PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Integrating Use of Beneficial Organisms with Chemical Crop Protection [and Discussion]

J. A. Pickett, L. P. J. J. Noldus, I. Harpaz, J. M. Franz, J. K. Wage, M. J. Way, P. T. Haskell and H. F. van Emden

Phil. Trans. R. Soc. Lond. B 1988 **318**, 203-211
doi: 10.1098/rstb.1988.0005

Phil. Trans. R. Soc. Lond. B **318**, 203–211 (1988)
Printed in Great Britain

Integrating use of beneficial organisms with chemical crop protection

By J. A. Pickett

AFRC Institute of Arable Crops Research, Rothamsted Experimental Station, Harpenden, Hertfordshire AL5 2JQ, U.K.

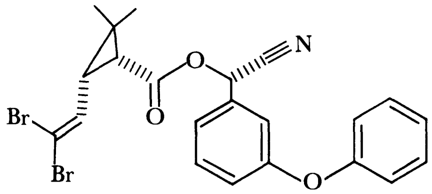
The selectivity of insecticides, particularly of pyrethroids, is described and possibilities are proposed for further development of selectivity. The production of beneficial organisms resistant to pesticides by techniques including genetic manipulation is discussed. Preliminary studies on the use of semiochemicals to improve the efficiency of entomophagous pathogens in controlling pest infestations, and for monitoring and manipulating populations of beneficial insects, are described. The prospects for genetic manipulation of crop plants to improve predation and parasitism of pests are also discussed.

Introduction

Although broad-spectrum pesticides are likely to remain the major means of crop protection for the next 15 years (Finney 1986), increased use of biological agents will be necessary to overcome problems of pesticide resistance and to reduce possible hazards to the environment. For the most part, more efficient use of biological agents will involve protecting and manipulating the natural populations of beneficial insects and pathogens of pests. This will necessitate improving the selectivity of chemical crop protection agents between pests and beneficial organisms and devising ways of manipulating beneficial organisms to enable them to function more effectively.

Selectivity of insecticides

Four main groups of insecticides are currently used in crop protection: the organochlorines, organophosphates, carbamates and pyrethroids. The pyrethroids are quickly replacing the earlier groups, and the more recent ones are generally the most selective in terms of relative activity between pest and beneficial organism. One of the most selective and yet most active is deltamethrin (**1**) (Elliott *et al.* 1974), and early bioassay studies using house flies and honey



1. Deltamethrin.

bees show the improvement in relative toxicity as successive pyrethroids were discovered (table 1) (Smart & Stevenson 1982). This difference in relative toxicity was subsequently found to be true for a moth and its parasite: for deltamethrin, the relative toxicity to the lepidopteran pest *Ephestia kuhniella* and its hymenopteran parasite *Venturia canescens* is 12:1 (Elliott *et al.* 1983). In the case of the predatory lacewing *Chrysoperla carnea*, the ability to hydrolyse pyrethroids selectively (Bashir & Crowder 1983) confers a considerable advantage over aphid pests, and makes these insecticides very much more selective than most organophosphorus compounds (table 2) (Stevenson *et al.* 1984). In the field, the pyrethroid cypermethrin causes less damage to hymenopteran aphid parasitoids than the organophosphorus compound, demeton-S-methyl (figure 1) (L. E. Smart, J. H. Stevenson &

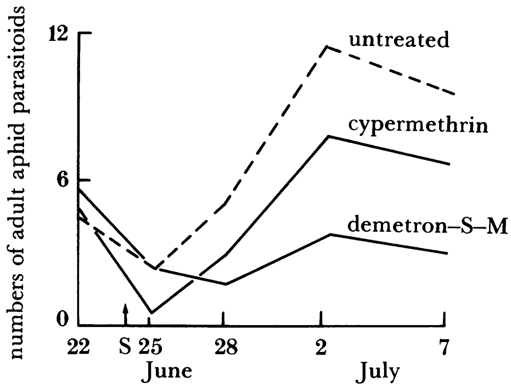


FIGURE 1. Numbers of adult aphid parasitoids caught by suction sampler, before and after insecticide application. (S = date of application.)

