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East Malling

**Review of Biological Control
of Apple and Pear Pests in the UK**

by

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REVIEW OF BIOLOGICAL CONTROL OF
APPLE AND PEAR PESTS IN THE UK

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Review of biological control of apple and pear pests in the UK

Summary

Previous research into natural enemies and biological control of apple and pear pests in the UK is reviewed and opportunities for development of new biological control methods appraised. Numerous opportunities for research, development and application of biological control agents were identified.

The first option to consider when reviewing possibilities for biological control in orchards is the exploitation of naturally occurring predators and parasites. Several groups of polyphagous predators, such as lacewings, ladybirds, hoverflies and spiders, prey on a number of pest species, contributing generally to the reduction in pest populations but are unlikely alone to prevent pest damage fully and reliably. In seeking biological control opportunities for a particular pest, these polyphagous natural enemies are unlikely to be a high priority. An exception, due to its abundance in orchards, is the common earwig. A means of fostering populations of earwigs whilst limiting fruit injury is an important research priority.

Many natural enemy species are specialised feeders and better able to respond to the population dynamics of particular pest species. The priority for research should be to study the specialist natural enemies of important pest species. Examples of these are *Anthocoris nemoralis* against pear sucker, *Cacopsylla pyricola*, and phytoseiid mites against phytophagous pest mites. Hymenopterous parasitoids have great potential to control pest populations but hitherto have received limited attention because they are very sensitive to broad-spectrum pesticides and are thus virtually absent from commercial orchards. The parasitoids of tortricids, apple sawfly, leaf miners and leaf midges should be prioritised for study. The aim of such studies should be to develop effective strategies for establishing a stable equilibrium between parasitoids and important pests, with pest damage rarely exceeding economic threshold levels. Key components of such studies should be the identification of the most effective parasitoids, elucidation of their biology, determination of the effects of pesticides on them, and the identification of possible ways of manipulating the habitat to favour them.

The second option to consider is the introduction of biological control agents into the orchard. The success rate of this approach, using arthropod predators and parasites to control pests of field crops, has been generally poor. Most successes have occurred where non-indigenous pests are controlled by introducing natural enemies from their native region. Furthermore, mass production methods for parasites and predators are likely to be difficult and very costly and so could be considered only where long-term populations can be established. Any change in this situation is dependent on the development of low cost mass culture techniques. The biological supplies industry is constantly seeking culture techniques, largely for arthropod biological control agents of pests of protected crops. It is possible that some future advance may be relevant to orchards though currently available predators or parasites do not appear promising. Negative results with mass release of *Trichogramma* egg parasites for control of tortricids

have not been encouraging for this approach. However, the potential of such biological agents needs to be reviewed regularly and research resources focussed where promising opportunities develop. A careful economic appraisal of the feasibility of use of any potential biological control agent would be prudent before embarking on research.

Microbial control agents and entomopathogenic nematodes, which can often be mass produced at low cost by bulk fermentation processes and applied as sprays, provide promising opportunities for research, development and application and should be considered as another priority area for the focus of research funding. However, registration procedures and associated fees for microbial agents, which are often host specific and thus offer restricted marketing opportunities, are a significant barrier to commercialisation. Such requirements do not apply currently to nematodes.

Baculoviruses are, in many respects, ideal biological control agents and the granuloviruses of codling moth, *Cydia pomonella* (CpGV), and the summer fruit tortrix moth, *Adoxophyes orana* (AoGV), have been researched extensively. However, commercial development and use in the USA and several other European countries has generally been poor to date because of their high costs relative to pesticides, slow action and short persistence. The widespread development of strains of codling moth, *Cydia pomonella*, multi-resistant to insecticides has transformed the commercial prospects of CpGV. The development of a genetically engineered fast-acting *egt*⁻ strain of CpGV by HRI Wellesbourne is a significant breakthrough providing opportunity for commercialisation. A high priority for future research and development should be the field testing and formulation (to reduce UV light sensitivity) of this strain and development of bulk *in vitro* mass production techniques. This should be followed by similar improvement of AoGV. A systematic search for baculoviruses of other apple and pear pests might also reveal important new opportunities.

To date, the most important bacterial pathogen used as a biological control agent is *Bacillus thuringiensis* (*Bt*). However, *Bt* products currently available in the UK have limited effectiveness against many orchard pests. The enormous advances in biotechnology and genetic engineering, in theory, provide opportunity for development of *Bt* strains designed specifically to control orchard pests. However, in reality, the market for such products for use in orchards has to date been too limited to attract commercial investment. However, new *Bt* products (containing novel combinations of toxin strains or formulations) developed for other markets worldwide should be evaluated for activity against orchard pests. A further option is to bioassay strains from *Bt* collections (e.g. at HRI Wellesbourne) for activity against selected target pests, firstly in the laboratory, then in the field.

Entomopathogenic fungi also provide an opportunity for development as biological control agents of apple and pear pests. However, the main factor limiting their effectiveness is the requirement for very high humidities and adequate temperatures for spore germination and development. Key areas for research are improved formulation together with the selection of low temperature-active strains. An interesting starting point might be the control of pear sucker, *Cacopsylla pyricola*, nymphs with isolates of *Paecilomyces fumosoroseus*. Pear sucker nymphs are immersed in honeydew for extended

periods, which might provide suitable conditions for infection. An alternative approach is to examine the exploitation of entomopathogenic fungi in soil, to which many species of entomopathogenic fungi are adapted ecologically. Apple and pear orchards provide long-term stable habitats where populations of entomopathogenic fungi in soil are likely to be large. Unfortunately, there are very few important soil pests of apple or pear, though many species spend part of their life in soil, mainly to pupate or overwinter (e.g. apple sawfly, (*Hoplocampa testudinea*), leaf midges (*Dasineura mali* and *D. pyri*) and some leaf miners (e.g. *Stigmella* sp.)).

Entomopathogenic nematodes have many attributes which favour them as biological control agents, not least the comparatively low cost of their *in vitro* mass production and the absence of any requirements for registration under the Control of Pesticides Regulations. However, their requirement for surface moisture for survival and movement means there are only remote prospects for using them as biological control agents for foliar pests. As with entomopathogenic fungi, there are better prospects for control of pests that occur in soil but such an approach is of lower priority.

When considering research opportunities for the biological control of apple and pear pests, it is important to consider opportunities in related areas including biotechnological and biologically-based control methods, such as plant breeding, the use of semiochemicals and host plant attractants, insect growth regulators, etc. An overall strategy for research and development into biologically and biological-based control methods needs to be developed within an Integrated Pest Management Strategy.

Introduction

Apple and pear are hosts to an extensive and diverse arthropod faunas. As long-term perennial plants they provide stable ecological habitats where this fauna has evolved over the millenia. Steiner (cited in Steiner *et al.*, 1970) recorded over 1,000 species in unsprayed apple orchards in Germany. Approximately 25% are pests and 25% are natural enemies of pests. The remaining species are benign though many act as 'buffers' and so provide ecological stability. Application of broad-spectrum insecticides, such as organochlorine, organophosphorus, carbamate or pyrethroid compounds, has a profound impact on the range and relative abundance of arthropods on apple and pear, especially if applications are frequent. Most species are highly sensitive to insecticides and are virtually eliminated by a single application. However others, especially those with cryptic habits or those that are dispersive, have alternative hosts or have developed insecticide-resistant strains, thrive as important pests. Treatment with broad-spectrum insecticides gives short-term control but usually eliminates or greatly reduces the numbers of their enemies, so making subsequent outbreaks more severe.

The most important key pests are codling moth (*Cydia pomonella*), rosy apple and pear bedstraw aphids (*Dysaphis plantaginea* and *D. pyri*), winter moth (*Operophtera brumata*) and apple sawfly (*Hoplocampa testudinea*). They frequently cause economic damage to flowers, fruitlets or fruits directly and their natural enemies are insufficiently effective to regulate their numbers below damaging levels.

The most important secondary pests are the fruit tree red spider mite (*Panonychus ulmi*), apple and pear rust mites (*Aculus schlechtendali* and *Epitrimerus pyri*), summer fruit tortrix moth (*Adoxophyes orana*) and pear sucker (*Cacopsylla pyricola*). On apple or pear trees not treated with insecticides these species do not cause significant damage because their numbers are regulated effectively by their natural enemies. Application of broad-spectrum pesticides, to which many of these pests are tolerant or have become resistant, eliminates or greatly reduces the numbers of their natural enemies, thus disrupting the ecological balance and enabling the pests to increase in numbers to cause economic damage. In addition, there are large numbers of less important and minor pests which are either of sporadic or local occurrence, or cause limited damage as they do not attack the fruit directly. Some of these can be very damaging if allowed to increase over a number of seasons but they are controlled readily with insecticides (e.g. apple blossom weevil, *Anthonomus pomorum*). The importance of pests of apple and pear in the UK has been reviewed recently by Umpelby, Solomon and Cross (1995).

Natural enemies and insecticide use thus play a crucial part in determining the importance of apple and pear pests. Adverse public attitudes to pesticides have intensified in recent years and this has led to a desire by fruit growers to reduce dependence on pesticides, especially broad-spectrum neurotoxic compounds that can adversely affect human health or the environment. Alternatives to the use of insecticides (as a means of controlling pests) are needed. Biological control provides one of the best alternatives. The development of an integrated mite management strategy for apple, whereby naturally-occurring OP-resistant strains of the orchard predatory phytoseiid mite *Typhlodromus pyri* have been harnessed to biologically control fruit tree red spider mite (*Panonychus ulmi*)

and apple rust mite (*Aculus schlechtendali*) which, hitherto, were serious secondary pests, has been an outstanding success. There are two other significant instances where biological control has been realised in UK apple and pear orchards. The first is the exploitation of predatory anthocorids to control pear sucker (*Cacopsylla pyricola*). Growers avoid using broad-spectrum insecticides after petal fall in pear orchards to allow anthocorid populations to increase and suppress pear sucker. This has been only partially successful as the migration of anthocorids into orchards in sufficient numbers in early summer is unreliable. The second instance, which is non-deliberate, is the suppression of woolly aphid (*Eriosoma lanigerum*) and a number of other pests by the large populations of the common earwig, *Forficula auricularia*, that occur in orchards. Growers do not appreciate the benefits that are gained from earwigs which are ubiquitous and abundant predators in orchards. It appears that they have developed resistance to OP and carbamate insecticides. As they are omnivorous and often feed on fruits, they are regarded widely, but wrongly, as pests by growers.

The benefits of biological control can thus be considerable, and this is recognised widely by growers. To date, the successes have depended on the exploitation of naturally-occurring arthropods, largely by avoiding the use of harmful pesticides. There is still considerable scope for further such exploitation. There is also extensive opportunity for the introduction or application of other biological control agents, including microbial agents, into orchards. Those that establish permanently or at least survive for several seasons are preferable. Short term biological control agents, referred to as 'biopesticides', also offer opportunities, though a careful economic appraisal of their mass culture and use is required to determine whether they are likely to be commercially viable. Biopesticides are often highly specific, controlling only the target species and occasionally closely related ones. To compete economically with broad-spectrum pesticides, the costs of production need to be very low, especially if the biopesticides need to be used frequently. Selectivity, whilst providing many benefits, poses a dilemma as large numbers of selective control agents may be needed to replace a single broad-spectrum one. The market opportunity for selective products may also be limited, making it un-economic for companies to invest in development and registration.

Where an arthropod or nematode biological control agent is not native to, or does not originate from the British Isles, a licence is required from the Department of the Environment before it can be introduced. A thorough appraisal of the possible impact of the biological control agent on the environment is necessary. Any microbial biological control agent (even if native to the UK) cannot be used without prior Approval from the Pesticides Safety Directorate. An extensive evaluation of the safety and efficacy of the agent is required in a similar way to that required for pesticides. A substantial fee (approximately £20k) is required. These regulatory requirements, though clearly essential, pose insurmountable hurdles to the development and use of many biological control agents. Nematodes and arthropods are exempt from these registration requirements though the classification of nematodes as microbial agents is being considered by the European Community.

The large numbers of natural enemies of apple and pear pests, plus the possibility of developing new biological control agents, including by genetic manipulation, provide many possibilities for developing new commercially viable biological control methods to

reduce dependence on chemical pesticides. However, the likelihood of success and the difficulties faced vary considerably. Here we review previous research and current knowledge of the natural enemies of apple and pear pests and appraise their suitability to be biological control agents, giving recommendations for future research. In prioritising research options, we have considered many factors including, in addition to the above, special relevance to the UK and existing expertise and facilities. Each family of natural enemies is covered in turn with a brief summary, conclusions and recommendations for future research. In this review the term 'biological control' is used in its classical sense, *viz.* the control of pests by predators and parasites. Biotechnological and related biologically-based control methods, such as plant breeding, the use of semiochemicals or host plant substances, the sterile insect technique, insect growth regulators, etc. are not included as subjects in their own right. This review will be used in the development of a strategy for UK research into biological, biotechnological and related control methods for apple and pear pests.

Predatory Mites

Phytoseiids

Phytoseiid mites have been shown to be capable of controlling *Panonychus ulmi*, the fruit tree red spider mite, and *Aculus schlechtendali*, the apple rust mite in several countries, (e.g. Dosse, 1960; Collyer, 1964a; Croft, 1975; Readshaw, 1975; Wearing *et al.*, 1978; Gruys, 1982; Easterbrook *et al.*, 1985). In 1985 eight different species of phytoseiid were considered to "play a role" in biological control in orchards and vineyards in Europe (Baillod, 1986). The most commonly found species were *Typhlodromus pyri*, *Amblyseius andersoni* and *Kampimodromus aberrans*.

Many species of phytoseiid mites are found on unsprayed apple trees in the UK (Chant, 1959) but in selectively sprayed orchards the species that generally colonises is *Typhlodromus pyri*. This species occurs in most other apple growing areas of the world where the climate is similar (e.g. McMurtry *et al.*, 1970; Baillod, 1986).

T. pyri has four developmental stages, an egg, larva, protonymph and deutonymph, and the adult stage. The larval stage does not feed, but the nymphal and adult stages are active predators. All stages of *P. ulmi* are eaten, but adult females are not the preferred prey. Chant (1959) determined in insectary trials that *T. pyri* consumed on average 133 *A. schlechtendali* or 18 *P. ulmi* during the total protonymph and deutonymph stages. He also determined that *T. pyri* developed more quickly when fed *A. schlechtendali* rather than *P. ulmi* (5-7 days and 11 days respectively). These results were confirmed in laboratory trials by Dicke *et al.* (1990). They determined that rates of population increase were greater for *T. pyri* fed on *A. schlechtendali* than *P. ulmi* although Dicke *et al.* (1988) had determined that in choice tests *T. pyri* prefers *P. ulmi* to *A. schlechtendali*.

At 26°C times for development from egg to adult were determined in laboratory trials to be 6.8 days when fed *A. schlechtendali* and 7.1 days when fed *P. ulmi* (Dicke *et al.*, 1990) and in an insectary at fluctuating temperatures in SE England they were 16.2 days when fed *P. ulmi* (Chant, 1959). The total fecundity of *T. pyri* is dependent on temperature and prey availability (Hayes, 1988). Fecundity increased from 0.14 eggs/day to 0.45 eggs/day at 20°C when consumption of *P. ulmi* larvae was increased from 2/day to 8/day (Hayes, 1988). At 20°C with consumption of 8 *P. ulmi* larvae/day a total of 20 eggs was laid by individual *T. pyri* (Hayes, 1988).

Collyer (1964b) found that *T. pyri* could reduce *P. ulmi* numbers to a lower level if *Aculus fockeui* was also present on the plants. This may have been due to the increased rate of population increase of *T. pyri* when feeding on rust mites (Dicke *et al.*, 1990).

T. pyri overwinter as diapausing fertilised adult female mites. Diapause is initiated by a short daylength of between 12.5 and 13.5 hours (Fitzgerald and Solomon, 1991), which occurs in mid September in SE England. Females commence laying eggs in early May (Fitzgerald and Solomon, 1991) before the overwintering eggs of *P. ulmi* begin to hatch. There are 3 or 4 generations per year in UK. Females need to mate before they

can produce eggs and they require multiple matings for maximum egg production (Overmeer *et al.*, 1982).

Sabelis and Van de Baan (1983) determined that phytoseiids respond to volatiles emitted from prey or leaves infested with prey. The role of these kairomones in the location of prey was reviewed by Sabelis and Dicke (1985).

T. pyri was found to be surviving in orchards receiving an organophosphorus-based insecticide programme in the UK in 1982 (Solomon and Fitzgerald, 1984). Bioassay results confirmed that these *T. pyri* had a high level of resistance to some OPs (Kapetanakis and Cranham, 1983; Cranham *et al.*, 1984). Resistance to OPs has also developed in *T. pyri* in other apple growing areas e.g. Hoyt (1972), Collyer and Van Geldermalsen (1975) and Penman *et al.* (1976) in New Zealand and Watve and Lienk (1975, 1976) in USA. The earlier development of OP-resistance in these countries may be due to differences in the pattern of pesticide use. As a result of field trials, a successful mite management strategy based on OP-resistant strains of *T. pyri* was devised for UK fruit growers by Solomon *et al.* (1993), in which OPs are used to control low threshold pests such as *Cydia pomonella*, codling moth, and OP-resistant *T. pyri* to regulate numbers of *P. ulmi* and *A. schlechtendali*. Pesticide programmes that allow the survival of OP-resistant *T. pyri* are now used in the vast majority of UK dessert and culinary apple orchards. The use of OP-resistant *T. pyri* to control phytophagous mites in orchards in Europe was reviewed by Blommers (1994).

The effects of some commonly used orchard pesticides on SE UK populations of *T. pyri* were given by Solomon (1987) and Croft (1990) reviewed the effects of pesticides on resistant phytoseiids worldwide. However, populations of *T. pyri* differed in their response to pesticides (Fitzgerald unpublished results); populations from cider orchards in SW England showed different levels of resistance to some OPs when compared to populations from dessert apple in the SE.

Once *T. pyri* has established in an orchard, the population will remain unless harmful pesticides are used (e.g. synthetic pyrethroids to which generally *T. pyri* are not resistant). They can survive and reproduce on alternative food sources if the numbers of *P. ulmi* and *A. schlechtendali* are small, e.g. apple powdery mildew (Chant, 1959) or apple pollen (Chant, 1959; Dosse, 1961; Overmeer, 1981). Thus there should be no necessity to mass culture and release this biological control agent. However, if populations are destroyed, mites can be introduced artificially by removing prunings from orchards containing large populations of mites and placing branches in the receptor trees (Solomon and Fitzgerald, 1984; Blommers, 1994). However, Fauvel and Gendrier (1992) were unable to introduce *T. pyri* successfully on prunings from vines to apple in France.

Overwinter mortality of female *T. pyri* can be high (Chant, 1959). Provision of sacking bands, especially on young trees that have few overwintering sites for mites, may enhance overwinter survival of *T. pyri*. Large numbers of overwintering *T. pyri* were extracted from bands collected from dessert (Greatorex, 1997) and cider apple orchards (Fitzgerald and Solomon, 1996). Cloth bands have been used to collect and release large

numbers of phytoseiids in orchards in Switzerland (Baillod and Guignard, 1984).

Other species of phytoseiid have been found in UK orchards e.g. *Amblyseius finlandicus*, *Phytoseius macropilus*. Their presence depends on the pesticide programme being used, as no species in the UK apart from *T. pyri* has been shown to exhibit any resistance to OPs. However, these species may play a role in biological control in organic systems.

Studies in the USA (Croft and Croft, 1993; Croft and MacRae, 1993; Zhang and Croft, 1995; MacRae and Croft, 1996) have shown that competition between species of phytoseiids and other predatory mites may cause displacement of some species in orchards. This may affect the biological control of phytophagous mites if the surviving species is less adapted to survive the pesticides used to control other pests in orchards.

The importance of phytoseiids as biological control agents in orchards has resulted in much work to improve the characteristics of the most widely used species. Resistance to pesticides is one characteristic that has received much attention. In New Zealand and UK, strains of *T. pyri* resistant to synthetic pyrethroids have been developed by selecting populations of mites in the field or laboratory with pyrethroids (Markwick, 1986; Solomon and Fitzgerald, 1993). Similar work has been done in the USA on the species most important in their growing systems (e.g. Strickler and Croft, 1982; Hoy *et al.*, 1983). Hoy (1985) reviewed the genetic improvement possibilities for phytoseiids and pesticide resistance selection (Hoy, 1990). With the rapid expansion of biotechnological techniques, such selection programmes can be implemented more rapidly (reviewed by Hoy, 1996). Novel DNA can now be injected into adult female phytoseiid mites and may be expressed in eggs laid by that mite (Presnail and Hoy, 1994).

Non-native phytoseiids may be of value as 'biological insecticides' if a licence can be obtained for their release. *Phytoseiulus persimilis* is used in this way to control *Tetranychus urticae* in strawberry and hop in UK; usually it does not overwinter and has to be released each year. *P. persimilis* has proved successful as a control agent for *T. urticae* in trials in apple in Israel (Steinberg and Cohen, 1992).

Stigmaeidae

The role of stigmaeids in the control of tetranychids was reviewed by Santos and Laing (1985) and in the control of eriophyids by Thistlewood *et al.* (1996).

Zetzellia mali is the only stigmaeid that has been found in UK apple orchards (Greatorex, 1997). *Z. mali* has been shown to feed on *P. ulmi* in apple (Böhm, 1960; Parent and LeRoux, 1956; Santos, 1976; Greatorex, 1997) and *A. schlechtendali* (Hoyt, 1969; Delattre, 1971, 1974; White and Laing, 1977a; Vogt *et al.*, 1990; Clements and Harmsen, 1993; Greatorex, 1997). White (1976) suggested that rust mite were the preferred prey of *Z. mali*; they are easier to capture than the active stages of spider mite and *Z. mali* oviposition rates are higher when fed on *A. schlechtendali* than *P. ulmi* (Santos, 1991). *Z. mali* can also survive on apple pollen (White and Laing, 1977a) or phytoseiid eggs (Santos, 1976) and they appear to feed on leaf tissue (Santos, 1982).

They are difficult to rear as they cannibalise their own eggs (Clements and Harmsen, 1993).

Z. mali has four developmental stages and passes through a brief quiescent stage between each motile stage. In Ohio, *Z. mali* has four generations per year (Ellingsen, 1971); in UK there appear to be 3-4 generations per year (Greatorex, 1997). *Z. mali* overwinter as adult females (White and Laing, 1977b) and in UK begin to emerge during April (Greatorex, 1997). *Z. mali* is less active than phytoseiid mites and this may result in low predatory activity (Knisley and Swift, 1972).

White and Laing (1977a) detected a numerical response of *Z. mali* to populations of *P. ulmi* and *A. schlechtendali*. *Z. mali* preferred eggs and quiescent stages of *P. ulmi* to active stages (Clements and Harmsen, 1993). Ellingsen (1971) calculated that an adult female *Z. mali* could consume 38 *P. ulmi* eggs in its lifetime.

