, fruit damage due to RBLR went down from 6.2% in 1970 to 3.7% in 1971, compared to an increase in the check area values of 7.0% for 1970 to 16.7% in 1971. In 1972 only 185 RBLR traps were used to capture 2700 males, with the crop damage remaining at 4.0%. The large RBLR populations in the surrounding environment makes mass trapping for control of this species difficult unless large areas, including buffer zones outside the vineyard, are employed.

The GBM should be more amenable to the mass trapping technique since it is found only on grape. The use of 226 GBM pheromone traps in the same vineyard section as described above for RBLR trapping caught 115 GBM males and resulted in a decrease of fruit damage from 16.2% in 1970 to 5.9% in 1971, as compared to 11.3% in 1970 and 13.0% in 1971 in the check area. Continuance of the experiment in 1972 resulted in a capture of 300 males with resulting 7.1% fruit damage, as compared to 16.0% damage in the check plot. The mass trapping technique appeared to have a substantial effect, but it did not suppress the pest population to commercially acceptable levels. Additionally, the cost and effort involved in mass trapping relative to grape grower bene-

fit did not justify continued experimentation along this line at this time. Research programs were then set up to investigate the use of sex pheromones in mating disruption programs.

Mating Disruption

Grape Vineyard - Widely-Spaced Evaporators. The sex pheromone mating disruption technique is based on the premise that continuous evaporation of pheromone in the atmosphere over large areas can eliminate the male moth's ability to locate a female in that area [see (3) and references therein]. In our initial studies in 1972, we used widely-separated evaporators as the method for air permeation. Shorey and co-workers (10, 11, 12) have conducted considerable research on this method with the cabbage looper moth, *Trichoplusia ni*, and the pink bollworm moth, *Pectinophora gossypiella*. Pheromone for the RBLR and GBM was evaporated in separate 2.5 cm planchets placed side by side in pheromone-release stations positioned on an 8 x 13 m spacing in a 0.4 ha vineyard (9). A smaller vineyard (0.2 ha) located 12 m away was used as a check. In the previous year, pheromone traps had caught 2900 and 3400 RBLR males, and 88 and 25 GBM males in the test vineyard and the check vineyard, respectively. During the disruption season, only 6 RBLR and 0 GBM were able to locate synthetic pheromone and virgin female traps in the test vineyard, whereas, 429 RBLR and 62 GBM males were captured in the check vineyard. The close proximity of the check vineyard was not ideal, since attractancy was probably affected by pheromone from the disruption plot and gravid females could readily fly from the check plot to the test vineyard. Nevertheless, the fruit injury due to RBLR in the test vineyard was reduced from 4.7% in 1971 to 3.8% in 1972, while it increased from 6.5% to 9.2% in the check vineyard. Fruit injury due to GBM decreased from 4.7% to 3.1% in the test vineyard and increased from 5.5% to 8.5% in the check vineyard.

The above experiments indicated a potential for using pheromones simultaneously for the control of several species. The method of using spaced pheromone release stations, however, appeared to be uneconomical and not completely efficient for the species studied due to possible layers and fenestellae of pheromone-free air. Efforts were then made to develop microencapsulated pheromone formulations that could be sprayed onto the foliage for a uniform distribution of pheromone.

Grape Vineyard - Microencapsulated Formulation. In 1974 some small test plots (0.12 ha) were set up to test several pheromone formulations for disruption of male GBM orientation to attractant traps. A microencapsulated formulation prepared by Pennwalt Corp. to contain ca. 10% by weight of GBM pheromone in polyamide capsules of 30-50 μ average diameter was diluted with water so that application of 90 l/ha of solution provided 25 g

of pheromone per ha. The formulation was applied to one side of the grape row with a roller pump sprayer driven by the power take-off on a tractor. Eight hundred fifty laboratory-reared GBM males were released in both the test and check plots (separated by 170 m) on 0, 2, 4, 6, and 9 days after applying the pheromone. Nine pheromone traps each in the treated and check plots caught 4 and 77 males, respectively over a period of 13 days. This indicated that the formulation could disrupt male orientation to the traps.

A 1% wettable powder of GBM pheromone was obtained from Zoecon Corp. and applied at the rate of 25 g of pheromone per ha in a similar test. In this case 160 laboratory-reared males were released in both the test and check plots on days 0 and 7 after treatment. Only 5 GBM males were attracted to the pheromone traps in the treated plot over the first 8 days, compared to 70 in the check plot, but on the 10th day the disruptant effect was gone and the treated plot traps caught 42 males, compared to 29 in the check plot. Again, the indication was that the formulation could disrupt orientation of GBM males to traps, in this case for less than 8 days.

Another microencapsulated formulation from Pennwalt containing 10% by weight of c11-14:Ac (11% trans) was used in a season-long experiment for disruption of RBLR. The 0.4 ha vineyard employed previously as the site of the disruption test with widely-spaced evaporators was used, but the 0.2 ha check plot was set up 100 m away this time. The formulation was applied 11 times at the rate of 22 g/ha every other week starting April 22, 1974. Only 9 RBLR males were trapped in the disruption block compared to 307 in the check. Fruit damage could not be used as an indicator of success in this test since both plots had less than 1% damage. Indications were that this formulation could disrupt male orientation to the traps at the rate used.

The above experiments with the mating disruption technique utilized the pheromone components in approximately their naturally-occurring ratios, such as c11-14:Ac + 11% t11-14:Ac for RBLR. Since the trans component when present in higher ratios greatly reduces male attractancy to a pheromone dispenser, there is a possibility that atmospheric permeation with t11-14:Ac or a 50:50 cis/trans mixture would be more effective than the compounds in the appropriate pheromone ratio. In 1975, 3 replicates of disruption plots (0.25 ha each) treated with microencapsulated (Pennwalt formulation) c11-14:Ac/t11-14:Ac mixtures in 89:11, 50:50 and 0:100 ratios and corresponding check plots were monitored with RBLR traps (see Fig. 2). The results are shown in Table II, indicating that the correct pheromone ratio, 89:11, was the most effective disruptant, whereas the t11-14:Ac component was the least effective disruptant for RBLR. There was very good consistency among the replicates of each treatment, making possible valid statistical separations among all treatments. The 89:11 ratio was very effective in disrupting male

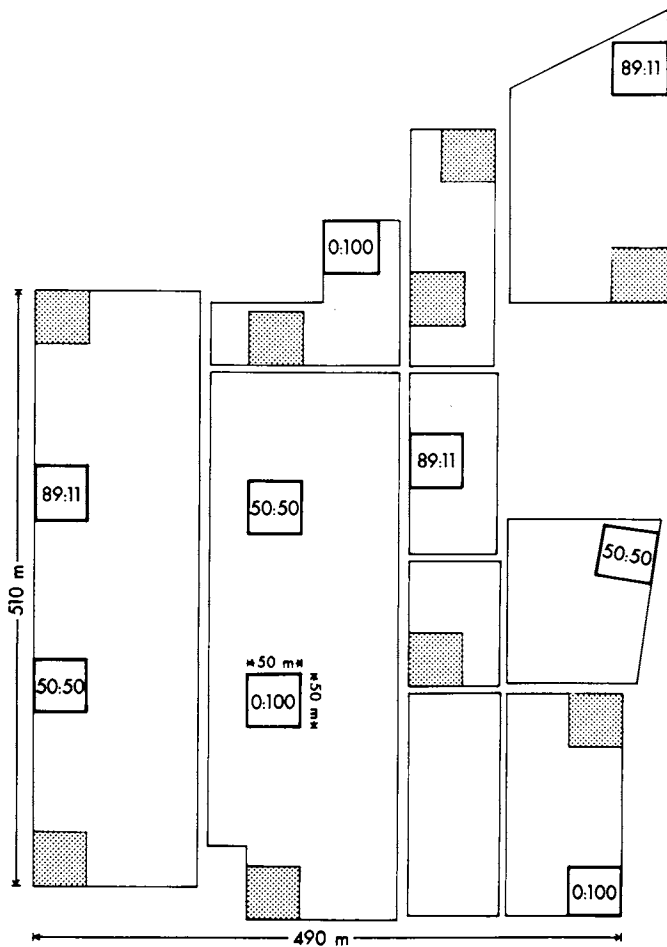


Figure 2. Placement of treatment and check plots in grape vineyards. Treatments of *c11-14:Ac/t11-14:Ac* (89:11, 50:50 and 0:100) were applied to the 50 x 50 m plots at 22g/ha. The corresponding check (no treatment) plots are stippled. Two pheromone-baited traps were used as an attraction monitor in all plots.

RBLR from orienting to the traps and, thus, shows excellent potential for use in mating disruption programs.

Table II. Disruption of communication of male redbanded leaf-roller moths using 11-tetradecenyl acetates in Fredonia, N. Y. Test conducted from May 8 to 19, 1975.

Treatment	\bar{x} males/plot ¹	$\bar{x}\%$ disruption ²
c11-14:Ac to t11-14:Ac		
89:11	1.0 d	98 a
check	49.0 a	
50:50	4.6 c	89 b
check	43.7 a	
0:100	13.0 b	67 c
check	39.3 a	

¹ Means followed by an uncommon letter differ at the 5% level according to an analysis of variance of the number of males per plot transformed to $\sqrt{x + 0.5}$ and Duncan's new multiple range test

² Percentages followed by an uncommon letter differ at the 5% level according to an analysis of variance of the percentages of disruption per plot transformed to the arcsin $\sqrt{\text{percentage}}$ and Duncan's new multiple range test

Apple Orchard - Microencapsulated Formulation. The Pennwalt microencapsulated formulation of c11-14:Ac (11% trans) was sprayed in small test plots in apple to test for disruption of male RBLR orientation to attractant traps (13). The test plots were 3 x 3 arrays of standard, mature apple trees planted on a 12 m spacing. There were 3 replicates of each treatment in both the spring and the summer flight of RBLR. Treatments consisted of 1) one application of pheromone at the initiation of flight, 2) application of pheromone at 5-7 day intervals, and 3) no pheromone. The microencapsulated formulation was added to 750 l of water along with 0.01 l of Triton B-1956 Spreader-Sticker (Rohm and Haas) and sprayed until runoff with a John Bean hand sprayer at ca. 26-38 l per tree in the spring (when there was little foliage) and ca. 57 l per tree in the summer. The micro-

encapsulated formulation (10.4% pheromone by weight) was diluted so that it was applied at the rate of 22 g of pheromone per ha. Laboratory emission rate studies had shown (13) that the pheromone was released at an initial rate of 0.7% per day, but that it was only 0.1% by the 8th day. The laboratory studies also revealed that the emission rate after 16 days was only 0.02% per day, even though only 3.7% of the total quantity of pheromone had been released. This underscores the need for more efficient formulations maintaining steady emission rates for several weeks.

The results in apple (Table III) show that this formulation effects good disruption of orientation to the traps, especially when applied at 5-7 day intervals to maintain a relatively consistent release of pheromone. Better disruption was effected in the summer flight, probably due to increased foliage that would retain the pheromone formulation more efficiently during application.

Table III. Disruption of communication in the RBLR with micro-encapsulated c11-14:Ac and t11-14:Ac (89:11)

Treatment	25 Apr-30 May 1974		12 July-23 Aug 1974	
	\bar{x} males/ plot ¹	\bar{x} % disruption	\bar{x} males/ plot ¹	\bar{x} % disruption
Experimental check	10.0 a ² 8.3 a		70.3 a	
Application at initiation of flight	2.3 b	75	6.0 b	91
Application at 5-7 intervals	1.3 b	86	1.0 b	99

¹ Means in the same column followed by the same letter do not differ at the 5% level according to analyses of variance and Duncan's new multiple range test.

² Two experimental check blocks in the spring test.

Although the c11-14:Ac (11% trans) formulation was successful in disrupting males from orienting to traps, it was not successful in preventing mating when RBLR moths, confined in small cages, were placed in sprayed areas. This lack of influence on mating

suggests that the c11-14:Ac (11% trans) pheromone affects the distance orientation response more strongly than the actual mating response. The addition of the third pheromone component, 12:Ac, could possibly exert more effect on the close-range responses.

Apple Orchard - Microencapsulated Formulation For Multiple Species. Since the leafroller complex on apple in New York uses c11-14:Ac as a common chemical in most of the pheromone systems, it is possible that disruption with this chemical, or possibly a mixture of several chemicals, would effect control over the whole tortricid complex. Experiments were initiated in 1975 in the Hudson Valley to test the effect of microencapsulated c11-14:Ac (11% trans) on orientation of males of several species to their corresponding pheromone traps. Two replicate plots (0.4 ha) were sprayed with the formulation on June 17, 23 and 27, and two plots (0.4 ha) were left as checks. The data from two monitoring traps for each species in each area are given in Table IV. It is apparent that the formulation is excellent in disrupting RBLR orientation, as shown previously, and that it apparently is almost as successful in disrupting orientation of the three-lined leafroller (TLLR). It is not surprising to find a lack of effect with the tufted apple bud moth (TABM), since this species does not use c11-14:Ac in its pheromone system, but it is surprising that no effect was observed with OBLR. The OBLR utilizes the same cis:trans ratio as RBLR, but without the dodecyl acetate (see Table I). The lack of disruption of OBLR with this formulation is unexplained at this time. Perhaps a higher concentration of pheromone in the air is required to disorient this species.

Table IV. Communication disruption of tortricid moths in Ulster, N. Y. utilizing microencapsulated c11-14:Ac (11% trans) at 22 g/ha and pheromone-baited traps as monitors. Test conducted from June 17 to July 3, 1975.

species	\bar{x} males/plot at 22 g/ha	\bar{x} males/plot check	\bar{x} % disruption
RBLR	0.4*	31.4*	99
TLLR	4.0	42.2 N.S.	91
OBLR	63.4	60.0 N.S.	0
TABM	92.0	62.0 N.S.	0

*Different at the 5% level according to an analyses of variance and Duncan's new multiple range test. N. S. Not significant at the 5% level.

The success of disruption programs may be dependent on the maintenance of a certain concentration of at least one pheromone component. The lowered success of the 50:50 cis/trans mixture with RBLR may have been due to a concentration of cis below that required for disruption. It should be possible to mix together compounds for various species in disruption programs as long as each compound is being released into the air at an appropriate rate. A new formulation that efficiently emits the pheromone at a steady rate for a long period of time would mean that lower amounts would need to be used and application would be less frequent. It is possible that a formulation could be developed that would emit 2 to 3 pheromone components found in tortricid pheromone systems at rates sufficient to disrupt all the leaf-roller pests of apple in New York.

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6

Pheromones in Agriculture – From Chemical Synthesis to Commercial Use

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Summary

This paper attempts to answer the question "why have no pheromones been registered for use in crop protection?" from an economic viewpoint. Based on the assumption that pheromones can be used to disrupt insect communication to prevent mating and larval damage, the various components of research and development needed to achieve registration for practical use are listed and their costs are estimated. For economic analysis, a specific case of codling moth control is used to estimate the acreage involved, the cost per season and the expense of developing and introducing a pheromonal method of pest control to derive the internal rate of return on the research and development investment. Assuming commercialization of the product, it appears from the calculated cash flow that the project could not break even on annual basis before the fourth year. Using discounted cash flow analysis, the internal rate of return is found to be 6%. This is significantly less than either the cost of providing capital to finance such a project, or of the value of alternate use of funds; on this basis, the project is therefore commercially unattractive.

Assuming that considerable portions of field testing would be conducted by non-industrial cooperators, the major costs to the commercial developer appear to be toxicology and chemical process development expenses. Partial solutions to the problems of the high cost of synthesis of pheromones are discussed with reference to pheromones of the pink bollworm moth and European grapevine moth.

Introduction

Research on pheromones spans numerous disciplines from sensory physiology to economics; a common aim of many research workers is to demonstrate the practical use of pheromones for crop insect control. Although the commercial use of pheromones and sex attractants for the monitoring of insect populations has progressed rapidly, their use for actual control of an insect population seems to be bogged down. This is hardly surprising since the amount of research and development work necessary to register the use of an agricultural chemical for pest control is very large compared with the work needed to develop and introduce monitoring traps.

Comparing agricultural chemical pesticides with pheromone chemicals for pest control, at least two major differences are immediately obvious. For pheromones, both the chemical structures and the optimum blend of active ingredients are defined by the insect in question. Thus the tedious and expensive process of discovery and refinement of the chemical structure to arrive at an active pesticide is circumvented. Secondly the formulation of a pheromone for pest control will be designed for volatility rather than for leaf-residual stability as in the case of a pesticide.

To simplify the consideration of development and registration of the use of a pheromone, this analysis will begin with the assumption that discovery and structure elucidation of the active pheromone blend has been completed elsewhere. Thus we shall consider only the steps from chemical synthesis to commercial use.

Development Costs

Four major areas of work can be separated out for the purposes of this analysis, and their associated costs for one pheromone are estimated conservatively below.

1. Chemical Process Development -	\$250,000
2. Formulation Research and Development-	\$ 60,000
3. Toxicology and Registration -	\$330,000
	\$640,000
4. Administrative Overhead (50%) -	\$320,000
Total -	\$960,000

The total of these costs is \$960,000, to be spent over a four-year period as shown in Table I. The derivation of these costs will be discussed below.

TABLE I. Calculation of Internal Rate of Return on Investment.
Codling Moth Control by Pheromonal Disruption of Mating.

A. DEVELOPMENT COSTS	Year: 1	2	3	4	5	6	7
1. Process Development (target \$200/lb)							
a.i. formulated	\$ (125)	(125)					
2. Toxicology & Registration (tolerance exemption)	\$ (50)	(130)	(150)				
3. Formulation (select and develop 1 formulation)	\$ (40)			(20)			
	\$ (215)	(255)	(150)	(20)			
4. G&A, overhead (50%)	\$ (108)	(127)	(75)	(10)			
Total Develop.& Regist.	\$ (323)	(382)	(225)	(30)			
B. SALES, Income & Expenditure							
1. Market Penetration		2,360A					
0.5% (Exp. Permit)							
1.0% (Exp. Permit)			4,730A				
3.0% (Full Registration)				14,190A			
5.0% (Full Registration)					23,650A		
5.5% (Full Registration)						26,015A	
5.0% (Full Registration)							23,650A
2. Sales (\$000) @\$20/Acre		24	95	284	473	520	473
3. Cost of goods @10g/A/Season		(10)	(21)	(62)	(104)	(114)	(104)
44¢/g a.i. formulated		(4)	(14)	(43)	(71)	(78)	(71)
4. Sales expense (15%)		(372)	(165)	149	298	328	298
5. Net cash flow	\$ (323)	x0.89	x0.84	x0.79	x0.75	x0.71	x0.67
6. Discount factor(6% rate)	x0.94	(331)	(139)	118	224	233	200
7. Discount cash flow	\$ (305)						
8. Discount cash flow, cumulated	\$ (305)	(636)	(775)	(657)	(433)	(200)	0

Chemical Process Development. These costs will be discussed after consideration of the manufacturing price of the active ingredient (a.i.) which we have derived by calculating back from the end-user price (see "Cost of the Pheromone Chemical").

Formulation Costs. We have assumed that a sustained release, sprayable formulation having an effective field life of 8-10 weeks (two sprays per season) can be developed within one year. This would involve preparation of a fairly large number of exploratory formulations, determination of their release rates, preparation of field test quantities of several formulations selected on the basis of release rates, and development of one of these formulas chosen on the basis of field test results. At the unusually low field use rates anticipated below, radiochemical methods would probably be required for measurement of release rates in the laboratory. We have assumed that additional formulation refinement would be necessary during the fourth year to correct minor problems anticipated at the start of commercial use in the field.

Toxicology and Registration Costs. The estimates shown in Table I, part A, are based on expectation that a petition for establishment of food residue tolerances (apples, pears, walnuts) or for exemption from the requirements of tolerances would form part of the request for registration of uses of the pheromone. In either case, toxicological work involving acute, subacute, chronic and reproduction studies would most likely be needed to support such petitions. Biochemical studies of the environmental fate and measurements of residue levels of the active ingredient have been assumed to be necessary for support of registration petitions in our estimate of "registration" costs, although the (assumed) low field use rate might justify omission of some of these studies. The costs of collecting, organizing and preparing the various parts of the registration petitions are covered by general and administrative overhead entries on line 4 of Table I, part A. A summary of the direct cost estimates is:-

	\$
Registration fees	10,000
Toxicology studies	180,000
Biochemistry studies	45,000
Residue studies	45,000
Field testing	50,000
Total direct costs	<u>\$330,000</u>

The estimate for costs of field testing is based on an assumption that considerable additional amounts of field work on smaller plots would be carried out by non-industrial cooperators.

