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Semiochemicals of Stored-product Insects: Research and Applications

THOMAS W. PHILLIPS

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Abstract—Development of semiochemical-based pest management systems in stored-products is being necessitated by the loss of traditional residual and fumigant pesticides. This review article evaluates our current state of knowledge and practice with semiochemicals for storage pests, it summarizes methods used for isolation and identification of semiochemicals, and it elaborates possible future research trends and applications. Pheromones are known from over 35 species of stored-product insects. The most successful applications of these compounds are as attractants in traps for detecting and monitoring pests in storage facilities. Recent research has focused on improving trapping technology by the discovery of additional pheromones, incorporation of food odor synergists, developing better slow-release formulations, and improving trap design. Direct control of storage pests with pheromones can be approached with the attracticide and mating disruption methods. Both techniques utilize synthetic female sex pheromones to prevent males from reproducing. Recent research is investigating attractants for female moths. Semiochemicals to manipulate female behavior will provide new tools for many different pest management approaches. Semiochemicals may be available to manipulate the behavior of beneficial natural enemies of storage pests. Host-finding efficiency of natural enemies in biological control programs could be improved with the use of kairomones in mass-rearing or release protocols. The role of semiochemicals in stored-product pest management is increasing as more biorational methods are employed. Published by Elsevier Science Ltd

Key words—pheromones, attractants, traps, lures, biological control, pest management, *Callosobruchus*

INTRODUCTION

Pheromones and other semiochemicals (behavioral chemicals) play important roles in the lives of stored-product insects and hold great potential as tools for pest management. Stored-product insects have been the subject of much research in chemical ecology, and some of the earliest pheromones to be identified were from important storage pests (e.g. Silverstein *et al.*, 1967a; Brady *et al.*, 1971). Pheromones in storage pests have been covered by several review articles in the past decade that listed species, pheromone compounds, and methods for use (Burkholder and Ma, 1985; Burkholder, 1990; Jones, 1993; Phillips, 1994). Pheromones of many of the major stored-product insect pests have been described and some are being used extensively for detection and population monitoring. With limitations on the use of pesticides and fumigants in stored products growing, and increasing public demands for wholesome and pest-free food products, the need for developing biorational pest management technologies in stored-products, such as those using semiochemicals, is greater than ever before. In this brief review, I attempt to summarize the applications of currently available pheromones and illustrate improvements that are suggested by new research. Also discussed is the methodology used for isolation and identification of semiochemicals, and a case study of a recently described pheromone system is presented. Lastly, I give a perspective of where future research directions and applications for semiochemicals of storage pests may lie. This review

covers mostly attractants, as repellents and natural toxicants are covered by other papers in this symposium.

PHEROMONES: CURRENT USES AND POTENTIAL IMPROVEMENTS

Pheromones, semiochemicals that are intraspecific signals, have been chemically identified from over 35 species of stored-product insect pests, all beetles and moths (see detailed lists in Burkholder and Ma, 1985; Burkholder, 1990; and Phillips, 1994). Behavioral chemicals for mites have also received research attention (e.g., Kuwahara *et al.*, 1982). As in other insects, pheromones of storage pests are volatile, low molecular weight organic compounds of various structures (Fig. 1). Pheromones are classified as either sex pheromones, which are produced by one sex (usually the female) and attract members of the opposite sex for mating, or as aggregation pheromones, which are produced by one sex (usually the male) and attract members of both sexes resulting in mating and aggregation at a food resource. In fact it is believed that both sex and aggregation pheromones evolved in the context of mating behavior, and thus all sex-specific adult pheromones of this nature could be considered 'sex' pheromones (see discussion related to bark beetles in Raffa *et al.*, 1993). Among storage insects, female-produced sex pheromones are utilized by all moths and by beetles in the families Anobiidae, Bruchidae, and Dermestidae. The adults of these insects with sex pheromones tend to be relatively short-lived (days to weeks) and feed very little (beetles) or not at all (moths) before they mate and die. Storage insects with male-produced aggregation pheromones include beetles in the families Bostrichidae, Cucujidae, Curculionidae, and Tenebrionidae, and these insects feed substantially and are relatively long-lived as adults (weeks to months) (Burkholder and Ma, 1985).

The most common uses of pheromones for storage pests are as attractant lures in traps to detect the presence of pests and to monitor the activities of pest populations. Pheromone traps provide an easy, efficient, and extremely sensitive way to detect insects in storage facilities, and managers can use information from traps to locate infestations and make management decisions. Widespread use of synthetic pheromones for certain species is facilitated by both biological effectiveness and economic cost-effectiveness. For example, the most commonly sold lures and traps in North America, by one accounting, are for the Indian meal moth, *Plodia interpunctella* (Hübner), and its pyralid relatives, and for the cigarette beetle, *Lasioderma serricorne* (F.) (Mueller *et al.*, 1990). For both species, the synthetic sex pheromones are perceived by users to be 'very strong' attractants because some insects are usually trapped if there is an infestation present in the target facility. Thus the pheromones for Indian meal moths and cigarette beetles are judged to be biologically very effective for detection and monitoring purposes. The economic cost-effectiveness that contributes to the commercial success of Indian meal moth and cigarette beetle pheromones probably lies in the size of the potential market for these products that offsets production and marketing costs. Many users of these traps and lures are managing high-value, or value-added, consumer products, and the cost of using traps for early pest detection is greatly offset by the cost-savings realized from protection of the product. The commercially available pheromone for the Indian meal moth has the added cost benefit of being used as a lure for four additional species of pyralid moth pests, a feature many pheromones lack due to their high species specificity.

Although only two species are cited in the example above, nearly half of the over 35 species of storage pests with known pheromones have synthetic pheromones that are commercially available and are used to various degrees (Phillips, 1984). The third most commonly sold pheromone lure during the survey of Mueller *et al.* (1990) was for *Trogoderma* spp. dermestid beetles. As with pyralid moth pests of stored products, several species of dermestid beetles in the genus *Trogoderma* share a common female-produced sex pheromone component, *Z*-14-methyl-8-hexadecenal, which is effective as a single component lure for different species (Barak and Burkholder, 1976; Cross *et al.*, 1976). *T. granarium* Everts, the khapra beetle, is a serious pest of raw grain in Europe and Asia, but it does not occur in North America. Hence *T. granarium* is an important quarantine pest for which detection with pheromone traps in and around ports of entry is practiced. Pheromone traps are also used to detect dermestids such as *T. variabile* Ballion, the warehouse beetle, in factories and food warehouses because this species is indicative of general filth and infestation problems. Although identified over 15 years ago (Kuwahara *et al.*, 1978), the sex pheromone for

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Effectiveness of pheromones and traps can be improved through use of optimal lures and deployment of better trap designs. Pheromone lures employ slow release technology so that