Croft and MacRae (1993) demonstrated that *Z. mali* could control pest mites on apple if the mites were present at high densities early in the season. However, according to (Ellingsen, 1971) winter mortality of *Z. mali* can be very high, so numbers are likely to be low at the beginning of the season. White and Laing (1977b) found that *Z. mali* was unable to control *P. ulmi* below levels of economic injury in their field trials in Canada. Hoyt (1969) and Vogt *et al.* (1990) have linked stigmatiid population cycles with those of its prey but these cycles have not always resulted in the control of the prey. Population density changes of *Z. mali* in the field were reported to follow *A. schlechtendali* densities more closely than changes in *P. ulmi* numbers (Woolhouse and Harmsen, 1984), confirming the preference of *Z. mali* for *A. schlechtendali*.

Thistlewood (1991) found *Z. mali* to be widespread in managed orchards in Canada, indicating some tolerance to pesticides, and Croft and Brown (1975) demonstrated that some populations were resistant to OPs.

Z. mali and phytoseiid mites may interact by feeding on each other or by competition for prey (Croft and MacRae, 1993). Stigmatiids have been reported to feed on phytoseiid eggs (Croft and McGroarty, 1977; Santos and Laing, 1985; Clements and Harmsen, 1990) and *T. pyri* sometimes feeds on eggs and immature *Z. mali* (MacRae, 1993).

Croft (1994) found that *Z. mali* displaced populations of *T. pyri* (and other phytoseiids) and, in field trials in Oregon, MacRae and Croft (1996) found that *Z. mali* had a greater effect on populations of another predatory mite *Metaseiulus occidentalis* than *T. pyri*. They concluded that this was because *M. occidentalis* laid more eggs in the primary foraging area of *Z. mali*.

In general, (Woolhouse and Harmsen, 1984) suggested that phytoseiids were more effective than *Z. mali* at controlling tetranychids. If pest mite numbers are high, stigmatiids may supplement the control provided by phytoseiids (White and Laing, 1977b; Santos and Laing, 1985; Croft and MacRae, 1992).

Erythraeidae

These mites are relatively large and fast moving. Little is known about their biology in UK orchards but in eastern Canada the most important species as a predator of tetranychids is *Balaustium putmani*. All mobile stages of *B. putmani* feed on *P. ulmi*. Cadogan and Laing (1977) reported that at 20°C adults could eat 30 *P. ulmi* eggs or 19 immatures per day, while Putman (1970) gave a higher predation rate of 106 eggs and 25 adult *P. ulmi* per day. Females fed on *P. ulmi* can lay up to 175 eggs during their lifetime (Putman, 1970).

B. putmani may also consume pollen (Childers and Rock, 1981) but larvae cannot complete their development on pollen alone (Cadogan and Laing, 1977).

As a result of field studies, Cadogan and Laing (1981) concluded that this mite is one of a group of predators that helps to maintain phytophagous mites at low levels.

Anystidae

These mites are fast running predators that move in a characteristic figure of eight pattern (Muma, 1975). The best known species is *Anystis agilis*. In North America this species has two generations per year with females producing an average of 31 eggs (Sorenson *et al.*, 1976). *A. agilis* is a non-specialised predator and is not thought to be a major consumer of spider mites; they require fresh water and also consume plant exudates (Sorenson *et al.*, 1976).

Summary and Conclusions

OP-resistant *Typhlodromus pyri* are the basis of integrated mite management in UK apple orchards. They can survive on alternative food when prey is scarce and so remain at low levels in orchards, unless inappropriate pesticides are used.

Stigmaeids are able to provide some control of *Panonychus ulmi* and *Aculus schlechtendali*. However, they are less efficient predators than phytoseiid mites and also interact with phytoseiids by feeding on their eggs and young stages.

Erythraeids and anystids are not sufficiently specialised as predators to be considered as major biocontrol agents for phytophagous mites.

Two areas for future research and development are the determination of the impact of new pesticides on *T. pyri* and the examination of the interactions between *T. pyri* and other species of native predatory mites found in orchards and non-native species that are or might be introduced.

Predatory Heteroptera (Anthocorids & Mirids)

The most widely occurring predatory Heteroptera found in UK apple and pear orchards are the anthocorids *Anthocoris nemoralis*, *A. nemorum* and *Orius* spp. and the mirids *Blepharidopterus angulatus*, *Pilophorus perplexus*, *Psallus ambiguus*, *Malacocoris chlorizans*, *Attractotomus mali* and *Phytocoris* spp. These species are described by Alford (1984) and the biology of the most commonly occurring species is described by Collyer (1953a).

Mirids and anthocorids have one or two generations per year. This makes them less responsive to increases in prey density than for example, phytoseiids which have four generations per year. Mirids overwinter as eggs that in most cases are inserted into the bark of trees; anthocorids overwinter as adults. They have six developmental stages, the egg and five larval instars.

Mirids and anthocorids are generalist predators and will feed on and thus help to control the numbers of the fruit tree red spider mite, *Panonychus ulmi* (Collyer, 1953a, b and c; Muir, 1965; Fauvel and Atger, 1981), the rosy apple aphid *Dysaphis plantaginea*, apple grass aphid, *Rhopalosiphum insertum*, the green apple aphid, *Aphis pomi* (Skinner, 1983), codling moth, *Cydia pomonella*, eggs and young larvae (MacLellan, 1961; Glen, 1975), and psyllids (Wille, 1950; Georgala, 1957; Bonnemaïson and Missonier, 1956; Fauvel and Atger, 1981; Viollier and Fauvel, 1984; Hodgson and Mustafa, 1984; Solomon *et al.*, 1989).

Anthocoris nemoralis is an important predator of pear sucker, *Cacopsylla pyricola*, in UK. If the pesticide programme allows it to survive, it can control the numbers of this pest in most years (Solomon *et al.*, 1989). Anthocorids migrate into pear orchards from early April. This migration is responsible for the major part of the population of the predator found during summer (Hodgson and Mustafa, 1984). Therefore broad spectrum insecticides can be used early in the season to control pests, without damaging anthocorid numbers in summer (Solomon *et al.*, 1989).

Windbreaks can provide a source of predatory mirids and anthocorids for orchards. The species that most often colonise selectively sprayed orchards are common in a wide range of hedgerow trees e.g. oak, hawthorn and alder. *B. angulatus* is especially abundant on alder where it feeds on alder aphid, *Pterocallis alni*, early in the season (Solomon, 1975a). *B. angulatus* colonised apple plots during the first year of a selective spray programme in response to high numbers of *P. ulmi* (Solomon, 1975a) and there was no similar response to mite numbers in the rate of colonisation of orchards by anthocorid adults. Anthocorids occur in large numbers on *Salix* spp. early in the season (Hill, 1957; Sands, 1957; Anderson, 1962). These anthocorids may then migrate into orchards in response to the presence of aphids and psyllids (Solomon, 1982).

Anthocorids and mirids are not resistant to the broad spectrum insecticides used in commercial fruit growing. Easterbrook *et al.* (1985) found few predatory insects in plots that had received applications of chlorpyrifos and azinphos methyl + demeton-S-methyl sulphone. Those that were present were adults that had flown into the plots after the

insecticide applications. They found that *B. angulatus*, *A. mali* and *P. perplexus* constituted 75-87% of the total mirid catch in selectively sprayed orchards. However, these mirids did not prevent several pest species from exceeding their treatment thresholds.

Scutareanu and Schoffemeer (1994) found that phenolic compounds detectable in HPLC from young pear leaves, cv. Conference, taken from sucker-infested trees were different from those from non-infested trees. Anthocorids have been shown to respond to these plant synomones (Drukker and Sabelis, 1990; Scutareanu *et al.*, 1993); migrating anthocorids aggregated around gauze-cage covered sucker-infested pear trees (Drukker *et al.*, 1995). Drukker *et al.* (1995) found significantly higher numbers of anthocorids on trees next to gauze-caged trees with high populations of suckers compared to uninfested trees. By covering some infested trees with airtight plastic, they determined that anthocorids were attracted to odours emitted from the infested trees. If these odours can be synthesised, they could be used to attract predators into orchards.

Flowering plants are attractive to some predators and parasitoids. Solomon and Fitzgerald (unpublished results) found that corn camomile, cornflower and corn marigold were attractive to anthocorids and Wyss (1995) found higher numbers of anthocorids and mirids on orchard strips that had been undersown with flowering plants.

It is possible to mass culture some anthocorid and orius species (Brönnimann, 1964) and recent trials are investigating the mass release of *A. nemoralis* to control pear sucker in France (Fauvel *et al.*, 1994).

Several species of anthocorid have been found to feed on predatory mites in orchards. In a laboratory study Cloutier and Johnson (1993) found that *Orius tristicolor* fed on *Phytoseiulus persimilis* (a predatory phytoseiid) even when its preferred prey, the thrips, *Frankliniella occidentalis*, were present. In an electrophoretic study of predation in orchards in Holland, field collected *Orius vicinus* were found to have the characteristic pattern of bands found in *T. pyri*, indicating that *O. vicinus* had recently fed on this predatory mite (Heitmans *et al.*, 1986). Therefore encouraging predatory mirids and anthocorids into orchards may affect the biological control exerted by predatory mites.

Summary and Conclusions

Several species of mirid and anthocorid are known to be predators of a range of orchard pest species, but they are susceptible to broad spectrum insecticides. *Anthocoris nemoralis* is the major predator of pear sucker and the current approach to the integrated management of this pest depends on avoiding pesticides damaging to the predator.

Areas for future research and development are 1) to examine the potential of flowering plants for attracting these predators and enhancing populations in orchards; 2) as the Dutch work on plant synomones progresses, review the potential for exploiting these materials as a means of attracting anthocorids and mirids into orchards; 3) using appropriate gut content analytical techniques, examine the extent to which mirids and anthocorids feed on predatory mites, thus undermining the effectiveness of current

integrated mite management practices; and 4) examine the impact of new pesticides on anthocorids and mirids.

Lacewings (Neuroptera)

There are 72 species of Neuroptera known to occur in the UK (Plant, 1994). The predators of main interest to apple and pear growers are confined to three sub-families, namely Chrysopidae (green lacewings), Hemerobiidae (brown lacewings) and Coniopterygidae (powdery lacewings). At least eight of the 16 species of Chrysopidae found in Britain have so far been recorded from top fruit (*Nineta flava*, *Chrysopa perla*, *C. pallens*, *Mallada flavifrons*, *M. prasina*, *Cunctochrysa albolineata* and *Chrysoperla carnea*). With the exception of *C. carnea*, most of these species are encountered rarely. All stages of Neuroptera are attacked by a wide range of predators and parasitoids (Alrouechdi *et al.*, 1984). Little is known of the importance of larval and pupal parasitoids as mortality factors in UK. Hymenopteran parasitoids of chrysopid eggs are common in USA, causing up to 76% loss in one study (Campbell and Cone, 1994), and in continental Europe (Johnson and Bin, 1982; Alrouechdi *et al.*, 1984). However, although several parasitoid species have been recorded in other countries from chrysopid and hemerobiid species that occur in UK, none has yet been recorded here. Continued vigilance will be required to prevent unintended importation, e.g. on perishable produce, or via a shipment of eggs from an overseas biocontrol supplier. Similarly, although an endoparasitoid of adult chrysopids is known from France and Italy (Alrouechdi *et al.*, 1984), it has yet to be recorded from UK.

Chrysopids are mostly generalist feeders taking almost any soft-bodied arthropods including siblings and other beneficial insects (Canard *et al.*, 1984). Their biology and ecology has been reviewed extensively (Hagen and van den Bosch, 1968; New, 1975, 1988; Canard *et al.*, 1984). An important consideration for IPM is the sensitivity of natural enemies to the pesticides that may be used. The pre-imaginal stages of chrysopids show greater physiological tolerance than most other predator groups to a variety of pesticides (Bigler, 1984; Bigler and Waldburger, 1994). The three larval instars are active and voracious predators in all species. In most species the adults are also predatory. In apple and pear orchards, larvae of *Chrysoperla carnea* have been recorded feeding mostly on aphids (Asgari, 1966; Wiackowski and Wiackowska, 1968; Bethell *et al.*, 1978; Fontanari *et al.*, 1993), although *Panonychus ulmi* is also taken (Böhm, 1960; Holdsworth, 1968; McMurtrey *et al.*, 1970; Injac and Dulic, 1992), as are mealybugs (Doutt and Hagen, 1950), codling moth (Holdsworth, 1970a) and pear sucker (Wilde, 1962; Nickel *et al.*, 1965; Bouyjou *et al.*, 1984; Westigard and Moffitt, 1984; Santas, 1987). Likewise, *Chrysopa perla* is regarded principally as a predator of aphids but Bognar and Csehi (1959) and Böhm (1960) reported it also preying on *P. ulmi* in Hungary and Austria, respectively.

Chrysoperla carnea is a cosmopolitan generalist predator found in a broad range of temperate zone habitats. It has been among the most-frequently detected species in surveys of pest natural enemies but there are few reports of confirmed regulatory effects on pest populations without artificial manipulation. *Chrysoperla carnea* is unusual among Chrysopidae by overwintering as an adult. That allows it to colonise crops early the following season when temperatures begin to rise and as soon as honeydew, which is an attractant and food for adults, becomes available. The provision of artificial hibernation sites has proved a useful tactic for increasing numbers on field crops early in the

following spring (Sengonca and Henze, 1992). Large numbers were recorded from similar artificial hibernation sites located in an organic fruit and hop farm in Kent (Campbell, unpublished results). If necessary, diapausing adults can be cold-stored for more than 6 months with less than 3% mortality (Tauber *et al.*, 1993). Attempts to enhance the numbers of adult *C. carnea* colonising crops by the use of attractants, such as artificial honeydews and L-tryptophan (van Emden and Hagen, 1976; McEwan *et al.*, 1993), produced few discernible effects (Hagley and Simpson, 1981; Dean and Satasook, 1983; Campbell, unpublished results).

Methods are available for rearing large numbers of *C. carnea* (reviewed by Tulisalo, 1984). Eggs and larvae may be obtained for predator introduction programmes from commercial suppliers in several countries including the UK (Lisansky, 1990). When released on crop plants as eggs or young larvae, the predators are confined largely to forage on them. Eggs and newly-hatched larvae are often supplied mixed with vermiculite or a similar medium for sprinkling on plants or, for larger scale application, eggs can be suspended in water and sprayed on to crops using a standard high pressure sprayer (Lochte and Sengonca, 1995). Wang and Nordlund (1994) reviewed the efficacy of inundative and inoculative release programmes using *Chrysoperla* spp. Good control was obtained in Poland with releases of first instar *C. carnea* larvae to control *Panonychus ulmi* on apple (Miszczak and Niemczyk, 1978). However, the mass introduction of eggs against this pest on pear in California provided only partial control and failed to prevent economic loss (Huffaker and Spitzer, 1950). Hagley and Miles (1987) found that the release of 100-1500 eggs per tree on glasshouse grown peach trees resulted in the virtual elimination of two-spotted mite (*Tetranychus urticae*). Later, Hagley (1989) reported a significant reduction in the numbers of *Aphis pomi* on apple in Ontario following the release of c.335000 eggs/ha of *C. carnea* which equated to predator/prey ratios of 1:10 and 1:19 in the two years of study. Sengonca *et al.* (1995) obtained only two-week control of aphids on sugar-beet (probably *Myzus persicae*) with releases of eggs of *C. carnea*, but only with a high predator/prey ratio of one egg to five aphids, whereas Scopes (1969) found that a ratio of one newly-hatched larva to 50 aphids produced effective control of *M. persicae* on glasshouse chrysanthemums. Raupp *et al.* (1994) saw no evidence of reductions in the populations of *Aphis fabae* on hawthorn following releases of *Chrysoperla* spp. In these examples, the wide variation in the predator/prey ratios and the subsequent degree of control achieved emphasise the need for adequate preliminary investigation before any releases are made. Mathematical models of predator/aphid systems such as that produced by Gutierrez and Baumgaertner (1984), using *C. carnea* and other predators, would provide useful interactive feedbacks for improving the efficacy of predator release experiments.

At least four of the 29 UK species of Hemerobiidae have so far been recorded feeding on apple and pear pests. Aphids are the prey cited most commonly for hemerobiids (Holdsworth, 1970a,b) but pear sucker (Madsen and Wong, 1964; Nickel *et al.*, 1965) and mites (Collyer, 1953b) have also been recorded as prey. *Hemerobius humulinus* and *H. lutescens* are the species recorded most commonly on top fruit in UK. Killington (1936), who reared Lachnid-specific hemerobiids from conifers on a diet of aphids, concluded that prey specificity was mediated largely by availability; in his study, the growth and development of predators was unimpaired by their novel diet.

Neuenschwander (1975) noted that the lower developmental threshold temperatures for hemerobiids were much lower than those of other groups of predators and their prey, giving them a potential advantage as biocontrol agents early in the season when aphid populations are still small. If this is confirmed for UK species, and in view of Killington's findings (above), then a potential avenue worth exploration may be to select biocontrol agents for release on fruit from those species normally confined to e.g. conifers. The efficacy of the biocontrol agent may be enhanced by physical separation from its own specific natural enemies.

Conwentzia psociformis is probably the most important predator of mites on apple and pear among the 12 known species of British coniopterygids. Collyer (1951) also recorded *Conwentzia pineticola*, *Coniopteryx tineiformis* and *Semidalis aleyrodiformis* on apple. *Conwentzia pineticola* is now considered restricted to conifers (Plant, 1994), throwing doubt on identifications by Marlé (1951), Blair and Groves (1952) and by Collyer (1951, 1953a,b), all of whom identified it as an important predator of *Panonychus ulmi* on apple in Kent and Essex. Similar reports from elsewhere in Europe (McMurtry *et al.*, 1970) may also be misidentifications. *Conwentzia psociformis* is an important predator of *P. ulmi* in Norway (Fjelddalen, 1952) as well as in England (Collyer, 1951). Withycombe (1924) reported the virtual elimination of *Bryobia praetiosa* on pear following the release of pupae of *C. psociformis*; however, the predator was less effective the following year as it was attacked by the parasitoid *Lygocerus* sp. Withycombe (l.c.) also recorded *C. psociformis* parasitised by an unknown *Ceraphron* sp. This parasitoid may have been *Aphanogmus steinitzi* (Ceraphronidae) which has been found attacking *C. psociformis* in Italy (Sinacori *et al.*, 1992). Withycombe (l.c.) further reported that, in September, the cocoons of *C. psociformis* were preyed on by larvae of *Chrysopa tenella* (= *Cunctochrysa albolineata*).

Summary and Conclusions

Several species of chrysopids (green lacewings) are known to occur on top fruit trees. The larvae are voracious consumers of a range of prey species and in most chrysopid species the adults also are predatory. They offer some promise as biological control agents against fruit tree pests, particularly aphids. Techniques exist for the mass culturing of some species so artificial introduction is a possibility. The cost of this, plus the mobility of the adults, mean that the encouragement of natural populations of chrysopids is likely to be a more promising approach than mass release. The development of artificial hibernation sites for chrysopids in orchards is a possible way of enhancing survival. Some species of hemerobiids (brown lacewings) and coniopterygids (powdery lacewings) also occur on fruit trees. Their prey range is similar to chrysopids, though coniopterygids, being smaller, consume prey including mites. They have attracted less research attention than chrysopids but the possibility that hemerobiids may be active early in the year is worth investigating.

The Common Earwig

The common earwig, *Forficula auricularia*, is an omnivorous insect that feeds on plant material as well as on arthropod prey. Buxton (1974) summarised the types of arthropods taken by earwigs; their diet included many species of Lepidoptera, Coleoptera, Diptera, Homoptera, Hymenoptera and Collembola.

Earwigs mate in late autumn and the female then excavates an underground nest in which the pair overwinter. Eggs are laid in late winter and early spring, the first batch typically containing 30-40 eggs. The female then ejects the male from the nest as males eat the eggs (Guppy, 1947). By late spring most males have died. Females often lay more than one batch of eggs but all eggs are fertilised before the first oviposition (Behura, 1956). Females display maternal care for their young. The young leave the nest after moulting to the second instar. There are four larval instars; larvae from the first egg batch become adult around mid-July and those from the second batch in September. Orchard populations are highest between July and September (Alford *et al.*, 1980). Earwigs forage at night and shelter by day so populations in orchards are often underestimated.

Earwigs are predators of many of the economic pests of apple and pear. Asgari (1966) found that a total of 8700 green apple aphid, *Aphis pomi*, were eaten during earwig larval development; in these trials earwigs were shown to be more voracious predators than *Chrysopa vulgaris*, *Coccinella septempunctata* or *Anthocoris nemorum*. In pre-bearing apple trees in USA, Carroll and Hoyt (1984a) found that numbers of *A. pomi* declined from 500 per tree to less than 50 per tree within three weeks of releasing earwigs into the trees at a rate of 5-6 per tree. However, earwigs failed to control *A. pomi* on bearing apple trees (Carroll *et al.*, 1985). In a serological assay to determine the diet of field-collected predators in Ontario, Hagley and Allen (1990) demonstrated that earwigs were an important predator of *A. pomi* in these orchards.

Ravensberg (1981) determined that the numbers of woolly aphid, *Eriosoma lanigerum*, increased in orchards that had received applications of diflubenzuron - an insect growth regulator that is toxic to earwigs. The side effects of diflubenzuron on earwigs were further investigated by Sauphanor *et al.* (1993a, b). They examined effects in the laboratory and field and discovered sub-lethal effects that included reduced predatory efficiency. Noppert *et al.* (1987) developed a simulation model of earwig predation on *E. lanigerum* from laboratory and other published work, which predicted that earwigs could destroy a field population of *E. lanigerum*. Stap *et al.* (1987) and Mueller *et al.* (1988) demonstrated that the numbers of *E. lanigerum* remained low in trees where earwigs were present compared to trees from which earwigs were excluded; 30-35% of new shoots were infested in earwig-excluded trees compared to 10% where earwigs were present. New colonies of aphids were discovered generally by earwigs within two weeks. However, Carroll *et al.* (1985) found that earwigs were unable to control *E. lanigerum* on apple stool beds in USA.

McLeod and Chant (1952) found that earwigs consumed large numbers of oystershell scale, *Quadrospidiotus* sp., and brown scale, *Parthenolecanium corni*, in

laboratory feeding tests. Karsemeijer (1973) found that earwigs were a locally important predator of mussel scale, *Lepidosaphes ulmi*, in The Netherlands.

Phillips (1981) demonstrated that earwigs feed on the fruit tree red spider mite, *Panonychus ulmi*, apple psyllids, *Psylla mali* and the apple grass aphid, *Rhopalosiphum insertum*, in the laboratory. She detected remains of *P. ulmi* and aphid eggs in the gut of field collected earwigs but could not show any significant effect of earwigs on aphid populations in a cider apple orchard in England.

