BIOLOGICAL CONTROL PROGRAMMES AGAINST INSECTS AND WEEDS IN CANADA

1959-1968

Technical Communication No. 4
Commonwealth Institute of Biological Control
Trinidad

COMMONWEALTH AGRICULTURAL BUREAUX

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IN CANADA

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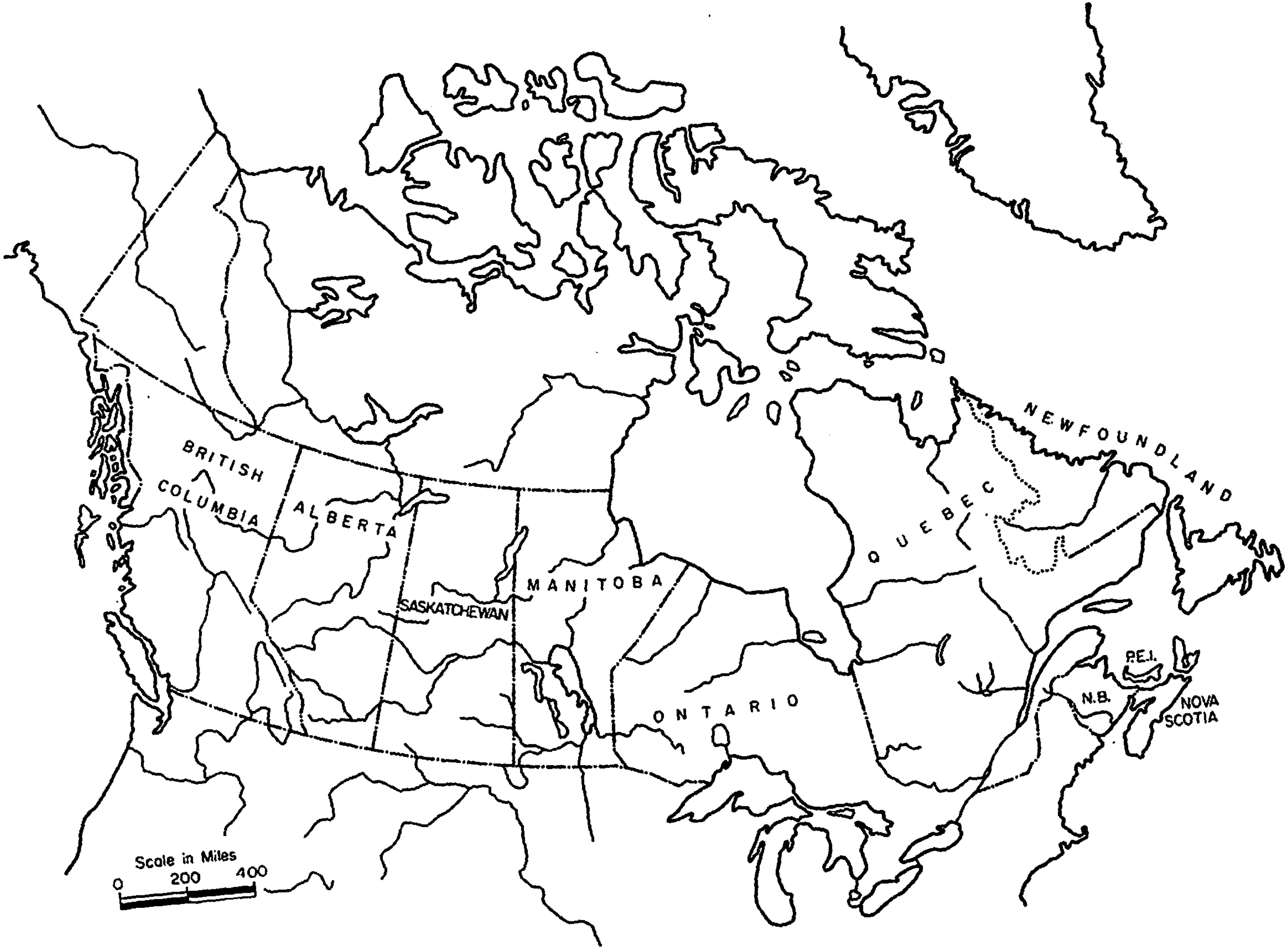
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TECHNICAL COMMUNICATION No. 4
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TRINIDAD

COMMONWEALTH AGRICULTURAL BUREAUX
FARNHAM ROYAL, SLOUGH SL2 3BN, ENGLAND

First published in 1971
by the
Commonwealth Agricultural Bureaux,
Farnham Royal, Slough SL2 3BN, England.
Price £2.50

SBN 85198 018 X

This publication can be obtained
through any major bookseller
or direct from :
Commonwealth Agricultural Bureaux,
Central Sales, Farnham Royal, Slough SL2 3BN, England

Printed in Great Britain by
Lamport Gilbert Printers Limited,
Reading, England

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FOREWORD

Whilst this volume is to a certain extent a timely supplement to that published in 1962, Technical Communication No. 2 in this series, it does more than simply bring the record of biological control operations in Canada up to date. The present *Review* gives in greater detail the results obtained against various pest species, and also deals more fully with attempts to utilize insect pathogens as biological control agents. Results are also given of trials using the sterile-male technique to reduce pest populations.

A further great improvement is that, with many of the examples given, an attempt has been made to give some idea of the cost-benefit figures for the results obtained, an aspect of biological control which has unfortunately in the past been rather ignored. An introduction of a natural enemy into a new area has often been stated to have been 'successful' without any accurate statement being given as to what this success has meant in economic terms, and hence such claims have often been rather discounted. Here we are given some examples where definite economic benefits are estimated as far as this is possible.

The division into sections dealing with agricultural and forest pests is both a logical and convenient grouping, and the treatment by which individual authors have contributed chapters dealing with their own particular speciality has given to this present volume a greater authority in detail.

A whole section of the book has been devoted to the general future prospects and research requirements for biological control, with particular reference to Canada, in all its aspects—from consideration of detailed long-term studies of pest and natural enemy complexes, through integrated control, to the type of organization for biological control work appropriate for optimal development of this aspect of pest control in Canada. In order to avoid any possibility of undue bias in favour of biological control in such an analysis, the preparation of this section was entrusted, not to a biological control specialist, but to a taxonomist well versed in the general organization of pest control in Canada. The result has been a very fair appraisal of the potential value of biological control in Canada and its rôle in pest control in general.

F. J. SIMMONDS,
Director,
Commonwealth Institute of Biological Control

PREFACE

The production of this *Review* testifies to the close working relationship that exists between the Canada Department of Agriculture and the Canada Department of Fisheries and Forestry, particularly in matters relating to biological control. The resolve to prepare the *Review* originated (in July 1968) from the Interdepartmental Advisory Committee on Entomology and Botany; and the task of assembling and integrating the separate contributions was undertaken jointly by members of the two Departments. The fact that the completed manuscript, comprising 48 chapters contributed by 60 authors, is being submitted for publication only two years after the project was conceived shows further how broadly based this cooperation has been. In prospect, this close community of interest augurs well for a future in which, to an increasing extent, the similarities in approach to management of agricultural and forestry pest species are becoming more important than are the differences.

This volume is intended to report progress in biological control in Canada, but especially to help towards charting a course for the future. It was with this second objective in mind that the Interdepartmental Committee recommended the inclusion of a general synopsis (Part IV) that would offer a critique of the principles of biological control, and a frank appraisal of its effectiveness. Though no two scientists would have approached this task in the same way, it is both significant and useful that the author of Part IV has identified organization and management as being the principal areas requiring attention. It will be recognized that the views expressed by the author in Part IV are his own personal ones and are not necessarily those of either Department or of any establishment engaged in biological control in Canada. It is unusual to include an appraisal of this nature in what is predominantly a report of Departmental research; but we consider that the usefulness of this exercise lies in the assessment being included (as it has been) without selective editing of content. It will have served its purpose well if it generates close constructive criticism of our ongoing programmes.

We welcome the publication of this *Review* as a serious attempt to take stock in an important field of activity and to offer guidelines for its future development. At this time, when there is such a great need to explore all possible alternatives to conventional pesticides, the appearance of this *Review* is especially appropriate.

B. B. MIGICOVSKY,
Director General,
Research Branch, Canada Department of Agriculture

M. L. PREBBLE,
Assistant Deputy Minister,
Canadian Forestry Service,
Department of Fisheries and Forestry

(*July 1970*)

GENERAL INTRODUCTION

In 1962 the Commonwealth Agricultural Bureaux published *A Review of the Biological Control Attempts against Insects and Weeds in Canada.* In Part I of that volume J. H. McLeod surveyed control attempts against agricultural pests and weeds up to 1959; in Part II B. M. McGugan and H. C. Coppel reviewed control attempts against forest insects up to 1958. The programmes were described in detail and thoroughly documented. In 1968 it was proposed that a sequel to the first *Review* be prepared that would cover developments during the decade 1959–1968. The present volume, which represents this sequel, is seen as having two main functions.

First, it updates information concerning biological control attempts in Canada, reports progress, and offers recommendations for programmes against specific pests. It provides records of releases and recoveries for the period 1959–1968 and an updated bibliography. Parts I–III serve this first function. As in the previous *Review*, the term 'biological control' is used to mean the manipulation of living organisms to reduce the numbers or viability of pests; but in this volume its scope is widened to include programmes utilizing disease organisms in the field (largely omitted before) and those involving the release of sterile individuals. The arrangement and authorship of material differs somewhat from that in the first *Review*. Here, sections devoted to individual pests have been written, for the most part as separate chapters, by the scientists primarily responsible for the work. Depending on its subject matter, a given chapter appears in Part I (agricultural insects), Part II (weeds) or Part III (forest insects). With a few exceptions (explained in Part I, p. 3), chapters within each Part are arranged in alphabetical order of the pest's generic name. The tables listing releases and recoveries are contained in the appropriate chapters and not, as before, in a composite appendix at the end of the text. Similarly each chapter has its own bibliography and is accordingly a self-contained contribution. The appropriate bibliographical citation to any part of this volume is therefore to the author of the chapter in question.[1] The full scientific name of each species referred to is given in the chapter heading (if it is a target species) and on the first occasion of mention, which can be found by consulting the index on p. 258. Two conventions of terminology require comment. Some authors have distinguished two categories of parasite (*sensu lato*): the 'parasitoid', a parasite that kills its host; and the 'parasite' (*sensu stricto*), one that generally does not. Except in Part IV it has not been found necessary to draw this essentially behavioural distinction, and both categories have been referred to as 'parasite'. In Part II the term 'parasite' has been used in the wide sense to describe a phytophagous insect that attacks a weed.

The second main function of this volume is one that its predecessor did not have: to try to evaluate the success, potential, and future of biological control as a method of reducing pest damage. For the intent of such an evaluation to be understood, it must be recognized that biological control is merely one of several available strategies, suited to some problems but not to others. Each case has to be judged according to its merits, and the unqualified rejection of biological control is as unjustifiable as its unqualified advocacy. The evaluation of biological control programmes reported in this volume has been attempted in the opening chapter of Parts I, II and III. The treatment in each of these chapters is somewhat different, depending on the subject matter and scale of operation; the relevant chapters in Parts II and III give cost-benefit analyses for certain programmes. Part IV offers an evaluation and recommendations at a broader level. Its author was invited to contribute as one who, not being a specialist in biological control, and at the same time possessing wide entomological, ecological and advisory experience, could be expected to offer a mature, detached appraisal of this approach, as it has been followed in Canada during the decade covered by the *Review*.

The evaluations included in each Part are perhaps appropriate to an extent that they would not have been ten years ago. Scientists concerned with resource protection and utilization have tradition-

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[1] For example: 'Peschken, D.P. (1971). *Cirsium arvense* (L.) Scop., Canada Thistle, pp. 79–83. *In* Biological control programmes against insects and weeds in Canada 1959–1968. *Tech. Commun. Commonw. Inst. biol. Control* 4, 266 pp.'

ally recognized the need to treat with respect and restraint the environment of which man is a part, even though this recognition has seldom been reflected in national and international policies. Today, however, the pressures man has to contend with, and the trends he is obliged to extrapolate, are of such a nature as to make time a dominant variable in any predictive equation he may formulate. When the first *Review* was written ecologists who warned of imminent world famine or irreversible destruction of the biosphere were seldom taken seriously. In 1970 (many million human births and tons of pesticide later) such warnings are being listened to with respect; indeed, concern now centres on whether present trends can be reversed and the damage repaired in time. It is now widely recognized that, if the increase in human population can be contained, solution of the related problems of food and environmental protection will depend partly on the rapid development of selective, non-polluting methods of pest control. It is perhaps less widely recognized that if the increase in human population cannot be contained, man himself will have become the major pest species, whereupon the control of insects or weeds will cease to be a relevant concern. If the pressures have become greater in the last decade, so also have the knowledge and techniques that can be harnessed to assist in their relief. It is obviously essential that potential applications of new discoveries to existing procedures be actively explored and exploited. An example that holds promise is the serious attention now being paid to the inundative release of biotic agents against agricultural pests on a scale significantly greater than could have been contemplated with the technology available ten years ago.

During the period covered by this *Review* the federal government agencies responsible for biological control programmes in Canada have for the most part performed the same functions and retained the same relationships as prevailed in 1958. The Department of Agriculture, and the Department of Fisheries and Forestry[2] operate programmes involving the manipulation of biotic agents in several of their regional establishments across Canada. The Canada Department of Agriculture Research Institute,[3] at Belleville, Ontario continues to serve both Departments in providing for the importation, quarantine and dispatch of biological control agents from abroad, and in providing liaison with the Commonwealth Institute of Biological Control. Testifying to the close relationship that is maintained with the C.I.B.C. are the joint authorship of chapter 29 and the publication of this *Review* as a Technical Communication of the Commonwealth Institute.

Preparation of this *Review* was the responsibility of an interdepartmental committee comprising: Dr. J. S. Kelleher, Dr. P. Harris and Mr. W. A. Reeks, who coordinated Parts I–III, respectively; Mr. G. D. Williamson, Quarantine Officer, Research Institute, Belleville, who prepared the release tables that appear throughout the text, and the index; and Mr. R. M. Prentice, Program Coordinator, Department of Fisheries and Forestry, and myself, who served as compilers. This committee expresses gratitude to: Dr. E. G. Munroe for accepting its invitation to write Part IV; Dr. F. J. Simmonds, Director, Commonwealth Institute of Biological Control for assistance with publication; and taxonomists of the Entomology Research Institute, Canada Department of Agriculture, Ottawa for guidance with insect nomenclature.

Contributions to this volume were prepared between March 1969 and July 1970. Addresses of all contributors are listed in the Appendix.

PHILIP S. CORBET, *Director*,
Research Institute, Canada Department of
Agriculture, Belleville, Ontario

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[2] Previously the Department of Forestry and Rural Development.
[3] Previously the Entomology Research Institute for Biological Control.

PART I

BIOLOGICAL CONTROL OF AGRICULTURAL INSECTS IN CANADA, 1959—1968

1. CURRENT APPROACHES TO BIOLOGICAL CONTROL OF AGRICULTURAL INSECT PESTS

J. S. KELLEHER

This Part includes insect and mite pests of crops, fruit trees, and ornamentals. In the previous review, McLeod (6) included only those projects in which parasites and/or predators had been moved from one area to another. The present review includes projects in which attempts were made to increase the biotic mortalities of pests by introduction, conservation, augmentation or inundation.

From 1948 to 1955, the Canada Department of Agriculture operated a biological control station at Vancouver which was very active in the importation and transfer of natural enemies of agricultural pests into British Columbia. In addition, prior to 1955, staff from the Research Institute, Belleville were actively engaged in agricultural insect problems in various parts of Canada. After 1955 the Vancouver station was closed and the responsibilities of Belleville staff were modified; regional pest problems became the sole responsibility of Research Stations, and Belleville provided only a service in the procurement and dispatch of information and natural enemies from overseas, as requested by those Stations. These changes markedly reduced the impetus to introduce biological control agents.

But an even more pronounced effect resulted from the standard of crop protection set by the use of organic chemicals, especially when the damage would have been done directly to the harvested product. Consumers have come to expect unblemished fruits and vegetables: growers have been forced to increase their production of such items in a highly competitive market. At one time *Macrocentrus ancylivorus* Rohwer was considered to be a successful introduction against oriental fruit moth because damage was reduced at a time when other control methods could not do so. But with the later development of potent insecticides, damage was much more markedly reduced and a new standard of production was set.

More recently the detrimental side effects of insecticides have led to studies in other aspects of biological control, especially integrated approaches and the use of biological insecticides, such as bacteria, viruses and nematodes.

In contrast, little has been done to augment the effectiveness of parasites and predators by providing them with certain amenities of life, e.g. food or shelter for adults. Leius (3, 4) has shown that, in the laboratory, egg-lay and longevity were higher for female parasites that were provided with pollen than for those that were denied it. He has also found (5) that parasitism was higher in orchards with a rich undergrowth of spring-flowering plants than in orchards without. However, not all field observations have shown that the provision of food sources for adult parasites increases parasitism. Although *Itoplectis conquisitor* (Say) preferred flowers of parsnip to those of other plants in laboratory tests, Bracken (1) found the parasitism of suitable hosts to be unrelated to the presence or absence of parsnip flowers in field tests.

Separate mention should be made of 'do-it-yourself' biological control. This operation mainly involves small growers who import natural enemies from suppliers in the U.S.A. on the basis of advertised claims that control can be obtained by their release. Such imports are subject to Plant Protection regulations; D. Henderson (2) has provided the information that *Trichogramma* spp., coccinellids, and European praying mantids have been imported for this purpose; but recent changes in certification are likely to restrict such operations in future importations. It is unlikely that the expected control is obtained when these parasites or predators are released. The numbers liberated are relatively small, and there is no assurance that the released individuals will remain within the area being treated. Perhaps many of the claims for success are related, not to the natural enemies released, but to the conservation of native species of biotic agents through restriction of chemical treatments that would have been detrimental to them.

Much of the evidence for successful biological control by introductions has been based on a simple correlation between high parasitism and reduced pest population. The use of more refined mathematical techniques to evaluate mortality factors which regulate insect pest populations has shown that an assumption based on the percentage parasitism can be erroneous. This has led to criticism of some claims for success of biological control. Differences of opinion are difficult to recon-

TABLE I

Evaluation of biological control measures[1] against agricultural insect and mite pests

Pest	Page reference	Method	Degree of success[2]
Acyrthosiphon pisum	3	Laboratory evaluation	++++
		Introduction	—
Agriotes obscurus	59	Inundation	—
Alsophila pometaria	59	Inundation	++++
Ancylis comptana fragariae	10	Introduction	—
Argyrotaenia velutinana	10	Introduction	—
Carpocapsa pomonella	12	Conservation	+++
		Inundation	+++
		Autocidal	++++
Coleophora malivorella	15	Introduction	+++
Euxoa messoria	16	Inundation	++++
Forficula auricularia	18	Introduction	+
Heliothis zea	59	Inundation	—
Hylemya brassicae	20	Conservation	++++
Hypera postica	43	Introduction	—
Lecanium coryli	23	Conservation	++++
Lepidosaphes ulmi	24	Conservation	++++
Malacosoma americanum	26	Inundation	++++
Melanopus spp.	27	Inundation	—
Panonychus ulmi and other orchard mites	28	Conservation	++++
		Introduction	—
Pieris rapae	30	Inundation	++++
Plutella maculipennis	30	Inundation	++++
Pseudexentera mali	59	Inundation	—
Psylla mali	31	Conservation	++++
Psylla pyricola	33	Introduction	+
Rhagoletis pomonella	38	Conservation	+
Rhopalosiphum maidis	41	Technique development	++
Sitona cylindricollis	43	Introduction	—
Sitona scissifrons	43	Introduction	+
Spilonota ocellana	47	Inundation	++++
		Introduction	+++
Swammerdamia lutarea	48	Introduction	—
Tetranychus urticae	49	Integration	++
Thymelicus lineola	51	Inundation	++++
Tipula paludosa	54	Introduction	—
Trialeurodes vaporariorum	57	Integration	+++
Trichoplusia ni	59	Inundation	++++
Various target species: attempts with DD–136	62	Technique development	++++

[1] Measures started during or extending into period 1959 to 1968.

[2] Degree of success:

—	No control
+	Slight pest reduction or too early for evaluation of control
++	Local control; distribution restricted or not fully investigated
+++	Control widespread but local damage occurs
++++	Control complete.

cile. Few mathematical workers will evaluate the regulating factors of a pest that has ceased to be a problem, especially since sampling would be a formidable task.

Life-table analyses are now being prepared for various agricultural pests. If similar information was obtained overseas this would provide a better basis for selecting species of natural enemies to import. In some instances it may be practicable to select candidate species from abroad by traditional methods and to introduce them against a Canadian pest for which life-table data have been prepared. A more satisfactory assessment of the results could then be made.

This Part of the review describes biological control attempts in 39 agricultural pest situations. Intentional introductions of parasites and/or predators were made against 11 species; field trials with bacteria, viruses or nematodes were directed against 18 species; integrated control by the restricted or selected use of chemical insecticides together with natural enemies are reviewed in nine pest problems; and in one instance the release of sterile individuals of a pest amongst field populations of the same species is described.

In Table I, an attempt has been made to evaluate the control obtained from each of these projects.

Agricultural entomologists often work alone rather than as part of a team, and not infrequently they are responsible for developing controls for several pest species. Biological control attempts usually account for only a portion of their activities, and as a result many contributions here are relatively brief. In particular microorganisms are often applied against a number of species; some of these contributions are incorporated into main chapters when other approaches were also made, but a few are grouped in a 'Miscellaneous' chapter; a coordinated programme with nematodes against several species is placed in a single chapter at the end of Part I.

Because of the wide diversity of biological control approaches covered in this review, it was necessary to solicit contributions from many Canada Department of Agriculture establishments and university departments. That the response was most encouraging is shown by the large number of contributors to this Part. Without this cooperation, and the support of supervisors, this review would not have been possible.

LITERATURE CITED

1. Bracken, G. K. (1964). *In Res. Rep. Res. Inst. Belleville, Ont.* (1962–1963): 14.
2. Henderson, D. (1969). *In litt.* Plant Protection Division, Canada Department of Agriculture, Ottawa, Ontario.
3. Leius, K. (1961). Influence of food on fecundity and longevity of adults of *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae). *Can. Ent.* **93**: 771–80.
4. Leius, K. (1963). Effects of pollens on fecundity and longevity of adult *Scambus buoliana* (Htg.) (Hymenoptera: Ichneumonidae). *Can. Ent.* **95**: 202–07.
5. Leius, K. (1967). Influence of wild flowers on parasitism of tent caterpillar and codling moth. *Can. Ent.* **99**: 444–46.
6. McLeod, J. H. (1962). Biological control of pests of crops, fruit trees, ornamentals, and weeds in Canada up to 1959. *In* A review of biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol. Control* **2**: 1–33.

2. *ACYRTHOSIPHON PISUM* (HARRIS), PEA APHID (HOMOPTERA: APHIDIDAE)

MANFRED MACKAUER[1]

PEST STATUS

The following is a review of a programme that was conceived as a basic study in biological control. The main objective of the study was to compare various hymenopterous parasites under laboratory conditions and to describe and measure characteristics that were assumed to determine the

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[1] Part of the experimental work described here was conducted while the author held a position at the Research Institute, Canada Department of Agriculture, Belleville, Ontario.

impact of each species as a mortality agent. The actual release of the most promising agent was considered mainly as a means to verify laboratory findings. In addition, it was hoped that the liberation of an exotic species would provide an opportunity to analyse adaptive changes in colonizing species and, in particular, factors that lead to the elimination of colonizers poorly adapted climatically. The target organism, *Acyrthosiphon pisum* (Harris), was selected for the reasons explained below.

The pea aphid is widely distributed in Canada, ranging from the Atlantic to the Pacific coast in areas which enjoy a temperate climate (Fig. 1). Its host range comprises many herbaceous Papilionaceae including *Cytisus*, *Lathyrus*, *Lens*, *Lotus*, *Medicago*, *Melilotus*, *Onobrychis*, *Ononis*, *Pisum*, *Trifolium* and *Trigonella* (10, 15). A number of plants in these genera are weeds which were accidentally introduced from Europe to North America by early settlers and which now form part of ruderal and agricultural biocenoses (11, 18). Other host plants, e.g. *Medicago sativa* L. and *Pisum sativum* L. are commercially important crops.

Acyrthosiphon pisum is believed to be of Palaearctic-Oriental origin; it probably invaded the North American continent somewhat before or during the second half of the 19th century. It was reported first from Illinois in 1878 (9) and about 20 years later was found in Ottawa, Ontario (16).

The life history and habits of the pea aphid are the subject of numerous detailed studies (5, 7, 9, 27, 28). The aphid overwinters chiefly in the egg stage, although some of the viviparous summer forms survive where the climate permits. In Ontario, eggs are laid mainly on sweetclover which also serves as the major host plant in spring and early summer. By the time sweetclover is in bloom it becomes less satisfactory as a host. Winged aphids appear and colonize alfalfa, peas and other summer host plants on which they can build up enormous populations within one or two weeks under favourable conditions. Taxonomically the pea aphid is composed of several biotypes which are either restricted to, or show preference for, certain host plants (6, 14, 29).

Although the pea aphid is moderately abundant locally, it is debatable whether this insect should be classified as an economically important pest in general. The aphid is known to be a vector of some 20 different plant viruses (17) but, normally, becomes most damaging as a direct pest during outbreaks. Loss of plant sap due to feeding by pea aphids may result in a reduction of yield of up to 50 per cent. in alfalfa (4). In Canada the pea aphid is not considered, or very rarely so, as an important pest of alfalfa or red clover that is grown for hay or seed production. This does not apply to areas where peas are grown for canning or freeze-processing, i.e. mainly in the Annapolis Valley in Nova Scotia and in southern Quebec. In these districts pea aphid damage is regarded as a significant economic factor requiring the regular application of insecticides.

The relevant literature contains numerous references to entomophagous insects and pathogens that contribute to the natural control of the pea aphid. For example, in eastern Canada the aphid is attacked by four endemic species of hymenopterous parasites: *Praon occidentale* Baker, *P. pequodorum* Viereck, *Aphidius pulcher* Baker (Aphidiidae) and *Aphelinus semiflavus* Howard (Aphelinidae) (23, 24). None of these parasites, however, exerts sufficient pressure to reduce pea aphid damage below the economic threshold. Although predators such as Coccinellidae, Syrphidae and Chrysopidae undoubtedly play an important role in the control of the aphid, no detailed account of their number and impact is available to date.

It follows that the pea aphid in Canada, thus, should offer an ideal situation for biological control. It is of exotic origin; in general, it behaves as a direct pest (damaging the harvested product) and it is insufficiently controlled by indigenous agents.

BACKGROUND

First attempts at increasing the impact of endemic mortality agents on *Acyrthosiphon pisum* in North America were made by the United States Department of Agriculture. It imported several of the more than 20 known parasite species belonging to the hymenopterous families Aphidiidae and Aphelinidae (12, 25) for release in the alfalfa-growing areas of the eastern United States and Cali-

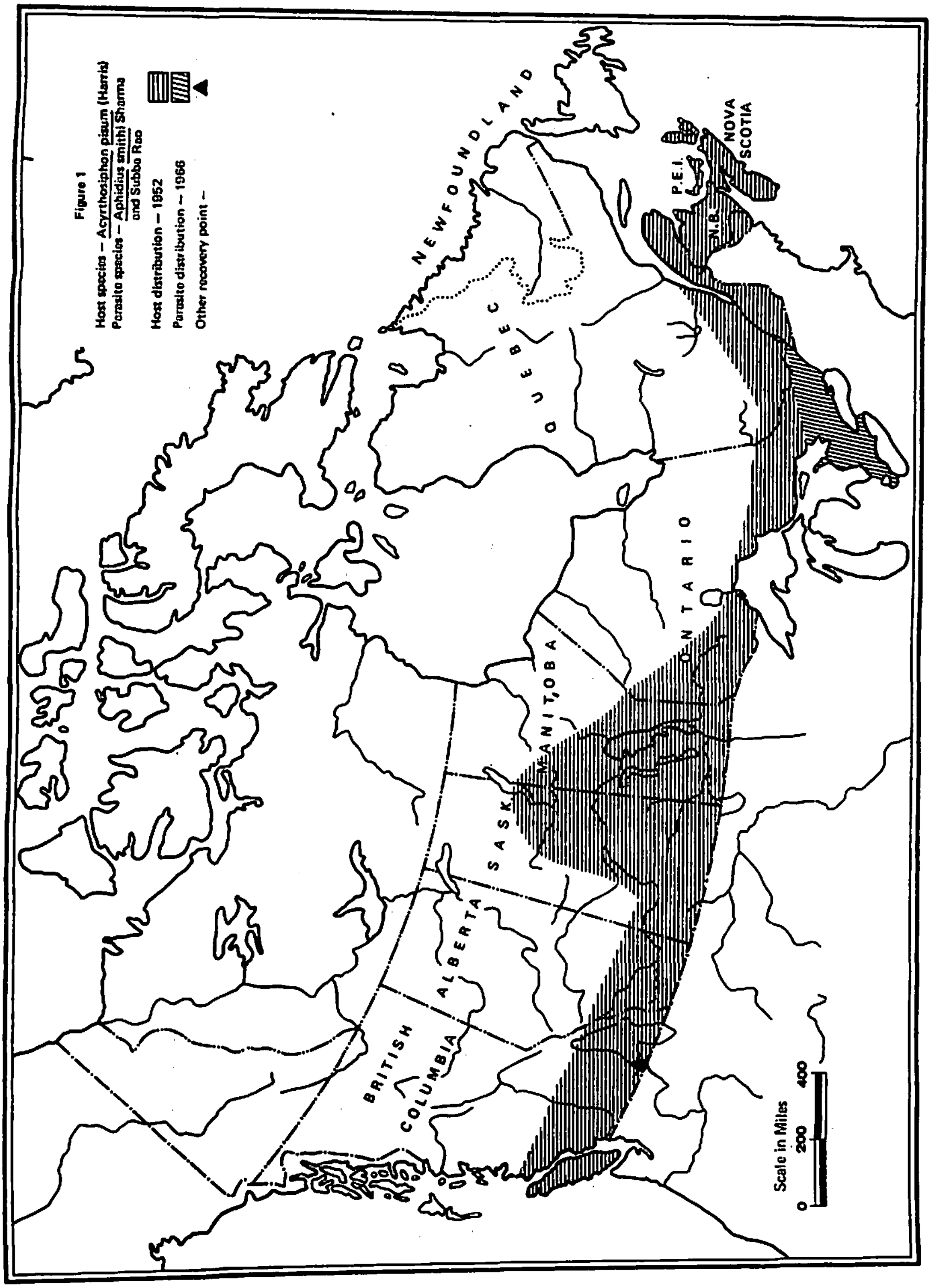

Figure 1

Host species – *Acyrthosiphon pisum* (Harris)
Parasite species – *Aphidius smithi* Sharma and Subba Rao

Host distribution – 1952 ▤
Parasite distribution – 1966 ▨
Other recovery point – ▲

fornia. The most successful of the imported parasites proved to be *Aphidius smithi* Sharma & Subba Rao which originated from India. It was released from 1958 onward and, within less than one year, became established in California (13). During subsequent years *A. smithi* spread over most of the alfalfa-growing districts of California, where it became one of the most important mortality agents, and also became established in areas of eastern Oregon and Washington (7). A similar success accompanied the introduction of *A. smithi* from California into the Hawaiian Islands (3, 8). Releases in the eastern United States did not result in the parasite becoming established, apparently because of its assumed inability to survive the winter months in diapause (13, 23).

In addition to *A. smithi*, two more parasites were considered for introduction into Canada. One was *Aphidius ervi* Haliday which is reported as being an effective parasite of *Acyrthosiphon pisum* on clover and alfalfa in Czechoslovakia (31), and *Praon barbatum* Mackauer which was found attacking the pea aphid in central Europe (24).

In 1963, a breeding colony of *A. smithi* was obtained at Belleville for laboratory evaluation. The colony consisted of *ca* 800 mummified parasites (i.e. parasite larvae and pupae encased in the indurated skin of the dead host) that had been field-collected on alfalfa in the San Joaquin Valley, in California (23). Also, breeding stocks of *A. ervi* were received from various central and southern European localities to be compared with *A. smithi* and respresentatives of the three major indigenous parasites, *A. pulcher*, *P. pequodorum* and *A. semiflavus* (24).

A four-year study in the laboratory showed *A. smithi* to be superior by far to any of the other species in searching behaviour, fecundity, developmental time, etc.[1] For example, in comparison tests conducted at 20°C and 55 per cent. relative humidity unmated females of *A. smithi* laid an average of 774 eggs (range 321–1,812) as compared with *P. pequodorum*, *A. ervi*, *A. pulcher* and *A. semiflavus* which laid 199 (84–369), 567 (109–1,011), 316 (90–597) and 312 (123–537) eggs, respectively; all females were provided with 60 three-to-four-day old aphid larvae per day throughout life. Under these conditions *A. smithi*'s performance was highly dependent on the number of potential hosts available. Densities of 5 to 10 aphids per day resulted in a decrease of longevity and of the total number of eggs laid as compared to densities of 40 and higher. The period of intensive egg laying lasted from six to eight days during which time each female deposited an average of some 100 eggs. This number was reached when a minimum of 40 hosts was available per day and increased only slightly at higher host densities. Discrimination between parasitized and unparasitized aphids was incomplete, resulting in a considerable degree of multiparasitism at lower host densities. As only one parasite larva per host is able to complete development, all superfluous eggs are wasted. This responsiveness of *A. smithi* to changes in abundance of the pea aphid was also observed in California alfalfa fields (33).

A. ervi, which also rated very highly because of its reproductive capacity, was imported from Europe by various United States agencies and was released in the eastern United States and in California, Oregon and Washington (24, 25). Conclusive evidence of its establishment there is lacking to date, perhaps because it is difficult to identify. Although *A. ervi* appeared to be better adapted climatically than *A. smithi* to conditions in eastern Canada (in particular its ability to undergo diapause was not in question) it was not considered suitable for release. Cross-breeding attempts under laboratory and field conditions showed that females of *A. ervi* would mate with males of *A. pulcher* to produce viable and fertile offspring, but that mating success in such interspecies crosses was reduced to about one third of the value to be expected in intraspecies crosses. Since *Aphidius* females generally mate only once and unfertilized females produced male offspring only, it was conceivable that the release of *A. ervi* in areas already occupied by *A. pulcher* could result in a reduction of female offspring during subsequent generations (20, 21). The possible benefits of heterosis were not considered to be sufficient grounds for accepting this risk.

Against this background it was decided to release *A. smithi* in preference to any other parasite in Nova Scotia in mid-1964. Establishment of the species was not anticipated. At best, it was hoped

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[1] A detailed account of this analysis will be published elsewhere.

that a release would eventually contribute to a reduction in numbers of alate aphids immigrating into pea fields from road-side vegetation and alfalfa fields.

At about the same time, a new *Aphidius* species parasitic on the pea aphid was discovered in southern Ontario which was later identified as *A. smithi* (23). The parasite was found quite commonly on alfalfa in Lincoln and Welland Counties and was often the most abundant mortality agent. As the possibility of an escape from the Belleville quarantine could be excluded, that discovery attested to the survival and establishment of the earlier U. S. D. A. releases and to the ability of *A. smithi* to go into diapause, which was confirmed later by Angalet & Coles (2).

Further experimental work at Belleville led to the discovery of genetic differences between the 'California' and 'Ontario' strains of *A. smithi.* Whereas the Ontario population is polymorphic for a gene called *Orange* (O), carriers of O are extremely rare in western populations and, so far, have not been found in material received from India. The most marked effect of gene O is on the pigmentation pattern, but there is some evidence that O is pleiotropic, affecting other characteristics of the species as well. Quite possibly, O arose as a new mutation among the offspring of the first releases in the eastern United States. Whether the gene actually conferred a selective advantage on the parasite and permitted it to become established in the initially adverse climatic conditions is subject to verification (19, 22).

Between 1964 and 1966, *A. smithi* spread very rapidly and invaded most alfalfa-growing districts in the Niagara Peninsula and north to a line roughly corresponding to latitude 45°N. along the lower St. Lawrence Seaway and into southwestern Quebec (Fig. 1). As the 'Ontario' strain succeeded very well in these areas it, too, was designated for release in Nova Scotia.

RELEASES

A programme to mass-produce exotic parasites of *Acyrthosiphon pisum* at Belleville for the subsequent release in the Annapolis Valley was started in 1964 and continued until 1967. Releases of predators, in particular the coccinellid, *Coccinella septempunctata* Linnaeus, were considered by H. B. Specht, who imported a small breeding colony for laboratory testing (Table II), but were evidently not released (30).

PARASITES

Aphidius smithi Sharma & Subba Rao (Hymenoptera: Aphidiidae)

First trial releases of some 10,000 mummified specimens of the 'California' strain were made in Hants and Kings Counties, Nova Scotia, in early June 1964 (Table III). About one month later another 10,000 specimens were liberated in the same general area. Some of the releases were open field releases on alfalfa and sweetclover which were inoculated with 300–500 mummies per site. Most of the parasites, however, were liberated on the Sheffield Farm, near Canard, into large field cages containing alfalfa and pea plants which had been infected with 2,000–5,000 greenhouse-bred pea aphids to provide sufficient suitable hosts. The cages were removed when the next generation of mummies appeared to allow the dispersal of emerging adults into neighbouring fields. However, a survey of the immediate release areas failed to reveal *A. smithi* later in 1964.

In 1965 1,000 more mummified specimens of the 'California' strain were liberated on the Sheffield Farm (Tables II, III) but, again, did not result in establishment of the parasite.

In 1966 and 1967 both a laboratory-bred stock of the 'Ontario' strain of *A. smithi* and material that had been field-collected in Prince Edward County, Ontario (the latter including some mummified *A. pulcher*), were released in the Annapolis Valley. These attempts, too, appeared to have failed when release sites were surveyed shortly after the liberations (30).

EVALUATION OF CONTROL ATTEMPTS

Various factors may have contributed to the apparent failure to get *A. smithi* established in Nova Scotia.

First, pre-release surveys had shown that hyperparasites, in particular *Coruna clavata* Walker and various *Asaphes*, *Charips* and *Lygocerus* species, are largely responsible for the sharp numerical decline of the primary parasites observed in late summer and fall. As these hyperparasites are not restricted to indigenous *Aphidius* species but also attack the exotic *A. smithi*, their action may have resulted in the loss of small founder colonies.

Second, van den Bosch *et al.* (32, 33) found evidence in California alfalfa fields of a deliberate movement of female *A. smithi* away from the site of development, unlike male wasps that in general remained there. This emigration would account for an additional reduction in parasite density.

Third, it is conceivable that the 'Ontario' strain of *A. smithi* is sufficiently well adapted to the climate of southern and central Ontario but does not tolerate conditions in Nova Scotia. A survey of the major mortality agents of *Acyrthosiphon* in the eastern United States revealed that *A. smithi* is the dominant *Aphidius* species west of about longitude 80°W. but that *A. pulcher* is dominant east of that line (1).

Lastly, the possibility must be considered that *A. smithi* specimens were recovered in post-release surveys but were misidentified. Morphological differences between *A. smithi* and *A. pulcher* are very slight and do not always permit the correct classification of individual specimens. Colour, although reliable for distinguishing specimens that were bred at 20°C, varies according to provenance, i.e. cool and humid climates induce a melanistic coloration in *A. smithi* which makes it practically indistinguishable from *A. pulcher* (24).

The loss or apparent loss of *A. smithi* due to hybridization with *A. pulcher* and introgression can be excluded on the basis of experimental evidence (21).

RECOMMENDATIONS

Recommendations for future action in the biological control of the pea aphid depend on a careful survey of the major release sites. Although available information, which is essentially that collected until 1968, points to the continued presence of the wasp in Ontario, there is also evidence of changes in population structure (22). It would be of importance to also survey central Ontario and areas along the St. Lawrence Seaway to determine the spread, if any, of *A. smithi* since 1966.

Depending on this information two options may be considered.

Assuming that the 'Ontario' strain can be shown to have successfully invaded areas east of Sherbrooke-St. Jean, Quebec, the first option would emphasize measures to speed up this process by inoculation releases in alfalfa-growing districts throughout Quebec, New Brunswick and Nova Scotia. Release of the parasite into field cages would seem preferable to open releases, as would the retention of field cages for one to two months to prevent the loss of adult wasps due to emigration. Furthermore it might be advisable to remove all hyperparasites and potential competitors from these cages by insecticide treatment and then to re-stock cages with insectary-bred pea aphids before releasing the parasite. Following the successful colonization of *A. smithi* in Nova Scotia, farmers should be advised to use strip-cutting of alfalfa in preference to solid harvesting procedures to maximize the economic impact of the parasite (32, 33).

Failing evidence of an eastward spread of *A. smithi* along the St. Lawrence Seaway, the mass production of the parasite and inundative releases would merit exploration. The enormous reproductive potential of the wasp supports such a decision. The first step in that programme should be to show that the inundation with *A. smithi*, which would have to be repeated annually, reduces the immigration of alate *Acyrthosiphon* into pea fields during the critical period between budding and harvesting.

It should be remembered that when the programme to control the pea aphid biologically in Nova Scotia was initiated in 1963, one important aspect of the study was to gain information (largely lacking to date) on why so many attempts to colonize exotic mortality agents have failed in the past. The eventual establishment of *A. smithi* was not considered to constitute success *per se*. It is beyond the scope of this review to expound on the merits of continuing with a long-term study of processes affecting colonizing species independent of economic considerations (20).

If an assessment must be based on economic criteria, however, an estimate of pest damage should precede all other decisions. It is likely that biological controls will compare favourably with current practices on a cost-benefit basis in a situation such as that found in Nova Scotia, even if other aspects of chemical control measures (such as toxicity to non-target organisms and accumulation of residues) were to be disregarded.

ACKNOWLEDGMENT

Dr. H. B. Specht, Research Station, Canada Department of Agriculture, Kentville, Nova Scotia, cooperated in making the field releases in Nova Scotia and carried out most of the post-release surveys.

TABLE II

Cage releases and laboratory studies of parasites and predators against *Acyrthosiphon pisum* (Harris)

Species and Province	Year	Origin	Number
Aphidius smithi Sharma and Subba Rao	1967	U.S.A.	100
Nova Scotia	1966	Canada	300
Coccinella septempunctata L.			
Nova Scotia	1967	U.S.A.	100

TABLE III

Open releases of parasites against *Acyrthosiphon pisum* (Harris)

Species and Province	Year	Origin	Number
Aphidius pulcher Baker and *A. smithi* Sharma and Subba Rao			
Nova Scotia	1966	Canada	700
A. smithi			
Nova Scotia	1964	U.S.A.	20450
	1965	U.S.A.	900
	1967	Canada	500

LITERATURE CITED

1. Angalet, G. W. (1967). Personal communication. United States Department of Agriculture, Moorestown, N.J.
2. Angalet, G. W. & Coles, L. W. (1966). The establishment of *Aphidius smithi* in the eastern United States. *J. econ. Ent.* 59: 769–70.
3. Beardsley, J. W. (1961). A review of the Hawaiian Braconidae (Hymenoptera). *Proc. Hawaii. ent. Soc.* **17**: 333–66.
4. Börner, C. & Heinze, K. (1957). Aphidina–Aphidoidea. Blattläuse, plantlice (aphids), pucerons (aphides). *In P.* Sorauer, *Handb. PflKrankh.* 5 Band, 2 Teil, 5 Aufl., 4 Liefg: Homoptera II, 402 pp. P. Parey, Berlin and Hamburg.
5. Campbell, R. E. (1926). The pea aphis in California. *J. agric. Res.* **32**: 861–81.
6. Cartier, J. J. (1959). Recognition of thee biotypes of the pea aphid from southern Quebec. *J. econ. Ent.* **52**: 293–94.
7. Cooke, W. C. (1963). Ecology of the pea aphid in the Blue Mountain Area of eastern Washington and Oregon. *Tech. Bull. U.S. Dep. Agric.* **1287**, 48 pp.

8. Davis, C. J. & Krauss, N. L. H. (1962). Recent introductions for biological control in Hawaii-VII. *Proc. Hawaii. ent. Soc.* **18**: 125–9.
9. Davis, J. J. (1915). The pea aphis with relation to forage crops. *Bull. U.S. Dep. Agric.* **276**, 67 pp.
10. Eastop, V. F. (1966). A taxonomic study of Australian Aphidoidea (Homoptera). *Aust. J. Zool.* **14**: 399–592.
11. Fernald, M. L. (1950). Gray's manual of botany, 8th ed. American Book Co., New York.
12. Ferrière, C. (1965). Hymenoptera Aphelinidae de l'Europe et du Bassin Méditerranéen. *In* Faune de l'Europe et du Bassin Méditerranéen, 1. Masson et Cie., Paris.
13. Hagen, K. S. & Schlinger, E. I. (1960). Imported Indian parasite of pea aphid established in California. *Calif. Agric.* **14**: 5–6.
14. Harrington, C. D. (1945). Biological races of the pea aphid. *J. econ. Ent.* **38**: 12–22.
15. Hille Ris Lambers, D. (1947). Contributions to a monograph of the Aphididae of Europe, III. *Temminckia* **7**: 179–319.
16. Johnson, W. G. (1900). The destructive green-pea louse. *Can. Ent.* **32**: 56–60.
17. Kennedy, J. S., Day, M. F. & Eastop, V. F. (1962). A conspectus of aphids as vectors of plant viruses. Commonw. Inst. Ent., London.
18. Lindroth, C. H. (1957). The faunal connections between Europe and North America. Wiley & Sons, New York.
19. Mackauer, M. (1968). Phenotypic polymorphism in *Aphidius smithi* Sharma and Subba Rao (Hymenoptera, Aphidiidae). *Entomophaga* **13**: 281–7.
20. Mackauer, M. (1968). Tiergeographische Aspekte der biologischen Schädlingsbekämpfung. *Natur u. Museum, Frankfurt* **98**: 491–5.
21. Mackauer, M. (1969). Sexual behaviour of and hybridization between three species of *Aphidius* Nees (Hymenoptera: Aphidiidae), parasitic on the pea aphid. *Proc. ent. Soc. Wash.* **71**: 339–51.
22. Mackauer, M. Unpublished observations.
23. Mackauer, M. J. P. & Bisdee, H. E. (1965). *Aphidius smithi* Sharma and Subba Rao (Hymenoptera: Aphidiidae) a parasite of the pea aphid new in southern Ontario. *Proc. ent. Soc. Ont.* **95**: 121–4.
24. Mackauer, M. & Finlayson, T. (1967). The hymenopterous parasites (Hymenoptera: Aphidiidae and Aphelinidae) of the pea aphid in eastern North America. *Can. Ent.* **99**: 1051–82.
25. Mackauer, M. & Starý, P. (1967). World Aphidiidae (Hym. Ichneumonoidea). *In* Index of entomophagous insects. Le François, Paris.
26. Markkula, M. (1963). Studies on the pea aphid, *Acyrthosiphon pisum* Harris (Hom., Aphididae), with special reference to the differences in the biology of the green and red forms. *Annls Agric. Fenn. Helsinki, Seria Animalia nocentia* N. 2, *Suppl.* 7, **1**: 1–30.
27. Meier, W. (1957). Über *Acyrthosiphon pisum* Harris 1776 (Hemipt. Aphid.). *Mitt. schweiz. ent. Ges.* **30**: 89–92.
28. Meier, W. (1958). Beiträge zur Kenntnis der auf Papilionaceen lebenden *Acyrthosiphon*-Arten (Hemipt. Aphid.). *Mitt. schweiz. ent. Ges.* **31**: 291–312.
29. Müller, F. P. (1962). Biotypen und Unterarten der 'Erbsenläuse' *Acyrthosiphon pisum* (Harris). *Z. Pflkrankh. Pflpath. Pflschutz* **69**: 129–136.
30. Specht, H. B. (1966–69). Personal communication. Research Station, Canada Department of Agriculture, Kentville, Nova Scotia.
31. Starý, P. (1962). Hymenopterous parasites of the pea aphid *Acyrthosiphon onobrychis* (Boyer) in Czechoslovakia. I. Bionomics and ecology of *Aphidius ervi* Haliday. *Zool. Listy* **11**: 265–78.
32. van den Bosch, R., Lagace, C. F. and Stern, V. M. (1967). The interrelationship of the aphid, *Acyrthosiphon pisum*, and its parasite, *Aphidius smithi*, in a stable environment. *Ecology* **48**: 993–1000.
33. van den Bosch, R., Schlinger, E. I., Lagace, C. F. and Hall, J. C. (1966). Parasitization of *Acyrthosiphon pisum* by *Aphidius smithi*, a density-dependent process in nature (Homoptera: Aphididae) (Hymenoptera: Aphidiidae). *Ecology* **47**: 1049–55.

3. *ARGYROTAENIA VELUTINANA* (WALKER), RED-BANDED LEAF ROLLER (LEPIDOPTERA: TORTRICIDAE)

A. Hikichi[1]

The red-banded leaf roller, *Argyrotaenia velutinana* (Walker), which commonly feeds on a number of broad-leaved trees in eastern North America, greatly increased in numbers in commercial apple orchards shortly after DDT came into general use for codling moth control. Though DDT and organophosphorus compounds effectively eliminate this pest from orchards, negligence in applying these materials has often resulted in loss of up to 25 per cent. of the fruit (4). Losses of this magnitude result mainly from poor control of the first generation; the survivors are able to multiply in subsequent generations when spray coverage is difficult to achieve because of denser foliage.

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[1] The work described here was conducted while the author held a position at the Research Station, Canada Department of Agriculture, Vineland Station, Ontario.

Twenty-five or more species of parasitic insects attack the red-banded leaf roller, but none are host-specific (3, 5). All species are polyphagous and depend on two or more hosts for survival. In some cases the alternative hosts were injurious pests in apple orchards.

A. velutinana is native to North America. The Commonwealth Institute of Biological Control showed (1) that on apple in Europe the species most closely related to it taxonomically and biologically is *A. pulchellana* Haworth; the C.I.B.C. showed also that *Colpoclypeus florus* (Walker) was the most abundant parasitic insect attacking *A. pulchellana*.

C. florus is an external gregarious parasite that attacks all host larval stages except the first. It has been recorded from various tortricids on deciduous trees and herbaceous plants. Two generations can be completed on one host generation. Hibernation usually takes place in the larval stage, and less frequently in the pupal stage. Mating frequently occurs before adults leave the host web. Female parasites enter the host web and contact the host, without paralyzing it. The host larva usually responds by additional web spinning that can be readily recognized. Eggs of the parasite are laid on the surface of the web. The life cycle lasts about 14 days. Parasitism of *A. pulchellana* increased from 10–12 per cent. early in the season to 46–68 per cent. later, in one locality, despite a ten-fold increase in host population. The parasite is recorded from Britain and Czechoslovakia, and has been found in northern and southern Germany, Switzerland, Austria, Italy and southern France (2).

C. florus was chosen for introduction into Canada because it is polyphagous on various tortricids, including the ones on fruit trees, and should adapt to *A. velutinana.* It is multivoltine, and increases in numbers rapidly during the season. Also it occurs over a wide geographical area in a variety of climatic conditions which suggested that it should adapt to a Canadian climate.

Studies in Canada were started in 1966 with *C. florus* adults reared from larvae collected near Montpelier, France and Verona, Italy. The numbers received alive at Simcoe were 395 and 359 respectively. These trials showed that under laboratory conditions, *C. florus* parasitized and developed on *A. velutinana* and the strawberry leaf roller, *Ancylis comptana fragariae* (Walsh and Riley). The latter was selected as the target species for the first release because it is more easily collected and it occurs in unsprayed fields whereas red-banded leaf roller is more abundant in sprayed orchards.

Parasites from Italy were cultured in the laboratory on *A. velutinana* and 250 *C. florus* adults were released near Simcoe, Ontario in the field against *A. comptana fragariae* on 26 August, 1966. No establishment has been recorded in the release area.

On 21 June 1967, 2,400 *C. florus* were released near Simcoe, Ontario in an orchard infested by *A. velutinana.* There has been no evidence of establishment.

Because laboratory tests indicated that *C. florus* is susceptible to spray chemicals, it was suspected that its establishment would be difficult. Therefore, strains of either *C. florus* or other parasitic species more resistant to our commonly used insecticides must be found before they can be established successfully in commercial apple orchards under present conditions.

LITERATURE CITED

1. Carl, K. (1963). Parasites of leaf rollers on apple in Europe. Unpublished Report, European Station, Commonw. Inst. Biol. Control, Delémont, Switzerland.
2. Carl, K. P. (1965). Natural enemies of *Argyrotaenia pulchellana*. Annual report of work in 1965. Unpublished Report, European Station, Commonw. Inst. Biol. Control, Delémont, Switzerland.
3. Hikichi, A. (1962). Notes on mortality factors affecting the red-banded leaf roller, *Argyrotaenia velutinana* (Wlkr.), (Lepidoptera: Tortricidae) in an unsprayed apple orchard in Ontario. *Proc. ent. Soc. Ont.* 92: 180–2.
4. Hikichi, A. (1962). Some factors influencing the control of the red-banded leaf roller, *Argyrotaenia velutinana* (Wlkr.), (Lepidoptera: Tortricidae) on apple in Norfolk County, Ontario. *Proc. ent. Soc. Ont.* 92: 182–8.
5. Hikichi, A. (1962). Unpublished annual progress report.

4. *CARPOCAPSA POMONELLA* (L.), CODLING MOTH (LEPIDOPTERA: OLETHREUTIDAE)

C. R. MacLellan, M. D. Proverbs and R. P. Jaques

PEST STATUS

The codling moth, *Carpocapsa pomonella* (L.), is potentially the most destructive insect pest of apples in Canada and indeed throughout most apple-growing areas of the world. It is also a pest of pears and occasionally of other fruits. Eggs are laid near or on the fruit and the larvae penetrate the fruit where they are protected from parasite attacks by natural enemies. Biological control by introductions of new species has not appeared promising (12). Chemical insecticides have been used extensively but, because of their adverse side effects, research on codling moth control in Canada has centred in three areas: integration by the use of selective insecticides and fewer and more timely application of them; inundation with a microbial insecticide; and autocidal control using the so-called sterile-male technique. These approaches are reviewed in this chapter.

NATURAL ENEMIES

(C. R. M.)

The use of native natural enemies of the codling moth has been studied, and in some instances evaluated, in commercial orchards of Nova Scotia for many years. With the recommendation of Ryania, a somewhat selective botanical insecticide, on a commercial scale in 1954, an opportunity arose for the study of natural enemies in an integrated control programme. The use of a pesticide in the most selective manner possible is indeed an important integral part of the programme. The use of Ryania kept damage by the codling moth below a commercially acceptable level and allowed the natural enemies of this and other pests to operate relatively unhindered. Many growers, after obtaining satisfactory chemical control with Ryania, maintained codling moth numbers at low levels with one or two applications each year or in alternate years, whereas others went as many as 7 years without any chemical control of codling moth.

The generally low levels of the pest made it desirable to study the effects of natural enemies on an extensive scale and those attacking the overwintering stage were studied first. The chief natural enemies of this stage are two species of woodpecker: the hairy woodpecker, *Dendrocopus villosus villosus* (L.), and the northern downy woodpecker, *Dendrocopus pubescens medianus* (Swainson). Woodpeckers attack according to the density of the pest, taking a greater portion at high numbers than at low numbers. They account for an annual average of slightly more than 50 per cent. mortality of the larvae overwintering on the tree trunks (7, 8). The larval parasite, *Ascogaster quadridentata* Wesm., similarly accounts for an average of 5–20 per cent.

Mortality due to low winter temperatures and the fungus, *Beauveria bassiana* (Balsamo) Vuillemin, is insignificant and seldom averages above 2 per cent. (6).

Larvae which attempt to overwinter by spinning cocoons in ground debris suffer heavy predation, in one study amounting to 94 per cent. (9).

The combined effects of natural winter mortality under an integrated control programme may be of sufficient significance to eliminate the use of a chemical spray for summer control of the codling moth.

After the trend of codling moth behaviour was established, more intensive studies were conducted on mortality of eggs and young larvae. The combined egg mortality caused by the parasite *Trichogramma* sp. and by a group of mite and insect predators averaged annually close to 20 per cent. (10, 11). The mite, *Atomus* sp., the thrips, *Haplothrips faurei* Hood and *Leptothrips mali* (Fitch), and the mirids *Diaphnocoris* spp., *Hyaliodes harti* Knight, *Pilophorus perplexus* D. & S. and *Blepharidopterus angulatus* (Falk.) are the chief egg predators, most of which are found throughout the apple-growing region of Nova Scotia.

Larvae, newly hatched from the egg, are subject to natural causes of death such as failure to find fruit, unsuccessful fruit penetration, dispersal, and predation. This mortality sometimes reaches 70 per cent. Predators which feed readily on young codling moth larvae under natural conditions include the mite *Anystis agilis* Banks, the mirids *B. angulatus*, *Diaphnocoris* spp., *H. harti*, *Phytocoris* sp., and *P. perplexus*, and other less common predacious species including coccinellids, pentatomids, clerids, and chrysopids.

When predators of eggs and young larvae are scarce and chemical controls are not used, codling moth survival is high, and conversely when effective predators are numerous codling moth survival is reduced (10, 11). Predation alone may be ineffective in preventing economic damage in which case growers will use a chemical (Ryania at present) to reduce the level of codling moth to manageable proportions. Where this method of control—the protection of natural enemies—has been followed faithfully, damage by codling moth has been light, harmful residual build-up has been minimized, and reduced costs of spray materials have resulted.

MICROBIAL INSECTICIDE

(R. P. J.)

Control of *Carpocapsa pomonella* by conventional insecticides frequently causes undesirable effects on the orchard fauna. *Bacillus thuringiensis* Berliner, a bacterium produced as a microbial insecticide, is specific for Lepidoptera and killed larvae of *C. pomonella* in preliminary tests (4).

Application of a commercial preparation of *B. thuringiensis* to bearing apple trees in large orchard plots at Kentville, Nova Scotia on five to seven occasions in each of 4 consecutive years reduced by 50–75 per cent. injury of fruit of the varieties McIntosh and Delicious by larvae of *C. pomonella* (5). The control was considered not acceptable economically, however. The degree of control of *C. pomonella* by *B. thuringiensis* was superior to that obtained in preliminary tests in which the bacterium *Bacillus cereus* F. and F., a close relative of *B. thuringiensis*, was applied to apple trees (13).

RELEASE OF STERILE MALES

(M. D. P.)

Work on the feasibility of releasing sterilized laboratory-reared moths to control or eradicate *Carpocapsa pomonella* was started in British Columbia in 1956 and in Washington State a few years later. In British Columbia, exposure of various stages of the insect to high temperatures indicated that heat could not be used to induce sexual sterility without causing prohibitively high mortality (14). Sterilization by gamma radiation was more successful. Exposure of fully mature pupae or adult moths to 40 krad induced 100 per cent. sterility in the female and at least 98 per cent. dominant lethality in the sperm of the male without seriously affecting the insects' life span, flight habits, or mating behaviour (15). Sperm from irradiated males were, however, less competitive in egg fertilization than were sperm from nonirradiated males, for, when an untreated female was mated both by an irradiated and a nonirradiated male, most of the eggs laid were viable (16). Despite this, it was shown in the laboratory and in field cages over dwarf apple trees that the reproductive rate was markedly reduced when sterilized moths were added to a population of untreated moths (3, 16, 17). These and later results indicated that it was necessary to employ a ratio of about 20 sterile to 1 native (fertile) male in order to initiate a rapid downward trend in a native population.

The sterility method of control was first assessed in a small abandoned apple orchard in the Okanagan Valley (18). In 1961, the codling moth population in this semi-isolated orchard was reduced to a manageable level (from 80 per cent. injured fruit at harvest in 1960 to 5 per cent. in 1961) by chemical sprays. From 1962–64, gamma-sterilized male moths, marked with fluorescent dusts, were released three times per week from the pink-bud stage of apple until late September when codling moth flight has virtually ceased. Because of rearing problems, the ratio of sterile to fertile males in the orchard in 1962 dropped to about 8:1 during the peak density of adult first brood moths. This resulted in a slight increase in the native population for at harvest 7 per cent. of the fruit was injured by second-brood larvae. During the following year the ratio of sterile to fertile males never fell below 20:1, a downward trend was induced in the population as indicated by sex-trap records, and fruit injury at harvest was reduced to 0·3 per cent. During the third year of release only one native moth was trapped in the orchard and fruit injury at harvest was further reduced to 0·05 per cent. The codling moth probably would have been eliminated completely if the test trees had been adequately isolated from infested commercial orchards.

Results of laboratory and field-cage tests had suggested that the release of sterile males alone would effect somewhat better control than the release of sterile males plus sterile females (3, 16, 17). However, since sexing is laborious and because unconfined moths and caged insects may behave differently, the effect of releasing mixed sexes was assessed in an abandoned 5-acre apple orchard (19). In 1964 and 1965, male and female moths, gamma-sterilized as adults, were released in the orchard three times weekly from the pink-bud stage of apple until the third week in September. A total of 265,000 sterile moths were released during the first year, resulting in a reduction of injured fruit at harvest from approximately 60 per cent. in 1963 to 2 per cent. in 1964. In the following year, 478,000 moths were released, resulting in an average ratio throughout the season of 129 sterile to 1 native male moth as determined by sex traps. At harvest, fruit injury by second-brood larvae was reduced to 0·09 per cent., and would have been lower still if native moths had not reinvaded the experimental orchard from nonsprayed apple trees 0·75 miles away.

The sterility method of control was next assessed in a commercial apple orchard (20). From 1966 to 1968, the release of radiation-sterilized male and female moths gave at least as good control as the usual chemical spray programme used in adjacent orchards. Useful information was also accumulated on methods of integrating chemical sprays with sterile-insect release.

Similar experiments in Washington State in 1964 and 1965 with tepa-sterilized male moths failed, probably because too few moths were released (2). Successful control was realized in 1966 with tepa- and radiation-sterilized males. Also, in 1967 when radiation-sterilized males and females were released by helicopter in a 93-acre orchard, the percentage of injured apples at harvest was approximately the same as in surrounding orchards where control was achieved by chemical sprays (1).

In 1969 and 1970, control by sterile moths in British Columbia will be extended to about 120 acres. An area release, involving 1,000 acres or more, will be initiated in 1971 to determine the economic feasibility of this method of control.

RECOMMENDATIONS

(1) Studies of the rôle of natural enemies in regulating the codling moth and techniques for conserving and increasing these mortality factors should be continued.

(2) Control of the codling moth by sprays of *Bacillus thuringiensis* is not economical at present. This method should be kept under review, however, as the situation may change and other considerations become more important.

(3) Field trials with releases of radiation-sterilized moths in British Columbia appear very promising and should be continued and extended. Cost analyses should also be prepared to appraise the feasibility of this method.

(4) Closer integration of the separate approaches reviewed above is needed.

LITERATURE CITED

1. Butt, B. A. (1967). Recent progress in the release of sterile codling moth. *Proc. Wash. St. hort. Ass.* 63rd Meeting: 17–8.
2. Butt, B. A., Hathaway, D. O. & Howell, J. F. (1965). Codling moth sterile male release program at White Swan, Washington. *U.S. Dep. Agr., Ent. Res. Div., Yakima, Wash., Spec. Rep.* AADFI–65–1, 18 pp.
3. Hathaway, D. O. (1966). Laboratory and field cage studies of the effects of gamma radiation on codling moths. *J. econ. Ent.* 59: 35–7.
4. Jaques, R. P. (1961). Control of some lepidopterous pests of apple with commercial preparations of *Bacillus thuringiensis* Berliner. *J. Insect Path.* 3: 167–82.
5. Jaques, R. P. (1965). The effect of *Bacillus thuringiensis* Berliner on the fauna of an apple orchard. *Can. Ent.* 97: 795–802.
6. Jaques, R. P. & MacLellan, C. R. (1965). Fungal mortality of overwintering larvae of the codling moth in apple orchards in Nova Scotia. *J. Invert. Path.* 7: 291–6.
7. MacLellan, C. R. (1958). Role of woodpeckers in control of the codling moth in Nova Scotia. *Can. Ent.* 90: 18–22.
8. MacLellan, C. R. (1959). Woodpeckers as predators of the codling moth in Nova Scotia. *Can. Ent.* 91: 673–80.
9. MacLellan, C. R. (1960). Cocooning behaviour of over-wintering codling moth larvae. *Can. Ent.* 92: 469–79.
10. MacLellan, C. R. (1962). Mortality of codling moth eggs and young larvae in an integrated control orchard. *Can. Ent.* 94: 655–66.
11. MacLellan, C. R. (1963). Predator populations and predation on the codling moth in an integrated control orchard—1961. *Mem. ent. Soc. Can.* 32: 41–54.
12. McLeod, J. H. (1962). Biological control of pests of crops, fruit trees, ornamentals and weeds in Canada up to 1959. *In* A review of biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol. Control* 2: 1–33.
13. Phillips, C. M., Bucher, G. E. & Stephens, J. M. (1953). Note on preliminary field trials of a bacterium to control the codling moth. *Can. Ent.* 85: 8.
14. Proverbs, M. D. & Newton, J. R. (1962). Effect of heat on the fertility of the codling moth, *Carpocapsa pomonella* (L.) (Lepidoptera: Olethreutidae). *Can. Ent.* 94: 225–33.
15. Proverbs, M. D. & Newton, J. R. (1962). Influence of gamma radiation on the development and fertility of the codling moth, *Carpocapsa pomonella* (L.) (Lepidoptera: Olethreutidae). *Can. J. Zool.* 40: 401–20.
16. Proverbs, M. D. & Newton, J. R. (1962). Some effects of gamma radiation on the reproductive potential of the codling moth, *Carpocapsa pomonella* (L.) (Lepidoptera: Olethreutidae). *Can. Ent.* 94: 1162–70.
17. Proverbs, M. D. & Newton, J. R. (1962). Suppression of the reproductive potential of the codling moth by gamma irradiated males in caged orchard trees. *J. econ. Ent.* 55: 934–6.
18. Proverbs, M. D., Newton, J. R. & Logan, D. M. (1966). Orchard assessment of the sterile male technique for control of the codling moth, *Carpocapsa pomonella* (L.) (Lepidoptera: Olethreutidae). *Can. Ent.* 98: 90–5.
19. Proverbs, M. D., Newton, J. R. & Logan, D. M. (1967). Autocidal control of the codling moth by release of males and females sterilized as adults by gamma radiation. *J. econ. Ent.* 60: 1302–6.
20. Proverbs, M. D., Newton, J. R. & Logan, D. M. (1969). Codling moth control by release of radiation-sterilized moths in a commercial apple orchard. *J. econ. Ent.* 62: 1331–4.

5. *COLEOPHORA MALIVORELLA* RILEY, PISTOL CASEBEARER (LEPIDOPTERA: COLEOPHORIDAE)

R. O. Paradis and E. J. Leroux[1]

Life tables, developed for natural population studies of the pistol casebearer, *Coleophora malivorella* Riley, in Quebec apple orchards, revealed that the parasite *Chrysocharis laricinellae* (Ratz.) and birds were the 'key' factors which reduced the casebearer population from epidemic levels in 1959–60 to endemic levels in 1962. Over the seven generations observed, the kill of summer larvae by *C. laricinellae* averaged 29 per cent., whereas the mortality of winter larvae due to this parasite and bird predation together were 2–99 per cent. (3). It was observed that *C. laricinella* has three generations a year, attacks all larval stages of *C. malivorella*, overwinters as larvae within the host body or shelter, and can well survive the lower temperatures experienced in apple orchard areas.

C. laricinellae was first introduced in Quebec, at Berthierville, in 1943 for the control of the larch casebearer, *Coleophora laricellae* (Hbn.) (1, 2), and the species was reared from larvae of the pistol casebearer in 1957, at Rougemont, 50 miles south of Berthierville. Thus, the species, already

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[1] Formerly of the Research Station, Canada Department of Agriculture, St. Jean, Quebec.

considered as a successful introduction for the control of *C. laricella* on forest trees (4), was afterwards found to be very effective against *C. malivorella* in apple orchard districts of southwestern Quebec (3).

LITERATURE CITED

1. Graham, A. R. (1944). The establishment of some imported parasites of the larch casebearer, *Haploptilia laricella* Hbn., in Ontario. *74th A. Rep. ent. Soc. Ont.* (1943): 48–52.
2. Graham, A. R. (1949). Developments in the control of the larch casebearer, *Coleophora laricella* (Hbn.). *79th A. Rep. ent. Soc. Ont.* (1948): 45–50.
3. LeRoux, E. J., Paradis, R. O. & Hudon, M. (1963). Major mortality factors in the population dynamics of the eye-spotted bud moth, the pistol casebearer, the fruit-tree leaf roller, and the European corn borer in Quebec. *Mem. ent. Soc. Can.* **32**: 67–82.
4. Turnbull, A. L. & Chant, D. A. (1961). The practice and theory of biological control of insects in Canada. *Can. J. Zool.* **39**: 697–753.

6. *EUXOA MESSORIA* (HARRIS), DARK-SIDED CUTWORM (LEPIDOPTERA: NOCTUIDAE)

G. E. Bucher

PEST STATUS

Euxoa messoria (Harris), the dark-sided cutworm, is perhaps the most serious pest of tobacco in Ontario. The light sandy soils of the main tobacco area along the north shore of Lake Erie are favourable for the development of this cutworm. Eggs laid in the summer hatch in the following spring and young larvae begin to feed on rye which is used as a rotation and cover crop, so that partly grown larvae are ready to feed on tobacco seedlings as soon as these are transplanted towards the end of May. Larvae damage the plants in several ways: they may cut the stem at ground level, thus causing complete destruction of the seedling; they may injure the terminal shoot and stimulate the plant to grow suckers, which do not produce a good yield of harvestable leaves; and they may eat the leaves themselves. Plants badly injured within 10 days of transplanting are usually replaced, so that early serious damage increases the cost of producing the crop, but is not represented by a total loss of yield. Damage done after 10 days results in loss of yield, because replacement transplants do not have sufficient time to produce a normal harvest of mature leaves before the first fall frost. Yields in fields not treated with insecticides may be reduced to half the normal values and fluctuate widely in response to the density of the cutworm populations. As tobacco acreage is strictly limited by regulation, any loss of yield is costly to the grower. No attempt is made to control cutworms in the rye rotation crop so that breeding adults are common and larvae are always present in the fields prepared for tobacco seedlings, though their numbers vary from year to year and from place to place. Present control consists of killing the young larvae before the tobacco seedlings are transplanted, by spraying insecticides (usually DDT) on the rye before it is ploughed, or on the soil prepared for the seedlings, or both. Present insecticidal control is adequate but continued addition of insecticides to tobacco land increases the residual insecticidal content of the soil, contributes to pollution and may well hasten the development of insecticide resistance of cutworms and root maggots, which are the other serious enemies of tobacco. Thus an alternative method of control is desirable.

BACKGROUND

Diseased larvae of *Euxoa messoria* have not been collected in the field in Ontario, but they are experimentally susceptible to three virus diseases isolated from a related cutworm, *E. ochrogaster*

(Guenée). The virus diseases are a nuclear polyhedrosis that attacks the tracheal matrix, fat body, hypodermis, and blood cells; a granulosis that infects the same tissues; and a cytoplasmic polyhedrosis that infects the cells of the midgut. Larvae are infected by eating food contaminated by the polyhedral or capsular inclusion bodies of all three viruses. The cytoplasmic virus develops slowly, and a proportion of infected larvae survive to form pupae and adults, so that it holds little promise for immediate control of cutworms in tobacco seedlings. The other two viruses produce lethal infections that reduce the activity and feeding of larvae within 7–10 days. The infective dose of polyhedra or capsules varies from larva to larva and increases markedly as larvae develop. Thus young larvae are very susceptible to infection and die rapidly, whereas late-instar larvae are more resistant and may live for a long period when infected.

CONTROL ATTEMPTS

In 1965 the author applied the nuclear polyhedrosis and the granulosis in bran baits to plots in a commercial tobacco field and to small experimental plots at the Canada Department of Agriculture Research Station, Delhi, Ontario, and their effect was compared with that given by various formulations of DDT applied in both baits and sprays. All baits were applied to soil tilled and prepared to receive tobacco transplants two days before the tobacco seedlings were transplanted, at the rate of 25 lbs of bran, 2×10^{11} to 2×10^{12} virus polyhedra, 3×10^{12} to 3×10^{13} virus capsules, and 0·25 to 1·0 lbs of DDT per acre. The viruses did not prevent heavy damage to tobacco seedlings under the conditions of the trials though 40–90 per cent. of larvae retrieved from the virus plots within two weeks of treatment were diseased. It appeared that larvae seriously damaged the tobacco seedlings before the virus diseases were capable of limiting their feeding or activity. Therefore virus pathogens would have to be applied to infect larvae at least 10 days before tobacco seedlings are planted in order to protect the seedlings from damage. This time element prevents the use of baits, and suggests that virus should be sprayed on the rye cover crop to infect cutworm larvae before the rye is ploughed and the fields are prepared for tobacco seedlings. The observation that baits containing 9×10^{11} nuclear polyhedra plus 0·25 lbs DDT per acre gave as good control as those containing 1·0 lbs DDT suggested that further investigations of combinations of virus and minimal doses of insecticides might be profitable.

In 1968 the author, with the cooperation of Dr. H. W. Cheng of the Canada Department of Agriculture Research Station, Delhi, Ontario, sprayed nuclear polyhedrosis on the rye cover crop at the end of April shortly after the young larvae were demonstrable in the field and about two weeks before the rye was tilled. The virus was sprayed at four dose levels of 0, 1×10^{9}, 1×10^{10}, and 5×10^{10} polyhedra per m^2 (*i.e.* 4×10^{12}, 4×10^{13}, 2×10^{14} polyhedra per acre) in an aqueous suspension containing 0·05 per cent. plyac spreader; and plots were replicated six times. Tobacco seedlings were transplanted towards the end of May, damage was recorded at weekly intervals for four weeks until the cutworms pupated, badly damaged seedlings were replanted for 10 days, as would be done commercially, and harvest was measured by the green weight of mature leaves from five pickings in August and September. Virus treatments reduced damage to tobacco plants in proportion to the virus dose. The damage followed a probit-log dose regression with a slope of $-0{\cdot}7$. Thus, in untreated plots 44 per cent. of the plants were completely lost and a further 29 per cent. suffered damage, whereas in the plots treated with the highest virus dose, only 5 per cent. of the plants were lost and a further 5 per cent. suffered light damage by the beginning of harvest. Sampling showed that the virus treatments reduced the number of larvae in the plots to between 1/6 and 1/10 the number in the untreated plots. The yields at harvest, however, did not show differences in the same proportions for a number of reasons. These included the replacement of badly damaged seedlings for the first 10 days, the fact that loss of one plant in a row stimulated the adjacent plants to greater growth, and the fact that a small number of cutworms can cause a disproportionate loss of yield.

Also in 1968 granulosis virus was sprayed on the rye cover crop of a 90 ft × 40 ft plot later commercially planted to tobacco. The virus was applied to 50 spots of 1 m^2 area arranged in a grid pattern to cover about 1/8 of the plot area at the rate of $4{\cdot}6 \times 10^{11}$ capsules on each square metre sprayed ($2{\cdot}8 \times 10^{14}$ capsules per acre). Though 26 per cent. of the larvae recovered from the plot were infected with granulosis, cutworm damage was not reduced in comparison to control plantings.

EVALUATION OF CONTROL ATTEMPTS

Cutworm control by spraying the rye cover crop with nuclear polyhedrosis was good enough to warrant planning further trials in 1969 to determine if combinations of the virus with bacterial pathogens or with sublethal doses of insecticides would provide satisfactory control at lower virus doses. The main factor preventing the economic use of virus as an insecticide for crop protection is its cost. Viruses must be propagated in living insects and extracted from them, a procedure that costs far more than the production of chemical insecticides. Thus viruses must be infective at low doses if they are to compete economically with insecticides for immediate crop protection.

There is the possibility that virus disease can be established as a permanent factor of mortality in a field population of insects, especially where the host crop is grown repeatedly on the same land, as is tobacco. The cytoplasmic virus of the gut and the granulosis, being less lethal in action than the nuclear polyhedrosis, have more chance of being transmitted by infected survivors to the following generation of cutworms. Future work is planned to investigate this aspect.

7. *FORFICULA AURICULARIA* L., EUROPEAN EARWIG (DERMAPTERA: FORFICULIDAE)

RAY F. MORRIS

PEST STATUS

The European earwig, *Forficula auricularia* L., is an important pest in many areas of eastern Canada and British Columbia. It is now widely dispersed throughout St. John's, Newfoundland, where it is considered a pest of economic importance. It has also recently been observed at Grand Bank, Mount Pearl and Topsail, Conception Bay. This pest thrives in Newfoundland's climate. Damage to vegetable and flower gardens is generally light. The most objectionable feature of this insect is its habit of invading homes in late summer and fall. Population levels are generally high.

