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Biological Control

1. Adult banana skipper, *Erionota thrax* (L.M. Nakahara). **2.** Young *E. thrax* larva commencing to roll a banana leaf (R.F.L. Mau). **3.** Rolled banana leaf sheltering a larger larva (D.P.A. Sands). **4.** Young banana plant stripped by *E. thrax* larvae (L.M. Nakahara). **5.** Adult spiraling whitefly, *Aleurodicus dispersus* (P.A.C. Ooi). **6.** Wax spiral deposited during *A. dispersus* oviposition (P.A.C. Ooi).

Biological Control Pacific Prospects — Supplement 1

D.F. Waterhouse
K.R. Norris

Australian Centre for International Agricultural Research
Canberra 1989

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Contents

Foreword

When *Biological Control: Pacific Prospects* by D.F. Waterhouse and K.R. Norris was published in 1987 under ACIAR's South Pacific Program I expressed the view that it would prove to be a valuable source of data, facilitating the selection and pursuit of target pests and weeds for biological control. In this it has already been highly successful and there has been a substantial increase in the number of biological control projects undertaken, one of which (the white peach scale on passion fruit in Western Samoa) has already resulted in effective control.

At each of the three regional plant protection meetings held since the decision at the Tongan/ACIAR/GTZ Workshop on Biological Control in 1985, to publish *Pacific Prospects,* ACIAR has been requested to arrange for the preparation of dossiers on additional pests. It is agreed that this is, indeed, a highly relevant and important activity for ACIAR to support, and furthermore it has become clear that the information is often required with some urgency. It has, therefore, been decided to publish dossiers in groups as they are written, a policy vindicated by the fact that two of the projects very recently initiated in the Pacific deal with newly-invading species which are treated here. These are the banana skipper *Erionota thrax,* which has recently spread rapidly in Papua New Guinea, and the spiraling whitefly *Aleurodicus dispersus,* which is living up to its specific name and dispersing widely and rapidly in the Pacific region.

ACIAR is very grateful for the wealth of information provided by many individuals in the Pacific, who have supplied unpublished observations and indicated great enthusiasm and support for the project; also to Dr Gabrielle Persley and Mr Paul Ferrar of its Crop Sciences program for helping to steer this important undertaking further along the road to success.

J.R. McWilliam
Director
Australian Centre for International
Agricultural Research, Canberra
1989

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Introduction

The six pest dossiers in this publication follow closely the format adopted in *Biological Control: Pacific Prospects*. Each was chosen following recommendations of the Plant Protection meetings in Apia in 1986 and Noumea in 1987. One of the pests, the western flower thrips *Frankliniella occidentalis* is not yet established in the oceanic south west Pacific, although it is perceived to be a significant threat if its frequent interception continues in both Guam and New Zealand in produce from California. Biological control programs have already been initiated against two others (the banana skipper and the spiraling whitefly), which have come to prominence since *Pacific Prospects* was completed. The distribution and importance in the Pacific of the six pests is shown in Table 1.1, using the conventions adopted previously.

No attempt has been made to present an exhaustive survey of all the literature on a particular pest, especially in relation to chemical control, in which recommendations often rapidly become outdated. On the other hand every effort has been made to cover the literature relevant to biological control, including the biological and ecological information upon which successful biological control often depends. Once again, the presentation of the material is heavily biased towards the south west Pacific and discussion is focussed on the relevance of the information to traditional and other agriculturists in this region. At the same time, the dossiers have very much wider relevance, since all of the pests are also important outside the region.

It would not have been possible to assemble the wide range of relevant information in this book without the ready assistance of many colleagues throughout the Pacific and elsewhere, who have given generously of their time and knowledge. This will become clear to the reader from the number of unpublished observations quoted.

The use of technical terms has been kept to a minimum and the widely used term 'parasite' has been employed again in this publication instead of the more technically correct 'parasitoid', since no confusion is thereby introduced amongst the main target readership.

Some 250 species of insects are referred to in the chapters and the author, order and family of each is provided in the index of scientific names of insects. There have been many changes to the names used in the literature quoted in the chapters. These changes have been incorporated as far as possible, although not all modern experts agree on what the correct terminology should be. In general, that of the Commonwealth Institute of Entomology and the British Museum of Natural History has been adopted where there is dispute. Since nomenclatural changes, particularly of genera, frequently make it difficult to use indexes to earlier literature, the practice has been adopted of listing superseded names used by earlier authors at the first citation of a species in a chapter by enclosing them, preceded by an equals sign in brackets following the name in current use, for example *'Nephaspis oculatus* (= *N. amnicolor*)'. Our action is not intended to imply that the two taxa are precise synonyms of one another, since frequently they are not, and the change has been made for other reasons.

At the front of each chapter there are two maps, one showing a stylised world distribution of the pest and the other the regional distribution and importance assigned to it in the Pacific. The lines on the map do not imply that all islands, archipelagos or land masses

Table 1.1 The distribution and importance of six insect pests of concern to the south west Pacific.

KEY:
* one of the country's worst pests
+++ widespread pest, causing important damage
++ less widespread, but of great importance
\+ important locally
P present, but unimportant
Blank = not recorded

Order and Family	Chapter	Scientific name	Common name	Cook Is	Fiji	French Polynesia	Guam	Hawaii	Kiribati	New Caledonia	Niue	Papua New Guinea	American Samoa	Western Samoa	Solomon Is	Tokelau	Tonga	Tuvalu	Vanuatu
Hemiptera																			
Aleyrodidae	3	*Aleurodicus dispersus*	spiraling white fly	+	+		+	P	+			+	+	+			+		
Thysanoptera																			
Thripidae	4	*Frankliniella occidentalis*	western flower thrips				?	+											
	5	*Thrips tabaci*	onion thrips		+			+		+		+	+		+		+		+
Coleoptera																			
Scolytidae	6	*Hypothenemus hampei*	coffee berry borer		* +++	+				* +++									
Lepidoptera																			
Pyralidae	7	*Hellula* spp.	cabbage centre grubs		+	P	* +++			P	+++	P	++		* ++	P			
Hesperiidae	8	*Erionota thrax*	banana skipper				P	P				* +++							

encircled are necessarily infested and the positions of the lines often follow political boundaries. As additional information becomes available, there will certainly be a need to adjust the extent of some of the areas included.

The precis at the front of each chapter is designed to serve not as a balanced summary, but as an aide-memoire to some of the key matters relating to prospects for biological control. We are happy to acknowledge the facilities generously provided by the Division of Entomology, CSIRO and the valuable assistance of many of its staff, in particular Dr M. Carver and Mr E.D. Edwards. Thanks are also due to many others with special knowledge of Pacific entomology, including Professor W.C. Mitchell, University of Hawaii and Dr P.A. Maddison, DSIR, Auckland. We are grateful also for the advice on taxonomic problems provided by the CAB International Institute of Entomology (Dr R.G. Booth, Dr M.L. Cox, Mr G.J. DuHeaume, Dr J.D. Holloway, Dr R.B. Madgi, Dr A. Polaszek, Dr G. Stonedahl, Ms A.K. Walker, Dr G.M. Watson, Dr I.M. White, Dr M.R. Wilson) and the British Museum (Natural History) (Mr S.J. Brooks, Mr M. Shaffer, Mr B.C. Townsend, Mr N.P. Wyatt).

2 Biological control and its implementation

Many of the topics in this chapter are dealt with in greater detail in *Biological Control: Pacific Prospects* (Waterhouse and Norris 1987), which is drawn upon extensively.

The concept of biological control

Biological control may be defined as the action of natural enemies (parasites, predators, phytophagous organisms and pathogens) in maintaining an organism at a lower average abundance than it would attain in their absence. The concept of biological control arose from the lower abundance of many animals and plants that was observed in their native range than in areas to which they had been introduced. These differences were frequently found to be due to the greater impact on them of natural enemies in their native range. The early spectacular examples of successful biological control all involved introduced organisms which, leaving behind their effective natural enemies, became major pests in the new country, instead of being inconspicuous, as they had been in their country of origin.

Classical biological control

Classical biological control consists of re-establishing the balance of nature in a country in which an introduced organism has become a pest. Organisms that will reduce the population of this pest to acceptable levels are introduced from their country of origin, after being carefully evaluated for host specificity.

No matter how effective, biological control very rarely leads to eradication. This approach is thus appropriate for pest problems where:

- a certain amount of damage is acceptable;
- the cost of other control methods is too high for the value of the crop; or
- available control measures are unsatisfactory on environmental or other grounds.

SOME ADVANTAGES OF CLASSICAL BIOLOGICAL CONTROL

- If the control agent has been properly screened (see later), it will be adequately specific to the pest and have little or no adverse effect on non-target organisms.
- Biological control may be the only method applicable in national parks, rangelands or forests, where other methods are inapplicable, uneconomic, ineffective or environmentally damaging.
- Once established, the control agents involved are self-perpetuating and no continuing inputs of energy are needed.
- No action is required of farmers or other beneficiaries except to avoid the unnecessary use of pesticides and, where necessary, to use them selectively or to use narrow-spectrum chemicals.
- All producers benefit, rich or poor.
- Land tenure arrangements impose no problems and sociological patterns are unaffected.
- The benefit/cost ratio is very high compared with most other control methods.

LIMITATIONS TO BIOLOGICAL CONTROL

- Since, in almost all cases, the pest continues to exist, even if at a low population level, biological control is unable to provide the absolute freedom from a pest or from pest damage which may be essential for some types of export produce. Chemical or physical means of disinfestation must be employed under these circumstances. Thus, biological control of fruit flies will not result in exportable produce although there may be far fewer fly maggots in fruit and vegetables available for local consumption.

- In some situations the only known controlling organisms may have undesirable attributes. For a few pests no organisms are known that have the attributes necessary to reduce their abundance to acceptably low levels. Examples include nutgrass and fruit flies.
- Where an organism is valuable in one situation (e.g. guava trees supplying fruit near villages) but a pest elsewhere (e.g. guava thickets in uncultivated land), biological control organisms make no distinction between the two situations, so they can only be used if the advantages of doing so clearly outweigh the disadvantages.

Some fears concerning biological control

The commonest fear concerning biological control, especially of weeds, relates to what will happen when the introduced natural enemy controls the pest and runs short of food. Will it then turn its attention to other hosts that it is desirable to protect? Fortunately, the vast majority of arthropods and other organisms attacking plants have clear food preferences and many are specific to a particular plant or a restricted group of related plants. In biological control projects, host specificity is carefully checked by carrying out appropriate tests and making field observations on other plant species. The validity of this approach is demonstrated by the fact that no biological control organisms have ever become pests anywhere in the world if they have been properly screened.

Another reservation that is sometimes expressed about biological control of weeds is what vegetation will replace the weed when it is controlled? Will its place be taken by another weed, perhaps even more difficult to control? Certainly, the space made available by the destruction of a weed is soon occupied by other plants but, where any reasonably intensive form of agriculture is practised, more desirable plants always appear to have moved in. The encouragement of appropriate species is certainly worth careful consideration.

Host specificity

Those selecting natural enemies for biological control generally look for organisms that are narrowly specific to the pest or group of pests concerned. A careful study of the biology and behaviour of candidate organisms and, if possible, detailed observations of them in their native home, often permits sound conclusions to be drawn about their probable host restriction in a new country. However, when the organism is phytophagous and there are crops or other valued plants in the new country that have never been exposed naturally to the candidate organism, it is necessary to carry out tests to determine whether or not such plants are safe from attack. References to suitable tests and criteria for selecting appropriate species for introduction are listed in Waterhouse and Norris (1987) and practical testing is considered in the next section.

Problems may arise with introducing predators of invertebrate pests, most of which attack a wide range of hosts. Thus, it is almost certain that the majority of predatory ladybird beetles (Coccinellidae) imported to attack scale pests have also brought about a reduction in abundance of a number of endemic and non-target scales in the Pacific and elsewhere. In view of the increasing environmental concern about effects of biological control agents on non-target native species, it must be concluded that general predators are less desirable than narrowly specific ones.

In general, there are far fewer problems of this nature with primary parasites since the majority are adequately host specific. Occasionally a parasite will attack a wide range of hosts in a particular location. For example, some species of the wasp *Trichogramma* oviposit in any lepidopterous eggs that are encountered. Since a number of species of

Lepidoptera have been used to control weeds, caution must therefore be exercised when considering parasites of low specificity. Regrettably, such consideration is seldom given. An example of host specificity testing currently in progress concerns the wasp *Apanteles erionotae* which attacks larvae of the banana skipper *Erionota thrax,* a serious pest of bananas recently introduced to Papua New Guinea (Chapter 8). This wasp is being tested against a relatively innocuous, closely related, palm skipper and also against two, quite unrelated, Papua New Guinea birdwing butterflies in order to obtain information on host specificity.

As a generalisation, it is desirable to evaluate the effects of having introduced host specific parasites before turning to the consideration of importing less specific parasites or predators.

Host specificity of insects attacking weeds

Host specificity of this group is conveniently considered in relation to species that are (i) monophagous (i.e. attack only one host); (ii) oligophagous (attack only a group of closely related plants); or (iii) polyphagous (attack more than one group of plants). Biological control agents may be selected from groups (i) and (ii), but from the latter only if none of the group of closely related plants is of economic importance. Group (iii) species are generally unsuitable for introduction as biological control agents.

Contrary to popular belief, only a minority of plant-feeding insects are polyphagous, the majority are either oligophagous or monophagous. This is because most insects must be able to satisfy a number of quite specific requirements before they can develop to reproductive maturity on a plant. The right sort of specific chemicals must be present, the stem must be thick enough if it is a stem borer, the plant surface must be smooth or hairy depending upon the behavioural requirements of the insect, and so on.

Plants that are closely related are far more likely to have the correct combination of attributes than those that are less closely related. Thus, it has been found that, if an insect attacks a small number of plants (i.e. it is oligophagous), those plants are almost always closely related. It is exceptional for a quite unrelated plant to be attacked.

For an insect to attack and develop to reproductive maturity on a plant a number of requirements have to be met sequentially:

OVIPOSITION

(i) The egg-laying female has to be attracted to the plant, either by sight or smell. Sometimes females fail to recognise plants that would serve as good hosts because of the absence of certain token chemicals. The female is thus unable to detect that it is suitable food for its offspring.

(ii) Once attracted, the female then has to be stimulated to lay. Oviposition is frequently influenced by the chemical composition and surface texture of the plant, sometimes by its colour, and sometimes by such environmental factors as whether it is growing in sunlight or shade.

LARVAL DEVELOPMENT

(i) The freshly-hatched larva needs at least two different and quite specific chemical messages for it to start feeding. One set triggers the biting reflex and the other the swallowing reflex.

(ii) Even when these two requirements are satisfied, toxic materials may kill the larvae or they may suffer from the plant lacking the correct balance of nutritive materials necessary for their development. Thus larvae may die after a period of feeding, or after pupation, or pupae may produce adults that are unable to reproduce.

ADULT FEEDING

If adults are produced there are four possibilities:

(i) feeding is normal and reproduction is normal;
(ii) feeding is normal but reproduction is reduced or inhibited;
(iii) feeding is abnormal and reproduction is reduced or inhibited; or
(iv) no feeding occurs.

If a larva or adult feeds only briefly on a plant, but is unable to complete its life cycle on that plant, it is a clear indication that the plant is not a satisfactory host. Such casual feeding should not necessarily exclude its consideration as a potential control agent.

Selection of plants for testing

The most relevant information on host specificity of a potential control agent comes from careful observations of the range of plants it attacks in its country of origin or in another country in which it has been established. It is safe to assume that any plants of economic or other importance that have not been attacked under these conditions are most unlikely to be attacked in a new country. The only plants that are possibly at risk in the new country are those which have not previously been exposed to attack under field conditions. It is customary to test such plants before arriving at a decision.

In addition to testing plants never before exposed to attack, valuable information on host specificity can be obtained by testing plant species closely related to the weed. If only the most closely related are attacked — or especially if none at all is attacked — it is very probable that the insect has highly restricted feeding requirements and hence that it is highly unlikely to be able to damage quite unrelated plants of economic importance.

Practical procedures

The practical procedures for testing are simple in the country of origin if it is practicable to carry out the tests there, since no quarantine facilities are necessary. Potted plants of the species to be tested are exposed in the field close to naturally-infested hosts. If any damage is observed on the plants under test, care must be taken to establish whether this is due to the activity of the candidate agent and not to that of polyphagous insects, such as grasshoppers.

Alternatively, potted plants may be put into cages, together with the potential biological control agent and its host plant. The plants are observed daily for at least 7 days. Up to 5 plant species can be tested at a time and all trials should be repeated at least 3 times. If it is not possible to use vigorously growing pot plants, trials may be performed using portions of terminal growth cut from the test plant. Complete absence of feeding will rapidly eliminate most test plants as potential hosts. Where any 'nibbling' occurs that plant is then subjected to repeated and more rigorous testing to see whether it is capable of supporting larval development and, if so, whether adults are produced that are capable of reproducing.

If these tests cannot be carried out where the candidate control agent already occurs, and must be carried out in the country of destination, secure quarantine conditions must be available to ensure that the potential agent does not escape. The difficulties are greater than in the country of origin, but one advantage is that the varieties of crop plants grown in the country of destination are readily available for testing.

A caution that must be issued here is that insects often do not behave entirely naturally under caged or quarantine conditions and are far more likely to oviposit on an unnatural host which they would not find acceptable under field conditions. Furthermore, exploratory 'nibbling' is also far more likely to occur. Thus, care must be taken not to exclude a potential agent because of false positive results obtained under unnatural conditions.

Constraints to implementing a program

The principal constraints in the oceanic Pacific are:

- the problem of selecting an appropriate target pest because of the lack of necessary information;

- the scarcity of trained personnel;
- the lack of quarantine or secure facilities; and
- the lack of funding

In the last few years there has been a significant improvement in all these regards, although there is still a considerable need for more trained personnel and appropriate facilities.

The importance of hyperparasites

When a parasite attacks a host that is not parasitic, it is termed a primary parasite. If, in turn, the primary parasite is itself parasitised, then its enemy is called a secondary parasite or hyperparasite. It is imperative to avoid the liberation of hyperparasites, because they may seriously reduce the impact of a primary parasite and jeopardise the success of a biological control program. Careful studies should therefore be made of candidate parasites in their home country or, less desirably, in quarantine in the country of destination, so as to ensure that no unwanted travellers will be liberated. The same basic precautions about eliminating all fellow travellers, known undesirables or otherwise, apply also in the handling of weed-feeding insects, insect pathogens, microsporidans and nematodes. All these should be eliminated before release of the primary natural enemy.

Guidelines for the introduction of biological control organisms

Because of the very great importance of adhering strictly to the necessary practical procedures involved in importing approved organisms, these are set out below in some detail. They apply even when it has been concluded that the degree of host specificity is adequate for an organism to be safe for introduction to a country for the biological control of an insect pest or weed. It is essential to make sure that no other organisms are introduced with it.

(i) Apart from exceptional cases, the organism should be bred through one or more (but not too many) generations under secure quarantine in the importing country before release. This is to enable confirmation of the identity of the imported species and the elimination of any undesirable fellow travellers, such as parasites, hyperparasites or disease organisms.

(ii) If there are no secure quarantine facilities or trained staff to service a breeding program it is permissible to accept stocks bred for one or more generations in secure quarantine in another country. Under these circumstances, after presumed 'clean' adult material has arrived in the importing country, it is desirable for each individual living biological control agent to be placed in a small container (a gelatin capsule or small tube) for careful examination under a microscope before being cleared for release. The transfer to a capsule or tube should be carried out in a sleeved cage to prevent escape of living material that has emerged from the imported material. When eggs are imported they should be held until they have hatched and when larvae or pupae are imported they should be bred through to adults. These activities should be carried out under such conditions that emerging parasites can be retained until they can be destroyed. Any diseased individuals should be preserved for later examination and, if there are many, the advice of an insect pathologist should be sought before any material is liberated. In certain cases great care must be taken not to introduce serious fungal infections of plants (e.g. coffee rust or leucaena fungus) as unintended contaminants of biological control agents.

(iii) If any fellow travellers are detected, a careful review of the situation should be made by the importing authorities before permitting the direct release of *any* material in the field, even after individual examination. Either the entire consignment should be destroyed or the species should be cultured for a generation in the laboratory under the most secure conditions available, examining each individual from this culture separately before field release, to make sure it is healthy and of the intended species.

(iv) Voucher specimens of the biological control agent(s) and of any fellow travellers should be killed and pinned, or preserved in alcohol, fully labelled and stored in-country. It would be highly desirable to lodge voucher specimens for safe-keeping with the Entomology Division, DSIR, Private Bag, Auckland, New Zealand which, for some years, has been building up a major reference collection of insects of importance to the south west Pacific.

(v) Except for healthy specimens of the desirable species all other imported material should be destroyed either by (a) placing in a deep freeze overnight and later burning, (b) immersing in alcohol or formalin, or (c) autoclaving.

(vi) It is extremely hazardous to make field collections of parasites or predators of a given pest (or of herbivorous insects attacking weeds) in one Pacific country and, without further processing as above, hand carry or despatch these to another Pacific country for liberation straight into the field. If, in spite of this strong discouragement, this procedure is proposed, skilled advice should be sought in each instance about how to minimise the risks involved. The procedures outlined above *must* be followed to make sure serious mistakes do not occur. One blunder could set back biological control in the Pacific for many years, just when it is gaining much needed momentum and important successes are emerging.

(vii) If the foregoing conditions cannot be met, then the importing country should seek assistance from outside agencies in the region that have appropriate facilities and experienced personnel (e.g. the Division of Entomology of the Commonwealth Scientific and Industrial Research Organisation, GPO Box 1700, Canberra, 2601, Australia, the Entomology Division, Department of Scientific and Industrial Research, Private Bag, Auckland, New Zealand, the Hawaiian Department of Agriculture, Box 22159, Honolulu, or the Plant Protection Service of the South Pacific Commission.

(viii) Prior written approval (a letter or import permit) *must* always be obtained from the relevant Authority of a country before introducing a living organism intended for biological control. This authorisation will often specify the conditions under which an introduction can be made. In some countries two authorisations are required, one to introduce into quarantine and the other to permit releases.

The importance of strains of a natural enemy

The first choice in seeking stocks of a natural enemy for biological control is from a region, within the area of origin of the pest species, that has climatic and other characteristics as similar as possible to those of the region into which it has been introduced. There are many examples of strains or biotypes of insects that cannot be distinguished on visible differences, but which may, nevertheless, differ greatly in habitat choice, host preference, physiology, behaviour and life cycle characteristics. In biological control it is often the behaviour of the natural enemy that determines its effectiveness. For example, those that can find hosts at low densities and those that can withstand adverse conditions will have an advantage as biological control agents over those lacking these qualities. It is desirable to introduce enough individuals to provide a wide representation of the genetic make-up of a local species population. Although smaller numbers have been adequate in the case of some natural enemies, it is desirable to introduce at least 100, and many more if possible, of a strain in order to ensure that the full range of genetic variability in the strain is represented.

It is also highly desirable to avoid breeding natural enemies through many generations under insectary conditions, since there is a great deal of evidence for rapid cage adaptation. This involves a reduction in genetic diversity and a loss of adaptation to life in the field.

Multiple importations

The introduction of more than one natural enemy will generally result in a greater total mortality of a pest, although there are many examples of an insect pest or weed being brought under effective biological control by a single species of natural enemy.

Multiple introductions may have the advantage that environmental variations adversely

Table 2.1 Possible 'fast track' targets for biological control in the Pacific (after Waterhouse 1987).

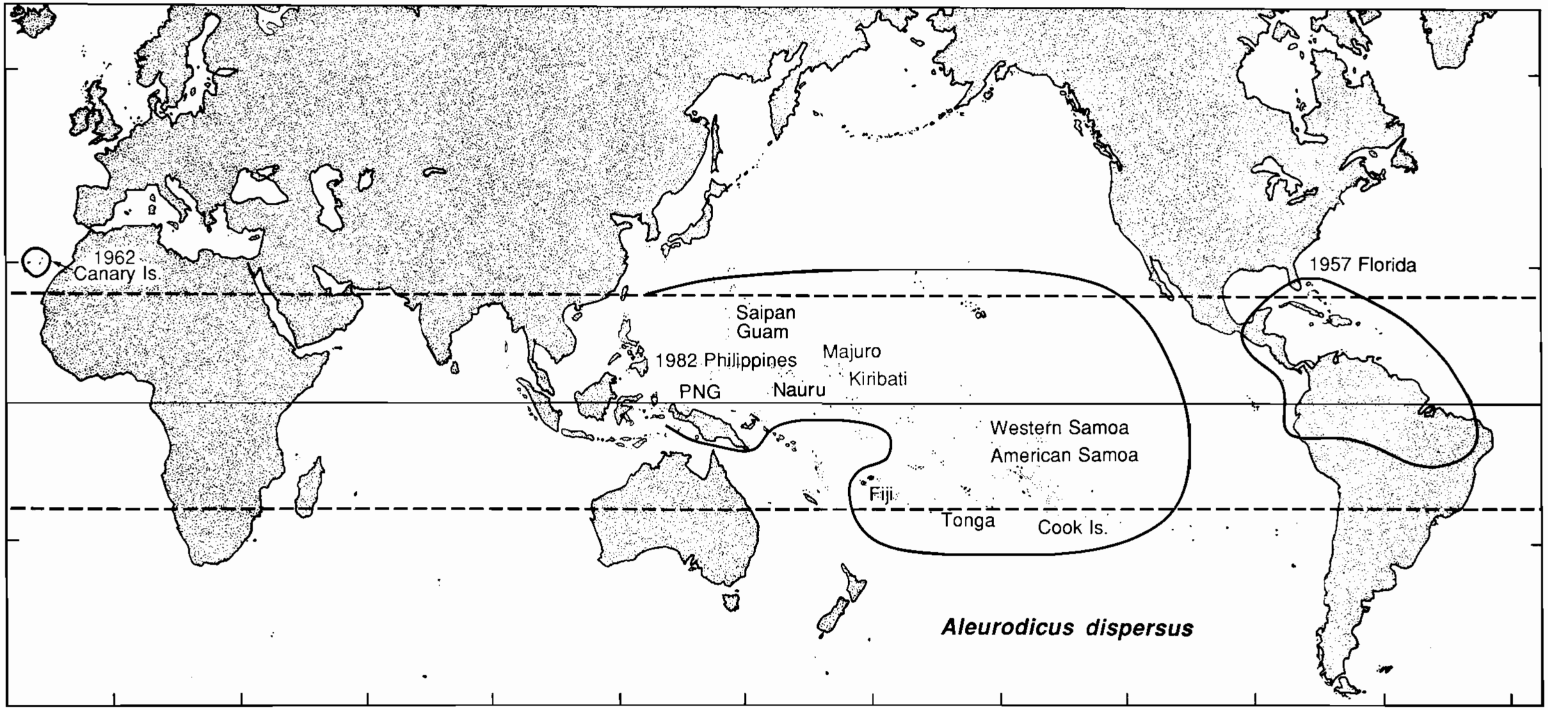
Order and Family	Scientific Name	Common Name
Phasmatodea		
Phasmatidae	*Graeffea crouanii*	coconut stick insect
Hemiptera		
Delphacidae	*Tarophagus proserpina*	taro planthopper
Aphididae	*Pentalonia nigronervosa*	banana aphid
Diaspididae	*Pseudaulacaspis pentagona*	white peach scale
	Unaspis citri	white louse scale
Pentatomidae	*Nezara viridula*	green vegetable bug
Coleoptera		
Chrysomelidae	*Brontispa longissima*	coconut leaf hispa
Diptera		
Agromyzidae	*Liriomyza* spp.	leaf miners
Lepidoptera		
Yponomeutidae	*Plutella xylostella*	diamondback cabbage moth
Noctuidae	*Othreis fullonia*	fruit piercing moth
Gastropoda		
Achatinidae	*Achatina fulica*	giant African snail
Asteraceae	*Mikania micrantha*	mile-a-minute weed
Malvaceae	*Sida rhombifolia*	paddy's lucerne
Melastomataceae	*Clidemia hirta*	Koster's curse
Mimosaceae	*Mimosa invisa*	giant sensitive plant
Pontederiaceae	*Eichhornia crassipes*	water hyacinth
Salviniaceae	*Salvinia molesta*	salvinia
Solanaceae	*Solanum torvum*	prickly solanum
Verbenaceae	*Lantana camara*	lantana

affecting one species may favour another, so that the second will tend to complement the first. Furthermore, a widely distributed pest attacking a range of hosts in many ecological situations generally has a complex of natural enemies, which may vary in numbers and species composition in these different situations. Any particular parasite may not be equally effective throughout the entire range of its host, so that a group of parasites is more likely to ensure that the host is effectively attacked wherever it occurs.

Selection of target pests

Organisms that are not pests in their native land are particularly appropriate candidates for biological control. Their natural enemies there are often under attack, both by general predators and more specific parasites. If they are freed from their parasites, hyperparasites, predators and diseases before introduction their effectiveness as control agents may be enhanced.

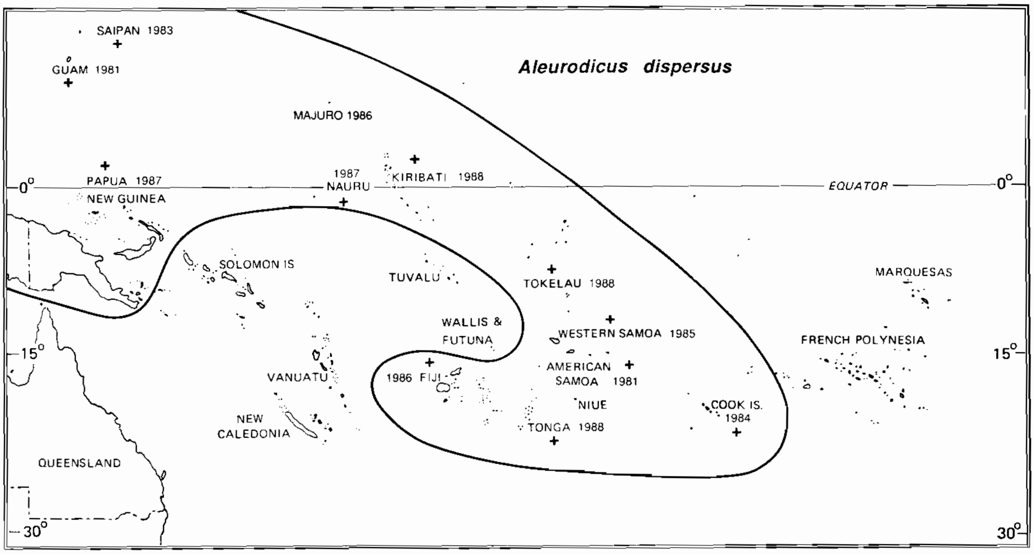
Because of the wide range of possible candidates for biological control, it is desirable to select each target carefully. Criteria on which a decision may be made are given by Waterhouse and Norris (1987). These include consideration of the importance of the crop(s) affected, the economic and social importance of the pest, the alternative control methods that are available and the evaluation of the chances of biological control being successful. Waterhouse (1987) placed 20 of the 47 pests dealt with in *Pacific Prospects* in a 'fast track' category (Table 2.1), because successful biological control had already been achieved with them elsewhere or because sufficient was known about their natural enemies to lead to the belief that they would be effective. Nine of these pests are now under investigation and work already has commenced on two of the pests in the present publication. As for the remaining pests, successful biological control is less certain, either because of the nature of the pest or the damage caused; uncertainty as to whether suitable natural enemies can be found; and the availability of a suitable donor to fund the substantial cost of a thorough overseas investigation in the area of origin of the pest.


1962
Canary Is.
Saipan
Guam
1982 Philippines
PNG
Nauru
Majuro
Kiribati
Western Samoa
American Samoa
Fiji
Tonga
Cook Is.
1957 Florida
Aleurodicus dispersus

3

Aleurodicus dispersus Russell

HEMIPTERA: ALEYRODIDAE
spiraling whitefly



Aleurodicus dispersus is native to the Caribbean region and Central America, where it is known from a very wide range of plants, but is not regarded as a pest.

After establishing a Pacific bridgehead in Hawaii in 1978 it has steadily spread westwards to many Pacific nations and also to the Philippines. Two parasitic wasps *Encarsia ? haitiensis* and *Encarsia* sp. and three not very specific coccinellid predators were introduced to Hawaii in 1979 and 1980 from Trinidad and rapidly reduced previously damaging populations of the whitefly. *E. ? haitiensis* is mainly responsible for effective biological control of the whitefly in Guam. It was found on the Hawaiian island of Lanai that *E. ? haitiensis* alone could achieve excellent control and elsewhere that *Encarsia* sp. was also an effective parasite, so it would appear to be unnecessary, perhaps even undesirable, to introduce the rather less specific coccinellids to any additional countries, at least until it is shown that the parasites alone are inadequate. *A. dispersus* is clearly an excellent target for biological control.

Origin

Aleurodicus dispersus is native to the Caribbean region and Central America. It was first recognised as a distinct species in 1965 from specimens accumulated over a period of some 60 years in the U.S. Department of Agriculture collection, many having been intercepted by plant quarantine personnel (Russell 1965). It was described from specimens collected on coconut in Florida. Eleven of the 28 other described species of the genus *Aleurodicus* also attack coconut, in addition to other hosts. However only one of these eleven (*A. destructor*) is known from the Pacific region (Australia, Papua New Guinea, Philippines, Solomon Is) (Mound and Halsey 1978).

Distribution

In the Caribbean and Central America *A. dispersus* is known from the Bahamas, Barbados, Costa Rica, Cuba, Dominica, Haiti, Martinique and Panama. In North America it occurs in southern Florida (first observed 1957) (Anon 1986, Russell 1965). It is not known from California, although it has been intercepted there many times by quarantine authorities.

In South America it occurs in Brazil, Ecuador and Peru; in Asia in the Philippines (1982) and in Africa in the Canary Is (1962) (Anon 1986, Paulson and Kumashiro 1985, Russell 1965).

In the Pacific it is known from Hawaii (1978), American Samoa (1981), Palau (1985), Majuro (1986) (Marshall Is), Pohnpei (1986) and the Mariana Is (Guam 1981, Saipan 1983), Cook Is (1984), Western Samoa (1985), Fiji (1985), Nauru (1987), Papua New Guinea (1987), Kiribati (June 1988), Tokelau (late 1988), Tonga (November 1988) (K. Englberger pers. comm. 1988, Ikin 1986, Kumashiro et al. 1983, Lauofo and Iwamoto 1982, R. Macfarlane pers. comm. 1989, Martin and Lucas 1984, L. Naseri pers. comm. 1989, Nechols 1981, P. Samuel pers. comm. 1987, I. Schreiner pers. comm. 1988, Schreiner and Nafus 1986, P. Sivan pers. comm. 1988, F. Dori pers. comm. 1988).

Life cycle

As in other whiteflies the eggs of *A. dispersus* have a characteristic short subterminal stalk or pedicel which is inserted during oviposition into the host plant, usually on the lower surface of a leaf. In *A. dispersus* and many other species the pedicel is inserted into the stomata (Paulson and Beardsley 1985). There are four immature instars, the first three being referred to as larvae. First instar larvae have distinct antennae and functional legs and can crawl actively. The legs and antennae of the remaining instars are atrophied and these instars tend to be sedentary. The final (fourth) instar larva is at first a feeding stage like earlier instars, but later ceases feeding and undergoes internal tissue reorganisation before moulting to the adult. The fourth instar cuticle on which most of the taxonomy is based is referred to as the 'pupal case'. Adult whiteflies copulate side-by-side and in this they are similar to psyllids but unlike aphids (Martin and Lucas 1984, Mound and Halsey 1978).

A characteristic structure of aleyrodids is the vasiform orifice, a large dorsal opening on the last abdominal segment of all stages. It receives the anus, is partly protected by a cover (the operculum), and contains a tongue-like process, the lingula. Honeydew accumulates there in globules and is flicked off from time to time by the lingula.

In *A. dispersus* the smooth surfaced, yellow to tan elliptical eggs (0.3 mm long) are laid singly at right angles to the leaf veins in association with irregularly spiraling deposits of waxy white flocculence (Plate 1, fig. 6), from which the whitefly derives its common name. Spiraling patterns of waxy material are produced also on non-host plants and inanimate surfaces, although the presence of eggs has not been confirmed on the latter (Henderson 1982).

On hatching, the tiny (0.32 mm long) first instar larvae (crawlers) generally settle in a spiral pattern near the eggs from which they were derived, although some move within the confines of their leaf. As they mature these larvae develop a characteristic row of anterior, mid-dorsal waxy tufts.

Second (0.5 mm long) and subsequent instar larvae usually remain feeding in the same place. Third instar larvae (0.65 mm long) can be distinguished by the numerous evenly-spaced short, glass-like rods of wax along the sides of the body. Fourth instar larvae (1.06 mm long) are soon covered with copious amounts of white material and long glass-like rods are produced from the single pair of cephalic and three pairs of abdominal pores. Rods up to 8 mm in length may occur, although most are shorter due to fragmentation.

Under glasshouse conditions (temperatures ranging from 20° to 39°C) development from egg to adult occupies 34 to 38 days (eggs 9 to 11 days, 1st instar 6 to 7 days, 2nd instar 4 to 5 days, 3rd instar 5 to 7 days, 4th instar 10 to 11 days). Only adults disperse beyond the leaf on which the egg was laid.

Under laboratory conditions, the maximum longevity recorded was 39 days. Females oviposit throughout their life, commencing within a day of emergence. Mated females produce offspring of both sexes, whereas unmated females produce male progeny only. In one experiment 20 pairs produced 1549 individuals of various stages of the life cycle in 37 days.

The wings of newly emerged adults (body length 2.28 mm in males and 1.74 mm in females) are clear on emergence, but develop a covering of white powder over the next few hours (Plate 1, fig. 5). The eyes are dark reddish-brown and the forewings each have two characteristic dark spots. Adults are particularly active during the morning hours.

