J Pest Sci (2012) 85:285–299
DOI 10.1007/s10340-011-0407-9

REVIEW

Advances in the use of pheromones for stored-product protection

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Received: 30 July 2011 / Accepted: 9 December 2011 / Published online: 22 December 2011

Abstract Considerable progress has been made in the monitoring and control of stored-product pests, mainly Lepidoptera and Coleoptera, by pheromones, which are used in mass trapping, attracticide and mating disruption methods. In integrated pest management programmes of stored-product protection, the use of pheromones can lead to a reduction in chemical treatments, with economic advantages and the improvement of food-product quality. In this article, I report some promising results offering efficient detection and control of stored-product pests based on pheromones and line up a number of remaining questions to be answered to improve the reliability and competitiveness of the methods used.

Keywords Pheromones · Monitoring · Mass trapping · Attracticide · Mating disruption · Stored-product insects

Introduction

Several research studies have been carried out, especially during the last two decades, with the aim of finding effective alternatives to methyl bromide and conventional chemical treatments or, in any case, the limitation of their use. In this regard, the use of pheromones is one of the most promising techniques aimed at the control of stored-product pests of Coleoptera and Lepidoptera (Fields and White 2002; Phillips and Throne 2010).

In fact, in the management of stored products, insect pheromones and other semiochemicals can be used to suppress and control the pest populations by means of mass trapping, attracticides and mating disruption methods, as well as acting as repellents and as specific behavioural stimulants or deterrents (Cox 2004; Phillips and Throne 2010).

In the integrated pest management (IPM) context, the use of these substances can lead to a drastic reduction in chemical treatments, thus conferring remarkable economic advantages and improvements in product quality, protecting goods from residual insecticides noxious to the consumer. IPM is defined as a comprehensive, systematic approach to commodity protection that emphasizes increased information for improved decision making to reduce purchased inputs and minimize social, economic and environmental consequences (Hagstrum and Flinn 1996). The IPM concept emphasizes the integration of disciplines and control measures including biological enemies, cultural management, sanitation, proper temperature utilization and pesticides into a total management system aimed at preventing pests reaching damaging levels. From an economic and ecological standpoint, IPM is based on the 'Economic Injury Level' (EIL) concept; this implies that management action is only taken when potential losses due to pest infestations exceed the costs of available control strategies (Trematerra 2002; Stejskal 2003; Carvalho et al. 2008). IPM will reduce the use of pesticides because control measures will only be used when sampling indicates that insect densities have exceeded the EIL (Stejskal 2003).

In managing stored-product pests, further reductions in chemical control can be achieved by replacing pesticides

A contribution to the Special Issue on Recent Advances in Stored-Product Protection.

Communicated by C. G. Athanassiou.

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with biological and physical control methods via biorational approaches (Phillips and Throne 2010).

In this article, a literature review on advances in the use of pheromones for stored-product protection is reported.

Pheromone utilization

Pheromones and other semiochemicals have been identified for about 40 species of stored-product insects over the past four decades. As reported, the use of pheromones fits very well with the idea of IPM. Pheromones provide highly sensitive tools for insect detection because a pheromone trap can detect the presence of an insect whereas numerous traditional sampling techniques would detect none, and pheromones are highly specific to target species. In this context, in recent years, considerable progress has been made not only in monitoring but also in the direct control of stored-product insects by pheromones (Burkholder and Ma 1985; Burkholder 1990; Phillips 1997; Trematerra 1997, 2002; Plarre 1998; Phillips et al. 2000; Cox 2004; Anderbrant et al. 2007).

Two general types of communication and reproductive strategies characterize stored-product insects (Levinson and Levinson 1995):

– adults, which are short-lived (<1 month) and require no feeding for reproduction to take place (predominated by species in Pyralidae, subfamily Phycitinae, and beetles in the families Anobiidae, Bruchidae and Dermestidae) rely on sex pheromones (usually produced by females) for communication. Clothes moths in the family Tineidae have interesting pheromone systems in which males orient towards larval food sources and then produce pheromones in a resource-based manner, whilst females produce attractant pheromones for males,
– adults, which are long-lived (>1 month) and must feed to reproduce (species in the families Bostrichidae, Curculionidae, Cucujidae, Silvanidae and Tenebrionidae) use male-produced aggregation pheromones for long-distance communication. Both males and females respond to these pheromones.

A sex pheromone is secreted by insects of one sex; it causes a response in individuals of the opposite sex, thus leading to copulation between females and males of the same species. An aggregation pheromone, being emitted by insects of one sex, causes conspecific females and males to join for the sake of feeding and reproduction. Males locate food, produce pheromones, attract females and other males and mate; females oviposit at that site, where the larvae ultimately develop.

Pheromones are commercially available for more than 30 species of stored-product insects as slow-release formulations of lures (Swords and van Ryckeghem 2010a, b). As reported before, these semiochemicals have been utilized for the implementation of four main methodologies: monitoring, mass trapping, mating disruption and attracticide methods.

Pheromones, like other semiochemicals, are generally considered to be safer and environmentally more acceptable than conventional pesticides because they occur naturally, are able to target the pest species only, possess low acute toxicities to vertebrates, and are usually volatile chemicals that do not leave behind harmful residues. However, products containing semiochemicals will still be required to go through some degree of formal registration. Government registration of a pheromone for the express purpose of controlling an insect pest population is required in Europe and in the United States of America (EU 1991; EPA 2006). Primary registration of the synthetic sex pheromone of stored-product moths, (*Z*,*E*)-9,12-tetradecadienyl acetate, was recently granted in mating disruption.

Traps and trapping procedure

Before mating, most male or female insects respond to their pheromone in combination with supplementary key stimuli (Levinson and Levinson 1995). This sequence of sensory stimuli can be utilized in the design of attractant traps to be employed in the manipulation of storage pests. Trapping procedures vary depending on whether the objective is monitoring or control.

To successfully capture attracted pest insects, a trap has to be escape proof; this can be achieved by a sticky surface to which the trapped insects become irreversibly attached or by some kind of funnel or pitfall system.

Trap design is crucial in developing trapping systems. It would be difficult to comprehensively review the numerous types that have been tested. In the monitoring of Lepidoptera, the most common types of traps in use employ a sticky surface to retain the attracted insect. If the surface on these traps is fresh, these kinds of traps retain most insects that come into contact with their sticky surfaces. As the sticky surface ages, its ability to retain new arrivals is reduced or even eliminated since it is covered by debris, dust or by the target insects. In this case, the trap must be replaced by a new one. In this situation insects can be trapped using funnel traps.

