

Pheromones - future techniques for insect control?

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Abstract: Four decades of pheromone research have provided the tools for environmentally safe control of insects through manipulation of male sexual behaviours. In Europe, disruption of mating by aerial dissemination of synthetic pheromones is used to control several economically important tortricids in orchards and vineyards on ca. 50 000 ha. In addition, attracticide lures have been developed for population control. The importance of pheromone-based methods is accentuated in view of increasing problems associated with the use of conventional insecticides. However, for a more widespread use of pheromones, application techniques must become more reliable and more economic. The key to further development is closer communication and collaboration between academic research institutions, plant protection industry and extension services.

Key words: sex pheromone, monitoring, mating disruption, attracticide

Introduction

"There are many reasons for using pheromones. One is that they are elegant." (Arn 1990). Pheromones are indeed elegant and safe tools for insect control. The fascination of being able to control insect populations through species-specific manipulation of sexual communication, without adversely affecting other, beneficial organisms, has been a driving force for research on insect pheromones during four decades.

The work done by chemists, biologists and plant protection experts has provided us with a solid knowledge of the chemistry and biology of the sex pheromones of many economically important insects. This know-how has been successfully used in some species, where people have gone beyond laboratory research and experimental trials and have established practical real-life applications which outcompete conventional insecticides.

The most important application technique for lepidopteran species is to permeate the atmosphere with synthetic pheromone, and to thereby prevent olfactory communication and mate-finding. Successful, area-wide applications of the mating disruption technique in Europe concern three lepidopteran insects from horticultural crops, codling moth *Cydia pomonella*, and the grape berry moths *Eupoecilia ambiguella* and *Lobesia botrana* (Ridgway et al. 1990, Witzgall and Arn 1997).

Will the use of pheromones expand in the future? Will established methods be used on a wider scale and will methods be developed against further insect species? An early and most successful development has been achieved with pink bollworm *Pectinophora gossypiella* - but the availability of Bt-transgenic cotton has led to a dramatic decrease in the use of pheromones (Jenkins 2002). In contrast, the surface treated by mating disruption against codling moth in the north-western United States increased from ca. 1.000 ha in 1991 to 9.000 ha in 1996 (Thom-

son 1997). What looked like a rather linear increase in 1996 then turned into an almost exponential increase - the area under mating disruption expanded to 45.000 ha in 2000 (Doerr and Brunner 2001, Brunner et al. 2002).

There is data in support of both pessimistic and optimistic projections into the future. The use of pheromone will continue to depend on cost and efficacy of pheromones vs. other methods. Failures of mating disruption at high population densities, elevated cost, and the occurrence of other insects which can only be controlled with insecticides are serious obstacles.

Only continued goal-oriented research will overcome these obstacles and lead to more reliable and more widespread applications. It is important to realize that all successful applications have been achieved through a combined effort made by researchers from universities, government institutions, extension services and the chemical industry. However, time is up for pheromone research at most academic institutions and the backup provided by research funded by the public hand will rapidly diminish. The future will tell whether chemical industries, plant protection sector and growers' associations are willing and able to continue the struggle.

Chances for success

Restrictions of insecticide use

Detrimental health effects, environmental issues, insect resistance, or marketing opportunities for organically-produced food are well-known arguments against the use of insecticides.

Increasing restrictions in the use of conventional insecticides in Europe further emphasize the need for new, environmentally safe methods of pest control. The "Environmental Action Programme" adopted by the European Union for the year 2000 aims at "*the significant reduction in pesticide use per unit of land under production, and conversion to methods of integrated pest control, at least in areas of importance for nature conservation*". The five-year-programs and resolutions adopted by European authorities are not always entirely realistic, but it remains a fact that a number of neuroactive insecticides have been or are being deregulated in several countries. In Germany, for example, the number of insecticides available for control of fruit insects has been decreasing steadily over the past decade, from 40 compounds in 1988 to 24 compounds in 1998 (Koch and Schietinger 1999).

Resistance against the available insecticides continues to be an important issue. In codling moth, for example, insecticide resistance is increasing all over Europe (Sauphanor & Bouvier 1995, Charmillot et al. 1999). In addition, it is a well-known fact that the overuse of insecticides induces outbreaks of secondary pests such as phytophagous mites, which are difficult to control with pesticides (Knisely and Swift 1972, Tanigoshi et al. 1983). Replacing insecticide with pheromone treatment against codling moth renders treatments against phytophagous mites superfluous, which, for example in South Tyrolian orchards, compensates for the cost of the pheromone treatment (Waldner 1997).