TABLE 1. TOXICITY OF PYRETHROIDS TO PEST AND BENEFICIAL INSECTS

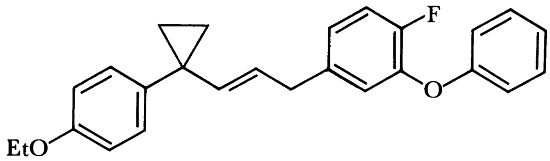
pyrethroid	discovery date	relative toxicity: house fly	relative toxicity: honey bee
bioresmethrin	1967	100	100
permethrin	1973	60	5
deltamethrin	1974	1700	11

TABLE 2. TOXICITY OF INSECTICIDES TO AN APHID AND ITS PREDATOR

insecticide	LD_{50} micrograms per insect: *Myzus persicae* (adult apterae)	LD_{50} micrograms per insect: *Chrysoperla carnae* (2nd-instar larvae)	approximate selectivity factor
demeton-S-methyl	0.0011	0.045	10
permethrin	0.00037	0.077	40
cypermethrin	0.000085	0.039	100
deltamethrin	0.0000038	0.029	1500

J. H. H. Walters, unpublished results), and a mustard crop sprayed with deltamethrin produced only 127 dead honey bees compared with 2968 dead bees when the crop was sprayed with the organophosphorus compound, dimethoate, even though active foraging continued (Garnier & Baumeister 1985). Further modification to the pyrethroid molecule, for example **2** (NRDC 200 (Elliott 1985)), may give even more selective compounds in this group.

Of the wide range of other insecticides now finding minor use or under development, several show promise for selectivity. For example, the formamidines and acylureas can be less toxic to



2

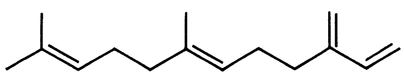
beneficial insects than most conventional insecticides, and although only in restricted use, the juvenoids and *Bacillus thuringiensis* endotoxins are highly selective in their activity. As these endotoxins are naturally occurring proteins, they can be targets for genetic manipulation studies resulting, for example, in crop plants that produce these materials in their leaves as a defence against chewing insects (Schell 1986). Highly selective, new insecticides may also be developed from the study of insect neuropeptides. These substances are effective at extremely low levels (less than 10^{-10} M) and are involved in the regulation of muscle, endocrine and metabolic activity, e.g. the muscle neurotransmitter proctolin and the adipokinetic hormone (AKH) (Menn & Henrick 1985). The baculoviruses currently being developed as biological control agents (Payne, this symposium) could be genetically modified to produce such neuropeptides within the target organism. The resulting disruption of the processes on which they act could have a more immediate effect than the gradual destruction caused by infection with the natural baculovirus.

Pesticide resistance in beneficial organisms

Pesticide resistance is currently causing considerable concern in agriculture (Jackson 1986). However, if this resistance could be transferred to beneficial organisms, the advantages would be substantial. Some work has been done in selecting insecticide-resistant beneficial organisms (Croft & Morse 1979) and, as has been mentioned above, the lacewing *Chrysoperla carnea* is inherently tolerant to certain insecticides. Already, resistance genes from pest species have been, or are being, cloned, such as the genes responsible for producing high levels of detoxifying esterases in mosquitoes (Mouchès *et al.* 1986) and in aphids (Devonshire *et al.* 1986). Although it is not yet possible to transfer these genes into beneficial insects, the notable success with the transposable P elements in *Drosophila* (Rubin 1985) suggests that this will become feasible.