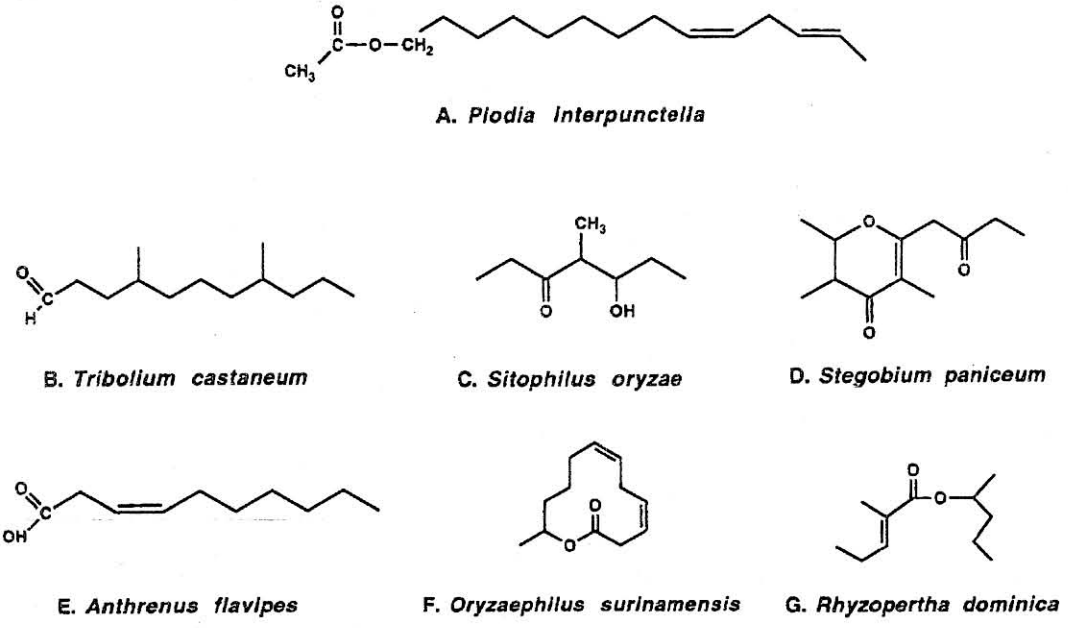


Fig. 1. Examples of structural diversity in pheromones among stored-products insects. A. Female-produced sex pheromone of *Plodia interpunctella*, the Indian meal moth; (*Z*, *E*)-9, 12-tetradecadienyl acetate (Brady *et al.*, 1971). B. Male-produced aggregation pheromone of *Tribolium castaneum*, the red flour beetle, and also the confused flour beetle, *T. confusum*; 4, 8-dimethyldecanal (Suzuki, 1980). C. Male-produced aggregation pheromone of *Sitophilus oryzae*, the rice weevil, and *S. zeamais*, the maize weevil; 4-methyl-5-hydroxy-3-heptanone, or 'sitophinone' (Schmuff *et al.*, 1984). D. Female-produced sex pheromone of *Stegobium paniceum*, the drugstore beetle, and also *Anobium punctatum*, the furniture beetle; 2,3-dihydro-2,3,5-trimethyl-6- (1-methyl-2-oxobutyl)-4*H*-pyran-4-one, or 'stegobinone' (Kuwahara *et al.*, 1978). E. Female-produced sex pheromone of *Anthrenus flavipes*, the furniture carpet beetle; (*Z*)-3-decenoic acid (Fukui *et al.*, 1974). F. One of the male-produced aggregation pheromones of *Oryzaephilus surinamensis*, the sawtoothed grain beetle, also produced by *O. mercator*, the merchant grain beetle; (*Z*, *Z*)-3,6-dodecadien-11-olide (Pierce *et al.*, 1985). G. Male-produced aggregation pheromone of *Rhyzopertha dominica*, the lesser grain beetle; 1-methylbutyl-(*E*)-2-methyl-2-pentenoate, or 'dominicalure 1' (Williams *et al.*, 1981).

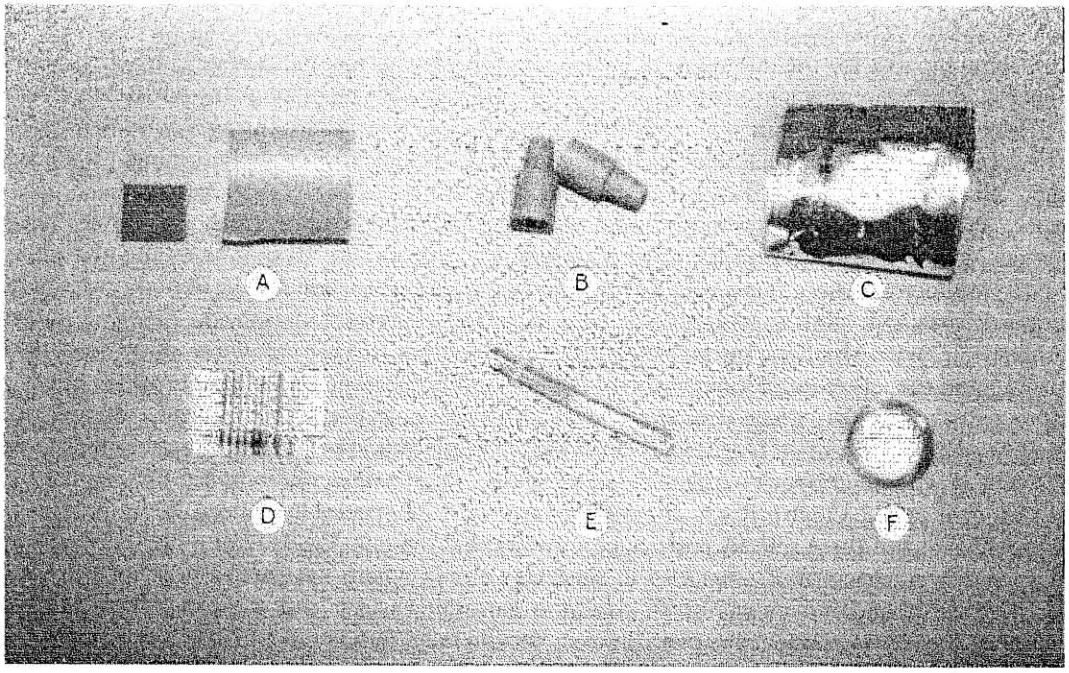
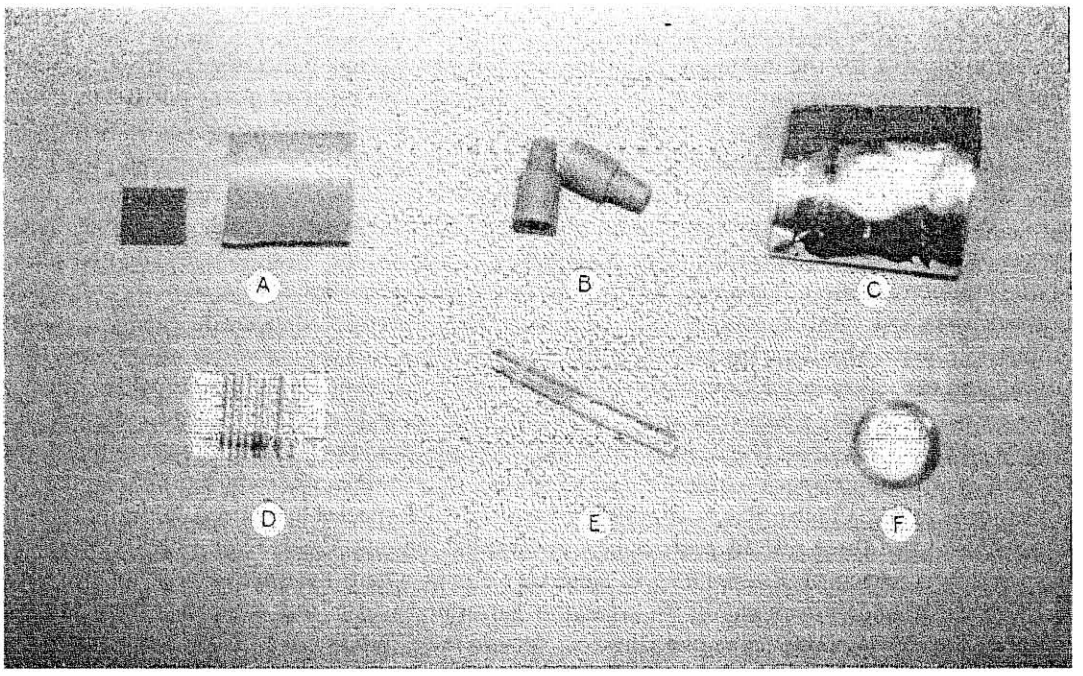