Recovering the Development Costs

If insect control by use of pheromone chemicals alone is to be paid for by government departments and funding agencies, in other words at the taxpayers' expense, then the recovery of development costs can be overlooked. One assumes that these costs will be recovered in some other form such as lower costs of crop or timber production, or increased property values from prevention of tree defoliation. However, in the USA the sector which has been and will be responsible for the introduction of virtually all new insect control agents and plant protection chemicals is industry and not the government. Clearly, university and government agency researchers play a major role in the discovery and the experimental field testing of pest control chemicals, particularly insect pheromones. Nevertheless the major costs listed above would probably be borne by industry, and it is relevant to consider how these costs might be recovered.

For the specific case of codling moth control by a pheromone, this analysis considers four elements which combine to produce income which offsets development costs, to give a net cash flow. These four elements are

1. Market penetration of the accessible acreage;
2. Net sales (manufacturer level);
3. Manufacturing cost of goods sold;
4. Marketing, general and administrative (G&A) expenses.

The net cash flow has then been calculated (Table I, line 5), to find the breakeven point, which occurs in the fourth year. From the seven-year analysis the internal rate of return on investment has then been calculated, by finding the interest rate at which the present value of expected future receipts equals the cost of the investment outlay.

Accessible Acreage

In the case of codling moth we estimate that a total of 473,000 acres in South Africa, Australia, and western North America (California, Oregon, Washington, British Columbia and Colorado) are areas where codling moth is the only or the primary pest. The bearing

acres involve apples, pears and English walnut (California only) and it should be noted that many additional thousands of acres exist where codling moth is one of a complex of pests. In these latter areas, insecticide sprays are often applied with the hope of controlling several pests simultaneously. On the 473,000 acres considered here, at least three insecticide spray applications are made specifically against codling moth each year. At the grower level we have used \$30 per acre per season as the current minimum total cost of these three sprays.

Market Penetration

The analysis in Table I, part B, shows the assumed penetration or coverage of circa 5.5% of the total of 473,000 acres which are suitable for this hypothetical codling moth control product. While this is a relatively small fraction of the total acres, a basic assumption is that it would be difficult to persuade growers to change completely to this new and comparatively untried method of insect control. Those expected advantages of lower chemical residues and fewer environmental effects of a pheromone disruption treatment (compared with standard insecticide treatment) by themselves do not motivate the grower to accept and use the new treatment. Only the prospect of a high quality fruit crop in the sense of low (ca. 1%) insect damage will significantly influence the grower to use the new method.

During the second year (Table I) we assumed that only one-half of the 2,360 acres treated will generate sales under an Environmental Protection Agency (EPA) Experimental Permit label. In the third year, we assumed that the 4,730 acres would all be treated on a commercial basis of sales, and that data gathered from these acres would allow a full commercial registration to be granted before the fourth season.

In considering the risks involved in such a project, the problem of competitive products entering the same market is substantial. Since the active ingredient pheromone is a natural product the establishment of a proprietary position would be difficult compared with the case of a novel synthetic chemical pesticide. For this reason we have assumed that the acreage covered would not increase significantly beyond 5% achieved in the fifth year. Declining sales in the seventh year (sixth year of marketing) are not unusual for crop protection chemicals. The assumption is therefore that

seven years would be the effective lifetime of the project, for conservative calculation purposes.

Cost of the Pheromone Chemical

Regardless of whether a development project such as this is undertaken by industry or by a government agency, one of the most important points is that the finished product, the formulated pheromone for crop insect control, must be available at a cost low enough to allow growers to use it economically. In other words it must compete in cost with other methods such as insecticide use under integrated pest management programs.

Since the hypothetical pheromone control product must be attractive compared to the current \$30 per acre cost, we have chosen an end-user price of \$25 per acre per season for the finished pheromone product. This figure of \$25 includes \$5 charged by the distributor of the product. The remaining \$20 received by the manufacturer is composed of:-

Active ingredient chemicals;	}	22%	\$ 4.40
Formulation ingredients;			
Containers or packages;			
Marketing expenses, general and administrative expense;	}	15%	\$ 3.00
Net margin before taxes			
		63%	\$12.60
		100%	\$20.00

A net margin of 63% is unusually large. However, if the analysis did not allow the manufacturer a net margin of 63%, the recovery of the initial investment in development costs would take proportionately longer, if it could be achieved at all.

One critical factor which will determine whether there is a need for chemical process development is the field use rate, defined in terms of active ingredient pheromone per acre per season. We have projected this figure to be 10 grams per acre per season for codling moth control, based on extrapolation from relevant literature (1), and from data presented in this symposium, although no such field use rates have yet been established. At this field use rate (1/45 lb per acre per season; 0.025 kg per ha per season) we can allow 22% of the manufacturer's selling price to be consumed by materials (cost of goods). This means that only \$4.40 per acre per season can be allowed for finished materials. Thus at \$4.40 for 10 grams, the active ingredient pheromone chemical or blend will cost the

manufacturer \$200 per pound or \$440 per kilogram, including the cost of formulation and packaging.

Chemical Process Development

One of the major development costs noted earlier is that of chemical process development, which requires some explanation. For this case study, the pheromone in question is (E,E)-8,10-dodecadienol (2) and so far no secondary chemicals have been reported as necessary for attraction of males to traps, or for disruption of communication among codling moths. The active chemical is the all-trans isomer but the influence of geometrical isomer impurities on the disruption performance of this isomer is unknown. Purity specifications must be defined before chemical process development can be completed, and should preferably be defined before alternative synthetic chemical processes are considered. In this particular case, the pheromone was found (3) to be crystalline, therefore purification by crystallization on an industrial scale might be possible. This would allow non-stereospecific processes to be considered for synthesis.

We can gain a fairly accurate idea of the scale of manufacturing operations that would be necessary, through the seven years covered by Table I, from the product of field use rate times acreage covered. The required quantities of active pheromone ingredient for the second through the seventh year are (lbs. wt.) 52, 104, 312, 520, 580, and 520 (production schedule).

For this analysis we have assumed that no new equipment would be required because capital investment in new plant for such a relatively small production schedule could hardly be warranted. This would be one of the goals of chemical process development - to use existing equipment - even though this would impose major constraints on the chemist, who is already constrained to use only relatively cheap and safely handled reagents.

In view of the complexity of the pheromone, a batch process would almost certainly be required, and the batch size might conveniently be 100 pounds (\$20,000 worth per batch!) followed in later years by scale-up to larger batch sizes as experience accumulates. With such expensive end product chemicals in the plant, the risk of accidental loss of even one batch must be absolutely minimal, and this can only be ensured by extensive chemical process development.

The manufacturing cost of any chemical includes both variable and fixed components, in an accounting

sense. The variable components usually comprise chemical raw materials, reagents, direct labor of process operators, and analytical in-process monitoring. The fixed components include property taxes, depreciation, management overhead, maintenance, supplies, utilities and incidental expenses. Some proportion of these fixed expenses must be allocated to the pheromone chemical unless the plant is solely devoted to the production of this single chemical (an unlikely case). Although these fixed expenses can be minimized by careful scheduling and management, they are mainly determined by plant occupancy time, so that a faster synthesis carries a lower overhead charge in addition to a lower direct labor cost. Thus a short convergent synthesis employing expensive materials could in principle be much cheaper than a lengthy stepwise process employing cheap raw materials.

Some idea of the nature of the chemical problem can be gathered from comparison of current and future costs of the pheromone chemical. Earlier in this analysis a future cost of \$440 per kilogram, including formulation and packaging, was derived (i.e. \$0.44/gm); the present cost of codling moth pheromone from one open market supplier is listed (4) at \$12 per gram falling to \$7.50 per gram at the 10-gram sample size. Clearly, these high prices cannot be applicable to multikilogram scale production, but they do illustrate the gap which exists for this and most other pheromones. One exception appears to be disparlure, the gypsy moth pheromone, cis-2-methyl-7,8-epoxyoctadecane, since unformulated material has been synthesized for the USDA at a cost around \$100 per pound. The synthesis of this chemical is considerably simpler than that of all-trans codling moth pheromone, but nevertheless a considerable amount of chemical process development was invested in disparlure synthesis (K. Greenlee, personal communication).

Synthesis - Problems and Partial Solutions

Synthesis of the sex pheromone of the female pink bollworm moth, Pectinophora gossypiella (Saunders), presents interesting and challenging problems, because a 50/50 mixture of isomers (gossyplure) is involved (5). Both isomers (7Z,11Z)- and (7Z,11E)-7,11-hexadecadien-1-ol acetate have been synthesized separately by methods involving acetylenic intermediates (6,7) but a recent novel synthesis (8) describes the direct preparation of the required mixture of cis and trans isomers by stereochemical control of the Wittig olefin synthesis. In

this scheme the 7Z olefin common to both isomers was introduced in pure cis geometry by the use of (Z,Z)-1,5-cyclooctadiene, which is readily available commercially. These authors (8) oxidized and opened cyclooctadiene to generate a difunctional intermediate, whose aldehyde group was allowed to react with pentyltriphenylphosphonium ylid. Various experimental conditions gave isomer ratios from 94:6 to 25:75 cis:trans at the newly formed olefin link. The particular conditions which formed a 49:51 mixture of isomers involve the critical temperature -40° at which ethanol is added to the reaction mixture 80 minutes after mixing of the aldehyde with ylid reagent.

Although the completion of the synthesis required cumbersome chain extension by three carbon atoms, a sequence hardly suitable for pilot plants, the controlled Wittig olefin synthesis appears to be well suited for mixed isomer manufacturing.

A recent synthesis of the sex pheromone (7E,9Z)-7,9-dodecadien-1-yl acetate, from (9) the European grapevine moth, Lobesia botrana (Schiff), again provides partial solutions to some of the problems in pheromone synthesis (10). In this scheme, acrolein reacted with 1-butynyl magnesium bromide to form 1-hepten-4-yn-3-ol. This alcohol was then converted by an orthoester Claisen reaction with trimethyl orthoacetate into methyl 4-nonen-6-ynoate, in 50% yield from acrolein. The remaining synthetic steps accomplished chain elongation by three carbon atoms, again a cumbersome operation, and selective hydroboration of the acetylene group with bis-(3-methyl-2-butyl)borane to produce the 7E,9Z diene alcohol, which was acetylated to provide the pheromone. During this sequence an intermediate 12 carbon acetylenic alcohol was crystallized from pentane at -35° to give the required 7E isomer in 98.6% purity, as the preferred alternative to the earlier separation by distillation of the olefin mixture resulting from the Claisen reaction. In considering the development of a chemical process for production of this pheromone, an early determination of the acceptability of the isomer mixture 7E/7Z would be essential, and a simple solution to the 3 carbon chain elongation problem would be desirable.

There is no doubt that synthetic chemistry could provide solutions to these problems. However, those solutions which are workable within the constraints of a chemical manufacturing operation can only be found with the expenditure of considerable amounts of time and money during chemical process development.

Conclusion

Based on the assumptions made in this analysis, the investment of almost \$1 million for development of codling moth control by disruption of pheromonal communication could not be justified on a commercial basis. Significant changes such as major reductions in development costs or expectation of substantially greater market penetration and sales would be necessary to allow the internal rate of return on investment to exceed 15%. With a 15% or greater return, the project might be expected to receive significant attention, provided that the most basic assumption of all is valid. This is the assumption that the pheromonal disruption method of insect control will actually work in the field to achieve damage levels acceptable to the grower.

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Control of the Gypsy Moth and Other Insects with Behavior-Controlling Chemicals

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Although insecticides continue to be our major means of defense against insects that attack our food, fiber, and other agricultural products, difficulties related to the use of insecticides have generated a sustained search for alternative means of insect control, or at least some means of reducing the use of insecticides required for pest management. In this regard, the behavior-controlling chemicals, and insect sex attractants in particular, have received considerable attention during the past several years.

The present paper describes some of the recent research conducted by the USDA and cooperators with behavior-controlling chemicals. Work with the sex pheromone of the gypsy moth (*Porthetria dispar* (L.)) will be used to illustrate this research for the most part because of the author's major involvement and familiarity with this project.

Insect Sex Attractant Pheromones

Insect sex attractant pheromones are chemicals emitted by one member of a species to call a mate to it for mating and propagation. These pheromones are highly specific in that they generally affect only their own species, and infinitesimal amounts often induce responses from great distances. Sex pheromones that excite without attracting will not be discussed because their value in pest control has not been demonstrated.

In recent years, progress in the identification of the sex attractant pheromones has been extremely rapid. Ten years ago, few had been identified; today, such pheromones are known for several hundred species. This phenomenal progress in an area of endeavor previously considered by many to be unrewarding (or much too difficult) was made possible in part by extraordinary improvements in chemical instrumentation and techniques. Improved chromatographic equipment, materials, and procedures have aided in the separation of the tiny amounts of pheromone in insects, and more sensitive spectrometric analyses -- along with

associated methodology and devices for manipulating microgram amounts of compound -- have made possible identifications of these pheromones at microgram and sometimes submicrogram levels (1). With new workers entering this fast-developing field, pheromone identifications can be expected to continue at a high rate for some time to come.

Unfortunately, progress in the application of these pheromones in pest management has not been equally rapid despite the availability of highly effective sex attractant pheromones for many economically important species and despite the potential of controlling these pests with non-toxic pheromones used either alone or as part of pest management programs. Experimental programs have nevertheless shown that the use of pheromones in pest management is a basically sound practice and of sufficient promise to warrant increased exploration. It is anticipated that pheromones, though generally not replacements for insecticides, can help by increasing the effectiveness of insecticides and by improving the selectivity of their attack, i.e., their attack will be focused on the damaging pest and not on beneficial or non-target organisms. In the pursuit of this quest, considerable technology must be developed, and a much greater understanding of the effect of pheromones on insects must be acquired before these chemicals can be utilized to best advantage.

How the Sex Pheromones May be Utilized

The sex pheromones have been used a) for detection and survey of insect species, b) for mass trapping, and c) for disruption of the odor-guidance system that normally brings the sexes together for mating and propagation.

Detection and Survey. The value of detection and survey traps is well recognized in pest management circles. The capture of insects in traps signals the presence of the targeted species, and insecticides or other control measures may then be directed to the place where they are needed and when they are needed. In this way, more effective control has been achieved with less pesticide, and the movement of pests into uninfested areas has been quickly recognized and prevented. Thus, more than 100,000 pheromone traps were set out in the area east of the Mississippi River last year to monitor or detect infestations of the gypsy moth. Also, 17,000 traps, baited in this case with synthetic lures, are being maintained by the USDA across the southern periphery of the U.S. to detect any accidental importation of three highly destructive subtropical pests -- the Mediterranean fruit fly (*Ceratitidis capitata* (Wiedemann)), the melon fly (*Dacus cucurbitae* Coquillet), and the oriental fruit fly (*Dacus dorsalis* Hendel) (2). This early warning system, in use since the late fifties, has saved the USDA millions of dollars in potential eradication costs by detecting incipient infestations of the

pests, and, on quite a few occasions, quickly wiping them out before they could spread.

Now, however, researchers working with pheromones have begun to realize that the availability of a pheromone is only the first step in utilization of these chemicals for pest control. Just as the pheromones for different insect species are different, so are the responses of the insects likely to differ from species to species. Thus, for efficient use of these materials, the methods of utilization must be built around the behavioral patterns of each species. Knowledge of the behavior of each species under the conditions of pheromone use is therefore just as necessary as knowledge of the properties of the chemical itself, and considerable experimentation may be required to achieve optimum performance of the pheromone against a given species.

To illustrate, some parameters that must be considered when traps are to be used in detection and survey of a specific species include trap design, trap height, trap placement, trap durability, type of bait dispenser and its position in the trap, trapping means (e.g. adhesive, insecticide), emission rate of the lure, lure stability and quantity, duration of effectiveness, ratio of the ingredients if the lure is multicomponent, effect of aging of the lure, effect of host crop, effective distance of attraction, time of insect response, cost of the trap, and, perhaps ultimately, the relationship between trap catch and number of insects in the vicinity of the trap. Some of these variables are critical enough to make the difference between success and failure. For example, gypsy moth traps tested at heights up to 4 m caught best between ground level and 2 m (3): traps of the oriental fruit moth (Grapholitha molesta (Busck)) tested similarly caught almost no moths at ground level, caught best at a height of 1 m, somewhat less at 2 m, and few at 3 m (4). With the pecan bud moth (Gretchena bolliana (Slingerland)), which responds to the oriental fruit moth pheromone and is found in the same vicinity but on a different host, trap captures were again very low near ground level (1.5 m) but increased progressively as trap heights were increased to 9.1 m, the greatest height tested (5).

Likewise, subtle differences in chemical composition of a pheromone were shown to affect the mean captures of the oriental fruit moth; captures varied from less than one to 109 per trap when the E-isomer content of (Z)-8-dodecenyl acetate was changed from 0 to 20%; the optimum catch occurred with about 6% E isomer (6). Oddly enough, with the sympatric pecan bud moth, the same 0 to 20% variation of E-isomer content in the same compound caused no appreciable difference in catch (Table I) (7). Unquestionably, more attention must be devoted to the study of such trap parameters if the erratic results sometimes reported by early investigators are to be avoided.

Table I. Effect of E isomer in (Z)-8-dodecenyl acetate on captures of male oriental fruit moths and pecan bud moths in baited traps (7).

<u>% E isomer</u>	<u>Mean no. of males captured per trap</u>	
	<u>Oriental fruit moth</u>	<u>Pecan budmoth</u>
0	1.5 a	253.8 a
2	36.0 cd	226.3 a
5	108.8 e	215.8 a
7.5	27.3 bcd	241.3 a
10	5.7 ab	251.5 a
20	0.33 a	244.3 a

a/ Means followed by the same letter are not significantly different at the 5% level of confidence based on Duncan's multiple range test.

As an aside and by way of rationalization, it is likely that the many differences in the response of species help maintain the reproductive isolation of species in nature, particularly of those located in the same vicinity at the same time.

When all of the trap parameters are optimized, results can be gratifying. Thus, Gentry et al. reported a recapture rate of 69% for 1000 marked oriental fruit moth males that he released in a 2-acre orchard containing 5 traps (8) of a design and at a height found best in previous studies (4).

The bait dispenser, because it controls the release of the pheromone, may be considered the heart of a trap. The ideal dispenser should emit lure at a constant rate, preferably the optimum rate for attraction, over a prolonged period and hopefully for an entire season. Nonvolatile diluents, called keepers (9), minerals, plastic caps and matrices, and other materials and devices (e.g. 10-13) have been used to slow the volatilization of pheromones and thereby extend duration of effectiveness. Recently, a 3-layer plastic laminate, called a Hercon[®] dispenser 1/, was found to approach ideal performance for extended but limited periods of time (14). The pheromone, which is concentrated in the inside layer of the laminate, gradually diffuses out through the outer plastic layers, and regulation of emission is readily achieved by varying the thickness of the laminate and the area exposed. As a further consequence of its location in the inner layer, the pheromone is protected from degradation by oxidation, hydrolysis, and light. The value of this protective effect should not be underestimated because degradation products are often potent inhibitors of attraction; e.g. many pheromones are

1/ Mention of a proprietary product does not imply endorsement by the USDA.

acetates, and a number of the alcohols that form on deacetylation proved to be powerful inhibitors of the attraction of the pheromone even when they are present to the extent of only a few percent (4). The prolonging of activity of unstable aldehyde pheromones has been especially noteworthy. Good results with the Hercon laminate have now been obtained with a number of pheromones, e.g., those of the gypsy moth, boll weevil (Anthonomus grandis Boheman), tobacco budworm (Heliothis virescens (Fabricius)), pink bollworm (Pectinophora gossypiella (Saunders)), cabbage looper (Trichoplusia ni (Hübner)), lesser peach tree borer (Synanthedon pictipes (Grote and Robinson)), peach tree borer (Sanninoidea exitiosa (Say)), and bark beetles.