In France, Causse (1976) attributed the winter mortality of larvae of codling moth, *Cydia pomonella*, to predation by earwigs. Glen (1977) observed that earwigs preyed on codling moth eggs in semi-field conditions but concluded that, because of their low density when distributed naturally, these eggs were unlikely to form a major component of the earwig diet.

In a field trial in France to assess the effects of pesticides on beneficials, Sauphanor *et al.* (1993b) demonstrated that earwigs play an important role in regulating the numbers of pear sucker, *Psylla pyri*, in pear; there was a correlation between the toxicity of pesticides to earwigs and the consequent size of pear sucker populations. Sublethal effects caused by some pesticides on earwig behaviour allowed an upsurge in pear sucker numbers in a field trial (Sauphanor *et al.*, 1993b). Lenfant *et al.* (1994) and Sauphanor *et al.* (1994) showed in laboratory studies that third instar earwigs consumed 1000 pear sucker eggs per day. Third and fourth instar larvae attacked all pear sucker life stages.

Earwigs also consume plant material and, for this reason, are sometimes classed as a pest. Earwigs often produce secondary damage to fruit by excavating pre-existing damage. This can be very serious on soft-skinned varieties such as Discovery. Phillips (1981) determined that the gut of 20% of field-collected earwigs in autumn contained apple fruit. Windfalls had more feeding damage than fruit on the trees but damage to the fruit at harvest was extensive (nearly 10%) in some years. Patternotte (1993) reported that 14-18% of apple fruit was damaged by earwig feeding in an experimental orchard in Belgium. However, when Carroll *et al.* (1985) caged earwigs on apple plants they could find no primary feeding damage to the fruits. Lenfant and Sauphanor (1992) discussed the relative role of earwigs as pest and predator; in their trials, fruit damage was not correlated with the size of earwig populations.

Summary and Conclusions

Earwigs have been shown to feed on many economic pests of apple and pear including *Aphis pomi*, *Eriosoma lanigerum*, scale insects, *Panonychus ulmi*, *Cydia pomonella* (larvae and eggs) and *Psylla pyri* and they have proved effective biocontrol agents of *A. pomi*, *E. lanigerum* and *P. pyri*. They are also known to feed on plant material and may cause fruit damage close to harvest.

Aspects for future research and development are to 1) determine the circumstances in which earwigs feed on fruit and whether or not they cause primary damage; 2) determine whether earwigs feed on all apple cvs, or only the softer cvs. such as Discovery; 3) establish consumption rates of earwigs on important pest aphid species and the pear sucker *C. pyricola*; 4) examine the population dynamics of earwigs to determine the pattern of movement within and between trees at different times of year; and 5) determine the impact of pesticides used in orchards on the numbers of earwigs.

Ladybirds (Coccinellids)

Forty-two species of coccinellid are resident in the British Isles with about a further six species recorded on one or two occasions (Majerus and Kearns, 1989; Rotheray, 1989). Majerus and Kearns (1989) provide simple taxonomic keys to adults and larvae of the commonest resident species, supplementing the more comprehensive keys of van Emden (1949) and Pope (1953, 1973). Most coccinellids of the subfamily Coccinellinae are aphid predators. Predators in the subfamily Chilocorinae, such as *Chilocorus bipustulatus* and *C. renipustulatus*, feed mostly on scale insects. However, *Exochomus quadripustulatus* seems less dependent on a scale insect diet, as Radwan and Lovei (1983) found it associated with aphids on apple in Hungary. They showed it able to complete its larval development when fed exclusively on *Dysaphis devectora*, *D. plantaginea* and *Aphis pomi*, but not when fed *Eriosoma lanigerum*. Adults and larvae of the eight species of *Scymnus* and *Stethorus punctillum*, the UK members of subfamily Scymninae, feed mainly on Tetranychoid mites.

Coccinellids are the most common and intensively studied predators of aphids (Frazer, 1988). Hagen (1962) and Hodek (1967, 1973, 1993) reviewed the biology and ecology of the family. Within orchards, their abundance and voracity make them among the most important predators of all the important aphid species (Asgari, 1966; Carroll and Hoyt, 1984b; van Driesche *et al.*, 1987; Bhagat *et al.*, 1988; Hagley and Allen, 1990; Grasswitz and Burts, 1995). However, there have been few rigorous empirical studies to determine the effectiveness of coccinellids as predators of aphids in the absence of other predators (Frazer, 1988). Most aphidophagous species will take other prey when aphids are scarce; for example, *Coccinella septempunctata* was considered an important predator of *Adoxophyes orana* on apple in Germany (Auersch, 1960) and Holdsworth (1970b) found that larvae of *Adalia bipunctata* would eat first-instar codling moth. Apparently, both last-named coccinellid species attack pear psyllids in Poland (Wojnarowska *et al.*, 1960), as do *Hippodamia convergens* and *Coccinella transversoguttata* in British Columbia (Wilde, 1962; McMullen and Jong, 1967). Interestingly, although the first two species occur on pear in UK and all four species now occur in Washington, none has been reported feeding on pear sucker species.

The appearance of coccinellids on particular crop plants is sporadic and difficult to exploit effectively (Frazer, 1988). Adult coccinellids require quite high thresholds of aphid density to stimulate oviposition (Wright and Laing, 1980), giving prey populations an opportunity to develop beyond the capacity of predators to exert a significant impact on their numbers (Carroll and Hoyt, 1984b). Early attempts in the USA at inundative release of field-collected adult coccinellids on high value crops were counter-productive, as a high proportion of healthy individuals dispersed from crops without ovipositing (Kieckheffer and Olsen, 1974; Ives, 1981), whereas the numbers of parasitised individuals (Iperti, 1964; Frazer, 1988) which, being less mobile are easily collected, were enhanced (Hatch and Tanasse, 1948). The latter problem could be avoided by releasing healthy mass-reared individuals but, with the exception of the mealybug predator *Cryptolaemus montrouzieri* in Europe and *H. convergens* in the USA (Lisansky, 1990), economic production methods for indigenous UK species are lacking at present. Coccinellid eggs are usually laid in batches attached to vegetation. The potential numbers of aphids consumed from each

group of eggs is rarely maximised. However, as newly hatched larvae often remain on the egg-mass, cannibalising unhatched eggs and siblings before beginning their search for aphid prey. Compared to some other predator groups, the searching behaviour of coccinellid larvae is generally recognised as inefficient (Hagen, 1962; Hodek, 1973; Frazer, 1988). Prey is detected by contact, yet larvae spend most of their time searching uninfested tissues; for example, those of *Coccinella septempunctata* were found to spend just 3% of their searching time on the aphid-infested leaf lamina (Marks, 1977).

The biology and ecology of *Stethorus* spp. was reviewed by McMurtry *et al.*, (1970) and by Chazeau (1985). *Stethorus punctillum* is economically the most important member of the Scymninae, preying on *Panonychus ulmi* in European apple and pear orchards (Geier, 1951; Grob, 1951; Blair and Groves, 1952; Collyer, 1953a, c; Bognar and Csehi, 1959; McMurtry *et al.*, 1970; Comai, 1985). In North America this niche is occupied by *S. punctum* (McMurtry *et al.*, 1970; Sirles, 1985; Houck, 1986). However, Putman (1955) recorded that the introduced *S. punctillum* had displaced the indigenous *S. punctum* in orchards in Ontario. Collyer (1953c) made an initial study of the development and feeding rates of *S. punctillum* on *P. ulmi* on apple at East Malling but in-depth information is lacking. Collyer recorded adult beetles consuming an average of 20 adult *P. ulmi* per day and larvae an average of 24 per day. Fecundity of *S. punctillum* was also high, with approximately 12 eggs laid per female per day for a total egg production of 743-1290 (Putman, 1955). The searching and oviposition behaviour of *S. punctillum* is similar to that of the aphidophagous coccinellids (see McMurtry *et al.*, 1970). Unlike some predatory phytoseiids, *Stethorus punctillum* is unhindered by the webbing of two-spotted spider mite (*Tetranychus urticae*) (Chazeau, 1985). Consequently, it has the potential of becoming increasingly important as a biological control agent for this pest also, which is becoming more prevalent on orchard and other high value outdoor perennial crops in UK.

Summary and Conclusions

Most of the coccinellid species found in orchards are principally predators of aphids, though some species are consumers of scale insects and mites. The rather poor prey-searching efficiency of larval coccinellids and the high prey density required to stimulate oviposition by adults are undesirable characteristics for potential biological control agents. The mobility of adult coccinellids and the sporadic nature of their appearance on particular crop plants adds to the difficulty of exploiting them as a component of a pest management programme. The observation that *Stethorus punctillum* is an effective consumer of *Tetranychus urticae* and is not hindered by the webbing produced by the mite means that this species merits some research attention as a potential biological control agent on those crops (not apple and pear in the UK) when *T. urticae* is a pest.

Hoverflies (Syrphids)

The biology of the aphidophagous syrphids has been reviewed by Schneider (1969) and Chambers (1988).

Eleven species of aphidophagous syrphids were found in apple in The Netherlands (Evenhuis, 1966). The most abundant species in a SE England plum orchard were *Eupeodes corollae*, *Episyrphus balteatus* and *Sphaerophoria scripta* (Hartfield, 1997).

Syrphids have four developmental stages, the egg and three larval instars. Most aphidophagous syrphids overwinter as larvae. Adult females need to feed on pollen for the maturation of eggs (Schneider, 1948). The adults are very mobile and search out aphid colonies amongst which to lay eggs. Each species has a preference for where to lay eggs; some species lay eggs within the aphid colonies, actively touching the aphid body, and some on nearby uninfested plants (Chandler, 1968a). Chandler (1968b) found that oviposition by syrphids varied with the size of the aphid colony and that different syrphid species had different preferences for the size of colony in which to oviposit. Many aphids do not exhibit escape responses to ovipositing syrphids. The average egg production of *E. corollae* females has been reported to be 400 (Barlow, 1961; Wilkening, 1961).

As syrphid larvae feed mainly at night and shelter during the day, their abundance may be underestimated. The larvae are voracious predators. *E. balteatus* larvae consumed, on average, 416 *Aphis pomi* individuals during their development and the third instar larvae consumed 84% of the aphids taken (Wnuk, 1977). A similar pattern is found in other species (Benestad, 1970). Some aphid species are unsuitable as food. Zeki and Kilincer (1992) determined that *E. corollae* developed on rosy leaf curling aphid, *Dysaphis devectora*, the peach potato aphid, *Myzus persicae* and the mealy plum aphid, *Hyalopterus pruni* but not on the green apple aphid, *Aphis pomi*. In field trials, syrphid larvae have been seen feeding on *Psylla pyri* and *Psylla pyrisuga* in France (Nguyen *et al.*, 1984), *A. pomi* in USA (Carroll and Hoyt, 1984b) and India (Bhagat *et al.*, 1988), and *Eriosoma lanigerum* in India (Veerma and Singh, 1985).

Syrphids can be effective control agents in top fruit. In a field trial in apple in France, there was a reduction in the populations of *A. pomi* within three weeks of the release of *E. balteatus* (Marboutie, 1976). Wnuk (1977) found that *E. balteatus* could control populations of this pest in Poland at predator : prey ratios of up to 1 : 200 if the rate of increases of the pest populations was less than 16% per day. In the USA Tracewski *et al.* (1984) found that syrphids were the least abundant of predator groups in *A. pomi* infested apples but that the abundance of syrphid larvae was correlated significantly with changes in prey density. Large numbers of syrphids were found in unsprayed apple orchards in France in May and June (Bonnemaison, 1972) and Brown and Schmidt (1994) found that syrphids were present in 20% of *E. lanigerum* colonies in June in the USA. Failure of aphid control may be caused by the late appearance of gravid females or low densities of syrphids.

Syrphids are affected adversely by broad-spectrum insecticides (e.g. Vickerman and Sunderland, 1977; Van Rensberg, 1978; Hellpap, 1982). Hassan *et al.* (1983)

tested a variety of pesticides against beneficials, including *Syrphus vitripennis* larvae, in the laboratory. Of twenty insecticides tested, only diflubenzuron was classified as harmless to the larvae. All ten commercially available aphicides tested were toxic to the syrphid.

Efforts to attract adult hoverflies by using flowering plants has had limited effects on the numbers of syrphids in the crops. Lövei *et al.* (1993) calculated that syrphids penetrated 15 m into a wheat field that had *Phacelia tanacetifolia* and coriander sown as 'islands' within the field and Harwood *et al.*, (1992) found that the numbers of syrphids were higher in winter wheat crops that had wild flowers sown around their margins than in crops with no surrounding wild flowers. However, MacLeod (1992) found that adult syrphids foraged on coriander sown around a winter wheat field but that this did not affect the numbers of syrphids within the field. Hickman and Wratten (1996) investigated the effects of strips of *Phacelia* around winter wheat fields on the numbers of pest and beneficial species within the crop but obtained conflicting results. In apple orchards in Switzerland, Wyss (1995) determined that the numbers of aphids were lower in orchards undersown with wild flower mixtures; the numbers of predatory insects, including syrphid larvae, were higher in these orchards. These conflicting results may be due to the timing of flowering of plants in each trial, or to the great mobility of adult syrphids.

Summary and Conclusions

Syrphid larvae have been shown to be active predators of several species of orchard aphids and psyllids. They are susceptible to many pesticides. Adult syrphids have been shown to be attracted by flowering plants but experiments with such plants adjacent to or within crops have yielded equivocal results on the impact of syrphids on pest populations. Syrphids alone are unlikely to control aphid numbers reliably. However, they could play an important role as a component of biological control on apple and pear if the pesticide programme used allows their survival.

Aspects for future research and development are 1) determination of species of syrphids found in apple and pear orchards; 2) examination of the potential of flowering plants to attract syrphids and enhance populations in orchards; and 3) determination of the impact of any syrphid population enhancement on orchard pest populations.

Spiders

Spiders are polyphagous predators. They display a variety of prey-capture tactics. Some spiders (for example those in the families Araneidae, Theridiidae and Linyphiidae) spin silk webs to ensnare prey; these may be cribellate webs, cobwebs, sheet webs, funnel webs or orb webs (Roberts, 1985). Other spiders actively hunt their prey, for example Salticidae, Clubionidae, Philodromidae and Lycosidae.

Approximately 40 species of spider may be found in orchards (Chant, 1956a) and some are active throughout the year. Some spiders complete their life cycle in 1-2 years, whereas other larger ones require 3-4 years to become adult. However, very little is known about the life cycle of many individual species (Jones, 1983). Most spiders become adult in spring and lay eggs in the summer. The eggs hatch into spiderlings within a few days to several weeks. The larger species of spider that require more than one overwintering period before they are adult usually mature in late summer and construct their egg sacs; the spiderlings undergo limited development before overwintering (Jones, 1983).

Spiderlings leave the egg sac when they are capable of feeding. This minimises the opportunity for cannibalisation (Jones, 1983). Dispersal tactics are varied, some species moving a short distance away from the egg sac and others taking to the air on short lines of silk. By means of this aerial dispersal technique, termed 'ballooning', spiders can travel considerable distances and their presence in an orchard therefore does not depend on a neighbouring population (Bishop & Riechert, 1990).

There have been two main reviews of spiders as biological control agents (Riechert & Lockley, 1984 and Nyffeler and Benz, 1987). However, there has been very little work done on this subject, particularly in orchards. The most recent information on spiders in apple orchards in Britain details studies carried out, from 1952 to 1956, in Kent and Essex (Chant, 1956a, b). He found that the web-spinning Linyphiidae, Theridiidae and Araneidae were the most abundant families present in orchards (Chant, 1956b).

Spiders as biocontrol agents

Spiders rarely show specificity towards their prey. Generally, they attack prey relative to the rate of encounter (Riechert & Lockley, 1984). Spiders usually feed on prey that are smaller than themselves, the optimal prey length ranging from 50-80% of the spider's length (Nyffeler *et al.*, 1994). Small and immature spiders prey upon phytophagous orchard mites, in particular fruit tree red spider mite, *Panonychus ulmi*. Spiders can maintain themselves at low densities of mites (Chant, 1956a). However, spiders live and remain active for a long time in comparison to their prey and spiders often capture prey in excess of the quantity they consume (Riechert and Lockley, 1984). The process of external digestion creates a delay between prey capture and ingestion. Spiders will continue to attack and secure prey until the first prey can be ingested. This may explain why spiders capture more prey than they eventually consume.

Larger spiders in orchards, for example adult Araneidae, usually feed on insects such as winter moth, (*Optheroptera brumata*) larvae and adults, codling moth (*Cydia*

pomonella) larvae, apple sucker, (*Psylla mali*), aphids and some predacious insects (Chant, 1956a, b). In Kent and Essex, spiders that were found commonly in orchards preyed on *Panonychus ulmi*, *Psylla mali*, *Aphis pomi*, *Blepharidopterus angulatus*, *Anthocoris nemorum*, *Psallus ambiguus*, *Optheroptera brumata* (winter moth) larvae and thrips sp. (Chant, 1956a).

Generalist feeding ensures survival and this should be considered when examining spiders as potential biological control agents. If a pest reaches high numbers, then spiders will feed preferentially on it. However, once the numbers decrease they may then turn to alternative types of food. This could be advantageous provided the preference remains until the pest is below the economic threshold. Thus, spiders may act as buffers to limit initial exponential growth of pest populations (Riechert and Lockley, 1984). However, as non-specific predators, spiders cannot fit the mould of 'traditional' biocontrol agents. Their overall impact could be negative in a situation where they prey heavily on beneficials (Nyffeler *et al.*, 1994). However, this may enable them to survive periods of low pest density (Specht & Dondale, 1960).

There have been several studies suggesting that spiders may be a significant factor in the control of certain pests. Mansour *et al.* (1980), in Israel, found that *Spodoptera littoralis* larvae did not reach damaging levels on trees occupied by spiders, whereas significant damage was observed on trees from which the spiders had been removed. Further studies (Mansour *et al.*, 1981a) showed that spiders were responsible for a 98% reduction in the larval density of *Spodoptera*.

Wyss (1995) studied the effects of weed strips on aphids and their predators in apple orchards in Switzerland. *Dysaphis plantaginea* eggs on apple hatch early in the year, when few predators are present. Established strips of early-flowering weeds attracted predators from nearby. The first predators Wyss observed on apple trees were spiders, some of which had overwintered in the weed strips. He also found that web-spinning spiders, mainly *Araniella* spp., reduced the numbers of *D. plantaginea* and *Aphis pomi* returning from their summer hosts in autumn. Thus, the early appearance of spiders in spring, aided by the weed strips, and their long activity to late autumn, make them potentially useful biocontrol agents for these pest species.

Spiders exhibit specific habitat preferences in orchards, which segregate the trees into many niches. Orchard pests often occupy several of these niches. Hence, spiders may act in a complementary manner to suppress pest populations (McCaffrey & Horsburgh, 1980). Experimental releases of spiders may be unsuccessful due to the self-limiting effect of spider populations (Riechert & Lockley, 1984); the availability of suitable web and foraging sites is the limiting factor and migration or cannibalism occurs where spiders are at high densities. A particular spider taxon by itself is unlikely to effect control, yet the spider community may as a whole. It is important, therefore, to consider the conservation of a diverse spider fauna (Riechert & Lockley, 1984). Further work is needed to establish the extent to which the spider fauna act as beneficial predators in the orchard.

The effects of pesticides

The effects of pesticides on spiders in orchards are considerable. In a five-year study of the species composition of spider communities in orchards in Kent and Essex, Chant (1956a) found a total of 20 species in sprayed orchards and 41 in unsprayed orchards. McCaffrey and Horsburgh (1980) examined the spider fauna in apple orchards in Virginia and found 63 species in an abandoned orchard compared to 11-17 species in commercial orchards. A study in a Quebec apple orchard found that a significant decline in the average density of spiders occurred when broad spectrum insecticides were introduced into the spray programme (Dondale *et al.*, 1979). Mechanical damage during spraying is also a factor; a study carried out in Virginia found that the proportion of web-building spiders was less in orchards where an air-blast sprayer was used (McCaffrey & Horsburg, 1980). This was due probably to mechanical disturbance caused by high air speeds produced by the sprayer.

Spiders are rare in sprayed orchards until several weeks after the spraying has finished, when migrants are able to settle without being affected by spray residues. Many species found in unsprayed orchards seem indigenous and the species found in surrounding habitats (such as hedgerows) are different (Chant, 1956a). Therefore, most spiders must colonise sprayed orchards by migration from distant sites, probably by 'ballooning', as the surrounding habitat may not act as a reservoir.

In a study of the population development of the pear suckers *Cacopsylla pyri* and *C. pyricola* in orchards in The Netherlands, van der Blom *et al.* (1985) found that those orchards in which the pear sucker population remained very small throughout the year had an abundance of spiders, whereas orchards in which a significant increase in pear sucker was observed had very few spiders. They suggested that this was due to the use of less-selective pesticides in the orchards with the greater population of pear sucker. The use of pesticides that are relatively harmless to spiders could increase the effectiveness of natural predation and significantly reduce pest populations in orchards (Mansour *et al.*, 1981b). In a study on the effects of certain pesticides on spiders in Israel, Mansour *et al.* (1981b) concluded that there are pesticides with a low acute toxicity for spiders, which may be used in an integrated control programme. The study was carried out mainly in the laboratory and further work is needed, particularly in the field.

Summary and Conclusions

Spiders are polyphagous predators, attacking many orchard pest species. Populations of spiders are reduced by many of the pesticides used in orchards.

Aspects for future research and development are to survey the species of spiders found in orchards and conduct experiments to examine spiders' diet and the effectiveness of web-spinning spiders as predators of host-alternating aphid species returning to apple in Autumn.

Predatory Midges (Cecidomyiidae)

In UK, larvae of two genera of cecidomyiid midges, namely *Monobremia* and *Aphidoletes*, are exclusively aphidophagous. Harris (1973) incorporated *Phaenobremia* as a junior synonym of *Aphidoletes*. As implied by its specific epithet, larvae of *Monobremia subterranea* are of subterranean habit. The midge has been recorded feeding on the apple aphid *Dysaphis plantaginea* on the aphid's secondary host (Harris, 1973). The biology, morphology, taxonomy and economic importance of aphidophagous cecidomyiids was reviewed by Nijveldt (1988).

Harris (1973) synonymised 33 previously described species as *Aphidoletes aphidimyza*, the commonest species of the genus. He noted that the morphometrically similar conspecific *A. urticariae* has overlapping prey range, habits and habitats with *A. aphidimyza*, concluding that some reports attributing predation to the latter species may be erroneous. *Aphidoletes aphidimyza* occurs in a diverse range of habitats and feeds on an extensive range of aphid prey, including the apple aphids *Aphis pomi*, *Dysaphis devectora* and *D. plantaginea*, but none from pear (Harris, 1973). The predator has been reported as an important native enemy of apple aphids in Bulgaria (Pelov, 1977), Poland (Olszak, 1979) and USA (Holdsworth, 1970a; Adams & Prokopy, 1980; Tracewski *et al.*, 1984; van Driesche *et al.*, 1987; Kozar *et al.*, 1994). Unusually, *Rhopalosiphum insertum* has not been recorded as a prey species for *A. aphidimyza*. This may be an oversight as *Rhopalosiphum padi*, a species related closely to *R. insertum*, was found to be nutritionally superior to other common aphid species for mass-rearing this predator (Kuo-Sell, 1989).