Fig. 2. Examples of slow-release dispensers for insect pheromones. A. Plastic laminate, in which the pheromone is in a porous material laminated between a permeable layer and an impermeable layer; pheromone evaporates from the sides and through the permeable layer. B. Rubber septa, on which pheromone solutions are absorbed; pheromone releases slowly from the rubber matrix. C. Membrane/reservoir formulation, in which the liquid pheromone is in an impermeable reservoir and evaporates through a permeable membrane that covers the reservoir. D. Hollow fibers, a series of open capillary tubes containing pheromone that evaporates directly through the openings. E. PVC matrix, a piece of polyvinyl chloride that had pheromone added directly to the medium before hardening. F. Modified membrane/reservoir, in which pheromone is absorbed on a filter paper disk and releases through a plastic membrane.

pheromones are evaporated at a fairly constant rate over a desirable period of time without chemical degradation or change (Fig. 2). In some cases, insect response is directly proportional to release rate, and high release levels simply catch more insects than lower levels (see Vick *et al.*, 1981, for data on *Plodia interpunctella*). However, in species such as the red flour beetle, *Tribolium castaneum* (Herbst), release rate may be critical to trap response. While testing the response of *T. castaneum* to different pheromone lure formulations in the laboratory, we found that lures newly opened from containers had high release rates of pheromone and were not attractive or repellent to beetles, while lures that were 1–8 weeks old (depending on formulation type) were more suitable for use (Hussain *et al.*, 1994). Thus optimizing release rate could improve efficacy of pheromone-baited traps for *T. castaneum*, and sub-optimal lures may contribute to poor performance noted for many commercially available *Tribolium* traps (Phillips, 1994). Trap design can also affect responses of insects to the same lures. Insect traps (Fig. 3) are designed for one of two purposes: aerial deployment to trap flying insects (Fig. 3A, B, C), and surface deployment (Fig. 3D, E) to catch walking and/or flying insects (Barak *et al.*, 1991). Grain probe traps (Burkholder, 1988; Cogan *et al.*, 1990; e.g. Fig. 3F), which could be considered surface or sub-surface traps, have the potential to utilize semiochemical lures, but typically are used without lures to sample insects moving through grain. Aerial flight traps either have sticky surfaces that are disposable, or they capture and kill insects in a reservoir. Non-sticky traps are generally re-usable and can be deployed for a longer time than sticky traps between servicing because many insects can be captured before the reservoir fills up. Surface traps capture insects on adhesives or in oils. Visual and tactile stimuli from traps apparently affect behavior of insects that are responding to attractants. Trematerra (1994) showed that male *Ephestia kuehniella* (Zeller) preferred pheromone-baited traps that displayed certain geometric figures compared to others. In a grain storage facility, I trapped significantly more *P? interpunctella* in pheromone-baited traps of the 'wing' design in Fig. 3b compared to traps of the 'diamond' design of Fig. 3a baited with the same lures, even though the wing traps had the larger sticky trapping surface (Phillips,



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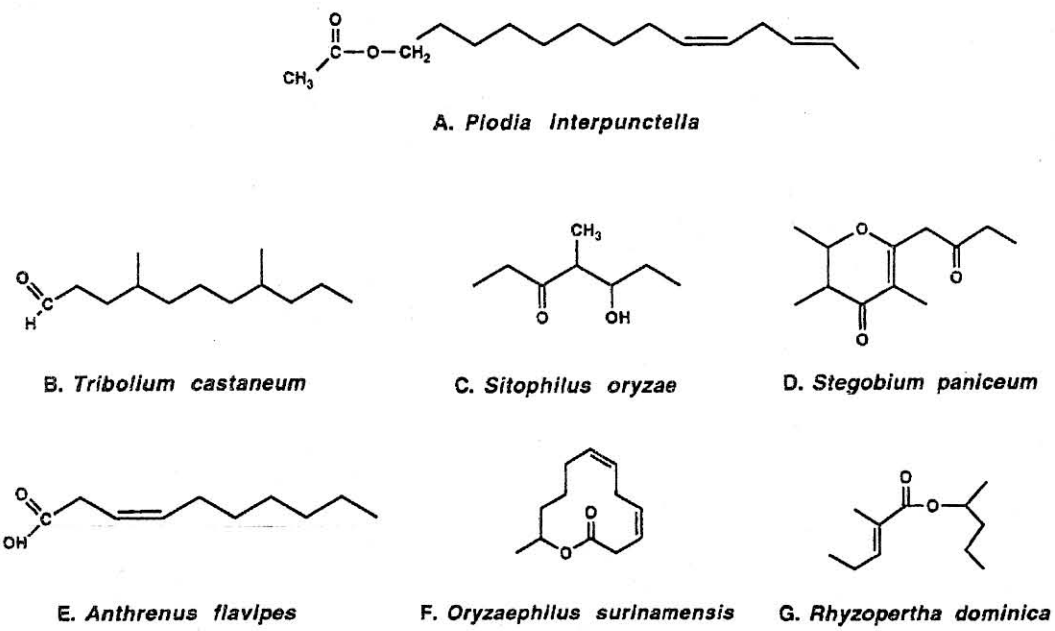