Insecticides do not work as well as often believed, and a long-term population decrease has never been achieved, not in any species. In comparison, a well-implemented mating disruption programme may clearly be more efficient than insecticides in some species. An observation shared by many working with mating disruption is that its long-term use results in continuously decreasing populations of the target species. This may be due to recovery of the beneficial insect fauna and an overall increasing stability of the orchard ecosystem.

Insecticide sprays harm the terrestrial and aquatic fauna. This is true even for chitin synthesis inhibitors, which have been long thought to be environmentally rather safe. In Scania (southern Sweden), the contamination of ground water resources with agrochemicals has risen to such a pitch that protected areas need to be established, where all use of insecticides is prohi-

bited in order to conserve drinking water resources. In such areas, farmers are forced by law to turn to organic production methods from one year to another.

It then is plain to see what we know, even though we are not always aware of it - that environmentally safe control methods are available only against a precious few insect species, and that biological control methods other than pheromones are often even more expensive or less reliable than pheromones. It then also becomes apparent that there is great potential in pheromone-based methods, once the "tools" have been developed properly. The tools are the knowledge of the pheromone chemistry and biology of a given species, economic synthesis, appropriate dispensers and the knowledge and experience of how to use them in the field. It was possible to elaborate pheromone-based methods against several species, and with the database on insect pheromones which is available today, it will certainly be possible to extend the use of pheromones to other species.

Economic aspects

The current conflict in Scania between cheap and rather efficient plant protection by insecticides and contamination of water resources by the same insecticides offers the trivial, but nevertheless important insight that the *price* of insecticides or pheromones should not be confounded with *economy of use*. Simple equations such as "insecticides are less expensive than pheromones - therefore, insecticide use is more economic" are no longer valid.

The economic importance of horticultural production in Scania is ever decreasing. More precisely: the revenue from the produced commodities is on the decline. As a result, the area covered by orchards has significantly decreased in the past decade. However, fruit production is, beyond fruit sales, of great significance for the attractiveness of this region. Tourism is an important source of income, as this is the case in other European fruit- and vine-growing regions. The farmer is becoming a landscape gardener and "landscape" is turning into "viewscape". A pleasant environment will not only attract tourists, but also new enterprises and investors, and people who wish to inhabitate this land. The character of the Scanian fruit-growing region will change and most likely suffer if the orchards are replaced with agricultural crops. This could accentuate already existing structural problems in this area.

Today, both the growers' economy and Scanian orchards are threatened by cheap fruit imports. At the same time, the consumer demand for unsprayed fruit has steadily increased over the past decade but cannot be met by the local production. A leading Swedish supermarket chain has based its marketing campaign on a green image, and all attempts to cut down on pesticide use receive much attention in local and national newsmedia. Employment of safe insect control techniques will improve fruit quality. This will be rewarded by the consumers and strengthen the competitiveness of local fruit production. The farmers' efforts to establish sustainable production methods will thus contribute to rural development.

Reasons for lack of success

Motivation

The main applications of the mating disruption technique in Europe are against codling moth on >10.000 ha and the grape berry moths on >30.000 ha (Arn and Louis 1996, Waldner 1997, Kast 2001, Zingg 2001). This clearly demonstrates the potential of the mating disruption technique for insect control and the figures are encouraging, until we take a closer look and realize that the area under mating disruption represents only a fraction of the several millions of hectares of European orchards and vineyards on which conventional insecticides are being used.

One reason for the comparatively limited use of mating disruption is that the technology currently in use must become more reliable. The most urgent shortcomings have been outlined in detail by many authors, and will be shortly mentioned below. However, one most important factor is certainly motivation and determination. A growers' association in Northern Italy has been determined to implement mating disruption against codling moth and has been successful (Waldner 1997). The conditions in Northern Italy for using pheromones are as favourable or poor as in most other European growing areas, but the main difference is that growers were determined to cut down insecticide use.

A similar situation is encountered with the grape berry moths. A significant part of German and Swiss vineyards are being treated with pheromones since many years (Kast 2001, Zingg 2001), but the river Rhine in Germany and the Jura mountains in Switzerland are natural borders for pheromone use. Admittedly, the climatic, economic and faunistic conditions may be less favourable for mating disruption in Southern European vineyards. However, pheromone use in grapes is rapidly increasing - in Northern Italy (Varner et al. 2001).