Mating occurs during the afternoon. Stationary males attract females by partially spreading their wings and beating them up and down rapidly on the leaf surface. Males then copulate with females that approach (Henderson 1982).

Heavy sporadic rains and cool temperatures may result in a temporary reduction in *A. dispersus* populations which, however, rise again in warmer, drier weather. Mortality of immature stages increases significantly between 40° and 45°C and of adults between 35° and 40°C : temperatures below about 10°C also cause mortality (Cherry 1979).

Pest status

A. dispersus is a pest of vegetables, fruit trees, ornamentals and shade trees. Its extensive host range covers at least 27 plant families, 38 genera and more than 100 species, including avocado, banana, breadfruit, capsicum, citrus, coconut, frangipani, guava, leucaena, macadamia, mango, pawpaw and rose.

Two other species of *Aleurodicus* occur in the Pacific on one or more of the same hosts, *A. destructor* on banana, coconut, *Canna indica* and *Vismia braziliensis* and *A. holmesii* on guava (*Psidium guajava*) in Fiji (Kumashiro et al. 1983, Mackie 1912, Martin and Lucas 1984, Mound and Halsey 1978).

Nymphs and adults suck sap from their host plants and can cause premature leaf drop, although the injury caused by even heavy infestations is usually insufficient to kill the plants. However, the copious white, waxy flocculent material secreted by the nymphs is readily spread elsewhere by wind and creates a very unsightly nuisance. Furthermore, much sticky honeydew is produced which serves as a substrate for dense growths of sooty moulds which interfere with photosynthesis. The sticky honeydew carried by the wind on the flocculent wax adheres to windows and cars and causes considerable annoyance. In Hawaii, at the height of the infestation, complaints were received of allergies and dermatitis, although it is not known whether the adult whitefly or the flocculent material (or both) were responsible (Anon 1981a, Kumashiro et al. 1983).

A. dispersus was once suspected as being a vector of the mycoplasma causing coconut lethal yellow disease in Florida (Weems 1971), although a planthopper (not present in Hawaii or the Pacific) is now implicated (Anon 1981a).

Of primary concern when the pest first became widely established in Hawaii was its threat to commercial fruit crops such as banana, guava and pawpaw and the potential threat of a quarantine being imposed on exported ornamentals, not least because the spiraling whitefly will deposit its eggs on both hosts and non-hosts (Anon 1981a).

Control measures

There are no publications dealing with insecticidal control measures, although a dilute aqueous solution of a dishwashing detergent has been suggested as helpful. It is probable that any of the contact insecticides recommended for other pests on the same plant hosts would temporarily reduce whitefly abundance and that systemic insecticides would be even more effective.

Associated pests

The extremely diverse host range of *A. dispersus* results in there being a very large number of associated pests, but there is no information available on what chemical control measures, if any, may have to be modified to avoid interference with biological control agents.

Attempts at biological control

HAWAII

A. dispersus was discovered on tropical almond, *Terminalia catappa,* in Honolulu in September 1978. It spread rapidly throughout Oahu, apparently moving with the prevailing trade winds and along major thoroughfares. Adult whiteflies were observed in buses and cars and new infestations were frequently found near bus stops and parking areas. By 1981 it had become established also on Kauai, Maui, Molokai, Lanai and Hawaii, being most abundant in coastal areas and less abundant above 300 m (Anon 1981a). Considering the initial infestation sites on the outer islands and the prevailing wind patterns, it is believed that adult whitefly reached Maui and Lanai on shipping, and Hawaii, Kauai and Molokai on infested plants. A smuggled plant harboring a few individuals may have initiated the infestation on Oahu (Anon 1981a).

By 1979 *A. dispersus* was considered to be an economic pest of major significance and a search was initiated for natural enemies in the Caribbean. Three species of coccinellid predator and two species of aphelinid parasite were introduced in 1979 and 1980, studied for host-specificity and liberated (Table 3.4). Of these, the coccinellid *Nephaspis oculatus* (= *N. amnicola*) and the parasites *Encarsia ? haitiensis* and *Encarsia* sp. were the most effective. As is characteristic of many coccinellids, *N. oculatus* was effective in reducing high populations of whitefly, but relatively less effective against low populations because its searching ability is poor. On the other hand, *E. ? haitiensis* and *Encarsia* sp. were effective in low whitefly populations and ultimately, therefore, the more valuable biological control agents. In 1980 to 1981 peak populations of *A. dispersus* around Honolulu were reduced by 79% in the lowlands and 98.8% in the highlands. It is particularly interesting that, from a single release of adult *E. ? haitiensis* in Lanai in September 1980, it was recovered in December 1980, when whitefly populations were at a peak. By July 1981 the whitefly was considered to be under control (Anon 1981a).

A number of predators, most of which had been introduced against other pests (Table 3.1), may have contributed to reducing high whitefly populations. Only one of the predators in this table had previously been recorded as attacking a whitefly, namely the coccinellid *Delphastus* (= *Nephaspis*) *pusillus* attacking *Trialeurodes packardi* (Mound and Halsey 1978) and, more recently, *Aleurothrixus floccosus, Orchamoplatus mammaeferus* and *Trialeurodes vaporariorum* (Funasaki et al. 1988). This coccinellid was introduced in 1980 (Anon 1981a).

Of the previously introduced predators *Allograpta obliqua* (Dip.: Syrphidae) was reported to be the most abundant and probably the most important. Its pupae were frequently parasitised by the encyrtid *Ooencyrtus guamensis,* which is believed to reduce its effectiveness (Nakahara and Marsden 1979a). Other useful predators that were parasitised were the lacewing *Chrysoperla* (= *Chrysopa*) *comanche* by the ichneumonid *Brachycyrtus nawaii,* the lacewing *Sympherobius barberi* by the encyrtid *Cheiloneurus*

Table 3.1 Natural enemies of *A. dispersus* in Hawaii (Paulson and Kumashiro 1985)

Coleoptera	Diptera	Neuroptera
Coccinellidae	Syrphidae	Chrysopidae
Bothrocalvia pupillata	*Allograpta obliqua*	*Chrysoperla comanche*
Cryptolaemus montrouzieri		Hemerobiidae
Curinus coeruleus		*Sympherobius barberi*
Delphastus pusillus		
Nephaspis bicolor	Hymenoptera	
N. oculatus	Aphelinidae	
Olla v-nigrum	*Encarsia ? haitiensis*	
O. v-nigrum var. *plagiata*	*Encarsia* sp.	
Serangium maculigerum		

sp., and the coccinellid *Bothrocalvia* (= *Coelophora*) *pupillata* by both the encyrtid *Homalotylus* sp. and the eulophid *Tetrastichus coccinellae*. None of these parasites was purposely introduced and it is not known when or how they became established in Hawaii. Of the predators listed in Table 3.1 only the coccinellids *D. pusillus, N. oculatus* and *N. bicolor* show a strong preference for whiteflies. All are general predators of scales, mealybugs and aphids as well as of whiteflies. Other general predators present included reduviid bugs, spiders, lizards and birds: these attacked the whitefly, but were never able to control it. No previously established parasites or any pathogens were recovered from the whitefly.

Although high rainfall and low temperature play a role from time to time in reducing whitefly populations, credit has been given to biological control as the main cause of the very great reduction in pest status of *A. dispersus* in Hawaii (Kumashiro et al. 1983). In particular, evidence from Lanai indicates that *Encarsia ? haitiensis* is the organism primarily responsible for bringing *A. dispersus* numbers to generally low levels (Anon 1981a). All 17 species of Aleyrodidae occurring in Hawaii are immigrants and in laboratory studies the *Nephaspis* species liberated exhibited a very strong preference for whiteflies (Yoshida 1982).

AMERICAN SAMOA

A. dispersus was found on Tutuila in 1981 on guava as a preferred host, although it also occurred on a very wide range of plants including ornamentals, citrus and other fruit trees (Kumashiro et al. 1983, Lauofo and Iwamoto 1982). Three coccinellid predators and the parasite *Encarsia ? haitiensis* (Table 3.4) were introduced from Hawaii in June 1984 and rapidly brought the pest under effective control, although scattered infestations continued to occur on pawpaw leaves and fruit, breadfruit leaves and taro leaves.

In 1987 the spiraling whitefly was found to be abundant on many crops on the outer islands of Ofu and Olosega (of the Manua group) and reached there in 1985 or earlier (P. Maddison pers. comm.). Infestations were first noted on banana leaves and later in vegetable gardens where capsicum, egg plant, tomato and guava were commonly attacked. Frangipani trees were also infested. *E. ? haitiensis* was taken from Tutuila in early 1988 to these infestations and by October 1988 the whitefly populations were low (A. Vargo pers. comm. 1988).

WESTERN SAMOA

A. dispersus was first recognised in 1985.

COOK IS

A. dispersus was discovered on Rarotonga in 1984 and is believed to have entered that year, possibly with fruit trees from Hawaii. Its hosts include frangipani, guava, hibiscus and mango. It has not yet been found on other islands of the group. *Nephaspis bicolor* and *Encarsia ? haitiensis* were introduced from Hawaii in 1985, but no information is available on their possible establishment although it is known that the area where they were released was sprayed on the following day. Until the end of 1987 the whitefly was not regarded as an important pest, but early in 1988, following a three-month drought, populations increased rapidly to pest proportions and *E. ? haitiensis* has been reintroduced (P. Samuel pers. comm. 1987, 1988).

FIJI

A. dispersus was discovered near Suva in April 1986, has since spread rapidly and come to be regarded as a serious pest. *E. ? haitiensis* was introduced from Guam and later, together with *N. oculatus* and *N. bicolor,* from Hawaii. *E. ? haitiensis* became well established within a year and the coccinellids had dispersed up to 2 km from their release site within a few months (Kumar et al. 1987).

Three predators present in Fiji prior to 1986 (Table 3.2) were found attacking *A. dispersus,* namely the coccinellids *Megalocaria (= Archaioneda tricolor) fijiensis* and *Serangiella* sp. and the neuropteran *Chrysopa* sp. (K. Kumar pers. comm. 1987).

Table 3.2 Natural enemies of *A. dispersus* in Fiji (K. Kumar pers. comm. 1987)

Coleoptera	Neuroptera
Coccinellidae	Chrysopidae
Megalocaria fijiensis	*Chrysopa* sp.
Serangiella sp.	

GUAM

The spiraling whitefly was first recorded in Guam in 1981 on coconut, frangipani, guava and mango (Lauofo and Iwamoto 1982, Nechols 1981). *N. oculatus* and *E. ? haitiensis* were imported from Hawaii and soon became established. On frangipani the population of whiteflies was reduced from 50 to 100 per leaf to less than 10 (Nechols 1982). However the whitefly is still common and there are periodic outbreaks, particularly on certain hosts such as sea grape (*Coccoloba* sp.) (Nafus and Schreiner 1989). A good correlation was established between decreasing densities of spiraling whitefly and increasing rates of parasitisation by *E. ? haitiensis*. A second parasite which resembled an *Encarsia* sp., but which had not been intentionally introduced, contributed to the effectiveness of parasitisation, so that the pest is kept at very low levels of abundance except during dry periods. *N. oculatus* responded to pest increases, but not until after high whitefly densities were reached. Parasites and predators attacking spiraling whitefly, but which had not been intentionally introduced are listed in Table 3.3 (Nechols 1982, 1983).

KIRIBATI

Spiraling whitefly was first recorded at Bikenibeu, Tarawa, in June 1988 and by December it had spread to Betio. By January 1989 it was established on 27 hosts belonging to 18 families, being most serious on chillies, bell peppers and tomatoes. It was also abundant on pawpaw, guava, breadfruit, banana and ornamentals, including frangipani and *Coleus.* A biological control project is to be commenced in the near future (G.S. Sandhu pers. comm. 1989).

PALAU

E. ? haitiensis was introduced from Guam in 1986 and *A. dispersus* was rapidly brought under control, although it is reported to be a problem in some outlying islands (I. Schreiner pers. comm. 1988) where the parasite is presumably not present.

Table 3.3 Natural enemies of *A. dispersus* in Guam (Nechols 1982, 1983)

Coleoptera	Hymenoptera	Neuroptera
Coccinellidae	Encyrtidae	Chrysopidae
Nephus roepkei	*Arrhenophagus albitibiae**	unidentified sp.
unidentified black sp.	Aphelinidae	
	? *Encarsia* sp.	

* This species is an armoured scale (diaspidid) parasite, so there may have been a misidentification.

POHNPEI

E. ? haitiensis was introduced from Guam in 1987 and was recorded in 1988 as established (I. Schreiner pers. comm. 1988).

PAPUA NEW GUINEA

A. dispersus was found in October 1987 in the Port Moresby area on guava and mango leaves and within a few months was infesting many other plants. Coccinellids and spiders have been observed preying on it (F.M. Dori pers. comm. 1988). Heavy infestations of *A. dispersus* were observed on young coconut palms near Madang in July 1988 (D.P.A. Sands pers.comm.)

TONGA

A. dispersus was recognised in November 1988 and was being attacked by an unidentified wasp (K. Englberger pers. comm. 1988).

Table 3.4 Introductions for the biological control of *A. dispersus*

Country and natural enemy	Liberated	From	Result	Reference
Cook Is				
Coleoptera				
Nephaspis bicolor	1985	Hawaii	?	P. Samuel pers. comm. 1988
Hymenoptera				
Encarsia ? haitiensis	1985	Hawaii	?	P. Samuel pers. comm. 1988
	1988	Fiji	+	B. Thistleton pers. comm. 1989
Fiji				
Coleoptera				
N. oculatus	1987	Guam	+	P. Sivan pers. comm.
	1987	Hawaii	+	B. Thistleton pers. comm. 1988
N. bicolor	1987	Hawaii	+	P. Sivan pers. comm.
	1987	Hawaii	+	B.Thistleton pers. comm. 1988

(continued on next page)

Table 3.4 (continued)

Country and natural enemy	Liberated	From	Result	Reference
Hymenoptera				
E. ? haitiensis	1987	Guam	+	B.Thistleton pers. comm. 1988
E. ? haitiensis	1987	Hawaii	+	B.Thistleton pers. comm. 1988
Guam				
Coleoptera				
N. oculatus	1981	Hawaii	+	Nechols 1981, 1982
Hymenoptera				
E. ? haitiensis	1981	Hawaii	+	Nechols 1981, 1982
Hawaii				
Coleoptera				
Delphastus pusillus	1980	Trinidad	+	Anon 1981a
N. oculatus	1979	Trinidad	+	Anon 1981a
	1979	Honduras	+	Anon 1981a
N. bicolor	1979	Trinidad	+	Anon 1981a
Hymenoptera				
E. ? haitiensis	1979	Trinidad	+	Funasaki et al. 1988
Encarsia sp.	1980	Trinidad	+	Anon 1981a
American Samoa				
Coleoptera				
Delphastus pusillus	1984	Hawaii	+	A. Vargo pers. comm. 1988
N. oculatus	1984	Hawaii	+	A. Vargo pers. comm. 1988
N. bicolor	1984	Hawaii	+	A. Vargo pers. comm. 1988
Hymenoptera				
E. ? haitiensis	1984	Hawaii	+	A. Vargo pers. comm. 1988
Palau				
Hymenoptera				
E. ? haitiensis	1986	Guam	+	I. Schreiner pers. comm. 1988
Pohnpei				
Hymenoptera				
E. ? haitiensis	1987	Guam	+	I. Schreiner pers. comm. 1988

Major natural enemies

Nephaspis oculatus

This coccinellid is very widespread in the Caribbean, having been reported from Barbados, Dominica, Curaçao, Trinidad, Honduras, Panama, Costa Rica and Florida. At 23 to 26°C, development of *N. oculatus* from egg to adult is completed in an average of 26 days. The light green, oblong eggs (0.38 × 0.21 mm) are inconspicuous and usually deposited flat on the leaf surface within the flocculent material produced by *A. dispersus*. They are often laid on or adjacent to 4th instar hosts. They hatch in an average of 6.9 days. When fed spiraling whitefly nymphs, the 1st, 2nd, 3rd and 4th larval stages were completed in an average of 3.1, 2.3, 2.6 and 5.3 days respectively. The average duration of the pupal stage is 6.2 days. The dorsal surface of the pupa bears scattered dark setae of varying length and, as the pupa matures, each seta develops a terminal droplet of clear liquid. Fully formed adults remain partially within the separated pupal cuticle in a quiescent state for about 48 hours. Mating occurs 9 to 10 days after emergence. Adult males live an average of 349 days and adult females 162 days, during which time they lay an average of 212 eggs. Prey-finding by larvae and adults depends upon chance contact. *N. oculatus* is an effective predator only when whitefly populations are high (Kumashiro et al. 1983, Yoshida 1982, Yoshida and Mau 1985). *N. oculatus* fed readily on four other species of whitefly, introduced to Hawaii, *Trialeurodes vaporariorum, Orchamoplatus mammaeferus, Paraleyrodes naranjae* and *Aleurothrixus floccosus,* but less readily on all stages of the mite *Tetranychus cinnabarinus* (Boisduval) and on damaged individuals of the aphid *Myzus persicae*. It did not feed on *Coccus viridis* (Funasaki et al. 1988, Yoshida 1982).

Encarsia sp.

The adult aphelinid wasp is brown with a white scutellum, the legs are generally pale, but the hind femora are dark. The developmental period from egg to adult is about 20 days at 25°C. The average length of females is about 0.1 mm, and they can survive up to a month in the laboratory. The species is parthenogenetic and no males were observed in Hawaii. Since 1981 *Encarsia* sp. has been one of the major agents in controlling the spiraling whitefly in Hawaii (Otsuka undated).

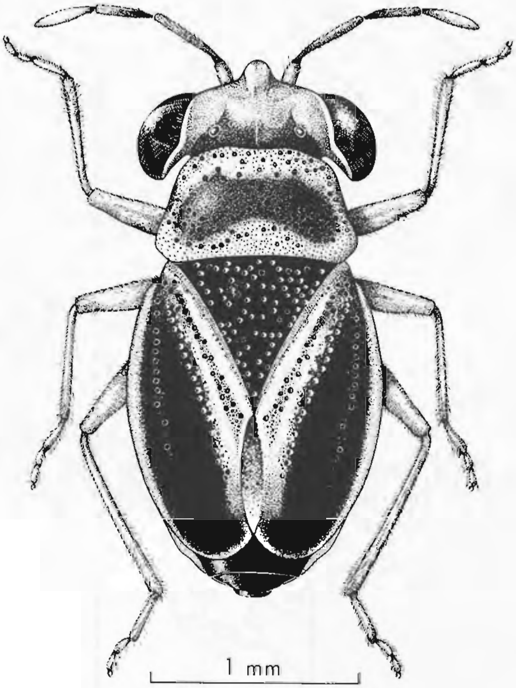
Encarsia ? haitiensis

Only 120 adults of this yellowish aphelinid wasp were sufficient to establish it on the island of Lanai (Anon 1981a), as few as about 80 in Palau, and fewer than 40 in Fiji (I. Schreiner pers. comm. 1988). It has a life cycle similar to that of *Encarsia* sp.

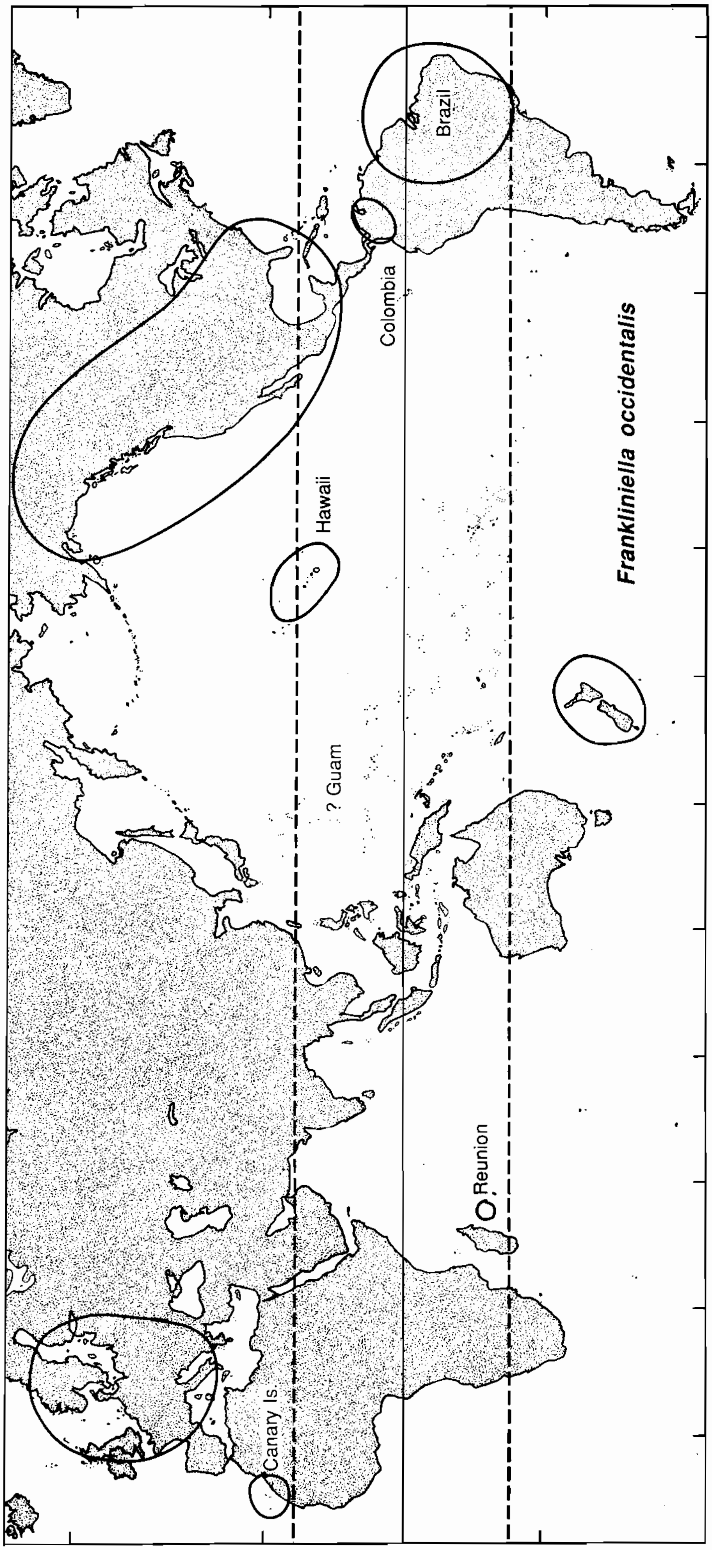
Comments

The steady spread of *A. dispersus* westwards in the Pacific suggests that, in the next few years, the spiraling whitefly may well be discovered to have reached additional oceanic countries and, quite possibly, also Australia. Strict quarantine procedures for introducing living plant material into countries currently uninfested may delay its entry, as action by Californian authorities seems to have done. Also any measures that will reduce its abundance in infested countries will tend to reduce the chances of such countries serving as the source of new infestations. Available evidence suggests that new infestations have often resulted from the transportation of infested plants. Furthermore, once in a country, both human activities and prevailing winds aid dispersal. There is no evidence that *A. dispersus* is transported far away to new countries in upper air movements, as seems to have been the case with the leucaena psyllid, *Heteropsylla cubana* (Waterhouse and Norris 1987).

It is fortunate that the work in Hawaii has led to the probability that spiraling whitefly populations can be readily reduced to sub-economic numbers by biological control agents. Since the parasite *Encarsia ? haitiensis,* which is believed to be host specific, has been shown in Hawaii to be capable of achieving this result unaided, it would seem to be highly desirable to introduce this first to any country seeking biological control. Only if *E.. haitiensis* and *Encarsia* sp. do not produce adequate reduction of whitefly populations should consideration be given to introduction of the less specific coccinellid predators *Nephaspis oculatus* and *N. bicolor*.



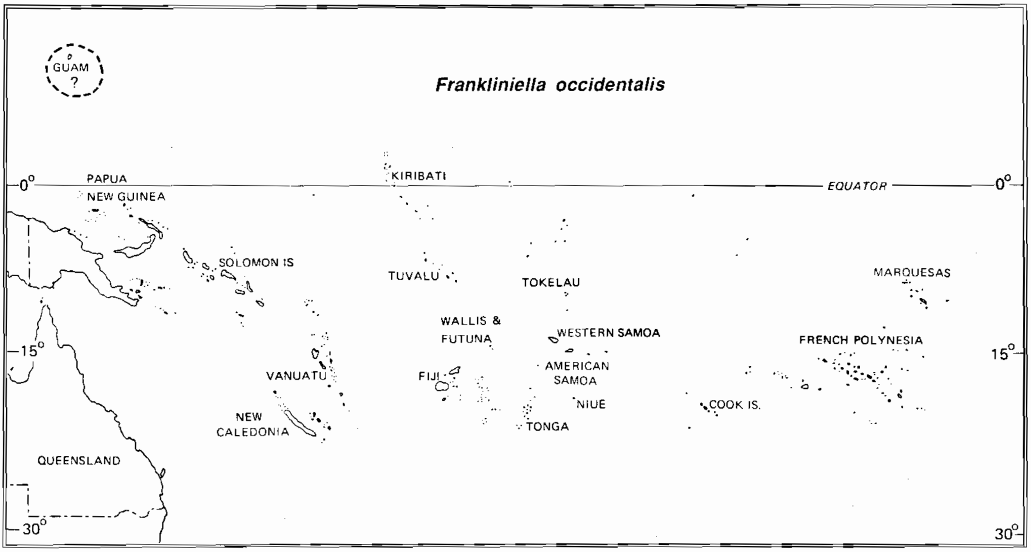
A predatory geocorid bug
(From *The Insects of Australia*, Melbourne University Press, 1970)


Frankliniella occidentalis
Brazil
Colombia
Hawaii
? Guam
Reunion
Canary Is

4

Frankliniella occidentalis
(Pergande)

THYSANOPTERA: THRIPIDAE
western flower thrips



Frankliniella occidentalis is native to North America, where it is very widespread and ranges from sea level to sub-alpine altitudes. It is the commonest thrips in California and occurs on an extremely wide range of plants. It has spread to northern South America, Europe and New Zealand and has also colonised Hawaii, Réunion and the Canary Islands. It is often intercepted in lettuce and flowers imported into Guam from North America, but is apparently not yet established there.

In addition to the unsightly damage and other adverse effects caused by its feeding, the thrips is an important vector of tomato spotted wilt virus. Insecticide sprays are relatively ineffective against it, although the use of systemic materials shows promise.

There have been no attempts at biological control. The most important natural enemy of the western flower thrips is the anthocorid bug *Orius tristicolor,* which is a general predator like the other species of *Orius* that are known to attack this thrips. Other general predators of *F. occidentalis* belong to the bug genera *Geocoris* and *Nabis* and also include the larvae of the lacewing *Chrysoperla* (= *Chrysopa*) *carnea.* Introduction of any or all of these general predators to a country lacking them would doubtless assist in reducing the numbers of *F. occidentalis* but, before deciding to do so, consideration should be given to what effects they might have on such non-target organisms as the beneficial thrips (*Liothrips urichi*) used in the effective biological control of the weed, *Clidemia hirta.*

Too little is known about the recorded wasp or nematode parasites to enable their potential to be evaluated.

Origin

F. occidentalis is native to North America and has been collected from sea level to sub-alpine altitudes throughout most of the continent. It has been recorded in the west over the vast region extending from Mexico to Alaska and, in the centre and east, from Texas and North Dakota to Connecticut. It is reported to be the commonest thrips in California.

Females occur in three colour forms (pale, intermediate and dark) which all mate readily with the uniformly pale males. The pale coloration of the female is dominant. This situation earlier resulted in a number of synonyms until the taxonomy was clarified by Bryan and Smith (1956). Pergande's (1895) type series contains both light and dark forms, although *F. occidentalis* was described as yellow. Characters for differentiating *F. occidentalis* from closely allied thrips are provided by Sakimura (1983).

Distribution

In addition to its native home in North America, the western flower thrips is known from South America (Brazil, Colombia), Europe (Britain, Denmark, France, Germany, Holland, Italy, Norway, Sweden), the Canary Is, Rèunion in the Indian Ocean and, in the Pacific, from Hawaii (1966) and New Zealand (prior to 1934) (L.A. Mound pers. comm. 1988). It is frequently intercepted in Guam in lettuce and flowers from North America, but not yet established there (R. Muniappan pers. comm. 1988). It has also been intercepted in New Zealand in flowers from California (Manson 1981). It was first collected in New Zealand from carnations in Christchurch as early as 1934. Adults from New Zealand are described as usually bicolored, abdomen brown, head mainly yellow, thorax intermediate orange brown and legs yellow with brown markings (Mound and Walker 1982). It has not been recorded from Australia.

Life cycle

The opaque, kidney-shaped eggs are inserted in the parenchyma cells of leaves, flowers or fruit. Eggs are susceptible to desiccation and mortality may be high in this stage.

The first instar larva emerges head first from the surface of the plant tissue and, in some plant species, mortality may be high during this process. Feeding commences almost immediately and mobility increases rapidly.

Second instar larvae are golden yellow. They move quickly and often seek crevices in which to hide and feed. This stage moults to disclose the third instar or 'prepupa', which is characterised by the appearance of wingpads and short erect antennae. In the next (4th) instar, the 'pupa', the antennae are laid back over the head.

The newly-emerged adult female is white to light yellow and is relatively quiescent for the first day. Thereafter it becomes very active and may live from 27 to 90 days, depending upon temperature and other factors, whereas males have about half this life expectancy (Bryan and Smith 1956).

The durations of life history stages are shown in Table 4.1. Oviposition normally begins within 72 hours of emergence and continues intermittently throughout life with an average at 26.6°C of 0.7 to 1.6 eggs per day (Bryan and Smith 1956). All life stages develop more rapidly as temperatures increase from 15° to 30°C, but adult female longevity decreases significantly as temperatures increase. Females lay significantly larger numbers of eggs at 20°C (95.5) than at 15° (24.2) or 30°C (43.8).

The relatively short life cycle at 20°C (22.4 days) and high reproductive potential provide for rapid population increase under temperate conditions. Decreased productivity at both 15° and 30°C suggests that either low or high temperatures do not favour massive population build up (Lublinkhof and Foster 1977). Movement was reduced by rain and mean daily temperatures below 10°C. Population increase was favoured by temperatures above 15°C (Harding 1961a, b).

Parthenogenesis occurs in *F. occidentalis,* a diploid female resulting if an egg is fertilised and a haploid male if it is not.

All stages tend to shelter in crevices or between touching leaves or flower parts. Individuals are gregarious and develop most rapidly when substantial numbers are present. In California the western flower thrips is more abundant when flowering peaks on native hosts in late spring and early summer than at other times of the year. There is a fall in population in autumn, correlated with a reduction in abundance of host flowers, followed by a steady rise from late winter when the first wild mustard flowers appear. An early spring peak is followed by an apparently sharp drop due to the dilution effect of rapidly increasing food and shelter. It appears that dark form females are better able to survive during wet cold periods and are more active than pale form females under these conditions.

When the attractiveness of white and yellow sticky board traps was compared in pear orchards, 91.1% of *F. occidentalis* were attracted to the white traps (Moffitt 1964) and greater numbers of this thrips were caught on white traps than on traps of other colours tested in an orange grove (Beavers et al. 1971). In lettuce farms in Hawaii white traps caught significantly more thrips than the 14 other colours tested. Of other colours, lighter shades were more attractive than darker shades, and yellow was more attractive than green (Yudin et al. 1987).

Leigh et al. (1984) developed a leaf-washing machine for recovering *F. occidentalis* and other minute arthropods from cotton and other plants.

Pest status

Frankliniella occidentalis is the most widespread thrips in California (Bryan and Smith 1956) and Arizona (Bibby 1958) and occurs in every vegetation unit and on almost every plant species that has been sampled. Its hosts range from plants growing in sands along the coast to those in subalpine areas as high as 3000 m. Bryan and Smith (1956) recorded it from 139 species in 45 families, favoured hosts occurring in the Fabaceae, Asteraceae and Brassicaceae.

It is found most frequently in the flowers, but it also occurs in all growing points and on the leaves. Smaller, more intricate flowers usually contain higher numbers than simpler ones, but *F. occidentalis* appears to have no very marked host preferences. In New Zealand, where it is widespread, it is particularly common from spring to autumn in flowers of *Lupinus, Melilotus, Chrysanthemum maximum* and nectarine (Mound and Walker 1982). Bailey (1933a, 1957) records *F. occidentalis* as a pest on many crops in California, including peaches, plums, nectarines, cotton, grapes, cut flowers and nursery stock. Other hosts include avocado, beans, lettuce, lucerne, lupin, mustard, onion, orange, spinach and

Table 4.1 Average developmental periods (days) for the life history stages of *Frankliniella occidentalis.* A: Bryan and Smith (1956), B: Lublinkhof and Foster (1977).

	15°C		20°C		26.7°C	30°C
Stage	A	B	A	B	A	B
1st instar	7	4.90	3.3	2.33	2.3	1.11
2nd instar	12	9.08	5.7	5.22	3.8	4.32
3rd instar	4.2	2.93	2.0	2.22	1.1	1.37
4th instar	8	5.56	4.8	2.85	2.7	1.56
adult pre-oviposition		10.44		2.43		2.39
longevity		70.80		56.75		27.50
eggs produced		24.20		95.50		43.83
egg incubation	13	11.18	6	6.37	4	4.26
egg to egg		44.10		22.40		15.0

sunflower. Nectarines are particularly susceptible to injury, scars produced by feeding damage on the young fruit leading to extensive disfigurement (Lewis 1973). The western flower thrips is one of the most abundant pests on cabbage in southern California (Oatman and Platner 1969) and a common pest on sesame (Carlson 1967).

The presence of ten or more thrips per strawberry flower resulted in the destruction of small flowers and the discoloration of fruit (Allen and Gaede 1963). On Chenin Blanc grapes in California 1 to 3 thrips per terminal after buds had opened or 1.6 per terminal during flowering resulted in stunting of growth, but did not affect the sugar content of the grapes at harvest (McNally et al. 1985a, b). Several varieties of grapes were scarred by larval western flower thrips (Jensen 1973, Jensen and Luvisi 1973), although under some circumstances thrips may improve pollination and lead to increased fruit set (Yokoyama 1977). Egg punctures of *F. occidentalis* on some apple varieties (e.g. McIntosh and Spartan) result in a skin discoloration known as pansy spot (Madsen and Jack 1966).

In Georgia *F. occidentalis* is an important glasshouse pest, damaging many kinds of flowers and newly formed fruits (Beshear 1983).

Insecticide control of *F. occidentalis* on early season cotton in Arizona and New Mexico caused a significant increase in yield (Race 1961, 1965, Tuttle and Wene 1959), although yield increases were not observed in California (H.T. Reynolds pers. comm. 1988).

In safflower (*Carthamus tinctorius*) in California, where *F. occidentalis* is one of the major pests, about three nymphs per bract or 18 to 20 per bud caused damage, whereas later feeding by 120 to 135 per maturing seed head caused only superficial injury. The degree of damage varied from 8% in an early planting to 40% in a late one. Damage was reduced from 31.9% to 6.8% by a single aerial application of insecticide to one late plot, but there was no striking increase in seed yield, indicating that the damage is of little economic significance (Carlson 1962, 1964a). When up to ten thrips, producing an average of 75 larvae, were caged on individual safflower buds seed yields were not affected. However the yield was reduced by up to 0.75 g per head when 20 or 40 thrips, producing 150 and 300 nymphs respectively, were introduced (Carlson 1966a, b).

F. occidentalis is common on sesame in California, but up to 20 adults caged on a single plant caused no significant damage and did not reduce pod set or seed yield (Carlson 1967).

Injury by *F. occidentalis* on onions grown for seed was primarily the result of feeding on the anther filaments of the florets, which resulted in a premature loss of pollen, leading to a decrease in pollination and seed set. Serious damage did not occur if the population was less than 10 thrips per floret. This suggests that 9,000 to 10,000 thrips would have to be present in each flowering head for a loss to be apparent. Appropriate insecticide treatment gave increased yield of seed (Carlson 1964b).

In Texas heavy infestations in onion fields resulted from breeding within the fields rather than through movement into them (Harding 1961a, b).

In Hawaii serious damage may occur on lettuce and chrysanthemums, but occasionally attack may also occur on the foliage of bush beans, capsicum, chinese peas, cucumber, egg plant, onion and watermelon and to the flowers of capsicum, egg plant and tuberose. On onion leaves tiny white scars are produced, generally on the upper part of the plant, and usually under a bend in a leaf (Nakahara and Marsden 1979b). In cucumber heavy damage is caused to the foliage, although the growing tips do not appear to be affected. Damaged leaves turn white and drop prematurely (Nakahara and Higa 1980).

Strip intercropping of beans *Phaseolus vulgaris* with sweet corn was reported to diminish the abundance of *F. occidentalis* (Capinera et al. 1985), but this does not appear to have been adopted as a control measure.

There is evidence of a degree of host resistance to *F. occidentalis* in some lines of cotton and of muskmelon *Cucumis melo* (Kishaba et al. 1971, Rummel and Quisenberry 1979). For example, cotton genotypes with pubescent leaves exhibit a high degree of resistance to injury compared with glabrous genotypes (Rummel and Quisenberry 1979).

F. occidentalis and five other species of thrips are vectors of tomato spotted wilt virus (Cho et al. 1987, Mound and Walker 1982, Paliwal 1976, Robb and Parrella 1988, Sakimura 1961, 1962, 1963, see also chapter 5 on *Thrips tabaci*) and *F. occidentalis* is also capable of transmitting tobacco streak mosaic virus from white sweet clover *Melilotus alba* to *Chenopodium quinoa* (Kaiser et al. 1982). Even when infestations were as light as three to five thrips per lettuce plant, spotted wilt diseased heads were observed in Hawaii.