Mass-rearing methods have been developed for *A. aphidimyza* (Rimpilainen, 1980; Markkula & Tiittanen, 1985) which can be obtained from commercial suppliers (Lisansky, 1990). Pupae can be cold-stored for up to 8 months with <9% mortality (Forsberg, 1980; Gilkeson, 1990).

The impact of inoculative releases of *A. aphidimyza* against aphid pests has been studied most often on protected crops (Mayr & El-Titi, 1973; Scopes, 1975; Asyakin, 1977; Bondarenko & Moiseev, 1978; Hansen, 1980; Markkula & Tiittanen, 1982, 1985; Gilkeson & Hill, 1987). Despite *A. aphidimyza* being a common predator outdoors, few studies have been reported of inoculative releases on unprotected outdoor crops (Meadow *et al.*, 1985; Markkula *et al.*, 1979; van Lenteren *et al.*, 1979). Those on apple are restricted to control of *Aphis pomi* in the USA (Bouchard & Hill, 1986; Morse & Croft, 1987; Lawson *et al.*, 1994; Grasswitz & Burts, 1995). Several reasons may contribute to this apparent limited interest in inoculative release on outdoor crops, not the least being the technical problems associated with containing such a mobile predator within defined experimental plots. Adult female midges require honeydew and aphids as an oviposition stimulus (El-Titi, 1973, 1974), so larvae are associated usually with high aphid densities. Newly-eclosed larvae have limited mobility and perceive prey by contact (Wilbert, 1973), starving when prey density is not high (Wilbert, 1972). Despite their requirement for a high prey density, actual prey consumption is relatively low, with as few as 7 adult *Myzus persicae* adequate for successful pupation (Uygun, 1971). Even a short period of starvation was found to induce premature pupation (Kuo-Sell, 1987). On a more positive

side, larvae are relatively unharmed by exposure to several acaricides, fungicides and some insecticides, but they are susceptible to several organophosphorus insecticides (Markkula & Tiittanen, 1976; Sell, 1984a,b; Helyer, 1991; Havelka & Bartova, 1992).

Larvae of *A. aphidimyza* are occasionally preyed upon by more generalist predators such as anthocorids (Olszak, 1979). They are host to a few hymenopteran parasitoids (Harris, 1973; Gilkeson *et al.*, 1993), the importance of which is unknown.

The midge *Feltiella* (= *Therodiplosis*) *persicae* is a little studied native predator of the two-spotted spider mite (*Tetranychus urticae*). It has not been recorded definitively on either apple or pear, although Collyer (1953a and b) reported larvae of an unidentified cecidomyiid preying on *Panonychus ulmi*. This was probably *F. persicae*. Its biology and distribution was summarised by Chazeau (1985). The predator is available commercially in UK. Introductions have been used successfully for the biological control of *T. urticae* in glasshouses (Helyer, 1993). Recent studies have been made of similar introductions of *F. persicae* for the control of the two-spotted mite on hop and on runner beans (Umpelby *pers comm.*, 1997). The taxonomic status of the genus *Feltiella* was reviewed recently by Gagne (1995).

Larvae of *Anthrocnodax fraxinella* have been recorded attacking eriophyoid mites on pome and stone fruits in Germany (Schliesske, 1992), but the predator has not been reported from UK.

Summary and Conclusions

Cecidomyiids have received relatively little research attention on apple and pear although some species are known to consume aphids on apple. The cecidomyiid species *Aphidoletes aphidimyza* can be mass cultured and has been the subject of much research on protected crops. It may have potential as a biological control agent against apple aphids. As growers move towards more-selective insecticides, natural populations of cecidomyiids may increase in orchards; although susceptible to organophosphorus insecticides, larvae of some species have been shown to be unharmed by several pesticides.

Parasitoids of aphids

Introduction

Apple and pear are attacked by a number of aphid species with varying degrees of severity (Blackman and Eastop, 1974, 1994; Savary, 1953; Solomon, 1987). The majority of these aphids attack the aerial parts of the trees causing some leaf damage. Of the two most common species on apple, the rosy apple aphid, *Dysaphis plantaginea*, is the most serious pest, as relatively small numbers can inflict economic damage on the crop. The aphids feed on developing leaves, resulting in yellowing and crinkling. More importantly, fruitlets close to the feeding site are small and distorted. *D. plantaginea* is also found on pear in warmer regions. For a review of the life history of this species see Bonnemaïson (1959).

Apple and pear aphids are attacked by at least one species of parasitoid, belonging to either the Aphidiidae (Ichneumonidea) or the Aphelinidae (Chalcidoidea) (Table 1). The majority of documented attempts to control apple and pear aphids with parasitoids have concentrated on using the aphelinid *Aphelinus mali* against the woolly apple aphid, *Eriosoma lanigerum*. This aphid can be a severe pest of apple (e.g. Weber and Brown, 1988). Feeding on roots, trunk or branches often causes hypertrophy and gall formation (Geoffrion, 1985). Much of the review will focus on the relationship between *A. mali* and *E. lanigerum*.

Biology of Aphelinus mali

Details of the life history of *Aphelinus mali* are given by Bonnemaïson (1965; 1974). Adult female parasitoids lay a single egg in each host, which develops through a number of larval stages, initially absorbing nutrients from the host's haemocoel, before feeding on internal organs. The parasitoid pupates inside the blackened aphid husk, from which the adult emerges. Records of the number of generations of the parasitoid each year in Europe range from 5 to 8, with an overwintering diapause at the pre-pupal stage. The extent of parasitism varies with environment conditions e.g. *A. mali* is not favoured by humid conditions. In comparison with its host, the adult parasitoid is more cold-hardy, but the aphid is able to develop at a lower temperature than the parasitoid.

In the field, the overall sex ratio of *A. mali* is slightly female-biased (Borg, 1952; Evenhuis, 1958). Asante and Danthanarayana (1993) showed that populations become increasingly female-biased as the host density increases. This was supported by observations of a seasonal effect, with the female bias at peak aphid population numbers during the summer. Increasing host size also leads to a predominance of females, with decreasing host size having the opposite effect (Mueller *et al.*, 1992). This study also showed that the levels of parasitism were inversely proportional to the size of the aphid colony. Extensive work on the effects of temperature on *A. mali* by Trimble *et al.* (1990) provides details of the post-diapause development threshold temperature and day-degree requirements for first and 50% emergence.

Table 1 Parasitoids of aphids attacking apple and pear (species which occur in UK are in bold)

Aphid Species		Economic Importance	Parasitoids
<i>Anuraphis farfarae</i>	Pear-Coltsfoot Aphid	0	<i>Ephedrus plagiator</i>
<i>Anuraphis subterranea</i>	Pear-Hogweed Aphid		<i>E. plagiator</i>
<i>Aphis pomi</i>	Green Apple Aphid	**	<i>E. plagiator</i> <i>Lipolexis gracilis</i> <i>Lysiphlebus fabarum</i> <i>Praon volucre</i> <i>Trioxys angelicae</i>
<i>Dysaphis devecta</i>	Rosy Leaf-curling Aphid	*	<i>Ephedrus persicae</i> <i>E. plagiator</i> <i>Praon sp.</i>
<i>Dysaphis plantaginea</i>	Rosy Apple Aphid	***	<i>Aphidius matricarae</i> <i>A. picipes</i> <i>E. persicae</i> <i>E. plagiator</i> <i>L. fabarum</i> <i>T. angelicae</i>
<i>Dysaphis pyri</i>		***	<i>E. persicae</i> <i>E. plagiator</i>
<i>Eriosoma lanigerum</i>	Woolly Aphid	**	<i>Areopraon lepelleyi</i> <i>Aphelinus mali</i> *
<i>Rhopalosiphum insertum</i>	Apple Grass Aphid	**	<i>E. plagiator</i> <i>Monoctonus cerasi</i> <i>Trioxys auctus</i>

Key to economic importance :
 0 - Not important
 * - Slight
 ** - Moderate
 *** - Most important

The biology and ecology of the interaction between the parasitoid and its host has been studied extensively, e.g. in Australia (Asante and Danthanarayana, 1993), China (Kuang *et al.*, 1989), France (Bonnemaïson, 1965), Iraq (El Haidari *et al.*, 1978), India (Thakur *et al.*, 1992), The Netherlands (Evenhuis, 1958), New Zealand (Dumbleton & Jeffereys, 1938), Palestine (Bodenheimer, 1947), Poland (Zawadska, 1962), Russia (Boldyreva, 1970), Spain (Castellari, 1967), Sweden (Borg, 1952) and the USA (Lundi, 1924).

All parasitoids listed belong to the Aphidiidae (UK species in bold), except *Aphelinus mali* (Aphelinidae). All host/parasitoid records are cited by Starý (1970, 1976), except for *A. mali*, which are cited by Bonnemaïson (1965).

Control of Eriosoma lanigerum with Aphelinus mali

The majority of biological control programmes using parasitoids against aphids on apple have focused on *Eriosoma lanigerum* and the parasitoid *Aphelinus mali*. Conclusions from these studies have been mixed, but have suggested mostly that biological control using *A. mali* is insufficient and should be included as part of an integrated control approach. Evenhuis (1958) considered that the longer generation time and lower fecundity of *A. mali*, relative to its host, were the principle reasons for inadequate control. The importance of selecting the most effective race of parasitoids was illustrated by Lung *et al.*, (1960, cited in DeBach, 1964) who showed that a Russian race of *A. mali* was more successful than the native parasitoid against *E. lanigerum* in China. Goryunova (1967) found that *A. mali* was not effective if the spring was cold and wet and the summer dull. In summarising twenty-five releases of *A. mali* between 1921 and 1939, DeBach (1964) reported that nine were considered to have achieved complete control, with 'substantial' control in twelve other cases. Wishart (1947) found that, following the introduction of *A. mali* into apple orchards in British Columbia, *E. lanigerum* outbreaks did not occur and the parasitoid had established successfully. Bénassy *et al.* (1964) reported good control of *E. lanigerum* by *A. mali* in France but noted that the parasitoid did not become established.

More recently, Bouchard *et al.* (1984) assessed a number of entomophagous species, including *A. mali*, for use against *E. lanigerum*. However, they suggested that Neuroptera offered the greatest potential as biocontrol agents. Tejada and Rumayor (1986) reviewed the pests and diseases of apple orchards in Mexico and found that *E. lanigerum* was present at very low densities with high (80%) parasitism by *A. mali*. Kuang *et al.* (1989) evaluated natural enemies of *E. lanigerum*, including *A. mali*, on apple in China. They found that the levels of parasitism peaked at 22-60% in June, but were too low in May (0.8-8%) when aphid numbers were highest. They also demonstrated in the laboratory that the intrinsic rate of increase of the aphid was higher than that of the parasitoid at 20 and 25°C, and recommended that integrated, rather than biological, control measures be used. Thakur *et al.* (1992) showed that the release of *A. mali* against *E. lanigerum* in apple orchards in India increased parasitism to between 49-69%, with an effective decrease in aphid populations of 23-36%. Similarly, Mohyuddin-Al (1992) reported a decrease in *E. lanigerum* populations following the release of *A. mali* in apple orchards in Pakistan.

Effects of insecticides on A.mali

Much of the literature suggests that aphid pests do better, or at least no worse, in orchards sprayed with pesticides compared to untreated orchards. In reviewing pest and beneficial arthropod management in apples, Croft (1993) discussed the problems associated with insecticide resistance and advocated a more biologically-based IPM approach. Stäubli *et al.* (1985) described a methodology for the field evaluation of pesticide applications in apple orchards.

Evenhuis (1959) examined the impact of DDT, gamma-HCH, diazinon and endosulfan on *A. mali* and found that these had little effect on parasitoid pupae. In assessing the impact of DDT on *E. lanigerum*, Carnegie (1965) found no subsequent upsurge in aphid populations which might have occurred had populations of *A. mali* been suppressed by the pesticide. In contrast, Schneider (1958) showed that DDT, gamma-HCH, parathion and diazinon eliminated populations of adult *A. mali* on apple in Germany. Van de Vrie (1965) examined the impact of a wide range of insecticides on *A. mali* and showed that only carbaryl and, to some extent, endosulfan were relatively harmless. Castellari (1967) found that infestations of *E. lanigerum* were larger on plots treated with insecticides, compared to those where *A. mali* was the principle controlling agent. For apple, Molinari (1986) recommended that systemic insecticides were used after flowering to encourage the development of natural populations of *A. mali*. Staubli and Chapuis (1987) showed that the use of pirimicarb in Swiss apple orchards was effective against young colonies of *E. lanigerum* and did not prevent the satisfactory development of *A. mali* populations. The assessment of four commonly used insecticides at four different time intervals after treatment on adult *A. mali* shows that phosalone was the least harmful, followed by endosulfan, when compared to methyl-demeton and phosphamidon (Gaffar *et al.*, 1989).

The distribution of *E. lanigerum* and its parasitoids was studied in insecticide-treated and non-treated apple orchards in Germany (von Kogler, 1989). Aphids were found in 22 out of 28 insecticide-treated orchards, but only in 2 out of 24 non-treated orchards. The presence of *A. mali* was noted wherever the aphid was found and the author suggested that selective insecticide treatments may allow biological control of *E. lanigerum* by the parasitoid. The effect of padding apple trees with monocrotophos against *E. lanigerum* was studied on apple trees in India by Natarajan (1990). The treatment was found to eliminate populations of *A. mali* and reduce aphid populations to levels comparable to those exposed to the parasitoid. Jenser and Balazs (1991) showed that the application of diflubenzuron in apple orchards led to an increase in the numbers of *Aphis pomi*, *Dysaphis devectora* and *D. plantaginea* and recommended the introduction of selective insecticides to promote the development of natural enemy populations.

More recently, Brown and Schmidt (1994) found that the use of pyrethroid sprays against *E. lanigerum* in US apple orchards did not affect aphid populations, or those of *A. mali*. Prokopy *et al.* (1996) examined the prospects for second-level IPM on apple in which chemically based control measures were used only for the first half of the growing season. They found that the level of damage on second-level plots did not differ from the level on those which had received chemical treatment throughout the season, and also

noted that parasitoids were more abundant on the former.

The effects of the fungicides carbendazim, mancozeb, captafol, difolatan and captan at five different concentrations were tested against *A. mali* mummies collected from apple trees in India (Rawat *et al.*, 1988). The authors concluded that the fungicides had no significant adverse effects on the mortality or emergence of adult parasitoids.

Alternative hosts

Olszak (1994) evaluated a number of plant species, including apple, as prospective sources of parasitoids in Poland. The parasitoids *Ephedrus* sp., *Praon* sp. and *Trioxys* sp. were found on apple which was infested by *A. pomi* and *D. plantaginea*. These parasitoids were also found commonly on spindle, *Euonymus europaea*, elder, *Sambucus nigra*, and snow-ball, *Viburnum opulus*, bushes. The author noted the presence of hyperparasitoids which significantly limited the abundance of parasitoids.

Hyperparasitism

The impact of hyperparasitoids on the primary parasitoids of *D. plantaginea*, *Rhopalosiphum insertum* and *Aphis pomi* (*Ephedrus nitidus*, *Monoctonus cerasi* and *Trioxys angelicae* respectively) was investigated by Evenhuis (1964) who noted that the three primary parasitoids were parasitised heavily by three to four hyperparasitoid species. Evenhuis (1968) found that populations of *Monoctonus cerasi*, the principle parasitoid of *R. insertum* in Dutch apple orchards, were not affected by the presence of hyperparasitoids. In contrast, the impact of primary parasitoids against *A. pomi* was affected adversely by hyperparasitoids. Von Kogler (1989) examined the potential for using *A. mali* against *E. lanigerum* in apple orchards, but noted the presence of four species of hyperparasitoid, *Asaphes vulgaris*, *A. suspensus*, *Pachyneuron solitarum* and *Aphidencyrthus aphidivorous*, which may have reduced the populations of *A. mali*.

Ant attendance

In a study of the effects of ant-tending of colonies of *D. plantaginea* on apple, Fontanari *et al.* (1993) used adhesive bands to exclude ants from trees. Where ants were absent, the numbers of predators, which included the aphid parasitoid *Ephedrus persicae*, were increased. The authors concluded that excluding ants from apple trees could result in decreased aphid damage through the action of natural enemies. Previous work on ant attendance using *A. mali* and *Aphidius colemani* against banana aphid showed that ants are particularly detrimental to the successful establishment of parasitoid species (Stechman *et al.*, 1996).

Summary and Conclusions

The extensive use of *Aphelinus mali* against woolly apple aphid throughout the world has produced a variety of, at times, conflicting reports as to its effectiveness and tolerance of insecticide programmes. If there is a consensus, it would appear to suggest a move towards selective insecticide use to encourage the development of natural or released

populations of this and other parasitoid species. No information is available concerning the use of this parasitoid in the UK and at present it is not available through the major suppliers of biological control agents e.g. CIBA-Bunting, BCP or Koppert.

Although parasitoids of apple and pear aphids, especially *A. mali*, have received considerable attention throughout the world, there is limited information available on the impact of these natural enemies in the UK. There is a requirement for research to determine the impact of UK parasitoid species on aphid pests of apple and pear.

Parasitoids of Codling and Other Tortricoid Moths

Tortricids have a reproductive capacity of approximately 50-200 per generation (Mills and Carl, 1991). The fruit tree tortrix, *Archips podana*, and the summer fruit tortrix, *Adoxophyes orana*, are common in apple and pear orchards; the codling moth, *Cydia pomonella*, is common in apple orchards and can occasionally be a pest of pear. *C. pomonella* and *A. podana* usually have one generation each year in the UK, but may have a second when conditions are favourable, whereas *A. orana* has two generations each year. Larvae of *C. pomonella* burrow into the fruit, whereas those of *A. orana* and *A. podana* cause surface damage. In all these species, however, each larva damages at least one fruit; thus they are all low threshold pests and intensive control measures are applied against them.

Parasitoids may play an important role in reducing the pest populations. Tortricids are attacked by a range of parasitoids but there is a major problem in their correct identification and association with the host species. There has been no comprehensive review of parasitoids of tortricid pests in the UK. However, there is a general review of tortricid parasitoids by Mills and Carl (1991) and Evenhuis and Vlug (1983) list and describe parasitoids of apple-feeding tortricids in the Netherlands.

Parasitoids may be grouped according to the host stage attacked, taking into account the mode of parasitism (ecto- or endo-parasites) and the form of parasitoid development (continuous or protracted) (Mills, 1992).

Egg parasitoids

The Trichogrammatidae is the only family that parasitises tortricid eggs. When an adult *Trichogramma* female encounters a suitable host egg, she examines it by drumming with her antennae. She then drills through the chorion with her ovipositor and lays one or more eggs, depending on the host egg's size (Hassan, 1994). The immature stages of *Trichogramma* eventually destroy their hosts by feeding on the egg contents (Schmidt, 1994). Parasitoid development is rapid; in the field *Trichogramma minutum* adults emerge about 17 days after *Choristoneura fumiferana* eggs are attacked (Houseweart *et al.*, 1983). Most egg parasitoids overwinter as quiescent or diapausing immature larvae inside their host egg (Boivin, 1994). The advantage of egg parasitoids as biocontrol agents is that they prevent hatching of the pest organism, leading to a considerable reduction in plant damage. In addition, egg parasitoids are mass reared more easily than other parasites of tortricids.

In 1926, the first mass production system for *Trichogramma* was developed using *Sitotroga cerealella* eggs (Flanders, 1929). Since then, large-scale *Trichogramma* production techniques have been improved and *Trichogramma* release developed as a biological control technique. In recent years, over 32 million ha of agriculture and forestry have been treated annually with *Trichogramma* to control insect pests (Li, 1994). However, there has been little work on the effectiveness of *Trichogramma* as a control agent for apple-feeding tortricids.

Wetzel *et al.* (1995) carried out investigations into the use of *Trichogramma* in apple orchards in Germany. The species they studied were *Trichogramma dendrolimi* and *Trichogramma cacoeciae*; *T. dendrolimi* is used in China and *T. cacoeciae* in Germany to control *A. orana* on apple. It was found that the dispersal radius for *Trichogramma* was very small. They discovered that, for effective control, 20,000 parasitised *S. cerealella* eggs were needed per tree. This produced a 50% reduction in fruit damage by *C. pomonella* and *A. orana* but was expensive, at a cost of 1000-2000 DM/ha - approximately ten times the cost of conventional pesticide treatments.

There are other problems pertaining to the use of *Trichogramma* as a biological control agent. *Trichogramma* overwinters inside the host egg. However, *C. pomonella*, *A. orana* and *A. podana* overwinter as larvae. There are other tortricids present in UK orchards but usually only in small numbers. Therefore, *Trichogramma* application is required every year. The predation of parasitised *S. cerealella* eggs by ants, earwigs and *Orius* is also a problem. The main users of *Trichogramma* are likely to be allotment-owners and organic growers who tolerate high levels of damage and don't consider the cost excessive (Wetzel *et al.*, 1995).

More work is needed to develop better *Trichogramma* strains, to look at the effectiveness of using a mixture of species and to examine further the conditions in apple orchards that limit the dispersal and efficiency of the parasite.

Egg-larval parasitoids

Egg-larval parasitoids are endoparasitic Braconidae that oviposit into the host egg. Development is then delayed until the host larvae are mature. An example is *Ascogaster quadridentatus*; the adult female oviposits a single egg into the host's egg, the parasitoid egg hatches in 2-3 days and the young larva penetrates the embryo of the host (Coutin, 1974). The parasitoid larva remains dormant until the host reaches its pre-pupal stage. Rapid development of the parasite then takes place; it moults twice before emerging from the host larva. After emergence, it spins a white cocoon in which it pupates (Rosenberg, 1934). *A. quadridentatus* overwinters as a 1st stage larva within the host, remaining inactive until spring (Coutin, 1974). *A. quadridentatus* appears to parasitise the Tortricidae Olethreutinae only (Evenhuis & Vlugg, 1983). These moths lay their eggs on the external surfaces of leaves and fruit, making them easily accessible to attack by parasitoids.

Larval parasitoids

There is a range of parasitoids of tortricid larvae, which are described briefly below. Examples are taken from parasitoids found commonly during studies on *A. podana*.

Braconidae - generally braconids are solitary endoparasitoids that attack young host larval instars.

Meteorus ictericus has three larval instars that develop inside the host. The third instar larva exits the host and spins a cocoon nearby. The host larva is not devoured entirely and remains alive for a period of time, eventually dying without further

development (Simmonds, 1947). Meteorinae overwinter as eggs or immature larvae within the host (Huddleston, 1980). They particularly parasitise Tortricidae, Hepialidae and Gelechiidae (Beech and Todd, 1985). *Macrocentrus linearis* completes its larval development externally. The fourth stage larva emerges from the host's body cavity and continues to feed, lying parallel to the host (Parker, 1931).

