

Pheromones of stored-product insects: current status and future perspectives

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Abstract

Pheromones have been isolated and identified from over 30 species of stored-product beetles and moths during the past 25 years. Existing gaps in our basic knowledge include: 1) discovery of new compounds in a few groups; 2) refined knowledge of chemical signals, response behaviours; and slow-release delivery systems; 3) development of cost-effective chemical syntheses on commercial scales; 4) identification of food attractants or pheromone synergists; and 5) identification of attractants for female moths. Application of new knowledge and improvements on existing pheromone-based technologies are expected. The most common application presently is with pheromone-baited traps for survey, detection, and monitoring, primarily of pyralid moths, cigarette beetles, and dermestids in processed food situations. Improvements in traps will occur in trap design, lure formulation, and data handling. Other applications of pheromones have been suggested or researched, but few have undergone extensive testing. Mass trapping of male moths is generally thought ineffective for control, but optimisation could result in biologically significant capture of males; mass trapping beetles with aggregation pheromones captures females and should be effective in control. Mating disruption was demonstrated many years ago and more work should be done on implementation. The 'attracticide' method holds numerous opportunities for pest suppression, especially as new and improved attractants are developed and more effective pesticides and pathogens for dissemination become available. Biorational alternatives are urgently needed to replace ineffective or unsafe methods of traditional pest control, and pheromone-based technologies can provide many solutions.

Introduction

The first stored-product insect pheromone was identified nearly 30 years ago from the black carpet beetle, *Attagenus unicolor* (= *megatoma*) (Silverstein et al. 1967), and since that time many advances in pheromones of storage pests have resulted in valuable tools for pest management (Burkholder 1990). From the hundreds of insects recorded from stored commodities and foods, pheromones for many of the common species have been investigated and synthetic formulations of pheromones are available for some of the most prevalent pests. Consequently, pheromone-based monitoring systems have been developed that facilitate early pest detection and

integrated pest management for overall reduction of pesticide use and increased product quality (e.g. Mueller and Pierce 1992). These trapping programs are mostly centred around detection of phycitine moths, cigarette beetles, dermestid beetles and other pests of processed foods in finished product warehouses and factories (Faustini et al. 1991).

Research is still required on some of the important warehouse pests and on pests of raw grain in order to develop effective monitoring systems with their pheromones. Sensitivity and levels of detection can be improved with more thorough knowledge of insect behaviour, semiochemistry, and redesigned trapping and formulation technology. Suppression methods employing pheromones were proposed decades ago, but their practical development in food storage systems has yet to come. In this brief review I will summarise the existing knowledge on available stored-product insect pheromones, I will identify research needs that could enhance pheromone-based monitoring in specific pest management systems, and I will review proposed strategies for using pheromones to suppress insect populations.

Pheromones Available for Use

Table 1 is a list of stored-product insects for which pheromones have been chemically identified. This list is similar to those published earlier (e.g. Burkholder and Ma 1985; Burkholder 1990), but with some recently reported entries. Of the 38 species listed, 50% have synthetic pheromones commercially available for use as formulated lures for traps. These 19 species include the most serious insect pests of stored grains and stored-food products worldwide. Some pheromones are active for multiple species of pests, thus enhancing their versatility as monitoring tools. For example, males of the first five moth species listed under Pyralidae can be trapped using the same compound, (*Z, E*)-9,12-tetradecadienyl-acetate. Some pheromones have been identified for stored-product mites (e.g. Kuwahara et al. 1982), but they have not been developed commercially and will not be considered here. In general, much of the basic research of discovery and identification has been done on pheromones of the major stored-product pests, hence refined understanding and new applications of pheromone systems provide the current challenges to researchers and pest managers.

Research Needs

New chemistry

Pheromone identification and synthesis is required for some species of important stored-product pests. One important species that remains to be fully studied is the cowpea weevil, *Callosobruchus maculatus*, a serious pest of stored legumes that uses a female-produced sex pheromone (Qi and Burkholder 1981). The sex pheromone for a closely related species, *C. analis*, was recently identified (Cork et al. 1991), but work is apparently still in progress on the pheromone for

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Table 1. Species of stored-product insects for which pheromones have been identified, and information on commercial availability.