As one small point in its favour *F. occidentalis* is recorded as attacking the weed, ragwort *Senecio jacobaea* (Frick 1964). A more important beneficial aspect of the presence of the western flower thrips in flowers is its role in increasing pollination, as has been recorded for onions (Carlson 1964b). Indeed, by penetrating a flower bud of the bean *Phaseolus vulgaris* before it opens, *F. occidentalis* can lead to earlier than usual pollination (Lewis 1973, Mackie and Smith 1935).

Control measures

There are many publications dealing with the chemical control of *Frankliniella occidentalis* and a wide range of insecticides has been tested, but generally with rather limited success. This is partly due to the considerable dispersive powers of adults when conditions are favourable, which results in sprayed crops soon being re-invaded. Other factors inimical to effective chemical control include the habit of larvae and adults of sheltering in cracks and crevices in flowers, growing points and leaf sheaths and of the females embedding their eggs into plant tissue. Insecticides with a systemic effect or persistency are therefore required, although these same qualities may lead to residue problems if edible portions of plants are treated. Persistency is a characteristic of some of the more effective chemicals formerly used, such as the chlorinated hydrocarbons and the cyclodienes, but these are no longer acceptable, both because of environmental considerations and the development of resistance.

Fumigation of thrips-infested strawberries with acetaldehyde in combination with carbon dioxide or oxygen produced 100% thrips mortality and reduced the extent of decay but the after effects of the treatments could generally be detected for several days in taste tests. This method has potential for post-harvest control on strawberries for shipment to countries that have quarantine regulations against *F. occidentalis* (Aharoni et al. 1979, 1980). However ethyl formate gave effective control without affecting taste (Aharoni et al. 1980, Dean 1981). Ninety per cent carbon dioxide for 48 hours killed all thrips and reduced decay, but it affected fruit flavour (Aharoni et al. 1981).

Although chlorinated hydrocarbons provided a significant increase in yield in early season cotton in Arizona, resistance appeared to be developing (Tuttle and Wene 1959). In New Mexico, cotton yields were also significantly increased by early control of *F. occidentalis* if populations reached five nymphs per plant, applications of the systemics disulfoton or phorate in the furrow during planting being most effective (Race 1961, 1965). In Texas several systemic insecticides dusted on seed the week before planting protected young plants from thrips for 4 to 6 weeks after planting (Hanna 1958). Application of the systemic insecticide aldicarb into the furrow when planting seed of glabrous cotton genotypes produced greater yields, but foliar application of dicrotophos did not (Rummel and Quisenberry 1979).

Application of methidathion or endosulfan reduced damage by *F. occidentalis* to safflower by 63% (Carlson 1969) and later studies showed that methidathion and oxydemeton-methyl at pre-bloom and onset of bloom were effective in reducing bud damage (Carlson and Witt 1977). However, in other trials successful thrips control produced little increase in yield of seed, suggesting that the thrips damage may be of little economic importance to safflower (Carlson 1962). Mexacarbate or carbaryl controlled western flower thrips on cauliflower (Shorey et al. 1962) and tomatoes (Shorey and Hall 1963).

More recently, western flower thrips control on tomatoes by permethrin, mevinphos or acephate did not extend beyond a day, either because of constant migration from adjacent crops or the occurrence of resistance to the insecticides, or both (Steenwyk 1979).

Aerial application of parathion or DDT and/or application of sprays of mexacarbate, dibrom, trichlorphon, azinphos-methyl, malathion, or fenchlorphos all gave control of the western flower thrips on lettuce in southern California (Shorey and Hall 1962).

F. occidentalis was controlled on lettuce and spinach by the systemic insecticides phorate or disulfoton applied as granules to the soil (Harding 1959, Harding and Wolfenbarger 1963), and thrips populations were reduced on potatoes by soil treatment with phorate granules (Gerhardt and Turley 1961). More recently, mortalities exceeding 90% have been obtained by spraying twice with oxamyl at 3-day intervals (M.W. Johnson pers. comm. 1988).

On bulb onions, the western flower thrips was controlled by granules of the systemic insecticides phorate or dimethoate that lodged between the leaves, or were applied to the soil, but disulfoton was less effective (Hale and Shorey 1965). When applied to onions grown for seed, dimethoate, azinphos-methyl, parathion and diazinon gave varying degrees of thrips control, but binapacryl was ineffective. Dimethoate gave increased yield of seed (Carlson 1964b).

Halo spotting (the production of a small dark scar surrounded by whitish tissue) and sunburst or starfish scarring of table grapes in California caused by *F. occidentalis* was greatly reduced by the application of dimethoate at the time of blooming (Jensen 1973, Jensen and Luvisi 1973). On Chenin Blanc wine grapes it was not possible to assess direct damage to the leaves and indirect effects of infestation on fruit yield and sugar content because shoots destroyed or stunted early in the season were later replaced in this vigorously growing variety (McNally et al. 1985b).

Because *F. occidentalis* colonised flowering weeds more readily than lettuce which does not flower under normal cultivation practices, weed trap crops have been suggested, preferably of species that do not harbour tomato spotted wilt virus (Yudin et al. 1988). Weeds with lighter coloured leaves and flowers would presumably be more attractive than those with darker colours. Since *F. occidentalis* shows a marked preference for buckwheat it is possible to consider this also as a trap crop, perhaps treated with a systemic insecticide.

Associated pests

The extremely wide host range of *Frankliniella occidentalis* results in there being a correspondingly wide range of associated pests. Those on beans, brassicas, onions and tomatoes are listed in chapter 5 on *Thrips tabaci*. To these might be added those on lettuce, including aphids, the leaf miners *Liriomyza huidobrensis* and *L. sativae,* two noctuid moths (the green looper *Chrysodeixis eriosoma* (= *Plusia chalcites*) and the black cutworm *Agrotis ipsilon)* and the vegetable weevil *Listroderes obliquus*. Other pests on chrysanthemums include the carmine spider mite *Tetranychus cinnabarinus* (Boisduval).

Natural enemies

Thrips as a group are attacked by a few parasitic wasps and flies and by a rather larger number of predators, notably anthocorid, nabid and lygaeid bugs, chrysopids, thrips, syrphid larvae, spiders and mites. They are also attacked by entomopathogenic nematodes. When a mixed population of thrips, mites and aphids is present in a crop, as is usually the case, it is not always easy from casual observations to determine which prey species are attacked by a particular general predator: nevertheless, there is good reason to believe that the natural enemies listed in Table 4.2 attack *F. occidentalis*.

Probably the most important natural enemy of the western flower thrips in its native California is the minute pirate bug *Orius tristicolor,* all stages of which (like those of many other species in the genus *Orius*) are important predators of thrips (Ananthakrishnan 1984, Bailey 1933a, van den Bosch et al. 1956, van den Bosch and Hagen 1966, Letourneau and

Table 4.2 Natural enemies of *Frankliniella occidentalis*

Species	Country	Reference
Hemiptera		
Anthocoridae		
Orius insidiosus	USA	Lewis 1973
O. persequens	Hawaii	Nakahara and Brennan 1977a, 1978a Nakahara and La Plante 1976a
O. tristicolor	USA (California, Utah)	Bailey 1933b, Gonzalez et al. 1982, Letourneau and Altieri 1983, Lewis 1973, Sakimura 1930, Stolz and Stern 1978b, van den Bosch and Hagen 1966, Yokoyama 1978
Paratriphleps laevisculus		Nakahara and Brennan 1976
Nabidae		
Nabis alternatus	California	Benedict and Cothran 1980
N. americoferus		Benedict and Cothran 1980
Lygaeidae		
Geocoris pallens	California	Stoltz and Stern 1978a Yokoyama 1978
G. punctipes	California	van den Bosch and Hagen 1966
Thysanoptera		
Aeolothripidae		
Aeolothrips fasciatus	Canada	Lewis 1973
A. kuwanaii	California	Bailey 1933b
Franklinothrips vespiformis	Hawaii	M.W. Johnson pers. comm. 1988
Neuroptera		
Chrysopidae		
Chrysoperla carnea (= *C. californica*)	California	Bailey 1933b, Russell 1912
Coleoptera		
Coccinellidae		
Hippodamia convergens	California	Bailey 1933b
Diptera		
Syrphidae		
Sphaerophoria sulphuripes	California	Russell 1912
Hymenoptera		
Chalcididae		
unidentified planidium	Texas	Wilson and Cooley 1972
Eulophidae		
Ceranisus (= *Thripoctenus*) *americensis*	USA	Ananthakrishnan 1984, Lewis 1973, Murai 1988
C. russelli	Crawford	Russell 1911, 1912
Acarina		
Amblyseius cucumeris	Canada	Steiner and Elliott 1987
A. mckenziei	Canada	Steiner and Elliott 1987
Anystis agilis Bks. (?)	USA	Sakimura 1930
Nematoda		
Howardula aptini	Texas	Wilson and Cooley 1972

Altieri 1983, Ryerson and Stone 1979, Sakimura 1930, Stoltz and Stern 1978b). A high correlation was found between numbers of *F. occidentalis* and of *O. tristicolor* in cotton fields in the San Joaquin Valley. Furthermore, in laboratory studies, as the number of thrips increased, adult and larval pirate bug mortality decreased and both bug longevity and production of offspring increased (Stoltz and Stern 1978a, b). An increase in thrips numbers followed mortality of predators, including *Orius,* caused by the application of insecticides (van den Bosch et al. 1956, Stoltz and Stern 1978a). *O. tristicolor* was more effective in controlling the western flower thrips on squash when this was interplanted with corn and cowpeas (Letourneau and Altieri 1983).

Other species of *Orius* also attack the western flower thrips, including *O. insidiosus* in California and Hawaii and *O. persequens* in Hawaii (Nakahara and Brennan 1977a, 1978b, Nakahara and La Plante 1976a).

Big eye bugs of the genus *Geocoris,* notably *G. pallens* and *G. punctipes,* are also important predators of *F. occidentalis* in California (van den Bosch and Hagen 1966).

Damsel bugs of the genus *Nabis,* including *N. alternatus* and *N. americoferus* are somewhat less important predators (Benedict and Cothran 1980).

The predatory thrips *Aeolothrips fasciatus* is reported to attack *F. occidentalis* in Canada (Lewis 1973), but it is not clear what overall impact this attack has. In Hawaii *Franklinothrips vespiformis* is reported to attack western flower thrips (M.W. Johnson pers. comm. 1988).

Several species of predacious mites are reported to attack the western flower thrips in North America and it is possible that they are capable of inflicting significant mortality. One of these is *Anystis agilis* (?), which was reported to be an effective factor in reducing thrips populations in Utah (Sakimura 1930). Under glasshouse conditions in Canada promising results have been obtained using *Amblyseius cucumeris* and *A. mckenziei,* especially the former (Elliott 1988, Johnson and Hill 1988, Steiner and Elliott 1987). Interestingly. *F. occidentalis* was observed feeding actively on eggs of mites (*Tetranychus* spp.) on cotton in California (Gonzalez et al. 1982).

Lewis (1973) provides a list of parasitic wasps recorded as attacking thrips. Of those listed the eulophid *Ceranisus* (= *Thripoctenus*) *americensis* is recorded from *F. occidentalis* in Canada, but no information is available on its impact. However the related species *C. russelli* has been reported to cause up to 70% mortality of larvae in some samples of the bean thrips *Caliothrips* (= *Hercothrips*) *fasciatus* (Russell 1912). *Ceranisus americensis* is also reported from the western flower thrips in USA and many other species of *Ceranisus* attack various species of thrips (Ananthakrishnan 1984). In Texas a planidium (the free living first instar larva of a wasp) of an unidentified chalcidoid was reported to become ectoparasitic on larval *F. occidentalis* (Wilson and Cooley 1972).

Many adult female *F. occidentalis* in Texas were found to be parasitised by all stages of the entomopathogenic nematode *Howardula aptini* (Wilson and Cooley 1972). This species was earlier known from the blueberry thrips *Frankliniella vaccinii* in New Brunswick (Nickle and Wood 1964).

Attempts at biological control

There have been none.

Hawaii

The current situation in Hawaii provides information relevant to other Pacific island nations. *Frankliniella occidentalis* was first recorded in May 1966 from Kauai and Maui (Anon. 1967). For almost a decade it was apparently not regarded as an important pest but, since the mid seventies, there have been sporadic and sometimes serious outbreaks of economic importance, particularly on lettuce and chrysanthemums.

For example, when there were ten or more thrips per head in one plot of lettuce, 75% of the crop was rendered unmarketable. In another plot 20 to 30% of plants showed symptoms of spotted wilt (Chun and Nakahara 1976). In yet another plot 25% of lettuce plants showed spotted wilt symptoms and had to be discarded (Nakahara and Brennan 1977b).

In recent years, and particularly in summer, tomato spotted wilt incidence has risen steadily to cause severe economic losses on Maui in lettuce (both *Lactuca sativa* and romaine, L. *sativa* var. *longifolia*), and to account for 50 to 90% of crop losses. *Thrips tabaci,* and particularly *F. occidentalis,* are responsible. High populations of *F. occidentalis* occur in the early blossoms of three woody legume species, *Leucaena leucocephala, Prosopis pallida* and *Acacia decurrens* (Yudin et al. 1986).

When weeds were in flower nearby they attracted more *F. occidentalis* than lettuce, but when flowering ceased or these hosts dried out mass movements of thrips into vegetable plantings occurred (Yudin et al. 1988). On one occasion 50% of the leaves in each head of lettuce had to be discarded before marketing because of feeding injury (Nakahara and Brennan 1978b).

F. occidentalis damage to onion leaves is similar to that caused by *Thrips tabaci,* but damage by the latter normally occurs only between the leaf axils, whereas *F. occidentalis* may damage the entire leaf surface (Nakahara and Higa 1980).

An immigrant predatory anthocorid bug, *Paratriphleps laevisculus,* was first recorded in 1974 in light traps and in *F. occidentalis* habitats (Nakahara and Brennan 1976). It was reported in Hawaii in January 1975, but was present still in only low numbers at the end of 1976 in areas where *F. occidentalis* was causing light to moderate damage to lettuce (Nakahara and La Plante 1976b).

In mid 1976 the predatory anthocorid bug, *Orius persequens,* was recorded in low densities (1 to 3 per head) in lettuce lightly infested with *F. occidentalis* (Nakahara and La Plante 1976a) and low densities of this same predator were also reported on thrips-infested lettuce early in 1978 (Nakahara and Brennan 1978a) and on heavily infested chrysanthemums in mid 1977 (Nakahara and Brennan 1977a). However, more recently *Orius insidiosus* has appeared and has become the commonest predator. *F. occidentalis* is also attacked by *Franklinothrips vespiformis* and it is possible that it may be attacked by the eulophid parasite *Ceranisus menes* (= *C. brui*) introduced in 1933 from Japan against *Thrips tabaci* (Sakimura 1937c). At least a dozen other species of *Ceranisus* attack many other species of thrips (Ananthakrishnan 1984).

Biology of the major species

Orius tristicolor

This species is widely distributed in North America (Kelton 1963) and is frequently mentioned as an important predator of many small arthropod pests of cotton, lucerne and other crops. It is the predator whose populations are most closely correlated with those of *F. occidentalis* (Stoltz and Stern 1978a). Known as a minute pirate bug, the adult *O. tristicolor is* a small (1.87 to 2.22 mm long) black and white, active bug, with a prominent proboscis with which it pierces soft-bodied prey. It can complete its development on a diet of mites alone (Askari and Stern 1972a). Cotton extrafloral nectar is also consumed (Yokoyama 1978) and, even when suitable prey is present, *Orius* may at times insert its proboscis into plant tissue to take in sap. There is no evidence that this activity causes damage to the plant, but the bug's life span is markedly shorter when plant sap is the only food available (Askari and Stern 1972a, van den Bosch and Hagen 1966).

O. tristicolor eggs are usually inserted singly into soft plant tissue with only the circular white egg caps protruding above the surface. In beans the leaf petiole is usually selected, with some eggs also in the bean stem or leaf midrib, but rarely in the leaf veins or blade. The incubation period is 3 to 5 days at 25.5°C. The nymphs are usually greenish yellow, but may be amber or brown and, in the later instars, are very active. Nymphal development takes 26, 14 and 8.5 days at 21.1, 25.5 and 33.3°C respectively. Females mate soon after moulting to the adult and commence laying eggs two to three days later. The average number of eggs laid is 129 ± 12 (Askari and Stern 1972b, Butler 1966). Adult longevity is about 35 days at 25.5°C, with abundant mites *Tetranychus pacificus* McGregor as food. Adult *Orius* are cannibalistic when placed in cages with nymphs, in spite of the presence of mites as food (Askari and Stern 1972b). In the laboratory *O. tristicolor* adults consumed an average of 1.4 spotted alfalfa aphids (*Therioaphis trifolii* forma *maculata*) per day (Goodarzy and Davis 1958).

Adults and nymphs of *O. tristicolor* are found on all above ground plant parts, but most commonly in terminal growth and flowers, where thrips, among their most favoured prey, occur. Adults are also attracted by spider mite aggregations that often occur on the undersides of leaves, especially of seedlings. They also attack aphids, whiteflies and, in cotton fields, the eggs and newly hatched larvae of the cotton bollworm *Helicoverpa zea*. *O. tristicolor* overwinters in California as an adult in rubbish and early in spring it may be found feeding upon larvae of *F. occidentalis* (Bailey 1933b).

Orius tristicolor was the most abundant predator in lucerne fields in summer and autumn in Utah (Goodarzy and Davis 1958, Knowlton et al. 1938).

O. tristicolor appeared to be less harmed by insecticides than most other beneficial insects in cotton fields (van den Bosch and Hagen 1966; van den Bosch et al. 1956). Four to eight times the number of bugs were found on untreated plants bearing abundant prey, than on insecticide-treated plants with far fewer prey (Gonzalez et al. 1982).

Orius insidiosus

The life history, predatory habits and abundance of this bug are dealt with by Garman and Jewett (1914), Marshall (1930) and Iglinsky and Rainwater (1950). It is an important predator of eggs and newly-hatched larvae of the bollworm *Heliocoverpa* (= *Heliothis*) *zea* (Barber 1936) and also attacks thrips and other small insect pests in a range of crops. Sweet corn pollen was found to be an important food for both nymphs and adults in that crop (Dicke and Jarvis 1962). Shelton and Edwards (1980) found that *O. insidiosus* was more abundant in soybean fields with grass and mixed weeds than in fields with broad-leaf weeds or that were weed free. This might have been due both to favourable microclimate and the presence of alternative prey.

Geocoris pallens and *G. punctipes*

These are known in California as big eye bugs and are important predators in cotton crops (Stoltz and Stern 1978a). Other *Geocoris* spp. occur on several Pacific islands.They move rapidly and fall readily from plants when disturbed. The greyish adults of *G. punctipes* range from 3 to 4 mm in length and are distinctly larger than the buff to black adults of *G. pallens*. The eggs (0.1 mm in length) have slender processes projecting from the anterior end. They are laid singly, often in the terminal growth of the plant, but sometimes amongst spider mite colonies on the undersides of leaves. The eggs turn black when parasitised by *Telenomus reynoldsi* (Hym.: Scelionidae). The effect of temperature on the rate of development of eggs and nymphs is reported by Butler (1966).

Big eye bugs appear early in the season and reach peak abundance in midsummer. They attack thrips, plant-feeding lygus bugs, leafhoppers, spider mites and small lepidopterous larvae (van den Bosch and Hagen 1966). In cotton they use extrafloral nectar as an alternative food to *F. occidentalis* (Yokoyama 1978).

Like *Orius*, *Geocoris* will take sap from cotton and other plants, but apparently without inflicting any damage (van den Bosch and Hagen 1966).

Eight to 17 times as many bugs were found on untreated cotton plants with abundant prey (especially mites) as on insecticide-treated plants with far fewer prey (Gonzalez et al. 1982). Reduction of *G. pallens* populations by dimethoate and naled-toxaphene applications in 1971 and by dimethoate treatments in 1972 allowed *F. occidentalis* populations on cotton in moulting to the adult and commence laying eggs two to three days later. The average number of eggs laid is 129 ± 12 (Askari and Stern 1972b, Butler 1966). Adult longevity is about 35 days at 25.5°C, with abundant mites *Tetranychus pacificus* McGregor as food. Adult *Orius* are cannibalistic when placed in cages with nymphs, in spite of the presence of mites as food (Askari and Stern 1972b). In the laboratory *O. tristicolor* adults consumed an average of 1.4 spotted alfalfa aphids (*Therioaphis trifolii* forma *maculata*) per day (Goodarzy and Davis 1958).

Adults and nymphs of *O. tristicolor* are found on all above ground plant parts, but most commonly in terminal growth and flowers, where thrips, among their most favoured prey, occur. Adults are also attracted by spider mite aggregations that often occur on the undersides of leaves, especially of seedlings. They also attack aphids, whiteflies and, in cotton fields, the eggs and newly hatched larvae of the cotton bollworm *Helicoverpa zea. O. tristicolor* overwinters in California as an adult in rubbish and early in spring it may be found feeding upon larvae of *F. occidentalis* (Bailey 1933b).

Orius tristicolor was the most abundant predator in lucerne fields in summer and autumn in Utah (Goodarzy and Davis 1958, Knowlton et al. 1938).

O. tristicolor appeared to be less harmed by insecticides than most other beneficial insects in cotton fields (van den Bosch and Hagen 1966; van den Bosch et al. 1956). Four to eight times the number of bugs were found on untreated plants bearing abundant prey, than on insecticide-treated plants with far fewer prey (Gonzalez et al. 1982).

Orius insidiosus

The life history, predatory habits and abundance of this bug are dealt with by Garman and Jewett (1914), Marshall (1930) and Iglinsky and Rainwater (1950). It is an important predator of eggs and newly-hatched larvae of the bollworm *Heliocoverpa* (= *Heliothis*) *zea* (Barber 1936) and also attacks thrips and other small insect pests in a range of crops. Sweet corn pollen was found to be an important food for both nymphs and adults in that crop (Dicke and Jarvis 1962). Shelton and Edwards (1980) found that *O. insidiosus* was more abundant in soybean fields with grass and mixed weeds than in fields with broad-leaf weeds or that were weed free. This might have been due both to favourable microclimate and the presence of alternative prey.

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California to increase significantly, an indication of the importance of *G. pallens* as a thrips predator. The numbers of other pests in the crop also increased (Stoltz and Stern 1978a).

Nabis alternatus and *N. americoferus* (= *N. ferus*)
These are known as damsel bugs in California. The active adult bugs are tan or grey, slender, 8 to 10 mm long and have a long proboscis and raptorial forelegs. They fall readily from plants when disturbed. Eggs are inserted into soft plant tissue with only the flat circular caps protruding. Nymphs first become abundant in mid-summer and remain common until autumn. The bugs feed on a range of hosts including thrips, aphids, leafhoppers, lygus bugs, spider mites and small caterpillars. They also feed on the eggs of their prey (Benedict and Cothran 1980, van den Bosch and Hagen 1966).

Chrysoperla carnea (= *C. californica*).
The green, yellowish green or brownish adults feed on honeydew and are not predacious. The stalked eggs are deposited singly and at random on plant surfaces. The predacious larvae puncture prey with their long sickle-like mandibles and suck out body fluids (van den Bosch and Hagen 1966). Further data on this species are presented in chapter 5.

Comment

The widespread abundance of *F. occidentalis* in its native home in North America is evidence that it is not kept under effective biological control. However its populations would undoubtedly be higher there, probably very much higher, were it not for the toll taken by its natural enemies. The more specific of the reported natural enemies, namely eulophid parasitic wasps of the genus *Ceranisus,* (especially *C. americensis*) may be worthy of further study. However, the anthocorid bug predators, *Orius tristicolor* and *O. insidiosus,* and especially the former, are more likely to establish readily in a new country and to produce considerable mortality. It is, perhaps, surprising that *O. tristicolor* has not been introduced to Hawaii, although there is a widespread and growing reluctance to introduce predators, unless studies show that the species concerned have a valuable degree of preference for the pest species involved. The problems caused by the presence already in the Pacific of beneficial thrips, which might also suffer predation, is dealt with in the comment section of chapter 5. Should there prove to be a conflict of interest, consideration should be given to whether or not other damaging thrips species (e.g. *Thrips tabaci*) are present and what overall magnitude of damage is produced by this group of pests.

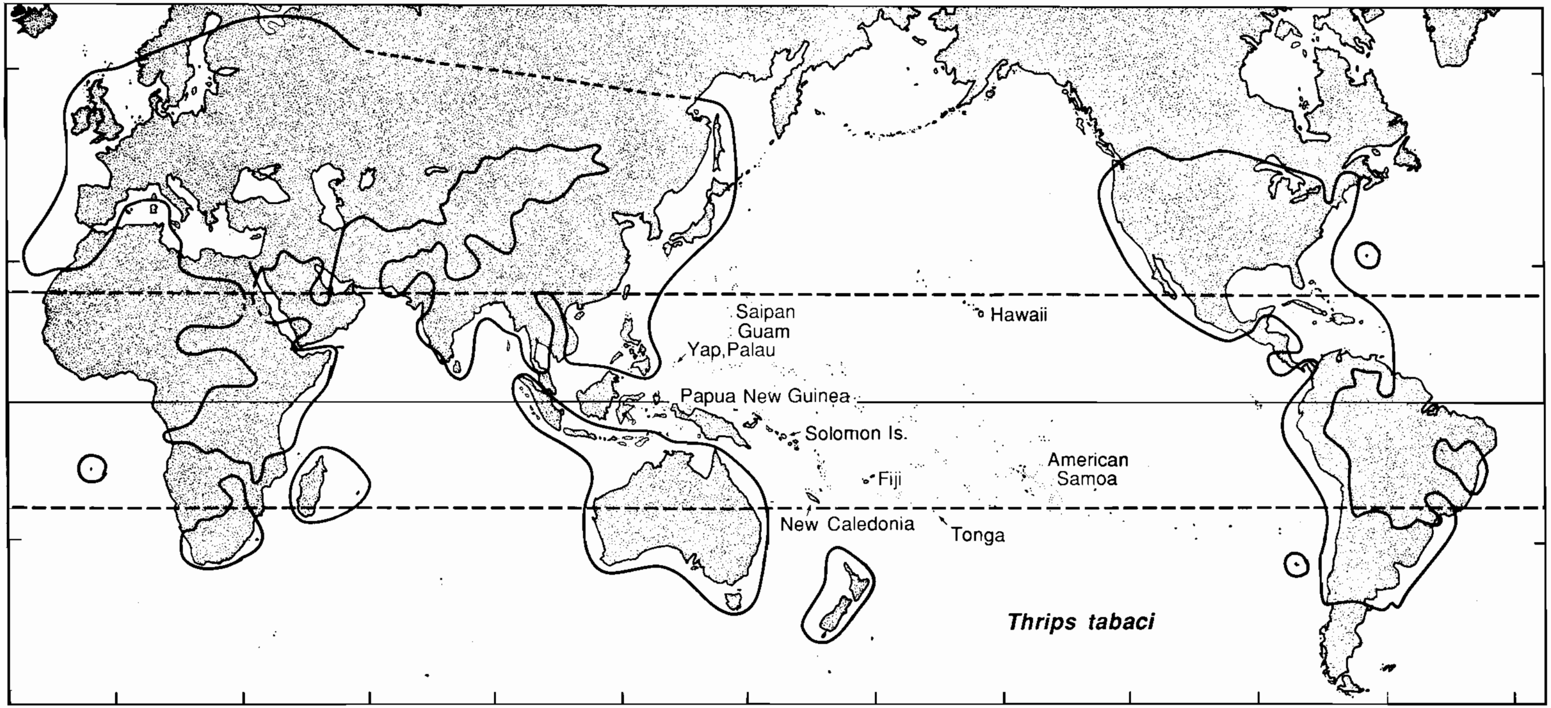
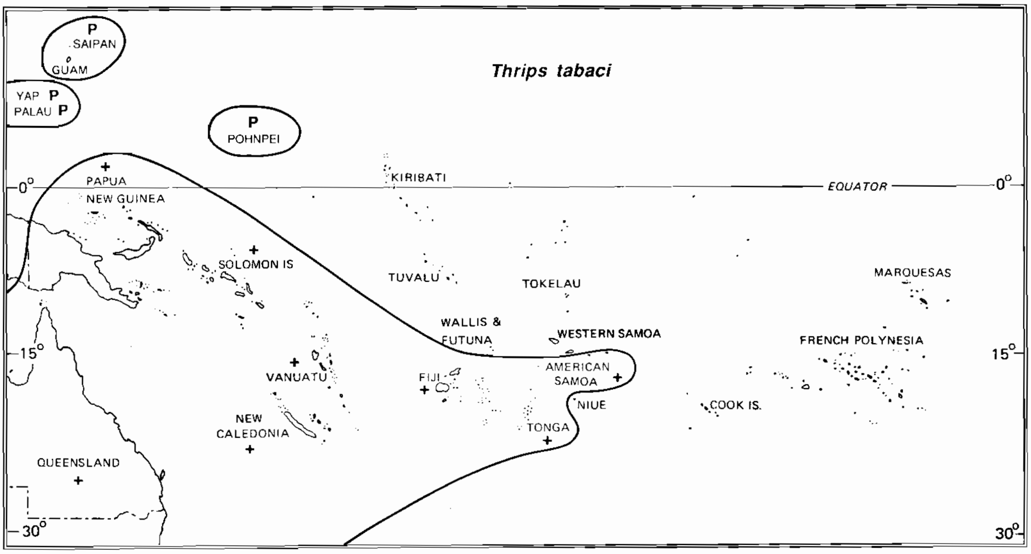


Fig. 5.1. World distribution of *Thrips tabaci* after Anon. (1969). The limits of distribution, particularly in the large land masses, follow political divisions. In consequence lack of records in many countries contributes heavily to the erratic course of the lines in some places. Real distribution would probably be broadly smoothed.

5

Thrips tabaci Lindeman

THYSANOPTERA: THRIPIDAE
onion thrips



Thrips tabaci probably originated in the Middle East and the countries bordering the Black and Caspian Seas, where one of its favoured host plants, the onion, is also thought to have originated. An attempt at biological control, using the hymenopterous parasite *Ceranisus menes,* imported from Japan into Hawaii, produced little effect, but the situation deserves reexamination. There are many general predators, especially in the Hemiptera, Coleoptera, Neuroptera, Diptera and Acari. Complexes of these appear to contribute to the control of the thrips in Bulgaria and other places within its reputed native range and it is possible that useful natural enemies could be transferred from there to other countries. However, their interaction would need to be examined and their degree of specificity would need to be carefully checked to ensure that they did not constitute a threat to such beneficial thrips as *Liothrips urichi.* Fungal pathogens and phytoseiid mites are proving of considerable value for the control of *T. tabaci* in glasshouses, but their potential value for use out-of-doors is unknown.

Origin

Lindeman's specimens were from Bessarabia (modern Moldavia, USSR). The thrips was doubtless very widespread even at that time (1888) and its country of origin cannot be assigned with certainty. However, Mound (quoted in Lewis 1973) states that, as the onion, a highly favoured food plant of the thrips, probably originated in the eastern Mediterranean region (Anon. 1973-74), this is the likely homeland of the thrips. This hypothesis is supported by the fact that in that region the sex ratio of *T. tabaci* is about 1 : 1, whereas in other parts of the world males are rare. They are unknown in Japan (Okada and Kudo 1982, Sakimura 1937a), Korea and Micronesia (Sakimura 1937a), Java (Kalshoven 1981), New Zealand (Mound and Walker 1982), and the Sudan (MacGill 1927), they occur in the ratio of only 1 male : 1000 females in Hawaii (Sakimura 1932), are usually rare in the U.K. (Morison 1957) although somewhat more plentiful but still uncommon (e.g. 1 male : 60 females, Harris et al. 1935) in the United States. This phenomenon of disparate sex ratios in different parts of the geographic range of a thrips species is a common occurrence associated with extension of geographic range and is thought to be due to the greater chances of successful establishment of parthenogenetic forms, of which one female is sufficient as a nucleus for a new population (O'Neill 1960).

As Lindeman's type series contained both sexes it is likely that Moldavia is part of the original range of the thrips (Lewis 1973, Mound and Walker 1982).

Distribution

The thrips is virtually cosmopolitan (Fig. 5.1) except for the southern tip of South America, the northern half of North America, northern Europe and Asia, the Tibetan plateau, large deserts and seemingly, much of the tropical rainforest areas of South America and West Africa (Anon. 1969). In the Pacific it is known from the Caroline Is, Fiji, Hawaii, Mariana Is, New Caledonia, New Zealand, Palau, Papua New Guinea, Solomon Is, Tonga, Vanuatu and Yap. A. Vargo (pers. comm. 1989) reports it from American Samoa and L.S. Yudin from Guam (pers. comm. 1989). Without doubt it is also present but not yet recorded, in other island groups with significant and diversified vegetation.

Life cycle

The duration of life history stages, according to various authors, is summarised in Table 1. Over much of its geographic range *Thrips tabaci* is usually parthenogenetic. The eggs are about 0.26 mm in length and 0.12 mm in width. They are whitish and kidney shaped when inserted, singly, into slits in the plant tissue made by the saw-toothed ovipositor of the female, but they swell somewhat and become elliptical while embedded in the plant tissue. The egg assumes an orange tinge as development proceeds and reddish eyespots eventually show through. Gawaad and Shazli (1969a) and Shazli and Gawaad (1971) observed that the development of eggs dissected from plant tissue was retarded, even though they were maintained on moist filter paper in a saturated atmosphere. It is possible, therefore, that absorption of tissue fluids from the plant is significant to the normal development of the egg. On emergence the first instar larva is initially covered with a pellicle, rather in the nature of that surrounding grasshopper hatchlings. This pellicle, or sheath, remains intact until the prelarva, as this stage is called, has wriggled out from the oviposition cavity onto the plant surface. The sheath then splits dorsally and discloses the active first stage larva. This stage (larva 1) is about 0.60 mm in length. It is pale yellow in colour, has short antennae and legs, rudimentary eyes and transverse rows of regularly arranged short bristles on each thoracic and abdominal segment. The lower aspect of the head is in the form of a mouthcone, comprised of the clypeus, labrum, galeae of the maxillae and the labium. Through this operate the single functional (left) mandible, and the delicate maxillary stylets which fit together to form a tube. The mandible, which is in the form of a slender dagger, is incapable of protrusion, but is brought into use by vigorous up and down movements of the entire head to tear the leaf cuticle and superficial mesophyll cells. The tube formed by the maxillary stylets, however, reaches deeper in, to lacerate cells the mandible cannot reach. Periodically the head movements operating the mandible cease, and the mouthcone is applied to the torn area to imbibe sap and cell fragments. The tube formed by the maxillary stylets also assists in the withdrawal of nutrients (Lewis 1973). During feeding, saliva is injected by a salivary pump into the mouth cavity near the opening of the cone (Kloft and Ehrhardt 1959). *T. tabaci* also employs the mandible alone in puncturing pollen grains to extract the contents (Grinfel'd 1959-60).

Although essentially phytophagous, *Thrips tabaci* larvae are reported to feed also on small mites (Mound and Walker 1982) and in addition they have been noted to attack a sawfly (presumably eggs and/or larvae) in Romania (Lewis 1973).

Moulting of the first instar larva occurs on the underside of a leaf, or in other places where it can hang down. A second instar larva (larva 2) is disclosed which eventually attains a length of about 0.77 mm. Separating the two larval stages on size is not reliable, but it can be achieved by examining the antennae: in larva 1 the terminal segment is pointed, whereas in larva 2 it is rounded. Larvae of both instars have claws, but these are reduced in the adults, which have protrusible adhesive tarsal bladders.

The larval stages tend to be somewhat gregarious, congregating in the axils of the leaves in onion plants, for instance, and in similar sheltered places on other hosts.

When under attack by predators, larvae of *Thrips tabaci,* like those of a number of other species of Thysanoptera, show evasive activity by repeatedly wagging the abdomen, usually at the same time producing a faecal droplet with which the attacker becomes smeared. Second instar larvae in particular use these tactics and are often successful in deferring or averting destruction by phytoseiid mites which are forced to withdraw and clean themselves (Bakker and Sabelis 1987).

When fully fed, larva 2 generally drops to the ground, rather than crawling down the stem (Binns et al. 1982), although some may move to the lower surface of the leaves or into leaf axils for 'metamorphosis'. Larvae that enter the soil do not form a cell, as do those of certain other species. Lying in a matrix of loose soil they soon transform into a non-feeding 'prepupa', with short antennae reverted back over the head, and short, backwardly directed wingbuds arising from the meso- and metathorax. This instar, which is about 0.8 mm long, is capable of limited crawling if disturbed, but normally remains immobile. The 'pupal' stage soon follows the 'prepupal'. This stage, which is also nonfeeding, is about the same length as the 'prepupa'. It has much longer antennae, reflected back over the head and prothorax, and very much longer wingbuds, reaching almost to the hind edge of the sixth abdominal segment. The 'pupal' stage is quite incapable of locomotion. (The terms 'prepupa' and 'pupa' are used in discussions on thrips life cycles in analogy with the true prepupal and pupal stage in higher insects such as beetles, flies, moths and wasps (endopterygotes), but in thrips these stages of metamorphosis into the adult have evolved quite independently.)

Larva 2, 'prepupa', 'pupa' and adult are somewhat more intensely yellow than larva 1 and some adults may be brownish. The eyes are red. Mound (1977) lists a combination of characters which will separate the adult female reliably from other species.

Recognition of males is less important, seeing that they are usually rare compared with females. Metcalf and Flint (1962), Swaine (1971) and Clausen (1978) are in error in stating that males of *T. tabaci* are apterous, since Priesner (1928) compares the forewing of the male with that of the female, Speyer (1934) presents a photograph of a male with wings and Hinds (1903), who evidently lacked American males of *T. tabaci* to describe in his monograph, quotes a description by Uzel (1895) which states that males are winged.

The data in Table 5.1 clearly illustrate the extreme brevity of both the 'prepupal' and 'pupal' stages. The duration of development from egg laying to emergence of adult ranges from 11 days at 30°C to 23 days at a mean of 22.4°C.