Mass Trapping. Traps may also be of value in the direct control of insect pests, e.g., for mass trapping of males before they can locate females for mating. However, the traps are apt to be useful only when infestations are very light, situations in which the ratio of traps to insects can be high enough to prevent the population of insects from growing (15, 16). However, a high population can be reduced to a low level with an insecticide (or by other means), and the traps may then be capable in themselves (without further use of insecticide) of preventing a population buildup. Recent trials have already shown that the mass-trapping approach is valid against low-level insect populations (17, 18).

An important theoretical advantage of mass trapping is its greater efficiency as the population diminishes -- to the point that it ultimately might be capable of eradicating a target species (16). This possibility focuses attention on the need for more efficient trapping devices and bait dispensers. Toward this end, the already-cited parameters needing attention in traps for survey and detection are likely to be important in traps used for control. Additional considerations are trap capacity, trap density (no./hectare) and distribution, and method of deployment.

Disruption of Pheromone-Guidance System of Insects. In 1960, the suggestion was made that insect sex pheromones could be released into the atmosphere (from small pheromone-containing particles) to confuse male insects seeking females for mating, and that in this way the reproduction of insect pests could be reduced (19). In other words, if synthetic pheromone were emitted from many dispersed particles, the males would be unable to distinguish between the odor of the synthetic and that the females generate to lead the males to them; the males would then not be able to find the females. This approach has special appeal in that the reproduction of the insect pest would be suppressed with an innocuous chemical, and the action of the lure would have no effect on the environment or on any but the offending species. (Toxicological data on disparlure, the gypsy moth sex pheromone, and on 8 other behavior-controlling chemicals

indicate that these chemicals have a very low order of toxicity (20). Such an approach to control the gypsy moth was further favored because of the extraordinary potency of disparlure (1 ng suitably formulated with a keeper remained effective for 3 months in the field (9)), the ability of the traps to monitor efficiently the whereabouts of the insect, the low cost of the synthetic lure (compared with most pheromones), the potential availability of the lure in large amount (1200 pounds were purchased in 1975), and the possibility of halting the spread of the gypsy moth from the presently infested Northeastern United States to the rest of the country.

As with mass trapping, the air-permeation or "confusion" approach theoretically becomes more efficient as the moth population declines (15). Accordingly, the population must be low for maximum or even adequate effectiveness; otherwise, males may find females by chance, a possibility that increases with increasing abundance of moths in a given searching area.

Formulation Research

We know now that the amounts of disparlure we used initially in our attempts to confuse the insect (actually only 50 mg/hectare) were much too low. However, even in these tests, we did disorient mate-seeking of males for as much as 3 weeks (21). We recognized that a suitable formulation had to be devised to demonstrate such disorientation for an entire season with sufficient lead time to allow for lure application (about 6-8 weeks), and because the area to be treated for gypsy moth is potentially enormous, we settled on aerial distribution of the confusant as the most feasible means of application.

Laboratory tests were conducted initially on formulations with a great variety of materials, and these tests were followed by field trials with laboratory-reared insects on 16-hectare plots to evaluate the performance of the most promising candidates. These tests were conducted out of season by our USDA APHIS laboratory at Otis Air Force Base, Mass. to avoid interferences that might occur during the season when unknown numbers of native insects would be in or near the test sites. A treatment was considered effective if a high proportion of the males released in the treated area was unable to find monitor traps baited with disparlure or females. Captures in treated areas were always compared with those in untreated ones. Tests were made with disparlure on or in hydrophobic paper, cork, molecular sieves, and microcapsules.

The microcapsules, which were supplied originally as a water slurry containing about 30% microcapsules, turned out to be the most promising of the formulations, and two types were evaluated further. One had a gelatine-base wall that was plastic coated, and the other had a nylon-based wall. Contracts were let with the manufacturers of the microcapsules to produce a variety of

these materials, which were then tested in our Beltsville laboratory to determine their rates of lure emission over prolonged periods. Some of the microcapsule parameters that were varied were diameter of the microcapsule, thickness of the capsule wall, solvent in the capsules and concentration of disparlure therein, degree of crosslinking of the plastic wall, and amount of plastic coating on the capsule.

Laboratory Tests. Even though the testing of pheromone formulations in the field, say as confusants, provides basic data concerning performance, complete reliance on field testing is impractical. Formulations generally require many changes in the course of development, and field tests to check each change would be prohibitively expensive and time-consuming, especially when such tests are limited to certain seasons and/or must be made over a large area, e.g., with flying insects. More appropriately, laboratory procedures can be utilized to determine the emission rates of pheromones (or similar behavior-controlling chemicals) from slow-release formulations at conditions approximating those encountered in the field; then these data can be compared and correlated with the results obtained in the field. For example, if a formulation performs well in the field for 2 weeks but poorly for the next 2 weeks, its performance in the laboratory can be characterized by periodic measurement of emission of lure at given conditions. The performance is then compared in the laboratory with that of others at identical conditions, and those providing adequate lure emission for longer periods can then be selected for field testing. Also, the effect of each change in formulation, e.g., addition or removal of an ingredient, on pheromonal emission and persistence can be determined in the laboratory, and ingredients can be selected to provide optimum performance.

Since the rate of emission of the pheromone is probably the single most important parameter governing the performance of a pheromone dispenser in a trap or a confusant broadcast on foliage in the field, the great value of the emission rates determined in the laboratory under controlled conditions can be readily appreciated.

In some of our early work, we tried to determine emission rates by periodic analysis of the amount of pheromone remaining in samples. A large series of identically made samples had to be prepared because samples were destroyed in the analysis. We found this procedure unreliable because the pheromone lost on aging often had not all volatilized; instead, some was lost by degradation, so the emission rates found were incorrect. Far better results were obtained by direct measurement of the pheromone taken up by air passed over the sample at a fixed rate. Since the sample was not destroyed in the analysis, the emission rate could be determined on the same sample for the duration of aging. In essence, far fewer samples were required for the

emission studies, and results were much more reliable.

A simple device used to collect volatiles from pheromone dispensers (usually from traps) is shown in Figure 1 (22). Air at 100 ml/min. and at a constant temperature is passed through a sintered glass gas dispersion tube into a glass tube containing the pheromone dispenser. The air picks up the vapors and carries them via an adaptor into a solvent contained in a centrifuge tube. With disparlure dispensers, a 4-hour collection period was usually necessary to obtain enough lure for a good analysis. After such a collection, the adaptor is washed with solvent (and the washings added to the collection solvent) to completely retrieve the volatilized pheromone. The combined solvent and washings are concentrated, an aliquot is analyzed by gas chromatography, and the emission rate is calculated in micrograms of lure emitted per hour.

Figure 2 shows a more complex device used to collect the emission of pheromones from confusant formulations spread on planchets 5 cm in diameter (22). A weighed sample (0.5 g) of wet microcapsules (residue from filtration of the aqueous slurry) is carefully dispersed with water on the planchets and then allowed to dry at room temperature for a day. Emission of pheromone from the microcapsules is then determined periodically, after aging at fixed conditions, by passing 100 ml of air/min. at a constant temperature over the microcapsules and collecting the vapors in a solvent. Operation of the apparatus is described in the legend of Figure 2. The inner surfaces of the petri dish N and the adaptor Q must be washed carefully with solvent to collect all the volatilized pheromone; as before, the washings are added to the collection solvent, and gas chromatographic analyses are made on the concentrated solvent. The samples in the planchets may be aged by exposure in a constant-temperature room. To speed our work, we used a special apparatus that accelerated the aging process and allowed 9 planchets to be aged at almost identical conditions so the emission rates could be compared (22). We included a known formulation (usually our best one) and determined emission rates relative to it. In other words, we determined relative emission rates, not absolute ones.

In addition to the foregoing, we sent important fresh and aged samples to our biological laboratory at Otis Air Force Base for bioassay to verify our chemical findings, i.e., high emission rates of lure should coincide with high biological activity, and vice versa. We also compared formulations of gypsy moth confusant by applying them directly onto oak leaves (a favored food) and then inserting the coated leaves into the apparatus of Figure 1 for collection and measurement of the disparlure emitted. Determinations were made periodically over a period of several months. At the same time, other leaves coated identically were evaluated biologically by exposing them in traps to male moths either in a bioassay chamber or in the

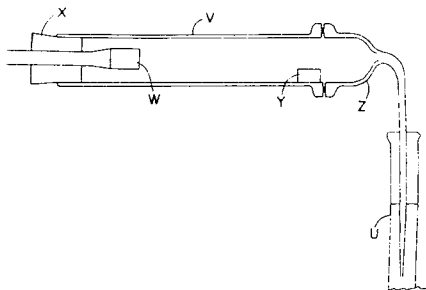


Figure 1. Emission collection from pheromone wicks. Air (100 ml/min), which enters glass tube V via gas dispersion tube W held by rubber stopper X, passes over sample Y and out through adapter Z, exiting through solvent in 12-ml centrifuge tube U (22).

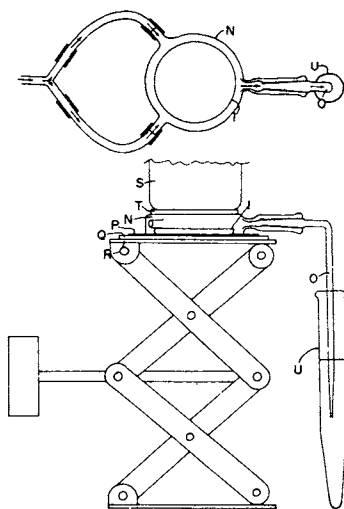


Figure 2. Emission collection from planchets. Above is top view of petri dish N with arrows showing air entering (100 ml/min) via 2 glass tubes (5-mm OD) and leaving via exit tube O; planchet I is held within. Bottom is side view of petri dish N mounted on rubber dam P, polyurethane foam sheet Q, and table R of lab jack. Weight S (water-containing jar) rests on rubber pad T, which presses on petri dish and prevents passing air from escaping from bottom edge of petri dish. Air, which leaves via exit tube O, passes through solvent in 12-ml centrifuge tube U. Drawn to scale (diam of planchet is 5 cm) (22).

field. The number of males caught with each formulation was considered a measure of attraction and very likely of disparlure emission. Of course, if inhibitors of attraction were formed on aging, the chemical and biological tests would not agree, and we would be alerted to this difficulty.

Since natural growth of the leaf and wind, rain, and other climatic factors would tend to remove the confusant microcapsules (or other such particles) from the leaves to which they were applied, a sticker was added to the formulations to assure adhesion of the particles to the leaves for the necessary interval. The stickers tried were water-dispersible, which once dried (generally less than 2 hours after application) were not again dispersed by water (or rain or high humidity). Stickers were tested by adding them to each formulation (in several concentrations), applying the combinations to oak leaves, allowing 1 to 2 hours for drying, spraying the leaves with a stream of water from a wash bottle, and then inspecting the leaves to determine the extent to which the confusant particles were removed by the action of the water. For formulations adjudged sufficiently adhering, the coated leaves were aged and periodically sprayed with the water stream to determine whether the confusant persisted. (Living leaves of oak seedlings were used for long aging periods.) In this way, the stickers were evaluated in terms of time required for drying and degree of adhesion over the desired interval. Coated leaves were also soaked in water for several hours (to simulate exposure to rain) and subjected to the action of the water stream to check adhesion of the confusant particles.

The method of application of confusant was determined from the type of formulation used. One of our earliest field trials was made with aerially dispersed disparlure-coated cork granules, which were tested with and without a sticker. The sticker in solution form was sprayed onto the dry cork granules as they emerged from the aircraft. The cork formulation with no sticker failed after the first rain; the formulation with sticker performed well for at least 6 weeks despite some very heavy rains (18). This result highlights the importance of a good sticker.

The microcapsule water slurries presently used are applied from aircraft with conventional spray equipment. Since these capsules are lighter than water and tend to separate on standing, a thickener was added, and the suspension was stirred during the spraying operation to disperse the microcapsules uniformly in the aqueous phase (18).

A typical formulation of the microcapsules consisted of the following ingredients:

17.6% capsules (25-200 μ diam., 10% gelatine-base wall, 1/4-coated with plastic) containing 2.2% disparlure in xylene or 1:3 amyl acetate-xylene, supplied by National Cash Register Company, Dayton, Ohio as a 30% aqueous slurry.

- 2% UCAR latex 680.
- 29% of 1% hydroxyethyl cellulose (Soilserve, Inc., Salinas, Calif.).
- 1.7% of 1% aqueous potassium hydroxide.
- 49.7% water.

For application of 2 g disparlure/acre (5 g lure/hectare), 575 ml/acre of the above formulation was applied. A similar nylon-base capsular formulation was supplied by Pennwalt Corp., King of Prussia, Pa. (18). The formulations were sprayed from Spraying Systems No. 8010 tips on spray boom nozzles.

Substantial losses of spray may occur from aircraft, and much depends upon the conditions of treatment. Flights must be made in calm air to avoid excessive drift of spray from the target area. The aircraft must fly close to the tree tops (about 20 m above the forest canopy) so the spray strikes the foliage while it is still wet. (It is presumed that formulation droplets will dry excessively in falling from great heights and then will be less likely to adhere to the foliage.) Rain occurring before the spray can dry fully (within 2 hours after spraying) may remove much of the confusant from the foliage. In general, the percentage of spray landing on target is far less from aircraft than from ground equipment, so allowances must be made for some losses of spray in aircraft applications. It is even conceivable that the best formulation could be rendered ineffective by an improper application.

Large Field Trials to Prevent Gypsy Moth Mating

At this point, some information on the gypsy moth is appropriate. The insect is a serious pest of forest, shade, and orchard trees in Europe and the Northeastern United States. About early May larvae emerge from eggs laid the previous summer and proceed to consume the leaves of their favored hosts; trees are ultimately defoliated and killed by heavy infestations. When fully grown, the larvae pupate. They emerge as adult moths some time in July or early August depending on the local climate. The male, a strong flier, seeks out the non-flying female, being guided to her by the wind-carried scent or sex pheromone she emits. The male mates with the female, she lays some 300-800 eggs in a mass, and another generation of the insect is on its way.

Following the identification and synthesis of the gypsy moth sex pheromone in 1970 (23), small field trials, usually on 16-hectare plots, were conducted (by USDA and by the Pennsylvania State University) to evaluate new formulations and techniques for the direct control of the gypsy moth. Results obtained with the microencapsulated confusant formulations in 1971 and 1972 were promising enough to justify a greatly expanded trial in a natural infestation in 1973.

The 1973 test was conducted in Massachusetts by the Massachusetts Department of Natural Resources in cooperation with the University of Maine and the USDA (24). The area treated was deliberately large -- about 60 km² or 24 mi.² -- in order to approach and evaluate practical conditions of operation and also to minimize any "edge effects" that might result from the incursion of males into the disparlure-treated areas during the moth flight season. On July 6-10, just before the anticipated moth emergence, the formulation described in the previous section (with xylene as the encapsulating solvent) was applied by three aircraft at a rate of 5 g disparlure/hectare. Another area of size similar to the treated area was left untreated to serve as a control.

In both areas, one hundred 0.1-hectare (0.25-acre) plots, suitably distributed, were monitored as follows:

In early spring before foliation of the trees, egg-mass counts were made.

In July and August (post-treatment) counts were made of moths captured by traps (2/plot) each baited with a cotton wick containing 10 µg disparlure plus 2 mg trioctanoin as keeper (which approximates a female in attraction) and by traps (2/plot) each baited with a female. In addition, fertilization of untethered females (2/plot) exposed on tree trunks (Figure 3) was determined. Females in the traps and exposed on tree trunks were replaced every third day.

In October and November, egg-mass counts were again made.

In the untreated area, the disparlure traps caught 2193 males; only 63 males were taken in the treated area. The decrease in captures was more than 97%. Results were even more striking with the female-baited traps. A total of 1136 males were captured in the untreated area, and only 1 was caught in the treated area. The trap captures are shown graphically in Figure 4 for the entire season. Undoubtedly, the odor-guidance system of the moth was seriously impaired by the disparlure treatment.

Figure 5 shows the percentages of the untethered females that were found fertilized in the treated and untreated areas during the period immediately after treatment with disparlure to the end of the moth flight season. For 2 1/2 weeks after treatment, mating of recovered females in the treated area remained low even though most of the time 95-100% of the females in the control area were mated. Subsequently, the percentage mated in the treated area climbed to high levels for 11 days though it then fell to about 56% during the last week of the test (which shows that the microcapsules were still exerting an effect at 5 weeks post-treatment). Thus, despite the apparent disruption of the odor-guidance system of the insects indicated by the greatly decreased trap catches throughout the flight season (Figure 4), males were probably numerous enough in the treated area to locate females by chance.



Figure 3. Placement of untethered female moth used in determining rate of fertilization in areas treated and not treated with disparlure microcapsules.

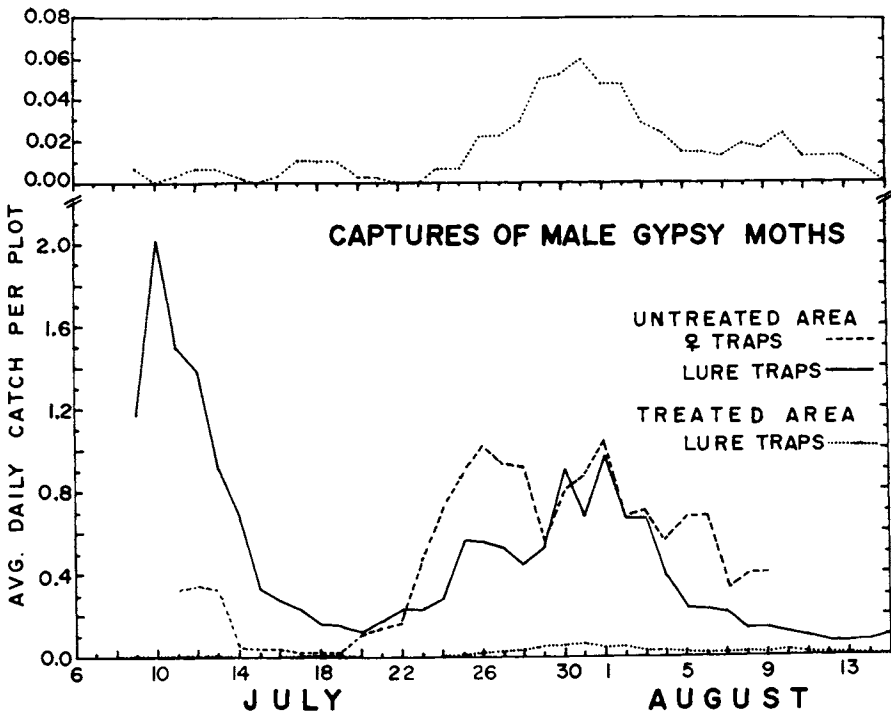


Figure 4. Captures of male gypsy moths by lure- and female-baited traps in untreated area and in area treated July 6-10 by application of microencapsulated disparlure at the rate of 5 g disparlure/ha. Upper graph shows captures by lure traps in treated area on a 10-fold expanded scale, (24).

However, the pre- and post-season egg-mass counts showed that the treatment did prevent a significant buildup of the moth population. These counts were not significantly different in the treated plots (though post-season counts were 1.4-1.6 times the pre-season values), but in the untreated plots, post-season counts were 3 to 3 1/2 times the pre-season counts, a significant difference.

In 1974, trials similar to those of 1973 were again undertaken (by the same groups) in a natural infestation in the same general vicinity of Massachusetts (25). Data were sought on a) the relative effect of doses of lure greater than those applied in 1973, b) the feasibility of reducing a high level population of gypsy moth larvae with insecticide before disparlure was applied during the mating flight, c) the effectiveness of mass trapping with high-potency traps (Figure 6) and d) the value of high-potency traps for monitoring disparlure-treated areas (Figure 7). The same microencapsulated formulation of disparlure (except that the solvent in the capsules was 1:3 amyl acetate-xylene) was used. The traps used in mass trapping and in monitoring were baited with high-potency plastic laminates containing 16 and 8 mg disparlure/trap, respectively; Tack-trap[®] adhesive was used to capture responding insects.

