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REVIEW ARTICLE

Sex Pheromones and Their Impact on Pest Management

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Abstract The idea of using species-specific behavior-modifying chemicals for the management of noxious insects in agriculture, horticulture, forestry, stored products, and for insect vectors of diseases has been a driving ambition through five decades of pheromone research. Hundreds of pheromones and other semiochemicals have been discovered that are used to monitor the presence and abundance of insects and to protect plants and animals against insects. The estimated annual production of lures for monitoring and mass trapping is on the order of tens of millions, covering at least 10 million hectares. Insect populations are controlled by air permeation and attract-and-kill techniques on at least 1 million hectares. Here, we review the most important and widespread practical applications. Pheromones are increasingly efficient at low population densities, they do not adversely affect natural enemies, and they can, therefore, bring about a long-term reduction in insect populations that cannot be accomplished with conventional insecticides. A changing climate with higher growing season temperatures and altered rainfall patterns makes control of native and invasive insects an increasingly urgent challenge. Intensified insecticide use will not provide a solution, but pheromones and other semiochemicals instead can be implemented for sustainable area-wide management and will thus improve food security for a growing population. Given the scale of the challenges we face to mitigate the impacts of climate change, the time is right to intensify goal-oriented interdisciplinary research on semiochemicals, involving chemists, entomologists, and plant protection experts, in order to provide the urgently needed, and cost-effective technical solutions for sustainable insect management worldwide.

Keywords Sex pheromone · Attraction · Monitoring · Attracticide · Mating disruption · Insect control · Integrated pest management · Food security

50 Years of Pheromone Research

Fifty years of curiosity driven pheromone research have yielded a profound understanding of sexual communication in insects. The discovery that minute amounts of species-specific chemical signals, encoded by discrete receptors on the antenna, instantaneously elicit a conspicuous upwind flight orientation behavior has been a source of inspiration for fundamental research on the insect olfactory system; research ranges from biosynthetic production of sex pheromones to peripheral perception by odorant receptor neurons, central processing of the olfactory input, and the resulting behavior (Jacquin-Joly and Merlin 2004; Jefferis et al. 2007; Xue et al. 2007; Cardé and Willis 2008; De Bruyne and Baker 2008).

The progress that has been made from the identification of the first sex pheromone in the silk moth by Butenandt and coworkers in 1959 to the identification of olfactory receptors in *Drosophila* (Clyne et al. 1999; Vosshall et al. 1999) and in the silk moth (Krieger et al. 2005) is spectacular. Pheromone communication, including the

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generation of behavioral responses, is now being dissected at a molecular level (Benton et al. 2007; Dickson 2008). Our imagination is not sufficient to envision knowledge in insect olfaction and chemical ecology another 50 years from now, provided that researchers have the mandate and the resources to carry on this work.

Fundamental research derives, in part, its motivation and justification from the prospect of applying the acquired knowledge. A characteristic of insect chemical ecology is that the know-how can be transferred and used for the control of insects that are noxious to plants or animals. The interconnection between fundamental and applied research, the academic sector, chemical industries, agriculture, horticulture, and forestry, has been a driving force in fundamental and applied pheromone research. Many who began pheromone research in the sixties were influenced by the concept of integrated pest management (Stern et al. 1959) and Rachel Carson's (1962) plea for biorational pesticides. The use of synthetic pheromones for environmentally safe insect control was postulated soon after the discovery of silk moth pheromone (Butenandt et al. 1959; Wright 1964), well before pheromones of economically important insect pests were known.

Fifty years after bombykol, the database of insect pheromones and related attractants contains hundreds of chemicals (Arn et al. 1992; El-Sayed 2008). Pheromones are used as monitoring tools worldwide, and pheromone-based control applications cover large areas (Ridgway et al. 1990b; Howse et al. 1998; Baker and Heath 2004). Behavior-modifying chemicals are elegant tools for insect control, and the prospect of a wide range of future applications in agricultural and medical entomology continues to fuel research in insect olfactory physiology and chemical ecology (Van der Goes van Naters and Carlson 2006). The idea of replacing hazardous insecticides with environmentally benign and species-specific odorants is still a current research challenge, but the emphasis is shifting. The motivating force for green, sustainable insect control is no longer merely the health of the rural work force, the safety of agriculture and horticultural products, nor even the attempt to promote organic farming. The matter is more urgent than it was 50 years ago, and our concerns are the necessity of establishing sustainable insect control methods in times of increasing food insecurity.

Sustainable Insect Control and Food Security

Population growth, creating an increased demand for food, intensifies the pressure on our natural resources, and the adverse effects of climate change on agroecosystems further accentuates the magnitude of this challenge (Ehrlich et al. 1993). Foremost among the Millennium Development Goals endorsed by the United Nations is to eradicate extreme hunger and poverty and, more precisely, to halve between 1990 and 2015 the proportion of people who suffer from hunger. (www.un.org/millenniumgoals). Obviously, our endeavor to secure food for a growing population is closely related to another millennium goal, i.e., to reduce the loss of environmental resources and biodiversity. As we approach the deadline for the fulfillment of these goals, advances have begun to slow or even to reverse.

Environmental security and food security are closely interrelated and mutually dependent. Intensified pressure on ecosystems leads to depletion of resources that are vital for agriculture, including natural enemies of insect pests, pollinators, and carbon sequestration (Ehrlich et al. 1993; Thrupp 2000; van Mantgem et al. 2009). Moreover, future crops will grow under a different climate. The predicted associated effects of higher growing season temperatures and altered patterns of precipitation will have substantial impact on all forms of land use, from agriculture land and forests to aquatic environments. (Battisti and Naylor 2009; Schlenker and Roberts 2009).

Climate changes also will influence plant health and vigor, directly and indirectly through a modified reproductive performance of their associated herbivores. Climatic change will alter outbreak patterns and geographical ranges of insects, including those that vector diseases. The consequences are difficult to predict, especially in view of the complex interactions between crops, herbivores, and pathogens, but climate-related changes most likely will combine to reduce yields (Hunter 2001; Gregory et al. 2009). Forest insects have provided the first conspicuous examples of how insect outbreaks are intensified by global warming. Higher temperatures and drought are blamed for violent bark beetle attacks across Northern America that impact forest structure and in consequence carbon sequestration (Kurz et al. 2008; Van Mantgem et al. 2009).

Up to one third of worldwide food production is destroyed by insects, not including the damage done in storage. During decades of insecticide use, a permanent decrease in the abundance of targeted insect populations never has been achieved. Many of our top agricultural pests instead have been created by the use of pesticides that often have a stronger effect on natural antagonists than on the target species, and also because of widespread insecticide resistance (Pimentel et al. 1992; Elzen and Hardee 2003; Oerke 2006). This is particularly relevant in developing countries, where agricultural production must be increased to feed the population (Thrupp 2000; Pretty et al. 2003; Nwilene et al. 2008).

While crop protection against insects has long relied on insecticides, it is clear that they alone cannot provide a solution, not even by further intensification of their application. Shortcomings are particularly obvious in regions with warm climates and long growing seasons. Recognition of pesticide limitations has, for example, led to the development of pheromone-based methods for control of the rice stem borer *Scirpophaga incertulas* in Bangladesh. Rice covers 70% of the land available for agriculture. Yield has increased by over 40% from 1996 to 2001, yet it does not match consumption. The annual insecticide application has increased from 7,000 t in 1997 to more than 16,000 t in the year 2000, some 90% of which is used in rice production. Even some agrochemical industries now have reached the view that a further increase is not feasible, and thus they support the development of mating disruption and mass trapping of rice stem borer in order to maintain a sustainable level of pesticide use (Cork et al. 2005b).