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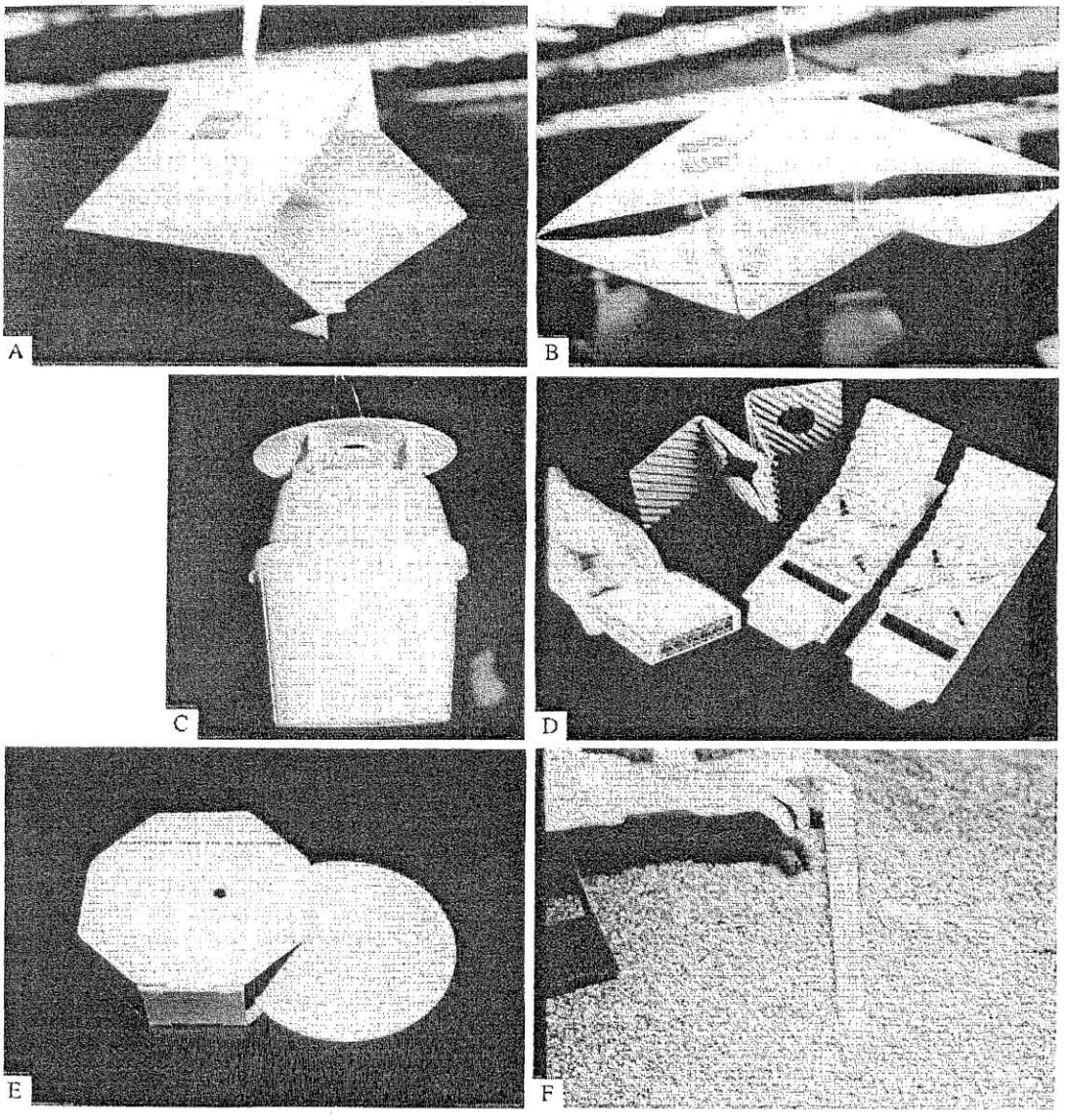
Additional semiochemicals, whether minor pheromone components or compounds from other sources, can improve responses of insects to traps. Although *Plodia interpunctella* responds to a single pheromone, *Z*,*E*-9,12-tetradecadienyl acetate (Fig. 1, commonly called ZETA), females also produce the corresponding alcohol to this acetate (referred to as ZETOH; Sower *et al.*, 1974) that can substantially increase response of males when the two compounds are deployed together (Vick *et al.*, 1981). However, ZETOH reduces the response of a related pyralid, *Cadra cautella* Walker,



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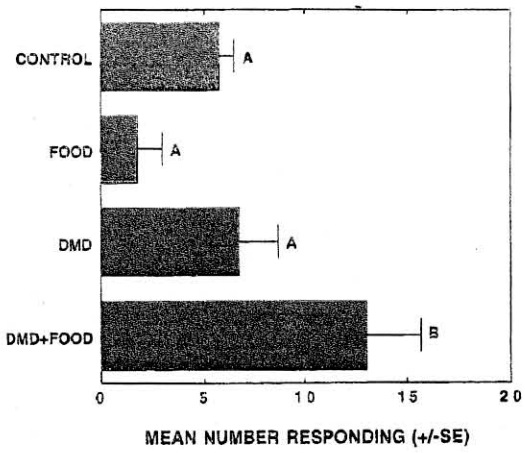

Fig. 4. Responses of *Tribolium castaneum* adults to synthetic pheromone (DMD) and a grain-based processed food (Food) separately or combined in a four-choice laboratory bioassay (see Phillips *et al.*, 1983 for details).

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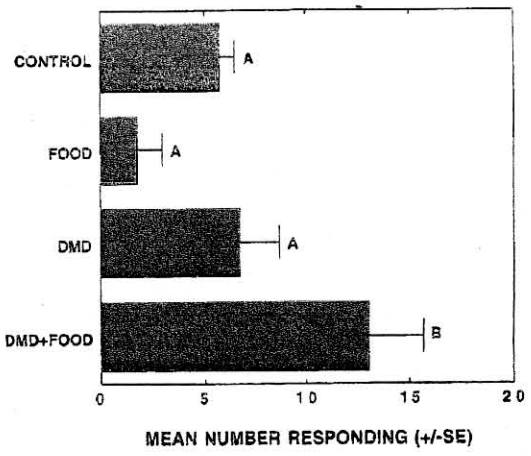
Trapping systems have not been developed for many species for which there are identified pheromones, due simply to a lack of commercial interest or the unavailability of practical commercial-scale chemical syntheses. Male-produced aggregation pheromones for five economically-important species of cucujid grain beetles were identified during the early 1980s (see review by Oehlschlager *et al.*, 1988), but commercialization was hindered by the lack of a high-yield, efficient synthesis of the compounds. Recently, Boden *et al.* (1993) reported new synthetic schemes for six of the seven macrolide pheromones of *Cryptolestes* and *Oryzaephilus* beetles that had higher yields and fewer steps than previous methods. Formulation of three of these pheromones into lures for the sawtoothed grain beetle, *O. surinamensis*, perhaps the most serious pest of the group, was accomplished and field tests showed that pheromone-baited traps can capture 11-times more *O. surinamensis* than unbaited traps; lures should be commercially available in the very near future (Paul Cogan, pers. comm.).

In addition to monitoring and detection, use of pheromones for suppressing stored-product pest populations has been proposed and studied over the years, but few if any methods have been put into practice. To cause a decline in a pest population, either a large majority of females need to be killed, or a similarly large majority of females need to go unmated. Mass-trapping pest insects