Ichneumonidae - the ichneumonids that parasitise young host larvae are generally solitary endoparasitoids. *Glypta fumiferanae* is a typical example. Oviposition occurs in 1st or 2nd instar host larvae. The mature parasitoids emerge from late host larval instars and construct characteristic 'cellophane-like' cocoons (Stairs, 1983). *G. fumiferanae* larvae overwinter within the host (Brown, 1946).

Tachinidae - tachinid parasitoids attack the host larvae in the mid to late instars and parasitoid development proceeds rapidly (Mills and Carl, 1991). Some tachinids, for example *Aplomyia ceaser*, oviposit eggs onto the host plant. These are consumed by the larvae and the larvae then hatch and bore through the gut wall into the haemocoel of the host. Others, for example *Hemisturmia tortricis*, deposit immature eggs onto the surface of the host larva; these hatch after 3-5 days and the parasitoid larvae bore through the host's intersegmental membranes. Other tachinids, for example *Lypha dubia*, deposit fully developed eggs on or near host larvae; these hatch immediately and the larvae locate and bore into their hosts.

Pupal parasitoids

The commonest tortricid pupal parasitoids belong to the family Ichneumonidae. *Itopectis maculator* is a solitary endoparasitoid that completes its development within the host pupa. The parasitoid oviposits into fresh host pupae or prepupae and the larvae develop continuously, eventually killing the host (Smith, 1932). *I. maculator* females also practice true predation on host larvae and pupae. The female impales the prey with her ovipositor and enlarges the hole with rotating movements. She then withdraws the ovipositor and imbibes the fluid flowing from the wound (Cole, 1967).

There have been many attempts at biological control of *C. pomonella*. Several parasitoids have been released in a number of countries but the only ones to establish were *T. minutum* in Australia and, temporarily, *A. quadridentata* in South Africa (Mills and Carl, 1991). The study by Wetzal *et al.* (1995) indicates that the reduction in fruit damage is not sufficient to make treatment with parasitoids in apple orchards economically viable.

Most studies of parasitoid occurrence have been conducted in unsprayed orchards. In these studies, egg parasitism has been in the range 0-30%, larval parasitism from 1-60% and pupal parasitism from 5-70%. Asynchronous (a different number of generations to the host) and synchronous parasitoids can act in a density-dependant manner (Mills and Carl, 1991). Thus, any species of parasitoid may provide some regulation of host population abundance and it is worth considering this when planning a control programme. It is unlikely that parasitoids can be used exclusively to control tortricid pests. However, the full impact of parasitoids on tortricid host populations remains uncertain and further work is needed to clarify the parasite-host relationship.

Summary and Conclusions

Aspects for future research are: to continue current MAFF-funded research to (i) determine the species of parasitoids attacking tortricids in orchards and the percentage parasitism by these species in orchards with different pesticide regimes and (ii) examine the biology of the effective parasitoid species and investigate possible means of enhancing their numbers in orchards.

Parasitoids of the European Apple Sawfly

Populations of the apple sawfly, *Hoplocampa testudinea* can be regulated naturally to some extent by a number of Ichneumonid parasitoids. In continental Europe the main parasitoid is *Lathrolestes ensator* (Zijp and Blommers, 1993; Carl and Kählert, 1993; Boevé, 1996; Badendreier, 1996); *L. ensator* occurs in the UK (Kloet and Hincks, 1978). *L. ensator* is an endoparasite which shows highly specialist host-finding behaviour as the parasitoid must locate larvae which are enclosed within apple fruitlets. The parasitoids are able to detect infested fruitlets while hovering above clusters (Badendrier, 1996). During host-location, the parasitoids may use chemical cues such as terpenoids emitted from the infested apples (Boevé, 1996). When an infested fruitlet has been located, the female searches for a few minutes and then probes her ovipositor into the apple near to a sawfly mine. She locates a suitable host and then oviposits. Badendrier (1996) found that only second instar larvae could be parasitised successfully. This was the case even when most of the larval instars were more mature. If only young larval instars are parasitised, then the searching period is limited; this may help to explain why female parasitoids and young sawfly larvae are synchronised closely (Zijp and Blommers, 1993).

Zijp and Blommers (1993) found between one and four eggs per host, although only one parasitoid pre-pupa was found per host. The parasitoid eggs are black and comma shaped and can be seen through the skin of the host by the time that the host leaves the fruitlet to overwinter and pupate. When the sawfly larva has formed a cocoon in the soil, the egg hatches and the parasitoid larva develops. It consumes its host and, by September, a parasite pre-pupa is found in the place of the sawfly pre-pupa. From the autumn until the following spring, the *L. ensator* pre-pupa develops gradually into an adult which emerges in May to June. This occurs at the end of the blossom period, when the host eggs and larvae are present. Some pre-pupae have a prolonged diapause and emerge after two winters rather than one.

Studies in Switzerland and France conducted by the International Institute of Biological Control (I.I.B.C.) have found parasitism levels by *L. ensator* of 40 % in one orchard in 1993 (Carl & Kählert, 1993). Rates of parasitism in The Netherlands were found to be up to 77 % in Integrated Pest Management orchards, and, estimated by rearing, between 14 and 44 % in an experimental orchard (Zijp & Blommers, 1993). The I.I.B.C. studies also found two other parasitoids, although these were present at lower levels: the larval parasitoid, *Lathrostizus macrostoma* which is not listed as a species which occurs in the UK, Kloet & Hincks (1978) and a cocoon parasitoid, *Aptesis nigrocincta*, which is found in the UK. The latter was responsible for parasitism levels of up to 15 %. The biology of *A. nigrocincta* was determined in a German study (Badendreier, 1996). *A. nigrocincta* can parasitise the apple sawfly for a longer period of time than *L. ensator*. It has two generations a year and so may be an important natural enemy. The first generation emerges in June, to coincide with the presence of cocoons. The females, which are nearly wingless, mate with the winged males and then oviposit in the host cocoon. The second generation occurs in close succession. The generations seem to overlap, oviposition by the second generation continuing until October. The main limitations of *A. nigrocincta* as a natural enemy of apple sawfly are that the numbers of mature eggs are small and the parasitoid has to search for cocoons within the soil.

In Poland, a different range of Ichneumonid parasitoids has been found to parasitise *H. testudinea*. The main species is *Lathrolestes marginatus* which has been found to parasitise up to 82% of *H. testudinea* (Karabash, 1966). *L. marginatus* can also be found in the UK (Kloet and Hincks, 1978). Like *L. ensator*, the life-cycle of *L. marginatus* closely follows that of the sawfly (Karabash, 1966; Jaworska, 1992). The parasitoid has one or two generations a year and overwinters in a cocoon inside the cocoon of the sawfly. The adults emerge after the sawfly, when sawfly larvae are present. The females oviposit into larvae in the fruit. The parasite completes its development when the host spins its cocoon. Jaworska (1992) also noted four other parasitoids, *Holocremna bergmani*, *Tersilochus jocator*, *Microcryptus abdominator* and *Hemiteles areator*, of which only *T. jocator* is listed as a British insect (Kloet and Hincks, 1978). Niezborala (1976) found that up to 33% of the sawfly larvae were parasitised by *L. citreus*, while 17.9 - 48.5% of the larvae were parasitised by an unidentified parasite whose eggs were encapsulated and melanized in the haemolymph. In Moldavia, Talickiej (cited in Jaworska, 1987) reared two other species, *Phygadeuon talitzkii* and *L. luteolus*. None of these species is found in the British Isles.

L. ensator is likely to be difficult to mass culture in the laboratory but fostering it as a natural enemy is still a promising control method. Once the parasitoid has been established in an orchard, it is likely that a natural population will build up as long as broad-spectrum insecticides are not used. One main disadvantage is that the adult parasitoids are likely to be very sensitive to insecticides. The main searching period is post-bloom when the young larval instars are present, which is also the time when spraying is likely. Other problems such as adverse weather conditions during this period may also affect the success rate. Although the mortality of larvae parasitised by Ichneumonidae may be as great as 60 - 100 % (Jaworska, 1992), entomogenous fungi and nematodes which infect larvae during their diapause in the soil may be more important control factors.

Summary and Conclusions

Research in other European countries has shown that several ichneumonid parasitoid species attack apple sawfly, particularly *Lathrolestes ensator*. Adults appear to be sensitive to broad-spectrum insecticides but studies in The Netherlands and Switzerland have shown high levels of parasitism by this species in orchards receiving only selective insecticides. The potential of *L. ensator* and other parasitoids as biological control agents against apple sawfly needs to be investigated in UK.

Parasitoids of the Apple Blossom Weevil

The apple blossom weevil, *Anthonomus pomorum*, is found mainly on apple and occasionally pear. It is still uncommon in commercial orchards in the UK, though it is increasing as a result of Integrated Pest Management (IPM) practices and the use of more selective insecticides. Birds such as sparrows, finches and tits have been found to account for up to 57 % of its mortality (Miles, 1923; Prieditis, 1975) and insects such as the thysanopteran *Haplothrips tritici*, which is found in the UK, can also act as predators of the larvae. However, the most important natural enemies are hymenopteran parasitoids.

Knowledge about the natural parasitoids of the apple blossom weevil is limited. The main parasitoid species in the UK is the ichneumonid *Scambus (Pimpla) pomorum* (Alford, 1984; Anon., 1985). Detailed studies of the biology of *S. pomorum* have been made in the UK by Imms (1918) and in The Netherlands by Zijp and Blommers (1992). The ichneumonid parasitises *A. pomorum* larvae while they are in the capped blossoms, depositing one egg on to each larva. The egg hatches after about three days and the ectoparasitic larva can be seen on the dorsal side of the host, with the mouth parts within the tissue. The larva progresses through four development stages. After 8 - 10 days, it leaves the host and spins a silken cocoon in the capped blossom. The adult wasp emerges in May or June, 15 - 23 days after spinning a cocoon. The adult is 5 mm long and is mainly black, with reddish brown legs. *S. pomorum* only has one generation on *A. pomorum*, although it may possibly parasitise a second host species in which to overwinter; whether it actually does so is unknown. In an experimental situation, it was possible for *S. pomorum* to overwinter in small conifer trees (Zijp and Blommers, 1996). *S. pomorum* can parasitise *A. piri*, the apple bud weevil; however, this pest is also found in the spring, albeit rarely in the UK (Alford, 1984).

Levels of parasitism by *S. pomorum* may be considerable. Imms (1918) examined 1270 infested apple buds and found that 27% contained larvae of *S. pomorum*. The levels of parasitism were much lower at Long Ashton, near Bristol (Miles, 1923), with only 12 specimens reared from 238 capped blossoms. Significant levels of parasitism have also been seen outside the UK, with 21.8% parasitism in orchards in The Netherlands (Zijp and Blommers, 1992) and up to 36% in Rumania. These levels of parasitism point to the potential benefits of conserving *S. pomorum* as a natural enemy of *A. pomorum*.

Zijp and Blommers (1992) also found two other parasitoid species in The Netherlands, *Habrocytus grandis* (Pteromalidae) and *Syrrhizus delusorius* (Braconidae), both of which are also found in the UK. *S. delusorius* targets the adult apple blossom weevil and has two generations a year. It overwinters as a larva in the abdomen of the adult weevil. The larva develops in the spring, feeding on teratocytes in the haemocoel of the host. The fully grown larva emerges in early May and spins a white cocoon in the soil, in which it pupates. The adult parasitoid emerges 3 - 3.5 weeks later in June. Emergence coincides with the presence of the next generation of adult blossom weevil. A partial second generation occurs, with the fully grown larvae leaving the hosts in July to pupate. The adult wasps emerge in August. The levels of parasitism by *S. delusorius* are variable, although reasons for this are unknown.

Imms (1918) has summarised other parasitoid species recorded from *A. pomorum*, of which those found in the UK include *Pimpla examinator*, *Scambus sagax* Hartig (Ichneumonidae), *Apanteles lateus* (Braconidae), *Apanteles impurus* (Braconidae) and *Meteorus ictericus* (Braconidae). The ichneumonid parasitoids *Scambus calobatus* and *Gregopimpla inquisitor*, which have been found to parasitise *A. pomorum* in Eastern Europe (Prieditis, 1975), are also found in Britain and may be important natural enemies. Lagowska and Winiarska (1982) reared larval parasitoids from *A. pomorum* in Poland. *H. fasciatus* and *S. annulatus* were the most abundant parasitoids, although neither of these species is found in the UK (Kloet and Hincks, 1978).

Broad-spectrum insecticides which were used originally to control *A. pomorum* have decreased almost certainly, the abundance of natural enemies also. In IPM orchards, selective insecticides should be applied to conserve the natural enemy population. The apple blossom weevil is a minor problem in orchards and so research into its natural parasitoids, which do not adequately naturally regulate numbers below the damage threshold, has a low priority.

Summary and Conclusions

Several species of ichneumonid and braconid parasitoids have been recorded as attacking apple blossom weevil in UK. Some old observations in UK, and a recent study in The Netherlands, have shown significant rates of attack by the ichneumonid parasitoid *Scambus pomorum*, suggesting that this would be a good starting point for any investigation of potential biological control agents against apple blossom weevil.

Parasitoids of Scale Insects

Karsemeijer (1973) reared three species of parasitoids from mussel scale, *Lepidosaphes ulmi*, in The Netherlands. They were the ectoparasites *Aphytis mytilaspidus* and *A. proclia*, and the endoparasite *Apterencyrtus microphagus*. However, he concluded that they were not important in reducing scale insect populations as the greatest extent of parasitism found was 26%; in most cases it was much lower. However, the parasitoids have been shown to be effective biocontrol agents in Nova Scotia (Pickett, 1965).

These three parasitoid species are recorded on the British list (Kloet and Hincks, 1978) but no research has been done on their presence in orchards or on their potential for biocontrol in the U.K. *L. ulmi* is often numerous on unsprayed trees in gardens, so these parasitoids may not be very effective at regulating numbers.

Witte and Lein (1992) studied the parasitism of overwintering *Lepidosaphes ulmi* and *Quadraspidiotus ostreaeformis* in an apple orchard in Germany from 1983-85. The degree of parasitism varied between years on average, and was higher on *L. ulmi* (8%) than on *Q. ostreaeformis* (3%); however, it was always low, the maximum recorded being 16%.

In the 1970s, Solomon (1973, 1974, 1975b) studied an outbreak of *Quadraspidiotus pyri* in an apple orchard at HRI-East Malling. In insectary and field experiments, he attempted to establish three species of parasites reared from *Q. ostreaeformis* and one raised from *L. ulmi* on *Q. pyri*. A species of *Prospaltella* and one of *Aphytis* from *Q. ostreaeformis* bred on *Q. pyri*, but both died after one generation.

The San Jose scale, *Quadraspidiotus perniciosi*, is a serious pest in many countries in Europe. It is not present in the U.K. but, if the climate becomes warmer, it could become a problem. There has been quite a lot of research on parasitoids of this species. Attempts at biological control have been made, using the aphelinid parasitoid *Encarsia perniciosi*, with some success (Katsoyannos and Argyriou, 1985; Mani *et al.*, 1995).

Summary and Conclusions

Several species of parasitoids have been shown to attack the scale insects *Lepidosaphes ulmi* and *Quadraspidiotus* spp. but the observation that population densities of these scale insects are sometimes high on unsprayed fruit trees suggests that natural populations of the parasitoids may not constitute a reliable regulatory mechanism. Little is known about their occurrence in orchards in UK. An examination of the species attacking populations of scale insects in orchards is a necessary starting point for any future research on their potential as biological control agents for scale insects in UK.

Parasitoids of Leafminers

Leafminer moths became serious pests in many apple and pear orchards in most European countries, particularly in southern Europe, from the 1950s onwards. It was surmised that one of the factors in this change in their pest status was the destruction of their natural enemies by pesticides. Surveys of parasitoids of leafminers were done in many countries. In general, these showed that each leafminer species was attacked by a complex (often over ten species) of parasitoids, though usually 2-3 species were numerically dominant. Several parasitoid species had more than one leafminer host. The results are discussed below in more detail, under the individual leafminer species that are most important in U.K. orchards.

Phyllonorycter (Lithocolletis) blancardella

In the Piedmont region of Italy, Arzone *et al.* (1983) found that *P. blancardella* was parasitised by a braconid, an encyrtid and twelve eulophids. The most active appeared to be *Sympiesis sericeicornis*, which was the last species to leave orchards when conditions became unfavourable, and *Apanteles lautellus*. The extent of parasitism differed markedly between orchards. In The Netherlands, van Frankenhuisen (1983) found that, in untreated orchards, *P. blancardella* was parasitised heavily (up to 65%), the main parasitoids being *Apanteles circumscriptus* and *Holcothorax testaceipes*. A later study by Blommers *et al.* (1990) found that *H. testaceipes* appeared to be synchronised badly with its host. By the time the adult parasitoids emerge in spring the host larvae have grown past the stage that the parasitoid prefers to attack. This poor synchronisation also occurs in the second generation and it is only in the third generation of the leafminer that much parasitism occurs. There is also a discrepancy between when the host and the parasitoid enter diapause and this may affect the survival of the parasitoid. Blommers *et al.*, (1990) speculated that the lack of synchronisation may be because *H. testaceipes* has only recently become a parasitoid of *P. blancardella*. It is not mentioned in several surveys of parasitoids in Europe in the 1960s and 1970s. Unlike many other parasitoids, such as *Sympiesis* spp. and *Pnigalio* spp., which attack many types of leafminers, *H. testaceipes* is more specialised, attacking only *Phyllonorycter* species on oak, willow and apple.

P. blancardella has become an important pest in parts of the USA and Canada and there have been several studies of its parasitoids there. Again, there is a complex of parasitoid species involved, usually from the same genera as in Europe, though different species are involved. There have been some attempts to import and release parasitoids from outside North America. Maier (1993) stated that *H. testaceipes* has several desirable attributes as a parasitoid, such as persistence at low host densities, oviposition in leafminer eggs and rapid dispersal after release.

Stigmella malella, Apple pygmy moth

Navone and Vidano (1983) reared a braconid and 13 eulophid species from *Stigmella malella* mines collected in orchards in the Turin region of Italy in 1976-81. Some of the eulophids sometimes acted as hyperparasites. Chambon (1981) surveyed the parasitoids of this leafminer in France. Again, a complex of species was involved with one, *Cirrospilus*

vittatus, parasitising up to 90% of the larvae in the third generation in October in the Paris region and *Tetrastichus pospielovi* attacking a large proportion of the pupae.

In East Germany, Mey (1989) reared thirteen parasitoids, mostly eulophids, from *S. malella*. *C. vittatus* and *Chrysonotomyia chlorogaster* were the commonest parasitoids of the larvae. He regarded *Chrysocharis prodice*, which attacks pupae and is restricted to the genus *Stigmella* as hosts, as the most important natural enemy. In unsprayed orchards, the extent of the parasitism often reached high levels and acted as a density-dependent mortality factor, working best at low host densities.

In The Netherlands, Eveleens and Evenhuis (1968) found that *C. vittatus* was by far the most numerous parasite of *S. malella*. Parasitism in the first generation of the leafminer was low but it was much higher in the second generation. Evenhuis and Soehardjan (1970) showed that the adult parasite also killed leafminer larvae by direct feeding; this could be an important mortality factor. However, phenological differences between the host and parasitoid meant that, in many cases, the parasitoid did not provide effective control. In a later paper, Evenhuis (1980) stated that *Chrysocharis prodice* was the most effective parasite of *S. malella* in The Netherlands, controlling the larvae within the mines at low population density. *C. vittatus* only regulated the leafminer at a level far above the economic threshold and the time of emergence between this parasitoid and the host did not coincide closely, possibly because it may have alternative preferred hosts. In contrast, *C. prodice* is well synchronised with *S. malella* and is specialised on this host (Gruys, 1980). It attacks all larval instars and can cause considerable mortality in the first and second generations. It caused high mortality in some years and the delayed density-dependence of this mortality suggested that it might be the agent regulating the population of *S. malella*. When collected and released into an orchard where it had been absent, its increase was associated with a gradual decline in the population of *S. malella*.

Leucoptera malifoliella (= *scitella*), Pear leaf blister moth

Santoro and Arzone (1983) reared nine eulophids and one braconid from *L. malifoliella* in Italy. *Chrysocharis nitetis* was the most widespread species and was the last to disappear from sprayed orchards. However, as it only became abundant late in the year, it could not contain the leafminer on its own. In Hungary, Balazs (1992) also found a complex of parasitoid species, with a different *Chrysocharis* species dominant, and showed that they were important in suppressing the pest. *C. nitetis* was the most frequent of sixteen parasitoids of *L. malifoliella* found in eastern Germany (Mey, 1993).

Effects of pesticides on parasitoids of leafminers

Several studies have shown that parasitoid populations are much larger in untreated than sprayed orchards. Balazs (1992) stated that parasitoids regulated numbers of *L. malifoliella* in untreated areas, whereas 4-5 insecticides per annum were required in treated areas. Mey (1988a) showed that pesticide treatments resulted in a strong decline in parasitism of *S. malella*, with the long persistence of many insecticides on the leaf surface important, as they could be toxic to parasitoids for some time. Regular insecticide treatments for codling moth usually coincided with the emergence and activity of

parasitoids of *S. malella*, causing severe mortality. He showed that dimethoate, cypermethrin, endosulfan, carbaryl and phosalone were highly toxic to the adults of three important parasitoid species (Mey, 1988b). The acaricides dicofol, propargite and azocyclotin also had high initial toxicity. Only diflubenzuron seemed to allow some survival. However, Gruys (1980) pointed out that there may be an indirect effect of diflubenzuron on parasitoids because of the reduction in numbers of available hosts.

Recent studies in Germany have looked at the effect of 'selective' insecticides used against tortricids or codling moth on leafminer parasitoids (Weiss and Vogt, 1994; Vogt, in press). They found that parasitism was less in plots treated with insect growth regulators (IGRs), such as fenoxycarb (Insegar), than in those treated with granulosis virus or left untreated, particularly in the early part of the season. Plots treated with diflubenzuron (Dimilin) or triflumuron (Alystin) had the least levels of parasitism. These reductions in parasitism were caused mainly by reductions in host numbers as a result of the insecticide treatments and could lead to problems with leafminer control later in the season.

In some cases, it may be possible to exploit 'biological windows' where a non-selective insecticide can be applied before a parasitoid has emerged in the spring, as has been used in the USA against *P. blancardella* before the parasitoid *Apanteles ornigis* emerges (Johnson *et al.*, 1976). However, persistent effects of the insecticide need to be considered. Celli (1972) showed that carbaryl had a long-lasting effect on parasitoids. Adult parasitoids, in particular, are very sensitive to insecticides.

Leafminer parasitoids in the U.K.