Taxa/Species	Sex producing	Commercial availability	Reference ^a
Coleoptera (beetles)			
Family Anobiidae			
<i>Stegobium paniceum</i>	Female	Yes	Kuwahara et al. 1978
<i>Lasioderma serricorne</i>	Female	Yes	Chuman et al. 1983
Family Bostrichidae			
<i>Rhyzopertha dominica</i>	Male	Yes	Williams et al. 1981
<i>Prostephanus truncatus</i>	Male	Yes	Hodges et al. 1984
Family Bruchidae			
<i>Acanthoscelides obtectus</i>	Male	No	Horler 1970
<i>Callosobruchus chinensis</i>	Female	No	Tanaka et al. 1981
<i>C. analis</i>	Female	No	Cork et al. 1991
Family Cucujidae			
<i>Ahasverus advena</i>	Male and Female	No	Pierce et al. 1991b
<i>Cathartus quadricollis</i>	Male	No	Johnston and Oehlschlager 1986
<i>Cryptolestes ferrugineus</i>	Male	No	Wong et al. 1983
<i>C. pusillus</i>	Male	No	Millar et al. 1985a
<i>C. turcicus</i>	Male	No	Millar et al. 1985b
<i>Oryzaephilus surinamensis</i>	Male	No	Pierce et al. 1985
<i>O. mercator</i>	Male	No	Pierce et al. 1985
Family Curculionidae			
<i>Sitophilus granarius</i>	Male	No	Phillips et al. 1987
<i>S. oryzae</i>	Male	No	Schmuff et al. 1984
<i>S. zeamais</i>	Male	No	Schmuff et al. 1984
Family Dermestidae			
<i>Attagenus unicolor</i>	Female	Yes	Silverstein et al. 1967
<i>A. brunneus</i>	Female	No	Fukui et al. 1977
<i>Anthrenus flavipes</i>	Female	Yes	Fukui et al. 1974
<i>A. sarnicus</i>	Female	No	Finnegan and Chambers 1993
<i>A. verbasci</i>	Female	Yes	Kuwahara and Nakamura 1985
<i>Dermestes maculatus</i>	Male	No	Levinson et al. 1978
<i>Trogoderma glabrum</i>	Female	Yes	Yarger et al. 1975
<i>T. granarium</i>	Female	Yes	Cross et al. 1976
<i>T. variabile</i>	Female	Yes	Cross et al. 1976
Family Tenebrionidae			
<i>Tribolium castaneum</i>	Male	Yes	Suzuki 1980
<i>T. confusum</i>	Male	Yes	Suzuki 1980
<i>Tenebrio molitor</i>	Female	No	Tanaka et al. 1986
Lepidoptera (moths)			
Family Gelichiidae			
<i>Sitotroga cerealella</i>	Female	Yes	Vick et al. 1974
Family Pyralidae			
<i>Cadra cautella</i>	Female	Yes	Brady 1973
<i>C. figulilella</i>	Female	Yes	Brady and Daly 1972
<i>Ephestia elutella</i>	Female	Yes	Brady and Nordlund 1971
<i>E. kuehniella</i>	Female	Yes	Brady et al. 1971a
<i>Plodia interpunctella</i>	Female	Yes	Brady et al. 1971b
<i>Pyralis farinalis</i>	Female	No	Landolt and Curtis 1982
<i>Amyelois transitella</i>	Female	No	Coffelt et al. 1979
Family Tineidae			
<i>Tineola bisselliella</i>	Female	Yes	Yamaoka et al. 1985

^aReferences are those giving the chemical identification or analysis of pheromones; more literature may exist on biology and application (see Burkholder 1990).