Semiochemicals to improve the efficiency of entomophagous pathogens

Semiochemicals (behaviour-controlling chemicals) such as the insect pheromones are already being developed for use in agriculture (Pickett 1984). These materials, by influencing the movement of pest organisms, may be used to bring them more efficiently into contact with biological control agents such as the spores of entomophagous fungal pathogens. Pathogens such as *Verticillium lecanii* are employed against resistant aphids in glasshouses in the U.K., but it is extremely important that the spores are picked up by the pest during the brief period in which they remain viable. The aphid alarm pheromone, (*E*)-β-farnesene (**3**) which



3. (*E*)-β-farnesene.

causes dispersal of aphids when they are attacked, can improve pick-up of *V. lecanii* spores by increasing aphid mobility: on plots which were untreated, treated with *V. lecanii*, and treated with *V. lecanii* plus pheromone, numbers of live aphids remaining were in the ratio 9:3:1 (Hockland *et al.* 1986). Attempts are being made to develop another fungal pathogen, *Erynia neoaphidis*, for use against aphids on arable crops (Wilding 1983) and preliminary laboratory results have shown that the alarm pheromone is again successful in improving the infection of aphids with this organism (N. Wilding, personal communication). The sex attractant pheromones of moths are currently being used commercially to control populations of pest species by interfering with mating (Reece 1985). An alternative use of these sex pheromones would be to attract moths to a source of an entomophagous pathogen held in the protected environment of a trap so that the moths, after becoming infected, could transfer the pathogen throughout the rest of the population during their normal mating and aggregation behaviour (E. D. M. Macaulay, personal communication).

Semiochemicals for monitoring beneficial insects

Although natural predator and parasitoid populations can be responsible for controlling pest infestations, their effects are erratic. However, with accurate monitoring of these populations, their value could be estimated and insecticide treatments planned accordingly. Semiochemicals such as aggregation pheromones could prove invaluable in providing accurate monitoring systems. The identification of such pheromones in the case of coleopteran pests has proved relatively simple, for example, the recent identification of the aggregation pheromone of the pea and bean weevil, *Sitona lineatus* (Blight *et al.* 1984). There is therefore considerable promise for use of aggregation pheromones to monitor beneficial coleopteran insects. Also, many hymenopteran parasitoids are attracted to plant compounds, and respond to oviposition stimulants and attractants produced by their host organisms (Powell & Zhang 1983; Decker & Powell 1985), which could provide the basis for monitoring systems.

Manipulation of beneficial insects by semiochemicals

Honey bees are valuable pollinators of crops and their behaviour is readily manipulated by pheromones; for example, the recently characterized Nasonov pheromone (Pickett *et al.* 1980) can be used to attract honey bees to flowers (Williams *et al.* 1981) and could be used to attract them away from crops being sprayed with insecticide; also, it has been shown that the sting gland and mandibular gland pheromones of the honey bee, which contain isopentyl acetate and 2-heptanone respectively, can act as repellents when applied to food sources (Ferguson & Free 1979). Oil-seed rape treated with a slow release formulation of this chemical attracts fewer foraging honey bees, but the effect is short-lived (table 3) (Free *et al.* 1985). However, by producing precursors that release the active material in sunlight, when honey bees are foraging, more persistence may be obtained (scheme 1) (Liu *et al.* 1984). Such materials could then be formulated with an insecticide to reduce hazard to foraging honey bees.

Hymenopterous parasitoids of aphids such as *Aphidius* spp. are known to make a significant contribution to the control of cereal aphid populations in certain conditions (Powell 1986). As parasitism by *Aphidius* has most impact early in the year, when parasitoid:aphid ratios are large, the aphid–host and plant attractants mentioned above may be useful in attracting and