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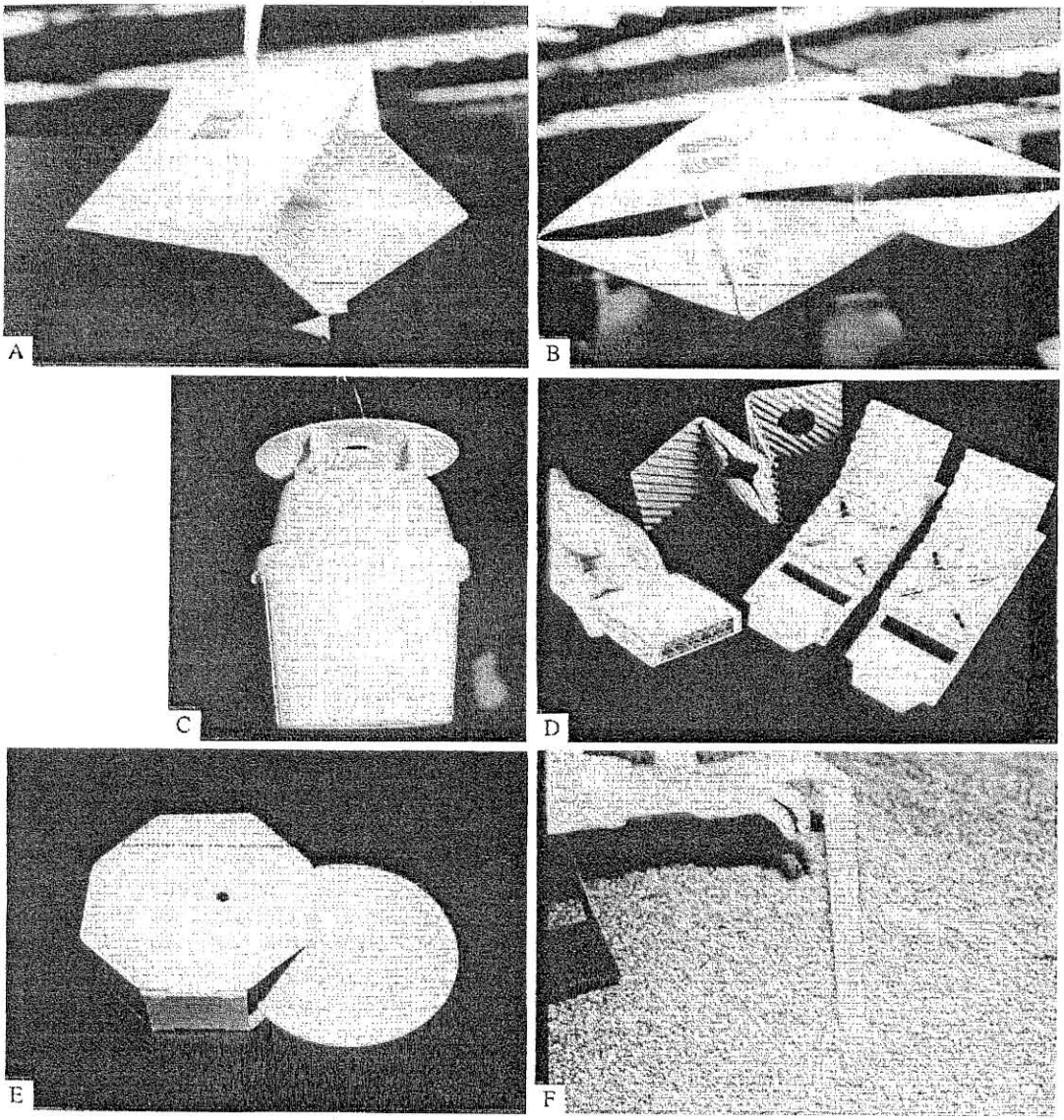

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SEMIOCHEMICAL ISOLATION AND IDENTIFICATION

Here I review a general method used in isolating and identifying pheromones and other semiochemicals. The method I refer to is bioassay-directed fractionation and isolation, which is used routinely in isolation of bioactive compounds, and which was elucidated previously with regard to insect pheromones (Silverstein *et al.*, 1967b). The differential diagnosis method (Vité and Renwick, 1970; Gries *et al.*, 1988), in which chromatographic peaks unique to active extracts relative to inactive extracts are identified, has been used with success by some, but can lack sensitivity in certain cases (e.g., Teale *et al.*, 1991). I reiterate the bioassay-directed fractionation method below with hopes that those working with stored-product insects may gain a better appreciation for how pheromones and other attractants are identified, and to demonstrate how collaborations between chemists and biologists can be successful. The hypothetical case of identifying a sex pheromone, and highlights of an actual sex pheromone identification are described below.

Initially there should be a convincing demonstration that a pheromone is operating, the pheromone should be separated from the insect and put into solution, and a bioassay should be developed. A demonstration of pheromone activity might be a simple experiment in which females are placed in a cage and males are observed flying or walking to the cage; a complementary experiment might show that males in a cage do not elicit the same response in other males. Next, perhaps as an outcome from initial experiments, a behavioral bioassay must be developed that will form the decision-making basis for the isolation. The bioassay should utilize the responding insect (e.g. males) in a simple, easily repeatable, procedure in which a pheromone-related response can be scored. Laboratory bioassays, although they remove the insect from its natural habitat, many times prove the most effective in pheromone isolation studies, provided the response is clear and can be interpreted in the context of a natural response. Typical laboratory bioassays might involve observing flight response in a wind tunnel or scoring walking response or directed orientation in an arena. The electroantennogram (EAG), a physiological bioassay that records the peripheral nervous system response of an insect to a volatile sample presented to the antenna (Roelofs, 1984), has been useful as a screening tool in many pheromone studies, but information about behavioral activity of EAG-active compounds is not obtained. Coupled gas chromatographic-electroantennographic detection (Arn *et al.*, 1975) is an excellent method for identifying EAG-active peaks in a

mixture, but it may be insensitive to small quantities and co-eluting peaks, and as with regular EAG analysis it must be followed by confirmation with a behavioral test. Following bioassay development a method is then needed for collecting or extracting the volatile pheromone from the living insect so it can be put into solution for use in bioassay and chemical analysis. Volatiles can be passively adsorbed on surfaces such as glass or paper, then extracted with solvent, or the air around pheromone-producing insects can be entrained to flow over or into a 'trap' such as an adsorbent polymer (Byrne *et al.*, 1975) or a chilled zone (Browne *et al.*, 1974) in which the pheromone is collected or condensed, then extracted into organic solvent. If volatiles are difficult to collect from living insects, then whole insects or pheromone-producing glands that are dissected from insects can be extracted in solvent. Whole body or gland extraction may result in a very complex mixture of compounds from which the pheromone must be isolated, and it extracts only the amount of pheromone present in the insect's body at the time of extraction. Collecting pheromone from volatiles produced by living insects over a period of time may result in more pheromone collected per insect than by tissue extraction, and the volatiles collection may result in a 'cleaner' extract since only airborne volatile compounds would be collected.

Once the pheromone is in solution the process of isolation can begin. The bioassay is used to confirm the activity of the crude pheromone extract, and then it must be used at each step of the isolation to confirm the presence of the pheromone. The crude extract, which usually contains a mixture of compounds, most of which are not pheromones, is subdivided into fractions by chromatography or other methods that will separate components of the mixture. Each fraction is bioassayed to determine the location of the pheromone. In cases in which multiple pheromones operate synergistically, it may be necessary to combine different fractions to find the activity, or combine all fractions to confirm that the activity was not lost (i.e., degraded or not recovered) during fractionation. Active fractions can be sub-fractionated, again following activity with the bioassay, until one or more individual compounds are isolated. Identification of isolated compounds involves proposal of a structure based on spectrometric data, synthesis of candidate compounds, and confirmation of the identification via chromatographic and or spectrometric congruence between synthetic and natural pheromone. Identity of the pheromone is then confirmed by activity of the synthetic material in the bioassay, and moreso by a field test of the synthetic pheromone that demonstrates activity similar to that of the natural pheromone.

