
GUEST EDITORIAL

Pheromones: will their promise in insect pest control ever be achieved?

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Do we need pheromones?

The demand is now greater than ever for new methods of pest control. One reason is the need to provide alternatives to pesticides where the development of resistance is preventing effective control. It is a serious mistake to assume that long term problems of resistance would be circumvented simply by devising approaches which involve new modes of action, or by employing chemical structures to which metabolic resistance has not yet developed. However, such novelty would provide valuable components of the Resistance Management Strategies now being investigated (Denholm, 1992). A further stimulus arises from the perception that the broad-spectrum eradicator pesticides in current use are highly hazardous to ourselves and the environment. Of course, science and technology must move forward, with every effort being made to develop more benign and efficient crop protection agents. Nonetheless, it would be quite wrong to imagine that crop protection would be made safer merely by deployment of natural products rather than synthetic ones. Of the pesticides that enter into our diet, Bruce Ames (1991) has calculated that at least 99.99% are natural compounds developed by plants to defend themselves against pests. Furthermore, many of these compounds would fail the rigorous toxicological testing for synthetic pesticides. Natural products can offer some advantages and where non-toxic modes of action are involved, as in the case of pheromones, then they would be expected to be more benign.

What are pheromones?

In terms of the scientific literature, pheromones are perhaps the best known of the behaviour-controlling chemicals, or semiochemicals. They act as chemical signals, often as packages of many compounds, between members of the same species. Other terms have to be used when different species are involved in the interaction:- allomones favour the emitting organism, kairomones favour the receiver, synomones favour both, and apneumones are released from non-living sources. Man himself is highly responsive to a tremendous range of semiochemicals including kairomones and apneumones arising from herbs and food plants. We still await confirmation of the existence of a human sex pheromone, even though commercial products are available for those, of both sexes, hoping to enhance their mate attraction. Although most animals and even some plants are known to respond to semiochemicals, it is only with relatively simple organisms that these signals can be used to effect behavioural changes. With the rapid growth in the identification of insect pheromones in the early 70s came very rash, but largely unfounded, claims for their potential, particularly in terms of their value in pest control. Sections of the agricultural industry and the public were led to believe that large scale replacement

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of pesticides would be possible through use of pheromones with which insects could be made 'to jump through hoops'. Unfortunately, such claims have remained largely unfulfilled, with the exception of certain lepidopteran sex attractant pheromones and aggregation pheromones of bark beetles (Ridgeway *et al.*, 1990). These can be used to catch insects for monitoring purposes and in some cases, mass trapping has been successful in controlling the pests. Another strategy, which has been particularly favoured for the lepidopteran sex attractants, is to use the pheromone or a closely related analogue to interfere with normal mate location. However, now that the demand for alternative pest control methods is so great, renewed efforts are providing fresh approaches that may allow these agents to achieve some of that originally claimed potential (Pickett *et al.* 1991). Nevertheless, the emphasis must be on 'some', because as argued in the previous guest editorial by Van Emden (*Bulletin of Entomological Research* 1991 Vol. 81(2), 123–126), control agents based on natural processes should be considered and used together with the other natural and artificial approaches available. One must also remember that pheromones alone will, like other biological agents, be insufficiently robust for the purpose of most agricultural production systems.

Pheromone-mediated behaviour as a component of insect chemical ecology

As realised by some of those involved in the early days of pheromone discovery, it is now becoming generally accepted that, for successful development, pheromones must be considered in combination with other behavioural cues and that, above all, a complete knowledge of the chemical ecology of the target pest is required. Insects interact with chemical signals in their environment by means of olfactory and gustatory sensilla or receptors on, for example, the antennae, mouthparts and tarsi. To identify the wide range of chemical stimuli that influence insect behaviour and interactions with their hosts, electrophysiological recordings from these sensilla, coupled with high resolution chromatography, play a vital role. Although further work is required on coupled gustatory studies, coupled analysis between the insect olfactory system and high resolution capillary column gas chromatography (GC) is now well developed. The electroantennogram, comprising a recording from the whole antenna, has been employed for a number of years, but this technique is now augmented by recordings from antennal sensilla, and even from single nerve cells within the sensilla (Wadhams, 1990). In addition, by using these techniques to analyse samples that closely represent the composition of the natural stimuli, their rôle and behavioural importance can be inferred. Entrainment onto a porous polymer of volatile components released from intact animals or plants has proved invaluable in providing appropriate samples. This type of strategic identification work is thereby of considerable value in reducing the number of behavioural studies required and allows efforts to be directed towards more sophisticated studies and simulated field experiments and field trials.