Chemical ecology produces the knowledge of non-toxic and species-specific pheromones and other semiochemicals that do not harm beneficial species and thus, the basis for efficient and sustainable insect management strategies. The paradox is that currently available know-how is not sufficiently exploited, and we may not be investing enough in research and development to provide breakthroughs quickly enough, especially in food-deficient countries in the developing world. Development aid to agriculture declined by almost 60% between 1980 and 2005, even though the total development aid bill increased over the same period (Fig. 1). In this review, one of our goals was to demonstrate that it is timely and meaningful to invest further in research on behavior-modifying chemicals for sustainable insect management.

Successes and Constraints of Pheromone-Based Methods

"There are many other reasons for using pheromones; one is that they are elegant" (Arn 1990). Three main elements account for the fascination of insect sex pheromones and their feasibility for insect management: 1) they are species-specific, 2) they are active in very small amounts, and 3) the vast majority are not known to be toxic to animals.

Pheromones are by definition species-specific, since the discrimination of conspecific and heterospecific pheromone signals is a key element in the evolution of specific mate recognition systems in many insects. Even synthetic, incomplete pheromone blends usually affect only the target, with the possible exception of taxonomically closely related species (Cardé and Haynes 2004).

Insects use extremely small amounts of pheromone for communication. For example, calling females of codling moth *Cydia pomonella* release pheromone at a rate of several ng/h. [In comparison, apple trees in orchards release one main volatile compound, (*E*,*E*)-α-farnesene, at an estimated rate of several g/ha/h (Witzgall et al. 2008)]. Pheromone trap lures used for detection and monitoring release typically ten to 100 times more than a calling female, and mating disruption dispensers used in orchards release up to 10,000 times more codlemone, which amounts to release rates of 10–100 mg/ha/h. The seasonal application rate of codlemone for mating disruption of codling moth in orchards is up to 100 g/ha. Worldwide annual production of codlemone is ca. 25.000 kg (Fig. 2), for codling moth control on ca. 210.00 ha.

Regulatory agencies in several countries consider it safe to use lepidopteran pheromones. This was corroborated by a recent evaluation by the California Environmental Protection Agency on the occasion of an area-wide eradication campaign against light brown apple moth (Ting 2009). Many pheromones have been registered for pest control, and there is no evidence of adverse effects on public health, non-target organisms, or the environment. Pheromones are applied in slow release formulations, thus resulting in low exposure; residues of lepidopteran pheromones in pheromone-treated food crops have not been detected (Tinsworth 1990).

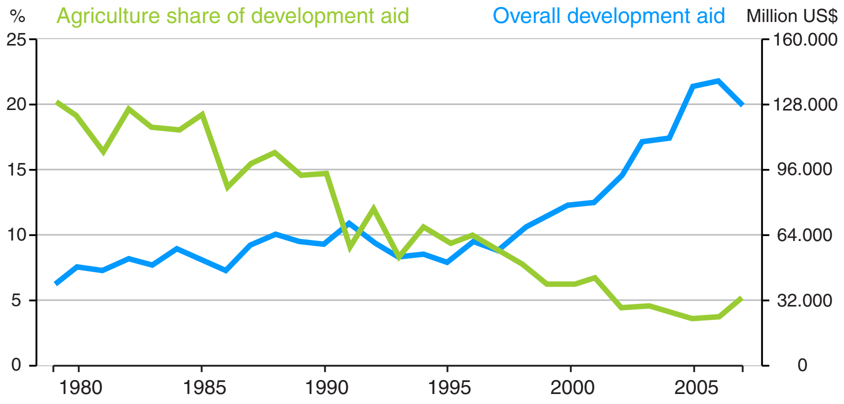

Fig. 1 Overall development aid (*right* scale, million US$), and the share dedicated to agriculture (*left* scale), 1979 to 2007 (Food and Agriculture Organization, FAO; World Summit on Food Security, Rome, November 2009)

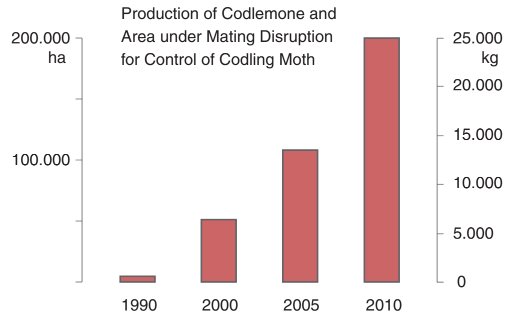

Fig. 2 Production of codling moth *Cydia pomonella* pheromone and area under mating disruption against codling moth worldwide (above; data courtesy of Shin-Etsu Chemical Co., Tokyo)

Insecticides vs. Pheromones

Insecticides do not achieve a long-term pest population decrease. In contrast, an observation shared by many working with pheromone-based control is that continuous long-term use *does* decrease population levels of target species (Fig. 3; Witzgall et al. 1999; Varner et al. 2001; Ioriatti et al. 2008; Weddle et al. 2009). This is attributable to a recovering fauna of beneficials, and to an increasing efficacy of pheromones at low population densities, when communication distance between sexes is increasing.

Insecticide overuse also induces outbreaks of secondary pests. Predatory and phytophagous mites provide the classic example of how the natural regulation of herbivores by their antagonists is disturbed by broad-spectrum pesticides (Agnello et al. 2003). Replacing insecticide with pheromone treatments in vineyards and orchards has rendered treatments against phytophagous mites superfluous, which compensates for the cost of the pheromone treatment (Louis et al. 1997; Waldner 1997; Jones et al. 2009). This emphasizes the contributing vital role of natural enemies for population control, and it corroborates that pheromone-based methods produce better results in the long run, due to recovery of the beneficial fauna.

Insects with hidden, protected lifestyles, including those with underground or woodboring larval habits, cannot easily be controlled with cover sprays of insecticides. Here, control with pheromones is advantageous, since it aims at the mobile adult life stage, and functions to prevent oviposition altogether. Examples of successful pheromone applications are provided in the sections below, and many of these concern insects that inflict severe damage and that are difficult or expensive to control with insecticides.

Slow Development of Pheromone-Based Pest Management

Despite their advantages, progress with practical implementation and commercial exploitation of pheromones has been slow. In Europe, pheromones have been used widely for almost two decades; against the grapevine moths *Lobesia botrana* and *Eupoecilia ambiguella* in Germany, Switzerland, and Northern Italy (Fig. 3; Arn and Louis 1996; Varner et al. 2001; Ioriatti et al. 2008) and against codling moth *Cydia pomonella* in Switzerland and Northern Italy (Mani et al. 1996; Waldner 1997). Although similar climatic, faunistic, and economic conditions exist in other

Mating Disruption in Mezzocorona vineyards 1992-2001

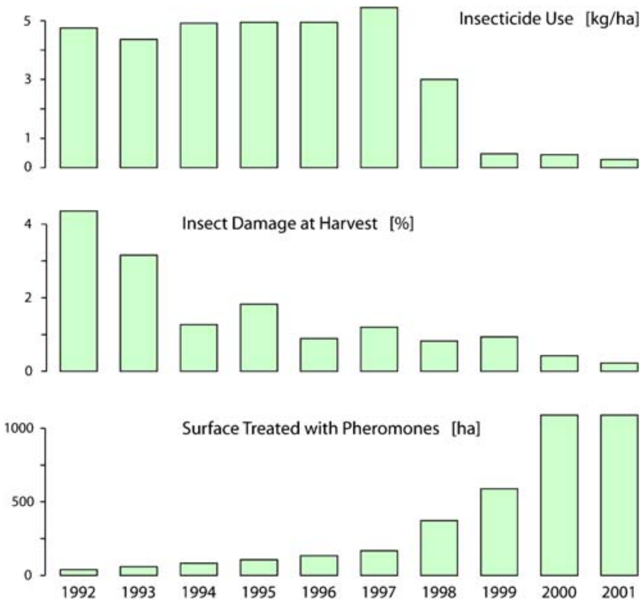

Fig. 3 Mating disruption in the Mezzocorona vineyards in Trento, Italy (Mauro Varner and Claudio Ioriatti, pers. comm.; photo by Mauro Varner)

European wine- and fruit-growing areas, pheromones have not been used much until very recently.