Motivation as a main factor for pheromone vs. insecticide use obviously concerns not only the farmers, but also researchers and chemical industries. Pheromone research, funded by the public hand over four decades, has provided the basic knowledge for the development of new pest control techniques. It is important to realize that only goal-oriented research will lead to reliable and more widespread applications. However, for many researchers at academic institutions it may instead be more rewarding to explore new directions and to point out the potential, future use of knowledge yet to be acquired. Some companies in the agrochemical sector may have used pheromones mainly as a public relation tool, whereas other chemical companies have made a most significant contribution to pheromone synthesis and dispenser systems. Work done by chemical companies was again driven by individuals motivated and determined to make pheromones work.

Integrated research

For future development, we must put stronger emphasis on a multidisciplinary approach. Clearly, there is a need for intensifying communication and collaboration, and for coordinating activities between academic research institutions, chemical industries and extension organizations. Insecticides are at least as complex chemicals as pheromones and they are difficult to formulate, market, and difficult to apply. However, in contrast to pheromones, the entire development, from research to application, is carefully planned and has often been done under one roof.

Already existing knowledge on pheromone technology can be contributed from various disciplines to achieve improvements or to rapidly establish new methods. Unfortunately, lab people all too often lack understanding for the difficulties associated with field implementation work. Chemical companies sometimes tend to believe that they "know all about pheromones" and that access to published information is sufficient. And farmers' organizations rarely manage to establish a dialogue with people from the academic circuit.

Summerfruit tortrix *Adoxophyes orana* is the most important leafroller moth in European orchards under mating disruption for codling moth and provides a good example of how people from different disciplines view the same problem and how lack of integration can become an important obstacle. A detailed account of female-produced compounds and their effect on male behaviours was published in 1986 by Guerin and coworkers, showing that the main pheromone compound of summerfruit tortrix is (Z)-9-tetradecenyl acetate and that it must be blended with additional minor pheromone compounds to attract males. Nonetheless, dispensers for summerfruit tortrix control were formulated to contain (Z)-11-tetradecenyl acetate (*e.g.* Neumann 1997, Rama 1997) and it comes to no surprise that satisfactory control was not achieved.

This explanation is brought forward by the author of this paper, who knows summerfruit tortrix only from lab rearings and wind tunnels. It takes field experience to realize that elevated population densities may be another cause for failures. Farmers tolerate high population levels of summerfruit tortrix, before populations further increase and start to cause damage. It may be impossible to control this species with pheromones once a certain population level has been attained, disregarding which pheromone blend is used (Charmillot *pers. comm.*, Neumann 1997).

The summerfruit tortrix reminds us that population biology rarely receives sufficient attention in mating disruption studies. Models on insect population dynamics have been elaborated during the seventies and eighties, and should always be incorporated into mating disruption studies. As long as population fluctuations are badly known, it is probably impossible to answer the question whether a full, partial or off-blend of pheromone chemicals is appropriate for summerfruit tortrix mating disruption.

Last not least, pheromone companies need to compete with the price of insecticides, and the amount of active ingredient or the number of compounds formulated in mating disruption dispensers is therefore critical. (Z)-11-tetradecenyl acetate is a pheromone component of many other leafrollers which are important especially in North America (Arn et al. 2000, Walker and Welter 2001) and this compound is easier to synthesize than (Z)-9-tetradecenyl acetate. It is obviously more economic to use one formulation all over and to include single compounds rather than complex blends into dispenser formulations.

Field implementation

Field implementation is the focal point of mating disruption research. All available knowledge of an insect's biology, its pheromone chemistry and biology, and dispenser technology needs to be integrated. Lack of success is often equivalent to lack of know-how, or the lack of knowledge transfer.

Heinrich Arn, the former convenor of the Pheromone Working Group, emphasized the need for field measurements on insect behaviour and pheromone dispersal as he coined the title of the the Neustadt meeting: "*Mating Disruption - The Behaviour of Moths and Molecules*" (Arn 1987). This meeting reflected the optimism that the necessary tools would soon be at hand. A quantum leap was then achieved by Uwe Koch and his working group, who managed to measure ambient pheromone concentrations using an insect antenna (Koch et al. 1992, 1997), and several behavioural studies, including work in field wind tunnels (Cardé et al. 1993, 1997), made a significant contribution to our understanding of insect behaviour in a pheromone-permeated atmosphere .

The optimistic attitude of the late eighties that collaboration between academic research and chemical industries would inevitably lead to the design of state-of-the-art mating disruption technology cooled off during the nineties. The 1994 meeting of our Working Group ran the provocative title "*The Wormy Apple Brainshop*", illustrating the general feeling that the methods available to study the behaviour of moths and molecules were all too often not taken into account when designing practical applications. Obviously, progress with optimizing dispenser density, dispenser load or the composition of the disruptant blend will be painstakingly slow as long as the "wormy apple" is our only bioassay. It goes without saying that a great many factors contribute to insect attack, many of which are not directly related to the efficacy of the mating disruption method.