BACKGROUND

Parasites considered effective against the European earwig in infested areas of British Columbia were introduced into Newfoundland in 1951, 1952 and 1953. The parasite, *Bigonicheta setipennis* (Fallén),[1] was successfully established but parasitism continued at an extremely low level and was therefore of little significance. Percentage parasitism during the period 1955 to 1959 is shown in Table IV. Low parasitism was partly attributed to the inability of the parasite to adapt to local climatic conditions. For this reason the Research Institute, Belleville imported supposedly hardier strains of the parasite from Sweden and Switzerland (Table V).

W. H. A. Wilde (2) provided additional information on parasite releases and recovery attempts at Creston, British Columbia. No recoveries were made in 1956, the year of release, but 2 per cent. of

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[1] Regarded as synonymous with *B. spinipennis* (Meigen); treated as separate in the previous *Review*.

the earwig population, at one release site, was parasitized in 1957. In 1958 no parasites were recovered in collections made from both release sites at Creston.

RELEASES AND RECOVERIES

PARASITES

Bigonicheta setipennis (Fallén) (Diptera: Tachinidae)

This parasite has been successfully established at St. John's. From 1964 to 1967 there was an average increase in parasitism from 0·6 to 8·2 per cent. (Table VI). However, this was followed by a decline in 1968 to 3·2 per cent. The highest parasitism recorded was 12·1 per cent. on 14 August 1967.

EVALUATION OF CONTROL ATTEMPTS

The introduced parasite has successfully established itself but there has been a rather slow increase in percentage of parasitism. Perhaps this indicates a gradual adaptation of the parasite to the life cycle of the European earwig. Although the introduction of parasites appears to have had a limited effect upon earwig populations, they complement traps as a means of control (1).

RECOMMENDATIONS

Annual evaluations to determine changes in the parasite population levels should be continued for five more years.

TABLE IV

Recoveries of *Bigonicheta setipennis* (Fallén) from *Forficula auricularia* L. at St. John's, 1955–9

Approximate dates of observation	Number of earwigs studied	% parasitism				
		1955	1956	1957	1958	1959
14 August	1000	0·3	0·0	1·5	0·9	0·9
31 August	1000	0·5	0·6	3·3	2·3	3·0
10 September	1000	0·1	0·3	0·0	0·5	1·9
Average		0·3	0·3	1·6	1·2	1·9

TABLE V

Open releases of parasites *Bigonicheta setipennis* (Fallén) against *Forficula auricularia* L.

Species and Province	Year	Origin	Number
B. setipennis (Fallén)			
Newfoundland	1959	Sweden	178
	1961	Switzerland	540
	1963	Switzerland	65

TABLE VI

Recoveries of the parasite *Bigonicheta setipennis* (Fallén) from *Forficula auricularia* L. at St. John's, 1964–8

Dates of observations	Number of earwigs studied	% parasitism				
		1964	1965	1966	1967	1968
14 August	1000	0·3	2·8	7·5	12·1	4·0
31 August	1000	0·4	4·0	4·5	6·9	3·0
10 September	1000	0·9	1·6	5·4	7·6	3·7
23 September	1000	0·7	0	6·8	6·0	2·0
Average		0·6	2·1	6·0	8·2	3·2

LITERATURE CITED

1. Morris, R. F. (1965). Note on the control of the European earwig, *Forficula auricularia* L., in Newfoundland with traps and attractants. *Can. Ent.* **97**: 1075–6.
2. Wilde, W. H. A. (1969). Personal communication. Department of Zoology, University of Guelph, Guelph, Ontario.

8. *HYLEMYA BRASSICAE* (BOUCHE), CABBAGE MAGGOT (DIPTERA: ANTHOMYIIDAE)

D. C. READ

PEST STATUS

Infestations of the cabbage maggot, *Hylemya brassicae* (Bouché), continue to plague growers of cruciferous crops in the Atlantic Provinces as well as in many other areas of Canada. Before the development of cyclodiene-type resistance (between 1959 and 1963 in most areas), the general practice of growers was to apply insecticide-fertilizer mixtures broadcast over the whole field, and to harrow them into the surface soil. Since 1963 growers have had to use the newer organophosphorus insecticides, and recommendations on methods of application vary in different regions across Canada. Surface sprays are recommended in many areas, and it is only in the three Maritime Provinces that preplanting subsurface applications alone are recommended. In other areas, no consideration appears to be given to the effect of the highly toxic sprays on predators above or on the soil surface that destroy flies and eggs of *H. brassicae* or to the parasite adults that also move freely through the surface soil.

BACKGROUND

During the period when cyclodiene-type insecticides gave almost complete control of root-maggot infestations, efforts to stop the broadcasting of insecticides in the Maritime Provinces were largely in vain, even though (as will be explained later) the insecticides were acting more against the predators and parasites than against the larvae of the pest. Most farmers insisted on continuing the use of broadcast fertilizer-insecticide mixtures because the application required no extra labour and could be applied with standard fertilizer-application equipment.

When resistance to aldrin and heptachlor first appeared in the Argyle area of Prince Edward Island in 1963, it was noted that damage by root maggots from 1963 until after a resistant strain of predator-parasites was developed was much more severe than had previously been observed in untreated plots or fields. Up to four-inch rutabagas were completely cut off just below ground level. Further examination revealed that there was no parasitism of the pupae in the soil, whereas parasitism by one species alone in untreated fields had reached as high as 96 per cent. in midsummer when parasites were most active and up to 78 per cent. in late fall.

Within 3 years cyclodiene resistance had spread to all major crucifer-growing areas of the province. In 1968, only one area (in the western section of Prince Edward Island) had not developed a resistant strain of the pest. Growers in this area had consistently followed the Departmental recommendations of placing the insecticide in a band in the row beneath the soil surface where it could not affect predators feeding on root-maggot eggs or attacking flies on the foliage.

An extensive field selection programme was undertaken in 1964 using cyclodiene insecticides broadcast in a sector of a field in the Argyle area of Prince Edward Island, and 4 years were required to select a resistant strain of the predator-parasite *Aleochara bilineata* (L.). The selected strain of this insect has a high level of resistance to the cyclodienes as compared to the susceptible strain.

PARASITE

Trybliographa rapae (L.) (Hymenoptera: Cynipidae)

The larvae of this insect enter different stages of the larvae of *H. brassicae* and usually cause early pupation. They then destroy the host pupae as they develop inside the puparium. This parasite has not been considered of major importance since percentages of parasitism are usually low (1) and, although varying in numbers from year to year, the parasite has not shown a marked increase in any year since 1959.

PREDATOR-PARASITE

Aleochara bilineata (Gyll.) (Coleoptera: Staphylinidae)

This species is considered to be the most important beneficial insect preying on root maggots because (a) the adults act as predators destroying root maggot eggs and larvae, and (b) the predator larvae are parasitic on root maggot pupae. No parasites were found in the resistant area at Argyle until after the resistant strain was selected, but within 2 years field plots in the vicinity of the selection site that were treated with double the recommended application of heptachlor showed an average parasitism of root maggot pupae of 76 per cent. in the overwintering generation. As root maggot eggs and larvae are destroyed by *A. bilineata* adults, and as the root maggot pupae of each generation are destroyed by the parasitic larvae, this predator-parasite must be considered an extremely important mortality factor of the root maggot. Unfortunately, it does not eliminate or control early injury by infestations of root maggots, because the predator develops more slowly at lower temperatures in early summer than do the root maggots. Therefore the first-generation root maggot larvae cause severe injury before the predators become prevalent (4).

PREDATORS

Coenosia tigrina (Fall.) (Diptera: Anthomyiidae)
Scatophaga stercoraria (L.) (Diptera: Anthomyiidae)

Both of these insects are adult predators that attack and destroy root maggot flies in the air or on plants; and sweeps made in a crucifer field with large trap cages usually contain many more predators than root maggot flies. However, since the predators have been observed attacking other insects collected in the trap cages as well as the root maggot flies, it is not possible to assess their overall effect on root maggot infestations. Nevertheless, they are assumed to be valuable biological control agents (2, 3).

Carabid beetles (various species)

These destroy root maggot eggs at or near the soil surface and their possible value as mortality factors of root maggots cannot be ignored. These predators are similar to *A. bilineata* in that they move freely in the soil between the rows; certain species are destroyed by as little as 0·1 ppm of dieldrin broadcast in the soil (1).

EVALUATION OF CONTROL ATTEMPTS

The aim of the recommendations for applying the insecticides in the Maritime Region has been to achieve integrated control. Growers are advised to apply the insecticides as a single preplanting treatment in a band in a ridged row about one inch below the soil surface, with the aim of concentrating the insecticide against the pest insect larva and at the same time giving predators and parasites the best chance to survive. The sub-surface application does not affect adult or egg predators operating above or at the soil surface. Also, the parasites attacking larvae or pupae of the pest species have at least the same chance to survive as the pest. Most *H. brassicae* pupae are found from 2 to 6 inches deep in the soil and thus are beneath the band of insecticide when attacked by the minute larvae of *A. bilineata.*

The success of this attempt at integrated control is difficult to measure because many growers in the major crucifer-growing areas followed the easier method of broadcast applications of fertilizer-insecticide mixtures. This practice may have led to early development of cyclodiene resistance in root maggots in these areas. In any event, resistance was accompanied by a tremendous increase in root maggot populations in Prince Edward Island as well as in other areas (1). An assessment of the value of the band-in-row treatment can only be made in more isolated areas where growers always placed the band of insecticide beneath the soil surface as recommended. In these areas, the cyclodiene insecticides were still effective in controlling *H. brassicae* after 15 years of continued use (now used in trial plots only because of the residue problem) and there are still no indications of resistance.

RECOMMENDATIONS

Since broadcast applications of the organophosphorus insecticides do not give efficient control of root maggot infestations, all treatments must be concentrated on or in the row. In many areas of Canada the recommendations state that an application should be made at planting time and followed by supplemental sprays applied during the season. The sprays are recommended because low preplanting rates of the materials do not give all-season control. However, because of the danger of destruction of the beneficial predators and parasites, only a single preplanting subsurface application of these materials at a higher rate is recommended in the Maritime Provinces. The insecticides now recommended for control, with the exception of thionazin, are as effective and persistent in alkaline as in acid mineral soils, and mid-season sprays should not be necessary in any mineral soil. Fensulfothion and chlorfenvinphos used as preplanting subsurface applications are almost as toxic to the root maggots 3 months after application as at or just after application. Similar investigations should be made in other areas of Canada where root maggots are still a problem.

LITERATURE CITED

1. Coaker, T. H. (1966). The effect of soil insecticides on the predators and parasites of the cabbageroot fly, (*Erioishia brassicae* (Bouché)) and on subsequent damage by the pest. *Ann. appl. Biol.* **57**: 397–407.
2. Perron, J. P., LeRoux, E. J. & LaFrance, J. (1956). Notes on *Coenosia tigrina* (F.) (Diptera: Anthomyiidae), mainly on habits and rearing. *Can. Ent.* **88**: 608–11.
3. Read, D. C. (1958). Notes on *Scatophaga stercoraria* (L.) (Diptera: Anthomyiidae) a predator of the cabbage maggot, *Hylemya brassicae* (Bouché). *Can. Ent.* **90**: 376.
4. Read, D. C. (1962). Notes on the life history of *Aleochara bilineata* (Gyll.) (Coleoptera-Staphylinidae), and on its potential value as a control agent for the cabbage maggot, *Hylemya brassicae* (Bouché) (Diptera-Anthomyiidae). *Can. Ent.* **94**: 419–24.
5. Read, D. C. (1964). Chemical control of the cabbage maggot integrated with natural controls. *Can. Ent.* **96**: 136–7.

9. *LECANIUM CORYLI* L., LECANIUM SCALE (HEMIPTERA: COCCIDAE)

A. W. MacPhee

PEST STATUS

The history of lecanium scale in Canada is given in the previous review (1). There is still some uncertainty of the taxonomy of this genus, but the present report refers to the species most commonly found on apple in Nova Scotia as *Lecanium coryli* L. which name is being retained until the taxonomy of the group is further clarified.

An outbreak of *Lecanium coryli* on elm at Indian Head and Regina, Saskatchewan was investigated by Peterson (2) who reported that weather was probably the most important factor influencing population density in the Prairie Provinces. Other mortality factors such as underdevelopment and parasitism were also considered significant.

This scale has been a serious pest in a small number of apple orchards in Nova Scotia where limbs and small branches may be killed when scale becomes heavy, although smutting of fruit by the black sooty fungus growing on the scale honeydew is a more common injury. It has never been a pest of neglected orchards nor on those receiving relatively selective pesticides, because parasites and predators flourish there and the scale density is usually very low. *L. coryli* may be a serious problem in a small number of orchards where broad spectrum sprays, such as DDT, have been used for a number of years and parasites and predators have been reduced. There are exceptions, for outbreaks occur on ornamental ash and oak trees. Where certain other broad spectrum materials, such as Guthion, are applied a number of times during the season, the scale is apparently controlled by the chemical. Unfortunately no selective pesticide to control this pest is available and a single application of a broad spectrum one, such as malathion or dormant oil, must be used to reduce its abundance until the natural biotic agents increase again.

NATURAL ENEMIES

The measurement of the influence of various factors on *L. coryli* populations in Nova Scotia has shown the relative value of a number of parasites and predators and how they affect the orchard management practices.

PARASITES

Blastothrix sericea Dalm. (Hymenoptera: Encyrtidae)

This parasite has been found wherever *L. coryli* is present. In some cases, notably where harmful sprays have been used, its rate of attack is low; in other situations where its numbers are high, *B. sericea* may kill 30–50 per cent. of the overwintering population and the first summer generation which attacks the maturing scale may then attack all or practically all the surviving scale. One to five or six, occasionally more, parasites develop in each scale but this attack is late and most scales produce a near-normal complement of eggs. Therefore, behaviour studies indicate, and observations support, the view that control of this scale by *B. sericea* alone is unlikely. This parasite is very sensitive to DDT sprays.

Coccophagus sp. (Hymenoptera: Eulophidae)

Populations of an undetermined species of *Coccophagus* are also commonly present and at peak numbers kill over 30 per cent. of the overwintered scale shortly after they begin development in the spring. Scale parasitized by *Coccophagus* do not mature. This parasite is relatively resistant to DDT sprays.

Aphycus sp. (Hymenoptera: Encyrtidae)

This parasite attacks the scale nymphs on the leaves in the summer and matures to emerge in late September in Nova Scotia; it has been observed only in very small numbers.

PREDATORS

The mirids *Diaphnocoris pellucida* (Uhler), *Hyaliodes harti* Knight, and *Deraeocoris fasciolus* Knight, and some chrysopids, in feeding tests in the laboratory, consumed up to about 10 *L. coryli* nymphs per day per individual predator. The mirid *Campylomma verbasci* (Meyer) and the anthocorid *Anthocoris musculus* (Say) fed only rarely under these conditions. During the summer many remnants of nymphs of *L. coryli*, with only the external skeleton remaining on the leaves, have been observed in orchards where predacious mirids were common.

The predacious mite, *Balaustium putmani* Smiley, was found to be numerous in one orchard where *L. coryli* was common and fed on the scale nymphs at least during their movement to the foliage just after hatching.

The larval stage of the encyrtid, *Microterys physokermis* Compere, preys on *L. coryli* eggs, living in the egg mass under the female scale in late June and early July, usually consuming most or all of the eggs before they hatch. Most members of the genus *Microterys* are true parasites but this species, in common with some others, is predacious on scale eggs.

The species of predators discussed and many others in addition, which are believed to prey on *L. coryli* are suppressed or practically eliminated by some broad spectrum pesticides and this greatly influences the survival of nymphs on the leaves during the months of July to October.

EVALUATION OF CONTROL ATTEMPTS

Biotic control agents keep *L. coryli* under control in most commercial apple orchards in Nova Scotia, including most of those in which integrated control is practised. Where other orchard pests cannot be controlled selectively, other chemicals are used, some of which interfere with biotic control of this scale, and outbreaks result. Orchardists who follow a preventive chemical control programme can obtain scale control when necessary with one of a number of materials including dormant oil treatments or summer applications of malathion.

It has proven relatively easy with present knowledge to manage the orchard pest control programme without special treatments for control of this pest. This is taken into consideration in making spray programme recommendations to growers. Special treatments for this pest are rare and direct costs therefore minimal. Chemical control in the rare outbreak situation costs about $10 to $12 per acre for material.

LITERATURE CITED

1. McGugan, B. M. & Coppel, H. C. (1962). Biological control of forest insects, 1910–1958. *In* A review of biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol. Control* **2**: 35–127.
2. Peterson, L. O. T. (1960). *Lecanium coryli* L. (Homoptera: Coccoidea) in Saskatchewan. *Can. Ent.* **92**: 851–7.

10. *LEPIDOSAPHES ULMI* (L.), OYSTERSHELL SCALE (HEMIPTERA: COCCIDAE)

F. T. Lord

Oystershell scale, *Lepidosaphes ulmi* (L.), is probably of European origin but it is now worldwide (3) as a pest of a number of woody plants such as fruit trees, ash, poplar, maple, lilac and others (10) on which branches may be killed or even mortality of the whole plant may occur (7). It has been known in Canada for many years, and is believed to have been introduced into British Columbia from Ontario on nursery stock (2).

There are two natural control agents in eastern Canada, a predacious mite, *Hemisarcoptes malus* (Shimer), and a chalcid parasite, *Aphytis mytilaspidis* (LeB.) (9). Both agents are of European origin and were introduced accidentally, possibly almost 400 years ago when the French settlers carried apple trees to this country. Either species working alone or both together can provide excellent natural control of oystershell scale (4) but the parasite does not survive cold winters such as occur in New Brunswick or Quebec (5). Lord and MacPhee (5) found that the parasite is killed when the winter temperatures drop much below —15°F whereas the predacious mite and the scale itself are sufficiently hardy to survive even when temperatures drop to —30°F or beyond, depending on the duration of the low temperature.

H. malus attacks all stages of the scale and passes the winter in the more advanced immature stages under dead scales or among the scale eggs. The parasite overwinters as a larva under the same conditions. The parasite has three generations per year in Canada and the predacious mite two or more. Tothill (9) failed to find *H. malus* in British Columbia and arranged for its introduction. In 1917 four colonies, each of more than 1,000 individuals, were obtained in New Brunswick and released in British Columbia at Aggasiz, Mission, Royal Oak and Vernon. Following its establishment, mite-infested material was transferred on numerous occasions to other fruit growing areas of southern British Columbia where *L. ulmi* was troublesome. The initial introductions and subsequent re-colonizations were reported to be quite successful (1). An outbreak near Trail, British Columbia prompted further introductions of *H. malus* from Ontario in 1952 and 1953. Neilson (6) described the mite as moderately effective in reducing the oystershell scale population.

Owing to the policy of using wide spectrum pesticides in fruit growing areas, the populations of scales and those of their two natural enemies are kept at low levels in orchards or eliminated. Where such sprays are avoided and only pesticides harmless to the two natural agents are used, natural control maintains scale populations well below the economic level (4, 8). Mainly because of the policy of avoiding destruction of natural enemies practically no dormant oil has been used in Nova Scotia or New Brunswick since the mid-1940's which in turn has greatly eased the natural control of other apple pests.

LITERATURE CITED

1. Baird, A. B. (1939). Biological control of insect pests in Canada with special reference to the control of European spruce sawfly, *Diprion polytomum* Htg. *70th Rep. ent. Soc. Ont.* 1939: 51–6.
2. Cunningham, T. (1911). Insects of the year in British Columbia. *Proc. ent. Soc. Brit. Columb.* 1: 15–21.
3. Griswold, G. H. (1925). A study of the oyster-shell scale, *Lepidosaphes ulmi* (L.) and one of its parasites, *Aphelinus mytilaspidis* LeB. *Mem. Cornell agric. Exp. Stn.* 93, 67 pp.
4. Lord, F. T. (1949). The influence of spray programs on the fauna of apple orchards in Nova Scotia. II. Oystershell scale, *Lepidosaphes ulmi* (L.). *Can. Ent.* 79: 196–209.
5. Lord, F. T. & MacPhee, A. W. (1953). The influence of spray programs on the fauna of apple orchards in Nova Scotia. VI. Low temperatures and the natural control of oystershell scale, *Lepidosaphes ulmi* (L.) (Homoptera: Coccidae). *Can. Ent.* 85: 282–91.
6. Neilson, C. L. (1957). Handbook of the main economic insects of British Columbia, Part 4. Ent. Branch Dep. Agric. Brit. Columb.
7. Parr, T. (1940). Oystershell scale (*Lepidosaphes ulmi* (L.)). *In* Important tree pests of the northeast. Boston Mass. For. Park Ass.
8. Pickett, A. D. (1965). The influence of spray programs on the fauna of apple orchards in Nova Scotia. XIV. Supplement to II. Oystershell scale, *Lepidosaphes ulmi* (L.). *Can. Ent.* 97: 817–21.
9. Tothill, J. D. (1918). Natural control investigations in British Columbia. *Proc. ent. Soc. Brit. Columb.* 12: 37–9.
10. Treherne, R. C. (1918). The oystershell scale (*Lepidosaphes ulmi* Linn.). *Circ.* (*New Hort. Ser.*), *Dep. Agric. Brit. Columb.* 41, 3 pp.

11. *MALACOSOMA AMERICANUM* (FABRICIUS), EASTERN TENT CATERPILLAR (LEPIDOPTERA: LASIOCAMPIDAE)

G. E. Bucher

The eastern tent caterpillar, *Malacosoma americanum* (Fabricius), destroys the leaves of almost any tree or shrub belonging to the family Rosaceae. Although gravid females oviposit exclusively on rosaceous plants, the larvae will eat the leaves of many deciduous plants outside this family. Commercial orchards are automatically protected by normal spray programmes for other insects, and damage to fruit and ornamental plants on residential property is easily prevented by several do-it-yourself methods such as burning, spraying, or hand-collection and destruction of nests when larvae are small. In eastern Canada the insect is commonly found on its preferred host, the eastern chokecherry, *Prunus virginiana* L., in fence rows, scrub land and wood lots where no control is applied. The ugly nests and denuded trees make the insect a public nuisance rather than an economic pest (7). Bucher (1, 3) isolated and described two new spore-forming bacteria, *Clostridium brevifaciens* Bucher and *C. malacosomae* Bucher as causes of a lethal disease of the western tent caterpillar, *Malacosoma pluviale* (Dyar), and cultured them vegetatively on a complex medium but was not able to induce sporulation in artificial culture. *C. brevifaciens* was the principal cause of disease in field populations but *C. malacasomae* was commonly associated with it and could cause the disease by itself when fed experimentally. The eastern tent caterpillar was highly susceptible to the disease but the forest tent caterpillar, *Malacosoma disstria* Hübner, was relatively resistant to the lethal results of infection though the bacteria would grow in its gut.

Individual larvae of all three species of tent caterpillar are readily infected by ingesting a small number of bacterial spores or infective vegetative rods. The bacteria grow and sporulate exclusively in the lumen of the insect's gut and are rapidly transmitted to sibling insects by contamination of the food with faeces and regurgitated fluid. Thus a whole nest or colony of tent caterpillars may catch the disease from a few individuals that were originally infected. The degree and speed of mortality depends largely on the age of larvae when infected. Larvae infected in the last instar frequently pupate, though they may produce small cocoons and pupae and a low proportion of emerging adults. Infected adult females carry spores in the meconium and may mechanically contaminate the foam of the egg capsule and transmit the infection to the following generation.

From 1957 to 1960 small chokecherry trees naturally infested with the eastern tent caterpillar were sprayed with the bacteria at the Institute Field Station about 14 miles north west of Belleville to determine the degree of control under field conditions (4). The bacteria were applied as pure vegetative cultures of both species, pure spore suspensions of both species, and mixed spore suspensions at concentrations of 10^5–10^7 bacteria or spores per ml and at rates of 20–40 ml per tree when larvae were in instars II to V. Spraying was confined to the nest itself or to the branches on which larvae were feeding and no attempt was made to secure complete coverage of the trees.

Vegetative cultures of the bacteria failed to produce infection of any larvae under field conditions. Vegetative bacteria were susceptible to drying, sunlight, oxidation and change of pH and lost viability before they were ingested by the insects.

Spore suspensions produced disease in all colonies of the tent caterpillar except some that were sprayed when they were in instar V. The degree of control, as measured by the mortality and the relative amount of defoliation, depended on the age of the caterpillars when sprayed and the speed at which the whole colony showed symptoms of disease and ceased to feed. Colonies infected when the larvae were in instar II caused very little defoliation before the larvae died in instar III. But colonies infected when larvae were in instar IV and V caused heavy defoliation, some of which occurred before they were sprayed.

Thus the eastern tent caterpillar can be controlled by spraying the nests or branches on which the larvae feed with a few millilitres of a suspension of spores of two species of *Clostridium*. As the spores must be produced by growing the bacteria in the living insect and extracting them from the excrement, the process is expensive and economically impracticable for an insect that does not cause financial loss. Although the disease persisted for several years in some areas of British Columbia in populations of *M. pluviale* (Dyar) (2), there was no indication that it was vertically transmitted to following generations of *M. americanum* from the small number of infection foci established near Belleville during the low population densities that prevailed during the tests.

Commercial preparations of *Bacillus thuringiensis* Berliner, which contain a mixture of bacterial spores and parasporal toxic crystals, killed most of the tent caterpillar larvae within 6 days in laboratory tests (5). The preparation, containing $7{\cdot}5 \times 10^7$ spores per ml and presumably an equivalent number of crystals, was sprayed on leaves that were fed to the larvae. Jaques (5) sprayed the commercial preparation on apple trees infested with the eastern tent caterpillar near Kentville, Nova Scotia. Excellent control of the insect was obtained at concentrations of 2 to 4 lbs of commercial concentrate per 100 gallons of water containing 50 ppm of wetting agent. These concentrations were from two to four times as great as the lowest laboratory dose or contained from $1{\cdot}5 \times 10^8$ to $3{\cdot}0 \times 10^8$ spores per ml. Larvae that were not killed outright were stunted, fed very little and did little further damage to apple foliage.

During a 4-year period Jaques (6) sprayed an experimental apple orchard near Kentville, Nova Scotia, with commercial preparations of *Bacillus thuringiensis* to determine its control of several apple pests, including the eastern tent caterpillar. The preparations consisted of a wettable powder used at a concentration of 1 to 4 lbs per 100 gallons of water or of an emulsifiable concentrate used at a concentration of 1 to 4 pints per 100 gallons. The applied sprays contained between 3×10^7 and 3×10^8 spores of *B. thuringiensis* per ml, plus a proportionate amount of toxic crystals. Five to seven cover sprays were applied per year and the orchard was treated with fungicides but not chemical insecticides. These treatments with *B. thuringiensis* preparations successfully controlled the eastern tent caterpillar. Only one active colony occurred on trees sprayed with 4 lbs or 4 pints of concentrate per 100 gallons during the four years of the test.

As mentioned above, the eastern tent caterpillar is not a pest in commercial orchards because it is controlled by insecticides applied against the codling moth and other economic insects. If, in the future, the use of chemical insecticides is reduced in favour of biological insecticides, such as *B. thuringiensis*, we may still expect the eastern tent caterpillar to be controlled.

LITERATURE CITED

1. Bucher, G. E. (1957). Disease of the larvae of tent caterpillars caused by a spore forming bacterium. *Can. J. Microbiol.* **3**: 695–709.
2. Bucher, G. E. (1959). Winter rearing of tent caterpillars *Malacosoma* spp. (Lepidoptera: Lasiocampidae). *Can. Ent.* **91**: 411–6.
3. Bucher, G. E. (1961). Artificial culture of *Clostridium brevifaciens* n.sp. and *C. malacosomae* n.sp., the causes of brachytosis of tent caterpillars. *Can. J. Microbiol.* **7**: 641–54.
4. Bucher, G. E. (1961). Control of the eastern tent caterpillar, *Malacosoma americanum* (Fabricius), by distribution of spores of two species of *Clostridium*. *J. Insect Path.* **3**: 439–45.
5. Jaques, R. P. (1961). Control of some lepidopterous pests of apple with commercial preparations of *Bacillus thuringiensis* Berliner. *J. Insect Path.* **3**: 167–82.
6. Jaques, R. P. (1965). The effect of *Bacillus thuringiensis* Berliner on the fauna of an apple orchard. *Can. Ent.* **97**: 795–802.
7. Stehr, F. W. & Cook, E. F. (1968). A revision of the genus *Malacosoma* Hübner in North America (Lepidoptera: Lasiocampidae): systematics, biology, immatures, and parasites. *Bull. U.S. natn. Mus.* **276**, 321 pp.

12. *MELANOPLUS* SPP., GRASSHOPPERS (ORTHOPTERA: ACRIDIIDAE)

G. E. BUCHER

Grasshoppers are considered to be one of the most serious pests in grain crops in Canada. Their greatest economic damage is done in the wheat-growing areas of the prairies where forecasts of abundance and damage are made on the basis of surveys of the numbers of adults and/or egg pods in the fall of the year plus consideration of weather conditions during winter and spring (4, 5, 6). Such forecasts allow the mobilization of resources for controlling the insects with insecticides in areas where serious damage is expected. Several species of the genus *Melanoplus* and *Camnula pellucida* (Scudder) are the most important members of the group.

During a study of the microbial flora and pathogens of western grasshoppers in Canada from 1949 to 1953, the bacterium *Pseudomonas aeruginosa* (Schroeter) Migula was found to be the most important pathogen of laboratory-reared grasshoppers, although it was not isolated as a cause of disease in the field (2, 3). The bacterium was associated in small numbers with a low proportion of field-collected egg pods and periodically invaded laboratory cultures of grasshoppers when these were established or supplemented with such eggs.

Baird (1) cultured and applied the bacterium in a fluid composed of nutrient broth, casein, sucrose, and gastric mucin (a formulation devised to give the maximum preservation of viability when the bacteria dried) to grasshopper egg beds near Lethbridge, Alberta before eggs hatched in the spring. He also formulated a bran-flour-peat bait moistened with a bacterial suspension in broth, casein, sucrose, and mucin, and broadcast this at the rate of 10 lbs dry bran per acre in grasshopper populations of mixed age and species.

Bait applications killed only 1–5 per cent. of the grasshoppers, a proportion of no economic importance. The bacteria were destroyed by drying and sunlight even when protected by the best formulations known, so that baits rapidly lost their infectivity and the disease did not spread through the population. Until the viability of vegetative bacteria can be preserved during exposure to drying and sunlight, their use against insects of dry environments, such as the grasshopper, is impracticable.

The number of nymphs that emerged from egg beds treated with fluid suspensions of the bacterium was so small that the results were inconclusive, though about half the nymphs were infected and died. Infection of the egg beds did not initiate a disease that spread through the population under the conditions of these trials. Unless bacterial infection of egg beds would result in establishing foci of infection from which a disease would spread widely, this method holds no promise for economic control of grasshoppers.

LITERATURE CITED

1. Baird, R. B. (1958). Field experiments with *Pseudomonas aeruginosa* (Schroeter) Migula to control grasshoppers. *Can. Ent.* 90: 89–91.
2. Bucher, G. E. (1959). Bacteria of grasshoppers of western Canada: III. Frequency of occurrence, pathogenicity. *J. Insect Path.* 1: 391–405.
3. Bucher, G. E. & Stephens, J. M. (1957). A disease of grasshoppers caused by the bacterium *Pseudomonas aeruginosa* (Schroeter) Migula. *Can. J. Microbiol.* 3: 611–25.
4. Edwards, R. L. (1962). A critical appraisal of grasshopper forecast maps in Saskatchewan, 1936–1958. *J. econ. Ent.* 55: 288–92.
5. Pickford, R. (1966). Development, survival and reproduction of *Camnula pellucida* (Scudder) (Orthoptera: Acridiidae) in relation to climatic conditions. *Can. Ent.* 98: 158–69.
6. Riegert, P. (1968). A history of grasshopper abundance surveys and forecasts of outbreaks in Saskatchewan. *Mem. ent. Soc. Can.* 52, 99 pp.

13. *PANONYCHUS ULMI* (KOCH), EUROPEAN RED MITE, (ACARINA: TETRANYCHIDAE) AND OTHER PHYTOPHAGOUS MITES ON FRUIT TREES IN CANADA

BENOIT PARENT and F. T. LORD[1]

The European red mite, *Panonychus ulmi* (Koch), is one of the most destructive of the pests attacking deciduous fruit trees in temperate regions. It has been in Canada for many years but did

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[1] In cooperation with W. L. Putman, R. P. Jaques and R. S. Downing.

not become an important fruit pest until DDT was used extensively after 1945. It readily attacks most kinds of fruit trees and a number of other plants as well. Besides being of economic importance, *P. ulmi* is well known because its natural control has been studied in detail on apple (3, 4, 8) and on peaches (11). Somewhat similar studies have been made in other parts of the world where *P. ulmi* is a pest.

In addition to *P. ulmi* about nine other species of phytophagous mites are of recognized importance on fruit trees in Canada. Some will feed on most kinds of fruit trees while others are more specific: some are found in all fruit growing areas but a few are found in one area and not in others, as for example the McDaniel spider mite, *Tetranychus mcdanieli* McG., which is found only in British Columbia.

Many of the predacious species that attack mites are common to all fruit areas and for the most part they feed on many species of insects and mites. A few appear to be fairly specific in the prey they will accept, such as some of the Cecidomyiidae which have a preference for eriophyid mites, whereas others attack a wide range of prey including the several species of pest mites. Some polyphagous predatory species, however, feed on mites only incidentally whereas others attack many insect and mite species. Because of this variation in habit it is not practicable to assess the influence they have on mite populations except in general terms and mostly in relation to their attacks on *P. ulmi.* The species most important in the natural control of Tetranychidae are found in the following groups: the mite family Phytoseiidae, and the insect groups, Anthocoridae, Miridae, Thysanoptera, Chrysopidae and a few Coccinellidae, notably *Stethorus* spp. Other, mostly larger, species have been observed to feed on phytophagous mites but there is little evidence to indicate that the mortality they cause is important. These are mostly larger species of Coccinellidae, spiders and Pentatomidae.

The side effects of chemicals on the fauna of fruit trees have been extensively studied in many parts of the world and the references are too numerous to cite. Those side effects that pertain to mite populations have received considerable attention, and it has been demonstrated in Canada that chemicals which destroy predators favour the build-up of mite populations (4, 8, 10). From these and other studies it is generally accepted that most mite species owe their abundance, in large measure, to the density of the predator populations and that the need for acaricides results from the destruction of predators.

P. ulmi became a major pest in Nova Scotia after 1930 following the use of dormant oil sprays for oystershell scale, *Lepidosaphes ulmi* (L.), and summer sprays of wettable sulphur to control apple scab, *Venturia inequalis* (Wint.). Later it was found that these materials were destructive to predators and that when the spray programme was changed to eliminate the use of oil and to substitute safer fungicides for sulphur, predator populations decimated the mites; they have continued ever since to maintain them at a low balance (4). Lists of many other materials examined for their effects on predators are given by MacPhee and Sanford (5, 6, 7). The latter information and studies on the ecology of pests and natural enemies has been used by growers in Nova Scotia to manipulate predator populations, mainly by avoiding their destruction, by using the most selective materials and techniques currently available. As a result *P. ulmi* causes trouble in commercial orchards only occasionally, when it becomes necessary to solve a pest problem with a material that is not selective. Similar studies in Quebec, Ontario and British Columbia have shown the potential of predators, but there is as yet no means by which this can be exploited.

In 1949 a colony of 14 adults of *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) was released in Ontario and 73 adults of *Stethorus punctillum* (Wse.) (Coleoptera: Coccinellidae) in Nova Scotia. Both species are, and were, present in Canada. Other species of predators received from Switzerland at that time for use in mite control were not released and none have been released since. Where studies have been made, such as on the predators attacking *P. ulmi*, there appears to be a sufficient potential of natural enemies to hold mites in check.

Dr. D. A. Chant, while at the Canada Department of Agriculture Research Station, Vineland Station, Ontario, released 650 individuals of the phytoseiid mite, *Phytoseiulus persimilis* Athias-Henriot, imported from South America in 1961 for use in the control of *P. ulmi.* No recoveries were made. Subsequent studies on seedling plum and peach indicated that the predator seemed unable to cling to the foliage and was flicked from the leaves by wind velocities in excess of 5–7 miles per hour. Releases were not repeated.

Two studies have been made on the use of pathogenic organisms against *P. ulmi* populations. These were *Bacillus thuringiensis* Berliner, in a commercial preparation of this entomophagous bacterium (2), and a virus disease discovered by Putman (9) and described by Bird (1). The *B. thuringiensis* preparation was repeatedly applied each year to mature apple trees in a test in Nova Scotia over a four-year period at rates of 1 to 4 lbs per 100 gallons of spray. Both *P. ulmi* and the brown mite *Bryobia rubrioculus* (Scheuten) were very scarce during the four-year test period but their scarcity was considered to be due to effective predation because *B. thuringiensis* is relatively harmless to predators. The virus disease, when introduced into laboratory and peach orchard populations of *P. ulmi*, resulted in high mortalities of the mite (11). The work on the virus suggested that the virus has considerable potential for control of *P. ulmi*, but further study on the factors influencing establishment and dissemination is needed.

LITERATURE CITED

1. Bird, F. T. (1967). A virus of the European red mite, *Panonychus ulmi* (Koch). *Can. J. Microbiol.* 13: 1131.
2. Jaques, R. P. (1965). The effects of *Bacillus thuringiensis* Berliner on the fauna of an apple orchard. *Can. Ent.* 97: 795–802.
3. LeRoux, E. J. (1960). Effects of "modified" and "commercial" spray programs on the fauna of apple orchards in Quebec. *Ann. ent. Soc. Queb.* 6: 87–121.
4. Lord, F. T. (1949). The influence of spray programs on the fauna of apple orchards in Nova Scotia. III. Mites and their predators. *Can. Ent.* 81: 202–30.
5. MacPhee, A. W. & Sanford, K. H. (1954). The influence of spray programs on the fauna of apple orchards in Nova Scotia. VII. Effects on some beneficial arthropods. *Can. Ent.* 86: 128–35.
6. MacPhee, A. W. & Sanford, K. H. (1956). The influence of spray programs on the fauna of apple trees in Nova Scotia. X. Supplement to VII. Effects on some beneficial arthropods. *Can. Ent.* 88: 631–4.
7. MacPhee, A. W. & Sanford, K. H. (1961). The influence of spray programs on the fauna of apple orchards in Nova Scotia. XII. Second supplement to VII. Effects on some beneficial arthropods. *Can. Ent.* 93: 671–3.
8. Parent, B. (1967). Population studies of phytophagous mites and predators in southwestern Quebec. *Can. Ent.* 99: 771–8.
9. Putman, W. L. (1970). Occurrence and transmission of a virus disease of the European red mite, *Panonychus ulmi*. *Can. Ent.* 102: 305–21.
10. Putman, W. L. & Herne, D. C. (1958). Natural control of phytophagous mites (Tetranychidae and Eriophyidae) in Ontario peach orchards. *Proc. 10th Int. Congr. Ent., Montreal* (1956) 4: 667–73.
11. Putman, W. L. & Herne, D. C. (1966). The role of predators and other biotic agents in regulating population density of some phytophagous mites in Ontario peach orchards. *Can. Ent.* 98: 808–20.

14. *PIERIS RAPAE* (L.), IMPORTED CABBAGEWORM (LEPIDOPTERA: PIERIDAE) AND *PLUTELLA MACULIPENNIS* (CURTIS), DIAMONDBACK MOTH (LEPIDOPTERA: PLUTELLIDAE)

R. P. Jaques

Larvae of *Pieris rapae* (L.), the imported cabbageworm, are the most important pests of cole crops in Canada. Control of the insect by chemical insecticides is usually acceptable economically. The larvae of *Plutella maculipennis* (Curtis) are leaf-feeding pests of secondary importance on cole crops in most of Canada.

A granulosis virus of *P. rapae* is known to be highly infective and has been applied quite extensively for control of the larvae in plot tests in the United States (3). *P. rapae* larvae also are highly susceptible to the toxins of the bacterium, *Bacillus thuringiensis* Berliner (3); the commercial microbial insecticide containing this bacterium as the active ingredient is now registered for use against this pest as well as against other insects on cole crops.

Plot tests by the author at Kentville, Nova Scotia, in 1960 (1) showed that three applications of *B. thuringiensis* or one application of DDT followed by two of *B. thuringiensis* gave good control of larvae of *P. rapae* and *P. maculipennis* on cabbage. Fewer applications of the bacteria did not retain the population of the pests below economic levels late in the season. Control by a single application was enhanced by addition of skim-milk powder or a latex preparation to the spray (4).

In plot tests at Kentville in 1963 and 1965, the effects of introducing the granulosis virus of *P. rapae*, the bacterium *B. thuringiensis* and the nematode DD136 into populations of *P. rapae* were compared (2). The control effected by introduction of the virus was equal to that attained by application of DDT or Phosdrin. Because the bacterium did not become established in the environment, two applications were not sufficient to protect the crop. The parasitic nematode DD136 gave good control late in the season.

Plot tests at Harrow, Ontario in 1967 and 1968 demonstrated that the introduction of the granulosis virus or the bacterium *B. thuringiensis* as foliar sprays reduced numbers of live *P. rapae* larvae by more than 90 per cent., thus protecting the crop. Application of the virus to soil had a more prolonged effectiveness.

The introduction of the granulosis virus was considered superior to that of the bacterium *B. thuringiensis* or that of the nematode DD136 for control of *P. rapae* in these tests because the virus became established in the environment. It is evident that the granulosis virus has considerable potential as a natural and applied agent for control of *P. rapae*. Further laboratory and field studies to determine long-term effectiveness of introduction of this pathogen are being carried out at the Canada Department of Agriculture Research Station, Harrow, Ontario.

LITERATURE CITED

1. Fox, C. J. S. & Jaques, R. P. (1961). Field tests with *Bacillus thuringiensis* Berliner and DDT for control of two pests of cabbage. *Can. J. Plant Sci.* **41**: 428–30.
2. Fox, C. J. S. & Jaques, R. P. (1966). Preliminary observations on biological insecticides against imported cabbageworm. *Can. J. Plant Sci.* **46**: 497–9.
3. Hall, I. M. (1963). Microbial control, pp. 477–517. *In* Insect pathology. An advanced treatise. Vol. 2. Academic Press, New York.
4. Jaques, R. P. & Fox, C. J. S. (1960). The influence of stickers on the effectiveness of sprays of *Bacillus thuringiensis* var. *thuringiensis* Berliner and *Bacillus entomocidus* var. *entomocidus* Heimpel and Angus. *J. Insect Path.* **2**: 17–23.

15. *PSYLLA MALI* (SCHMIDBERGER), APPLE SUCKER (HEMIPTERA: PSYLLIDAE)

R. P. JAQUES

The apple sucker, *Psylla mali* (Schmidberger), became an important pest of apple in Nova Scotia with the widespread use of organic fungicides in the early 1950's. Work by Dustan (1) had suggested that mortality of *P. mali* in the adult stage by the entomogenous fungus *Entomophthora sphaerosperma* (Fresenius) was largely responsible for reducing an earlier infestation to an economically acceptable level. Jaques and Patterson (2) showed that the fungal disease developed naturally in populations of *P. mali* adults in non-sprayed orchard plots in Nova Scotia and killed large numbers of adults before oviposition in August and September (Table VII) thus reducing the density of the following generation. Application of an organic fungicide, such as captan, to an orchard (see Nash orchard Table VII) or to orchard plots, reduced mortality of adults by the disease and this resulted in greater oviposition (2). Plot tests and observations on several orchard populations (Table VIII)

TABLE VII

Mortality caused by *Entomophthora sphaerosperma* in four populations of adult *Psylla mali* in 1958 and 1959 at Kentville, Nova Scotia

Orchard[1]	Year	Adults per 500 leaves										Eggs laid
		6–11 July		22–24 July		3–7 Aug.		18–21 Aug.		9–12 Sept.		(100 buds)
		Living	Dead[2]	Living	Dead	Living	Dead	Living	Dead	Living	Dead	
North Sawler (Check plot)	1958	204	26	135	123	17	201	14	118	3	45	75
	1959	57	0	37	3	26	15	5	27	2	20	30
Herbert	1958	420	11	105	113	13	219	9	148	3	104	75
	1959	108	1	42	27	19	43	6	52	1	36	—
Nash	1958	134	0	75	0	158	0	129	0	134	1	880

[1] Nash orchard was sprayed with captan; other orchards were not sprayed in years of observation.

[2] Only adults killed by *E. sphaerosperma* are included.

TABLE VIII

Prevalence of disease in population of adult *Psylla mali* during egg-laying (20–31 August) in unsprayed orchards and plots examined in 1955 to 1959 inclusive[1]

Year	Not sprayed	Sprayed with fungicides				
		Glyodin	Captan	Ferbam	Other	Total
1955	$\frac{2}{2}$	$\frac{1}{4}$	$\frac{0}{3}$	$\frac{0}{0}$	$\frac{0}{2}$	$\frac{1}{9}$
1956	$\frac{2}{3}$	$\frac{0}{3}$	$\frac{0}{6}$	$\frac{0}{2}$	$\frac{0}{5}$	$\frac{0}{16}$
1957	$\frac{1}{2}$	$\frac{0}{3}$	$\frac{0}{2}$	$\frac{0}{2}$	$\frac{0}{5}$	$\frac{0}{12}$
1958	$\frac{3}{3}$	$\frac{1}{2}$	$\frac{1}{6}$	$\frac{0}{4}$	$\frac{1}{2}$	$\frac{3}{14}$
1959	$\frac{4}{4}$	$\frac{0}{2}$	$\frac{0}{4}$	$\frac{0}{3}$	$\frac{0}{2}$	$\frac{0}{11}$
1955–9	$\frac{12}{14}$	$\frac{2}{14}$	$\frac{1}{21}$	$\frac{0}{11}$	$\frac{1}{16}$	$\frac{4}{62}$

[1] If more than one observation was made between 20–31 August, data from the first observation only are recorded here. The numerator for each entry is the number of sites in which more than 20 per cent. of the adults found were killed by *Entomophthora sphaerosperma*; the denominator is the number of orchards or plots examined.

confirmed that the mortality of *P. mali* by naturally occurring *E. sphaerosperma* was affected by application of certain organic fungicides. This work is significant because it demonstrated that the effectiveness of a pathogen can be influenced by manipulation of the environment.

LITERATURE CITED

1. Dustan, A. G. (1924). The control of the European apple sucker, *Psylla mali* Schmidb., in Nova Scotia. *Can. Dep. Agr. Pamphlet* 45 (new series), 13 pp.
2. Jaques, R. P. & Patterson, N. A. (1962). Control of the apple sucker, *Psylla mali* Schmidb., by the fungus *Entomophthora sphaerosperma* (Fresenius). *Can. Ent.* 94: 818–25.

16. *PSYLLA PYRICOLA* FORSTER, PEAR PSYLLA (HEMIPTERA: PSYLLIDAE)

R. D. McMullen

PEST STATUS

The pear psylla, *Psylla pyricola* Förster, was introduced from Europe to the eastern United States in about 1832 (22) and first appeared in Canada at Freeman, Ontario in 1894 (21). It has since spread to nearly all areas of Canada where pears are grown. In 1918, *P. pyricola* was reported from Nelson, British Columbia, but this was either a case of misidentification or the infestation has since died out.

The pest did not become a problem in British Columbia until 1942 when it spread north from established infestations in the State of Washington (13).

Pyrus spp. are the only true hosts of *P. pyricola*. Overwintering occurs in the adult stage and oviposition commences very early in the spring about three weeks before pear buds start to break. In Ontario, up to three generations have been recorded (26), whereas in southern British Columbia five generations occur in some years (25). Uncontrolled infestations can cause total loss of salable fruit and it is not uncommon for crop value to be reduced by 20 per cent. in orchards where chemical control measures are not properly applied or timed. The adult and nymphal stages feed on tender twig growth, buds, and leaves, and only rarely on fruits. One of the injuries caused by *P. pyricola* is leaf necrosis which results from feeding and the smothering effect of honeydew produced by the nymphs. The principal economic injury is marking of the fruit by honeydew. Various microorganisms grow in the honeydew, turning it black. These blackish stains may be washed off but lenticels in the skin of the fruit covered by honeydew enlarge and suberize, permanently marking the fruit. In addition, *P. pyricola* is suspected of transmitting fireblight bacteria (*Bacillus amylovorus* (Burr) Trev.) and is a proven vector of pear decline virus (9) and pear leaf curl virus (6).

Four parasites native to Canada have been reared from the nymphal stages of *P. pyricola* (4, 15, 20). *Trechnites insidiosus* (Crawford) and *Prionomitus mitratus* (Dalm.) (Hymenoptera: Encyrtidae) are primary parasites, and two, *Pachyneuron californicum* Grlt. and *Asaphes vulgaris* Walker (Hymenoptera: Pteromalidae) are hyperparasites. Accurate assessments of the degree of population suppression effected by these parasites have not been made.

Several species native to Canada have been recorded as predators of *P. pyricola* (3, 12, 17, 18, 23, 24, 26). In British Columbia the list includes: *Chrysopa oculata* Say and *C. carnea* Steph. (Neuroptera: Chrysopidae); *Hemerobius pacificus* Banks (Neuroptera: Hemerobiidae); *Anthocoris antevolens* White, *A. melanocerus* Reuter and *Orius tristicolor* White (Hemiptera: Anthocoridae); *Campylomma verbasci* (Meyer), *Deraeocoris brevis piceatus* Knight, *D. fasciolus* Knight, *Diaphnocoris provancheri* (Burque) (Hemiptera: Miridae); *Adalia frigida* Schn., *Calvia duodecimmaculata* Gebl., *Coccinella transversoguttata* Fald., *Hippodamia convergens* Guérin-Meneville, *H. quinquesignata* Kirby and *Megilla fuscilabris* Mulsant (Coleoptera: Coccinellidae); *Platypalpus* sp. near *pluto* (Diptera: Empidae) and *Sphaerophoria* sp. (Diptera: Syrphidae). In southern Ontario two *Chrysopa* spp., one *Anthocoris* sp., one *Orius* sp. and three coccinellids, *Hippodamia* sp., *Cycloneda* sp. and *Ceratomagilla* sp., are listed. Definitive studies on the effectiveness of these predator complexes in the regulation of *P. pyricola* populations are lacking, although some information is available on the effects of pesticides on certain of the predacious species and the response of *P. pyricola* populations to reduced rates of predation (16).

BACKGROUND

P. pyricola in British Columbia is heavily attacked by a relatively large number of species of predacious insects (15), and the native parasitic species, both of which attack the nymphal stages, are subject to hyperparasitism (15). Therefore, the choice of candidate species for importation and release must be carefully made. None of the native predators prey exclusively on *P. pyricola* but feed on a wide variety of other insect and mite species in the orchard environment. These polyphagous habits may well be advantageous. Most of the predators tend to occupy the arboreal portion of the orchard habitat, to which *P. pyricola* is restricted except for its overwintering adults. In the case of the most abundant of the predators, there is good seasonal synchrony with the life cycle of *P. pyricola*. Little is known about the natural factors which may limit the effectiveness of native predators in suppressing *P. pyricola* populations, such as parasitism of the predator species and interspecific competition for prey. Thus, it is difficult to list a set of desirable attributes required for the introduction of a candidate predator. *Anthocoris nemoralis* (F.) is the only predator released and successfuly established for control of *P. pyricola* in British Columbia to date. The criteria for selection were that in Europe *A. nemoralis* shows a marked preference for psyllids as prey and has a greater rate of growth when fed on psyllids than on other prey (1, 2).

Parasitism of *P. pyricola* and the related species, *P. pyri* (L.) and *P. pyrisuga* Förster, on pear trees has been widely studied (9). No egg parasites of any psyllid species have yet been discovered. Records of primary parasites of the nymphal stages of psyllids on pear include *Prionomitus mitratus* on *P. pyricola* in Europe and British Columbia and on *P. pyri* and *P. pyrisuga* in Europe; *Trechnites insidiosus* on *P. pyricola* in eastern and western North America and *Trechnites psyllae* (Ruschka) on *P. pyricola* and *P. pyri* in Europe. In Europe, *P. mitratus* is invariably associated with *P. pyrisuga* and reared only from *P. pyricola* when these are coexistent with *P. pyrisuga* (7). In British Columbia, *P. mitratus* has only been recovered from the first of four to five generations of *P. pyricola* for a number of consecutive years, but breeds throughout the growing season on two unidentified psyllid species on willows near orchards (16). This suggests that *P. pyricola* is not an entirely acceptable host for *P. mitratus*. *T. insidiosus* and *T. psyllae* are very similar and were considered as conspecific at one time. Both are subjected to hyperparasitism by a number of species (7, 15). This plus the likelihood that any primary parasite of the nymphal stage of *P. pyricola* introduced into British Columbia will be subject to attack by hyperparasites already present, reduces the probability of the success of such introductions.

One species, *Endopsylla agilis* de Meijere (Diptera: Itoniidae), has been recorded as parasitic on adult *P. pyricola* in the British Isles and northern Europe. A brief description of its biolology (10) lists the psyllids *P. peregrina* Förster, *P. mali* Schmidberger, and *P. melanoneura* Förster as additional hosts in Scotland. Other reports from Holland (19) and England (5) list *P. foersteri* Flor. as a host. No hyperparasites are known to date and no adult parasites of *P. pyricola* were found in British Columbia after an extensive search. For these reasons and because the adult of *P. pyricola* is less subject to predation than are the immature stages, *E. agilis* has been chosen for study and possible introduction into British Columbia to augment biological control of *P. pyricola*. The choice is not without weaknesses for the preference of *E. agilis* for *P. pyricola* compared to other psyllids is unknown, the percentage parasitism in *P. pyricola* populations in Europe is low and the climate of northern Holland and northwestern Germany where *E. agilis* is most abundant is cooler and moister than that of the southern interior of British Columbia.

RELEASES AND RECOVERIES

PARASITES

Prionomitus mitratus (Dalman) (Hymenoptera: Encyrtidae)

A total of 167 adults, 72 males and 95 females, were released in a group of nonsprayed mature pear trees heavily infested with *P. pyricola* immediately south of the entomology laboratory at the Canada Department of Agriculture Research Station, Summerland, British Columbia during the latter two weeks of July 1963. In June 1964, adult *P. mitratus* emerged from parasitized fifth-instar nymphs of the first generation of *P. pyricola* collected at the release site. Also recovered were adults of another primary parasite, *Trechnites insidiosus*, and two hyperparasites, *Pachyneuron californicum* and *Asaphes vulgaris*. The level of parasitism by *P. mitratus* was less than 1 per cent. (15). *P. mitratus* has been recovered each year since but only from the first generation of *P. pyricola* and always in small numbers. There is doubt as to whether these collections of *P. mitratus* are attributable to the introduction of *P. mitratus* in 1963 (15). In June 1964, *P. mitratus* adults were also reared from *P. pyricola* nymphs collected 33 miles south, 45 miles north, and 36 miles west of the release site. It is unlikely that the released parasites, or their progeny, could have dispersed over these distances, particularly westward where a mountain range separates the western collection sites from the release site. The dispersal would have had to occur in, at most, only three generations. Also, *P. mitratus* had previously been reported from a number of native psyllids on a variety of host plants in California and Utah (8), and Washington (10).

PREDATORS

Anthocoris nemoralis (Fabricius) (Hemiptera: Anthocoridae)

On 19 June 1963, a single liberation of 55 *A. nemoralis* adults, the number of each sex not specified, was made in a small unsprayed mature pear orchard due east of the soils laboratory at the Summerland Research Station. Small numbers of adults and nymphs were observed at the release site in August 1966. In July 1968, *A. nemoralis* was the most abundant *Anthocoris* present in an unsprayed pear orchard 0·75 miles east of the release site. Maximum dispersal from the release site in August 1968 was approximately 1·5 miles.

Two other species of *Anthocoris* were also released in June 1963 (see Table X) but none of these have been recovered.

Anthocoris melanocerus Reuter (Hemiptera: Anthocoridae)

After determining the absence of *A. melanocerus* in the area of Paris, Ontario, Dr. W. H. A. Wilde of the University of Guelph released 90 female and 55 male adult *A. melanocerus* in a pear orchard 1·2 miles south west of Paris on 15 July and 24 August 1964. The specimens of *A. melanocerus* were obtained from the Okanagan Valley and the Kootenay Valley of British Columbia. The latter valley has a climate similar to that of Paris, Ontario. Eggs of *A. melanocerus* were observed on an aphid-infested alfalfa crop near the point of release on 22 July and adults were observed in pear trees through September 1964. No recoveries were made in 1965 or 1966.

LABORATORY STUDIES OF IMPORTED PARASITES AND PREDATORS

PARASITES

Endopsylla agilis de Meijere (Diptera: Itoniidae)

In 1968, 1343 mature larvae and pupae of *E. agilis* were imported from Germany (Table IX). Because of poor survival and emergence of adults over a prolonged period, these insects have been reserved for the study of methods of colonization in the laboratory to obtain adequate numbers for free release purposes. To date, a viable laboratory colony has not been established. Approximately 900 pupae in hibernal diapause were retained for work in 1969.

PREDATORS

Anthocoris nemoralis (Fabricius) (Hemiptera: Anthocoridae)

In 1962 and 1963, 113 *A. nemoralis* nymphs were received from Switzerland (Table IX), for laboratory evaluation as a predator of *P. pyricola.* Rates of prey consumption by adult *A. nemoralis* and *A. melanocerus* in cage experiments with *P. pyricola* eggs and nymphs on potted pear seedlings were about equal, although *A. nemoralis* exhibited a slight preference for *P. pyricola* eggs over nymphs as compared to *A. melanocerus* (25).

EVALUATION OF CONTROL ATTEMPTS

For reasons given above there is little doubt that the importation and release of *Prionomitus mitratus* was an unsuccessful attempt to introduce an additional species into a complex of native parasites and predators presently exerting considerable population regulating pressures against *P. pyricola.* In contrast, the introduction and establishment of *Anthocoris nemoralis* may be of significance because of its demonstrated ability to compete with and, in part, displace native *Anthocoris* spp. in pear orchards. In addition, after a winter (1968–1969) of record low temperatures, *A. nemoralis* has shown a marked superiority in cold hardiness over *A. antevolens.* However, in 1968 the suppression of *P.*

pyricola populations by the predator-parasite complex in nonsprayed orchards where *A. nemoralis* was established was not significantly greater than in orchards where *A. nemoralis* was not yet established.

RECOMMENDATIONS

Prior to the further introduction of exotic parasites or predators there should be additional research on the biologies of *P. pyricola* and the more numerous native predators and parasites. Particular emphasis should be placed on life-table and key mortality factor studies of *P. pyricola* so that more reliable criteria may be available for the selection of species for introduction. Information available through such additional studies would also provide a firm basis for considering the manipulation of populations of native predators through cultural practices, modification of chemical control practices for pests of pear other than *P. pyricola* to conserve predators and parasites, and other means of enhancing the efficiency of native and introduced biological control agents.

TABLE IX

Cage releases and laboratory studies of predators and parasites against *Psylla pyricola* Förster

Species and Province	Year	Origin	Number
Predator			
Anthocoris nemoralis (Fabricius)			
British Columbia	1962	Switzerland	18
	1963	Switzerland	95
Parasite			
Endopsylla agilis de Meijere			
British Columbia	1968	Germany	1343

TABLE X

Open releases and recoveries of predators and parasites against *Psylla pyricola* Förster

Species and Province	Year	Origin	Number	Year of recovery
Predators				
Anthocoris nemoralis (Fabricius)				
British Columbia	1963	Switzerland	50	1966
A. melanocerus Reuter				
Ontario	1964	British Columbia	145	—
A. nemorum (L.)				
British Columbia	1963	Switzerland	2	—
A. pilosus (Jakovliev)				
British Columbia	1963	Switzerland	10	—
Parasite				
Prionomitus mitratus (Dalman)				
British Columbia	1963	Switzerland	167	1964[1]

[1] Probably present as a native species before the release. See text.

LITERATURE CITED

1. Anderson, N. H. (1962). Bionomics of six species of *Anthocoris* (Heteroptera: Anthocoridae) in England. *Trans. R. ent. Soc. Lond.* **114**: 67–95.
2. Anderson, N. H. (1962). Growth and fecundity of *Anthocoris* spp. reared on various prey (Heteroptera: Anthocoridae). *Entomologia exp. appl.* **5**: 40–52.
3. Anderson, N. H. (1962). Anthocoridae of the Pacific Northwest with notes on distributions, life histories, and habits (Heteroptera). *Can. Ent.* **94**: 1325–34.

4. Armstrong, T. (1946). *In* A. Rep. Ent. Lab., Canada Dep. of Agriculture, Vineland Station, Ontario (unpublished).
5. Bagnall, R. R. & Harrison, H. (1924). New British Cecidomyidae. V. *Entomologist's Rec. J. Var.* 36: 38.
6. Griggs, W. H., Jensen, D. D. and Iwakiri, B. T. (1968). Development of young pear trees with different rootstocks in relation to psylla infestation, pear decline, and leaf curl. *Hilgardia* 39: 153–204.
7. Hagen, K. S. (1966). Personal communication. Department of Biological Control, University of California, Albany, California.
8. Jensen, D. D. (1957). Parasites of the Psyllidae. *Hilgardia* 27: 71–99.
9. Jensen, D. D., Griggs, W. H., Gonzales, C. Q. & Schneider, H. (1964). Pear decline virus transmission by pear psylla. *Phytopathology* 54: 1346–51.
10. Krombein, K. V., *et al.* (1958). Hymenoptera of America north of Mexico, synoptic catalog. *U.S. Dep. Agric. Monogr.* 2, 1st Suppl., 305 pp.
11. Lal, K. B. (1934). Insect parasites of Psyllidae. *Parasitology* 26: 325–34.
12. Madsen, H. F. (1961). Notes on *Anthocoris melanocerus* Reuter (Hemiptera: Anthocoridae) as a predator of the pear psylla in British Columbia. *Can. Ent.* 93: 660–2.
13. Marshall, J. & Olds, H. F. (1946). The pear psylla in British Columbia. *Proc. ent. Soc. Brit. Columb.* 43: 1–3.
14. McMullen, R. D. (1964). Biological control of pear psylla. *Proc. Wash. St. hort. Ass.* 60: 79–82.
15. McMullen, R. D. (1966). New records of chalcidoid parasites and hyperparasites of *Psylla pyricola* Förster in British Columbia. *Can. Ent.* 98: 236–9.
16. McMullen, R. D. Unpublished observations.
17. McMullen, R. D. & Jong, C. (1967). New records and discussion of predators of the pear psylla, *Psylla pyricola* Förster, in British Columbia. *Proc. ent. Soc. Brit. Columb.* 64: 35–40.
18. McMullen, R. D. & Jong, C. (1967). The influence of three insecticides on predation of the pear psylla, *Psylla pyricola*. *Can. Ent.* 99: 1292–7.
19. Meijere, J. C. H. de. (1907). Eerste supplement op de niewe naamlijst van Nederlandsche Diptera. *Tijdschr ent.* 50: 151–95.
20. Peck, O. (1966). An emendation. *Can. Ent.* 98: 448.
21. Ross, W. A. (1918). The pear psylla. *Agric. Gaz. Can.* 5: 1134–6.
22. Slingerland, M. V. (1892). The pear-tree psylla. *Bull. Cornell Univ. agric. Exp. Stn* 44: 161–8.
23. Watson, T. K. & Wilde, W. H. A. (1963). Laboratory and field observations on two predators of the pear psylla in British Columbia. *Can. Ent.* 95: 435–8.
24. Wilde, W. H. A. (1962). Bionomics of the pear psylla, *Psylla pyricola* Foerster in pear orchards of the Kootenay Valley of British Columbia, 1960. *Can. Ent.* 94: 845–9.
25. Wilde, W. H. A. & Watson, T. K. (1963). Bionomics of the pear psylla, *Psylla pyricola* Foerster, in the Okanagan Valley of British Columbia. *Can. J. Zool.* 41: 953–61.
26. Wilde, W. H. A. (1965). The pear psylla, *Psylla pyricola* Foerster, in Ontario (Homoptera: Chermidae). A review. *Proc. ent. Soc. Ont.* 95 (1964): 5–10.

17. *RHAGOLETIS POMONELLA* (WALSH), APPLE MAGGOT (DIPTERA: TEPHRITIDAE)

L. G. Monteith

PEST STATUS

Rhagoletis pomonella (Walsh) remains a perennial and potentially destructive pest throughout certain areas of Canada and the United States (2, 3, p. 463), and there has been no detectable change in its food preferences. It continues readily to attack hawthorns (*Crataegus* spp.) and crab apples (*Pyrus* spp.) which were its principal hosts before *R. pomonella* first attracted attention by attacking commercial apples and prunes (3, 6, 7, 8, 15, 16).

Control methods used against this pest are greatly influenced by the sporadic, unpredictable appearance of adults and by its choice of food plants. Emergence is influenced by the weather, so that numbers of adults fluctuate widely at one place from year to year, or from one site to another in any one season. The period of greatest emergence and the duration of adult activity vary widely at a site in successive years. The adults facultatively attack a variety of food plants.

Biotic agents have contributed little to apple-maggot control in commercial orchards because all methods used against this pest have been more detrimental to its parasites and predators, perhaps sometimes eliminating them from such orchards (12, 13). Parasites and predators occur throughout the area of infestation, and contribute to apple-maggot mortality in non-commercial environments (12, 13). Data on the pest, its parasites and predators, and the effect of integrated control methods on them are insufficient to allow recommendations to be made that might increase the contribution by biotic agents.

BACKGROUND

In Canada, studies directly related to the use of biotic agents are being conducted by the Canada Department of Agriculture at the Research Institute, Belleville, Ontario, and at the Research Station, St. Jean, Quebec. In Europe, studies on the biology and collection of parasites for the Belleville project are being conducted by the Commonwealth Institute of Biological Control (1, 4, 5).

So far, all parasites imported have been used in laboratory experiments, and there have been no field releases.

PARASITES

The only parasites obtained during a recent collecting survey across southern Ontario were two species of *Opius* in the Region of Niagara. They are well adapted to attack the apple maggot but tend to be restricted to situations with unsprayed trees and grassy undergrowth. *Opius lectus* Gah. and *O. alloeus* Mues. attack the apple maggot in Quebec (17), and *O. melleus* Gah. and *O. lectus* in New Brunswick (14).

A number of parasites attack various European fruit flies (1). As these fruit flies are closely related to the apple maggot and cherry maggots of North America and attack the same or closely related food plants, the possible use of European parasites against the apple maggot is being investigated.

Phygadeuon wiesmanni Sachtl. is a parasite of the European cherry fruit fly, *Rhagoletis cerasi* (L.). Initially samples were obtained from Poland and Switzerland. There was a difference in the responses of *P. wiesmanni* from these areas. The Polish stock showed considerably more interest in the apple maggot than did the Swiss stock. Both attacked mature larvae or forming puparia but no further development occurred in the host. Later *P. wiesmanni* from Austria was obtained; it readily attacks apple maggot pupae at a later stage than did the Polish stock, and has produced a first filial generation. *P. wiesmanni* was sent to Dr. P. S. Messenger who tested them on *R. completa* Cresson and *R. indifferens* Curran, obtaining a first filial generation on *R. completa* (9).

Opius rhagoleticolis Sachtl. is also a parasite of *R. cerasi*. In the laboratory it has been seen to mate, visit apple fruit (entire or sliced), investigate and probe mature larvae of the apple maggot, but not to oviposit. This parasite showed as much interest in larvae of the golden rod gall fly, *Eurosta solidaginis* Fitch, and the apple seed chalcid *Torymus druparum* Boh. as in those of the apple maggot.

PREDATORS

Crickets, *Gryllus* and *Nemobius*, were found to be major predators of apple maggot pupae under unsprayed trees with grassy undergrowth, destroying 54 per cent. of samples of buried pupae during the fall, but not contributing to a further 25 per cent. mortality by predators during the pre-emergence period in the spring and early summer (10, 11, 12). In the laboratory crickets were very efficient in finding and destroying apple maggot larvae and pupae (11, 12).

At St. Jean, Quebec carabid beetles are important predators of the larvae and pupae (18).

RECOMMENDATIONS

Since no biotic agents have yet been released in Canada against the apple maggot, the effective ness of such an approach remains unknown. Also, the economic significance of native parasites and predators in commercial orchards has yet to be studied: such a study will require the maintenance of an environment favourable to the biotic agents and therefore the modification of current chemical control methods.

If biological control of *R. pomonella* is to become feasible, a critical consideration will be the extent to which the parasites and predators can tolerate the environment of most commercial orchards. Perhaps sufficiently tolerant species may be found by testing additional parasites of other fruit flies. A parasite able to attack apple maggot on hawthorns as well as on apples and plums would be able to parasitize it over the greater part of its range.

P. wiesmanni can develop on *R. pomonella*. It remains to be discovered whether or not it can establish itself in Canada. It is bivoltine in Europe. Hopefully both generations would find hosts in Canada, with the first attacking *R. fausta* (Osten Sacken) and *R. cingulata* (Loew) and the second (or both) *R. pomonella*. If *P. wiesmanni* could be established, its importance as a control agent, relative to the native *Opius*, might well depend on its ability to synchronize its winter diapause with that of the apple maggot.

It is recommended that:

(1) Tests for host-preference and survival in Canada be continued with exotic parasites that attack hosts related to the apple maggot or that have similar food plants, with a view to finding species suitable for use in a biological control attempt.

(2) Particular emphasis be given to developing methods that manipulate parts of the orchard environment so as to trap or deter the pest and favour its parasites and predators.

LITERATURE CITED

1. Ahmad, M. & Carl, K. P. (1965). The natural enemies of *Rhagoletis* in Europe. A literature review. *Rep. Commonw. Inst. biol. Control*, 9 pp.
2. Anon. (1965). *Can. Insect Pest Rev.* 43: 95.
3. Bush, G. L. (1966). The taxonomy, cytology, and evolution of the genus *Rhagoletis* in North America (Diptera: Tephritidae). *Bull. Mus. comp. Zool. Harv.* 134: 431–562.
4. Carl, K. (1966). Collection of parasites of *Rhagoletis cerasi* (L.). Report of the work in 1966. *Rep. Commonw. Inst. biol. Control*, 7 pp.
5. Carl, K. (1968). Collection of and observations on the natural enemies of *Rhagoletis cerasi* (L.). Report of the work in 1968. *Rep. Commonw. Inst. biol. Control*, 8 pp.
6. Comstock, J. H. (1882). The apple maggot. *Rep. U.S. Commnr Agric.* (1881–1882): 195–8.
7. Good, C. A. (1915). The apple maggot in Nova Scotia. *Proc. ent. Soc. Nova Scotia* 1: 54–69.
8. Harvey, F. L. & Munson, W. M. (1900). Apple insects of Maine. *Rep. Me agric. Exp. Stn* (1899): 136–40.
9. Messenger, P. S. (1969). Personal communication. Division of Biological Control, Agricultural Experiment Station, University of California, Berkeley.
10. Monteith, L. G. (1968). *In Res. Rep. Res. Inst. Belleville, Ont.* (1967): 90.
11. Monteith, L. G. (1969). *In Res. Rep. Res. Inst. Belleville, Ont.* (1968): 185.
12. Monteith, L. G. Crickets as predators of the apple maggot, *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae). *Can. Ent.* (in press).
13. Monteith, L. G. Parasites of the apple maggot, *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae), in Ontario. *Can. Ent.* (in press).
14. Neilson, W. T. A. (1969). Personal communication. Research Station, Canada Department of Agriculture, Kentville, Nova Scotia.
15. Petch, C. E. (1924). The apple maggot and its control in Quebec. *Circ. Dep. Agric. Can.* 28: 1–4.
16. Riley, C. V. (1872). The apple-maggot fly. *Am. agric.* 31: 263–4.
17. Rivard, I. (1967). *Opius lectus* and *O. alloeus* (Hymenoptera: Braconidae), larval parasites of the apple maggot, *Rhagoletis pomonella* (Diptera: Trypetidae), in Quebec. *Can. Ent.* 99: 895–6.
18. Rivard, I. (1969). Personal communication. Research Station, Canada Department of Agriculture, St. Jean, Quebec.
19. Wellhouse, W. H. (1920). Wild hawthorns as hosts of apple, pear and quince pests. *J. econ. Ent.* 13: 388–91.
20. Woods, W. C. (1915). *Biosteres rhagoletis* Richmond, sp. n., a parasite of *Rhagoletis pomonella* (Walsh). *Can. Ent.* 47: 293–5.

18. *RHOPALOSIPHUM MAIDIS* (FITCH), CORN LEAF APHID (HEMIPTERA: APHIDIDAE)

B. C. SMITH

PEST STATUS

The corn leaf aphid, *Rhopalosiphum maidis* (Fitch), occurs yearly on barley, corn, and other cereals. High density populations cause appreciable damage. The severity of the damage depends on weather, soil fertility, plant susceptibility to aphid attack, time of planting, and disease (1). *R. maidis* is found in North America wherever corn is grown, and in recent years its numbers have been increasing in Ontario and the American corn belt (6). The damage to corn includes barrenness, interference with pollination, propagation of moulds on leaves where honeydew accumulates, increase in numbers of corn earworms, *Heliothis zea* (Boddie), because of the attraction of adults to honeydew, and reduction in yield. Treatment with insecticides is usually not recommended unless aphid density is very high or the crop is grown for seed.

Though insect predators, including chrysopids, coccinellids, and syrphids, attack *R. maidis* on corn, they have so far been unable to prevent aphid outbreaks that cause serious damage. In the area of Belleville, Ontario the alatae of *R. maidis* usually occur in the last two weeks of July when corn is in the whorl stage. Populations are well established on susceptible plants by the end of July, and large numbers are found on the tassels, leaves, and ears in the first week of August.

The abundance of *R. maidis* varies much in different years and is generally greater on field (Pride 432) than on sweet (Seneca chief) varieties of corn. In 1967, high-density populations on field corn variety Pride 432 reduced ear weight of infested plant by about 38 per cent. Damage was slight in 1966 and 1968. In 1968, *R. maidis* was more numerous on the tassels and upper parts of the plant than on the ears and lower foliage.

BACKGROUND

Work to date has been concerned with the occurrence of coccinellids on corn infested with *R. maidis*, the ecology of the predator and aphid, and the possibility of manipulating coccinellids so as to render them effective control agents. This work, mostly unpublished and still in progress, has been undertaken by the author in the vicinity of Belleville, Ontario.

OCCURRENCE

Adults of 11 coccinellid species occur on corn and four of these reproduce and become common when *R. maidis* is abundant. They are: *Coleomegilla maculata lengi* Timberlake, *Coccinella novemnotata* Hbst., *Coccinella transversoguttata richardsoni* Brown, and *Hippodamia tredecimpunctata tibialis* Say. The less common species in descending order of abundance are: *Adalia bipunctata* (L.), *Hippodamia parenthesis* (Say), *Coccinella trifasciata perplexa* Muls., *Hippodamia convergens* (Guérin-Menville), *Cycloneda munda* (Say), *Hippodamia glacialis* (F.), and *Anatis mali* Auct.

ECOLOGY

An experiment was done on field corn (DeKalb) in 1963 which confirmed an earlier observation that coccinellid adults form aggregations in places where pollen is present.

Coccinellid adults are more numerous on high-density than on low-density populations of *R. maidis*, although their numerical response is not sensitive to small changes in aphid density. An increase of about ×23 in *R. maidis* produces an increase in adult predator density of ×1·5.

The density of coccinellid eggs, larvae, and pupae is not directly related to the density of *R. maidis*. This indicates that females do not respond to prey stimuli for oviposition. The availability of foods other than *R. maidis*, particularly pollen, may mask the relationship between coccinellid larvae and this aphid.

MANIPULATION

Various interacting factors, some of which offer promise for manipulation, affect the numbers and concentration of coccinellids and therefore their ability to contain pest outbreaks. Coccinellids can be manipulated in two ways: first, by attracting them to places where aphids cause damage and by limiting their dispersal from these places; and second, by increasing their numbers, both in nature—and in the laboratory for release in nature.

Synthetic food supplements may be applied to the foliage of corn to encourage aggregations of predators at a particular place and time (5). This may be done before, during, or after the occurrences of *R. maidis* and pollen. Sucrose is effective in July; 149 per cent. more adults were recorded on treated than on control plots. *C. maculata* can be aggregated with turkey starter and liver diets in the last week of July. *C. maculata, C. transversoguttata,* and *H. tredecimpunctata* were present on a higher percentage of plants to which a liver diet was applied than on the controls with pollen. *C. novemnotata, C. transversoguttata* and *H. tredecimpunctata* were scarcer on plants with no pollen (tassels removed) than on controls with pollen. Plots treated with yeast diet had fewer egg batches than did controls, though the proportion of larvae developing to the pupal stage was unaffected.

Coccinellid adults display preferences for particular species and varieties of plants, particular locations within a crop, and sites on an individual plant (3, 4). They respond to gradients of light, temperature and humidity, and to gravity (2).

On plots of Seneca 60, Pride 5, Pride K300, or a mixture of these, adult numbers varied in the respective proportions 1: 2: 3: 2. *H. tredecimpunctata* was 76 per cent. more abundant on varieties of Pride than on Seneca, whereas the numbers of *C. transversoguttata* did not differ on these varieties. *C. maculata* was less abundant on Pride K300 than on other varieties in July but more abundant in August.