Designs of traps for moths (*Ephestia*, *Plodia*, *Sitotroga*, *Tineola*, etc.) and beetles (*Cryptolestes*, *Lasioderma*, *Oryzaephilus*, *Prostephanus*, *Rhyzopertha*, *Sitophilus*, *Stegobium*, *Tribolium*, *Trogoderma*, etc.) infesting stored products have been developed, generally on an empirical basis (Levinson and Buchelos 1981; Barak et al. 1990;

Burkholder 1990; Cogan et al. 1990; Mullen 1992; Phillips 1997; Plarre 1998).

In survey and detection programs, the foremost concern is the sensitivity of the system. Similarly, when a trap catch is used to time phenological events, such as the onset of adult emergence, trap saturation may be of no concern. On the contrary, in other trapping programmes, saturation can pose serious problems. When a trap catch is used as an indicator of population density, the limited capacity will make it difficult to develop predictable relationships between the trap catch and density. In mass-trapping applications, the superior trap efficiency necessary for management would appear to abolish the use of sticky traps, except at very low pest densities.

A variety of non-sticky traps with a large capacity and unvarying efficiency offer alternative approaches in detection and monitoring of moths. Insects can be trapped and kept alive with lures in funnel traps. Their capacity exceeds several thousand insects, in contrast to sticky traps that become saturated, depending on the species, at 150–400 adults. However, when a funnel trap contains an insecticide to kill the insects, some attention should be paid to the possibility of the insecticide repelling the insects before they enter the trap.

For beetles that tend to land and crawl to an odour source, traps are designed to sit on a floor or flat surface and capture insects that walk into the trap, which eventually become stuck to the trapping surface or ensnared inside the trapping receptacle. These insects, both larvae and adults, can be successfully trapped in corrugated paper traps; insects retreat into and hide in the corrugations just as they do in the cracks of floors or walls.

Barak and Burkholder (1985) developed a trap with horizontal layers of corrugated cardboard, where responding beetles walked through tunnels of corrugations to reach a cup of oil, into which they fell and suffocated. A popular alternative design is what appears to be a ramp-and-pitfall trap, where beetles walk to the trap, climb up the inclined side of the trap, and fall into a receptacle of oil (Mullen 1992).

The oil in floor traps serves both as a trapping medium and as a pheromone synergist or additive attractant, as many formulations are grain derived (Phillips et al. 1993, 2001). Dome traps were used by Kaltsikes et al. (2008) in the monitoring of insect populations in a pasta factory and related facilities in Greece.

In Sweden, it was also noted that ingredients of chocolate attract moths (males and females), and a series of studies involving the head-space collection of volatiles, solvent extraction, chemical identification, electrophysiology and behavioural experiments were undertaken to reveal which compounds were active and which behavioural responses they induced (Olsson et al. 2006a, b). Ethyl vanillin, phenylacetaldehyde and nonanal were found to elicit electrophysiological responses in *Ephestia* and *Plodia*. A preliminary test in a pet store showed that both male and female *P. interpunctella* (Hübner) can be trapped using this three-component blend.

In addition to specific trap designs, which have improved insect catches for monitoring purposes over the years, it was found that the females of sex pheromone-producing species and, in certain cases, even the larvae could also be attracted by a combination of pheromones and food attractants. The advantage of also trapping female moths is obvious from both population suppression and monitoring points of view.

In the monitoring of *E. kuehniella* (Zeller) by pheromone traps in flour mills and bakeries in Belarus, Kozich (2008) used kairomene substances based on the fatty acids from grain cereals, which are attractive to both male and female adults. Odours from larval foods that also serve as attractants for adult moths, technically considered as kairomones, were investigated to monitor females of *P. interpunctella* and other stored-product moths (Sambaraju and Phillips 2008).

Other traps include sticky traps, pitfall traps and light traps. The behavioural response of insects was the key influence in the development of these types of traps. Food traps and sex-food-baited traps have also been used for crawling Coleoptera. Synergistic effects of pheromones and food attractants in the trapping of *S. oryzae* (L.) were reported by Trematerra and Girgenti (1989). But, as reported for *Tribolium castaneum* (Herbst), the activity of traps can be negatively influenced by accumulated numbers of trapped specimens (Trematerra et al. 1996). Regular inspection and the removal of trapped insects are important because dead insects can cause repellency and reverse the effects of attractants.

The precise position of a trap within a habitat can significantly affect the levels of trap catch. The placement of traps in food-processing facilities is partly dependent on the size of the facility and on available supporting posts or other places where there is little or no traffic. In general, a trap should be placed away from open doors or windows to avoid attracting insects into a facility from the outside. However, traps can also be placed outside the premises to catch migrant insects, thus intercepting them before they have a chance to move inside.

In particular, stored-product Lepidoptera are often found outside storage and food facilities and are sometimes able to cause heavy infestations before and after harvest (Wohlgemuth et al. 1987; Doud and Phillips 2000; Campbell and Mullen 2004; Campbell 2007; Trematerra and Gentile 2010). For instance, Doud and Phillips (2000) and Trematerra and Gentile (2010) reported high numbers of *P. interpunctella* (Hübner) and *E. kuehniella* around flour mills and food-processing facilities. According to Bowditch and Madden (1996), the presence of moths outdoors is mainly caused by dispersal patterns. It is generally expected that, in the enclosed environment of a storage facility, the negative influence of the immigration of mated females will be lower in comparison to the presence of field pests. However, Trematerra (1990) and Süss et al. (1996) recorded the rapid reinfestation of *E. kuehniella* in a flour mill after fumigation with methyl bromide and attributed this increase to immigration from outdoor sources. Campbell and Arbogast (2004) also assessed the seasonal trends in *E. kuehniella* trap captures in a flour mill, the relationships between catch data inside and outside the plant and between the number of trapped moths and the level of product infestation, and the impact of fumigation on the pest population with similar results.

These findings suggested that broader landscape processes may be more important than generally recognized in pest management, but this is certainly an area that needs additional research (Campbell 2007). Still, even in the case of the existence of an outdoor reservoir of moths and beetles, their role may be limited in comparison to other field pests and their immigration rate could be reduced as part of an IPM programme.

