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Production of behaviour-controlling chemicals by crop plants

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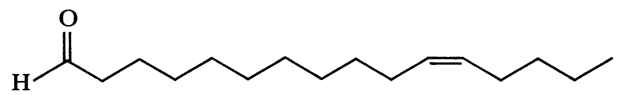
The possibilities of breeding crop plants that produce insect pheromones and other behaviour-controlling chemicals and of obtaining antifeedants from natural sources for protection against invertebrate pests are discussed. The possible role of genetic manipulation in these approaches to crop protection is also considered.

Introduction

Future developments in protection of crops against damage by invertebrate pests will involve integrating the use of pesticides with other control strategies that use behaviour-controlling chemicals, biological agents or pest-resistant crop plants. This will lead to safer and more effective crop protection procedures and is necessary to overcome the rapid development of pesticide resistance and to accommodate increased concern for the environment. However, many problems must be solved before integrated régimes achieve wide agricultural use.

Pheromones

Behaviour-controlling chemicals can be highly potent. For example, 10 μg of the synthetic diamondback moth (*Plutella xylostella*) sex attractant pheromone (compounds **1** and **2**), slowly released from a polythene closure, is highly attractive for over two weeks and can be used to lure the moths into sticky traps (Rothamsted 1979). However, because of chemical instability and high volatility, synthetic pheromones are difficult to use directly on crops and attempts are being made to develop special formulation (Hall *et al.* 1982) or chemical precursors called propheromones (Pickett *et al.* 1984).



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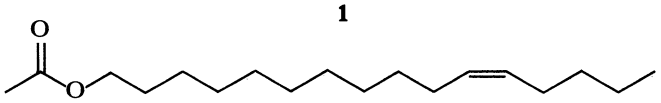

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Pheromones used by invertebrate pests can be closely related or even identical to secondary plant substances. The aphid alarm pheromone, which causes rapid dispersal when aphids are attacked, is for most species the sesquiterpene hydrocarbon (*E*)-β-farnesene (**3**). Synthetic (*E*)-β-farnesene can be used to improve the effectiveness of contact insecticides, but is too volatile and unstable for long-term protection of plants (Griffiths & Pickett 1980). Although (*E*)-β-farnesene occurs commonly in plants it does not generally interfere with colonization by

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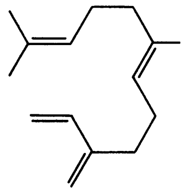

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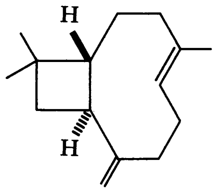

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aphids. It was thought that the aphids could not detect (*E*)-β-farnesene within the plant, but an alternative explanation is now being advanced. In plants, the biosynthesis of (*E*)-β-farnesene from farnesyl pyrophosphate is accompanied by cyclization of the farnesyl carbenium ion to give other sesquiterpenes including (−)-β-caryophyllene (**4**), which we have shown to be a potent inhibitor of the alarm pheromone activity of (*E*)-β-farnesene (Dawson *et al.* 1984). However, this problem has been overcome in the wild potato *Solanum berthaultii*, a close relative of the commercial potato *Solanum tuberosum*, which releases (*E*)-β- farnesene from glandular hairs on its leaves in such a way as to alarm the aphids (Gibson & Pickett 1983) and prevent colonization. Already at the Plant Breeding Institute in Cambridge there has been some success in crossing the two species. Thus, production of the aphid alarm pheromone by commercial potatoes for protection against aphid-mediated damage is a realistic objective.

Attractants and repellents

Secondary plant substances can affect the behaviour of invertebrate pests in other ways. Some compounds attract herbivores such as slugs (Pickett & Stephenson 1980) and crop plants could be bred to produce lower levels of these kairomones. Alternatively, plants bred to release higher levels could be used to attract pests away from a commercial crop. There are also secondary plant substances that benefit the plant, and these allomones present more promise. Plant allomones include compounds that attract pollinators and other beneficial invertebrates, such as predators and parasitoids of insect pests. Certain *Aphidius* wasps, useful as parasitoids of aphids, can be attracted to infestations by volatiles released from crop plants (Powell & Zhang 1983).