Adult distribution and species composition vary at different sites and times on one variety of plant in response to changes in plant height, amount of sunlight and shadow, and plant diversity along crop boundaries.

Plant density and date of planting of corn seed affect coccinellid numbers. Adult density is generally greater at a plant density of 3·2 than at 1·6, 6·4, or 11·4 plants per m^2. (The density of 6·4 is about equivalent to 18,000 plants per acre and generally recommended for corn.) *C. maculata* and *H. tredecimpunctata* are most abundant at a plant density of 3·2 plants whereas *C. novemnotata* and *C. transversoguttata* are most abundant at a density of 1·6 plants per m^2. Adults are generally more abundant on early than on late planted corn.

RECOMMENDATIONS

At this stage in the current investigation, the prospects of controlling *R. maidis* by manipulating predator density are uncertain. An urgent need, if this possibility is to be tested, is a rational system for measuring damage to the crop.

The most effective, non-chemical measures available to reduce damage by *R. maidis* are: to use aphid-resistant varieties of corn, and to plant early, and at a density of about three plants per m^2.

LITERATURE CITED

1. Everly, R. T. (1960). Loss in corn yield associated with the abundance of the corn leaf aphid, *Rhopalosiphum maidis* in Indiana. *J. econ. Ent.* **53**: 924–32.
2. Ewert, M. A. & Chiang, H. C. (1966). Effects of some environmental factors on the distribution of three species of Coccinellidae in their microhabitat. *Ecology of aphidophagous insects.* IV: 195–219. *Czechoslovak Academy of Sciences, Academia Prague.*
3. Iperti, G. (1965). Contribution a l'étude de la spécificité chez les principales coccinelles aphidophages des Alpes-Maritimes et des Basses-Alpes. *Entomophaga* **10**: 159–78.
4. Klausnitzer, B. (1966). Relation of different species of Coccinellidae to the habitat of fir-forests. *Ecology of aphidophagous insects* IV: 165–6. *Czechoslovak Academy of Sciences, Academia Prague.*
5. Smith, B. C. (1966). Effects of food on some aphidophagous Coccinellidae. *Ecology of aphidophagous insects* I: 75–81. *Czechoslovak Academy of Sciences, Academia Prague.*
6. Wressell, H. B. & Hudon, M. (1968). Common insects of corn in eastern Canada. *Publ. Can. Dep. Agric.* **945**: 18.

19. *SITONA CYLINDRICOLLIS* FAHR., SWEETCLOVER WEEVIL, AND *HYPERA POSTICA* GYLL., ALFALFA WEEVIL (COLEOPTERA: CURCULIONIDAE)

C. C. LOAN

PEST STATUS

Species of *Sitona* in Canada breed on legumes, especially forage crops, and usually the feeding effects of their populations are not evident. However, the sweetclover weevil, *S. cyclindricollis* Fåhr., became prominent because of its relatively rapid spread from eastern to western Canada; because its crescent-shaped feeding pattern on foliage and occasional severe damage to seedling sweetclover were clearly evident to the farmer; and because it posed a threat to sweetclover which is unique as a green manure crop. The sweetclover weevil occurs in Canada from Quebec west to British Columbia. It has no known specific parasites or predators and natural control is effected chiefly by weather (2). Where suppression of local populations is needed, tilling or plowing (2, 19) effectively destroy a large proportion of larvae and pupae. The biology of this species has been studied by numerous workers, but the work of Bird (2) is especially thorough and informative. Except for a study on plant resistance to weevil feeding there is no research underway on *S. cylindricollis* in Canada at this time.

Hypera postica Gyll., a serious pest of alfalfa that has been in the eastern United States since 1951 (3), was first reported in Alberta in 1954 (5), and is now established there and in Saskatchewan. It has recently become established in southern Ontario along Lake Ontario and the St. Lawrence River, and in southwestern Quebec (3). *H. postica* is attacked by a complex of insect parasites in the United States of which one species, *Bathyplectes curculionis* (Thoms.), occurs in Alberta. The occurrence of parasites in eastern Canada has not been investigated.

BACKGROUND

Research on biological control of *S. cylindricollis* in the United States by the United States Department of Agriculture was discontinued in 1957 (5). An appraisal of the control programmes involving this species and also *H. postica* in North America is given by J. R. Coulson (6). Brunson and Coles (3) discuss the introduction of parasites of *H. postica* into the United States. A spectacular and unique success is the confirmed establishment in New Jersey on *H. postica* of the braconid *Microctonus aethiops* (Nees). First released in 1957, *M. aethiops* has spread over an area of 100 square miles and its incidence has reached 70 per cent. It is the only introduced parasite of adult weevils to become an important mortality factor.

The sweetclover and alfalfa weevils are serious pests only in North America and so the need for control attempts with insect parasites has not developed elsewhere. Apparently their populations in Europe and Asia are not controlled by natural enemies as no parasites of the adult stage of *S. cylindricollis* are known, and the incidence of parasitism of *H. postica* in France is relatively low (1). In other European areas parasitism of *Sitona* species is also low (4, 6, 7, 8, 9, 10, 21). Exceptions are the 75 per cent (in a sample of 100 weevils) of *S. lineata* L. parasitized in Sweden (18); the 40 per cent. (in 100) of *S. scissifrons* Say parasitized in Canada (14); and the 65–70 per cent. (in 100) of *H. postica* in the United States (3). The potential parasitism of this braconid group is apparently high despite the low incidence reported for most associations.

The objective of parasite introductions was to decrease populations of *S. cyclindricollis* and *H. postica* by adding a mortality factor to a susceptible stage, in this example the adult. The Canadian programme on the sweetclover weevil developed directly from one initiated by the United States Department of Agriculture in North Dakota. It was based on the supposition that European parasites reared from a complex of *Sitona* and *Hypera* weevils on alfalfa would parasitize *S. cylindricollis* on sweetclover in Manitoba. The indigenous parasites of *Sitona* were not considered initially because none was known and because relatively large numbers of various European species were available from the United States Department of Agriculture. A complex on *S. scissifrons* of two braconids, *M. sitonae* Mason (Nearctic) and *Centistes excrucians* Hal. (Holarctic) was not discovered until the conclusion of the release phase of the project.

There were two separate attempts to colonize European parasites in Canada, both of which dealt chiefly with *S. cyclindricollis* in Manitoba. Adult braconids reared from imported cocoons of French origin were released directly into the field in 1952–1954. When this attempt failed, Swedish braconids were obtained and released in 1958–1960 as first-instar larvae in laboratory-parasitized weevils. Surveys to recover the released species in Manitoba extended from 1960 to 1964. With the end of this five-year period the project was discontinued.

McLeod (20) briefly reviewed the Canadian attempts from 1952–1958. Loan reported life-cycle and related studies of the European and indigenous parasite species (11, 13, 14, 15, 17, 18), the progress of the project (12), and its final results (16). This chapter provides information subsequent to McLeod's review and an assessment of the control attempts. It deals chiefly with *S. cylindricollis*, as relatively little work was done with *S. hispidula* (F.) and *S. scissifrons* Say in Ontario, and *H. postica* in Alberta.

RELEASES AND RECOVERIES

PARASITES

The following parasite species were used in the control attempts: *Microctonus aethiops* (Nees), *Perilitus rutilus* (Nees), *Pygostolus falcatus* (Nees), *Campogaster exigua* (Meig.) (against *S. cyclindricollis*); *P. rutilus* (*H. postica*, *S. hispidula*); and *Pygostolus falcatus* (*S. scissifrons*). The numbers released and dates of release are shown in Table XI. The species are discussed in more detail below.

Microctonus aethiops (Nees) (Hymenoptera: Braconidae)

Adults were reared at Belleville from cocoons supplied by the European Parasite Laboratory, United States Department of Agriculture, France, and were released near Portage la Prairie, Manitoba. No progeny were found in *S. cylindricollis* and the attempt is considered a failure.

Perilitus rutilus (Nees) (Hymenoptera: Braconidae)

This species was reared at Belleville from live weevils, chiefly *S. lineata* L., field-collected in Sweden. The programmes featuring this braconid in 1958 and 1959 were based on the release in western Canada of laboratory-parasitized, summer-emerged weevils, rather than on release of adult parasites, as with *M. aethiops*. This was done: to avoid parasitism in the field of overwintered weevils in July which have a short life-span; to take advantage of the diapause of the braconid first-instar larvae in summer-emerged weevils; to release the parasite population in positive association with its intended host; and to increase the size of the released parasite population.

Despite this improved release method, *P. rutilus* failed to establish in Manitoba on *S. cylindricollis* and in Alberta on *H. postica*. The release of adult *P. rutilus* in Ontario to establish on *S. hispidula* was not evaluated.

Pygostolus falcatus (Nees) (Hymenoptera: Braconidae)

P. falcatus also reared from weevils collected in Sweden was released in laboratory-parasitized weevils at three points in Manitoba, and recoveries in 1959 and 1960 near Brandon indicated initial establishment. None, however, was recovered after 1960 and it was concluded that the colony perished (16). *P. falcatus* was also released in 1960 near Belleville, Ontario by the same method in populations of *S. scissifrons*. This attempt was made to see whether *P. falcatus* would establish more successfully in a perennial legume such as vetch rather than in the transient, biennial type of growth of sweetclover; and to determine whether *P. falcatus* would also parasitize *S. cylindricollis*, *S. hispidula*, and *S. lepidus* Marsh. in vetch and adjacent clovers. The parasite was found in *S. scissifrons* collected near the release point in mid-June of 1961, 1963 and 1964, and in *S. cylindricollis* collected in 1961. From 1964 to 1968 no *P. falcatus* were found in the annual dissections. However, *P. falcatus* was recovered from *S. scissifrons* and *S. cylindricollis* in 1969 near the 1960 release point.

Campogaster exigua (Meig.) (Diptera: Tachinidae)

Adults were shipped to Belleville from the European Parasite Laboratory, United States Department of Agriculture, France. Survival was poor and relatively few were released in Manitoba (Table XI). None was recovered from *S. cylindricollis*.

EVALUATION OF CONTROL ATTEMPTS

The reasons why European parasites failed to establish in Manitoba are unknown. For *M. aethiops* the most likely reason is the physiological unsuitability of *S. cylindricollis* as a host: for on this host a high proportion of first-instar larvae died or were diseased (17). Possibly, *M. aethiops* is chiefly a parasite of *H. postica* in Europe; and if so, such preference might explain its successful establishment on this species in the United States.

Relationships that ensure the survival of the parasite and its host decrease the usefulness of these braconid groups as control agents. The most important factor of these relationships may be the diapause of first-instar larvae in summer-emerged weevils. The parasite larva develops to the imago only in spring and early summer, when weevils are most active and relatively concentrated on breeding plants. The diapause also makes certain that the species remains associated with the host when it disperses in late summer, and over winter. The obligatory diapause of the parasite prevents further reduction of weevil populations before they become sexually mature. Though parasitism in early summer by the generation arising from overwintered larvae may be relatively high, it occurs near the end of the normal life-span of the host after a lengthy period of oviposition that establishes the new weevil generation. The maximum incidence of parasitism occurs in populations of overwintered weevils and the minimum in summer-emerged weevils. This relationship is important for the survival of the association, as otherwise the weevil population would be drastically decreased by emergence of a

TABLE XI

Open releases and recoveries of parasites against *Sitona* spp. and *Hypera postica* Gyll.

Species and Province	Year	Origin	Numbers	Year of recovery
Campogaster exigua (Meig.)[1]	1952	France	11♂♂ 54♀♀	—
Manitoba	1953	France	1 10	—
Microctonus aethiops (Nees)[1]	1952	France	350 425	—
Manitoba	1953	France	420– 587	—
Perilitus rutilus (Nees)[1]	1958	Sweden	750–1000	—
Manitoba				
Perilitus rutilus (Nees)[2]	1960	Sweden	78	Establishment not monitored
Ontario				
Perilitus rutilus (Nees)[4]	1959	Sweden	35	—
Alberta	1960	Sweden	13	—
Pygostolus falcatus (Nees)[1]	1958	Sweden	5000–7000	1959, 1960
Manitoba	1959	Sweden	250	—
Pygostolus falcatus (Nees)[3]	1960	Sweden	150– 200	1961, 1963–4
Ontario				

[1] Against *Sitona cylindricollis* Fåhr.
[2] Against *Sitona hispidula* (F.).
[3] Against *Sitona scissifrons* Say.
[4] Against *Hypera postica* Gyll.

high number of parasite larvae in the spring. Reasons for low parasitism of summer-emerged weevils are unknown, but a changed ecosystem and different behaviour of the sexually immature host population may influence the success of parasitism.

RECOMMENDATIONS

(1) The specificity of insect parasites of adult Coleoptera should be determined by rearings of field material before the species is released.

(2) *Microctonus aethiops* and *M. colesi* Drea are suitable candidates for release in eastern Canada on *H. postica*. Establishment attempts should be considered if populations of *H. postica* continue to spread and increase.

LITERATURE CITED

1. Berry, P. A. & Parker, H. L. (1950). Notes on parasitism of *Sitona* in Europe with special reference to *Campogaster exigua* (Meig.). *Proc. ent. Soc. Wash.* 52: 251–8.
2. Bird, R. D. (1949). Studies in the biology and control of the sweetclover weevil (Coleoptera: Curculionidae) in Manitoba, 1945–1949. *80th Rep. ent. Soc. Ont.* 1949: 1–6.
3. Brown, G. S. (1968). *In litt.* Plant Protection Division, Canada Department of Agriculture, Ottawa, Ontario.
4. Brunson, M. H. & Coles, L. W. (1968). The introduction, release and recovery of parasites of the alfalfa weevil in eastern United States. *Rep. U.S. Dep. Agric.* 101, 12 pp.
5. Coulson, J. R. (1969). *In litt.* Insect Identification and Parasite Introduction Branch, United States Department of Agriculture, Beltsville, Maryland.
6. Coulson, J. R. (1969). Unpublished mss.
7. Grossheim, N. A. (1928). Data for the study of the genus *Sitona* German. (In Russian.) *Trudy moldov. nauchno-issled. Inst. Sadov. Vinogr. Vinod.* (*Bull. Mleev Hort. Exp. Stn*) 17, 57 pp. (Abstract in *Rev. appl. Ent.* (*A*) 17: 434–6.)
8. Hobbs, G. A., Nummi, W. O. & Virostek, J. F. (1959). History of the alfalfa weevil, *Hypera postica* (Gyll.) (Coleoptera: Curculionidae) in Alberta. *Can. Ent.* 91: 562–5.
9. Jackson, D. J. (1920). Bionomics of weevils of the genus *Sitona* injurious to leguminous crops of Britain. *Ann. appl. Biol.* 7: 269–98.
10. Jackson, D. J. (1922). Bionomics of weevils of the genus *Sitona* injurious to leguminous crops of Britain. *Sitona hispidula* F., *S. sulcifrons* Thun., and *S. crinita* Herbst. *Ann. appl. Biol.* 9: 93–115.
11. Jackson, D. J. (1924). Insect parasites of the pea-weevil. *Nature, Lond.* 113: 353–4.
12. Jackson, D. J. (1928). The biology of *Dinocampus* (*Perilitus*) *rutilus* Nees, a braconid parasite of *Sitona lineata* L. *Proc. zool. Soc. Lond.* 1928: 597–630.
13. Jackson, D. J. (1934). Parasites of weevils of the genus *Sitona*. *Scott. Nat.* 207: 75–9.
14. Loan, C. C. (1960). A hymenopterous parasite of *Sitona scissifrons* Say (Coleoptera: Curculionidae). *Can. J. Zool.* 38: 837.
15. Loan, C. C. (1961). Introduction of European parasites of *Sitona* spp. for control of the sweetclover weevil *Sitona cylindricollis* in Canada. *J. econ. Ent.* 54: 1026–31.
16. Loan, C. C. (1962). Braconid parasitism of *Sitona* weevils with special reference to *S. scissifrons* Say and *S. cylindricollis* Fahr. *Proc. N. cent. Brch ent. Soc. Am.* 17: 145.
17. Loan, C. C. (1963). The bionomics of *Sitona scissifrons* (Coleoptera: Curculionidae) and its parasite *Microctonus sitonae* (Hymenoptera: Braconidae). *Ann. ent. Soc. Am.* 56: 600–12.
18. Loan, C. C. (1964). Observations on the biology of *Centistes excrucians* (Haliday) (Hymenoptera: Braconidae). *94th Rep. ent. Soc. Ont.* 1963: 56–61.
19. Loan, C. C. (1965). Status of *Pygostolus falcatus* as a parasite of *Sitona* spp. following releases in Manitoba and Ontario. *J. econ. Ent.* 58: 798–9.
20. Loan, C. C. & Holdaway, F. G. (1961). *Microctonus aethiops* (Nees) auctt. and *Perilitus rutilus* (Nees) (Hymenoptera: Braconidae) European parasites of *Sitona* weevils (Coleoptera: Curculionidae). *Can. Ent.* 93: 1057–79.
21. Loan, C. C. & Holdaway, F. G. (1961). *Pygostolus falcatus* (Nees) (Hymenoptera: Braconidae) a parasite of *Sitona* species (Coleoptera: Curculionidae). *Bull. ent. Res.* 52: 473–88.
22. Manglitz, G. R. & Calkins, C. O. (1963). Plowing for sweetclover weevil control. *J. econ. Ent.* 56: 716–7.
23. McLeod, J. H. (1962). Biological control of pests of crops, fruit trees, ornamentals, and weeds in Canada up to 1959. *In* A review of the biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol. Control* 2: 1–33.
24. Ulaskevitch, M. I. (1935). Nodule weevils of the species *Sitona lineata* L., and *Sitona crinita* Herbst. [In Ukranian.] *Vinnitza reg. agric. Exp. Stn.* 23, 75 pp. (Abstract in *Rev. appl. Ent.* (*A*) 24: 452–4.)

20. *SPILONOTA OCELLANA* (D. & S.), EYE-SPOTTED BUD MOTH (LEPIDOPTERA: OLETHREUTIDAE)

R. P. JAQUES,[1] E. J. LEROUX[1] and R. O. PARADIS

MICROBIAL INSECTICIDES
(R. P. J.)

The eye-spotted bud moth, *Spilonota ocellana* (D. & S.), is a prevalent pest of apple in eastern Canada, particularly in orchards in which broad spectrum insecticides are used. Laboratory tests (3) showed that larvae of *S. ocellana* were highly susceptible to the toxins of the bacterium *Bacillus thuringiensis* Berliner, the active ingredient of a microbial insecticide. Tests elsewhere suggested that pollinating insects were not killed by the bacterium, an important consideration when timing applications of insecticides for control of larvae in the spring.

In an initial orchard test at Kentville, Nova Scotia, a wettable powder preparation of the bacterium containing $1{\cdot}4 \times 10^{13}$ spores/lb was applied to apple trees in August at rates of 1, 2, or 4 lbs per 100 gallons of spray to assess effectiveness against newly hatched larvae (3). Counts of live larvae in webs two weeks after treatment gave no evidence that larval populations were affected by the treatments. This ineffectiveness was attributed to protection of the larvae by the web. In a second orchard test at Kentville the bacterium was applied in May when larvae of *S. ocellana* were nearly full grown. Death of about 75 per cent. of the population was caused by application of the preparation at rates of 4 and 6 lbs per 100 gallons of spray.

A long-term test to assess the effect on the orchard fauna of introducing *B. thuringiensis* was carried out at Kentville (4). An emulsifiable concentrate preparation containing $2{\cdot}7 \times 10^{13}$ spores of *B. thuringiensis*/quart was applied to bearing apple trees in large orchard plots on 5–7 occasions in each of 4 consecutive years at rates of 0·5 or 2 quarts per 100 gallons of spray. Numbers of webs formed by small *S. ocellana* larvae, and numbers of spinups formed by sixth-instar larvae were reduced by about 30 and 75 per cent. by the respective dosages of the bacterium. Injury to fruit was proportional.

The tests had value in demonstrating the control of pest species without affecting pollinating, parasitic and predacious species of insects (4). The use of the bacterium for control was not considered economically feasible, however.

PARASITES
(R. O. P. and E. J. L.)

Life tables for the eye-spotted bud moth, *Spilonota ocellana* (D. & S.), in Quebec apple orchards revealed that from 1957 to 1962, *Chrysocharis laricinellae* (Ratz.) parasitized on an average 20 per cent. of the summer larvae and 17 per cent. of the winter larvae of this pest (5).

As mentioned for the pistol casebearer (p. 15), *C. laricinellae* was first introduced at Berthierville, Quebec in 1943 for the control of the larch casebearer, *Coleophora laricella* (Hübner), while from 1957 it was found at Rougemont and other apple districts located about 50 miles south of Berthierville (1, 2). In this new environment, the parasitism caused by *C. laricinellae* has been closely linked to the rise and fall of the eye-spotted bud moth and especially the pistol casebearer larval populations.

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[1] The work described here was conducted while the first and second authors held positions at the Canada Department of Agriculture Research Stations at Kentville, Nova Scotia, and at St. Jean, Quebec respectively.

LITERATURE CITED

1. Graham, A. R. (1944). The establishment of some imported parasites of the larch casebearer, *Haploptilia laricella* Hbn., in Ontario. *74th Rep. ent. Soc. Ont.* 1943: 48–52.
2. Graham, A. R. (1949). Developments in the control of the larch casebearer, *Coleophora laricella* (Hbn.). *79th Rep. ent. Soc. Ont.* 1948: 45–50.
3. Jaques, R. P. (1961). Control of some lepidopterous pests of apple with commercial preparations of *Bacillus thuringiensis* Berliner. *J. Insect Path.* 3: 167–82.
4. Jaques, R. P. (1965). The effect of *Bacillus thuringiensis* Berliner on the fauna of an apple orchard. *Can. Ent.* 97: 795–802.
5. LeRoux, E. J., Paradis, R. O. & Hudon, M. (1963). Major mortality factors in the population dynamics of the eye-spotted bud moth, the pistol casebearer, the fruit-tree leaf roller, and the European corn borer in Quebec. *Mem. ent. Soc. Can.* 32: 67–82.

21. *SWAMMERDAMIA LUTAREA* (HAWORTH), A HAWTHORN DEFOLIATOR (LEPIDOPTERA: YPONOMEUTIDAE)

RAY F. MORRIS

PEST STATUS

This pest was first observed in Newfoundland in 1954. It is of European origin and is not known to occur in any other area of North America. Repeated attacks on hawthorn shrubs and trees have caused high mortality in ornamental plantings of this species in and around St. John's. In some instances damaged hawthorn hedges have been removed. Satisfactory chemical controls are now available.

BACKGROUND

Eckstein (1) recorded *Swammerdamia lutarea* (Haworth) as a pest on *Crataegus* and *Sorbus* and stated that it was widely distributed in central Europe. Meyrick (2) stated that it was common in England. Seasonal life-history studies were conducted at St. John's during 1959 to 1966 (3). In central Europe, Zwölfer (4) recorded two important larval parasites, *Apanteles xanthostigma* (Haliday) and *Horogenes* sp. nr. *soridipes* Thoms.

RELEASES AND RECOVERIES

PARASITES

Open releases of *Apanteles xanthostigma*, from Germany were made against *Swammerdamia lutarea* in Newfoundland in 1963 (174 specimens) and 1964 (276 specimens).

Studies to determine what parasites were present, and whether or not *A. xanthostigma* was established, were made from 1962 to 1966. Although *A. xanthostigma* was never recovered the following native parasites were observed:

Year	Species	Parasitism (%)
1962	*Herpestomus* probably *nasutus* Wesmael	1
1963	*Meteorus* n. sp. near *trachynotus* Viereck	1
1964	*Meteorus* sp. near *trachynotus* Viereck	1
	Tranosema sp.	5
	Itoplectis quadricingulatus (Prov.)	4

1965	*Apanteles* sp. (not *xanthostigma* (Haliday))	3
	Campoletis sp.	1
	Itoplectis quadricingulatus (Prov.)	2
1966	*Itoplectus quadricingulatus* (Prov.)	2

Parasites were identified by Dr. W. R. M. Mason and Mr. G. S. Walley, Entomology Research Institute, Canada Department of Agriculture, Ottawa, Ontario.

EVALUATION OF CONTROL ATTEMPTS

Attempts at control with *A. xanthostigma* were unsuccessful since the parasite was never successfully established. The low percentage parasitism by native parasites shows them to be of limited significance as control agents.

RECOMMENDATIONS

These studies were discontinued in 1967 and no further attempts to recover the parasite, *A. xanthostigma*, are contemplated. The pest is now of little economic importance.

LITERATURE CITED

1. Eckstein, K. (1933). Die Schmetterlinge Deutschlands, 5. Die Kleinschmetterlinge Deutschlands. K. G. Lutz Erlong, Stuttgart.
2. Meyrick, E. (1927). A revised handbook of British Lepidoptera. Watkins and Doncaster, London.
3. Morris, R. F. (1961). Life-history and habits in Newfoundland of *Swammerdamia lutarea* (Haw.) a pest new to North America. *Can. Ent.* 93: 130–5.
4. Zwölfer, H. (1964). Notes on the parasites of *Swammerdamia lutarea* Hw. and *S. caesiella* Hb. (Lep. Hyponomeutidae) in central Europe. *Tech. Bull. Commonw. Inst. biol. Control* 4: 121–46.

22. *TETRANYCHUS URTICAE* (KOCH), TWO-SPOTTED SPIDER MITE

(ACARINA: TETRANYCHIDAE)

R. J. McCLANAHAN

PEST STATUS

The two-spotted spider mite, *Tetranychus urticae* (Koch), is a problem on greenhouse cucumbers but is not often found on greenhouse tomatoes. Good acaricides are available, but control is limited by the difficulty of obtaining complete underleaf coverage, and limitations are imposed by the long continuous harvest. Two-spotted mites from greenhouses have not yet shown evidence of resistance to commonly used acaricides.

BACKGROUND

Experimental work has been done with the predacious mite *Phytoseiulus persimilis* Athias-Henriot in a number of European countries. In England releases were made in cucumber greenhouses by growers provided with *P. persimilis* by the National Agricultural Advisory Service (5). Control of the two-spotted mite was not accomplished until 9 weeks after the predator introduction, and considerable yield loss was involved. *P. persimilis* had a higher biological potential than a native predator *Typhlodromus fallacis* (Garman) (3). Russian work with *P. persimilis* demonstrated 50 per cent. cucumber-yield increase over plots sprayed 15 times a year with acaricides (1).

RELEASES AND RECOVERIES

P. persimilis was obtained by Dr. D. A. Chant from Dr. G. Dosse in Germany in 1959. This mite was originally found in Chile. In a controlled greenhouse release at Belleville, Ontario, the predator virtually eliminated *Tetranychus telarius* (L.) from bean plants in 21 days whereas plants without predators were severely damaged (2). A colony of *P. persimilis* was started at Vineland, Ontario about 1960 and at Harrow, Ontario in 1961.

At the Canada Department of Agriculture Research Station, Harrow experimental work was primarily on the response of *P. persimilis* at various temperatures and the susceptibility to many acaricides (3, 4).

One release on large cucumbers in a greenhouse showed that the predacious mite multiplied and spread. The population of *T. urticae* was fairly high at the time of introduction and the predators never gained the advantage. In another situation, primarily to study control of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), two-spotted mites were successfully controlled when they first were noticed, by an introduction of *P. persimilis* to infested leaves.

EVALUATION OF CONTROL ATTEMPTS

P. persimilis could be an important biological control agent on greenhouse cucumbers. It must be introduced before the two-spotted mite reaches a density of 5 adults per leaf, and the released predators are most efficient when placed on each plant. Only a few chemicals are selective against the two-spotted mite (4) and an integrated control programme is not fully developed.

RECOMMENDATIONS

Research on release timing and rates is needed before the predator can be released in commercial greenhouses. Efficient methods of mass rearing and holding stocks of *P. persimilis* are known but have not been tried in Canada. The best recommendation for cucumber pest control should jointly consider predator releases, whitefly control and mildew control.

LITERATURE CITED

1. Begljarow, G. A. (1967). Ergebnisse der Untersuchungen und der Anwendung von *Phytoseiulus persimilis* Athias-Henriot (1957) als biologisches Bekämpfungsmittel gegen Spinmilben in der Sowjetunion. *Nacht Bl. dt. PflSchutzdienst., Berl.* 21: 197–200.
2. Chant, D. A. (1961). An experiment in biological control of *Tetranychus telarius* (L.) (Acarina: Tetranychidae) in a greenhouse using the predacious mite *Phytoseiulus persimilis* Athias-Henriot (Phytoseiidae). *Can. Ent.* 93: 437–43.
3. McClanahan, R. J. (1968). Influence of temperature on the reproductive potential of two mite predators of the two-spotted spider mite. *Can. Ent.* 100: 549–56.
4. McClanahan, R. J. (In press). Integrated control of *Tetranychus urticae* by selective acaricides and the predacious mite *Phytoseiulus persimilis. Advances in Acarology* 3.
5. Parr, W. J. & Hussey, N. W. (1967). Biological control of the red spider mite on cucumbers: effects of different predator densities at introduction. *Rep. Glasshouse Crops Res. Inst.* 1966: 135–9.

23. *THYMELICUS LINEOLA* (OCHS.), AN INTRODUCED SKIPPER (LEPIDOPTERA: HESPERIIDAE)

A. P. Arthur

PEST STATUS

The introduced, or Essex skipper, *Thymelicus* (=*Adopaea*) *lineola* (Ochs.) was first recorded in North America in 1910 at London, Ontario (12). By 1927 it had spread into the Detroit area of Michigan where it was very abundant in 1930 (10). To the east it was "extremely abundant" at St. Catharines by 1952 (4). It was found in Belleville, Ontario by 1959 (10) and in Ottawa by 1964 (1). In 1956 *T. lineola* was first recorded as causing economic damage by defoliating hayfields and pastures in the Durham and Priceville areas of Grey County (10). This infested area was under observation by the present author each year from 1957 until 1968 when an infestation of similar magnitude was discovered at Read (Hastings County), Ontario. Further to the north and west in Ontario the skipper was recorded near Sudbury by 1960, and in the Sault Ste. Marie and Fort William areas in 1965 (1) (Fig. 2).

Localized infestations have been recorded in other provinces. In Quebec *T. lineola* was recorded at Lanoraie in 1962 and near Montreal in 1965 (1). It has been observed in the Edmunston area of New Brunswick since 1957 (5), and in Halifax, Nova Scotia (2) since 1966. It was also recorded from Terrace, British Columbia as early as 1960 (8) (Fig. 2).

T. lineola has been recorded from several localities in the north central and north eastern parts of the United States, in addition to Michigan. Local infestations were found at Chicago and Streator, Illinois (7); North Manchester, Indiana (13); Columbus, Ohio; Niagara Falls, New York; Lancaster and Reading, Pennsylvania; and Portland and Rockfall, Connecticut (5). The species was also abundant at several localities in New Jersey (5).

These data indicate that *T. lineola* is capable of surviving in eastern and central North America. The fact that it has become abundant in at least four widely scattered areas leaves little doubt that it is a potentially dangerous pest on a variety of important grasses.

BACKGROUND

Surveys show that *T. lineola* is not abundant in Europe, possibly because of the more intensive farming practices and the presence of natural enemies there (6). In Europe, it is consistently attacked by two larval parasites, *Phryxe vulgaris* Fall. and *Rogas tristis* Wesm., and by a pupal parasite *Stenichneumon scutellator* (Grav.) (6). *P. vulgaris* is multivoltine and attacks many species of macrolepidoptera. Females attacking *T. lineola* usually larviposit on instars IV and V. In Europe it parasitized 8-44 per cent. of final-instar larvae collected in the field. *R. tristis* has a fairly wide host range attacking many Lepidoptera occupying the same habitat as *T. lineola*. It is multivoltine and completes the first generation and sometimes the second on *T. lineola*. It usually attacks and completes its larval development in the third instar of the host. Its abundance fluctuated, and parasitism was generally 10–30 per cent. in field-collected material. *S. scutellator* has a more limited host range. It is univoltine, its life cycle being well synchronized with that of *T. lineola*. Parasitism by this species was 30–50 per cent. (6).

Some attempts have been made at the Research Institute, Belleville to study the European species of parasites of *T. lineola* prior to release, but they are difficult to obtain in sufficient numbers because the host is rare in Europe. Small numbers of *T. lineola* larvae parasitized by *R. tristis* were received from Austria for study at Belleville in 1963. The *R. tristis* adults emerged too late to attack *T. lineola* larvae in the field during the same year, but attempts to maintain the stock in the laboratory on alternative hosts were unsuccessful. *S. scutellator* is especially difficult to hold for release because

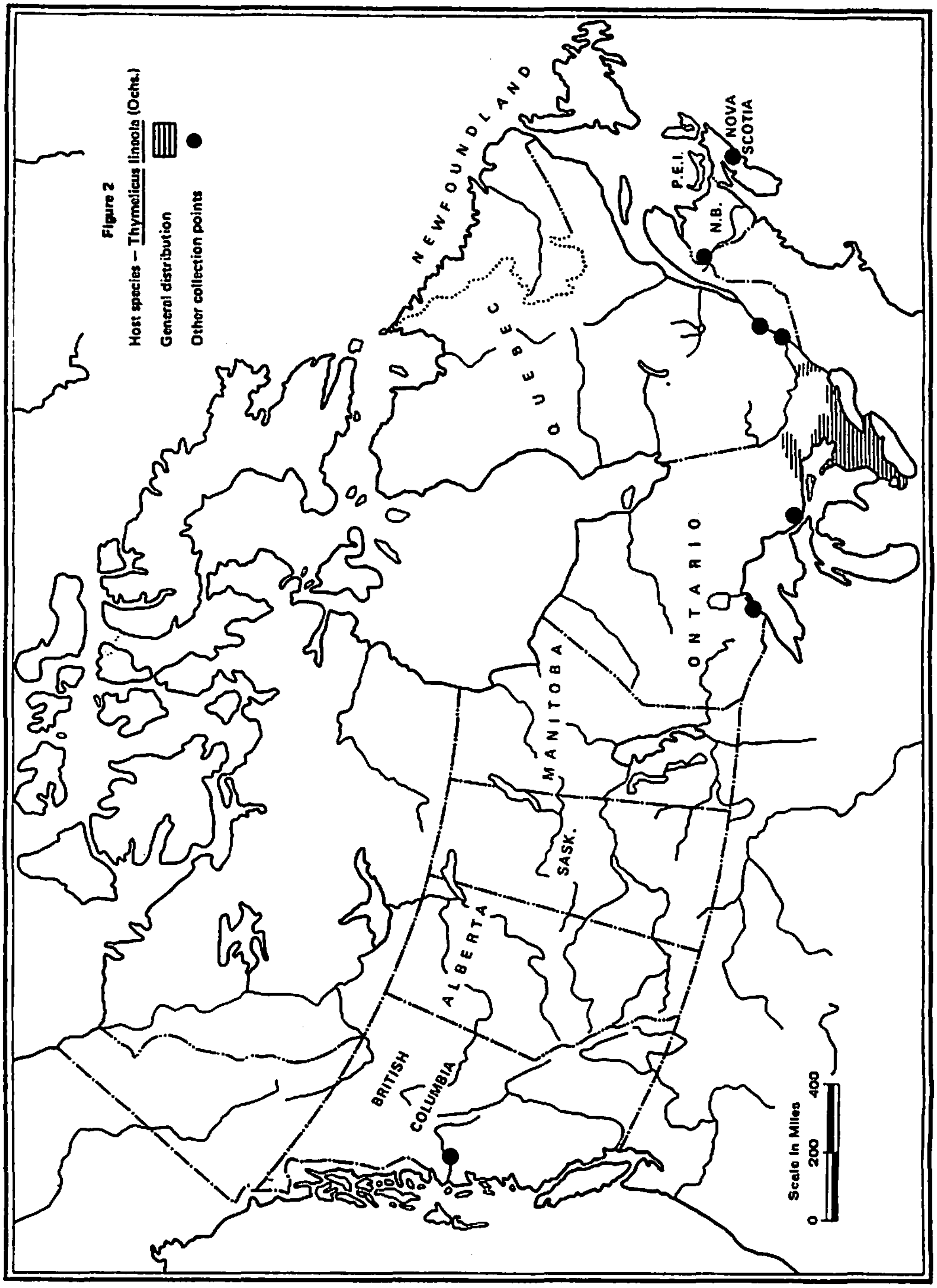

Figure 2

Host species – Thymelicus lineola (Ochs.)

females that emerge from *T. lineola* in July hibernate as adults and do not oviposit until June of the following year. High mortality has occurred when hibernating females were kept in the laboratory. In 1966 approximately 60 females were placed in a styrofoam box containing moist sphagnum and peat moss. This box was stored at 34 ± 2°F during the winter months. Two females survived the winter and resumed activity in the spring. They lived through the summer, but failed to deposit eggs when skipper pupae were exposed for attack. In 1968, 30 females in rearing cages were placed in a dark room at 62 ± 2°F for the winter, except that they were fed in a lighted room at 74 ± 2°F on Mondays, Wednesdays, and Fridays. On 15 May seven females remained alive, but all died before hosts were available in the field.

Persistent chemical insecticides cannot be used against *T. lineola* because of the danger of contamination of milk or meat if animals are pastured on, or fed, hay from treated areas. Commercial preparations containing spores and toxins of *Bacillus thuringiensis* Berliner have been used effectively as a biotic insecticide against the alfalfa caterpillar, *Colias philodice eurytheme* Boisduval (14), and the imported cabbageworm, *Pieris rapae* L. (9). These successes indicated that *Bacillus thuringiensis* might also be effective against *T. lineola*.

Field-cage studies conducted by Arthur (1) showed that females of *T. lineola* would not oviposit on stubble of timothy, *Phleum pratense* L. Pengelly (11) showed that if a field was mowed after oviposition by *T. lineola* some eggs would still be present on the stubble. Carl (6) stated that in Europe the larvae of *T. lineola* were often eliminated when the crop was harvested. The only area in Europe where *T. lineola* was present in significant numbers in hay fields was in eastern Austria where harvesting is done after completion of larval development. These data indicate that harvesting of a hay crop before the larvae have completed feeding would be an effective cultural control.

FIELD EXPERIMENTS WITH *BACILLUS THURINGIENSIS* BERLINER

Field experiments using commercial preparations of *Bacillus thuringiensis* were conducted each year from 1964 to 1967 in the Durham area of Grey County, Ontario, and in 1968 near Read, Hastings County, Ontario. These experiments showed that Thuricide 90T, containing 3×10^{10} spores per gram, applied at the rate of 1·5 to 2 pints per acre would result in approximately 80 per cent. mortality of the field population (3).

Later experiments showed that Thuricide 90TS, also containing 3×10^{10} spores per gram, applied at the rate of 1 pint per acre and Biotrol BTB-183 containing $2{\cdot}5 \times 10^{10}$ spores per gram, applied at the rate of 10 oz per acre, would produce approximately the same mortality (2). A *B. thuringiensis* dust, Biotrol 183-2·5D, containing $2{\cdot}5 \times 10^{9}$ spores per gram, was also tested against *T. lineola* in the Read area in 1968. Although the exact dosage required was not determined, this product was also effective against *T. lineola*.

Surveys of treated plots showed that field populations of the skipper were significantly reduced 10 days after treatment (3). Since larvae affected by *B. thuringiensis* stop feeding almost immediately and die within 48 hours, such treatment is expected greatly to reduce damage to the crop, especially if it is applied against the more susceptible instars III or IV. However, unlike most other forms of biological control, this pathogen does not maintain itself under field conditions and therefore no long-term benefits can be expected from its application to limited areas.

RECOMMENDATIONS

(1) Efforts should be made to obtain the three species of parasites, *P. vulgaris*, *R. tristis* and *S. scutellator*, which consistently attack *T. lineola* in Europe, in sufficient numbers for release in Canada.

(2) The cost of controlling *T. lineola* with commercial preparations of *B. thuringiensis* is expected to be in excess of $1 per acre. Thus, this method can be applied only as an emergency measure to limited areas until other less expensive methods are developed and applied.

(3) Field experiments to determine the value of mowing the crop before adult emergence as a means of control in hay fields are planned. The observations on possible cultural control methods by Pengelly (11), Arthur (1) and Carl (6), indicate that an occasional change to earlier harvesting dates may be effective in reducing populations of *T. lineola* in hay fields to below economic levels.

LITERATURE CITED

1. Arthur, A. P. (1966). The present status of the introduced skipper, *Thymelicus lineola* (Ochs.) (Lepidoptera: Hesperiidae) in North American and possible methods of control. *Can. Ent.* **93**: 622–6.
2. Arthur, A. P. (1968). Further information on the control of the introduced European skipper, *Thymelicus lineola*, with *Bacillus thuringiensis*. *J. Invert. Path.* **10**: 146–50.
3. Arthur, A. P. & Angus, T. A. (1965). Control of a field population of the introduced European skipper, *Thymelicus lineola* (Ochsenheimer) (Lepidoptera: Hesperiidae) with *Bacillus thuringiensis* Berliner. *J. Invert. Path.* **7**: 180–3.
4. Bailey, E. G. (1953). *Erratum. Lepid. News* **7**: 56.
5. Burns, J. M. (1966). Expanding distribution and evolutionary potential of *Thymelicus lineola* (Lepidoptera: Hesperiidae), an introduced skipper with special reference to its appearance in British Columbia. *Can. Ent.* **98**: 859–66.
6. Carl, K. P. (1968). *Thymelicus lineola* (Lepidoptera: Hesperiidae) and its parasites in Europe. *Can. Ent.* **100**: 785–801.
7. Irwin, R. R. (1968). *Thymelicus lineola* (Hesperiidae) in Illinois. *J. Lepid. Soc.* **22**: 21–6.
8. MacNay, G. C. (1965). A European skipper (*Adopaea lineola* (Ochsenheimer)). *Can. Insect Pest Rev.* **43**: 46.
9. McEwen, F. L. & Hervey, G. E. R. (1959). Microbial control of two cabbage insects. *J. Insect Path.* **1**: 86–94.
10. Pengelly, D. H. (1961). *Thymelicus lineola* (Ochs.) (Lepidoptera: Hesperiidae) a pest of hay and pasture grasses in Southern Ontario. *Proc. ent. Soc. Ont.* 91 (1960): 189–96.
11. Pengelly, D. H. (1965). Oviposition sites and the viability of eggs of *Thymelicus lineola* (Ochs.) (Lepidoptera: Hesperiidae). *Proc. ent. Soc. Ont.* 95 (1964): 102–5.
12. Saunders, W. E. (1916). European butterfly found at London, Ont. *Ottawa Nat.* **30**: 116.
13. Shull, Ernest M. (1968). *Thymelicus lineola* (Hesperiidae) in Indiana. *J. Lepid. Soc.* **22**: 20.
14. Stern, V. M., Hall, I. M. & Peterson, G. D. (1959). The utilization of *Bacillus thuringiensis* Berliner as a biotic insecticide to suppress the alfalfa caterpillar. *J. Insect Path.* **1**: 142–51.

24. *TIPULA PALUDOSA* (MEIG.), EUROPEAN CRANE FLY (DIPTERA: TIPULIDAE)

A. T. S. WILKINSON[1]

PEST STATUS

The first North American record of this European pest was in 1955 on Cape Breton Island (3) where lawns and flowers were attacked. The infestation was thought to have originated in soil used for ships' ballast and dumped ashore. In 1959 damage to cabbage transplants and turnip seedlings was reported in Newfoundland (4). In British Columbia the larvae (leather jackets) were first found in 1965 causing severe damage to lawns in the eastern outskirts of Vancouver (10). In the past 4 years they have become well established in lawns in and around Vancouver and in pastures and forage crops on large dairy farms up to 65 miles east of Vancouver. Their spread to the south has been confirmed by the capture of adults in light traps along the British Columbia–Washington State border (9). Distribution as of 1968 is shown in Fig. 3. Pastures and hay meadows heavily infested have shown little if any, growth before 15 May. The first cutting of hay, of about three tons per acre and normally taken before the end of May, is lost in heavily infested fields.

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[1] The section on pathogens was contributed by R. F. Morris.

The only predators observed were starlings and seagulls that feed on the larvae and adults, and spiders that feed on the adults. During the adult emergence period, the gut contents of seagulls and of European starlings shot on an airport in the first week of September 1968 consisted primarily of crane flies. The control effected by these birds is known only from work in England (2). In the 4 years that this pest has been studied we have encountered no parasites or diseases in the hundreds of larvae that have been reared in the laboratory; nor have there been any observed in the field.

BACKGROUND

The literature indicates that *Siphona geniculata* (DeGeer) is the primary control agent of *T. paludosa* (Meig.). Parasitism by this tachinid has been recorded at 21·3 per cent. and 17·6 per cent. in England in two consecutive years (6). From this study a partial life history was worked out. The climate appears to be ideal for the host and so it is probably suitable for the parasite.

RELEASES

A small number (11) of *S. geniculata* adults were received in 1967 from Germany but failed to parasitize *T. paludosa* in a laboratory cage. In 1968 a larger number (331) were received from the same source. From this material a culture was established. From the progeny 565 adults were released in British Columbia in 1968. None have yet been recovered.

PARASITES

Siphona geniculata (DeGeer) (Diptera: Tachinidae)

Approximately 600 host larvae were collected from the release site in February and March 1969 and examined under the microscope for the presence of parasites. More than 1,200 have been caged to trap emerging flies. To date no recoveries have been made.

EVALUATION OF CONTROL ATTEMPTS

It is too early in the project to determine the ecological impact of the parasite on pest numbers and damage.

A single application of DDT during fall or early spring gives excellent control on lawns, boulevards and golf greens, and similarly a single application of parathion followed by a 2-week safety period will give very good contol on pasture and forage crops without incurring the danger of harmful residues.

The winter of 1968–9, one of the longest and coldest in several years, may have reduced populations in some areas.

RECOMMENDATIONS

It is recommended that every attempt be made to establish the tachinid fly, *Siphona geniculata*, and that a search for other biological control agents be made. Chemical controls for leather jackets should be considered temporary because of the danger that they may reduce the abundant parasites and predators that keep other pests below the economic threshold.

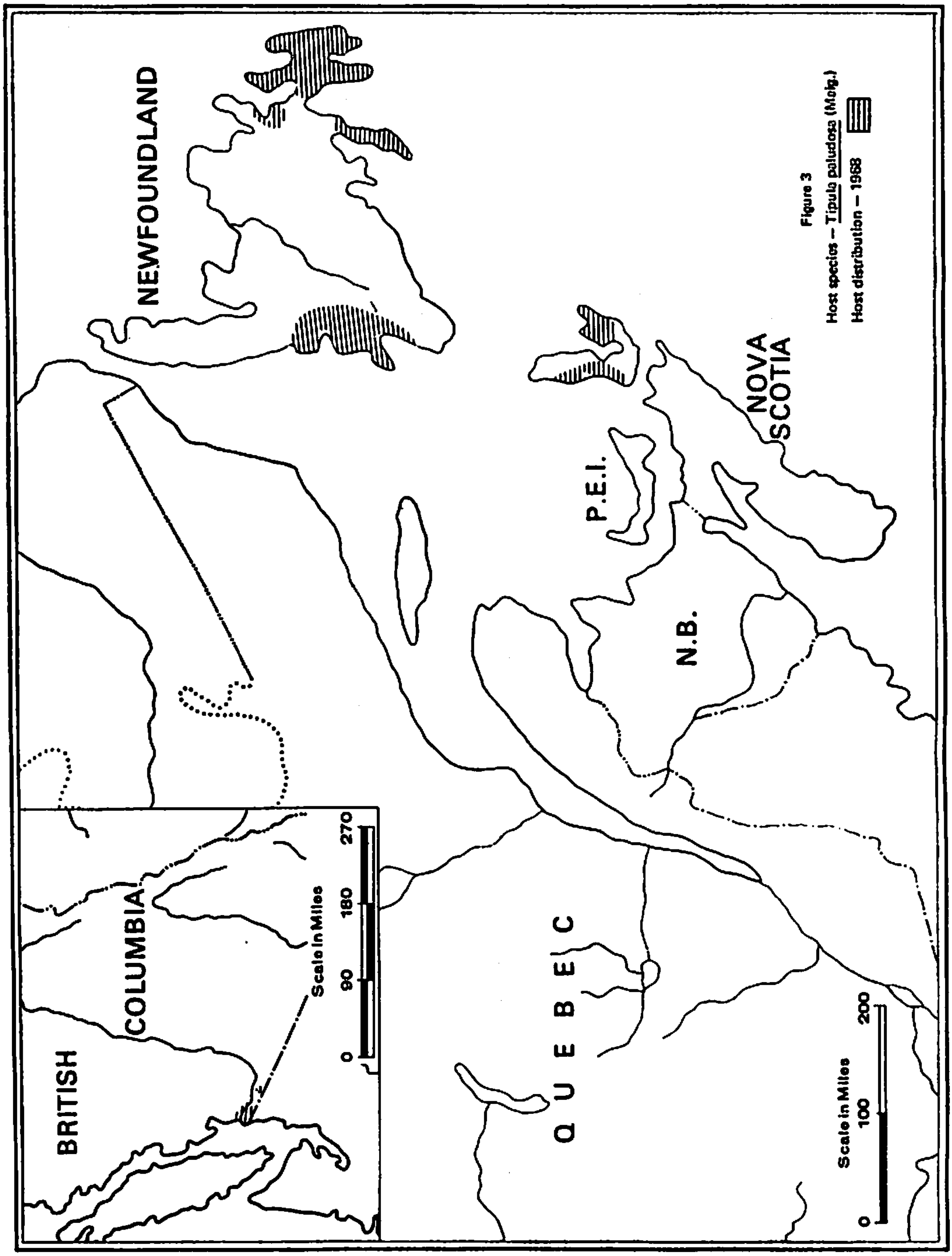

Figure 3

Host species – *Tipula paludosa* (Meig.)

Host distribution – 1968 ▥

PATHOGENS

(R.F.M.)

In September 1960 diseased *T. paludosa* larvae were noted in field collections at Calvert, Newfoundland. Since diseased larvae failed to pupate, samples were submitted to Dr. F. T. Bird, Insect Pathology Research Institute, Sault Ste. Marie, Ontario to determine what diseases, if any, were present. Dr. Bird confirmed the presence of a nuclear polyhedrosis virus discovered by Rennie (7) and Smith and Xeros (8). Infected larvae were collected in the field each year during the period 1960 to 1968. On average, 17·2 per cent. of the larvae collected were infected. In 1965, 40 per cent. of larvae examined at Baine Harbour were diseased. The disease is widely dispersed in Newfoundland and has been found at: Cape Broyle, Calvert, Tors Cove, Aquaforte, Harricot, Peter's River, Ferryland, Garnish, Baine Harbour, Gaskiers, Drook, Fermeuse, Renews and Trepassey.

This virus disease provides a partial but not an effective control (5). Experiments conducted by Dr. F. T. Bird (1) to determine if the virus could be propagated by feeding it to larvae were unsuccessful.

LITERATURE CITED

1. Bird, F. T. (1969). *In litt.* Insect Pathology Research Institute, Department of Fisheries and Forestry, Sault Ste. Marie, Ontario.
2. Dennett, G. M. (1955). The breeding of the starling, *Sturnus vulgaris* in relation to its food supply. *Ibis* **97**: 619–62.
3. Fox, C. J. S. (1957). Note on occurrence in Cape Breton Island of *Tipula paludosa* Mg. (Diptera: Tipulidae). *Can. Ent.* **89**: 288.
4. Morris, R. F. (1960). Newfoundland. Vegetable, field crop and other injurious insect pests predominating during 1959. *Can. Insect Pest Rev.* **38**: 104–6.
5. Morris, R. F. & Fox, C. J. S. (1963). Control of the European marsh crane fly in Newfoundland and Nova Scotia. *Publ. Can. Dep. Agric.* **1193**, 4 pp.
6. Rennie, J. (1923). Polyhedral disease in *Tipula paludosa* (Meig.). *Proc. R. phys. Soc. Edinb.* (*A*) **20**: 265–7.
7. Rennie, J. & Sutherland, C. H. (1920). On the life history of *Bucentes* (*Siphona*) *geniculata* (Diptera: Tachinidae) parasite of *Tipula paludosa* (Diptera) and other species. *Parasitology* **12**: 199–211.
8. Smith, K. M. & Xeros, N. (1954). An unusual virus disease of a dipterous larva. *Nature, Lond.* **173**: 866–7.
9. United States Department of Agriculture (1966). *Cooperative Bionomic Insect Report* **16**: 946–9, 956.
10. Wilkinson, A. T. S. & MacCarthy. H. R. (1967). The marsh crane fly, *Tipula paludosa* Mg., a new pest in British Columbia (Diptera: Tipulidae). *J. ent. Soc. Brit. Columb.* **64**: 29–34.

25. *TRIALEURODES VAPORARIORUM* (WESTWOOD), GREENHOUSE WHITEFLY (HOMOPTERA: ALEYRODIDAE)

R. J. McClanahan

PEST STATUS

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), has been a persistent problem on greenhouse vegetable and flower crops. The whitefly's preference for upper foliage, the natural tolerance of some stages to many insecticides, and this pest's ability to persist outdoors and reinfest greenhouses, all contribute to the difficulty of controlling it.

The parasite *Encarsia formosa* Gahan has proven to be an effective control agent against the whitefly. From 1958 to 1968 releases in Canada have been limited compared to the previous programme which saw nearly 2 million parasites sent from Belleville in 1952. Laboratory research at Belleville has determined some factors which have limited *Encarsia formosa* efficiency (1). At the Canada Department of Agriculture Research Station, Harrow, Ontario the objective has been to develop an integrated control programme for greenhouse vegetables.

BACKGROUND

The parasite *Encarsia formosa* has been released in many countries and can easily be propagated on a colony of whiteflies on tobacco, cucumbers or beans. Recent work in England (6) has shown renewed interest in biological control of whiteflies, to fit in with biological control of the two-spotted spider mite. Previous mass rearing in England had ceased in 1954. Parr's studies indicated that *Encarsia formosa* multiplied slowly on whiteflies on tomato in a greenhouse kept at 63°F or higher, and did not prevent sooty mould. He suggested that a succession of parasite introductions at 2-week intervals might give better control.

There are several endemic parasites of *T. vaporariorum* in California. Biological studies were conducted on *Encarsia pergandiella* Howard, *Eretmocerus californicus* Howard and *Encarsia formosa* (2, 3, 4). The host-parasite interactions of various whiteflies and parasites on cotton in California, over a 3-year period, were presented in detail by Gerling (5). *Encarsia meritoria* Gahan is listed as a parasite of *T. vaporariorum*.

RELEASES AND RECOVERIES

PARASITES

In Canada, releases of whitefly parasites had mainly involved shipments made to commercial greenhouse growers, with little information being obtained on the success or failure of the parasite. In the period 1959–68 parasite shipments were primarily to Research Stations interested in keeping whitefly populations under control without using insecticides (Table XII).

Encarsia formosa Gahan (Hymenoptera: Eulophidae)

This parasite is usually successful in greenhouses where there is a supply of whitefly nymphs or pupae on tomatoes or cucumber. Adult parasites are susceptible to most insecticides and fumigants. When the greenhouse is cleared out at the end of the season the parasites die off and have to be reintroduced when whiteflies infest the next crop. The species is no longer reared at the Research Institute, Belleville, but a colony is maintained at the Research Station, Harrow.

Eretmocerus californicus Howard (Hymenoptera: Eulophidae)

The two releases were made at Canada Department of Agriculture Research Stations. The 150 specimens released at Fredericton were successful in parasitizing whiteflies but the interacting populations were only kept for a short time.

EVALUATION OF CONTROL ATTEMPTS

Encarsia formosa is a valuable parasite for control of whiteflies on greenhouse cucumbers and tomatoes. It must be released when whitefly numbers are reasonably low and reintroduced on subsequent crops. The main obstacle to widespread use is the parasite's susceptibility to phosphate acaricides and most chemicals used against whiteflies. An integrated control programme, with low doses of oxythioquinox (Morestan), has provided very good control in a small greenhouse section.

RECOMMENDATIONS

Research should be conducted to evaluate the success of *Encarsia formosa* in commercial greenhouses, both as a biological control agent and as a component of integrated control programmes.

TABLE XII

Releases of parasites against *Trialeurodes vaporariorum* (Westwood)

Species and Province	Year	Origin	Number
Encarsia formosa Gahan			
Newfoundland	1961	Ontario	2000
Prince Edward Island	1962	Ontario	5000
	1964	Ontario	200
	1968	Ontario	1000
Nova Scotia	1960	Ontario	7000
	1964	Ontario	150
New Brunswick	1964	Ontario	150
Ontario	1961	Ontario	4000
Manitoba	1960	Ontario	5000
Eretmocerus californicus Howard			
Nova Scotia	1964	California	50
New Brunswick	1964	California	150

LITERATURE CITED

1. Burnett, T. (1967). Aspects of the interaction between a chalcid parasite and its aleyrodid host. *Can. J. Zool.* 45: 539–78.
2. Gerling, D. (1966). Studies with whitefly parasites of southern California. I. *Encarsia pergandiella* Howard (Hymenoptera: Aphelinidae). *Can. Ent.* 98: 707–24.
3. Gerling, D. (1966). Studies with whitefly parasites of southern California. II. *Eretmocerus californicus* Howard (Hymenoptera: Aphelinidae). *Can. Ent.* 98: 1316–29.
4. Gerling, D. (1966). Biological studies on *Encarsia formosa*. *Ann. ent. Soc. Am.* 59: 142–3.
5. Gerling, D. (1967). Bionomics of the whitefly-parasite complex associated with cotton in southern California. *Ann. ent. Soc. Am.* 60: 1306–21.
6. Parr, W. J. (1968). Biological control of greenhouse whitefly (*Trialeurodes vaporariorum* West.) by the parasite *Encarsia formosa* Gahan on tomatoes. *Rep. Glasshouse Crops Res. Inst.* 1967: 137–41.

26. MISCELLANEOUS AGRICULTURAL INSECTS

R. P. JAQUES

AGRIOTES OBSCURUS (L.), AN ELATERID WIREWORM (COLEOPTERA: ELATERIDAE)

Mortality of a wireworm, *Agriotes obscurus* (L.), by the fungus *Metarrhizium anisopliae* (Metch.) was noticed in plots near Dartmouth, Nova Scotia. Mortality of larvae, pupae and adults totalled about 10 per cent. (1). Application of large doses of spores of the fungus to soil in plots at Digby and Dartmouth, Nova Scotia, did not increase incidence of the disease in 15 months following treatment (2). The failure to increase disease incidence is explained by the low susceptibility of the wireworm to the fungus as demonstrated in laboratory tests and by the difficulty of establishing an introduced organism in soil.

ALSOPHILIA POMETARIA (HARRIS), FALL CANKERWORM (LEPIDOPTERA: GEOMETRIDAE)

Alsophilia pometaria (Harris), the fall cankerworm, is often a pest of apple in eastern Canada. Because insecticides for control must be applied in early spring when broad-spectrum chemical insecticides may affect pollinating, predacious and parasitic insects, a microbial insecticide containing the bacterium *Bacillus thuringiensis* Berliner was tested. Applications at rates of 2 lbs of preparation

($1{\cdot}4 \times 10^{13}$ spores/lb)/100 gallons of spray reduced numbers of half-grown larvae by as much as 95 per cent. (4, 9). Although this degree of control was acceptable it is doubted that inundation with the bacterium is a practical method of controlling this species.

HELIOTHIS ZEA (BODDIE), CORN EARWORM (LEPIDOPTERA: NOCTUIDAE)

Heliothis zea (Boddie), the corn earworm, is a serious pest of corn, particularly sweet corn, in central and eastern Canada in some years. Because residues of chemicals applied to sweet corn near harvest may be harmful to human health, control by biological agents is desirable.

Laboratory tests at Kentville, Nova Scotia, and elsewhere have shown that larvae of *H. zea* are highly susceptible to a nuclear-polyhedrosis virus disease and to the toxins produced by the bacterium *Bacillus thuringiensis* Berliner. Two applications of the virus to plots of corn at Kentville, Nova Scotia, in 1967 at rates up to 500 virus units per acre ($7{\cdot}4 \times 10^{8}$ polyhedra/m^{2}) reduced the population of *H. zea* larvae in ears by about 75 per cent., being less satisfactory for control than was the chemical insecticide DDT. Populations of the insect at Harrow, Ontario were too sparse to yield dependable data on control of the insect by the virus and *B. thuringiensis* in tests carried out in 1967.

Further tests on both biological agents using better methods of introduction are recommended.

PSEUDEXENTERA MALI (FREEMAN), PALE APPLE LEAFROLLER (LEPIDOPTERA: TORTRICIDAE)

Pseudexentera mali (Freeman), the pale apple leafroller, feeds on buds and young leaves of apple trees in May and June in Nova Scotia. In some seasons this insect is an important pest. *P. mali* pupates in the soil, where mortality is often high. *Beauveria bassiana* (Balsamo) Vuillemin was among several fungi isolated from pupae killed by fungi in non-treated orchard soil in a laboratory test at Kentville, Nova Scotia. Laboratory tests showed that the entomogenous fungi *B. bassiana* and *Metarrhizium anisopliae* (Metch.) (2) and the entomogenous nematode DD–136 (6) could cause high mortality of *P. mali* in the late larval and pupal stages.

Square-foot plots of soil enclosed by cages in an apple orchard at Kentville, Nova Scotia, were treated in June 1965 and 1966 with spores of *B. bassiana* and *M. anisopliae*, and the nematode DD–136 in a series of tests on mortality of overwintering pupae (10). Up to 100 late-instar larvae were put into each cage. The fungus *M. anisopliae* reduced survival to less than 5 per cent. in most tests but *B. bassiana* had little effect. The survival of *P. mali* in cages treated with the nematode DD–136 was reduced to about 10 per cent. Natural mortality in non-treated cages approached 50 per cent.

The tests showed that introduction of a fungal pathogen or a nematode into soil could reduce survival of a susceptible insect species. The possibility of establishment of biological agents such as *M. anisopliae* or the nematode DD–136 in soil should be exploited further as a means of regulating numbers of insects that are in or near the soil for all or a part of the life cycle.

TRICHOPLUSIA NI (HÜBNER), CABBAGE LOOPER (LEPIDOPTERA: NOCTUIDAE)

The cabbage looper, *Trichoplusia ni* (Hübner), is one of the most important pest insects on cole crops in Canada, being particularly prevalent in Ontario. The insect is particularly difficult to control in late larval instars.

A nuclear-polyhedrosis virus disease is widespread in populations of *T. ni*, often causing high mortality late in the season. The virus is highly infective, the LD_{50} being about 100 polyhedra per third-instar larva. Two other viruses, a granulosis and an atypical polyhedrosis virus that kill *T. ni*, have been found in field populations at Harrow, Ontario (8). The typical nuclear-polyhedrosis virus has given good control when introduced into populations of *T. ni* as foliar sprays by numerous investigators in the United States (3, 11). In most cases the populations were reduced to economically acceptable densities.

The typical nuclear-polyhedrosis and granulosis viruses and a bacterium, *Bacillus thuringiensis* Berliner, were introduced into field populations of *T. ni* in plot tests at Harrow, Ontario in 1967 and 1968. In the 1967 tests four foliar applications of the nuclear-polyhedrosis virus at a rate of 100 virus units/acre/application ($1{\cdot}5 \times 10^8$ polyhedra/m^2/application) reduced populations more than did four applications of the bacterium *Bacillus thuringiensis* at 1 quart/acre (Table XIII). The biological agents had an effect on the population of *T. ni* larvae equal to or greater than foliar applications of the chemical insecticide Phosdrin. Numbers of live larvae in plots in which soil was treated with *T. ni* virus on two occasions earlier in the season approximated numbers in plots in which foliage was treated. In 1968 tests, application of the typical nuclear-polyhedrosis virus to soil or foliage reduced populations of host larvae in plots more than did applications of the granulosis virus.

TABLE XIII

Numbers of larvae of *Trichoplusia ni* (Hübner) on cabbage plants in plots treated in 1967 with foliar or soil applications of the nuclear-polyhedrosis virus, the bacterium *Bacillus thuringiensis*, or the chemical insecticide Phosdrin

		Numbers of live larvae/10 plants				
Material/acre/application[1]	Surface treated	Aug. 23	Sept. 1	Sept. 7	Sept. 25	Oct. 6
None (check)	—	8	11	17	10	5
Virus 100 units	Foliage	2	4	5	1	1
Virus 500 units	Foliage	1	2	0	1	0
Virus 500 units	Soil	2	4	5	2	2
Bacillus thuringiensis 1 qt	Foliage	6	3	6	1	1
Phosdrin 6 fl. oz	Foliage	4	4	6	5	4

[1] One virus unit is 6×10^9 polyhedra. The preparation of *Bacillus thuringiensis* contained $2{\cdot}7 \times 10^{13}$ spores per quart. All foliage applications were made on 16, 24 August and 1, 12 September; soil treatments were on 19 July and 16 August.

The establishment of the nuclear-polyhedrosis virus in the environment after introduction was demonstrated by the sparse populations of *T. ni* in 1968 in plots in which soil was treated in 1967 but not in 1968. Bioassays on soils showed that substantial residues of virus persisted from the previous year. It is known that the virus persists for relatively short periods on foliage exposed to sunlight (5). It persists for long periods in soil, however, and can be transmitted to foliage by rain and dust to initiate epizootics (7). The nuclear-polyhedrosis virus persisted better in soil and on foliage than did the granulosis virus. Partly because of greater persistence, the nuclear-polyhedrosis virus predominated in soil treated with the granulosis virus within 10 weeks after treatment.

Residues of the nuclear-polyhedrosis virus in soil increased with repeated epizootics of disease in populations of the host on cabbage plants grown in plots not treated with a virus (8). In one year residues of the virus in soil in non-treated plots attained concentrations nearly equal to those resulting from treatment of soil with virus at a rate of $1{\cdot}5 \times 10^9$ polyhedra/m^2. These substantial residues of the virus in the soil resulted in higher mortality of larvae of *T. ni* in the second year that a cole crop was grown in a non-treated plot than in the first year of cropping.

These tests show that the nuclear-polyhedrosis virus of *T. ni* is a useful biological agent for control of larvae of the host. The virus becomes established in the environment, particularly when applied to soil, and has a marked effect on the population in the year of treatment and in at least one year following treatment.

LITERATURE CITED

1. Fox, C. J. S. (1961). The incidence of green muscardine in the European wireworm, *Agriotes obscurus* (Linnaeus) in Nova Scotia. *J. Insect Path.* **3**: 94–5.
2. Fox, C. J. S. & Jaques, R. P. (1958). Note on the green-muscardine fungus, *Metarrhizium anisopliae* (Metch.) Sor., as a control for wireworms. *Can. Ent.* **90**: 314–5.
3. Getzin, W. L. (1962). The effectiveness of the polyhedrosis virus for control of the cabbage looper, *Trichoplusia ni. J. econ. Ent.* **55**: 442–5.
4. Jaques, R. P. (1961). Control of some lepidopterous pests of apple with commercial preparations of *Bacillus thuringiensis* Berliner. *J. Insect Path.* **3**: 167–82.
5. Jaques, R. P. (1967). The persistence of a nuclear-polyhedrosis virus in the habitat of the insect host, *Trichoplusia ni.* I. Polyhedra deposited on foliage. *Can. Ent.* **99**: 785–94.
6. Jaques, R. P. (1967). Mortality of five apple insects induced by the nematode DD–136. *J. econ. Ent.* **60**: 741–3.
7. Jaques, R. P. (1967). The persistence of a nuclear-polyhedrosis virus in the habitat of the host insect, *Trichoplusia ni.* II. Polyhedra in soil. *Can. Ent.* **99**: 820–9.
8. Jaques, R. P. (1970). Natural occurrence of viruses of the cabbage looper in field plots. *Can. Ent.* **102**: 36–41.
9. Jaques, R. P. & Fox, C. J. S. (1960). The influence of stickers on the effectiveness of sprays of *Bacillus thuringiensis* var. *thuringiensis* Berliner and *Bacillus entomocidus* var. *entomocidus. J. Insect Path.* **2**: 17–23.
10. Jaques, R. P., Stultz, H. T. & Huston, F. (1968). The mortality of the pale apple leafroller and winter moth by fungi and nematodes applied to soil. *Can. Ent.* **100**: 813–8.
11. McEwen, F. L. & Hervey, G. E. R. (1958). Control of the cabbage looper with a virus disease. *J. econ. Ent.* **51**: 626–31.

27. VARIOUS TARGET SPECIES: ATTEMPTS WITH DD–136

H. E. Welch[1]

In the last decade considerable research and development have been conducted on this curious nematode-bacterium complex, but its application as a self-reproducing agent of biological control remains to be tested on a significant scale. Its potential as a biological insecticide is limited by certain definable conditions, and as such it is a weapon of restricted use in the armoury of pest control.

BIOLOGICAL RESEARCH

This nematode-bacterium complex was first described by Dutky and Hough (1, 8) from larvae of the codling moth, *Carpocapsa pomonella* (L.), from Virginia, U.S.A. The biology of the complex was clarified by Dutky (6). The nematode is consumed by an insect, passes through the gut wall, and enters the haemocoele. Here it releases the associated bacterium that multiplies and creates a septicaemia that kills the host insect. The nematode feeds on the dead host tissue and bacteria, passes through several generations, and increases dramatically in number in the cadaver. Juvenile nematodes eventually leave the host cadaver and carry the bacteria with them. They infect the next suitable host that they encounter.

In 1955 Weiser described *Neoaplectana carpocapsae* from larvae of the codling moth collected in Czechoslovakia. The possible synonymy of this worm with the North American form was suspected by Schmiege (31) and Welch (41, 43). Poinar (20) identified the North American nematode as a strain of *N. carpocapsae* and its associated bacterium as *Achromobacter nematophilus* Poinar and Thomas, 1965. The identity of the bacteria may be more complex than this for Bucher (27) failed to identify this strain of bacterium and suggested that different strains may have developed under different conditions of nematode culture. For example, both Weiser (38) and Lysenko (16) reported *Pseudomonas aeruginosa* (Schroeter) Migula, and later Weiser (39) reported *Pseudomonas septica* Bergey *et al.* as the bacterial member of the complex.

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[1] Formerly of the Research Institute, Canada Department of Agriculture, Belleville, Ontario.

The potential host list of DD–136 seems unlimited, as many kinds of insects have been infected by this nematode-bacterium complex in both laboratory and greenhouse experiments (8, 14, 17, 30). However, in the field many factors could be limiting.

Welch and Bronskill (46) reported the first observations of host melanization and encapsulation of the nematodes in mosquito larvae in both laboratory and field infections. Bronskill (2) studied the phenomenon in detail and recorded expulsion of the encapsuled nematode from the host body. She has also reported a similar encapsulation of the nematode by the sawfly, *Pristiphora erichsonii* (Hartig), and a different type of capsule with few melanin particles in the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (28).

The complex has been examined from several other points of view. Reed and Wallace (22) reported a peculiar 'leaping' mode of locomotion in the juvenile nematodes. Sherman and Jackson (32) studied the esterases and phosphatases of the nematode. It is known that the nematode derives its essential sterol from the cholesterol of the insect host (8, 11, 12).

DEVELOPMENT RESEARCH ON THE NEMATODE-BACTERIUM COMPLEX

The use of the complex both as a biological control agent and particularly as a biological insecticide requires mass-culture techniques that can produce large numbers of nematodes quickly, cheaply, and simply. Dutky, Thompson, and Cantwell developed a mass-culture technique for the wax moth (9) and subsequently for the nematode (10). Welch (42) compared this technique with other techniques and found it best with respect to nematode fecundity and infectivity, retention of associated bacteria, and inhibition of contaminants. The simplest technique for mass-culture of the nematode was developed by House, Welch and Cleugh (13). Commercial dog food was used and produced yields of 4×10^5 nematodes in a single petri plate at a cost of one cent. Various culture harvesting techniques were developed, that of Carne and Reed (3) perhaps being the best for harvesting nematodes from insect cadavers.

Several studies were made on the shelf-life of the complex. Infective third-stage juveniles were usually stored in aqueous suspensions. Nematodes were viable and infective after two years' storage. In mass concentrations vibrating or aerated flasks must be used. Care against fungal infections is essential.

The nematodes may be applied most conveniently with standard chemical spray equipment. Nematode tolerance to pressure, temperature and insecticide was tested experimentally. Nematodes withstood pressures of up to 250 p.s.i. Exposures to 34°C for more than an hour were lethal, but the concentration of oxygen in the water influenced the lethal temperature. Oxygen consumption per unit weight by the nematode was proportional to temperature. Nematodes withstood cold temperatures down to 0°C and exposure trials in the field revealed survival in light sandy soil over winter.

The nematode-bacterium complex was apparently unharmed and just as infective when exposed to DDT, BHC or dieldrin in solutions of 0·04 to 5·0 ppm for 72 hours. This confirmed the report (7, 8) that the nematodes can survive exposure to chemical insecticides and herbicides, and indicates their potential value in control programmes in which both biological and chemical agents are required.

Spraying of the nematodes in water suspensions exposes them to desiccation. Spray droplets quickly evaporate and without this thin film of moisture the nematode quickly dies (15, 17, 30). Various readily available chemicals (sugar, honey, and glycerine suspensions) were tested (44) to determine if the rate of droplet evaporation could be retarded. The chemicals produced little retardation and were either nematicidal or phytotoxic, or they enhanced fungal development. Webster and Bronskill (35) tested a number of chemicals and found that a suspension containing Gelgard^R, Folicate^R and Arlatone^R retarded evaporation and increased mortality of larch sawfly larvae (*P. erichsonii*) from 24 to 90 per cent. in laboratory tests.

FIELD TRIALS

DD–136 was tested as both a biological control agent and as a biological insecticide. In the former, emphasis is on the continued passage of the nematode from one host generation to the next and its rôle as an additional mortality factor in the life history of the pest insect. In the latter emphasis is on the massive destruction of one particular generation of the pest insect.

Dutky's early test of the nematode against the codling moth in an apple orchard in Virginia, U.S.A., and subsequent recovery in periodic examinations over 11 years remains the major example of the use of the nematode and bacterium as a biological control agent. Similar attempts against woodland mosquitoes (*Aedes* spp.) and subsequent recovery at Belleville were unsuccessful (23, 24, 25, 26).

Attempts to use DD–136 as a biological insecticide have been more numerous. Dutky, for example, carried out successful trials against pest insects of peaches, cotton boll weevil larvae, and fly maggot infestations in chicken ranches (7). Chamberlin and Dutky (4) used the complex against tobacco budworm, *Heliothis virescens* (F.), and obtained 80–85 per cent. mortality under conditions of high humidity. Dutky sent culture material to entomologists in Germany, Netherlands (see appendix of Rühm (29)), Egypt, Japan and Chile. There have been successful trials in Peru against crop and vegetable insects (34).

The DD–136 was tested at Belleville against field infestations of five species of insects representing five types of habit and habitat. Inoculation of the nematode suspension around the roots of cabbages and rutabagas reduced damage by the cabbage maggot, *Hylemya brassicae* (Bouché), by about half as much as chemical treatment (45). Experiments in which predacious carabid beetles were excluded from the plots showed that the mortality to low-density root maggot populations caused by the nematodes was about equal to that caused by carabids. Inoculation of young cabbage heads with nematode suspensions gave little mortality of the imported cabbageworm, *Pieris rapae* (L.), but treatment of mature cabbage produced mortality equivalent to that caused by chemical insecticides. Optimal control procedures for this pest species could involve early treatment with chemicals followed later by application of nematodes. The importance of moisture in the control of the Colorado potato beetle, *L. decemlineata*, by nematodes sprayed in suspension was confirmed by high mortality obtained in a plot that was covered by a plastic tent and had humidities of 90 per cent. or more. When the growing tips of corn plants and tassels of corn cobs were inoculated with nematode suspensions, the mortality of the European corn borer, *Ostrinia nubilalis* (Hübn.), was equivalent to that resulting from treatment with DDT. Although control was achieved, it was similar to that observed in field tests of DD–136 against corn earworm, *Heliothis zea* (Boddie) (33), where death occurred after insect invasion and consequent damage of the cob. This precludes the use of DD–136 as a control agent against insects of low economic threshold. Treatment of mosquito-infested pools partially reduced larval density and adult mosquito emergence. Highest mortalities occurred when insect cadavers containing the nematodes were added to the pools.

Investigators in Europe and North American have reported additional trials. Moore (17) carrying out tests similar to those of Tanada and Reiner (33) obtained 42–46 per cent. mortality of *H. zea* in the field. Jaques (14) compared the nematode with entomophagous fungi for the control of the soil stage of the pale apple leaf roller, *Pseudexentera mali* (Freeman) and the winter moth, *Operophtera brumata* (L.). He found reduced survival of overwintering forms. Drooz (5) observed only a few dead sawfly larvae following treatment of sphagnum bog with DD–136. The cool temperatures of the soil may reduce infections, as suggested by Carne and Reed (3) in their infection trial of DD–136 against the curl grub.

Niklas has reviewed the literature on this complex (18, 19).

RECOMMENDATIONS

Despite Dutky's statement that the nematode-bacterium complex has an "enormous potential for the control of a large number of insect species", I consider the complex to be a specialized tool.