The cowpea weevil, *Callosobruchus maculatus* (F.), is a cosmopolitan internal-feeding pest of stored pulses, and one of the few major storage pests for which a pheromone has not previously been identified. Bioassay-directed isolation and fractionation recently resulted in the identification of five female-produced sex pheromones (Phillips *et al.*, 1996); an overview of the study is presented here. Male *C. maculatus* display a very dramatic response to female-produced pheromone (Qi and Burkholder, 1981), which allowed for the development of a simple bioassay in which a single male is scored for locomotory behavior when presented with pheromone in a small glass vial. Female volatiles were collected from individuals by adsorption on filter paper discs followed by hexane extraction; air entrainment of volatiles from groups of females yielded extracts of lower activity, presumably due to reduced pheromone production caused by crowding or irritation from an air flow. Bioassay response of males was very clear: within one second of being exposed to less than one female-day-equivalent of natural pheromone on filter paper, the test male would rapidly walk around the perimeter of the vial floor, jump or fly up to the filter paper that was suspended 1 cm overhead, and usually attempted copulation with the paper. Weaker extracts elicited responses of lower magnitude or the initial locomotory response of the male began several seconds following exposure. This response could be easily scored for a number of males within an hour, thus the bioassay was simple and effective for detecting the presence of pheromone in extracts or fractions.

Gas chromatographic (GC) fractionation of *C. maculatus* female volatiles gave unsatisfactory resolution of pheromone activity, and silica gel column chromatography with solvents of increasing polarity failed to find activity in any single fraction or in a combination of all the fractions. A final elution of the silica gel column with methanol yielded a fraction with very high activity, suggesting the pheromone was a highly polar molecule such as a carboxylic acid. Since other bruchid pheromones were known to be carboxylic acids (Tanaka *et al.*, 1981; Cork *et al.*, 1991), we performed a simple acid-base partitioning of the crude extract. We neutralized all acids in the

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extract with sodium bicarbonate, extracted all non-acid polar compounds in methylene chloride (a strong polar solvent), reacidified the remaining aqueous solution with strong hydrochloric acid, and extracted this with methylene chloride to yield a fraction containing all organic acids. Only the organic acid fraction was active in bioassay, indicating the pheromone was an acid, and other fractions from the reaction were inactive. This procedure accomplished a substantial purification of the pheromone into a fraction that was much less complex than the original extract (Fig. 5), thus simplifying the subsequent isolation of the pheromone. The acid fraction was subfractionated on packed column GC and the bulk of activity was found in one fraction. Analysis of this fraction with capillary column GC revealed five compounds that were given tentative structural assignments following coupled GC-mass spectrometry. Synthesis of all possible structural isomers resulted in five 8-carbon acids that matched peaks in the active GC fraction, both in their retention times on column and in their mass spectra, and that proved to be active as pheromones in bioassays with male *C. maculatus* (see Phillips *et al.*, 1996 for details). Identification of the five acid pheromones from female *C. maculatus* exemplifies the rigor of bioassay-directed fractionation and isolation. The *C. maculatus* pheromones were very minor components in the original extract of female volatiles that contained probably hundreds of compounds (Fig. 5, note that the pheromones are not resolved from the baseline in the chromatogram of the acid fraction, Fig. 5b). To identify and bioassay every compound in the original extract in search of the pheromone is impractical, and differential diagnosis by comparing GC analyses of males and females would not reveal the very small pheromone peaks that would have been obscured by other non-pheromone peaks. Close collaboration between chemists and entomologists was essential in this project, as it is in most pheromone identifications, for the specialized skills each group brought to the research.

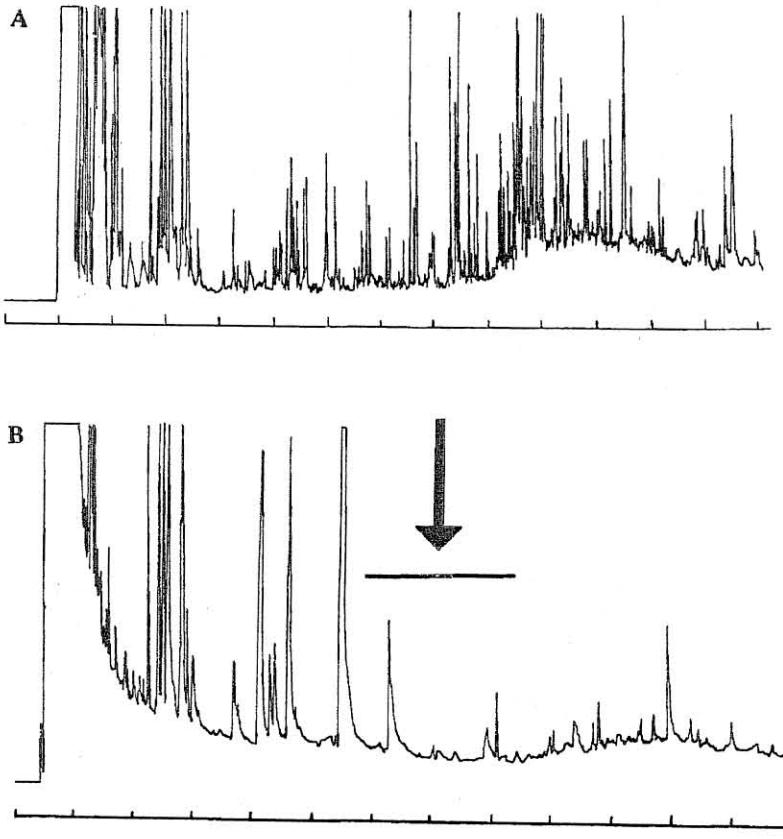

Fig. 5. A. GC record of the whole extract of volatiles from female *Callosobruchus maculatus*. B. GC record of the acid fraction of female *C. maculatus* volatiles; note that peaks in the area where sex pheromones were ultimately isolated, indicated by arrow, are not the pheromones. Both GC records were acquired with a 50 m DB-1 column under the same conditions.

FUTURE RESEARCH AND APPLICATIONS

There is much basic research, both in chemistry and biology, that can improve the use of semiochemical-based pest management methods and also increase the number of techniques available to the practitioner. For species that have identified pheromones that have not been commercialized (Phillips, 1994), research is needed to determine the usefulness of their pheromones in trapping or other field applications. Common pest species that need work beyond pheromone identification and laboratory studies include bruchid seed beetles such as *Callosobruchus maculatus*, *C. chinensis* (L.), and *Acanthoscelides obtectus* (Say); *Cryptolestes* flat grain beetles; *Sitophilus* grain weevils; carpet beetles (Dermestidae) in the genera *Anthrenus*, *Attagenus*, and *Dermestes*; the yellow meal worm, *Tenebrio molitar* L.; pyralid moths such as the meal moth, *Pyralis farinalis* (L.), the rice moth, *Corcyra cephalonica* (Stainton), and the wax moth, *Galleria melonella* L.; and the webbing clothes moth, *Tineola bisselliella* (pheromone identifications referenced in Mayer and McLaughlin, 1991). Other important pests for which pheromones or attractants have not been developed, but for which these could prove useful, include the larger black flour beetle, *Cynaeus angustus* (LeConte) (Tenebrionidae); the Mexican bean beetle, *Zabrotes subfasciatus* (Boheman) (Bruchidae); and the case-making clothes moth, *Tinea pellionella* (L.) (Tineidae).