Antifeedants

Many plants produce allomones that prevent feeding by herbivores. Brassicas produce mustard oils, mostly comprising organic isothiocyanates (e.g. allyl isothiocyanate, **5**) that act as antifeedants; oilseed rape (*Brassica rapae*) cultivars low in the glucosinolate precursors (e.g. sinigrin, **6**) are more readily eaten by a range of herbivorous animals. Other antifeedants include some polyphenolic compounds commonly found in plants. However, both these and the isothiocyanates are only weakly active and to protect crops would have to be used at the level of tonnes per hectare. But some plants produce highly potent antifeedants; one of the best known is obtained from the nuts of the neem tree (*Azadirachta indica*), which contain several limonoid tetranortriterpenoids including azadirachtin (**7**), active against larvae of Lepidoptera down to parts per million (Zanno *et al.* 1975). This molecule is too complicated for economic synthesis, but numerous laboratories are investigating the agricultural use of crude neem extracts and limonoids obtained from the neem tree and from some other trees of the

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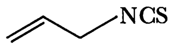

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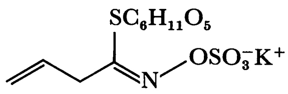

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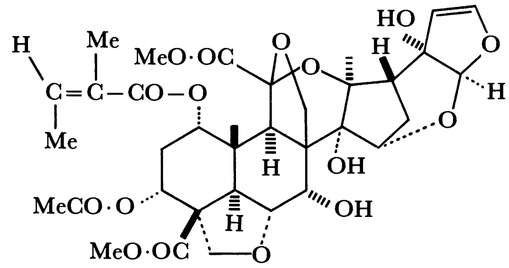

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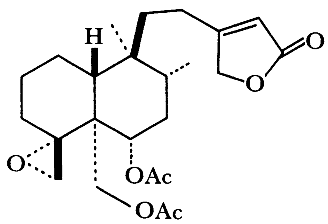
Meliaceae, for example, *Melia azedarach*. An alternative to direct natural production of azadirachtin is to modify plant-derived compounds that are chemically more readily available. The limonoid bitters produced as a by-product from citrus fruits may provide such a starting material.

Other potent antifeedants have less complicated structures and are more accessible by synthesis. Ajugarin 1 (**8**), an oxygenated clerodane from *Ajuga remota*, has recently been synthesized for the first time at Imperial College, London by Ley *et al.* (1983). Although the route is unlikely to allow commercial synthesis, it does facilitate structure-activity studies to identify the structural requirements for this type of antifeedant. One of the most simple and yet most active antifeedant molecules is (−)-polygodial (**9**) from marsh pepper (*Polygonum hydropiper*) (Nakanishi & Kubo 1977). Plants treated in the laboratory with (−)-polygodial



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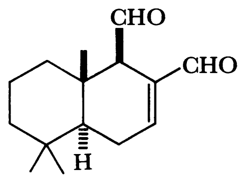

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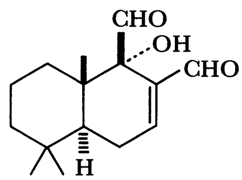

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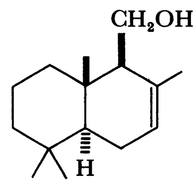

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resist colonization by aphids, including those highly resistant to conventional insecticides. Also, infection by plant-virus diseases is substantially lowered by treatments equivalent to only tens of grams per hectare, even when transmission takes place in seconds as with potato virus *Y* (Gibson *et al.* 1982). Again, Ley's group has provided an excellent synthetic route but the racemic product is highly phytotoxic. At Rothamsted we have recently succeeded in resolving this mixture and have shown that a 0.01 % solution of the (+)-isomer causes considerable leaf damage. The resolution is extremely laborious and traces of the (+)-isomer remaining with the resolved natural isomer still give some leaf damage. Therefore, the plant-derived material is at present of greater value for agricultural development. Workers at the Royal Botanic Gardens, Kew, are studying germination of seeds gathered from wild plants and C. J. W. Brooks's group at the University of Glasgow is looking for ways of increasing the yield from plant material. Again, an alternative to production by the parent plant is to obtain polygodial as the correct optical isomer by modification of a natural and more abundant precursor. Recently the related antifeedant warburganal (**10**) has been synthesized in a few simple steps from (−)-drimenol (**11**) (Ley 1985), which is readily available from the tree *Drimys winteri* (Appel *et al.* 1959).