The dosage tests consisted of 1) one treatment of 5 g disparlure/hectare as in 1973, 2) two treatments of 10 g lure/hectare 2 1/2 weeks apart, and 3) one treatment of 20 g lure/hectare. The treatment with 5 g lure/hectare gave definite though less than adequate suppression: mating success of exposed females was reduced 47% compared with the control, and both male trap captures and post-treatment egg-mass counts indicated about 50% control. The higher dosages were highly effective: mating success of the untethered females was reduced 94-97%, and male captures and post-treatment egg-mass counts were likewise markedly suppressed. In essence then, the dosage tests established that 20 g lure/hectare (8 g lure/acre) were enough to suppress drastically the low-level moth population (from 10-15 egg-masses/hectare pre-season).

The test to reduce a potentially high-level population to a low level before disparlure treatment was conducted on two islands (one island being the control) in the Quabbin Reservoir to minimize any influx of male moths from adjoining territory. It turned out that the insecticide applied to the 6-km² treated island (two application of carbaryl as Sevin[®] 4-oil at 1.14 kg AI/hectare 11 days apart) depressed the moth population to too low a level, and the females found mated and the post-season egg-mass counts were simply too low to establish significant differences among the following three treatments that were superimposed on the insecticide treatment: 1) 20 g lure/hectare as microcapsules, 2) mass trapping with 25 high-potency traps/hectare, and 3) no treatment. The three treatments all showed the same degree of mating by the exposed females, 2.4-3.2%

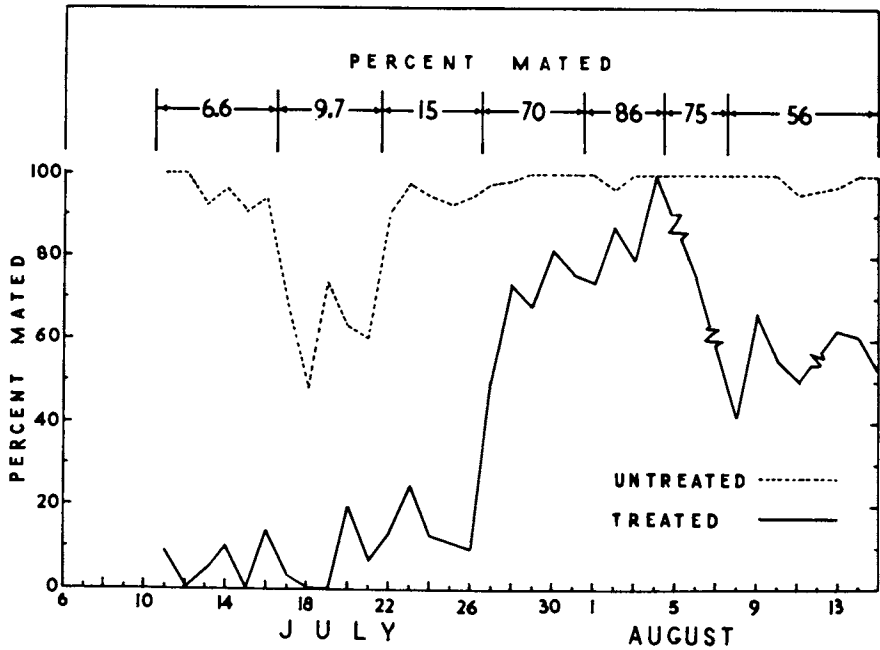


Figure 5. Percentage of recovered female gypsy moths found fertilized in the treated and untreated areas. The relative percent mated (treated/untreated) is shown above the graph for the different periods of the test. Data were not obtained on Aug. 5, 7, and 12 (indicated by breaks in solid-line graph), (24).



Figure 6. Triangular trap being stapled to tree in experiment to determine effectiveness of mass trapping.

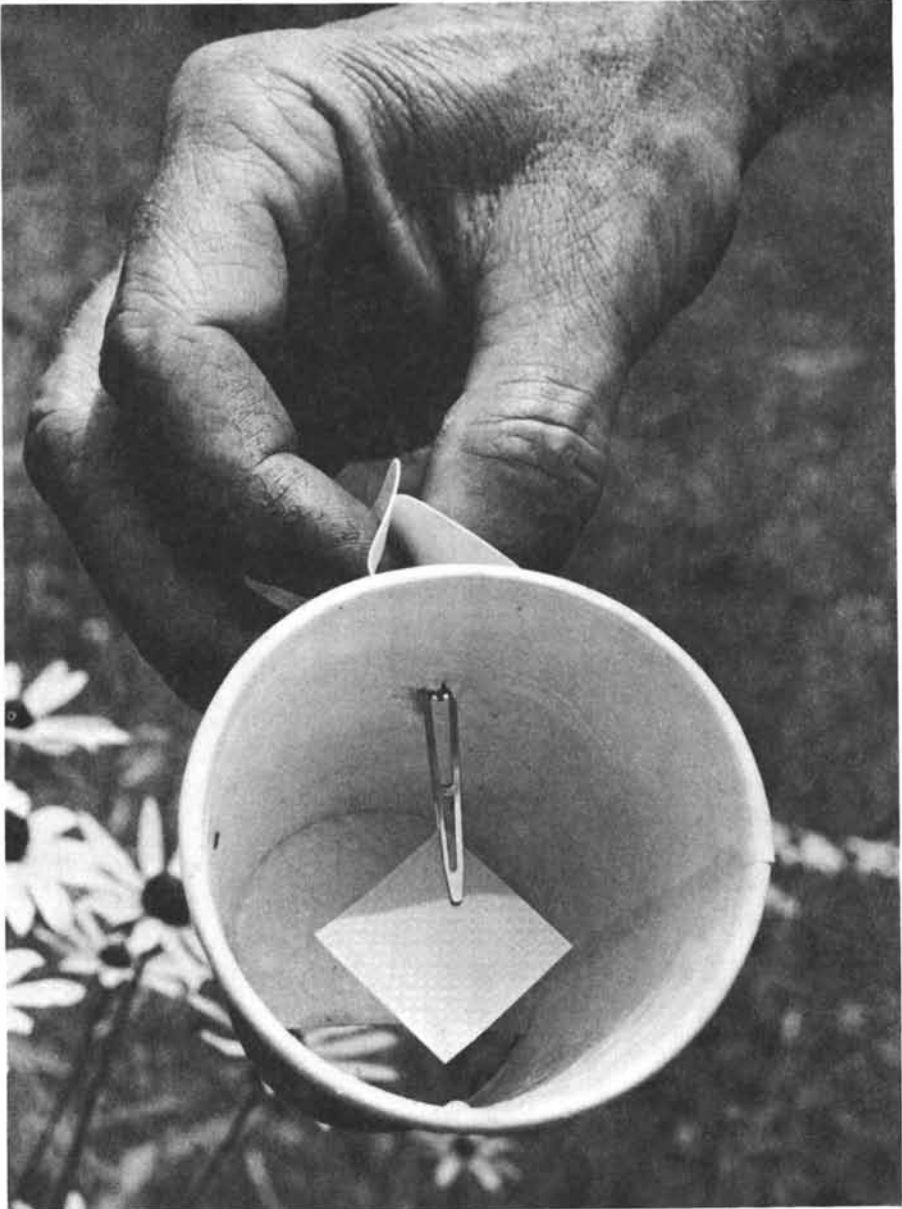


Figure 7. Drinking cup monitor trap showing high-potency plastic laminated dispenser of disparture.

relative to mating on the untreated island where 85.4% mated despite a very low initial population. However, the trend of the data, trap captures and post-season egg-mass counts, definitely showed the effect of the disparlure confusant and of the mass trapping. For example, captures in monitor traps totalled 14 in the area treated only with insecticide compared with 5 each in the other two treated areas and 467 in the untreated control. (Because of an unexplained natural collapse of gypsy moth populations throughout the Northeastern U.S. in 1974, post-season egg-mass counts were low in all plots, including the control.) It is considered encouraging that the only area in which no post-season egg masses at all were found was the one treated with insecticide and then with the disparlure microcapsules. In the area treated with insecticide only, 8 egg masses were recovered. Also, 1151 moths were taken in the area that was treated with insecticide and mass trapped, which shows that a substantial number of males were left in the insecticide-treated area and were available for mating with the untethered females. In addition to the potential usefulness of mass trapping in controlling low-density populations, mapping of the trap captures could at the same time provide an assessment of the distribution and size of incipient infestations in spotty but generally infested areas.

By utilizing the high-potency Hercon bait dispensers in the monitor traps, we found that males could be captured in the disparlure-treated areas. (Very few insects were captured by the monitor traps baited with 10- μ g disparlure in the 1973 tests, an indication that much more potent traps would be needed to monitor the lure-treated areas.) Indeed, the numbers of males taken in the high-potency traps greatly exceeded the numbers of untethered females found mated. For example, only 1 and 2 untethered females were found mated in the areas treated with 10 + 10 and 20 g lure/hectare when 32 and 22 males, respectively, were captured by the high-potency monitor traps in the same areas. Thus, the high-potency traps should be useful in monitoring disparlure-treated areas, in designating areas that require additional treatment or attention, in signalling at an early stage (before mating occurs) that the disparlure concentration in the air is falling below the level required to disrupt orientation so another treatment can be made to maintain disruption, and in providing a measure of the mating potential and perhaps even of the residual male population in an area.

Overall, the 1974 field results indicate that air permeation with slow-release disparlure microcapsules applied at the rate of 20 g lure/hectare is effective in reducing mating success in low-level infestations of the gypsy moth or in infestations brought to low levels with an insecticide.

Need for Monitoring Populations

If we are to make optimum progress in direct insect control with such population-dependent tools as pheromones, accurate means of estimating insect populations have to be developed. With such estimates a proper judgment can be made as to whether the pheromone approach is applicable in a given situation, and they can also be valuable in assessing progress as insect populations are reduced to very low levels. Presently, traps are the chief tool for such assessments, and a high-potency trap with a uniform and constant attraction would be invaluable. Toward this end, a bait dispenser that emits sufficient lure at a constant rate (aside from the effect of temperature) is needed. In this regard, it is recognized that captures by pheromone-baited traps may not be proportional to insect populations when infestations are of moderate to high density because native females compete with lure-baited traps. Thus, at least theoretically, the traps should make fewer captures proportionally as competition from native females increases. We believe this effect was operating in the 1973 gypsy moth trials (24).

Other Studies

Microencapsulated pheromones have also been tested as confusants against the codling moth (Laspeyresia pomonella (L.)) and the oriental fruit moth. In areas treated with codling moth pheromone, trap captures of the moth in monitor traps were substantially suppressed (compared with those in an untreated area) for up to two weeks (Moffitt et al., unpublished). Similar results were obtained with the oriental fruit moth with trap captures being suppressed for up to 5 weeks (8).

In addition, attempts were made to disrupt mate-finding of the gypsy moth with the olefin precursor of disparlure, which has been shown to be an effective inhibitor of the response of males to disparlure in traps (26). Applications up to 61.75 g of the olefin/hectare in microcapsules were found ineffective in trials conducted before and during the moth flight season. In concurrent tests with 15 g disparlure/hectare fertilization of females was significantly reduced (27). A similar attempt to disrupt mate-finding with an inhibitor of the codling moth pheromone (28) was likewise unrewarding (Moffitt et al., unpublished).

Summarizing Comments

Sex attractant pheromones provide a promising means of controlling insect pests. Their use in the detection of pest buildups, particularly for the guidance of control measures, appears to be established. However, for the use of pheromones in direct control of insects, as in mass trapping or air-

permeation, considerable technology needs to be developed, especially since much of this technology is likely to differ with different species. Efforts thus far have shown promise against several important insect pests.

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Use of Kairomones to Promote Action by Beneficial Insect Parasites

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Parasites and predators have been used successfully to control insect pests. However, efforts to control insect pests with parasites, especially the release of parasites, have often failed. These failures occurred because of a number of factors, most of which could be corrected if more information was available concerning the host-parasite relationship. Information concerning the roles of chemicals (kairomones) in this relationship has recently appeared. These chemicals play a major role in the host selection sequence of the parasite and can be used to manage parasites to make them more effective as a pest control measure.

The following discussion will be limited to insect parasites, but most of the principles are applicable to predators as well.

Host Selection

An understanding of the host-selection phase of the host-parasite relationship is a prerequisite to a study of the role of kairomones.

Salt (1) and Flanders (2) divided the host-selection processes into four phases. These steps are: (a) host habitat finding, (b) host finding, (c) host acceptance, and (d) host suitability. The first two steps have been expanded by Lewis et al. (3) to provide a better understanding of the process, which is shown in Figure 1. This figure was designed to accommodate a variety of parasites, and the behavior of any particular species might vary to some extent from this design (4).

The transition (T_1) from inactivity to initial random movement is initiated by an innate appetitive drive (S_1) together with prevailing environmental conditions and the physiological state of the parasite. Upon detecting the appropriate olfactory, visual, or physical cues (S_2), the parasite passes (T_2) into a habitat-scanning phase (5,6,7,8). Then upon reception of the appropriate stimuli, the parasite enters a find and attack cycle

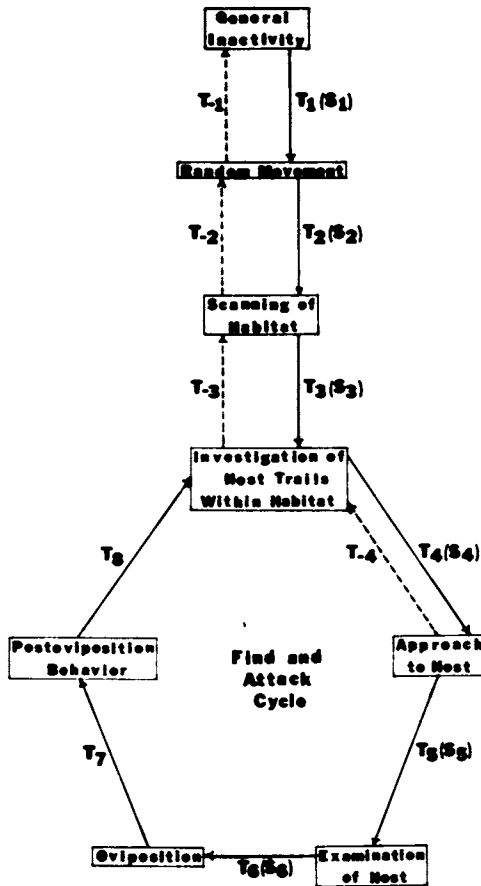


Figure 1. Basic sequence of host-finding activities of female insect parasites (3)

(T₃). These stimuli include such host evidence as frass, moth scales, decomposition products, and other cues associated with the host (6,7,9,10,11,12,13)

There are usually two or three substeps associated with the search of host trails, all of which are apparently released by stimuli from the host (14). Detection of the host results in an approach to the host (T₄). This transition is stimulated (S₄) by olfactory, visual, auditory, and other chemical and physical cues (9,15,16,17,18,19,20). The examination of the host and oviposition, (T₅) and (T₆), are responses to chemical, visual, and tactile stimuli S₅ and S₆ (1,15,21,22,23,24,25,26,27). Post oviposition behavior is variable and apparently innate. Some parasites make an intense search of the surrounding area immediately after oviposition (16,28). The female then reverts (T₈) to search for other hosts within the habitat.

The ability to manipulate the parasite at the T₃ transition is of great importance to the effective use of parasites in a pest control program. It is this step that determines whether a parasite remains in a given area or moves to another habitat. Contact with the stimulus (S₃) must occur periodically to reinforce and maintain the find and attack cycle (3).

The pathway from a newly emerged or resting parasite to a parasitized host is complex and dependent upon many outside factors. A knowledge of these factors and the ability to influence them are very important in parasite management.

Insect Kairomones

A number of chemicals have been identified as the kairomones that affect parasitization of these insect hosts. These are summarized in Table 1.

The chemical, 13-methylhentriacontane, was identified by Jones et al. (29) as the component of the feces of larvae of Heliothis zea that elicits the host-seeking response of the larval parasite, Microplitis croceipes. (The adult female parasite oviposits in the larvae. Upon hatching the parasite larvae live inside the larvae until maturity. At that time it emerges from the dying Heliothis zea larvae and pupates.) Upon detection of larval feces, the parasite initiates an intense antennal investigation of the surrounding area. This same behavior was observed when the female was exposed to synthetic 13-methylhentriacontane. In petri dish bioassays, the parasite responded to as little as 50 ng of this chemical, and 150 ng elicited a consistent and strong response. Thus this chemical acts as an S₃ type stimulant in the scheme shown in Figure 1, and may have some role as S₄. Microplitis croceipes also responded to a lesser extent to the other methylhentriacontanes that were shown to be present in the larval feces (Table II), but mixtures of the isomers resulted in a dilution of the most active

Table I
Chemicals identified as kairomones of parasitic insects

Parasite	Host	Type of stimulus (refer to Figure 1)	Chemical(s)	Source	Reference
<u>Microplitis croceipes</u> (Cresson)	<u>Heliothis zea</u> (Boddie)	S3	13-methylhentriacontane	hemolymph, cuticle, frass	(29)
<u>Cardiophiles nigriceps</u> Viereck	<u>Heliothis virescens</u> (F.)	S3 and S4	11-methylhentriacontane 16-methyldotriacontane 13-methyltriacontane	mandibular gland	(30)
<u>Orgilus lepidus</u> Musebeck	<u>Phthorimaea operculella</u> (Zeller)	S3 or S4	heptanoic acid	mandibular gland	(13)
<u>Trichogramma evanescens</u> (Westwood)	<u>Heliothis zea</u>	S3	tricosane	hemolymph adult cuticle	(31)
<u>Archytas marmoratus</u> (Townsend)	<u>Heliothis zea</u>	S6	protein	feces, hemolymph	(33)
<u>Venturia canescens</u> (Grav.)	<u>Anagasta kuehniella</u> (Zeller)	S6	unknown	mandibular gland	(32)
<u>Itoplectis conquisitor</u> (Say)	<u>Galleria mellonella</u> (L.)	S6	amino acids	hemolymph	(26, 27)
<u>Cheiloneurinus noxius</u> Compire	<u>Coccus hesperidum</u> L.	S5	protein	hemolymph	(34)

components (Table III). The response to a mixture of 50 ng of each of the two most active isomers was 0.92, which was roughly an average of the responses to 50 ng of each component alone.

Table II

Response of female Microplitis croceipes to 150 ng of synthetic kairomones

Compound	Score ^{a/}
9-Methylhentriacontane	0
11-Methylhentriacontane	.22
12-Methylhentriacontane	.48 a
13-Methylhentriacontane	2.32 c
15-Methylhentriacontane	1.68 b

^{a/} Scores not followed by the same letter are significantly different at the 0.05 level of probability. The 9- and 11-isomers are not included in the statistical comparison because only one replication (8 observations) was tested. Scores based on observation of behavior. 0 - no response, 3.0 - strongest response.

Table III

Response of Microplitis croceipes to various mixtures of synthetic host-seeking stimulants

Compound	Concentration (ng)	Score ^{a/}
13-Methylhentriacontane	50	1.21 c
15-Methylhentriacontane	50	.63 ab
13- and 15-Methylhentriacontane	25 each	.39 a
13-Methylhentriacontane	100	2.49 e
15-Methylhentriacontane	100	1.76 d
13- and 15-Methylhentriacontane	50 each	.92 bc

^{a/} Scores not followed by the same letter are significantly different at the 0.05 level of probability. Scores based on observation of behavior. 0 - no response, 3.0 - strongest response.

A similar group of compounds has been identified as host-seeking stimulants for Cardiochiles nigriceps, a larval parasite of Heliothis virescens (30). The active chemicals were several

methylhentriacontanes, methyl-dotriacontanes, and methyltritriacontanes. The response of the parasite to 5 μg of each chemical is shown in Table IV. The most active compounds were 11-methylhentriacontane, 12-methyl-dotriacontane, and 13-methyltritriacontane, and the parasites were more responsive to mixtures of the most active components. Table V reports responses to some of the most active mixtures and the results of a dose response test. There was an optimum amount of material for activity that produced a bell-shaped curve of response. Optimum activity was obtained with 500 ng of a mixture of the three most active chemicals. These materials are active in the T_3 and T_4 transitions since they acted as stimulants S_3 and S_4 . Their role in transitions T_5 and T_6 with both Microplitis croceipes and Cardiochiles nigriceps is unknown. However, it is very probable that they have a part here also.