A pessimistic and possibly somewhat arrogant point of view is that implementation of mating disruption relies even today largely on an empirical trial-and-error approach. Roger Bartell manifested in 1982 the need to study the "behavioural mechanisms underlying mating disruption". Despite numerous discussions and scientific publications devoted to this topic we still

cannot claim of having succeeded in deciphering these mechanisms or that we are taking advantage of the knowledge acquired. Let alone the fact that the study of insect behaviour in the field, including migration and dispersal, may simply be beyond our means, one may also argue that distinct mechanisms do not suffice to explain or describe the extremely heterogeneous and complex field situation (Bengtsson et al. 1994).

False trail following, i.e. male upwind orientation requires structured plumes and a pheromone blend which is attractive to the males. Camouflage of female-released plumes requires a homogenous and sufficiently concentrated pheromone cloud. Sensory overload requires that males are exposed long enough to large enough amounts of pheromone. All of these conditions may be met at the same time, in the same pheromone-treated orchard: structured plumes in the tree tops and along the borders, a thick and homogenous pheromone cloud within tree canopies in the centre of the orchard, and males with long-term exposure to pheromone vs. newly emerging or migrating, sensorily largely unaffected males. And, the situation will change as soon as dispenser density, dispenser load or the pheromone blend are modified.

Dispenser technology

The discussion above tacitly assumes dispenser technology as a constant. Pheromone synthesis, dispensers and dispenser application dictate the cost of mating disruption. Discussions of behavioural mechanisms may turn out to be futile if only we were able to afford or to achieve sufficiently high aerial pheromone concentrations.

Major achievements have been made with large-scale industrial synthesis of insect pheromones (e.g. Yamamoto and Ogawa 1989). It is important to realize that commercial use of codling moth mating disruption became possible only after economic synthesis of codlemone became available. The price for this compound has been diminished by a factor of 50 to 100 since the eighties.

A major flaw of currently used commercial pheromone dispensers is that they are "passive" and that pheromone release depends on ambient temperature. In Swedish apple orchards, ca. 90% of pheromone applied is released outside codling moth 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, while their release rates decrease during the season, as population densities start to increase (Ogawa 1997). These problems are circumvented by using active pheromone "puffers", releasing large amounts of pheromone when the insects are active (Shorey et al. 1996, Baker et al. 1997). However, their commercial use is still limited.

Hand-application of dispensers does not pose a problem in labour-intensive horticultural crops, but precludes the use of mating disruption in most field crops. The formulation of sprayable pheromone dispensers has been attempted in the past (Hall et al. 1982, Weatherston 1990), and is subject of recent efforts (Polavarapu et al. 2001).

Outlook

More reliable and economic applications of communication and mating disruption by pheromone can probably be achieved, and a more widespread use of this technology is not unlikely. Most technical difficulties can certainly be overcome, if progress with mating disruption is deemed useful and desirable, and if a joint effort is made by people from different disciplines and organizations.

A most important obstacle, however, will probably remain. Laboratory assays to predict the behavioural effect of field treatments with a particular dispenser formulation are not at hand.

Development of mating disruption technology still relies on repeated field trials and will therefore remain to be costly and slow. In addition, the focus of research in chemical ecology is turning away from lepidopteran pheromones and future improvements will increasingly depend on work done by commercial companies, extension services and farmers' associations.

A clear drawback of pheromone-based methods is that only male moth behaviours can be manipulated. This, and the considerable effort and cost associated with development of mating disruption stimulates current work on attracticides (Charmillot and Hofer 1997; Suckling et al. 1999). Attracticide lures can be optimized in laboratory windtunnel assays - a more attractive lure will show a better effect. Formulation of experimental dispensers requires comparatively small amounts of chemicals and can be done in any laboratory. Attracticide lures make it also possible to use attractants for egg-laying females. A volatile compound from pear has recently been shown to attract codling moth males and females (Light et al. 2001). Semiochemical-based methods directed at females are expected to become a most important complement to mating disruption.

Last not least, more emphasis should be placed on the integration of different biological control methods. Microbial pesticides and resistant plants can be used to reinforce the effect of behaviour-modifying chemicals. All biological methods are species-specific to varying degree and do not cover all insects associated with a crop. In addition, biological insect control methods produce rather subtle effects compared to conventional insecticides, which are lethal upon contact. Single biological control methods can therefore rarely replace insecticide treatments and the available biological tools should be developed as components of an integrated crop management programme, rather than as sole agents.

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