Table 5.1 Duration of life history stages (days) and egg production of females of *Thrips tabaci*. Numbers in parentheses are means.

Reference and country	Temperature (0°)	Egg	Larva 1	Larva 2	Prepupa	Pupa	Pre-oviposition	Oviposition	Egg production	Longevity
Fedorov (1930) Crimea	–	4–5.0	4.0	4.0	1.5–2.0	1.5–2.0			up to 100	20–25
Ghabn	22.2	7–10	2–4	2–4	2	3			3–14	22–28
(1948)		(8.4)	(3.0)	(3.5)	(2.0)	(3.0)			(4.2)	(23.8)
Egypt	27.1	5–9	1–4	1–4	1–2	1.3			3–22	1–12
		(6.1)	(2.0)	(2.2)	(1.2)	(1.7)			(4.8)	(6.9)
Harris et al.	25.0	6	4.5–7.0		1.0–2.0	2–2.5				
(1935) USA	30.0	4								9–39
										(20.0)
Watts (1934)		2–9	1–4	1–6	1–4	1–5	1–5			
USA		(4.6)	(2.0)	(2.8)	(1.1)	(2.7)	(3.1)		(44.3)	(18.3)
Sakimura		4–7	6–13		1–2	3–5				
(1932)	(22.4)	(4.9)	(9.3)		(1.6)	(3.5)				
Hawaii							4–12	22–35	31–55	32–52
	(22.8)						(7.0)	(26.6)	(42.0)	(40.3)
		3–6	6–9		1–2	1–5				
	(24.7)	(4.2)	(7.7)		(1.5)	(2.8)				
							4–7	4–30	12–51	11–35
	(25.0)						(4.8)	(14.0)	(34.4)	(21.0)
Lall and	15.8	8.5	6.5		2.0	4.0				
Singh (1968)									(49.8)	(18.8)
India	30.8	4.8	5.3		1.4	2.4				
									(28.2)	(20.2)
MacGill	15.0	8–11	16–19		3–5					
(1927) U.K.	19.0	8	10–14		8–12					
Eddy and	(24.5)	(4.7)	(2.3)	(2.8)	(1.4)	(3.2)				
Clarke (1930)	Mean of						(1–7)	(1–26)	(1–46)	(4–28)
USA	four generations									

Perhaps the most erratic statistic given by the sources quoted in Table 5.1 is the number of eggs laid. Clearly this is difficult to measure because of the implantation of the eggs into plant tissue, but overall the generalisation by Kalshoven (1981) that the total egg production is 'about 80' seems to indicate a possible average. Egg production is influenced by species of food plant and nutritional status of the tissues. In Iraq Al-Faisal and Kardou (1986) showed that age of food plant had a pronounced effect on population. Maturation of cotton plants made them less favourable to *T. tabaci*, so that thrips moved to younger food plants, including onion, cucumber and tomato. Younger food plants favoured higher fecundity, higher hatch rate, shorter life cycle and greater adult longevity.

Although mass movements occur in some species, in general thrips are poor fliers. They do not fly at night and *Thrips tabaci* requires sunshine and air temperatures of 26.5°C and upwards to initiate flight. Thrips of the suborder Terebrantia to which *T. tabaci* belongs, usually take off from leaf tips and other high points. Flight is preceded by preening of the wing fringes by the hind legs, which also assist take-off by a kicking action. Morison (1937) and Binns et al. (1982) observed females of *T. tabaci* in glasshouses jumping, especially when disturbed, and it may be assumed that in nature *T. tabaci* females are leg-assisted at take-off, as other thrips are known to be. Directional flights are made between plants, and Shelton and North (1986a) obtained evidence that *Thrips tabaci* females move from the crowns of senescing weeds and crop plants to infest adjacent crops, such as cabbage, that are growing more vigorously. In view of their very small size, however, directional flight of thrips between host plants may be very much influenced by wind. Greatest displacements of *T. tabaci* populations undoubtedly occur by means of mass flight which is initiated when weather conditions are suitable. Mass flights involve large numbers of airborne thrips being caught in warm updrafts, which may transport them over considerable distances, their wings in motion but adding little to the distance travelled.

Adult thrips overwinter in sheltered positions in various crop plants such as lucerne, red clover, cereals and also weeds (North and Shelton 1986) and not, as so often stated, in trash, nor does any life history stage overwinter in the soil. This information throws doubt on the value, in relation to *T. tabaci*, of early USSR recommendations (cited by Binns et al. (1982)) to plough deeply when fallowing, thus encouraging infection of overwintering adult thrips by the fungus disease organism *Beauveria bassiana*. There is considerable mortality during the winter, but when the weather warms up the surviving adults are soon capable of resuming feeding and maturation of eggs. There is no true diapause, merely cold quiescence. Thrips populations may reach very high levels. Thus Harris et al. (1936) estimated that in onion crops in the U.S.A. there were up to 74 million *T. tabaci* per hectare (Fedorov 1930, Gawaad and Shazli 1969a,b, Ghabn 1948, Harris et al. 1935, Hill 1983, Horsfall and Fenton 1922, Lewis 1973, MacGill 1927, Mound 1971a, 1977, North and Shelton 1986, Sakimura 1932, Shirck 1951).

Pest status

Thrips tabaci has been recorded from more than 300 species of host plant scattered through diverse plant groups. The host plant list in Hawaii, for example, embraces members of at least 25 families (Sakimura 1932) and that of Egypt 37 families (Ghabn 1948). In the Crimea Fedorov (1930) recorded host plants in 33 families and in Bulgaria Dimitrov (1983) recorded *T. tabaci* on 158 species of food plants in 44 families. In temperate regions the thrips is common on various Asteraceae (such as *Senecio* and *Achillea*) and Brassicaceae. In warmer climates heavy infestations occur on cotton, cucurbits, tobacco, tomatoes, and various weeds such as *Emilia sonchifolia* (Asteraceae) (Mound 1977). The extent of its polyphagy is illustrated by reports of significant attack on seedlings of *Pinus radiata* in nurseries in Chile (Cerda 1980). However, onions in particular; and other closely allied Liliaceae are undoubtedly preferred hosts.

Oviposition alone has been suggested by Ghabn (1948) as making a significant contribution to plant damage; but this is contrary to the view of the author he cites (Pearson 1930). Ferrari (1980) claimed that the saliva injected by *T. tabaci* when feeding on onions is toxic, but there is little mention of this elsewhere in the literature. Undoubtedly the feeding by the thrips, and its by-products, fouling of plant surfaces and virus transmission, are the overwhelming sources of losses. The feeding of the thrips drains underlying cells of their contents, leaving air-filled spaces which impart a silvery sheen, and causing distortion during growth and great reductions in photosynthetic capacity. Young plants are particularly susceptible, and there may be total losses at the seedling stage in crops of onions, cabbages and cotton (Mound 1977). On onions, bulbs, leaves and flowers are attacked. In the United States in earlier years losses of onion crops due to *T. tabaci* attack were frequently as high as 25 to 50%, and the volume of literature on chemical control in recent years indicates that the pest is still a problem with onions. Edelson et al. (1986) in fact showed that populations of 50 thrips per plant halved yields in Texas, and *T. tabaci* populations often greatly exceed that level (Harris et al. 1935). Onion seed crops are particularly vulnerable and Pearson (1930) attributed severe losses in seed production to *T. tabaci* feeding on the flowers.

On broadleaved plants such as tobacco the thrips tend to shelter alongside the veins on the underside, so that damage may be particularly severe in strips following the leaf venation (Fedorov 1930). Klein et al. (1986) observed that attack by *T. tabaci* on cotton seedlings in Israel caused proliferation and branching, early damage significantly reducing yields of fibre and seed. Attack on other species of plants is of the same general nature, resulting in discoloration and necrosis of leaves, malformation of plant parts, reduction in yields and even death of entire crops (Mound 1971b, Hill 1983, Horsfall and Fenton 1922, Sakimura 1932).

Although there is ample evidence of major economic losses due to *T. tabaci,* some forms of damage may be chiefly cosmetic in nature, being of questionable significance to the welfare of consumers but evoking buyer resistance or even over-reaction on the part of authorities regulating marketing. This is true of onion thrips damage to cabbage grown for sauerkraut in the U.S.A., where chemical treatment is used to reduce visible injury to very low levels (Shelton 1982, Shelton et al. 1983).

The faeces deposited by the thrips near their feeding site provides a medium for fungus growth which may be very disfiguring when populations are high. An interesting sidelight on fouling of leaf surfaces by insects is reported by Morison (1957) who stated that thrips very seldom occur in any abundance on plants supporting numerous Hemiptera of the families Aleyrodidae, Aphididae or Coccidae, due, he considered, to the excretions of these insects on the plants, and the fungi growing on them, discouraging colonisation by the thrips. There seems to be no practical way of exploiting this aversion by the otherwise undiscriminating feeder, *Thrips tabaci.*

Larvae and adults of *Thrips tabaci* have been observed carrying on their bodies spores of the black mould *Aspergillus niger* and insects of this species are also thought to disperse spores of mildew on grapevines, rose, strawberry and cantaloupe.

Bhangale and Joi (1983) showed that feeding by *Thrips tabaci* on onion seedlings could result in infection by *Alternaria porri* causing purple blotch disease, if spores were present, but that undamaged leaves did not become infected. However, any impact that mechanical transfer of plant pathogens may have is far transcended by the status of *Thrips tabaci* as a vector of the virus of spotted wilt disease of tomatoes. The virus, which is also transmitted by three species of *Frankliniella,* including the western flower thrips *F. occidentalis* (see chapter 4), infests a number of other cultivated plants, causing symptoms which have resulted in a variety of different names.

Losses in host plants other than tomatoes can also be serious. Thus Jankowski et al. (1979) reported devastation of tobacco crops by this disease in Poland in 1977 which resulted in about 91,000 tonnes of tobacco being lost. Various weeds also act as reservoirs from which thrips can contract infection and transmit it to cultivated plants. Weeds display an ambivalence which complicates consideration of their control for the reduction of damage by *T. tabaci.* They harbour tomato spotted wilt virus and generate considerable populations of the thrips (Sakimura 1932) but, to offset this, they may afford valuable reservoirs from which natural enemies can recolonise crops.

Thrips tabaci can become infected with tomato spotted wilt virus only during the larval stages, but adult thrips so infected also readily transmit the disease (Best 1968). The readiness with which *T. tabaci* can reinfest chemically treated crops under favourable meteorological conditions defies attempts to control spotted wilt of tomatoes with contact toxicants directed on to foliage to kill the feeding stages (Mound 1971b).

Control measures

There is an extensive literature on the chemical control of *Thrips tabaci,* whose habits of embedding eggs in plant tissue, sheltering in leaf sheaths, inflorescences, etc. and 'pupating' underground constitute refractory life history features. Persistency in a chemical, of course, helps in some measure to overcome these problems and formerly DDT and the cyclodienes afforded good control. However, environmental considerations eventually resulted in the prohibition of the use of these materials for most purposes and moreover *T. tabaci* became resistant to DDT (Rossiter and Giesemann 1976). Omethoate and methidathion proved effective against DDT-resistant *Thrips tabaci* in Australia. Groen and Lans (1985) advanced evidence suggesting that *T. tabaci* was becoming resistant to endosulfan and diazinon in the Netherlands and Deryabin (1979) reported resistance to trichlorphon and dimethoate in *T. tabaci* on seed lucerne in Kazakhstan, USSR. The vast populations of the thrips provide an ideal basis for the operation of selective processes for the elicitation of insecticide resistance. Examination of recent literature suggests that, even in the absence of resistance, difficulties persist in the control of *Thrips tabaci* with modern chemicals. Thus Gupta et al. (1984) found that to control the pest on onion crops five sprays of demeton-S-methyl or malathion at 15-day intervals were necessary. It seems likely that in these spraying experiments reinfestation by flying thrips must have been of overwhelming importance. Shelton and North (1986b) found that parathion or dimethoate were usually effective in eliminating blemishes on peas due to moderate populations of *T. tabaci,* if applied no later than the bloom stage, but when infestations were heavy, no worthwhile reduction in scarring was produced. Hajdu and Nagyimre (1984) found methomyl to be very effective for the control of *T. tabaci* on onion. Bhamburkar (1986) emphasised the importance of systemic qualities in pesticides used against insects such as *T. tabaci,* with its embedded eggs and cryptic feeding stages. In his experiments phosphamidon was outstanding. In glasshouses the penetrating avermectin B1, used primarily for the control of a dipterous leafminer, was shown to have possibilities for eradicating *T. tabaci* (Green and Dybas 1984) and Hassan (1982) drew attention to a useful side effect of a fungicide, pyrazophos in controlling *Thrips tabaci.*

Mutton and Treverrow (1985) showed that tomato spotted wilt could be substantially controlled by sowing granules of the systemic insecticides carbofuran, disulfoton, aldicarb, fenamiphos or terbufos 50 mm below the seeds. Chemical control of tomato spotted wilt, seemingly impossible with contact toxicants (Mound 1971b), is thus feasible with systemics. Sticky yellow traps were used in Italy by Nucifora and Vacante (1982) to reduce abundance of *T. tabaci* in glasshouses, but the method would not be applicable out-of-doors. The use of sticky traps beneath cucumber plants in glasshouses virtually eliminated the thrips by entrapping second stage larvae when they dropped to the ground to seek 'pupation' sites (Binns et al. 1982), but this too would be ineffective out-of-doors, not only because of maintenance problems but because of the high invasive powers of thrips.

Cultural methods have been advocated from very early times, but seldom with any evidence as to their value. Crop sanitation, or rather maintenance of clean fallow after cropping (Mound 1977) may be of value. The practice eliminates weeds and volunteer crop plants in the heads of which adult thrips overwinter, but what it cannot do, as Mound suggests, is simultaneously destroy metamorphosing stages in the soil, since burial in the soil is not a feature of the overwintering biology of *Thrips tabaci* (North and Shelton 1986). In New Zealand Townsend and Watson (1984) demonstrated a link between the degree of weed and litter control in asparagus crops and subsequent populations of thrips, which included *T. tabaci.* They found that the proximity of overwintering sites increased the chances of infestation of asparagus spears, but there was no indication that overwintering management would reduce spear infestation by air-borne thrips to the extent that there would be no need for post-harvest decontamination of export asparagus. The contribution of *T. tabaci*, as against other thrips, was not assessed, but there is no doubt that the problem of risks of reinvasion of treated areas is crucial to protection by cultural methods. As pointed out earlier, the importance of trash in the overwintering of *Thrips tabaci* in cold areas has been grossly overemphasised.

Crop rotation is also stated to be of value for reducing the impact of *T. tabaci*, particularly if successive replanting with onions is avoided. In Bulgaria Dimitrov (1975a) claimed that a three year rotation of cereals and tobacco eliminated damage to the tobacco by the onion thrips. The value of such measures, in the light of the considerable invasive powers of the pest when conditions are right for flight, needs to be assessed.

Deliberate campaigns for widespread weed control, as advocated by Georgiev (1984) in Bulgaria to protect tobacco crops from *T. tabaci*, require quantitative evaluation to determine whether weeds act more as reservoirs of thrips and virus diseases than of natural enemies.

Mound (1977) also recommended the manipulation of planting dates to avoid population peaks, which seems to be sound practice. He also advocated appropriate spacing of plants according to crop, to minimise damage.

Location of host plants by insects can be disturbed by the fact that non-host plants in their vicinity provide camouflage or diversionary or repellent compounds, such as are usually found in diverse ecosystems. This is the basis of companionate planting, which has been investigated for reducing damage by various pests. Uvah and Coaker (1984) used carrots as non-host plants for *T. tabaci* in interplanting with onions. This reduced the numbers of onion thrips on onions by 43%, it is thought, due to the reduced 'apparency' of the onion plants to the thrips, but the authors concluded that the effect of companionate planting was insufficient to provide the level of control required. Intercropping with the aromatic French marigold *Tagetes patula* (Asteraceae) was ineffective.

Varietal resistance to *Thrips tabaci* has received a considerable amount of attention. The leaf structure of different varieties of onions affects the numbers of *T. tabaci* they can support. In susceptible varieties the young leaf blades generally have one flat side which is closely pressed to the flat surface of the opposite leaf, thus providing many crevices into which the larvae can creep for protection. In contrast, other varieties have leaves almost circular in cross section with a wide angle between the two youngest leaves, thereby reducing the number of crevices suitable as larval shelter. Tying the leaves of such varieties together resulted in increasing the numbers of acceptable crevices and a consequent increase in thrips numbers per plant. Differences in susceptibility to thrips attack appeared not to have a chemical basis (Jones et al. 1934, Sleesman 1943). Over 40 years after this pioneer study Coudriet et al. (1979) confirmed the validity of those views on the influence of onion leaf anatomy on *Thrips tabaci* susceptibility. Maugham and MacLeod (1936) added further comparisons of onion varieties which showed that 'sweet Spanish' onion plants carried fewer *Thrips tabaci* than other varieties. They concluded that no single quality determined the capacity of a plant variety to resist thrips attack. In India, as in the United States, white varieties of onion have been shown to be less susceptible to *Thrips tabaci* attack than red ones (Lall and Singh 1968, Verma 1966). Molenaar (1984) found that the more glossy the foliage of onion plants the less they were preferred by *Thrips tabaci.* Nonglossy leaves had abundant wax crystals in the form of rods and toothed platelets, whereas glossy plants had sparse, amorphous platelets only. This relationship seems counter-intuitive, but thin-layer chromatography demonstrated chemical differences between the waxes, so the observed differences in thrips preference may have had a chemical rather than a mechanical basis. Mound (1977) states that crop losses in tomatoes have been reduced by growing least susceptible varieties. McKinney (1938) found that in the semi-arid climate of Arizona sticky exudates from the tips of short stocky spines on tomato leaves clogged the feet of thrips in such fashion as to make them lose their hold, or even become fatally entangled. In beans the same author observed *Thrips tabaci* impaled on the numerous minute hooked hairs, the numbers affected being augmented by the movement and rubbing together of the leaves. Cabbages grown for sauerkraut have been shown to exhibit varietal differences in susceptibility which may help to circumvent the damage which insecticidal treatment will not reduce to legally acceptable limits in susceptible varieties (Shelton et al. 1983).

In pigeonpea Wardle and Simpson (1927) showed that very dense hairs on the undersurface of leaves probably prevented attack by *T. tabaci* by making the surface inaccessible. Cotton varieties also show differences in susceptibility to *Thrips tabaci* attack. In contrast with the condition in pigeonpea, Wardle and Simpson (1927) found that, in cotton, sparse hairs favoured the thrips rather than bare leaves, perhaps because the hairs were at such a density as not to impede feeding, but to offer shelter and create a suitable microenvironment.

Zareh (1985) studied infestation of *T. tabaci* on six varieties of cotton in Iran and found a significant correlation between thrips abundance on the under surfaces of leaves and the densities of hair and glands there. A variety with dense hairs and few glands had significantly fewer thrips than one which had few hairs and many glands. Baloch et al. (1982) tested 20 varieties of cotton and found that hairy varieties (i.e., hairy so far as cotton goes) were more susceptible to attack by *T. tabaci*. Gawaad and Shazli (1969c) considered that cotton seedlings were either toxic or repellent to *T. tabaci* up to 12 to 15 days after germination, resulting in very low thrips fecundity in comparison with those feeding on castor oil seedlings. Some varieties remained less susceptible than others for much longer periods, but complete destruction of young cotton is so common that we must assume any protective qualities eventually disappear completely. In Bulgaria, Georgiev (1983) tested 59 varieties of tobacco and 28 wild species of *Nicotiana* for resistance to *Thrips tabaci* and found that the wild species were generally more resistant to attack. Significant differences were found between certain groups of cultivated varieties.

The above is by no means an exhaustive survey of the field of resistance to *T. tabaci* in cultivated plants. A difficulty in relation to this approach in vegetables, with the possible exception of onions, is the number of other important pests that also have to be taken into consideration.

Integrated control involving *T. tabaci* has been studied extensively in glasshouses, and Saxena (1975) proposed programs for the integrated control of *T. tabaci* on onions under field conditions, involving augmentation of natural enemies, the use of resistant varieties and the strategic application of insecticides, but his proposals do not appear to have been put into practice. *Thrips tabaci* and various combinations of insect pests attack cotton in all major producing countries and a number of sophisticated predictive methods and integrated control practices have been developed. There is little reason to discuss these in detail here. Heavy rain is well known to destroy many *T. tabaci*, and it has been widely noted that irrigation reduces infestations (Mound 1977). Thus we must accept with caution an oft-quoted claim by Passlow (1957) that unthrifty onions in his trials were more susceptible to attack by *T. tabaci* than healthy ones, when 'unthriftiness' had been brought about by the discontinuation of irrigation.

Associated pests

The diverse host range of *Thrips tabaci* results in there being a very large number of associated pests, chemical control of which may have to be modified if biological control of the thrips is to be attempted. For present purposes it may be sufficient to consider pests attacking mainly onions, tomatoes, beans and brassicas.

onions: Important pests, other than *T. tabaci*, include: Diptera: *Delia platura;* Lepidoptera: *Agrotis* spp., *Spodoptera litura.*

tomatoes: Hemiptera: *Nezara viridula;* Diptera: *Dacus* spp.; Lepidoptera: *Agrotis* spp. (including *A. ipsilon*), *Chrysodeixis* spp., *Spodoptera litura, Phthorimaea operculella.*

beans: Hemiptera: *Nezara viridula, Aphis craccivora;* Thysanoptera: *Megalurothrips usitatus, Thrips palmi;* Diptera: *Smittia aterrima* (= *S. macleayi*), *Ophiomyia phaseoli, Delia platura;* Lepidoptera: *Agrotis* spp., *Chrysodeixis* spp., *Helicoverpa* (= *Heliothis*) *armigera, Spodoptera litura, Acrocercops caerulea, Etiella zinckenella, Maruca testulalis;* Acari: *Tetranychus* spp., *Polyphagotarsonemus latus.*

brassicas: Hemiptera: *Brevicoryne brassicae; Lipaphis erysimi; Myzus persicae;* Diptera: *Delia platura; Liriomyza brassicae;* Lepidoptera: *Agrotis* spp., *Chrysodeixis* spp., *Thysanoplusia* (= *Diachrysia*) *intermixta, Helicoverpa armigera, Spodoptera litura, Plutella xylostella, Pieris rapae, Crocidolomia pavonana* (= *C. binotalis*), *Hellula* spp..

Natural enemies

The wide range of host plants of *Thrips tabaci* results in its occupying very diverse habitats and so coming into contact with many polyphagous predators and non-specific disease organisms. Most of the natural enemies for which records have been published are listed in Table 5.2. The main predators involved are Hemiptera, Thysanoptera, Neuroptera, Coleoptera, Diptera and Acari, and the parasites Hymenoptera and Fungi (Zygomycetes). With the possible exception of *Entomophthora thripidum,* none is specific to *T. tabaci.*

Hymenopterous parasites have been quite impressive in Japan, where Sakimura (1937b) found that parasitisation of *T. tabaci* by *Ceranisus menes* was sometimes as high as 88%, although it was generally much lower. In India Narayanan (1970) reported up to 10% parasitisation of *T. tabaci* by *Ceranisus* sp. in some fields, but no attack at all in other fields nearby.

There is a considerable volume of literature on the biological control of *T. tabaci* in glasshouses, where it is a member of pest complexes requiring the manipulation of chemical, mechanical, cultural and biological control measures.

Various research workers have measured the rate of consumption of *T. tabaci* by natural enemies. In India nymphs of the predatory bug *Orius albidipennis* consumed 30 *T. tabaci* larvae per day and the adults 23 larvae per day (Saxena 1975). In Egypt Tawfik and Ata (1973) found that bugs of the same species consumed 189 *T. tabaci* during the course of the nymphal stages. In Bulgaria Dirimanov and Dimitrov (1975) found that *Macrolophus rubi* consumed 450-500 *T. tabaci* in the course of its life cycle. Bournier et al. (1978) showed that in France adults of *Aeolothrips intermedius* each consumed about 10 *T. tabaci* larvae per day, whereas in India Saxena (1975) found that adults of *A. collaris* consumed 34 *T. tabaci* larvae per day. Saxena (1975) also found that the melyrid beetle *Laius externenotatus* and the coccinellid *Scymnus nubilus* devoured 48 and 47 thrips larvae per day respectively, and that *Chrysopa* sp. consumed 96 *T. tabaci* larvae per day, whilst in Bulgaria Dirimanov and Dimitrov (1975) showed that the larvae of *Chrysoperla carnea* consumed 600–900 *T. tabaci* in the period from hatching to pupation. MacGill (1939) showed that adults of *Amblyseius cucumeris* each ate 5 to 6 thrips larvae per day. Such in vitro studies give some measure of the voracity of predators when given no choice, but do not indicate what impact a polyphagous organism would have on *Thrips tabaci* populations in the presence of diverse other prey in nature.

Table 5.2 Natural enemies of *Thrips tabaci*.

Species	Country	Reference
ORTHOPTERA		
Gryllidae		
Oecanthus longicauda	Japan	Hori 1927
Oecanthus turanicus	Egypt	Ghabn 1948
HEMIPTERA		
Anthocoridae		
Orius albidipennis	Egypt	Tawfik and Ata 1973
	India	Saxena 1981
Orius insidiosus	USA	Horsfall and Fenton 1922
Orius laevigatus	Egypt	Ghabn 1948
Orius maxidentex	India	Muraleedharan and Ananthakrishnan 1978
Orius minutus	Switzerland	Ramakers 1978
	Netherlands	Ramakers 1978
	Poland	Niemczyk 1978
Orius niger	Armenia	Akramovskaya 1978
	Bulgaria	Bailov 1929
	USSR	Suchalkin 1983
Orius persequens	Hawaii	Illingworth 1931
Orius tantillus	India	Muraleedharan and Ananthakrishnan 1978
Orius tristicolor	USA	Pearson 1930
Orius vicinus	USSR	Akramovskaya 1978
Orius sp.	Egypt	Ghabn 1948
Orius sp.	India	Narayanan 1970
Miridae		
Deraeocoris punctulatus	USSR	Suchalkin 1983
*Deraeocoris zarudni**	USSR	Suchalkin 1983
Dicyphus eckerleini	Bulgaria	Suchalkin 1983
Macrolophus rubi	Bulgaria	Dimitrov 1975b
(= *M. costalis*)	USSR	Suchalkin 1983
Macrolophus sp.	USSR	Eremenko 1984
Nabidae		
Nabis alternatus	USA	Knowlton 1953
Nabis americoferus	Bulgaria	Dirimanov and Dimitrov 1975
*Nabis pollifer**	USSR	Suchalkin 1983
Nabis pseudoferus	Bulgaria	Dirimanov and Dimitrov 1975
THYSANOPTERA		
Aeolothripidae		
Aeolothrips collaris	Egypt	Ghabn 1948
	India	Saxena 1975

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* This taxon unknown to CAB International Institute of Entomology.

Table 5.2 (cont'd)

Species	Country	Reference
THYSANOPTERA (cont'd)		
Aeolothrips ericae	USSR	Suchalkin 1983
Aeolothrips fasciatus	Italy	Ferrari 1980
	USSR	Suchalkin 1983
Aeolothrips intermedius	France	Bournier et al. 1978
	USSR	Suchalkin 1983
Aeolothrips kuwanii	USA	Lewis 1973
Thripidae		
Scolothrips priesneri	Hawaii	Jacot-Guillarmod 1974
COLEOPTERA		
Coccinellidae		
Adalia bipunctata	Bulgaria	Dirimanov and Dimitrov 1975
Calvia quatuordecimguttata	Bulgaria	Dirimanov and Dimitrov 1975
Coccinella quinquepunctata	USSR	Dirimanov and Dimitrov 1975
Coccinella novemnotata	USA	Horsfall and Fenton 1922
Coccinella septempunctata	USSR	Suchalkin 1983
Coccinella transversalis (= *C. repanda*)	Java	Franssen and van Heurn 1932
Coccinella undecimpunctata	Egypt	Ghabn 1948
Coleomegilla (= *Ceratomegilla*) *maculata*	Cuba	Russo 1928
Hippodamia convergens	USA	Horsfall and Fenton 1922
Hippodamia oculata (= *H. undecimnotata*)	Bulgaria	Dirimanov and Dimitrov 1975
Hippodamia variegata	USSR	Suchalkin 1983
Propylea quatuordecimpunctata	Bulgaria	Dirimanov and Dimitrov 1975
Scymnus nubilus	India	Saxena 1975
Melyridae		
Laius externenotatus	India	Saxena 1975
NEUROPTERA		
Chrysopidae		
Chrysopa orestes	India	Patnaik and Bhagat 1984
Chrysopa perla (= *C. chrysops*)	Bulgaria	Dirimanov and Dimitrov 1975
*Chrysopa phyllochroma**	Bulgaria	Dirimanov and Dimitrov 1975
Chrysopa septempunctata	Bulgaria	Dirimanov and Dimitrov 1975
Chrysopa vulgaris aegyptiaca†	Egypt	Ghabn 1948
Chrysopa sp.	India	Saxena 1975

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* The authors spell this trivial name *'polychroma'*, but it seems highly likely that *Ch. phyllochroma* is intended.

† This taxon unknown to CAB International Institute of Entomology: however *Chrysopa vulgaris* = *Chrysoperla carnea*.

Table 5.2 (cont'd)

Species	Country	Reference
NEUROPTERA (cont'd)		
Chrysoperla (= *Chrysopa*) *carnea*	Bulgaria USA	Dirimanov and Dimitrov 1975 Caltagirone 1985
Mallada (= *Anisochrysa*) *prasina*	Bulgaria	Dirimanov and Dimitrov 1975
DIPTERA		
Syrphidae		
Episyrphus balteatus	Bulgaria	Dirimanov and Dimitrov 1975
Mesograpta (= *Mesogramma*) *marginata*	Bermuda N. America	Suchalkin 1983 Stone et al. 1965
Metasyrphus corollae	Egypt	Ghabn 1948
Metasyrphus nitens	Bulgaria	Dirimanov and Dimitrov 1975
Paragus cinctus	Bulgaria	Dirimanov and Dimitrov 1975
Scaeva pyrastri	Bulgaria	Dirimanov and Dimitrov 1975
Sphaerophoria rueppellii	Egypt	Tawfik et al. 1974
Syrphus opinator	Bulgaria	Dirimanov and Dimitrov 1975
Syrphus rectus	Bulgaria	Dirimanov and Dimitrov 1975
Syrphus sp.	USA	Horsfall and Fenton 1922
HYMENOPTERA		
Ceraphronidae		
Aphanogmus fumipennis	France	Dessart and Bournier 1971
Eulophidae		
Ceranisus menes (= *Thripoctenus brui*)	Europe, Indonesia, West Indies, Hawaii, Japan	Franssen and van Heurn 1932 Sakimura 1937b
*Ceranisus nigrifemora**	Argentina	Lewis 1973
*Ceranisus rosilloi**	Argentina	Lewis 1973
Ceranisus russelli (= *Thripoctenus russelli*)	USA	Fullaway and Dobroscky 1934
Ceranisus sp.	India	Narayanan 1970
Ceranisus sp.	India	Saxena 1971
Goetheana parvipennis (= *Dasyscapus parvipennis*)	Java, West Indies	Clausen 1978
Trichogrammatidae		
Megaphragma sp. nr *mymaripenne*	India	Narayanan 1970
ACARI		
Anystidae		
Anystis astripus (Karsch)	Japan	Sakimura 1937a

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* These species were not listed from South America by De Santis (1979).

Table 5.2 (cont'd)

Species	Country	Reference
ACARI (cont'd)		
Erythraeidae		
Hauptmannia brevicollis Oudemans	USSR	Ananthakrishnan 1984
Phytoseiidae		
Amblyseius aurescens Athias-Henriot	Netherlands	Suchalkin 1983
Amblyseius cucumeris (Oudemans) (= *Typhlodromus thripsi* MacGill)	Europe	Beglyarov and Suchalkin 1983
Amblyseius mckenziei Schuster and Pritchard	Europe	Beglyarov and Suchalkin 1983
Amblyseius potentillae (Garman)	Netherlands	Suchalkin 1983
Amblyseius swirskii Athias-Henriot	USSR	Suchalkin 1983
Typhlodromips (= *Amblyseius*) *sessor* (DeLeon)	USA Europe	Sciarappa and Swift 1977 Suchalkin 1983
FUNGI		
Zygomycetes		
Entomophthora thripidum	Netherlands*	Samson et al. 1979
Entomophthora sp.	Austria, France, Germany, Switzerland*	Carl 1975
Entomophthora (*Tarichium*) sp.	Switzerland	Stradling 1968
Neozygites parvispora	Australia	Glare and Milner 1987
	Chile	Aruta et al. 1984
	Europe*	MacLeod et al. 1976
	USSR	Tsintsadze et al. 1984
Zoophthora radicans (= *Entomophthora sphaerosperma*)	USA	Bourne and Shaw 1934
Hyphomycetes		
Aspergillus ochraceus	India	Narayanan 1970
Aspergillus sp.	? India	Ananthakrishnan 1984
Beauveria bassiana	USSR	Dyadechko 1964
Cephalosporium sp.	? India	Ananthakrishnan 1984
Metarhizium anisopliae	UK†	Gillespie 1986
Paecilomyces fumosoroseus	UK†	Gillespie 1986
Verticillium lecanii	UK†	Binns et al. 1982

* = observed in glasshouse.
† = infected in laboratory test.

Larvae of ***Chrysoperla carnea***, for example, are known to attack over 80 species of insects and 12 species of tetranychid mites, so that in the field ***Thrips tabaci*** would be accorded only a small fraction of their attention (Beglyarov and Ushchekov 1974). Indeed some insects are recorded as being more suitable as food for ***C. carnea*** than ***T. tabaci*** and so may be preferred prey (Awadalla et al. 1975). This is confirmed by Adashkevich et al.(1972) who found that ***C. carnea*** larvae attacked first aphids, then thrips, finally turning to tetranychid mites when the other prey ran out. In other regards, also, the mere listing in Table 5.2 of an organism as a natural enemy may give an entirely false idea of its potential value. Thus the record of predation by the bug ***Nabis alternatus*** seems to be based on a naked-eye field observation of a ***Nabis*** nymph having impaled one adult ***T. tabaci*** (Knowlton 1953), and the recording of the hymenopteran ***Aphanogmus fumipennis*** (Dessart and Bournier 1971) is unique. The record of parasitisation by ***Megaphragma*** sp. nr ***mymaripenne*** is based on laboratory tests only, and two at least of the records of entomogenous fungi are also based on laboratory infectivity tests only. Mere listing of ***Aeolothrips intermedius*** as a predator does not take into account the fact that the females must feed on plants to become fertile and, although the larvae thrive well on ***T. tabaci***, they also feed on plant tissue and their value as predators is diminished not only by polyphagy but by cannibalism as well (Bournier et al. 1979). Another predator, the cricket ***Oecanthus longicauda*** is listed in publication after publication without consideration of the fact that its predation on ***T. tabaci*** was observed only in laboratory cultures, and that in the field it feeds on a variety of cultivated plants, including soybean (Hori 1927).

In Iraq El-Serwiy et al. (1985) found that ***Aeolothrips fasciatus*** controlled ***T. tabaci*** abundance when the bug ***Orius albidipennis*** had become scarce, but the latter, in addition to attacking ***T. tabaci*** preyed so significantly on the larvae of ***A. fasciatus*** that the numbers of this predator itself were distinctly depressed. It is clear, therefore, that compatibility of predators must be considered. Other species listed may also have undesirable features and all should be very carefully assessed before deciding they are suitable for introduction to a new country.

Although caution is very necessary, some reports of the efficacy of natural enemies seem enthusiastic enough to suggest that further study might be rewarding. For example great importance has been claimed for predatory bugs in some countries in the reputed native range of ***Thrips tabaci***. In Armenia Akramovskaya (1978) found that the bugs ***Orius niger*** and ***O. vicinus*** were highly significant predators of ***T. tabaci*** on cucurbits and eggplant. Dimitrov (1975b) suggests that early introduction each season of the bug ***Macrolophus rubi*** into Bulgarian tobacco fields in the ratio of one predator to 30–35 thrips offers promise of useful control. This author (Dimitrov 1976) claimed that supplementary releases of ***Macrolophus rubi, Hippodamia*** (= ***Adonia***) ***variegata*** and ***Chrysoperla carnea*** kept ***Thrips tabaci*** populations at low levels. The feasibility of establishing periodical release programs of this type in developing countries, if the candidate organism is not suitable for classical biological control, would need critical study.

Phytoseiid mites and fungal pathogens assume importance chiefly in glasshouses, though there are many records, particularly of fungal attack, in the field. Perhaps the most impressive is that of Tsintsadze et al. (1984) of a high incidence of ***Neozygites parvispora*** on ***Thrips tabaci*** on soybeans in Georgian USSR in 1976. Seemingly, because of the absence of further mention, a comparable degree of attack was not observed again before the appearance of their publication.

In glasshouses Hussey and Bravenboer (1971) mentioned only chemical control of ***T. tabaci*** and Ramakers (1978), after discussing the use of ***Orius minutus, Amblyseius*** spp. and ***Entomophthora*** spp. concluded that ***T. tabaci*** still needed to be controlled by chemicals. Since that time, however, marked advances have been made in the selection of suitable phytoseiids and fungal pathogens. In particular ***Amblyseius mckenziei*** has proven a highly effective predator, and ***A. cucumeris*** and ***Typhlodromips sessor*** very useful supplements

(Beglyarov and Suchalkin 1983, Eremenko 1984, de Klerk and Ramakers 1986, Ramakers 1980, 1983). Mass production methods for *A. mckenziei* and *A. cucumeris* have been developed (Ramakers 1983). Newly recognised pathogenic fungi such as *Entomophthora thripidum* and *Neozygites parvispora* have also been assessed for use in integrated pest management programs in glasshouses.