These data do not imply that these chemicals act alone to effect the transitions discussed. Preliminary tests indicate that chemicals released from the plant as a result of host feeding may act in combination with the identified kairomones.

Hendry et al. (13) identified the host-seeking stimulant of Orgilus lepidus Musebeck, a larval parasite of the potato tuber worm, Phthorimaea operculella, as heptanoic acid. The parasite also responded to hexanoic acid and to a much lesser extent to octanoic acid. Again the dose response curve was bell-shaped; optimum activity occurred at 100 ng. This kairomone acts as an S_3 and/or S_4 stimulant at the T_3 and T_4 transitions.

Kairomones for the egg parasite, Trichogramma evanescens were identified by Jones et al. (31). This parasite oviposits in the egg of the host wherein the parasite larvae matures and pupates following hatch. The adult parasite emerges from the host egg to mate and repeat the life cycle. The active chemicals, isolated from scales of adult Heliothis zea, were docosane, tricosane, tetracosane, and pentacosane. Responses to kairomones by this parasite were determined by recording the increases in parasitism brought about when these chemicals were applied to the host egg substratum. Synthetic tricosane, the most active of the four identified chemicals, increased parasitism 1-1/2 to twofold when it was used at a rate of 6 pg/cm^2 with host eggs held in a petri dish and exposed to the parasites for 45 minutes. In similar tests with pea seedlings as a substratum in the greenhouse, parasitism was markedly increased by tricosane applied at a rate of 250 pg/cm^2 . Studies indicate that tricosane is active at the T_3 transition and acts as an S_3 stimulant.

Extracts of Heliothis zea moth scales elicited a similar response in Trichogramma pretiosum Riley, but the active chemicals have not been identified. Tricosane caused no significant response, though dotriacontane increased parasitism 1-1/2 to twofold in the laboratory petri dish bioassays; however, its presence in moth scales has not been demonstrated.

Table IV
 Response of female *Cardiochiles nigriceps* to 5 μ g of synthetic methyl-branched hydrocarbons found in fractions active as host-seeking stimulants (30).

Hydrocarbon chain	Response rating ^{a/} of compound with position of methyl branch indicated									
	9	10	11	12	13	14	15	16	17	
Hentriacontane	0.82	-	1.65	1.45	0.53	-	0.76	-	-	
Dotriacontane	-	1.12	-	1.59	0.31	1.46	0.44	2.29	-	
Tritriacontane	1.32	-	0.92	-	1.81	-	0.18	-	0.41	

^{a/} Based on a minimum of 30 observations. The insect response was rated from 0 to a maximum of 3.

Table V
 Response of *Cardiophiles nigriceps* to 4 concentrations of compounds active as host-seeking stimulants and of 3 of their mixtures (30)

Compound	Response rating ^{a/} with total concentration in μg indicated			
	50	5	0.5	0.05
11-Methylhentriacontane	0.36	1.65	0.50	0.12
12-Methylhentriacontane	0	1.45	0.22	0
12-Methyldotriacontane	0	1.08	0.89	0.17
16-Methyldotriacontane	0	1.79	1.60	0.38
9-Methyltriotriacontane	0.29	1.32	0.25	0.09
13-Methyltriotriacontane	0.13	1.81	2.37	0.52
11-Methylhentriacontane + 12-Methyldotriacontane + 13-Methyltriotriacontane	-	1.87	2.50	0.75
12-Methylhentriacontane + 12-Methyldotriacontane + 13-Methyltriotriacontane	-	2.60	2.83	1.98
11-Methylhentriacontane + 16-Methyldotriacontane + 9-Methyltriotriacontane	-	2.25	2.75	2.12
9-Methyl-9-triacontene	1.95	1.28	0.89	-

^{a/} Based on a minimum of 24 observations.

Several other kairomones have been shown to exist although their identity is unknown. Corbet (32) and Mudd and Corbet (12) isolated a chemical from Anagasta kuehniella that elicited ovipositional behavior in Venturia canescens. This material acts as an S_6 stimulant, but step T_6 is most often a two-step process composed of the "sting" and the egg release, each with its own stimulus. The material isolated from A. kuehniella effects the "sting". Chemicals that elicited egg release by the parasite, Itoplectis conquisitor, a larval parasite of Galleria mellonella, were identified by Arthur et al. (26) and Hegdekar and Arthur (27) as several amino acids in the hemolymph of the host. Nettles and Burks (33) isolated a protein in the feces of Heliothis zea larvae that serves as an S_6 stimulant for Archytas marmoratus (Townsend), a parasite of Heliothis zea larvae. Also Weseloh and Bartlett (34) isolated a protein from Coccus hesperidum that activates the T_5 transition of the parasite, Cheiloneurinus noxius.

Origin of Insect Kairomones

The sources of the kairomones isolated and identified to date are shown in Table 1. Most of these chemicals, with the possible exception of the A. kuehniella material, are not confined to any one tissue or organ within the insect though when a mixture of chemicals is involved, the optimum ratio may be found in one organ; for example, gas chromatographic data showed the presence of similar hydrocarbons with dissimilar ratios in samples of mandibular gland, cuticle, hemolymph, and frass of several lepidopteran larvae. However, the primary function of the kairomones has not been elucidated. For example, the saturated hydrocarbons are part of the waxy layer of the cuticle and serve as a water barrier that protects the insect from desiccation, but the reason for their presence in the mandibular gland is not as clear though they probably lubricate the ingested food. In the hemolymph, they probably serve as precursors to new cuticle formation (35). Synthesis probably occurs in the oenocytes (36). The presence in frass then is the result, in part at least, of mandibular gland secretion and exuvia consumption. The amino acids are, of course, common intermediary metabolites, and proteins can serve any of a large number of functions. The function of the heptanoic acid is unknown.

Kairomone Effects on Field Behavior

Field Treatments. The effects of an H. zea moth scale extract on Trichogramma evanescens is shown in Table VI (37). Cadra cautella (Walker) eggs were placed on alternately treated (sprayed with a diluted hexane extract of moth scales) and untreated (sprayed with hexane only) leaves in a cotton field. For 5 successive days eggs were placed on the leaves and

Table VI

Parasitism of Cadra cautella eggs by Trichogramma evanescens when fresh eggs were placed on cotton leaves sprayed with hexane extract of moth scales and on control leaves sprayed with hexane only each day for 5 days after treatment (parasites released day 1 only) (37)

Day and treatment ^{a/}	Host eggs dissected		
	No.	No. dissected	No. with 1 or more parasites ^{b/}
1 T	132	40	10
C	143	40	4
2 T	167	39	11
C	157	40	6
3 T	170	44	21
C	149	46	7
4 T	140	40	12
C	146	40	7
5 T	102	39	4
C	102	39	0
Total			
T	711	202	58 a
C	697	205	26 b

a/ T=treated, C=control.

b/ Treated and control totals, by column, not followed by the same letter are significantly different at the 0.05 level as determined by paired t-test.

collected after 3 hours exposure (38). Trichogramma evanescens adults were released on day 1 only. As shown by the data in Table VI, twice as many eggs collected from treated leaves had been parasitized.

Likewise, effectiveness of synthetic tricosane in increasing parasitization in the field by naturally occurring Trichogramma species was demonstrated by Lewis et al. (37). The chemical was sprayed on five 10 ft. X 10 ft. plots at a rate of 1.2 grams per acre; another 5 plots of equal size were used as checks. Heliothis zea eggs (75) were placed in each plot and collected after 24 hours of exposure. Parasitization in treated plots (15%) was significantly higher than that in control plots (4%). Also, doses as low as 150 mg per acre produced increased parasitization. In addition, increased parasitization, by released Trichogramma species as a result of synthetic tricosane was demonstrated by Jones et al. (31) and Lewis et al. (37).

The increased parasitization elicited by the synthetic kairomones occurs as a result of at least 3 mechanisms of behavior modifications (14), (1) activation, (2) retention, and (3) egg distribution.

Activation. Pea seedlings grown in 440-cm² pie pans were subjected to moth scale extract applied in three patterns. In the first pattern, complete coverage, all seedlings were sprayed. In the second pattern, partial coverage, the seedlings were sprayed in 5 of 10 areas of 7 cm². In the third pattern, untreated check, no seedlings were sprayed. Two Heliothis zea eggs were placed in each of the 10 areas in the partial coverage test, and 20 eggs were placed similarly in the other two tests. The eggs were exposed to Trichogramma pretiosum for an hour, and then collected and dissected to check parasitization. These results are shown in Table VII. The highest parasitization was obtained with complete coverage. Thus the extract elicited a released behavior type of activity. Parasitization was directly related to the amount of area sprayed, so the kairomone apparently caused a more intensified search pattern rather than acting as a guide to the host egg. The kairomone acts as an S₃ type stimulant functioning to keep the parasite in the search and attack cycle.

Retention. Kairomones also serve to increase the retention of the parasites in a treated area, a not unexpected phenomenon. This function is readily demonstrated with the larval parasite, Microplitis croceipes. Table VIII shows the results of a field experiment in which M. croceipes was released over pea seedlings of 3 types: (a) Heliothis zea larvae were present after 12 hours of feeding, (b) H. zea larvae were removed after 12 hours of feeding but frass remained, (c) no larvae and no feeding damage. Plainly, plants containing frass retained the parasites about as well as plants infested with larvae, but the parasites

Table VII

Mean percentage parasitization of H. zea eggs by T. pretiosum when the eggs were exposed on pans of pea seedlings completely or partially treated with a moth scale extract

Complete	% Parasitism ^{a/}		
	Partial		Control
	Treated areas	Overall	Untreated areas
71 ^a	52 ^b		29 ^c
	57 ^x		47 ^y

a/ Means followed by a, b, and c are significantly different (P0.01). Means followed by x and y are significantly different (P0.05).

Table VIII

Retention of adult Microplitis croceipes released among plants with and without host larvae or with previous exposure to larvae

Plant condition	% Parasites remaining after indicated time (minutes)						
	5	10	20	30	40	50	60
Larvae present	100	93	86	86	57	21	7
Larvae removed	100	93	64	50	43	21	7
Control (no larvae)	100	71	43	21	0	0	0

deserted the clean seedlings rapidly. Similar retention experiments with Trichogramma species have not been attempted because of the small size of the parasite and the resultant difficulty in field observation. However, all other evidence indicates that retention is a mechanism with this species.

Egg Distribution. A study of the distribution of Trichogramma species eggs in host eggs revealed that host eggs collected from plots treated with kairomones contained fewer parasite eggs per host egg than host eggs collected from control plots (14). The level of parasitization that would occur with a random distribution of host eggs can be calculated by the method of Wadley (39) by determining the mean number of parasite stings per host. However, with Trichogramma species the mean number

can only be obtained by dividing the mean number of parasite eggs by 2 because the parasite generally deposits 2 eggs per sting. Then the percentage parasitization (R) based on the calculated, random distribution of eggs, compared with the observed percentage parasitization (O) is a measure of the ability of the parasite to avoid a previously parasitized egg or, more simply, its egg distribution efficiency. The lower the R/O, the greater the efficiency of the parasite. In fact, host eggs from treated plots had an average R/O of 1.08 whereas those from control plots had an average R/O of 1.34. Probably the presence of the kairomones on the plant induces the parasite to depart the host egg more rapidly after oviposition in search of a new host. The absence of the kairomone from the surrounding substratum causes the parasite to linger on and repeat the sting in the host egg.

Kairomones and Parasite Establishment. Successful establishment of released parasites has been difficult, mainly because of the innate tendency of the insect to disperse upon release. Studies by Gross et al. (40) showed that kairomones can overcome this tendency by inducing a host-seeking behavior that will dominate until habitat establishment is achieved. Kairomones acting in this manner are defined as sign stimulants or releasers (41). For example, Microplitis croceipes has an intense escape response. Female Microplitis croceipes were allowed to examine Heliothis zea frass (prestimulation) prior to release at a central point among 3 petri dishes; each containing some frass and a Heliothis zea larva feeding on a pea leaf. Then 30 minutes after the release, the larvae were collected and checked for parasitism. As shown in Table IX, larvae exposed to these

Table IX

Comparative parasitization of larvae of Heliothis zea by frass-stimulated and unstimulated Microplitis croceipes released in the greenhouse (40)

Parasite condition	% Larvae parasitized ^{a/} after indicated days						
	1	2	3	4	5	6	7
Stimulated	33.3	33.3	13.3	40.0	13.3	33.3	26.6
Unstimulated	0	0	0	0	0	0	0
Difference=	27.6	t=6.927 ^{b/}					

a/ 15 total larvae available for parasitization on each day.

b/ Significant at the 0.01 level of probability.

prestimulated parasites are readily parasitized; those exposed to unstimulated parasites were unparasitized. Also, visual observation revealed that the untreated parasites exhibited a positive phototaxis at release and remained at the greenhouse ceiling. The treated parasites assumed a host-seeking pattern among the infested petri dishes.

The same principle was demonstrated with Trichogramma pretiosum in a field situation (40). Parasites that were stimulated before release by exposure to Heliothis zea moth scales caused higher rates of parasitism (30.5%) on naturally occurring Heliothis species eggs than did unstimulated parasites (21%). This difference was significant at the 0.05 level of probability (Student's T-test). Kairomones can therefore be used to activate the host-seeking instinct before release, which greatly increases the probability that parasites can be used effectively in pest control.

Summary

Results, to date, indicate that insect parasites have a complex behavioral scheme by which they effect parasitization. Some of the chemicals associated with the host insect (kairomones) which have a major part in this scheme have been identified. No phase of the parasitization process is influenced by a single factor but rather a number of factors; a fact that makes the progress we have achieved only a good beginning. However, work underway at a number of laboratories should produce enough information so we can soon understand the entire sequence for at least one or two parasites. Such an understanding should make utilization of that parasite much simpler and much more effective.

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EPA's Registration Requirements For Insect Behavior Controlling Chemicals—Philosophy and Mandates

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For those of you who do not know, I regretfully report that Dr. Len Axelrod suffered a fatal heart attack a few weeks ago, and needless to say, I feel very humble standing here in his place.

During the few years in which I had the distinct pleasure of associating with Len, he always received my deepest respect, not only as a scientist, but as a humanitarian who was greatly concerned with the welfare and survival of man and his environment.

So, without any further adieu, I would like to dedicate this presentation to Dr. Leonard R. Axelrod.

During the past year, Criteria and Evaluation Division has worked closely on a contract with the Zoecon Corporation. The purpose of this contract was to provide scientific and technical data to enable the Environmental Protection Agency to develop guidelines for the registration of pheromones and insect growth regulators. Part of what I am about to present is from the Zoecon Contract, as we take our first major step in developing the necessary guidance and criteria for the development and registration of chemicals for insect behavior control.

Since we are just beginning to develop these guidelines, I am not going to discuss the specifics on what needs to be done for evaluating efficacy, environmental chemistry, safety, etc. However, I will attempt to address the past, present, and future in our association with these materials for use not only as alternatives for some of the more highly persistent traditional pesticides, but also as an aid in reducing the chemical load entering the environment.

Historical Background

Although European naturalists as early as the 17th Century utilized caged virgin female moths to lure males for their collections, the field of chemical communication did not acquire appreciable sophistication until quite recently. In 1959,

Karlson and Luscher coined the term "Pheromone" to refer to substances which are emitted to the outside by an individual and received by a second individual of the same species which responds in a specific manner, such as a behavioral response. (The singular term "Pheromone" refers to one or several chemical compounds eliciting the response). Two years later, the German chemist Butenandt and co-workers culminated a 20-year effort by identifying the male sex attractant from 500,000 silkworm moth females, the first such natural chemical message system to be decoded. These two events plus an increased interest in alternate pest control methods have helped stimulate numerous research programs directed toward the understanding of the biological function of the chemical structure of pheromones.

For the purposes of the EPA Guidelines for Registration, the term "Pheromones" will also include non-pheromone chemicals, which elicit or modify behavioral responses. Included in this category will be attractants discovered by empirical screening.

A Sampler of Behavioral Functions

To date pheromones have been found to mediate a diverse repertoire of behavior patterns ranging from those in unicellular organisms to those in the primates. As a partial sampler, insect pheromones have been found to regulate such phenomena as aggregation responses, including trail following as in ants and termites, host colonization as in attraction or mass attack of bark beetles to trees, and recruitment ("Calling") of sexual partner as in attraction of males to female moths. In other chemical stimuli systems, dispersion away from the released pheromone occurs. This occurs in the case of an alarm substance emitted from an attacked aphid which causes the aphid's neighbors to escape predation by rapidly dropping from the plant. Alarm pheromones can also serve to mark an enemy for attack by additional individuals, a phenomenon many of us have encountered after being stung by a social hymenopteran such as a bee or a wasp. Other patterns of pheromone response include colonial behavior in many social *Hymenoptera* (such as bees and ants) and the *Isoptera* (termites). Generally, the queen emits the "master" pheromone which serves many functions including colony membership identification and eliciting the retinue behavior of feeding and grooming the queen. Examples of some of the chemicals that mediate behavior are listed in Table I. More extensive information can be found in recent reviews by Jacobson and Shorey.

The sensitivity of the messenger reception system to the pheromone is of an extraordinary nature. In the male silkworm moth, a single pheromone molecule can elicit firing of an olfactory neuron on the male antenna, whereas some 200 molecules are required for an overt behavioral response as male movement toward the odor source.

Table I: Examples of Chemicals Mediating Various Behavioral Responses in Insects*

<u>Scientific Name</u>	<u>Common Name</u>	<u>Chemical Name</u>	<u>Response</u>
<i>Limonius californicus</i>	Sugar Beet Wireworm Beetle	Valeric Acid	Male Attraction
<i>Ponthetria dispar</i>	Gypsy Moth	<u>cis</u> -7,8-Epoxy-2-Methyloctadecane	Male Attraction
<i>Trichoplusia ni</i>	Cabbage Looper Moth	(<u>Z</u>)-7-Dodecen-1-ol Acetate	Male Attraction
<i>Anthonomus grandis</i>	Boll Weevil	1) (+) <u>cis</u> -2-Isopropenyl-1-Methylcyclobutanethanol 2) (<u>Z</u>)-3,3-Dimethylcyclohexylideneethanol 3) (<u>Z</u>)-3,3-Dimethylcyclohexylideneacetalddehyde 4) (<u>E</u>)-3,3-Dimethylcyclohexylideneacetalddehyde	Female & Male Attraction (Aggregation)
<i>Apis mellifera</i>	Honeybee	1) 2-Heptanone 2) Isopentyl Acetate	Alarm
<i>Zootermopsis nevadensis</i>	Termite	Hexanoic Acid	Trail-marking

*References can be located in Jacobson, M., In Rockstein, The Physiology of Insecta, 2nd ED., 3:229-276. 1974 (Academic Press, New York)

Elucidation of the chemical structures of pheromones has lagged behind the description of the general behavioral functions. Generally, evidence of the presence of a pheromone by observation of the specific behavior must precede bioassay and isolation. In 1966, several insect pheromones were chemically identified, and since then the number of compounds characterized has increased steadily, due in part to the increased sophistication of the instrumentation for chemical analysis. As the synthetic pheromones have become available, biologists have been able to decipher their exact behavioral function and applied entomologists and zoologists have been able to initiate programs designed to utilize pheromones for pest population manipulation.

Principles

Generally, the development of pheromones into a chemical system for pest population manipulation, such as mass trapping or disruption of pheromone communication, initially involves chemical characterization of the pheromone system, chemical synthesis, and laboratory and field documentation of the behavioral responses elicited by the pheromone. Once the structure and evoked biological response are described, evidence of the effectiveness and usefulness of the pheromone for population manipulation must be established through field testing under natural conditions.

Use of Pheromones in Pest Monitoring

The most immediate and obvious use of synthesized pheromones has been for population monitoring, essentially an extension of the early naturalists' use of female moths to lure males. A synthetic pheromone in a sticky trap, for example, lures and ensnares the pests. The numbers caught can be used to estimate the pest's relative abundance and seasonal development. This information may permit decisions to be made as to the exact timing of insecticide applications for maximum effectiveness or even a determination of the necessity for a conventional pesticide application. For certain crops, this precise population sampling technique may allow substantial reductions in the standard pesticide application, with the use of only 0.015 to 0.00003 gram of synthetic pheromone per acre in a single trap.