This suggests that motivation and determination among those involved in development and operation of pheromonal pest control methods is a key factor. A certain inertia in the pest control sector to adopt new technologies may be sustained by the lack of interest among research scientists in promoting and transferring existing knowledge. Ehrlich et al. (1993) convincingly argued that the historical separation of agriculture and pure biology at most universities has prevented the implementation of ecological principles in agriculture. To some extent, this may still be true today.

Another key to a more widespread use of pheromones is that the technologies currently in use must become more reliable. Continued goal-oriented research will lead to both more reliable and hence more widespread applications, but funding for applied research at academic institutions and extension services is being cut in many countries (Jones et al. 2009). Field implementation should become a focus of future pheromone research.

Few conventional chemical industries have invested in pheromones, and this lack of engagement has led to the belief that pheromone technology is not viable economically. More smaller companies that specialize in a particular product type, and have the flexibility and low overheads to make their investments in semiochemical products financially viable, are needed.

Practical pheromone applications depend on availability of efficient dispenser materials and on the economic synthesis of pheromone chemicals. The price of synthetic codlemone in the beginning of the nineties, for example, was far too elevated for commercial area-wide applications, but development of large-scale synthesis (Yamamoto and Ogawa 1989) made it possible to exploit it commercially. The annual production of codlemone, the main pheromone compound of codling moth, is on the order of 25 t (Fig. 2), and the price of codlemone is now well below 1,000 US$/kg.

Motives for Area-Wide Pheromone Use

The pheromone application concept goes beyond the conventional control paradigm of protecting plants against larval infestation with sprays of toxic compounds. Conditions for pheromone use are more favorable in area-wide programs, where the effect of immigrating, mated insect females becomes negligible. Successful use is frequently based on a joint effort that involves research scientists, extension entomologists, growers' associations, and also pheromone industries. Area-wide projects facilitate and provide support for this organizational effort (Ioriatti et al. 2008; Jones et al. 2009; Weddle et al. 2009).

The economic benefits of implementing sustainable techniques become evident at the landscape level. A close inspection of pheromone technologies that have been in place over several years shows that the price of pheromones vs. insecticides should not be confounded with economy of use. Farmers' efforts and successes in establishing sustainable production methods contribute to rural development (Ioriatti et al. 2008).

Safe insect control techniques not only improve product quality, but also contribute to the image of a region. Insecticide drift and run-off pollutes air and groundwater, and reduction of insecticide sprays alleviates growing conflicts between rural and urban areas. Orchards and vineyards, where pheromone-mediated mating disruption is widely used, are a part of cultural landscapes that produces, in addition to horticultural products, revenues by attracting tourists, enterprises, investors, and people who wish to inhabit this land.

Detection and Monitoring

The most widespread and successful applications of sex pheromones concern their use in detection and population monitoring. Captures in traps baited with synthetic pheromone lures accurately show whether a specific insect is present, and when its seasonal flight period starts. A simple and widespread strategy is to time insecticide sprays accordingly.

Population monitoring relates trap captures to the abundance of, or to the damage caused by an insect species. The magnitude of trap captures is used to determine thresholds, either for the timing of control procedures, or for making the decision whether or not remedial action is to be taken. One of the first widely used monitoring systems that include an action threshold based on trap captures was established for pea moth *Cydia nigricana* (Wall et al. 1987). Pheromone traps are sensitive enough to detect low-density populations, and are, therefore, effective for tracking invasive species in the establishment phase (El-Sayed et al. 2006; Liebhold and Tobin 2008).

Since pheromones lures are inexpensive and usually reliable, they facilitate the Integrated Pest Management (IPM) concept, which relies on frequent scouting of target species for planning of control measures and evaluating their efficacy. This is particularly so when more specific tools such as semiochemicals, microbials, or beneficials are used, rather than broad-spectrum insecticides.

Invariably, pheromone traps capture adults, and often only males, as is the case with lepidopteran pheromones. When trapping information is to be used in a predictive manner, such as in the damage done by the next generation of larvae, a good understanding of the biology of the pest and the effect of weather and crop stage on development is needed. For pheromone-based monitoring it is further essential that a number of parameters, including the attractant, dispenser, trap design, and trap location are standardized and kept constant. The attractant and dispenser material must be under strict quality control, since release rates and chemical impurities, even in trace amounts, will strongly affect the attractiveness of a lure (Arn et al. 1997). Lure constancy, not overall attractiveness, is decisive.

One future goal is data capture. Insect monitoring can be facilitated by supplying farmers with additional information that includes current and historical seasonal records of trap catch, infestation rates, climate data, and possibly even the geographical distribution of the crop and target insect. This can be aided by the use of geographical information systems (GIS), for example, in area-wide control programs in forests (see below; Tobin et al. 2004, 2007).

Practical Use of Pheromone-Baited Traps

Hundreds of pheromone compounds have been identified, most of them in Lepidoptera, but also in other insect orders, particularly beetles and flies (Arn et al. 1992; El-Sayed 2008). Table 1 shows widely used pheromone lures. In several species, such as the tomato leafminer *Tuta absoluta* and in stored product insects, lures are used for both monitoring and mass trapping (see below). Lures are distributed by many companies worldwide, and there are no reliable data on the total number used, especially in emerging markets in Asia and South America. We estimate that at least 20 million pheromone lures are produced for monitoring or mass trapping every year. This includes all pest control sectors, horticulture, agriculture, stored products, forests, and also private use in households and gardens.

Gall midges (Diptera: Cecidomyiidae) are, because of their small size, difficult to see, and pheromones are cost-effective tools for tracking these tiny flies. Gall midge pheromone identifications require state-of the-art analytical techniques, since they are produced in pico- to femtogram amounts. The chemical structures are carbon chains with one or two ester functionalities, and have been identified from several species including Hessian fly *Mayetolia destructor* (Andersson et al. 2009), swede midge *Contarinia nasturtii* (Hillbur et al. 2005), and raspberry cane midge *Resseliella theobaldi* (Hall et al. 2009). Swede midge traps have been deployed along the US-Canadian border to determine the geographical range of this invasive insect. A combination of a predictive model with pheromone traps accurately assesses and times control strategies (Hallett et al. 2009).

The tomato leafminer, *Tuta absoluta*, is an example of how the absence of an efficient conventional chemical control or other biological method encourages the use of an immature pheromone technology for insect control, merely because other methods are not available. *T. absoluta* is a multivoltine species that mines leaves and fruits of solanaceous plants. Effective chemical control is difficult to achieve (Pereyra and Sanchez 2006). Originally of neotropical distribution, *T. absoluta* recently has been introduced to Southern Europe and Northern Africa. This has fuelled the demand for monitoring lures, which are now employed in mass trapping campaigns in greenhouses. The main sex pheromone component is a triene, (E,Z,Z)-3,8,11-tetradecatrien-1-yl acetate (Svatos et al. 1996), but the lack of an economic synthesis currently precludes mating disruption tests.

Pheromone identifications in beetles are less advanced than in moths. Aggregation pheromones currently are used for mass trapping of weevils and scarabs (see below), and sex pheromones of several other families are under investigation. Larvae of click beetles are hard to control with pesticides due to their underground life habit. One main compound of click beetle pheromones is geranyl octanoate, and specific blends have been identified in several species. Pheromones have been used to survey species distributions and to monitor in the field, for example, *Agriotes* sp. in Europe and North America (Vernon and Toth 2007; Toth et al. 2008).