The importance to the multiplication and infectivity of pathogenic fungi of high relative humidity, free water on surfaces and perhaps other factors have been demonstrated by Milner and Lutton (1986). Even in conditions that are ideal from the point of view of water relations a certain degree of mobility in the host insect may be a necessary feature to ensure maximum infection. One pathogenic fungus, *Verticillium lecanii,* is now available commercially as a preparation for use in glasshouses, specifically against whitefly and aphids, but it also produces a useful level of infection in *Thrips tabaci.* Distinct progress has therefore been made in the biological control of *T. tabaci* in glasshouses, but this has involved a great deal of intensive research. Similar detailed study will be needed to further the progress of classical biological control of *T. tabaci* in the field.

Attempts at biological control

Several unsuccessful attempts were made before 1923 to introduce the eulophid wasp *Ceranisus russelli* into Hawaii from California, where it had been shown in laboratory experiments to parasitise *Thrips tabaci* (Fullaway and Dobroscky 1934). However, this parasite, whose primary host is *Caliothrips* (= *Hercothrips*) *fasciatus,* failed to propagate on *T. tabaci* in Hawaii. Fullaway and Dobroscky therefore turned their attention to the Philippines where they obtained another parasite *Ceranisus vinctus.* The normal host of this hymenopteran is *Megalurothrips usitatus* (= *M. nigricornis* = *Taeniothrips longistylus*). Failure also resulted from attempts to rear this wasp on *Thrips tabaci* in Hawaii. Clausen (1978) states that at the same time *Ceranisus femoratus* was introduced to Hawaii from the Philippines, but in fact Fullaway and Dobroscky (1934) recorded only the collection of a single specimen, host unknown, along with numbers of *C. vinctus,* the single specimen being used as the type. Baltazar (1966) seems to be in error in recording *Megalurothrips usitatus* as host, since the single specimen was extracted as an adult from flowers, and likewise in suggesting that an attempt was made to introduce *C. vinctus* into Japan as well as Hawaii, since this is not borne out by Fullaway and Dobroscky. Thrips cultures were brought on board ship in Kobe harbour, Japan, and exposed to parasites from the Philippines that had already emerged, but seemingly only with the intention of adding further material to the parasitised cultures that were in transit to Hawaii.

The eulophid *Ceranisus menes,* reared from *T. tabaci,* was introduced from Japan to Hawaii by Sakimura (1937c), and became established. Apart from a specimen recorded on nasturtium by Swezey (1936, 1937) and some new locality records (Swezey 1950), no follow-up investigations have been published, and the account by Ananthakrishnan (1984, p. 96) of the sweeping success of this wasp against *T. tabaci* in Hawaii is unsubstantiated and may be based on confusion with Sakimura's (1937b) account of the bionomics of *C. menes* in Japan.

The eulophid parasite *Goetheana parvipennis* was introduced in 1935 from Ghana, Africa, to Trinidad for the control of the red-banded thrips *Selenothrips rubrocinctus* on cacao (Callan 1943). Whereas it was originally described from *Thrips tabaci* in Java there is no indication that it was ever intended to contribute to the control of this species in Trinidad, although this was claimed by Clausen (1978), who stated that it has had no effect on the abundance of *T. tabaci* there. Dohanian (1937) recommended the introduction of *G. parvipennis* into the United States for the control of *T. tabaci,* and according to Clausen (1978) this was done in 1936 and 1962. The insect was also introduced to other countries and became established in Puerto Rico and Jamaica (Clausen 1978). Again it is unclear whether these transfers were intended in any way as a campaign against *T. tabaci.*

Table 5.3 Attempts at biological control of *Thrips tabaci*.

Country and Species	Liberated	From	Result	Reference
GRENADA				
Goetheana parvipennis	1936	Trinidad	–	Clausen 1978
HAWAII				
Ceranisus menes	1933–34	Japan	+	Sakimura 1937c
Ceranisus russelli	(pre-1925)	California	–	Fullaway and Dobroscky 1934
Ceranisus vinctus	(1931)	Philippines	–	Fullaway and Dobroscky 1934
Goetheana parvipennis	1936	Trinidad	–	Clausen 1978
JAMAICA				
Goetheana parvipennis	1937	Trinidad	+	Clausen 1978
PUERTO RICO				
Goetheana parvipennis	1936–38	Trinidad	+	Clausen 1978
TRINIDAD				
Goetheana parvipennis	1935–36	Ghana	+	Callan 1943
USA				
Goetheana parvipennis	1936, 1962	Trinidad	–	Clausen 1978

For control of *T. tabaci* in glasshouses, extensive use of phytoseiid mites has occurred, chiefly *Amblyseius mckenziei, A. cucumeris* and *Typhlodromips sessor*. Fungal pathogens such as *Neozygites parvispora* and *Verticillium lecanii* have also been extensively dispersed for use in glasshouses in Europe and USSR, but there is no indication of the deployment of such natural enemies against field populations of *T. tabaci*.

Comment

A feature of the biology of *Thrips tabaci* that may create difficulties in the field of biological control is the occurrence of mass flights over considerable distances when atmospheric conditions are favourable. In this respect its dispersal is analogous to that of *Helicoverpa armigera* which is described as a facultative migrant (Waterhouse and Norris 1987), erupting under favourable conditions in such large numbers into areas previously sparsely populated that resident predators are unable to cope with them.

Working on one of the basic principles of biological control, that it is most profitable to search for effective and specific natural enemies in the country of origin of a pest, attention should be concentrated upon the Middle East and the environs of the Black and Caspian Seas, taking into account as far as possible climatic homologs. However, the number of publications relating to the high pest status of *Thrips tabaci* in this region gives some cause for concern. It is uncertain how far this situation is due to the use of chemicals, perhaps also intended for the control of pests other than *T. tabaci*. Dirimanov and Dimitrov (1975) indicate that in Bulgaria periods as long as three years can elapse without the use of chemicals on tobacco, the predation on and parasitisation of *T. tabaci* usually being sufficient in the meantime to keep the thrips below pest abundance. The same authors (1973) had shown that chemical pest control measures applied in May, June, July and August each abruptly reduced the abundance of predators on tobacco crops and after the completion of the spraying program, thrips (and aphids) were significantly more abundant on sprayed than on unsprayed areas. On farms where, following recommendations, only two sprays had been applied, thrips and aphids were not abundant. Thus there seems to be substantial evidence that natural enemies keep *T. tabaci* under control in Bulgaria if the use of chemicals is minimised.

An ideal type of predator for the control of *T. tabaci* would be an egg-sucking bug similar in its habits to *Cyrtorhinus fulvus* which is so important in the biological control of the taro planthopper *Tarophagus proserpina* (Waterhouse and Norris 1987). Although the egg of *T. tabaci* is embedded in plant tissue, it is sufficiently exposed to be accessible to a sucking bug (Harris et al. 1935, Plate 2a). No such predators have been described, but it seems improbable that a biological resource as plentiful as *T. tabaci* eggs would go quite unexploited. Any entomologist studying the biological control of *T. tabaci* should be alert for the possible occurrence of such organisms.

The lack of specificity of the arthropod predators listed in Table 5.2 is a serious problem, as almost all would be capable of attacking beneficial as well as pest insects. Elucidating the full impact of potential natural enemies would be a laborious task, but specificity or near specificity is highly desirable. It is particularly important in relation to the safety of beneficial thrips, such as *Liothrips urichi*, an effective agent in the biological control of the weed Koster's curse *Clidemia hirta*, and *Liothrips mikaniae* which is soon to be employed for the biological control of mile-a-minute weed *Mikania micrantha* in a number of Pacific countries (Waterhouse and Norris 1987).

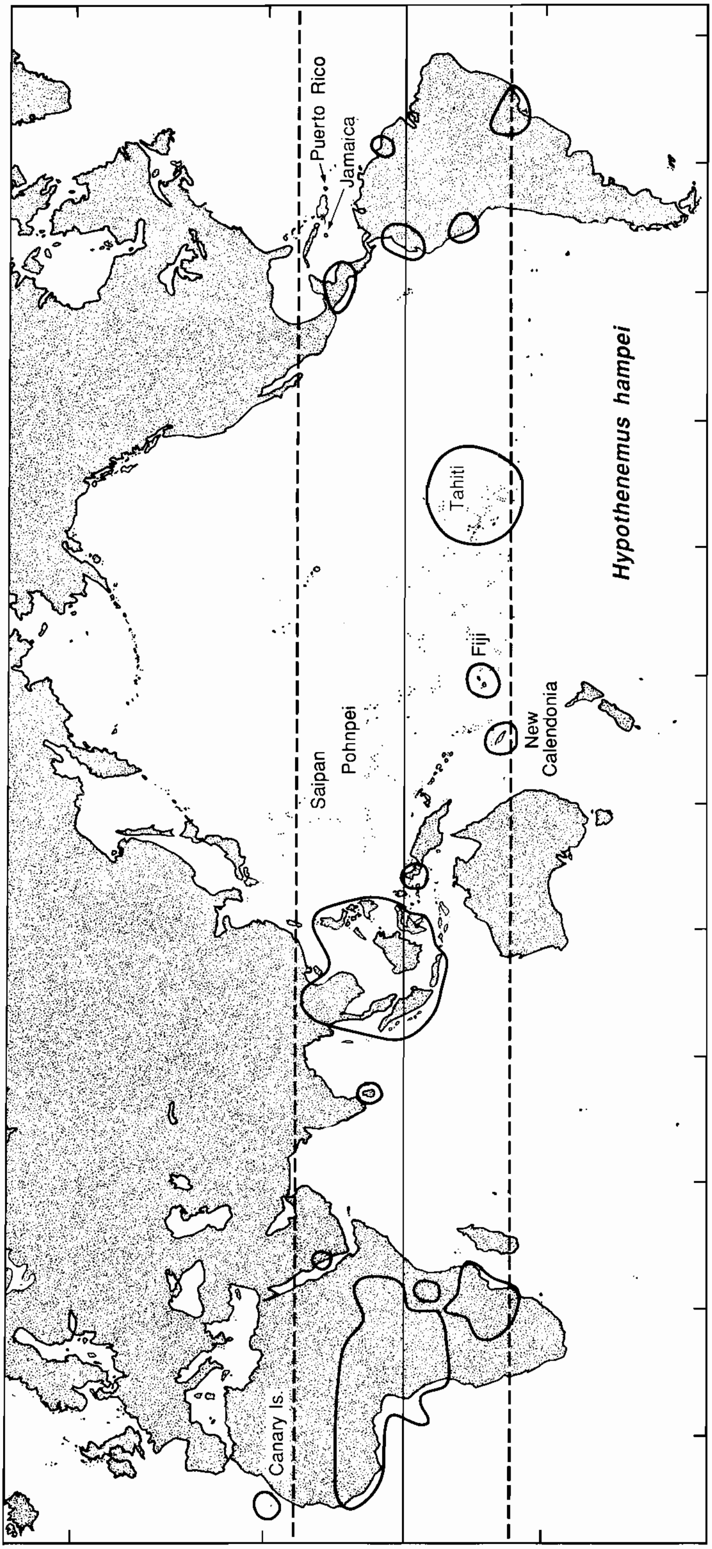
Perhaps the most promising predators for initial study are anthocorid bugs such as *Orius niger*, *O. vicinus* and *O. minutus*, and mirid bugs such as *Macrolophus rubi*, *Deraeocoris punctulatus* and *Dicyphus eckerleini*. If they are specific enough, freeing them from their natural enemies before transfer to new countries might raise their status as biological control agents even higher than claimed for them in Bulgaria (Dimitrov 1975b) and Armenia (Akramovskaya 1978). These bugs are not specific to *T. tabaci*, but to some of them the thrips may be preferred prey.

The parasitic Hymenoptera, generally so valuable in classical biological control projects, seem of somewhat limited value in relation to *Thrips tabaci* control. Although Caltagirone (1985) points out that *Ceranisus menes* is parthenogenetic in Europe and biparental in Japan (implying that this is an indication of useful genetic diversity) the effectiveness of this hymenopteran in biological control so far is not impressive. The material which Sakimura (1937c) used to establish the species in Hawaii came from a seemingly vigorous population in Japan, but despite this its impact in Hawaii seems to have been insufficient to warrant follow-up studies after its establishment. The adult insects emerging from thrips larvae collected in Japan were liberated direct into thrips-infested areas in Hawaii, and although scrutinised for freedom from hyperparasites, no search seems to have been made for the presence of disease organisms. It is possible that some unconscious selective process in the course of the transplantation resulted in the establishment of a uniparental population, lacking the invigorating effect of genetic diversity produced by sexual reproduction. Further study of *Ceranisus menes* in Japan and Hawaii seems justified. A puzzle in the field of biological control of *Thrips tabaci* by Hymenoptera is why *Ceranisus russelli* readily parasitised *T. tabaci* in culture in California, but could not be induced to do so in Hawaii. In this case genetic diversity in the thrips may have been the important factor. It would be of interest to have this situation explored further.

Caltagirone (1985) also draws attention to the genetic diversity of *Chrysoperla carnea* in the United States. This predator seems to be highly regarded in the USSR (e.g., Tulisalo 1984) and, particularly if it could be shown to have biotypes oriented to predation on *T. tabaci*, could be of value for thrips control. New (1975) assesses the possibilities of chrysopids as biological control agents, discussing particularly *C. carnea*. This species is marketed commercially in the USA for supplementary releasing for pest control. Chrysopids which, like *C. carnea,* have non-predatory adults, have the advantage that they can be conserved in culture during periods of low pest numbers by the provision of inanimate food supplies. This, coupled with a high reproductive potential, relatively long adult life and oviposition period, physiological and ecological tolerance to a variety of pesticides (Bigler 1984), and the highly efficient searching behaviour of the larvae, are points in favour of their use as biological control agents, which, however, may well be outweighed by the polyphagous and cannibalistic behaviour of the larvae. Consideration of such pros and cons for the employment of this species in classical biological control may, however, be completely overshadowed by a possible need to infect entire land masses with the yeasts required by the adult chrysopid to mediate its digestive processes. Thus Hagen and Tassan (1972) considered that their failure to establish California stock of *C. carnea* in New Zealand (to 'remedy' a complete lack of native chrysopids) may have been due in part to the lack of appropriate endemic yeasts in the New Zealand microflora.

Further information is required on the prey range of phytoseiid mites such as *Amblyseius mckenziei, A. cucumeris* and *Typhlodromips sessor,* how they perform under field conditions, and whether they have biotypes which are safe for release in new countries. The same applies to pathogens such as *Entomophthora thripidum.*

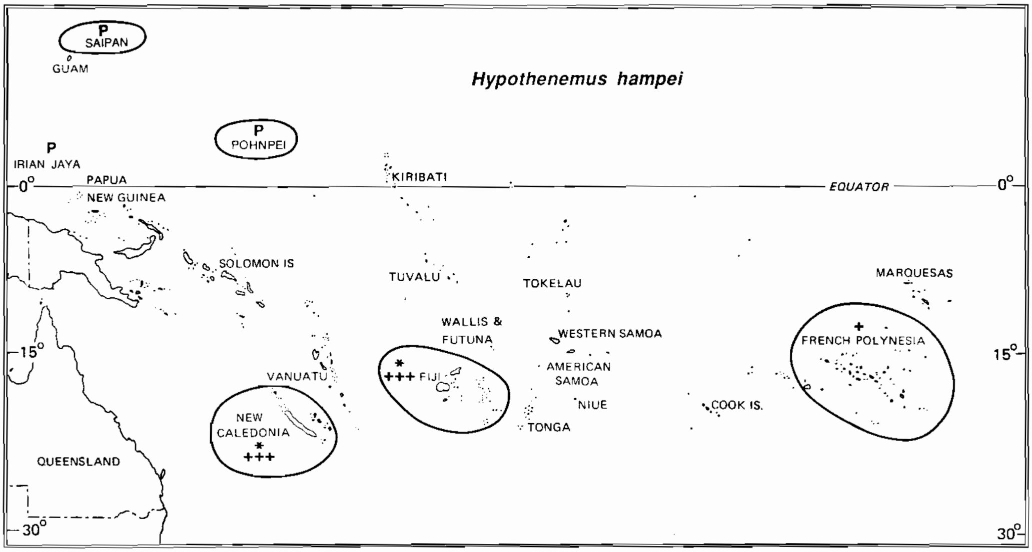
To sum up, improvement in the biological control of *Thrips tabaci* is not to be viewed as impossible, but long and costly programs of research seem inevitable if the prospects for biological control are to be thoroughly explored.


Puerto Rico
Jamaica
Tahiti
Fiji
New Calendonia
Pohnpei
Saipan
Canary Is.
Hypothenemus hampei

6

Hypothenemus hampei
(Ferrari)

COLEOPTERA: SCOLYTIDAE
coffee berry borer



Hypothenemus hampei is native to Central Africa but has spread to many coffee producing countries in Central and South America, to Southeast Asia and to several Pacific countries. Significant coffee-growing areas not yet infested are Hawaii, Papua New Guinea and Solomon Islands.

It is a pest exclusively of coffee berries and does not damage the vegetative parts. It is difficult to control with chemicals and although plantation management methods can reduce damage the coffee berry borer remains an important pest.

The most important natural enemies appear to be three parasitic wasps native to Africa, *Prorops nasuta, Heterospilus coffeicola* and *Cephalonomia stephanoderis.* The former has been established in Brazil and Ecuador without its own natural enemies, but has not so far produced spectacular results. The two other parasites have not yet been established elsewhere, but this is being attempted. A thorough study is in progress of the interactions of the parasites and other natural enemies of *H. hampei* and the influence on them of various components of the environment. Optimism has been expressed about the outcome of this program.

Origin

Ferrari's specimens, described in 1867 under the generic name *Stephanoderes,* were obtained from trade coffee beans in France. There appears to be no record of the country of origin of the material, but in 1867 infested beans could only have come from Africa or Saudi Arabia, because *Hypothenemus hampei* did not obtain a footing in other continents until the twentieth century. The seed used to establish *Coffea arabica* in Saudi Arabia was probably obtained from the Ethiopian highlands centuries ago.There the coffee berry borer is native, though scarce (Davidson 1967), but if it did not accompany the original seed it could easily have reached Saudi Arabia through Arabian–African commerce over the centuries.

The generic name *Cryphalus* has also been applied to this species in early taxonomic literature.

Distribution

This was given by Anon. (1981d) as: Africa (Angola, Benin, Burundi, Cameroun, Canary Is, Central African Empire, Chad, Congo, Ethiopia, Fernando Poo, Gabon, Ghana, Guinea, Ivory Coast, Kenya, Liberia, Malawi, Mozambique, Nigeria, Principe, Rio Muni, Rwanda, São Tomé, Senegal, Sierra Leone, Sudan, Tanzania, Togo, Uganda, Zaire and Zimbabwe). Middle East (Saudi Arabia). Asia (Indonesia, Kampuchea, Laos, Malaysia, Philippines, Sri Lanka, Thailand, Vietnam). Central America (Guatemala, Honduras, West Indies). South America (Brazil, Peru, Surinam). Pacific (Caroline Is, Irian Jaya, Marianas Is, New Caledonia, Society Is).

To these must be added: South America (Colombia in 1988 (D. Moore pers. comm. 1989), Ecuador (CIBC 1988a, b)). Central America (El Salvador, Mexico (Baker 1984)). Pacific (Fiji (Anon. 1979a), Tahiti (Johnston 1963)). In the West Indies, Reid (1983) reported the beetle from Jamaica and Puerto Rico.

Significant coffee-growing or potential coffee-growing areas not yet infested are Papua New Guinea, Solomon Is, and Hawaii.

Life cycle

An important aspect of the life cycle of any insect pest is its host range. In Africa, in addition to its regular hosts in the genus *Coffea, Hypothenemus hampei* has been reported from fruit, pods or seeds of species of *Centrosema, Crotalaria, Phaseolus* and *Tephrosia* (Fabaceae), *Leucaena* (Mimosaceae), *Caesalpinia* (Caesalpiniaceae), *Hibiscus* (Malvaceae), *Rubus* and *Oxyanthus* (Rubiaceae), *Vitis* (Vitaceae) and *Ligustrum* (Oleaceae), but these associations are all considered to reflect only casual feeding by adults. In Africa, the only species outside of the genus *Coffea* in which immature stages have been found is *Dialium lacourtianum* (Caesalpiniaceae) (Le Pelley 1968).

A review of hosts of the genus *Hypothenemus* was made by Johanneson and Mansingh (1984) who concluded that *H. hampei* was monophagous according to their criteria, as it attacked only six species of the genus *Coffea*. However, they listed 23 other species of plants in 11 families from which *H. hampei* has been recorded, but only as adult females. In contrast, in the Philippines, Morallo-Rejesus and Baldos (1980), whose paper was overlooked by Johanneson and Mansingh, reported finding eggs, larvae and pupae of *H. hampei* in *Leucaena leucocephala* (Mimosaceae), *Gliricidia sepium* (Fabaceae), two species of *Psychotria* (Rubiaceae) and one of *Dioscorea* (Dioscoreaceae). In laboratory tests they found that adults of *H. hampei* fed on pods of four of those species and also on the pods of 19 other species in 9 orders.

Such feeding tests may be of little significance, however, since the survival times recorded are greatly exceeded by the periods for which the beetles are capable of withstanding starvation (Corbett 1933). If the insects were correctly identified the host plants recorded in the Philippines may help to support a population of *H. hampei* when no coffee berries are available. Reexamination of the host range is necessary. For example Cohic (1958) found *H. hampei* attacking loquat in New Caledonia, and this relationship, though abortive in the end, has not been reported anywhere else in the world. In connection with 'host' records Johanneson and Mansingh (1984) drew attention to the problem of misidentification of species of *Hypothenemus,* a notoriously difficult genus, and also to misinterpretation of the relative roles of various 'host' plants. Hargreaves (1935) found adults of four species of *Hypothenemus* other than *H. hampei* in seed of *Phaseolus lunatus* (Fabaceae) in Uganda, and Gonzalez (1978) alludes to species of *Hypothenemus,* known as false coffee borers, which occur from Mexico to northern Argentina and greatly complicate quarantine procedures. Such insects would, of course, also raise difficulties in host plant studies. A thorough review of true hosts of *H. hampei* would be relevant to a number of aspects of the control of this pest. Meanwhile the following description of the life cycle refers exclusively to the relationship of the beetle with *Coffea* spp., and principally with Arabian coffee *C. arabica* and robusta coffee *C. canephora,* the most important cultivated species.

Infestations of *H. hampei* occur in coffee seeds while they are enclosed in berries on the trees and in berries that fall to the ground. They will also continue vigorously in processed beans in storage, but not if the moisture content has been reduced below 12.5% (robusta beans) or 13.5% (arabica beans) (Hargreaves 1935). Apart from dispersive flight by adult females, no part of the life cycle of the coffee berry borer is passed through outside of the coffee bean.

The length of adult females of *H. hampei* of Central American origin was given in a taxonomic study by Wood (1982) as 1.4 to 1.7 mm and the width as about 0.43 of the length. Hargreaves (1926) gave the length of Ugandan females as about 1.9 mm and that of males 1.3 mm. Malaysian females measured by Corbett (1933) averaged 1.58 mm in length and 0.77 mm in width and males 0.99 × 0.53 mm. These figures are based on specimens from the native range in Africa and from widely separated regions that the beetle has invaded, and indicate the real dimensions of the adults, but attention should be drawn to a grossly inaccurate statement by Koch (1973) to the effect that females are 10 to 12 mm in length and to an illustration by Hill (1983), whose accompanying scale makes the female depicted about 8.5 mm in length. Males are much smaller on the average, but stunting of some females sometimes results in overlap. Females outnumber males by at least 10 to 1 and the ratio is frequently much higher.

The elytra are striate and the exoskeleton in general closely punctate and covered with short bristles. The beetle is brown when it first emerges from the pupa but in the course of 4 or 5 days it becomes generally black, although the prothorax has a slightly reddish tinge. The prothorax is markedly humped, so that the down-turned head is not visible from above. The antennae are short, elbowed and strongly clubbed, and the tibiae have strong spines which doubtless assist in such activities as tunneling through the pulp of coffee berries, ejecting the resulting frass, and forcing a way to the soil surface should the berry become interred.

Beetle attack tends to be aggregated on some trees or on particular branches within trees, rather than evenly distributed (Baker 1984). The fertilised female flies to coffee berries that have begun to ripen and bores an entrance hole at the apex, either in the terminal pore or in the calyx ridge or annulus of differentiated tissue that surrounds the pore. Sometimes this annulus is perforated by several holes, but boring into the fruit elsewhere is unusual. The colour of berries appears not to influence choice by females seeking oviposition sites (Morallo-Rejesus and Baldos 1980). Young berries, containing seeds with a watery endosperm, usually do not come under attack if more advanced berries are plentiful. If they do they are soon abandoned, after the female has fed on some of the pulp, and they then tend to fall prematurely, being particularly vulnerable to infection by disease organisms. The falling of such immature berries after being attacked often contributes significantly to the amount of crop lost. After the endosperm has passed from the watery to the milky stage in the course of maturation, beetles invading the berry will wait in the pulp until the seed tissue is firm enough to excavate (Penatos and Ochoa 1979). Rhodes and Mansingh (1981) cite opinions to the effect that females that become static in this fashion for several weeks (May to mid-July in the Jamaican lowlands) are in a state of reproductive diapause. When available, berries are selected that are already suitable for colonisation. To quote Corbett (1933) 'The green berry is favoured for feeding and the ripe (i.e. red) berry for breeding purposes', but the ripe berries are also very suitable for feeding. In a ripe berry the female bores in one operation through skin, pulp and the endocarp and pellicle surrounding one of the two seeds (beans) present in each berry. Ejected frass may surround the entrance hole during boring (Hutson 1936). Several days may be occupied in this boring process, and the female then tunnels into the endosperm, the substance of the seed, which is the basis of the world's $8 billion annual coffee crop (Bardner 1978). Berries that fall to the ground may generate considerable numbers of beetles, but these are from their on-tree infestation, seeing that the female berry borers appear not to visit fallen fruit (Baker 1984).

The eggs are bean-shaped, about 0.6 mm in length, translucent and whitish in colour. They are laid at the rate of two or three a day in batches of 8 to 12 in chambers chewed out of the maturing bean tissue. Oviposition extends over a period of three to seven weeks, each female producing from about 30 to over 70 eggs. According to some authors, laying is not necessarily confined to one bean because the female that has initiated an infestation may fly to other berries during the oviposition period. According to others (e.g. Bergamin 1943) the female that has initiated an infestation only quits the bean when the first of her progeny emerge as adults. Others again (e.g. Hargreaves 1935) state that she remains until all the bean tissue is consumed or has deteriorated in some way. Most likely the pattern is quite flexible. Eggs hatch in three to nine days, disclosing legless white larvae with brown, sclerotised head capsules. These may possibly feed at first on frass remaining from the tunneling of the female, but they also bore readily into intact bean tissue, making pockets opening off the main tunnel bored by the parent female. Some early authors assumed that the larvae feed on an ambrosia fungus inoculated by the female into the cavity in the bean, much as some bark-boring platypodids do, but this has long been considered not to be the case, the larvae supposedly eating only tissue chewed from the endosperm. However CIBC (1986) reports tests on an ambrosia fungus cultured from *H. hampei,* but the present status of this research is unknown. Attacked beans, even lightly bored, have a distinctive blue-green staining (McNutt 1975).

Male larvae pass through their two instars in the course of about 15 days, and the females pass through three instars in about 19 days (Bergamin 1943). Morallo-Rejesus and Baldos (1980) state that the female, like the male, passes through only two instars, indicating the need for further biological study. The long period over which oviposition is spread results in larvae in all stages of development being present in one bean. At the end of the larval stage there is a non-feeding or prepupal stage lasting about two days.

The insect then pupates, without any cocoon formation, in the galleries excavated by the larvae. The pupal stage is passed through in four to nine days. The period from egg-laying to the emergence of the adult is 25 to 35 days. The temperatures at which the preceding records were made are generally not specified, but chiefly they relate to warm lowland coffee plantations. Bergamin (1943) recorded that at 24.5°C in Brazil the period from egg-laying to emergence of adult averaged 27.5 days. De Oliveira Filho (1927) found that in Brazil shade temperatures of 20 to 30°C suited the females best. Below 15°C they became inactive, endeavouring to hide, preferably in coffee berries, but sometimes by boring into beans, maize, peanuts or cotton seed of suitably low moisture content. They can survive temperatures just below 0°C, which however are rarely experienced in Brazilian coffee growing areas. At higher elevations development is somewhat prolonged (Le Pelley 1968) and *H. hampei* has a low pest status in highland coffee growing areas in East Africa and Java (Haarer 1962).

The adult males emerge from the pupa earlier than the females. Their hindwings are short and they do not fly, but remain in the bean, fertilising their female siblings as they emerge.

Each male can fertilise two females a day and up to 30 in his lifetime which may extend to 103 days, although averaging less. Corbett (1933) states that the males seldom leave the berries, and then only when they are near death. The vast majority of observers confirm that males never leave the berries. Baker (1984) suggested that males may leave the berries and perhaps walk to others in search of more females, but he does not state that this was observed. Quite likely they may move from bean to bean within a fruit, thereby gaining access to females other than their sisters. Parthenogenesis does not occur, and although unfertilised females may produce some eggs, these do not hatch. One insemination is sufficient to allow a female to lay fertile eggs throughout her reproductive period. Corbett (1933) stated that, if there are no males in the seed when the females emerge from the pupal skin after their hardening period of a few days, they leave via the entrance hole and seek males in other infested berries. Morallo-Rejesus and Baldos (1980) suggest that sex pheromones secreted by the males guide such females to appropriate berries.

Females that have been fertilised remain in the 'parental' bean for three or four days, by which time they have become sexually mature. They then leave the berries via the entrance holes and enter others and, after a preoviposition period of 4 to 20 days, commence egg laying. Females have been known to live up to 282 days, and longevity was stated by Bergamin (1943) to average 156 days. According to Corbett (1933) in Malaysia females survived 81 days without food. There is time for a succession of seven or eight generations a year in lowland coffee growing areas but, on account of the long reproductive period, there are few clearcut population peaks to indicate generations.

Morallo-Rejesus and Baldos (1980) observed that in the Philippines beetles are to be observed in flight from 3.00 p.m., considerable numbers being visible in the air between 4.00 and 5.00 p.m. Corbett (1933) observed that, in Malaya, females fly at any time during the day, but in greatest numbers between 2.00 and 5.00 p.m., reaching a peak between 3.30 and 4.30 p.m. De Oliveira Filho (1927) states that in Brazil females 'are active' on warm nights, but it is unclear whether this implies flight activity. Kalshoven (1981) states that in Java females start flying during the midday period, and that they assemble under leaves and in other places where they dance up and down like gnats. Such activity can have no sexual significance, seeing that the males do not leave the seeds, and its function is obscure. In Java flights up to 345 m have been measured (Leefmans 1920). In Mexico, Baker (1984) carried out experimental studies on flight. Females flew freely in the laboratory for up to 22 minutes, tending to hover or move forward only slowly. In tethered flight, and thus relieved of supporting their own weight, they could fly non-stop for 100 minutes, with an aggregate of three hours. Such enduring activity, with so little progress on the part of such a small insect, combined with its afternoon peak of activity, suggests that, in their habits, the beetles resemble aphids and thrips in being adapted to exploiting periods of maximum convection in the atmosphere, so achieving long-distance travel with their own contribution serving chiefly to keep them aloft. De Oliveira Filho (1927) states that local flight occurs when the fertilised female is seeking a place to lay, when (oviposition having commenced) she emerges to seek moister berries after having been driven out by the heat of the sun, when unfertilised females seek males (as they do if there is none in the berry when they emerge), when seeds are waterlogged or becoming destroyed or are overcrowded with adults and larvae, or when the beetles are disturbed.

Rhodes and Mansingh (1981) state that, in the Jamaican lowlands, beetles in dry berries remain in diapause for five months, from mid-December to mid-May. Baker (1984) found that in mid-spring in Mexico females tended to remain in fallen coffee berries at a time when temperatures in berries in the trees ranged up to an inimical 37°C. Soaking the fallen berries in water induced many to emerge, but they did so in a specific pattern, some seven to eight hours after dawn. Possibly the soaking simulated rain that would have made the environment generally more favourable, although at the time there were few berries around for the released females to infest. Baker reminds us that coffee is naturally an understorey plant in tropical forest, and, by sheltering cumulatively in fallen berries beetles may avoid the harmful effects of strong, direct sunlight in certain seasons.

Infestations are carried over between peaks of fruiting by breeding that occurs in late-maturing berries, or else in those that have fallen to the ground. Females can survive for up to two months in buried beans (Clausen 1978) and mobile females can also survive by feeding on immature berries.

It is probable that intercontinental travel is brought about by the agency of man, rather than by travel in moving air masses. Infested beans are an obvious vehicle for dispersal, but there are other avenues to which quarantine measures should be applied. In Jamaica Reid (1983) observed females among banana trash used in packing boxes on their way to the boxing plant. Commonly beetles dispersed in sacks, empty or otherwise, and on the clothing and equipment of plantation workers. Under some conditions beetles bore for protection into wood or other materials to the extent that Baker (1984) suggested that authorities in beetle-free areas should think very carefully before allowing entry of untreated plant material from an infested area. A rather bizarre, if minor, means of dispersal is in seeds swallowed whole by the Javanese berry-eating palm civet, the loewak (*Paradoxurus hermaphroditus,* Carnivora: Viverridae), and passed intact in its faeces (Leefmans 1922). In former times the pellets were collected and the seed extracted and marketed at premium prices as 'loewak' coffee. The high quality of the seed was ascribed to the loewak's selecting only the choicest berries (Le Pelley 1968). Thus, unconsciously, a four-footed epicure catered for an odd taste in human epicures.

Pest status

Hypothenemus hampei is a pest exclusively of the immature and mature coffee berries and does no damage whatsoever to the vegetative parts of the plant. In physiological terms this is illustrated by the experiments of Prates (1969), which showed that adults of *H. hampei* were strongly attracted to extracts of green or ripe coffee berries, but not to extracts of coffee leaves or flowers. Significant losses are caused by the female beetles feeding on young berries which are too immature to colonise but which, after the beetle has gone, are invaded by decay organisms, and so fall prematurely. In Java Leefmans (1920) found that 80% of green berries that had fallen through being bored by the beetle contained decayed beans as against 46.5% in unbored beans that had fallen through other causes. In the Congo Schmitz and Crisinel (1957) found that 64 to 82% of shed berries had fallen on account of *H. hampei* attack. Such losses through attack on immature fruits are serious enough, but the bulk of the damage done by this beetle is to the endosperm of the mature beans. These may be extensively damaged or even completely destroyed. Even lightly bored beans acquire a distinctive blue-green staining which significantly reduces their market value (McNutt 1975), but the further tunneling by the beetles and their larvae brings about progressive degradation so that the coffee bean is only a dusty mass of frass. Damaged beans contain remnants of the brood killed during processing and also of their accumulated frass or faeces, and this further downgrades them. Market requirements demand the removal of damaged berries from the harvested crop, which is done by various mechanical processes (fortunately bored beans float), supplemented even by handpicking. The beans removed by such processing are not necessarily a total loss, but can go into only low grade fractions at a much reduced market rate.

In New Caledonia *H. hampei* was found to have attacked 80% of berries where no control measures had been implemented (Cohic 1958). Other examples of losses due to *Hypothenemus hampei* are given by Le Pelley (1968). Severe infestations in Uganda may result in 80% of berries being attacked. In the Ivory Coast, damage of 5 to 20% of berries is common, rising to 50 to 80% in some cases. In the Congo boring of up to 84% of green berries and up to 96% of hard berries has been recorded and in Tanzania records indicate up to 96% boring of hard berries. In Malaysia there have been records of up to 90% of damaged beans. In Java crop loss of 40% was recorded in 1929, and in Brazil 60 to 80% losses have been experienced. The above figures apply for the most part to poorly managed situations, and crop losses can be reduced by appropriate management, but the beetle is a constant latent threat if vigilance is relaxed. In Jamaica, Reid (1983) estimated that 27% of the berries harvested were damaged. The studies of Reid and Mansingh (1985) showed that *H. hampei* was responsible for 20.9% reduction of exportable beans in the Jamaican crop of 1980-81. Baker (1984) reported that in southern Mexico the attack of *H. hampei* on coffee plantations was so severe that, in spite of application of insecticides in some places in 1982, no berries were harvested because it would not have been economical to do so.

In Brazil a particular problem arises from the common practice of stripping berries from the trees and allowing them to remain on the ground until raked up, mixed with naturally fallen (and usually heavily infested) berries, and carrying them off for processing, along with a generous helping of earth and debris. This treatment and the 'dry' extractive process to which the crop is then subjected often provides ideal conditions for the further propagation of *H. hampei* (Haarer 1962).

Proper processing results in beans of moisture content too low to permit the borer to multiply. This is below 13.5% for arabica coffee and below 12.5% for robusta coffee. If, however, coffee beans are stored with significantly higher moisture content, beetle reproduction continues. Thus Morallo-Rejesus and Baldos (1980) found that in the Philippines infestation in coffee beans stored before drying rose from 20% to 100% in six weeks.

Control measures

Hypothenemus hampei has established itself in most of the coffee growing areas of the world, but there are still uninfested countries, such as Australia, Hawaii, Papua New Guinea and the Solomon Islands. Quarantine is of critical importance to these countries, the various habits of the beetle mentioned under Life Cycle giving some guidance to the orientation of inspections. It is important to ensure that seed coffee imported into clean areas has been completely disinfested. In the past fumigants suggested for this purpose ranged from turpentine to hydrocyanic acid gas. McNutt (1975) advocated methyl bromide or phosphine. Morallo-Rejesus et al. (1980) suggested aluminium phosphide as a source of phosphine. Le Pelley (1968) mentions techniques involving submersion in water under pressure and also exposure to shortwave and infrared irradiation. Thorough drying of the seed grains is an indispensable supplement to disinfestation techniques. Some methods suggested for destroying the pest in trade coffee are unsuitable for seed coffee.