Pest control strategies incorporating pheromones

As pheromones and additional semiochemical components of insect chemical ecology are identified, their use must be integrated with other approaches, and in particular biological control. Although semiochemicals have long been seen as components of integrated pest management, this has rarely been exploited. The integration of these approaches should follow the semiochemical development programme, and not simply involve combining separately evolved systems at the end.

Strategies for employing semiochemicals in pest control should initially include monitoring systems to indicate the presence or population density of the pest. At the next stage, pest and disease resistant crop cultivars and deterrent semiochemicals would be used to decrease pest numbers within the crop. At the same time, semiochemicals would be employed to cause aggregation on trap crops chosen for their attractiveness to the pest. On the trap crop, highly selective pesticides or biological agents should be deployed and this combined approach allows slow-acting control agents to be used. For certain crop pests, and also for vectors of human and animal diseases, semiochemicals can be used as lures at sites where biological agents can most effectively survive. The general

approach of using semiochemicals to decrease colonisation on the crop or the part of the crop to be harvested, and causing aggregation on a trap crop or on part of the plant of little value, has been called the push-pull or stimulo-deterrent diversionary strategy (SDDS) (Miller & Cowles, 1990). This is being investigated by our laboratory in a number of ways, but particularly for a range of pests attacking oilseed rape (*Brassica napus*), a crop now very prevalent in temperate Europe. Already, components of SDDS have been shown to work: for example, plant-derived antifeedants have been used in simulated field trials to protect the upper parts of the plant, allowing slow destruction of the pest by an insect growth regulator applied deeper within the canopy. In addition, application of the analytical approaches described above to the study of aphid chemical ecology is giving rise to a comprehensive range of semiochemicals for use against these insects at the various vulnerable stages of their life cycle (Dawson *et al.*, 1990).

Advantages as natural products

Merely by being natural products, pheromones must not automatically be expected to be intrinsically safer, but as their mode of action does not involve a toxic effect, there is a high probability that these compounds would be more benign. Nonetheless, synthetic pheromones will be subject to registrations and control, as are pesticides.

There are advantages that pheromones have as natural products: since pheromones and other semiochemicals are produced by naturally existing biosynthetic pathways, in the long term there are prospects for use of molecular biology in their development for crop protection. Semiochemicals are often secondary plant metabolites or closely related compounds, and although many practical difficulties have still to be overcome, crop plant secondary metabolism could be modified through genetic manipulation to produce semiochemicals useful in new control strategies. The wild predecessors of crop plants defended themselves against insect herbivores by a variety of mechanisms, but defence based on secondary metabolism in particular has been sacrificed in order to obtain high-yielding cultivars and highly nutritional plant produce. With the advent of growth stage and tissue specific gene expression, it may be possible to exploit further the secondary metabolism already present in the plant or to incorporate alien genes from other plant or even animal sources. Secondary metabolites are the products of a series of enzymes but, in some plants, it is possible to identify existing pathways which could provide valuable semiochemicals after incorporation of one or a limited number of enzymes from another organism. To this end, the enzymology of cyclases that provide the basic structure for certain terpenoid antifeedants and pheromones is under investigation. Other targets include the desaturase enzymes involved in the biosynthesis of lepidopteran sex attractant pheromones, and the strategic modification of biosynthetic pathways already present in crop plants to provide protection against pests and diseases, particularly of oilseed rape (Dawson *et al.*, 1989).

Conclusions

With new techniques for identifying the full range of compounds mediating pest behaviour and interactions with the host, and with new truly integrated approaches to semiochemical usage such as the SDDS, demands for alternative methods of pest control could be met. This prospect is considerably enhanced by the rapidly developing techniques of molecular biology. Currently, most effort is directed at pests of agriculture, but these strategies could be equally well applied to the control of insects vectoring diseases of man and his animals.

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