C. maculatus. Pheromones for cucujid beetles in the genera *Cryptolestes* and *Oryzaephilus* have been identified (Table 1), but the lack of an efficient large-scale chemical synthesis of the pheromones has prevented their commercial application. Additionally, some pheromones have been identified and could be synthesised commercially, but they have not been put to use because data on field activity are lacking or their use in a pest management scheme has not been developed (e.g. *Anthrenus* spp., *Callosobruchus* spp., and *Sitophilus* spp.).

Formulation and delivery systems

The performance of certain commercially available pheromone systems could be improved with changes in chemical formulation or delivery systems. A pheromone-based trapping system is being used for *Tribolium* flour beetles, but effectiveness of traps in detecting pest populations is equivocal (David Mueller, pers. comm.). Males of *T. castaneum* and *T. confusum* produce 4,8-dimethyldecanal, a molecule that can exist as four distinct optical isomers or enantiomers. A complete mixture of all four enantiomers yield fairly low activity in baited traps (Javer et al. 1990), but the pure 4R, 8R isomer gives optimal response (Levinson and Mori 1983). Hence suppliers of *Tribolium* pheromone may produce sub-optimum lures if they do not use synthetic pheromone with the proper enantiomeric composition.

Formulation of *Tribolium* pheromone into slow-release devices is also very important for eliciting optimum response of beetles. Work in my laboratory has investigated the response of *T. castaneum* to different pheromone lure formulations using a two-choice pitfall bioassay (see Phillips et al. 1993 for details of bioassay). Commercial lures of different ages were tested against blank controls (see Hussain 1993 for complete listing of lures tested). Examples of variation in response to two different lure designs are given in Figure 1. Membrane lures, in which liquid pheromone was held in an impermeable reservoir and evaporated through a semi-permeable membrane on one surface, were repellent to *T. castaneum* when new, and did not elicit significant attraction until five weeks of age (Fig. 1a). However, laminate lures, in which the pheromone was formulated into a plastic matrix and then released through a semi-permeable membrane, were attractive when initially removed from the package, and remained active for the 14-week course of the study (Fig. 1b). Differences in activity of these lures over time is likely to be due to the amount of pheromone being released at a given time. Other work has shown that high doses of 4,8-dimethyldecanal, like those probably coming from new membrane lures (Fig. 1), are repellent to *T. castaneum* in laboratory bioassays (Hussain 1993). Proper release rate, and the formulation required to achieve it, are therefore very important for effective pheromone lures for *Tribolium*. We also know that the aldehyde group on the pheromone molecule reacts with air over time to form the carboxylic acid, which is inactive. *Tribolium* pheromone, as with other unstable pheromones, should probably be protected with an antioxidant while in the slow release device.

Minor components

Despite successful use of some pheromones in traps, the pheromone system of the pest insect in question may not be fully understood. Minor components may exist that could improve trap performance, particularly under low population densities. A single component pheromone, (Z, E)-9, 12-tetradecadienyl acetate (referred to as ZETA), is available for the Indianmeal moth, *Plodia interpunctella*, and four other species of stored-product Pyralidae (Table 1). The corresponding alcohol to ZETA, (Z, E)-9, 12-tetradecadienol