A number of pheromones have been elucidated in cerambycid beetles over the past decade. Even weak attraction to generic blends may be sufficient for monitoring distribution and phenology. However, some pheromones even attract females, and many of these species have long life cycles with short adult stages, which should favor the use of pheromones for control (Maier 2008; Ray et al. 2009; Rodstein et al. 2009). The coffee white stem borer *Xylotrechus quadripes* is a serious pest of coffee in South Asia. Male beetles have been shown to attract females, and (S)-2-hydroxy-3-decanone has been identified as the main attractive compound. Pheromone traps have been rapidly adopted for mass trapping (Table 1; Hall et al. 2006) reflecting exceptional grower interest in the absence of acceptable alternative control methods.

Mass Trapping and Annihilation

Control of insect populations with pheromones is achieved by two principle techniques, mating disruption and mass annihilation. Mating disruption (see below), causes disorientation and communication disruption between the sexes, and thus delays, reduces, or prevents fertilization of females. Mass annihilation, by mass trapping or attract-and-kill, relies on attraction of one or both sexes to a lure, in combination with a large-capacity trap or an insecticide-

Table 1 Use of sex pheromone lures for detection (D) and population monitoring (M), and for mass annihilation tactics, by mass trapping (MT) and attract-and-kill (AK)

Species	Purpose	Region	Lures/year
Horticulture			
Coleoptera			
Red palm weevil *Rynchophorus ferrugineus*	MT	Asia	1.175.000
American palm weevil *Rhynchophorus palmarum*	MT	Central and South America	25.000
Palm fruit stalk borer *Oryctes elegans*	MT	Asia	125.000
Banana weevil *Cosmopolites sordidus*	MT	Worldwide	120.000
Coffee white stem borer *Xylotrechus quadripes*	MT	India	40.000
Diptera			
Olive fruit fly *Bactrocera oleae*	MT, AK	EU	–[a]
Lepidoptera			
Grapevine moth *Lobesia botrana*	M	EU, Mediterranean countries, Chile, USA	–
Codling moth *Cydia pomonella*	M, AK	Worldwide	–
Oriental fruit moth *Grapholita molesta*	M, AK	Worldwide	–
Tomato leafminer *Tuta absoluta*	M, MT	South America, EU, North Africa	2.000.000
Brinjal fruit and shoot borer *Leucinodes orbonalis*	MT	India, Bangladesh	400.000
Fall armyworm *Spodoptera frugiperda*	MT	Central America	50.000
Agriculture			
Coleoptera			
Cotton boll weevil *Anthonomus grandis*	MT (AK)	North and South America	2.600.000
Click beetles *Agriotes spec.*	M	Europe	–
Lepidoptera			
Pink bollworm *Pectinophora gossypiella*	M, AK	North and South America, South Asia	–
Old World bollworm *Helicoverpa armigera*[b]	M, MT		830.000
Cotton leafworm *Spodoptera litura*[b]	M, MT		480.000
African armyworm *Spodoptera exempta*	D	East Africa	–
Spotted bollworm *Earias vittella*[b]	M, MT		280.000
Yellow rice stem borer *Scirpophaga incertulas*	M, MT	India	100.000
Southwestern Corn Borer *Diatraea grandiosella*	D	USA	–
Potato tuber moth *Phthorimaea operculella*	AK	South Africa	–
Forestry			
Coleoptera			
Spruce bark beetle *Ips typographus*	MT	Europe, China	800.000
Mountain pine beetle *Dendroctonus ponderosae*	MT	North America	–
Douglas-fir beetle *D. pseudotsugae*	MT	North America	–
Lepidoptera			
Gypsy moth *Lymantria dispar*	D	USA, EU	250.000
Spruce budworm, *Choristoneura fumiferana*	D	Canada, USA	–
Pine processionary moth, *Thaumetopoea pityocampa*	D, M	EU	–
Stored products			
Cigarette beetle *Lasioderma serricorne*	M, MT	Worldwide	2.500.000
Indian meal moth, *Plodia interpunctella*	M, MT	Worldwide	2.000.000
Households and gardens			
Japanese beetle *Popillia japonica*	MT	North America	–
Oriental beetle *Anomala orientalis*	MT	North America	–
House fly *Musca domestica*	MT	Worldwide	2.000.000
German cockroach, *Blattella germanica,* American cockroach, *Periplaneta americana*	MT	Worldwide	1.000.000

Examples of widely used lures. A distinction between monitoring and mass trapping is not always possible. The estimated number of lures used worldwide, based on turnover of leading companies in the US and Europe, exceeds 20 million lures

[a] No data available

[b] Data concern South Asia only

impregnated target. Unlike detection and monitoring, where only a small proportion of a population needs to be sampled, mass annihilation requires the use of the most attractive lure.

For attract-and-kill strategies, two different approaches are taken. Either, a semiochemical formulation, consisting of an attractant and inert carriers, is deployed as an additive tank-mix to insecticide products, or an attractant and insecticide are incorporated into a fully integrated matrix that can be applied as a stand-alone intervention. Each approach has specific merits. The additive approach has an advantage in that registration of semiochemicals is facilitated. When applying an integrated matrix product, blanket spray coverage of the crop is not necessary, so the amount of insecticide can be significantly reduced. However, specialized application technology is required.

With female-produced sex pheromones, only males are caught. Since male insects typically mate more than once, a high proportion of the male population must be removed to produce an effect. Male protandry, eclosion before females, will improve the effect of removing males. In addition, even a delay in mating, via a reduction in the number of available males, may also contribute to population control, as has been shown in mating disruption studies (Vickers 1997; Fraser and Trimble 2001; Jones et al. 2008; Stelinski and Gut 2009). These studies underscore the importance of integrating population biology and life history data into development of pheromone-based control applications. Population control is a dynamic and quantitative phenomenon, as illustrated by the importance of the Allee effects in the management of biological invasions (Liebhold and Tobin 2008).

Features of the biology and ecology of the target species that determine the efficacy of annihilation techniques include: the duration of the life cycle, the number of generations per season, the duration of the flight period, and the rate of population growth. Univoltine insects with short seasonal flight periods and a limited host range are easiest to control. Annihilation techniques become far more efficacious when using lures that attract females or both sexes, and when they include male-produced pheromones, aggregation pheromones, floral or plant volatiles that serve as ovipositional cues.

Mass trapping and attract-and-kill are cost-effective compared to mating disruption, since much smaller amounts of pheromones are needed. The insecticide component is environmentally rather safe, since small amounts are used and since crop contamination during application is much reduced. Nonetheless, the insecticide component is an obstacle to public acceptability of attract-and-kill methods. Fungal or viral insect pathogens might be used instead, but their slow mode of action and the short field-life of formulations have not been solved.

Practical Use of Mass-Trapping

Brinjal Fruit and Shoot Borer Eggplant is an important vegetable in South Asia, commercially produced by approximately 700,000 farmers on 570,000 ha in India alone. In Bangladesh, 40% of all vegetables produced are eggplants, providing farmers with a regular, year-round income. Severe yield losses are caused by the fruit and shoot borer *Leucinodes orbonalis*. Insecticides appear to be largely ineffective for control of *L. orbonalis*, because of protection offered by the fruit itself and because of insecticide resistance. A pheromone-based mass trapping strategy has been developed, from optimization of the pheromone blend and dose, trap design, and placement to field implementation (Cork et al. 2001, 2003, 2005a). Mass trapping, without the use of insecticides, has led to a 50% and higher increase in marketable fruit, which has been attributed to the combined effects of mass trapping and enhanced impact of natural enemies. Additionally, secondary pests, such as mites and whitefly, were reduced in the pheromone plots. The yield increase translates to earnings of $1,000 US$ per ha and yr for resource-poor families. Given estimated sales of pheromone lures reported in India and Bangladesh (Table 1), at least 15% of all farmers have now adopted the technology, and this is increasing year on year (A. Cork, unpublished).