One new area of research that could result in useful semiochemicals is the study of female attractants, especially for the case of moths in which there are many known male attractants. Early work on female-produced moth pheromones was so successful for so many important species (Roelofs and Cardé, 1977), that it was not until recently that it became apparent that semiochemicals affecting female behavior, such as host plant odors and male-produced pheromones, were biologically common and approachable with modern research methods (e.g. Landolt, 1989, Landolt and Heath, 1989, 1990; Mitchell *et al.*, 1990). Barrer and Jay (1980) reported that female almond moths, *Cadra cautella* (Walker), could orient to grain odors, and Corbet (1973) found that a secretion from Mediterranean flour moth larvae, *Ephestia kuehniella* (Zeller), larvae elicited oviposition responses by adult female conspecifics. The Indian meal moth, *Plodia interpunctella*, also responds to grain odors and larval secretions when presented separately, but we found that a combination of grain plus larval secretions elicited a much larger oviposition response than either stimulus presented separately as a choice (Phillips and Strand, 1994). In the same study we showed that female *P. interpunctella* would fly upwind to grain odors, but contacts with the odor source and oviposition were increased by the presence of larval secretions. Male-produced pheromones that function in courtship behavior have been reported from storage moths (Krasnoff and Vick, 1984), and potential exists for male pheromones being described that may affect long range orientation (Landolt and Heath, 1990). If attractants for female moths can be identified and synthesized, then manipulation of females for population suppression will be possible.

Interest is growing in research and the implementation of biological control of storage pests using parasitoids and predators (Brower *et al.*, 1995), and the efficacy of these natural enemies could be enhanced by semiochemicals. Kairomones, interspecific chemical signals that benefit the receiver, many times direct the orientation of predators and parasitoids to their prey and hosts, respectively. Habitat or host plant odors, termed synomones because they benefit both the producer (host plant) and the receiver (natural enemy) can also be utilized in host or prey location (see Nordlund, 1981, for terminology). The idea of actually using kairomones and/or synomones to facilitate biological control, both by enhancing proper rearing and deployment of natural enemies and in affecting searching behavior in the field, has been discussed for some time and addressed by numerous research projects in pre-harvest systems (e.g., review of Lewis and Martin, 1990). In storage systems kairomones have been studied in *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae) and in *Bracon hebetor* Say (Hymenoptera: Braconidae), both parasitoids of pyralid moth pests. *V. canescens* is arrested and immediately begins probing the substrate in response to host larval secretions or extracts of host larval mandibular glands (Corbet, 1971). Some of the same compounds identified from host mandibular glands as kairomones for *V. canescens* also elicited trail-following in *B. hebetor* (Strand *et al.*, 1989). Recent work showed that female *B. hebetor* require prior experience with host larval secretions before orienting to host odors over a distance (Fig. 6). In another stored-products example, the parasitoid *Cephalonomia waterstoni* Gahan (Hymenoptera: Bethylidae) was shown to respond strongly to a hexane-extractable kairomone

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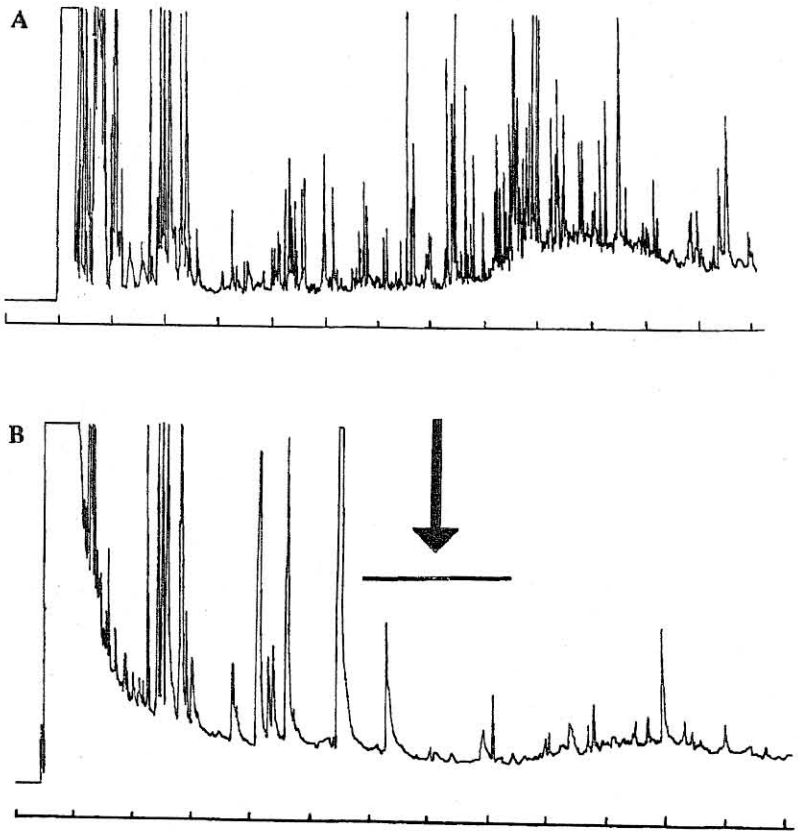
extract with sodium bicarbonate, extracted all non-acid polar compounds in methylene chloride (a strong polar solvent), reacidified the remaining aqueous solution with strong hydrochloric acid, and extracted this with methylene chloride to yield a fraction containing all organic acids. Only the organic acid fraction was active in bioassay, indicating the pheromone was an acid, and other fractions from the reaction were inactive. This procedure accomplished a substantial purification of the pheromone into a fraction that was much less complex than the original extract (Fig. 5), thus simplifying the subsequent isolation of the pheromone. The acid fraction was subfractionated on packed column GC and the bulk of activity was found in one fraction. Analysis of this fraction with capillary column GC revealed five compounds that were given tentative structural assignments following coupled GC-mass spectrometry. Synthesis of all possible structural isomers resulted in five 8-carbon acids that matched peaks in the active GC fraction, both in their retention times on column and in their mass spectra, and that proved to be active as pheromones in bioassays with male *C. maculatus* (see Phillips *et al.*, 1996 for details). Identification of the five acid pheromones from female *C. maculatus* exemplifies the rigor of bioassay-directed fractionation and isolation. The *C. maculatus* pheromones were very minor components in the original extract of female volatiles that contained probably hundreds of compounds (Fig. 5, note that the pheromones are not resolved from the baseline in the chromatogram of the acid fraction, Fig. 5b). To identify and bioassay every compound in the original extract in search of the pheromone is impractical, and differential diagnosis by comparing GC analyses of males and females would not reveal the very small pheromone peaks that would have been obscured by other non-pheromone peaks. Close collaboration between chemists and entomologists was essential in this project, as it is in most pheromone identifications, for the specialized skills each group brought to the research.