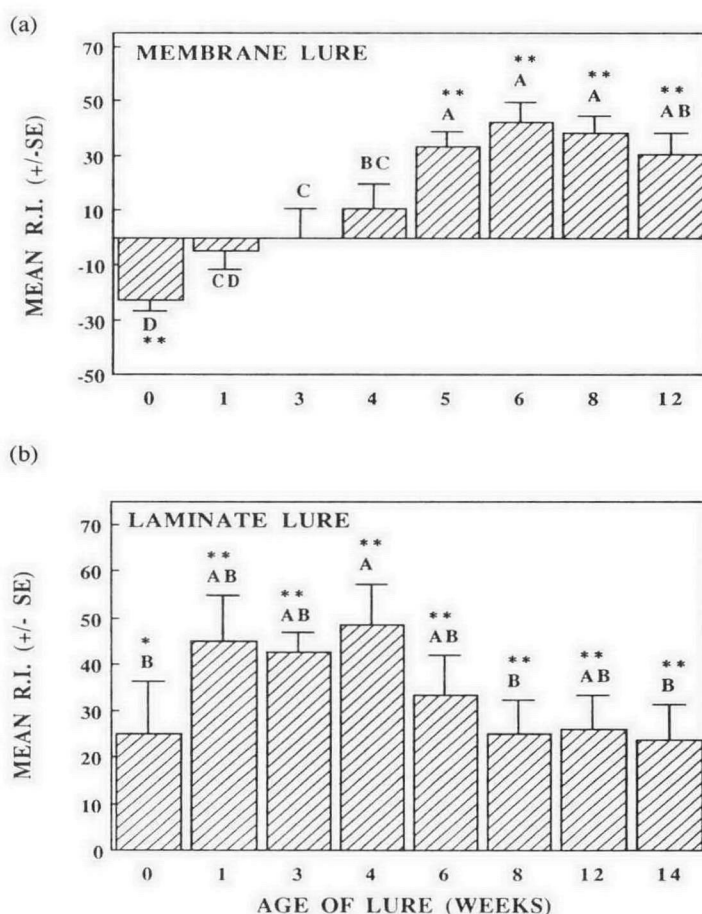


Fig. 1. Responses of *Tribolium castaneum* to pheromone lures of different ages in a two-choice pitfall bioassay. Histograms show means and standard errors for response index (R.I.), calculated as $[(T-C)/total] \times 100$, for which 'T' is the number responding to the treatment (a lure), 'C' is the number responding to the control (blank), and 'total' refers to the total number of beetles released (usually 20 one-week-old adults of mixed sex). Means for response to lures of different ages with different letters are significantly different ($P < 0.05$, ANOVA and Fishers PLSD test), and stars indicate significant differences in response to treatment and control within an experiment (*, $P < 0.05$, **, $P < 0.01$, Student's t-test). (a) Membrane lure; (b) Laminate lure.

(ZETOH), is produced by female *P. interpunctella* and it also enhances responses of male moths when combined with ZETA (Vick et al. 1981; Phillips unpublished). However, ZETOH has the opposite effect of inhibiting responses by the almond moth, *Cadra cautella* (Sower et al. 1974), hence the material is not added to commercial lures intended for multiple species. I studied the responses of male *P. interpunctella* natural and synthetic pheromone sources in a wind tunnel (Fig. 2). When a small cage containing a virgin female *P. interpunctella* was presented upwind, all male moths tested flew upwind and contacted the cage. A one-week-old pheromone lure (rubber septum) in the wind tunnel elicited upwind flight in male moths, but very few males actually contacted the pheromone source; a similar response occurred when 1.0 mg of ZETA was applied to filter paper and presented. When 100 ng of ZETA on filter paper was tested in the wind tunnel I observed flight and contact responses of males similar to those elicited by virgin females. However, this dose of 100 ng represents about 10 times the amounts produced by a virgin female (Sower and Fish 1975). When 10 ng of ZETA was tested, a