Much evidence has been accumulated and the conditions can be partially defined for its use as a biological insecticide. The use of the complex as a biological control agent, however, remains unexplored. Insect pests, particularly forest species, with life histories similar to that of the codling moth, should be examined. Research on the complex, particularly critical definition of the microclimatic conditions favourable to it, should be continued.

LITERATURE CITED

1. Anonymous (1956). Nematodes on our side. *Agric. Res.* **4**: 3–4.
2. Bronskill, J. F. (1962). Encapsulation of rhabditid nematodes in mosquitoes. *Can. J. Zool.* **40**: 1269–75.
3. Carne, P. B. & Reed, E. M. (1964). A simple apparatus for harvesting infective stage nematodes emerging from their insect hosts. *Parasitology* **54**: 551–3.
4. Chamberlin, F. S. & Dutky, S. R. (1948). Tests of pathogens for the control of tobacco insects. *J. econ. Ent.* **51**: 560.
5. Drooz, A. T. (1960). The larch sawfly. Its biology and control. *Tech. Bull. U.S. Dep. Agric.* **1212**, 52 pp.
6. Dutky, S. R. (1959). Insect microbiology. *Adv. appl. Microbiol.* **1**: 175–200.
7. Dutky, S. R. (1968). An appraisal of the DD–136 nematode for the control of insect populations and some biochemical aspects of its host—parasite relationships. *Proceedings of the Joint U.S.-Japan Seminar on Microbial Control of Insects*, Tokyo: 139–40.
8. Dutky, S. R. & Hough, W. S. (1955). Note on a parasitic nematode from codling moth larvae, *Carpocapsa pomonella*. *Proc. ent. Soc. Wash.* **57**: 244.
9. Dutky, S. R., Thompson, J. V. & Cantwell, G. E. (1962). A technique for mass-rearing the greater wax moth (Lepidoptera: Galleridae). *Proc. ent. Soc. Wash.* **64**: 56–8.
10. Dutky, S. R., Thompson, J. V. & Cantwell, G. E. (1964). A technique for the mass propogation of the DD–136 nematode. *J. Insect Path.* **6**: 417–22.
11. Dutky, S. R., Kaplanis, J. N., Thompson, M. J. & Bobbins, W. E. (1967). The isolation and identification of the sterols of the DD–136 insect parasitic nematode and their derivation from its insect hosts. *Nematologica* **13**: 139.
12. Dutky, S. R., Robbins, W. E. & Thompson, J. V. (1967). The demonstration of sterols as requirements for the growth, development, and reproduction of the DD–136 nematode. *Nematologica* **13**: 140.
13. House, H. L., Welch, H. E. & Cleugh, T. A. (1965). A prepared dog food as an artificial food medium for rearing a *Neoaplectana* sp. *Nature, Lond.* **206**: 847.
14. Jaques, R. P. (1967). Mortality of five apple insects induced by the nematode DD–136. *J. econ. Ent.* **60**: 741–3.
15. Jaques, R. P., Schultz, H. T. & Huston, F. (1968). The mortality of the pale apple leafroller and winter moth by fungi and nematode applied to the soil. *Can. Ent.* **100**: 813–8.
16. Lysenko, O. (1963). The mechanisms of pathogenicity of *Pseudomonas aeruginosa* (Schroeter) Migula. 1. The pathogenicity of strain N–06 for larvae of the greater wax moth, *Galleria mellonella* (L.). *J. Insect Path.* **5**: 78–82.
17. Moore, G. E. (1935). The bionomics of an insect-parasitic nematode. *J. Kansas ent. Soc.* **38**: 101–5.
18. Niklas, O. F. (1967). Die Nematoden DD–136 (*Neoaplectana* sp.) and *Neoaplectana carpocapsae* Weiser, 1955 (Rhabditoidea) als Insektenparasiten eine. Literaturübersicht. *Mitt. biol. Bund. Anst. Ld-u. Forstw.* **124**, 40 pp.
19. Niklas, O. F. (1967). Ergänzungen zum Literaturberichtüber die Nematode DD–136 (*Neoaplectana carpocapsae* Weiser, 'strain DD–136'; Rhabditida). *Nachr. Bl. dt. PflSchutzdienst., Braunschweig* **21**: 71–8.
20. Poinar, G. O. (1967). Description and taxonomic position of the DD–136 nematode (Steinernematidae, Rhabditoidea) and its relationship to *Neoaplectana carpocapsae* Weiser. *Proc. helminth. Soc. Wash.* **34**: 199–209.
21. Poinar, G. O. & Thomas, G. M. (1965). A new bacterium, *Achromobacter nematophilus* sp. nov. (Achromobacteriaceae: Eubacteriales) associated with a nematode. *Int. Bull. bact. Nomencl. Taxon.* **15**: 249–52.
22. Reed, E. M. & Wallace, H. R. (1965). Leaping locomotion by an insect-parasitic nematode. Studies on the behaviour of the unnamed species referred to as DD–136. *Nature, Lond.* **206**: 210–11.
23. Research Report (1960). *Res. Rep. Ent. Res. Inst. for Biological Control, Belleville, Ont.* (1956–1959): 15–41.
24. Research Report (1962). *Res. Rep. Ent. Res. Inst. for Biological Control, Belleville, Ont.* (1960–1961): 14–8.
25. Research Report (1964). *Res. Rep. Res. Inst., Belleville, Ont.* (1962–1963): 19–32.
26. Research Report (1966). *Res. Rep. Res. Inst., Belleville, Ont.* (1964–1965): 32.
27. Research Report (1967). *Res. Rep. Res. Inst., Belleville, Ont.* (1966): 15.
28. Research Report (1968). *Res. Rep. Res. Inst., Belleville, Ont.* (1967): 87.
29. Rühm, W. (1956). Nematodes und biologische Bekämpfung der Insekten. *Nematologica* **2** (Suppl.): 349–54.
30. Schmiege, D. C. (1963). The feasibility of using a neoaplectanid nematode for control of some forest insect pests. *J. econ. Ent.* **56**: 427–31.
31. Schmiege, D. C. (1964). A note on the taxonomy of an undescribed insect parasitic nematode in the genus Neoaplectana. *Parasitology* **54**: 233–6.
32. Sherman, I. W. & Jackson, G. J. (1963). Zymograms of the parasitic nematodes, *Neoaplectana glaseri* and *N. carpocapsae* grown axenically. *J. Parasit.* **49**: 392–7.

33. Tanada, J. & Reiner, C. (1962). The use of pathogens in the control of the corn earworm, *Heliothis zea* (Boddie). *J. Insect Path.* 4: 139–54.
34. Tang, J. L. (1958). Notas generales sobre nematodes portadores de bacterias como un método di control biologico. *Revta peru. Ent. agric.* 1: 19–22.
35. Webster, J. M. & Bronskill, J. F. (1968). Use of Gelgard M and an evaporation retardant to facilitate control of the larch sawfly by a nematode-bacterium complex. *J. econ. Ent.* 61: 1370–3.
36. Weiser, J. (1955). *Neoaplectana carpocapsae* n. sp. nový cizopasník housenek oblaeče jablečného, *Carpocapsa pomonella* L. *Věst. čsl. Spol. zool.* 19: 44–52.
37. Weiser, J. & Kohler, W. (1955). Hlístice jako cizopasnici larev ploskohřbetky, *Acantholyda nemoralis* Thoms. v Polsku. *Česk. Parasitol.* 2: 185–90.
38. Weiser, J. (1962). Ueber die Benutzung der Nematoden zur biologischen SchädlingsbeKämpfung. *Verh. XI Int. Kongr. Ent., Wien* (1960) 2: 880–2.
39. Weiser, J. (1963). Diseases of insects of medical importance in Europe. *Bull. Wld Hlth Org.* 28: 121–7.
40. Welch, H. E. (1962). Nematodes as agents for insect control. *Proc. ent. Soc. Ont.* 92: 11–9.
41. Welch, H. E. (1963). Nematode infections, *In* Insect pathology, E. A. Steinhaus, ed. Academic Press, New York.
42. Welch .H. E. (1963). The mass production of entomophilic nematodes. *Wld Hlth Org.*, E.B.L./Working paper, No. 23, 3 pp.
43. Welch, H. E. (1965). Entomophilic nematodes. *A. Rev. Ent.* 10: 275–302.
44. Welch, H. E. and Briand, L. J. (1961). Tests of the nematode DD–136 and an associated bacterium for control of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say). *Can. Ent.* 93: 759–63.
45. Welch, H. E. & Briand, L. J. (1961). Field experiment on the use of a nematode for the control of vegetable crop insects. *Proc. ent. Soc. Ont.* 91: 197–202.
46. Welch, H. E. & Bronskill, J. F. (1962). Parasitism of mosquito larvae by the nematode, DD–136. *Can. J. Zool.* 40: 1263–8.

PART II

BIOLOGICAL CONTROL OF WEEDS IN CANADA, 1959-1968

28. CURRENT APPROACHES TO BIOLOGICAL CONTROL OF WEEDS

P. HARRIS

My purpose here is to put the Canadian projects on biological control of weeds, described in the remainder of this Part, into perspective by describing the procedures followed and the general considerations that apply to them. Some of the weaknesses in the programme are indicated and an assessment is made of the value of biological control in solving weed problems.

DIFFERENCES BETWEEN BIOLOGICAL CONTROL OF WEEDS AND THAT OF INSECT PESTS

There are several major differences between biological control of weeds and that of insect pests although both are based on the same premise—that pest density can be lowered by increasing the level of parasitism. In both cases this is usually done by the addition of parasite species. One striking difference is the emphasis placed on determination of host specificity of weed parasites before use to ensure that they will not damage desirable plants as well as the weed. Thus, before a weed parasite is released in North America it is cleared at the national level in both Canada and the United States. Parasites of insect pests are not subjected to similar, rigid scrutiny because it is very unlikely that they could be a direct nuisance to man. It is easier to integrate the chemical and biological control of a weed than that of an insect pest because insecticides (unlike herbicides) tend to counteract by killing both the pest and its insect parasites. Little use has been made of this difference. Insect pests typically harm a crop or man directly, whereas the importance of most weeds is that they compete for space, light and nutrients with plants desired by man. This leads to differences in the application of biological control as there are usually fewer parasites than competitors of an individual crop. Successful biological control of one important insect pest may eliminate the need for insecticide treatment of the crop. On the other hand, most crops of arable land have many species of weeds competing with them and even if one species is controlled it is still necessary to spray or cultivate to control the rest. There are, however, situations in which control of a single weed species is valuable. High diversity of weed species is a characteristic of newly cultivated ground; but as succession advances a few species come to dominate. Dominance is usually well established on rangeland, although it is often a matter of the dominant species having only a small edge over its competitors. Such a dominant species is a very suitable subject for biological control because even a slight increase in pressure against it has a large effect. The effectiveness of the control agent can be enhanced by increasing the competitiveness of forage plants by good pasture management. Conversely, it can be decreased or nullified if the land is exploited by overgrazing or in other ways, and in extreme examples the result may merely be the replacement of one noxious weed with another.

PROCEDURES: BIOLOGICAL CONTROL OF A WEED

The biological control of a weed should not be started lightly: the decision to do so will probably involve obtaining international cooperation and a programme that, if there are no setbacks, will remain in the experimental stage for about ten years. Provision should be made for periodic review so that the programme can be modified or terminated if the initial results prove unsatisfactory because, unless monitored, biological control attempts often drift into obscurity with a series of indecisive results. To make such a review as systematic as possible, our programme is divided into six successive steps. In Table XIV the result required for termination or continuation at each step is shown, as well as the status of the Canadian projects. Excepting the four weeds in the survey stage, each project is described in the following chapters.

TABLE XIV

Evaluation of biological control measures against weeds

Weed	Page reference	Start of programme in Canada	Estimated cost to end of 1968 (thousands of dollars)		Principal planned benefits	Degree of success[1]
			Abroad	Canada		
Carduus spp.	76	1968	45	20	Protection of forage	++[3]
Cirsium arvense	79	1963	45	320	Protection of forage and crops	+
Euphorbia spp.	83	1965	25	100	Protection of forage and crops	+
Hypericum perforatum[2]	89	1952	10	410	Removal of threat	++++
					Protection of forage	+++
Linaria vulgaris	94	1957	10	120	Protection of forage and crops	+
Senecio jacobaea	97	1961	10	220	Protection of forage	+++[3]
					Protection of cattle	++++[3]

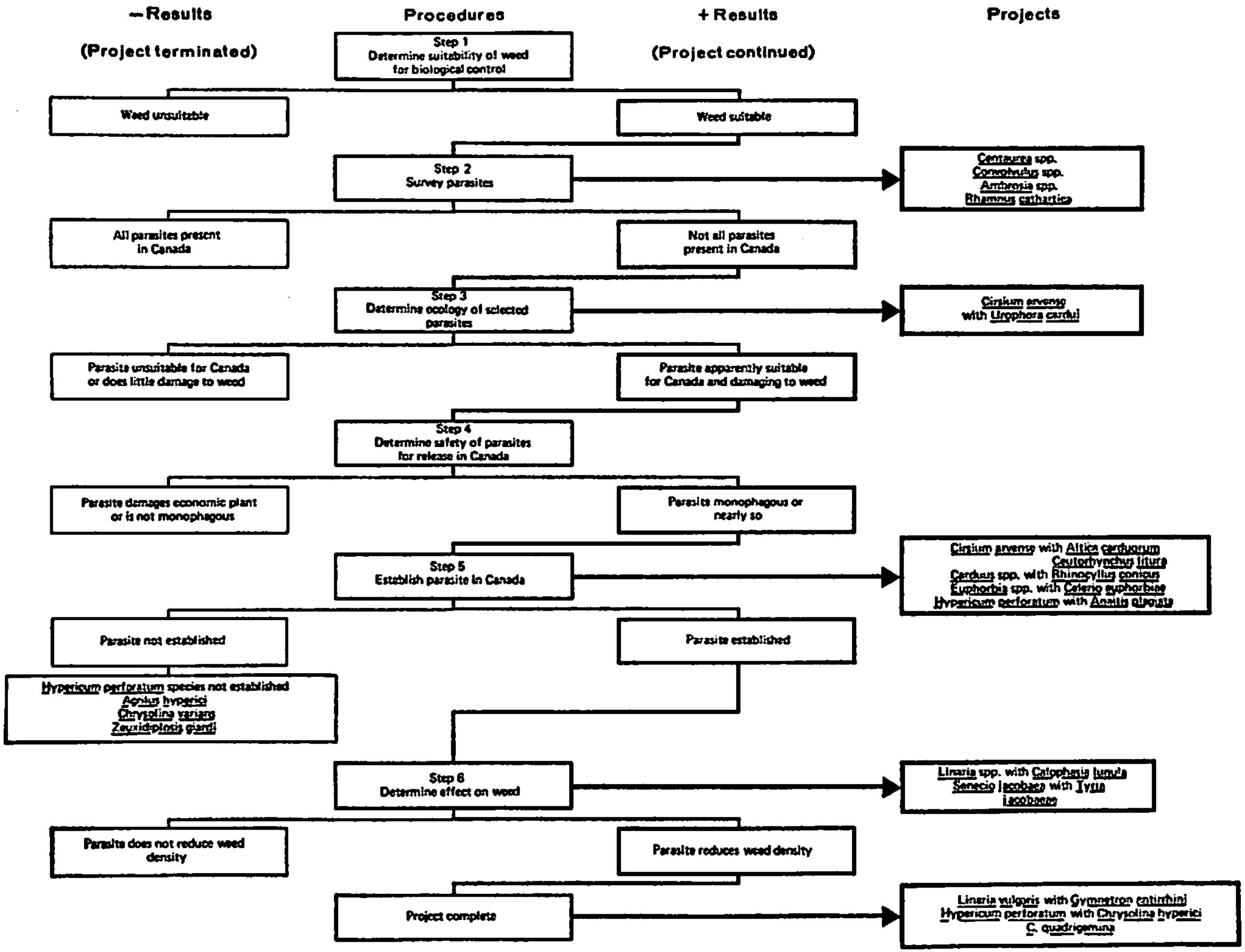
[1] Degree of success:
— No control
\+ Slight pest reduction or too early for evaluation of control
++ Local control; distribution restricted or not fully investigated
+++ Control widespread but local damage occurs
++++ Control complete.

[2] In British Columbia.

[3] Prospects.

Not all weed problems are amenable to biological control, and the first step (Fig. 4) is to determine whether the method is applicable. Seven main considerations are involved. (i) The target weed should not be a plant valued in other situations into which the control agent may spread. For example, blue weed, *Echium vulgare* L., is both a pasture weed and a honey plant in Ontario; so unless its honey production can be sacrificed, biological control should not be pursued. Occasionally it is possible to reconcile such a conflict of interest, although this probably means accepting less efficient control. For example, a seed-eating insect might be introduced against broom, *Cytisus scoparius* (L.)Lk., in British Columbia to reduce its spread without affecting its use as an ornamental shrub. (ii) The specificity of a biological control agent to a single weed or at most to a few closely related species largely eliminates its use for problems in which many weed species are involved, as is usual on arable land. However, specificity is an advantage on rangeland or waste areas where it is desirable to control a dominant weed species while retaining the diversity of grasses, forbs and shrubs. (iii) The weed should not be related closely to an economic plant: the closer the relationship, the greater the possibility that a biotic agent will attack both of them. For this reason wild oats and some cruciferous weeds are unsuitable for biological control. (iv) The intensity of weed control achieved by biological means is generally much lower than by chemical or mechanical control. The size of a weed population that can be tolerated tends to decrease with increasing intensity of land use, and so does the applicability of biological control. (v) Introduced weeds are generally more amenable to biological control than are native species. They tend to have an impoverished complement of parasites, and therefore the addition of another has proportionately more effect than it would have in the case of the larger

Figure 4 Procedure and Status of Canadian Projects for Biological Control of Weeds



complex usually associated with most native weeds. Also, the origin of the introduced weed is a source from which parasites can be introduced; for native weeds there may be no source of additional parasite species. However, Harris and Piper (6) argue that there may be such a source of parasites for the biological control of native ragweeds (*Ambrosia artemisiifolia* L. and *A. trifida* L.) in Canada. (vi) Biological control does not provide quick results, but may provide permanent solutions for persistent problems. Temporary weed problems caused by short-term crop rotations are not good candidates for biological control. (vii) The cost of biological control increases little with the area involved which gives it a considerable cost advantage over other methods against widespread weeds, but a disadvantage against localized problems.

The second step (Table XIV) is to survey the parasites of the weed at home and abroad. The parasites of greatest interest for introduction are those affecting parts of the plant that are lightly attacked in Canada. For example leaf- and stem-feeding insects have been introduced against *Cirsium arvense* (L.) Scop. in preference to seed insects, as a high proportion of seed heads (often up to 70 per cent.) are already attacked by a European tephritid, *Orellia ruficauda* F. This level of attack is usually much higher than that accomplished by a complex of insects, including *O. ruficauda*, which attack the heads of this thistle in Europe. The difference is not caused by an absence of natural enemies of *O. ruficauda* in Canada as it is attacked by at least two European and one native parasite. It is possible that the lower incidence of attack in Europe is the result of interspecific competition. If so, the introduction of several parasites using the same part of the plant should be avoided. This is a controversial issue. In examples examined by Zwölfer (15) the parasite complexes with few species were more efficient in preventing outbreaks of the pest than those with many species. On the other hand, competition between parasites does not necessarily have much effect on the level of parasitism (4) and DeBach (3) advocates introduction of all promising natural enemies.

Sometimes the parasites of a weed are so well known that species for introduction can be selected from the literature. However, it is usually desirable that a field survey should be made on the weed and plants of related species and genera. This provides information on preferences and host ranges of the parasites and helps to determine the species that are most promising for biological control. Thus, the basis of introduction of thistle insects into Canada is a survey by Zwölfer (16) of the phytophagous insects attacking the tribe Cynareae in Europe. The richest source of parasite species is likely to be at the centre of origin and diversification of the weed or its glacial refugia. If only limited surveys can be done, these places should be given preference regardless of their climatic similarity to the release area. This is not to say that the provenance of the parasite is not important, but I think it has been overemphasized. For example the impoverished association of insects on *Cirsium arvense* in Britain probably arises as much from their inability to get there as it does from the unsuitability of an Atlantic climate. Hence, even if the parasite is to be released in a climatically similar area, restriction of the survey to Britain may eliminate suitable species from consideration. Likewise, surveys of *Hypericum perforatum* L. in Sweden, which is climatically similar to British Columbia, revealed no parasite species that were not present in the richer association on the weed in France (8, 9, 13). Control of the weed might have occurred sooner if the *Chrysolina* spp. used had been introduced from Sweden; but the fact that they were introduced from climates contrasting with that of the release area in British Columbia did not prevent them from eventually controlling the weed, presumably after adapting to the new environment. Insects with broad ecological tolerances should generally be favoured as biological control agents over species with narrow tolerances, as being more likely to thrive in the new habitat. *A priori*, this means that the precise matching of the source and release areas is not of crucial importance.

Four surveys are listed in Fig. 4 (Step 2). The main target of the Commonwealth Institute of Biological Control survey on *Centaurea* spp. in Europe is *C. diffusa* Lam., an extremely serious weed in the dry belt of British Columbia. No monophagous insects have been found on it in western Europe but surveys nearer the origin of the weed in Rumania and Turkey have been more rewarding. Likewise the diversity of insects on *Rhamnus cathartica* L. tends to increase from west to east in Europe. The results of a field survey in Ontario and a world literature review of *Convolvulus* insects have been compiled and discussed by Mohyuddin (11). The list of *Ambrosia* insects compiled by Harris and Piper (6) is the result of field surveys in eastern North America supplemented by a literature review. *Ambrosia* spp. are native weeds and the possibility for their biological control depends on there being a source of additional cold-hardy parasites in the mountains of Mexico and/or South America. The southwestern origin of the genus and the barrier effect of the Sonoran deserts make this a possibility.

A biological control agent must be damaging to the weed and be able to survive in the country of introduction. If possible, these abilities should be demonstrated in the laboratory before release (Fig. 4, Step 3). Insects released in Canada will be subjected to cold winters and if there is any doubt of their hardiness this should be checked in the laboratory, as was done with *Celerio euphorbiae* (L.). The beetle *Chrysocloa tristis* F. (*Chrysomelidae*) which was found to require damp, cool conditions for breeding, was rejected for introduction against *Centaurea* spp. in British Columbia because the infestations were in areas with dry, hot summers. The moth *Anaitis plagiata* (L.) was selected for release in the province against *Hypericum perforatum* L. because it seemed to be preadapted to this type of habitat (5), and no insect seemed to have broad enough ecological tolerances to control the weed in all its habitats.

It is often difficult to select the most damaging parasites for introduction as conspicuousness of attack is not necessarily an indication of the harm done to the plant. Most plants have more leaves than they need and a proportion of them can be removed without affecting the plant's metabolic rate. Apparently many leaves do no more than maintain themselves, although they tend to be shed when they become an energy drain. The damage done by many leaf miners probably does not produce an energy deficit in the leaf (or it would be shed and the larva killed) and so is of little value for biological control. The extent to which particular species of plants are damaged by leaf chewing, sucking, skeletonizing or other types of attack or the time when they are most vulnerable to attack (in the spring, just before flowering, or at another stage) is not known. The study on the effects of the stem gall of *Urophora cardui* L. is a start towards correcting our ignorance, but more extensive studies are needed if parasites for biological control of weeds are to be selected on a rational basis. A successful biological control agent needs other qualities besides the ability to damage the weed and survive in the country of release and it may be possible to recognize some of them. It is likely that many of the attributes that Baker (1) found to be associated with weediness in plants, such as broad ecological tolerance, quick development and a large amount of genetic material, might be important.

Step 4 (Fig. 4) involves showing that the agent chosen will not damage desirable plants. To ensure adequate safeguards before release of a weed control agent, North American investigators are required to prepare reports for review in both the United States and Canada, substantiating their claims that the agent involved will not become a pest. These reports cover the six criteria proposed and discussed by Harris and Zwölfer (7), namely: (i) investigation of the insect's biology with attention being given particularly to features likely to restrict its host range; (ii) review of the plants attacked by related insects; (iii) determination of the range of plants that the insect can be induced to eat or accept for oviposition in the laboratory; (iv) investigation of the basis of host recognition; (v) starvation tests on economic plants representing as many families as possible; and (vi) establishment that the insect is potentially effective for weed control. The investigations made within this framework have been purposely left flexible with the onus on the investigator to use the test most appropriate for the insect concerned. It is hoped that in this way the procedures will evolve, leading to increased emphasis being placed on determination of the basis of host acceptance, whether this involves the visual host recognition characters used by many adult trypetids or the chemical feeding stimulants used by many lepidopterous larvae.

The release of the parasite in Canada is Step 5 (Fig. 4). It is often helpful to make several trial releases of an insect in contrasting habitats to identify the major causes of mortality. This can be done with quite small numbers and the use of field cages to determine phenology and the ability of the insect to survive the climate. Attempts to obtain establishment should be made initially in the most favourable habitat because the species is likely to be subjected to heavy selection pressure until it adapts to the new environment. The value of identifying the major mortality factors in order to find a favourable habitat is evident from the establishment of *Tyria jacobaeae* L. in British Columbia. The first releases, made at Abbotsford, failed partly because of prepupal predation by carabids (12). A release site was found with a much lower carabid population and the moth became established. Several years later the moth from this colony was established at Abbotsford without difficulty. It is likely that the initial failure was due to a combination of high predation and environmental selection, but that predation was not sufficient to exterminate an adapted strain. Likewise, the failure of most releases of *Celerio euphorbiae* (L.) in Canada have been partially related to high ant predation. The moth is established on one site with a low ant density and it is hoped that after several years of natural selection it can be spread to sites where it had previously failed. If this is not possible, at least it is known that an alternative biological control agent for spurge should be selected on the basis of immunity to ant predation.

The number of insects needed to obtain establishment depends on mortality, dispersal and fecundity and so varies widely for different species. In view of the high initial mortality of *T. jacobaeae* and of *C. euphorbiae*, survival is not likely unless the release is made with 1,000 to 5,000 larvae. This figure is much smaller than was used in many releases against weeds in Australia (14) but, rather than make larger releases, I would prefer to supplement the colony in the following year. Larger releases necessitate mass rearing or the direct release of imported stock and both of these procedures greatly increase the likelihood of disease problems. The use of diseased stock is apparently the reason why many Lepidoptera released against weeds in Australia and other parts of the world failed to become established (1, 2). Virulent diseases can usually be eliminated by individual rearing of the larvae for two or three generations, and this should be routine practice for Macrolepidoptera. It is more difficult to eliminate benign diseases such as the cytoplasmic virus on *Calophasia lunula* (Hufn.) and *Celerio euphorbiae*. Such diseases have not prevented establishment of these insects and hopefully they will not prevent the successful control of the weeds. Conceivably the diseases could be beneficial by stabilizing the weed-parasite equilibrium; but without knowing their effect, one cannot judge how much effort is justified in trying to eliminate them before release of the insect.

Step 5 continues until either the parasite fails to survive and the attempt to establish it is abandoned, or the parasite population builds up. In my experience, if a colony of an introduced weed insect survives the sharp reduction in numbers during the first year, it usually persists at a low density for several generations (although it may need some nursing to do so) before starting to increase. With *T. jacobaeae* the increase did not start until the fourth year after release whereas in various colonies of *Chrysolina* spp. this initial phase lasted 6–13 years. The parasite cannot affect the prevalence or vigour of the weed until it has built up a large population. Hence there is little to be gained in starting to measure an effect (Step 6, Fig. 4) until the insect shows itself capable of increase in the area involved. To determine when detailed measurements of the vegetation should be started, it is necessary to monitor the parasite population. I suggest that this should be done annually until the fifth year after release and then biennially until the tenth year, although it may be necessary to sample more frequently in a climate warmer than that of Canada. If there has been no increase by this time, basic investigations of the ecological requirements of the parasite are appropriate.

Methods of evaluating the effects of biological control on a weed are reviewed and discussed by the National Academy of Sciences (10). The results of biological control of weeds are sometimes so conclusive that there is no difficulty in demonstrating them. For example there was a dense infestation of *Senecio jacobaea* L. at Nanaimo, British Columbia in the spring of 1968; but by mid-summer *T. jacobaeae* larvae had eaten every leaf of the weed on 35 acres around the release site. For less conclusive results the usual method for demonstrating the effects of biological control is a sequence of density measurements taken before and after build-up of the parasite. However, unless the sequence is long, even a large reduction in the weed is not proof that the biological control agent is responsible. This is especially true for a biennial such as *S. jacobaea* because fluctuations in density may merely reflect germination conditions. Also, in spite of intensive control by *T. jacobaeae*, the reservoir of seeds in the soil may enable the weed to persist at a high density for many years. An alternative approach is to measure the decrease in seed production resulting from the parasite attack and determine the recruitment level needed to maintain the weed at its present density. For example if only 10 per cent. of the present production of seeds is needed for population maintenance, seed reduction by the parasite must exceed 90 per cent. to be effective.

A perennial weed such as *Euphorbia cyparissias* L. presents different problems. The seed is obviously of no importance in the sterile form, and even fertile stands perpetuate themselves vegetatively. Severe grazing by *C. euphorbiae* does not kill the weed but over several years produces a gradual decline in vigour. This may be demonstrated by comparing the weed density in the grazed areas with check plots from which larvae are excluded. However, exclusion either by caging or by chemical treatment may affect other environmental factors and hence negate the use of the plot as a control. Alternatively the effects of the insect can be determined from a series of energy budgets that relate various *C. euphorbiae* grazing levels with spurge production; and these results in turn can be related to the ratio of spurge biomass and to the number of larvae in the field. This involves considerably more work than the check-plot method but has the advantage that the effect of the larvae can be experimentally supplemented with other biological control agents and a pasture management scheme to determine the most effective combination. The need for this has been neglected in biological control of weeds, but the combination is probably usually required for satisfactory control. Also largely neglected are financial estimates of the benefits achieved by biological control of a weed. The increased calorie value of forage production (probably equal to the decreased weed production) provided by an energy budget is a basis from which the benefits might be calculated.

WEAKNESSES IN PRESENT PROCEDURES

Some of the deficiencies in the practice of biological control of weeds have been indicated in the discussion of procedures. For example the absence of comparative studies of the effects of different types of insect damage results in an intuitive rather than a rational selection of parasites for introduction. The information might be provided by feeding test insect species on standard plants until a given number of calories had been removed and then comparing the assimilation rates of the damaged plants. There is also a basic difficulty in establishing priorities among weeds to control, because economic losses, rates of spread and exact distribution of many species in Canada are not known. For example, although *Senecio* poisoning was known to occur in British Columbia there were no statistics on the number of cattle killed by it, or on the proportion of slaughtered cattle with affected livers, and the infestation of the weed on the mainland in 1969 was a hundred times as great as reported in 1955. A toxic weed spreading at this rate should have a high priority for control, but its seriousness was not known at the time it was selected.

One of the most serious deficiencies in most biological control programmes is the lack of attention given to a newly released biotic agent. Some insects can be established even if casually dumped; but others such as *Tyria jacobaeae* and *Celerio euphorbiae* require care for several years after release, apparently while they adapt to the new environment. This may involve locating a more favourable release site or making supplementary releases to keep the colony above the critical level for survival. In a country as large as Canada this requires a cooperator living within driving distance of the release site and willing to spend some time following the survival of the parasite. This has not always been possible to arrange. For example *Anaitis plagiata* (L.) (5), *Calophasia lunula* and *Agrilus hyperici* (Cr.) were not followed closely enough, so that reasons for their failure are not known. To continue releasing these species without more information is likely to be a wasted effort; yet to abandon them is a waste of the initial studies. The answer seems to be not to undertake the biological control of a weed without prior commitment from someone in the region concerned to follow the survival of any parasite released.

Another weakness in many biological control attempts is the tendency to 'go-it-alone' without regard to other methods of control. This probably arises from the unsuitability of many of the projects for other methods of control. Also the tremendous success of biological control against prickly pear in Australia and *Hypericum perforatum* L. in California has created the unfortunate impression that the method is self-sufficient. More often the result is a partial success with the parasite achieving some reduction in the vigour or density of the weed but not enough to eliminate it as a problem. A rangeland improvement scheme in Ontario which involves an initial herbicide treatment to remove the dominant weeds followed by seeding and fertilizing may founder because of the rapidity with which *Carduus acanthoides* L. reinvades the treated areas. Biological control can assist by reducing the vigour and seed production of the thistle. Alone biological control would be inadequate because the insects available for introduction against the thistle are unlikely to control it without the assistance of increased pasture competition. Even if they did, the thistle would tend to be replaced by other coarse weeds. Hence the benefits of integrating weed control may be considerably greater than those achieved by using biological, chemical or mechanical methods individually.

EVALUATION OF CONTROL ATTEMPTS

The cost and benefits of the six Canadian biological control projects are summarized in Table XIV. Most of the attempts are too recent to be evaluated fully: the populations of the insects concerned are still increasing and additional expenses will be incurred. Nevertheless it is possible to rate the prospects on the basis of present results. For example, the prospects of the *Cirsium* project are rated as low, indicating that neither of the two insects introduced against it are likely to control the weed. This does not necessarily mean that the prospects of its control with other agents are poor.

The cost of each project is based on the approximate number of scientist-years spent on it (each costing the Canada Department of Agriculture Research Branch an average of $40,000) plus the cost of overseas exploration, which has been mainly done by the Commonwealth Institute of Biological Control. The direct costs of this work are met from a grant given for each project, but the overhead costs of the Commonwealth Institute of Biological Control are met on a different basis. To cover part of the overheads the direct costs have been doubled. The fairly large sums spent on Commonwealth Institute of Biological Control studies of *Centaurea*, *Rhamnus* and other weeds for which there is no Canadian project at present have been covered by dividing them arbitrarily between the projects listed in Table XIV. The resulting cost figures are by no means exact but do indicate an order of magnitude of the cost of biological control of a weed. The costs are highest for the *H. perforatum* project partly because it is the only one completed and partly because it was a first attempt. The cost would have been still higher had it not been possible to capitalize on the experience of others against this weed. Likewise, the *S. jacobaea* project has benefited from New Zealand and Australian studies and, in particular, from the promise of early results with *Tyria jacobaeae* in the United States. The cost of the *Cirsium* and *Carduus* projects for which Canada has sponsored the foreign exploration and screening and trial of biological control agents will undoubtedly be higher and the benefits less certain than in the former projects. In round figures the cost of biological control of a weed may be as much as $500,000 if it is possible to use agents that have been shown to be safe and effective elsewhere and twice this sum if it is necessary to do the development work. These costs compare favourably with that of developing a new herbicide and have the further advantage that they do not involve a continuing expense for materials and labour. However, the cost is sufficiently high that the benefits of biological control cannot justify them for many weed species. Biological control can be done more cheaply if safeguards are reduced, the results not assessed and the reasons for the success or failure of individual agents not determined. However, to do this would retard development and future use of the method.

Ideally, the benefits of biological control should be expressed in financial terms so that a cost-benefit analysis can be made. This is impossible without more information on the economic effects and distributional limits of the weeds concerned. For example the biological control of *H. perforatum* was undertaken because continued northward spread of the weed could have largely extinguished the large ranching industry in the interior of British Columbia. The establishment of biological control agents in the province has removed this threat as the weed is now unable to monopolize good quality rangeland. Perhaps the project should be credited with saving the ranching industry; but as much of the grazing area may be near the northern limit of the weed, it is possible that it never would have been a serious problem. Hence, realistic appraisal is dependent on detailed ecological studies of the weed. The project was also done to gain experience with biological control of a weed—*H. perforatum* was presumed to be an easy project to start on in view of this weed's successful biological control in California. The experience gained is reflected in the subsequent projects but cannot readily be expressed in monetary terms. It is easier to evaluate the increased forage production resulting from control of the weed, but the figure is small: the weed did not infest an extensive part of the range and many of the stands were on unfarmed sites. Furthermore, the project was only a partial success in this respect as the weed is still a problem on dry grassland sites where presumably cattle may consume enough of it to develop ill effects.

The most promising among recent projects is *S. jacobaea.* Annual cattle deaths in Canada from this weed may represent a loss of the order of $10,000, but the social consequences of the loss are greater than the sum indicates because most of the weed occurs in marginal farming areas. It is likely that a moderate level of *S. jacobaea* control will eliminate these losses as cattle do not eat the weed if they can avoid doing so and the poisoning is cumulative, so that occasional consumption of small amounts is not harmful. The forage lost from the weed is of more consequence than the cattle lost but is harder to evaluate. The present results indicate that *S. jacobaea* will be eliminated as a dominant weed of impoverished pasture. This should eliminate cattle losses, and most of the forage losses, as well as the need for any herbicide treatment. On the other hand, good pasture management will still be needed, and if biological control removes the stimulus for this, the total benefits of the project will be small. The project has also been valuable for developing ideas and techniques because the establishment and build-up of the control agent has been followed more closely than in other examples of weed control.

The least rewarding project has been *Linaria vulgaris* Mill. The decline of the weed on the prairies removed the urgency for new control methods with the result that attention given to the project declined. The introduced moth can probably be used against *L. dalmatica*, which is increasing in British Columbia, but local studies will have to be made to overcome the difficulties of establishment. *Cirsium arvense* is likely to continue to be a difficult biological control problem because the choice of agents is small. The immediate prospects for control of *Euphorbia* are poor as the moth released against it has only survived at one place. It is possible that it can be more widely colonized after a period of adaptation; but even if this is not possible, there is a wide choice of other agents that can be tried. The weevil released against *Carduus* is likely to achieve a large reduction of the seed produced by *C. nutans* but is less promising against *C. acanthoides.*

CONCLUSIONS

Biological control is applicable to a different type of weed problem from that suited to chemical or mechanical control. Hence its use is not going to end 'chemical pollution' by herbicides, although it may sometimes reduce their use. On the other hand, biological control can help make farming profitable on marginal land by reducing the seriousness of dominant weeds for which other methods of control are economically unavailable. The rewards from its use are likely to be greatest if it is supplemented by good land management and sometimes even chemical control, and almost non-existent if the land is exploited.

LITERATURE CITED

1. Baker, H. G. (1965). Characteristics and modes of origin of weeds; pp. 147–69. *In* H. G. Baker and G. L. Stebbins (eds.), The genetics of colonizing species. Academic Press, New York.
2. Bucher, G. E. & Harris, P. (1961). Food plant spectrum and elimination of disease of cinnabar moth larvae, *Hypocrita jacobaeae* (L.) (Lepidoptera: Arctiidae). *Can. Ent.* 93: 931–6.

3. DeBach, P. (1966). The competitive displacement and coexistence principles. *A. Rev. Ent.* **11**: 183–212.
4. DeBach, P. & Sundby, R. A. (1963). Competitive displacement between ecological homologues. *Hilgardia* **34**: 105–66.
5. Harris, P. (1967). Suitability of *Anaitis plagiata* (Geometridae) for biocontrol of *Hypericum perforatum* in dry grassland of British Columbia. *Can. Ent.* 99: 1304–10.
6. Harris, P. & Piper, G. (1970). Ragweed (*Ambrosia* spp. Compositae), its North American insects and the possibilities for its biological control. *Tech. Bull. Commonw. Inst. biol. Control.* **13**: 117-140.
7. Harris, P. & Zwölfer, H. (1968). Screening of phytophagous insects for biological control of weeds. *Can. Ent.* **100**: 295–303.
8. Johansson, S. (1962). Insects associated with *Hypericum* L. 1. Host plant and Coleoptera. *Opusc. ent.* **27**: 128–46.
9. Johansson, S. (1962). Insects associated with *Hypericum* L. 2. Lepidoptera, Diptera, Hymenoptera, Homoptera and general remarks. *Opusc. ent.* **27**: 175–92.
10. Mohyuddin, A. I. (1965). The insect complexes of *Calystegia* and *Convolvulus*, the biology, phenology, host spectrum and its chemical basis in four oligophagous species feeding on these in the Belleville, Ontario area. Ph.D. thesis, Queen's University, Kingston, Ont. 152 pp.
11. National Academy of Sciences (1969). Principles of plant and animal pest control. Vol 2, Weed control. National Academy of Sciences, Washington, Publ. **1597**, 471 pp.
12. Wilkinson, A. T. S. (1965). Release of cinnabar moth, *Hypocrita jacobaeae* (L.) (Lepidoptera: Arctiidae) on tansy ragwort in British Columbia. *Proc. ent. Soc. Br. Columb.* **62**: 10–3.
13. Wilson, F. (1943). The entomological control of St. John's wort (*Hypericum perforatum* L.) with particular reference to the insect enemies of the weed in southern France. *Bull. Coun. scient. ind. Res., Melb.* **169**: 5–87.
14. Wilson, F. (1960). A review of the biological control of insects and weeds in Australia and Australian New Guinea. *Tech. Commun. Commonw. Inst. biol. Control* **1**, 102 pp.
15. Zwölfer, H. (1963). Untersuchungen über die Struktur von Parasitenkomplexen bei einigen Lepidopteren. *Z. angew. Ent.* **51**: 346–57.
16. Zwölfer, H. (1965). Preliminary check list of phytophagous insects attacking wild Cynareae (Compositae) species in Europe. *Tech. Bull. Commonw. Inst. biol. Control* **6**: 81–154.

29. *CARDUUS ACANTHOIDES* L., WELTED THISTLE, AND *C. NUTANS* L., NODDING THISTLE (COMPOSITAE)

P. Harris and H. Zwölfer

PEST STATUS

The thistle genus *Carduus* is native to Eurasia and North Africa, but three species, *C. acanthoides* L., *C. nutans* L. and *C. crispus* L. have become established in Canada. The first two are serious pasture weeds that have undoubtedly not reached their potential limits of spread (5). *C. acanthoides*, which may be annual or biennial, is most abundant in Ontario, with the largest stands occurring in Grey County. It also occurs in Nova Scotia, Quebec and British Columbia. *C. nutans* is biennial and occurs in Newfoundland, New Brunswick, Quebec, southern Ontario, Manitoba and Saskatchewan. The two species hybridize where they occur together in Grey Country, Ontario (4). *C. crispus* is confined to Nova Scotia and is of little consequence as a weed.

The status of *C. nutans* in Saskatchewan was investigated by Alex (1): before 1965 *C. nutans macrolepsis* was restricted to a triangle with a 60-mile base (from Mortlach to Craven) and an apex at Dundurn, about 100 miles NNW of the centre of the base line—generally between Regina and Saskatoon—plus one outlier at Wilkie (100 miles WNW of Dundurn). By 1967 the triangle had extended 40 miles southeast to Regina and McLean, 65 miles northeast to Ituna and about 10 miles west to Broderick. This increase doubled the area of occurrence and within the original triangle there was a marked increase in both size and number of patches.

The infestations were most noticeable in non-cultivated, ungrazed areas: roadsides, railroad rights-of-way, vacant land around gravel quarries, fence lines and stone piles or shrub patches in pastureland. The thistle is less obvious in pastures because trampling and some grazing prevent it from growing as large as in ungrazed areas. Nevertheless, extensive infestations occurred on permanent or semi-permanent tame pasture and hayland as well as occasionally in native grassland pastures.

In contrast with Saskatchewan the most important *Carduus* species in Hastings County, Ontario is *C. acanthoides* and the problem is largely confined to non-arable pasture that has suffered sustained overgrazing. Such areas have provided good grazing in the past and after complete rest for about six years the grass is usually thick enough to eliminate most of the thistle. This solution is unacceptable to most of the farmers who are short of summer pasture. A pilot project started on about 10,000 acres in 1968, involving spraying with herbicide, fertilizing and sowing grasses or trefoil may offer a partial solution, although it appears that some measure of biological control will be needed as well. The area is generally not favoured for afforestation because it is difficult to plant the trees in the rocky soil.

Both *C. nutans* and *C. acanthoides* can be controlled by cultivation and some selective herbicides. However, they are not being controlled effectively because of inaccessibility and because the infested areas yield a return too low to justify large expenditures. In the long run the problem in Saskatchewan is more serious than in Ontario because the thistle maintains itself in the absence of grazing.

BACKGROUND

No biological control attempts against *Carduus* have been reported from other parts of the world. The European insects attacking *Carduus* as well as those from other Cynareae have been listed by Zwölfer (6). The most interesting of these as biological control agents are *Rhinocyllus conicus* Frl., *Lixus elongatus* Goeze (Coleoptera: Curculionidae), *Tingis cardui* L. (Hemiptera: Tingidae) and *Urophora solstitialis* L. (Diptera: Trypetidae). In addition detailed studies of host specificity and ecological requirements have been made on three thistle-feeding species of *Cassida* (Coleoptera: Chrysomelidae) (8); several species of *Larinus* (Coleoptera: Curculionidae) (7); and *Terellia serratulae* (Diptera: Tephritidae) (3). Also investigations on *C. nutans* insects in Italy have been made by the United States Department of Agriculture and an annotated list of *Carduus* insects has been compiled by Coulson (2).

Three insects are commonly associated with *Carduus* in Canada: *Vanessa cardui* L. (Lepidoptera: Nymphalidae), *Cassida rubigionosa* L. (Coleoptera: Chrysomelidae) and *Cleonus piger* L. (Coleoptera: Curculionidae). The former species, a native, is widespread and occasionally of local value in defoliating thistle, but it is also a pest of sunflower and other crops. Both the latter insect species are of European origin and are confined to eastern Canada. The larvae and adults of *C. rubiginosa* skeletonize the leaves and are capable of damaging thistles severely, but high parasitism seems to prevent the build-up of a population high enough to control thistles. The larvae of *C. piger* develop in the root crowns of thistles, but infested plants usually suffer little damage. *Carduus* is also attacked by many polyphagous insects, but no species attacking seeds or flower heads are prevalent.

RELEASES AND RECOVERIES

Rhinocyllus conicus Frl. (Coleoptera: Curculionidae)

R. conicus is found in the Mediterranean basin, south and central Europe and parts of western Asia. It overwinters as an adult in the soil litter and emerges to feed on the thistle leaves in the spring. The eggs are laid externally on the involucral bracts, usually close to the peduncle. Each egg is covered by a crust of masticated particles of the host plant and up to 20 eggs may be laid on a single flower head. After an incubation of 6 to 8 days the larva hatches and mines its way into the receptacle on which it develops. Up to 16 larvae have been found in a single *C. nutans* flower head. Depending on the size of the thistle head, the number of larvae present and probably the maturity of the head when attacked, all or some of the seeds are prevented from developing. *R. conicus* may be either uni- or bivoltine. Observations in Austria suggest that the adults maturing early produce a second generation but that the bulk of the population, emerging in July and August, do not lay until the following year. The weevil in Europe is most commonly found in large flowered species of *Carduus*, but it also attacks *Cirsium* and *Silybum*, and rarely *Onopordum* (Compositae: Cynareae). They are seldom associated with *C. acanthoides* in Europe in spite of its close relationship to *C. nutans*.

R. conicus was released in Canada at the end of July 1968, on *C. nutans* near Regina, Saskatchewan and on *C. acanthoides* near Belleville, Ontario (Table XV). In Europe these individuals would overwinter, but at Belleville they completed a second generation. As a result, in September many attacked heads were found, usually containing a single larva and occasionally two.[1] The weevil has survived near Regina with the first eggs being laid the year following release in early July.

EVALUATION OF CONTROL ATTEMPTS

The release of *R. conicus* at Belleville was disappointing because of the failure of most of the progeny to complete development before winter and their consequent mortality. However, it did establish that (1) *R. conicus* will freely attack and develop on *C. acanthoides*; (2) none of the attacked heads developed seed, so that the weevil is a potentially effective control agent for this thistle; and (3) *R. conicus* can survive in the Belleville area, although not many did so. The poor survival was probably associated with the late development of the thistles in Canada relative to those at the source of the weevil, in the upper Rhine valley. Thus, the weevils released in July encountered thistles characteristic of a June developmental stage in their original habitat. So, behaving as early emerging adults, they produced a second generation that could not be matured before winter.[2] The initial results from *C. nutans* near Regina, Saskatchewan are more promising.

This project for the biological control of *Carduus* differs from most attempts made against weeds in that it is part of a larger programme for upgrading permanent pasture in Ontario with chemical and pasture improvement practices. To a large extent the two parts of the programme complement each other. Without pasture improvement even the elimination of *Carduus* would be of little value: other weeds would remain and in the face of continued overgrazing, would replace *Carduus*. The weakness of the chemical control programme by itself is that it leaves a seed source of *Carduus* in the properties of non-cooperating neighbours and in inaccessible areas.

RECOMMENDATIONS

(1) *Rhinocyllus conicus* offers prospects for reducing seed production of both *Carduus nutans* and *C. acanthoides* in Canada. This will be of particular value for preventing the thistle from reinfesting pasture improvement areas; therefore continued efforts should be made to establish the weevil in Canada.

(2) *Urophora solstitialis* L. (Diptera: Tephritidae) is apparently confined to *Carduus* spp. (6) and could be introduced to restrict seed production if *R. conicus* fails to become established or destroys only a small percentage of the seed.

(3) Insects such as *Ceutorhynchus horridus* Panz., *Lixus elongatus* Goeze (Coleoptera: Curculionidae) and *Tingis cardui* L. (Hemiptera: Tingidae) have host ranges approximately similar to that of *R. conicus* and might be introduced to attack the stems and leaves of the thistles. The prospects of finding *Carduus* insects suitable for Canada with a more restricted host range are poor.

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[1] These larvae as well as pupae and most of the young beetles remained in the heads during winter and were dead in the spring. However, two live *R. conicus* were recovered from the soil litter, the normal overwintering site, in the spring of 1969. Whether they were individuals that did not develop their ovaries after release, or whether they had matured early enough to leave the heads before winter is not known.

[2] In 1969, to overcome this difficulty the releases were made in May with overwintering weevils; but this resulted in a wastage of eggs. The weevils were ready to lay, but there were no buds available until early June. Consequently the eggs were laid on the leaves or concentrated on the first buds to appear. These problems may disappear if the weevil can be synchronized with the thistle in Canada.

TABLE XV

Open releases and recoveries of insects against *Carduus* spp.

Species and Province	Year	Origin	Number released	Year of recovery
Rhinocyllus conicus Froelich				
Saskatchewan	1968	France	400	1969
Ontario	1968	France	370	1969

LITERATURE CITED

1. Alex, J. L. (1967). *In litt.* Department of Botany, University of Guelph, Guelph, Ontario.
2. Coulson, J. R. (1969). Insects associated with *Carduus* thistles. *U.S. Dep. Agric., Ent. Res. Div. Beltsville, Maryland* (mimeographed).
3. Ghani, M. A. Unpublished reports. Commonw. Inst. Biol. Control (1960–7). Pakistan Station, Rawalpindi.
4. Moore, R. J. & Mulligan, G. A. (1956). Natural hybridization between *Carduus acanthoides* and *Carduus nutans* in Ontario. *Can. J. Bot.* 34: 71–85.
5. Mulligan, G. A. & Frankton, C. (1954). The plumeless thistles (*Carduus* spp.) in Canada. *Can. Fld Nat.* 68: 31–6.
6. Zwölfer, H. (1965). Preliminary list of phytophagous insects attacking wild Cynareae (Compositae) species in Europe. *Tech. Bull. Commonw. Inst. biol. Control* 6: 81–154.
7. Zwölfer, H. Unpublished observations.
8. Zwölfer, H. and Eichhorn, O. (1966). The host ranges of *Cassida* spp. (Col. Chrysomelidae) attacking Cynareae (Compositae) in Europe. *Z. angew. Ent.* 58: 384–97.

30. *CIRSIUM ARVENSE* (L.) SCOP., CANADA THISTLE (COMPOSITAE)

D. P. PESCHKEN

PEST STATUS

Cirsium arvense (L.) Scop. is indigenous to Europe, western Asia and northern Africa and was probably first introduced into the French settlements of Canada early in the 17th century (4, 7). This noxious weed now occurs throughout the agricultural areas of Canada and the northern half of the United States (3, 5). Growing under a wide variety of conditions it thrives on fertile, well drained soils in overgrazed pastures and small-grain fields. It is one of the most frequently encountered weeds in Canada: it occurred on 77 per cent. of survey check plots from the Maritime Provinces to eastern Saskatchewan inclusive, and on 40 per cent. from there to the Pacific coast (6). Twenty-five shoots per square yard can reduce the yield of wheat by 60 per cent. (10). At an initial density of 18 plants per square yard, Canada thistle can reduce the production of alfalfa by 7·4 tons per acre and consumption by sheep by 4·7 tons per acre in a four-year period (16). Control measures must extend for several years and aim at starving the aggressive and extensive root system by clean cultivation, mowing, and planting competitive crops (10). Picloram (4-amino-3,5,6-trichloropicolinic acid) seems to be the only commercial herbicide that enters and destroys the roots, but it harms many other plant species and may persist in the soil for several years (9).

BACKGROUND

In Canada, the most conspicuous enemies of *C. arvense* are: the insects *Cassida rubiginosa* Muell. (Coleoptera: Chrysomelidae), *Cleonus piger* Scop. (Coleoptera: Curculionidae) and *Orellia ruficauda* F. (Diptera: Trypetidae) and the rust *Puccinia suaveolens* Rostr. However, these do not control Canada thistle below the economic level.

The Commonwealth Institute of Biological Control began work on the biological control of Canada thistle in 1961 with a study of its parasites in Europe. Zwölfer (20) lists 80 insect species feeding on the weed in Europe, from which *Altica carduorum* Guer., *Ceutorhynchus litura* (F.) and *Urophora cardui* L. were selected for further study because of their apparent host specificity and possible climatic suitability.

RELEASES AND RECOVERIES

Altica carduorum Guer. (Coleoptera: Chrysomelidae)

ECOLOGY. In Europe, *A. carduorum* has a Mediterranean and partly Atlantic distribution which corresponds closely with areas where 'heat days' occur regularly, i.e. days during which the temperature does not drop below 20°C (19). The beetle usually occurs in regions with high precipitation or humidity during the summer. In dry continental areas it prefers relatively moist sites. After hibernation, the adults are present from April to July, and eggs and larvae from May to July. Third-instar larvae pupate in the upper 2 cm of soil or duff and the adults which will overwinter are found from June to September. There is one generation a year. *A. carduorum* is potentially very destructive, both adults and larvae feeding on the leaves of *C. arvense*. The host range of this flea beetle is restricted to the genera *Cirsium*, *Carduus* and *Silybum*, all of which are in the tribe Cynareae (8, 11). In his field surveys Zwölfer (19) found *A. carduorum* only on *C. arvense*.

RELEASES. Colonies of 24 to 1,160 beetles were released on pastures or roadsides heavily infested with *C. arvense*, at six places in Ontario, three in British Columbia, and one each in Nova Scotia and Alberta during 1963–8 (Table XVII) (13). However, the beetle probably did not become established. Outside field cages, no survivors were found in the fall of the same year in which the releases were made, except for a few adults and eggs in the following year at Summerland, British Columbia, and a small colony which survived for three years at Lacombe, Alberta.[1] In Ontario, survivors were found in the spring following a release made in the previous fall, but none thereafter. Five cage colonies thrived in three Provinces with different climates, but the mortalities of eggs and/or larvae of field colonies reached 91 per cent., which indicates that predators took many of the immature stages. Near Belleville, Ontario, *Erythraeus* sp. near *regalis* (Koch), *Leptus* sp. near *curtipes* Schweizer and *Sphaerolophus* sp. (Acarina: Erythraeidae) were implicated in tests with *A. carduorum* eggs labelled with P^{32}. The adults start flying at 21°C and disperse strongly on hot summer days. This may have contributed to failures of releases made in late May to July. Dry continental summers, such as occur at Summerland, British Columbia and Lacombe, Alberta, were probably not detrimental to the development of the immature stages, but laboratory experiments indicate that eggs would desiccate without the occurrence of dew (13).

Ceutorhynchus litura (F.) (Coleoptera: Curculionidae)

ECOLOGY. *C. litura* has a European-Atlantic distribution, and occurs more frequently in the northern than in the southern part of its range (22). It is found in a wide variety of habitats but more abundantly in cultivated fields than in grassland, forest borders or swamps. In early spring, the adults feed on the young shoots of *C. arvense*. The females oviposit in the main vein of thistle leaves, from the end of March to mid-May. The larvae mine through the midrib of the leaf into the stem and the root collar, and occasionally into the root. The third instar pupates in the ground. Teneral adults are found from early June to mid-July (22). In Europe, adult feeding does not seriously damage the host. Vigorous plants, if attacked by only one or two larvae, may smother and kill the larvae with callus tissue or localize a stronger attack by formation of a gall in the region of the root collar. On the

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[1] No survivors were found at Lacombe in the spring of 1969.

other hand, thistles growing under stress suffer severely from larval attack (22). As with *A. carduorum*, the host range of *C. litura* is restricted to the *Cirsium-Silybum-Carduus* group within the tribe Cynareae (22).

RELEASES. *C. litura* was released in field cages at four locations near Belleville, Ontario in 1965 and 1967 (12) (Table XVII). On three sites, where only 22–56 adults were released and the thistle infestation was low to moderate, the colonies died out. On the fourth site (a heavily infested permanent pasture) 150 beetles were released in May and 80 in August, 1967. The cage was removed in late fall of 1967, and the colony had spread from the area of the field cage (3·25 m^2) to 135 m^2 by May 1968. At that time, oviposition marks were found on 39 per cent. of a sample of 390 thistles, indicating that initial establishment had occurred (12). Observations are being continued.

Urophora cardui L. (Diptera: Trypetidae)

ECOLOGY. *U. cardui* is widely but sporadically distributed over Europe, and has also been recorded from Siberia (21). This patchy distribution cannot be explained by local climate, biotope or altitude. There seems to be a preference, however, for thistle stands in half shade. *U. cardui* galls were found exclusively on *C. arvense* which indicates a high degree of host specificity. In the laboratory, the female usually oviposits into the terminal bud and the larvae induce the development of a gall, in which they develop. After hibernating as mature larvae, they pupate in spring inside the gall from which the adults emerge in May and June (21). *U. cardui* has not been released in Canada but is cultured at Belleville for preparatory studies on its host specificity and ecological requirements. In the laboratory, the flies mate and oviposit at a light intensity of 4,000 lux. The larvae pupate without the delay of a diapause if they are dissected from the galls (14, 15). The life cycle is completed in about six weeks at 21°C.

Laboratory experiments show that the vigour of galled thistles is significantly reduced, particularly when there are multiple galls on one plant, as measured by the dry weight of the plants, the number of new shoots produced by the lateral roots and the number of dead plants (Table XVI) (12). *U. cardui* galls have only been found on *C. arvense* in the field (21). This apparent host specificity, the effect on its host and climatic suitability make *U. cardui* an attractive candidate insect for use against *C. arvense*.

EVALUATION OF CONTROL ATTEMPTS

C. arvense differs from most other weeds against which biological control has been tried in that it is a serious problem within its indigenous range (1, 7, 17) as well as in newly colonized areas. Despite the stresses imposed by numerous insect species, the rust *Puccinia suaveolans* and the virus causing yellow top, all feeding on or parasitizing 'creeping thistle' in Europe, the weed is not controlled below the economic level. However, Wilson (18) states that the 'intrinsic capacity' of an insect species to regulate plant numbers is more important from the standpoint of biological control than the extent to which they do so in their natural habitat. *A. carduorum*, *C. litura* and *U. cardui* do have the capacity to destroy or at least to reduce seriously the vigour of their host (11, 12, 22).

High mortalities of the larvae and eggs of *A. carduorum*, probably caused by predation and excessive dispersal by the adults, may have prevented the establishment of this flea beetle. Also, *A. carduorum* is probably not adapted to the Canadian climate, because 30 or more 'heat days' occur in most of its habitats in Europe (19), whereas only 14 such days occur in southern Ontario, this being the highest number recorded from any of the release sites in Canada. In this respect it is surprising that the only release site where *A. carduorum* survived for three years was Lacombe, Alberta, where no heat days occurred, and where temperatures are cooler than at any other release site during every month of the year except July, when the average temperature equals that at Saanichton, British Columbia. Reduced adult dispersal due to lower temperatures and less predation may account for the better survival of the flea beetle at Lacombe (12).

In contrast, *C. litura* has survived and is spreading at one release site in Ontario where *A. carduorum* failed. Inside the plant tissue, the eggs and larvae of *C. litura* are probably protected from those predators that prevented establishment of *A. carduorum*, and the weevil's native range indicates climatic requirements similar to those found in southern Ontario. Furthermore, the muscid fly, *Phaonia trimaculata* Bouché, which is the most important enemy of *C. litura* in at least one locality in Europe (22), is not recorded in North America.

The stimulation of sideshoot development in the laboratory by infestations with *U. cardui* larvae in the terminal vegetative bud of *C. arvense* may give rise to concern that infested thistles would produce more sideshoots and eventually more seedheads in the field. However, this is not expected to occur for the following reasons. In the laboratory, very young thistles were used. The single-gall group was infested several weeks before sideshoot development would normally have taken place. In the case of the multiple-gall group, sideshoot development had to be stimulated first by pruning the terminal shoot to allow oviposition into several buds on one plant. In contrast, oviposition and sideshoot development in the field occur approximately simultaneously. Thus several galls on one plant with the resultant increased reduction in host vigour are possible, particularly if *U. cardui* becomes more abundant in North America than in Europe. This is hoped for, because the most important biotic mortality agents of *U. cardui*, the chalcid wasps *Eurytoma serratulae* F. and *E. robusta* Mayr (2), are not recorded in America north of Mexico.

TABLE XVI

Effect of *Urophora cardui* L. galls on the vigour of *Cirsium arvense* (L.) Scop. in the laboratory

	Plants with one gall each (n = 15)		Plants with an average of two galls each (n = 16)	
	Not galled	Galled	Not galled	Galled
Mean dry weights per plant in grams of:				
Roots	1·35	0·46	1·23	0·25
Stems and leaves	3·34	1·75	3·12	1·28
Galls	—	0·96	—	0·66
Mean number per plant of:				
Side shoots	1·0	4·7	2·8	4·1
Root shoots	0·53	0·27	0·69	0·06
U. cardui larvae	—	7·1	—	3·9
Total number of dead plants	0	0	0	3

TABLE XVII

Open releases and recoveries of insects against *Cirsium arvense* (L.) Scop.[1]

Species and Province	Year	Number	Year of recovery
Altica carduorum (Guérin-Meneville)			
Nova Scotia	1966	50	—
Ontario	1963	21	—
	1964	600	—
	1965	1460	1966
	1966	517	—
	1967	480	—
	1968	291	—
Alberta	1963	24	1964–68
	1965	149	1966–68
	1968	1267	—
British Columbia	1964	99	—
	1965	72	—
	1967	431	1968
	1968	1237	—
Ceutorhynchus litura (Fabricius)			
Ontario	1965	22	—
	1967	270	1968

[1] All insects originated from Switzerland, and all *A. carduorum* from laboratory culture.

RECOMMENDATIONS

(1) No further releases of *A. carduorum* should be made, except perhaps in Kent and Essex Counties, southwestern Ontario, where 'heat days' occur annually.

(2) Further releases of *C. litura* should be made throughout Canada, preferably using specimens from the release near Belleville.

(3) *U. cardui* should be tested for its host specificity and released if its host range is sufficiently restricted.

LITERATURE CITED

1. Brenchley, W. E. (1920). Weeds of farm land. Longmans, Green, London, New York.
2. Carl, K. & Zwölfer, H. (1965). Untersuchungen zur biologischen Bekämpfung einiger Schädlinge in Landwirtschaft und Obstbau. 2. Bericht über die Arbeiten der europäischen Station des Commonwealth Institute of Biological Control, Delémont, Schweiz. *Anz. Schädlingsk.* **38**: 81–7.
3. Detmers, F. (1927). Canada thistle, *Cirsium arvense* Tourn. Field thistle. *Bull. Ohio agric. Exp. Stn* **400**, 45 pp.
4. Dewey, L. H. (1901). Canada thistle. *Circ. Div. Bot. U.S. Dep. Agric.* **27**, 14 pp.
5. Frankton, C. (1955). Weeds of Canada. Queen's Printer, Ottawa.
6. Groh, H. & Frankton, C. (1949). Canadian Weed Survey. *7th Rep. Can. Dep. Agric. Div. Bot. Pl. Path.* 144 pp.
7. Hansen, A. A. (1918). Canada thistle and methods of eradication. *Fmrs' Bull. U.S. Dep. Agric.* **1002**, 15 pp.
8. Harris, P. (1964). Host specificity of *Altica carduorum* Guer. (Coleoptera: Chrysomelidae). *Can. J. Zool.* **42**: 857–62.
9. Heikes, E. E. (1964). Tordon and other herbicides. . . . Field testing for the control of deep-rooted perennial weeds in Colorado. *Down to Earth* **20**: 9–12.
10. Hodgson, J. M. (1968). The nature, ecology, and control of Canada thistle. *Tech. Bull. U.S. Dep. Agric.* **1386**, 32 pp.
11. Karny, M. (1963). *Haltica carduorum* Guer. (Col.: Chrysomelidae), attacking *Cirsium arvense*. *Tech. Bull. Commonw. Inst. biol. Control* **3**: 99–110.
12. Peschken, D. (1968). Unpublished data.
13. Peschken, D., Friesen, H. A. & Tonks, N. V. (1970). Releases of *Altica carduorum* Guer. (Chrysomelidae: Coleoptera) against the weed Canada thistle (*Cirsium arvense* (L.) Scop.) in Canada. *Can. Ent.* **102**: 264–71.
14. Quentin, R. M. (1954). Remarques liminaires sur les galles de *Cirsium arvense* Scop., dues à *Urophora cardui* Linné (Dipt. Trypetidae). *Bull. Soc. ent. Fr.* **59**: 147–9.
15. Ruppolt, W. (1958). Gallenentwicklung an *Cirsium arvense* L. im Winter hervorgerufen durch *Euribia cardui* L. (Trypetidae). *Naturwissenschaften* **45**: 275–6.
16. Schreiber, M. M. (1967). Effect of density and control of Canada thistle on production and utilization of alfalfa pasture. *Weeds* **15**: 138–40.
17. Wehsarg, O. (1954). Ackerunkräuter. Biologie, allgemeine Bedeutung und Einzelbekämpfung. Akademie Verlag, Berlin.
18. Wilson, F. (1964). The biological control of weeds. *A. Rev. Ent.* **9**: 225–44.
19. Zwölfer, H. (1965). Observations on the distribution and ecology of *Altica carduorum* Guer. (Col. Chrysom.). *Tech. Bull. Commonw. Inst. biol. Control* **5**: 129–41.
20. Zwölfer, H. (1965). Preliminary list of phytophagous insects attacking wild Cynareae (Compositae) species in Europe. *Tech. Bull. Commonw. Inst. biol. Control* **6**: 81–154.
21. Zwölfer, H. (1967). Observations of *Urophora cardui* L. (Trypetidae). *Prog. Rep. Commonw. Inst. biol. Control* (*Weed Projects for Canada*) **19**, 11 pp.
22. Zwölfer, H. & Harris, P. (1966). *Ceutorhynchus litura* F. (Col. Curculionidae), a potential insect for the biological control of thistle, *Cirsium arvense* (L.) Scop. in Canada. *Can. J. Zool.* **44**: 23–37.

31. *EUPHORBIA ESULA* L., LEAFY SPURGE, AND *E. CYPARISSIAS* L., CYPRESS SPURGE (EUPHORBIACEAE)

P. HARRIS and J. ALEX

PEST STATUS

Euphorbia esula L. and *E. cyparissias* L. are two closely related perennial weeds of European origin. They thrive on a wide variety of soils in Canada and dominate most other herbaceous vegetation (7, 11). Like other species of *Euphorbia* they contain an acrid latex that produces blisters and dermatitis in man and cattle. Cattle avoid eating them as a rule but may do so if forage is scarce or if the weeds are in hay. When these weeds are eaten in small amounts a severe irritation of the mouth and digestive tract results; large amounts cause death (3).

E. esula is found in every province of Canada except Newfoundland. It is estimated to infest 35,000 to 40,000 acres, most being in the prairies, although the weed was unknown there at the beginning of the century (11). The weed is difficult to control because of persistent regeneration from the roots. Plants can be killed by soil applications of herbicides at high rates or by repeated removal of shoots over several years. Two consecutive seasons of intensive cultivation will prevent nearly all regrowth but such a programme is costly and in the prairies invites soil erosion. Alternating intensive summer fallow with cropping to grain sprayed with 2, 4–D to kill seedlings and regrowth reduces competition from the weed to a negligible level but the weed remains as a nuisance. Eradication is only achieved when the seed in the soil has lost its viability. Seed remains viable for at least 5 years under field conditions in Saskatchewan and for 13 years in dry storage (11). Picloram is recommended (9) for leafy spurge on non-crop land; it gives 95–99 per cent. control but has the disadvantage of leaving residues in the soil. There is no known economic method of controlling large stands of the weed in non-arable sandy or rocky soils and in such areas the weed is still spreading. These stands reduce the forage available to cattle and wildlife and provide a seed source for reinfestation of arable areas reclaimed from the weed by intensive control programmes.

E. cyparissias occurs largely in eastern Canada where it presents the same problems as *E. esula* except that most stands are sterile. Hence spread is slow and infestations are usually restricted to a few acres. One exception is at Braeside, Ontario, where a fertile form was scattered over approximately 9 square miles in 1952 (7) and has since spread considerably.

BACKGROUND

Biological control has not been reported against *Euphorbia* in other parts of the world and no comprehensive studies of the insect fauna of either *E. esula* or *E. cyparissias* are known except for surveys of their indigenous insect enemies made by the Commonwealth Institute of Biological Control (C.I.B.C.). The indigenous distribution of *E. esula* is centred in the Caucasus (11) and extends through central Russia to western Europe, north to Finland and southern Sweden and south to northern Spain and central Italy (6). The distribution of *E. cyparissias* is centred slightly to the south and west of *E. esula* (7). The C.I.B.C. has not surveyed either plant at its distribution centre (probably the richest source of monophagous insects) but surveys made in Austria, Germany and Switzerland show that the plants share a highly specialized and mostly little known complex of insects. The best known of these is *Celerio euphorbiae* (L.), the spurge hawk moth, which was released in Canada after extensive tests confirmed its host specificity (2). At present D. Schröder at the C.I.B.C. Station, Delémont, Switzerland, is studying the root-boring aegeriid, *Chamaesphecia empiformis* Esp., as a possible alternative to *Celerio euphorbiae* as a biological control agent.

The most noticeable parasite of both *E. esula* and *E. cyparissias* in Canada is the rust *Uromyces striatus* Schroat (alfalfa, *Medicago sativa* L. and clovers, *Trifolium* spp., are the alternate hosts). It does little damage to the spurge stands although infected plants are weakened. The few insects, all of which are polyphagous, found attacking the spurges do negligible damage and are not likely to impede the establishment of a control agent.

RELEASES AND RECOVERIES

Celerio euphorbiae (L.) (Lepidoptera: Sphingidae)

ECOLOGY. *C. euphorbiae* is indigenous to southern and central Europe, northern India and central Asia. The moth occurs in Britain and northern Europe as an immigrant but normally does not propagate itself, probably because the summers are too cool for larval development. A female lays

70–110 eggs (8) singly or in clusters (up to 50) on many *Euphorbia* spp. Although light frosts are survived both eggs and larvae require high temperatures to develop: at 13°C the larvae fed little and eventually died, but at 32°C a generation was completed within six weeks. The moth is univoltine in Canada although it is sometimes bi- or multivoltine in parts of Europe. The larvae are conspicuously coloured, grow to a large size and, provided there is enough spurge foliage for them to feed on, move little until ready to pupate. Hence, larval survival counts can be readily made under field conditions. *C. euphorbiae* overwinters as a pupa, either under a rock or just below the soil surface.

The ability of *C. euphorbiae* to withstand freezing temperatures is important for its survival in Canada. The occurrence of the moth in regions of Europe with severe winters indicates that cold-hardiness should not be a problem. However, Wittdstat (16) suggested that pupae are unable to survive in Germany if there is poor snow cover. Salt (10) has criticized early workers who concluded that the pupae were completely frozen at −4·5°C for assuming that physical rigidity implies a frozen condition. Bachmetjew (1) found that the undercooling temperature of the pupae was about −6·3°C, but as he measured this with a thermocouple piercing the cuticle this is not necessarily a reliable value for undamaged pupae.

The ability of the Belleville laboratory stock of *C. euphobiae* to withstand low temperatures was determined on 318 pupae. The pupae were kept in damp vermiculite at 2°C for a month and then exposed to freezing temperatures which were decreased from −6 to −21°C in five stages at weekly intervals. At the end of each week the pupae were brought to room temperature. Those that wriggled when stimulated with a 45-volt B cell were considered to be alive and returned to a lower temperature. The accumulated mortality curve (Fig. 5) show that temperatures −20°C are unlikely to kill all the pupae.

The following soil temperatures (Canada Department of Transport) indicate conditions that the pupae are likely to encounter at our release sites. Good snow cover at Ottawa (Braeside release site) usually keeps the soil temperature at 1 cm within a few degrees of freezing although occasionally it falls to −9°C. The temperature at Toronto (Belleville release site) at 5 cm is frequently −5°C and falls to −12°C for short periods. At Swift Current, Saskatchewan, which is likely to be colder than the prairie release sites, the 5 cm temperature remains at −12 to −15°C for long periods and reaches −20°C briefly. We infer from this that although winter kill could be a problem on the prairies, it is unlikely to be one in Ontario. This conclusion is supported by the survival of pupae at Belleville and Braeside, Ontario. At Regina, Saskatchewan, only 1/12 of the pupae set out in the course of the winter survived; but only a few survivors might be needed to develop a hardier strain.

RELEASES. The following is a summary of work to be treated in detail in a later paper. The location and number of *C. euphorbiae* released given by Williamson (13, 14, 15) are summarized in Table XVIII. The only recoveries made were 68 widely scattered, nearly mature larvae at Braeside, Ontario, on 30 July 1968.

The first releases, made in 1965, were not followed in detail, but a rapid disappearance of the larvae was noted. It was thought that a cytoplasmic virus, causing many deaths in the laboratory stock, might be responsible. This disease was controlled by rearing each larva individually and as long as this procedure was followed the disease was not apparent. Hence the disease can be discounted as an important cause of mortality in the subsequent releases.

Most of the releases of *C. euphorbiae* larvae made in 1966 and 1967 suffered a mortality of over 95 per cent. during the two weeks after release. The exceptions were at Braeside, Ontario, where 23 per cent. of the larvae were alive at the end of the two-week period and in a series of late releases at Belleville. However, in the late releases development was so slow that many larvae were unable to pupate before winter and died. Even confining the larvae to a field cage (20-mesh screen with its edges buried) did not prevent them from disappearing. For example, at Belleville, only 20·6 per cent of 360 larvae put in a cage on 13 July 1966 were recovered two weeks later, although in a similar test started on 31 August, 90 per cent. were recovered. The main predators taking the caged larvae were ants and the mouse *Peromyscus leucopus leucopus* (Raf.). Outside the cage the following predators

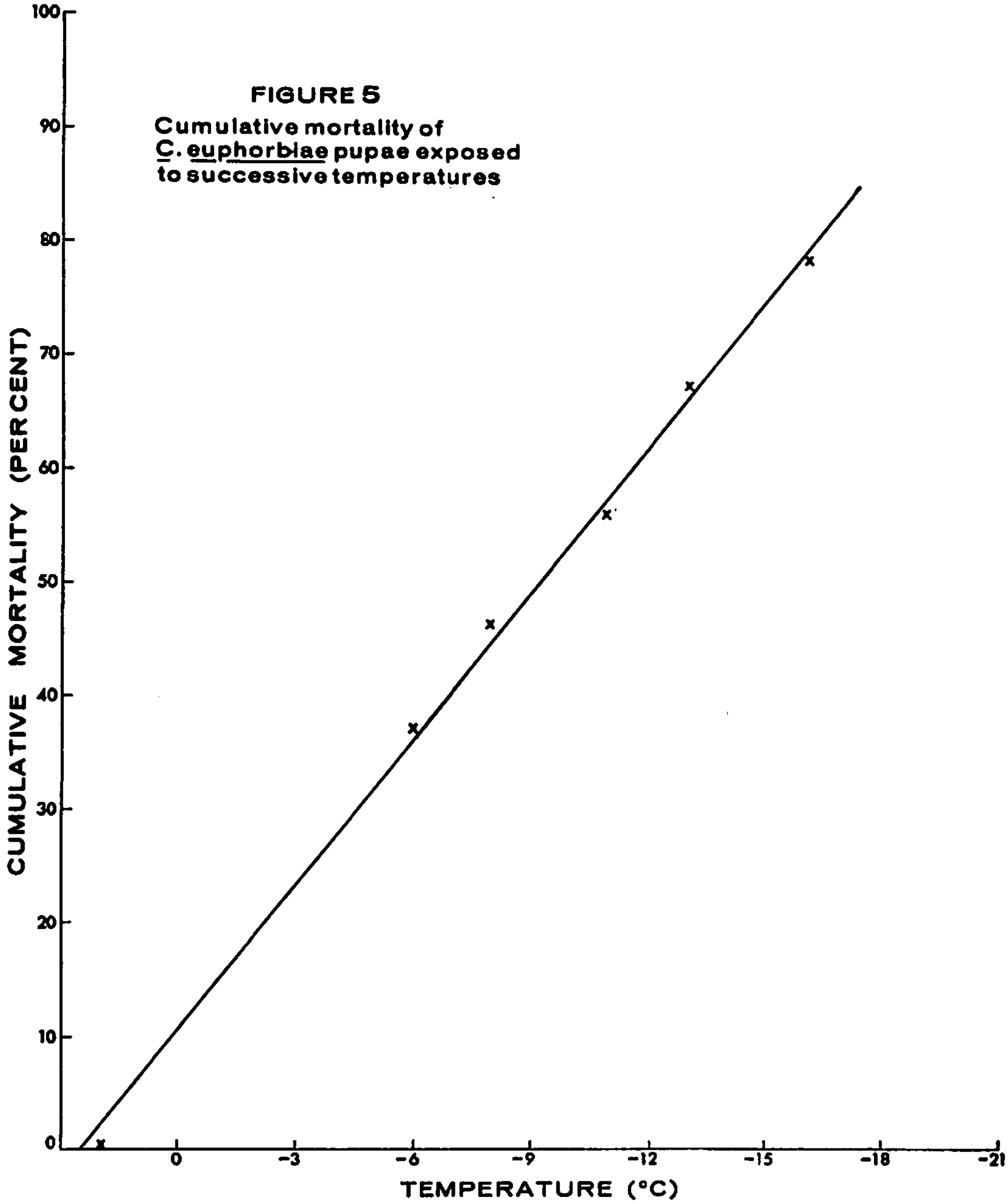

FIGURE 5
Cumulative mortality of *C. euphorbiae* pupae exposed to successive temperatures

were seen taking larvae: the spider *Xysticus emertoni* Key., the wasp *Polistes fuscatus pallipes* Lep., and in Saskatchewan the pentatomid *Apateticus bracteatus* Fitch. Following the release of *C. euphorbiae* larvae made radioactive with P^{32} four species of carabids (*Calosoma calidum* Fab., *Pterostichus melanarius* Ill., *Amara obesa* Say and *Calathus gregarius* Say) became radioactive as well as eight species of ants (*Myrmica americana* Web., *Lasius* sp., *Formica lasioides* Emery, *F. pallidefulva nitidiventris* Emery, *F. obscuripes* For., *F. haemorrhoidalis* Emery, *Campanotus herculeanus* (L.) and *Crematogaster lineolata* (Say)). The percentage of *C. euphorbiae* larvae disappearing over a four-day period at three places in Ontario varied directly with the number of ants caught in pitfall traps.