BIOLOGICAL SCIENCES THE ROYAL SOCIETY PHILOSOPHICAL TRANSACTIONS OF

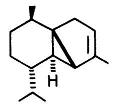
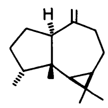
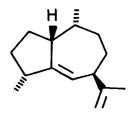
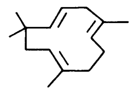
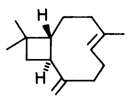
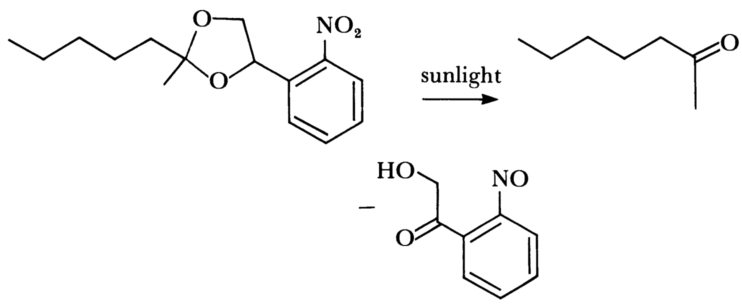
sesquiterpene	relative concentration (EBF=1)	difference from control (EBF alone) P
 (−)-α-cubebene	30	not active
 (+)-aromadendrene	30	not active
 (+)-γ-gurgunene	3	<0.01
 α-humulene	3	<0.01
 (−)-β-caryophyllene	0.03	<0.05

FIGURE 2. Inhibition of aphid alarm pheromone activity: lowest relative concentration of some hop sesquiterpenes causing inhibition of activity of (*E*)-β-farnesene (EBF).



SCHEME 1

TABLE 3. REDUCTION IN NUMBERS OF HONEY BEES FORAGING ON RAPE AFTER TREATMENT WITH THE PHEROMONAL REPELLENTS, ISOPENTYL ACETATE AND 2-HEPTANONE

time after treatment min	reduction in no. of bees relative to untreated plots (%)
0–30	85
36–60	67
60–90	34

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

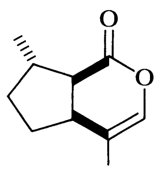
retaining parasitoids in the crop at the most strategic stage. The aphid alarm pheromone, (*E*)-β-farnesene, is a component of hop plants, which are readily colonized by aphids. In investigating this anomaly, it was discovered that a series of related sesquiterpenes present in plants (figure 2) acted as inhibitors of the pheromone, thus allowing aphids to colonize plants that contained (*E*)-β-farnesene (Dawson *et al.* 1984). Many plants contain this compound, although at lower levels than found in hops, and usually it is associated with a larger amount of β-caryophyllene, the most active inhibitory compound (figure 2). Thus air from above the leaves of certain plants, particularly potatoes and hops, prevents aphids responding to (*E*)-β-farnesene (Pickett *et al.* 1984). Under laboratory conditions, β-caryophyllene is also shown to lower the dispersal of aphids, when attacked by the predator *Chrysoperla carnea*, by about 50%. This compound could therefore be applied directly to crops to improve predation of aphids.

Genetic manipulation of crop plants to improve predation of pests

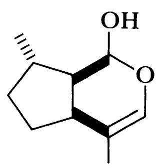
Because β-caryophyllene is produced by many plants, it may be possible, by employing plant breeding programmes or genetic modifications, to enhance production of this compound in crop plants. This may improve predation of aphids by reducing their dispersal. β-Caryophyllene is also an attractant for predatory lacewings (Flint *et al.* 1979), so could be used to increase numbers of predators on the crop.

Some predators and parasitoids locate their insect hosts by detecting compounds released from plants during feeding by the pests. It is possible that crop plants could be genetically manipulated to produce more of these compounds without the need for prior damage. This might attract predators and parasitoids into the crop at a more timely stage.

The sex pheromone for a number of aphids has recently been shown to comprise two compounds, the nepetalactone (**4**) and the nepetalactol (**5**) (Dawson *et al.* 1987). This



4. Nepetalactone.



5. Nepetalactol.

pheromone is responsible for attracting males to females on the primary or winter host. These compounds are closely related to known lacewing attractants (Sakan *et al.* 1970), and may act as kairomones in enabling lacewings to locate populations of aphids during periods when these are scarce. Because these compounds are also produced in plants, particularly those in the *Nepeta* genus, the possibility exists for transferring genes into crop plants to attract lacewing predators.

References

Bashir, N. H. H. & Crowder, L. A. 1983 Mechanisms of permethrin tolerance in the common green lacewing (Neuroptera: Chrysopidae). *J. econ. Entomol.* **76**, 407–409.