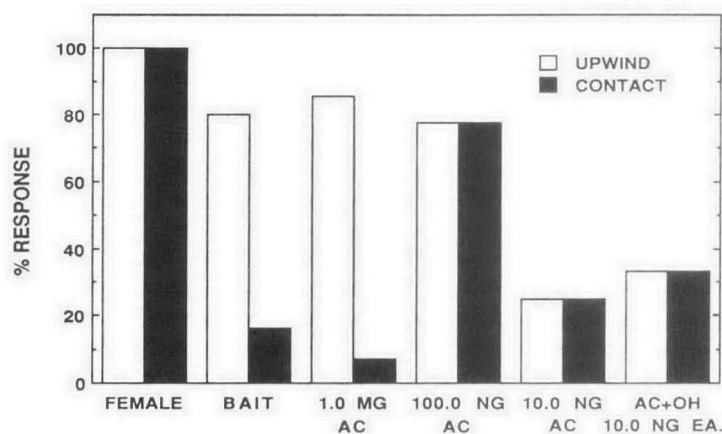


Fig. 2. Responses of male *Plodia interpunctella* to natural and synthetic sources of sex pheromones in a wind tunnel bioassay. Histograms represent the percentage of females ($n=10-20$) to: 1) take flight and initiate characteristic upwind orientation; and 2) to contact the source for a minimum of 10 seconds. Sources of attraction listed along the bottom of the graph are: 1) a single virgin female, one day old, in a small cage; 2) a one-week old pheromone lure (Trécé Inc.) containing ZETA in an open 60 mm glass Petri dish; 3) 1.0 mg of ZETA (referred to as AC for acetate) applied to filter paper in a dish; 4) 100.0 ng of ZETA on paper in a dish; 5) 10.0 ng of ZETA on paper in a dish; and 6) 10.0 ng each of ZETA and ZETOH on paper in a dish. Individual males, one-day old, were released downwind and given 3 minutes to respond.

biologically relevant dose, both flight and contact responses were very low; addition of ZETOH at 10 ng had no effect (Fig. 2). Thus synthetic pheromone components released at levels similar to one or a few virgin females failed to elicit attraction in *P. interpunctella*. Male moths obviously respond from a distance to high levels of ZETA coming from commercial lures, but moth capture in traps is probably dependent on relatively high population levels. Analysis of volatile chemicals produced by female *P. interpunctella* revealed individual variation in the number and amounts of compounds produced (Fig. 3). In addition to ZETA and ZETOH, which may vary quantitatively between females, several other unidentified compounds were detected. It is clear from behavioral studies (Fig. 2) that ZETA alone cannot account for pheromone-mediated mate finding in *P. interpunctella*, and potential exists for discovery of new pheromones that may yield improved pest management tools.

Female attractants

Sex pheromones produced by female insects attract only males. Traps baited with synthetic sex pheromones can only monitor populations of males and impact on overall population increase is limited since females are not affected. Work is underway in various laboratories to develop attractants for female moths of agricultural importance (e.g. Mitchell et al. 1990; Landolt 1989). Work in my laboratory has focused on attractants and oviposition stimulants for the Indianmeal moth (Phillips and Strand 1994). In close-range oviposition experiments, mated female *P. interpunctella* oviposited on dishes containing cornmeal-based rearing medium. While investigating the potential for epideictic (spacing or dispersal) pheromones, we found that females preferred to oviposit on cheesecloth patches that had been contaminated by conspecific wandering fifth instar larvae. A similar oviposition response was reported by Corbet (1973) for the Mediterranean

flour moth, *Ephestia kuehniella*. With *P. interpunctella* we found that a combination of food plus larval secretions elicited a greater oviposition response than either food alone or larval secretions alone. In wind tunnel bioassays female moths flew upwind only when food was present, and contacts by females were highest to the combination of food plus larval secretions (Phillips and Strand 1994). We are currently isolating the material that elicits oviposition in *P. interpunctella* in hopes of identifying new semiochemicals that can be used to manipulate behaviour of female moths.

Food odours

Our results with a combination of food odours and insect produced volatiles in *P. interpunctella* reflect a recurring theme on the importance of food and food volatiles in the pheromone systems of insects. Several examples are known from stored-product insects in which food is very important for pheromone production and food volatiles serve as attractants or synergists to pheromones. Grain oils are known to be attractive to stored-grain insects (e.g. Nara et al. 1981), as are volatiles from fresh grains and from fungus-infected grains (e.g. Pierce et al. 1990; 1991a). Recently we compared the responses of two ecologically different beetle species, *T. castaneum* and *S. oryzae*, to a collection of grain oils and found that the two species responded quite differently to the same oils (Phillips et al. 1993). In the same study we also showed that male *T. castaneum* responded to food volatiles at levels higher than females, and that responses of both sexes to synthetic pheromone was increased by the addition of food volatiles. Hussain (1993) found that male *T. castaneum* produced pheromone only when feeding on cracked wheat, and that pheromone production ceased when beetles were removed from food. A scenario involving food and mate-finding can be proposed for *T. castaneum*: male beetles locate food sources at which they feed, produce pheromone, and attract females for mating and reproduction. Walgenbach et al. (1987) had similar results with *S. zeamais*, in which weevils responded stronger to a combination of pheromone and food volatiles compared to pheromone or food separately. Synergism of host plant volatiles with beetle-produced pheromones is a common phenomenon in scolytid bark beetles (reviewed in Raffa et al. 1993), and a synergistic role for plant volatiles in pheromone systems in various insect groups is now being realised (Dickens et al. 1990). Potential certainly exists to improving existing trapping technology for stored-product insects by addition of food volatiles to increase insect response to pheromone lures.