Hence, although the species of ants involved varied from place to place, it is concluded that ant density is one of the most important factors in determining whether *C. euphorbiae* can survive. The only place where they have done so—Braeside, Ontario—has a relatively low density of ants.

EVALUATION OF CONTROL ATTEMPTS

Climatically Canada appears to be suitable for *C. euphorbiae*: summer temperatures are high enough for larval development and winter temperatures are above the minimum tolerated by the pupae except perhaps in some regions on the prairies. That the moth has failed to become established in most places where it was released is the result of high larval mortality. Larval mortality was especially high immediately after release. This may have been partly caused by failure of the larvae to cling to the foliage: but predation by ants seems to be the major single factor causing mortality. Most stands of spurge in Canada occur on sites (well drained, sandy soil) on which ants are numerous; but the presence of spurge may encourage them further by providing an abundant source of nectar. Except for Braeside which is on a heavier, damper soil than are most spurge stands, there seems to be little chance of finding stands without many ants.

The recovery of 68 nearly mature *C. euphorbiae* larvae at Braeside in 1968 suggests that the species may be established there. It is proposed to propagate these survivors in the laboratory in the early spring to complete a generation before field emergence. The progeny will then be released at Braeside again. Hopefully the pre-adaptation of this stock to the region will increase larval survival over previous years. It is felt that the size of the spurge stand at Braeside and the public interest in its control justify these additional releases. Also the effectiveness of this technique is of interest for other biological control attempts.

Since *C. euphorbiae* appears to have little value as a biological control agent in most of Canada, alternative *Euphorbia* insects should be sought. The root borers, *Oberea euphorbiae* Germ. (Buprestidae) and *Chamaesphecia empiformis* Esp. (Aegeriidae) are probably the most promising candidates because they are not likely to be found by ants and most other predators. *C. empiformis* is probably the more host-specific of the two insects. Its larvae cause a progressive weakening of the host over a year. If this damage reduces the capacity of the plant to regenerate, it could be more effective than the dramatic defoliation caused by *C. euphorbiae.*

RECOMMENDATIONS

(1) To suspend releases of *Celerio euphorbiae* except at Braeside, Ontario.

(2) To resume releases of *Celerio euphorbiae* in other areas using Braeside stock after it has undergone a period of adaptation.

(3) To continue studies on *Chamaesphecia empiformis* with the object of releasing it in Canada.

ACKNOWLEDGMENTS

We thank Mr. K. Bertrim of the Research Institute, Belleville for rearing the large number of *C. euphorbiae* used and for making survival counts on the ones released in Ontario; and Messrs. D. Arnott, J. Awmack and A. Kolach for the releases at Kamloops, and Invermere, British Columbia, and in Manitoba respectively.

TABLE XVIII

Open releases and recoveries of *Celerio euphorbiae* (L.) against *Euphorbia* spp.[1] in Canada

Weed	Province	Year	Number[2]	Year of recovery
Euphorbia cyparissias L.	Ontario	1965	206	—
		1966	5246	—
		1967	13680	1968
		1968	4366	—
Euphorbia esula L.	Ontario	1967	825	—
	Manitoba	1966	578	—
		1967	3700	—
	Saskatchewan	1965	1980	—
		1966	1200	—
		1967	5241	—
	British Columbia	1966	300	—
		1967	4900	—

[1] All material of *C. euphorbiae* originated from laboratory culture of European stock.
[2] All larvae.

LITERATURE CITED

1. Bachmetjew, P. (1901). Experimentelle entomologische Studien vom physikalisch-chemischen Standpunkt aus. Band I. Engelmann, Leipzig.
2. Canada Department of Transport. (1960–1968). Monthly Record. Meteorological observations in Canada. Canada Dep. Transport, Toronto.
3. Harris, P. Unpublished observations.
4. Kingsbury, J. M. (1964). Poisonous plants of the United States and Canada. Prentice-Hall, Englewood Cliffs, N. J.
5. Meyrick, E. (1928). A revised handbook of British Lepidoptera. Watkins and Doncaster, London.
6. Moore, R. J. (1958). Cytotaxonomy of *Euphorbia esula* in Canada and its hybrid with *Euphorbia cyparissias*. *Can. J. Bot.* 36: 547–59.
7. Moore, R. J. & Lindsay, D. R. (1953). Fertility and polyploidy of *Euphorbia cyparissias* in Canada. *Can. J. Bot.* 31: 152–63.
8. Moscardini, C. (1947). Osservazioni morfologico-biologiche su *Deilephila euphorbiae* L. *Atti Soc. Nat. Mat.* 78: 210–13.
9. National Weed Committee. (1968). Report of the Research Appraisal Committee for Western Canada, 65 pp.
10. Salt, R. W. (1936). Studies on the freezing process in insects. *Bull. Minn. agric. Exp. Stn* 116, 41 pp.
11. Selleck, G. W., Coupland, R. T. and Frankton, C. (1962). Leafy spurge in Saskatchewan. *Ecol. Monogr.* 32: 1–29.
12. Wilkinson, A. T. S. (1965). Release of cinnabar moth, *Hypocrita jacobaeae* (L.) (Lepidoptera: Arctiidae) on tansy ragwort in British Columbia. *Proc. ent. Soc. Brit. Columb.* 62: 10–13.
13. Williamson, G. D. (1965). Summary of parasite and predator liberations in Canada and of insect shipments from Canada in 1965. *Can. Insect Pest Rev.* 43: 127–39.
14. Williamson, G. D. (1967). Summary of parasite and predator liberations in Canada and of insect shipments from Canada in 1966. *Can. Dep. Agric. Research Institute, Belleville, Ont.* 13 pp.
15. Williamson, G. D. (1968). Insect liberations in Canada; parasites and predators, 1967. *Can. Dep. Agric. Research Institute, Belleville, Ont.* 18 pp.
16. Wittstadt, H. (1966). Wanderfalterbericht für das Jahr 1965. *Ent. Z.* 76: 241–3.

32. *HYPERICUM PERFORATUM* L., ST. JOHN'S WORT (HYPERICACEAE)

P. Harris and D. P. Peschken

PEST STATUS

Hypericum perforatum L. is a perennial of Eurasian origin that has become a troublesome range weed in Australia, the western United States and other places where it has suppressed forage species. It causes loss of weight, thrift and even death when eaten by livestock, although it is usually avoided by them unless forage is scarce (16). Hence the appearance in the early 1940's of small but dense and rapidly spreading stands of *H. perforatum* in interior British Columbia was viewed with alarm. Vigorous attempts to eradicate the weed with chemicals failed: the stands required repeated treatment as the seeds germinated, and the cost was high because of poor accessibility and the number of patches involved.

H. perforatum also occurs in central Ontario where it has a frequency of 32·5 per cent. in check-point lists compared with only 2·3 per cent. in British Columbia (5), but it is a less serious problem because dense stands only form on gravelly or sandy soils. It is prevalent in the Maritime Provinces (frequently 26·7 per cent.) where its continuing spread is of concern. The weed is absent from the prairies except for a small patch at Winnipeg, Manitoba.

BACKGROUND

Biological control of *H. perforatum* was pioneered in Australia (3) and has since been used with varying success in at least six regions of the world. In Australia, it was most successful on potentially good quality, open grazing land, although it was often necessary to supplement it with pasture improvement practices to achieve control. It was least successful on barren rocky ground, where there was little competition from other plants, and in shade (24). The reliability and rapidity of biological control of the weed decreased as the summer rainfall increased (11). On the other hand, in California, biological control rapidly reduced the weed, and has kept it well below the economic threshold without the aid of pasture improvement practices.

The basis for the choice of the insects introduced against *H. perforatum* in both Australia and California was a study of its insect enemies in the south of France, and to a lesser extent of Britain (23). Nelson (18) investigated several insects attacking the weed in Germany and, on the behalf of Canada, Johansson (13, 14) made a detailed study of its Swedish fauna. These and other less comprehensive studies show that the weed is attacked by a large complex of oligophagous insects with individual species tending to be restricted to a small part of its geographical or ecological range. It is likely that the known complex would be still larger if detailed surveys on the weed were extended to the parts of its native range outside western Europe. Geographically the weed is native to Europe (where it occurs as far north as the boundary of mixed deciduous forests (13)), north Africa and large parts of Asia, including northern India, China and Japan. Ecologically it ranges from open to partly shaded sites, from small pockets of humus on rock to steppe grassland, moist meadows and woodlands. It avoids wet or boggy soil and dense shade.

RELEASES AND RECOVERIES

Most of the insects introduced against *H. perforatum* were released in the early 1950's which is prior to the period covered by this review, and so this aspect of the project is not covered in detail. Instead, emphasis is placed on the reasons for the success or failure of the various insects in controlling the weed. All aspects of the project are described and discussed in more detail by Harris, Peschken and Milroy (7).

Zeuxidiplosis giardi Kieff. (Diptera: Cecidomyiidae)

ECOLOGY. *Z. giardi* forms leaf galls on *Hypericum* in southern and central Europe including Britain. Wilson (23) suggested that its range is limited by winter kill of its host-plant foilage and that even in southern France loss from this cause is severe.

RELEASES. *Z. giardi* is established in both Australia (24) and California (9) but is ineffectual in controlling H. *perforatum*. The midge was released in Hawaii in 1965 and shows promise (4). It was introduced into British Columbia at two places in 1955 by transplanting infested plants, and became abundant during the summer of its release; but it did not survive the first winter (21).

Agrilus hyperici (G.) (Coleoptera: Buprestidae)

ECOLOGY. *A. hyperici* is found in the drier regions of southern, central and eastern Europe, but is only numerous in the south of its range (23). The larvae bore into the root crown of *H. perforatum*, destroying or weakening the plant.

RELEASES. The beetle is established in Australia (24) and in California, where it showed excellent ability to destroy the weed until displaced by *Chrysolina quadrigemina* Suffr. (8). Adult *A. hyperici* from California were released in early summer in British Columbia at two sites in 1955 but did not survive. Another release was made in the summer of 1964 (Table XIX) and larvae were found mining the root crowns in the fall, but no survivors were found the following year. Wilson (23) mentioned that larvae are prone to fungal attack in damp sites, and this may have contributed to their failure in British Columbia.

Chrysolina varians (Schall.) (Coleoptera: Chrysomelidae)

ECOLOGY. *C. varians* is common in northern and alpine regions of Europe where the summers are moist and there is a good snow cover if winters are rigorous (13). Panin (19) correlated its occurrence in Rumania with a value of 35–45 on Martonne's aridity index.[1] Both adults and larvae feed on the foliage, and breeding continues through the summer with several generations a year (13) which explains its absence from places where the *Hypericum* foliage dries up in summer. Kanervo (15) considered that the principal host in Finland was *H. maculatum Cr.* which, unlike *H. perforatum*, always grows on wet ground; but in Sweden Johansson (13) found it most abundant on *H. perforatum* growing in moist places along forest edges and in bushy sites.

RELEASES. *C. varians* was released in Australia (24) and in California and Idaho (8) but failed to survive. In British Columbia 250 beetles were released in 1957 in a park-like stand of ponderosa pine (*Pinus ponderosa* Laws.) with an aridity index of about 17. This site was clearly too dry for the beetle and no survivors were found in the following years. A release of 500 beetles was made in 1958 in an area supporting a fairly dense stand of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) that had an aridity index of about 35, which is the lower limit for the beetle in Rumania. A few survivors were found in 1959 but none subsequently.

Chrysolina hyperici (Först.) (Coleoptera: Chrysomelidae)

ECOLOGY. *C. hyperici* is predominant in the Atlantic region of Europe. Its range extends into Scandinavia where it is largely confined to the coast (13). Panin (19) correlated its occurrence in Rumania with an aridity index of 30–45, indicating that the species is more tolerant of dry conditions than is *C. varians*. The beetle lays during winter and early spring and the new adults appear about mid-summer. These feed for a short period and then aestivate until early winter. All stages, but particularly the adults and larvae, are killed by frost unless protected by snow or litter (1). The eggs are susceptible to desiccation and the larvae cannot pupate in dry hard soil (12). Aestivation is not

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[1] Aridity index $= \frac{\text{Average annual precipitation in mm}}{\text{Average annual temperature in °C} + 10}$

terminated until the adults have been exposed to moist conditions for several months; thus in California oviposition does not reach its peak until February or March, which is too late for the brood to complete development before the summer drought (12). Hence the beetle is absent from sites with early summer droughts.

RELEASES. *C. hyperici* was introduced against *H. perforatum* in Australia (24), New Zealand (10) and western United States (8). In both Australia and the United States this beetle was less effective than *C. quadrigemina*. However, in New Zealand *C. hyperici* controlled the weed in one area whereas *C. quadrigemina* failed to survive.

C. hyperici was released in British Columbia in 1952 and subsequently was distributed to many places in the southern interior of the Province. It is thriving in sites with an aridity index of 30–40 (characterized by vigorous stands of Douglas fir) and has reduced the weed to an acceptable level in these places. On drier sites, where ponderosa pine occurs, *C. hyperici* has been completely or partly replaced by *C. quadrigemina*.

Chrysolina quadrigemina (Suffr.) (Coleoptera: Chrysomelidae)

ECOLOGY. *C. quadrigemina* has a more southerly distribution than the other two species of *Chrysolina*: its range extends from north Africa to Denmark (but not the Swedish mainland) (13). It is more tolerant of dry conditions than is *C. hyperici*: it occurs in Rumania at an aridity index of 24–45 (19), and its eggs have a greater resistance to desiccation (1). *C. quadrigemina* is the *Hypericum*-feeding species of *Chrysolina* pre-eminently adapted to a Mediterranean climate. It has one generation a year and an obligatory aestivation which it cannot enter in wet conditions (11). Aestivation is ended rapidly after the first autumn rains; then the beetles lay and the larvae develop on the basal winter foliage of *H. perforatum*. Feeding is completed before the foliage dries up in the summer drought. The species requires the protection of snow cover or litter in regions that have severe frosts.

RELEASES. The introduction of *C. quadrigemina* to the western United States has reduced the weed well below the economic threshold, and in Australia it has returned much good quality pasture to full production (11). In New Zealand the beetle failed to survive (10) and a release at 7,100 feet in Hawaii is not thriving (4). In British Columbia, *C. quadrigemina* was originally released in 1952 (21) and subsequently beetles were distributed to many places in the interior of the Province. The beetle has reduced *H. perforatum* to an acceptable level or is extensively damaging it in sites with an aridity index of 24–30. These sites are characterized by the presence of ponderosa pine, either in pure stands or mixed with Douglas fir. The beetle is present but not controlling the weed in the grassland sites where the aridity index is 17–24, and has died out, or survived in low numbers, in areas with an index above 30.

Anaitis plagiata (L.) (Lepidoptera: Geometridae)

ECOLOGY. *A. plagiata* occurs in dry areas, such as rocky ground, open sandy places and limestone regions, from central France to the northern limit of *H. perforatum* in Sweden (14). It is bivoltine and overwinters as a larva. The early-spring feeding and the ability of the larva to withstand both high and low temperatures in dry places makes it an attractive insect for biological control of *H. perforatum* in the Kettle valley of British Columbia (6).

RELEASES. Attempts to establish *A. plagiata* failed in Australia where predators, particularly ants, were incriminated (24). Harris (6) suggested that a virus disease imported with the larvae also contributed to this failure. To eliminate virus from the stock before liberation in British Columbia, the larvae were reared individually for two generations. The laboratory colony (then apparently healthy) was released at three places in the Kettle valley in the spring of 1967 (Table XIX). The release sites were visited the same year, two or more weeks later, to check on survival. Several full-grown larvae were recovered on one site and some feeding damage characteristic of *A. plagiata* was seen on the second site. On a third site *C. quadrigemina* had defoliated the *H. perforatum*. No *A. plagiata* or signs of feeding were found in 1968, although small colonies may have been overlooked because larvae are difficult to see and often hide in the duff during the day.

EVALUATION OF CONTROL ATTEMPTS

Intense competition between sympatric insect species should either eliminate the poorer competitor or reduce competition by divergent specialization. This may involve the evolution of different host preferences within the ancestral host range or the acceptance of new hosts. Alternatively, the competing species may retain their ancestral host range and specialize by evolving different ecological tolerances. Both processes appear to have occurred in the five European species of *Chrysolina* specialized on the genus *Hypericum*. *C. brunsvicensis* Grav. selects the species containing hypericin (20). On the other hand *C. quadrigemina*, *C. hyperici* and *C. varians* did not distinguish between species of *Hypericum* in laboratory tests (21) although they are adapted to different moisture zones. Panin (19) related their occurrence in Rumania to values of Martonne's aridity index. The overlap of the three species he found at high index values almost certainly arises because Martonne's index does not distinguish between summer and winter precipitation whereas the *Chrysolina* spp. are largely influenced by the mositure supply during the growing season. Thornthwaite's (22) moisture index avoids this difficulty by taking into account the monthly supply and demand for moisture. The application of this index to the British Columbia release sites shows that *C. quadrigemina* thrives in a dry subhumid climate (index minus 10–0) and *C. hyperici* in a moist subhumid climate (index 0–20), and that *C. varians* would probably succeed in a humid climate (index 20–40). These climatic types are reflected by the forest composition (17). Thus the presence of ponderosa pine, Douglas fir without ponderosa pine, or western red cedar indicates a site suitable for *C. quadrigemina*, *C. hyperici* or *C. varians* respectively. The existence of sympatric insects with a similar host range is an indication that the species have narrow ecological tolerances. Much time and energy can be saved by determining these before introductions are made.

The time taken for *C. quadrigemina* or *C. hyperici* to achieve control of the weed has differed in different regions of the world, apparently having depended on the extent to which they were preadapted to the region. Thus in the Mediterranean-like climate of California *C. quadrigemina* was a rapid success whereas *C. hyperici*, which has more Atlantic requirements, failed to increase. These and similar results led Clausen (2) to postulate that a biological control agent would show evidence of success within three generations or not at all. However, his postulate does not fit the results in other parts of the world. In Australia the numbers of both beetles dropped to such low densities that specimens could not be found for several years (24); yet eventually they were successful. In British Columbia it has taken the various releases 5–13 years to show success in the form of a population build-up (7). The reason for this delay would seem to be that the interior of the Province is neither Mediterranean nor Atlantic in climate, but on release both beetles behaved as if they were in their original biotopes: both species starting to lay in the fall or early winter. The larvae were not able to develop in the winter and they as well as the ovipositing adults suffered a heavy mortality. The eventual success of the beetles indicates that they have adapted to local conditions. It is suggested that *inter alia* this may involve an increase in the threshold temperature at which the adults seek shelter in the litter. This would tend to delay oviposition until spring and make the adults less vulnerable to frost. It is likely that the average time for a biological control agent to succeed is least in the tropics and progressively greater at higher latitudes. If Clausen's postulate has merit, then the criterion of three generations should be increased to five or even eight generations in Canada.

RECOMMENDATIONS

(1) The susceptibility of *Zeuxidiplosis giardi* to winter kill and its ineffectiveness in both Australia and California indicate that no further attempts should be made to establish it in British Columbia.

(2) The distribution of *Agrilus hyperici* in Europe indicates that it should not only survive in British Columbia, but also help to control the weed on dry sites. If another attempt is made to introduce this species, the stock should be obtained from eastern Austria or other areas climatically similar to interior British Columbia.

(3) Further releases of *Chrysolina varians* should not be made unless it is desired to control the weed where the moisture index is over 20. This situation could arise if *H. perforatum* invades grazing lands in the north of the Province. The presence of western red cedar is probably a good indicator of the site conditions required by this species in southern British Columbia.

(4) *Chrysolina hyperici* should be used to control *H. perforatum* where the moisture index is between 0 and 20. The beetle's site requirements are approximately the same as those of Douglas fir.

(5) *Chrysolina quadrigemina* should be used to control the weed where the moisture index is between 0 and — 10. Optimum sites are characterized by vigorous ponderosa pine, and the beetle is ineffective at the dry end of the pine range.

(6) *Anaitis plagiata* appears suitable for controlling *H. perforatum* on sites with a moisture index below — 10; but it is not known whether the species is established.

(7) *Chrysolina hyperici* should be introduced to Nova Scotia to combat the increasing spread of *H. perforatum.*

TABLE XIX

Open releases and recoveries of insects against *Hypericum perforatum* L.

Species and Province	Year	Origin	Number	Year of recovery
Agrilus hyperici (Crotch)				
British Columbia	1964	California	156	Not recovered in 1965
Anaitis plagiata (L.)				
British Columbia	1967	Germany[1]	1375	Not recovered in 1968

[1] Laboratory culture.

LITERATURE CITED

1. Clarke, L. R. (1953). The ecology of *Chrysomela gemellata* Rossi and *C. hyperici* Forst. and their effect on St. John's Wort in the Bright District, Victoria. *Aust. J. Zool.* 1: 1–69.
2. Clausen, C. P. (1951). The time factor in biological control. *J. econ. Ent.* 44: 1–9.
3. Currie, G. A. & Garthside, S. (1932). The possibility of the entomological control of St. John's Wort in Australia—Progress report. *Pamph. Coun. Scient. ind. Res. Aust.* 29: 1–28.
4. Davis, C. J. & Krauss, N. L. H. (1966). Recent introductions for biological control in Hawaii. *Proc. Hawaii. ent. Soc.* 19: 201–7.
5. Groh, H. & Frankton, C. (1949). Canadian Weed Survey, Seventh Report 1948, including cumulative reports 1–7. *Can. Weed Surv.* Rep. 7: 1–144.
6. Harris, P. (1967). Suitability of *Anaitis plagiata* (Geometridae) for biocontrol of *Hypericum perforatum* in dry grassland of British Columbia. *Can. Ent.* 99: 1304–10.
7. Harris, P., Peschken, D. & Milroy, J. (1969). The status of biological control of the weed *Hypericum perforatum* in British Columbia. *Can. Ent.* 101: 1–15.
8. Holloway, J. K. (1964). Projects in biological control of weeds. *In* Biological control of insect pests and weeds, 650–70, ed. by P. DeBach. Chapman and Hall, London.
9. Holloway, J. K. & Huffaker, C. B. (1953). Establishment of a root borer and a gall fly for control of Klamath weed. *J. econ. Ent.* 46: 65–7.
10. Hoy, J. M. (1964). Present and future prospect for biological control of weeds. *N.Z. Sci. Rev.* 22: 17–19.
11. Huffaker, C. B. (1967). A comparison of the status of biological control of St. John's Wort in California and Australia. *Mushi* 39: 51–73.
12. Huffaker, C. B. & Kennett, C. E. (1952). Ecological tests on *Chrysolina gemellata* (Rossi.) and *C. hyperici* Forst. in the biological control of Klamath weed. *J. econ. Ent.* 45: 1061–4.
13. Johansson, S. (1962). Insects associated with *Hypericum* L. 1. Host plant and Coleoptera. *Opusc. ent.* 27: 128–46.
14. Johansson, S. (1962). Insects associated with *Hypericum* L. 2. Lepidoptera. Diptera, Hymenoptera, Homoptera and general remarks. *Opusc. ent.* 27: 175–92.
15. Kanervo, V. (1939). Übersicht über die Generationszahl einiger Chrysomeliden (Cole.) in Finnland sowie einige andere allgemeine biologische Beobachtungen. *Suom. Hyönt. Aikak.* 5: 140–64.

16. Kingsbury, J. M. (1964). Poisonous plants of the United States and Canada. Prentice-Hall, Englewood Cliffs, N.J. 626 pp.
17. Kirk, D. W. (1951). Moisture regions in the east Kootenay lowlands of British Columbia. *Scient. Agric.* **31**: 15–24.
18. Nelson, H. S. (1962). Untersuchungen zur biologischen Bekämpfung von *Hypericum perforatum* L. mit Hilfe von Insekten (*Chrysomela varians* Schall., Coleoptera, und *Semasia hypericana* Hb., Lepidoptera). *Z. angew. Ent.* **50**: 290–327.
19. Panin, S. (1944). Les Chrysomela de la Roumanie (Gen. *Chrysomela* (L.)). *Bull. Sect. scient. Acad. roum.* **26**: 601–25.
20. Schoonhoven, L. M. (1968). Chemosensory bases of host plant selection. *A. Rev. Ent.* **13**: 115–36.
21. Smith, J. M. (1958). Biological control of Klamath weed, *Hypericum perforatum* in British Columbia. *Proc. 10th int. Congr. Ent., Montreal* (1956), **4**: 561–65.
22. Thornthwaite, C. W. (1948). An approach toward a rational classification of climate. *Geogrl Rev.* **38**: 55–94.
23. Wilson, F. (1943). The entomological control of St. John's Wort (*Hypericum perforatum* L.) with particular reference to the insect enemies of the weed in southern France. *Bull. Coun. scient. ind. Res., Melb.* **169**: 5–87.
24. Wilson, F. (1960). A review of the biological control of insects and weeds in Australia and Australian New Guinea. *Tech. Commun. Commonw. Inst. biol. Control.* **1**, 102 pp.

33. *LINARIA VULGARIS* MILL., YELLOW TOADFLAX, AND *L. DALMATICA* (L.) MILL., BROAD-LEAVED TOADFLAX (SCROPHULARIACEAE)

P. Harris and A. C. Carder

PEST STATUS

Linaria vulgaris Mill. and *L. dalmatica* (L.) Mill. are perennial weeds of Eurasian origin that have become widely established in Canada. *L. vulgaris* is found in all the provinces, but although common it is of little consequence except on the prairies. This weed, first recorded in Saskatchewan in 1918, spread rapidly to infest 134,602 acres (86 per cent. under cultivation) by 1954 (5). A typical example of the rate of spread between 1952 and 1954 is the increase of one infestation from 114 to 311 acres; seed production of *L. vulgaris* during this period was estimated to average 5,584 seeds per flowering stem (11). The situation changed when a beetle, *Brachypterolus pulicarius* (L.), which feeds on *Linaria* flowers, appeared on the prairies in large numbers in the late 1950's. Its attack reduced seed production by over 90 per cent. in 1958 (6) and probably was the main reason for the subsequent decline in the seriousness of the weed. For example, extensive *L. vulgaris* infestations near Regina in the mid-1950's were represented by only scattered plants ten years later. However, the distribution of the weed mapped by Alex (2) shows that it has been more persistent north of this area.

L. vulgaris was probably introduced into the Peace River area of Alberta in the mid- to late 1920's with alfalfa seed imported from the U.S.A. It was well established by late 1930's and spread rapidly to become an exceedingly serious grain and pasture weed by the late 1940's. In 1956 it infested 8,000 acres at Codessa and 8,900 acres at Berwyn. *B. pulicarius* was noticed at about the same time as it appeared in Saskatchewan. Subsequently the incidence and aggressiveness of the weed declined.

L. vulgaris can be controlled in pasture with 2,4-D at 2 lb per acre, particularly in bromegrass which is a stronger competitor than is creeping red fescue (4). This dosage cannot be used on cereal crops, but intensive summer fallow alternated with grain production usually controls the weed at an acceptable level.

L. dalmatica is less prevalent than *L. vulgaris* and although it occurs in at least six provinces of Canada (1), it is likely to become a serious problem only on the non-arable coarse textured soils of the prairies and the British Columbia dry belt. In these regions it tends to exclude other herbaceous vegetation, and hence causes loss of forage because cattle generally eat only the flower shoots.

BACKGROUND

No biological control attempts are known against the genus *Linaria* except for those in Canada and cognate attempts in the United States. Surveys of insects attacking *Linaria* in western Europe have been made by the Commonwealth Institute of Biological Control (12). Three insect genera that are particularly characteristic of *Linaria* are *Gymnaetron*, *Mecinus* (Coleoptera: Curculionidae) and *Calophasia* (Lepidoptera: Noctuidae). Malicky (9) discussed the geographical distribution of *Calophasia* spp. in relation to their climatic suitability as biological control agents in Canada. The most promising species appeared to be *C. lunula* Hufn. on which further investigations were made by Karny (8). Host-specificity studies on this species (7) showed that although the larvae would do at least some feeding on most plants in the tribe Antirrhineae (Scrophulariaceae), only a few species of *Linaria* (including *L. vulgaris* and *L. dalmatica*) were suitable as hosts. Investigations of European *Linaria* insects are also being sponsored by the United States Department of Agriculture.

Investigations by Smith (10) on the insect complex attacking *L. vulgaris* show two species of Coleoptera to be of particular interest in Canada: *Brachypterolus pulicarius* (L.) (Nitidulidae) and *Gymnaetron antirrhini* (Payk.) (Curculionidae). Both are monophagous *Linaria* insects of European origin that were unintentionally introduced to North America. The adult *B. pulicarius* emerges in the spring to feed on the young toadflax stems, causing stooling. Adults lay eggs in the flowers of both *L. vulgaris* and *L. dalmatica* on which the young larvae feed, chiefly on the anthers and ovaries, although the older larvae may also attack the maturing seeds in the capsules. In southern Ontario larval feeding is responsible for almost complete destruction of bloom in the early summer. By mid-August feeding is usually complete and the larvae descend to pupate in the soil. *B. pulicarius* was absent or rare on the prairies before 1950, but was present in large numbers by the end of the decade. During this period *L. vulgaris* seed production dropped by 90 per cent. in Saskatchewan, a condition for which this beetle is believed to be largely responsible. In contrast with its behaviour in Ontario, this beetle continues to feed on the flowers until freeze-up in Saskatchewan.

G. antirrhini adults also feed on the young toadflax shoots in the spring. They lay their eggs in the ovary of *L. vulgaris* during flowering and the larvae feed on the seeds inside the capsules which become swollen as a result of the attack. In Ontario, the destruction of flowers by *B. pulicarius* in the early summer means that few *G. antirrhini* larvae can be found until mid-August. They then become common, infesting a high proportion of the capsules. The weevil was first introduced on the prairies in 1957 with the release of 2,000 adults at Marsden, Saskatchewan and the same number at Codessa, Alberta. The hope was that its presence would further supplement the seed reduction resulting from *B. pulicarius*. It did not become established at Marsden, but did at Codessa where about three times as many flowers per stem escaped destruction by *B. pulicarius*. At Codessa it partly displaced *B. pulicarius* and to this extent did not have the additive effect that had been hoped for (6). By 1960 the weevil had spread at least 700 feet from the release point and by 1966 it was found 1¼ miles away.

RELEASES AND RECOVERIES

Calophasia lunula (Hufn.) (Lepidoptera: Noctuidae)

ECOLOGY. *C. lunula* occurs over all of central Europe as far north as Sweden and as far west as Britain; it is recorded from southern Russia, parts of south-central Asia and the Amur region on the Pacific (9). Except for its absence from regions with high rainfall or cool summers, its climatic tolerances are wide: winter temperatures acceptable to it may be as low as −40°C and summer temperatures as high as +40°C or more. The moth has one to three generations a year depending on the summer temperature and the length of the growing season. At Belleville, Ontario larvae are present in the field continuously from early June to the end of August. The eggs are laid singly on *Linaria* foliage and the newly hatched larvae feed preferentially on the flowers or, if these are not present, on the young foliage. Karny (8) calculated that during the course of its development a larva consumed the foliage from an average of 38·6 cm of *L. vulgaris* stem (range 24–61 cm). Larvae pupate in a cocoon composed of plant or soil debris, usually on the ground but sometimes attached to stems.

The stock of *C. lunula* imported from Europe contained two virus diseases: a cytoplasmic and a nuclear polyhedrosis. The nuclear virus was eliminated by rearing the larvae individually for three generations and destroying all siblings if any became diseased. The cytoplasmic virus was not eliminated by this procedure and has been found in the field population at Belleville, Ontario. Bucher and Harris (3) found that this virus, which attacks the cells of the midgut, produced a relatively benign infection with symptoms of malnutrition.

RELEASES. *C. lunula* were released, mostly as second-instar larvae, in five provinces of Canada from 1962–8 (Table XX). The only release followed in detail was that made at Belleville, Ontario in 1962. Two hundred and eighty second-instar larvae were released on 1 June; over the subsequent two weeks the population declined to 148 fifth-instar larvae which were mostly ready to pupate within a week. There was a partial second generation of which 229 larvae were counted on 14 August. The following year (1963) fewer than 30 larvae were found in either of the generations and no larvae were found in 1964.

The next attempt (Ontario in 1965) was made with a much larger release and the small number of progeny the following year was supplemented by an additional release. Larvae were found 250 yards downwind from the release site in 1966 and two miles away in 1968. On 24 June there was a density of 3·4 larvae per 100 *L. vulgaris* stems and by 8 August this had risen to 5·2. At this density small patches of toadflax stems were stripped.

The 1965 release at Codessa, Alberta was made at the end of the summer and the larvae were probably killed by frost shortly after release. A further release was made in the early summer of 1967 but with no recovery in the subsequent year. The 1965 release in British Columbia (at Rock Creek on *L. dalmatica*) was in an area grazed by cattle; in later years it was noticed that cattle were eating the flowering shoots. This habit would destroy any larvae feeding there and might have prevented establishment of the moth. The 1968 release in British Columbia was made to test the ability of the species to overwinter at Kamloops. Its failure was probably due to heavy contamination of the release stock with cytoplasmic virus rather than to climatic conditions.

EVALUATION OF CONTROL ATTEMPTS

L. vulgaris, and to a lesser extent *L. dalmatica*, are adequately endowed in Canada with insects that directly reduce seed production (*B. pulicarius* and *G. antirrhini*) but lack species that damage other parts of the plant. *C. lunula*, a foliage feeder, could correct this deficiency and increase the ecological pressures on the weeds. So far the moth is established only at Belleville, Ontario. The demise of the first colony released and some of the others probably occurred because there were too few individuals released to allow for a heavy selection mortality during the first year. With a larger initial release and supplementation of the survivors with laboratory stock, *C. lunula* became established and has shown some ability to damage *L. vulgaris* in the field. If there is sufficient interest, the moth can undoubtedly be established in other areas of Canada.

RECOMMENDATIONS

(1) The establishment of *Calophasia lunula* at Belleville indicates that the species can survive in Canada. Its establishment in other parts of the country would increase the amount of insect damage done to *Linaria vulgaris* and *L. dalmatica* and hence reduce the competitive ability of these weeds. However, further releases are not recommended unless they can be closely monitored.

(2) The threat of *L. dalmatica* spread in the dry belt of British Columbia probably justifies greater efforts to establish the moth there.

(3) No studies should be made on additional *Linaria* biocontrol agents unless justified by a re-evaluation of this weed's pest status.

TABLE XX

Open releases and recoveries of insects against *Linaria vulgaris* Mill. and L. *dalmatica* L.

Species and Province	Year	Origin[1]	Number	Year of recovery
Calophasia lunula Hufnagel				
Ontario	1962	Europe	280	—
	1965	Europe	1535	1966–8
	1966	Europe	1109	—
	1967	Europe	100	—
Manitoba	1967	Europe	210	—
Saskatchewan	1965	Europe	690	—
Alberta	1965	Europe	580	—
	1967	Europe	1105	—
British Columbia	1963	Europe	95	—
	1965	Europe	1250	—
	1968	Europe (*via* Ontario)	201	—

[1] All European material came from laboratory culture.

LITERATURE CITED

1. Alex, J. F. (1962). The taxonomy, history, and distribution of *Linaria dalmatica*. *Can. J. Bot.* **40**: 295–307.
2. Alex, J. F. (1966). Survey of weeds of cultivated land in the prairie provinces. Can. Dep. Agric., Exp. Farm, Res. Br., Regina, Sask. (mimeographed).
3. Bucher, G. E. & Harris, P. (1968). Virus diseases and their interaction with food stress in *Calophasia lunula*. *J. Invert. Path.* **10**: 235–44.
4. Carder, A. C. (1963). Control of yellow toadflax (*Linaria vulgaris*) by grass competition plus 2,4–D. *Weeds* **11**: 13–4.
5. Coupland, R. T. (1955). The Saskatchewan weed survey. *Circ. Dep. Agric. Sask.* **35**: 1–14.
6. Harris, P. (1961). Control of toadflax by *Brachypterolus pulicarius* (L.) (Coleoptera: Nitidulidae) and *Gymnaetron antirrhini* (Payk.) (Coleoptera: Curculionidae) in Canada. *Can. Ent.* **93**: 977–81.
7. Harris, P. (1963). Host specificity of *Calophasia lunula* (Hufn.) (Lepidoptera: Noctuidae). *Can. Ent.* **95**: 101–5.
8. Karny, M. (1963). The possibilities of *Calophasia lunula* Hufn., (Lep.: Noctuidae) in the biological control of toadflax, *Linaria vulgaris* Mill. *Tech. Bull. Commonw. Inst. biol. Control* **3**: 1–26.
9. Malicky, H. (1967). Climatological and ecological aspects of the geographical distribution of the genus *Calophasia* Steph. (Lep., Noctuidae). *Tech. Bull. Commonw. Inst. biol. Control* **8**: 103–16.
10. Smith, J. M. (1959). Notes on insects, especially *Gymnaetron* spp. (Coleoptera: Curculionidae) associated with toadflax, *Linaria vulgaris* Mill. (Scrophulariaceae) in North America. *Can. Ent.* **91**: 116–21.
11. Zilke, S. & Coupland, R. T. (1954). Basic studies—*Linaria vulgaris*. *Res. Rep. natn. Weed Comm. west. Sect. Can.* 1954: 104–7 (processed).

34. *SENECIO JACOBAEA* L., TANSY RAGWORT (COMPOSITAE)

P. HARRIS, A. T. S. WILKINSON, M. E. NEARY and L. S. THOMPSON

PEST STATUS

Senecio jacobaea L. or tansy ragwort is a European biennial or short-lived perennial that has been introduced to North and South America, New Zealand, Australia and South Africa. According to Harper and Wood (12) its range in Europe has been extended by man's activities: it occurs from the Mediterranean to Denmark and south Sweden with scattered records as far north as 62° 30′ in Norway, and from Ireland in the west to Siberia in the east. The weed favours open, well-drained sites and avoids strongly acid soils. It will not stand cultivation or intense competition from other plants, but on poor or run-down pastures and undisturbed open ground it tends to be monopolistic.

In Canada, *S. jacobaea* is still restricted to coastal regions except for a small but persistent stand near Guelph, Ontario (11). On the east coast the weed was introduced into Nova Scotia probably at Pictou around 1850 (21) and is now widespread over the eastern part of the province and present as isolated stands in the remainder (Fig. 6). This distribution coincides with that of the heaviest snow cover, which suggests that the whole province is not equally vulnerable to the weed. On Prince Edward Island the weed was first recorded at Tignish in 1888 and now is found in all parts of the Island (5). In New Brunswick the main infestation is around the mouth of the Miramichi River, and in Quebec the only known infestation is by the York River in the Gaspé Peninsula. There are records of two minor infestations in Newfoundland. On the west coast there is an infestation of recent origin, on 25,000 acres at Abbotsford on the British Columbia mainland, and a more serious infestation near Nanaimo on Vancouver Island which probably dates from about 1913; in 1955 this was estimated to cover 40 square miles including Gabriola Island nearby. It is still spreading, particularly along the gaps in the forest growth provided by logging roads and hydroelectric easements (27).

The toxic alkaloids jacobine, jacodine and jaconine (20) make the weed a hazard to livestock whether they eat it fresh, in hay or in silage. Mature plants are usually avoided by cattle but young plants are often eaten with forage. This results in chronic, cumulative poisoning, leading to liver necrosis, vascular and neuromuscular damage and other effects. There may be a latent period of one to five months following a lethal dose before the poisoning is apparent but death often follows less than a week after the symptoms appear (19). There is evidence that the problem may be worsened by periods of drought, by scarcity of forage, and by mineral deficiency (24). Sheep are more tolerant of the poison than are cattle, and within limits can be used as a control agent for *S. jacobaea* since they readily acquire a taste for it (1).

Losses from the weed in Canada are hard to assess. A great deal of *Senecio* poisoning probably goes unrecognized because of the latent period involved (19) and because sublethal symptoms are almost unknown (12). Most of the cattle from the Nanaimo area are reported to have 'spotty livers' when slaughtered (26) and there has been mortality from the weed. The reductions in pasture yield by the weed are not large in British Columbia because most problem areas are on poor hillside pastures. On Gabriola Island a switch from cattle to sheep farming has largely eliminated the problem. Hence, the main importance of the infestations is that they are a nucleus from which the weed could spread to the whole southwestern part of the province.

By contrast, the weed is a serious problem in the Maritime Provinces. In Prince Edward Island, where it is increasing rapidly, it rates as one of the most important pasture weeds. It caused estimated losses in 1968 of 30–50 cattle in King's County (16) and 10–15 head in Queen's County (17). Pasture yields have been reduced by 50 per cent. or more in heavily infested fields, and hay is often abandoned after cutting when it contains too much weed to pick out by hand. The weed is also of major importance in Nova Scotia where it is spreading slowly. In a recent survey 22 of 61 farms reported losing cattle to it (24). It is less serious in New Brunswick, Quebec and Newfoundland, perhaps because of differences in climate and agriculture.

The difficulty of controlling *S. jacobaea* results partly from its ability to regenerate from the roots (12). It is susceptible to 2,4–D although two applications are usually required for control. This treatment is used in British Columbia but rarely in the Maritime Provinces, where herbicide use is limited by cost and made impractical by the rapid reinfestation of land with seed blown from neighbouring fields and headlands. The preferred control in both regions is to replace a degenerating pasture with a cultivated crop for two years, and then to establish a vigorous sward. Unfortunately this method is not applicable to stump pastures and waste areas.

BACKGROUND

The biological control of *S. jacobaea* was pioneered by Cameron's (3) investigation of the weed's insect enemies in Britain. His list of species has since been revised by Harper and Wood (12). Two of

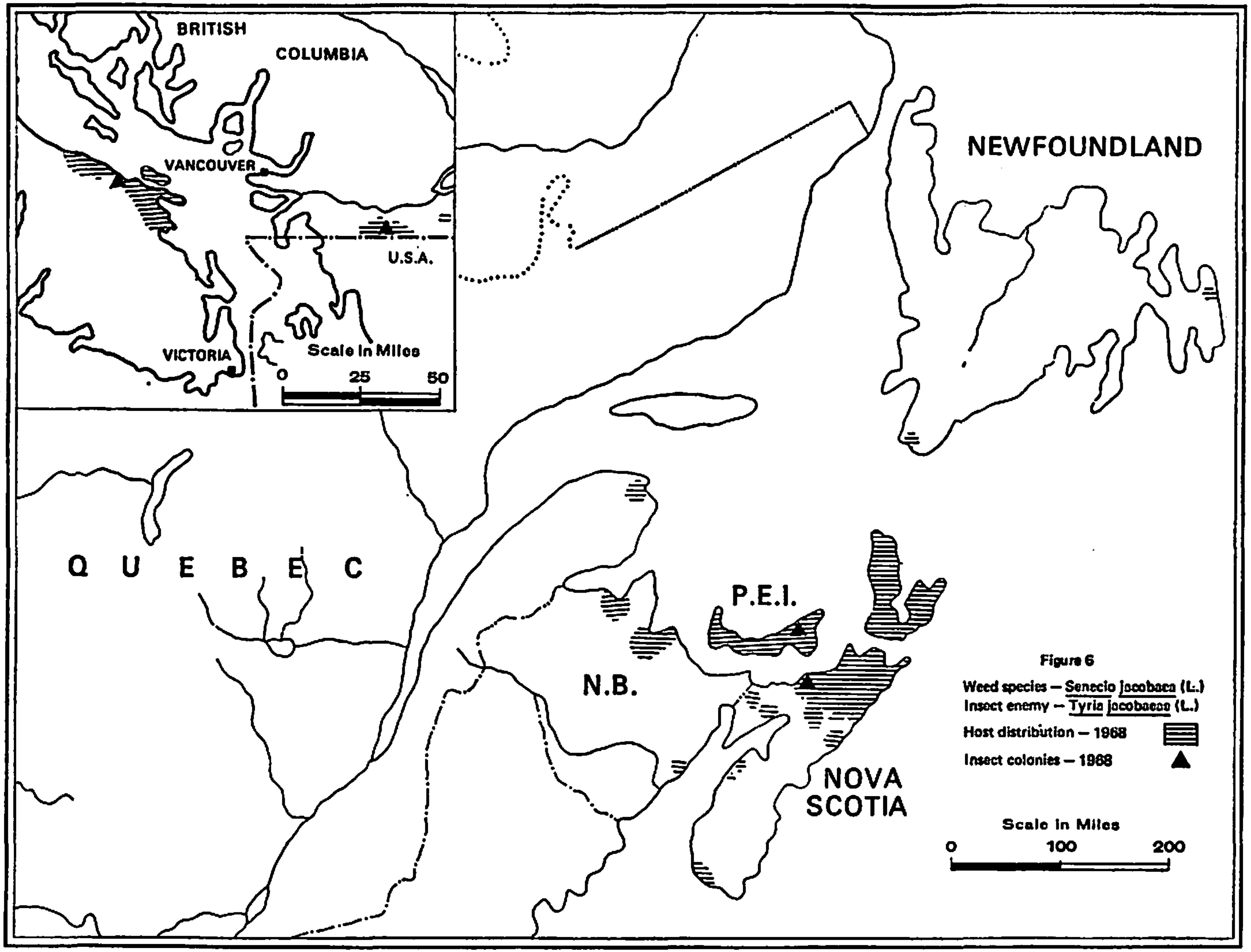

Figure 6

Weed species – *Senecio jacobaea* (L.)
Insect enemy – *Tyria jacobaeae* (L.)

these insects were introduced into New Zealand: *Tyria jacobaeae* L. (Arctiidae) the cinnabar moth, and *Hylemya seneciella* Meade (Muscidae), the ragwort seed fly. *T. jacobaeae* built-up to a high density in several places but eventually all the colonies died out for unknown reasons (1). When introduced, the stock was carrying a virus disease that made insectary rearing difficult (22), whereas larvae in the field were attacked by native parasites and birds (23). By contrast the seed fly survived and spread. In the growing seasons of 1949–50 and 1953–4 it attacked about 80 per cent. of the early and main crop of seed heads, which as a result did not produce viable seed, although it missed the late crop of flowers (18). In the 1958–9 season poor synchrony between the seed fly and the flowers greatly reduced the level of attack (14). Opinions differ as to the value of the fly as a control agent (15); enough seed is produced to perpetuate the weed as a problem, but presumably the fly makes it easier to control by conventional means.

The attempts at biological control in New Zealand were followed by unsuccessful attempts to establish *T. jacobaeae* in Australia. The reason for the failure given by Currie and Fife (4) was predation by a scorpion fly, *Harpobittacus nigriceps* Selys (Mecoptera), but the stock was known also to be diseased, since so-called 'bacterial wilt' frequently destroyed the insectary cultures. *H. seneciella* was not released because the fly would not oviposit in captivity (29). Another attempt to establish these two insects was started in 1955. This time *T. jacobaeae* survived in the field for five generations before succumbing to fungal infections; predation, chiefly by *H. nigriceps*; parasites; and a virus (1). No details are given for the effectiveness of *H. seneciella*, but on the basis of preliminary results Bornemissza (1) indicates that the species is unlikely to be of value as a control agent.

The cinnabar moth was first introduced into California in 1959 and then to other parts of the western United States (13). The initial results were disappointing: where the species survived, the number of larvae found the following year was only a small fraction of those liberated. The colonies maintained themselves for the next two years (10) and it was not until the fifth year that there was a marked increase in the population. The increase has since continued and the moth has spread and caused considerable defoliation of the weed. It is noteworthy that the United States populations are virus-free and have apparently adapted to the long growing season in California with an extended period of adult emergence. Moths are found there from about mid-April to the end of August (13), whereas in Britain the flight period is from mid-May to the end of June (3).

After host-specificity tests had been conducted, *H. seneciella* was introduced in 1967 into other parts of the western United States (8). Extensive feeding tests have been made with the ragwort flea beetle, *Longitarsus jacobaeae* Wat. (Chrysomelidae) as a preliminary to its release (9).

Endemic insect fauna of S. jacobaea

The commonest insect collected from *S. jacobaea* in Nova Scotia was the leaf roller, *Cnephasia virgaureana* Treit (Lepidoptera: Tortricidae), which in places had a density of about one per plant. The other tortricids found were *Archips purpuranus* Clem. and *Aphelia pallorana* Rob. The tarnished plant bug, *Lygus lineolaris* (Beauv.) and a spittle bug were also common. Three insects found on the weed in British Columbia were *Phragmatobia fuliginosa* L. (Lepidoptera: Arctiidae), *Aphis lugentis* Williams (Homoptera: Aphididae) and *Phytomyza atricornis* (Diptera: Agromyzidae) (28). All are polyphagous and some are minor agricultural pests. They should not interfere with the establishment of specialized *Senecio* insects. The lack of any endemic specialized insect on the weed in Canada is surprising since there are several native species of *Senecio* that might be expected to be a source. Frick (7) in a detailed survey of the weed in the western United States noted a similar absence of monophagous species.

RELEASES AND RECOVERIES

Tyria jacobaeae L. (Lepidoptera: Arctiidae)

ECOLOGY. The cinnabar moth is indigenous from the Mediterranean to Sweden and east- to west-central Asia. The insect is normally associated with *S. jacobaea* although feeding tests showed that closely related plants in the genera *Senecio* and *Erechtites* were suitable hosts. A small amount of feeding sometimes occurred on other genera in the same tribe (2, 25). The moth is univoltine, overwintering as a pupa under rocks or in soil debris to emerge in late spring. The female lays clusters of about 40 eggs on the underside of the foliage. On hatching larvae feed near the oviposition site and then move to the the top of the plant to feed on the young foliage or flowers if present. Later, the lower foliage and even the tender parts of the stem may be consumed. When the original plant is stripped, the larvae seek other *S. jacobaea* plants, including rosettes. The larvae and moths are distasteful to vertebrate predators (6) but are susceptible to attack by invertebrates (20).

The stock of *T. jacobaeae* imported into Canada carried two known diseases: a cytoplasmic polyhedrosis and a microsporidian (2). These were eliminated by rearing each larva individually for two generations and destroying the whole brood if any died from disease.

RELEASES. The first release was made in Cape Breton, Nova Scotia, with 114 mated females of Swedish origin (Table XXI). A survival count on 60 egg masses showed that 73 per cent. of the eggs disappeared during the night, presumably being taken by predators and most of the remainder were parasitized by a chalcid, *Telenomus* sp. Later, 500 third-instar larvae were released in the same field, but they did not become established.

The next releases were made at Abbotsford, British Columbia, in 1962; these have been reported by Wilkinson (28). He found that there was a loss of about 30 per cent. of the second- and third-instar larvae within two hours of their release but little subsequent mortality until the larvae descended to the ground to pupate, when they were attacked by carabid beetles. This was presumed to be the reason for the failure of establishment. A new release site was found at Nanaimo on Vancouver Island, where there was a lower density of carabids. In 1967 field-collected larvae from the successful Nanaimo colony and stock from Fort Bragg, California were released at Abbotsford. These resulted in a field colony of 900 larvae the following year, which was infested with a microsporidan disease. The disease may have been introduced with the Californian stock because it was not found in Nova Scotia where no Californian stock was liberated.

No attempt was made to assess mortality in the releases made after 1963 but the population trend was followed by annual counts of larvae. These showed that in British Columbia, Nova Scotia and Prince Edward Island there was heavy and sometimes complete mortality of the released stock during the first year. Where some individuals survived the colonies were supplemented with releases in the following years.

The establishment pattern of the moth is similar in the three provinces (Table XXI). There was high mortality of the laboratory-reared, European stock during the first year after release, approximate maintenance of the larval population in the following two years, and finally in the fourth and later years a four- to five-fold annual increase. In British Columbia, where the largest releases were made, half- to one-acre patches of the weed were defoliated by the larvae in the third year after release. Complete defoliation of the weed on 20 acres occurred in the fourth year and on 35 acres in the fifth year. The smaller releases in Nova Scotia follow the same pattern two years later. The colonies in Prince Edward Island are still in the early stages of establishment and their effect on the weed has yet to be determined.

Hylemya seneciella Meade (Diptera: Muscidae)

ECOLOGY. *H. seneciella* is a univoltine seed-fly found on *S. jacobaea* in western Europe. It emerges in the early summer to oviposit in the flower heads. The larvae feed on the immature seeds and basal parts of the flower, causing a characteristic dark centre (3). The use of the fly as a biological control agent in New Zealand and Australia and host-specificity studies made by Dr. K. Frick, United States Department of Agriculture, Albany, California were accepted as clearance for its use in Canada.

RELEASES. The stock released in Canada was supplied by the United States Department of Agriculture from collections made in Italy. The 2,000 puparia received were kept at 4°C. until July and then divided equally between British Columbia and Prince Edward Island. Emergence was poor: only 80 and 105 flies were obtained respectively (Table XXI). These were released as soon as possible;

holding them in the laboratory is reputed to reduce breeding success. It is doubtful if the flies became established in either Province because flowers with darkened centres were not seen. It is planned to make further releases when stocks become available, either from Europe or from colonies established in the western United States.

EVALUATION OF CONTROL ATTEMPTS

Attempts to establish *T. jacobaeae* in Canada and the United States were characterized by poor survival of the initial releases. A female lays 200–300 eggs (3) so that in theory the F_1 generation could have been produced by a single pair of moths. At least two pairs were involved at Durham, Nova Scotia, and at Nanaimo, British Columbia, since two age groups of larvae were found, but to judge from the few plants attacked, there probably were not many more. It is fairly certain that only a single pair bred in the first year at St. Charles, Prince Edward Island. Thus well under 1 per cent. of the released larvae survived to breed the following year and not surprisingly most of the releases made with less than 1,000 larvae failed to establish themselves. Percentage survival increased over the next three generations, presumably as poorly adapted individuals were eliminated. The population at Durham, Nova Scotia increased successfully from a nucleus of only a few hundred larvae. Therefore, provided preadapted stock is used, a release of 500 larvae should ensure survival. With preadapted stock, F_1 progeny were obtained at Salt Springs, Nova Scotia and Abbotsford, British Columbia, when much larger releases of laboratory stock failed. It follows that a biological control agent should not be written-off because it does not maintain itself in the first few generations. Provided there is some survival, the species may adapt. The chances of success can be increased by making the initial release in the most favourable site available or in the partial protection of a field cage.

It was noticed in British Columbia and Nova Scotia that the length of the oviposition period increased during the years of establishment. A natural consequence of a small population is that moths emerging early or late are unlikely to find mates. There may thus be a strong selection for synchronous emergence which becomes less severe as the population increases. Eventually, when the population has expanded to the limit of its food supplies and if the climate permits, there may even be selection for moths emerging early and late, whose progeny will have less competition for food than those produced in mid-season. This may explain the prolonged emergence now found in California. A similar occurrence in British Columbia should reduce the incidence of defoliated plants regenerating to produce seed. The oviposition period is likely to remain short in the Maritimes because the season is brief but this circumstance also gives the defoliated plants little time to regenerate.

The presence of a microsporidian disease in some Canadian colonies is unfortunate. However, at Fort Bragg, California, this rather benign disease has not prevented the moth from building up a high population and severely damaging the weed. Presumably the diseased populations will increase somewhat more slowly and may not attain such high densities as do disease-free populations, but whether this makes them less effective remains to be seen. Even disease-free cinnabar moths are unlikely to solve the weed problem completely. The moth prefers open sites and may be less effective in the shade. It may also be ineffective in some regions because of high predation or lack of pupation sites. These limitations may be overcome by establishing other insect species such as the seed fly, *Hylemya seneciella*, and the flea beetle, *Longitarsus jacobaeae*. Besides having a restricted host range, these attack different parts of the plant and so do not compete directly with *T. jacobaeae*.

RECOMMENDATIONS

(1) *Tyria jacobaeae* is well established in Canada and promises to be a valuable biological control agent for *Senecio jacobaea*. It is recommended that the moth should be distributed from existing colonies to all infestations of the weed.

(2) The presence of a microsporidian disease in some colonies has not prevented the moth

from spreading and increasing. Nevertheless the disease may reduce the effectiveness of the moth. We recommend that a comparative study be made of the degree of weed control obtained with diseased and healthy colonies as a guide to the value of excluding relatively benign diseases in future biological control attempts.

(3) Ecological restrictions on the moth in certain areas will probably prevent it from controlling *S. jacobaea*. The seed fly *Hylemya seneciella*, may supplement the damaging effects of the moth in these areas. We recommend that further attempts be made to establish it.

TABLE XXI

Open releases and recoveries of insects against *Senecio jacobaea* L.

Species and Province	Year	Origin	Number	Form	Year of recovery
Hylemya seneciella (Meade)					
Prince Edward Island	1968	Europe[2]	105	adults	—
British Columbia	1968	Europe[2]	80	adults	—
Tyria jacobaeae (Linnaeus)					
Prince Edward Island	1964	Switzerland[1]	211	larvae	—
	1965	Switzerland[1]	150	larvae	1966–8
	1966	California[2]	5700	larvae	—
			47	adults	—
	1967	California[2]	620	larvae	—
			154	adults	—
	1968	Nova Scotia[2]	1000	larvae	—
Nova Scotia	1961	Sweden[1]	500	larvae	—
			114	♀adults	—
	1963	Switzerland[1]	1633	larvae	1964–8
	1964	Nova Scotia[2]	650	larvae	—
	1965	Nova Scotia[2]	75	larvae	—
British Columbia	1962	Switzerland[1]	856	larvae	—
	1963	Switzerland[1]	5000	larvae	—
	1964	Switzerland[1]	2800	larvae	1965–8
	1965	Switzerland[1]	6800	larvae	—
	1966	British Columbia[2]	21285	larvae	—
	1967	British Columbia and California[2]	9700	larvae	—

[1] Laboratory culture.
[2] Field.

LITERATURE CITED

1. Bornemissza, G. F. (1966). An attempt to control ragwort in Australia with the cinnabar moth, *Callimorpha jacobaeae* (L.) (Arctiidae: Lepidoptera). *Aust. J. Zool.* **14**: 201–43.
2. Bucher, G. E. & Harris, P. (1961). Food-plant spectrum and elimination of disease of cinnabar moth larvae, *Hypocrita jacobaeae* (L.) (Lepidoptera: Arctiidae). *Can. Ent.* **93**: 931–6.
3. Cameron, E. (1935). A study of the natural control of ragwort (*Senecio jacobaea* L.). *J. Ecol.* **23**: 265–322.
4. Currie, G. A. & Fyfe, R. V. (1938). The fate of certain European insects introduced into Australia for the control of weeds. *J. Coun. scient. ind. Res. Aust.* **11**: 289–301.
5. Erskine, D. S. (1960). The plants of Prince Edward Island. *Canada Dep. Agric. Publ.* **1088**, 272 pp.
6. Frazer, J. F. D. & Rothschild, M. (1962). Defence mechanisms in warningly-coloured; moths and other insects. *Proc. 11th int. Congr. Ent., Vienna* (1960) **3**: 249–55.
7. Frick, K. E. (1964). Some endemic insects that feed upon introduced tansy ragwort (*Senecio jacobaea*) in western United States. *Ann. ent. Soc. Am.* **57**: 707–10.
8. Frick, K. E. (1969). Attempt to establish the ragwort seed fly in the United States. *J. econ. Ent.* **62**: 1135–8.
9. Frick, K. E. (1970). *Longitarsus jacobaeae* (Coleoptera: Chrysomelidae), a flea beetle for the biological control of tansy ragwort. 1. Host plant specificity studies. *Ann. ent. Soc. Amer.* **63**: 284–96.
10. Frick, K. E. & Holloway, J. K. (1964). Establishment of the cinnabar moth *Tyria jacobaeae* on tansy ragwort in the western United States. *J. econ. Ent.* **57**: 152–4.
11. Groh, H. (1946). Canadian weed survey, third annual report, 1944. *Rep. Dep. Agric. Can.* **3**, 70 pp.
12. Harper, J. L. & Wood, W. A. (1957). Biological flora of the British Isles. *Senecio jacobaea* L. *J. Ecol.* **45**: 617–37.
13. Hawkes, B. H. (1968). The cinnabar moth, *Tyria jacobaea*, for control of tansy ragwort. *J. econ. Ent.* **61**: 499–501.

14. Hoy, J. M. (1958). The collection of *Hylemyia seneciella* (Meade) (Diptera: Muscidae) for shipment to Australia. *N.Z. Jl Sci.* 1: 417–22.
15. Hoy, J. M. (1964). Present and future prospects for biological control of weeds. *N.Z. Sci. Rev.* 22: 17–9.
16. Ings, A. E. (1969). *In litt.* Montague, King's County, Prince Edward Island.
17. Kelly, H. H. (1969). *In litt.* Director of Veterinary Services, P.E.I. Department of Agriculture, Box 2000, Charlottetown, Prince Edward Island.
18. Kelsey, J. M. (1955). Ragwort seed-fly establishment in New Zealand. *N.Z. Jl Sci. Technol.* 18: 762–7.
19. Kingsbury, J. M. (1964). Poisonous plants of the United States and Canada. Prentice-Hall, Englewood Cliffs, N.J.
20. Leonard, N. J. (1950). *Senecio* alkaloids. *In* The alkaloids, chemistry and physiology, 107–64, ed. by R. H. F. Manske, & H. L. Holmes. Academic Press, New York.
21. MacKay, A. H. (1915). In *Senecio jacobaea* and *Callimorpha jacobaeae* (the cattle killing ragwort and the cinnabar moth) by Henry S. Poole. *Proc. Trans. Nova Scotian Inst. Sci.* 13: 279–88.
22. Miller, D. (1929). Control of ragwort: experimental work with cinnabar moth. *N.Z. Jl Sci. Technol.* 11: 112–9.
23. Miller, D. (1936). Control of weeds by means of insects. Ragwort, piri-piri and gorse. *Bull. Cawthron Inst. Scient. Res. Chem. Dep.* 23, 3 pp.
24. Palfrey, G. D., MacLean, K. S. & Langille, W. M. (1967). Correlation between incidence of ragwort (*Senecio jacobaea* L.) poisoning and lack of mineral in cattle. *Weed Res.* 7: 171–5.
25. Parker, H. L. (1960). Starvation tests with larvae of the cinnabar moth. *J. econ. Ent.* 53: 472–3.
26. Putman, N. (1969). *In litt.* Field Crops Commissioner, British Columbia Department of Agriculture, Victoria, British Columbia.
27. Renney, A. J. (1955). Tansy ragwort (*Senecio jacobaea* L.) in British Columbia. *Res. Rep. natn. Weed Comm. west Sect. Can.* 1955: 125.
28. Wilkinson, A. T. S. (1965). Release of cinnabar moth, *Hypocrita jacobaeae* (L.) (Lepidoptera: Arctiidae) on tansy ragwort in British Columbia. *Proc. ent. Soc. Brit. Columb.* 62: 10–3.
29. Wilson, F. (1960). A review of the biological control of insects and weeds in Australia and Australian New Guinea. *Tech. Commun. Commonw. Inst. biol. Control* 1, 102 pp.

PART III

BIOLOGICAL CONTROL OF FOREST INSECT PESTS IN CANADA, 1959—1968

35. CURRENT APPROACH TO BIOLOGICAL CONTROL OF FOREST INSECTS

W. A. REEKS and J. M. CAMERON

It is over a decade since McGugan and Coppel (10) reviewed half a century of progress in the biological control of forest insects in Canada. These authors recognized that some of their comments and conclusions would require modification with the passing of time. They forecast supplements that would provide information on future projects and would reappraise the long-term effects of past releases. This review is the first supplement as envisaged by McGugan and Coppel.

Balch (1) observed that the term 'biological control' is sometimes used very broadly to cover all methods of encouraging the action of biotic factors. In this discussion, as in the earlier one (10), the term is used with reference to the introduction of parasites, predators, or pathogens against accidentally introduced insects and, in a few instances, against native ones. The term 'control' (19), often causes confusion because of two commonly accepted definitions. One relates to the process that determines the amplitude of populations, and the other to acceptable economic damage. We feel that economic control is achieved when insect populations are reduced to the point where further reduction would cost more than the additional benefits gained, a concept in which several benefits looked for in current control attempts are implicit. Among these benefits are prevention of loss of wood volume, prevention of reduction of wood quality, protection of foliage for aesthetic reasons, and improvement of operational techniques.

The scope of recent biological control attempts has been somewhat narrower than that for the period 1910 to 1958 (10). All control operations reported herein were directed against 12 of the 36 pests discussed earlier. The present review provides new information on control attempts involving the 12 target species and reports on 27 additional taxonomic entities brought to Canada since 1958 to combat four of the pests or to make preliminary tests in cages. Excluded from the review are a number of pests for which no information has accrued during the review period, *e.g.* a sawfly, *Diprion frutetorum* (F.), and the lodgepole needle miner, *Evagora starki* (Free.), and other pests on which studies have only recently begun, *e.g.* two birch pests, *Fenusa pusilla* Lep. and *Coleophora fuscedinella* (Zell.).

Of the 12 pests considered in this review, eight are considered to be of European origin, viz. balsam woolly aphid, *Adelges piceae* (Ratz.); larch casebearer, *Coleophora laricella* (Hübner); European spruce sawfly, *Diprion hercyniae* (Hartig); European pine sawfly, *Neodiprion sertifer* (Geoff.); winter moth, *Operophtera brumata* (L.); European pine shoot moth, *Rhyacionia buoliana* (Schiff.); satin moth, *Stilpnotia salicis* (L.); and the larch sawfly, *Pristiphora erichsonii* (Hartig), although proof of the European origin of the last species is lacking. Of the eight apparently introduced pests, two are frequently reported as pests in Europe, one is occasionally reported as a pest, and five are seldom, if ever, reported as pests. This gives credence to Balch's (1) theory that ". . . . chances of success will be least when the introduced pest is also a pest in its native habitat". Eleven of the target species are indirect pests, a category claimed by Turnbull and Chant (19) to be suitable candidates for biological control. The twelfth species, the balsam woolly aphid, can be classed as a 'direct' and 'indirect' pest because of its attack on both the bole and shoots of trees.

Unlike the format of the former review (10), each chapter in the present review is authored by those who have been most intimately associated with the programmes. The chapters are in alphabetical, generic sequence. Each chapter attempts to outline the problem area, status of the pest, changes in the distribution of control agent and target species, relevant work conducted in Canada or elsewhere, releases since 1958 (with tabular data provided by the Research Institute, Canada Department of Agriculture, Belleville, Ontario), evaluation of control attempts and an expression of need for continuance of the programme. Most of the control projects are sufficiently discrete to be treated adequately under the above format and deviations are required only in a few cases, especially those involving pathogens or those for which there had been no releases since 1958.

Our approach to the biological control of introduced pests by means of parasites and predators has followed a logical sequence of steps that embrace an appreciation of the pest situation, survey of the biotic factors of the pest in its country of origin, selection of candidate species for introduction, importation and rearing, field trials, and establishment evaluation. The only planned introduction of a pathogen from a foreign country is the virus of *N. sertifer* and in this case the more *ad hoc* approach was adopted. The virus was found in a few cadavers submitted for examination, extracted and tested in the laboratory, and then introduced in the field. Actually, because of the host-specific nature of viruses, this may be a very sound approach in many cases.

SELECTION OF SPECIES FOR INTRODUCTION

Appreciation of a pest problem is usually accomplished through a study of the population dynamics of the pest in Canada. As soon as a pest is recognized as one of foreign origin the possibility of biological control is investigated through cooperation with the Commonwealth Institute of Biological Control. The latter organization, chiefly by its staff at the Delemont Station, Switzerland, surveys and appraises the natural enemies in the countries where the pest is indigenous. Two additional features have been added to the C.I.B.C. studies during the present reporting period. More emphasis has been placed on studying competition between species of parasites to determine which ones are intrinsically or extrinsically superior, and in the case of *N. sertifer* studies, the relationship between parasitism and prey density has been examined more critically within limits imposed by availability of staff.

In the preliminary search for candidates for introduction, the first step was to find host species identical or allied to the pest in Canada. When considering allied host species as a source of suitable material, care was taken to assure that the forest communities in both countries were similar in composition and ecology. Both monophagous and polyphagous biotic agents were considered in the preliminary selection of candidates and invariably there had to be strong evidence that the organism would attack the prey species in its new environment. This consideration is consistent with theories of Turnbull and Chant (19) but they chose a poor example to demonstrate their point. They suggested that *Dahlbominus fuscipennis* (Zett.) was an unsuitable parasite for use in the biological control of the European spruce sawfly programme because it was "never found parasitizing *D. hercyniae* or its close relative, *D. polytomum*, in their native environments. . . ." Actually, it has been known for over 30 years that the parasite does attack *D. polytomum* in its native environment (11), and the failure of *D. fuscipennis* in Canada must be explained by a combination of other factors, as reviewed by Reeks (15).

The selection process continued throughout the European and Canadian programmes, and decisions took into account the controversial question as to the number of species or organisms that should be introduced against a single pest. Several candidates were generally selected for importation and rearing with the view to releasing more than one species if circumstances warranted. Multiple-species releases are contrary to the views of Turnbull and Chant (19) who favour release of only one or two promising species against each target species. One must agree with these authors that the selection of 27 species for releases against the European spruce sawfly could have been narrowed. However, on biological grounds there has been nothing to indicate that single-species releases have any advantage over multiple-species introduction. The multiple releases against the European spruce sawfly evidently did not have a detrimental effect because, as shown by Neilson, Martineau, and Rose (pp. 138), either parasites, the virus, or combination of both are capable of regulating host densities. Furthermore, there is now excellent evidence from recent experience and inductive population models of Hassell and Varley (7) that the practice of multiple or successive introduction is sound, the advantages of multiple introductions being: (a) greater chance that at least one species will be established; (b) possibility of better control offered by two species than by one; and (c) dominance of different species by competitive displacement in different climatic zones.

IMPORTATION, REARING, AND RELEASE OF PARASITES AND PREDATORS

The importation and rearing of parasites and predators were conducted by the Research Institute, Canada Department of Agriculture, Belleville, Ontario. During the past decade the Institute has not attempted to multiply parasites for inundative release programmes of the magnitude described for *D. fuscipennis* in the earlier review (10).

Recent programmes of the Canadian Forestry Service have devoted more attention to observing the results of cage releases before making free releases in the field. Based on the success of cage rearings, *Lophyroplectus luteator* (Thunb.) (pp. 157) was chosen as a suitable candidate for free releases against *N. sertifer*, while *Lamachus* complex was withheld from field releases because of its failure to perform satisfactorily under cage conditions. However, performance of parasites in field cages is not always a sound criterion for selection, especially in the case of tachinid parasites, and in some instances free releases were tested after cage releases failed. Initial field releases were usually made on permanent plots where the populations and behaviour of both host and parasite can be studied simultaneously. Recent policy calls for releasing only one species on each plot or on series of widely separated plots. In one programme, three colonies of a parasite species were released during two consecutive years on each plot, thereby providing a degree of assurance of synchrony between parasite and host, and only mated females were released as a safeguard against mating failure due to rapid dispersal. In other programmes, pre-release mating was not always feasible and the number of specimens in a colony for release was largely determined by material available in relation to rigid shipping schedules. A minimum of 500 females in each colony is generally desirable but establishment of *Olesicampe benefactor* Hinz. on the larch sawfly was demonstrated at five points in New Brunswick and Maine where colonies of 149–388 mated females were released. The spacing between release points or study plots varied with the supply of material and the distances between plots which are usually established with the view to cover the spectrum of ecosystems occupied by the host species.

ESTABLISHMENT STUDIES

The first recoveries of a released parasite, predator or pathogen mark the beginning of long, arduous studies if one is to obtain a meaningful appreciation of the impact of the organism on its host. In the assessment of biological control of major pests, the Canadian Forestry Service largely depends on the life-table approach, which has been used for six of the 12 target species listed for biological control (Table XXII). This approach requires long series of life tables before and after establishment. For example, to the end of 1968, specialists of the Canadian Forestry Service developed 55 larch sawfly life tables in Manitoba, but only nine relate to plots on which the introduced parasite, *O. benefactor*, had been released. Many more will be required before the impact of this parasite will be fully understood.

Ecologists studying establishment are primarily concerned with the performance of the released organism on and near the life-table plots, but the Forest Insect and Disease Survey is called upon to assess gross parasitism and distribution after dispersal extends appreciably beyond the study plots. The Survey is also responsible for studying the establishment of released control agents of less important species that do not warrant the life-table approach. In such cases, the Survey must resort to extensive sampling, rearing, and dissection procedures because they lack the manpower required to assess the interaction of complex biotic and abiotic control factors. The section on the satin moth, *Stilpnotia salicis* (L.) (pp. 205–12), illustrates valuable assessments of parasite establishment undertaken by the Survey organization.

USE OF PATHOGENS

Some of the following chapters feature field trials with pathogens against forest insect species, *e.g Malacosoma disstria* Hübner, *Neodiprion lecontei* (Fitch), *N. sertifer* (Geoff.) and *N. swainei* Midd. Although success in the control of forest insects with pathogens has been somewhat variable, these field trials and other small scale tests have provided an insight into the potential of pathogens as well as methods of dissemination. To date, virus diseases have shown more promise of success than have bacteria, fungi, or protozoa.

Testing the efficiency of new viruses is done first in the laboratory. If results are at all promising, small scale tests are done in the field, the technique being governed by the habits of the insect. Colonial feeders such as *Neodiprion* spp. are comparatively easy to work with because the colony can be treated as a unit and application can be reasonably well controlled. With solitary feeders and highly mobile species, on the other hand, a tree must usually be used as a unit. Sampling is more arduous, but quantitatively satisfactory estimates of disease incidence and population trends are obtainable. Establishment and spread of the virus may be more effective when the female distributes her eggs rather than laying them in one or two places.

Once the preliminary field trials are complete, and show promise, the next step is to treat a significant area. This may be done by ground equipment of the fogging or mist-blowing type, or if sufficient material is available and larger areas are infested, aerial spray may be applied. Assessment of the results then determines whether or not it can be recommended as a means of control.

Various other methods for initiation of infection have also been tried. In early work, Bird[1] attempted to use the virus as a systemic insecticide by injection into the phloem of the tree, but this was not successful. The fact that the virus persists from the larva through the pupa to the adult suggests that diseased, but still living, pupae might be scattered in the forest, so that diseased adults would produce infected progeny, thus providing foci of infection. The method might be satisfactory to introduce disease into an incipient population but the numbers of infected pupae required to be effective against an outbreak are so large and the effective speed of development of an epizootic so much slower than by direct virus spray, the method would seem to be impractical.

In the dissemination of pathogens, it is important to know something of the habits of the host insect. Bird (2), for instance, has shown that application of virus to colonies of *N. sertifer* on the lower part of the tree results in a much less successful introduction than when colonies in the upper crown are infected. In the latter case, the virus spreads downward by weathering action as the insects die, and those on the lower branches that may have escaped at first, will be subject to later infection thus increasing the efficiency of spreading. Similarly, initiation of an epizootic in populations of *M. disstria* is more effective in the upper than in the lower crown of trees.