Seven species of stored-product Coleoptera pests were found outside a grain store by Kucerova et al. (2005): *Ahasverus advena* (Waltl), *Cryptolestes ferrugineus* (Linnaeus), *Cryptophagus* sp., *Oryzaephilus surinamensis* (Linnaeus), *Sitophilus granarius* (Linnaeus), *T. castaneum* and *Typhaea stercorea* (Linnaeus). Toews et al. (2006), monitoring the flight activity and immigration rate of *Rhyzopertha dominica* (Fabricius) into seed wheat warehouses also captured other stored-product beetles, including *A. advena*, *C. ferrugineus*, *S. oryzae*, *T. castaneum*, *Trogoderma variabile* (Ballion) and *T. stercorea*.

Limited published data are available pertaining to the seasonal flight activity, routes of immigration into warehouses and food industries, and the use of commercially available pheromones in monitoring programs for Coleoptera such as *Lasioderma serricorne* (Fabricius), *Prostephanus truncatus* (Horn), *R. dominica* and *Sitophilus* spp.

Monitoring

Pheromone traps in stored insect management can be used to detect both the presence and density of pests. Their purpose is to achieve a more accurate control and to limit insecticide usage to only when strictly necessary. In addition, pheromone traps can be used to help determine the efficacy of a management tactic, such as fumigation or heat treatment, by comparing trap captures before and after the treatment.

Pheromone traps are generally effective when pest numbers are very low and they can be qualitatively used to provide an early warning of pest incidence. They are useful in defining areas of pest infestation, particularly in cases when the overall distribution and life cycle are poorly understood. Typical recommendations are provided for the placement of a grid-work of traps and their monitoring for the capture of insects at regular time intervals (Subramanyam and Hagstrum 1996). If one or more traps in a particular area captures a higher number of insects, then an increased density of traps should be deployed in that area to determine the source of the pests.

Further developments in the use of pheromone-baited traps could improve their application in pest management schemes. New trap designs are being realized that appear promising for the improvement of detection limits of some insect species (Mullen 1992; Quartey and Coaker 1992; Trematerra et al. 1996).

A list of the factors known to affect trap catching that should be addressed during the design, execution and reporting of trapping studies was reported (Cuperus et al. 1990; Wright and Cogan 1995; Mankin et al. 1999; Hugget et al. 2010). Using identical lures, differences in trap effectiveness were shown to be based on either the visual clues of traps or their accessibility by pest insects (Plarre 1998). The results of monitoring insect populations by using rectangular cardboard traps of different colours (black, green, blue, white and yellow) and with adhesive surfaces in a dried fig warehouse in Southern Greece were reported by Karlis et al. (2008). The outer geometry of a trap has a major influence on its ability to catch flying insects.

Multiple pheromones for different species can be employed in single traps where no interspecific influence of the semiochemical attractants has been shown. The multiple pheromone trap is a new trapping system for use by professional pest managers. Sex pheromones for *Ephestia* (*Cadra*) *cautella* (Walker), *E. kuehniella*, *P. interpunctella*, *L. serricorne*, *Trogoderma granarium* (Everts) and *T. variabile* and aggregation pheromones for *T. castaneum* and *Tribolium confusum* J. du Val are incorporated into natural food attractant oils. The pitfall trap is a plastic trap where oil is placed into the pit; the oil in these floor traps serves as a trapping medium and as a pheromone synergist or additive attractant, as many formulations are grain derived. Over 20 stored-product pest species have been captured in field traps (VanRickeghem et al. 1999).

In storage environments, which are often inhabited by a range of different pest species, multi-species semiochemicals are likely to be more cost effective than species-specific ones. Using a single multiple pheromone trap to monitor several stored-product insect species will reduce the material land labour costs of maintaining a pest surveillance programme (Wakefield 2006).

In the practical situation of a tobacco store, Trematerra and Zanetti (1998) compared the activity of commercial pheromone dispensers in the capture of *L. serricorne*. Burks et al. (2010) performed experiments in commercial and pilot scale facilities to examine the effect of a pheromone dose on the detection of *P. interpunctella* in the presence of mating disruption. When *P. interpunctella* males were released into 1,000-m^3 rooms with traps baited with 0,1 or 10 mg (*Z,E*)-9,12-tetradecadienyl acetate (or TDA), the traps that contained 10 mg captured more of the insects than those baited with 1 mg in both the presence and absence of mating disruption. After testing various concentrations of a pheromone, Mueller and Pierce (1992) found that some insects preferred higher concentrations of the pheromone, whilst some preferred lower concentrations. In *T. castaneum*, strain-specific pheromone concentrations were found to be very important for the successful trapping of these insects in the field (Trematerra et al. 2007).

As reported, the performance of a pheromone product is a dynamic among the choice of a formulation, the age of a formulation and the release rate and population pressure. For example, solutions need to be found in the following areas: synthesis; stabilization and longevity (pheromone molecules are environmentally labile and need to be stabilized from photochemical, thermal, oxidative and hydrolytic degradation, and from isomerization and polymerization); blend quality (purity, composition), amongst others. Adequate determination of the release rates of dispensers should become a part of the standard protocol of dispenser evaluation trials to introduce hard facts rather 'guesstimates' for the interpretation of field trial results.

The female-produced sex pheromones of the above phycitids comprise (*Z,E*)-9,12-tetradecadienyl acetate (TDA) as a common and predominant component, acting as the main sex attractant for males of those sympatric species. The sex pheromone of female *E. cautella* also includes (*Z*)-9-tetradecenyl acetate (TA) which synergizes the attractiveness of TDA for conspecific males and subdues the attractiveness od TDA for male *E. kuehniella* and *P. interpunctella*. (*Z,E*)-9,12-tetradecadienol (TDO), (*Z,E*)-9,12-tetradecadienal an additional sex pheromone component of female *E. kuehniella*, *E. cautella*, *E. elutella* and *P. interpunctella* was found to enhance the attractiveness of TDA for male *E. elutella* and *P. interpunctella* as well as to suppress the responsiveness of male *C. cautella* to TDA and TA (Plarre 1998; Levinson and Levinson 2002). The reinvestigation of the sex pheromone of *P. interpunctella* revealed the presence of a fourth component, (*Z*)-9-tetradecenyl acetate (Zhu et al. 1999). Flight-tunnel experiments showed that the four-component blend was superior to blends in which one or more of the substances had been removed. Furthermore, trapping studies in Sweden indicated that the four-component blend was best since catches with this blend were about five times higher than for traps containing TDA only (Zhu et al. 1999). The four-component blend developed for *P. interpunctella* also improved catches of *E. cautella*, by approximately five times (Anderbrant et al. 2009).