There have been no surveys of leafminer parasitoids in commercial apple or pear orchards in the U.K. The main records consist of species reared from *Phyllonorycter* mines in the leaves of *Malus* trees in northern England (Askew and Shaw, 1974). They listed eleven species of chalcids, all of which were also reared from mines of other *Phyllonorycter* species on other types of tree. They found the commonest species to be *Sympiesis sericeicornis*, *Pnigalio pectinicornis*, *Chrysocharis laomedon* and *Enaysma atys*. From limited sampling of mines of *Leucoptera malifoliella*, they found the commonest parasitoid to be *Chrysocharis nitetis*.

These records suggest that the important parasitoids of leafminers in the U.K. may be similar to those in The Netherlands and other parts of northern Europe. However, it is vital to get information from commercial orchards in the main fruit-growing areas, in terms of parasitoid species lists and relative numbers and also details of the phenology of the parasitoids and their leafminer hosts. Without such information, it is impossible to design a selective spray programme that will allow key parasitoids to survive in sufficient numbers to regulate leafminers at non-damaging levels. Reliance on chemical control is dangerous because of the ability of these pests to develop resistance to insecticides, as has been demonstrated in several regions of Europe and North America. Because most of these parasitoids have hosts on other tree species, it is also important to consider the environment around orchards and make it as attractive to these beneficials as possible.

Summary and Conclusions

Parasitoids play an important part in naturally regulating populations of several leafminer species on pome fruits in the UK. Severe local outbreaks of leafminers on occasions in recent years, possibly due to elimination of parasitoids by broad-spectrum pesticides, has highlighted the need for research and development into leafminers and their parasitoids, which have been little studied in the UK. Aspects which require study are as follows:

1. Obtain information on the species of parasitoids of leafminers present in U.K. apple and pear orchards.
2. Establish which are the key parasitoid species and study their phenology and that of their leafminer hosts.
3. Investigate the effects of pesticides on these key parasitoids.
4. Using information from (2) and (3), devise a spray programme for other key pests in which leafminer populations will be regulated.

Parasitoids of Midges

Relatively little research has been done on parasitoids of midges, in comparison to those that attack other pest groups such as aphids and moth caterpillars. However, in New Zealand, Todd (1956, 1959) showed that natural enemies, in particular parasitoids such as *Platygaster demades*, were important in regulating the numbers of leaf midge.

Coutin (1981) recorded ten species of parasitoids attacking *Dasyneura pyri*, the pear leaf curling midge, in France. In the South Tyrol, Carl (1980) found that the parasitoids *Inostemma contariniae*, *Platygaster marchali*, *Gastrancistrus* sp. and *Torymus rubi* caused the collapse of several outbreaks of the leaf curling midges *Dasyneura mali* and *Macrolabis* sp. on apple.

In The Netherlands, Van der Vooren *et al.* (1980) found three parasitoids of *D. mali*. The most important were the egg parasite *Platygaster demades* and the larval parasite *Torymus* sp. In 1979, *Platygaster* adults synchronised with the presence of the eggs of the first and second generations of the midge but parasitism of the second generation was low in most of the study orchards because few parasites were present during the main egg period. The effect on *D. mali* was apparently low in four out of five orchards but possibly considerable in the other. In later research in the same country, Trapman (1988) found the same species of parasitoid to be important and showed that, where endosulfan, which allowed parasitoids to survive, was used, the numbers of shoots attacked by midges fell dramatically. High levels of parasitism of *D. mali* could be found at the end of the summer and, where this exceeded 80% in August, monitoring for midges could be omitted the following spring.

Summary and Conclusions

Although little-studied in the UK, several species of parasitoids have been shown to be important natural enemies of apple and pear leaf midges in New Zealand and Europe.

A recent study in The Netherlands showed the egg parasite *Platygaster demades* to be a potentially effective biological control agent for apple leaf midge. Research on apple and pear leaf midges in UK should begin with an investigation of the species attacking midges in unsprayed or selectively sprayed orchards.

Parasitoids of Pear Sucker

The predominant pear sucker species in Britain and America is *Cacopsylla pyricola*. In continental Europe, the predominant species is *C. pyri*.

No systematic study of parasitoids of *C. pyricola* appears to have been done in Britain, though there are several *ad hoc* records of parasitoids including those of *Endopsylla agilis* (Diptera: Itonididae), *Prionomitus mitratus*, *Psyllephagus* sp. and *Trechnites psyllae* (Hymenoptera: Encyrtidae). British records of hyperparasitoids include *Asaphes vulgaris* and *Pachyneuron* sp. (Hymenoptera: Pteromalidae) (all records cited by Philogene and Chang (1978)). However, our experience is that parasitoids of pear sucker are very scarce in commercial pear orchards in UK.

Philogene and Chang (1978) reviewed the world status of parasitoids of *C. pyricola* and reported first records of *Trechnites psyllae*, a *Pachyneuron* sp. and a *Coccidencyrthus* sp. on pear in the Niagara Peninsula, Ontario. Parasitism levels of fifth instar nymphs ranged from 30 to 45%. *T. psyllae* was reared from 58% of mummified suckers and *Pachyneuron* sp. from 40%. *T. psyllae* was considered to be a primary parasitoid and the *Pachyneuron* sp. a hyperparasitoid.

The parasitoids of *C. pyri* have been studied more extensively in continental Europe, especially France. Rieux *et al.* (1990) and Armand *et al.* (1992) studied the parasitism of *C. pyri* in pear orchards in the Avignon-Montfavet area of France. The primary parasitoids which attack 4th and 5th instar nymphs are *Trechnites psyllae* and *Prionomitus mitratus* and the main hyperparasitoids are *Syrphophagus mamitus* (Hymenoptera: Encyrtidae) and *Pachyneuron muscarum*. However, Armand *et al.* (1992) found *T. psyllae* to be the only important primary parasitoid in a treated commercial orchard. They considered *P. mitratus* to be less well adapted to commercial conditions. *T. psyllae* was found to be effective against first generation *P. pyri*. *S. mamitus* was the main hyperparasitoid. *Psylla pyrisuga* was found to act as a relay host between the first and second generation of *P. pyri*. The primary parasitoid was found to be an important natural limiting factor in the population dynamics of pear sucker. Total parasitisation levels exceeded 30% in summer. Rieux *et al.* (1990) gave a bibliographic review of the species of parasitoids of the pear sucker species in Europe and America. Several records of the above parasitoids in France, Switzerland, Italy, Germany, Yugoslavia, Poland, USA and Canada are cited.

The scarcity of parasitoids of pear sucker in UK pear orchards is probably due to the intensive use of broad-spectrum insecticides to control pear sucker and other pests. Adult parasitoids are particularly susceptible to insecticides including their residues on plant surfaces. A study of the occurrence of pear sucker and its parasitoids on unsprayed pear trees in Britain might reveal the potential of exploiting parasitoids as natural enemies. An important aspect for study is the effects of pesticides on parasitoids and hyperparasitoids.

Summary and Conclusions

Levels of parasitism of *Cacopsylla pyricola* in UK orchards are very low, although high levels have been recorded in Canada; in Europe, high levels of attack by several parasitoid species have been recorded in populations of the non-UK sucker species *C. pyri*. A starting point for an investigation of parasitoids of *C. pyricola* in UK would be a search for parasites in sucker populations on unsprayed pear trees.

Parasitoids of Leafhoppers

Leafhoppers have increased in abundance in commercial apple orchards in recent years. They feed on the mesophyll cells on the underside of the leaves, leaving a characteristic white speckling: this may reduce the photosynthetic activity and hence the vigour of the plant. Excrement may also spot the fruit, reducing the quality. The main species on apple is *Edwardsiana crataegi*, with *E. rosae* and *Alnetoidia alneti* occurring in small numbers. These species are in the sub-family Typhlocybinae (Cicadellidae). A survey of leafhoppers and damage to apple has been conducted recently by Jay and Cross (1997). Similar species are found on pear though in much smaller numbers in commercial orchards (Alford, 1984).

Spraying with insecticides such as carbaryl can control leafhoppers although there is increasing concern about insecticide resistance (Charles *et al.*, 1994); other control methods such as biological control should be considered. In the UK, the main parasitoids of leafhoppers belong to the families Pipunculidae (Diptera) and the Dryinidae (Hymenoptera). These target the nymphal or adult stages and the Typhlocybinae are common hosts. Egg parasitoids belong to the families Mymaridae (Hymenoptera) and the Trichogrammatidae (Hymenoptera) and are important egg parasites of leafhoppers. However, most records occur in the US, southeast Asia, Australia and New Zealand. Parasitoids of leafhoppers have been reviewed by Freytag (1985) and Waloff and Jervis (1987).

Pipunculid parasitoids of the Typhlocybinae belong to the genus *Chalarus*. There are ten British species of *Chalarus*: *C. argenteus*, *C. basilis*, *C. fimbriatus*, *C. griseus*, *C. latifrons*, *C. parmentari*, *C. pughi* and three species which are unnamed (Jervis, 1980a, b). Female *Chalarus* generally select only 3rd, 4th and 5th instar nymphs in which to oviposit, probably on a size basis (Jervis, 1980a). Eggs are deposited singly and are injected into the host's abdominal haemocoel. There are two larval instars, the second only occurring in the adult host. The larva consumes most of the host's tissues and emerges by rupturing an intersegmental membrane. The parasitoid then pupates in the soil, leaf litter or the host's food plant. Only one parasitoid develops per host. However, super-parasitism has been recorded in most species. For example, with *C. fimbriatus* parasitising *A. alneti*, there was 20% mortality of the progeny. Mortality of 16.5% was also found due to encapsulation by *A. alneti*. In 1976, Jervis (1980b) recorded levels of parasitism from leafhoppers collected from mixed broad-leaved woodlands in Wales. Levels of parasitism due to *Chalarus* sp. were higher for *A. alneti* at 21.2% but lower for samples of *Edwardsiana* sp. (14.5% for the first generation and 7.6% for the second generation). Jervis (1980b) summarised the host relationships of British *Chalarus*; the potential parasitoids of host species found on apple and pear are shown in Table 2.

Table 2. Pipunculid species which parasitise Typhlocybinae of importance on UK apple and pear.

Host	<i>Chalarus fimbriatus</i>	<i>Chalarus pughi</i>	<i>Chalarus parmenteri</i>	<i>Chalarus</i> sp. A	<i>Chalarus</i> sp. C
Erythroneurini					
<i>Alnetoidia alneti</i>	✓				✓
Typhlocybini					
<i>Edwardsiana rosae</i>				✓	
<i>Edwardsiana</i> sp.	✓	✓		✓	
<i>Typhlocyba quercus</i>			✓	✓	

From Jervis (1980b).

The main Dryinid parasitoids in Britain belong to the genus *Aphelopus*, with five main species (*A. carnus*, *A. holomelas*, *A. melaleucus*, *A. nigriceps* and *A. serratus*) (Jervis, 1977 & 1980b). The Dryinidae may be wingless and may have chelate front legs with which they seize their prey. *A. nigriceps* and *A. serratus* do not have chelae but catch the nymph and hold it with the front and middle pairs of legs. Oviposition can take place in any of the host's five nymphal instars, with the egg being injected into the abdomen, as with the Pipunculidae. The eggs hatch when the host has reached the fourth or fifth nymphal instar, or adulthood. Dryinid parasitoids have five larval instars, although only the 1st and 2nd instars are spent within the host's haemocoel; the late second and subsequent instars are semi-external. The parasitoid's head and part of the tail region remain inside the host; the remainder of the body is external and, contained in a brown/black sack composed of moulted exuviae, curves between the attachment points in an arc. Larval development takes about six weeks and then the fifth instar splits the sack, with the head remaining attached to the host while the parasitoid consumes it. The larva then moves away and spins a cocoon in the soil or the leaf litter; the cocoon develops into a pre-pupa. Emergence of the adults occurs three weeks after formation of the cocoon. Most *Aphelopus* are either uni- or bivoltine. *Aphelopus* sp. have been found to cause up to 20% parasitism of first generation *Edwardsiana* sp., 23% parasitism of second generation *Edwardsiana* sp. and 3.4% parasitism of *A. alneti* (Jervis, 1980b). *Aphelopus* sp. which parasitise host species found on apple and pear are shown in Table 3.

Table 3. Dryinid species which parasitise Typhlocybinae on UK apple and pear

Host	<i>Aphelopus melaleucus</i>	<i>Aphelopus holomelas</i>	<i>Aphelopus serratus</i>
Erythroneurini			
<i>Alnetoidia alneti</i>	✓		✓
<i>Zygina</i> sp.		✓	✓
Typhlocybini			
<i>Edwardsiana crataegi</i>	✓*		
<i>Edwardsiana rosae</i>	✓		
<i>Edwardsiana</i> sp.	✓	✓	
<i>Typhlocyba quercus</i>	✓	✓	✓

From Jervis (1980b), * Richards (1939).

Although egg parasitoids are not major control agents of leafhoppers in the UK, they do control species of importance and so are mentioned briefly in this section. The Mymaridae, known as fairy flies, develop endoparasitically and have four main genera: *Anagrus*, *Anaphes*, *Gonatocerus* and *Polynema* (Waloff and Jervis, 1987). In New Zealand, the summer eggs of *T. froggatti* were parasitised by *Anagrus armatus* (Teulon & Penman, 1986a). The presence of a parasite is shown generally by a red pigmentation of the eggs. By counting the numbers of red eggs, Teulon and Penman (1986b) showed an average of 74.2% parasitism in March to May, which is similar to the value obtained by Dumbleton (1937). *Anagrus atomus* has also been shown to parasitise *E. rosae* and *R. debilis* on *Rubus* spp. and *T. quercus* on *Quercus robur* in Italy. *A. atomus* has a high biotic potential and a number of generations per year (Arno *et al.*, 1987). British species of *Anagrus* do occur, although mostly on grassland leafhoppers (Walker, 1979).

The effects of parasitism on cicadellid hosts are similar for the Pipunculidae and the Dryinidae. The internal reproductive organs are reduced or suppressed for both sexes. This is known as 'parasitic castration'. Parasitism can also reduce the development of the external genitalia if the leafhopper is parasitised in the nymphal stage. In males, the aedeagus and styles may be reduced while, for females, the ovipositor is shortened. Parasitic castration is an important contributory factor in biological control as the breeding potential of the host may be reduced. Other visible differences are that males parasitised by the Pipunculidae may be paler and resemble females more closely and that wing venation may be altered. Although the pipunculid larvae are internal parasitoids, locomotion of the host is not affected usually until the pipunculid larva has reached the late first instar development stage (Jervis, 1978; Waloff, 1980).

It is helpful to have some knowledge of the biology of the parasitoids and hosts if parasitoids are to be used for biological control. Most *Aphelopus* and *Chalarus* species occur as adults in the spring and early summer. This is because some species such as *A. serratus* are univoltine and species which are bivoltine generally enter diapause early in the season (Jervis, 1980b). Most parasitoids show good temporal synchronisation with their hosts, for example *C. exiguus* emerges later than *C. fimbriatus* and *C. sp. A nr. spurius*, as it has a late emerging host, *A. alneti* (Jervis, 1980c). Parasitoids emerge to synchronise with the occurrence of the correct host stage and they often emerge slightly later than the adult leafhoppers. For example, adult parasitoids of the mymarid *A. armatus* emerge after the leafhopper adults, when the eggs will be present. If insecticide is applied after the leafhopper nymphs have emerged, but before the parasitoid emerges, parasitoid populations will be safeguarded while affording some control of the pest (Teulon & Penman, 1984). This type of situation can also be seen with *E. rosae*. The majority of *E. rosae* adults disperse from rose to their secondary host between the 2nd and 4th weeks of June in UK, leaving only a small population of leafhoppers comprising individuals infested with dryinid or pipunculid parasitoids together with some apparently healthy late-hatching insects (Chiswell, 1964). If an IPM programme is to be developed, it is also important to know if there are any such periods when an insecticide could be applied, while safeguarding the parasitoids.

Summary and Conclusions

1. Parasitoids may be important natural enemies of leafhoppers.
2. The presence and abundance of leafhopper species in the UK, especially *E. crataegi*, should be monitored.
3. The harmful effects of pesticides (used for controlling other pests) on the parasitoids should be investigated and how the choice and use of pesticides can be manipulated to minimise adverse effects.
4. Mass rearing and inundative release of leafhopper parasitoids is unlikely to succeed due to the difficulty and cost involved. However, the possibility of 'seeding' absent parasitoids in orchards should be considered.
5. Priorities for research should include screening pesticides for their effects on parasitoids of leafhoppers, conducting bioassays to determine the levels of resistance to insecticides in leafhopper populations, and monitoring leafhopper species and abundance in UK orchards.

Virus diseases

Viruses are amongst the most important groups of pathogens of insects and have perhaps the greatest potential for exploitation as biological control agents. Morphologically, they can be divided into two categories: 1) viruses with occlusion bodies where the infectious agents or virions are embedded in a regularly shaped protective protein crystal, 2) non-occluded, free virions.

The most extensively researched insect viruses belong to the family Baculoviridae with characteristic rod shaped virions containing double-stranded DNA. Two different types of Baculovirus can be distinguished: 1) nucleopolyhedroviruses (NPV) with many virions in their occlusion bodies, 2) granuloviruses (GV) which contain only one virion in their occlusion bodies. General information about Baculoviruses is given by Kurstak (1991).

Numerous insect viruses have been catalogued by Martignoni and Iwai (1981, 1986). Most records are of viral diseases which have been reported as naturally occurring in their hosts. However, in a few instances, the disease results from inoculation with a virus isolated originally from another host.

Several naturally occurring virus diseases of insect pests of apple and pear have been identified, mainly of tortricids, and have been exploited as biological control agents (Zimmerman and Weiser, 1991; Huber and Hassan, 1991). The best known and most extensively researched example is the codling moth (*Cydia pomonella*) granulovirus (CpGV). The virus diseases of the summer fruit tortrix moth, *Adoxophyes orana*, have also been studied extensively. Three baculoviruses of *A. orana*, including a nucleopolyhedrovirus (NPV) and two granuloviruses (GV) have been tested for use in the field (Flückiger, 1982).

Insect virus diseases are usually highly host-specific. In most cases a given virus can be applied as a biological control agent only against a single pest species, whereas the fruit grower usually has to deal with a whole complex of pests. High selectivity is desirable from many points of view. However, the potential sales market for the virus preparation is limited. The high costs of product development, registration and manufacture have been the main barriers to the commercial exploitation of insect viruses which, in many other respects, are ideal biological agents.

An important limitation to the effectiveness of baculoviruses as biological control agents is their sensitivity to degradation by UV light. They are of short persistence in the field outside their host. Improved formulation to overcome this problem might improve their effectiveness significantly.

Advances in genetic engineering have made possible the development of recombinant baculoviruses. The pathogenicity of the virus is combined with the insecticidal action of a toxin, hormone or enzyme. This speeds up the action of the virus on the pest which dies from the effect of the foreign protein expressed by the recombinant virus rather than from the viral infection. The technology has been overviewed recently by Bonning and Hammock (1996). From a technical point of view, the genetic modification of insect virus

diseases has great potential for the future. However, strong public concerns about the release of genetically modified material, especially microbial agents, into the environment and tough regulatory hurdles, are strong barriers to the commercial exploitation of this technology.

Below, the known virus diseases of pests of apple and pear are each covered briefly and the potential for their exploitation as biological control agents and opportunities for further research are discussed.

Codling moth (Cydia pomonella) granulovirus (CpGV)

The identification, mass production, testing and commercial exploitation of CpGV, an important event in the annals of insect pathology and biological control, have been reviewed recently by Falcon and Huber (1991).

The virus was isolated first from dead overwintering codling moth larvae collected in Mexico (strain CpGV M) in 1963 (Tanada, 1964; Thomas and Poinar, 1973). Several other wild type isolates were identified subsequently from Russia and England. CpGV was field tested first in California and subsequently in many other areas of the world including Europe and the United Kingdom (Glen and Payne, 1984; Ballard, 1988). Extensive field trials demonstrated CpGV to be an effective biological control agent for codling moth.

The most important points pertaining to the use of CpGV as a biological control agent are as follows:

- 1 On apple and pear it is highly host specific to codling moth, though it is also an effective biological control agent for the pea moth, *Cydia nigricana*, and is moderately active against the pine shoot moth, *Rhyacionia buoliana*. It is ineffective against the plum fruit moth, *Cydia funebrana*. The high selectivity allows natural enemies of other pests to flourish, so avoiding outbreaks of secondary pests.
- 2 It is highly virulent against codling moth larvae, particularly neonates. The normal dosage is $0.5-1.0 \times 10^{14}$ granules per hectare.
- 3 Until now, the virus has been produced commercially in its host, larvae of the codling moth, though larvae of the false codling moth, *Cryptophlebia leucotreta*, have been used as an alternative (see below). Mass production in host insects is labour intensive and costly. Current formulations of the product available in USA and continental Europe are expensive, making an effective control programme with the virus several times more costly than a control programme using conventional insecticides. The high cost of achieving control with CpGV relative to the costs of insecticides is the main barrier to the commercial use on a large scale. Little progress will be made in the UK or elsewhere until the costs of CpGV to the grower are reduced substantially or until the codling moth develops multiple insecticide resistance so that it cannot be controlled with insecticides. Commercially available products have a shelf life of up to two years when stored in fridge and/or freezer conditions.
- 4 The persistence of the virus outside its host in orchards is short. It has been

demonstrated that the application of weekly one-tenth dose sprays, added to regular fungicide sprays, is an effective strategy of use, overcoming the need for precise timing (Dickler and Huber, 1986). Local research is needed to identify the best way of using CpGV in an IPM strategy meeting local requirements.

- 5 The efficacy of CpGV in numerous field experiments has ranged from 70 to 90% control, somewhat lower than for the best insecticides where codling moth populations have not developed resistance to insecticides. However, considerable additional winter mortality is caused by the virus. The use of CpGV in combination with insecticides is probably the most appropriate strategy for exploiting the virus in an IPM programme in the UK.
- 6 Current 'wild type' strains of CpGV act more slowly than conventional insecticides. Young codling moth larvae are able to cause limited surface injury to apple fruits before they die. This injury can be of economic significance and is a significant barrier to the widespread commercial adoption of the virus. A fast-acting *egt*⁻ strain of CpGV is being produced at HRI-Wellesbourne by genetic modification (see below).

The first commercial CpGV product, SAM406, was developed by Sandoz Inc in USA in 1980, but, despite good results in field tests, commercial development ceased in 1982. It was re-started in 1985 by Microgenesys Inc, USA, who produced a product named 'Decyde'.