Host specificity of viruses is a very favourable characteristic because it practically eliminates the possibility of injuring parasites, predators, or other beneficial animals such as pollinators, birds, and fish. This characteristic, however, seems to belong to the nuclear polyhedroses; cytoplasmic polyhedroses are less specific, although the host range is still narrow, almost certainly not extending to vertebrates. Another significant feature of all viruses is their functional response, which leads to the collapse of the pest outbreak. Sometimes, as in the spruce sawfly and the forest tent caterpillar, parasites may be an important factor while in other cases the virus seems to be the prime control agent.

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[1] Insect Pathology Research Institute, Canadian Forestry Service, Sault Ste. Marie, Ontario. Unpublished data.

Bacillus thuringiensis Berliner is so far the most widely used bacterium. In most cases it apparently acts more like an insecticide than a pathogen, because its effect depends largely on the toxic proteinaceous crystal that accompanies the spore. On agricultural crops at least two or three applications are usually recommended because the bacterium has little 'epizootic' effect. The same procedure may prove to be essential for forest insects; if this is so it will undoubtedly decrease its general usefulness. There is no evidence that this type of organism becomes established as a continuing control against our major pest insects.

Numerous attempts have been made to create fungal epidemics in insect populations. Generally, when an epidemic has occurred in treated areas it has also occurred almost simultaneously over large untreated areas, leaving the question whether the entire phenomenon had been natural. The conditions governing sporulation and spore germination of entomogenous fungi are not completely understood, hence the difficulty in obtaining predictable results. Natural epizootics are so highly effective in an insect outbreak that continuation of efforts to explain and exploit them is well worthwhile.

Only recently has the impact of protozoans on insect populations been recognized. Seldom do the protozoa—usually microsporidia—have spectacular effects, but they do exert a continual pressure, frequently in the form of reduced growth, feeding, adult longevity, and fecundity. In at least one case a microsporidian, *Perezia fumiferanae* Thom., has been credited with 'control' of a population of spruce budworm, although it required several years to achieve this effect (18). There are problems in producing, storing, and using these organisms, although recent work by Ishihara (9) has suggested that the first may be nearing solution, and Weiser (20) has reported the artificial establishment of infection by *Thelophania hyphantriae* Weiser in a population of *Hyphantria cunea* Drury.

CONTROL EVALUATION

Due to justifiable criticism by Turnbull and Chant (19) of failure to assess early control programmes, the chapter authors have made a serious attempt to evaluate the operations outlined in the present review. Clearly, success of the operations must be considered in the light of all benefits, both primary and secondary. None of the operations could be classed as complete failures because each strengthened elements of research or experience of value in planning subsequent operations. Two of the operations were planned mainly to study techniques. One operation was principally concerned with protecting wood quality, and the remaining nine attempted to protect wood volume and/or foliage. A general appraisal of all 12 operations is presented (Table XXII), based on the success classification of Simmonds (16). The degree of control success ranges from negligible to very high, with the frequency of partial or complete success predominating.

Unfortunately, it is generally impossible to express success of operations in meaningful monetary terms, because of indeterminate variables such as size of target area, realistic value of wood saved, and importance of secondary benefits, *e.g.* aesthetic improvement. Difficulties in the interpretation of some of these variables in relation to monetary savings achieved by control operations can be illustrated by examining case histories of the European spruce sawfly and the winter moth, which are our best documented introduced pests with respect to their impact on forest stands.

The greatest destruction of spruce by the sawfly in Canada occurred in the Gaspé Peninsula, where the total spruce inventory in 1937 was approximately 17 million cords of living and insect-killed trees. The outbreak collapsed in the early 'forties, due to the combined effects of released parasites and a virus disease although delayed tree mortality continued for another year or two. By 1940 it was estimated that 66 per cent. of spruce volume had been destroyed by the combined attacks of the sawfly and eastern spruce beetle (14). The latter species was particularly destructive, but had it been absent the sawfly alone could have killed some of the white spruce that were actually killed by the beetle. It would not be unreasonable to estimate that the sawfly was responsible for killing half of the merchantable spruce in the Gaspé up to 1946, or the equivalent of 8·5 million cords, excluding additional heavy losses that were caused by windfall after insect attack led to opening of the stands.

TABLE XXII

Evaluation of biological control[1] measures against forest insect pests

Pest	Page reference	Principal planned benefit	Degree of success[2]
Adelges piceae	113	Protection wood volume	—
Choristoneura fumiferana	127	Technique development	—
Coleophora laricella	131	Protection wood volume	++++
Diprion hercyniae	136	Protection wood volume	++++
Malacosoma disstria	144	Technique development	+
Neodiprion lecontei	148	Protection wood volume	+++
Neodiprion sertifer	150	Protection of foliage and wood volume	++
Neodiprion swainei	162	Protection wood volume	++
Operophtera brumata	167	Protection of foliage and wood volume	++++
Pristiphora erichsonii	175	Protection wood volume	++
Rhyacionia buoliana	194	Protection wood quality	+
Stilpnotia salicis	205	Protection of foliage and wood volume	+++

[1] Measures started during or extending into period 1959 to 1968.
[2] Degree of success:

—	No control
+	Slight pest reduction or too early for evaluation of control
++	Local control; distribution restricted or not fully investigated
+++	Control widespread but local damage occurs
++++	Control complete.

If the sawfly outbreak had continued unabated, there is no reason to doubt that all the white spruce and some of the black would have been killed so one could argue that the control operations protected trees with a total volume of 8·5 million cords. But what does the volume mean in terms of dollars? The monetary value could be expressed in terms of Crown stumpage dues, value of the wood at the mill, or the conversion return. The first is an artificial value set by the state, the second includes the added cost of harvesting and transportation and the third includes a margin for profit, risk and uncertainty. None of these values reflects the true value of the loss. According to Dr. R. Forster[1] the true loss is the stumpage value of the wood which would have been cut if it had not been destroyed, discounted or compounded to the present from the time it would have been hypothetically cut. One must also appreciate that market prices and accessibility during the period of mortality were not conductive to harvesting. Nevertheless, to appreciate the magnitude of the hypothetical loss described above let us assume that 75 per cent. of the wood saved was harvested and that this wood was sold for $1 a cord. It can then be theorized that the sawfly programme, which cost $300,000,[2] between 1932–46, produced a benefit of over $6,000,000.

Additional benefits can also be attributed to this programme. By the end of 1968 the sawfly was known to have occurred in very small numbers throughout the Maritime Provinces, Quebec, Newfoundland, and most of Ontario. Both the virus and the parasite were operating on endemic populations throughout this large region. It is possible that, had controls not operated in these provinces, destruction would have occurred at the same level (50 per cent.) as in the Gaspé. The 1966 inventory estimates of spruce volume in the larger region exceeds one billion cords. If this insect had caused the same percentage of damage in this region as occurred in the Gaspé, trees totalling 500 million cords would have died. It is impossible to determine the effect this would have on the economy. The destruction would have occurred over a time span of perhaps 40 years. During this 40-year span some of the affected trees could have been salvaged but salvage operations add to the cost of harvesting wood. There would be substitution of spruce by balsam but the yield of spruce, according to Frost (5),

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[1] Forest Economics Research Institute, Canadian Forestry Service, Ottawa. Personal communication.
[2] Rough estimate.

is 15 per cent. greater than that of balsam and this would increase the cost of processing. It is doubtful if the estimated hypothetical loss of 500 million cords of wood could have been sold at a price equal to the present Ontario stumpage dues of $2·80 per cord, because the surplus of dead trees would have depressed the market value. One may also speculate on what impact destroyed timber has on the labour force, but estimates on loss of work days resulting from catastrophic insect outbreaks hold little meaning without an appreciation of the value of work days of displaced persons in new employment.

The cost-benefit relationship in the winter moth programme is equally interesting and speculative. This subject is under study by D. G. Embree[1], whose unfinished work has already provided interesting statistics on volume losses. The highest losses occurred in the Counties of Lunenburg and Queens, Nova Scotia, where about 200,000 cords of oak were killed. Had the insect outbreak continued unabated, it is likely that the remaining oak would have been killed for a total loss of about 450,000 cords, without taking into account some damage to other hardwoods. The economist would reason that only a portion of the killed or damaged tree could be harvested, and he could justifiably claim that the value of the loss should be based solely on stumpage values, currently $1–$1·50 per cord. Less conservative loss evaluations could also be based on roadside values including stumpage and harvesting (up to $4·50 per cord) or on mill-site values (from $12–$18 a cord at a local hardboard plant in 1969). Because the entire northeastern seaboard could have been affected by the winter moth, and the cure being self-perpetuating, the benefits are continuing while the costs virtually terminated in the mid 1960's. It should also be noted that from 1954 to 1962 four cities or towns in Nova Scotia spent $11,000 a year for spraying against the insect. These spraying operations ceased when biological control became effective.

Against any estimates of savings accruing from the winter moth control operations, one must consider costs, which include several years of part-time studies by the Commonwealth Institute of Biological Control, at least 3 man-years of study and rearing by the Research Institute, Canada Department of Agriculture, Belleville, Ontario, and about 13 years of ecological studies by the Canadian Forestry Service in Nova Scotia. Finally, one could challenge the need for including all research input in a control operation of this kind. The final cost-benefit relationship of the winter moth operation will have to await completion of the study referred to above.

The above illustrations indicate that even the best figures on economic evaluation of insect control operations lack precision, so it is not surprising that the chapter authors generally expressed their control successes in terms other than dollars.

FUTURE CONSIDERATIONS IN BIOLOGICAL CONTROL

The present review will have served no useful purpose unless we can draw on our experience for future direction in biological control programmes involving forest insects. Smallman (17) expressed the view that the interplay between the search for principles and the solution of practical problems characterized entomological research in Canada in the 'fifties, while Turnbull and Chant (19) clearly showed that too often solutions were being attempted without adequate attention to principles. We share the opinion of Huffaker and Kennett (8) that case histories viewed retrospectively are the real test of the efficacy of released organisms, and hope that case histories reported herein will ultimately assist in the development of principles in biological control.

Intuitive decisions still play a role in our choice of organisms for release in Canada. Intuition cannot be eliminated but in many cases it could be narrowed by more research on often-repeated questions on the stage of pest species that should be controlled and single- versus multiple-species releases against pest insects. Both questions relating to any programme should be examined by a study of competition or predation and mode of action of abiotic influences. Ideally, such process studies should attempt to test the new 'parasite quest' theory (7) or they should yield sub-models

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[1] Department of Fisheries and Forestry, Fredericton, New Brunswick. Unpublished data.

that fit into an overall mathematical model describing the functioning of a life system and showing how all key influences contribute to variance (4). Griffiths' and Holling's (6) sub-models on competition could be used with field data and programmed to calculate the properties of an 'ideal' predator. Unfortunately, however, a parasite or predator is often extremely rare and difficult to propagate for the purpose of matching its properties with those of a programmed 'ideal'. The search for the 'ideal' parasite or predator should not be confined to programmes dealing with only introduced pests, because Pimentel (12) has shown a fairly high degree of control of native pests by the introduction of parasites or predators of allied species or genera. If careful searching in a foreign country or different habitat fails to locate an organism that matches the programmed 'ideal', we see no reason why a small colony of a parasite with less than 'ideal' characteristics cannot be imported for cage or free releases. Although we accept the idea of narrowing the number of biotic agents in the control of any one forest pest, we favour multiple species releases when reasons are sound. We support the views of Price (13) who implies that criticism of multiple species releases too often has failed to appreciate the adaptive capacity of parasites to coexist in the exploitation of a common host.

Agricultural entomologists have devoted a good deal of thought to developing models to show the number of colonies of parasites and the numbers of individuals in a colony that should be released for each level of host population. These models have been most popular in programmes involving control by the sterilized male technique. Parallel studies are needed in programmes on the biological control of forest insects by the use of parasites and predators.

Considerable research and additional testing will be required before the use of pathogens in forest insect control becomes as common as chemical insecticides. A major problem not yet seriously attacked is the best way to provide adequate quantities of virus when needed. So far the only method of production is to infect healthy larvae, wait until the disease develops and kills them, then collect the cadavers and process the virus. This is expensive, because the insects require a great deal of handling. It could be reasonably streamlined in a unit designed for the purpose, but whether or not it can be feasible without high subsidization is not known. More work on antagonism between viruses is warranted. So far there is no evidence of a single insect being infected by two different nuclear polyhedroses, but Bird (3) has shown that a nuclear and a cytoplasmic polyhedrosis are antagonistic in *Choristoneura fumiferana* (Clemens). Finally, combining pathogens with chemical insecticides should be a rewarding area of research and trials in the control of forest pests in Canada.

LITERATURE CITED

1. Balch, R. E. (1960). The approach to biological control in forest entomology. *Can. Ent.* **92**: 297–310.
2. Bird, F. T. (1961). Transmission of some insect viruses with particular reference to ovarial transmission and its importance in the development of epizootics. *J. Insect Path.* **3**: 352–80.
3. Bird, F. T. (1969). Infection and mortality of spruce budworm, *Choristoneura fumiferana*, and forest tent caterpillar, *Malacosoma disstria*, caused by nuclear and cytoplasmic polyhedrosis viruses. *Can. Ent.* **101**: 1269–85.
4. Clark, L. R., Geier, P. W., Hughes, R. D. & Morris, R. F. (1967). The ecology of insect populations in theory and practice. Methuen, London.
5. Frost, F. (1958). Is artificial regeneration necessary in Newfoundland? *For. Chron.* **34**: 194–200.
6. Griffiths, K. J. & Holling, C. S. (1969). A competition submodel for parasites and predators. *Can. Ent.* **101**: 785–818.
7. Hassell, M. P. & Varley, G. C. (1969). New inductive population model for insect parasites and its bearing on biological control. *Nature, Lond.* **223**: 1133–7.
8. Huffaker, C. B. and Kennett, C. E. (1969). Some aspects of assessing efficacy of natural enemies. *Can. Ent.* **101**: 425–47.
9. Ishihara, R. (1968). Growth of *Nosema bombycis* in primary cell cultures of mammalian and chick embryos. *J. Invert. Path.* **11**: 328.
10. McGugan, B. M. & Coppel, H. C. (1962). Biological control of forest insects 1910–1958. *In* A review of the biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol. Contr.* **2**: 35–127.
11. Morris, K. R. S., Cameron, E. & Jepson, W. F. (1937). Insect parasites of the spruce sawfly (*Diprion polytoma* (Htg.) in Europe. *Bull. ent. Res.* **28**: 341–93.
12. Pimentel, D. (1963). Introducing parasites and predators to control native pests. *Can. Ent.* **95**: 785–92.
13. Price, P. W. (1970). Characteristics permitting coexistence among parasitoids of a sawfly in Quebec. *Ecology* **51**: 445–54.

14. Reeks, W. A. & Barter, G. W. (1951). Growth reduction and mortality of spruce caused by the European spruce sawfly, *Gilpinia hercyniae* (Htg.) (Hymenoptera: Diprionidae). *For. Chron.* **27**: 1–16.
15. Reeks, W. A. (1953). The establishment of introduced parasites of the European spruce sawfly (*Diprion hercyniae* (Htg.)) (Hymenoptera: Diprionidae) in the Maritime Provinces. *Can. J. agric. Sci.* **33**: 405–29.
16. Simmonds, F. J. (1969). Brief resume of activities and recent successes achieved. Commonwealth Institute of Biological Control. C.A.B., Trinidad, West Indies. 16 pp.
17. Smallman, B. N. (1959). Trends in entomological research in Canada. *A. Rep. ent. Soc. Ont.* **89**: 26–31.
18. Thomson, H. M. (1960). The possible control of a budworm infestation by a microsporidian disease. *Bi-mon. Progr. Rep., Can. Dep. Agric.* **16** (4): 1.
19. Turnbull, A. L. & Chant, D. A. (1961). The practice and theory of biological control of insects in Canada. *Can. J. Zool.* **39**: 697–753.
20. Weiser, J. & Veber, J. (1955). The possibilities of biological struggle with *Hyphantria cunea* Drury II. *Česk. Parasitol.* **2**: 191–9.

36. *ADELGES PICEAE* (RATZ.), BALSAM WOOLLY APHID (HOMOPTERA: ADELGIDAE)

R. C. CLARK, D. O. GREENBANK, D. G. BRYANT and J. W. E. HARRIS

PEST STATUS

The balsam woolly aphid, *Adelges piceae* (Ratz.), continues to be a serious pest of true firs, *Abies* spp. and infestation boundaries have expanded in both eastern and western Canada. In the east, it occurred in 1958 in Nova Scotia, Prince Edward Island, southern and eastern New Brunswick, and southwestern Newfoundland. Since 1958, infestations have been found in northwestern New Brunswick, the eastern tip of the Gaspé Peninsula (17), the Magdalen Islands (3), and in stands throughout central and eastern Newfoundland (Fig. 7). A total area of about 40,000 square miles is affected in eastern Canada, an increase of 4,000 square miles since 1958. The area infested in western Canada now involves about 4,000 square miles of southwestern British Columbia (Fig. 7).

The insect feeds on the bark cortex of all parts of the tree from the root collar to the crown. On the stem, the favoured sites are beneath lichens, at lenticels, and in crevices in the bark. On *Abies balsamea* (L.) Mill. heavy stem populations of 20 aphids or more per square inch of bark surface are capable of killing trees in 3 years. In the crown, aphids tend to aggregate in staminate flowers and at 2- and 3-year-old nodes. Distortion of the current shoots is frequently the first evidence of a new infestation. This symptom appears when there are five or more aphids per node but even one aphid can cause swellings visible on close examination. If the attack persists, subsequent forms of damage are pronounced swelling of the shoots (gout), die-back of branches, inhibition of height growth, and the eventual death of the trees. The levels of stem and crown populations which cause serious damage to western species of *Abies* are being determined in British Columbia.

Greenbank (14) has shown that in New Brunswick aphid abundance and the amount and type of aphid damage can be related to climate. Low winter temperature is a limiting factor in the survival of populations because the formation of ice in the tissues is fatal to the aphid. The probability of freezing increases as temperatures fall below — 5°F and there are no survivors below — 35°F no matter how brief the exposure. Coastal regions have relatively mild winters and aphid survival on all parts of the tree is high. Crown populations predominate and large concentrations on the tree stem occur mainly in localized spots in newly infested areas. Aphid damage is severe in maritime climatic regions. In the more continental climate of northwestern New Brunswick, temperatures each winter fall well below — 5°F and populations are mainly restricted to the base of trees where snow provides protection. Damage accumulates at a slow rate and the aphid is not as serious a problem in this inland region as it is in areas with a maritime climate.

Because of extension of crown infestations since 1958, the search for biological control agents in Europe has been concentrated on species associated with low-density, twig-inhabiting adelgids as

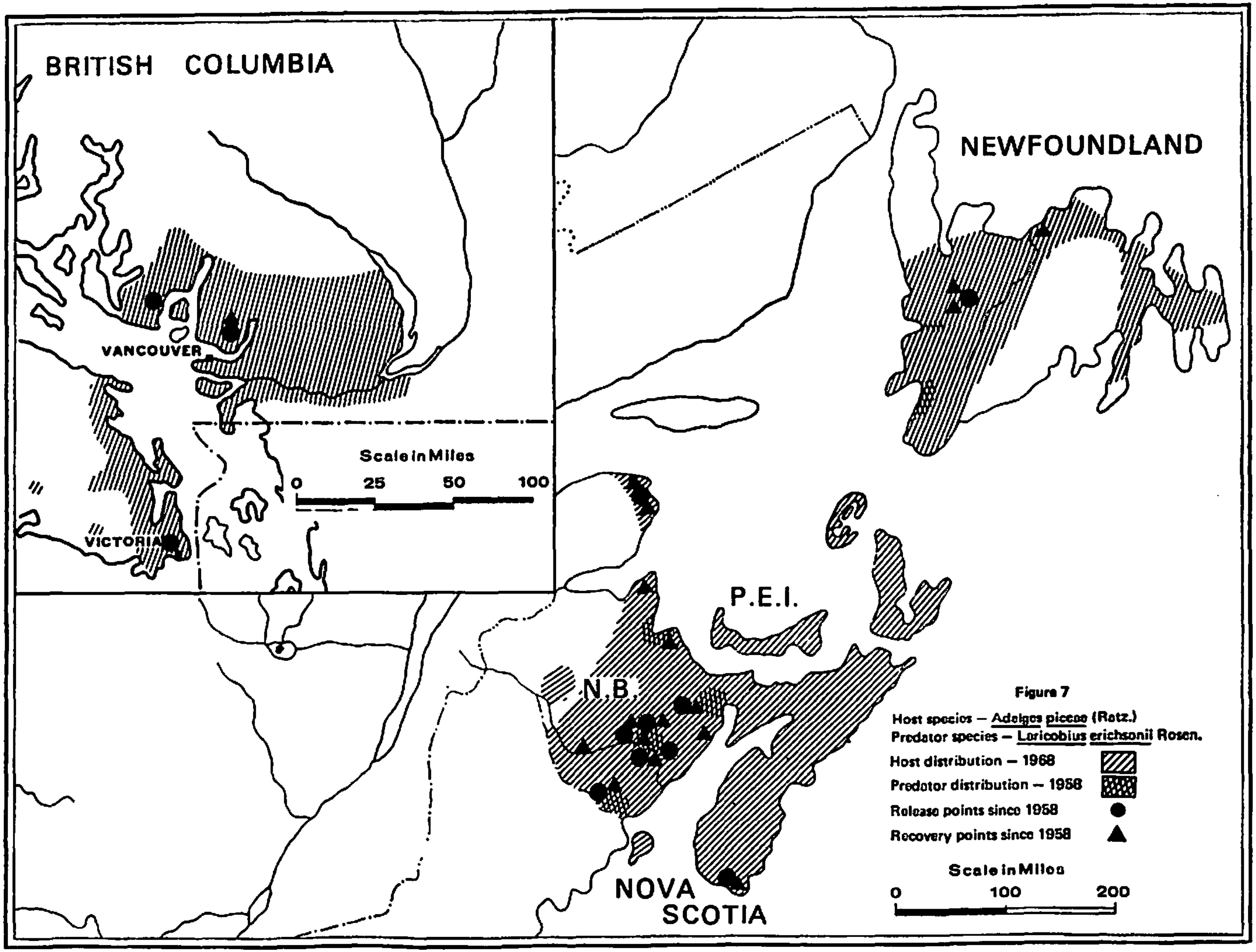

Figure 7

Host species — *Adelges piceae* (Ratz.)
Predator species — *Laricobius erichsonii* Rosen.

suggested by Pschorn-Walcher (20). As a result, new species, such as the *Leucopis* spp. complex, as well as large number of *Scymnus pumilio* (Weise) and *Aphidoletes thompsoni* Möhn., have been released in aphid-infested forests.

BACKGROUND

Biological control studies have been conducted in the United States where the aphid occurs in both the northeast and the northwest and in Europe where the majority of predators are collected. The United States Department of Agriculture Forest Service imported a total of 23 species of insect predators and began releases in the northwest in 1957 and in the east in 1959 (1, 19). A few of the species became established but aphid damage continued to increase. In Europe, predation on stem populations was 'inverse density dependent' and not 'regulative' (13). However, there was some evidence that twig populations of *Adelges nüsslini* C. B. were being controlled by *Leucopis* n. sp.

Chemical control of the balsam woolly aphid, through contact insecticides, requires saturation of the infested trees and appears to be impractical for protection of forests (23). With the development of combined contact and systemic insecticides, laboratory and field experiments were initiated in Canada in 1963 (21). Of the 46 insecticides used in the laboratory and greenhouse experiments, four showed promise, but none of them caused acceptable levels of aphid mortality under field conditions. A recent observation (7) suggests that populations may be reduced, or at least held at a constant level, if insecticides are applied during the hatching and crawler period of the aphid. Systemic insecticides proved successful in Europe when used against an allied species, *Adelgea nüsslini* (16).

Silvicultural control conducted on a non-operational basis in Newfoundland (12) has: (a) temporarily limited spread of the aphid by cutting spot infestations and burning the slash and (b) reduced the amount of balsam fir stands by converting them to black spruce. (Black spruce seed is broadcast following cutting and burning.) In western Canada, Carrow and Graham (8) inferred that nitrogen fertilizers, as foliar sprays, inhibited the establishment of crawlers on *Abies*. Results of these experiments, however, do not offer a permanent solution to the aphid problem in natural stands.

RELEASES AND RECOVERIES

The balsam woolly aphid in Canada is attacked by several native predacious insects, and the importation of predator species was begun in 1933 to improve the biological control complex. Of the 13 species released before 1958 only four became established. These were *Leucopis* (*Neoleucopis*) spp., *Laricobius erichsonii* Rosenhauer, *Pullus impexus* Mulsant and *Cremifania nigrocellulata* Czerney. Since 1958, *Aphidoletes thompsoni* Möhn. became established in Newfoundland and British Columbia and *C. nigrocellulata* in Nova Scotia. Searches for additional predators were extended by the Commonwealth Institute of Biological Control to India, Pakistan, Australia, and Japan. These searches resulted in the introduction, release, and study in Canada of 15 additional predator species of which none became established.

The biology, habits, and control value of established species are given below and details of all releases during the past decade are presented in Tables XXIII and XXIV. The present predator complex of both introduced and native species in Canada is listed in Table XXV.

PREDATORS

Aphidecta obliterata L. (Coleoptera: Coccinellidae)

Results of studies by Brown and Clark (5) indicated that, although *A. obliterata* was capable of completing one generation in the year of release, it was unable to survive the severe winter conditions and thus failed to become established. Additional releases were made in New Brunswick and in Nova Scotia between 1959 and 1968 (Tables XXIII and XXIV) from collections made in colder regions of

Europe, *i.e.*, Norway and Czechoslovakia. As in the earlier releases, there was no establishment in New Brunswick. In Nova Scotia, where winter conditions are less severe, one adult was successfully reared from a field collection of eggs in the spring of 1967. This recovery offers slight evidence that *A. obliterata* is capable of survival in Nova Scotia.

In Newfoundland, releases have been made each year since 1958, except 1961. It was not until 1966 that overwintered adults were recovered and in 1968 all stages were found. The adults in 1966 were found in protected areas on the bark of infested balsam fir, but all stages were found on infestations of *Adelges cooleyi* (Gillette), an adelgid which infests the needles of *Picea glauca* (Moench) Voss. Studies indicate that predation is evident only when there are more than 25 *A. cooleyi* per 4-inch twig. The species is apparently established but ineffective because it does not prey at low levels of *A. piceae* populations.

In British Columbia, releases have been made in most years since 1960. As in New Brunswick, adults and progeny have been recovered only in the year of release and the species is not established.

Aphidoletes thompsoni Möhn. (Diptera: Cecidomyiidae)

Releases of this predator in New Brunswick after 1958 were made in 1959, 1960, 1965 and 1966 (Tables XXIII and XXIV). Limited larval recoveries in 1960 and 1961 indicated that the species could successfully overwinter, but no further recoveries have been made and the species is not considered established. Similar observations were made in Newfoundland following releases in 1959, and 1965, but recoveries of immature stages in 1966, 1967 and 1968 indicate that the species is established. These predators were found only when there were more than 15 aphids per node on branches. In British Columbia, recoveries were made on Vancouver Island in 1967, following releases in 1966, and the species is considered established in that province.

Cremifania nigrocellulata Cz. (Diptera: Chamaemyiidae)

This small predator is established and well dispersed from earlier releases over most of the range of *A. piceae* in New Brunswick and Nova Scotia. Recoveries have been consistent but low in number and additional releases were made in 1963 and 1966 (Table XXIII, Fig. 8). Studies of the life history and habits showed that this species, although well dispersed, has failed to achieve effective economic control because major feeding is restricted to *A. piceae* adults that have already laid the majority of their complement of eggs (11).

No recoveries followed releases in either British Columbia or Newfoundland.

Leucopis (*Neoleucopis*) spp. (Diptera: Chamaemyiidae)

Initial releases in New Brunswick, Nova Scotia, and Prince Edward Island between 1933 and 1947 and in Newfoundland in 1955 and 1956 were identified as *Leucopis obscura* Haliday. Recent information (unpublished) from the Entomology Research Institute, Canada Department of Agriculture, indicates that these early releases were probably mixed and could have included specimens of *Leucopis atratula* Ratzeburg, *Leucopis obscura* Hal., and *Leucopis* n. sp. which was formerly recognized as *Leucopis* or *Leucopina americana* (Malloch), a native species. Further complexity was introduced with releases in 1959, 1960, 1965, 1966 and 1968, of two additional species, *Leucopis* (*Leucopis*) n. sp. nr. *melanopus* and *Leucopis* (*Neoleucopis*) n. sp. nr. *obscura*, in New Brunswick, Newfoundland and British Columbia (Tables XXIII and XXIV). There is now a possibility that a complex of five *Leucopis* species exists in New Brunswick and Newfoundland. Until the taxonomy is clarified we will consider the group as *Leucopis* (*Neoleucopis*) spp.

The species established readily from the early releases and by 1948 had dispersed over most of the range of *A. piceae* in New Brunswick, Nova Scotia and Prince Edward Island (4).

Recoveries were made at Cap Desrosiers on the Gaspé Peninsula of Quebec in 1966 (Fig. 9). *A. piceae* was first discovered in this area in 1964 and is thought to have originated by wind dispersal about 1958 from northeastern New Brunswick infestations. The *Leucopis* species probably arrived in the same way.

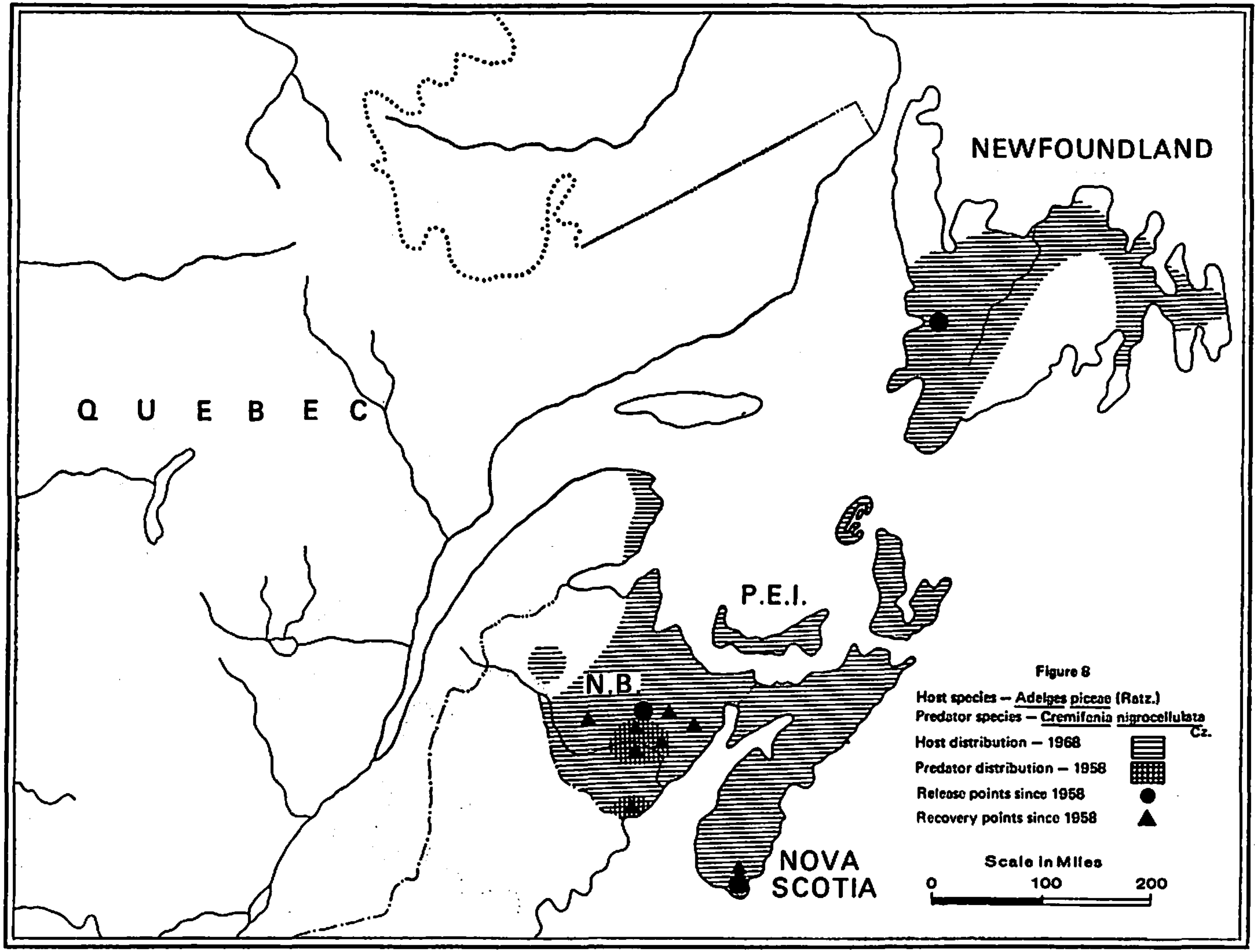

Figure 8

Host species — *Adelges piceae* (Ratz.)

Predator species — *Cremifania nigrocellulata* Cz.

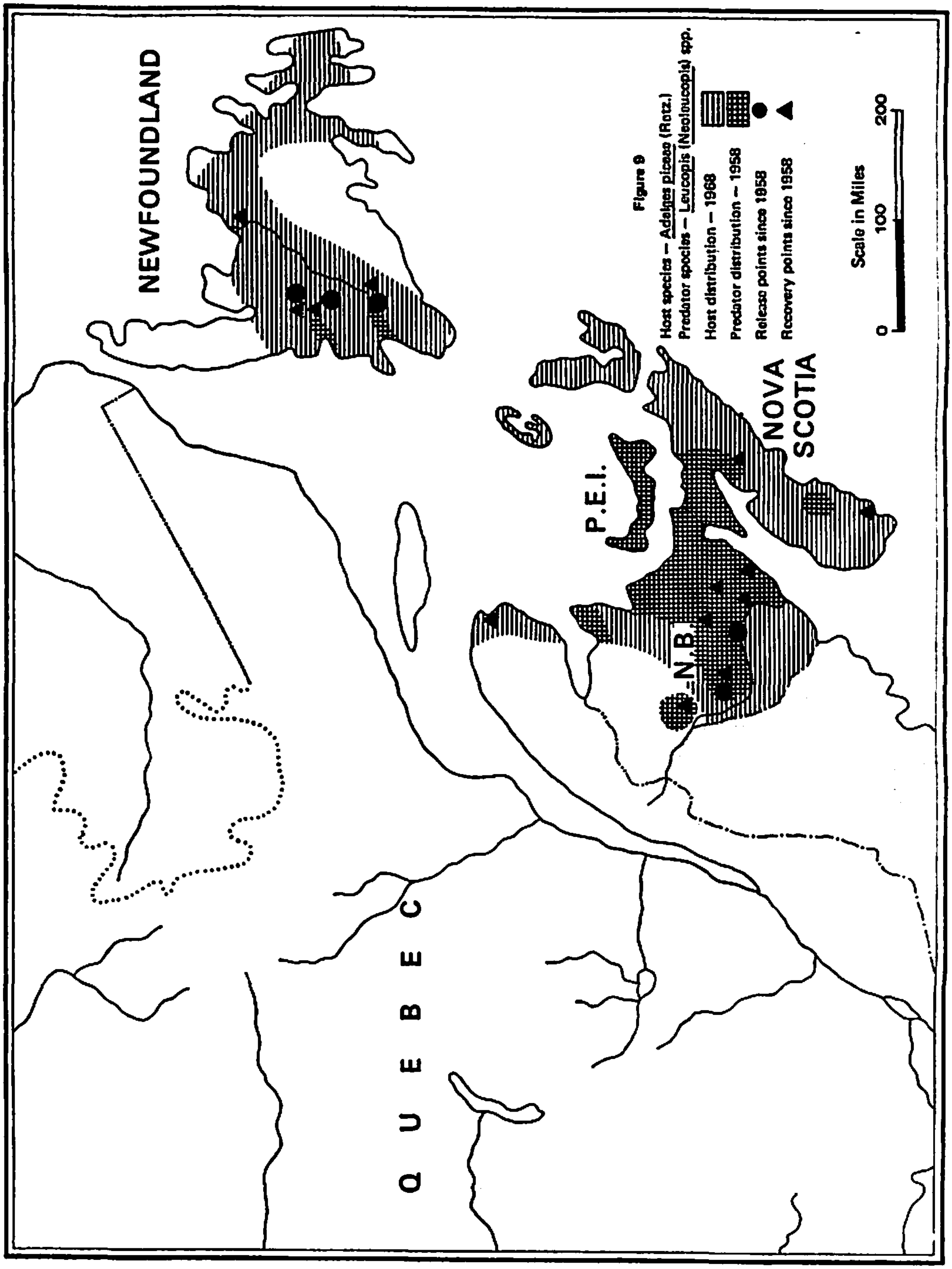

Figure 9

Host species – *Adelges piceae* (Ratz.)

Predator species – *Leucopis* (*Neoleucopis*) spp.

In Newfoundland, the *Leucopis* species established quickly from releases made in 1955 and 1956, and by 1968 had dispersed over most of the range of *A. piceae* in that province.

The only *Leucopis* releases in British Columbia were made in 1968. These were identified as *Leucopis* n. sp. nr. *melanopus* and as yet no recoveries have been made.

Although established and well distributed throughout the range of *A. piceae* in the Atlantic Provinces, the *Leucopis* species failed to provide effective control for a variety of reasons. The main ones are:

(a) The predators occur primarily on moderate to heavy stem infestations or only when aphid populations exceed 35 aphids per node on twigs.

(b) Feeding takes place after the aphids have laid large numbers of eggs which are not generally susceptible to attack under field conditions.

(c) Their searching ability in the larval stage is limited.

(d) The aphid is capable of increasing more rapidly than the predator.

Laricobius erichsonii Rosen. (Coleoptera: Derodontidae)

This small predator from Europe became established prior to 1959 throughout most of the range of *A. piceae* in New Brunswick and Nova Scotia (18). The species showed promise and additional releases were made between 1959 and 1968 in New Brunswick, Nova Scotia, Newfoundland and British Columbia (Table XXIII, Fig. 7).

In New Brunswick, Clark and Brown (9) found that *L. erichsonii* has one generation per year that feeds in the early spring on all stages of the hiemosistens prey generation on the stem, and never on twig infestations. Also, when *L. erichsonii* larval populations exceed 0·1 per 1,000 square inches of bark area, the aestivosistens generation of the aphid was reduced to an average of 39 per cent. of the hiemosistens generation. However, these figures were obtained from areas where large numbers of the predator had been released within 1 or 2 years, and natural population levels of this magnitude have seldom been observed.

In Newfoundland, *L. erichsonii* is established in aphid-infested stands but it does not reduce aphid populations significantly and tree mortality occurs (6). Unlike New Brunswick, where *L. erichsonii* occurs only on stem infestations of *A. piceae*, in Newfoundland it has been found on the stems, at the bases of branches, and among staminate flower buds and cups, and at nodes (6). All stages have also been found on *Adelges cooleyi*, which feed on needles of *Picea glauca*. On this host, the females of *L. erichsonii* oviposit only when there are more than 35 *A. cooleyi* per 4-inch twig (equivalent to 35 aphids/node). Thus, *L. erichsonii* is not expected to occur when aphid population levels are low and as a result will not provide effective control.

In British Columbia, *L. erichsonii* was first released in 1960, both on the mainland and on Vancouver Island. It is established on the mainland but limited recoveries indicate that neither establishment nor dispersal has been as successful as in other areas of Canada. Mitchell and Wright (19) believe that low-host stem populations and poor overwintering conditions are the major factors reducing survival in the western regions.

Pullus impexus (Muls.) (Coleoptera: Coccinellidae)

P. impexus was recovered, and apparently established, following extensive releases in New Brunswick between 1951 and 1955. Thereafter, predator numbers declined rapidly until 1960 when no further recoveries were made. Similar trends followed releases in Newfoundland. Clark and Brown (10) showed that the disappearance was due to inability of eggs, which are laid on the bark, to survive the low winter temperatures of central New Brunswick. This, however, would not necessarily apply in Newfoundland. Between 1962 and 1966 additional releases were made in more southern areas of New Brunswick and in Nova Scotia (Table XXIII, Fig. 10) where the winters are less severe. Annual recoveries of larvae, pupae, and adults have been made each year but it is too early to determine if successful establishment has occurred. In British Columbia, only one recovery was made following several releases between 1960 and 1968.

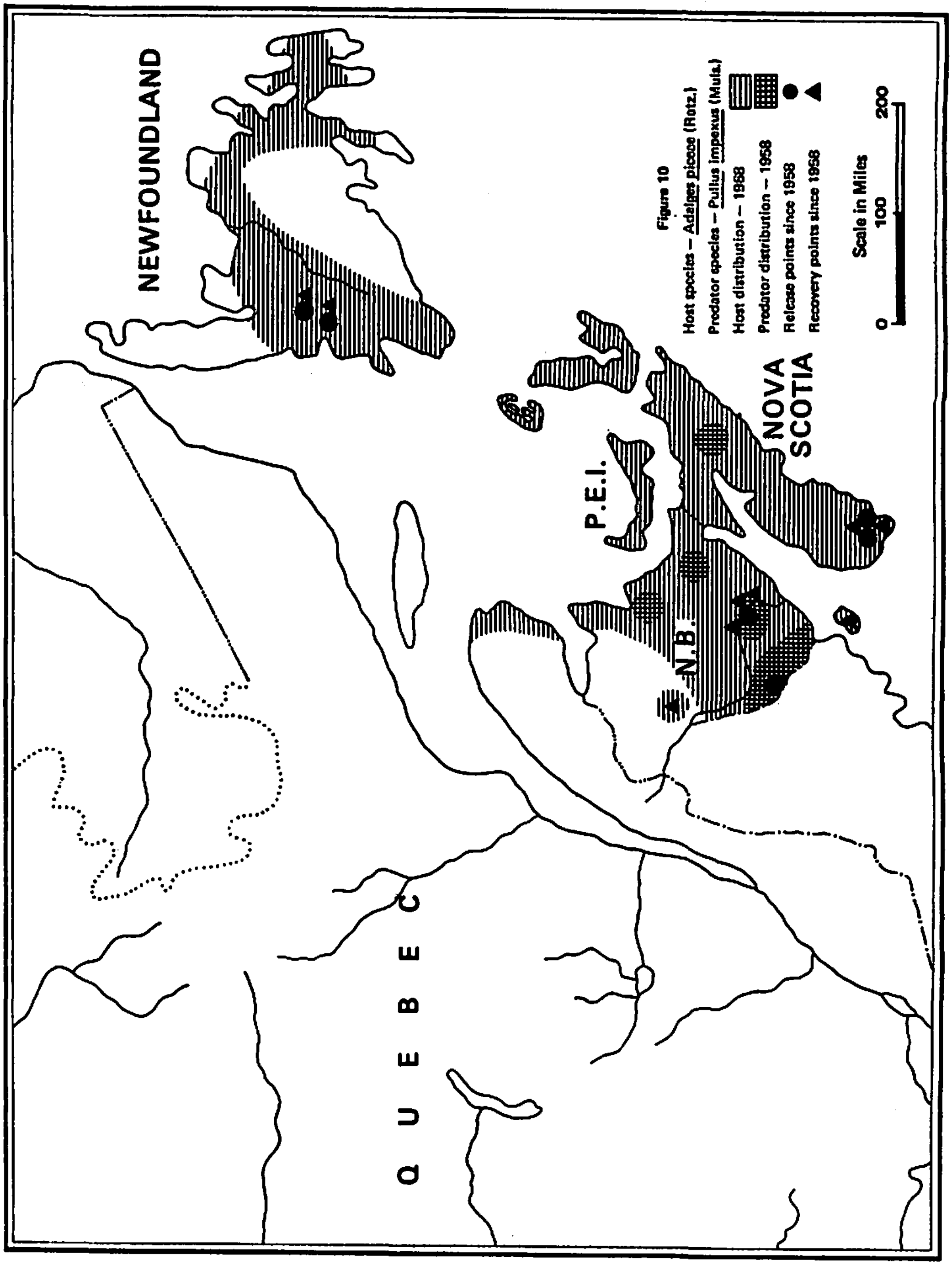

Figure 10

Host species — Adelges piceae (Ratz.)

Predator species — Pullus impexus (Muls.)

Species from India and Pakistan

Shipments of 13 predator species (Coleoptera and Hemiptera) were introduced from the Himalayan regions of both India and Pakistan (Table XXIII). Most of the releases and studies of these species in Canada were carried out in New Brunswick and Nova Scotia; however, some have been tested in Newfoundland and British Columbia. Limited numbers of adults and immature stages of a few species have been recovered in the year of release but there has not been any evidence of successful overwintering. Studies indicate that the inability to adapt to a new and different host and unsuitable overwintering conditions are the most probable reasons for failure to establish.

Coleoptera from Australia and Japan

Several shipments of *Scymnus pumilio* (Weise) from Australia and *Adalia ronina* (Lewis) from Japan have been released in New Brunswick, Nova Scotia, Newfoundland, and British Columbia (Table XXIII). A few adults and immature stages of both species were collected in the years of release but there has been no evidence of establishment.

PARASITES AND DISEASE ORGANISMS

There are no known parasites of the balsam woolly aphid and, until recently, no known disease organisms other than one possible saprophytic fungus reported by Balch (2) and Schimitschek (22). Two fungi, identified as *Fusarium larvarum* Forbel, a possible pathogenic species, and *Cephalosporium coccorum*, a facultative species, were found on stem infestations of *A. piceae* in the Gaspé region of Quebec.[1] Neither species reduced aphid numbers in laboratory and greenhouse experiments. Field trials in New Brunswick and Newfoundland are now in progress. In British Columbia, Harris *et al.* (15) also reported two fungi, *Cephalosporium* sp. and *Penicillium* sp., attacking adults of the balsam woolly aphid.

EVALUATION OF CONTROL ATTEMPTS

The longest history of the aphid in Canada is in southwestern Nova Scotia where it has been present for well over 50 years. Initial infestations caused heavy mortality in merchantable stands in the 1920's and 1930's. Damage and mortality resulted mainly from populations affecting the twigs but in some stands heavy stem populations also killed trees (2). The young stands survived but most became severely infested later. Infestations currently develop in maturing stands and these appear no less damaging than the earlier ones. Most trees are eventually killed or survive as dwarfed, dead-topped, or flat-topped trees of little commercial value. Thus, there is little evidence that the present predator complex, which includes *Leucopis* (*Neoleucopis*) spp., *A. obliterata*, *L. erichsonii*, and *P. impexus* is significantly reducing aphid populations.

There is some evidence (9) that introduced predators have improved the control of heavy stem populations. Such control is of more value in continental climatic regions, where low temperature restricts populations mainly to the lower stem. In maritime climatic regions, most of the damage results from twig infestations and the spread of aphids is mainly by wind dispersal of twig populations.

Biological control has not proved effective in British Columbia where *L. erichsonii* and *A. thompsoni* have become established. The scattered distribution of heavily infested stems and the light twig populations have not offered these introduced predators an ecological opportunity for explosive multiplication or striking reduction of the aphid. Similarly, in the states of Washington and Oregon, these predators together with *P. impexus*, *C. nigrocellulata*, and *L. obscura* have failed to produce significant control of new aphid infestations (19).

Studies in Newfoundland on the numerical response of predators to changes in prey density provide an explanation for the ineffectiveness of predators. Four species of predators, *Leucopis* spp.,

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[1] Smirnoff, W. A. Department of Fisheries and Forestry, Ste. Foy, Quebec 10, Quebec. Personal communication.

A. thompsoni, *A. obliterata*, and *L. erichsonii*, became established in populations of *Adelges* spp. when there were more than 15 aphids per node. However, serious damage to balsam fir can occur at considerably lower levels of balsam woolly aphid populations.

Complexes of introduced predators have become established in Canada and from comparisons of populations before and after predator release, it is concluded that, in maritime climatic regions, native and introduced predators are not reducing populations of the balsam woolly aphid to economically tolerable levels. Although predators appear more effective on stem populations than on twig populations, the key mortality factor in continental climatic regions is winter temperature and not predation.

Although studies are still continuing, the few pathogens associated with balsam woolly aphid also appear to be ineffective in limiting aphid numbers.

RECOMMENDATIONS

Limited scope exists for additional study in the field of biological control of the aphid, but this control method may still be possible through use of pathogens. Current studies on the potential value of entomogenous fungi should be given full support, and the possibility of combining these with the most promising of chemical insecticides should not be overlooked. Intermittent field trials over a period of about 35 years provide solid evidence of the ineffectiveness of predator complexes in areas where twig infestations predominate. Releases of predators should be discontinued until surveys and research can produce a species that offers effective control of low-density twig-infesting adelgids.

TABLE XXIII

Open releases and recoveries of predators against *Adelges piceae* (Ratz.)

Species and Province	Year	Origin	Number	Year of recovery
Adalia luteopicta Mulsant				
Newfoundland	1960	India	159	
Adalia ronina (Lewis)				
Newfoundland	1961	Japan	67	
Nova Scotia	1963	Japan	290	
New Brunswick	1960	Japan	25	1960
	1962	Japan	37	1962
	1963	Japan	585	1963
Adalia tetraspilota (Hope)				
Newfoundland	1960	India	33	
Aphidecta obliterata (L.)				
Newfoundland	1959	Czechoslovakia	735	
	1960	Germany	934	
	1962	Czechoslovakia	848	
	1963	Germany	989	
	1964	Germany	1187	
	1965	Czechoslovakia	185	
		Germany	267	
	1966	Czechoslovakia	509	
	1966	Austria	1380	1966
	1967	Austria	4288	1967
	1968	Germany and Austria	1096	1968
Nova Scotia	1964	Germany	1773	1967
	1966	Austria	370	
		Norway	47	
	1967	Norway	422	
New Brunswick	1962	Germany	1827	1962
	1963	Germany	3157	1963

TABLE XXIII (continued)

Species and Province	Year	Origin	Number	Year of recovery
Aphidecta obliterata (L.)				
British Columbia	1960	Germany	1050	
	1961	Germany	1141	
	1962	Germany	796	
	1963	Germany	1997	
	1965	Czechoslovakia	660	
	1968	Germany	1069	
Aphidoletes thompsoni Möhn				
Newfoundland	1959	Czechoslovakia	3124	
		Germany	25952	
	1962	Germany	270	1961
	1963	Germany	5201	
	1965	Germany	826	1967
	1966	Germany	35119	
	1968	Germany	7248	
Nova Scotia	1965	Germany	450	1965
	1966	Germany	37110	1966–7
New Brunswick	1959	Germany	36131	1959–61
	1965	Germany	551	1965
	1966	Germany	6300	1966
British Columbia	1962	Germany	280	
	1963	Germany	516	
	1965	Germany	1080	
	1966	Germany	6845	
Balaustium sp.				
Quebec	1967	Pakistan	126	
Ballia eucharis Mulsant				
Newfoundland	1960	India	32	
New Brunswick	1959	Pakistan	79	
	1960	India	55	
Coccinella septempunctata L.				
New Brunswick	1959	India	28	
	1960	India	22	
Cremifania nigrocellulata Czerny				
Newfoundland	1959	Germany	198	
	1961	Germany	17	
Nova Scotia	1966	Germany	169	1966
New Brunswick	1963	Germany	48	1964–5
	1966	Germany	17	1966–8
British Columbia	1966	Germany	137	
	1968	Germany	706	
Exochomus lituratus Gorham				
Newfoundland	1960	Pakistan	110	
Nova Scotia	1963	Pakistan	991	
New Brunswick	1963	Pakistan	209	
Exochomus uropygialis Mulsant				
Newfoundland	1960	India	226	
	1960	Pakistan	2839	
Nova Scotia	1963	Pakistan	8782	
New Brunswick	1959	Pakistan	2550	
	1963	Pakistan	247	
	1964	Pakistan	238	
Harmonia breiti Mader				
Newfoundland	1960	Pakistan	88	
New Brunswick	1959	India	85	
Laricobius erichsonii Rosenhauer				
Newfoundland	1959	Czechoslovakia	1043	1959
		Germany	2159	1960
	1960	Germany	8228	1961
	1961	Germany	1118	1963
	1962	Germany	7940	1964
	1963	Germany	1869	1965
		Newfoundland *via* Europe	1984	1966

TABLE XXIII (continued)

Species and Province	Year	Origin	Number	Year of recovery
	1964	Germany	1819	1968
		Newfoundland *via* Europe	300	
	1965	Germany	152	
Nova Scotia	1966	Germany	2575	1967
New Brunswick	1960	Germany	14266	1958–68
	1966	Germany	3497	
British Columbia	1960	Germany	800	
	1961	Germany	1432	
	1963	Germany	4871	1962–6
	1965	Germany	612	
	1968	Germany	3164	
Leucopis (*Leucopis*) n. sp. nr. '*melanopus*' Authors[1]				
Newfoundland	1959	Germany	160	1959–62
	1968	Germany	1040	
New Brunswick	1960	Germany	166	1959–68
	1966	Germany	241	
British Columbia	1968	Germany	2273	
Leucopis (*Neoleucopis*) *obscura Holiday*				
Newfoundland	1965	Austria	24	1959–68
Leucopis (*Neoleucopis*) *atratula* Ratzeburg				
New Brunswick	1965	Germany	385	
Pullus impexus (Mulsant)				
Newfoundland	1959	Germany	9500	
	1960	Germany	1146	1960
	1961	Germany	131	1961
	1966	Germany	18036	
Nova Scotia	1963	Germany	1000	1965–7
	1964	Germany	2031	
	1966	Germany	4700	
New Brunswick	1962	Germany	685	1958–9
	1963	Germany	397	
	1964	Germany	200	
	1966	Germany	26550	
British Columbia	1960	Germany	1240	
	1963	Germany	1400	
	1965	Germany	2417	
	1966	Germany	18513	
	1968	Germany	2079	
Scymnus pumilio (Weise)				
Newfoundland	1960	Australia	9687	
New Brunswick	1959	Australia	5590	
	1960	Australia	7286	
British Columbia	1960	Australia	2930	
Tetraphleps abdulghani Ghauri				
Nova Scotia	1965	Pakistan	949	
New Brunswick	1962	Pakistan	1972	
	1963	Pakistan	1157	
	1964	Pakistan	45	
	1965	India	278	
		Pakistan	2921	
British Columbia	1965	India	19	
		Pakistan	1257	
Tetraphleps raoi Ghauri				
Nova Scotia	1965	India	59	
New Brunswick	1965	India	59	

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[1] Species 'M'.

TABLE XXIV

Cage releases and laboratory studies of predators against *Adelges piceae* (Ratz.)

Species and Province	Year	Origin	Number
Adalia ronina (Lewis)			
New Brunswick	1959	Japan	16
	1963	Japan	150
Adalia tetraspilota (Hope)			
New Brunswick	1959	India	41
Aphidecta obliterata (L.)			
Newfoundland	1964	Germany	328
	1965	Czechoslovakia	70
		Germany	30
Nova Scotia	1964	Germany	56
	1967	Norway	9
New Brunswick	1963	Germany	30
	1965	Czechoslovakia	155
	1968	Germany, Austria	1736
British Columbia	1965	Czechoslovakia	20
	1968	Germany	30
Aphidoletes thompsoni Möhn			
Newfoundland	1965	Germany	969
	1968	Germany	67
New Brunswick	1960	Germany	200
	1965	Germany	155
Balaustium sp.			
Quebec	1967	Pakistan	198
Ballia eucharis Mulsant			
New Brunswick	1959	Pakistan	89
Bdella muscorum Ewing and *Neomolgus* sp. nr. *thorianus* (Berlese)			
Quebec	1967	Pakistan	18
Chrysopa spp.			
New Brunswick	1965	India	17
		Pakistan	1
	1966	Pakistan	768
Coccinella septempunctata L.			
New Brunswick	1960	India	31
Cremifania nigrocellulata Czerny			
New Brunswick	1966	Germany	36
Exochomus lituratus Gorham			
Nova Scotia	1963	Pakistan	970
New Brunswick	1959	Pakistan	242
	1964	Pakistan	23
Exochomus uropygialis Mulsant			
New Brunswick	1959	Pakistan	11
	1964	Pakistan	100
Laricobius erichsonii Rosenhauer			
New Brunswick	1965	Germany	61
	1968	Germany	1201
		Switzerland	255
Quebec	1968	Germany	74
Leis dimidiata (Fabricius)			
New Brunswick	1959	India	62
Leucopis spp.			
New Brunswick	1965	India	95
Leucopis (*Leucopis*) sp. 'M'			
New Brunswick	1960	Germany	419
	1966	Germany	226
	1967	Turkey	325
	1968	Germany	586
Leucopis (*Neoleucopis*) *obscura* Holiday			
Newfoundland	1965	Austria	55
New Brunswick	1967	Germany, Austria	231
	1968	Austria	305

TABLE XXIV (continued)

Species and Province	Year	Origin	Number
Leucopis (*Neoleucopis*) *atratula* Ratzeburg			
New Brunswick	1965	Germany	60
Metasyrphus lapponicus Zetterstedt			
New Brunswick	1965	Germany	41
	1966	Germany	126
Scymnus pumilio (Weise)			
New Brunswick	1959	Australia	1006
	1960	Australia	145
Synharmonia conglobata (L.)			
New Brunswick	1959	India	19
Tetraphleps abdulghani Ghauri			
New Brunswick	1962	Pakistan	769
	1963	India	340
		Pakistan	129
	1964	Pakistan	75
	1965	Pakistan	123
Tetraphleps raoi Ghauri			
New Brunswick	1963	India	120
	1965	India	2337

TABLE XXV

The native and introduced predator complex of *Adelges piceae* (Ratz.) in Canada in 1968

Native species	Introduced species
New Brunswick, Nova Scotia, and Prince Edward Island	
Anatis quindecimpuncta Oliv.	*Aphidecta obliterata* L.
Chilocorus stigma Say.	*Leucopis* (*Neoleucopis*) spp.
Cnemodon coxalis (Curr.)	*Laricobius erichsonii* Rosen.
Hemerobius humulinus L.	*Pullus impexus* Muls.
Hemerobius stigmaterus Fitch.	*Cremifania nigrocellulata* Cz.
Leucopina americana (Mall.)	
Laricobius rubidus Lec.	
Metasyrphus lapponicus (Zett.)	
Metasyrphus wiedemanni (Johns.)	
Mulsantina hudsonica Csy.	
Syrphus torvus O. S.	
Tetraphleps canadensis Prov.	
Newfoundland	
Tetraphleps uniformis Parsh.	*Aphidecta obliterata* L.
Tetraphleps latipennis Van. D.	*Aphidoletes thompsoni* Möhn.
Tetraphleps canadensis Prov.	*Laricobius erichsonii* Rosen.
Chrysopa sp.	*Leucopis* (*Neoleucopis*) spp.
Hemerobius stigmaterus Fitch.	
British Columbia	
Allothrombium mitchelli Davis	*Aphidoletes thompsoni* Möhn.
Anystis sp.	*Laricobius erichsonii* Rosen.
Hemerobius sp.	
Leucopis sp.	
Metasyrphus aberrantis (Curr.)	
Neocnemodon rita (Curr.)	
Scymnus phelpsii Cress.	

LITERATURE CITED

1. Amman, G. D. & Speers, C. F. (1964). Release of predators of the balsam woolly aphid in North Carolina. *Res. Note, U.S. Dep. Agric. For. Serv.*, SE–32, 4 pp.
2. Balch, R. E. (1952). Studies of the balsam woolly aphid, *Adelges piceae* (Ratz.) and its effects on balsam fir, *Abies balsamea* (L.) Mill. *Can. Dep. Agric. Publ.* 867, 76 pp.
3. Blais, J. R. (1965). Discovery of the balsam woolly aphid, *Adelges piceae* (Ratz.), on the Magdalen Islands. *Bi-mon. Progr. Rep., Can. Dep. For.* 21 (1): 1–2.
4. Brown, N. R. & Clark, R. C. (1957). Studies of the predators of the balsam woolly aphid, *Adelges piceae* (Ratz.) (Homoptera-Adelgidae). IV. *Neoleucopis obscura* (Hal.) (Diptera: Chamaemiidae), an introduced predator in Eastern Canada. *Can. Ent.* 89: 533–46.
5. Brown, N. R. & Clark, R. C. (1959). Studies of the predators of the balsam woolly aphid, (*Adelges piceae* (Ratz.) (Homoptera: Adelgidae). VI. *Aphidecta obliterata* (L.) (Coleoptera: Coccinellidae), an introduced predator in Eastern Canada. *Can. Ent.* 91: 596–9.
6. Bryant, D. G. (1963). Notes of *Laricobius erichsonii* an introduced predator of the balsam woolly aphid in Newfoundland. *Bi-mon. Prog. Rep., Can. Dep. For.* 19 (6): 1.
7. Bryant, D. G. (1968). Effect of sumithion on the balsam woolly aphid in Newfoundland. *Bi-mon. Res. Notes, Can. Dep. Fish. For.* 24: 47.
8. Carrow, J. R. & Graham, K. (1968). Nitrogen fertilization of the host tree and population growth of the balsam woolly aphid, *Adelges piceae* (Homoptera: Adelgidae). *Can. Ent.* 100: 478–85.
9. Clark, R. C. & Brown, N. R. (1958). Studies of predators of the balsam woolly aphid, *Adelges piceae* (Ratz.) (Homoptera: Adelgidae). V. *Laricobius erichsonii* Rosen. (Coleoptera: Derodontidae), an introduced predator in Eastern Canada. *Can. Ent.* 90: 657–72.
10. Clark, R. C. & Brown, N. R. (1961). Studies of predators of the balsam woolly aphid, *Adelges piceae* (Ratz.) (Homoptera: Adelgidae). IX. *Pullus impexus* (Muls.) (Coleoptera: Coccinellidae), an introduced predator in Eastern Canada. *Can. Ent.* 93: 1162–8.
11. Clark, R. C. & Brown, N. R. (1962). Studies of predators of the balsam woolly aphid, *Adelges piceae* (Ratz.) (Homoptera: Adelgidae). XI. *Cremifania nigrocellulata* Cz. (Diptera: Chamaemyiidae), an introduced predator in Eastern Canada. *Can. Ent.* 94: 1171–5.
12. Dickson, W. A. (1968). Forest Improvement Committee Report. *In A. Rep. Nfld For. Prot. Assoc.* (1968), 67 pp.
13. Eichhorn, O. (1969). Naturliche Verbreitungsareale und Einschleppungsgebiete der Weisseannen-Wollause (Gattung *Dreyfusia*) und die Moglichkeiten ihrer biologischen Bekampfung. *Z. angew. Ent.* 63 (2): 113–31.
14. Greenbank, D. O. (1970). Climate and the ecology of the balsam woolly aphid. *Can. Ent.* 102: 546–78.
15. Harris, J. W. E., Allen, S. J., Collis, D. G. & Harvey, E. G. (1966). Studies of the balsam woolly aphid *Adelges piceae* (Ratz.) in British Columbia. *Can. Dep. For., For. Res. Lab., Victoria. Inform. Rep. B.C.-X*-5, 5 pp.
16. Jahn, E. & Sinreich, A. (1961). Verbreitung der Tannen-trieblaus *Dreyfusia nusslini* C.B. in Österreich and neue Methoden der Bekämpfund. *Anz. Schädlingsk.* 34: 97–102.
17. Martineau, R. (1965). *Rep. Forest Insect Dis. Surv. Can.* 1964: 43–7.
18. McGugan, B. M. & Coppel, H. C. (1962). Biological control of forest insects 1910–1958. *In* A review of the biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol. Contr.* 2: 35–127.
19. Mitchell, R. G. & Wright, R. H. (1967). Foreign predator introductions for control of the balsam woolly aphid in the Pacific Northwest. *J. econ. Ent.* 60: 140–7.
20. Pschorn-Walcher, H. (1964). Comparison of some *Dreyfusia* (*Adelges*) infestations in Eurasia and North America. *Tech. Bull. Commonw. Inst. biol. Contr.* 4: 1–20.
21. Randall, A. P., Hopewell, W. W. & Nigam, P. C. (1967). Chemical control studies on the balsam woolly aphid (*Adelges piceae* (Ratz.)). *Can. Dep. For. Rural Dev., Bi-mon. Res. Notes* 23: 19.
22. Schimitschek, E. (1952). Ein neur entomophager Phiz and *Dreyfusia nusslini* C.B. *Anz. Schädlingsk.* 23: 115–6.
23. Smith, R. K. (1964). Fraser fir stands threatened. *Forest Farmer* 23 (5): 8–10.

37. *CHORISTONEURA FUMIFERANA* (CLEMENS), SPRUCE BUDWORM (LEPIDOPTERA: TORTRICIDAE)

C. A. Miller and T. A. Angus

PEST STATUS

The outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clemens), that caused severe damage to unsprayed pulpwood forests in eastern Canada in the 1940's and 1950's had largely subsided by the late 1950's. In Ontario and western Quebec, populations had collapsed, whereas in the

Lower St. Lawrence-Gaspé areas of Quebec and New Brunswick, the last major region to be attacked, large-scale spraying operations coupled with unfavourable weather had drastically reduced the extent of severely defoliated areas. By 1959 a total population collapse appeared imminent. However, a resurgence occurred in the early 1960's in New Brunswick and, although it was largely confined to the central part of the province from 1960 to 1966, its severity necessitated continued aerial spraying to save susceptible softwood stands. Favourable weather in 1967 and particularly 1968 triggered an increase in the extent of the New Bunswick outbreak and by 1970 it is expected that the budworm will still be abundant and causing appreciable defoliation in the central and southern areas of the province. The budworm is also increasing in Ontario and Quebec. After a period of scarcity in the early 1960's, severe defoliation was noted in northwestern Ontario (40,000 acres) in 1967 and an attempt was made to contain this infestation by aerial spraying in 1968. Defoliation was also recorded in northeastern Ontario and in the Ottawa River valley. These increases over widely scattered areas of eastern Canada may be the forerunners of extensive outbreaks in the 1970's.

Outbreaks of spruce budworm have been recorded in British Columbia and other parts of western Canada but they have not caused serious losses.

BACKGROUND

The lack of success from introducing parasites from western Canada and Europe into eastern Canada in the 1950's, and failure to show that native budworm parasites exert any significant regulation (7) tended to dampen interest in new introductions. However, prolongation of the central New Brunswick outbreak and new background information on parasites of *Choristoneura* spp. (11, 12) renewed interest and in 1966 and 1967 unsuccessful attempts were made to obtain the following species, which attack *C. murinana* (Hbn.) from Europe: *Apanteles murinanae* Čapek and Zwölfer; *Cephaloglypta murinanae* (Bauer); *Phaeogenes maculicornis* Steph. We were particularly interested in these species because they are relatively specific to *C. murinana* and could complete their life cycle on *C. fumiferana* without reliance on an alternate host. Also more data are available on the oviposition behaviour of *C. murinanae* and *P. maculicornis* under laboratory conditions (6). To date, population levels of the host, *C. murinana*, have been too low to supply material for experimental studies or releases in Canada.

Detailed field and experimental studies of virus diseases of the spruce budworm have also failed to reveal an effective biological control agent. These studies are continuing.

More promising results have been attained with *Bacillus thuringiensis* Berliner. Although it had long been known that certain isolates of spore-forming bacteria were pathogens of some insects it was not until after 1954 that the importance of parasporal inclusion protein as an aid to infection was demonstrated (1, 8). The bacterial species now referred to as *Bacillus thuringiensis* was shown to be an effective pathogen for a wide range of Lepidoptera including the spruce budworm, *Choristoneura fumiferana* (2). In 1959 wettable powder formulations of commercially produced *B. thuringiensis* became available and their usefulness was evaluated in limited field trials.

EVALUATION OF CONTROL ATTEMPTS

PARASITES

There have been no releases of parasites against the spruce budworm since 1958 and attempts to transfer budworm parasites from western to eastern Canada during the 1950's met with failure.

DISEASES

Bacillus thuringiensis was tested against the spruce budworm in New Brunswick in 1960. The material utilized was Thuricide concentrate SO–75 containing 60 billion spores per gram, manufactured by the Bioferm Corporation of Wasco, Calif., U.S.A. (now part of International Minerals and Chemical Corporation, Skokie, Illinois). At this time the Thuricide formulation was based on the *Berliner* serotype of *B. thuringiensis* (3). The method of spray formulation, toxicity, diagnosis and bacteriological assay of spray deposit has been described elsewhere (4).

The Thuricide formulation was applied at a rate of 2 pounds per acre in furnace oil (1 U.S. gal) and also in water (1 U.S. gal) on two 30-acre plots. A 30-acre control plot was treated with 12½ per cent. DDT in oil at 1 gal per acre.

Counts of colonies growing on petri plates of nutrient agar that had been exposed in the spray plots immediately before spraying revealed that the deposit was almost uniformly higher than 500 colonies per plate and that the counts declined with distance from the flight path swaths; a few colonies still appeared 2,000 feet downwind. Larvae collected about 8 hours after spraying were reared in the laboratory at room temperature. Mortality was observed in about 100 hours and vegetative rods of *B. thuringiensis* were present in dead larvae.

Field sampling at 3-day intervals did not reveal any clearly defined reduction of population in the Thuricide-treated plots whereas the DDT-treated plots showed about a 95 per cent. reduction. It was found that most of the dead larvae in the Thuricide-treated plots were contaminated with *B. thuringiensis* and a higher percentage of dead insects occurred in these plots than in the control plot. The maximum differences between the control and treated plots were: oil-Thuricide, 31 per cent. on 16 June; water-Thuricide, 22 per cent. on 16 June; and DDT, 66 per cent. on 9 June. Development of the Thuricide-treated population appeared to be retarded, possibly because the larger, more rapidly feeding larvae were killed.

It was concluded that although *B. thuringiensis* (formulation Thuricide SO–75) had produced some insecticidal effect as applied, this was not sufficiently high to warrant consideration of its use in place of DDT (10).

RECOMMENDATIONS

A considerable body of knowledge has been accumulated on the characteristics of large-scale spruce budworm outbreaks and the following points should be considered in planning further attempts at biological control of this serious pest:

(1) The extent and severity of spruce budworm outbreaks are such that, at or near the peak of an outbreak, only the application of a direct and very lethal control agent will ensure survival of host trees in vulnerable stands. The probability that a control agent with a lagging numerical response (parasites) might be effective under such circumstances is not high enough to warrant the risk of large-scale tree mortality.

(2) If the climate (warm, dry summers) and food supply (contiguous stands of maturing balsam fir) are optimal, the budworm can increase from less than five small larvae per tree to 20,000 per tree in the interval of six generations. This could severely tax the effectiveness of an introduced biological control agent with a lagging numerical response as opposed to one with a direct density dependent action. The lack of a regulatory effect among native parasites supports this conclusion.

(3) As an outbreak develops, budworm adults tend to disperse over wide areas. This 'escape' mechanism limits the effectiveness of those parasites and predators that are less dispersive.

(4) Studies of past budworm outbreaks (5) have revealed eight 'outbreak regions' in eastern North American and Blais has also tabulated the frequency of outbreaks in these regions. It is further suspected, but yet to be proven, that sub-areas or epicentres exist within these regions where the local environment (food quantity, food quality, local climate, etc.) permit and enhance the initial release of a budworm population. If this assumption is correct then it is within these epicentres and during the pre-release phase of a budworm population cycle that control studies and experiments must be largely directed. We require a biological agent that will operate at a low pest density and, supplemented with management of the food supply, will minimize the explosive potential of a budworm population.

Furthermore, management of both the host and pest should insure that the pest population peaks below the density level that results in an economic loss.

(5) A comparison of the severe tree mortality in unsprayed check areas in New Brunswick in the 1950's and the very low degree of mortality in sprayed areas clearly indicates man's ability to save a forest in the face of a severe budworm outbreak. Some would argue, however, that the cost in environmental pollution is too high, particularly if DDT is used exclusively. Tests with *B. thuringiensis* in 1960 were conducted as an attempt to reduce pollution problems. Although the results were not too encouraging, commercial formulations have been improved since that time in a number of ways: stable emulsions are now available; toxicity of preparations has been increased; more effective stickers are available; resistance to the destructive effects of sunlight on spores has been increased. However, recent trials (1963) by Klein and Lewis (9) indicate that further improvements are required especially in the field of application techniques.

In view of the continued and substantial improvements that are being made in commercial preparations of *B. thuringiensis*, trials of the best products available should be conducted periodically against the budworm as improvements in formulations warrant. A second small-scale aerial application of this organism was made in New Brunswick during the 1969 field season, but results are not yet available.

As pointed out above, once a budworm population has been 'released', parasites have very little regulating effect. In spite of this there is the possibility that a more efficient parasite complex would greatly reduce the chances of such 'releases' taking place. Attempts to improve the budworm parasite complex should continue. As soon as European populations of *C. murinanae* reach levels where it becomes feasible to collect sufficient numbers of parasites, introductions of the three parasite species, *A. murinanae*, *C. murinanae* and *P. maculicornis* should be attempted.

LITERATURE CITED

1. Angus, T. A. (1956). The reaction of certain lepidopterous and hymenopterous larvae to *Bacillus sotto* toxin. *Can. Ent.* 88: 280–3.
2. Angus, T. A. & Heimpel, A. M. (1959). Inhibition of feeding, and blood pH changes, in lepidopterous larvae infected with crystal-forming bacteria. *Can. Ent.* 91: 352–8.
3. Angus, T. A. (1968). The use of *Bacillus thuringiensis* as a microbial insecticide. *Wld Rev. Pest Control* 7: 11–26.
4. Angus, T. A., Heimpel, A. M. & Fisher, R. A. (1961). Spray formulation, toxicity, diagnosis, and bacteriological assay of spray deposit. *Bi-mon. Prog. Rep., Can. Dep. For.* 17: 1–2.
5. Blais, J. R. (1968). Regional variation in the susceptibility of eastern North American forests to budworm attack based on history of outbreaks. *For. Chron.* 44 (3): 17–23.
6. Capek, M. (1967). Parasites of *Choristoneura murinana* (Hb.), pp. 185–95. *In* Preservation of forests in Slovakia. Publishing House Slovak Academy of Sciences, Bratislava.
7. Miller, C. A. (1963). Parasites and the spruce budworm, pp. 228–41. *In* The dynamics of epidemic spruce budworm populations. *Mem. ent. Soc. Can.* 31, 332 pp.
8. Heimpel, A. M. & Angus, T. A. (1960). Bacterial insecticides. *Bacteriol. Rev.* 24: 266–88.
9. Klein, W. H. & Lewis, F. B. (1966). Experimental spraying with *Bacillus thuringiensis* for control of the spruce budworm. *J. For.* 64: 458–62.
10. Mott, D. G., Angus, T. A., Heimpel, A. M. & Fisher, R. A. (1961). Aerial spraying of Thuricide against the spruce budworm in New Brunswick. *Bi-mon. Prog. Rep., Can. Dep. For.* 17 (3): 2.
11. Zwölfer, H. (1961). A comparative analysis of the parasite complexes of the European fir budworm, *Choristoneura murinana* (Hb.) and the North American spruce budworm, *C. fumiferana* (Clem.). *Tech. Bull. Commonw. Inst. biol. Contr.* 1, 162 pp.
12. Zwölfer, H. (1968). Die parasitenkomplexe due Europaischen und Nordamerikanischen tannenwickler (*Choristoneura* spp., Lep. Tortricidae) in Biogeographischer sicht. *Z. angew. Ent.* 61: 448–52.

38. *COLEOPHORA LARICELLA* (HÜBNER), LARCH CASEBEARER (LEPIDOPTERA: COLEOPHORIDAE)

F. E. Webb and F. W. Quednau

PEST STATUS

The larch casebearer, *Coleophora laricella* (Hübner), now occurs throughout the range of tamarack in the Atlantic Provinces and as far north as 49–50° N. latitude in Quebec and Ontario. During the past 10 years, it has been discovered progressively westward from Lake Superior to the Manitoba border in western Ontario (Fig. 11) and in 1965 was discovered in the extreme southeastern corner of Manitoba (5).

Outbreaks have been reported in all eastern provinces in the past decade but these have been relatively local and of short duration. This represents a significant change from earlier decades when outbreaks tended to be widespread and of greater intensity, particularly in newly invaded areas. This change is attributed to the action of two introduced parasites, *Agathis pumila* (Ratz.) and *Chrysocharis laricinellae* (Ratz.). European collections of both species were released in the Atlantic Provinces and southern Quebec and Ontario from the mid 1930's to the mid 1940's (7). The last major outbreak of the casebearer in eastern Canada occurred in the late 1940's and early 1950's in newly invaded areas of central Ontario where the introduced parasites had not then become established. Additional relocations of *A. pumila* in northern Michigan in 1951 and in Wisconsin in 1953 assisted in colonizing this species at the forefront of the spreading infestation and help to explain its appearance in northwestern Ontario almost simultaneously with the host. Indeed, the simultaneous spread of parasite and host in recent years may account, in part, for the failure of the casebearer to appear in epidemic proportions in these newly invaded areas (17).