These two experiments show that lures for monitoring based on female sex pheromones can be made much more sensitive by adding minor pheromone compounds to the commercially used main component. However, it is still unclear whether or not it is possible to combine improved sensitivity with the ability to catch all three species using the same lure. Results shown by Anderbrant et al. (2009) indicate that this is indeed possible for *P. interpunctella* and *E. cautella*, whereas the necessary experiments with *E. kuehniella* still need to be performed.

A variety of different dispensers are applied, ranging from simple rubber tubing, rubber septa, polyethylene capsules and glass or plastic beads in plastic capsules covered by specific membranes into or onto which the active pheromone can be embedded into the glue of the sticky trap surface, for example.

Simple mathematical models are needed to interpret pheromone trap catches and to provide predictions of pest population dynamics and distributions (Subramanyam and Hagstrum 1996). The optimization of traps and lures will enable the realization of new computer-based methods aimed at the organization and interpretation of data, which will make it easier to face pest attacks properly (Wileyto et al. 1994; Longstaff 1997; Campbell 2007; Burks et al. 2010). During recent years, computer-assisted decision support systems have also been developed that estimate insect population growth and the spatial distribution of insects as a function of environmental factors in various commodities and types of food industries and storage facilities (Arbogast et al. 2000a, b, 2002a, b, 2004; Campbell et al. 2002; Campbell and Hagstrum 2002; Athanassiou et al. 2005).

The data from trapping, along with spatial analysis or geographic information software, can be used to visualize locations in a building that have a high or low probability of encountering a pest insect or infestation (Arbogast et al. 1998; Shumann and Epsky 1998; Arbogast and Mankin 1999; Phillips et al. 2000; Trematerra and Sciarretta 2002, 2005; Nansen et al. 2003; Trematerra et al. 2004, 2007; Athanassiou et al. 2011).

Mass trapping

The idea of mass trapping is to attract so many individuals of the population to the traps that the trapping itself controls the population.

Early mass-trapping attempts were conducted using pheromone blends of many target insect species. The trap designs were generally developed on an empirical basis: various release mechanisms were devised to distribute the pheromones at a controlled rate. A major problem is quantification of the number of traps necessary per unit area to achieve effective control. Mass trapping with pheromones, or simply catching as many insects a possible to reduce their overall numbers, has immediate appeal but has gained limited success.

In the case of female-produced sex pheromones, which are most commonly used in storage systems against Lepidoptera, only males are trapped. Hence, any attempt to suppress the population by trapping males would require a sufficient number of trapped males 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 its lifetime (Lanier 1990). If a male can mate with 6–10 females in a lifetime, as is the case for *P. interpunctella* (Brower 1975), then up to 90% of the male population can be trapped without affecting the number of mated females or the subsequent larval generation.

Under high population levels, the rate of female encounters would be high and mass trapping would be more difficult to achieve. However, under low population levels, males locate females less frequently and intensive trapping could conceivably reduce male populations to biologically significant levels (Cardé and Minks 1995).

Proper experiments of mass trapping are not easy to conduct due to inadequate controls or poor replication. However, various studies have reported success in the control of *E. cautella* in the US; *P. interpunctella* in a vegetable and flower seed storage room in France; *E. kuehniella* in some Italian mills; *L. serricorne* and *P. interpunctella* in two food warehouses in Hawaii and *L. serricorne* in tobacco stores in Greece, in a cigarette factory in Portugal and in a Hawaiian bakery (Fleurat-Lessard et al. 1986; Trematerra 1990, 1994a, b; Buchelos and Levinson 1993; Pierce 1994, 1998; Süss et al. 1996; Carvalho and Mexia 2002; Campos-Figueroa 2008; Pease and Storm 2010; Trematerra and Gentile 2010).

In practice, the effectiveness of the mass-trapping technique can be reduced by factors such as inefficient trap design, the saturation of traps, especially in situations of high pest density, poor pheromone release or duration, the attraction of only one sex, inappropriate positioning of traps, the expense and the immigration of new pests from outside the treated area.

Mass trapping both sexes of a population using aggregation pheromones should be more effective than mass trapping only males or only females. Aggregation pheromones are known from several beetle species that infest stored products, but few studies have been conducted to suppress the populations of these insects.

Likewise, food lures used in combination with pheromones may offer a way of enhancing the effectiveness of mass-trapping systems for stored-product pests (Cox 2004). Recent studies have investigated the potential of pheromone-based mass-trapping methods for controlling indoor populations of *E. kuehniella* (Trematerra and Battaini 1987; Trematerra 1989, 1990, 1994a, b; Süss et al. 1996; Athanassiou et al. 2003; Anderbrant et al. 2007; Ryne et al. 2007; Trematerra and Gentile 2010).

Trematerra and Battaini (1987) showed that the integrated control of *E. kuehniella* can be achieved by mass trapping. Furthermore, Trematerra (1989, 1990) reported the results of surveys of a practical application of mass trapping to control the infestation of *E. kuehniella* in the whole of a large flour mill. In a recent article, Trematerra and Gentile (2010) presented the results of a mass-trapping method to contain the Mediterranean flour moth population that had infested a large traditional flour mill. The study also investigated the effectiveness of mass trapping combined with other pest control techniques in improving the procedures used to combat infestation by *E. kuehniella* in an IPM approach. Over 5 years, the pheromone funnel traps, baited with 2 mg TDA, attracted a total of 54,170 males. The constant presence of the traps caused a marked decrease in the population of *E. kuehniella*. The results of the surveys showed that the population density of this moth could be notably reduced and maintained at a low level in flour mills by mass-trapping techniques accompanied by localized insecticide treatments and careful cleaning of the various departments and of all equipment.