The world's coffee is grown on a great variety of production units ranging from large, well-capitalised and scientifically conducted estates to small, poorly managed domestic plantations. In Kenya, for example, many thousands of dollars may be expended on machinery in large concerns, whereas about half Kenya's production of arabica coffee comes from plantings of 10 down to 1/10 hectare, and in the latter even the cost of an oilcan for injecting dieldrin into stem borer holes may be beyond the resources of the producer (Bardner 1978). Species and varieties of coffee under cultivation vary widely with terrain, altitude, soil type, rainfall regime, markets and the fancies of growers. Production practices also show great variation — whether plantations are uniformly of one variety or mixed, how the trees are spaced and pruned, whether shade trees are employed, and if so their species, whether mulching, cover cropping and weed control is practised and what techniques are used in harvesting and processing. The mix of all these factors bears heavily on pest incidence and impact, and from time to time technological changes may result in the reordering of the status of pests. For example in East Africa it was found that mulching to counteract the effects of drought and poor soil conditions lessened the importance of a thrips, which throve previously, but increased the pest status of a moth which found the new conditions more congenial (Le Pelley 1973). In common with all other fields of agriculture, applications of pesticides to coffee crops is an important overriding factor influencing the status of arthropod pests.

Plantation sanitation is an old-established tradition in pest control, and the coffee berry borer has long been attacked from this angle. The life cycle of the borer, indeed, lends itself to this approach, as it is narrowly specific to the coffee berries. In Java Leefmans (1920) recommended the collection from coffee bushes and ground surface of blackened berries (with tissues discolored by disease organisms in the pulp, and almost invariably with heavily infested beans) and their burning or burial at least 20 cm deep under well-tamped soil. Corporaal (1921) recommended that all infested berries be collected from the bushes and ground surface and placed in bags of closely woven material with flaps to prevent beetle escape. The bags had to be immersed in boiling water for a period and then soaked for four days to ensure that all life history stages were killed. Corbett (1933) also advised keeping factories clear of rubbish in which the beetles could either breed or shelter.

In various forms strategic picking and collection of vulnerable or infested (even potentially nutritive) berries has remained important in the control of *Hypothenemus hampei* since the second decade of the century.

In Java, Roepke (1912) and Leefmans (1924b) applied the method of 'rampassen' to the control of the coffee berry borer. Rampassen is a system worked out by Zehnter in 1902 for controlling the cacao moth in Java (Roepke 1915). It involves the total removal or destruction of breeding medium over a period long enough to break the life cycle of a pest. In the case of the coffee berry borer a period of three months was aimed at, although some records of the longevity of beetles exceed this. Measures taken involve the collection of all fallen berries and the picking of any that may have escaped the harvest, plus the continuous removal of all young berries on which adult female beetles might feed. Friederichs (1922) and Rutgers (1922) reported successful application of the method in Java. The latter reported that, on estates which had applied the measures, the percentage of infested berries fell from 40 to 90% to between 0.5 and 3.0%.

In Brazil, Do Amaral Castro (1924) drew attention to the advantages of picking coffee berries as they ripen, thereby minimising the breeding of *H. hampei.* The rampassen method was early recommended in Brazil. Escherich (1926) claimed reduction of infestation from 90% to 100% to 1 to 5% and Neiva (1928) a reduction from 60 to 90% to less than 1%, but Le Pelley (1968) appears to have reservations about these claims. Quantitative studies were first made in Brazil by Bergamin (1944). In his experiments he compared the results of stripping all berries from trees only, collection from the ground only, and a combination of both procedures. The last treatment gave highly significant reductions of damage in succeeding crops and the other two treatments also produced significant results in particular situations. The term applied to the technique in Brazil is 'repasse' (in Portuguese meaning gleaning or going over). The word bears a suggestive resemblance to 'rampassen', the derivation of which appears to be unknown (Anon: footnote in Rev. App. Ent. (A) 1: 57).

In New Caledonia application of the 'repasse' method reduced infestation from 80% to 10% (Cohic 1958).

In Africa attention was only tardily directed to strategic picking and gathering as a coffee berry borer control measure. Thus Hargreaves (1926) in Uganda emphasised the importance of favouring the parasites at all costs. He pointed out that harvesting the ripe coffee berries involves the elimination of a greater percentage of parasites than of beetles. He conceded that it could be advantageous to pick and destroy a minor crop that occurred in April, but only if borer numbers were low, and he deprecated the cost of this action anyway. The same emphases were evident in a second paper (Hargreaves 1935) in which attention was drawn to 'rampassen' as used in Java and 'repasse' in Brazil, without this technique being recommended. In fact growers were advised to leave overripe berries on the ground as harborage for parasites, and emphasis was again placed on reduction of shade to favour the parasites. The same advice about shade was offered by Jervis (1939) in Tanzania, although the collection and burning of fallen berries after harvest was advised. Ingram (1969) recommended to Ugandan growers that they abandon their tendency to pick only when there is a large flush overall, regardless of the condition of individual trees, and instead to pick all ripe berries at least every two weeks, at the same time gathering and destroying fallen berries. This harvesting pattern was stated to reduce berry fall to the extent that it obviated the need for collecting and destroying fallen berries, the small percentage finishing up on the ground being allowed to lie there as a reservoir for parasite breeding. McNutt (1970) also placed the emphasis on regular picking and the reduction of shading to encourage parasites, and in a second paper (1975) McNutt made no recommendations regarding patterns of harvesting, but emphasised again the encouragement of conditions favouring parasites. Rampassen or breaking the life cycle of the coffee berry borer, therefore does not seem to have been adopted or even encouraged in Africa. Instead the emphasis seems to have been on patterns of berry picking that do not allow the beetle time to do much damage, and on management methods that do not discourage parasites.

In Sri Lanka Hutson (1936) recommended that all bored berries on the bushes and all fallen berries should be collected for destruction at least once a fortnight and by early afternoon, before the flight period. However, the latter must be of only minor importance, as it is relevant only on the day of collection. In Malaysia Corbett (1933) recommended picking at weekly intervals (or the shortest period practicable, according to size of holding) of all bored green, ripe and blackened berries on the bush and from the ground. A rampassen period of six months was recommended for the eradication of the beetle from isolated plantations. Reid (1983) advocated the use of the rampassen method in Jamaica, and Cohic (1958) did likewise for New Caledonia, but there are no reports of results.

Baker (1984) experimented with berry collection in Mexico. He found that the manual gathering of infested berries from the trees reduced the proportion of these in the carpet on the ground where, however, the number of infested berries per unit area remained low and almost constant. He concluded that berries are not infested while lying on the ground surface. Nevertheless the infested berries allowed to lie where they fell ultimately generated large numbers of beetles. Le Pelley (1968) stated that 'the value of this form of control was undoubted, and it should be practised in all cases other than in the exceptional ones where at any time the insect can be shown to be under effective biological control'. On the other hand, in his world review of the control of coffee pests, Bardner (1978) implies that hand picking for control of coffee berry borer was practised only in Java, and commented that it decreased the risk of carry-over of the beetle between seasons, but did require a great deal of labour. Neglect of weed control and the adoption of practices such as mulching and the use of cover crops makes the gathering of berries from the ground surface almost impossible (Ingram 1969).

Differences in susceptibility to *H. hampei* attack exist between species and varieties of *Coffea*. For example Ticheler (1961) claimed that berries with thick pulp and lacking a protruding disk (the calyx ridge) are less susceptible to attack. However, reports on the topic of resistance are not consistent, and there does not appear to have been any sustained tendency to exploit this factor. The perennial nature of the plant, which may be cropped profitably for a century or more if carefully managed, and a lead period of three years to first harvest makes large-scale replacement a problem. Moreover, in many areas, susceptibility to other pests and diseases may be of much greater importance than susceptibility to *H. hampei,* posing a complex problem for plant breeders. In addition there can be a conflict of interests in the field of varietal differences. Thus in Uganda Hargreaves (1926) considered that planting of robusta near the more valuable arabica would help to protect the latter from *H. hampei* because the year-round berry burden of robusta would afford reservoirs for the production of parasites, whereas Cohic (1958) found this feature in mixed plantations a serious impediment to the implementation of rampassen in New Caledonia. The interplay of disease and pest is well illustrated by the experience in New

Caledonia (Cohic 1958). Before 1911 only *C. arabica* was grown there, but then there was extensive mortality of the bushes due to the invasion of the island by coffee rust *Hemileia vastatrix*. The resulting gaps in the plantations were filled with *C. canephora,* which is relatively rust resistant, but when *Hypothenemus hampei* gained access to the northern part of the island and spread southwards from 1948, it was found that the different fruiting patterns of *C. canephora* and *C. arabica* made it impossible to arrange a three month berry-free period necessary to implement the principle of rampassen.

Plantation management has important bearings on the degree of *H. hampei* attack. McNutt (1970, 1975) stressed that the heavy shading, brought about usually by inefficient pruning, is not only unfavourable to natural enemies, but results in many berries, too high to reach, being left on the bushes, thus favouring the borer. Proper pruning is therefore necessary for direct and indirect control of *H. hampei.* It is vital anyway, since only new wood bears flowers, and hence fruits, each year. Roepke (1919), from his studies in Java, suggested that *Coffea liberica,* which is highly susceptible to borer attack, could be used as a trap crop (presumably by total destruction of berries each year), but there seems to have been little or no adoption of this approach. Baker (1984) also suggested the use of trap crops in Mexico, where he considered that *C. canephora* was more susceptible to attack than *C. arabica.* This reflects the current view in East Africa, where *C. arabica* is said to be less heavily attacked than *C. canephora,* although to some extent this may reflect the fact that *C. arabica* crops are generally grown there at higher altitudes, where the incidence of the coffee berry borer is lower (D. Greathead, pers. comm. 1989).

A few authors (e.g. Morallo-Rejesus and Baldos 1980, Reid 1983) advocate the eradication of alternative hosts as a control measure, but this is inadvisable until there has been further study of the host relationships and the taxonomy of the beetles involved. The main alternative hosts in Africa may be *Coffea* species, either indigenous or plantation escapes, which may be of significance in the economy of native peoples. There should, however, be no bar to the destruction of abandoned plantations. According to Cohic (1958), for example, in New Caledonia numerous plantations have been abandoned for want of manpower, and these are foci from which populations of *H. hampei* invade the groves of active coffee producers. Escherich (1926) listed this measure among recommendations which he claimed had brought about a phenomenal reduction in losses due to *H. hampei* in Brazil.

The biology of the coffee berry borer makes it difficult to control with chemicals, seeing that all the immature stages, the adult males, and, for a significant part of their lives, the adult females, are protected within the beans, deep inside the berry. In the early days only adult females on exploratory travel were in any way vulnerable, and then only to contact poisons. Females boring entrance holes are not even susceptible to stomach poisons, since they reject the portions of the skin of the berry that they remove in the process (Hargreaves 1935).

In coffee crops fungicides generally seem to have a higher priority than insecticides, and spraying equipment is generally designed primarily with disease control in view (Haarer 1962). However, in New Caledonia and southern Asia insecticides are considered to be of greater importance (L.O. Brun pers. comm. 1989).

Many coffee crops are grown on mountain slopes, on which the use of motorised spraying equipment is impracticable, but on lowland crops in large estates mounted airblast and hydraulic sprayers are used extensively. Flying conditions in mountainous areas and the frequent use of shade trees make aerial spraying of limited value. Thus in many coffee growing areas chemicals are applied by men on foot, equipped at best with motorised sprays, knapsack sprays or stirrup pumps.

The advent of synthetic insecticides brought a new aspect to the chemical control of *H. hampei* and other coffee pests, although bringing some environmentally unacceptable features as well, such as destruction of natural enemies of coffee pests. BHC received extensive testing in South America, and dusting the ground surface with BHC in lieu of collecting all fallen fruits became a widespread practice in Brazil, along with dusting of the bushes (Le Pelley 1968). A systemic effect from the application of lindane to coffee bushes was demonstrated by Ribas et al. (1976). There was considerable concern over the possibility that BHC would impart a taint to coffee and Haarer (1962) states that this was definitely demonstrated in Kenya. In Brazil also, De Oliveira et al. (1979) and Do Amaral et al. (1973) showed that BHC imparted an unacceptable flavour to coffee liquor, though a number of earlier Brazilian reports were negative. BHC appears not to have been viewed in Africa with as much appreciation as in South America. Sprayed on the foliage it had a very destructive effect on the parasites of the coffee leafminer (Bardner 1978). Much work was also carried out on other organochlorines and on cyclodienes, which will not be discussed because environmental considerations have now ruled out their use. Ingram (1968) showed that endosulfan, sprayed on to the branches bearing the crop, was valuable for the control of heavy attacks by *H. hampei* in Uganda, bringing about a significant destruction of the pests in the berries, leaving no taint in the coffee liquor and having no side effects on natural enemies, but not producing a significant improvement in yield. Hernandez Paz and Penagos Dardon (1974) found, in tests in Guatemala, that low-volume sprays of endosulfan could completely destroy infestations of *H. hampei* in berries on the bushes, and according to Mansingh and Rhodes (1983) this chemical is in extensive use in Central and South America. However these authors state that it is quite expensive and dangerous for operators and environment. Ingram (1968) looked for evidence of a fumigative effect of endosulfan on *H. hampei* in coffee berries, but seems not to have considered the possibility of a systemic effect. Resistance to endosulfan in *H. hampei* is reported in New Caledonia (Brun and Ruiz 1987).

Rhodes and Mansingh (1981) and Mansingh and Rhodes (1983) carried out comprehensive screening tests by dipping detached maturing and ripe coffee berries in solutions or suspensions. Their work clearly evaluates systemic effects, although the term is not used. Such a mode of action is desirable in a chemical to cope with the cryptic nature of the life history stages of *H. hampei*. The work of these authors suggested that the organophosphorus compounds perfekthion, carbicron and perhaps actellic, alone or admixed with endosulfan, might provide effective, economic and safe alternatives to endosulfan on its own. If true systemic action is involved in the mode of operation of the chemicals tested, the results of application to berry-laden bushes would be of interest, since absorption by the foliage would also contribute to the toxicosis. The results of Ribas et al. (1976) clearly demonstrate systemic effects from spraying coffee bushes, the chemical translocating in measurable quantities into the beans. Such a factor might well have accounted for the differences between laboratory and field tests with lindane mentioned by Mansingh and Rhodes (1985). In the treatment of dried berries lying on the ground pending harvesting, Rhodes and Mansingh (1985) recommended fast-acting non-persistent insecticides such as some synthetic pyrethroids. Bardner (1978) states that side effects on the parasites of the coffee leafminer are now avoided by the application of systemic insecticides to the soil.

It is obvious that great advances have been made in the chemical control of *H. hampei*, but indications are that it would be a great advantage to have a significant level of biological control in any coffee-growing system. Rhodes and Mansingh (1986) found chemical control inadequate on its own in Jamaica and advocated its integration with cultural practices. Bardner (1978) emphasised the need to harmonise cultural, biological and chemical control of coffee pests, indicating that integrated control, based on threshold values obtained from frequent inspections by trained but non-professional staff, has been long established in Africa, where, he states, 'great care is taken to minimise disturbance of the environment and to encourage the maximum possible control (of all coffee insects) by parasites and predators'. The position would appear to be less satisfactory in South and Central America.

Associated pests

Some insect pests, of which *Hypothenemus hampei* is the most important, have spread from their African homeland along with coffee plants, but for the most part in countries where coffee has been introduced, it is the native insect species that attack it. There are many rubiaceous genera related to the Afro-Oriental genus *Coffea* in the tropics in both the Old and New World, and their associated insects readily adapt to *Coffea* spp. Most of these secondary pests, however, remain local, and specific pests like *H. hampei* are exceptional, and 'because the crop is perennial, evergreen and only grown in areas without climatic extremes, pest populations only rarely become intolerable, being held in check for most of the time by parasites, predators and diseases' (Bardner 1978). If this generalisation is true it should be a matter for comfort to coffee growers, since Le Pelley (1973) states that 850 species of arthropods are known to attack coffee: 400 in the Ethiopian region, 250 in the Oriental Region, 200 in the Neotropical Region and a few Pantropical in nature. Bardner, himself, (1978) places the total of known coffee pests at 900. Quite an extensive fauna of arthropod herbivores may already be present in areas to which *Hypothenemus* has not yet spread. This is true in Papua New Guinea (Barrett 1966, Szent-Ivany and Stevens 1966, Williams 1986), where the diversity of the insect fauna approaches continental proportions. However there are fewer native species capable of attacking coffee in Hawaii and Marianas (Le Pelley 1968) and the Solomon Is, few also in Fiji (Anon. 1979a, Swaine 1971) and probably even fewer in Tahiti. Pacific situations will undoubtedly present progressively less complex secondary problems, arising from the presence of native insect pests should *H. hampei* spread to more island groups.

Natural enemies

The cryptic nature of the immature stages and the male of *H. hampei* makes them relatively inaccessible victims for predators, and the only one recorded is the non-specific Javanese bug *Dindymus rubiginosus*. This bug draws the borers from the berries with its beak and sucks them dry. Le Pelley (1968) states that it is of little importance.

The most important parasitic wasps, *Prorops nasuta, Heterospilus coffeicola* and *Cephalonomia stephanoderis* are, of course, African in origin and are dealt with in some detail by Klein et al. (1988). The potential of *H. coffeicola* in biological control requires further study because its larvae are not very specific, but the other two species appear to have a narrow enough host range to make them acceptable from this point of view.

In addition to the identified arthropod natural enemies (Table 6.1), Hargreaves (1926) found an undetermined hymenopterous parasite in Uganda which could escape through fine mesh gauze capable of retaining *H. hampei*. Koch (1973) hinted that this may have been *Cephalonomia stephanoderis*. Morallo-Rejesus and Baldos (1980) reported the presence in the Philippines of a braconid and an encyrtid parasite of *H. hampei*, both unidentified, and presumably non-specific members of the local fauna.

Some ants attack the borer. Swallows and other small birds that feed on the wing consume flying adults of *H. hampei*.

The parasitic fungus *Beauveria bassiana* has been observed infesting *H. hampei* in Brazil (Averna-Saccá 1930, Villacorta 1984), Jamaica (Rhodes and Mansingh 1986), Cameroun (Pascalet 1939), Congo (Sladden 1934, Steyaert 1935), Ivory Coast (Ticheler 1961) and in Java (Friederichs and Bally 1922). Steyaert (1935) and Averna-Saccá (1930) studied the seasonal cycle and the former also made studies of the infectivity and epidemiology of the fungus of which there are many strains, some of particular value against a pest species or a related group of species. Moist, warm conditions favour the incidence of this pathogen, and heavy rain is thought to enhance the rate of infection by driving the adult female berry borers to crowd into the coffee trees for shelter. Friederichs (1922) recommended the encouragement of heavy shade to increase the incidence of fungal pathogens, but this runs counter to the fact that intensity of shade must often be reduced to encourage hymenopterous parasites which, however, may still prove to be of minor significance in population regulation.

Table 6.1 Natural enemies of *Hypothenemus hampei.*

Species and type	Country	Reference	Comment
HYMENOPTERA			
Bethylidae (ectoparasites of immature stages)			
Cephalonomia stephanoderis	Ivory Coast	Betrem 1961	A promising parasite
	Togo	Klein et al. 1988	
Prorops nasuta	Cameroun	Klein et al. 1988	
	Congo	Klein et al. 1988	
	Ivory Coast	Klein et al. 1988	
	Kenya	Klein et al. 1988	
	Tanzania	Rangi et al. 1988 Klein et al. 1988	
	Togo	Klein et al. 1988	
	Uganda	Klein et al. 1988 Waterston 1923	
Scleroderma cadavericus	Uganda	Benoit 1957	Causes severe dermatitis in man
Eulophidae			
Tetrastichus sp. (attacks adult beetles)	Togo	Klein et al. 1988	
Braconidae (ectoparasite and predator)			
Heterospilus coffeicola	Uganda	Schmiedeknecht 1924	Kills larvae with sting. Attacks larvae of other parasites of *H. hampei*—also may be cannibalistic
	Tanzania	CIBC 1988b	
	Cameroun	Klein et al. 1988	
	Congo	Klein et al. 1988	
Formicidae (predator)			
Crematogaster curvispinosa	Brazil	Pinto da Fonseca and Araujo 1939	
HEMIPTERA			
Pyrrhocoridae (predator)			
Dindymus rubiginosus	Java	Wurth 1922	Not specific
NEMATODA			
Heterorhabditis sp.	?	Moore and Prior 1988	
FUNGI			
Hyphomycetes			
Beauveria bassiana	Java	Friederichs and Bally 1922	Cosmopolitan, in a variety of strains
	Cameroun	Pascalet 1939	
Metarhizium anisopliae		Moore and Prior 1988	
*Nomuraea rileyi**		Moore and Prior 1988	
Paecilomyces (= *Spicaria*) *javanicus*	Java	Friederichs and Bally 1922	Indonesia, Asia, Africa (Samson 1974)
P. tenuipes		Moore and Prior 1988	

* Normally recorded from Lepidoptera.

Pascalet (1939) advocated the spraying of suspensions of spores, before sunrise. No records of the result of this treatment are available, and no recent papers refer to attempts to utilise this parasitic fungus for *H. hampei* control. As with so many parasitic fungi, its application would be limited by intolerance of dry conditions. *Paecilomyces javanicus* is Afro-Asian in distribution and wide spectrum in its host range (Samson 1974), attacking also Lepidoptera. Its use against *H. hampei* appears not to have been attempted. Methods of rearing and despatch of natural enemies and freeing them of disease organisms are discussed by Moore and Prior (1988) and Rangi et al. (1988).

Attempts at biological control

Published information is summarised in Table 6.2, but there were probably a number of transfers of parasites within Africa and perhaps South America that have gone unrecorded.

AFRICA

CAMEROUN

Pascalet (1939) recommended the introduction of *Heterospilus coffeicola, Prorops nasuta* and *Beauveria bassiana* to any plantations lacking them. There is no record that this was implemented anywhere, nor whether any or all of the organisms were not already generally distributed in Cameroun.

CONGO

Sladden (1934) and Leroy (1936) suggested that, by breeding and liberating them, it would be possible to increase the efficiency of *P. nasuta* and *H. coffeicola* which he knew to be already present in the Congo and he made a similar suggestion for fungus diseases. However, there is no indication of the extent to which this was done.

KENYA

Prorops nasuta was sent from Uganda to Kenya in 1930 (Greathead 1971), but according to Evans (1965) that wasp and *H. coffeicola* were probably native there. Abasa (1975) considered that parasites were of doubtful value in controlling *H. hampei* in Kenya.

UGANDA

Prorops nasuta and *Heterospilus coffeicola* are both native to Uganda. Hargreaves (1935) considered that some areas lacked these parasites, and so he introduced cultures from Kampala County, north of Lake Victoria, to Bwamba County on the western border. He stated that this introduction resulted in a great reduction in the previously intense infestation of coffee berry borer, but in view of the natural occurrence of *P. nasuta* over a wide area to the west of the Ugandan border (Le Pelley 1968), it seems unlikely that the distribution was discontinuous and that it was lacking in Bwamba County. Hargreaves' claims that the introduction brought about a great reduction in the impact of the coffee berry borer in Bwamba County must be treated with reserve.

ASIA

SRI LANKA

Stock of *P. nasuta* and *H. coffeicola* from Uganda were liberated in Sri Lanka in 1938, but neither species became established (Hutson 1939).

CARIBBEAN

JAMAICA

CIBC (1987) states that *P. nasuta* is being screened in UK for shipment to Jamaica. Stocks are being freed of possible hyperparasites and diseases, and plant pathogens by culturing them in coffee berries sent from Jamaica.

CENTRAL AMERICA

MEXICO

Prorops nasuta is being screened in UK to eliminate parasites, pathogens and plant disease organisms before despatch of cultures to Mexico. The cultures are raised in coffee berries imported from Mexico (CIBC 1987). Stocks of *Cephalonomia stephanoderis* have been sent by CIBC to Mexico and are thriving in culture there (D. Moore pers. comm. 1989).

INDONESIA

JAVA

The introduction of *Prorops nasuta* to Java from Uganda in 1923 was the earliest attempt to bring about the biological control of *H. hampei.* It was found to be easily propagated (Leefmans 1924a) and was distributed widely in considerable numbers (Begeman 1926). It was still being bred for distribution in 1928 (Ultée 1928) and in 1932 (Betrem, in Ultée 1932, Schweizer 1932).

Table 6.2 Introductions for the biological control of *Hypothenemus hampei.*

Country and species liberated	Year	From	Result	Reference
BRAZIL				
Prorops nasuta	1929	Uganda	+	Hempel 1933
ECUADOR				
Cephalonomia stephanoderis	1988	Togo via UK	?	CIBC 1988b
Prorops nasuta	1986 –1987	Kenya via UK	+	CIBC 1988a
	1988	West Africa	?	Rangi et al. 1988
JAVA				
Prorops nasuta	1923 –1925	Uganda	-	Begeman 1926 Kalshoven 1981
Heterospilus coffeicola	1923	Uganda	? not liberated	Begeman 1926
KENYA				
Prorops nasuta	1930	Uganda	already present	Evans 1965
MEXICO				
Cephalonomia stephanoderis	1988	Togo via UK	?	CIBC 1988b
UGANDA (Bwamba county)				
Prorops nasuta	1932	Uganda (Kampala county)	+ ? already present	Hargreaves 1935
PERU				
Prorops nasuta	1962			Clausen 1978
	1964?	Brazil	-	De Ingunza 1964
SRI LANKA				
Prorops nasuta	1938	Uganda	-	Hutson 1939

Leefmans (1924a) drew attention to the fact that the parasite did not thrive in shade, and that it flourished best in black berries which tend to be most abundant after harvest, when the parasite is least needed. The former problem was later solved by appropriate pruning, but despite improvements in management to favour it and the long period spent in breeding and disseminating it, the parasite seems not to have become established in Java (Clausen 1978, Kalshoven 1981).

Cultures of *Heterospilus coffeicola* were taken to Java from Uganda along with those of *P. nasuta* in 1923, but the wasp appears not to have been released. Leefmans (1924a) seems to have concluded that it was likely to be incompatible with *P. nasuta*.

SOUTH AMERICA

BRAZIL

Prorops nasuta was imported into Brazil from Uganda in 1929, and by 1933 it was established in several coffee plantations (Hempel 1933, 1934). As in Java, breeding and distribution continued and in 1937 (Anon. 1937) it was stated to be of considerable value in controlling the coffee berry borer in São Paulo, but only if its numbers were boosted by rearing between coffee production seasons. Puzzi (1939) studied the reproduction of the parasite in relation to that of its host in Brazil and concluded that, in theory it was more prolific, but that the efficiency of the parasite was limited by the tendency of the female to remain in one berry. De Toledo (1942) examined rates of parasitisation, but his figures do not suggest that the wasp could have been having any significant impact. De Toledo et al. (1947) were only mildly enthusiastic about the value of the wasp, mentioning a continuing need for repeated liberations and the requirement for boosting the effect of the parasite by cultural practices. Le Pelley (1968) stated that, at that time, Brazilian entomologists appeared satisfied that *P. nasuta* was of value in their country, but he could find no conclusive evidence that the amount of routine work required for the control of *H. hampei* had decreased. Yokayama et al. (1978), considered that the climate of the São Paulo district in Brazil was unfavourable for this wasp, in which the growers lost interest when BHC was found to give satisfactory control. They reported that it had recently been 'recovered' in coffee plantations in São Paulo.

ECUADOR

Prorops nasuta from Kenya was bred in the UK on coffee berries from Ecuador to free the cultures of possible hyperparasites, diseases and plant pathogens. The wasp was then successfully reared in Ecuador and released. Recoveries have been made from berries in plantations and establishment seems likely (CIBC 1988b). Stocks of West African *P. nasuta* (a different ecological strain) have also been sent to Ecuador (D. Moore pers. comm. 1989). Cultures of *Cephalonomia stephanoderis* have been sent to Ecuador and are thriving there (D. Moore pers. comm. 1989). Liberations were commenced in 1988 (CIBC 1988b).

PERU

According to De Ingunza (1964) *Prorops nasuta* was introduced from Brazil to Peru in 1962, but failed to become established.

Major parasite species

Prorops nasuta

Prorops nasuta is a dark brown bethylid wasp about 2.3 mm in length, with a short, extrusible ovipositor, pale, honey coloured parts in the antennae and legs, forewings faintly tinted brown, hindwings clear and wing veins smoky or blackish-brown. The name *nasuta* refers to the characteristic bilobed 'nose' protruding forwards above the antennal bases. The antennae are shortish and comparatively massive. This wasp parasitises and preys upon several species of *Hypothenemus*. On coffee the fertilised female enters a blackened (thus very over-ripe and diseased) berry, via the borehole of the adult *H. hampei*, choosing berries on the trees rather than those on the ground. If the parent borer beetle is still present she may kill it and use the cadaver to plug the entrance hole, over which she stands guard. According to CIBC (1987) the female wasp does not feed upon borer beetles she may kill, but other authors state that she will do so if no other life history stages are available, but that she cannot mature eggs on a diet of adults alone. Several larvae and pupae may be injured with the ovipositor before any oviposition occurs, and these victims succumb in a few days. The hosts chosen for oviposition are also stung, sometimes several times, and thus paralysed before one, or sometimes two, eggs are laid upon them. Eggs are placed ventrally on larvae and on the abdominal dorsum of pupae. The eggs (0.55 × 0.18 mm) are large for a wasp of this size. They hatch in an average of about three days and the larval stages last three to eight days. The ectoparasitic larva may consume more than one host. The fully grown larva is 1.8 mm in length and 0.65 mm at its widest point. It is devoid of bristles and protuberances, and is blunt anteriorly and tapering posteriorly. There is a prepupal (non-feeding) period of about three days, passed inside a silken cocoon spun by the fully fed larva. It is common to find 20 cocoons in a coffee bean, and up to 62 have been recorded. The pupal stage lasts on an average about 21 days, varying from 9 to 27 days according to temperature.

The life cycle from egg to adult lasts 17 to 33 days (average 29) at 25°C and may be as long as 66 days at 18°C. There are considerable discrepancies between figures given by various authors for the duration of the life history stages, but there is general agreement that the female is quite long-lived—up to 135 days being cited in Brazil, given an abundant supply of larvae and prepupae as food. By contrast it appears that the males do not feed and they do not survive longer than 13 days. Females outnumber the males, a figure of three to one being recorded. Statements as to duration of the preoviposition period give rather diverse figures. Usually a few days are indicated but one record is of 17 days. Parthenogenesis may occur, when only male progeny are produced. Females may lay up to 66 eggs at a rate of one or two a day, utilising several berries in the process.

In feeding, females consume several eggs and unparasitised larvae per day and they will also eat pupae. Normally all stages of the beetle in a berry are killed either by parasitisation, predation or merely by stabbing before the female leaves (Begeman 1926, De Toledo 1942, De Toledo Piza and da Fonseca 1935, Hargreaves 1935, Hutson 1936, Leefmans 1924a, Le Pelley 1968, Puzzi 1939).

Heterospilus coffeicola

Heterospilus coffeicola is a braconid wasp about 2.5 mm long bearing an ovipositor 0.6 mm long. The antennae are filiform and about 2.5 mm long. The body and much of the antennae are very dark brown, and the legs, ovipositor and basal four antennal segments pale brown. In addition to its lacking an ovipositor the male is distinguished by having a small dark area or stigma near the base of the hind wing.

In contrast with the preceding species *H. coffeicola* is free living. It does not enter the borehole of the beetle, but travels from berry to berry inserting its ovipositor into the boreholes in the course of seeking *Hypothenemus* larvae. Only one small egg (0.38 × 0.13 mm) is laid in each berry, and the larva that emerges after about six days feeds on beetle eggs and larvae over a period of 18 to 20 days, consuming 10 to 15 eggs and larvae per day. In this regard it is more of a predator than a parasite. Full-grown larvae (1.80 × 0.63 mm) are translucent white, with sparse minute hairs and paired segmental prominences which distinguish it from the smooth larvae of *Prorops nasuta*. According to De Toledo Piza and Pinto da Fonseca (1935) the larva kills the adult beetle before pupating inside a white silken cocoon. The wasp emerges after a comparatively brief pupal period (De Toledo Piza and Pinto da Fonseca 1935, Hargreaves 1926, Le Pelley 1968).

Hargreaves (1926, 1935) stated that *Heterospilus coffeicola* contributed substantially to the control of *H. hampei* in Uganda. The Brazilian entomologists De Toledo Piza and Pinto da Fonseca (1935) studied the wasp in Uganda with a view to assessing its potential value as a biological control agent in Brazil. They concluded that *H. coffeicola* can thrive only in areas with a continuous production of coffee berries throughout the year, and as such conditions prevail nowhere in Brazil they recommended against its importation. One possible disadvantage of this wasp is that its larvae feed on the larvae of other wasps as well as those of *H. hampei*, and it may even be cannibalistic (Hargreaves 1924). If these statements are verified then there may be reservations about the employment of *H. coffeicola* in biological control. A further difficulty associated with this species as a biological control agent is that a number of workers have been unable to breed it in the laboratory, a problem also experienced by CIBC (1987) during its current program, although Rangi et al. (1988) have reported limited success. The free-living existence of the adults may involve special nutritional or mating requirements that have not yet been met experimentally.

Cephalonomia stephanoderis

Cephalonomia stephanoderis is a small black bethylid wasp. The females, which are 1.6 to 2.0 mm in length, deposit eggs on the ventral surface of larvae and prepupae of *H. hampei.* The larvae feed as ectoparasites, exhausting the tissues of the host in 4 to 6 days, then spinning a silken cocoon in which to pupate. The pupal stage lasts about 15 days. Fertilisation takes place in the berry where the wasps emerge, and seemingly, the males, although fully winged, remain there after the females have left. Autogeny does not occur, and the females must feed for two days at 27°C or 6 to 11 days at 24°C before they can mature eggs. Adult females feed on *H. hampei* eggs, larvae and prepupae and they also chew holes in the membrane of adult beetles, between the prothoracic and mesothoracic tergites and feed on the haemolymph. Females cannot produce eggs on a diet of borer eggs or adults alone, but need to feed first on the larvae and/or prepupae of the borer. Koch (1973), who made a detailed study of this species in the Ivory Coast, found that adult *C. stephanoderis* each required two eggs, two larvae or two adults per diem for survival. Koch found that harvesting procedures deprive *H. hampei* and hence *C. stephanoderis* of food supplies and appropriate conditions for laying. He considered it likely that in the Ivory Coast the pattern of predation/parasitisation of *C. stephanoderis* might well result in greater populations of *H. hampei* being produced, to tide the species over the 'off' season. The parasite, seasonally having greatly reduced previous beetle populations, then suffered a population crash, leaving considerable quantities of endosperm in which new beetle populations could regenerate, but not itself multiplying soon enough to prevent this. This hypothesis requires further study.

Scleroderma cadavericus

Scleroderma cadavericus is listed by Herting and Simmonds (1973) as a natural enemy of *H. hampei*, but only some of the specimens before Benoit (1957) when he prepared the taxonomic description had been reared from that species, others being stated to come from small beetles boring in cane furniture. The North American species of *Scleroderma* are stated by Krombein et al. (1979) to be parasitic on the larvae of small wood-boring beetles, the female wasps frequently stinging people inhabiting infested houses. The African specimens of *S. cadavericus* were submitted to European specialists for identification and description because stinging by females (which may be either winged or apterous) had caused severe dermatitis to African and European people. No responsible person would consider using this insect in biological control projects.

Comments

Hargreaves' (1926, 1935) enthusiastic claims for the great importance of parasites in contributing to the reduction in the pest status of *Hypothenemus hampei* in its native range in Uganda are not supported by the views of Ingram (quoted by Le Pelley 1968, p.125) to the effect that the parasites appear to have little influence on the number of bored berries, whether or not the number of berry borers inside is reduced. Elsewhere in Africa critical opinions have been voiced on the value of parasites in reducing the pest status of the coffee berry borer, for example in Kenya (Abasa 1975), Congo (Sladden 1934, Schmitz and Crisinel 1957) and Ivory Coast (Ticheler 1961). Experience in biological control suggests that these negative assessments of the value of parasites in Africa may reflect the restraining influence of hyperparasites (such as *Aphanogmus* (= *Ceraphron*) *dictynna*), predators, competitors and diseases, but it seems that no such impediments were taken to Brazil with the original stocks of *Prorops nasuta*. Nevertheless, Le Pelley (1968) stated that there was no evidence that 35 years after the introduction Brazilian coffee growers had to invest less effort in other control measures and Yokayama et al. (1978), 45 years after its introduction, gave a depressing picture of its impact.

Greater success may attend the employment of *Cephalonomia stephanoderis,* which may thrive better in an exotic environment than in Africa.

Heterospilus coffeicola requires careful study to assess whether the predation by its larvae on the brood of *P. nasuta,* as well as that of *H. hampei,* really matters, considering the allegedly dubious value of the former species. It is encouraging that CIBC (1988a) is making a thorough study of the interactions of the parasites and other components of the environment in Kenya. Recommendations for such an approach were made half a century ago in a thoughtful paper by Mendes (1938), but his views have been lost sight of during the long hiatus that followed in the study of the biological control of *Hypothenemus hampei.* Optimism has recently been expressed by Moore and Prior (1988) for an integrated control program involving parasites, perhaps with augmentative release, entomopathogenic nematodes for suppression of borer populations in fallen berries and applications of *Beauveria bassiana* as a mycopesticide to the aerial parts of the plants.