Blight, M. M., Pickett, J. A., Smith, M. C. & Wadhams, L. J. 1984 An aggregation pheromone of *Sitona lineatus*. *Naturwissenschaften* **71** *S*, 480.

Croft, B. A. & Morse, J. G. 1979 Research advances on pesticide resistance in natural enemies. *Entomophaga* **24**, 3–11.

Dawson, G. W., Griffiths, D. C., Pickett, J. A., Smith, M. C. & Woodcock, C. M. 1984 Natural inhibition of the aphid alarm pheromone. *Entomologia exp. appl.* **36**, 197–199.

Dawson, G. W., Griffiths, D. C., Janes, N. F., Mudd, A., Pickett, J. A., Wadhams, L. J. & Woodcock, C. M. 1987 Identification of an aphid sex pheromone. *Nature, Lond.* **325**, 614–616.

Decker, U. M. & Powell, W. 1985 *Rothamsted report for 1985*, 96–97.

Devonshire, A. L., Searle, L. M. & Moores, G. D. 1986 Quantitative and qualitative variation in the mRNA for carboxylesterases in insecticide-susceptible and resistant *Myzus persicae* (Sulz). *Insect Biochem.* **16**, 659–665.

Elliott, M., Farnham, A. W., Janes, N. F., Needham, P. H. & Pulman, D. A. 1974 Synthetic insecticide with a new order of activity. *Nature, Lond.* **248**, 710–711.

Elliott, M., Janes, N. F., Stevenson, J. H. & Walters, J. H. H. 1983 Insecticidal activity of the pyrethrins and related compounds. Part XIV. Selectivity of pyrethroid insecticides between *Ephestia kuhniella* and its parasite *Venturia canescens*. *Pestic. Sci.* **14**, 423–426.

Elliott, M. 1985 Lipophilic insect control agents. In *Recent advances in the chemistry of insect control, Royal Society of Chemistry monograph* (ed. N. F. Janes), pp. 73–102. London: Royal Society of Chemistry.

Ferguson, A. W. & Free, J. B. 1979 Production of a forage marking pheromone by the honeybee. *J. Apicult. Res.* **18**, 128–135.

Finney, J. 1986 The future of the pesticide industry. Paper presented at SCI Meeting 'Novel Approaches in Agrochemical Research', December 1986.

Flint, H. M., Salter, S. S. & Walters, S. 1979 Caryophyllene: an attractant for the green lacewing. *Envir. Ent.* **8**, 1123–1125.

Free, J. B., Pickett, J. A., Ferguson, A. W., Simpkins, J. R. & Smith, M. C. 1985 Repelling foraging honeybees with alarm pheromones. *J. agric. Sci., Camb.* **105**, 255–260.

Garnier, P. & Baumeister, R. 1985 Results obtained in France in 1983 and 1984 in the experimentation on bees with *Decis* on cereals and crucifers. In *International Commission for Bee Botany report: Third symposium on the harmonization of methods for testing the toxicity of pesticides to bees, March 1985*, A17. 1–2.

Hockland, S. H., Dawson, G. W., Griffiths, D. C., Marples, B., Pickett, J. A. & Woodcock, C. M. 1986 The use of aphid alarm pheromone (*E*-β-farnesene) to increase effectiveness of the entomophilic fungus *Verticillium lecanii* in controlling aphids on chrysanthemums under glass. In *Fundamental and applied aspects of invertebrate pathology* (ed. R. A. Samson, J. M. Vlak & D. Peters), Wageningen: Foundation of the Fourth International Colloquium of Invertebrate Pathology, pp. 252.

Jackson, G. J. 1986 Insecticide resistance – what is industry doing about it? In *Proceedings of the British Crop Protection Conference – Pests and Diseases*, pp. 943–949. Croydon: BCPC Publications.

Liu, X., Macaulay, E. D. M. & Pickett, J. A. 1984 Propheromones that release pheromonal carbonyl compounds in light. *J. chem. Ecol.* **10**, 809–822.