Bark Beetles Bark beetles are of tremendous importance in coniferous forests worldwide, and the discovery of the aggregation pheromones of the most destructive European and North-American species was soon followed by area-wide mass trapping campaigns (McLean and Borden 1979; Bakke 1982). A more recent study corroborates that mass trapping is indeed a viable control strategy. In an isolated 2,000-ha forest reserve in China, traps for the double-spined spruce bark engraver *Ips duplicatus*, baited with a 2-component pheromone blend of ipsdienol and *E*-myrcenol, were employed at a rate of 1 trap/25 ha for 3 years. Yearly beetle captures between 0.5 and 1.7 million strongly reduced average tree mortality to 17% according to a 20-year record (Schlyter et al. 2003). This particular forest is isolated, but treatments on larger areas that use the same trap density should produce the same effect.

Palm Weevils Palm weevils are the most destructive pests of palm trees and cannot be efficiently controlled with insecticides. Adult weevils are not very susceptible to toxic compounds, and mining larvae are protected inside tree trunks. They provide an outstanding example of sustainable area-wide insect control by mass trapping, covering thousands of hectares of palm in all growing regions, particularly in Central America, the Middle East, and South Asia (Table 1). The beetles use aggregation pheromones for sexual communication prior to mating, attracting both males and females. A facilitating factor is that overall population densities are lower than in smaller insects. Attractancy of the lures can be augmented by the use of plant and associated fermentation volatiles (Giblin-Davis et al. 1996; Oehlschlager et al. 2002).

Males of the American palm weevil, *Rhynchophorus palmarum*, release an aggregation pheromone, rhynchophorol: (4S)-2-methyl-(5E)-hepten-4-ol (Rochat et al. 1991; Oehlschlager et al. 1992). Captures with pure rhynchophorol increase considerably with the addition of plant material, leading to the development of an efficient control method based on mass trapping (Oehlschlager et al. 1993). Laboratory studies corroborate that aggregation is mediated by a male-produced pheromone and host-plant volatiles that include acetoin and ethyl acetate (Said et al. 2005). The American palm weevil is an important pest of several palm species in tropical America. Besides damaging the trees, it vectors a nematode that cause red ring disease. At less than one trap per 5 ha, even high palm weevil populations and nematode infestation rates have been reduced to very low infection levels, after only 1 year of trapping in combination with removal of infected palms (Oehlschlager et al. 2002).

The red palm weevil, *Rhynchophorus ferrugineus* originates in South-East Asia and is now widely distributed in Asia, Africa, and Oceania. It infests a range of tropical palms, including date, oil, and coconut palms. The larvae develop in the tree trunk, where they destroy the vascular system. Tens of thousands of date palm trees have been destroyed in the Middle East and North Africa since its appearance in the eighties because insecticide-based control is not sufficiently efficient (Soroker et al. 2005; Blumberg 2008). Mating in red palm weevil is mediated by an aggregation pheromone produced by the male weevil, composed of the main compound (4S,5S)-4-methyl-5-nonanol (ferrugineol) and 4-methyl-5-nonanone (Giblin-Davis et al. 1996; Perez et al. 1996). Traps loaded with ferrugineol, supplemented with ethyl acetate and plant volatiles, and a fermenting mixture of dates and sugarcane molasses, are placed at densities of up to 10 traps/ha for monitoring and mass trapping. Pheromone traps have played a significant role in the suppression of red palm weevil populations, for example in date palm plantations in Israel (Hallett et al. 1999; Soroker et al. 2005).

Banana Weevil The banana root borer *Cosmopolites sordidus* is a major pest of bananas throughout the world. The male-produced aggregation pheromone sordidin attracts both sexes, and mass trapping by using ground traps has the potential to replace inefficient insecticide treatments (Reddy et al. 2009).

Japanese Beetle The Japanese beetle is a devastating pest of urban landscape plants in the eastern United States and traps are sold in many garden centers. These are baited with a combination of synthetic pheromone, japonilure, and with floral compounds, phenethyl propionate, eugenol, and geraniol. This powerful lure can attract thousands of beetles. However, due to limited trapping efficacy, the spillover onto surrounding host plants is counterproductive, unless traps are placed at some distance from the plants needing protection (Switzer et al. 2009).

Practical Use of Attract-and-Kill

Cotton Boll Weevil The cotton boll weevil *Anthonomus grandis* is a major pest of cotton in the Americas. Males produce an aggregation pheromone, grandlure (Tumlinson et al. 1969), that has been successfully incorporated into a pheromone-baited killing station known as "Boll Weevil Attract and Control Tubes". These tubes are produced in large numbers every year (Table 1). A density of 14 traps per ha achieves a strong reduction in weevil populations, at minimal crop damage. After successful control and eradication programs in the USA, bollweevil trapping is now also used in South America on at least 250,000 ha (Ridgway et al. 1990a; Smith 1998).

House Fly In addition to feeding attractants, house flies *Musca domestica* are attracted to pheromone, (Z)-9-tricosene (muscalure), which is widely used in combination with co-attractants in lure-and-kill approaches indoors and in livestock stables (Table 1; Butler et al. 2007; Geden et al. 2009).

Fruit Flies Male fruit flies (Diptera, Tephritidae) produce pheromones that attract females (Jang et al. 1994; Landolt and Averill 1999). However, these sex pheromones have not been a main research target, because of the efficacy of parapheromones and plant volatiles as attractants (methyl eugenol, trimedlure, cuelure, angelica seed oil, enriched ginger oil, raspberry ketone), and hydrolyzed protein baits (e.g., GF-120). These have been most widely used for monitoring and annihilation of several fruit flies, including Oriental fruit fly *Bacterocera dorsalis*, melon fly *Bacterocera cucurbitae*, and Mediterranean fruit fly, *Ceratitis capitata* for almost 50 years. Methyl eugenol, which is a male pheromone precursor, is a highly effective attractant and is used in IPM programs and for eradication of *Bactrocera* flies by male annihilation in the Pacific region, including Hawaii and California (Cunningham et al. 1990; Hee and Tan 2004; Vargas et al. 2008; El-Sayed et al. 2009).

A female-produced pheromone, a blend of (1,7)-dioxaspiro-[5,5,]-undane (olean), α-pinene, n-nonanal, and ethyl dodecanoate is exploited for control of the olive fly *Bactrocera oleae* by a lure-and-kill technology that incorporates the food attractant ammonium bicarbonate (Mazomenos and Haniotakis 1985; Broumas et al. 2002).

Orchard Tortricids A fully integrated attract-and-kill product, containing 0.16% pheromone and 6% permethrin, has provided control of codling moth at economic levels of less than 1% harvest infestation in apple orchards in Switzerland. Based on reductions in trap catch and the mating frequency of tethered moths, efficacy of the attract and kill droplets lasted 5–7 wk, requiring two seasonal applications. Subsequent experiments replaced permethrin with an alternative toxicant, the insect growth regulator, fenoxycarb, which has a sterilizing effect. Field tests showed that autosterilization, i.e., transfer of the insect growth regulator from a contaminated male to the female moth at mating, contributes to the control effect (Charmillot et al. 2000, 2002).

Studies of competition have shown that attracticide droplets are more attractive to male moths than calling females, and that the number of point sources is key to the ability of males to locate calling females (Krupke et al. 2002). Commercial applications require applications of 3,000 droplets per ha. At this rate, disruption of male orientation is likely to be a contributing mechanism. This has been substantiated with two further key orchard tortricids, Oriental fruit moth *Grapholita molesta* and lightbrown apple moth *Epiphyas postvittana* (Suckling and Brockerhoff 1999; Evenden and McLaughlin 2004).

Disorientation and Communication Disruption by Air Permeation

Insects rely on volatile sex pheromones to communicate for mating. Permeation of the crop with synthetic sex pheromone can disrupt chemical communication and thus prevent mating. Indeed, the mating disruption technique has become the most commonly utilized application of semiochemicals for population control (Baker and Heath 2004; Witzgall et al. 2008). Unlike with mass trapping, the natural pheromone is not required for mating disruption to be effective. Both attractive and non-attractive pheromone blends have been used, since off-blends can result in considerable cost savings (Bengtsson et al. 1994; Cork et al. 1996; Stelinski et al. 2008). Negative signals, including antiaggregation pheromones, have been combined with attractants into push-pull techniques (Borden 1997; Schlyter and Birgersson 1999; Cook et al. 2007).