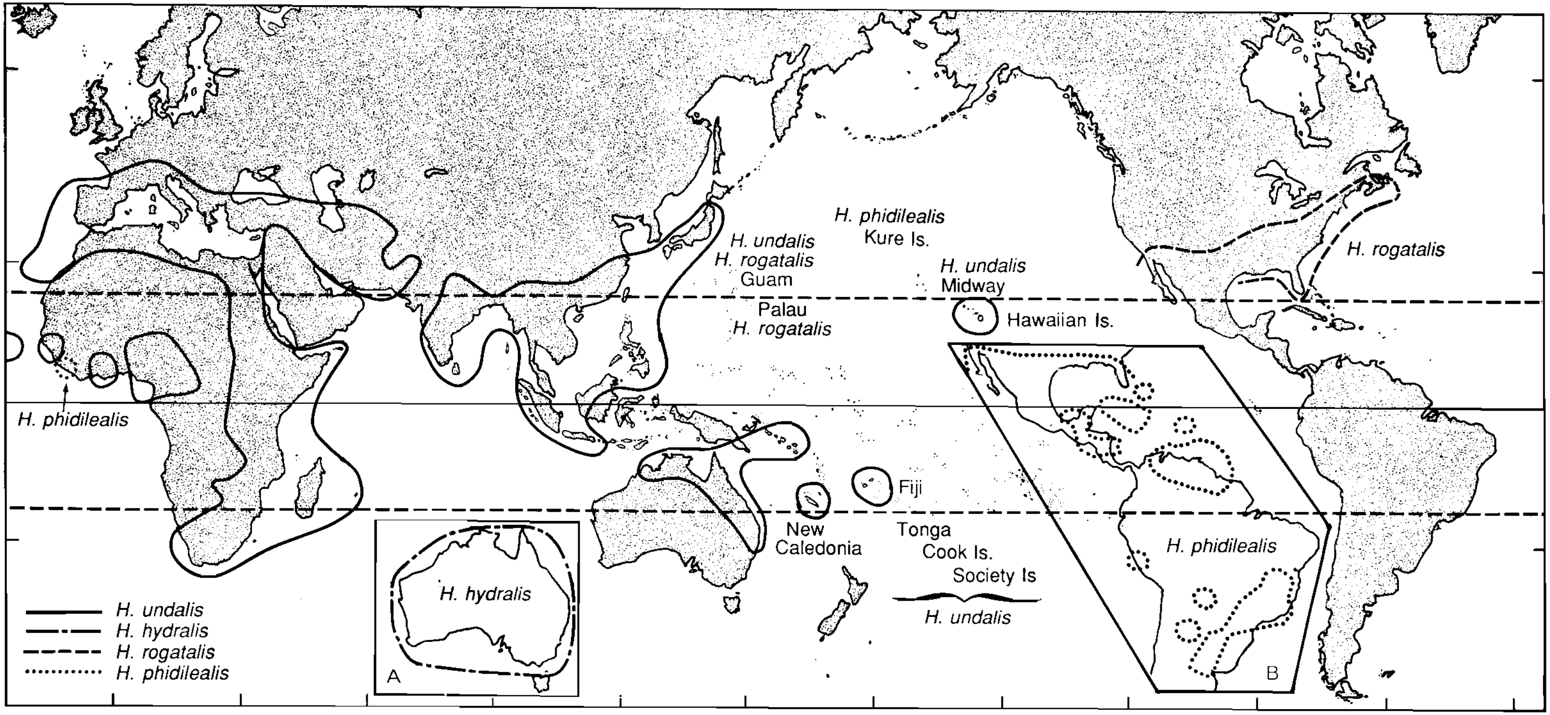
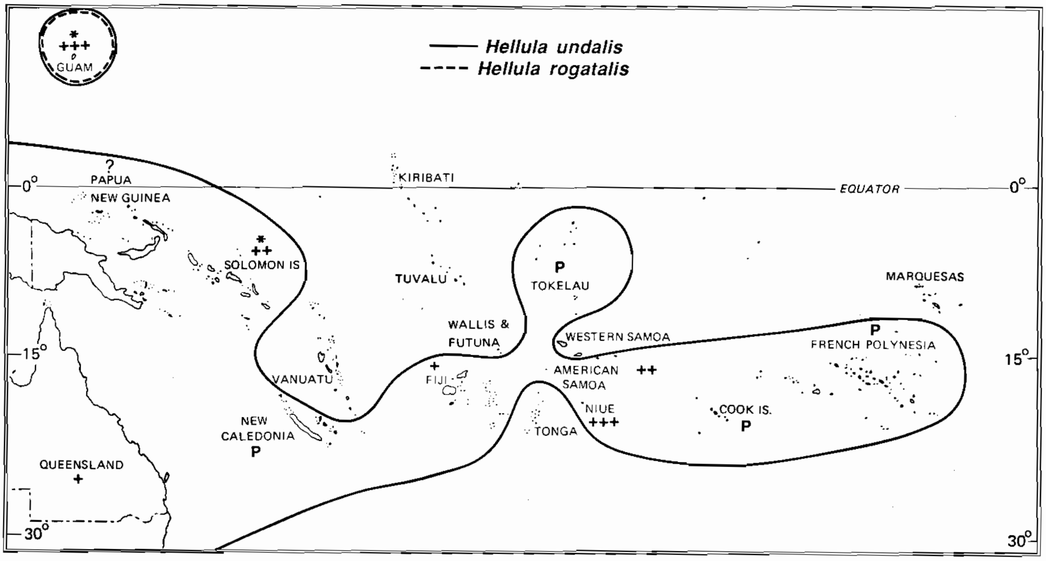


Fig. 7.1. World distribution of *Hellula* species of economic importance. The African, Asian and European limits of *H. undalis* are largely after Anon. (1981). Inset A: *H. hydralis*. The extension of *H. rogatalis* into Central America seems probable. Inset B. *H. phidilealis*. The northern boundary across southern USA seems probable from the records of Munroe (1972). South and Central American records, based on Anon. (1964) reflect political divisions, with lack of records from many countries contributing heavily to a very disjunct distribution. It seems likely that this species is much more generally distributed in these regions.

7

Hellula species

LEPIDOPTERA: PYRALIDAE
cabbage centre grubs



Hellula undalis is native to Europe, Africa and much of Asia. *H. hydralis* is confined to Australia. *H. rogatalis* is North American and *H. phidilealis* occurs in South America and northwards to southern U.S.A.

The array of parasites attacking the four pest species of *Hellula* is not impressive. None of the arthropod parasites is specific even to members of the genus. However, those listed for *H. undalis* in Egypt, although not specific, may yet repay further study since they appear to be quite abundant in some seasons, and might be more effective if freed of their own parasites. Refinement of knowledge of the original homeland of *H. undalis* may lead to a more effective search for natural enemies.

Four species of the genus *Hellula* figure in the literature of economic entomology: *H. undalis, H. hydralis, H. rogatalis* and *H. phidilealis*. All are of actual or potential concern in the Pacific. These four species may well be very similar in their biology, and some of the apparent differences in the descriptions that follow may result from differing emphases by the various authors.

The generic name *Oeobia* Hübner (sometimes misspelled *Oebia)* has been applied to these insects from time to time, but this was suppressed by the International Commission of Zoological Nomenclature in 1959 and should no longer be used.

Hellula undalis (Fabricius)

cabbage-centre grub (Australia); imported cabbage webworm (Hawaii); centre grub (Fiji); cabbage webworm, turnip webworm

Origin

The specimen described by Fabricius in 1794 came from Italy.

Distribution

Mediterranean littorale, Middle East, southern USSR, eastern half of Africa and a number of places in West Africa, Canary Is, Cape Verde Is, Malagasy Archipelago, Iran, Iraq, Pakistan, Asia generally, including Japan, Philippines and western Indonesia, Papua New Guinea, north and northeastern Australia, Cook Is, Fiji, Hawaii, Midway Is, Marianas [including Guam (Thompson 1914)], New Caledonia (Anon. 1981b). The Solomon Is are also infested (Macfarlane 1982). Suehiro (1960) records *H. undalis* from Midway Atoll. The record from Papua New Guinea is a very old one based on three specimens from Port Moresby (Meyrick 1889). It has not been recorded since then (F.M. Dori pers. comm. 1989), there are no specimens from Papua New Guinea in either the British Museum or the Australian National Insect Collection, and the record must therefore be regarded as very doubtful.

Anon. (1981b) is in error in relation to the Australian distribution of *H. undalis,* seemingly having confused this moth with the widespread native species, *H. hydralis*. In eastern Australia no specimens of *H. undalis* are known from further south than Singleton, N.S.W. (32°34'S) and in Western Australia it is known only from the Kimberleys, in the extreme north. The occupation of the entire North and South Islands of New Zealand by *H. undalis,* shown in the same map is also wrong, since P. Maddison (pers. comm. 1988) states that the only New Zealand specimens of *Hellula* are vagrant *H. hydralis* from Australia. A specimen of *H. undalis* has been taken on Norfolk Island (Holloway 1977). This was considered as probably a vagrant, but climatic conditions on the island would seem to offer no bar to colonisation. Swaine (1971) records *Hellula rogatalis* from Fiji, but almost certainly he is referring to *H. undalis*.

Hellula undalis is not known from North and South America or the West Indies.

Hellula undalis is considerably more widespread than any other species in the group, and, in consequence, has a rather more extensive treatment in the literature.

Life cycle

The egg is ovoid, and flattened where attached to the plant. It is about 0.47 mm in length. Pearly white when laid, it becomes pinkish over the next day, and, just before hatching, brownish-red, with the dark head of the larva visible at one end (Harakly 1968a). The eggs are deposited singly, or in groups or 'chains' on the leaves of cabbage. In Hawaii (Awai 1958) eggs hatched in 2 to 3 days at mean temperatures of 28°C. Rawat et al. (1968) state that in India they hatch in 3 to 4 days and Bhalani (1984) in 2 to 9 days at 29°C. Assem and Nasr (1968) state that in Egypt development takes 3 to 4 days but Harakly (1968b) indicates

1 to 6 days in summer and up to 13.6 days in winter. An incubation period of 1 day is to be doubted.

The most complete and best controlled laboratory studies of the larval stages are those carried out by Awai (1958) in Hawaii. Newly hatched larvae are 1.0 mm in length and at the end of the first instar the larvae measure 2 to 3 mm. The head capsule is blackish-brown, with a pale suture extending down from the vertex and forking out around the mouthparts. The thoracic shield is prominent, shiny and purplish-grey; and there is also a spotted anal shield. The larval cuticle is initially whitish-yellow, soon turning to greyish-yellow and exhibiting five broad, irregular brownish-purple bands on the dorsum extending from the second thoracic to the terminal abdominal segment. There are also two weak and broken ventro-lateral lines and a very weak mid-ventral line. Striping such as this is similar in the other three species being considered. Instars 2 to 4 are generally similar to the first instar, but grow to 5.2, 8.5 and 11.0 mm respectively, with the head capsules 0.33, 0.53 and 0.74 mm in width. The fifth (usually final) instar has the thoracic shield somewhat dull and greyish-yellow, instead of shiny purplish-grey, but is otherwise similar to the preceding instars. It grows to 14.0 mm in length with a head capsule width of 1.15 mm. At a mean laboratory temperature of 28°C the duration of the instars is 2.1, 2.2, 1.8, 2.1 and 4.3 days respectively (total 12.5). The optimal temperature for the larvae, as judged by percentage survival, was about 31°C. At lower temperatures (20 to 25.5°C) a small percentage of larvae moulted into a sixth instar, following an abbreviated fifth instar. The fifth instar was the most critically affected by temperature, none surviving at 43°C and less than half at 23°C. Harakly (1968b) and Youssef et al. (1973) give the number of instars in Egypt as five. Rawat et al. (1968) state that there are four, rarely five instars in India. Eggs laid by adults resulting from larvae exposed to temperatures lower than 20°C or higher than 46.7°C did not hatch (Awai 1958). Newly hatched larvae suffer considerable mortality while seeking to become established in leaf tissue. Free water is inimical [although heavy rain does not affect established populations (Talekar and Lee 1985)], and inanition also claims many hatchlings before they enter the leaf tissue. After penetration into plant tissues the larvae may either mine the leaf lamina, midribs and stems or graze on the leaf surface under a protective silken web. Larvae tend to continue to feed in later instars in the same manner as they chanced to do in the first. They often feed on terminal buds, causing distortion and stunting, and in the case of seedlings, death. Older larvae bore into the compact heads of cabbages and cauliflowers. Larvae tend to feed solitarily, and cannibalism may occur if first instar larvae are crowded and presumably it occurs also in later instars under similar circumstances.

Species of host plant may affect duration of the larval stage. On cabbage, for example it was 16 to 19 days at a time when it was 11 to 13 days on cauliflower (Youssef et al. 1973).

Cocoon spinning and pupation occurs in the feeding tunnels, among leaves rolled or spun together with silk, but more usually in a cocoon spun in an earthen cell just below the soil surface. The tenth abdominal segment of the pupa bears a cremaster comprising four hooklike spines which anchors the pupa securely in its silken cocoon (Youssef and Hammad 1977). At 26.3°C the pupal stage lasts 6 to 8 days. Youssef et al. (1973) reported that the duration of the pupal stage was also influenced by larval food, cabbage-fed larvae, for example, yielding pupae that took a mean of 8.4 days to disclose adults, when pupae from cauliflower-fed larvae were taking 7.6 days and radish-fed larvae 10 days. In Egypt El-Sherif et al. (1976) showed that larval food plant had a significant effect on reproductive processes in the adult, cabbage, cauliflower, radish and garden rocket being a series in descending order of suitability. In Japan Tanaka and Tanimoto (1979) found that at 20°C the egg, larval and pupal stages averaged 5, 21 and 13 days respectively. A mass rearing method was described by Yamada and Koshihara (1981) and a synthetic diet by Jayanth and Nagarkatti (1981).

The moths are nocturnal. Females mate once only, but males may do so a number of times. A female sex pheromone of this species was chemically identified by Arai et al. (1982). Oviposition may commence within 24 hours of mating and may last from one to three days. The eggs are laid rather randomly on the plant. In Egypt the maximum number of eggs laid by females raised on cabbage may range from 40 (January) to 281 (September) (Harakly 1968b). Assem and Nasr (1968) state that in Egypt the females lay from 50 to 120 eggs. Females die soon after laying, but in culture they live longer if provided with sugar solution or flowers. In Japan Tanaka and Tanimoto (1979) found that females lived for 7 to 9 days and laid a mean of 150 eggs. The seasonal history on cabbage in central Japan was described by Yamada (1981). Watanabe (1927) and Ishii (1938) state that in Japan *H. undalis* hibernates as larvae and pupae, but in Egypt Harakly (1968b) states that there is no true hibernation, merely a prolongation of developmental period. This reflects the climatic differences between these two parts of the geographic range. Holdaway (1944) in Hawaii and Sachan and Gangwar (1980) in India found that increase in altitude at which a crop was planted resulted in a decrease in the importance of *H. undalis* as a pest. This, of course, reflects an effect of temperature.

The adult moths have a wingspan of 12 to 16 mm. They are greyish brown, the forewings having wavy grey markings and a curved subterminal pale patch. The kidney-shaped spot at one third length from apex is much less sharply marked than in the American species *H. rogatalis* and *H. phidilealis.* The hindwing is pale, with light brown suffusion apically.

Pest status

H. undalis attacks principally Brassicaceae, but also Amaranthaceae and eggplant (Solanaceae) (Singh and Verma 1976, Fletcher 1921). In Hawaii Holdaway (1944) listed this moth as a major pest of all Brassicaceae. Losses are serious at the seedling stage but boring by advanced larvae ruins cabbage and cauliflower heads. Radish and turnip also suffer severe damage. In India *H. undalis* attacks cabbage and cauliflower during summer in Punjab and it is a pest of a range of Brassicaceae in southern India (Sandhu and Bhalla 1973).

In Turkey *H. undalis* is a serious pest of sugarbeet (Sevket 1934). Secondary rotting of damaged plants may complete the destruction of a crop. In Iraq Al-Janabi et al. (1983) found that damage to kohlrabi inflicted by *H. undalis* initiated rots which attracted adults of the fly *Atherigona orientalis* bearing the bacterium *Erwinia carotovora,* which infects the plants and causes 'soft rot'.

Control measures

Chemical control is complicated by the presence of a complex of other pests (especially on Brassicaceae), by the difficulty of penetrating the webbing produced by the larvae and by problems of pesticide residues on sprayed plants. Earlier literature revolved largely around the use of arsenicals and insecticides of vegetable origin. Carbaryl and quinalphos are highly effective (Rao et al. 1979). In Taiwan profenfos, EPN (a phosphonothionate) and triazophos at weekly intervals gave better control than the standard parathion treatment (Anon. 1985). In Western Samoa Hollingsworth et al. (1984) found that acephate, permethrin and trichlorphon at 8 to 10 day intervals gave excellent control of *Hellula* sp. (probably *H. undalis*).

In Egypt Harakly (1969) found in laboratory and field tests that *Bacillus thuringiensis* was less effective than a DDT-lindane mixture against third instar larvae and also less persistent. *B. thuringiensis* was ineffective against *H. undalis* in Singapore compared with diazinon, mevinphos or methomyl (Chang and Pegn 1971). Tanada (1956a) found that very heavy dosages of *B. thuringiensis* were required to make any impact on *H. undalis* in the field in Hawaii, although Prasertphon (1975) observed in laboratory tests in Thailand that larvae of '*H. rogatalis*' (probably *H. undalis*) were highly susceptible. Tanada attributed his poor success to the presence of resistant individuals but presumably field populations are difficult to infect because of their burrowing in the plant tissues.

The value of manipulating planting dates of cabbage was studied in Mauritania (Anon. 1982). In view of the generally marked severity of autumn damage to seedlings there may be profit in this approach. Varietal resistance in Chinese cabbage is being investigated in

Taiwan (Anon. 1985), but there is little other literature on this approach, or on the use of cultural control methods.

Associated pests

Common associates of *H. undalis* on cabbage are: Hemiptera: *Brevicoryne brassicae, Lipaphis erysimi, Myzus persicae;* Lepidoptera: *Agrotis* spp., *Helicoverpa* (= *Heliothis*) spp., *Crocidolomia pavonana, Pieris rapae, Plutella xylostella* and many others of lesser importance. Biological control measures against *H. undalis* would face a heavy challenge from chemical control.

Hellula hydralis Guenée

cabbage-centre grub (Australia)

Origin

Guenée's type locality is Australia.

Distribution

The species is widespread in mainland Australia, extending into the Bass Strait islands (Hardy et al. 1980). Holloway (1977) recorded a number of specimens from Norfolk Is. but they may have been non-breeding vagrants. Vagrant specimens have also been collected in New Zealand (P. Maddison pers. comm. 1988). The range of latitudes over which this species extends in Australia suggests that it could become widespread elsewhere.

Life cycle

This has not been studied in detail in Australia, where the species has often been confused with *H. undalis*. Holloway (1977) describes it as the 'Australian duplex of *H. undalis*', inferring close anatomical resemblance in the adults, so presumably the biological details are rather similar. Anon. (1970) gives meagre details generally confirming this, except that 'it pupates on the plant'. Adults may be distinguished from those of *H. undalis* by their having a straight, instead of a curved, subterminal pale band on the forewing.

Pest status

This insect's pest status is unclear, partly due to confusion with *H. undalis,* but any literature referring to infestations with *Hellula* spp. in Bass Strait islands, Victoria, South Australia and the southwest of Western Australia will certainly refer to this species, since *H. undalis* has not been recorded there. *H. hydralis* attacks Brassicaceae and Amaranthaceae, being very abundant throughout the Nullarbor Plain, where the former group is scarce, but Amaranthaceae well represented (E.D. Edwards pers. comm. 1987).

It is a sporadic minor pest of turnips in Victoria, causing little damage to other brassicaceous crops.

Control measures

Kessell (1972) described experiments in southwestern Australia with insecticides on flowering rape to obtain information on dangers to honeybees. Recommendations were drawn up for the use of carbaryl, DDT, methidathion, demeton-S-methyl and trichlorphon to reduce risks, yet bring about the control of pests of Brassicaceae. One of these, given as *Hellula* sp., was almost certainly *H. hydralis.*

Associated pests

As for *H. undalis.*

Hellula rogatalis Hulst

cabbage webworm (USA)

Origin

The type locality is Texas, USA.

Taxonomic notes

This species was referred to in early North American literature as *H. undalis,* but Capps (1953) indicated that the species were quite distinct, *H. rogatalis* then being confined to North America, whereas *H. undalis* did not occur in the New World at all (see also Anon. 1981b). Thus it has been assumed herein that all literature referring to '*H. undalis*' in North America in fact refers to *H. rogatalis.*

Apart from three species, so uncommon that their host plants were unknown in 1972 (Munroe 1972), the only other species of the genus which economic entomologists are likely to encounter in the USA is *H. philidealis* (Walker), which occurs along the southern fringe of the USA, but, according to Munroe the adults of the two species are 'abundantly distinct', and Capps (1963) indicates that the colour of the head capsule readily distinguishes the larvae. Thus it is clear that all references to *H. rogatalis* in America north of Mexico are likely to be correct, and also that all references to *H. undalis* in North America also refer to *H. rogatalis.*

Distribution

The distribution of *H. rogatalis* is given by Munroe (1972) as 'from North Carolina to Florida and westward through Texas to southern California. It ranges north at least to Kentucky and Arkansas, and Nova Scotia.' Presumably it occurs also in central America, outside of the region to which Munroe restricted his study. It is now also recorded from the Marianas, including Guam, and possibly occurs in Palau (R. Muniappan pers. comm. 1987).

Hinckley (1963) records the species from Fiji and Prasertphon (1975) from Thailand, but both records probably refer to *H. undalis.*

Life cycle

Chittenden and Marsh (1912) described the life history stages. When laid, the light grey egg is ovoid, about 0.5 mm in length and flattened on the surface attached to the plant. It becomes pinkish the day after laying and on the following day the dark head of the developing larva can be seen at one end. At 28°C hatching occurs three days after laying. The slender first instar larva has a dark head and thoracic plate. As in *H. undalis* the body is pale yellowish grey with five well-marked brownish-purple dorsal and dorso-lateral bands. There is a sparse coating of long fine hairs. Other instars are similarly coloured and striped. The fully grown larva is about 15 mm in length, tapering at both ends. The head is uniformly black or dark brown except for a white adfrontal suture extending down from the vertex and forking down around the mouthparts. Both the head capsule and the thoracic shield are shiny. The latter is purplish-grey, with brown markings. The anal shield bears 10 to 12 round purplish spots, the central posterior one larger, and standing alone, with the remainder arranged in a crescentic pattern in front of it. The striping of the fully fed larva is well marked: the five purplish bands referred to in the first instar larva are all prominent, the two lower sublateral bands weak and interrupted on each side, and a mid-ventral stripe very weak (Allyson 1981, Chittenden and Marsh 1912). There appears to be no record of the number of larval instars in this species, nor of the duration of the larval stage. (The abundant data of Chittenden and Marsh (1912) on the duration of life history stages in Hawaii refer, of course, to *H. undalis.*)

The larvae spin webbing on their food plants, sometimes binding leaves together or rolling a leaf edge in the process. Young larvae burrow into tissues or may mine leaves, or else issue periodically from their shelters to consume leaf tissue. Older larvae bore deep into midribs and firm tissues such as cabbage hearts. Cannibalism may occur if smaller larvae venture into the shelters of advanced ones.

Pupation may occur in a cavity on the plant resulting from the feeding of the larvae, in a leaf roll, or more usually underground, the larva encasing itself in a cocoon. The obtect pupa is light yellowish-brown in colour, with a whitish bloom. The eyes are dark and there is a mid-dorsal stripe.

The adults of *H. rogatalis* are grey and have a wingspan of 18 to 21 mm. The forewings have a kidney-shaped spot about one third of their length from the apex and elsewhere are marked with brown, ashen and black, with irregular white lines running from front to rear and a sub-terminal white band. The adults are strong fliers. They mate soon after emergence. Chittenden and Marsh (1912) state that the females lay 300 to 350 eggs over several days, but comparison with other species suggests the average may be much lower.

The data on seasonal incidence are meagre, investigations on brassicaceous insects usually embracing other lepidopterous pests whose study receives greater emphasis. *H. rogatalis* is an important autumn pest in Virginia (Latheef and Irwin 1979). It does not survive the winter in North Carolina, but repopulates the area in the summer or early autumn (Brett and Sullivan 1974). In South Carolina this species is most abundant from mid-July to early September, surviving in small numbers until early November (Reid and Bare 1952). In studies in northeast Florida the larvae occurred on cabbage from late April to June in 1974, reaching a peak of abundance in May, but in the same plots in 1975 numbers were consistently low (Ru and Workman 1979). Latheef and Irwin (1983) rightly state that 'Much needs to be known about its biology, ecology and its role as a cole crop insect in the United States'.

Pest status

Food plants of this moth are chiefly Brassicaceae, including all cultivated varieties and such common weeds as *Capsella bursa-pastoris*. It also attacks Amaranthaceae and Chenopodiaceae, including beet and spinach, and some Portulacaceae including the weed *Portulaca oleracea*. Cabbage, cauliflower, turnip and radish are prominent among the records of damage. Seedlings are particularly vulnerable, the boring of the larvae in the stem of young cabbage and turnip often resulting in wilting and death. Reports include the destruction of entire crops, for example over a hundred hectares of turnips in Mississippi (Anon. 1930), and a plot of 500 cabbage plants in Virginia (Latheef and Irwin 1983). Damage to more advanced plants by large larvae may also be severe, the heart then being riddled, but at this stage it is likely that losses due to *H. rogatalis* tend to be additive to those due to other pests, such as the diamondback cabbage moth *Plutella xylostella* and the cabbage white butterfly *Pieris rapae*. Although the mechanical damage inflicted by larval feeding may be sufficient to make brassicaceous crops unacceptable for market, rots caused by microorganisms invading damaged and fouled areas hasten the ruin and make them unacceptable for any purpose.

Control measures

Early literature stressed the importance of cultural practices, such as ploughing to destroy pupae, and the elimination of crop residues to deny the insect breeding sites. The chemicals available then for moth control were few and their application hampered by the webbing spun by the larvae. Emphasis was on the importance of treatment at the critical seedling stage, in which the pest is more vulnerable. More recent literature seems largely to omit specific mention of cultural approaches to the control of *H. rogatalis*. However Brett and Sullivan (1974) advocated crop residue destruction and the establishment of new plantings in areas as remote as possible from earlier ones to assist in the control of *Pieris rapae* and *Plutella xylostella*, and these measures could possibly have some effect also on the abundance of *H. rogatalis*.

Blanket spraying with permethrin preparations (Waites et al. 1978) may result in adequate control of *H. rogatalis* on advanced plants where, however, this moth appears to be of relatively less importance than on seedlings. More recent tests with chemicals for the control of *H. undalis* in other countries may give a useful guide to the control of *H. rogatalis*.

Brett and Sullivan (1974) demonstrated that some varieties of radish were markedly more resistant than others to *H. rogatalis*. The variety Cherry Belle was resistant to both diamondback cabbage moth and *H. rogatalis*, but comparatively susceptible to the striped flea beetle, *Phyllotreta striolata*. Reconciling such discordant findings poses serious problems in employing resistant varieties, although Cherry Belle might well be a valuable variety where the striped flea beetle does not occur.

The use of *Bacillus thuringiensis* (as 'Dipel') was less effective than spraying with permethrin formulations (Waites et al. 1978).

Companionate planting with six species of herbs (marigold, nasturtium, pennyroyal, peppermint, sage and thyme) had no worthwhile effect against the common Lepidoptera of cabbage, including *H. rogatalis* (Latheef and Irwin 1979). If anything, there was a suggestion that some of the companionate plants used may have been attractive to *P. rapae*, resulting in a greater threat to the cabbages than if they had been in monoculture.

Associated pests

Literature on the control of *H. rogatalis* reflects strongly the fact that it is only one member of an extensive complex of insects attacking Brassicaceae. In the USA these include: Hemiptera: *Brevicoryne brassicae* and *Murgantia histrionica;* Coleoptera: *Epilachna varivestis* and *Phyllotreta striolata;* Diptera: *Delia radicum* (= *Hylemya brassicae*); Lepidoptera: *Agrotis* spp., *Trichoplusia ni*, *Pieris rapae* and *Plutella xylostella.* If the moth assumes pest status in other areas, some of these species may be lacking in the fauna.

***Hellula phidilealis* (Walker)**

cabbage budworm (Trinidad, Barbados); mustard stem-borer (Virgin Is)

Origin

Walker's material came from Venezuela.

Distribution

This is given (Anon. 1964) as USA, Mexico, El Salvador, Guatemala, Nicaragua, West Indies, Argentina, Brazil, British Guiana, Paraguay, Peru, Surinam, Venezuela and Sierra Leone. The Sierra Leone record (Hall 1955) was stated to indicate a probable recent establishment. Butler and Usinger (1963) record specimens from Kure Is, in the Midway group, where it seems likely to have been introduced also. The distribution within the United States is given as Florida (south of about latitude 29°N), Texas, Arizona (Munroe 1972), New Mexico and California (Anon. 1964).

Life cycle

Eggs are laid singly or in clusters on the leaves near the main bud of the plant (Razuri and Hinostroza 1974). They are 0.5 mm long, ovoid and translucent and have a longitudinal ridge. Fertilized eggs turn brown soon after deposition. At a mean temperature of 26.5°C they hatch after 3 days. The larvae then feed for a few hours on the tender parts of the leaves and next enter the main stem usually at the junction with the leafstalks (Monte 1944). Later stages may bore in leaf veins, stems and the hearts of cabbages. There are five or six instars, which at 25.6°C occupy respectively mean periods of 14 and 16.3 days (Cadogan 1983). In Peru Razuri and Hinostroza (1974) found that in cultures at 27°C the first two generations went through five or six instars but in the third and fourth generations there were only five instars. No detailed descriptions of the larvae are available, but according to Allyson (1981) they are striped similarly to that of *H. rogatalis*. A clear difference between the two species is shown in the head capsule, which is paler and mottled rather than uniformly brown or black as in *H. rogatalis,* and has the adfrontal suture pale, but not white. The larvae are leaf-webbers, like those of *H. rogatalis* (Allyson 1981). A non-feeding prepupal stage, lasting two days, follows the larval stage, and during this period a translucent silken cocoon is spun in a cell just below the soil surface. Pupation then occurs, and at 26.5°C the moth emerges 7.3 days later (van Dinther 1956, Monte 1944, Razuri and Hinostroza 1974).

The adult moth differs from that of *H. rogatalis* in having a very strongly curved termen (apical edge) to the forewing. It is paler than *H. rogatalis,* with whitish, rather than yellowish or buff ground colour on the forewings, which also lack the dark median band across the forewing, that is present in *H. rogatalis,* just bodywards of the dark kidney-shaped spot that is at two-thirds the wing length in both species. There is a preoviposition period of 3 days, eggs are laid over 4 to 5 days and the females may live about 4 days after that (Cadogan 1983). The mean number of eggs produced is 64, laid usually in about 4 batches. Adults in culture will consume honey, and they doubtless feed on nectar in the wild state.

There are no data on seasonal incidence and behaviour etc. in the field.

Pest status

The pest status is broadly similar to that of *H. rogatalis*. Brassicaceae and Amaranthaceae are the only hosts quoted (Allyson 1981), and attack on young plants is important (Cadogan 1983; van Dinther 1956; Pastrana 1946; Razuri and Hinostroza 1974). Cadogan (1983) comments that the damage caused by larval feeding on the shoot apex of cabbage and cauliflower seedlings in Barbados induces lateral growth and multiple false heads. Fungal attack usually follows damage (Monte 1944).

Control measures

Monte (1944) advised the removal and destruction of infested plants and cultivating to destroy pupae. The use of arsenicals and cubé was recommended in early papers. In Trinidad Parasram (1969) found that weekly applications of trichlorphon, fenitrothion, methyl-parathion and a mixture of this with toxaphene gave 70% more insect-free heads of cabbage. Such a regimen of sprayings seems likely to leave residues dangerous to humans, and more acceptable treatments may perhaps be found in the literature on *H. undalis.*

Associated pests

The cosmopolitan pests of Brassicaceae mentioned under *H. rogatalis* would also be associated with *H. phidilealis* throughout most of its range. The beetle *Epilachna varivestis* does not occur south of Mexico, but there are additional Lepidoptera attacking cabbage. In Surinam, for example, cabbage may be infested also by the Lepidoptera *Spodoptera* (= *Laphygma*) *frugiperda, Symphysa amoenalis* and *Ascia monuste monuste.*

Natural enemies of *Hellula* spp.

Records of natural enemies identified at least to genus are presented in Table 7.1. In addition unidentified braconids are reported from Egypt (Youssef et al. 1973) and the Sudan (Johnston 1930), an unidentified ichneumonid from Egypt (Youssef et al. 1973) a possible braconid from Cyrenaica (Turati and Zanon 1922) and 'parasites' from South Africa (Brain 1928). Jack (1914) reported that in Zimbabwe *H. undalis* was 'little attacked by parasites', which may suggest that some were there in low numbers. Although the tachinid fly *Nemorilla pyste* was repeatedly reared from *H. rogatalis* in autumn, none of the North American insects attacking *H. rogatalis* appears to be specific. Latheef and Irwin (1983), in their studies in Virginia, reared no parasites from *H. rogatalis,* and Ru and Workman (1979)

Table 7.1 Natural enemies of *Hellula* spp. (except those identified only to family level).

Pest species and natural enemies	Country in which attack recorded	Reference
H. undalis		
HYMENOPTERA		
Ichneumonidae		
Casinaria (= *Charops*) *infesta*	Hawaii	Awai 1958
Diadegma (= *Nythobia*) sp.	Egypt	Harakly 1968b
Diadegma sp.	Hawaii	Awai 1958
Pristomerus hawaiiensis	Hawaii	Awai 1958
Trathala (= *Zaleptopygus*) *flavoorbitalis*	Hawaii	Awai 1958
Venturia (= *Idecthis*) sp.	Hawaii	Awai 1958
Braconidae		
Agathis (= *Bassus*) sp.	Egypt	Youssef et al. 1973
Apanteles sp.	Egypt	Harakly 1968b
Apanteles sp.	Egypt	Youssef et al. 1973
Bracon (= *Habrobracon*) *hebetor*	Egypt	Harakly 1968b
Chelonus blackburni	India	Rawat et al. 1968
	Hawaii	Zimmerman 1958a
Trichogrammatidae		
Trichogramma minutum	ex USA	Veitch 1928
MICROSPORIDA		
Perezia or *Glugea*	Hawaii	Awai 1958
H. hydralis Nil		
H. rogatalis		
HYMENOPTERA		
Ichneumonidae		
Campoletis (= *Limnerium*) *tibiator*	USA	Chittenden and Marsh 1912
Diadegma insulare	West Indies, USA, Mexico south to Venezuela, Hawaii	Krombein et al. 1979
Rubicundiella annulicornis	USA	Krombein et al. 1979
Temelucha facilis (= *T. macer*)	USA	Krombein et al 1979
Braconidae		
Apanteles choreuti	USA	Krombein et al. 1979
Meteorus leviventris (= *M. vulgaris*)	Holarctic, Neotropical	Krombein et al. 1979
DIPTERA		
Tachinidae		
Nemorilla (= *Exorista*) *pyste*	USA	Chittenden and Marsh 1912
Stomatomyia (= *Plagioprospherysa*) sp.	USA	Chittenden and Marsh 1912
ACARI		
Acaridae		
'*Tyroglyphus americanus* Banks'	USA	Chittenden and Marsh 1912
H. phidilealis		
HYMENOPTERA		
Braconidae		
Bracon (= *Microbracon*) *hellulae*	Brazil	da Costa Lima 1938, Monte 1944

also failed to rear any parasites from 513 larvae of this species collected in the field. Chemical control measures may contribute to this situation, so that any search for natural enemies should take non-crop situations into consideration. The host range of *Bracon hellulae,* described from *H. phidilealis* in Brazil, is unknown. In view of the fact that Monte (1944) claimed that *B. hellulae* afforded some control of *H. phidilealis* in Rio de Janeiro, this species should be studied; but Yaseen (1978), who doubtless knew of the species, indicated that no suitable biological control agent could be recommended for use against this moth in Trinidad.

The natural enemies reared from *H. undalis* in Egypt remain to be assessed. Their presence in abundance there from August to October obviously does not prevent *H. undalis* from becoming an economic problem, and they may propagate principally on species other than *H. undalis.* However, several of them, if shown to be adequately specific, might produce a greater impact in other countries if freed of their own natural enemies. The cosmopolitan *Bracon hebetor* may be discounted. It is chiefly a parasite of stored product Lepidoptera, but it is known to attack phytophagous species in culture. None of the ichneumonoid Hymenoptera recorded from *H. undalis* in Hawaii is specific, and *Trichogramma minutum* is a cosmopolitan parasite of lepidopterous eggs. For purposes of biological control it would have to be employed on an inundative basis, making it unsuitable for use in many communities.

Awai (1958) observed a pathogenic rod-shaped bacterium attacking *H. undalis* larvae in Hawaii. Chittenden and Marsh (1912) mentioned a 'wilt' disease in caged *H. undalis* larvae in Hawaii, but the pathogen concerned was not identified. Tanada (1956b) reported the occurrence of a microsporidan infection of *H. undalis* larvae in the field in Hawaii, and so did Awai (1958), who stated that it belonged either in the genus *Perezia* or *Glugea*. R. Muniappan (pers. comm. 1988) states that no natural enemies of *H. undalis* are known from Guam.