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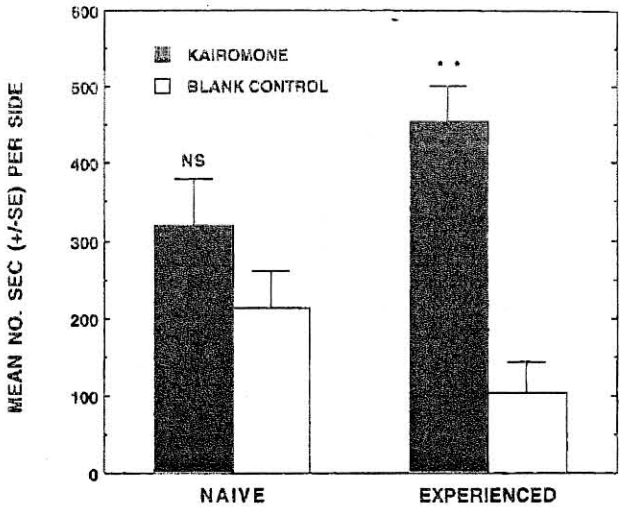

Fig. 6. Responses of female *Bracon hebetor* to host kairomone in a laboratory bioassay as a function of prior host experience (see Franqui-Rivera, 1995). The bioassay device was a glass tube, open at both ends, with a central opening for introduction of the test wasp; filter paper containing kairomone from the host *Plodia interpunctella* was at one end of the tube, and untreated filter paper was at the other end. The amount of time spent by a female at each end of the tube was recorded over a ten-minute period. Histograms represent means of 20 replicates. Naive wasps were isolated as pupae, mated, and allowed access to sugar water only for 4 days prior to testing. Experienced wasps were mated, held 3 days with sugar water, then held one day in a dish with cracked corn and 4 host larvae, which they parasitized. Only experienced wasps displayed a significant response to the kairomone (** = $P < 0.01$, t-test).

from its host, *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Cucujidae), and prior experience played an important role in this response (Howard and Flinn, 1990). The need for prior experience, or learning, of host volatiles to facilitate subsequent responses to host cues is a common theme in host selection by parasitoids (Lewis and Martin, 1990). If parasitoids produced in mass-rearing facilities do not learn the proper host cues upon adult emergence, then they may perform sub-optimally when released for augmentative biological control. Additionally, if parasitoids remain in an area and search longer when kairomone is present, then slow-release application of synthetic or naturally mass-produced kairomones in storage facilities may enhance the searching and host-finding activities of released parasitoids (Lewis and Martin, 1990). I am unaware of published reports on kairomone-mediated behavior of predators of storage insects, but functional response studies suggest that predators utilize experience with prey to increase predation rates (Parajulee *et al.*, 1994). Clearly there are many areas for future research on semiochemicals that mediate behavior of natural enemies of stored-product insects.

CONCLUSIONS AND PROSPECTS

Although there is much basic work to be done on semiochemicals of storage insects and their natural enemies, at this date, there has been enough research on pheromones of the major pests for the field to progress and mature. Pheromone-baited traps are clearly playing an important role in early pest detection in facilities concerned with production or storage of high-value commodities, and they have undoubtedly contributed to reduced use of pesticides and improved product quality. However, application of our knowledge needs to go beyond these cases. Management of post-harvest commodities is facing a potential crisis with increased consumer demand for high quality food products, the regulatory loss of chemical pesticides and fumigants, the increased occurrence of genetically-based resistance to existing insecticides, and relaxation of international trade barriers that may allow increased spread of pests. I expect that semiochemical-based methods will become important components of integrated pest management (IPM) of various commodity systems. Conventional technology with pheromone traps and identified pheromones could expand to encompass all the major pests in their respective habitats, e.g., on-farm storage, terminal grain elevators, flour mills and food factories, warehouses and distribution centers, grocery stores, and homes. Education of resource managers, from quality control officers of multinational food

companies to homeowners, will facilitate implementation of IPM. I am hopeful that we will see improved pheromone formulations, more effective and more practical traps, more commercial-scale chemical syntheses of known pheromones, and chemical identifications of unknown pheromones and additional components to improve activity of existing pheromones. I am also hopeful that innovations drawn from existing knowledge or as a product of new discoveries will add to our arsenal of semiochemical-based pest management tactics. The need for developing new and effective biorational methods to suppress or eliminate pests in stored-products is greater now than ever before. Potential exists with semiochemicals for such methods to come forward, but the pace of research and development should not slow.

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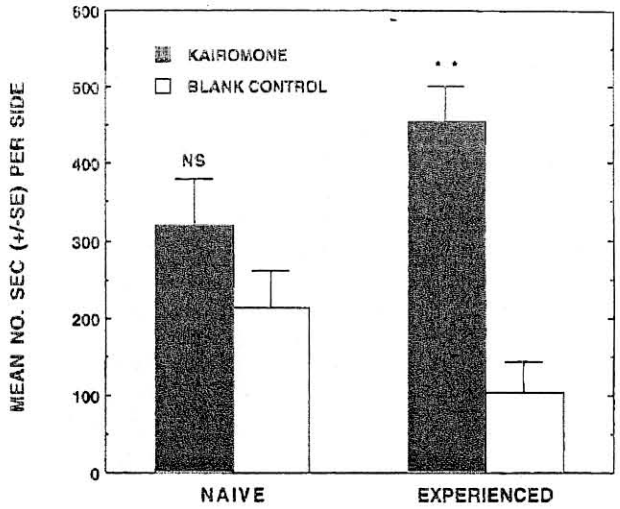

Fig. 6. Responses of female *Bracon hebetor* to host kairomone in a laboratory bioassay as a function of prior host experience (see Franqui-Rivera, 1995). The bioassay device was a glass tube, open at both ends, with a central opening for introduction of the test wasp; filter paper containing kairomone from the host *Plodia interpunctella* was at one end of the tube, and untreated filter paper was at the other end. The amount of time spent by a female at each end of the tube was recorded over a ten-minute period. Histograms represent means of 20 replicates. Naive wasps were isolated as pupae, mated, and allowed access to sugar water only for 4 days prior to testing. Experienced wasps were mated, held 3 days with sugar water, then held one day in a dish with cracked corn and 4 host larvae, which they parasitized. Only experienced wasps displayed a significant response to the kairomone (** = $P < 0.01$, *t*-test).

from its host, *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Cucujidae), and prior experience played an important role in this response (Howard and Flinn, 1990). The need for prior experience, or learning, of host volatiles to facilitate subsequent responses to host cues is a common theme in host selection by parasitoids (Lewis and Martin, 1990). If parasitoids produced in mass-rearing facilities do not learn the proper host cues upon adult emergence, then they may perform sub-optimally when released for augmentative biological control. Additionally, if parasitoids remain in an area and search longer when kairomone is present, then slow-release application of synthetic or naturally mass-produced kairomones in storage facilities may enhance the searching and host-finding activities of released parasitoids (Lewis and Martin, 1990). I am unaware of published reports on kairomone-mediated behavior of predators of storage insects, but functional response studies suggest that predators utilize experience with prey to increase predation rates (Parajulee *et al.*, 1994). Clearly there are many areas for future research on semiochemicals that mediate behavior of natural enemies of stored-product insects.

CONCLUSIONS AND PROSPECTS

Although there is much basic work to be done on semiochemicals of storage insects and their natural enemies, at this date, there has been enough research on pheromones of the major pests for the field to progress and mature. Pheromone-baited traps are clearly playing an important role in early pest detection in facilities concerned with production or storage of high-value commodities, and they have undoubtedly contributed to reduced use of pesticides and improved product quality. However, application of our knowledge needs to go beyond these cases. Management of post-harvest commodities is facing a potential crisis with increased consumer demand for high quality food products, the regulatory loss of chemical pesticides and fumigants, the increased occurrence of genetically-based resistance to existing insecticides, and relaxation of international trade barriers that may allow increased spread of pests. I expect that semiochemical-based methods will become important components of integrated pest management (IPM) of various commodity systems. Conventional technology with pheromone traps and identified pheromones could expand to encompass all the major pests in their respective habitats, e.g., on-farm storage, terminal grain elevators, flour mills and food factories, warehouses and distribution centers, grocery stores, and homes. Education of resource managers, from quality control officers of multinational food

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