The most important development in the spread of the casebearer in recent years was its appearance on western larch, *Larix occidentalis* Nutt., in northwestern United States and southeastern British Columbia. It was first noticed in north-central Idaho in 1957 (2) and in British Columbia in 1966 (1). Its current distribution includes most of the western larch in Washington, Idaho and Montana[1] and a strip of approximately 200 miles along the international boundary in British Columbia (Fig. 11).

The initial outbreak on western larch in the United States followed a similar pattern to that of early outbreaks on tamarack in eastern North America. Lack of effective natural control permitted a tremendous population increase and rapid spread within a few years of its introduction. High populations have persisted over wide areas for 10 years or longer and have resulted in serious damage to host stands.[1] This is in contrast to the sporadic, short-lived outbreaks that now characterize this insect's occurrence in the east.

In 1960, about 2,500 adult *A. pumila* obtained from infestations in eastern United States were released at the original infestation point in Idaho. Recoveries in 1962 and 1963 confirmed the successful establishment of the parasite (2). In 1964, a large-scale programme was undertaken to propagate additional collections of *A. pumila* from eastern states and to colonize the species more widely in the newly infested areas. Unpublished reports[1] indicate that a measure of success has been achieved in establishing the parasite at widely distributed release points, but that natural spread of the parasite from these points thus far has been limited. *A. pumila* has not yet been found in British Columbia but is expected to spread northward from United States releases near the border.

BACKGROUND

A number of important studies of the larch casebearer and its parasites have been published in the past decade. A monograph by Eidmann (4) represents the most comprehensive study yet

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[1] Denton, R. E. United States Forest Service, Moscow, Idaho. Personal communication.

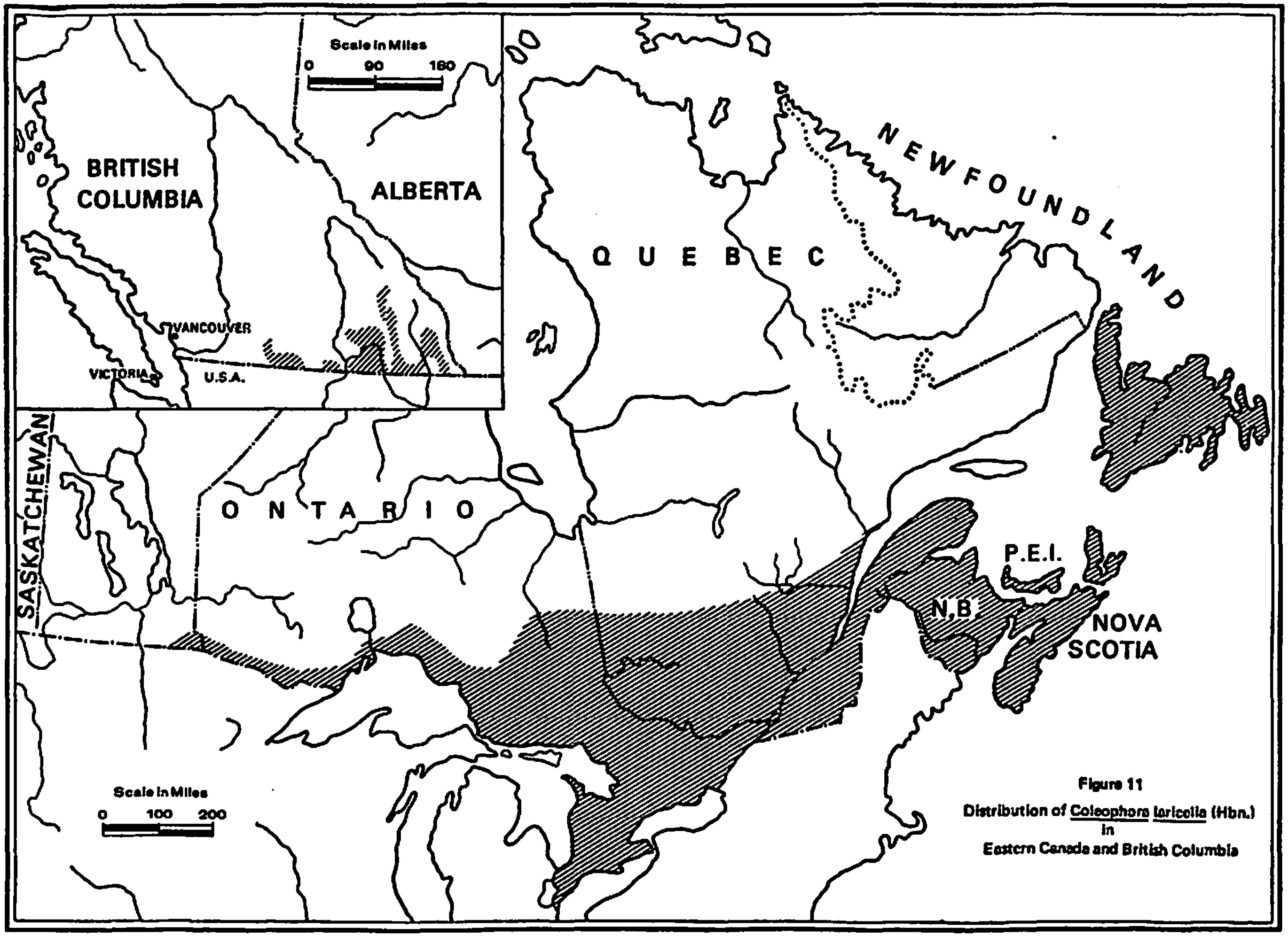

Figure 11
Distribution of *Coleophora laricella* (Hbn.)
in
Eastern Canada and British Columbia

published of this insect and includes original research on its biology, physiology and population behaviour in Sweden. Other European studies suggest that population increases are a function of suitable weather during the periods of adult emergence, copulation and oviposition, of site conditions, and of the vigour of foliage growth on the host (15, 16). Schindler (15) found that parasitism in Germany was related to climatic conditions.

Studies by Sloan (18) and Sloan and Coppel (19, 20, 21, 22) add to the knowledge of the factors influencing population behaviour of the larch casebearer in North America. A model life equation was attempted by these authors for the conditions in the University of Wisconsin Arboretum, 1962–4 (20). Climate, weather, avian predation on overwintering cases, invertebrate predators of eggs, and native and introduced parasites all were found to be implicated in population fluctuations.

Canadian studies of the larch casebearer during the past decade have been centered in the Quebec Laboratory of the Canadian Forestry Service. The results of studies by Quednau (8, 9, 10, 11, 12, 13, 14) of the biology, behaviour and effectiveness of *A. pumila* and *C. laricinellae* in the Quebec Region are detailed below.

RELEASES AND RECOVERIES

No releases or relocations of imported parasites have been made in Canada in the past 10 years. The following importations were used for laboratory cage studies.

Species and province	Year	Origin	Number
Chrysocharis laricinellae (Ratz.) Quebec	1967	France, Austria and Germany	509
Diadegma nana (Grav.) Quebec	1968	Austria	35

PARASITES

Chrysocharis laricinellae (Ratz.), (Hymenoptera: Eulophidae)

C. laricinellae is well established throughout the Atlantic Provinces and in southern Quebec and Ontario. The extent of its occurrence in the northern fringe of the host's range in Quebec and Ontario and in the newly invaded areas of northwestern Ontario is less certain, but scattered recoveries from the casebearer and alternate hosts suggest that it is almost as widely distributed as the casebearer but relatively rare in the fringe areas.

The life history and behaviour of this multivoltine parasite has been studied in detail by Quednau (8, 11). The species is long-lived as an adult but cannot breed in the small needle-mining stages of the casebearer and has only limited success in parasitizing the pupal stage (10). Because this parasite depends on good synchronization with the case-dwelling larval stage of the host, and on suitable stages of alternate hosts, control is reduced in years when host development is delayed by cool periods in early summer and autumn. In years of favourable weather, parasitism may reach 60 per cent. and there may be as many as four generations per year (13).

Agathis pumila (Ratz.), (Hymenoptera: Braconidae)

Although recovery records (7) suggest that this univoltine species colonized more slowly than *C. laricinellae* in the Atlantic Provinces, it is now the more widely and uniformly distributed of the two species and has shown a remarkable ability to keep pace with the host in invading new territory[1] (17). Quednau (14) believes that the species is well synchronized with its host during warm summers on the North American continent and as a consequence of this is a more effective control agent than

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[1] Cody, J. B. (1963). Unpublished M.F. thesis, University of Michigan, Ann Arbor, U.S.A.

in the areas of its origin in Europe. Its effectiveness is less evident in the northern fringe of its range, probably owing to less consistent synchronization with the host during the relatively short adult life of the parasite.

A. pumila attacks first- and second-instar larvae and hibernates in the diapausing third-instar of the host. Development continues in the spring while the host continues to feed. The host never pupates but continues to live for up to 2 weeks after the unparasitized hosts have pupated. This sequence results in close synchronization between the emergence of adult parasites and the hatching of host larvae.

Diadegma nana (Grav.), (Hymenoptera: Ichneumonidae)

Although releases of this parasite in Ontario in the 1930's apparently failed, interest in the possibilities of its introduction has continued because of its importance in Europe. In 1968, 35 specimens were imported from Switzerland to Quebec for laboratory studies. Experiments are underway on the autecology of this species and on its coexistence with *A. pumila*.

EVALUATION OF CONTROL ATTEMPTS

The importation of foreign parasites against the larch casebearer in eastern Canada has been cited as an example of successful biological control (23). Considerable support of this evaluation is provided in the annual reports of the Forest Insect and Disease Survey for the past decade, which reveal an absence of periodic mass outbreaks of the type that characterized this insect's occurrence prior to the colonization of the two introduced parasites. Recent studies by Quednau have focused on the biological mechanism by which the two introduced parasites effect significant control of casebearer populations.

Observations by Webb[1] in the early 1950's indicated that each of the successfully introduced parasites is capable of reaching high levels of apparent effectiveness in the absence of the other. Recent releases of *A. pumila* in northwestern United States will provide an additional test of the effectiveness of this species alone, but further study of the effectiveness of one species in the absence of the other would be academic in eastern North America with the spread of both over virtually the entire eastern range of the host.

The existence of a form of mutualistic competition between the two species was first reported by Graham (6) from studies in Ontario during the 1940's. He noted that the presence of casebearer larvae parasitized by *A. pumila* for up to 2 weeks after the pupation of healthy casebearers provided additional opportunity for multiparasitism by *C. laricinellae*, thus improving the synchronization of this species with suitable host material. *C. laricinellae* is the successful competitor in such cases and, therefore, the occurrence of appreciable parasitism by *A. pumila* enhances the opportunity for *C. laricinellae* to complete three generations per year and to contribute significantly to the reduction of the casebearer population. Observations by Cody[2] in Michigan also indicated that where both species were present in relatively high infestations of the casebearer, *A. pumila* increased first to a point where it provided sufficient hosts to enable *C. laricinellae* to produce a large third generation. He hypothesized that the reduction in the numbers of *A. pumila* that results inevitably reduces the population of *C. laricinellae* the following season and that at very low host densities, this extrinsically inferior species may depend on alternate hosts for survival.

Quednau (13) has used the life-table approach to analyse the mechanism of this interaction and concludes that it is essentially cooperative and potentially host-regulative. Although intrinsic competition sacrifices part of the *A. pumila* population, it helps *C. laricinellae* to increase to the point at which it may become host-regulative by massive attack. Extrinsic competition of *C. laricinellae* with *A. pumila* is counteracted by a notable decline of the populations of both *A. pumila* and the casebearer

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[1] Webb, F. E. (1953). Unpublished Ph.D. thesis, University of Michigan, Ann Arbor, U.S.A.

[2] Cody, J. B. (1963). Unpublished M.F. thesis, University of Michigan, Ann Arbor, U.S.A.

after the interaction and by other factors. Competitive displacement of *A. pumila* by *C. laricinellae* is prevented by the extrinsic superiority of the former at low host densities. Quednau hypothesizes that *A. pumila* alone cannot become host regulative, but that through cooperative interaction with *C. laricinellae*, it is able to contribute significant partial control of the larch casebearer.

The validity of Quednau's hypothesis when applied to host-parasite interactions in western larch types is uncertain due to a lack of knowledge of the comparative influence of other regulatory factors, notably climate. Some clarification of this may be forthcoming from the degree of success achieved by the recent colonization programme.

The limited commercial values represented by tamarack in recent years and the effectiveness of the imported parasites have thus far obviated the need for chemical control measures in eastern Canada. The threat of serious losses in the higher-value stands of western larch, however, prompted tests of aerial applications of various insecticides in 1962 and 1963 (3).

RECOMMENDATIONS

Life-table studies now underway in Quebec should be continued for several casebearer generations to establish the validity of the hypotheses developed thus far by Quednau. Results of current studies by entomologists in northwestern United States will be watched with interest in relation to the need for releases of introduced parasites in British Columbia.

A second attempt to colonize *D. nana* in eastern Canada is under consideration. The object of this would be to supplement the already established parasites by additional sequential parasitism on small casebearing larvae that are unsuitable as hosts for *A. pumila*. This species would also offer further aid to *C. laricinellae* by prolonging the development of parasitized hosts. Mass rearing methods are being developed to provide sufficient stocks of *D. nana* for effective releases.

LITERATURE CITED

1. Andrews, R. J. (1966). First record of the larch casebearer on western larch in British Columbia. *Bi-mon. Res. Notes, For. Br., Dep. For. Rural Dev.*, **22** (6): 3.
2. Denton, R. E. (1965). Larch casebearer in western larch forests. *Forest Pest Leaflet 96, U.S. For. Serv., U.S. Dep. Agric.*, 6 pp.
3. Denton, R. E. & Tunnock, S. (1968). Low-volume application of Malathion by helicopter for controlling the larch casebearer. *J. econ. Ent.* **61**: 582–3.
4. Eidmann, H. H. (1965). Ökologische und physiologische Studien über die Lärchenminiermotte, *Coleophora laricella* Hbn. *Studia Forestalia Suecica* **32**, 1–226.
5. Elliott, K. R. & Hildahl, V. (1966). First record of the larch casebearer in Manitoba. *Bi-mon. Res. Notes, For. Br., Dep. For. Rural Dev.*, **22** (4): 3–4.
6. Graham, A. R. (1958). Effectiveness of two introduced parasites of the larch casebearer, *Coleophora laricella* (Hbn.) (Lepidoptera: Coleophoridae), in Ontario. *88th Rep. ent. Soc. Ont.* 37–41.
7. McGugan, B. M. & Coppel, H. C. (1962). Biological control of forest insects, 1910–1958. *In* A review of the biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol. Contr.* **2**: 35–127.
8. Quednau, F. W. (1966). Notes on life-history and morphology of *Chrysocharis laricinellae* (Ratz.) (Hymenoptera: Eulophidae), a parasite of the larch casebearer (*Coleophora laricella* (Hbn.)). *Ann. ent. Soc. Quebec* **11**: 200–5.
9. Quednau, F. W. (1967). Notes on mating, oviposition, adult longevity and incubation period of eggs of the larch casebearer, *Coleophora laricella* (Lepidoptera: Coleophoridae), in the laboratory. *Can. Ent.* **99**: 397–401.
10. Quednau, F. W. (1967). Ecological observations on *Chrysocharis laricinellae* (Hymenoptera: Eulophidae), a parasite of the larch casebearer (*Coleophora laricella*). *Can. Ent.* **99**: 631–41.
11. Quednau, F. W. (1967). Notes on mating behaviour and oviposition of *Chrysocharis laricinellae* (Hymenoptera: Eulophidae), a parasite of the larch casebearer (*Coleophora laricella*). *Can. Ent.* **99**: 326–31.
12. Quednau, F. W. (1968). Distribution and effectiveness of larch casebearer parasites in southwestern Quebec. *Bi-mon. Res. Notes, For. Br., Dep. For. Rural Dev.*, **24**: 22–3.
13. Quednau, F. W. (1970). Competition and cooperation between *Chrysocharis laricinellae* and *Agathis pumila* in larch casebearer populations in Quebec. *Can. Ent.* **102**: 602–12.
14. Quednau, F. W. (1970). Notes on life-history, fecundity, longevity, and attack pattern of *Agathis pumila* (Hymenoptera: Braconidae), a parasite of the larch casebearer. *Can. Ent.* **102**: 736–45.

15. Schindler, U. (1968). Massenwechsel eines typischen forstlichen Dauerschädlings, der Larchenminiermotte *Coleophora laricella* (Hbn.). *Z. angew. Ent.* **61**: 380–6.
16. Schwenke, W. (1958). Über die Standortsabhängigkeit des Massenwechsels der Larchenminiermotte, *Coleophora laricella* (Hbn.) und der Ahorneule *Acronycta aceris* L. *Beitr. Ent.* **8**: 241–90.
17. Sippell, W. L., Dance, B. W. & Rose, A. H. (1966). Ontario Region. *Rep. Forest Insect Dis. Surv. Can.* 1965: 44–65.
18. Sloan, N. F. (1965). Biotic factors affecting populations of the larch casebearer, *Coleophora laricella* (Hbn.), in Wisconsin. Ph.D. Thesis, Univ. of Wisconsin.
19. Sloan, N. F. & Coppel, H. C. (1965). The insect parasites of the larch casebearer, *Coleophora laricella* (Hbn.) (Lepidoptera: Coleophoridae), in Wisconsin with keys to the adults and mature larval remains. *Wisconsin Acad. Sci. Arts Letters* **54**: 125–46.
20. Sloan, N. F. & Coppel, H. C. (1965). Population fluctuations of the larch casebearer, *Coleophora laricella* (Hbn.), in the University Arboretum, Madison, Wisconsin 1962–1964. *Univ. Wisconsin Res. Notes* **122**, 4 pp.
21. Sloan, N. F. & Coppel, H. C. (1965). Seasonal history and parasite complex of the larch casebearer, *Coleophora laricella* (Hbn.), in Wisconsin. *Univ. Wisconsin Res. Notes* **123**, 6 pp.
22. Sloan, N. F. & Coppel, H. C. (1965). Oviposition patterns and egg predation of the larch casebearer, *Coleophora laricella* (Hbn.), in Wisconsin. *Univ. Wisconsin Res. Notes* **124**, 4 pp.
23. Turnbull, A. L. & Chant, D. A. (1961). The practice and theory of biological control of insects in Canada. *Can. J. Zool.* **39**: 697–753.

39. *DIPRION HERCYNIAE* (HARTIG), EUROPEAN SPRUCE SAWFLY (HYMENOPTERA: DIPRIONIDAE)

M. M. Neilson, R. Martineau and A. H. Rose

PEST STATUS

The European spruce sawfly, *Diprion hercyniae* (Hartig), was considered a major threat to the spruce forests in eastern Canada during the 1930's (1). This threat was largely removed in 1945 with the termination of the infestation in the Gaspé Peninsula and in northern New Brunswick. By 1958 the insect could be relegated, at least in terms of economic importance, to the status of an unimportant insect. The situation has changed very little since then. Although *D. hercyniae* is still one of the more common defoliators found on spruce, populations have seldom exceeded endemic levels anywhere in its range and minor resurgences have been local and of short duration. Changes in its distribution have also been minor (Fig. 12). The insect has still not been reported west of the Ontario-Manitoba border and there have been no significant extensions in its northward spread. Increases in range have been largely confined to the filling in of gaps in the 1959 distribution.

The Forest Insect and Disease Survey has monitored *D. hercyniae* populations annually in all areas since 1959 but the greatly reduced economic importance of this species and the pressures of other commitments have not permitted the special collecting and rearing methods that must be used to obtain valid measurements of mortality from disease and parasitism. As a result, information on the factors that have been responsible for regulating populations of this sawfly at endemic levels throughout its range is somewhat fragmentary. However, Survey data can be used to show substantial differences between regions in both population levels and the relative importance of mortality factors, particularly if the intensive investigations that have been conducted in the Maritimes Region since 1938 are used as a basis for comparison.

MARITIMES

The role of an accidentally introduced nucleopolyhedrosis virus, *Borrelinavirus hercyniae*, and two species of introduced parasites, *Drino bohemica* (Mesn.) and *Exenterus vellicatus* Cush., as key factors in regulating *D. hercyniae* populations at very low levels has been well documented (4, 9). Other mortality factors such as predation of cocoons by small mammals and insects are of lesser importance and tend to damp oscillations about the endemic level. With the exception of a short-

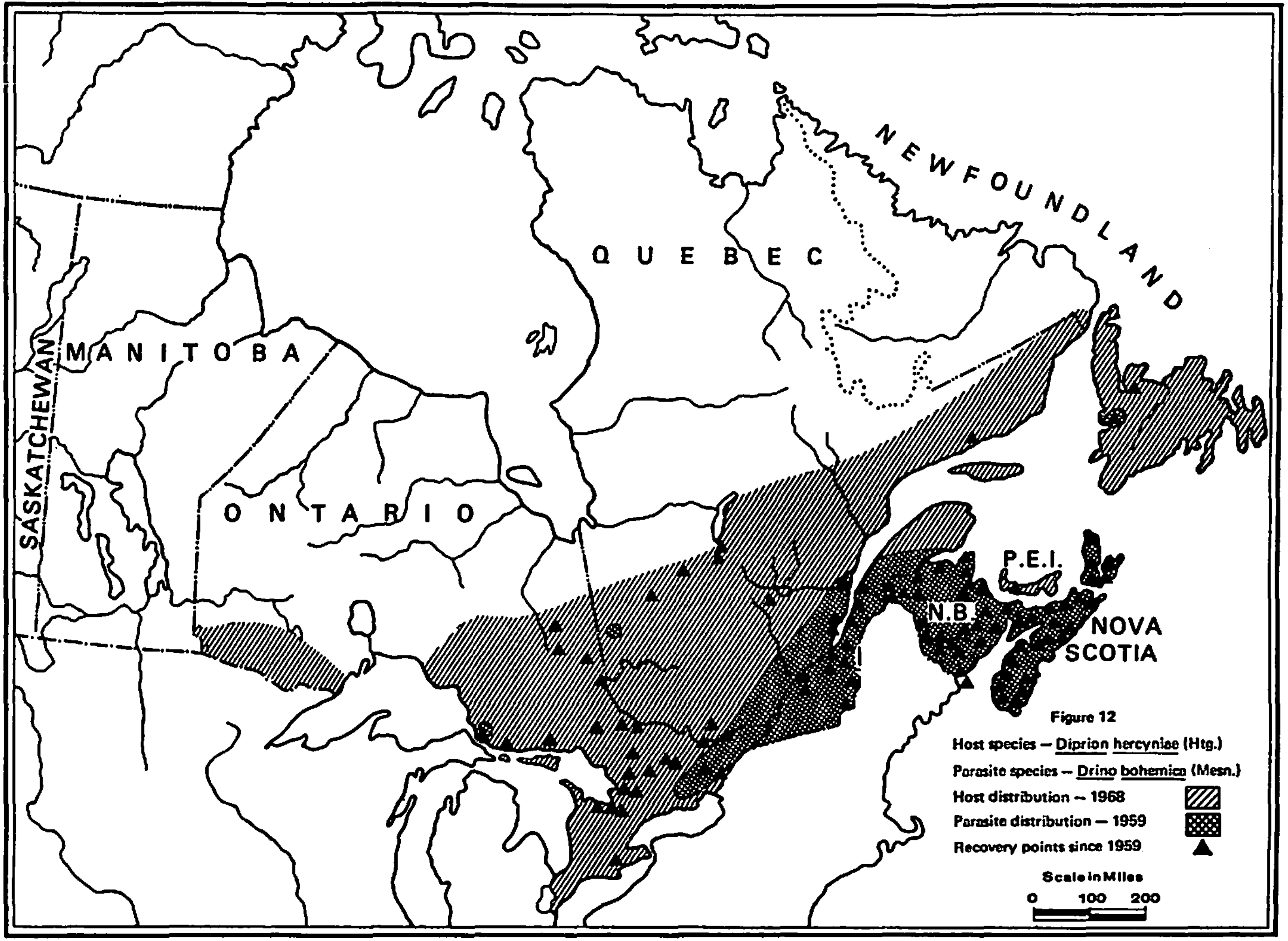

Figure 12

NEWFOUNDLAND
QUEBEC
MANITOBA
SASKATCHEWAN
ONTARIO
P.E.I.
N.B.
NOVA SCOTIA
Host species — Diprion hercyniae (Htg.)
Parasite species — Drino bohemica (Mesn.)
Host distribution — 1968 ▨
Parasite distribution — 1959 ▩
Recovery points since 1959 ▲
Scale in Miles
0 100 200

lived but dramatic population resurgence that occurred in some areas that had been sprayed with DDT, populations in the Maritimes have fluctuated about an average density of less than one insect per tree sample since the end of the outbreak about 1945.

The relative roles of disease and parasitism are difficult to assess because either may be capable of regulating host densities without the presence of the other. Bird and Burk (3) have shown in Ontario that the virus, in the absence of introduced parasites, is able to reduce sawfly populations and maintain them at levels where economic damage will not occur. Similarly, sawfly populations on Grand Manan Island off the coast of New Brunswick have been contained at endemic levels by introduced parasites in the absence of the virus[1] (10). Usually, however, the average host density when only one of these mortality factors is operating is several times higher than when both are present. The virus and introduced parasites seem to constitute an ideal regulating complex. The parasites are effective even at very low host densities and are sensitive to minor fluctuations at these levels. The virus, while less sensitive to minor fluctuations, responds to density changes of greater magnitude or to minor increases of prolonged duration.

NEWFOUNDLAND

D. hercyniae has now spread throughout much of Newfoundland and specimens have been collected almost everywhere substantial numbers of spruce trees have been sampled. Although populations are endemic, fluctuations in densities are much more pronounced than in the Maritimes; samples of 35 larvae or more per tree are not rare and defoliation on isolated clumps of white spruce has occasionally reached 5–10 per cent. These minor increases in density, however, have always been of short duration and have been terminated by a virus epizootic. The virus, first introduced into Newfoundland in 1943, now appears to be widespread. Introduced parasites appear to exert only a minor influence on host populations but their role is uncertain. Only four specimens, two of which were identified, have been recovered over the past decade. These few recoveries, however, do not necessarily reflect the importance nor the true distribution of parasites because in several years larvae were not reared and, when they were, most of them succumbed to the virus.

QUEBEC

D. hercyniae populations in this region have also remained endemic over the past 10 years but have fluctuated about an average density of over five times that in the Maritimes. Martineau (6) concluded from a study of the factors regulating sawfly densities in southern Quebec from 1949 to 1959 that the virus was the key regulating factor and that other sources of mortality, including introduced parasites, exerted only minor influences. No significant changes in this situation have been observed since. Both *D. bohemica* and *E. vellicatus* have been recovered from most of the range of *D. hercyniae* in Quebec but numbers have been small.

ONTARIO

It is difficult to compare Forest Insect and Disease Survey population sampling records for *D. hercyniae* in Ontario with similar records obtained in the Maritimes. Nevertheless, it is obvious that sawfly populations have remained endemic since 1958 throughout the province, and average larval densities have been higher than in the Maritimes. It is also difficult to evaluate the role of controlling factors in this region because records on recoveries and distribution of the virus are not available after 1962. The virus and one species of introduced parasite, *D. bohemica*, however, have become firmly established throughout most of Ontario and appear to be the key population regulators. A comparison of sawfly densities before 1958, when neither the virus nor *D. bohemica* was common, with those since indicate a considerable reduction in densities. Samples of 100 larvae per tree were not uncommon before 1958 and a few samples yielded as many as 400 larvae per tree (10). Average densities since 1958 have been considerably lower (12). Bird and Burk (3) successfully introduced the

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[1] Neilson, M. M. & Elgee, D. E. Department of Fisheries and Forestry, Fredericton, N.B. Unpublished data.

virus into an infestation in the Kirkwood area in 1950 when introduced parasites were rare. Ten years later they concluded that the virus was maintaining sawfly populations below the level where damage of economic consequence would be inflicted. *D. bohemica* has since become more abundant in the area and now roughly equal proportions of the host succumb to the virus and the parasite. However, this increase in importance of the parasite has not been accompanied by a further reduction in host densities.[1]

Neither introduced parasites nor the virus have been recovered from northwestern Ontario and yet densities of *D. hercyniae* have remained endemic. This area may be close to the northern and western limits of the insect and climate may be exerting the controlling influence.

RELEASES AND RECOVERIES

There have been no releases of parasites, predators, or diseases against *D. hercyniae* since 1958. Recoveries after 1958 are discussed below.

PARASITES

Drino bohemica (Mesn.) (Diptera: Tachinidae)

D. bohemica is by far the most common species of parasite recovered from *D. hercyniae.* Although its spread has not always been rapid (120 miles in 12 years in Ontario) it has now been recovered throughout much of the range of its host (Fig. 12). A notable exception is northwestern Ontario where isolated releases were made before 1959 against other sawflies but where no recoveries have been made since. Long-term intensive population studies of *D. hercyniae* in the Maritimes have shown that *D. bohemica* can be recovered from any area where the host occurs if large enough numbers of larvae are collected and reared. This species is also the most sensitive of all mortality factors in responding to minor fluctuations in host densities about endemic levels and, as such, has been the most important factor in regulating sawfly numbers. In Newfoundland, only two recoveries of *D. bohemica* have been made but these are not indicative of the distribution or importance of this species as no special effort has been made in this region since 1958 to rear sawfly larvae for parasite recoveries. In Quebec and Ontario, *D. bohemica* is commonly recovered from *D. hercyniae* but it is not as abundant or as effective in host population regulation as in the Maritimes. Nevertheless, it is well established and still increasing in abundance and distribution in both of these regions.

D. bohemica has been released against and recovered from several other sawfly species. Its distribution with respect to four other hosts is shown in sections of this bulletin. The numbers of recoveries since 1958 from other species of sawflies are as follows:

Species	Province				
	Nfld.	N.S.	N.B.	Que.	Ont.
Croesus latitarsus Nort.	0	1	0	0	0
Neodiprion abietis complex	0	0	0	2	4
Neodiprion nanulus Schedl.	0	1	0	0	6
Neodiprion pratti banksianae Roh.	0	0	0	1	19
Neodiprion pratti paradoxicus Ross	0	0	0	0	3
Neodiprion virginianus complex	0	0	0	1	7
Pikonema alaskensis Roh.	0	0	0	6	10
Pikonema dimmokii Cress.	0	0	0	1	0

Exenterus vellicatus Cush. (Hymenoptera: Ichneumonidae)

E. vellicatus has not been recovered from as many points or in as large numbers in the Maritime Provinces as *D. bohemica*; of 1907 parasite recoveries made since 1958, 274 were *E. vellicatus* while 1630 were *D. bohemica.*

In spite of its lesser occurrence, *E. vellicatus* exerts a substantial effect on host populations, especially in those years when host densities are increasing (10). The proportion of *E. vellicatus* to *D. bohemica* recoveries in Quebec has been much the same as in the Maritimes but both species have been of lesser importance in this region. *E. vellicatus* has not been recovered in Newfoundland or Ontario since 1958. The distribution of recoveries of this species is shown in Fig. 13.

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[1] Bird, F. T. Insect Pathology Research Institute, Sault Ste. Marie, Ontario. Personal communication.

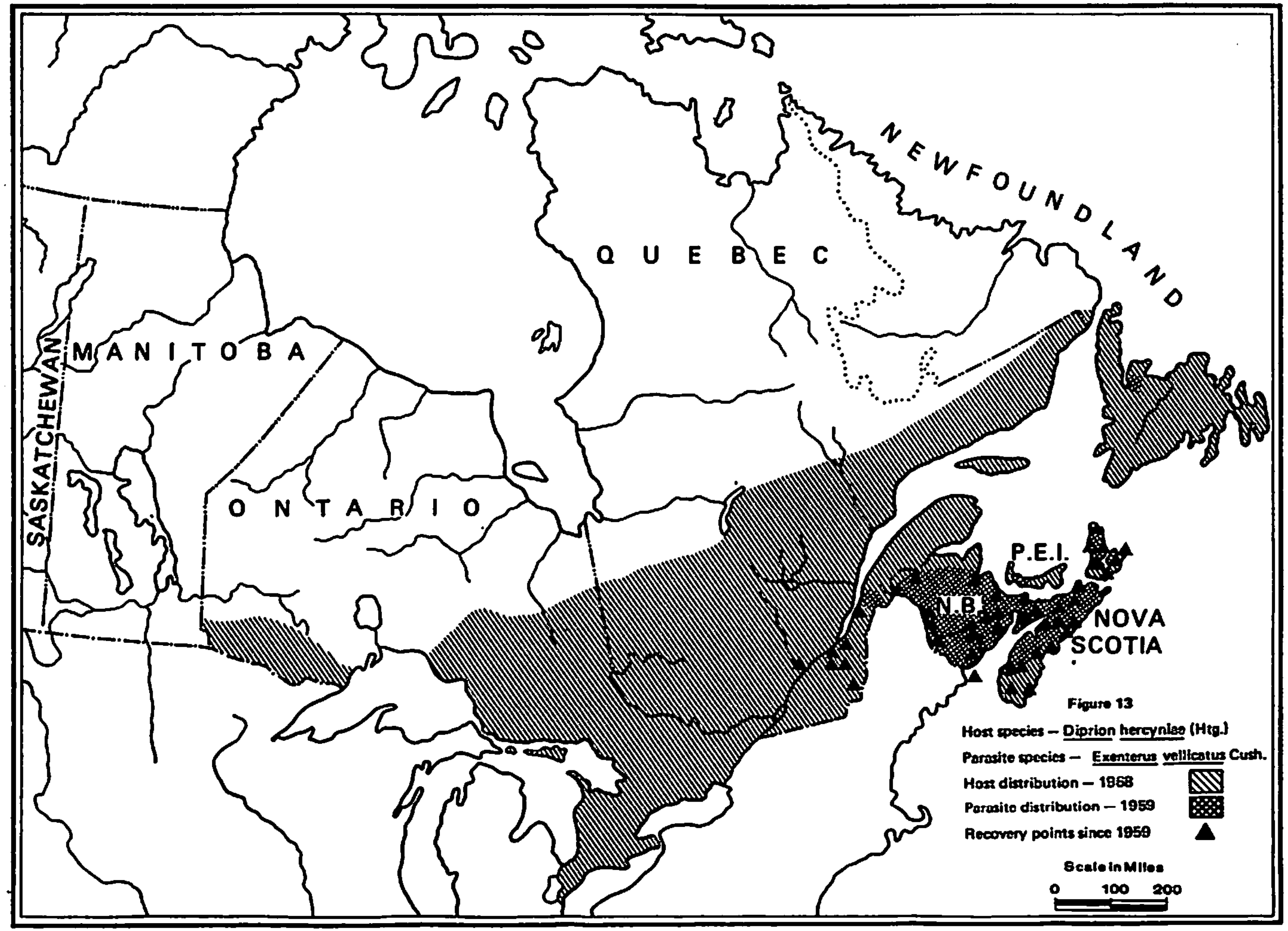

Figure 13

Host species — *Diprion hercyniae* (Htg.)

Parasite species — *Exenterus vellicatus* Cush.

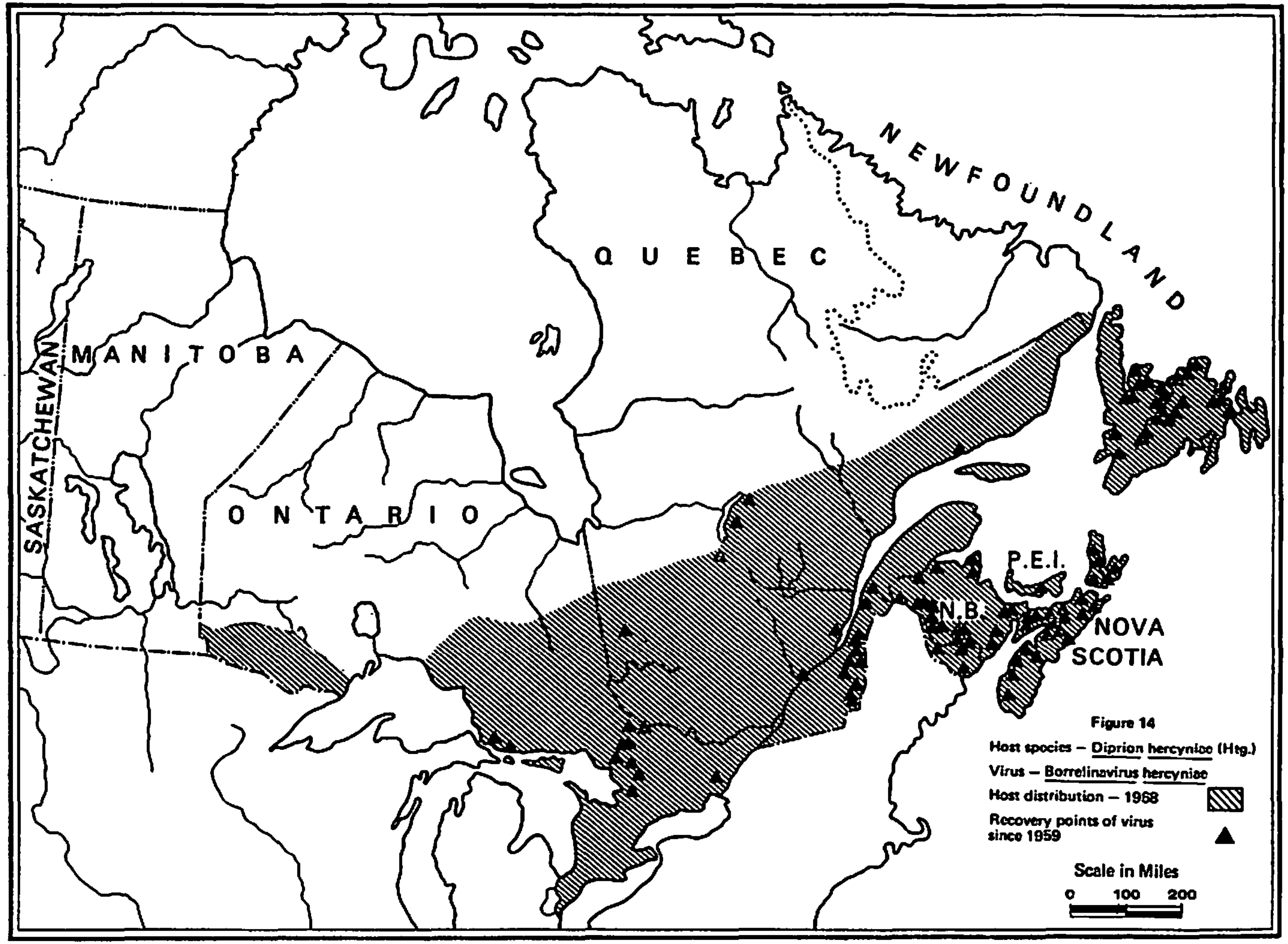

Figure 14

Host species – *Diprion hercyniae* (Htg.)

Virus – *Borrelinavirus hercyniae*

Host distribution – 1968 ▨

Recovery points of virus since 1959 ▲

Exenterus spp.

At least five other species of *Exenterus* were released against *D. hercyniae* in eastern Canada before 1959 (7) but only two of these have been recovered from this host during the past 10 years. *Exenterus amictorius* (Panz.) has been recovered five times in Ontario and once in Quebec; and *Exenterus tricolor* Rom. has been recovered three times in New Brunswick. These two species have no effect on *D. hercyniae* populations, but both are commonly recovered from other sawfly species.

None of the other species of parasites released against *D. hercyniae* before 1959 (7), has been recovered from this host in the past decade.

DISEASES

Borrelinavirus hercyniae

Although there have been no releases of *B. hercyniae* since 1958 this virus has continued to spread within the range of the host and is probably more widely distributed than the recovery points shown in Fig. 14 indicate. This is especially true for Ontario where recoveries are shown only up to 1963. With the exception of rearings of larvae collected near Kirkwood in connection with special virus studies (3), suspected cases of polyhedrosis in rearings of the host collected after 1962 were not checked by examining the insects for polyhedra. Neilson and Elgee (8) have shown that the virus can remain undetected during periods of low host density in spite of intensive larval sampling to detect it. This is evident from the behaviour of the virus in both Newfoundland and Quebec where localized increases in densities of *D. hercyniae* have occurred in areas where larval sampling had been conducted previously without detecting the virus. Such increases have always been short-lived because of the seemingly sudden appearance of the virus. There is little doubt that the virus was actually present in the populations in most of these areas before the increase in host densities, and it is probably present in other areas that have not experienced increases in sawfly densities and where larval sampling to detect the virus produced negative results. This is especially true for Ontario where Reeks (10), concluded as early as 1963 that recovery points for the virus up to 1963 did not adequately portray its distribution.

In the Maritimes, where *D. hercyniae* populations are the lowest of all regions, the virus is nearly always present but it is not as effective in regulating host densities at these low levels as parasites (9). However, in all the other regions host densities are considerably higher and the virus appears to be the key regulating factor.

Notable gaps in the distribution of the virus occur in northwestern Ontario, on Grand Manan Island off the coast of New Brunswick and in Shelburne, Queens and Lunenburg counties of Nova Scotia.

EVALUATION

The threat that the European spruce sawfly once posed to the forest economy of eastern Canada may be appreciated from the immense damage inflicted on spruce stands in the relatively short period from the time it was discovered to the end of the infestation that subsequently developed. About 11,400,000 cords were lost through tree mortality and additional losses were sustained from reductions in increment on surviving trees (11). Before the initiation of the biological programme against this insect a continuation and expansion of the infestation with accompanying increase in losses was indicated. The collapse of the sawfly infestation in eastern Canada by 1945, primarily through the action of an accidentally introduced virus, and the subsequent regulation of sawfly densities at endemic levels by introduced parasites and/or the virus has often been cited as an excellent example of successful biological control (2, 5, 13). This programme and the attendant studies must rank as one of the best documented and most successful attempts to control and regulate an insect pest in the history of biological control.

The results of population studies on *D. hercyniae* in New Brunswick prompted the hypothesis that a balance or equilibrium had been achieved between the sawfly and its enemies and that the virus and introduced parasites had reached their maximum effectiveness in the regulation of host populations (9). This hypothesis is supported by the sequence of population changes that took place after the study area was sprayed for three consecutive years with DDT against the spruce budworm, starting in 1960.[1] During the spray years sawfly densities were reduced to the lowest levels ever recorded, and the parasites and virus were virtually eliminated from the area. Immediately upon cessation of spraying, and in the absence of disease and parasitism, sawfly populations began to recover and within five generations approached those of the latter years of the oubreak. Parasites reappeared three generations after spraying, and mortality from parasitism increased from 12 to 37 per cent. in the six subsequent host generations. The virus was not detected until the seventh generation after spraying. By the second generation of 1966, host populations receded to levels characteristic of the prespray years—the equilibrium had become re-established and at the same level as before the disturbance.

An equilibrium similar to that in the Maritimes does not yet appear to exist in other areas within the range of *D. hercyniae*. Both the parasites and the virus are continuing to spread and increase in abundance and this has been accompanied by a gradual decline in average host densities. Sawfly populations in both Ontario and Quebec have been generally lower during the past decade than in the previous decade. Because of climatic and other differences between widely separated areas within the range of *D. hercyniae* it is unlikely that an equilibrium will be established at the same host level as in the Maritimes. There is not much doubt, however, that such an equilibrium will develop in these other areas and at host densities somewhat lower than presently exist.

Although the natural spread of *D. hercyniae* westward and northward appears to be slowing considerably, there is always the possibility that the insect could be accidentally introduced, without its parasites and disease, to an area well outside its present range. In view of the ease and success with which the major enemies of the insect can be introduced into an area, such an event would not really pose a serious problem.

Now, 24 years after the collapse of the outbreak, it can be stated with confidence that *D. hercyniae* is presently not a problem in Canada and, furthermore, barring major disruptions such as widespread forest spraying, it is not likely to become one in the foreseeable future.

LITERATURE CITED

1. Balch, R. E. (1937). The spruce sawfly outbreak in 1936. *Pulp Pap. Can.* **38**: 249–55.
2. Balch, R. E. (1958). Control of forest insects. *A. Rev. Ent.* **3**: 449–68.
3. Bird, F. T. & Burk, J. M. (1961). Artificially disseminated virus as a factor controlling the European spruce sawfly, *Diprion hercyniae* (Htg.), in the absence of introduced parasites. *Can. Ent.* **92**: 228–38.
4. Bird, F. T. & Elgee, D. E. (1957). A virus disease and introduced parasites as factors controlling the European spruce sawfly, *Diprion hercyniae* (Htg.) in central New Brunswick. *Can. Ent.* **89**: 371–8.
5. De Bach, P. (ed.) (1964). Biological control of insects and weeds. Chapman and Hall, London.
6. Martineau, R. (1963). Facteurs naturels de régulation des populations de la tenthrède Européenne de l'épinette, *Diprion hercyniae* (Htg.), dans le sud du Quebec. *Can. Ent.* **95**: 317–26.
7. McGugan, B. M. & Coppel, H. C. (1962). Biological control of forest insects, 1910–1958. *In* A review of the biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol. Contr.* **2**: 35–127.
8. Neilson, M. M. & Elgee, D. E. (1968). The method and role of vertical transmission of a nucleopolyhedrosis virus in the European spruce sawfly, *Diprion hercyniae. J. Invert. Path.* **12**: 132–9.
9. Neilson, M. M. & Morris, R. F. (1964). The regulation of European spruce sawfly numbers in the Maritime Provinces of Canada from 1937 to 1963. *Can. Ent.* **96**: 773–84.
10. Reeks, W. A. (1963). The European spruce sawfly in Ontario, 1936 to 1962. *Bi-mon. Prog. Rep., For. Ent. Path. Br., Can. Dep. For.* **19** (6): 2–3.
11. Reeks, W. A. & Barter, G. W. (1951). Growth reduction and mortality of spruce caused by the European spruce sawfly, *Gilpinia hercyniae* (Htg.) (Hymenoptera: Diprionidae). *For. Chron.* **27**: 1–16.
12. Sippell, W. L. *et al.* (1967). *Rep. Forest Insect Dis. Surv. Can.* 1966:60.
13. Turnbull, A. L. & Chant, D. A. (1961). The practice and theory of biological control of insects in Canada. *Can. J. Zool.* **39**: 697–753.

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[1] Bird, F. T. Insect Pathology Research Institute, Sault Ste. Marie, Ontario. Personal communication.

40. *MALACOSOMA DISSTRIA* HÜBNER, FOREST TENT CATERPILLAR (LEPIDOPTERA: LASIOCAMPIDAE)

F. T. Bird

PEST STATUS

Records of the Forest Insect and Disease Survey, Department of Fisheries and Forestry, show that 1958–68 was a period of forest tent caterpillar, *Malacosoma disstria* Hübner, outbreaks and collapses throughout most of Canada. About 177,000 square miles of trembling aspen in Ontario, Manitoba, Saskatchewan, and Alberta were severely defoliated. The remaining provinces were less severely affected. The Maritime Provinces escaped the outbreak except for a very small infestation in New Brunswick. High population densities continued for a period of about 5 years and then, as with most forest tent caterpillar outbreaks, populations suddenly declined or collapsed (9, 14).

A review of the Forest Insect and Disease Survey records, as well as other published data (6) has also shown that, although insect parasitism, predation, and disease all contribute to the reduction of forest tent caterpillar populations and their prevalence is considered as evidence that the collapse of an outbreak is imminent, low temperatures in the spring and immediately following larval emergence are considered chiefly responsible for controlling outbreaks.

Forest tent caterpillar larvae are susceptible to bacterial, fungal, protozoan and virus diseases which may occur singly or in mixed infections. A study of these diseases, particularly of the virus diseases, has been made to determine their usefulness as biological control agents.

BACKGROUND

Four species of bacteria have been isolated from forest tent caterpillar larvae (1, 12): *Clostridium brevifaciens* Bucher, *Bacillus cereus* Frankland and Frankland, *Serratia marcescens* Bizio, and a *Pseudomonas* sp. It is also susceptible to *Bacillus thuringiensis* Berliner varieties (2). In this case, the disease produced is a coupled toxemia—septicaemia. Under natural conditions, *B. thuringiensis* does not seem to cause a great deal of mortality among Lepidoptera because very few spores and toxic crystals are produced. However under highly artificial conditions it is possible to obtain material that has a much higher count of spores and crystals. The distribution of such material in the field exposes insects to a risk of infection and mortality very much higher than would ever occur under natural conditions.

Several species of fungi have been isolated from the tent caterpillar (10, 12): *Beauvaria bassiana* (Balsamo) Vuillemin, *B. globulifera* (Spegazzini) Picard, *Isaria farinosa* (Dickson) Fries, *Aspergillus fumigatus* Fresenius, and an *Entomophthora* sp. In one collection 47 per cent. of the larvae were killed by fungi, but apart from this record (10), there is little evidence that fungi are responsible for any marked mortality.

A microsporidian (protozoan) disease is commonly found in forest tent caterpillar larvae and pupae (20). As high as 90 per cent. of the larvae have been infected with the disease toward the end of an outbreak (12). A microsporidian disease of the larch sawfly, *Pristiphora erichsonii* (Hartig), is also infectious for the tent caterpillar (13).

The effect of a microsporidian disease is difficult to measure. The disease is lethal for young forest tent caterpillar larvae and, while it may not kill older larvae, it is a type of disease that causes a reduction in larval, pupal, and adult sizes, in the number of progeny produced, and perhaps also a reduction in the vigour of the progeny (19).

The disease considered to be most important in the natural control of the forest tent caterpillar is a nuclear polyhedrosis virus or 'wilt disease' (7). This disease reaches epizootic proportions before the collapse of most outbreaks. A second virus, a cytoplasmic polyhedrosis virus introduced from Europe and originally isolated from larvae of *Vanessa cardui* (L.) (4), is also infectious for the tent caterpillar. These viruses have been studied as single and double infections in the laboratory (5, 16) and have been tested as biological control agents in the field (15, 17, 18). An indigenous cytoplasmic polyhedrosis virus has been reported affecting populations in Quebec (12) but has not been discovered in other parts of Canada.

The nuclear polyhedrosis virus (NPV) of the forest tent caterpillar multiplies in the nuclei of fat, blood, epidermal, and other cells of the insect but not in mid-gut cells. The rod-shaped virus particles contain DNA and become occluded by protein to form polyhedral bodies about 2 μ in diameter. The cytoplasmic polyhedrosis virus (CPV) multiplies only in the cytoplasm of mid-gut cells. The virus particles are icosahedra, about 80 mμ in diameter, contain RNA, and they also become occluded by protein to form polyhedra about 2 μ in diameter (4). After ingestion, the polyhedra break down in the gut fluids liberating the infectious virus particles to start the infection process. The polyhedra are very resistant to aging and in water suspensions or in the dry state remain infectious for many years.

First- and early second-instar forest tent caterpillar larvae are extremely susceptible to the NPV but resistance, which begins to develop almost as soon as the eggs hatch, becomes very strong by the third instar (5, 16) and increases even more as the larvae mature. It has been estimated (16) that first-instar larvae are 1,000 times more susceptible to NPV than third-instar larvae, and 68,000 times more susceptible than fourth-instar larvae.

The CPV of the forest tent caterpillar is not quite so infectious for first-instar larvae but slightly more infectious for second-instar larvae, and much more infectious for third- fourth- and fifth-instar larvae (5). Resistance to the CPV also develops but much more slowly and to a far less degree than that which develops against the NPV.

First-instar tent caterpillar larvae fed a mixture of both viruses develop both diseases but as the susceptibilities of the larvae to the viruses change and they become relatively more susceptible to CPV than to NPV, the CPV disease develops first and retards or prevents infection by the NPV (5). CPV interferes with infection by NPV in first- and second-instar larvae if the larvae are fed CPV 1 day or more before being fed the NPV (5). The nature of this interference has not been determined. It may simply be a physical blockage since the mid-gut through which the NPV must pass is greatly disrupted by CPV multiplication.

The NPV of the forest tent caterpillar is a lethal disease and all larvae infected with the virus die except those infected so late in larval development that pupation occurs before or soon after cell infection takes place. The CPV is lethal for first- second- and most third-instar larvae but older larvae, even though heavily infected, may survive. The survivors however suffer debilitating effects as in the case of the microsporidian disease (5).

EVALUATION OF CONTROL ATTEMPTS

Small-scale field studies in which virus was smeared or sprayed on foliage being eaten by forest tent caterpillar larvae showed that both the nuclear and the cytoplasmic polyhedrosis viruses were as infectious and lethal under field conditions as they were under laboratory conditions. Larger-scale field trials in which power-operated mist blowers were used to disseminate the viruses were not as successful due to the difficulty of obtaining satisfactory patterns of spray deposit at the stage of larval development most susceptible to infection. Both the small- and large-scale field tests demonstrated the necessity of disseminating virus as soon as possible after hatching and before larvae reached the virus-resistant third instar.

Dissemination of relatively large quantities of NPV (10^7 polyhedra per ml of water sprayed at the rate of 150 ml per tree 3–5 inches in diameter) with a power-operated 'Micro-Hart' mist blower during the first instar produced, 92 per cent. mortality; during the third instar, 11 per cent. mortality; and during the fourth instar, no mortality (15). Only a trace of disease was found when a 20-gallon application of NPV (10^7 polyhedra per ml of water) was disseminated by the author with a large power-operated mist blower, ('Microsol Model 304') mounted on a truck and driven slowly along the edge of an infestation near Iron Bridge, Ontario, when larvae were in the second and third instars. No infection or mortality resulted when the same concentrations of NPV and CPV were disseminated against second- and third-instar larvae with a 'Micro-Hart' mist blower in an infestation near Sault Ste. Marie.

The NPV (and possibly also the CPV) is transmitted from one generation to another via the egg (18). This appears to result largely from external contamination of the egg mass since it can be greatly reduced by treating the egg masses with 'Javex' (8). Experiments by the author whereby egg masses were sprayed with virus and then treated with 'Javex' showed that virus could be completely inactivated by this treatment.

As high as 59 per cent. of egg masses collected in one infestation were contaminated with virus (18). On the basis of results obtained in similar studies of the transmission of viruses by sawflies (3), one would expect a severe virus epizootic to develop. However, only about 10 per cent. of the larvae died from disease. Similarly, only 2 per cent. of the larvae died from disease in an area where 25 per cent. of the egg masses were contaminated with virus. This very low mortality was probably due to the rapid increase in larval resistance to virus (the sawfly larvae studied showed no increase in resistance with age). Insect parasites were considered to be important in the transmission of sawfly viruses (3) and also in the transmission of the NPV of the forest tent caterpillar (18).

The NPV of the forest tent caterpillar has been shown to spread from the areas of artificial dissemination (17) but the virus, being indigenous, is naturally widely distributed and this has limited the amount of information obtained from artificial dissemination. Widespread dissemination of virus early in the development of an outbreak would be necessary to influence population trends.

RECOMMENDATIONS

Bacteria, fungi, microsporidia, and viruses are potentially useful agents for the biological control of the forest tent caterpillar. The bacteria appear to be the least important in natural control. The fungi are sporadic and cause severe localized mortality when conditions are favourable. The microsporidia appear to be the most prevalent of all the diseases. The viruses appear to cause the greatest mortality. Much further study, however, is required to verify these generalizations, and to determine the precise role of disease in the natural control complex.

Forest tent caterpillar larvae are susceptible to *Bacillus thuringiensis* varieties but it has not yet been determined whether it is economically feasible to use 'B.t.' on a large scale.

Very high percentages of larvae are infected with the microsporidian disease toward the end of most outbreaks. All stages of insect development, including the egg, are susceptible to infection and while the disease may not kill the host, it has pronounced debilitating effects: retardation of larval development, reduction in pupal and adult weights and adult fecundity, and perhaps also a reduction in the vigour of the progeny. Low temperatures in the spring are considered chiefly responsible for controlling outbreaks. An interesting and very important project would be the study of the effects of temperature on the survival of the progeny of adults infected with microsporidia and other diseases. An investigation of the mortality of fully developed embryos which die for no apparent reason (11) would be particularly interesting.

Microsporidia have not been tested as biological control agents. Laboratory propagation and storage of microsporidia might be difficult but it would be relatively easy to collect large quantities of infected larvae from one area and disseminate the organisms they contained in another area.

The nuclear and cytoplasmic polyhedrosis viruses are potentially very useful agents for biological control of the forest tent caterpillar but methods of disseminating the viruses to infect larvae almost as soon as they hatch must be worked out. Experiments using aircraft would be expected to yield the best results since, except for the first two instars, larvae feed from the tops of the trees downwards. It is therefore important to establish disease in the tops of the trees. The objective would be to initiate infection at the tops of the trees when larvae were very young and susceptible and depend on an ever increasing amount of virus to overcome increased larval resistance.

Further study is required before any of these pathogens can be recommended as operational control agents.

LITERATURE CITED

1. Angus, T. A. (1951). Bacteria associated with the forest tent caterpillar. *Bi-mon. Prog. Rep., Can. Dep. Agric.* 7 (4): 2.
2. Angus, T. A. (1968). The use of *Bacillus thuringiensis* as a microbial insecticide. *Wld Rev. Pest Contr.* 7 (1): 11–26.
3. Bird, F. T. (1961). Transmission of some insect viruses with particular reference to ovarial transmission and its importance in the development of epizootics. *J. Insect Path.* **3**: 352–80.
4. Bird, F. T. (1965). On the morphology and development of insect cytoplasmic polyhedrosis virus particles. *Can. J. Microbiol.* **11**: 497–501.
5. Bird, F. T. (1969). Infection and mortality of spruce budworm, *Choristoneura fumiferana* (Clemens), and forest tent caterpillar, *Malacosoma disstria* (Hübner) caused by nuclear and cytoplasmic polyhedrosis viruses. *Can. Ent.* **101**: 1269–85.
6. Blais, J. R., Prentice, R. M., Sippell, W. L. & Wallace, D. R. (1955). Effects of weather on the forest tent caterpillar, *Malacosoma disstria* Hbn., in central Canada in the spring of 1953. *Can. Ent.* **87**: 1–8.
7. Chapman, J. W. & Glaser, R. W. (1915). A preliminary list of insects which have wilt with a comparative study of their polyhedra. *J. econ. Ent.* **8**: 140–9.
8. Grisdale, D. G. (1968). A method for reducing incidence of virus infection in insect rearings. *J. Invert. Path.* **10**: 425.
9. Hildahl, V. & Reeks, W. A. (1960). Outbreaks of the forest tent caterpillar, *Malacosoma disstria* Hbn., and their effects on stands of trembling aspen in Manitoba and Saskatchewan. *Can. Ent.* **92**: 199–209.
10. Macleod, D. M. (1951). Fungus diseases of the forest tent caterpillar. *Bi-mon. Prog. Rep., Can. Dep. Agric.* 7 (1): 2.
11. Prentice, R. M. (1954). Decline of populations of the forest tent caterpillar in central Saskatchewan. *Bi-mon. Prog. Rep., Can. Dep. Agric.* **10** (5): 2.
12. Smirnoff, W. A. (1968). Microorganisms isolated from *Malacosoma americanum* and *Malacosoma disstria*. *Bi.-mon. Res. Notes, Can. Dep. For. Rural Dev.* **24** (1): 4.
13. Smirnoff, W. A. (1968). Adaptation of the microsporidian *Thelohania pristiphorae* to the tent caterpillars *Malacosoma disstria* and *Malacosoma americanum*. *J. Invert. Path.* **11**: 321–5.
14. Sippell, W. L. (1962). Outbreaks of the forest tent caterpillar, *Malacosoma disstria* Hbn., a periodic defoliator of broadleaved trees in Ontario. *Can. Ent.* **94**: 408–16.
15. Stairs, G. R. (1964). Dissemination of nuclear polyhedrosis virus against the forest tent caterpillar, *Malacosoma disstria* (Hübner) Lepidoptera: Lasiocampidae. *Can. Ent.* **96**: 1017–20.
16. Stairs, G. R. (1965). Quantitative differences in susceptibility to nuclear-polyhedrosis virus among larval instars of the forest tent caterpillar, *Malacosoma disstria* (Hübner). *J. Invert. Path.* **7**: 427–9.
17. Stairs, G. R. (1965). Artificial initiation of virus epizootics in forest tent caterpillar populations. *Can. Ent.* **97**: 1059–62.
18. Stairs, G. R. (1966). Transmission of virus in tent caterpillar populations. *Can. Ent.* **98**: 1100–4.
19. Thomson, H. M. (1958). The effect of a microsporidian parasite in the development, reproduction, and mortality of the spruce budworm, *Choristoneura fumiferana* (Clem.) *Can. J. Zool.* **36**: 499–511.
20. Thomson, H. M. (1959). A microsporidian parasite of the forest tent caterpillar, *Malacosoma disstria* Hbn. *Can. J. Zool.* **37**: 217–21.

41. *NEODIPRION LECONTEI* (FITCH), RED-HEADED PINE SAWFLY (HYMENOPTERA: DIPRIONIDAE)

F. T. BIRD

PEST STATUS

The red-headed pine sawfly, *Neodiprion lecontei* (Fitch), has always been a common enemy of young pines but since 1934 it has become increasingly serious. This increase is associated with the practice of planting pure stands of pine (10). In Canada the species shows a decided preference for open-growing trees and for those established in poor sites (9). Its Canadian distribution includes only New Brunswick, Quebec, and Ontario.

The red-headed pine sawfly will feed on many native and exotic conifers; however, only the hard pines are known to be suitable for the deposition of its eggs. Its principal hosts in Canada are red pine, jack pine, and Scots pine. In general, trees less than 15 feet high are preferred, thus the species is often a major problem in young plantations where hard pines predominate. Following the nearly complete defoliation of the initial host, the larvae may crawl to adjacent pines or other coniferous trees to complete their development (9). Rapid decline in numbers is usually attributed to hot, dry weather and parasitism of eggs.

Annual Reports of the Forest Insect and Disease Survey, Department of Fisheries and Forestry, show that high populations of the sawfly prevailed in Ontario from 1958 to 1960 and from 1964 to 1968. In many cases chemical insecticides were used to prevent serious defoliation. In Quebec, severe infestations were discovered in 1962, 1965, 1966, and 1967. There was no report of a serious infestation in New Brunswick during the 1958–68 period.

Three species of egg parasites occur in Ontario: *Tetrastichus* sp., *Telenomus* sp. and *Achrysocharis* sp. (11). *Closterocerus cinctipennis* Ashm. is also reported to be a significant egg parasite (11). Four primary species of larval parasites also occur in the province (12): *Lamachus contortionis* Davis, *Phorocera hamata* A. & W., *Spathimeigenia spinegira* Tns., and *Perilampus hyalinus* Say. Although *P. hyalinus* has been considered by many to be a hyperparasite, recent investigations (12) indicate that it is principally a primary parasite when attacking *Neodiprion* species. These were also found to be the most important larval parasites in Quebec (8). In Ontario, egg parasitism as high as 87 per cent. and larval parasitism as high as 58 per cent. have been recorded (12).

BACKGROUND

The red-headed pine sawfly is susceptible to a nuclear polyhedrosis virus discovered in Ontario in 1950 (5) and reported in 1951 in the United States (16). The virus is similar to those affecting other species of sawflies (7). It multiplies in the nuclei of the digestive cells of the mid-gut epithelium. The rod-shaped virions, about 210×50 mμ, are occluded by protein as single rods to form polyhedra about 1μ in diameter. On the basis of number of polyhedra consumed, it is about 10 times more infectious than the virus which controlled outbreaks of the European spruce sawfly, *Diprion hercyniae* (Hartig), in eastern Canada (1) and the virus of the European pine sawfly, *Neodiprion sertifer* (Geoff.), introduced into North America about 20 years ago (2). The virus of *D. hercyniae* spreads very rapidly from areas where it is artificially disseminated (6). The effectiveness of the virus of *N. sertifer* as a biological control agent has been repeatedly demonstrated (2).

The red-headed pine sawfly is also susceptible to *Bacillus thuringiensis* Berliner (13, 15). One study (13) indicated that the sawfly was only slightly susceptible. A second study (15) showed that it was susceptible to a commercial preparation 'Bakthane'. Pine foliage dipped in 'Bakthane' produced averages of 80 per cent., 72 per cent., and 45 per cent. mortality at dosages of 5 mg, 2·5 mg, and 1·25 mg per ml of water respectively.

EVALUATION OF CONTROL ATTEMPTS

Controlled experiments with the nuclear polyhedrosis virus have been carried out in a small infestation of about 5 acres on St. Joseph Island, Ontario, in a 15-acre infestation near Massey, Ontario, and it was used to control an infestation on Cockburn Island, Ontario. Heavy infestations near Sault Ste. Marie have been sprayed with virus for the purpose of virus propagation.

Over 98 per cent. of the larvae were killed by virus when red pine, infested with the sawfly, were sprayed with virus suspensions containing 10^4, 10^5, 10^6, 10^7 and 5×10^7 polyhedra per ml of water at the rate of about 50 ml per 6-foot tree. Period of mortality varied from 8·6 to 13·1 days after spraying with the higher virus concentrations producing the more rapid mortality. The yield of polyhedra from red-headed pine sawfly larvae killed by virus is low relative to that obtained from *D. hercyniae* and *N. sertifer* but total infectivity (free virus plus polyhedra) is high. Freeze-drying appears to retain the infectivity of the free virus as well as that of polyhedra and has replaced polyhedra extraction. Virus dosages are based on the weight in grams of freeze-dried virus-infected larvae per gallon of water. Sawfly populations are destroyed with 0·04 gm of freeze-dried virus-infected larvae per gallon of water sprayed at the rate of about 1 gallon per acre. The propagation of the virus is relatively inexpensive. About 45,000 diseased larvae were collected from one infestation at the expense of about 10 man days. This is sufficient material to prepare about 10,000 gallons of virus suspension.

The amount of virus necessary to induce an epizootic in a sawfly-infested plantation can be greatly reduced by disseminating the virus as soon as the eggs commence hatching, when natural transmission will produce the epizootic. As the period to cocoon spinning shortens and the time for virus development decreases, the amount of virus disseminated has to be increased to the 1 gallon per acre dosage. Virus dissemination must be completed about 2 weeks before cocoons are spun. After this period, the virus is ineffective. Cocooned larvae developed a temporary immunity to infection (3) and only those larvae in an advanced stage of infection die after cocoons are spun.

The progeny of sawflies which escape death following virus dissemination usually die during an epizootic occurring the following year. The virus is transmitted chiefly via the eggs of infected females (5, 14). Larvae hatching from these eggs commence dying during the second and third instars and the virus is rapidly transmitted from colony to colony (5). Larval parasites appear to be the chief means of viral transmission from tree to tree but many factors (rain, frass drop, scavengers, etc.) are responsible for intra-tree transmission (5).

The virus spreads rapidly from the areas of artificial dissemination. It was found within a 5-mile radius 1 year after an infestation of about 3 acres was sprayed near Sault Ste. Marie. It persisted 5 years after it was disseminated on St. Joseph Island, and an incipient infestation about 8 miles distant was destroyed by the virus. There are, of course, natural virus epizootics but these are infrequent. It appears most probable that, in each case, the virus originated from the area of artificial dissemination.

The virus of the red-headed pine sawfly as well as viruses of other sawflies have been studied for many years (5) and there is no evidence of any tendency towards a development of a more resistant strain of sawfly.

RECOMMENDATIONS

It is recommended that the nuclear polyhedrosis virus be used to control the red-headed pine sawfly. Not only can infestations be completely destroyed by artificially disseminating the virus, but incipient and undetected outbreaks may be destroyed by natural transmission of the virus.

Widespread use of the virus would require facilities for virus propagation, processing, and storage. By taking advantage of, and disseminating virus in heavily infested plantations, large amounts of virus-killed larvae can be obtained at very low cost. It is recommended that facilities be provided for the propagation, processing, and storage of the virus of the red-headed pine sawfly.

LITERATURE CITED

1. Balch, R. E. & Bird, F. T. (1944). A virus disease of the European spruce sawfly, *Gilpinia hercyniae* (Htg.) and its place in natural control. *Sci. Agric.* **25**: 65–8.
2. Bird, F. T. (1953). The use of virus in the biological control of the European pine sawfly, *Neodiprion sertifer* (Geoffr.) *Can. Ent.* **85**: 437–46.
3. Bird, F. T. (1953). The effect of metamorphosis on the multiplication of an insect virus. *Can. J. Zool.* **31**: 300–3.
4. Bird, F. T. (1955). Virus diseases of sawflies. *Can. Ent.* **87**: 124–7.
5. Bird, F. T. (1961). Transmission of some insect viruses with particular reference to ovarial transmission and its importance in the development of epizootics. *J. Insect Pathol.* **3**: 352–80.
6. Bird, F. T. & Burk, J. M. (1961). Artificially disseminated virus as a factor controlling the European spruce sawfly, *Diprion hercyniae* (Htg.). *Can. Ent.* **89**: 371–8.
7. Bird, F. T. & Whalen, M. M. (1954). Stages in the development of two insect viruses. *Can. J. Microbiol.* **1**: 170–4.
8. Daviault, L. (1951). Le tenthrède de Leconte *Neodiprion lecontei* (Fitch) dans la province de Quebec. *33rd Rep. Que. Soc. Prot. Pl.*: 165–84.
9. Davidson, A. G. & Prentice R. M. (1967). Important forest insects and diseases of mutual concern to Canada, the United States and Mexico. *Can. Dep. For. Rural. Dev. Publ.* **1180**, 248 pp.
10. Graham, S. A. & Knight, F. B. (1965). Principles of forest entomology. McGraw-Hill, Toronto.
11. Griffiths, K. J. (1956). Parasitism of the eggs of *Neodiprion lecontei* in Ontario. *Bi-mon. Prog. Rep., Can. Dep. Agric.* **12** (4): 2.
12. Griffiths, K. J. (1961). Larval parasites of *Neodiprion lecontei* (Fitch) in Northern Ontario. *Bi-mon. Prog. Rep., Can. Dep. For.* **17** (4): 2.
13. Heimpel, A. M. (1961). Pathogenicity of *Bacillus cereus* Fr. and Fr. and *B. thuringiensis* Berliner varieties for several sawfly larvae. *J. Insect Path.* **3**: 271–3.
14. Neilson, M. M. & Elgee, D. E. (1968). The method and role of vertical transmission of the nucleopolyhedrosis virus in the European spruce sawfly, *Diprion hercyniae*. *J. Invert. Path.* **12**: 132–9.
15. Shaikh, M. V. & Morrison, F. O. (1965). Notes on the susceptibility of *Neodiprion lecontei* (Fitch) (Hymenoptera: Diprionidae) to bakthane L–69, a commercial preparation of *Bacillus thuringiensis* Berliner. *Ann. Soc. ent. Quebec* **10** (1): 11–2.
16. Steinhaus, E. A. (1951). Report on diagnosis of diseased insects, 1944–50. *Hilgardia* **20**: 625–78.

42. *NEODIPRION SERTIFER* (GEOFF.), EUROPEAN PINE SAWFLY (HYMENOPTERA: DIPRIONIDAE)

K. J. Griffiths, A. H. Rose and F. T. Bird

PEST STATUS

The first North American collection of the European pine sawfly, *Neodiprion sertifer* (Geoff.), was made in 1925 (22) and it was first recorded in Canada near Windsor, Ontario, in 1939 (20). By 1958, it was distributed throughout southwestern Ontario west of a line from Toronto to Owen Sound (Fig. 15) (23). In the past decade, its eastward dispersal has continued, but much more slowly at the northern end of its distribution than at the southern end (Fig. 15). The more rapid dispersal at the southern end may have resulted partly from the appearance of three 'spot' infestations in 1961, approximately 10, 50 and 80 miles east of the infested area, and along the shore of Lake Ontario (26). These isolated populations were subsequently engulfed by the eastward advance of the general infestation, but no doubt contributed to this advance through dispersal from these local foci.

In the first half of the past decade populations of *N. sertifer* were generally low. Isolated pockets of severe defoliation were noted in areas where the sawfly had been present 10 years or more and also where it had been present only 2 or 3 years. Some of these outbreaks lasted only 1 year others, as in

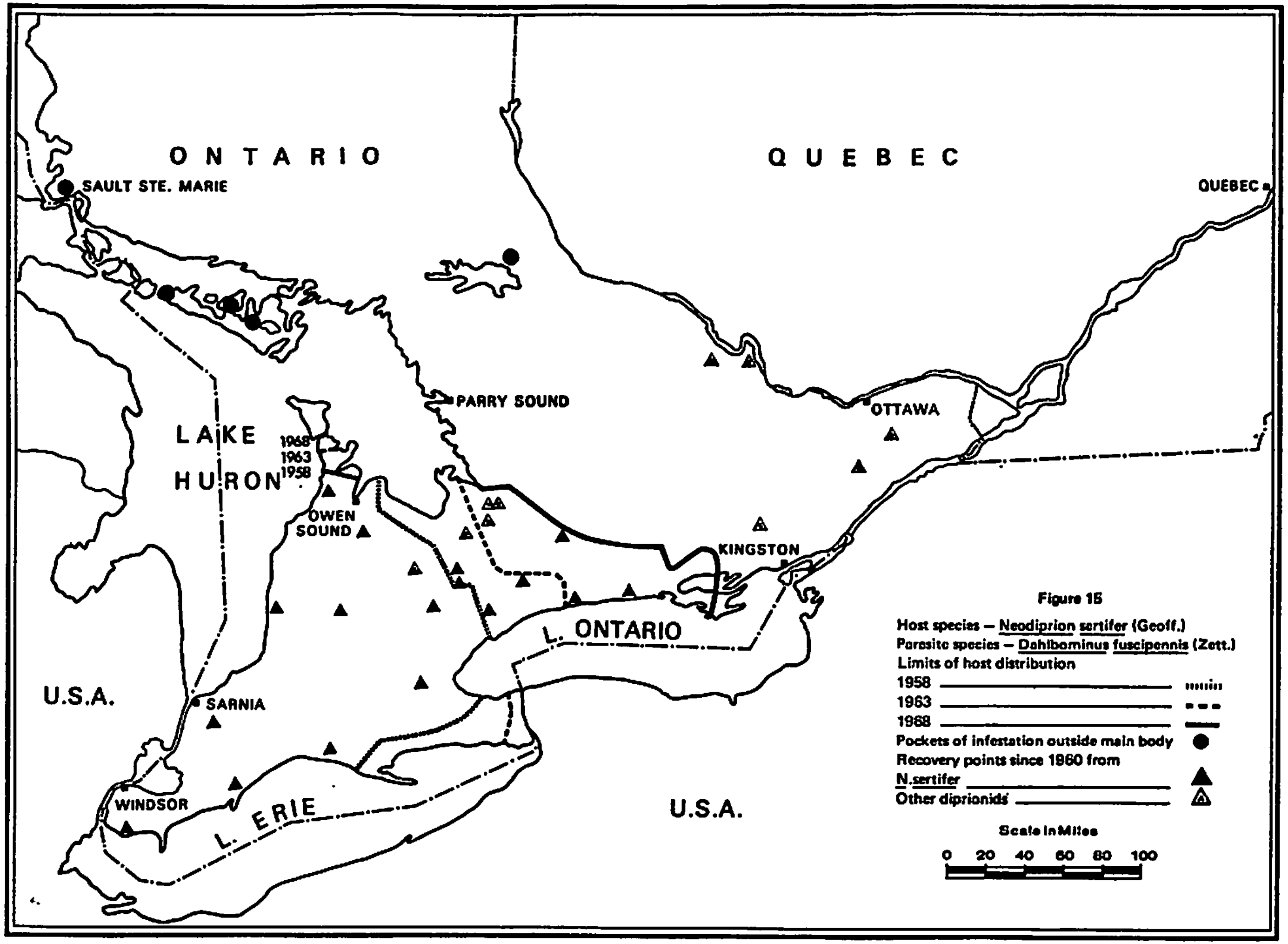


Figure 15

Host species – Neodiprion sertifer (Geoff.)

Parasite species – Dahlbominus fuscipennis (Zett.)

Norfolk County and in the Hepworth-Owen Sound area, continued to cause severe defoliation for several consecutive years. In 1964, a marked increase in the number of areas of heavy defoliation was noted, not only in the older infestation areas, but in those parts of the range where the sawfly had been present only 1 year. These increases were attributed to greater flight activity of adult sawflies in the fall of 1963, and to the unusually mild winter of 1963–64, which resulted in lower over-wintering egg mortality (27). High population levels and severe defoliation were again noted in many parts of the range in 1965. In the three following years, populations were lowered to tolerable levels by control measures taken by private Christmas tree growers and the Ontario Department of Lands and Forests.

The three isolated infestations mentioned above apparently did not result from natural dispersal, but from the introduction of infested nursery stock (26). The definite implication of infested nursery stock in the initiation of isolated infestations was obtained in 1966, when hatched eggs and larvae of *N. sertifer* were found on Manitoulin Island in recently planted stock obtained from a commercial nursery in southwestern Ontario. *N. sertifer* had been collected for the first time in two widely separated areas on Manitoulin Island the previous year (24). The appearance of *N. sertifer* for the first time in Sault Ste. Marie and North Bay, in 1968, was again attributable to the shipment of infested stock from private nurseries in southern Ontario (25).