Applications

Monitoring and detection

The predominant application of pheromones of stored-product insects is as tools for monitoring and detection of pest populations. Pheromone-baited traps are used extensively to monitor populations of pyralid moths, cigarette beetles (*Lasioderma serricorne*), and dermestid warehouse beetles (*Trogoderma* spp.) in processed food warehouses and factories. Typical recommendations are for a grid-work of traps to be established in a structure and monitored at regular intervals for the capture of insects. If one or more traps in a particular area captures more insects than others, then an increased density of traps should be deployed in that area in order to localise the source of the pests (Burkholder 1990). Monitoring of insects infesting raw grains has relied mostly on probe traps that do not require pheromone lures, although synthetic phe-

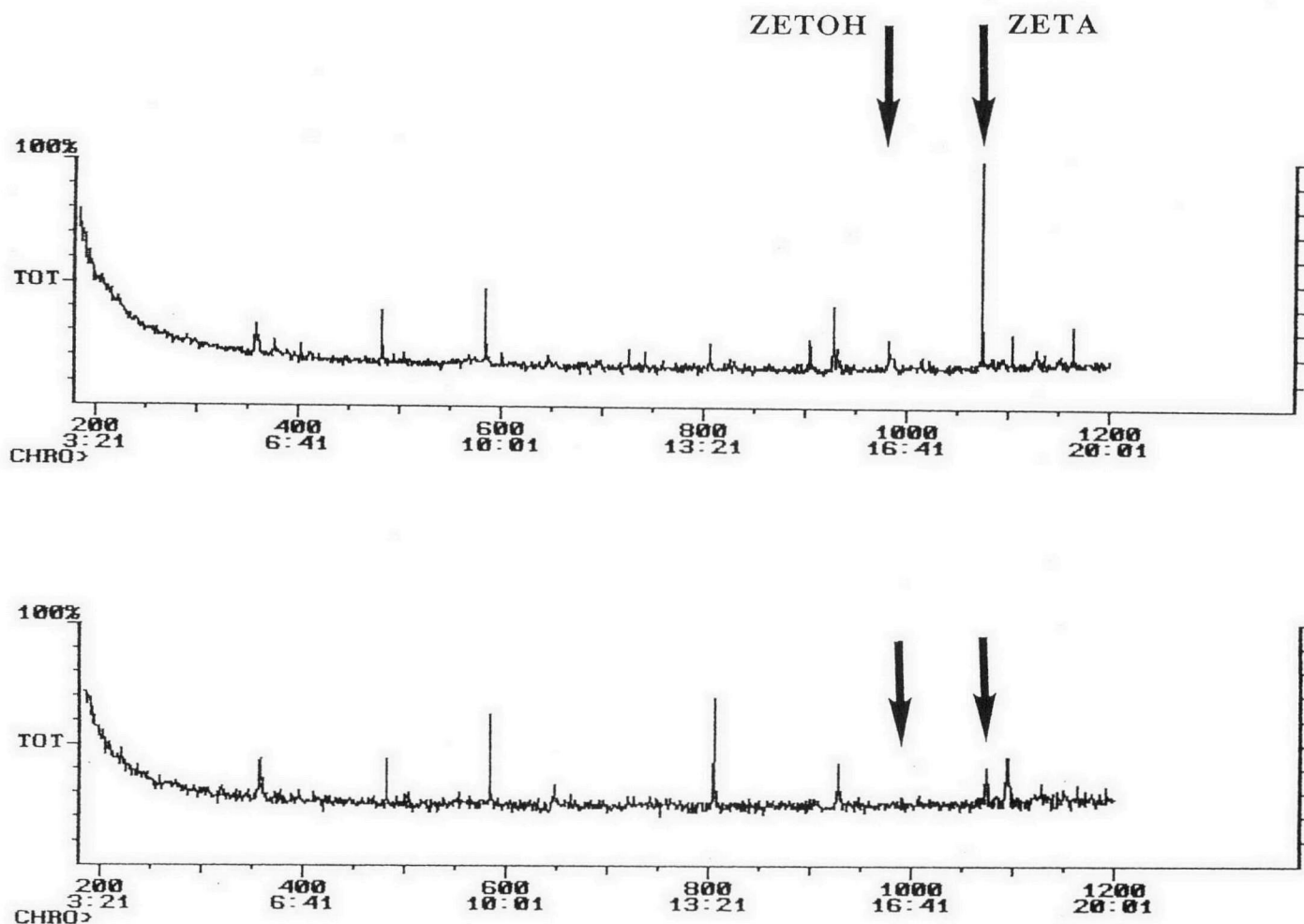


Fig. 3. Total ion chromatograms (GC) of volatiles collected from two different one-day old *P. interpunctella* for 16 hours through the scotophase. Arrows indicate the retention times for ZETOH and ZETA. The x-axis is the retention time in seconds and minutes:second, and the y-axis is ion current relative to the largest peak. Volatiles were collected on Super-Q polymer, extracted with hexane, and analysed on a Schimadzu GC-14A with a 30 m DB-1 column (J & W Scientific) coupled to a Finnegan 800 series Ion Trap Detector.

romones for the grain borers *Rhyzopertha dominica* and *Prostephanus truncatus* have been used to study the geographic spread of these pests within regions of new range extension (e.g. Fields et al. 1993; Hodges et al. 1984).

New developments in the use of pheromone-baited traps could improve their application in pest management schemes. New trap designs are being developed and some show promise in improving the detection limits with certain insects (e.g. Mullen 1992; Quartey and Coaker 1992). Once traps and lures are optimised, new computer-based methods to organise and interpret data from traps will greatly enhance the value of the data and facilitate informed decision-making based on trap catch (e.g. Insects Limited 1994). Warehouse managers could then maintain long-term databases on insect activity in their facilities and easily detect changing trends in pest numbers in a relatively short time. In addition to estimating relative numbers of insects by observing changes in trap catch over time, pest managers may also employ new techniques to estimate absolute numbers of insects in a facility. Wileyto et al. (1994) have developed a trapping-marking-re-trapping method to estimate population sizes of insects using pheromone traps. In a validation experiment of their mark-recapture model, Wileyto et al. (1994) estimated sizes of known populations within statistically acceptable levels of confidence. Population estimation may provide a more realistic numerical