The behavioral mechanisms by which mating disruption is achieved have been subject to investigation and discussion since Bartell (1982). If we understand the underlying mechanisms that cause or result in the behavioral modification that leads to disruption of mating, we will be better placed to understand why some applications are successful and others not (Cardé and Minks 1995; Sanders 1996, Miller et al. 2010). Attempts to interpret the behavioral response to air permeation treatments should, however, also build on field data on both the behavior of moths and molecules. Male moth behavior depends on a number of factors, including pheromone blend, release rate, and aerial concentration. Measurement of these factors and their contribution to efficacy will help to predict the outcome of mating disruption (Bengtsson et al. 1994).

Resistance to mating disruption is a remote risk in many species, because changes in female pheromone biosynthesis or male response are unlikely to lead to a new communication channel that is unaffected by synthetic pheromone treatments that do not precisely match the female-produced blend. However, resistance to treatments with a single pheromone component has occurred in the small tea tortrix *Adoxophyes honmai*. The efficacy of (Z)-11-tetradecenyl acetate, a ubiquitous leafroller pheromone component, decreased after 16 years. The composition of the pheromone blend produced by the females was unaltered, but the pheromone response was broader in resistant males. Efficacy of mating disruption returned to its former level, after changing to the natural 4-component pheromone blend (Mochizuki et al. 2002; Tabata et al. 2007a, b).

Commercial use of mating disruption became possible only after industrial scale synthesis became available at the end of the eighties. As a general guide, application rates of between 10 g and 100 g per ha per season are required to achieve communication disruption, thus resulting in aerial concentrations of at least 1 ng/m3 (Bengtsson et al. 1994; Cork et al. 2008).

A wide range of controlled release formulations has been developed for use in mating disruption. Early on, it had been assumed that a very high density of point sources was required to produce an effective fog of pheromone to disrupt male moths, and, therefore, formulations such as aqueous suspensions of micro-capsules and hollow fibers were developed. However, with the advent of hand-applied reservoir-type formulations, it was realized that fewer point sources that release higher quantities of pheromone could achieve the same result, by generating plumes with high concentrations of synthetic pheromone. Season-long field life is a main advantage of hand-applied dispensers. Renewed efforts to develop sprayable formulations is motivated by reduced application cost, either in combination with fungicides in orchards, or for applications on large areas (Leonhardt et al. 1990; Weatherston 1990; Trimble et al. 2003; Tcheslavskaia et al. 2005; Il'ichev et al. 2006).

A major flaw of current commercial pheromone dispensers is that pheromone release increases with ambient temperature. In apple orchards treated against codling moth, ca. 90% of pheromone applied is released outside the diel flight period, mainly during daytime at peak ambient temperatures (Witzgall et al. 1999). In addition, dispensers must be applied early in season when population densities are still low and release rates decrease during the season, as population densities start to increase. These problems can be circumvented by using timed and metered pheromone sprayers that release constant and large amounts of pheromone only when the insects are active (Shorey and Gerber 1996; Mafra-Neto and Baker 1996; Fadamiro and Baker 2002). Such "puffers" are now increasingly used against navel orangeworm *Amyelois transitella* and codling moth.

Mating disruption is more efficacious over large areas. This is in part because large areas reduce the impact of gravid females that immigrate into treated plots, but also because homogenous air permeation is facilitated. Incomplete permeation with pheromone, especially along crop borders, is an obstacle. This has been confirmed by field EAG measurements of aerial pheromone concentrations (Milli et al. 1997). Border effects become negligible when large surfaces are treated. Indeed, dispenser spacing and overall pheromone application rate can be reduced as the treated area increases, resulting in considerable cost savings to farmers.

Adoption of mating disruption and reduction of insecticide leads to a decrease in the incidence of secondary pests due to conservation of natural enemies. In orchards and vineyards, mating disruption renders treatments against phytophagous mites superfluous since outbreaks are typically induced by the overuse of insecticides.

Other biological techniques rarely permit stand-alone containment of insects, and mating disruption, in addition to annihilation techniques, is often the only option when insecticides cannot be applied, as in organic crops, allotment gardens, or against insecticide-resistant insect populations (Suckling et al. 1990; Albert and Wolff 2000). From the nineties onwards, the area under mating disruption saw an almost exponential expansion into the first decade of this century (Fig. 2; Brunner et al. 2002; Ioriatti et al. 2008).

Mating Disruption in Vineyards

The history of mating disruption of grape moths in Europe, reviewed by Arn and Louis (1996) and Ioriatti et al. (2008), exemplifies the weight of interfacing research among extension people, growers, and pheromone industries for the development and implementation of this new technology.

The complete identification of the sex pheromones of the key European grape insects as a prerequisite for the development of mating disruption (Arn et al. 1986; Guerin et al. 1986; El-Sayed et al. 1999b) was the incentive for the development of techniques that still are widely used in chemical ecology research, such as the electroantennographic detector (Arn et al. 1975) and a wind tunnel bioassay with quantitative, controlled stimulus application (Rauscher et al. 1984; El-Sayed et al. 1999a, b).

A portable electroantennogram apparatus was designed for live measurements of ambient pheromone concentrations with an insect antenna, and for rapid optimization of pheromone dispenser placement (Sauer et al. 1992; Koch et al. 2009b). Field tents were used to determine the mating status of female moths and critical population densities, above which mating disruption is no longer effective (Feldhege et al. 1995). The latest methodological progress is appreciably simple but facilitates replicated field measurements of the behavioral effect of dispenser formulations or dispenser densities. Insects are released into portable 8.5 m^3 field cages that contain traps with live females and synthetic pheromone. The cages are placed in vineyards, into 20×20 m pheromone dispenser arrays that simulate full-scale vineyard treatments. The plot size is convenient for the investigation of experimental dispenser formulations (Koch et al. 2009a).

Experimental trials in vineyards were expanded to area-wide campaigns by involving plant protection entomologists, growers associations, and pheromone industries (Rauscher and Arn 1979; Neumann et al. 1993; Vogt et al. 1993). The coordination of mating disruption field campaigns is a complex task, indeed: 1,447 growers participated in Northern Italy in 1999 (Varner et al. 2001). By the end of the nineties, mating disruption had led to an area-wide reduction in population densities and it became widely accepted by growers in Germany, Switzerland, and Northern Italy (Fig. 3; Varner et al. 2001). A challenge in these European vineyards is now to develop novel strategies against new pests that are not affected by mating disruption, especially leafhoppers that vector plant diseases (Mazzoni et al. 2009).

Meanwhile, European grapevine moth *Lobesia botrana* has been found in Chile and Napa County, California. In Chile, 40,000 ha now are under mating disruption in an attempt to eradicate the newly established population (V. Veronelli, pers. comm.)

Mating Disruption in Orchards

Pheromone use in orchards concerns mainly the codling moth *Cydia pomonella*, Oriental fruit moth *Grapholita molesta* (Table 1), and lightbrown apple moth *Epiphyas postvittana*.

Lightbrown apple moth *Epiphyas postvittana* is native to Australia and New Zealand. It is a serious threat to agriculture, because of its polyphagous lifestyle on many fruit and ornamental crops and because it is a quarantine pest in many countries. Suckling and Clearwater (1990) demonstrated that a 2-component blend provided better communication disruption than the main compound alone. Mating disruption then was conceived as a strategy to achieve, in combination with a reduced spray program, economically acceptable control in insecticide resistant populations in apple in New Zealand (Suckling et al. 1990; Suckling and Shaw 1995). More recently, efficient population control has been demonstrated in Australian citrus (Mo et al. 2006). Lightbrown apple moth now has been found in California. A mating disruption campaign uses ground-based sprays and hand-applied dispensers (Garvey 2008; Varela et al. 2008).