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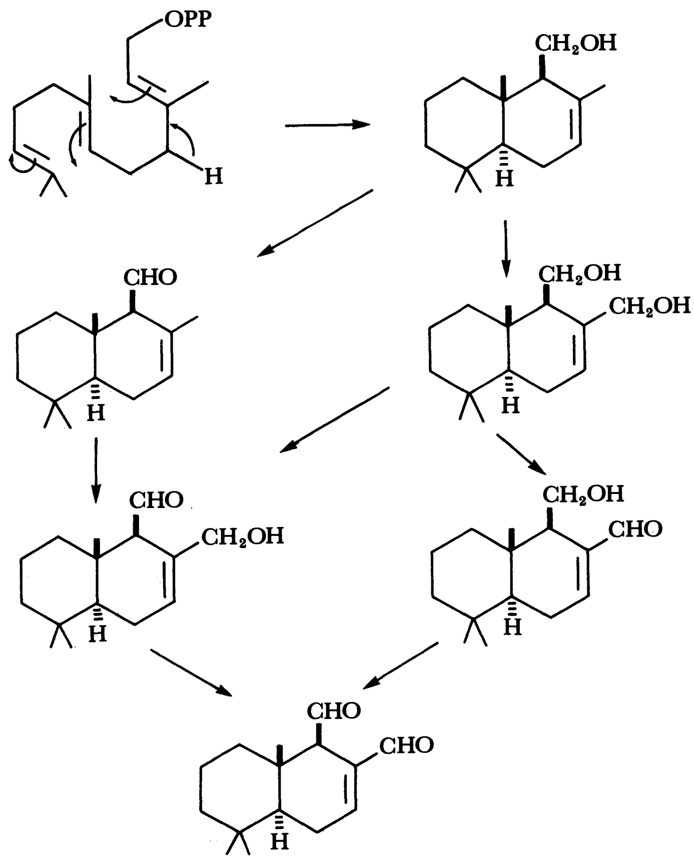
Genetic manipulation

Earlier paragraphs have outlined the potential for modifying the production of behaviourally active secondary plant substances in crops by plant breeding programmes and of cultivating a new generation of crop plants to provide antifeedants and other behaviour-controlling chemicals for use in agriculture. However, the rapid developments in genetic manipulation of plants mean that a synthesis of the two approaches can be considered. Thus, crop plants may in the future be genetically modified to produce new behaviour-controlling chemicals for their own protection. Schneidermann (1984) has suggested that production by plants of insecticides similar to those synthesized commercially is unlikely, but that genetic manipulation of plants to produce the entomophagous peptides employed by fungal insect pathogens is possible. A disadvantage of this approach is that such compounds are metabolically unstable and are unlikely to reach the site of action. However, genetic manipulation of crop plants to produce beneficially active secondary plant substances is potentially more valuable because, although these compounds are not direct gene products, their biosynthesis is often relatively simple and employs precursors found abundantly in most plants. The biosynthesis of (–)-polygodial, although not fully elucidated, formally involves the oxidation of (–)-drimenol, which may be obtained in one step by the cyclization of the ubiquitous farnesyl pyrophosphate and may involve relatively few enzymically controlled steps (scheme 1).



Scheme 1. Proposed biosynthetic route from farnesyl pyrophosphate to polygodial.

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Conclusions

For the future, production of behaviour-controlling chemicals by crop plants seems feasible and with developments in genetic manipulation may give better and safer protection of crop plants against damage by invertebrate pests. Furthermore, such advances in the management of pests and biological control agents by means of behaviour-controlling chemicals produced by crop plants would place the development of pest-resistant crop plants on a more rational basis and would thus fully integrate the three alternative approaches to crop protection mentioned at the beginning of this discussion.

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