value that can be used with greater confidence than simply uncalibrated trap catches for making pest management decisions.

Suppression

Although population monitoring is the primary use of pheromones in agriculture, the idea of actually suppressing insect populations with pheromones has been proposed from the very beginning of pheromone research. Mass trapping with pheromones, or simply catching as many insects as possible to reduce overall numbers, has immediate appeal but has received limited success. In the case of female-produced sex pheromones, those used most commonly in storage systems, only males are trapped. Hence any attempt to suppress the population by trapping males would require a sufficient number of males to be trapped so that nearly all females would go unmated. Theoretical considerations of mass trapping males take into account the density of males in the population and the potential number of matings a male is able to secure in a lifetime (Lanier 1990; Roelofs et al. 1970). If a male can mate with ten females in his lifetime, as is the case for the Indianmeal moth (Brower 1975), then up to 90% of the male population can be trapped and not have any effect on mated females or the subsequent larval generation. Under high popu-

lation levels the rate of female encounter would be high and mass trapping more difficult to achieve. However, under low population levels males would locate females less frequently and intensive trapping could conceivably reduce male populations to biologically significant levels. Proper experiments of mass trapping are difficult to conduct due to inadequate controls or poor replication, although various studies have reported successful suppression of storage pests by mass trapping males with sex pheromones (e.g. Mueller and Pierce 1992; Suss and Trematerra 1986). Mass trapping both sexes of a population using aggregation pheromones should be intuitively more effective than mass trapping just females. Aggregation pheromones produced by males are known from several beetle species that infest stored products (Table 1), but no studies have been conducted to suppress populations of these insects by mass trapping.