Codling moth *C. pomonella* exemplifies some main requirements for competitive pheromone use (Brunner et al. 2002; Witzgall et al. 2008). (1) The larvae damage the crop directly, and the economic damage threshold in apple, pear, and walnut is very low. (2) The hatching larvae are difficult to control with insecticides since they immediately bore into the fruit. A most efficient and widely used insecticide, azinphos-methyl, has been banned in many countries due to its acute neurotoxicity. Resistance problems have occurred with several other insecticides (Reyes et al. 2009). New insecticides, including neonicotinoids that provide more specific control than organophosphates are more costly and still harmful to beneficial arthropods (Beers et al. 2005; Brunner et al. 2005; Poletti et al. 2007). (3) Other, stand-alone biological control techniques are not available. (4) Overuse of insecticides is well-known to harm predatory mites and induce phytophagous mites (Waldner 1997; Epstein et al. 2000; Agnello et al. 2003). Miticide sprays are costly; avoiding them balances the cost of the pheromone treatment. (5) IPM was initiated in orchards and vineyards, and much emphasis has been placed on crop protection education. (6) Consumers are more wary of pesticide residues in fruit than in other food. (7) Sustainable pest control helps to reconcile conflicts between urban and adjacent rural areas, and corroborates the contribution of orchards to the aesthetic value of a region. The worldwide orchard area treated with codling moth mating disruption has now surpassed 200,000 ha, corresponding to, for example, almost half of the European orchard area (Table 2; Fig. 2).

Mating Disruption in Forests

Antipheromones and Bark Beetle Control Bark beetles, including mountain pine beetles *Dendroctonus* sp. can convert large regions of boreal and temperate forest from carbon sinks to carbon sources. It is, therefore, urgent to determine whether pheromones and other semiochemicals become effective in suppressing bark beetle outbreaks. Conifer-inhabiting bark beetles have evolved several olfactory mechanisms for finding, colonizing, and killing their hosts, and also for avoiding unsuitable, overcrowded host trees and resistant nonhost trees. The battery of semiochemicals, attractant and repellent, produced by beetles, host plants, and non-host plants is available for the design of innovative control technology (Borden 1997; Schlyter and Birgersson 1999; Zhang and Schlyter 2004; Seybold et al. 2006).

An alternative strategy to mass trapping with attractant pheromones (see above) are push-pull tactics. These combine aerial permeation of forest stands with anti-aggregation pheromone or repellent non-host volatiles with attractant pheromones. Recent tests confirm the potency of the anti-aggregation pheromones verbenone and methylcyclohexenone (MCH) in aerial forest treatments against mountain pine beetle *Dendroctonus ponderosae* and Douglas-fir beetle *D. pseudotsugae*, respectively (Gillette et al. 2009a, b). These compounds also have been combined with pheromone-based mass-trapping in a push-pull fashion, using hand-applied dispensers (Borden et al. 2006, 2007).

Gypsy Moth The largest application of mating disruption over many years is part of the area-wide management of gypsy moth *Lymantria dispar*, an invasive forest insect in the Eastern US. The “Slow the Spread” program has significantly reduced the spread of gypsy moth by detecting isolated populations in grids of pheromone-baited traps placed along the expanding population front. The detected populations are treated by using *Bacillus thuringiensis* or more frequently by mating disruption, by using aerial applications of plastic flakes (Sharov et al. 2002; Tcheslavskaia et al. 2005).

A prerequisite to the success of managing the spread or establishment of invasive insects is the availability of practical methods for detecting low-density populations. Much of the credit for the success of gypsy moth containment efforts is attributed to the availability of pheromone-baited traps that are inexpensive yet highly sensitive (Liebhold and Tobin 2008).

Area-Wide Programs

Natural insect populations are known to fluctuate in large-scale synchrony. Such spatio-temporal fluctuations are particularly conspicuous in unmanaged forest insects, which can defoliate entire regions (Peltonen et al. 2002). Population fluctuations have been largely neglected in horticultural and agricultural insects while conventional insecticides are the dominating management tactic. The knowledge of population changes on a regional scale is, however, vital for pheromone-based pest management programs (Kobro et al.

Table 2 Use of mating disruption and air permeation with pheromones and antipheromones

Species	Main crop	Region	Area (ha)
Mating disruption			
Gypsy moth *Lymantria dispar*	Forest	USA	230.000
Codling moth *Cydia pomonella* [a]	Apple, pear	Worldwide	210.000
Grapevine moth *Lobesia botrana*	Grape	EU, Chile	100.000
Oriental fruit moth *Grapholita molesta*	Peach, apple	Worldwide	50.000
Pink bollworm *Pectinophora gossypiella* [b]	Cotton	USA, Israel, South America, EU	50.000
Grapeberry moth *Eupoecilia ambiguella*	Grape	EU	45.000
Leafroller moths, Tortricidae	Apple, pear, peach, tea	USA, EU, Japan, Australia	25.000
Striped stem borer *Chilo suppressalis*	Rice	Spain	20.000
Other species	Fruit, vegetables		40.000
Total			770.000
Antipheromones			
Mountain pine beetle *Dendroctonus ponderosae*	Pine	USA, Canada	– [c]
Douglas-fir beetle *D. pseudotsugae*	Douglas-fir	USA, Canada	– [c]

[a] Annual estimated codlemone production is 25 tons (Fig. 2)

[b] Usage dropped significantly upon widespread adoption of transgenic cotton varieties

[c] No data available

2003). In addition, landscape ecology affects insect dynamics, and this should be taken into account for more efficient crop protection (Ricci et al. 2009).

Pheromone-based methods have been shown to produce reliable results especially in area-wide programs, and future applications should, therefore, be planned on a landscape level. Geographic information systems (GIS) make it possible to capture, organize and evaluate insect population data and to visualize spatial and temporal fluctuations on a regional scale. Geo-referenced insect monitoring data can, in addition be correlated with relevant parameters such as distribution of the crop and other vegetation, geography, climate, and insect control programs.

GISs are already in use, especially in forest insects, to document geographic variation, predict outbreaks, and to delimit invasive species (Tobin et al. 2004, 2007). The web adds yet another dimension to the analytical power of geographical information systems, as it provides worldwide connectivity. A web-based GIS permits one to quickly disseminate and share information, and it enables interactivity between end users, extension people, and researchers. A rigorous effort should be made to apply such techniques for landscape-level applications of semiochemical-based insect control.

Other Semiochemicals

Semiochemicals that attract insect females are tools for monitoring the occurrence and reproductive status of females. This is particularly important in species in which sexual communication relies on female-produced sex pheromones that attract only males. Moreover, some powerful annihilation strategies are based on female attractants (Table 3). Plant-derived chemicals also are known to improve attraction to pheromone lures (Giblin-Davis et al. 1996; Oehlschlager et al. 2002; Knight and Light 2005; Knight et al. 2005; Bengtsson et al. 2006; Schmidt-Büsser et al. 2009).

Even non-host volatiles may play a significant role in insect management, since some insects avoid volatiles of non-host plants. The know-how of negative plant volatile signals can be used to design push-pull techniques (Borden 1997; Zhang and Schlyter 2004; Cook et al. 2007).

Floral Compounds that Target Moths Floral scents play a key role in the coevolution of flowering plants and their pollinators (Raguso 2004; Bergström 2008). The bouquets of flowering plants, for example, Canada thistle and *Buddleja* butterfly bush, are strong attractants for Lepidoptera, Coleoptera, Diptera, and Hymenoptera (El-Sayed et al. 2008; Guedot et al. 2008). Synthetic floral attractants composed of phenylacetaldehyde and other volatiles, such as β-myrcene are known for several noctuid moths (Haynes et al. 1991; Heath et al. 1992; Landolt et al. 2006). Noctuids also respond to attractants that encode fermenting food sources, such as acetic acid and 3-methyl-1-butanol (Landolt and Alfaro 2001; Landolt et al. 2007).