A typical case of such a benefit occurs with the monitoring of the summer fruit tortrix moth in the Netherlands. The maximum benefit for an insecticide spray with this species is derived when the application occurs a few days after egg hatch, just as the larvae are migrating to their feeding sites. This susceptibility window can be predicted accurately through the use of pheromone traps, and their widespread use in the Netherlands has resulted in the use of fewer insecticide applications with more effective control.

Similar monitoring programs for a number of pests such as the codling moth, the peach twig borer, and the oriental fruit moth are in the research and development stage. Population monitoring with commercially available pheromone traps has been adopted by some commercial growers as part of integrated pest management programs. Monitoring systems are not regulated by the EPA since this pheromone use is neither designed nor claimed to suppress population levels.

Mass Trapping for Population Suppression and Control

Several distinct methodologies for pheromone utilization in direct population manipulation have been described. The technique of mass trapping utilizes compounds which lure one or both sexes to a mating and/or aggregation locus. In mass trapping these compounds are emitted from a dispenser and the attracted pest becomes ensnared in a sticky trap or a device of similar principle. Success of this method depends upon removal of a sufficient portion of the pest population so as to reduce damage or nuisance to an economically or medically acceptable level.

Efficacy in mass trapping involves not just the description of the actual number of pests captured in a test, but, additionally, it requires some independent estimate of the effect on the total pest population and/or of the damage reduction.

In some successful mass trapping experiments, the quantity of pheromone used per acre was less than 0.04 grams (0.0009 lbs) or roughly 1/10,000 the quantity per acre for several conventional pesticides. In the case of other pest species, the total amount of pheromone per acre could be substantially less than this amount.

In mass trapping an attractant-baited trap generally serves to capture the pest. Traps are set out at a density which is sufficient enough to remove the proportion of the breeding pest population necessary for population suppression.

For example, in the case of the redbanded leafroller moth, a species in which the female-produced pheromone lures the male for mating, 40 attractant traps per acre in an apple orchard will remove enough males to effect control of this pest, providing that this technique is used on low initial populations. For this species, a low population could be achieved by application of a conventional insecticide prior to the initiation of the pheromone program. A low population also would exist in a well-managed commercial apple orchard.

A mass trapping population manipulation technique would possess the following advantages over conventional pesticides:

1. Highly specific control of the target organism;
2. Facilitation of biological control of non-target pests;
3. Use of a compound which is designed to attract rather than kill at rates comparable to natural pheromone levels.

Population Suppression by Disruption of Communication

Another promising means of using pheromones or attractants in an integrated pest management program is through disruption of pheromone communication, a procedure first demonstrated by Gaston and co-workers. Population manipulation involving disruption of communication is dependent upon atmospheric permeation with a sufficient concentration of communication component chemicals to prevent or greatly alter the pest's olfactory perception and orientation toward the natural pheromone sources.

Research experiments with many moth species have demonstrated that emission of these communication disruptants into the air prevents the male's successful location of the female, thereby effecting a reduction or elimination of mating. The disruptant employed could be the natural pheromone chemicals reconstituted in a different proportion or rate, or a compound which by itself is not part of the natural communication system but which affects the behavioral response. Successful communication disruption thus generally prevents crop damage in the following generation by reduction or elimination of mating in the present generation. Efficacy evaluation again requires precise sampling of total pest populations and accurate estimates of crop damage.

One technique for dispersal of the pheromone into the atmosphere is emanation of the compound from point source dispensers. Such evaporating devices can be deployed at a set number per unit area and are recoverable (i.e., can be removed after use), so that the pheromone is dispersed only into the atmosphere and not sprayed directly onto the foliage, crops, soil and target or non-target organisms.

Another method of pheromone application is similar to that used for conventional pesticides. In this procedure, a pheromone formulation (involving microencapsulation, wettable powders, or other volatile release matrices) is sprayed with standard pesticide equipment.

Experiments conducted to date indicate that rates of only 10 grams (0.02 lbs) or less of pheromone per acre per application may be more than adequate for communication disruption for several weeks. The specific test protocol necessary to demonstrate efficacy will be dependent on the characteristics of the pheromone compound, the nature of the manipulation technique chosen, the nature of the crop, the timing of the application, and the biology of the organism.

Current EPA Philosophy

The public's concern for the environment is one of the factors motivating the development of new agents for insect population control. At the present time, most research, notably in industry is still concentrated on hard chemical insecticides,

especially directed toward modifications of existing structural types such as organophosphates, organotins and carbamates. The emphasis is on agents with less persistence, improved efficacy, and greater specificity to target organisms.

Insect pheromones in general are highly selective; each pheromone is limited to a particular insect, or at most, to several related species. The most efficient pheromones appear to be chemicals which are produced by the insects themselves, or by host plants. They are effective in extremely small quantities. They are attractive to a particular stage of the pest insect, generally the adult stage, and they are used only during a limited time of the year. By their very nature, natural pheromones have been presumed to be relatively non-toxic to man and other non-target organisms. However, extensive investigations concerning the possible hazards or adverse effects of pheromones to man and the environment are necessary to determine the safety of their use as pesticides, especially when synthesized.

Although pheromones exhibit highly desirable characteristics as insect control agents, commercial interest in chemicals which are effective against a single species on a sporadic need basis is generally limited. Understandably; the chemical industry does not wish to bear the high cost of research and development for materials with limited profit, however, the USDA is carrying out the development of pheromones as part of their thrust toward integrated pest management systems.

At the present time pheromones are mainly used as survey tools for monitoring populations and many investigators feel that this use of pheromones will be the key to integrated pest control programs for many crops. Pheromone baited traps for monitoring purposes have the following specific uses:

1. To determine proper timing of sprays;
2. To locate sources of infestation from over-wintering areas;
3. To detect a new pest coming into a region;
4. To determine if a pesticide spray is actually needed.

In the future, pheromones may be used for control of certain insects. Current thinking is that control with pheromones may be effective in two ways.

1. By mass trapping of one or both sexes;
2. By confusion of the insects through communication disruption, i.e., the insects become confused and die before mating occurs.

Certain of the compounds are included in major programs being carried out as part of the thrust toward integrated pest management, in particular, gossyplure for pink bollworm, grandlure for boll weevil and disparlure for gypsy moth.

Pheromones for numerous insects are available for experimental purposes and a small number are available for commercial uses. Because of the long experience of industry and government with chemical pesticides, the registration requirements and

development procedures are best defined for the "traditional" chemical control agents. Safety, efficacy and environmental requirements which have evolved for traditional insecticides are the standards by which practically every new chemical control agent is evaluated by the EPA. The cost of developing any new and novel method of insect control, falling within the jurisdiction of the EPA, is going to be at least as expensive as the cost of developing a traditional chemical insecticide. In addition to the baseline requirements established for the traditional insecticides, new agents (even in the "experimental permits" and "temporary tolerance" phases), may be required to undergo additional studies some of which may be new and unique.

Proposed Regulations and Recommendations

Safety-Hazard Evaluation. Hazard evaluation requirements should strongly consider the use pattern and the basic safety of the individual materials. The requirements may be entirely different if the pheromone is applied by point-source release versus being broadcast over an area in the form of a spray or granular formulation. Also, with a pheromone, one must consider whether or not the compound occurs in nature, and possibly in what concentrations. A further distinction in the requirements might also be made between a point-source release mechanism which is not recoverable versus a point-source release mechanism which is recoverable.

Efficacy - Use Pattern Criteria - Labeling. With pheromones it is felt that some term should be used other than "control". There is a wide variation of terms that could be used, but, generally, it is felt that terms such as "population suppression" or "aids in control" are more suitable particularly where the usefulness and efficacy of the product are based on its ability to protect foliage and/or on its ability to prevent mating, thus leading to possible population reduction in a manner other than by direct kill as experienced with traditional hard chemicals. Perhaps the most controversial area in obtaining pheromone registration revolves around the fact that even though there may be a reduction in mating this does not necessarily mean there is a reduction in the population of a species. This is why the term "aids in control" may be more appropriate for pheromones which are employed as an integral part of an integrated pest management system. In addition, resistance to pheromones, especially those used for monitoring, should not develop, thus insuring a longer market life for pheromones.

Catches in pheromone baited or organism-baited traps or mating incidence in the treated areas are supportive of efficacy but such data do not constitute a demonstration of efficacy.

Field Plot Techniques. Field plot techniques acceptable for traditional pest control in general are acceptable for pheromones but may vary depending upon the biology of the insect and

adaptability of the product to certain pest management practices. Each individual pheromone development must be considered on a case-by-case basis, and criteria such as plot size, number of replicates, geographical test locations, etc., should, out of necessity, be subject to revision depending upon the problem at hand.

Areas which may have to be investigated in addition to what is presently done with traditional pesticides are as follows:

- (A) Necessity for obtaining more details on the biology of the insect, the stage of development present at time of application and the percentage of the population in each stage.
- (B) The necessity for compiling past history records on insect populations, on the treated area and in adjacent areas.
- (C) The necessity for compiling records on adjacent crops and areas, for the season of the experiment and, possibly, for the seasons before and after treatment.

Current Registration Status

When used as survey tools in integrated pest management programs, the pheromones are not subject to the Federal Insecticide, Fungicide and Rodenticide Act, unless used in conjunction with a pesticide which is subject to the Act. If used as an attractant in a control procedure or in insect mitigation, pheromones are subject to regulation under the Act.

The pheromone field, as a part of the science of entomology has advanced rapidly in the past decade, and in particular, in the past few years. At present, muscalure is registered as an attractant in fly baits. This pheromone is specific to houseflies, for which the baits are so intended; however, other species of flies may be attracted by other ingredients in the bait. The rationale for registering muscalure differed from other basic attractants in that its action as a sex attractant incorporated in the bait, permitted a reduction in the concentration of a more toxic chemical pesticide and increased the efficacy of the product. This constituted the first registration of a pheromone for insect control.

Extensive field experiments have been conducted by the USDA to assess the potential of disparlure in controlling the gypsy moth by communication disruption techniques. Due to the method used and type of results obtained, it will be necessary to employ criteria for registration based on foliage protection and/or inability of the insect to mate and propagate the species, rather than on the basis of population reduction obtained through direct kill. Disparlure is in the advanced stages of development under an experimental permit, and registration appears possible within a year or two.

Experimental permits have also been issued by EPA for codlemone, a sex attractant for codling moth, and grandlure, the

boll weevil aggregation pheromone, which is currently in for registration.

Current Progress

Scientists in the Registration and Criteria and Evaluation Divisions have begun a joint effort to develop guidance and criteria for the efficacy and safety evaluation of pheromones. The purpose of this guidance will be to assist registrants with the registration requirements for developing and testing these compounds, and to assist the review process with the evaluation of such products when submitted for registration.

The "Guidance and Criteria" package will be developed in a separate document paralleling the general registration guidelines in format, but applicable specifically to the development and testing of these type compounds.

This will further enable us to circulate and work on this document with the Registration Division until the requirements and methods are suitable to both Criteria and Evaluation Division and the registration process, thereby preventing the problem of constantly modifying the general registration guidelines. The anticipated completion date for the pheromone guidance and criteria will be the end of the current calendar year, as we move forward in the area of new pesticide products.

Insect-Behavior Chemicals Active in Field Trials

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To be of practical value in insect control, a chemical or combination of chemicals that affects insect behavior should evoke an approaching or departing response or nullify one of these responses. Furthermore, the action should be demonstrable in the normal habitat of the insect. The more compelling the response to the chemical, the greater will be its potential as an insect control agent.

A compilation of such "insect-behavior" chemicals is given in Table I. Many of the compounds have been identified as pheromonal components, but many found active in field trials are not known to be present in the responding insect. Footnotes in the table indicate whether a compound is produced by males (g) or females (h), or derived from mixed sexes (q). Compounds not known to be present in the insect are also designated by a footnote (d); this broad category includes compounds foreign to the insect as well as those strongly suspected of being major pheromonal components but whose presence has not been rigorously proved.

The compounds are arranged by general chemical structure; within each grouping the order is determined by increasing number of carbon atoms in the straight-chain part of the molecule, by the number of double bonds, and generally by increasing complexity. For the esters, the acid moiety is considered first (e.g., formates precede acetates).

To describe the action of a compound, the following classifications and definitions are used: attractant, a compound, often found through a screening program, that produces a significant increase in trap captures over captures in unbaited traps but that does not produce responses similar to those evoked by sex pheromones; sex attractant, a compound that produces increased trap captures of insects of one sex and also elicits additional responses similar to those evoked by natural sex pheromonal emissions; aggregant, a compound that attracts insects of both sexes and evokes responses similar to those observed with natural pheromonal emissions; inhibitor, a compound that causes

a reduction in trap captures when exposed in a trap baited with an attractant, a pheromonal extract, or live insects; disruptant, a compound that interferes with the ability of insects to locate mates when the material is disseminated throughout a test area; synergist, a compound that is not attractive in itself but that causes a significant increase in trap captures when exposed with an attractant; trail compound, a compound that causes an insect to follow an artificial trail; kairomone, a compound from an insect that attracts or stimulates a parasite or predator of that insect; larval attractant; and oviposition stimulant. Other materials such as feeding stimulants, food baits, and repellents have not been included.

With further reference to Table I, a sex attractant is a male attractant unless there is a footnote indicating that it is produced by males (g) or that it attracts females (m). By the definitions used here, an attractant that becomes less attractive at higher concentrations is classed as an inhibitor as well; this also applies to two-component attractants that require a specific ratio of components for optimum attractancy. Distinctions between categories are sometimes quite arbitrary and are subject to change as additional results are reported. Thus, a compound listed here as a synergist may ultimately prove to be an obligatory component of a multicomponent attractant. Compounds for which activity has been reported but that have failed to show activity in subsequent field tests have been deleted; it is quite possible that some of these may prove to be active when additional requirements have been elucidated. Conversely, some compounds included here on the basis of preliminary reports may prove to be inactive when extensive field tests are made.

Many of the compounds in the table have more than one effect on insects. Insects affected similarly by a given compound are listed together alphabetically. However, when a compound educes more than one action from a given insect, all actions for that insect are listed together.

For the sake of conciseness, much important information is not included in the table. Thus, there is no indication of the relative activity of different compounds that attract the same insect, no indication of optical activity is given, and the optimum ratios of two-component attractants are not specified. The original references must be consulted for further details. Some early synthetic attractants of low activity have not been listed.

In this table compounds are dealt with solely in terms of activity measured by empirical criteria such as trap catches. Readers with interest in insect pheromones and their action (1) will wish to consult other sources, such as the "Annotated Compendium of Insect Sex Pheromones" (2), for further information.

Table I. Insect Behavior-controlling Chemicals

<u>Compound^a</u>	<u>Insect affected^b</u>	<u>Action^c</u>	<u>Notes</u>	<u>Ref.</u>
<u>Alcohols</u>				
1. Ethanol	<u>Dendroctonus pseudotsugae</u> Hopkins, Douglas fir beetle	synerg	d	3
2. (Z)-4-Phenyl-3-buten-1-ol	<u>Coptotermes formosanus</u> Shiraki <u>Reticulitermes speratus</u> (Kolbe)	trail trail	d d	4 4
3. 4-Methyl-3-heptanol	<u>Scolytus multistriatus</u> (Marsham), smaller European elm bark beetle	aggr	he(157) f(185)	5
4. 6-Methyl-5-hepten-2-ol (sulcatol)	<u>Gnathotrichus sulcatus</u> LeConte	aggr	g	6
5. 3,7-Dimethyl-1,6-octadien-3-ol (linalool)	<u>Ips paraconfusus</u> (Lanier), California fivespined ips	inhib	h	7,8
6. 2-Methyl-6-methylene-7-octen-4-ol (ipsenol)	<u>Ips confusus</u> (LeConte) <u>Ips grandicollis</u> Eichhoff <u>Ips paraconfusus</u> (Lanier) Other <u>Ips</u> spp. ¹ <u>Ips pini</u> (Say)	aggr aggr aggr aggr inhib	eg eg eg eg d	9 10 11 7
7. 2-Methyl-6-methylene-2,7-octadien-4-ol (ipsdienol)	<u>Ips calligraphus</u> (Germar) <u>Ips confusus</u> (LeConte) <u>Ips paraconfusus</u> (Lanier) <u>Ips sexdentatus</u> (Börner) Other <u>Ips</u> spp. ¹	aggr aggr aggr aggr aggr	efg eg eg g g	12 9 11 13
8. 8-Propoxy-1-octanol	<u>Grapholitha molesta</u> (Busck), oriental fruit moth	synerg	d	14

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
9. (E)-6-Nonen-1-ol	<u>Ceratitidis capitata</u> (Wiedemann), Mediterranean fruit fly	sex at	e(107) g	15
10. (E)-5-Decen-1-ol	<u>Anarsia lineatella</u> Zeller, peach twig borer	sex at	hk(42)	16
11. 1-Undecanol	<u>Laspeyresia pomonella</u> (L.), codling moth	inhib	d	17
12. 1-Dodecanol	<u>Archips argyropilus</u> (Walker), fruittree leafroller	synerg	h	18
13. (Z)-7-Dodecen-1-ol	<u>Grapholitha molesta</u> (Busck), oriental fruit moth	synerg	d	14, 19, 20
	<u>Dicentra semirufescens</u> (Walker)	sex at	d	21
	<u>Exartema</u> sp.	sex at	d	22
	<u>Harpiteryx xylostella</u> auct. (L.)	sex at	de(49)	21
	<u>Raphia frater</u> Grote	sex at	d	21, 22
	<u>Pseudoplusia includens</u> (Walker), soybean looper	inhib	d	23
	<u>Trichoplusia ni</u> (Hübner), cabbage looper	inhib	d	24
14. (Z)-8-Dodecen-1-ol	<u>Celypha striana</u> (Schiffermüller)	sex at	d	25
	<u>Epiblema scudderiana</u> (Clemens)	sex at	d	21
	<u>Hedia nubiferana</u> (Haworth)	inhib	d	25
	<u>Grapholitha molesta</u> (Busck)	inhib	d	26
15. (E)-8-Dodecen-1-ol	<u>Hedia chionosema</u> (Zeller)	sex at	de(52)	21
16. (E)-9-Dodecen-1-ol	<u>Dichrorampha</u> sp.	sex at	de(54)	21
17. (Z,Z)-3,6-Dodecadien-1-ol	<u>Coptotermes formosanus</u> Shiraki	trail	d	4
	<u>Reticulitermes speratus</u> (Kolbe)	trail	d	4

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
18. (E,E)-8,10-Dodecadien-1-ol (codlure)	<u>Eucosma nigromaculana</u> (Denis and Schiffermüller) <u>Hedra nubiferana</u> (Haworth) <u>Laspeyresia pomonella</u> (L.), codling moth	sex at sex at sex at, disrup	d d h	27 25 28,29 30
19. (Z,Z,E)-3,6,8-Dodecatrien-1-ol	<u>Reticulitermes flavipes</u> (Kollar) and other termites <u>Reticulitermes santonensis</u> Feytaud <u>Reticulitermes virginicus</u> (Banks)	trail trail trail	d d g	4 31 32
20. (Z,E)-3,7,11-Trimethyl-2,6,10-dodecatrien-1-ol (farnesol)	<u>Tetranychus urticae</u> Koch, twospotted spider mite	sex at, inhib	h	33 33
21. (E,E)-3,7,11-Trimethyl-2,6,10-dodecatrien-1-ol (farnesol)	<u>Zootermopsis nevadensis</u> (Hagen) <u>Tetranychus urticae</u> Koch	trail inhib	d d	34 33
22. (Z)-11-Tridecen-1-ol	<u>Argyrotaenia velutinana</u> (Walker), redbanded leafroller	inhib	d	35
23. (Z)-11-Tetradecen-1-ol	<u>Choristoneura fractivittana</u> (Clemens) <u>Clepsis melaleucana</u> (Walker) <u>Nedra imosula</u> (Guenée) <u>Sparganothis niveana</u> (Walsingham) <u>Zygaena transalpina</u> Esper <u>Platynota stultana</u> (Walsingham), omnivorous leafroller <u>Archips argyrospilus</u> (Walker), fruittree leafroller <u>Argyrotaenia velutinana</u> (Walker), redbanded leafroller <u>Platynota idaeusalis</u> (Walker), tufted apple budmoth	sex at sex at sex at sex at sex at synerg, inhib inhib inhib inhib inhib	d de(77) d d d h h h d	21 21 36 21,36 37 38,39 39 18 35
24. (E)-11-Tetradecen-1-ol	<u>Platynota idaeusalis</u> (Walker), tufted apple budmoth <u>Platynota stultana</u> (Walsingham), omnivorous leafroller	sex at synerg, inhib	h h	40 38,39 39