Attracticide method

The more common concept of an attracticide method involves the formulation of an insecticide with a feeding stimulant and a long-range attractant that can be applied evenly over large areas. Target insects orientate to the formulation where they feed on or contact the insecticide and then die. In stored-product protection the attracticide method, or lure-and-kill or attract-and-kill, concept-based method involves using a pheromone or another attractive semiochemical to lure insects to a specific point or an area where they come into contact with a toxicant that causes a rapid kill or contamination with some kind of pathogen (Trematerra and Capizzi 1991). This method is in some ways analogous to mass trapping, although many more insects are affected because the attracticide method is broadcast over a large area and the killing effect is not limited to individual traps.

The attracticide method is desirable because of the reduced input of insecticides in food storage areas since a specific pest is coaxed via the pheromone lure to come into contact with a small amount of an effective and locally contained killing agent.

There are many promising results in the use of the attracticide method concept in flour mills and confectionary industries for the control of *E. kuehniella* and *E. cautella* in Italy and for the control of *L. serricorne* in food warehouses in Hawaii (Trematerra and Capizzi 1991; Pierce 1994; Trematerra 1995, 1997; Süss et al. 1999). Preliminary results for the lure-and-kill method for *P. interpunctella* have been also reported in the US (Nansen and Phillips 2002, 2004; Campos-Figueroa 2008).

In stored-product protection, the attracticide method concept is promising in flour mills for the control of *E. kueniella* (Trematerra 1995, 1997) and in confectionary industries for the control of *E. cautella* (Süss et al. 1999).

In Italian mills, Mediterranean flour moth males were successfully lured to laminar dispensers (2 × 2 cm) baited with 2 mg TDA (daily release of 13 μg) and treated with 5 mg cypermethrin; this caused a marked decrease in moth population. Furthermore, Trematerra and Capizzi (1991) performed behavioural tests involving olfactometer, electroantennogram and insecticide activity to clearly determine the effectiveness of these elements in the attracticide method. Therefore, in field tests, a practical application was performed to determine the degree of control of *E. kuehniella*. In olfactometer tests, 80–90% of *E. kuehniella* males responded to pheromone-insecticide dispensers, confirming the low repellency of cypermethrin in their sexual behaviour. The possible interaction between optical and pheromone stimuli was also studied by recording the choices of *E. kuehniella* males and females between nine different light-brown cardboard figures varying in shape and position. A significantly higher number of *E. kuehniella* males were attracted to the sub-triangular forms resembling females than to any of the other figures.

Encouranging results were obtained by Trematerra (1995) using attracticide method applications in flour mills at 220- to 280-m^3 intervals. This experiment was undertaken in Central Italy in a large mill 16,000 m^3 in size that produced flour and semolina from *Triticum aestivum* L. and *T. durum* Desf. Throughout the 2 years of application of the attracticide method, the males were removed from *E. kuehniella* populations, preventing an increase in the residual population. The prolonged presence of the treated dispensers in the flour mill, particularly during periods when the moths were able to breed, led to a population reduction throughout the mill, including areas where no processing occurred. After 2 years of using the attracticide method, the usual second fumigation proved unnecessary. The continuous presence of attracticide dispensers in the mill also caused a marked decrease in the *E. kuehniella* population during the third year.

In the USA, Nansen and Phillips (2004) evaluated a commercially formulated attracticide for *P. interpunctella* in which TDA was used as the attractant and the synthetic pyrethroid permethrin was the killing agent. The experiments were designed to determine to what extent the subtle contact of *P. interpunctella* males with the attracticide would affect their survival and ability to mate; the positive anemotactic flight response of *P. interpunctella* males to the attracticide in a wind tunnel; and the potential of the attracticide method to suppress *P. interpunctella* populations under controlled, simulated warehouse conditions with different moth densities. The overall conclusions found that pyrethroids and naturally derived pyrethrins, both applied to surfaces at registered label dose, had the highest toxicity against adult male Indian meal moths.

In addition, from the US, Campos and Phillips (2010) clearly showed that attracticide formulations could control *P. interpunctella* for up to 8 weeks and could be developed using adequate application doses of permethrin to a variety of surfaces.

Another attracticide method utilized pheromones in an inoculation device contaminated with some kind of pathogen. Adult *Trogoderma glabrum* (Herbst) males were successfully drawn to a sex pheromone source containing the pathogenic protozoan *Mattesia* spp. and became externally contaminated with the pathogen (Burkholder and Boush 1974). After leaving the treated attractive source, they transmitted infective spores to the females and subsequently spread the disease throughout about 96% of the test population. Under simulated warehouse conditions, the following generations of *T. glabrum* were suppressed after a single introduction of *Mattesia trogodermae* Canning into the dense, adult male population via pheromone-baited spore-transfer sites (Shapas et al. 1977). Population growth in the first generation after treatment was reduced to one-sixth of the untreated control population and it further fell to below the pre-treatment level by the second generation.

Adult males of *P. interpunctella* were contaminated with a powder formulation of a homologous granulosis virus when attracted to a source of this virus by a pheromone lure (Vail et al. 1993). Surface contamination of males was transferred to adult females during copulation and larval food was contaminated by females during oviposition. Both the first and second larval generation acquired the infection, resulting in 60 and 50% mortality, respectively.

More recently, *Beauveria bassiana* (Bals.-Criv.) Vuill. was used in laboratory tests to attract and kill *Prostephanus truncatus* (Smith et al. 1999).

Whilst bacteria, fungi, protozoa and viruses all have the potential to be natural microbial control agents (biopesticides), it is insect-specific (entomopathogenic) fungi such as *B. bassiana* and *Metarhizium anisopliae* (Metsch.) Sorokin which are the most well known and the best candidates at present. Research to investigate the potential of entomopathogenic fungi for the control of stored-product insects has increased over the past decade, with studies examining the potential of both *B. bassiana* and *M. anisopliae* on a range of pest species (Wakefield et al. 2010).

Mating disruption

Mating disruption is assumed to work via permeating the area under treatment with a synthetic pheromone so as to reduce mate finding or aggregation, the result being mating suppression.

The mechanisms involved in mating disruption can consist of one or a combination of any of the following:

- constant exposure of the insect to a relatively high level of a pheromone leads to adaptation of the antennal receptors, thus determining a refractory state in the central nervous system,
- a sufficiently high background level of the applied pheromone masks the natural pheromone plume and therefore trail following is not possible,
- the synthetic pheromone plume is applied to a relatively large number of discrete sources so that insects flying within the treatment area can be diverted from naturally occurring plumes, i.e. a false-trail following,
- the auto-confusion system is a novel pheromone-based mating disruption method for the control of stored-product moth pests. New research has shown that electrostatically charged powders can adhere to insect cuticles and be used as carrier particles for active ingredients (Armsworth et al. 2006) such as entomopathogens, insecticides and pheromones.