Attempts at biological control

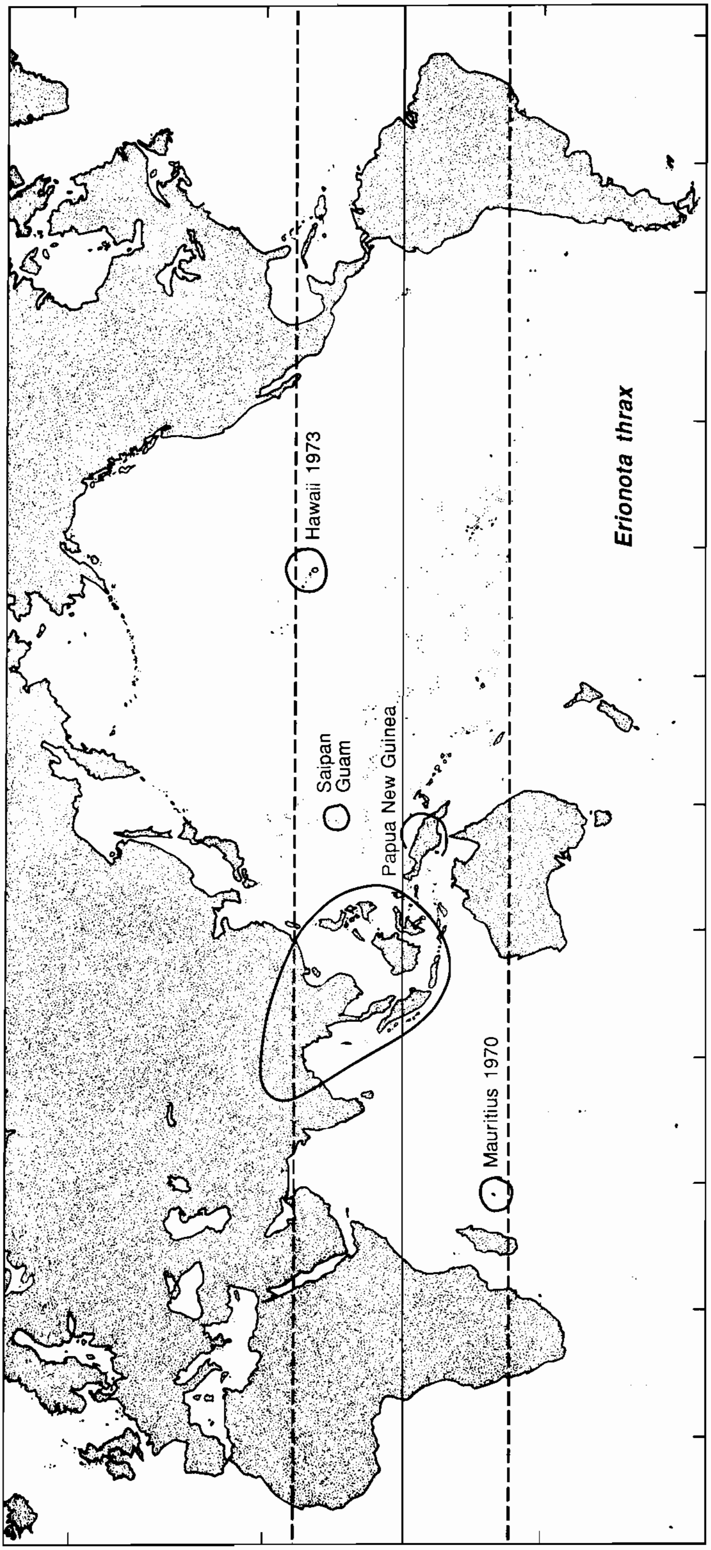
There have been none.

Comments

The prospects for bringing about the biological control of any *Hellula* species do not seem very bright, but the subject has not been properly studied. In this respect it is surprising that *H. undalis* is now either absent from, or very rare in, Papua New Guinea, since it was recorded there a hundred years ago, although not since. This situation merits further study. The potential of Egyptian and North and South American natural enemies should be investigated, studying particularly non-crop situations.

There are few reports of damage from the European littorale of the Mediterranean. Climatic effects may be partly responsible for this, but the situation may repay study. Pemberton and Williams (1938) quoted Fletcher (1921) as stating that *H. undalis* is a pest of only minor importance in India, Burma and Sri Lanka, arguing from this that these countries would offer greatest promise of yielding effective natural enemies. However there are sufficient reports of *H. undalis* attaining high pest status in Southeast Asian countries since those days to raise doubts as to the validity of Fletcher's statement, and on the other hand there are singularly few reports of natural enemies attacking the pest there. Nevertheless, from this aspect, refinement of the knowledge of the original geographic range of *H. undalis* is desirable.

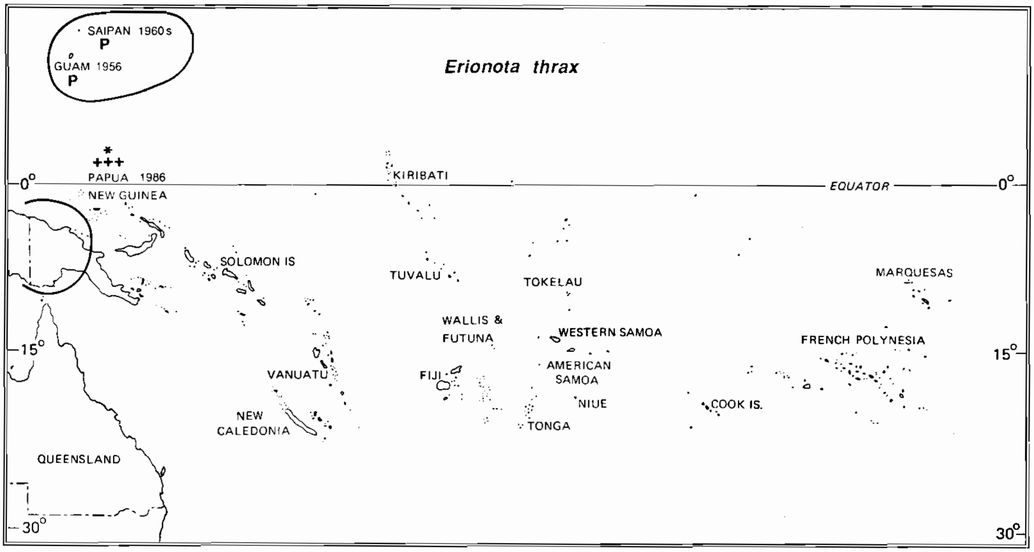
The microsporidan reported to attack *H. undalis* larvae in Hawaii is probably not specific to this pest, since *H. undalis* is an introduced insect in Hawaii, and the disease has not been reported elsewhere. Anyone attempting to employ it as a biological control agent against *Hellula* spp. should consider risks to beneficial Lepidoptera such as those used for the biological control of weeds.


Hawaii 1973
Saipan
Guam
Papua New Guinea
Mauritius 1970
Erionota thrax

8

Erionota thrax (Linnaeus)

LEPIDOPTERA: HESPERIIDAE
banana skipper, banana leaf-roller (Mauritius)



The hesperiid butterfly, *Erionota thrax,* is native to Southeast Asia.

It is attacked there by a number of parasitic wasps and flies. Together these natural enemies, many of which are themselves parasitised, exert a very considerable measure of biological control, although from time to time damaging outbreaks may occur.

After establishment of *E. thrax* in Guam, Hawaii and Mauritius it was brought under biological control by the egg parasite *Ooencyrtus erionotae* and the larval parasite *Apanteles erionotae.* Although both of these appear to be adequately host specific, their specificity should be evaluated before introduction to countries with a native hesperiid fauna. If adequate control is not brought about by these two species, the following are worth considering: *Agiommatus* sp. nr *sumatraensis* (egg parasite), *Scenocharops* sp. (larval parasite) and *Brachymeria* sp. from Sabah (pupal parasite).

Heavy rains cause considerable mortality of first instar larvae and, the shredding of banana leaves by high winds depresses populations of the banana skipper.

Origin

Southeast Asia. *E. thrax* was described in 1767 by Linnaeus from specimens collected in Indonesia, India and Malaysia.

Distribution

Asia: Burma, southern China, Hongkong, India, Indonesia, Laos, Malaysia, Philippines, Singapore, Thailand, Vietnam. Africa: Mauritius (since 1970). Pacific: Guam (since 1956), Saipan (late 1960s), Hawaii (since 1973), Papua New Guinea (Sepik since 1986, Madang, Eastern Highlands and Morobe since 1987, Port Moresby since September 1988). It is not present in the other Mariana islands (Anon. 1981c, Arura 1987, Davis and Kawamura 1975, F. Dori pers. comm. 1988, Monty 1970, Muniappan pers. comm. 1988), Sands et al. 1988).

There are three subspecies, which can be distinguished by the upper side cell spot of the fore wing, the widespread *E. thrax thrax* (which is now present in Papua New Guinea), *E. thrax mindana* Evans from the Philippines, and *E. thrax hasdrubal* Fruhstorfer from the northern Moluccas (Evans 1949). *E. thrax* has sometimes been incorrectly assigned to the genera *Hidari* (Evans 1949, Hoffmann 1935) or *Pelopidas* (Mau et al. 1980).

Life cycle

The 2 mm diameter, yellow eggs are laid at dusk or at night, either singly or irregularly in groups of up to about 25, more frequently on the lower than the upper surface of the leaves and usually about halfway between the midrib and the outer edge of the leaf. Syed (1974) obtained fertilized eggs in the laboratory by keeping adults in a large cage of green nylon mesh and feeding them with dilute honey in small tubes placed in the middle of pink plastic flowers. After a couple of days the eggs turn bright red and, before hatching, the black head capsule of the developing larva becomes visible through the chorion. Five to eight days after oviposition the pale green larva with a shiny black head hatches and proceeds to the edge of the banana leaf where it starts feeding and begins to roll and tie the leaf (Plate 1, figs 2, 3). If there is a single larva on a leaf it often starts near the apex and, as it grows, forms a roll towards the midrib, after which it returns to near the apex and repeats the rolling process on the opposite side of the midrib. If there are several larvae on the same leaf, one larva rolls and ties a portion of the leaf until it approaches the roll of another larva, when it abandons its roll and proceeds to another portion of the leaf or to another leaf to commence another roll. There are five instars which occupy some 23 to 30 days according to the temperature. All except the first instar larvae are covered with a whitish waxy powder, some of which is transferred to the inside of the leaf roll. As the larva develops the waxy powder increases in quantity. Rain causes high mortality of young larvae due to their lack of protective waxy powder and the poor construction of their leaf rolls. Older larvae close their rolls more securely and produce enough waxy powder to be water repellent.

Pupation occurs inside the leaf roll and the pupal period is about 10 days. The pupa is also covered with waxy powder. It is very sensitive to movement and wriggles violently on the slightest provocation. The adults usually emerge in the afternoon and fly rapidly and apparently erratically about the banana plants in the evening and early morning. They are occasionally attracted to lights. They feed on nectar from banana flowers and mate in flight. They are brownish (Plate 1, fig. 1), with three yellowish spots on the forewings. The wingspan is 70 to 75 mm in the male and up to 80 mm in the female. In southern China there are at least two generations a year and probably three or more, eggs being observed in the field as early as May. In Java there are five generations a year.

Food plants include, in particular, banana *Musa sapientum*, but *E. thrax* is also recorded from Manila hemp or fibre pisang *Musa textilis*, bamboo, coconut *Cocos nucifera*, oil palm *Elaeis guineensis*, nipa palm and other palms (Ashari and Eveleens 1974, Corbett 1923, Corbet and Pendlebury 1978, Dammerman 1929, Hoffmann 1935, Kalshoven 1951, 1981). In Guam, Hawaii, Mauritius and Papua New Guinea *E. thrax* is known only from cultivated and wild species of banana (R. Muniappan pers. comm. 1987, J.W. Beardsley pers. comm. 1988, J. Monty pers. comm. 1988, D.P.A. Sands pers. comm. 1988), which raises the possibility that other species may be responsible for the records on bamboo and palms or that there are host specific strains of the banana skipper. In Papua New Guinea *E. thrax* ocurs on *Musa* spp., *Australimusa* spp. and *Eumusa* spp., but not on the closely related *Ensete glaucum,* nor on a range of palms (Sands et al. 1988).

Pest status

Heavy infestations of the banana skipper leave only the midrib with numerous leaf rolls attached to it. In some instances no leaf surface at all may be left on young banana plants (Plate 1, fig. 4). In Malaysia damaged leaves are often conspicuous on banana plants in villages near the edge of the forest (Corbet and Pendlebury 1978). At the height of the attack in Oahu, Hawaii, more than 80 percent of all banana plants and leaves were damaged and *E. thrax* was regarded as a serious threat to the banana industry (Mau et al. 1980).

The banana plant produces leaves in excess of its needs for fruit production. Defoliation at 0, 10, 20, 30 and 40% at 35 day intervals for four years showed that there was no significant loss in fruit weight until 20% or more leaf area had been removed (Ostmark 1974). Defoliation at the time of appearance of the fruiting bud caused the greatest reduction in fruit weight. Fifty per cent defoliation at this time caused 28% loss in fruit weight. The longer the period before or after the fruiting bud emerges that damage occurs, the less fruit weight is lost (Hartman and Bailey 1929).

Outbreaks in Manila hemp (pisang) plantations are sporadic in Indonesia, but more frequent in the eastern part, particularly in localities protected from wind. Much damage has been done in south Sumatra. In Malaysia, drought conditions are thought to favour outbreaks (Kalshoven 1951, 1981), possibly because of the reduction of drowning of young larvae by rain. In Malaysia, *E. thrax* is at times a serious pest of plantain, sometimes entirely defoliating plants (Susainathan 1924), and coconut palms appear to be equally or more seriously attacked (Hoffmann 1935). In the spring of 1935 in southern China, scarcely a single uninfested banana plant could be found. Not only were the banana leaves damaged, but the plants were rendered unsightly, an important consideration to many Chinese families who grow banana plants in their gardens as much for aesthetic pleasure as for the production of fruit (Hoffmann 1935).

Control measures

Control measures are seldom required in Indonesia, but such infestations as occur may usually be dealt with by hand removal of infested leaf rolls or, if this is impracticable, organophosphorus sprays may be timed so as to synchronise with the appearance of newly hatched larvae (Ashari and Eveleens 1974). In southern China, Hoffmann (1935) advised collecting eggs and larvae and placing them in screened receptacles close to banana plants, so that any parasites could emerge and escape. In earlier days in Malaysia (Richards 1914), lead arsenate was used as a spray on coconut leaves. In Mauritius, before effective biological control, sprays of methomyl or monocrotophos were recommended for use on commercial plantations (Monty 1977).

Associated pests

On bananas in Australia fruit-spotting bugs, thrips, certain moth larvae and tetranychid mites are the subject of insecticidal recommendations (Anon. 1979b). Insecticides are no longer recommended for the general control of the banana aphid *Pentalonia nigronervosa* but are selectively applied only to plants exhibiting bunchy top disease and neighbouring ones. Insecticides are applied only to the developing bunches of fruit for the control of the banana scab moth *Lamprosema octasema.* The cluster caterpillar, *Spodoptera litura,* is probably the only pest of bananas in the Pacific whose insecticidal control would be likely to interfere with effective biological control of *E. thrax*, but this is such an occasional minor pest of bananas (Waterhouse and Norris 1987) that little interference is likely.

Natural enemies

CHINA

Eggs of *E. thrax* are parasitised by *Ooencyrtus papilionis*, but neither *Ooencyrtus erionotae* nor *Apanteles erionotae* appears to be recorded (Li Li-Ying pers. comm. 1988).

INDONESIA

In West Java there are five separate generations of *E. thrax* a year, each occupying about 70 days. The larvae damage the foliage of bananas, especially at high altitudes. Egg, larval and pupal parasites (Table 8.1) kill some 94% of the population and control measures are seldom required (Ashari and Eveleens 1974). Several egg parasites (*Ooencyrtus erionotae, Agiommatus* sp., *Anastatus* sp.) are present, resulting in 50 to 70% of the eggs being killed (Kalshoven 1951). About half of the larvae are attacked by *Apanteles erionotae* and 41 to 66% of pupae are attacked, chiefly by *Brachymeria euploeae*, but also by *Xanthopimpla* sp. or a tachinid fly (Ashari and Eveleens 1974). *B. euploeae* also attacks the pupae of *Hidari irava*, which is closely related to *E. thrax* and feeds on coconut and other palms in Southeast Asia. This may be the source of records of *E. thrax* on palms (Kalshoven 1951).

MALAYSIA

Ferrière (1931) described *Ooencyrtus erionotae* from the eggs of *E. thrax* and of an unknown lepidopteran on the leaf of wild plantain. These might have been *E. thrax* eggs, but no details are given. Susainathan (1924) states that larvae are highly parasitised by *Brachymeria* (= *Chalcis*) *marginata* and Corbet and Pendlebury (1978) record attack by *Apanteles erionotae* on larvae.

For several years a survey of natural enemies of *E. thrax* was carried out in Sabah (Malaysia) by Syed (1970, 1971, 1972, 1973, 1974). This resulted in records of thirteen species of Hymenoptera (5 egg, 4 larval, 4 pupal parasites), of two species of Diptera (1 larval, 1 pupal parasite) and of a fungus that attacked larvae (Table 8.1).

The total egg parasitisation found in 1971 (Syed 1971) was 36.7% (*Pediobius* sp. 30%, *Ooencyrtus erionotae* 4%, *Agiommatus* sp. 2%, *Leurocerus ovivorus* 0.5%). All species seemed to prefer eggs one day old or less. Total larval parasitisation was 43% (*Apanteles erionotae* 25%, *Scenocharops* sp. 17%): the former was apparently more abundant when *Erionota* populations were high and the latter when populations were lower. Both parasites are occasionally very heavily hyperparasitised (up to 62%), *Apanteles erionotae* by *Eurytoma* sp., which in turn was parasitised by *Pediobius elasmi* (= *P. lividiscutum*) and *Pediobius* sp. Larval-pupal and pupal parasitisation amounted to 28% (*Brachymeria* 15.8%, *Xanthopimpla* sp. 7.2% and *Sarcophaga* sp. 4.7%).

Cultures of *Ooencyrtus erionotae, Agiommatus* sp. and *Apanteles erionotae* were established and material from these, together with *Scenocharops* sp. adults, were sent to Mauritius. The last two species were later sent to Hawaii (Table 8.2).

THAILAND

E. thrax thrax attacks bananas (Cantelo and Pholboon 1965) and its parasites *Ooencyrtus erionotae, Apanteles erionotae* and *Brachymeria euploeae* are widespread. *O. erionotae* has been recovered from the eggs of *E. thrax*, but not from those of other hesperiids. *A. erionotae* appears to be specific to larvae of *E. thrax* whereas *B. euploeae* which attacks pupae is less host specific having been recorded from *Papilio demoleus, P. polytes* and the teak defoliator, *Hyblaea puera* (Chaiglom 1976). Other less important chalcidoid parasites are listed in Table 8.1. *E. thrax* caused problems from time to time in northern Thailand

Table 8.1 Natural enemies of *Erionota thrax.*

Country	Species	Family	Stage attacked	Reference
Hawaii	*Anastatus* sp.	Eupelmidae	eggs	Mau et al. 1980
	Brachymeria lasus	Chalcididae	pupae	Mau et al. 1980
	Echthromorpha agrestoria (= *E. fuscator*)	Ichneumonidae	larvae	Mau et al. 1980
	Trichogramma sp.	Trichogrammatidae	eggs	Mau et al. 1980
Hong Kong	*Leurocerus hongkongensis*	Encyrtidae	eggs	Subba Rao 1971
Indonesia	*Agiommatus* sp.	Pteromalidae	eggs	Kalshoven 1951, 1981
	Anastatus sp.	Eupelmidae	eggs	Kalshoven 1951
	Apanteles erionotae	Braconidae	larvae	Ashari and Eveleens 1974, Kalshoven 1951, 1981
	Brachymeria euploeae	Chalcididae	pupae	Ashari and Eveleens 1974, Kalshoven 1951, 1981
	Elasmus brevicornis	Elasmidae		Thompson 1945
	Ooencyrtus erionotae	Encyrtidae	eggs	Kalshoven 1951, 1981
	Xanthopimpla sp.	Ichneumonidae	pupae	Ashari and Eveleens 1974, Kalshoven 1951, 1981
	tachinid fly	Tachinidae	pupae	Ashari and Eveleens 1974
Malaysia	*Apanteles* sp.	Braconidae	larvae	Gater 1925
	Brachymeria albotibialis	Chalcididae		Hoffmann 1935
	B. marginata	Chalcididae	larvae	Susainathan 1924
	Elasmus brevicornis	Elasmidae		Dammermann 1929
	E. philippinensis	Elasmidae		Dammermann 1929
	Ooencyrtus erionotae	Encyrtidae	eggs	Ferrière 1931
	Scenocharops sp.	Ichneumonidae	larvae	Nakao and Funasaki 1976
	Xanthopimpla sp.	Ichneumonidae	larvae	Dammermann 1929
Malaysia (Sabah)	*Agiommatus* sp. nr *sumatraensis*	Pteromalidae	eggs	All Sabah records from Syed 1971
	Apanteles erionotae	Braconidae	larvae	
	Brachymeria sp. nr *marginicollis**	Chalcididae	pupae	
	Brachymeria sp. nr *lasus*	Chalcididae	pupae	
	Leurocerus ovivorus	Encyrtidae	eggs	
	Ooencyrtus erionotae	Encyrtidae	eggs	
	Pediobius sp.	Eulophidae	eggs	
	Pediobius sp.	Eulophidae	larvae	
	Pediobius sp.	Eulophidae	pupae	
	Scenocharops sp.	Ichneumonidae	larvae	
	Sympiesis sp.	Eulophidae	larvae	
	Telenomus sp. nr *attaci*	Scelionidae	eggs	
	Xanthopimpla regina	Ichneumonidae	pupae	
	tachinid fly	Tachinidae	larvae	

(continued on next page)

* This taxon unknown to CAB International Institute of Entomology.

Table 8.1 (continued)

Country	Species	Family	Stage attacked	Reference
Malaysia (Sabah)	sarcophagid fly	Sarcophagidae	pupae	
	Cordyceps sp.	a fungus	larvae	
Papua New Guinea	*Anastatus* sp.	Encyrtidae	eggs	Sands et al. 1988
	Ooencyrtus erionotae	Encyrtidae	eggs	Arura 1987
	Ooencyrtus sp.	Encyrtidae	eggs	Sands et al. 1988
Philippines	*Brachymeria albotibialis*	Chalcididae	pupae	Thompson 1945
	Elasmus philippinensis	Elasmidae		Thompson 1945
Southern China	unidentified chalcidoids	Chalcididae	eggs	Hoffmann 1935
Thailand	*Apanteles erionotae*	Braconidae	larvae	All Thailand records are from Napompeth 1976 or 1978b
	Brachymeria albotibialis	Chalcididae	pupae	
	Brachymeria euploeae	Chalcididae	pupae	
	Brachymeria marginata	Chalcididae	pupae	
	Ooencyrtus erionotae	Encyrtidae	eggs	
	Scenocharops sp.	Ichneumonidae	larvae	
	unidentified scelionid	Scelionidae	eggs	
	tachinid fly	Tachinidae	larvae	
	Bessa remota	Tachinidae	larvae	
	Exorista sp.	Tachinidae		
	ants	Formicidae		
	small house gecko			
	smooth skin chameleon			
	Dicrurus aeneus	Aves (the bronze drongo)		
	bacteria and viruses			

where no *A. erionotae* were found. Liberation of this parasite in the early seventies resulted in a decrease in damage (Napompeth 1976). *E. thrax* is reported to be no longer a pest of bananas except in a few pockets along the Laotian, Burmese and Malaysian borders (Napompeth 1976, 1978a, b, pers. comm. 1988).

Attempts at biological control

GUAM

When *E. thrax* first appeared in Guam in 1956 it caused serious damage to banana leaves. The egg parasite *Ooencyrtus erionotae* may have been introduced with the pest as there is no record of its introduction (R. Muniappan pers. comm. 1988). If this is so, this egg parasite alone was evidently unable to prevent economic damage occurring at times.

A larval parasite *Apanteles erionotae* was, therefore, introduced in 1974 from Hawaii, where material from Thailand had been liberated that year. Two pupal parasites *Brachymeria albotibialis* and *B. lasus* (= *B. obscurator*) were also introduced, although their origin and other details are not available (Muniappan 1982, pers. comm. 1988). It is possible that these records resulted from confusion of species names with the introduction of *B. euploeae* from Papua New Guinea mentioned below (I. Schreiner pers. comm. 1988).

The non-specific *Brachymeria albotibialis* (as *B. euploeae*) was introduced in 1973 from Papua New Guinea as a potential controlling agent for the poinciana looper, *Pericyma cruegeri*, a serious seasonal pest of the ornamental royal poinciana *Delonix regia* (Nafus and Schreiner 1989). About the same time *B. albotibialis* was introduced from northern Australia against *P. cruegeri*, but it was found to parasitise only a small percentage of its hosts (Schreiner and Nafus 1986). *B. albotibialis* had been recorded as a pupal parasite of *E. thrax* in Malaysia and/or the Philippines by Hoffmann (1935). A large *Brachymeria* species parasitises small numbers (usually less than 5%) of many Lepidoptera, including *P. cruegeri* and corn borers, but appears to prefer *Euploea* pupae (I. Schreiner pers. comm. 1988). A local species of *Trichogramma* also attacks *E. thrax* eggs (Nafus & Schreiner 1989).

Counts in central Guam from February to May 1977 revealed that *O. erionotae* was present in 85.6% of those banana plantings where *E. thrax* eggs were found and *A. erionotae* in 80% of plantings where *E. thrax* larvae were present. In southern Guam, the corresponding figures were 89.9% and 56.3% respectively. In northern Guam, no egg parasites were found and *A. erionotae* was present in only 40% of the sites where larvae were present. In November 1977 to March 1978 populations of *E. thrax* were lower, but the percent parasitisation only slightly lower. *Brachymeria albotibialis* was not recovered and *B. lasus* was present only at low levels, never rising above 0.9% parasitisation.

The general level of control of *E. thrax* on Guam is now regarded as satisfactory although in some years, particularly at the beginning of the wet season, there may still be seasonal defoliation sufficient to reduce fruit yield (Muniappan and Stevens 1978, R. Muniappan, pers. comm. 1987) and it has been concluded that the combined effects of both the egg and the larval parasites is responsible for a satisfactory level of control (Stevens and Kikuchi 1978). Neither *O. erionotae* nor *A. erionotae* has been recorded from other hosts on Guam (R. Muniappan pers. comm. 1988). *A. erionotae* is established on Saipan.

HAWAII

E. thrax was first reported on banana leaves at Hickam Air Force Base in August 1973 and soon after it was found to occur elsewhere on Oahu (Davis and Kawamura 1975). Within a few years it had spread to the other islands in the group. Three species of parasitic wasps were introduced and liberated in 1973 and 1974 (Table 8.2). Of these *Apanteles erionotae* and *Ooencyrtus erionotae* are credited with bringing the banana skipper under effective biological control in less than a year. By December 1975 populations had subsided and only trace to light infestations occurred from 1976 onwards (Nakao and Funasaki 1979). Parasitisation rates recorded were 24 to 99% (average 62%) for *A. erionotae* and 0 to 80% for *O. erionotae*.

In addition to the above, four other species of parasitic Hymenoptera which were already present in Hawaii were occasionally reared from field collected *E. thrax* eggs and pupae (Table 8.1), but the level of parasitisation was low by comparison with that by *A. erionotae* and *O. erionotae*. Mau et al. (1980) considered that a high degree of control would have been achieved had only one of the parasite species been introduced.

MAURITIUS

E. thrax was first recorded in Mauritius in 1970, although adults are thought to have been introduced in military aircraft based in Malaysia in 1968. It soon became a serious pest in summer in urban areas, especially on tall banana varieties such as Ollier or Gingeli. It was never a pest in rural commercial plantations of dwarf cavendish type bananas. It did not attack coconuts (J. Monty pers. comm. 1988). Egg and larval parasites were introduced from Malaysia from 1971 to 1973 (Table 8.2) and these resulted in successful control. However, in 1975 a cyclone severely damaged banana plants and drastically reduced banana skipper populations which, nevertheless, built up again in 1976. None of the three parasites established earlier was recovered in the two years following the cyclone (Anon. 1979c, 1980, Monty 1977), but damage to banana by the skipper was recorded as being very low in 1978

Table 8.2 Introductions for the biological control of *E. thrax*.

Country	Species	Liberated	From	Result	Reference
Guam	*Apanteles erionotae*	1974	Thailand via Hawaii	+	Muniappan 1982, Stevens and Kikuchi 1978
	*Brachymeria albotibialis**	between 1971 and 1976	Australia	-	Schreiner and Nafus 1986, Stevens and Kikuchi 1978
	*B. euploeae**	1973	Papua New Guinea	?	R. Muniappan pers. comm. 1988
	*B. lasus**	?	?	+	Stevens and Kikuchi 1978
	Ooencyrtus erionotae	?	?	+	Stevens and Kikuchi 1978
Hawaii	*A. erionotae*	1974	Thailand	+	Nakao and Funasaki 1976, Mau et al. 1980
		1974	Malaysia (Sabah)	+	
	O. erionotae	1973	Guam	+	Nakao et al. 1975
	Scenocharops sp.	1974	Malaysia (Sabah)	+ +	Mau et al. 1980, Nakao and Funasaki 1976, Syed 1974
Mauritius	*Agiommatus* sp. nr *sumatraensis*	1971, 1972	Malaysia (Sabah)	(+)	Anon 1975, J. Monty pers. comm. 1987, Syed 1971, 1972
	A. erionotae	1971, 1972, 1973	Malaysia (Sabah)	+	Monty 1970, 1977 Syed 1971
	O. erionotae	1971, 1972	Malaysia (Sabah)	+	Monty 1977, Syed 1971
	Scenocharops sp.	1971, 1972	Malaysia (Sabah)	-	J. Monty pers. comm., Syed 1971, 1972
Saipan	*A. erionotae*	1974, 1975	Thailand via Guam	+	Muniappan 1982, Nafus and Schreiner 1989

* It is possible that the material introduced was all of the same species, but the situation is a confused one (I. Schreiner pers. comm. 1988).

(Anon. 1980) and it is now quite uncommon (J. Monty pers. comm. 1988). The myna *Acridotheres tristis* (Aves: Sturnidae) is recorded as attacking the larvae of the banana skipper, often splitting open the rolls to expose them (Anon 1975, J. Monty pers. comm. 1987).

Four species of Hesperiidae occurred in Mauritius prior to the introduction of *E. thrax*. Two belong to the same subfamily (Hesperiinae) as *E. thrax*, namely the common *Borbo borbonica* and the moderately common *Parnara naso* (= *P. marchalii*). The former is a minor pest of rice and both feed on a range of grasses (Poaceae). The other two species are *Coeliades forestan* (subfamily Coeliadinae), which is a minor pest of *Canavalia ensiformis* and also occurs on *Terminalia catappa;* and the uncommon *Eagris sabadius* (subfamily Pyrginae) which feeds on *Hibiscus rosasinensis* (Vinson 1938). None of these species is known to be parasitised by either of the parasite species introduced against *E. thrax* (J. Monty pers. comm. 1987).

PAPUA NEW GUINEA

A specimen of *E. thrax* was first collected in Vanimo in August 1983 (H. Roberts pers. comm. 1988). It was next recorded in numbers in the East Sepik Province in July 1986. In March 1987 it was found defoliating banana plants in the Markham Valley of Morobe Province (Arura 1987 pers. comm. 1988, Arura et al. 1987) and in July 1987 it was causing extensive damage to banana leaves in the Madang area (D.P.A. Sands pers. comm. 1987). By the end of the year it had spread to nearly all of Morobe Province and to some parts of the Eastern Highlands and by September 1988 it was present in the Port Moresby area (F. Dori pers. comm. 1988). After sweet potatoes, bananas are the next most important food crop for indigenous Papua New Guineans, so this rapidly spreading pest is of considerable importance. In addition banana leaves are used for baskets, table cloths, wrapping food for market, cooking, protection against flies and for protecting the fruit from bats and birds during ripening. By mid 1988 up to 94% of leaves were infested with *E. thrax* at Bulolo. Up to 70% defoliation was recorded near Busu Village in the Markham Valley and the maximum number of rolls per leaf, six, was recorded at Goroka in the Eastern Highlands. On seasonal occasions individual plants were completely defoliated, with only the leaf stalks remaining (Sands et al. 1988).

Three banana skipper egg parasites have been recorded, one of which has been identified as *Ooencyrtus erionotae* (Arura 1987, Arura et al. 1987, Sands et al. 1988). Since this egg parasite has not been introduced intentionally it is probable that, as in Guam, it came in with its host, presumably as parasitised eggs on the leaf of a banana or other host plant. Alternatively, if non-specific, it was already present on other hosts: but there is no evidence that it is non-specific. Indeed it was not reared from eggs of the related palm skipper, *Cephrenes moseleyi,* even when both hesperiids were present at the same sites. On the other hand, a chalcidid wasp uncommonly reared from pupae of *E. thrax* was frequently found in pupae of *C. moseleyi.* Less than 5% of pupae collected were parasitised. In a survey in May and June 1988, 31.3% of *E. thrax* eggs were found to be parasitised by *O. erionotae.* As in Guam, this parasite alone appears incapable of preventing important damage to banana plants. Two other egg parasites were occasionally found, *Ooencyrtus* sp. and *Anastatus* sp. (Sands et al. 1988). Two larval/pupal parasites, a tachinid fly and three predatory Hemiptera were also present, but not *Apanteles erionotae* (Sands et al. 1988, D.P.A. Sands pers. comm. 1988). Biological control introductions are proposed when the specificity of *Apanteles erionotae* and perhaps other parasites has been investigated.

Biology of the major parasites

Agiommatus sp. nr *sumatraensis*

This species completed development in 13 to 15 days and only a single parasite emerged from each egg (Syed 1974).

Apanteles erionotae

Females, which measure 2.2 to 3.0 mm, oviposit in young larvae, with a preference for those in the second instar. The parasite larvae develop within the host larva, which shows no external signs. At an average temperature of 26.7°C, mature parasite larvae emerge through the larval cuticle between 16 and 24 days after oviposition. They pupate in whitish silken cocoons on both sides of the host larva, which usually dies within a day. Adult *Apanteles* emerge in 5 to 7 days. On average, 69 adults (range: 18 to 150, Mau et al. 1980; 36 to 87, Napompeth 1978b) emerged from each parasitised larva. In Guam adult emergence from each host larva averaged 25, with a sex ratio (female/male) of 1.95:1 (Stevens and Kikuchi 1978). In many locations in Thailand 60 to 100% *E. thrax* larvae were parasitised (Napompeth 1978b).

Ooencyrtus erionotae
Adult females measure 0.8 to 1.0 mm and males 0.6 to 0.9 mm (Napompeth 1978b). Females lay in banana skipper eggs up to 3 days old, but seldom oviposit in older eggs. In a period of about 10 minutes each female may oviposit at several different sites in the same host egg. *O. erionotae* eggs hatch in 2 days and, following a larval period of 6 to 7 days, pupation occurs within the host egg. Adult parasites emerge 8 to 10 days later by chewing holes through the chorion. *O. erionotae* is polyembryonic (Napompeth 1978b) and, on average, 5 parasites are reared from each parasitised egg. There is a 2-day pre-oviposition period and adults live up to 2 months (Mau et al. 1980). In Guam parasite emergence from each parasitised egg averaged 4, with a sex ratio of 2.3:1 (Stevens and Kikuchi 1978). In Thailand from 70 to 100% parasitisation of banana skipper eggs has been recorded (Napompeth 1978b).

Scenocharops sp.
Adults mated fairly readily when kept in large jars. Females preferred third instar *E. thrax* larvae for oviposition, but second instar larvae were also attacked. The development period within the host larvae varied from 17 to 25 days. The pupal period lasted 10 days (Syed 1974).

Brachymeria euploeae
Females oviposit in host pupae and the resultant larvae feed internally. Adults emerge after 7 to 10 days through exit holes chewed in the pupal cuticle. The number of parasites per pupa ranges from 1 to 24, the smaller the number the larger the adult size. Normally the size range is from 3.0 to 6.0 mm. Adults aggregate on the underside of the banana leaf and males perform a 'nuptial dance' (Napompeth 1978b).

Comments

It is highly probable that *E. thrax* will extend its distribution significantly over the next decade or so. It will certainly spread throughout Papua New Guinea and, doubtless, into Irian Jaya if not already there, partly by adult flight and partly either on banana suckers used as planting material or on infested banana leaves used to wrap fruit and vegetables for transport. The water gaps between southern Papua New Guinea and Northern Australia are probably well within the flight range of adults. Thus there are good reasons for believing that, in due course, it will reach Australia and then possibly extend into the banana growing areas of northern New South Wales. Southwest Pacific islands will be at risk if inter-island movement of fresh banana leaves is not prohibited. In any case adults may be able to fly to nearby islands and establish themselves.

The prospects for achieving effective biological control of *E. thrax* in countries it invades appear excellent, judging from the experience in Guam, Hawaii and Mauritius and from the generally low level of damage in countries where *E. thrax* is native. There is, however, a complication for Papua New Guinea and Australia. Whereas Guam (Swezey 1942) and Hawaii (Zimmerman 1958b) have no native Hesperiidae, and hence the host specificity of *Apanteles erionotae* and other parasites was not an issue, both Papua New Guinea and Australia have rich and diverse hesperiid faunas of great scientific interest and it is possible that effective non-specific natural enemies may transfer from them to *E. thrax.* Although there are no records of the two major introduced parasites attacking eggs or larvae of other Lepidoptera in Guam (R. Muniappan pers. comm. 1988), Hawaii (C.J. Davis pers. comm. 1988) or Mauritius (J. Monty pers. comm. 1987), these localities have afforded them very limited opportunities for attacking these stages of other Hesperiidae. There are, however, no records in the literature of *Apanteles erionotae* attacking any species other than *E. thrax* and the only record suggesting that *Ooencyrtus erionotae* may not be completely host specific is in its original description by Ferrière (1931), who recorded it from the eggs of an unknown lepidopteran laid on a wild plantain leaf. It is, of course, possible that they were *E. thrax* eggs.

A study of collections in the Bishop Museum (J. Beardsley pers. comm. 1988) and the British Museum (K.M. Harris pers. comm. 1988) and checks on the local collections and literature in Malaysia failed to reveal any records of hosts other than *E. thrax* (P.A.C. Ooi pers. comm. 1988).

Before deciding to introduce *A. erionotae* or other parasites to Papua New Guinea it would appear desirable to determine whether or not they are capable of developing in eggs or larvae of other representatives of the hesperiid subfamily Hesperiinae to which *E. thrax* belongs.

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