Menn, J. J. & Henrick, C. A. 1985 Newer chemicals for insect control. In *Agricultural chemicals of the future* (*BARC symposium 8*) (ed. J. L. Hilton), pp. 247–265. Totowa: Rowman & Allanheld.

Mouchès, C., Pasteur, N., Bergé, J. B., Hyrien, O., Raymond, M., Vincent, B. R. de St., Silvestri, M. de & Georghiou, G. P. 1986 Amplification of an esterase gene is responsible for insecticide resistance in a California *Culex* mosquito. *Science, Wash.* **233**, 778–780.

Pickett, J. A., Williams, I. H., Martin, A. P. & Smith, M. C. 1980 Nasonov pheromone of the honeybee, *Apis mellifera* L. (Hymenoptera: Apidae). Part I. Chemical characterization. *J. chem. Ecol.* **6**, 425–434.

Pickett, J. A. 1984 Prospects for new chemical approaches to insect control. *Chemy. Ind., Lond.* 657–660.

Pickett, J. A., Dawson, G. W., Free, J. B., Griffiths, D. C., Powell, W., Williams, I. H. & Woodcock, C. M. 1984 Pheromones in the management of beneficial insects. In *Proceedings of the British Crop Protection Conference – Pests and Diseases*, pp. 247–254. Croydon: BCPC Publications.

Powell, W. & Zhang, Z. 1983 The reactions of two cereal aphid parasitoids, *Aphidius uzbekistanicus* and *A. ervi* to host aphids and their food-plants. *Physiol. Ent.* **8**, 439–443.

Powell, W. 1986 Enhancing parasitoid activity in crops. In *Insect Parasitoids – Proceedings 13th Symposium of the Royal Entomological Society of London* (ed. D. J. Greathead & J. K. Waage), pp. 319–340. London: Academic Press.

Reece, C. H. 1985 The role of the chemical industry in improving the effectiveness of agriculture. *Phil. Trans. R. Soc. Lond.* B **310**, 201–213.

Rubin, G. M. 1985 P transposable elements and their use as genetic tools in *Drosophila*. *Trends Neurosci.* **8**, 231–233.

Sakan, T., Isoe, S. & Hyeon, S. B. 1970 The chemistry of attractants for Chrysopidae from *Actinidia polygama* Miq. In *Control of insect behaviour by natural products* (ed. D. L. Wood, R. M. Silverstein & M. Nakajima), pp. 237–247. New York: Academic Press.

Schell, J. St. 1986 The development and use of gene transfer systems and efficient expression vectors for the genetic engineering of plants. Paper presented at SCI Meeting 'Novel Approaches to Agrochemical Research', December 1986.

Smart, L. E. & Stevenson, J. H. 1982 Laboratory estimation of toxicity of pyrethroid insecticides to honeybees: relevance to hazard in the field. *Bee Wld* **63**, 150–152.

Stevenson, J. H., Smart, L. E. & Walters, J. H. H. 1984 Laboratory assessment of insecticide selectivity – practical relevance. In *Proceedings of the British Crop Protection Conference – Pests and Diseases*, pp. 355–358. Croydon: BCPC Publications.

Wilding, N. 1983 The current status and potential of entomogenous fungi as agents of pest control. In *Proceedings of the 10th International Congress of Plant Protection*, pp. 743–750. Croydon: BCPC Publications.

Williams, I. H., Pickett, J. A. & Martin, A. P. 1981 Attraction of honeybees to flowering plants by using synthetic Nasonov pheromone. *Entomologia exp. appl.* **30**, 199–201.

Discussion

L. P. J. J. Noldus (*Department of Entomology, Wageningen Agricultural University, The Netherlands*). I would like to make a point regarding the use of semiochemicals to manipulate the behaviour of noxious or beneficial insects. Aphids, for example, can avoid predation by alarm-pheromone-induced dispersal which, however, can also enhance mortality from contact pesticides. If these responses are important in the population dynamics of the insect, does Dr Pickett think that selection may occur for individuals that no longer react to the alarm pheromone? Please also comment on whether beneficials might become resistant to semiochemicals.