Knowing which disruption mechanisms are operating is important, as otherwise the design of appropriate formulations would be just guesswork. In fact, the situation can differ for various insect species.

The limitations and theoretical bases of mating disruption are similar to those for the mass trapping of males: a substantial proportion of the male population has to fail to locate females, and success is more likely under relatively low population levels. For practical pest control, the technique of mating disruption generally requires the use of much larger quantities of semiochemicals than mass trapping, and so will only be practical if the chemicals are cheap enough to produce. In addition, there may be concerns about possible contamination of the stored product where high concentrations of the pheromone come into direct contact with it.

The synthetic pheromone is usually enclosed in slow-release dispensers capable of releasing it over weeks or even months. Therefore, the application of this method requires the simultaneous development of a reliable system to monitor whether or not the method works.

Mating disruption is a potentially effective pheromone-based control method for storage moths and requires further consideration. The response of females in the presence of high concentrations of pheromones must be considered. The low level presence of males and the pheromone substance present inside the structure could induce females to leave internal areas in favour of outdoor zones (Trematerra 1994a), and the absence of males could also stimulate dispersal. Also, it has been suggested that insects may evade the effect of mating disruption by a progressive elevation of pheromone production and response threshold or a change in pheromone composition over consecutive generations to enable them to compete with background pheromones.

Studies carried out in the field indicate that there is a significant correlation between some of these factors and the spatial distribution of several insects in food-processing facilities and in flour mills (Nansen et al. 2003; Trematerra and Sciarretta 2005; Trematerra and Gentile 2010).

Although several successful experiments have been reported, such as for: *E. cautella* and *P. interpunctella* in the laboratory and in simulated and field situations including a chocolate factory, pet food distributor and pet shop; *Sitotroga cerealella* (Olivier) and *E. kuehniella* in food industries and mills; mating was also found to be reduced in *Attagenus megatoma* (Fabricius) and *Trogoderma inclusum* LeConte; other mating-inhibition compounds are also known for *L. serricorne* and *Stegobium paniceum* (Linnaeus) (Sower and Whitmer 1977; Hodges et al. 1984; Levinson and Levinson 1987; Prevett et al. 1989; Trematerra 1989; Mafra-Neto and Baker 1996; Süss et al. 1999; Ryne et al. 2001, 2006, 2007; Shani and Clearwater 2001; Fadamiro and Baker 2002; Sieminska et al. 2009; Phillips and Throne 2010; Savoldelli and Süss 2010; Trematerra et al. 2011a, b).

The main disadvantage of mating disruption is that this method does not prevent mated female immigration from adjacent areas, thus oviposition and subsequent infestation are still likely to occur (Cardé and Minks 1995; Jones 1998). Hence, the monitoring of female activity and/or oviposition is essential when developing a mating disruption-based control programme. The stored-product ecosystem is an 'enclosed' environment, which may render stored-product facilities as ideal candidates for the implementation of mating disruption, as many of the limiting factors that exist in the case of field pests have a reduced effect in these ecosystems.

The pheromone (*Z,E*)-9,12-tetradecadienyl acetate is the male attractant for several stored-product moth species of Pyralidae, thus, this 'multi-pheromone' has been successfully used for mating disruption in stored-product facilities.

In particular, the use of mating disruption against pyralid moths has been evaluated for stored-product facilities with promising results in both laboratory and field tests. Brady and Daley (1975) and Hodges et al. (1984) conducted studies of mating disruption in *E. cautella*, with promising results for the wider use of this technique in large storerooms. Sower et al. (1975) showed a 90–95% reduction in mating in small rooms when *P. interpunctella* densities were low. Sower and Witmer (1977) and Prevett et al. (1989) noted a significant reduction in mating and the population growth of both *P. interpunctella* and *E. cautella* in warehouse rooms treated with high TDA densities. Fadamiro and Baker (2002) reported that pheromone puffs suppressed the mating of *P. interpunctella* and *S. cerealella* in an infested corn store. Shani and Clearwater (2001) noted that an increased pheromone presence disrupted the mating of *E. cautella* adults and significantly influenced progeny production. Moreover, for the same species, Ryne et al. (2006), in a chocolate factory in Sweden, noticed a 94% reduction in the capture of *E. cautella* males in pheromone-baited traps, which is an additional indication that this method is effective against this species. In the same study, a reduction was also noted in moth captures in water traps, also suggesting that the total moth population was reduced.

Several studies, from many parts of the world, have shown more or less similar results for *E. cautella*, *E. kuehniella* and *P. interpunctella* (Phillips 1997; Trematerra 1997, 2002; Plarre 1998; Süss et al. 1996, 1999; Ryne et al. 2001, 2006, 2007; Anderbrant et al. 2007; Sieminska et al. 2009; Mueller 2010; Trematerra et al. 2011a, b). However, there are consistent methodological problems with evaluating mating disruption in practice, such as defining what a replicate is and the estimation of control based on trap captures (Cardé and Minks 1995; Anderbrant et al. 2009; Sieminska et al. 2009). Ryne et al. (2007) compared two adjacent storage rooms, one that was treated with mating disruption and one that was not, and, using electrophysiological recordings (male antennal response), found that there was a leakage of pheromone into the untreated room. Mating disruption-based experiments usually use a single or a low number of treatment and control rooms. Each food processing and storage facility is unique, which makes finding a 'control facility' that is similar to the treated facility extremely difficult (Sieminska et al. 2009). As a result, there is still inadequate information regarding mating disruption effectiveness under different microclimates and in different types of facilities.

Sieminska et al. (2009) presented the results from a long-term monitoring trial of *E. kuehniella* populations in two similar flour mills in Poland: one mill was treated with pheromones for mating disruption for 2 years, whereas the second was left untreated. The mating disruption mill was located in Piaseczno and was a four-storey building with an area of $\sim$460 m^2 and an air volume of about 3,000 m^3. The untreated mill was located in Warka and also has four floors, but it was larger, $\sim$940 m^2, with an air volume of about 6,100 m^3, and it produces grains in addition to flour. Thirty pheromone dispensers (one per 100 m^3 factory volume), each releasing about 2 mg TDA per day, were used. Pheromone-baited traps were used to monitor the moth populations in the mating disruption mill and in the nearby untreated mill. The reduction in trap catch during the mating disruption treatment was about 90% or more compared to the untreated mill and the pre-treatment periods of the mating disruption mill. The reduction was larger during the second year of mating disruption than during the first year. These results contribute to the picture that mating disruption is an effective method for controlling moth species infesting stored products.