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
	<u>Archips argyrospilus</u> (Walker), fruittree leafroller	inhib	h	18
	<u>Choristoneura fumiferana</u> (Clemens), eastern spruce budworm	inhib	h	41,42
25. <u>(Z,E)-9,12-Tetradecadien-1-ol</u>	<u>Cadra cautella</u> (Walker), almond moth	inhib	d	43
26. <u>(Z)-7-Hexadecen-1-ol</u>	<u>Pectinophora gossypiella</u> (Saunders), pink bollworm	inhib	d	44
27. <u>(Z)-11-Hexadecen-1-ol</u>	<u>Scotogramma trifolii</u> (Rottenberg), clover cutworm	sex at	de(90)	45
28. <u>(Z)-14-Methyl-8-hexadecen-1-ol</u>	<u>Trogoderma granarium</u> Everts, khapra beetle	sex at	dk	46
29. <u>(E)-14-Methyl-8-hexadecen-1-ol</u>	<u>Trogoderma inclusum</u> LeConte	sex at	hk	47
30. <u>(E,Z)-10,12-Hexadecadien-1-ol</u> (bombykol)	<u>Trogoderma glabrum</u> (Herbst)	sex at	hk	48
31. <u>3-Methyl-2-cyclohexen-1-ol</u> (seudenol)	<u>Bombyx mori</u> (L.), silk worm	sex at ¹	h	49
	<u>Dendroctonus pseudotsugae</u> Hopkins, Douglas fir beetle	synerg	h	50,3
32. <u>cis-2-Isopropenyl-1-methylcyclo-</u> <u>butaneethanol</u> (component of grandlure)	<u>Anthonomus grandis</u> Boheman, boll weevil	sex at, aggr, disrup	eg	51
	<u>Rhabdoscelus obscurus</u> (Boisduval), New Guinea sugarcane weevil	sex at	dem	52 53
33. <u>(Z)-3,3-Dimethyl-1,β -cyclohex-</u> <u>aneethanol</u> (component of grandlure)	<u>Anthonomus grandis</u> Boheman, boll weevil	sex at, aggr, disrup	eg	51 52

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
34. <u>cis</u> -2-Pinen-4-ol (<u>cis</u> -verbenol)	<u>Rhabdoscelus obscurus</u> (Boisduval)	sex at	dem	53
	<u>Ips calligraphus</u> (Germar)	aggr	efg	12
	<u>Ips confusus</u> (LeConte)	aggr	eg	9
	<u>Ips paraconfusus</u> (Lanier)	aggr	eg	11
	Other <u>Ips</u> spp. ¹	aggr		
35. <u>trans</u> -2-Pinen-4-ol (<u>trans</u> -verbenol)	<u>Dendroctonus ponderosae</u> Hopkins, mountain pine beetle	aggr	efh	54
<u>Esters</u>				
36. (<u>Z</u>)-9-Tetradecen-1-ol formate	<u>Heliothis virescens</u> (Fabricius), tobacco budworm	disrup	d	55
37. (<u>Z</u>)-11-Tetradecen-1-ol formate	<u>Heliothis zea</u> (Boddie), corn earworm	disrup	d	55
	<u>Argyrotaenia velutinana</u> (Walker), redbanded leafroller	inhib	d	35
38. Triacetin (glycerol triacetate)	<u>Heliothis zea</u> (Boddie)	ov st	d	56
39. 3,7-Dimethyl-1,6-octadien-3-ol acetate (linalyl acetate)	<u>Pectinophora gossypiella</u> (Saunders), pink bollworm	synerg	d	57
40. 8-Butoxy-1-octanol acetate	<u>Adoxyphes orana</u> (Fischer von Rösler- stamm)	inhib	d	58
41. 1-Nonanol acetate	<u>Paralobesia viteana</u> (Clemens), grape berry moth	synerg	d	59
42. (<u>E</u>)-5-Decen-1-ol acetate	<u>Anarsia lineatella</u> Zeller, peach twig borer	sex at	hk(10)	16
43. (<u>Z</u>)-7-Decen-1-ol acetate	<u>Battaristis</u> sp. <u>Lobesia aeolopa</u> Meyrick	sex at sex at	d d	21 60

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
44. 11-Methoxy-1-undecanol acetate	<u>Adoxypbes orana</u> (Fischer von Röslerstamm)	inhib	d	58
45. 11-Ethoxy-1-undecanol acetate	<u>Adoxypbes orana</u> (Fischer von Röslerstamm)	inhib	d	58
46. 11-Propoxy-1-undecanol acetate	<u>Adoxypbes orana</u> (Fischer von Röslerstamm)	inhib	d	58
47. 1-Dodecanol acetate	<u>Archips argyrospilus</u> (Walker), fruittree leafroller <u>Argyrotaenia velutinana</u> (Walker) redbanded leafroller <u>Paralobesia viteana</u> (Clemens), grape berry moth <u>Choristoneura rosaceana</u> (Harris), obliquebanded leafroller <u>Grapholitha molesta</u> (Busck), oriental fruit moth <u>Grapholitha prunivora</u> (Walsh), lesser appleworm <u>Pectinophora gossypiella</u> (Saunders), pink bollworm <u>Rhyacionia buoliana</u> (Schiffermüller), European pine shoot moth	synerg synerg synerg inhib inhib inhib inhib	h h d d d d d	18 35,61 59 62 14,19 19 63,57 64
48. (Z)-5-Dodecen-1-ol acetate	<u>Autoplusia esena</u> (Guenée), bean leafskeletonizer <u>Chionodes fuscomaculella</u> (Chambers) <u>Scrobipalpa atriplicella</u> (Fischer von Röslerstamm)	sex at sex at sex at	d d d	65 21 21

<u>Compound</u>	<u>Insect Affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
51. (Z)-8-Dodecen-1-ol acetate (orfralure, with ~6%(48))	<u>Aphania infida</u> (Heinrich)	sex at	d	21
	<u>Cnephasia alternella</u> Stephens	sex at	d	27
	<u>Cryptophlebia ombrodelta</u> (Lower)	sex at	d	60
	<u>Epiblema desertana</u> (Zeller)	sex at	d	21
	<u>Epiblema scudderiana</u> (Clemens)	sex at	d	27
	<u>Epiblema scutulana</u> (Schiffermüller)	sex at	d	77
	<u>Grapholitha funebrana</u> (Treitschke)	sex at	d	78,79
	<u>Grapholitha molesta</u> (Busck), oriental fruit moth	sex at	he(52)	80
	<u>Grapholitha prunivora</u> (Walsh), lesser appleworm	sex at	de(52)	78
	<u>Grapholitha tenebrosana</u> Duponchel	sex at	d	27
	<u>Gretchena bolliana</u> (Slingerland), pecan bud moth	sex at	d	81
	<u>Pammene albuginana</u> (Guenée)	sex at	d	27
	<u>Pammene argyrana</u> (Hübner)	sex at	d	27
	<u>Pammene fasciana</u> (L.)	sex at	d	27
	<u>Pammene inguilina</u> Fletcher	sex at	d	27
	<u>Pammene nemorosa</u> V. Kusnetsov	sex at	d	60
	<u>Pseudexentera maracana</u> (Kearf tt)	sex at	d	21
<u>Hedia rubiferana</u> (Haworth)	inhib	d	25	
<u>Laspeyresia pomonella</u> (L.), codling moth	inhib	d	25	
52. (E)-8-Dodecen-1-ol acetate	<u>Ecdytolopa insitificiana</u> (Zeller)	sex at	d	21
	<u>Grapholitha molesta</u> (Busck), oriental fruit moth	sex at	de(51)	79,19
	<u>Grapholitha packardii</u> (Zeller)	inhib	d	78
	<u>Grapholitha prunivora</u> (Walsh), lesser appleworm	sex at	d	78
	<u>Grapholitha prunivora</u> (Walsh), lesser appleworm	sex at	de(51)	19
	<u>Hedia chionosema</u> (Zeller)	inhib	d	19
	<u>Hedia chionosema</u> (Zeller)	sex at	de(15)	21

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
53. (Z)-9-Dodecen-1-ol acetate	<u>Cosmopterix</u> sp. <u>Episimus argutatus</u> (Clemens) <u>Paralobesia viteana</u> (Clemens), grape berry moth <u>Spodoptera frugiperda</u> (J. E. Smith), fall armyworm <u>Rhyacionia buoliana</u> (Schiffermüller)	sex at sex at sex at disrup sex at disrup inhib	d d h h e d	60 21 59 82 83 74 64,84
54. (E)-9-Dodecen-1-ol acetate	<u>Caradrina morpheus</u> (Hufnagel) <u>Dichrorampha</u> sp. <u>Loxostege chortalis</u> (Grote) <u>Rhyacionia buoliana</u> (Schiffermüller), European pine shoot moth	sex at sex at sex at sex at	d de(16) d h	25 21 21 64
55. (Z)-10-Dodecen-1-ol acetate	<u>Argyrotaenia quadrifasciana</u> (Fernald) <u>Hedia nubiferana</u> (Haworth) <u>Laspeyresia pomonella</u> (L.), codling moth	sex at inhib inhib	d d d	85 25 25
56. (E)-10-Dodecen-1-ol acetate	<u>Argyroloce autofasciana</u> (Haworth) <u>Hedia nubiferana</u> (Haworth) <u>Laspeyresia pomonella</u> (L.)	sex at inhib inhib	d d d	25 25 25
57. 11-Dodecen-1-ol acetate	<u>Diparopsis castanea</u> Hampson, rad bollworm	synerg	h	86
58. (E,Z)-7,9-Dodecadien-1-ol acetate	<u>Lobesia botrana</u> (Schiffermüller)	sex at	h	87,88
59. (E,E)-8,10-Dodecadien-1-ol acetate	<u>Laspeyresia pomonella</u> (L.)	inhib, disrup	d	17 30
60. (E)-9,11-Dodecadien-1-ol acetate	<u>Diparopsis castanea</u> Hampson	sex at	hn	86
61. 9-Dodecyn-1-ol acetate	<u>Adoxypbes orana</u> (Fischer von Röslerstamm)	inhib	d	89

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
62. Tridecan-1-ol acetate	<u>Argyrotaenia velutinana</u> (Walker), redbanded leafroller	inhib	d	35
63. (Z)-11-Tridecen-1-ol acetate	<u>Argyrotaenia velutinana</u> (Walker)	sex at	d	36
64. (Z,Z)-7,10-Tridecadien-1-ol acetate	<u>Trichoplusia ni</u> (Hübner)	sex at	d	90
65. (Z,Z)-7,11-Tridecadien-1-ol acetate	<u>Phthorimaea operculella</u> (Zeller), potato tuberworm	sex at inhib	do	90
66. 9-Tridecyn-1-ol acetate	<u>Adoxyphes orana</u> (Fischer von Röslerstamm)	inhib	d	89
67. Tetradecan-1-ol acetate	<u>Pectinophora gossypiella</u> (Saunders), pink bollworm	inhib	h	91,92
68. (Z)-3-Tetradecen-1-ol acetate	<u>Archips semiferranus</u> (Walker), oak leafroller	sex at	hk	93
69. (Z)-4-Tetradecen-1-ol acetate	<u>Archips semiferranus</u> (Walker), oak leafroller	sex at	hk	93
70. (E)-5-Tetradecen-1-ol acetate	<u>Rhynchopacha</u> sp.	sex at	d	94
71. (Z)-7-Tetradecen-1-ol acetate	<u>Amathes c-nigrum</u> (L.), large <u>Lacinipolia lorea</u> (Guenée) <u>Adoxyphes orana</u> (Fischer von Röslerstamm)	sex at sex at inhib	d d d	21 21 58
72. (E)-7-Tetradecen-1-ol acetate	<u>Amathes c-nigrum</u> (L.), small <u>Zeiraphera diniana</u> (Guenée), larch bud moth	sex at sex at, inhib	d d	21 95 95
73. (Z)-8-Tetradecen-1-ol acetate	<u>Spilonota ocellana</u> Fabricius	sex at	d	25

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
74. (Z)-9-Tetradecen-1-ol acetate	<u>Adoxyphes fasciata</u> Walsingham, smaller tea tortrix	sex at	he(77)	96
	<u>Adoxyphes orana</u> (Fischer von Röslerstamm), summerfruit tortrix (= <u>A. reticulana</u> Hübner)	sex at	he(77)	97,98
	<u>Amphipoea interoceanica</u> (Smith)	sex at	d	21
	<u>Apotomis auricristana</u> Walsingham	sex at	d	60
	<u>Archips semiferanus</u> (Walker), oak leafroller	sex at	hk	93
	<u>Bryotropha similis</u> (Stainton)	sex at	d	100
	<u>Cacoecimorpha pronubana</u> Hübner	sex at	de(77)	99
	<u>Clepsis spectrana</u> (Treitschke)	sex at	de(77)	101
	<u>Cucullia intermedia</u> Speyer	sex at	d	21
	<u>Hermonassa cecilia</u> Butler	sex at	d	60
	<u>Leucania phragmitidicola</u> Guené	sex at	d	21
	<u>Nemapogon apicisignatellus</u> (Dietz)	sex at	d	21
	<u>Pandemis heparana</u> (Denis and Schiffermüller)	sex at	de(77)	99
	<u>Pandemis limitata</u> (Robinson), three-lined leafroller	sex at, disrup	de(77)	102
	<u>Pyreferra citromba</u> Franclemont	sex at	d	21
	<u>Spotoptera cilium</u> Guenee	sex at	de(83)	103
	<u>Spotoptera exempta</u> (Walker)	sex at	he(83)	104
	<u>Anagasta kuehniella</u> (Zeller)	inhib	d	105
	<u>Cadra cautella</u> (Walker), almond moth	inhib	h	105,106
	<u>Plodia interpunctella</u> (Hübner), Indian meal moth	inhib	d	105

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
75. (E)-9-Tetradecen-1-ol acetate	<u>Bryotropha sp.</u>	sex at	d	96
	<u>Bryotropha terrella</u> (Hübner)	sex at	d	25
	<u>Loxostege neoblitalis</u> Capps	sex at	d	21
	<u>Polia grandis</u> (Boisduval)	sex at	d	21
	<u>Adoxypbes orana</u> (Fischer von Röslerstamm), summerfruit tortrix	inhib	d	107
76. (Z)-10-Tetradecen-1-ol acetate	<u>Argyrotaenia velutinana</u> (Walker), redbanded leafroller	inhib	d	35
	<u>Apotomis corticana</u> (Hübner)	sex at	d	25
	<u>Archips semiferranus</u> (Walker), oak leafroller	sex at	hk	108,93
	<u>Endothenia carbonana</u> (Douglas)	sex at	d	25
	<u>Exartema sp.</u>	sex at	d	85
77. (Z)-11-Tetradecen-1-ol acetate (riblure)	<u>Adoxypbes orana</u> (Fischer von Röslerstamm)	inhib	d	58
	<u>Adoxypbes fasciata</u> Walsingham, smaller tea tortrix	sex at	he(74)	96
	<u>Adoxypbes orana</u> (Fischer von Röslerstamm) (= <u>A. reticulana</u> Hübner), summerfruit tortrix	sex at	he(74)	97,98
	<u>Archips argyrosipilus</u> (Walker), fruittree leafroller	sex at, inhib	he(78)	18
	<u>Archips longicellanus</u> (Walsingham)	sex at	d	60
	<u>Archips podana</u> (Scopoli)	sex at	he(78)	109
	<u>Archips semiferranus</u> (Walker), oak leafroller	sex at	hk	93
	<u>Argyrotaenia pulchellana</u> (Haworth)	sex at	d	111
	<u>Argyrotaenia velutinana</u> (Walker), redbanded leafroller	sex at, disrupt	he(78)	110,61
	<u>Cacoecimorpha pronubana</u> (Hübner)	sex at	dk(74)	99
			(78)	112

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
77. contd.	<u>Ceramica picta</u> (Harris), zebra caterpillar	sex at	d	21
	<u>Choristoneura rosaceana</u> (Harris), obliquebanded leafroller	sex at	h	62
	<u>Clepsis melaleucana</u> (Walker)	sex at	de(23)	21
	<u>Clepsis spectrana</u> (Treitschke)	sex at	he(74)	101
	<u>Ostrinia nubilalis</u> (Hübner), European corn borer	sex at, inhib	he(78), P	113,114, 115
	<u>Ostrinia obumbratalis</u> (Lederer), smartweed borer	sex at	de(78)	116
	<u>Pandemis heparana</u> (Denis and Schiffermüller)	sex at	de(74)	99
	<u>Pandemis limitata</u> (Robinson), three-lined leafroller	sex at, disrup	de(74)	102
	<u>Platynota stultana</u> (Walsingham), omnivorous leafroller	sex at, inhib	he(78)	38
	<u>Pyrausta purpuralis</u> L.	sex at	de(78)	112
	<u>Thyris maculata</u> (Harris)	sex at	d	21
	<u>Yponomeuta padellus-malinellus</u> (Gl.)	sex at	d	25
	<u>Zygaena transalpina</u> Esper	sex at	d	37
	<u>Argyrotaenia citrana</u> (Fernald), orange tortrix	synerg	h	117
	<u>Platynota idaeusalis</u> (Walker)	inhib	d	41
78. (E)-11-Tetradecen-1-ol acetate	<u>Archips argyrospilus</u> (Walker), fruittree leafroller	sex at, inhib	he(77)	18
	<u>Archips podana</u> (Scopoli)	sex at	he(77)	109
	<u>Argyrotaenia velutinana</u> (Walker), redbanded leafroller	sex at, inhib, disrup	he(77) 114,61	35 118
	<u>Cacoecimorpha pronubana</u> (Hübner)	sex at	de(77)	112
	<u>Choristoneura viridis</u> Freeman	sex at	d	119
	<u>Croesia holmiana</u> (L.)	sex at	d	25

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
87. 9-Pentadecyn-1-ol acetate	<u>Adoxyphes orana</u> (Fischer von Röslerstamm)	inhib	d	89
88. (Z)-7-Hexadecen-1-ol acetate (hexalure)	<u>Euxoa tessellata</u> (Harris)	sex at	d	21
	<u>Pectinophora gossypiella</u> (Saunders), pink bollworm	sex at, disrup	d	134
	<u>Sitotroga cerealella</u> (Olivier), Angoumois grain moth	sex at	d	135, 68
	<u>Autographa californica</u> (Speyer), alfalfa looper	disrup	d	136
	<u>Heliothis virescens</u> (Fabricius), tobacco budworm	disrup	d	68
	<u>Spodoptera ornithogalli</u> (Guenée) <u>Trichoplusia ni</u> (Hübner), cabbage looper	disrup disrup	d d	68 68
89. (Z)-10-Hexadecen-1-ol acetate	<u>Mamestra configurata</u> Walker, bertha armyworm	sex at	d	137
90. (Z)-11-Hexadecen-1-ol acetate	<u>Amphipoea velata</u> (Walker)	sex at	d	21
	<u>Amphipyra monolitha</u> Guenée	sex at	d	60
	<u>Mamestra configurata</u> Walker, bertha armyworm	sex at	dk	138
	<u>Morristonia confusa</u> (Hübner)	sex at	d	21
	<u>Pseudorthodes crenulata</u> (Butler)	sex at	d	21
	<u>Pseudorthodes vecors</u> (Guenée) <u>Scotogramma trifolii</u> (Rottenberg), clover cutworm	sex at sex at	d de(27)	21 21, 45
	<u>Telorta divergens</u> (Butler)	sex at	d	60
	<u>Argyrotaenia velutinana</u> (Walker), redbanded leafroller	inhib	d	35