A highly effective technique to control *Helicoverpa* spp. combines floral attractants and feeding stimulants with insecticide. The blend is sprayed on one out of 36 or 72 rows of a cotton field, thus minimizing the environmental

Table 3 Use of other semiochemicals in insect detection (D) and control by mass trapping (MT) and attract-and-kill (AK)

Species	Lure	Purpose	Region	Lures/year
Horticulture				
Mediterranean fruit fly *Ceratitis capitata*	Trimedlure	MT	Worldwide	3.000.000
Melon fly *Bactrocera cucurbitae*	Cue-lure	AK	South Asia, USA	300.000
Oriental fruit fly *Bactrocera dorsalis*	Methyl eugenol	AK	South Asia, USA	400.000
Agriculture				
Corn rootworm *Diabrotica spp.*[a]	Kairomone	AK	USA	40.000 ha
American bollworm *Helicoverpa armigera* [a]	Kairomone	AK	Australia	10.000 ha
Forestry				
Emerald ash borer *Agrilus planipennis*	Kairomone	D	USA	150.000
Medical entomology				
Sheep blowfly *Lucilia cuprina*	Kairomone	MT	Australia, South Africa	350.000
Tsetse fly, *Glossina pallidipes, G. morsitans morsitans*	Kairomone	AK	Southern Africa	–[b]
Bed bug, *Cimex lectularis*	Kairomone	D	USA, Canada, EU, Australia	50.000
Homes				
Social wasps	Food bait		USA, EU	–
Vinegar fly *Drosphila melanogaster*	Food bait		USA, EU	50.000

[a] Treated surface

[b] No data available

impact of the insecticide component. The attractant primarily targets female moths and removes them from the crop ecosystem prior to oviposition, showing that plant volatiles can be used to control insect populations (Del Socorro et al. 2003, 2010a, b; Gregg et al. 2010). The dispersal activity of insects, which is generally perceived as an obstacle for mating disruption and mass trapping, can be turned into an advantage when using female attractants.

This breakthrough development is based on a paradigm shift, since the attractant does not mimic a particular plant, it is instead a combination of compounds from several plants, producing a supernatural floral blend not found in nature (Del Socorro et al. 2003, 2010a, b; Gregg et al. 2010). Clearly, olfactory space would accommodate different floral attractants, since noctuid moths have been exposed to a changing guild of flowers during evolution. It is conceivable, given a more complete knowledge of olfactory receptor ligands, that such synthetic blends can be created also for other insect species.

Social Wasps Blends of acetic acid, with either butyl butyrate, heptyl butyrate, or isobutanol elicit food-finding behavior in a range of social wasps (Landolt et al. 2000). Lures for these wasps are widely distributed for the home and garden market (Table 3).

Corn Rootworms Diabroticine chrysomelid beetles evolved in the prairie ecosystem with larvae that feed on grass roots and adults that feed on vegetative parts of a broad range of plants, including maize. The western corn rootworm, *Diabrotica virgifera virgifera* is a species that is of particular concern in Europe, since it was introduced into the Balkans (Hummel 2003). Adult beetles are attracted to the volatiles of squash blossoms (Cucurbitaceae), and compulsive feeding and arrestment responses on cucurbit foliage are triggered by cucurbitacin secondary plant compounds (Metcalf et al. 1980). This behavior is exploited in the development of floral-baited traps for monitoring (Toth et al. 2007) and flowable and sprayable bait formulations that contain insecticides for area-wide management (Siegfried et al. 2004; French et al. 2007).

Emerald Ashborer The metallic and bright coloration of the elytra of jewel beetles (Buprestidae) points to the significance of visual cues in mate finding. However, host finding is likely mediated by olfactory cues, since many buprestids oviposit on stressed or dying trees. This has been demonstrated in the genus *Melanophila*, where females, which oviposit on wood of trees freshly killed by fire, can detect substances emitted in smoke from burning wood (Schütz et al. 1999).

The emerald ash borer is a rapidly spreading invasive species in the Eastern USA that kills ash trees. The cooperative emerald ash borer project includes a considerable trapping program (Table 3) for early detection in and around the Great Lakes district. Bark volatiles from green ash *Fraxinus pennsylvanica* contain a range of antennal active sesquiterpenes. Natural oil distillates, containing high concentrations of some of these ash volatiles, are currently used as a lure (Crook et al. 2008; Crook and Mastro 2010 this volume). Emerald ash borer trapping is another example of how even immature technology is adopted, due to the absence of other management tools.

Tsetse Flies African trypanosomiasis is transmitted by tsetse flies *Glossina* spp., that are obligate haematophages. The prospect of eradicating tsetse over large areas has appeared to be a serious possibility because of the development of cost-effective semiochemical-based control technologies, notably odor-baited targets that mimic host odor. The search for further host volatiles is ongoing (Harraca et al. 2009). The best known attractant identified from cattle volatiles and buffalo urine comprises a blend of 3-n-propyl phenol, 1-octen-3-ol, and 4-methylphenol (p-cresol), and a separate dispenser containing methyl ethyl ketone or acetone, (Bursell et al. 1988; Vale et al. 1988). Importantly, the odor-baited targets are treated with a fast acting insecticide, typically deltamethrin, and provide visual cues, typically colored in panels of blue and black, that attract and elicit landing in tsetse flies (Torr et al. 1997). There has been a steady increase in the use of odor-baited targets for mass trapping in Southern Africa, with a concomitant insecticide treatment of cattle. In Zimbabwe, an area-wide vector management program reduced typanosomiasis in cattle from several thousand cases per year to two in 1995 (Lindh et al. 2009; Torr et al. 2010).

Sheep Blowflies Australian sheep blowfly *Lucilia cuprina* and related species are potentially controlled by a rather selective synthetic kairomone attractant (Table 3). Insecticidal control is problematic, because of the demand for residue-free wool and the resistance of blowflies to many insecticides. Fly population changes also are driven largely by climate, rather than by biotic factors, and are expected to increase under likely scenarios of climate change (Goulson et al. 2005).

Traditionally, blowfly traps have been baited with liver and sodium sulfide, but a synthetic kairomone, consisting of 2-mercaptoethanol, indole, butanoic acid, and a sodium sulfide solution is far more effective and selective for *L. cuprina* than the standard liver attractant. More importantly, the synthetic mix can be packaged in controlled-release dispensers to generate constant, prolonged release of the attractant. Field studies have confirmed that kairomone traps are a useful component of a blowfly control program (Ward and Farrell 2003; Urech et al. 2004, 2009).

Outlook

Future applications of pheromones and other semiochemicals depend on the availability of odorants that enable efficient manipulation of mate- and host-finding behavior in insects and other animals. It is now within our reach to facilitate the discovery of relevant chemical signals with emerging molecular tools. An odorant binding protein recently has been used in a “reverse chemical ecology” approach to select oviposition attractant candidate compounds in a mosquito (Leal et al. 2008; Pickett et al. 2010 this volume). The next step towards identifying ligands of odorant receptors is to express them in heterologous cell systems for a high-throughput screening of candidate chemicals, by imaging or electrophysiological techniques (Wetzel et al. 2001; Hallem et al. 2006; Kiely et al. 2007). Another, complementary approach is to use structural chemistry software combined with statistical analyses and thus to calculate a physicochemical odor metric that predicts neuronal responses (Haddad et al. 2008). These methods are still in the experimental stage and classic chemical ecology research will meanwhile deliver results. Continued, goal-oriented research aimed at the identification of behaviorally relevant odorants will continue to bring forth novel insect control methods that contribute increasingly to food and environmental security.

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