One of the basic drawbacks of the mating disruption method is that oviposition by mated females from untreated areas that enter areas under treatment can still occur (Jones 1998; Athanassiou et al. 2003; Campbell and Arbogast 2004; Trematerra and Gentile 2010). Consequently, the number of captured males in pheromone-baited traps may not be a clear indicator of the suppression of mating and the concomitant oviposition. Shani and Clearwater (2001) noted that the application of mating disruption may cause an increase in the natural pheromone production of *E. cautella* adults in comparison to undisturbed populations. Hence, mating can occur in the treated area, but remains undetected by pheromone-based trapping protocols.

To avoid these methodological issues, Trematerra et al. (2011a, b) conducted 2-year-large-scale experiments that included eight experimental facilities located in three European countries (Czech Republic, Greece and Italy) in flour mills, food and drug storage facilities, raisin warehouses, pasta warehouses, organic food warehouses and wheat warehouses. The mating disruption dispensers consisted of a cellulose pad loaded with $\sim$50 mg of the TDA pheromone and sealed in a polyethylene sachet. The cellulose pad dispensers, each with 50 mg of TDA, were placed at a rate of one dispenser per 9 m^2 (or one per 54 m^3). Based on the results reported in some of the storage facilities and from certain trap-checking dates, the suppression of capture in the mating disruption-treated areas was $<$95% compared to the untreated areas, and thus mating might have occurred. For instance, in the Greek facilities, where untreated areas were used as 'controls', the reduction in captures was approximately 87 and 93% for 2007 and 2008, respectively.

Generally, there is no clear indication that the species of moth makes a difference in mating disruption programme effectiveness, so Trematerra et al. (2011a, b) proposed that the mating disruption method had the same level of efficacy for *E. kuehniella*, *E. cautella* and *P. interpunctella*. The use of a single pheromone, (*Z*,*E*)-9,12-tetradecadienyl acetate, for the simultaneous suppression of more than one pest species is an additional advantage for the use of mating disruption in storage facilities (Anderbrant et al. 2009).

Still, in large-scale experiments with mating disruption dispensers, the 'untreated' areas may not accurately serve as 'controls' because of the potential permeation of pheromones in the air from treated areas. Also, mating disruption may have a cumulative effect after multiple years of implementation and at several locations a trend was found for lower capture levels in the second year of the study in the facilities under mating disruption.

Historical data from previous years, concerning both adult captures and larval presence in target facilities, could more accurately serve as 'controls' because they can also reflect seasonal patterns in activity. Oviposition and/or immature emergence should be monitored in conjunction with adult activity in pheromone-baited traps to indicate whether successful mating disruption occurred or not.

One of the most important factors impacting the efficacy of mating disruption is the population density. Results from mills and storerooms suggest that structures with high initial moth captures had reduced mating disruption efficacy. However, in all of the experiments conducted, male captures in pheromone-baited traps were reduced under mating disruption. Application of dispensers earlier in the season, or throughout the entire year, is likely to provide increased efficacy in comparison to application of the dispensers late in the season, even though this is the 'critical season' for infestation.

Burks et al. (2011) compared the impact of mating disruption and aerosol-space treatment using synergized pyrethrins on Indianmeal moth, *P. interpunctella*, in 2,200- to 2,900-m^3 structures at a dried bean storage and processing facility in California. A single microsprayer (Isaacs et al. 1999) was suspended from roof beams in the centre of this structure, and emitted 0.07 mg TDA in 95% ethanol every 2.5 min. The resulting rate was 1.9 mg/d/100 m^3 [i.e. similar to the release rate used in a recent study by Sieminska et al. (2009)].

Burks et al. (2011) compared the biological effects of mating disruption between areas treated with mating disruption, aerosol-space treatments, and an untreated part of the facility. The ability of males to orient to a pheromone source and to mate with calling females and the fertility of resident females were examined using pheromone traps, sentinel females and oviposition bait cups, respectively. Compared to an untreated area, the number of males in the pheromone traps and female mating were greatly reduced in both the aerosol-space treatment and mating disruption treatment areas.

After the second week of the study, *P. interpunctella* progeny were recovered in the untreated area and the aerosol-space treatment area but not in the mating disruption area, despite an active infestation in this area at the start of the study. Burks et al. (2011) concluded that the mating disruption treatment was just as effective as the aerosol-space treatment in suppressing population growth under the conditions in this facility, and discussed the potential for mating disruption using high-volume timed aerosol dispensers for phycitine moths in stored products.

Two main issues still remain to be solved. The first is to develop a method of measuring population densities of *P. interpunctella* and *E. kuehniella* that does not rely on pheromone communication. The second issue is to evaluate by how much the sensitivity of a pheromone-based monitoring trap can be increased whilst still being able to catch all three target species (Anderbrant et al. 2009).

Baxter et al. (2008) and Hugget et al. (2010) reported preliminary results from laboratory studies that examined behavioural effects of auto-confusion on virgin male *P. interpunctella*. The auto-confusion system is a novel pheromone-based mating disruption method for the control of stored-product moth pests. The method uses TDA combined with a patented electrostatic powder delivery system known as Entostat Exosex™ SPTab (Exosect Ltd., Winchester, UK) to disrupt mating and interrupt the lifecycle of several moth pests. Male moths are attracted to a compressed tablet of the powder impregnated with synthetic TDA at about 1% of the weight of the plug. The powder adheres to a moth's cuticle via electrostatic attraction and the moth leaves the tablet coated in TDA. Males that have been contaminated in this way will become habituated to the female pheromone and will be less capable of detecting pheromones released by females. Contaminated males can also act as attractive sources to other males, thus increasing the mating disruption and confusion effect amongst males.

Laboratory flight-tunnel studies with *P. interpunctella* have shown that SPTab auto-confusion disrupts the ability of males to locate female moths and they become attractive sources to other males (Hugget et al. 2010).