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
91. (E)-11-Hexadecen-1-ol acetate	<u>Epiplema moza</u> Butler <u>Telorta edentata</u> (Leech)	sex at sex at	d d	60 60
92. (Z,Z)-7,11-Hexadecadien-1-ol acetate (gossypure, with (93))	<u>Pectinophora gossypiella</u> (Saunders), pink bollworm	sex at, disrup	he(93)	139,92 140
93. (Z,E)-7,11-Hexadecadien-1-ol acetate (gossypure, with (92); angoulure)	<u>Pectinophora gossypiella</u> (Saunders), pink bollworm <u>Sitotroga cerealella</u> (Olivier), Angoumois grain moth	sex at, disrup sex at	he(92) h	139,92 140 141
94. (E,Z)-7,11-Hexadecadien-1-ol acetate	<u>Pectinophora gossypiella</u> (Saunders), pink bollworm	inhib	d	92
95. (E,E)-7,11-Hexadecadien-1-ol acetate	<u>Pectinophora gossypiella</u> (Saunders), pink bollworm	inhib	d	92
96. (Z,Z)-3,13-Octadecadien-1-ol acetate	<u>Sannioidea exitiosa</u> (Say), peachtree borer <u>Synanthedon pictipes</u> (Grote and Robinson), lesser peachtree borer	sex at, disrup inhib, disrup	h d	142 143 142 143
97. (E,Z)-3,13-Octadecadien-1-ol acetate	<u>Synanthedon pictipes</u> (Grote and Robinson), lesser peachtree borer <u>Sannioidea exitiosa</u> (Say), peachtree borer	sex at disrup disrup	h d	142 143 143
98. (E,E)-8,10-Dodecadien-1-ol propionate	<u>Laspeyresia pomonella</u> (L.), codling moth	inhib	d	144
99. Phenethyl propionate	<u>Popillia japonica</u> Newman, Japanese beetle	att	de(161)	145
100. Hexyl butyrate	<u>Neophyllomyza</u> sp.	att	d	146
101. 2,4-Hexadienyl butyrate	<u>Vespula</u> spp., yellowjacket wasps <u>Chloropid</u> gnats	att att	d d	147 148,149

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
102. Heptyl butyrate	<u>Vespula</u> spp., yellowjacket wasps <u>Chloropid</u> gnats	att att	d d	150 148,149
103. Octyl butyrate	<u>Vespula</u> spp., yellowjacket wasps <u>Siphonella</u> spp.	att att	d d	151 146
104. (Z)-5-Decenyl 3-methylbutyrate	<u>Nudaurelia cytherea</u> (Fabricius)	sex at	h	152
105. Hexyl hexanoate	<u>Forcipomyia</u> sp.	att	d	146
106. Butyl (E,E)-2,4-hexadienoate (butyl sorbate)	<u>Amphimallon majalis</u> (Razoumowsky), European chafer	att	d	153
107. Methyl (E)-6-nonenoate	<u>Ceratitidis capitata</u> (Wiedemann), Mediterranean fruit fly	sex at	ge(9) j	15
108. Methyl (Z)-3-decenoate	<u>Anthrenus flavipes</u> LeConte, furniture carpet beetle	sex at	d	154
109. Methyl (E)-2,4,5-tetradecatrien- oate	<u>Acanthoscelides obrectus</u> (Say), dried bean beetle	sex at	g	155,156
110. Methyl (Z)-7-hexadecenoate	<u>Trogoderma glabrum</u> (Herbst)	sex at	hk	48
111. Methyl (Z)-14-methyl-8-hexa- decenoate	<u>Trogoderma inclusum</u> LeConte	sex at	hk	47
112. Methyl (E)-14-methyl-8-hexa- decenoate	<u>Trogoderma glabrum</u> (Herbst)	sex at	hk	48
113. Ethyl 3-isobutyl-2,2-dimethylcyclo- propanecarboxylate(chrislure, ethyl dihydrochrysanthemumate)	<u>Oryctes rhinoceros</u> (L.), coconut rhinoceros beetle	att	d	157

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
114. Ethyl 2,2-dimethyl-3-(2-methyl-propenyl)cyclopropanecarboxylate (ethyl chrysanthemumate, rhinolure)	<u>Oryctes rhinoceros</u> (L.), coconut rhinoceros beetle	att	d	158
115. Propyl cyclohexaneacetate	<u>Blattella germanica</u> (L.), German cockroach	att	d	159
116. Methyl cyclohexanepropionate	<u>Popillia japonica</u> Newman, Japanese beetle	att	de(161)	160
117. <u>sec</u> -Butyl 6-methyl-3-cyclohexene-carboxylate (siglure)	<u>Ceratitidis capitata</u> (Wiedemann), Mediterranean fruit fly	att	d	161
118. <u>tert</u> -Butyl 4 (or 5)-chloro-2-methyl-cyclohexanecarboxylate (trimedlure)	<u>Ceratitidis capitata</u> (Wiedemann), Mediterranean fruit fly	att inhib	d	162 163
119. Propyl 1,4-benzodioxan-2-carboxylate (amlure)	<u>Amphimallon majalis</u> (Razoumowsky), European chafer	att	d	164
120. Methyl 4-methylpyrrole-2-carboxylate (attalure)	<u>Atta cephalotes</u> (L.), <u>Atta texana</u> (Buckley), Texas leafcutting ant	trail trail	q q	165 166
121. Methyl 4-chloropyrrole-2-carboxylate	<u>Atta texana</u> (Buckley)	trail	d	167
122. Methyl 4-bromopyrrole-2-carboxylate	<u>Atta texana</u> (Buckley)	trail	d	167

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
<u>Acids</u>				
123. Hexanoic acid	<u>Trogoderma glabrum</u> (Herbst) <u>Lasius fuliginosus</u> (Latreille) <u>Zootermopsis nevadensis</u> (Hagen)	sex at trail trail	hk qk q	48 168,169 34
124. Heptanoic acid	<u>Lasius fuliginosus</u> (Latreille) <u>Orgilus lepidus</u> Muesebeck [<u>Phthorimaea operculella</u> (Zeller)]	trail kair	qk r	168,169 170
125. Octanoic acid	<u>Lasius fuliginosus</u> (Latreille)	trail	qk	168,169
126. Nonanoic acid	<u>Lasius fuliginosus</u> (Latreille)	trail	qk	168,169
127. Decanoic acid	<u>Lasius fuliginosus</u> (Latreille)	trail	qk	168,169
128. (Z)-5-Decenoic acid	<u>Anthrenus flavipes</u> LeConte, furniture carpet beetle	sex at	h	154
129. (E,Z)-3,5-Tetradecadienoic acid (megatomomic acid)	<u>Attagenus elongatulus</u> Casey <u>Attagenus megatoma</u> (Fabricius), black carpet beetle	sex at sex at	d h	171 172
130. (E)-9-Oxo-2-decenoic acid (queen substance)	<u>Apis cerana</u> Fabricius <u>Apis dorsata</u> Fabricius <u>Apis florea</u> Fabricius <u>Apis mellifera</u> L., honey bee	sex at sex at sex at sex at	h h h h	173 173 173 174
131. Dodecanoic acid	<u>Lasius fuliginosus</u> (Latreille)	trail	qk	168,169
<u>Aldehydes</u>				
132. Nonanal	<u>Galleria mellonella</u> (L.), greater wax moth	sex at	ge(133)	175

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
133. Undecanal	<u>Achroia grisella</u> (Fabricius), lesser wax moth <u>Galleria mellonella</u> (L.), greater wax moth	sex at sex at	ge(140) ge(132)	176 177, 175
134. (Z)-9-Tetradecenal	<u>Heliothis virescens</u> (Fabricius), tobacco budworm	sex at	he(137)	178, 179
135. (Z)-11-Tetradecenal	<u>Argyrotaenia citrana</u> (Fernald), orange tortrix	sex at	h	117
136. (E)-11-Tetradecenal	<u>Acleris emargana</u> (Fabricius) <u>Choristoneura biennis</u> Freeman <u>Choristoneura fumiferana</u> (Clemens), eastern spruce budworm <u>Choristoneura occidentalis</u> Freeman <u>Argyrotaenia citrana</u> (Fernald), orange tortrix	sex at sex at sex at sex at inhib	d d h d d	22 119 180 180 117
137. (Z)-11-Hexadecenal	<u>Heliothis virescens</u> (Fabricius), tobacco budworm <u>Heliothis zea</u> (Boddie)	sex at inhib	he(134) h	178, 179 181, 178
138. (Z)-14-Methyl-8-hexadecenal	<u>Trogoderma inclusum</u> LeConte <u>Trogoderma variabile</u> Ballion	sex at sex at	hk hk	182 182
139. (E)-14-Methyl-8-hexadecenal	<u>Trogoderma glabrum</u> (Herbst)	sex at	hk	48
140. (Z)-11-Octadecenal	<u>Achroia grisella</u> (Fabricius), lesser wax moth	sex at	ge(133)	176
141. (Z)-3,3-Dimethyl- Δ^1, α -cyclohexanecetaldehyde (component of grandlure)	<u>Anthonomus grandis</u> Boheman, boll weevil	sex at, aggr, disrup	ge	51 52

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
142. (E)-3,3-Dimethyl-Δ ^{1,4} -cyclohexaneacetaldehyde (component of grandlure)	<u>Anthonomus grandis</u> Boheman, boll weevil	sex at, aggr disrup sex at	ge dem	51 52 53
<u>Ketones</u>	<u>Rhabdoscelus obscurus</u> (Boisduval)			
143. (Z)-6-Heneicosen-11-one	<u>Orgyia pseudotsugata</u> (McDunnough), Douglas-fir tussock moth	sex at	h	183
144. 3-Hydroxy-2-methyl-2-butanone	<u>Xyloterus domesticus</u> (L.) <u>Xyloterus lineatus</u> (Oliver)	aggr aggr	q q	184 184
145. 4-(p-Hydroxyphenyl)-2-butanone (Willison's lure)	<u>Dacus tryoni</u> (Froggatt) Other <u>Dacus</u> spp.	att att	ds ds	185 186
146. 4-(p-Hydroxyphenyl)-2-butanone acetate (cue-lure)	<u>Dacus cucurbitae</u> Coquillett, melon fly <u>Dacus ochrosiae</u> Malloch <u>Dacus tryoni</u> (Froggatt) <u>Dacus umbrosus</u> Fabricius Other <u>Dacus</u> spp., <u>Callantra</u> spp.	att att att att att	ds ds ds ds ds	187 187 188 189 186
147. 3-Methylcyclohexanone	<u>Dendroctonus pseudotsugae</u> Hopkins, Douglas fir beetle	inhib	d	190
148. 2-Isopropyl-5-methylcyclohexanone (menthone)	<u>Dendroctonus pseudotsugae</u> Hopkins	inhib	d	190
149. 2-Isopropylidene-5-methylcyclohexanone (pulegone)	<u>Dendroctonus pseudotsugae</u> Hopkins	inhib	d	190
150. 3-Methyl-2-cyclohexen-1-one	<u>Dendroctonus pseudotsugae</u> Hopkins, Douglas fir beetle	aggr. inhib, synerg, disrup	hk	191, 192 192 193
	<u>Dendroctonus rufipennis</u> (Kirby), spruce beetle	inhib, disrup	d	194 195

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
151. 2-Isopropyl-5-methyl-5-cyclohexen-1-one (piperitone)	<u>Dendroctonus pseudotsugae</u> Hopkins	inhib	d	190
<u>Miscellaneous Compounds</u>				
152. (E,E)-8,10-Dodecadien-1-ol ethyl ether	<u>Laspeyresia pomonella</u> (L.), codling moth	inhib	d	144
153. (E,E)-8,10-Dodecadien-1-ol propyl ether	<u>Laspeyresia pomonella</u> (L.)	inhib	d	144
154. cis-7,8-Epoxy-2-methyloctadecane (disparlure)	<u>Lymantria dispar</u> (L.) (= <u>Porthetria dispar</u> (L.)), gypsy moth <u>Lymantria dispar japonica</u> (Motschulsky) <u>Lymantria fumida</u> Butler <u>Lymantria monacha</u> (L.), nun moth <u>Lymantria obfuscata</u> Walker	sex at, disrupt sex at sex at sex at sex at	h d h d	196 197,198 199 199 200,201 202
155. 7-Ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane (brevicomin)	<u>Dendroctonus brevicomis</u> LeConte, western pine beetle Other <u>Dendroctonus</u> spp. 1 <u>Temnochila chloridia</u> (Manmerheim) [<u>Dendroctonus brevicomis</u> LeConte]	aggr aggr kair	hkf d	203 204
156. 1,5-Dimethyl-6,8-dioxabicyclo[3.2.1]octane (frontalin)	<u>Dendroctonus brevicomis</u> LeConte, western pine beetle <u>Dendroctonus frontalis</u> (Zimmerman), southern pine beetle <u>Dendroctonus pseudotsugae</u> (Hopkins) Other <u>Dendroctonus</u> spp. 1 <u>Medetera bistriata</u> Parent [bark beetles] <u>Thanasimus dubius</u> (Fabricius) [<u>Dendroctonus frontalis</u> (Zimmerman)] <u>Thanasimus undatulus</u> Wolcott	aggr aggr aggr aggr kair kair kair kair	gkf hkf hkf df d d	205 206 207 208 209 207

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
157. 5-Ethyl-2,4-dimethyl-6,8-dioxabicyclo[3.2.1]octane (multistriatin)	<u>Scolytus multistriatus</u> (Marsham), smaller European elm bark beetle	aggr	he(3) f(185)	5
158. 5-Ethylidihydro-2(3H)-furanone (δ-caprolactone)	<u>Trogoderma glabrum</u> (Herbst) <u>Trogoderma inclusum</u> LeConte <u>Trogoderma variabile</u> Hallion	sex at sex at sex at	hk hk hk	48 182 182
159. Phenol	<u>Costelytra zealandica</u> (White), grass grub beetle	sex at	h	210
160. 2,6-Dichlorophenol	<u>Amblyomma americanum</u> (L.), lone star tick <u>Rhipicephalus sanguineus</u> (Latreille), sex at brown dog tick	sex at sex at	h h	211 212
161. 4-Allyl-2-methoxyphenol (eugenol)	<u>Popillia japonica</u> Newman, Japanese beetle	att	de(99) (116)	145 160
162. 4-Allyl-1,2-dimethoxybenzene (methyl eugenol)	<u>Chrysopa basalis</u> Walker <u>Chrysopa</u> sp. <u>Dacus dorsalis</u> Hendel, oriental fruit fly <u>Dacus umbrosus</u> Fabricius Other <u>Dacus</u> spp.	att att att att att	d d ds ds ds	213 189 214 186,189 186
163. 1-Methoxy-2-phenylbenzene (o-phenylanisole)	<u>Dendroctonus rufipennis</u> Kirby	aggr	d	215
164. 5-Methyl-3-butyloctahydroindolizine	<u>Monomorium pharaonis</u> (L.), Pharaoh's ant	trail	q	216
<u>Hydrocarbons</u>				
165. Undecane	<u>Blaberus craniifer</u> Burmeister	aggr	qe(168)	217

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
166. (Z,E)-3,7,11-Trimethyl-1,3,6,10-dodecatetraene ((Z,E)- α -farnesene)	<u>Laspeyresia pomonella</u> (L.), codling moth	larv at ov st	t	218,219 220
167. (E,E)-3,7,11-Trimethyl-1,3,6,10-dodecatetraene ((E,E)- α -farnesene)	<u>Laspeyresia pomonella</u> (L.)	larv at ov st	t	218,219 220
168. Tetradecane	<u>Blaberus cranifer</u> Burmeister	aggr	qe(165)	217
169. 2-Methylheptadecane	<u>Holmelina</u> spp.	sex at	h	221
170. (Z)-2-Methyl-7-octadecene	<u>Lymantria dispar</u> (L.), gypsy moth	inhib	h	222
171. Docosane	<u>Trichogramma evanescens</u> Westwood [<u>Heliothis zea</u> (Boddie)]	kair	uk	223
172. Tricosane	<u>Trichogramma achaeae</u> Nagaraja and Nagarkatti [<u>Heliothis zea</u> (Boddie)] <u>Trichogramma evanescens</u> Westwood [<u>Heliothis zea</u> (Boddie)] <u>Trichogramma pretiosum</u> Riley [<u>Heliothis zea</u> (Boddie)]	kair kair kair kair	u uk u	224,225 223 225
173. (Z)-9-Tricosene (muscalure)	<u>Musca domestica</u> L., house fly	sex at	h	226
174. Tetracosane	<u>Trichogramma evanescens</u> Westwood [<u>Heliothis zea</u> (Boddie)]	kair	uk	223
175. Pentacosane	<u>Trichogramma evanescens</u> Westwood [<u>Heliothis zea</u> (Boddie)]	kair	uk	223
176. 11-Methylhentriacontane	<u>Cardiochiles nigriceps</u> Viereck [<u>Heliothis virescens</u> (Fabricius)]	kair	q	227

<u>Compound</u>	<u>Insect affected</u>	<u>Action</u>	<u>Notes</u>	<u>Ref.</u>
177. 13-Methylhentriacontane	<u>Cardiochiles nigriceps</u> Viereck [<u>Heliothis virescens</u> (Fabricius)] <u>Microplitis croceipes</u> (Cresson) [<u>Heliothis zea</u> (Boddie)]	kair kair	q q	227 228
178. 12-Methyldotriacontane	<u>Cardiochiles nigriceps</u> Viereck [<u>Heliothis virescens</u> (Fabricius)]	kair	q	227
179. 13-Methyltrtriacontane	<u>Cardiochiles nigriceps</u> Viereck [<u>Heliothis virescens</u> (Fabricius)]	kair	q	227
180. 12-Isopropenyl-1,5,9-trimethyl- cyclohexadeca-1,5,9-triene (neocembrene-A, nasutene)	<u>Nasutitermes exitiosus</u> (Hill)	trail	q	229, 230
181. 2-Methylene-3-dimethylbicyclo- [2.1.1]heptane (camphene)	<u>Dendroctonus pseudotsugae</u> Hopkins	syner	v	207
182. 2,6-Trimethylbicyclo[3.1.1]- hept-2-ene (α-pinene)	<u>Dendroctonus frontalis</u> Zimmerman <u>Dendroctonus pseudotsugae</u> Hopkins <u>Dendroctonus ponderosae</u> Hopkins	syner syner syner	v v v	231, 232 233 232
183. 2,6,6-Trimethylbicyclo[3.1.1]- hept-3-ene (3-carene)	<u>Dendroctonus brevicornis</u> LeConte <u>Dendroctonus frontalis</u> Zimmerman	syner syner	v v	232 232
184. 7-Methyl-3-methylene-1,6-octadiene (myrcene)	<u>Dendroctonus brevicornis</u> LeConte	syner	v	234
185. 3a,3b,4,5,6,7-Hexahydro-4α-iso propyl-3,7β-dimethyl-1H-cyclo penta[1,3]cyclo[1,2]benzene (α-cubebene)	<u>Scolytus multistriatus</u> (Marshall), smaller European elm bark beetle	syner	v	5

Notes for Table I

- a Order used: alcohols, esters, acids, aldehydes, ketones, miscellaneous O- and N- containing compounds, and hydrocarbons. Other designations frequently used are given in parentheses.
- b Some non-insects (ticks and mites) are included. With kairomones, the source insect is listed in brackets.
- c att = attractant, sex at = sex attractant, syner = synergist, inhib = inhibitor, disrupt = disruptant, trail = trail compound, ov st = ovipositional stimulant lar at = larval attractant.
- d Not shown to be present in insect or produced by insect.
- e Other compound(s) required for activity (compound number in parentheses).
- f Synergized by compound(s) from host plant (compound number in parentheses).
- g Produced by males.
- h Produced by females.
- i Listings of bark beetles are incomplete. See Silverstein and Young, in this volume, for additional listings.
- j Certain fatty acids also required for activity.
- k Other active compounds also.
- l Data on field activity lacking.
- m Attracts females.
- n 20% E isomer present. Action of individual isomers not reported.
- o Mixture of isomers; major component = Z,Z isomer.
- P Major component of attractant is (77) for Iowa strain and (78) for New York strain.
- q From the insect.
- r From frass.
- s Primarily attracts males.
- t From apple skins.
- u From moth scales.
- v From host.

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