J. A. Pickett. I think it is certain that such insects could become unresponsive to semiochemical treatments but if, as is becoming the case for pesticides, carefully controlled integrated régimes are employed, this should be avoided.

I. Harpaz (*Department of Entomology, Hebrew University of Jerusalem, Israel*). Another aspect relevant to the topic in this paper is where pesticides can be used for enhancement of biological control. This is done in the control of prickly pear (a noxious plant in South Africa and Australia) by cochineal scale insects of the genus *Dactylopius*. When the infested prickly pear plants are treated with DDT, the pesticide kills predators and parasites of the scale insect, but not the scale insect itself which is not susceptible to DDT. As a result, the control of prickly pear is significantly improved by this unusual, selective pesticidal treatment. Possibilities of using this particular method of integrating biological and chemical measures should not be overlooked.

J. A. Pickett. I take note of this interesting point.

J. M. Franz (*Gundolfstrasse* 14, 6100 *Darmstadt, F.R.G.*). The recommendation was given to use methods established by the IOBC/WPRS Working Group 'Pesticides and Beneficial Organisms', for tests on the toxicity of established and new pesticides on beneficial athropods. These standard methods would seem to be more realistic than simple relative toxicity studies in the laboratory and are applicable to pesticides in general.

J. A. Pickett. I am aware of the methods recommended by the Working Group; indeed my own staff were involved in drawing up these protocols, and I agree that these should be used when considering selectivity between pests and beneficial organisms. However, our laboratory studies on selective toxicity provide a good indication of chemical structures likely to be less hazardous to beneficial organisms. In addition, I did report numbers of live parasitoids surviving in the field after use of the more selective pyrethroid cypermethrin compared with the non-selective organophosphorus demeton-S-methyl which is the final test of selectivity.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

J. K. Waage (*C.A.B. International Institute of Biological Control, Ascot, U.K.*). A problem with the use of semiochemicals to attract natural enemies is that one may thereby force natural enemies to forage where they would not normally, instead of in response to natural kairomones which would presumably bring them to high densities of their pest populations. As a result, the searching efficiency of these natural enemies could be reduced, and consequently their reproduction and future population size. The value of such chemicals may therefore be negative in the long term, unless they were used in conjunction with augmented natural enemies. In these circumstances the chemicals might then be of special value in directing released natural enemies to the target pest population.

J. A. Pickett. I agree with your general point but although we may have to consider augmentation of natural enemies, I feel that this would best be achieved by cultural means.

M. J. Way (*Imperial College at Silwood Park, Ascot, U.K.*). It seems inevitable that there will often be problems in rectifying a pest-resistant situation once it has developed. I therefore suggest that you have not given sufficient emphasis to the development and use of natural enemies that are resistant to broad-spectrum pesticides that would otherwise harm them. Surely such natural enemies can play a crucial role by killing residues of resistant pests that might be left after pesticide application, and which would otherwise form the nucleus from which wholly resistant pest populations could develop.

J. A. Pickett. This is a theoretically sound proposal and we are making efforts in this direction. It would be compatible with my view that we must help the agricultural industry to continue use of chemical control agents in ways that minimize possibly harmful consequences.

P. T. Haskell (*Department of Zoology, University College, Cardiff, U.K.*). As regards attraction of predators and parasites into a crop by using semiochemicals, is there not a limit to the increase that can be caused by density-dependent inhibitory reactions by the parasites and predators involved?

J. A. Pickett. I agree that inhibition can occur but comment that semiochemicals could allow the balance to be tipped in favour of control.

H. F. van Emden (*Departments of Horticulture, and Pure and Applied Zoology, University of Reading, U.K.*). Plant odours will attract parasitoids regardless of presence of prey; if there are few prey they may not all stay, but they would never be any use unless you could get them into the crop in the first place!

J. A. Pickett. I agree, and that is why the work concentrates on both host and host–plant chemicals.