Mating disruption is a potentially effective control measure in which the air in the area containing the pest population is permeated with sex pheromone. Although the mechanism of mating disruption is incompletely understood, it seems that males fail to mate with females due to either a physiological affect on pheromone perception or due to a behavioural inability to locate and contact a real female amongst all the synthetic sources of pheromones (Cardé 1990). The limitations and theoretical bases of mating disruption are similar to those for mass trapping of males: a substantial proportion of the male population must fail to locate females, and success is more likely under relatively low population levels. Mating disruption has been successfully applied to Lepidoptera in field crops (e.g. the pink bollworm on cotton) and has been commercialised in such cases. Although several successful experiments have been reported using mating disruption with stored-product pyralid moths (e.g. Prevett et al. 1989; Sower and Whitmer 1977), no commercial applications of this method are currently available. Clearly mating disruption is a potentially effective pheromone-based control method for storage moths that requires further consideration.

Attracticide

One final application of pheromones for insect pest suppression in stored-products is the 'attracticide' or 'lure-and-kill' method. The attracticide concept involves using a pheromone or other attractive semiochemical to lure insects to an area or a specific point source whereby they contact a toxicant or are destroyed or disabled by other means. Attracticidal control is analogous in a way to mass trapping, although many more insects are affected because the attracticide is broadcast over a large area and the killing effect is not limited to individual traps. Trap cropping represents a variation of the attracticidal method in agriculture whereby the target insects are lured to a plot of crop plants (or one or more trees in the case of bark beetles), and the crop is subsequently destroyed. The more common concept of an attracticide involves the formulation of an insecticide with a feeding stimulant and a long-range attractant, either in liquid droplets or in some encapsulated or solid matrix, that can be applied evenly over large areas. Target insects orient to the formulation where they feed on or contact the insecticide and then die. In agriculture the attracticide method has been used with success against tephritid fruit flies (Cunningham et al. 1990) and cotton boll weevils (Ridge-way et al. 1990). In stored-products there are many promising results on the use of the attracticide concept in flour mills and warehouses (Trematerra, these proceedings). One variation on the attracticide concept is for the dissemination of pathogenic organisms into the pest population. Instead of an insecticide, the attractive source could contain inoculum of an insect pathogen that could be spread among contacting insects and then

amplified in the next generation to bring about an epizootic. Suppression of experimental dermestid beetle populations using a protozoan pathogen and pheromone-based dissemination was reported by Shapas et al. (1977). Current work on microbial insect pathogens and biotechnology could conceivably produce inoculum of maximal virulence and high environmental tolerance that would be applicable to the attracticide method.

Conclusions

The practice of stored-product protection is facing serious challenges worldwide as important issues arise regarding food safety, government regulation, and biological pressure from insects that become increasingly more difficult to control. In the United States, for example, one fumigant and two residual protectants are available for use on raw grain, and finished food warehouses and factories have very limited options for chemical pest control. Insect populations are rapidly evolving resistance to the few chemicals being used, and the general public is calling for limited use of pesticides on food while also approaching a zero-tolerance attitude toward insect contamination in agricultural commodities. Safe and effective alternatives to conventional pesticides are needed, and potential exists for development of pheromone-based methods. Basic research on the isolation and identification of pheromone compounds flourished during the 1970s and 1980s, and consequently pheromones are known from most of the major pest insects in stored-products. It is time now to move forward and apply existing knowledge of pheromones and insect behavior into effective biorational methods to manage insect pests in stored-product systems.

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