Three commercial formulations of CpGV are available currently in Europe as follows:

- 1 Granupom, a liquid product registered in Germany (registration in Belgium and Italy pending), formulated for AgrEvo by a German intermediary company, GAB, from virus produced at the Chelchize Institute, Budweis, Czechoslovakia. This product is of high quality but is sold mainly to gardeners by a garden products retail company, Neudorff. Early formulations developed by AgrEvo were contaminated by yeasts and bacteria which fermented in the pesticide container, causing the containers to explode when being handled by growers. The fermentation problem was solved by adding ascorbic acid to lower the pH of the formulation but this severely reduced the activity of the virus. These occurrences damaged the reputation of CpGV in Germany. A further difficulty arose when the false codling moth, *Cryptophlebia leucotreta*, a species with larger larvae than *C. pomonella* and which is easier to mass culture because it is not cannibalistic, was used for mass culture of the virus in an attempt to reduce production costs. CpGV was contaminated heavily by the granulosis virus of the false codling moth (ClGV). The use of *C. leucotreta* for mass production was discontinued. These difficulties have undermined grower confidence in CpGV in Germany.
- 2 Carpovirusine, produced in France by INRA and a private company. Carpovirusine is a solid, deep frozen product containing artificial codling moth larval diet in addition to CpGV.
- 3 Madex, a liquid formulation produced on a small scale by Andermatt, Switzerland, registered in Switzerland.

In the late 1980s, the Agricultural Genetics Company, UK, began the development of a CpGV product but commercialisation was not pursued for financial reasons. In UK, where codling moth usually has only one, but sometimes two, generations per annum, control is achieved easily by insecticidal sprays, including the selective chitin synthesis inhibitor diflubenzuron. It is also controlled by several OPs and carbamates used for controlling other pests, especially those used for control of the summer fruit tortrix moth, *Adoxophyes orana*. Registration of the juvenile hormone analogue insect growth regulator fenoxycarb (Insegar) in February 1997 has provided a further new means of control of *C. pomonella*, against which it has strong ovicidal activity.

An important recent development is the production at HRI Wellesbourne (D Winstanley, pers comm) of a genetically engineered *egt*⁻ strain of CpGV, which has a faster action on its host which stops feeding at an early stage of infection. This is probably the first genetically-modified granulosis virus, though several genetically-modified nuclear polyhedrosis viruses (for control of pests of other crops overseas) have been available for some time. Important progress has been made at HRI Wellesbourne, where a genetically manipulated CpGV lacking the *egt*⁻ (ecdysteroid-UDP glucosyl transferase) gene is being developed. Preliminary studies suggest that the recombinant virus kills faster and reduces feeding in the infected larvae compared to the wild type CpGV (D. Winstanley, pers. comm.). This recombinant CpGV may provide the basis for the first commercial genetically improved granulosis virus product. It is believed that the problem of surface injury to fruits will be reduced or greatly eliminated by the use of this genetically manipulated CpGV, though this has not yet been demonstrated in the field. The enzyme, which occurs naturally in the virus and the host, is responsible for naturally regulating concentrations of the moulting hormone ecdysone in the host. First instar codling moth larvae stop feeding at an early stage of infection and die more rapidly. Cessation of feeding is a normal physiological response to increases in ecdysone concentration which occur shortly before moulting. This genetically modified virus offers exciting prospects for overcoming one of the main barriers to the widespread commercial use of CpGV. It is hoped that the regulatory and public view of this form of genetic modification by the deletion of such a gene will be more acceptable than adding genes from other organisms.

The commercial development of CpGV has been hampered severely by the limited market for such a specific biological control agent coupled with the high costs of commercial production and, in the UK, by the substantial fees levied by the Pesticides Safety Directorate for the registration of microbial biological control agents. These fees (£20k), though half those charged for conventional pesticides, are the main barrier to registration of one or more of the formulations currently available in Europe. It should be noted that registration fees for biological products are zero in several other European countries. It can only be hoped that these inconsistencies will be ironed out with the advent of the common EC pesticide registration arrangements.

However, it is our view that the registration of a CpGV product for codling moth control, preferably of HRI's *egt*⁻ strain, should be held firmly as a medium to long term objective for the UK apple and pear industry. It is an essential part of a comprehensive IPM strategy for apple and pear. Codling moth has developed resistance to conventional and IGR insecticides in central and southern Europe, as far north as the Netherlands. Some UK growers and the Farm Advisory Services Team have reported a much higher incidence

of codling moth damage in the last year or two than hitherto. They have expressed the view that control with insecticides is breaking down in the UK, though these views are conjecture. Where resistance develops, CpGV and the pheromone mating disruption technique are the only alternative remaining means of control. The advent of insecticide resistance has led to the use of the pheromone mating disruption technique on approximately 5,000 ha of apples in Northern Italy and on approximately 10,000 ha of apples in Washington State, USA. The pheromone mating technique is costly. CpGV produced by current *in vivo* techniques is also costly but less so than the pheromone mating disruption technique. However, CpGV does not control other tortricid pests of apple or pear such as *Adoxophyes orana* or *Pandemis heparana*.

Further research into CpGV should concentrate on techniques of reducing the costs of production, on improved formulation to reduce sensitivity to UV light and into field testing and the commercial development of the *egt*⁻ CpGV strain. Codling moth larvae are cannibalistic and have to be reared individually, so leading to high handling costs. A cell culture method suitable for large scale, low-cost *in vitro* production needs to be developed. A cell culture line has been developed and used at HRI Wellesbourne. This line, the first to support the replication of a granulovirus, is not suitable however for use in large scale production. *Adoxophyes orana* granuloviruses (AoGV) require similar research and development so that they can also be made available at low cost (see below).

Summer fruit tortrix moth (Adoxophyes orana) Nucleopolyhedrovirus (AoNPV)

The first field trials with AoNPV were carried out in the Netherlands from 1966-68 by Ponsen (1966) and continued in the late 1970s and early 1980s (Peters *et al.*, 1984; Dickler, 1984). These trials demonstrated that AoNPV could control *A. orana* very effectively but that the virus was highly host-specific, leading to increases in other tortricid species, notably *Pandemis heparana* (Dickler and Huber, 1983). However, the main problem encountered was the low yields of the virus, which has a large particle size, from culture in the host. This made the production of the virus uneconomic and commercial development was not pursued.

Summer fruit tortrix moth (Adoxophyes orana) Granuloviruses (AoGV)

A granulovirus of *Adoxophyes orana* was first found in Japan (AoGV-J) (Shiga *et al.*, 1973; Ito *et al.*, 1977; Sekita *et al.*, 1984). However, the cost of producing the virus was considered too high. In the late 1970s a more potent granulosis virus of *A. orana* was isolated by A Schmid, Valais, Switzerland (AoGV-S) and was then tested in the laboratory (Flückiger, 1982; Schmid *et al.*, 1983). AoGVs are characterised by a very slow pathenogenesis. Neonate larvae infected with the virus usually only die in the last instar and often have an even longer larval life than uninfected insects. Therefore, despite the high eventual mortality due to virus dissemination, the injury to apple trees caused by *A. orana* does not decrease in the generation treated with GV. Adequate control is only achieved if large areas are treated, thus minimising the effect of immigration from untreated areas. However, early trials in Japan (with AoGV-J) indicated that the virus persisted in populations over several seasons. Shiga *et al.* (1973) observed a greater incidence of virus in the second generation after application than in the first and a 57% reduction in pupal numbers in the third generation after treatment.

Andermatt (1989) evaluated early spring applications of AoGV-S against overwintered caterpillars after emergence in the field at 5-25% of concentrations that of AoGV-J used by Ito *et al.* (1977). In nine field experiments, 80-100% mortality was achieved by a spray of 5×10^{13} capsules per hectare. Good results were also achieved with two applications of 5×10^{12} capsules per hectare, corresponding to 500 larval equivalents per hectare. The reduction in costs resulting from the effective use of the lower concentration was an important step towards the commercialisation of ApGV-S. Andermatt (1989) also found that the virus persisted until the following season, causing 20% mortality in the summer generations and 20% mortality the following spring. However, although the virus was still traceable the year after treatment, it did not prevent a strong increase of the *A. orana* population. The soil was shown to be the main reservoir of the virus. It is believed that the virus is spread by wind and rain.

Drs. M. and I. Andermatt have formed a company, Andermatt Biocontrol AG, which produces a commercial formulation of AoGV-S (Capex 2) which is registered for use in Switzerland. It is principally used by organic growers and private gardeners due to its high cost relative to insecticides. As with CpGV, the main barriers to the commercial exploitation of AoGV are its high specificity, coupled with the high cost of its production compared to commercial insecticides. Registration fees are also a significant barrier in the UK. A strain of *Adoxophyes orana* granulovirus was recorded on overwintering caterpillars from two orchards in Kent in March 1993. Caterpillars gathered by A Warley of the Farm Advisory Services Team (FAST), Faversham, Kent and supplied to P Jarrett, Insect Pathology Unit, HRI-Littlehampton (for bioassay with *Bacillus thuringiensis* strains) were found to be infected heavily with AoGV. An interesting observation was that the virus caused mortality in the second to third instar stage of overwintered caterpillars (D Winstanley, pers comm). These were the first records of AoGV in the UK. Samples have been kept in cold storage at HRI-Wellesbourne. Circumstantial evidence suggests this is the same, or a very similar, strain to the AoGV-S strain in Capex 2. However, genetic profiling is necessary to demonstrate that the strain of AoGV recorded in Kent is the same as the AoGV-S strain in Capex 2 in order to obviate the need for a Department of the Environment licence to introduce AoGV-S into the British Isles.

As with CpGV, much cheaper *in vitro* mass production methods need to be developed to make AoGV viable for use in commercial production in the UK. Although *A. orana* caterpillars are not cannibalistic like *Cydia pomonella*, mass production in the host remains expensive. The immediate R&D priority is to profile genetically the AoGV-UK and AoGV-S strains. This would enable an experimental permit to be obtained from PSD at reasonably low cost (£2,000) so that the field evaluation of Capex 2 could be pursued. However, the main priority for research must be the development of cheaper mass production methods, perhaps by the use of cell culture techniques.

Virus diseases of other pests of apple and pear

Virus diseases have been recorded from a small number of other pests of apple and pear. The nucleopolyhedrovirus of the tortricid *Pandemis heparana* is infective only for neonate larvae. The virus induces diapause in the third instar development stage, death occurring in the fifth or sixth instar stage (Amargier *et al.*, 1981). The exploitation of PhNPV as a biological control agent has not been studied hitherto. An NPV of the bud

moth, *Spilonota ocellana*, a local species of minor importance in the UK, has also been recorded (Martignoni and Iwai, 1986; Tchubianishvili *et al.*, 1982) as well as an NPV of codling moth (Martignoni and Iwai, 1986). No virus diseases of the fruit tree tortrix, *Archips podana*, have been recorded, though granuloviruses, nucleopolyhedrovirus and entomopoxviruses have been recorded from other *Archips* sp (Martignoni and Iwai, 1981 and 1986). The NPV of the light brown apple moth, *Epiphyas postvittana*, a serious insecticide-resistant tortricid pest of apple in New Zealand and Australia, has been studied by Geier and Briese (1979). *E. postvittana*, a species non-native to the UK, has been introduced inadvertently into the UK where it was first reported feeding on spindle at Newquay, Cornwall, England, in 1936 (Alford, 1984). It is now established locally on a wide variety of plants in Devon and Cornwall, though not yet on apple in southern England (Cross, 1996). Virus diseases of a number of other Lepidoptera of minor pest status in the UK, including the clouded drab moth (*Orthosia incerta*), and of the cockchafer (*Melolontha melolontha*) are also listed by Martignoni and Iwai (1981 and 1986). Nucleopolyhedro- and cytoplasmic polyhedroviruses have also been recorded for the winter moth *Operophtera brumata* (Wigley, 1976; Martignoni and Iwai, 1981, 1986). Baculoviruses of free-living diprionid sawflies have also been studied extensively and exploited as biological control agents for forest pests (Cunningham and Entwistle, 1981). The nucleopolyhedrovirus of the pine sawfly *Neodiprion sertifer* is the only baculovirus currently registered for use in the UK. These sawfly baculoviruses are highly active, being effective at doses several orders of magnitude lower than CpGV. However, no baculoviruses of apple sawfly (*Hoplocampa testudinea*) or of other related sawfly species that are pests of fruit (none of which are free-living) have been recorded (Cunningham and Entwistle, 1981).

Summary and Conclusions

1. Virus diseases, of which the baculoviruses of codling moth and summer fruit tortrix moths have been studied most extensively and exploited, provide potentially ideal biological control agents for orchard pests, particularly tortricids.
2. Because of the development and spread of resistance in codling moth and summer fruit tortrix moth to neurotoxic and IGR insecticides in continental Europe and the recent increase in the incidence of codling moth in the UK, the registration of CpGV, preferably of the 'egt-' strain, and of AoGV in the UK should remain a firm medium to long term objective.
3. The main barrier to the commercial exploitation of granuloviruses appears to be the high cost of *in vivo* production which makes granulovirus products several times more costly than conventional insecticides. A careful economic appraisal of development, production and commercialisation costs of CpGV and AoGV, including R&D costs, with reference to the UK and to wider overseas opportunities, needs to be made to determine whether commercialisation can be viable. Many factors need to be taken into account including the occurrence of resistance, the availability of produce and public attitudes to insecticides. The main priority for future research must be the development of means of production at much lower cost, probably by the use of cell culture techniques. The identification of insect cell lines suitable for *in vitro* production of virus is potentially a costly, protracted and speculative research activity.

However its importance should not be underestimated. Field evaluation to develop optimum, locally appropriate strategies for the commercial use of viruses will be necessary.

4. The persistence of baculovirus is limited by their sensitivity to UV light. An important area for research is the improved formulation of baculoviruses to increase their persistence.
5. A systematic search for new insect viruses of important apple and pear pests might reveal important opportunities.

Entomopathogenic fungi

Entomopathogenic fungi are common in the environment, particularly in soil. Most have probably adapted and evolved from soil inhabiting saprophytes. The flora is dominated by a few species belonging to the Hyphomycete family with septate hyphae and no sexual stage. The most important species are *Beauveria bassiana*, *Metarhizium anisopliae*, *Paecilomyces farinosus*, *P. fumosoroseus* and *Verticillium lecanii*. The former four species have a broad host range though, in the same species of fungus, strains can have very different activity spectra. *V. lecanii* is more host-specific, parasitising aphids and scale insects most frequently. There have been several recent major reviews of entomopathogenic fungi in general (Ferron *et al.*, 1991; Roberts *et al.*, 1991; Goettel, 1992; Roberts and Hajek, 1992; Leathers *et al.*, 1993). The infection of insects by Hyphomycete fungi follows a broadly similar pattern. In the first phase of infection, the fungus grows in a yeast-like phase inside the host, forming budding spores (blastospores). In the second phase, after death, conidia are formed externally on the insect's surface. A further group of entomopathogenic fungi, the Entomophthorales, are Zygomycetes with broad, non-septate hyphae. In these, conidia are produced outside the host on club-shaped conidiophores. They are discharged forcibly, forming a white halo around the infected insect.

The main factor limiting the use of insect pathogenic fungi as biological control agents is their requirement for high humidities and adequate temperatures for spore germination, growth and sporulation. In contrast to entomopathogenic bacteria and viruses that pass through the gut wall from contaminated food, insect pathogenic fungi infect the insect through the cuticle or possibly the mouthparts. There is often a positive correlation between the numbers of infective spores and mortality by mycosis. Examples of the successful use of entomopathogenic fungi as biological control agents are few and limited mainly to tropical environments or glasshouses. However, the highly humid conditions necessary for infection occur sporadically and only transiently on the aerial parts of fruit trees so the prospects for exploiting insect pathogenic fungi as biological control agents are slight. An important recent development is the discovery that oil-based formulation can greatly improve the effectiveness of insect pathogenic fungi, at least in larger insects such as locusts (Prior *et al.*, 1988). The mechanism is not known but it may be speculated that germination and possibly the attachment of spores is improved. Suitable formulation is clearly a key area for future research. A further area of concern about the use of entomopathogenic fungi as biological control agents is their compatibility with fungicides, including residual deposits. Such effects, if any, are most likely to occur in apple and pear crops which are treated intensively with programmes of fungicides to control scab and mildew. However, limited research has indicated that entomopathogenic fungi are fairly tolerant of fungicides. Prospects for controlling pests that occur, at least for part of their development, in soil are perhaps better and worthy of exploration. Long term perennial crops such as apple and pear provide stable permanent habitats where greater populations of entomopathogenic fungi could be fostered in soil.

The above entomopathogenic fungi are non-fastidious and are easy to produce in bulk fermentation. However, in liquid media, they assume a yeast-like morphology, producing the blastospores, probably in response to the accumulation of CO₂, which are less effective. Solid substrate culture is preferable as conidia are produced. However, a strong

barrier to their exploitation as biological control agents is that they are classified as microbial agents and must be Approved by the Pesticides Safety Directorate before they can be used. A wide range of environmental and human safety and efficacy data is needed to satisfy the requirements for Approval, as well as a substantial fee (£20K). If the agent cannot be shown to be native to the UK, a licence for release from the Department of the Environment is also required. The use of each of the main species of entomopathogenic fungi for control of apple and pear pests is reviewed below.

Beauveria

Most previous research into the biological control of apple and pear pests using insect pathogenic fungi has involved the control of codling moth, *Cydia pomonella*, by *Beauveria bassiana*. The production, formulation and application of *B. bassiana* for insect control has been comprehensively reviewed recently by Feng *et al.* (1994). The fungus has a wide host range with over 200 insect species (mainly Lepidoptera and Coleoptera) recorded as hosts (Li, 1988) and causes epizootics in some species (e.g. pine caterpillars, *Dendrolinis* sp. in China) particularly in warm wet conditions. *B. bassiana* is one of the most common species found infecting codling moth in nature (Ferreira, 1943; Russ, 1964; Jaques and MacLellan, 1965; Hagley, 1971). It has also been studied as a biological control agent for codling moth. Extensive research has been conducted in the USSR (Dyadechko, 1959; Archipova, 1965; Evlakhova, 1971; Pristavko and Yanishevskaya, 1971), where a commercial preparation of conidia, Boverin, was mass produced by submerged fermentation. Mixtures of Boverin with reduced doses of pesticides (one-fifth to one tenth dose of trichlorophon, chlorophos or malathion) were found to be effective against the second generation (Droza and Lappa, 1974). Fungicides used for the control of scab (*Venturia* sp.) in spring prevent the simultaneous use of the fungus against the first generation of codling moth (Sikura, 1974). Reductions of codling moth damage to fruit and of numbers of hibernating larvae have been reported to be comparable to that achieved by the full chemical insecticide dose alone (Sikura, 1976; Lappa, 1978). Ferron and Vincent (1978) and Audemard and Ferron (1980) sprayed the trunks and lower branches of apple trees with a suspension of conidia in early August as larvae were searching for their overwintering sites. There was an increase in the infection of the larvae by the fungus but the overall efficacy was poor. Puterka *et al.* (1994) found that *B. bassiana* (isolate ARSEF #2860) was effective against pear sucker (*Cacopsylla pyricola*) nymphs in the laboratory. Jaworska (1979, 1992) studied the effect of entomopathogenic fungi, including *B. bassiana* isolated from dead Colorado beetle larvae, on apple sawfly (*Hoplocampa testudinea*) and found high levels of larval mortality in the laboratory and that development and reproduction were adversely affected by application to soil in the field.

The only other insect, which is a minor pest of apple in the UK, against which a *Beauveria* sp. has been evaluated as a biological control agent is the cockchafer, *Melolontha melolontha*. The cockchafer is occasionally a serious pest of forestry in continental Europe, causing extensive defoliation in spring. Field trials in Switzerland and France demonstrated that blastospores of *B. brongniartii* were highly effective, causing epizootics and population collapse. Swarming adults treated with a blastospore suspension, using skimmed milk as a sticker and UV-protectant, passed on the infection to their brood which established and persisted for two generations (Keller *et al.*, 1986;

Keller and Zimmermann, 1989; Keller, 1991).

There are apparently no commercially available *B. bassiana* formulations in western Europe or America at present. However, there is massive production in China (10,000 ton per annum) using an automatically mechanised solid fermentation process. A pure conidial powder of high quality is produced. It can be used in aqueous or mineral oil sprays at low or ultra-low volumes (Feng *et al.*, 1994). The product is used to control pine caterpillars, European corn borer and rice leaf hoppers. It is not used to control orchard pests though Xu (1988) reports 80-85% control of *Adoxophyes privatana* on tea by aerial spraying of conidial suspensions.

Metarhizium anisopliae

M. anisopliae is an important entomopathogenic fungus which occurs world-wide as part of the natural soil flora and can be isolated easily from soil using selective media. It has a wide host range and has been isolated from over 200 insect hosts, mainly Coleoptera. Strains of *M. anisopliae* differ considerably in their host ranges. There have been many attempts to use *M. anisopliae* as a biological control agent against a range of pests including termites, locusts, cockroaches, spittlebugs and various Coleoptera including scarabaeids (most notably the rhinoceros beetle, *Oryctes rhinoceros*), curculionids (notably the vine weevil (*Otiorhynchus sulcatus*)) and chrysomelids. *M. anisopliae* and its potential as a biological control agent have been reviewed by Zimmermann (1993).

There has been little study of the use of *M. anisopliae* for control of apple or pear pests. It has been recorded naturally parasitising codling moth, *Cydia pomonella* at low levels (Müller-Kögler, 1971; Pristavko *et al.*, 1975). Puterka *et al.* (1994) found *M. anisopliae* to be less virulent and pathogenic to nymphs of pear sucker, *Cacopsylla pyricola*, than *Beauveria bassiana*, *Paecilomyces fumosoroseus*, *P. farinosus* or *Verticillium lecanii* in the laboratory (see below).

There is clearly scope for evaluating the use of *M. anisopliae* for the control of apple and pear pests, particularly those that occur for at least part of their development cycle in soil in summer. The optimal growth temperature for *M. anisopliae* is high (about 23°C) so prospects for success in the UK are, perhaps, poor. Selection of strains with low temperature optima would be necessary. Such research might be considered to have only low prospects for success.

Paecilomyces sp.

The most important species are *Paecilomyces fumosoroseus* and *P. farinosus* which have been isolated from numerous insect hosts worldwide. *P. farinosus* is a common fungal pathogen of codling moth, *Cydia pomonella*, sometimes causing high mortality especially in mixtures with *Beauveria bassiana* (Harris, 1960; Weatherston and Retnakaran, 1975; Nussbaum, 1979; Zimmerman and Weiser, 1991). It is found usually on overwintering larvae. Jaworska (1992) found isolates of *P. fumosoroseus* and *P. farinosus* gave 100% mortality of apple sawfly, *Hoplocampa testudinea*, larvae in the laboratory.