Using auto-confusion, Pease and Storm (2010) presented practical trials that were conducted in two flour mills in the UK and a spice factory in the Netherlands. Populations of target moth species of *E. kuehniella* and *P. interpunctella* were monitored alongside the deployment of the SPTab system and compared with untreated control areas and historical data from the test areas in the years before deployment. In all cases, the populations were reduced in number compared to the same area in the previous year and compared to untreated control areas under local pest control practices.

The efficacy of the SPTab auto-confusion system for mating disruption of *P. interpunctella* was also studied in field trials conducted in the US during 2008 and 2010 by Phillips et al. (2011).

The SPTab system was also evaluated in several storage facilities in Italy and Greece during 2010 (Trematerra et al. 2011a, b). In these cases, the SPTab dispensers were placed in a 5 × 5-m grid and were replaced at roughly 8–12-week intervals. In Greece, this method was assessed in a large retail store and an organic food store. The moth populations were monitored by pheromone-baited traps and also by cups containing semolina, which were used as oviposition traps. The most abundant moth species were *P. interpunctella* followed by *E. kuehniella*. After dispenser placement, the captures were generally found to be lower compared to the corresponding captures from the previous year, especially in the retail store, until the end of 2010. At the same time, the presence of larvae in the oviposition traps was low.

In Italy, the auto-confusion method was assessed in an industrial feed mill composed of six floors; the trials were conducted from April to Dec 2010. Floors II–V were protected by auto-confusion; the ground floor, floors I, III and VI were used as controls. The most abundant moth species was *E. kuehniella.* After the SPTab dispensers were put in place, captures in the pheromone traps were reduced, particularly during the summer period, compared to the corresponding captures from the control floors. All of these data clearly indicate that this technique could be used with success against stored-product Pyralidae pests.

Future prospects

The development of IPM programmes has been considered by the food industry for both raw and processed commodities. The food industry will need to use IPM programs more extensively in the future to satisfy the increased demands of consumers and regulatory agencies for the reduced use of pesticides.

Crucial factors for IPM of stored products include understanding the factors that regulate systems, monitoring insect populations, maintaining good records, and using this information to make sound management decisions. In this context, ‘insectistasis’ can be readily achieved by the continual supervision of environments by attractant traps in combination with a limited number of curative measures that are appropriately timed (Levinson and Levinson 1985, 2002).

As reported, the utilization of pheromones could lead to a drastic reduction in chemical treatments with consequent economic and qualitative advantages, protecting goods from residual products that are noxious to the consumer and improving the image of the firm.

In stored-product protection, different tolerance thresholds should be established for the various pests depending on their economic impact and the place in the processing chain at which they are found. For example, a limited number of insects can be tolerated at times in a storehouse containing raw materials, but in food-processing plants and storehouses containing finished products, the Injury Level must necessarily be zero. However, it was found that it is not possible to eliminate infestation or even reduce the level of insectistasis if pheromone applications are not accompanied by insecticide treatment and general cleaning of the facilities, particularly in corners and inside machinery where the insects can hide and reproduce undisturbed. If such measures are not observed, the pheromones will, at best, only reduce the number of insecticidal operations, which, in such cases, remain indispensable.

I believe that pheromones, and indeed all semiochemicals, will play a greater role in future IPM programmes than they do at present. However, we must obtain a sound ecological understanding to accompany advances in the fields of chemistry, biochemistry, physiology and genetics.

The available data clearly indicate that many factors influence both female and male behaviour. Furthermore, the relative importance of the different factors varies between species and different populations of the same species, undoubtedly reflecting the different ecological conditions to which they are normally subjected. In recent years, new tools have been developed for detecting insects in stored products, for estimating insect population growth, and for administering fumigants, as well as for natural methods of insect control, such as grain temperature manipulation. Existing or potential new technologies include pheromone traps, sampling devices, acoustic sampling methods and chemical tests that detect live or dead insects through the presence of enzymes. Computer-assisted decision support systems have also been developed that estimate insect population growth and the spatial distribution of pests as a function of environmental factors (Arbogast et al. 1998; Shumann and Epsky 1998; Arbogast and Mankin 1999; Phillips et al. 2000; Trematerra and Sciarretta 2002, 2005; Nansen et al. 2003; Trematerra et al. 2004, 2007; Athanassiou et al. 2005, 2011). The use of trapping data with spatial analysis or geographic information software can visualize locations in a building with a high or low probability of encountering a pest insect or infestation, but sometimes simple observations of trap capture data collected over time will be highly useful information to pest managers. Traps provide relative population samples. The manager should be attentive to increases in insect numbers in traps at one or more locations relative to other locations, and to increases or decreases in numbers at one time compared to past sampling times.

Phillips and Throne (2010) reported that biorational alternatives are urgently needed to replace inefficient or health hazardous methods for pest control. The use of pheromones as a tool shows promising results, and it is worthwhile continuing the development of such a tool.

Research should optimize or further develop other semiochemicals (attractants and repellents) to aid in the monitoring of some stored-product insects and to provide new tools. In this regard, future stored-product protection combinations of repellents and attractants may also find use in push–pull tactics. Push–pull strategies involve the behavioural manipulation of insect pests and their natural enemies via the integration of stimuli that act to make the protected resource unattractive or unsuitable to the pest (push) whilst luring them towards an attractive source (pull) from where the pests are subsequently removed (Cook et al. 2007).

Deterrent or repellent semiochemicals can be used to discourage pests from entering a premise; at the same time, attractants or stimulants can encourage pests to congregate in an adjacent area where they can be controlled more effectively and safely by chemical pesticides or biocontrol agents. So far, these strategies have only been used in the field and glasshouse trials for pests of growing crops (Pickett et al. 1997; Cook et al. 2007). However, there seems to be no serious obstacle preventing similar techniques being adapted for use against stored-product pests.

Thus, it might be worthwhile considering the use of repellents and attractants in traps or other dispensers. For example, to clean up residual pest populations in empty stores before fresh grain arrives, a repellent could be applied to the fabric of the store to deter pests from seeking refuge there and to flush out any insects already established, driving them towards traps containing attractants and control agents that are centrally placed. A similar strategy could be employed for stored grain; here, traps containing repellents could be placed on the surface of and within bulk grain storage devices to drive insects out towards traps positioned around the edge of the bulk storage that contain attractants and insecticides or biocontrol agents.

Obviously, there is a need to improve other methods, including the use of semiochemicals to manipulate the behaviour of target pest species.

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