Recently, Sterk *et al.* (1996) reported the commercial development by Biobest N.V., Belgium, of the Apopka 97 strain of *P. fumosoroseus* isolated from mealy bug in Florida in 1986 as a mycopesticide, PFR97. It is recommended for the control of the greenhouse whitefly, *Trialeurodes vaporariorum*, on greenhouse vegetables. As with other entomopathogenic fungi, high humidities and temperatures are required for infection, rendering the product only suitable for use in greenhouse conditions. G. Sterk (pers. comm.) reported PFR97 to be active against pear sucker, *Psylla pyri*. Puterka *et al.* (1994) used a detached-leaf bioassay to evaluate the pathogenicity of aqueous suspensions of conidial isolates of *P. fumosoroseus*, *P. farinosus*, *Beauveria bassiana*, *Metarhizium anisopliae* and *Verticillium lecanii* against first and second instar pear sucker, *Cacopsylla pyricola*. They found that *P. fumosoroseus* (isolate ARSEF #2658) was the most virulent fungal isolate with an LT₅₀ of 1.8 days. Over 92.5% mortality occurred in 7 days.

Field evaluation of the use of *Paecilomyces* sp. against *C. pyricola* is worthy of further investigation in the UK, especially if formulations can be manipulated to foster activity at lower humidities.

Verticillium lecanii

Verticillium lecanii is a widespread entomopathogen, principally of aphids and scale insects, but spectacular epizootics are only observed in tropical and sub-tropical regions. Its biology and use as a microbial insecticide against aphids and scales was reviewed by Hall (1981). Spores are dispersed by rainsplash or by contact with fungus-bearing material, e.g. soil or sporulating aphid cadavers. Spores can survive a few months in cold humid conditions but are very sensitive to desiccation. There are few references to *V. lecanii* parasitising orchard pests in temperate regions. Glen (1982) reported that, on tree trunks protected from bird attack, 5-30% of overwintering codling moth, *Cydia pomonella*, were killed by fungi, of which *V. lecanii* was the most important.

Two strains of *V. lecanii* available as the commercial formulations 'Vertalec' and 'Mycotal' are Approved for control of aphids and whiteflies respectively in glasshouse crops in the UK. The warm humid conditions necessary for the effective action of the products are provided only in the glasshouse.

Summary and Conclusions

The effective exploitation of entomopathogenic fungi for the biological control of orchard pests is limited severely by the humid, warm conditions required for infection. Key areas for research are improved formulation, together with the selection of low temperature-active strains. An interesting starting point might be the control of pear sucker nymphs, *Cacopsylla pyricola*, by the currently available formulations and other available isolates of *Paecilomyces fumosoroseus*. Pear sucker nymphs are immersed in honeydew for extended periods and this might provide suitable conditions for infection. Large populations of pear sucker in many orchards would facilitate the investigation. However, the strain of *P. fumosoroseus* in the Biobest formulation PFR97, selected for activity against the glasshouse whitefly *Trialeurodes vaporariorum*, might be inappropriate. Systematic bioassay, selection and formulation to develop biopesticides for

specific insect pests of apple or pear is one approach worthy of R & D exploration. The effects of foliar application of fungicides on the entomopathogens is an important issue.

A second alternative approach is to examine the exploitation of entomopathogenic fungi in soil. Apple and pear orchards provide longer term stable habitats where populations of entomopathogenic fungi are likely to be high. A survey of the occurrence of entomopathogenic fungi infecting orchard pests in soil (e.g. sawfly, leaf midge, leaf miners) would be a useful starting point.

Bacteria

Although bacteria are present on the cuticle and in the gut of all living insects, most species are part of the insects' natural flora or are only secondary pathogens (Bucher, 1981). To date, the most important bacterial pathogen that has been found to be exploitable as a biological control agent is *Bacillus thuringiensis* Berliner (*B. t.*). This pathogen is found occasionally in the wild associated with insects (e.g. in orchards in overwintered tortricid larvae) but usually it occurs only in connection with field applications of biocontrol formulations. A recent detailed account of the use of *B. t.* as an environmental biopesticide is given by Entwistle *et al.* (1993). A few other species of bacteria have also been used as biological control agents in specific circumstances, including *Bacillus popilliae* for the control of chafer larvae (Klein, 1981) and *Bacillus sphaerius* for the control of mosquito larvae (Singer, 1981).

B. t. was first discovered 90 years ago but the discovery of a strain of *B. t.* subsp. *kurstaki* (known as the HD-1 strain), up to 200 times more active than previous strains, and the establishment of a standardized system for the determination of potency (based on bioassay against the cabbage looper, *Trichoplusia ni*) in the 1960s, led to the development of commercial products for use in forestry, agriculture and horticulture. The developments were led by extensive field trials on formulations of the HD-1 strain against forest Lepidoptera in North America, especially the spruce bud worm, *Choristoneura fumiferana* and the gypsy moth, *Lymantria dispar*.

For several decades, a number of formulations of the HD-1 strain have been available for use in various crops in the UK including Bactospeine, Biobit, Dipel, Novosol and Thuricide. Before the advent of the 1986 Control of Pesticide Regulations, available products containing the HD-1 strain were not Approved under the ACAS Approvals Scheme and, as they were regarded as containing a biological control agent, may not have been 'cleared' under the scheme until latterly. The HD-1 strain has been evaluated fairly extensively for the control of apple and pear pests (see below).

The pathogenicity of *B. t.*, which has to be ingested to act, is due primarily to the production, during sporulation, of a crystal protein toxin. Upon ingestion and solubilisation of the crystal, the toxins act on the gut epithelial cells, causing an increase in membrane permeability followed by swelling and lysis; contamination of the haemolymph by the toxin and death ensue. The commercial products are produced by fermentation and contain spores and the associated protein crystal toxins.

An important feature of *B. t.* is that different strains have species-specific activity. This specificity is due mainly to the combination of endotoxins present in the toxin crystal and the ability of the insect gut to solubilise the crystals into lethal toxins. Important more recent developments were the isolation of the sub-species *B. t. israelensis* and *B. t. tenebrionis*, with specific activity against Diptera (including mosquitoes) and Coleoptera respectively. A large collection of some 6000 *B. t.* strains is kept at HRI-Wellesbourne. The collection is being screened against a range of agricultural and horticultural pests of world importance.

In the last two decades, advances in molecular and genetic techniques have led to a

new phase in *B. t.* development. The crystal toxin genes have been located on plasmids and a means of transferring them between strains of *B. t.* has been developed. This has provided a means of constructing strains with novel insecticidal activity (Jarrett and Burges, 1986). Numerous sequences have now been determined and many sub-classes of genes based on sequence homology and toxicity spectra have been identified. Another important development was the cloning of the toxin genes in *Escherichia coli* (Schnepf and Whiteley, 1981).

Because of their proteinaceous composition, the activity of *B. t.* preparations is degraded significantly in 24 to 48 hours by sunlight (300-380 nm) and heat in the field (Pusztai *et al.*, 1991; Gelernter, 1990). Antagonistic interactions with other leaf colonising bacteria, dilution by rainfall and foliar expansion also contribute to the degradation. An important development in recent years has been the development of transgenic microorganisms to overcome these difficulties. One such development is that of the 'Cell Cap' system by the Mycogen Corporation, USA. This involved the transfer of a cloned toxin gene into the leaf-colonising, non-pathogenic bacterium, *Pseudomonas fluorescens*, which is killed at the end of fermentation to overcome regulatory restrictions on the release of living transgenic microorganisms. The encapsulation is claimed to increase foliar persistence by 2 to 3 fold (Gelernter, 1990). Two commercial products are based on the Cell Cap system. One ('MVP bioinsecticide') is active against Lepidoptera and the other ('M-Trak bioinsecticide') is active against Coleoptera.

There is intense commercial interest by several large commercial companies in the development and exploitation of *B. t.* transgenic technology including the development of transgenic crop plants. However, this is targeted generally for insect pests of crops of major world importance where there are substantial marketing opportunities. Pests of apple and pear, except perhaps codling moth, *Cydia pomonella*, against which sprays of *B. t.* have low activity (see below), do not provide such lucrative market opportunities. For this reason, it is unlikely that strains of *B. t.* selected specifically for high activity against orchard pests will be developed by commercial companies in the foreseeable future.

Activity of B. t. against orchard pests

The majority of research and development has focussed on use of the HD-1 strain of *B. t.* subsp. *kurstaki* for control of lepidopterous larvae, against which the isolate is primarily active. *B. t.* deposits on plant surfaces are of short persistence (a few days at most) in the field. As *B. t.* has to be ingested to act, warm weather conditions so that caterpillars are feeding actively are necessary at the time of *B. t.* application for effective control, especially early in the season.

Many investigations have been conducted into the control of tortricids, including *Adoxophyes orana* (Van der Geest, 1971; Van der Geest and Veltrop, 1971; Dickler and Huber, 1983; De Reede *et al.*, 1985), *Archips rosana* (Niemczyk *et al.*, 1975; Niemczyk, 1980), *Pandemis heparana* (Injac and Dulic, 1982; Injac and Bakic, 1983; De Reede *et al.*, 1985) *Spilonota ocellana* (Jaques, 1961; Jaques, 1965; Niemczyk, 1980; De Reede *et al.*, 1985) and *Cydia pomonella* (see below).

Great differences in efficacy were determined, not only between species but also within the same species. In laboratory bioassays, Undorf and Huber (1986) found first instar larvae of the different species had very similar LC_{50} values for *B. t.* Tortricid larvae are generally less susceptible than other caterpillar species to *B. t.*, e.g. than *Plutella* or *Pieris* sp. However, the main reason for the inconsistent field efficacy of *B. t.* seems to be due to the biology of the larvae. *B. t.* has to be ingested to act. The important orchard tortricids listed above are either leaf rollers (*A. orana*, *P. heparana*), bud borers (*S. ocellana*) or are carpophagous (*C. pomonella*). They do not feed openly on their host plant. Sprays of *B. t.* have to be timed to coincide with egg hatch and then may only have limited efficacy. It is possible that efficacy could be improved by the use of feeding stimulants e.g. skimmed milk powder or sugar.

The use of *B. t.* for the control of codling moth (*Cydia pomonella*) has been researched extensively (Roehrich, 1964; Falcon, 1971; Fedorinchik and Korostel, 1972; Vervelle, 1975; Lappa, 1978; De Reede *et al.*, 1985). Undorf and Huber (1986) found codling moth to be susceptible but, due to its feeding behaviour, the larva ingests little of the bacteria deposited on the surfaces of fruit or foliage. Niemczyk *et al.* (1976) achieved 75% control of a light infestation in the field using a programme of three sprays. Galetenko *et al.* (1976), Videnova and Ismail (1985) and Malevez (1978) investigated enhancement of the activity by combining *B. t.* with low doses of conventional pesticides. Results were mixed and it was not possible to identify a marked synergistic effect.

In Italy, Forti and Ioriatti (1992) achieved good control of young larvae of the fruitlet mining tortrix, *Pammene rhediella*.

The use of *B. t.* for the control of winter moth, *Operophtera brumata*, has been researched extensively in forestry and in orchards (Arru and Lapietra, 1978). Over 100 research papers have been published reporting varying degrees of success. Much of the work was done in Russia and eastern Europe in the 1960s - 1970s. Variable results may be due partly to the effects of temperature which are often low at the green cluster growth stage when sprays are applied. The effects of temperature were investigated by Svestka (1976) who showed that, when temperatures were low (4-12°C), substantial feeding damage occurred before mortality which took over 22 days at 4°C. The use of *B. t.* at low doses in admixture with low doses of insecticides (including pyrethroids) for control of winter moth has also been investigated by several authors (Niemczyk, 1980; Svestka, 1976; Svestka and Vankova, 1980; Lipa and Bakowski, 1981). A synergistic effect is apparent, better control occurring with the mixtures than with the sums of the effects of either constituent alone.

B. t. is effective against several other caterpillar species, including the clouded drab moth, *Orthosia incerta* (Wagner *et al.*, 1996). Efficacy can be limited if weather conditions are cool at the time of application (Van Frankenhuyzen, 1990).

The use of *B. t.* strains to control other, non-lepidopterous, apple and pear pests does not appear to have been investigated. Many species have cryptic living habits and do not ingest parts of the plant where sprays are deposited. *B. t.* strains active against sucking pests such as aphids have not been identified to date.

Summary and Conclusions

The limitations of the *B. t.* products currently available in the UK for the control of apple and pear pests are well understood. In theory, the enormous advances in biotechnology and genetic engineering provide an unparalleled opportunity for the development of *B. t.* strains designed specifically to control orchard pests. However, in reality, the market for such products is too limited to attract the interest of commercial companies willing to invest in the development of such products. Research opportunities are, thus, confined to the following:

1. The screening for activity against orchard pests of existing and new *B. t.* products already developed for the control of other pests worldwide. Such products contain novel combinations of toxin strains (e.g. Agree, Ciba Agriculture; Cutlass, Ecogen; Condor, Ecogen) or new means of 'formulation' (e.g. the Cell Cap system products MVP and T-Trak bioinsecticides, Mycogen Inc.). Appropriate formulation may improve their suitability for ULV application which is likely to enhance efficacy.
2. Select strains from the collections of *B. t.* strains (e.g. at HRI-Wellesbourne) likely to be active against specific orchard pests and screen them against selected target pests, firstly in the laboratory, then in the field.

Nematodes

Since the majority of apple and pear pests spend most or all of their active life on the aerial parts of the tree, they do not usually come into contact with the soil where parasitic nematodes usually occur, except in some instances to pupate and/or overwinter.

Nematodes are soft-bodied, invertebrate animals which need surface moisture to move and survive. These conditions do not occur on leaf, bud, flower or fruit surfaces, except very transiently. For this reason, there is only a remote prospect of successfully exploiting parasitic nematodes as biological control agents for apple and pear pests on the aerial parts of the tree. There is limited opportunity for using nematodes for control of those pests that occur in bark crevices or burr knots, especially close to the soil, or for control of pests which occur in the soil for at least part of their development cycle, e.g. during pupation or diapause. Little is known about nematode parasites of mites.

Entomopathogenic nematodes

The most interesting and widely studied nematode parasites for biological control of insects belong to the families Steinernematidae and Heterorhabditidae. These two families are mutualistically associated with, and are vectors of, bacteria of the genera *Xenorhabdus* and *Photorhabdus* respectively. The bacteria infect the insect host which dies from the bacterial infection rather than from the effects of nematode invasion. The bacteria are carried in the nematode's intestinal lumen. For this reason, they are termed 'entomopathogenic' nematodes. Entomopathogenic nematodes have many advantages as potential biological control agents. These include active movement, a broad host range, high pathogenicity and low susceptibility to most pesticides (Kovács, 1982). Entomopathogenic nematodes principally inhabit the soil environment. They are most active at warmer temperatures. They appear to have little host specificity (Peters, 1996) and can attack beneficial insects and non-target hosts (Bathon, 1996). Currently, 13 indigenous species of entomopathogenic nematodes are known from the UK.

The use of entomopathogenic nematodes as biological control agents has been reviewed recently by Kaya and Gaugler (1993). A comprehensive book has also been published by the same authors (Gaugler and Kaya, 1990). An important step in the development of nematodes as biological control agents has been the development of low cost *in vitro* techniques for mass-production (Bedding, 1981 & 1984). Formulation development and spray application methods were reviewed by Georgis (1990).

An important point is that entomopathogenic nematodes are not classified currently as microbial biological control agents under the Control of Pesticides Regulations. This means that PSD Approval is not required to produce, market or use them in the UK. This makes it far easier to commercialise them than other microbial agents which require Approval from PSD, a very costly exercise requiring the generation of extensive safety and efficacy data as well as payment of a substantial fee. However, if the nematode is not a native species or strain, a Department of the Environment Licence is required for the release of non-native organisms into the UK. Producing the data necessary to demonstrate that the agent poses no risk to humans or the environment is likely to be a costly and protracted exercise. For this reason, species and strains indigenous to the UK are preferred. British and European legislation regulating the use of entomopathogenic

nematodes as biological control agents has been reviewed recently by Richardson (1996).

There are currently four main commercial entomopathogenic nematode products available in the UK.

1. Nemasys (MicroBio Ltd). Powder formulation containing an indigenous strain of *Steinernema feltiae* recommended for control of sciarid fly larvae in compost in mushroom houses (Nemasys M) and glasshouse ornamentals. Active at moderately warm temperatures (~ 18 - 25°C).
2. Nemasys H (Microbio Ltd). Powder formulation containing an indigenous strain of an *Heterorhabditis* species known as the North West European (NWE) type, a species close to but different from *H. megidis* described from America. Nemasys H is recommended for the control of vine weevil larvae in compost in glasshouse ornamental crops. It has been tested with variable results for the control of vine weevil in field crops.
3. Exhibit SF-WDG. Water dispersible granule formulation containing *Steinernema feltiae* recommended for control of sciarid fly larvae in compost in mushroom houses and glasshouse ornamentals.
4. Exhibit SC. Powder formulation containing *Steinernema carpocapsae* recommended for the control of vine weevil larvae in glasshouse ornamentals and in field crops in the UK.

The entomopathogenic nematode *Steinernema carpocapsae* Weiser (= *Neoaplectana carpocapsae* Weiser) has been recovered from natural populations of codling moth, *Cydia pomonella*, in various parts of the world. Each isolate is considered to be a separate strain: Czechoslovakian (Weiser, 1955); DD-136 Virginia USA (Dutky and Hough, 1955); Mexican (Poinar, 1979); Sierra, California, USA (Poinar, 1985); XI, Poland (Stanuszek, 1974). *S. carpocapsae* has a wide host range including insects from most orders, millipedes, spiders, isopods and symphylids and occurs in many ecological niches. However, it appears that *S. carpocapsae* is able to live on the surface of soil and to search for insects on tree trunks close to the soil level (Poinar, 1991).

In several cases, populations of *S. carpocapsae* have been recovered from codling moth larvae and then mass-produced and used as a biological control agent (Anon., 1956; Dutky, 1959; Dutky, 1974; Sledzevskaia, 1980, 1984; Kaya *et al.*, 1984; Nachtigall, 1991; Dickler and Nachtigall, 1992). The results of field trials were variable but in every case some mortality was recorded. The best results were achieved where applications were made to trunk bands to control overwintered pre-pupae or pupae. Anon. (1956) and Dutky (1959) claimed 60% or higher mortality from spray applications to trunks and branches. Sledzevskaia (1984) examined the survival of *S. carpocapsae*, *S. feltiae* and *Heterorhabditis bacteriophora* after foliar spray applications to fruit trees in the Moscow region. Survival time was related mainly to humidity. It was considered that prolonged survival on fruit trees would require rainfall every third day. In soil, nematodes survived in damp shady areas, remaining active throughout summer. Nachtigall and Dickler (1992)

compared the efficacy of a trunk spray application of infective *S. feltiae* (= *S. bibionis*) juveniles with a sponge collar application to control fifth instar *Cydia pomonella* larvae hibernating in corrugated cardboard bands in September. Whereas the trunk spray treatment resulted in 30% parasitisation by 5 days after treatment, the collar treatment resulted in 85% parasitisation.

Deseo *et al.* (1984) and Deseo and Miller (1985) studied the efficacy of *Steinernema* sp. against the apple clearwing moth, *Synanthedon myopaeformis*, in Italy and Kaya and Brown (1986) studied the control of clearwing moths in alder and sycamore trees. They demonstrated the parasitising capability of the infective (J3) juveniles against insects in protected habitats. Nachtigall (1991) and Nachtigall and Dickler (1992) studied the control of the apple clearwing moth *Synanthedon myopaeformis* occurring in galleries around the graft union of apple trees, particularly round the rugged part of the grafting knot with M9 rootstocks. Miller and Bedding (1982) had successfully applied *Steinernema* nematodes for the control of larvae of the currant clearwing moth, *S. tipuliformis*, boring in the stems of currants in Australia. Nachtigall and Dickler achieved good control of *S. myopaeformis* with *Steinernema feltiae* or *S. carpocapsae*. As with control of *Cydia pomonella*, better results were achieved by the use of a sponge collar application than by a spray to the trunk.

Deseo (1982) also demonstrated good control of larvae of the goat moth, *Cossus cossus*, and the leopard moth, *Zeuzera pyri*, by introducing *Steinernema carpocapsae* into their galleries.

There are better prospects for using entomopathogenic nematodes for the control of apple and pear pests in soil, especially for those that occur in soil in summer when temperatures are higher and favourable for nematode activity. Two interesting investigations of the use of entomopathogenic nematodes for control of soil pests are reported.

Vincent and Bélair (1992) investigated the parasitisation of apple sawfly, *Hoplocampa testudinea*, in the laboratory by *Steinernema carpocapsae* (strains DD136 or All), *S. feltiae* or *Heterorhabditis bacteriophora*. All the strains caused 100% mortality after 72 hours. Promising results (up to 80% mortality) were achieved in the field with soil applications of all strains of *S. carpocapsae*. In a further experiment, a single foliar application significantly reduced the percentage of fruit showing damage.

Brown *et al.* (1992) examined the control of edaphic populations of woolly aphid (*Eriosoma lanigerum*) using *S. carpocapsae* and an experimental aphicide, RH-7988. Laboratory experiments showed that the presence of the nematode in a colony of *E. lanigerum* increased the mortality rate, nematodes being found in the body cavity of several individuals. It was believed that the nematodes entered the anus via a droplet of honeydew. In the field, a broadcast spray (at 376,600 nematodes per m²) had fewer aphid colonies on roots than untreated controls, but a top dressing treatment was ineffective. Reductions were still apparent one month after treatment, but no differences were found four months after treatment.

Other parasitic nematodes

Mermithid nematodes have been recorded parasitising codling moth larvae (Von Linstow, 1898) including larvae feeding in apple fruits (Von Siebold, 1853; Stiles, 1907; Leidy, 1850, 1875). Von Siebold (1848) also recorded a mermithid parasite of the tortricid *Pandemis heparana*. As obligate insect parasites, with a wide host range in some cases, they would probably be difficult to mass culture and do not appear to have been evaluated as biological control agents (Poinar, 1991). However, several other mermithids have been used for the control of blackfly and mosquito.

Summary and Conclusions

Entomopathogenic nematodes have many attributes which favour them as biological control agents, not least the comparatively low cost of their *in vitro* mass production and the absence of any requirements for registration under the Control of Pesticides Regulations (for indigenous species).

However, their requirement for surface moisture for survival and movement means that there are only remote prospects for using them as biological control agents for control of most foliar pests of apple and pear. Improved formulation to prolong their survival on the aerial surfaces of plants might transform their prospects, but research to develop such formulations would be more appropriate for pests on other crops in the first instance. Any such breakthrough might change research priorities.

Some limited success has been achieved using specialised methods of application or dispensing of nematodes, mainly treated bands or sponge collars round the trunk of apple trees, for control of apple clearwing moth larvae or L5 codling larvae seeking hibernation sites in bark crevices. However, such methods are likely to be costly and labour intensive and thus regarded as impractical by growers.

There are better prospects for the control of pests that occur for at least part of the year in soil, the normal habitat of entomopathogenic nematodes. Various insect species might prove interesting, especially species which occur in the soil in summer when soil temperatures are high, e.g. leaf miners (*Stigmella* sp.), leaf midge (*Dasineura mali*) and apple sawfly (*Hoplocampa testudinea*). A feasibility study of the use of currently-available formulations of entomopathogenic nematodes for the control of these pests should be pursued.

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