Concern over the appearance of *N. sertifer* on Manitoulin Island and at Sault Ste. Marie and North Bay is justified since these 'spot' infestations lie well within the range of commercially usable stands of red pine and jack pine, species which this exotic defoliator readily attacks. Sullivan (28) has investigated the supercooling point of eggs from *N. sertifer* populations and the increase in their coldhardiness with exposure to non-lethal conditioning temperatures and has indicated that low winter temperatures will not limit the distribution of this species.

There has been considerable change in the parasite complex of *N. sertifer* in the past decade. The published list of parasites of this sawfly up to 1958 included 14 native primary parasites, three native hyperparasites and four European parasites introduced and known to be established before 1958 (14, 15). Since that time the list of parasites has been increased by 14 indigenous and two introduced species (Table XXVI). One of the latter was introduced in 1962 and will be dealt with below. The other is *Drino bohemica* Mesn. Large numbers of *D. bohemica* were released in Ontario in the period 1942–51, but recoveries were limited, and only from *Diprion hercyniae* (Htg.), *Neodiprion pratti banksianae* Roh. and *Pikonema alaskensis* Roh. (15). In the past 10 years, only two specimens of this species have been recovered from *N. sertifer*. Since extensive larval collections were made through

TABLE XXVI

Numbers of parasites attacking *Neodiprion sertifer* (Geoff.) and other pine feeding diprionid sawflies

Order and family	*N. sertifer*	Other
Hymenoptera		
Braconidae	1	1
Eulophidae	2	7
Eupelmelidae	1	1
Encyrtidae	0	2
Ichneumonidae	19	34
Perilampidae	0	2
Pteromalidae	5	2
Scelionidae	0	1
Torymidae	1	0
Diptera		
Bomyliidae	1	0
Metopiidae	0	1
Muscidae	1	2
Phoridae	1	1
Tachinidae	5	8
	37	62

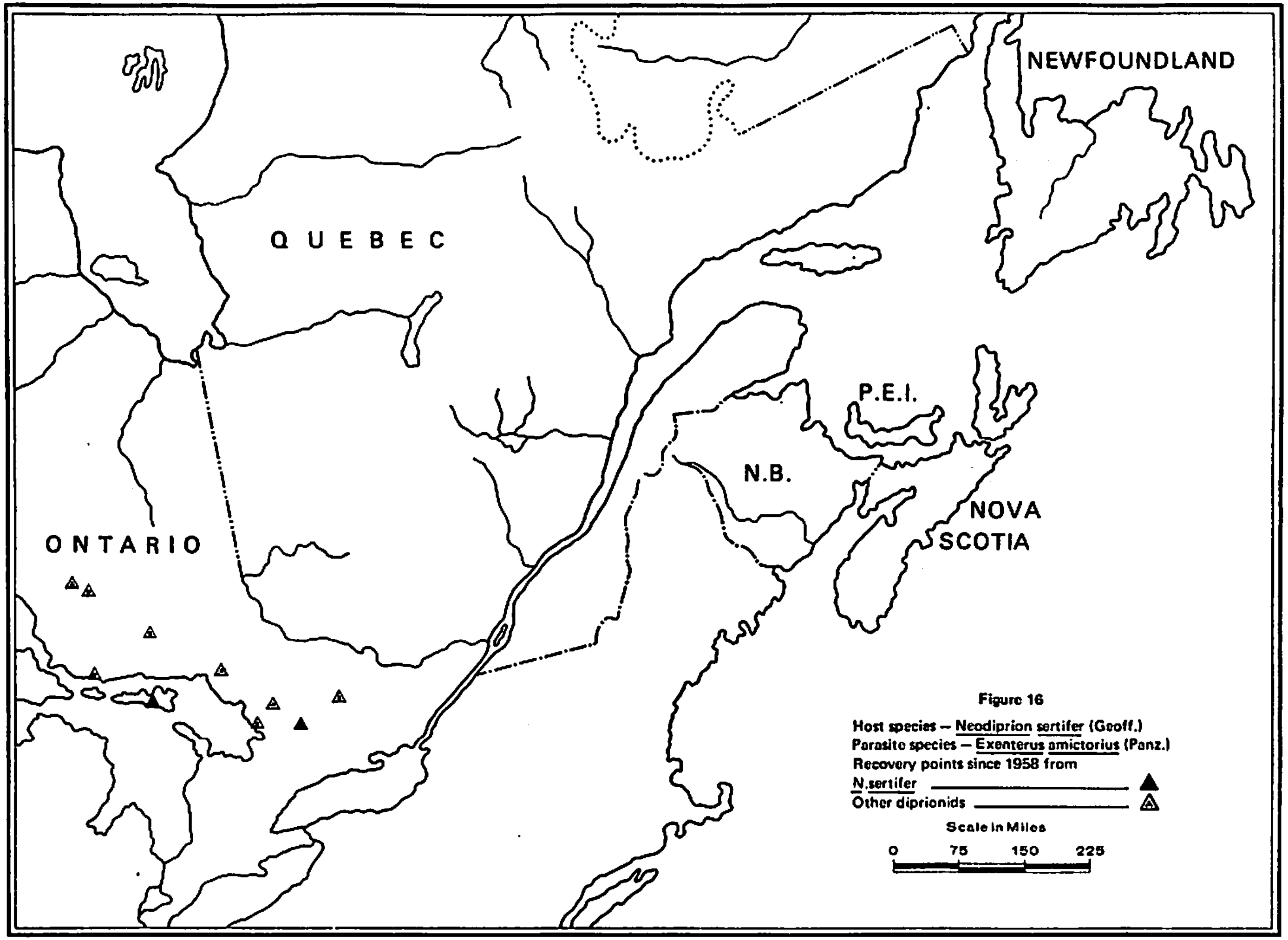
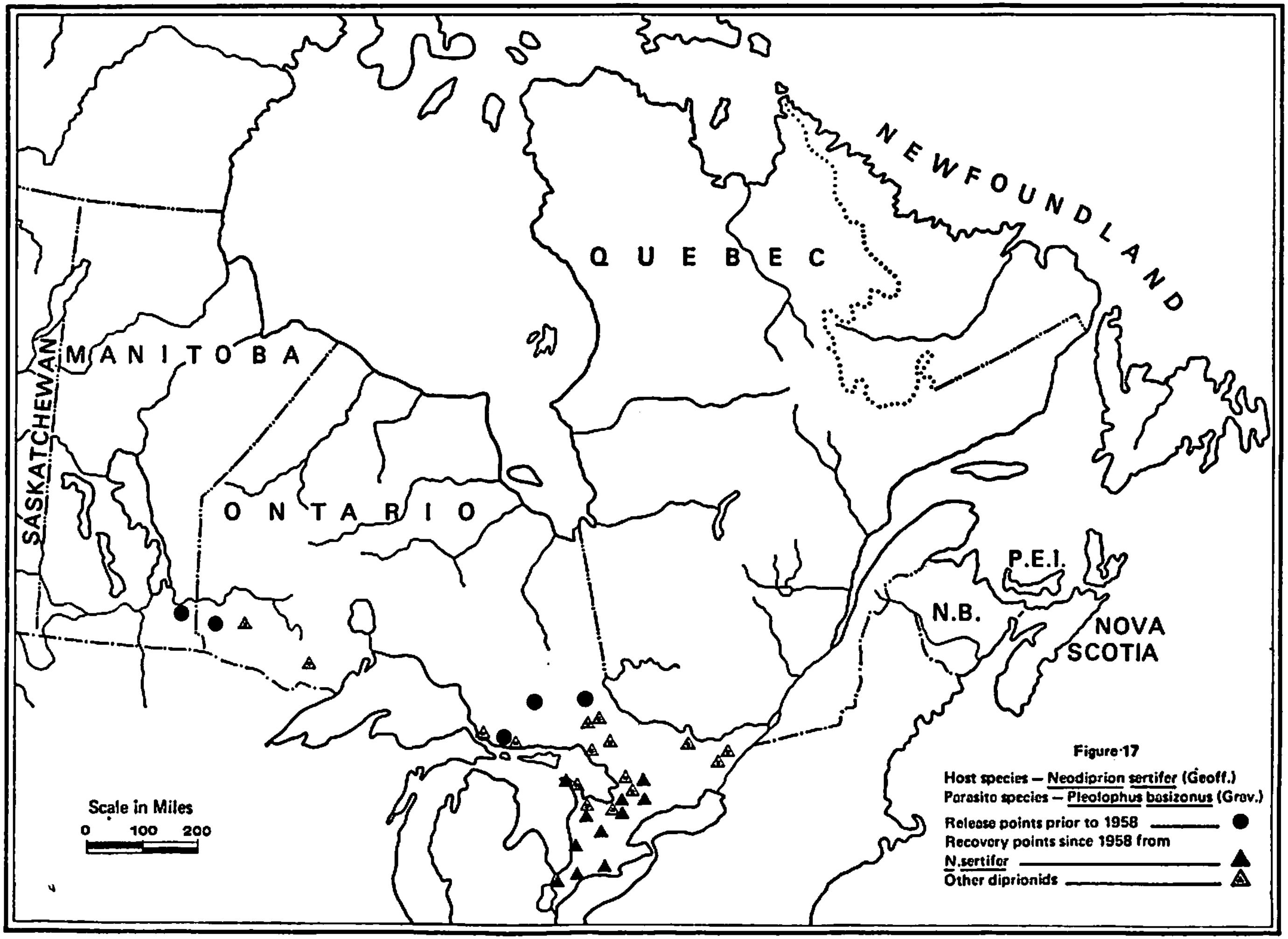


Figure 16

Host species – Neodiprion sertifer (Geoff.)
Parasite species – Exenterus amictorius (Panz.)
Recovery points since 1958 from
N.sertifer ▲
Other diprionids △



Figure·17

Host species – *Neodiprion sertifer* (Geoff.)

Parasite species – *Pleolophus basizonus* (Grav.)

the whole of the sawfly's range during this period, and since *D. bohemica* has been recovered from numerous other hosts in the same period in the *N. sertifer* range, we must assume that this larval parasite rarely attacks *N. sertifer*.

Monodontomerus dentipes (Dalm.), which was earlier recorded from *N. sertifer* in Lambton County in 1946 and from *Diprion frutetorum* (F.) in Grey County in 1951 (15), has now been recovered in Grey County from *N. sertifer*. Twenty-five of the 27 *N. sertifer* cocoons containing *M. dentipes* were found in trees. Since only 3 per cent. or less of *N. sertifer* cocoons are normally found in the trees (14) this parasite must play an insignificant role in the economy of *N. sertifer*.

Additional information has been obtained in the last 10 years on several other parasites released prior to 1958. *Dahlbominus fuscipennis* (Zett.) is spreading at the same rate as *N. sertifer*, as documented by maps in McGugan and Coppel (15), Rose and Sippell (21) and Fig. 15. In spite of large numbers of rearings of cocoons exposed to attack outside the range of *N. sertifer* it has not been recovered except in an outbreak of native diprionids along the eastern boundary of Ontario in 1966 and 1967, where it had not been recovered since the years of its release, 1942–44.

Exenterus amictorius (Panzer), another species released in the years 1935–48 and recovered only in limited numbers in that period, is now widely distributed in the eastern half of the province (Fig. 16). Low populations of *N. sertifer* and other sawflies have made assessment of this species difficult, but it is regularly recovered from four introduced and eight native diprionid hosts and has moved a distance of 280 miles from the closest known release point, La Morandiere Township in Quebec.

Pleolophus basizonus (Grav.) has the widest distribution of any of the parasites released against *N. sertifer* (Fig. 17). Rose and Sippell (21) reported recovery of this species throughout the range of *N. sertifer* in Ontario, and, subsequently, exposure of various diprionid cocoons at many locations has indicated successful establishment and dispersal following releases beyond this area. For example, releases were made at Hawk Lake, just east of Kenora in 1940, and in the Whiteshell Forest in eastern Manitoba in 1949, and recoveries were made recently from *Neodiprion virginianus* complex at Wabigoon near Dryden and Kashabowie, west of Port Arthur, at least 180 miles from the release points. In addition to *N. sertifer*, this parasite has been recovered from two other introduced species, *Diprion similis* (Htg.) and *Pristiphora geniculata* (Htg.) (21), and from seven native diprionids.

The recovery of these introduced species beyond *N. sertifer's* present distribution indicates that we may expect them to exert some influence on this sawfly as it extends its range. In addition, we can predict an increase in native sawfly parasite attack as *N. sertifer* spreads into more northern areas. We have already indicated that there are 31 indigenous parasites now attacking *N. sertifer*. From compilations of Forest Insect and Disease Survey data and unpublished data of the authors we have determined that there are at least 62 species of parasites now known to attack pine-feeding sawflies other than *N. sertifer* in Ontario, many of which can be reasonably expected to attack *N. sertifer* when they are present (Table XXVI). In the group are several important species such as the ichneumonids *Lamachus* spp. and the tachinids *Spathimeigenia* spp. which attack diprionid larvae in considerable numbers (9, 29). At the present time, parasites attacking the cocoon stage are more common on *N. sertifer*, but if experience with other more northern diprionids is a criterion, parasites attacking the larval stage will assume increasing importance as *N. sertifer* moves into more northern areas.

BACKGROUND

Two excellent review papers on *N. sertifer* have appeared in the past decade (14, 31). Research at the Forest Research Laboratory, Sault Ste. Marie, Ontario, is directed to the biology, parasitism, and population dynamics of this species in southern Ontario. In this long term study, it is already clear that there is a definite pattern in the population fluctuations of *N. sertifer* in seven of the eight sample plots being used. In these plots, which are all in plantations of young red and Scots pines, there was a rapid increase in *N. sertifer* numbers after the initial appearance of the sawfly in the stand, followed by a slow decline to low levels. To date, there have been no consistent increases following this decline. Mortality is the result of egg freezing, starvation, parasitism, and predation. In the eighth plot, which is in a stand of 40-foot jack pines, populations have been consistently higher, and prolonged diapause has played an important rôle in determining the course of population fluctuations, with a fungus disease *Beauveria bassiana* (Bals.) Vuill. being one of the main mortality agents of cocooned larvae.[1]

A number of important contributions on the parasites of *N. sertifer* have also appeared in the past 10 years. Pschorn-Walcher (17, 18, 19) has provided much useful information on the biology of European species, while Finlayson (5) dealt with the identification of parasites attacking *N. sertifer* in Canada in one of a valuable series of papers on sawfly parasite taxonomy. In addition, the biology of the introduced eulophid *Dahlbominus fuscipennis* has been reported on by Bobb (1) and that of an indigenous ichneumonid, *Mastrus argeae* (Vier.) by Bobb (2) and Wingfield and Warren (32). A number of papers have also appeared on the introduced ichneumonid *Pleolophus basizonus* (6, 7, 8, 10) and this species has proved to be a valuable experimental animal for the theoretical study of host-parasite interactions (11, 12). Dowden (4) has published a summary of parasite and predator releases in the United States up to 1960 in which he lists seven species released against *N. sertifer*, most of them apparently being obtained from Canada, rather than directly from Europe. He states that *P. basizonus*, *D. fuscipennis* and *Exenterus abruptorius* (Thnb.) became established, although the evidence for the success of the last-named species is based on the recovery of 'a few specimens' 7 years after release, and is similar to recovery data noted by McGugan and Coppel (15) for this species. Dowden also lists *E. amictorius* in the releases, but indicates that it was not recovered from *N. sertifer*. This is contrary to Canadian results, since this species is established here.

In the past decade, there has been a gradual change in the approach to biological control of the European pine sawfly, and this is reflected in the exotic parasite species that have been studied in Canada and *not* released, compared to those that have been released. The only species to be released in this period without preliminary study of their potentialities were liberated in 1959 and 1961. Since then, of four European and one Japanese species studied, only one was thought to be worthy of release. The change embraces not only an attempt to put decisions on a more objective basis than heretofore, but also a realization that the transfer of foreign parasites to new areas offers a unique opportunity for basic research. Preliminary study of candidate species may permit us to do simulations of the effect of the proposed introduction, and successfully introduced species make ideal subjects for basic studies of dispersal and interspecific competition. The discussion of candidate species in the following paragraphs and in the next section can thus best be understood as reflecting our gradual attempts to escape from the older naïve techniques of parasite introduction and a move to more sophisticated methods of dealing with this subject.

Exenterus abruptorius (Thunberg) (Hymenoptera: Ichneumonidae)

Over 1,200,000 specimens of this species were released in Canada from 1935 to 1949, mainly against *Diprion hercyniae*, but also against native species of *Neodiprion* and *N. sertifer*. Recoveries were very limited, and although it has been suggested that this species may be established at very low density throughout at least part of the release area (15) there have been no recoveries by the *N. sertifer* study group or by the Forest Insect and Disease Survey in Ontario. Pschorn-Walcher (19) describes this species as the most 'important' parasite of *N. sertifer* in Europe and probably the most commonly obtained. In addition, it is specific to *N. sertifer*. The latter may explain our failure to establish it on other sawflies earlier, and Pschorn-Walcher's description of its European reputation made it appear a likely candidate for more intensive study here. It also is a good experimental animal for studies on interspecific competition because *N. sertifer* is already attacked by two species of the same genus. The species has been studied through cage releases at Chatsworth for 4 years during the 1-month period when appropriate host stages are present (Table XXVII). Preliminary results are

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[1] Lyons, L. A. Department of Fisheries and Forestry, Sault Ste. Marie, Ontario. Personal communication.

as follows: *E. abruptorius* shows the same host stage preferences as the native *E. canadensis* Prov. and the previously introduced *E. amictorius* and has the same adult life span and distributes its eggs among hosts in a manner similar to these species. However, its daily oviposition rate is intermediate between the two species that already attack *N. sertifer*, its development rate is slower, and there are significantly fewer successful attacks by *E. abruptorius* than by the other two species. When competition between immature stages is induced by obtaining eggs of two species on one host, *E. amictorius* is most frequently the successful contender and there is no significant difference between the other two species. It should be noted that interspecific competition occurs in approximately 20 per cent. of attacked larvae in the field. The reaction of these three species to host density is now being studied, and we may soon be able to make an objective decision about the introduction of *E. abruptorius.*

Lamachus eques complex (Hymenoptera: Ichneumonidae)

This species was selected as a candidate for introduction on the basis of its abundance in European populations of *N. sertifer* (19).

Studies began in 1961 (Table XXVIII). In insectary tests, nearly 17 per cent. of the larvae exposed to attack contained parasite eggs, but there was no development in hosts dissected later in the season, nor any emergence of adult parasites from the remaining exposed hosts. Further tests were conducted using a large nylon cage that completely surrounded a 6-foot Scots pine. Approximately 2,000 host cocoons were obtained from this cage, but there was no attack, as indicated by dissections of samples before and after cold storage, nor was there any emergence of parasite adults.

In 1962, four large cages completely enclosing trees were used, and parasite adults were released in these cages at intervals throughout the larval period. Sixty-one female parasites were used in these cages, and nearly 800 host cocoons obtained from them. Although immature stages of an internal parasite were obtained in 4 per cent. of the 80 hosts dissected before cold storage, there was no emergence of parasite adults after cold storage, and dissection of the remainder gave no indication of attack. Because of the consistent failure of this species to develop in Canadian *N. sertifer*, it was decided that field releases were not justified.

Lophyroplectus luteator (Thunberg) (Hymenoptera: Ichneumonidae)

This species will be dealt with in the next section, where free releases are discussed.

Lophyroplectus nipponensis Cushman (Hymenoptera: Ichneumonidae)

This species was obtained by the Entomology Research Institute in Belleville, Ontario. Twenty-five females were tested in the insectary at Chatsworth in June, 1962. There was no attack and the parasite adults all lived less than 3 days. These results, plus the success of introduction of the European *L. luteator* in the same year, discouraged further attempts to study this parasite.

Synomelix (= *Zemiophorus*) *scutulata* (Hartig) (Hymenoptera: Ichneumonidae)

Although this species is uncommon on *N. sertifer* in Europe it was tested in Canada. Four living adult female parasites were obtained at Chatsworth, and these failed to oviposit on *N. sertifer* larvae in insectary tests. No further tests were attempted.[1]

RELEASES AND RECOVERIES

PARASITES

Achrysocharella ruforum (Krausse) (Hymenoptera: Eulophidae)

Adults of this species were released 1 September, 1959 (Table XXIX) in a mixed red, Scots and jack pine plantation in which a population of *N. pratti banksianae* had been present the previous year. At the time of release there were no eggs of this species or of *N. sertifer* in the plantation, nor, in the normal course of events, would there be any until 2 weeks after the release. There has been no follow-up of this poorly timed release.

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[1] Lyons, L. A. Department of Fisheries and Forestry, Sault Ste. Marie, Ontario. Personal communication.

Lophyroplectus luteator (Thunberg) (Hymenoptera: Ichneumonidae)

This European larval endoparasite is specific to *N. sertifer* and one of the most important parasites of this sawfly in Europe (19). Previous unsuccessful attempts had been made to introduce it into Canada, principally against *Diprion hercyniae* in the Maritime Provinces, Quebec and northern Ontario. These attempts probably failed because of the specificity of the parasite for *N. sertifer*. A small release made against *N. sertifer* in 1940 failed because of poor synchronization. Further tests of this species started in 1961 (Table XXVIII). They indicated that attack and development did occur on Canadian *N. sertifer*, and two introductions were made in 1962 (Table XXIX). In the Williamsford Tract of the Grey County Forest 234 males and 316 females from the U.S.S.R. were liberated in seven releases from mid-May to mid-June. In the Main Tract of the Grey County Forest, approximately 20 miles away, eight males and 10 females from Austria were liberated in three releases. There have been no recoveries of *L. luteator* in the Grey Main Tract in the 6 years since the liberation (Table XXVII), but recoveries have been made every year since release in the Williamsford Tract. Dispersal from this release point averaged approximately one-third of a mile per year in the first 4 years after release, but in the fifth year (1967) dispersal became more rapid and parasites were obtained from all plantations within a 3-mile radius of the release point, except in a southwesterly direction. Preliminary results of the 1968 surveys indicate that the species has dispersed 7 miles from the release point.

TABLE XXVII

Attack by and dispersal of *Lophyroplectus luteator* (Thunb.) released against *Neodiprion sertifer* (Geoff.) in 1962 and 1964

		Attack within release area			Dispersal	
Release areas	Year	Host density (colonies per tree)	Number of hosts reared	Number of parasites emerged	Radius of area sampled	Most distant recovery point
Grey Main Tract	1963	low	896	0	—	
	1964	low	2165	0	—	
	1965	low	1481	0	—	
	1966	low	534	0	—	
	1967	low	388	0	—	
	1968	low	147	0	—	
Williamsford Tract	1962	2·69	951	49	150 yd	110 yd S 100 yd E
	1963	0·33	1620	14	0·6 mi	380 yd E 150 yd NW 150 yd N
	1964	0·06	1749	18♂ 22♀	1·1 mi	475 yd ESE 150 yd NW
	1965	0·05	19267	361♂ 233♀	1·5 mi	0·7 mi SE 0·6 mi NNW
	1966	1·06	3749	158♂ 68♀	2·0 mi	1·3 mi WSW 1·4 mi N 1·1 mi SW
	1967	0·09	1386	108♂ 92♀	3·0 mi	3·0 mi[1]
	1968	0·02	95		7·0 mi	
Jackson Tract	1964	6·51	1720	30♂ 4♀	—	
	1965	2·92	7920	6♂ 0♀	—	
	1966	1·24	5087	240♂ 208♀	—	
	1967	0·71	903	132♂ 124♀	2·0 mi	2·0 mi SE
	1968	0·61	704		3·0 mi	

[1] Parasites were obtained at all collection points within 3·0 miles of the release point except in a southwesterly direction where the most distant recovery point was 1·1 miles.

In 1964, a release was made in the Jackson Tract in Norfolk County, roughly 100 miles south of the previous release points. This release has also been successful (Table XXVII) and our records of dispersal from this release indicate a dispersal rate of approximately 0·5 miles per year in the first 4 years since release (13).

Tetracampe diprioni Ferriere (Hymenoptera: Tetracampidae)

Three shipments of this species were received and released in 1959 (Table XXIX). The first was released on 28 July, the second, 13 August and the third, 1 September. As *N. sertifer* oviposition does not normally begin until mid-September, the probability of success of these poorly timed releases is minimal. Two more shipments were received in 1961 and were released on 23 and 29 September, in a plantation in which *N. sertifer* eggs were known to be present. However, there was no evidence of attack by this parasite in 43 egg clusters collected within 100 feet of the release point in April 1962, nor has there been any evidence of attack in egg samples taken each year in a population dynamics sample plot approximately 0·5 mile from the release point.

PATHOGENS

A nuclear polyhedrosis virus of *N. sertifer* was introduced in *N. sertifer* infested Scots pine plantations near Strathroy, Ontario, in 1950 (3). It has since been disseminated in most infested areas by growers of Scots pine, by officials of the Ontario Department of Lands and Forests and by officials of the Canada Department of Fisheries and Forestry. There has also been some natural spread of the virus. This virus causes an extremely virulent and lethal disease and there is no evidence of its becoming less virulent or less effective over the nearly 20 years it has been in use in Canada, or in the United States and Europe where Ontario-produced virus has been used. *N. sertifer* populations can be destroyed by spraying infested trees with the virus extracted from 5–10 larvae in 1 gallon of water. If the virus is applied at the time of *N. sertifer* egg hatch, larvae die in the second or third instar with no more than a trace of defoliation. Therefore, Christmas trees crops are afforded good protection by early application of virus. The sawfly will be destroyed by viral sprays when larvae are halfway through their development, but the longer spraying is delayed the more severe defoliation will be. If the virus is disseminated as the larvae approach maturity, many will survive because viral development ceases soon after cocoons are spun. These survivors transmit disease to their offspring and it is chiefly in this way that the disease is carried over from one generation to the next.

N. sertifer virus is currently being used to suppress the outbreak on Manitoulin Island. The sawfly was discovered there in two widely separated Scots pine plantations in 1965, and in 1966 was found in four more plantations. In that year all six plantations were treated with virus, and in 1967 populations in most of the areas were less than 0·01 colony per tree. Parts of three plantations where more than 0·1 colony per tree was found were re-sprayed and one newly discovered infested plantation was also treated. In 1968, populations averaged only 0·02 colony per tree in all infested plantations on the Island.

EVALUATION OF CONTROL ATTEMPTS

If we accept the position of Turnbull and Chant (30) that an insect is controlled when it does not cause economically intolerable damage, then we must admit that *N. sertifer* is not being controlled in Canada. In cooperation with the Ontario Department of Lands and Forests, the *sertifer* virus has been disseminated in plantations throughout most of southern Ontario and can be found in nearly all pine plantations not being treated with insecticides, but it is having little effect in the overall control of the sawfly or in preventing its spread. Transmission of virus from one generation to another is effective only at high host densities and thus it does not always prevent damage to small trees that can support only relatively low populations. It is therefore necessary to use virus as an insecticide in

Christmas tree plantations and spray whenever the numbers of insects become potentially harmful. This treatment has, of course, prevented economic damage in plantations in many instances.

Although we have not brought *N. sertifer* under complete biological control, there have been several successes in the introduction of biological control agents. The success of the earlier releases of *E. amictorius*, *D. fuscipennis* and *P. basizonus* and their dispersal throughout much of Ontario must be noted. The more recent introduction of *L. luteator* and its dispersal to date is also gratifying, as is the level of attack which this species has attained. Within the Williamsford Tract, where this species was released in 1962, 14 per cent. of the *N. sertifer* cocoons collected in 1967 produced the parasite. In the same year, over 28 per cent. of *N. sertifer* cocoons produced adult *L. luteator* in collections made in the 1964 release area in the Jackson Tract. These levels of attack are occurring at low and declining levels of host populations (Table XXVII). These data are the result of our intensive study of *L. luteator* dispersal after its recent introduction. They do not indicate its role in regulating *N. sertifer* numbers. This will have to be determined from future analysis of many yearly samples from population study plots, as will any conclusion on the effectiveness of the other introduced parasites.

Perhaps the place where the most pressing need for control exists is in those areas where *N. sertifer* has recently been found beyond the general area of infestation. Sawfly numbers have been greatly reduced by the use of virus in the outbreaks on Manitoulin Island, but these measures must be continued until the danger of reinfestation from adults emerging after prolonged diapause disappears. Efforts to eradicate the sawfly in North Bay and Sault Ste. Marie have not yet been started, since these extensions of the range were not discovered until 1968. As two of these three extensions are known to be the result of infested stock, shipments from infested areas should be restricted. It is also disturbing to note that a fumigation procedure that causes 100 per cent. mortality of *N. sertifer* eggs has been known for several years (16) and not yet utilized.

No information is as yet available on the effectiveness of the virus in permanently controlling populations of the sawfly in forested areas in Canada. Only a few small plantations with large trees have been available for study and these are pure stands of closely planted pine and not typical of a forested area. In these stands the virus has provided excellent continuous control, producing epizootics each year and preventing harmful defoliation. However, in Europe, where by the sawfly and the virus are endemic, severe outbreaks occur from time to time in forests, and although the virus appears to be one of the chief factors causing the collapse of the outbreaks, the fact that outbreaks do occur shows that the virus does not provide continuous control. Apparently one of the reasons that the virus is not as effective as it could be here and in Europe is its slow rate of intertree dispersal within one sawfly generation. This is probably due to the lack of larval parasites which accidentally carry virus from one colony to another in their search for hosts. Indigenous ichneumonid and tachinid larval parasites which are important elements in the parasite complex of native pine sawflies, may therefore play an important dual rôle in the regulation of *N. sertifer* when it reaches our northern forests.

RECOMMENDATIONS

Due to the relation between attack by larval parasites and virus disease mentioned in the previous section, work should continue on the recently introduced larval parasite, *L. luteator*, to determine the interaction between its activities and the effectiveness of virus disease. Also, studies of the interaction between *N. sertifer*, the virus disease and native larval parasites might be profitably undertaken to predict their future effect in northern Ontario, or even with a view of transferring the parasites to areas infested with *N. sertifer* in southern Ontario. However, because all parasites now attacking *N. sertifer* and also nearly all indigenous sawfly parasites either attack the host in its cocoon directly, or undergo most of their development within or on the host prepupa in the cocoon, the introduction of more exotic larval parasites is not recommended. Our attention should now be directed to the possibility of introducing one or more of the European egg parasites of *N. sertifer*, subject to the outcome of European studies by Pschorn-Walcher of the Commonwealth Institute of Biological Control.

The virus has not been used to the extent that it should be. Although some growers of Christmas trees use virus and even propagate their own virus, most use chemical insecticides. There are several reasons for this: (1) information has not been distributed to the growers on the advantages of virus over insecticides, (2) facilities are not available for large scale production of the virus, and (3) virus requires exact timing and in this respect is more difficult to use than chemical insecticides. These problems should be overcome and the great advantages of virus over chemicals made evident to all, especially in view of the ever-increasing level of pollution of the environment with chemical insecticides. Further study of the usefulness of the fungus disease *Beauveria bassiana*, as a regulating agent should also be undertaken, as a possible substitute for chemicals.

Although it is now apparently too late to prevent the dispersal of this species into northern Ontario, the establishment of further, isolated outbreaks could be prevented by an embargo on shipment of planting stock from within the infested area into uninfested areas, unless such stock has been subjected to the fumigation treatment recommended by Monro and Kirby (16).

TABLE XXVIII

Cage releases and laboratory studies of parasites against *Neodiprion sertifer* (Geoff.)

Species and Province	Year	Origin	Number
Exenterus abruptorius (Thunberg)			
Ontario	1963	Austria	249
	1966	Austria	98
	1967	Austria	544
	1968	Austria	559
Lamachus eques complex			
Ontario	1961	Austria	99
	1962	U.S.S.R.	105
		Austria	4
Lophyroplectus luteator (Thunberg)			
Ontario	1961	Austria	204
Lophyroplectus nipponensis Cushman			
Ontario	1962	Japan	89
Synomelix scutulata (Hartig)			
Ontario	1965	Switzerland	21

TABLE XXIX

Open releases and recoveries of parasites against *Neodiprion sertifer* (Geoff.)

Species and Province	Year	Origin	Number	Year of recovery
Achrysocharella ruforum (Krausse)				
Ontario	1959	Czechoslovakia	282	
Lophyroplectus luteator (Thunberg)				
Ontario	1962	Austria	18	
		U.S.S.R.	550	1962
	1964	Austria	443	1964
Tetracampe diprioni Ferriere				
Ontario	1959	Czechoslovakia	3996	
	1961	Czechoslovakia	1576	

LITERATURE CITED

1. Bobb, M. L. (1962). The biology of *Dahlbominus fuscipennis* (Zett.) (Hymenoptera), an introduced parasite of pine sawfly prepupae. *Bull. Brooklyn ent. Soc.* **57**: 102–8.
2. Bobb, M. L. (1965). The biology of *Mastrus argeae* (Viereck) (Hymenoptera: Ichneumonidae), a parasite of pine sawfly prepupae. *Bull. Brooklyn ent. Soc.* 19–20: 53–62.
3. Bird, F. T. (1950). The dissemination and propagation of a virus disease affecting the European pine sawfly, *Neodiprion sertifer* (Geoff.) *Bi-mon. Prog. Rep. Can. Dep. Agric.* 6 (5): 2–3.

4. Dowden, P. B. (1962). Parasites and predators of forest insects liberated in the United States through 1960. *U.S. Dep. Agric. Handb.* **226**, 70 pp.
5. Finlayson, T. (1960a). Taxonomy of cocoons and puparia, and their contents, of Canadian parasites of *Neodiprion sertifer* (Geoff.) *Can. Ent.* **92**: 20–47.
6. Finlayson, T. (1960b). Occurrence of diapause in *Aptesis basizona* (Grav.) (Hymenoptera: Ichneumonidae). *Entomologist's mon. Mag.* **96**: 177.
7. Finlayson, T. (1961a). Notes on effects of some minerals on fecundity of *Aptesis basizona* (Grav.) (Hymenoptera: Ichneumonidae). *Can. Ent.* **93**: 626–8.
8. Finlayson, T. (1961b). Effects of temperatures of rearing on reproduction of *Aptesis basizona* (Grav.) (Hymenoptera: Ichneumonidae). *Can. Ent.* **93**: 799–801.
9. Griffiths, K. J. (1960). Parasites of *Neodiprion pratti banksianae* Rohwer in northern Ontario. *Can. Ent.* **92**: 653–8.
10. Griffiths, K. J. (1961). The life history of *Aptesis basizona* (Grav.) on *Neodiprion sertifer* (Geoff.) in southern Ontario. *Can. Ent.* **93**: 1005–10.
11. Griffiths, K. J. (1969). The importance of coincidence in the functional and numerical responses of two parasites of the European pine sawfly, *Neodiprion sertifer* (Geoff.). *Can. Ent.* **101**: 673–713.
12. Griffiths, K. J. & Holling, C. S. (1969). A competition submodel of parasites and predators. *Can. Ent.* **101**: 785–818.
13. Griffiths, K. J. & Lyons, L. A. (1968). The establishment of *Lophyroplectus luteator* (Hymenoptera: Ichneumonidae) on *Neodiprion sertifer* (Hymenoptera: Diprionidae) in Ontario. *Can. Ent.* **100**: 1095–9.
14. Lyons, L. A. (1964). The European pine sawfly, *Neodiprion sertifer* (Geoff.) (Hymenoptera: Diprionidae). A review with emphasis on studies in Ontario. *Proc. ent. Soc. Ont.* **94**: 5–37.
15. McGugan, B. M. & Coppel, H. C. (1962). Biological control of forest insects, 1910–1958. *In* A review of the biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol. Contr.* **2**: 35–127.
16. Monro, H. A. U. & Kirby, C. S. (1963). Fumigation of nursery stock as a possible means of retarding the spread of the European pine sawfly. *Bi-mon. Prog. Rep., Can. Dep. For.* **19** (3): 2.
17. Pschorn-Walcher, H. (1962). Zur Kenntnis der gesellig lebenden Kiefernbuschhornblattwespen (Hymenoptera: Diprionidae) der Ostalpen. Teil II. Die Parasiten der untersuchen Diprionidae. *Pflanzenschutzberichte* **27**: 153–64.
18. Pschorn-Walcher, H. (1965). The ecology of *Neodiprion sertifer* (Geoffr.) (Hymenoptera: Diprionidae) and a review of its parasite complex in Europe. *Tech. Bull. Commonw. Inst. biol. Contr.* **5**: 33–97.
19. Pschorn-Walcher, H. (1967). Biology of the ichneumonid parasites of *Neodiprion sertifer* (Geoffrey) (Hymenoptera: Diprionidae) in Europe. *Tech. Bull. Commonw. Inst. biol. Contr.* **8**: 7–51.
20. Raizenne, H. (1957). Forest sawflies of southern Ontario and their parasites. *Div. Forest Biol., Can. Dep. Agric. Publ.* **1009**, 45 pp.
21. Rose, A. H. & Sippell, W. L. (1966). Distribution of cocoon parasites of the European pine sawfly, *Neodiprion sertifer* (Geoffrey), in southern Ontario. *Can. Ent.* **98**: 40–5.
22. Schaffner, J. V. (1939). *Neodiprion sertifer* (Geoff.), a pine sawfly accidentally introduced into New Jersey from Europe. *J. econ. Ent.* **32**: 887–8.
23. Sippell, W. L. & MacDonald, J. E. (1959). *Rep. Forest Insect Dis. Surv. Can.* **1958**: 38–56.
24. Sippell, W. L., Dance, B. W. & Rose, A. H. (1966). *Rep. Forest Insect Dis. Surv. Can.* **1965**: 44–65.
25. Sippell, W. L., Gross, H. & Rose, A. H. (1969). *Rep. Forest Insect Dis. Surv. Can.* **1968**: 54–66.
26. Sippell, W. L., MacDonald, J. E. & Rose, A. H. (1962). *Rep. Forest Insect Dis. Surv. Can.* **1961**: 55–72.
27. Sippell, W. L., MacDonald, J. E. & Rose, A. H. (1965). *Rep. Forest Insect Dis. Surv. Can.* **1964**: 51–67.
28. Sullivan, C. R. (1965). Laboratory and field investigations on the ability of eggs of the European pine sawfly, *Neodiprion sertifer* (Geoff.) to withstand low winter temperatures. *Can. Ent.* **97**: 978–93.
29. Tripp, H. A. (1960). *Spathimeigenia spinigera* Townsend (Diptera: Tachinidae), a parasite of *Neodiprion swainei* Middleton (Hymenoptera: Tenthredinidae). *Can. Ent.* **92**: 347–59.
30. Turnbull, A. L. & Chant, D. A. (1961). The practice and theory of biological control of insects in Canada. *Can. J. Zool.* **39**: 697–753.
31. Wellington, W. G., Sullivan, C. R. & Green, G. W. (1966). Biometeorological research in Canadian forest entomology—a review. *Int. J. Bioclim. Biomet.* **10**: 3–15.
32. Wingfield, M. T. & Warren, L. O. (1968). Notes on the biology of *Mastrus argeae* (Vier.), a parasite of *Neodiprion taedae linearis* Ross and other sawflies. (Hymenoptera: Ichneumonidae). *J. Ga ent. Soc.* **3**: 63–6.

43. *NEODIPRION SWAINEI* MIDD., SWAINE JACK-PINE SAWFLY (HYMENOPTERA: DIPRIONIDAE)

J. M. McLeod and W. A. Smirnoff

PEST STATUS

The Swaine jack-pine sawfly, *Neodiprion swainei* Midd., has been a threat to jack-pine stands in Quebec and is now the major forest insect problem in the Province (3). Although infestations have also occurred in Ontario, they were less severe and widespread than in Quebec (1). Extensive tree mortality and general stand deterioration have resulted from outbreaks of this sawfly in Quebec (3, 7), but the principal danger is expected to occur in the 1970's as extensive pure stands of jack-pine, most of which originated from fires in the early 1920's, reach maturity and become more susceptible to sawfly defoliation (8).

Recent severe and moderate infestations have been generally restricted to the areas outlined in Fig. 18 where outbreaks are expected to recur. Cold weather apparently determines the northern limit of outbreaks (1, 3, 23).

Sawfly populations erupt periodically at intervals of as little as 6 years, and complete defoliation and tree mortality may start 3–4 years after the beginning of particularly severe outbreaks. Feeding is more prevalent in the upper crowns of dominant trees and thus they are the first to show the effects of defoliation (7).

Some outbreaks have been controlled by natural factors mainly low-temperatures during the developmental period (9, 23); predation by small mammals may also be a control factor.

RELEASES AND RECOVERIES

PARASITES

Before 1958, only small numbers of *Pleolophus basizonus* (Grav.) and *Drino bohemica* Mesn. were released against *Neodiprion swainei* in a few localities in Ontario. However, massive releases of these two parasites, as well as *Exenterus amictorius* Panzer and *Dahlbominus fuscipennis* (Zett.) were also made in the early 1940's against *Diprion hercyniae* Htg. in both Ontario and Quebec. All four species have been recovered from *N. swainei* in a number of localities in Quebec since 1958 (Table XXX), but none in Ontario. *E. amictorius* and *P. basizonus* were most abundant, *D. fuscipennis* was less common, and only one specimen of *D. bohemica* was found.

TABLE XXX

Recoveries of parasites from *Neodiprion swainei* Midd. in Quebec 1958–68

Species	Lat.	Long.	Year	Host
Exenterus amictorius Panzer	(See below)		1961–8	*Neodiprion swainei* Midd.
Pleolophus basizonus (Gravenhorst)	(See below)		1964–8	*Neodiprion swainei* Midd.
Dahlbominus fuscipennis (Zett)	(See below)		1960–8	*Neodiprion swainei* Midd.
Drino bohemica (Mesn.)	48°10′	71°01′	1968	*Neodiprion swainei* Midd.
Localities				
Lac des Iroquois, Lac St-Jean W.Co.	48°22′	72°28′		
R.-à-Mars, Chicoutimi Co.	48°10′	71°01′		
L. Potherie, St. Maurice Co.	47°13′	73°49′		
L. Baude, Champlain Co.	47°05′	73°18′		
L. Chevalier, St. Maurice Co.	47°03′	73°43′		
L. McLaren, Champlain Co.	47°11′	73°30′		
L. Oriskany, Champlain Co.	47°31′	73°43′		
L. Caousacouta, Champlain Co.	47°16′	73°37′		

Exenterus amictorius Panzer (Hymenoptra: Exenterini)

This species has appeared regularly in collections from 1961 and since then has dominated the complex of native *Exenterus* spp. attacking this sawfly (2). It lays its eggs on pre-spinning eonymphs. Adult *E. amictorius* emerge from *N. swainei* cocoons in early June and the secood generation develops on alternate hosts, notably the egg-overwintering *Neodiprion pratti banksianae* Roh. and *Neodiprion nanulus* Schedl. which are fairly widely distributed through the recovery areas on jack-pine (6). It also attacks *Diprion hercyniae* which is usually present in low numbers on black spruce scattered through jack-pine stands. Thus second generation *E. amictorius* adults emerge from host cocoons in mid-August, just in time to lay on pre-spinning eonymphs of *N. swainei* which are present in late August and September. Parasitism by this species on *N. swainei* in the localities sampled (Fig. 18) averages 1 per cent. over a 6-year period.

Pleolophus basizonus (Grav.) (Hymenoptera: Ichneumonidae)

This species parasitizes *N. swainei* cocoons. It was first recovered in samples in 1964 (5), and since then has been recovered consistently from all areas sampled (Fig. 18). It is bivoltine, on *N. swainei*, lays on eonymphs in cocoons in the fall, on eonymphs in extended diapause, and pronymphs, pupae, and adults in cocoons in June and July. Alternate hosts available during the summer include egg-overwintering *Neodiprion* spp. on jack-pine, and *Diprion hercyniae*. First generation parasitism on *N. swainei* averaged 2 per cent. over a 6-year period but its greatest impact probably occurs during the second generation which presently cannot be estimated precisely.

Dahlbominus fuscipennis (Zett.) (Hymenoptera: Eulophidae)

This species has been recovered sporadically in all sampled areas (Fig. 18) since 1962. Its populations are generally quite low, and its attacks occur mainly on pupae and adults in cocoons during June and July.

Drino bohemica (Mesn.) (Diptera: Tachinidae)

One specimen was identified in dissections of *N. swainei* cocoons collected from Rivière-à-Mars, Chicoutimi County, Quebec, in 1968. However, it is a common parasite of *N. pratti banksianae* and *N. nanulus* in Quebec.

PATHOGENS

The *Borrelina* virus was first discovered in a larva of *N. swainei* in a forest insect survey sample from Bear Island in Lake Timagami, northeastern Ontario, in August 1953. It was next reported in September 1956 near Lake Gagnon, in the St. Maurice Region of Quebec where it caused a moderately heavy infestation. Studies on the nuclear-polyhedrosis of this insect have been in progress since 1957 (12). The disease develops in the nuclei of the cells of the mid-gut epithelium. Polyhedral bodies ranging from 0·5–1·7 microns in diameter fill the nuclei of infected cells. Infected larvae begin to lose their appetite within a few days, their greenish colour changes to yellow, and the intestinal track becomes cream-coloured and fragile (12). Although the virulence of the original strain of the virus was low, a more virulent strain was obtained by selection. The latter caused 40–80 per cent. mortality of first-instar larvae with polyhedra concentration $2{\cdot}00^4$ per ml. Mortality is proportional to the virus concentration and inversely proportional to the age of the larvae. Effective virus concentrations ranged from $5{\cdot}10^5$–$3{\cdot}10^6$ polyhedra per ml. The higher concentrations neither hastened the development of the disease nor increased mortality of larvae. Best results were obtained when spray was applied at the end of the first or beginning of the second instar. Spraying was done in a severely defoliated jack-pine stand where tree mortality was insignificant and where, 3 years after spraying, the foliage density had returned to normal. The virus has persisted in the stand, and *N. swainei* populations continue at low levels.

An experimental aerial dispersion of the virus was made in 1960 over heavily infested jack-pine stands (15, 16). The virus at polyhedra concentration $2{\cdot}10^6$ per ml was mixed with two formulae; a water-latex dry ox-blood solution, and an oil-magma bentonite-spane water emulsion. The virus was applied at the rate of 0·5 and 4·0 gallons per acre. The results obtained were excellent. The year following the spray application, the plots and surrounding 0·25 mile zone were completely protected from defoliation and the disease had spread 2 miles from the plots.

In 1964, 7,000 acres of infested jack-pine forest were sprayed operationally with virus in a water-latex, dry ox-blood solution (22). The results obtained were not as good as those in 1960 mainly because unseasonable cold and rainy weather accompanied and followed the treatment (20, 21).

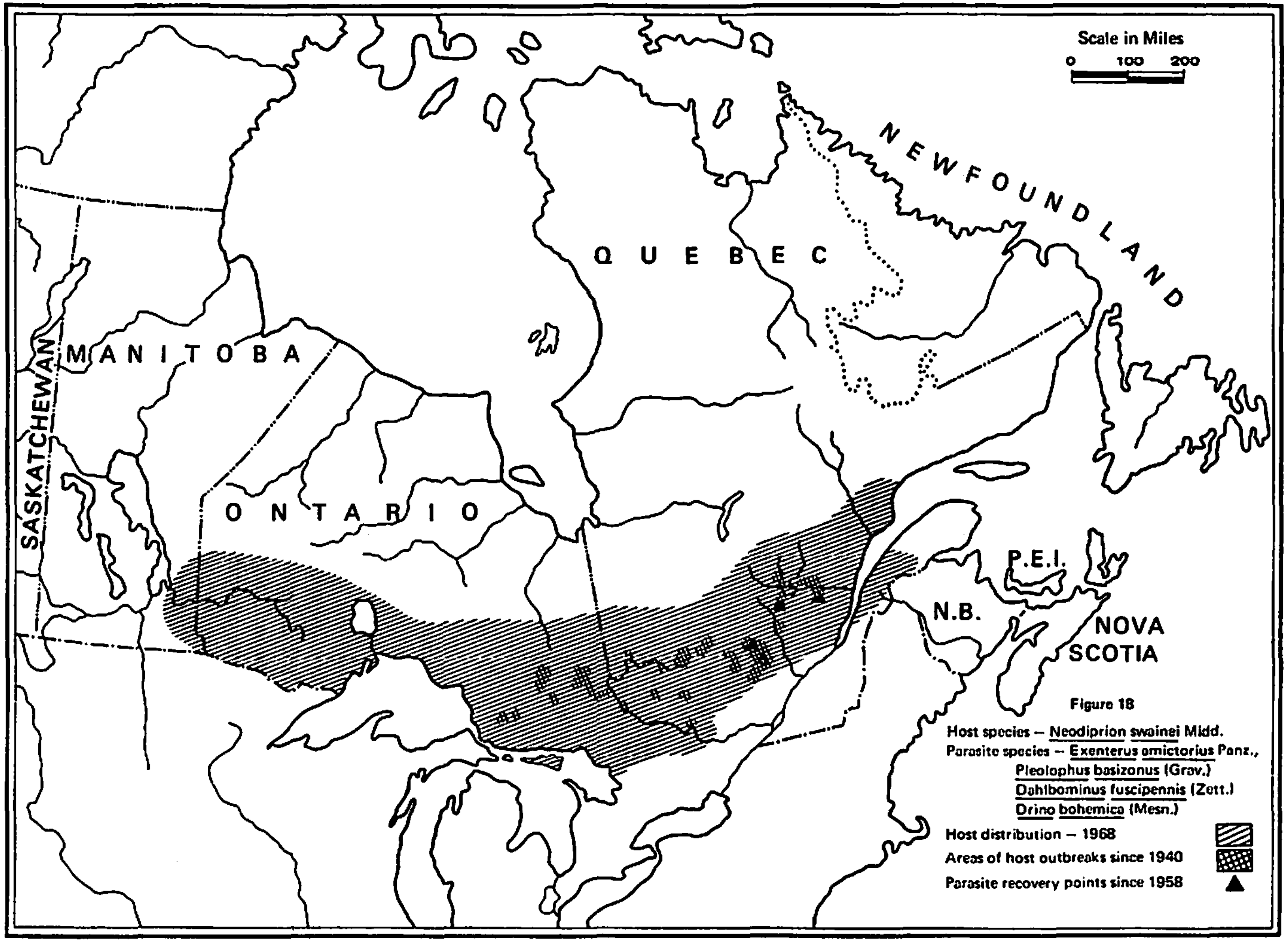

Figure 18

Host species – *Neodiprion swainei* Midd.
Parasite species – *Exenterus amictorius* Panz.,
Pleolophus basizonus (Grav.)
Dahlbominus fuscipennis (Zett.)
Drino bohemica (Mesn.)

Host distribution – 1968	▨
Areas of host outbreaks since 1940	▩
Parasite recovery points since 1958	▲

The phenomenon of virus transmission from parent sawflies to their progeny, accompanied by the spread of infection to healthy individuals (trans-ovum transmission) (14) might be used effectively for control instead of treating large areas with concentrated spray. The method would consist of an application of weak dosage of virus at specific spots in an infected stand, or the dissemination of infected cocoons.

The ecology of the virus on its host and the effects of several external factors, namely temperature, darkness and sunlight, were studied (1, 11, 17, 18, 19, 20, 22). Experiments have also revealed that predators, mainly wasps and pentatomids, act as vectors of virus diseases (10, 13). The disease is also disseminated through migration of *N. swainei* larvae.

EVALUATION OF CONTROL ATTEMPTS

Both of the introduced parasites, *E. amictorius* and *P. basizonus*, appear to dominate their respective parasite communities at high host densities, and *N. swainei* is one of a number of alternate hosts which are exploited by these two parasites when numbers of *D. hercyniae*, against which they were released, are low. Thus, their introduction appears beneficial. A more precise evaluation of their impact should be available in 1 or 2 years following completion of studies in progress in Quebec.

The value of the virus disease for direct control of *N. swainei* is promising. Although the first experimental aerial spraying programme with virus in 1960 was phenomenally successful (15), the operational programme in 1964 showed rather conclusively that an uncontrollable variable, weather, contributed materially to a reduction in effective control (20, 21). Experiments have suggested, however, that effective control might be achieved in incipient outbreaks through trans-ovum transmission following spot spraying of areas with weak virus concentrations or through dissemination of infected cocoons.

Two highly successful aerial spray operations with the chemical insecticides Phosphamidon and Sumithion were carried out in Quebec (7, 8). Sawfly mortality attributable to spray averaged 99 per cent. in both operations, and a minimum of disturbance to birds, small mammals, parasites, and predators occurred as a result of spray application (4, 7).

RECOMMENDATIONS

It seems that aerial application of the insecticide Phosphamidon at the recommended dosages offers the only sure means of controlling *N. swainei* outbreaks. The method is cheap, efficient, and apparently causes a minimum of side effects.

Research should be initiated to determine the efficacy of controlling incipient outbreaks by virus through trans-ovum transmission by spot spraying areas with low virus concentrations (5×10^5 — 1×10^6 polyhedra per ml applied at 2 gallons per acre) or through dissemination of infected cocoons.

Population dynamics studies in Quebec, now nearing completion, may provide clues to the successful manipulation of the parasite complex. Studies in progress will determine whether *E. amictorius* and *P. basizonus* complement or hinder each other and their respective indigenous parasite communities. (Studies in progress by P. W. Price in Quebec are expected to provide answers to these problems).

LITERATURE CITED

1. Anon. *Rep. Forest Insect Dis. Surv. Can.* 1958–67.
2. McLeod, J. M. & Desalliers, G. (1966). Notes on *Exenterus amictorius* Panzer, an introduced parasite now established on the Swaine jack-pine sawfly, *Neodiprion swainei* Midd. *Bi-mon. Prog. Rep., Can. Dep. For.* 22 (2): 2.
3. McLeod, J. M. (1967). The Swaine jack-pine sawfly. *In* Important Forest Insects and Diseases of Mutual Concern to Canada, the United States, and Mexico. *Publ. Can. Dep. For. Rural. Dev.* **1180:** 138–41.

4. McLeod, J. M. (1967). The effect of phosphamidon on bird populations in jack-pine stands in Quebec. *Can. Fld Nat.* **81**: 102–6.
5. McLeod, J. M. (1967). First record of *Pleolophus basizona* parasitising *Neodiprion swainei*. *Bi-mon. Res. Notes, Can. Dep. For. Rural Dev.* **23** (4): 27–8.
6. McLeod, J. M. (1968). An infestation of the jack-pine sawfly, *Neodiprion pratti banksianae* Roh., in Quebec. *Bi-mon. Res. Notes, Can. Dep. For. Rural Dev.* **24** (1): 5–6.
7. McLeod, J. M. (1968). Results of an aerial spraying operation against the Swaine jack-pine sawfly, *Neodiprion swainei* Middleton, in Quebec utilizing the insecticide phosphamidon. *For. Chron.* **44**: 14–20.
8. McLeod, J. M. (1969). Spraying for jack-pine sawfly in Quebec. *Pulp Pap. Can.* **70** (22): 105.
9. Pilon, J. G., Tripp, H. A., McLeod, J. M. & Ilnitzky, S. L. (1964). Influence of temperature on prespinning eonymphs of the Swaine jack-pine sawfly, *Neodiprion swainei* Midd. (Hymenoptera: Diprionidae). *Can. Ent.***96**: 1450–7.
10. Smirnoff, W. A. (1959). Predators of *Neodiprion swainei* Midd. (Hymenoptera: Tenthredinidae) larval vectors of virus diseases. *Can. Ent.* **91**: 246–8.
11. Smirnoff, W. A. (1960). Observations on the migration of larvae of *Neodiprion swainei* Midd. (Hymenoptera: Tenthredinidae). *Can. Ent.* **92**: 957–8.
12. Smirnoff, W. A. (1961). A virus disease of *Neodiprion swainei* Midd. (Hymenoptera: Tenthredinidae) *J. Insect Path.* **3**: 29–47.
13. Smirnoff, W. A. (1961). Predators of larvae of *Neodiprion swainei* Midd. (Hymenoptera: Tenthredinidae). *Can. Ent.* **93**: 272–6.
14. Smirnoff, W. A. (1962). Trans-ovum transmission of a virus of *Neodiprion swainei* Midd. (Hymenoptera: Tenthredinidae). *J. Insect Path.* **4**: 192–200.
15. Smirnoff, W. A., Fettes, J. J. & Haliburton, W. (1962). A virus disease of Swaine's jack-pine sawfly, *Neodiprion swainei* Midd., sprayed from an aircraft. *Can. Ent.* **94**: 477–86.
16. Smirnoff, W. A. (1964). Preparation and application of viral material in biological control of the jack-pine sawfly. *For. Chron.* **40**: 187–94.
17. Smirnoff, W. A. & MacLeod, C. F. (1964). Apparent lack of effect of orally-introduced polyhedrosis virus on mice and of pathogenicity of rodent-passed virus for insects. *J. Insect Path.* **6**: 537–8.
18. Smirnoff, W. A. & McLeod, J. M. (1966). Modification of diapause in a population of *N. swainei* Midd. *Bi-mon. Prog. Rep., Can. Dep. For.* **22**: 3.
19. Smirnoff, W. A. (1967). Influence of light on the development of a nuclear-polyhedrosis of *Neodiprion swainei*. *J. Invert. Path.* **9**: 269–271.
20. Smirnoff, W. A. (1967). Influence of temperature on the development of a virus disease of *Neodiprion swainei* (Hymenoptera: Tenthredinidae). *Can. Ent.* **99**: 244–9.
21. Smirnoff, W. A. (1967). The biological control of *Neodiprion swainei* Midd. with a nuclear-polyhedrosis virus. *Bi-m. Res. Notes, Can. Dep. For. Rural Dev.* **23**: 5.
22. Smirnoff, W. A. (1968). The nature of cysts found in pupae and adults of *Neodiprion swainei* Midd. *Can. Ent.* **100**: 313–8.
23. Tripp, H. A. (1965). The development of *Neodiprion swainei* Middleton (Hymenoptera: Diprionidae) in the Province of Quebec. *Can. Ent.* **97**: 92–107.

44. *OPEROPHTERA BRUMATA* (L.), WINTER MOTH (LEPIDOPTERA: GEOMETRIDAE)

D. G. Embree

PEST STATUS

The status of the winter moth, *Operophtera brumata* (L.), has changed dramatically since 1958 (15) owing to the success of two introduced parasites, *Cyzenis albicans* (Fallén) and *Agrypon flaveolatum* (Gravely) (3). The severity of damage on red oak, the principal forest host, is minimal, and the insect is now one of the less common defoliators of hardwoods. In a few towns, populations still occur on shade trees but below a level that would require the application of insecticides. The winter moth has persisted in commercial apple orchards where it is controlled through normal spray programmes. Occasional outbreaks occur in abandoned orchards. The range of distribution has not expanded appreciably since 1958[1] and the insect occurs throughout Nova Scotia and in isolated pockets of New Brunswick and Prince Edward Island (Fig. 19). A key factor in the regulation of winter moth populations in the absence of parasitism was the mortality that resulted when the degree of synchronism

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[1] Forbes, R.S. Department of Fisheries and Forestry, Fredericton, New Brunswick. Personal communication.

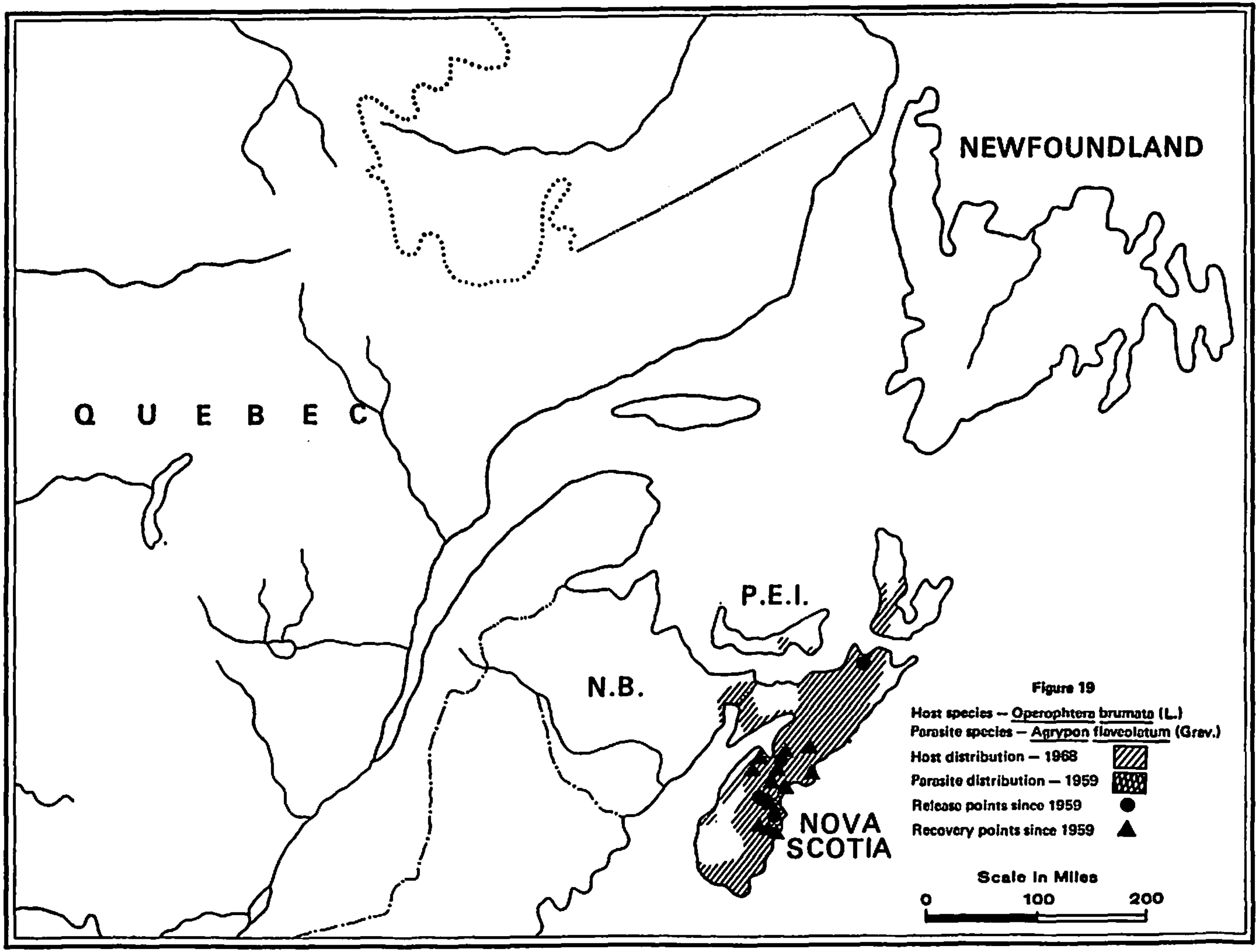

Figure 19

Host species — *Operophtera brumata* (L.)
Parasite species — *Agrypon flaveolatum* (Grav.)

between hatchlings and budbreak of the host was poor. Larvae that hatch before the buds burst usually starve (2). At the extremely low populations which now exist natural selection for better synchronized individuals tends to intensify and as the females are flightless and do not disperse readily, the chances of mating between siblings also increases. Such assortative mating could conceivably result in the appearance of a new population that is better adapted to the phenology of its host.

A nuclear polyhedrosis which was first detected in isolated larvae in 1961 is now generally present throughout the area of winter moth distribution and has contributed to the collapse of at least two infestations.

BACKGROUND

Only six of 63 known parasites of the winter moth were selected for release. Apparently the two that eventually became established, *C. albicans* and *A. flaveolatum*, were selected simply because they were the most abundant in Europe (15). However, when success appeared likely, field releases of other species were discontinued to avoid the risks of introducing a parasite which would compete with the established species. Subsequent releases were made experimentally in field cages. One of the six species originally introduced, *Lypha dubia* Fallén, a tachinid, was released in cages in 1962; an ichneumonid *Pimpla contemplator* Müller, first recorded as a parasite of the winter moth in 1960 and believed to parasitize mature larvae (20), was released in 1964 (Table XXXI). Neither species overwintered successfully.

Detailed studies of the population dynamics of the host were carried out in England by Varley and Gradwell (19) and associates at Oxford University starting in 1949, and in Canada by the author beginning in 1954 when the initial releases of the parasites were made. Work in Canada led to the development of a series of winter moth life tables from 1954 to 1962, which explained through a mathematical model, the change that occurred in the population behaviour of the winter moth after the parasites became established (2). A cytoplasmic polyhedrosis virus obtained from K. M. Smith, and which appeared to be a promising control agent in England, was tested in Canada by M. M. Neilson. Although the virus caused high mortality to winter moths in the laboratory it was ineffective in the field (16).

Varley and Gradwell, on the basis of mathematical models developed in England, have forecast that in Canada strong oscilations in interacting populations of the winter moth and its parasites will cause damaging outbreaks of the winter moth at 9 or 10 year intervals (19). Canadian studies suggest that other factors besides the parasites, such as the presence of the virus disease and the probability of the occurrence of a series of years of favourable synchronism between winter moth hatching and bud break of its host, will determine the frequency and course of future outbreaks. If outbreaks develop in forest populations, they will most likely result from invasions of winter moths from shade- and orchard-trees, which are better synchronized with winter moth hatching.

RELEASES AND RECOVERIES

Releases and recoveries are listed in Table XXXI. *C. albicans* had already reached some of the areas by the time the releases were made (3). Hence the year of recovery is listed as the same year as the release.

PARASITES

Agrypon flaveolatum (Gravely) (Hymenoptera: Ichneumonidae)

This parasite appears in the field when the winter moth is in its early larval instars, but only late instars are attacked. The parasite larva matures in the host pupa in late summer or fall and overwinters in the pupal stage within the pupal case of the host. First released in 1956, it had spread at least 1 mile from the original release site by 1960. It usually appeared in new areas at least 2 years after *C. albicans* and by 1965 had spread to most areas where the winter moth was found (Fig. 19). It has not been recovered from northern Nova Scotia, Prince Edward Island, or New Brunswick although it is probably present in at least the mainland areas. It is most effective at low densities and exhibits a typical parasite functional response in that the proportion of hosts attacked per parasite decreases with increasing host density. Regulation only occurs in combination with the numerical response of the parasite (3).

Cyzenis albicans (Fallén) (Diptera: Tachinidae)

Adults emerge early in May about the time of winter moth hatch. Oviposition begins when the winter moth is in the late 3rd or early 4th instar in early June and continues throughout the development period of the host larva, which lasts until the end of June. The parasite female, which lays about 1,300 microtype eggs, is apparently attracted to sap issuing from damaged leaves and oviposits near feeding host larvae. Eggs ingested by the host hatch in its midgut. The parasite larvae pass through the gut wall and enter the salivary glands. After the host pupates the parasite develops rapidly, pupating within the pupal case of the host by midsummer (20).

C. albicans became firmly established within 2 years at the site of the first release (5). The first record of spread was made 4 years later when larvae parasitized by *C. albicans* were found 0·5 mile from the liberation site. The following year an additional 0·5 mile spread was recorded and the next year the parasite was collected from some areas over 50 miles distant (2). As shown in Fig. 20, it has since spread throughout almost the entire range of the winter moth (3). It has not been recovered from Prince Edward Island but it is probably present there.[1]

C. albicans kills a higher proportion of winter moth larvae at high host density than does *A. flaveolatum*. However, the most interesting characteristic of *C. albicans* is that it has a sigmoid functional response curve. This means that percentage parasitism increases with an increase in host density over the portion of the curve with an increasing slope. Consequently, within the range of host densities represented by this section of the curve, unlike *A. flaveolatum*, *C. albicans* has regulatory properties (3). Laboratory studies now in progress have duplicated the sigmoid curves previously demonstrated only from data on field populations. The results of these studies suggest that the unusual functional response occurs because the degree of synchronism between winter moth development and parasite oviposition is related to winter moth density, an increase in density increasing the chances of favourable synchronism by slowing the larval development of the host. Field data suggested that the nature of the functional response was due to the presence at low winter moth densities of higher proportions of associated defoliators. The damage caused by these insects attracted ovipositing *C. albicans* females and caused the parasite population to waste a high proportion of its egg capacity on non-host insects when winter moth densities were low. This explains the greater effectiveness of *A. flaveolatum* at low host densities as compared to *C. albicans*. Since *A. flaveolatum* oviposits directly on the host larvae, it is presumably not influenced by the presence of other defoliators. At high host densities the immature stages of *A. flaveolatum* cannot compete with *C. albicans* in cases of multiparasitism because the latter develops more rapidly in the host (3).

The rate of attack of *C. albicans* may vary with different stand types. Lightly infested trees in areas of generally heavy infestations attrack a smaller proportion of the *C. albicans* population than similarly infested trees in less severe outbreaks.

Lypha dubia (Fallén) (Diptera: Tachinidae)

Recorded from winter moth and several species of Lepidoptera in Europe (18), this parasite has a life cycle similar to that of *C. albicans* except that the parasite eggs hatch on the foliage and the puparium is formed outside the host cocoon (20). The parasite apparently failed to establish, possibly because the initial release in 1955 was very small and the 1961 release was made at the time the outbreak was collapsing.

Phobocampe crassiuscula (Gravely) (Hymenoptera: Ichneumonidae)

This parasite has been recorded from winter moth and other geometrids in Europe (18). It

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[1] Forbes, R.S. Department of Fisheries and Forestry, Fredericton, New Brunswick. Personal communication.

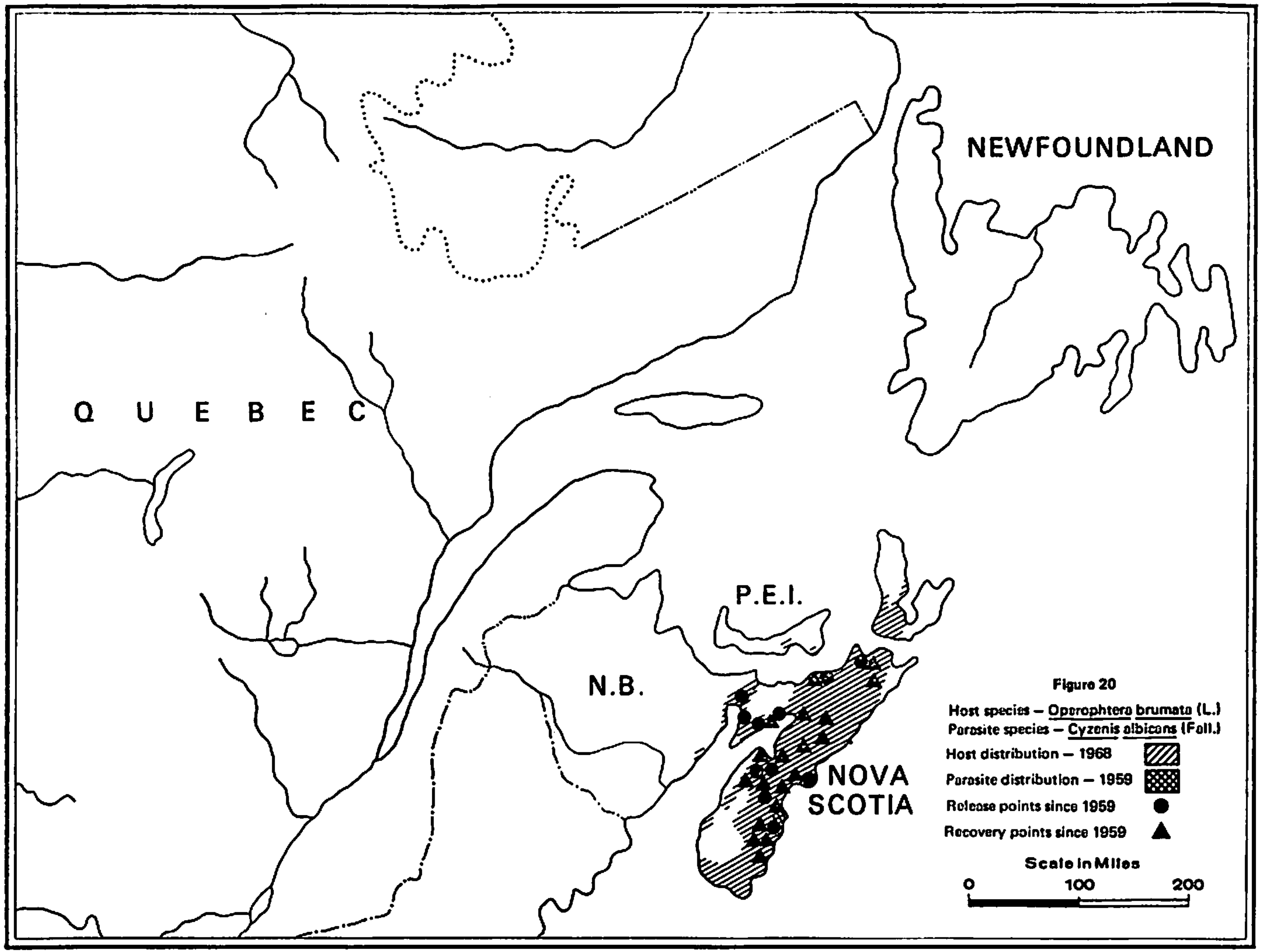

Figure 20

Host species – *Operophtera brumata* (L.)

Parasite species – *Cyzenis albicans* (Fall.)

develops in winter moth larvae, emerges from mature larvae and spins a cocoon on the foliage. Adults emerge about 3 weeks later and are believed to produce a second generation on another host species (20). No recoveries were made from field releases in Nova Scotia and experimental releases on caged winter moth populations were also unsuccessful. Its chances of establishment were minimal probably because of the need for an alternate host.

Phorocera obscura Fallén (Diptera: Tachinidae)

A common parasite of various Lepidopterous hosts, this parasite has a similar life cycle to *L. dubia* except that it lays macrotype eggs on late instar larvae (20). Although released in relatively large numbers in 1955 and 1958 and again in 1959 and 1961, it has never been recovered.

PATHOGENS

The bacterium *Bacillus thuringiensis* Berliner, the active ingredient of a registered microbial insecticide, was tested extensively for control of larvae of the winter moth on apple at Kentville, Nova Scotia. Orchard tests in 1959 and 1960 showed that economically acceptable control could be obtained by applications of preparations of the bacterium in water at rates of 2 pounds of wettable powder per 100 gallons (7, 10). Applications of the bacterium when the larvae were about half grown and feeding on exposed foliage gave better results than earlier treatments. In a long-term study on the effect of the bacterium against the fauna of apple orchards, including larvae of *O. brumata*, an emulsifiable concentrate preparation of *B. thuringiensis* was applied on five to seven occasions in each of four consecutive years to bearing apple trees at rates of 0·5 to 2 quarts/100 gallons of spray (8). Numbers of winter moth larvae were reduced by 75–99 per cent. and damage to fruit was reduced proportionally. Predaceous and pollinating insects were not affected and numbers of red mite were consistently low. The bacterium may be particularly useful when the beneficial insects must be preserved but owing to the cost, widespread commercial usage is not practical.

Laboratory tests showed that larvae of *O. brumata* were readily killed by the entomogenous nematode DD–136 (9). But applications of the nematode to foliage of apple trees had no effect on *O. brumata* in the orchard apparently because the nematode is killed by desiccation (9). Experiments with the nematode showed that survival of *O. brumata* in soil was reduced from 35 to 12 per cent. by treatment of soil with the nematode at the time of pupation (11). The fungus *Metarrhizium anisopliae* applied to soil reduced survival to 4 per cent. in laboratory tests but was not consistently effective under orchard conditions. The studies demonstrated effectiveness of pathogens applied to soil and suggested that "the effectiveness of naturally occurring pathogens and of applied pathogens might be increased by suitable manipulation of the soil environment".

EVALUATION OF CONTROL ATTEMPTS

Population models based on life tables developed before the parasites became established, showed that the key factor regulating population levels was the degree of synchronism between pest and host plant. After the establishment of *C. albicans* and *A. flaveolatum* parasitism became the key factor, reducing winter moth populations to extremely low levels, well below that where economic damage could occur (3). For example, in the principal study area, population densities dropped from over 1,000 adults per tree in 1954 to less than one per tree in 1963. There were 0·03 adults per tree in 1968.

Outbreaks generally collapsed 3 years after parasitism by *C. albicans* reached 10 per cent. *C. albicans* parasitism sometimes exceeded 80 per cent. and at one point in the outbreak the ratio of potential *C. albicans* eggs to winter moth larvae in the principal study area was 1,600 to 1. In the year before population collapse, parasitism by *A. flaveolatum* always exceeded that of *C. albicans* (3).

The main infestation of the winter moth was in the South Shore area of Nova Scotia and the effect of the successful control of the winter moth on the forest economy in this area is complex. The principal damage was to red oak, up to 40 per cent. mortality occurred in some areas after 3 years of heavy defoliation (4). After the drop in winter moth populations, tree recovery was complete. Total merchantable volume of oak was about 124 million cubic feet or about 3 per cent. of the total hardwoods in the Province.

At the time of the initial biological control attempts, oak was not harvested in large quantities, but was used extensively in the ship building industry in the area. Apart from the loss of wood, the associated white pine regeneration stood to lose a large part of its protective overstory and would be made more vulnerable to attacks of the white pine weevil. However, the winter moth was just beginning to infest forested areas and the main threat seemed to be to shade- and ornamental-trees in towns and cities. Communities were forced to purchase sprayers and apply insecticides each spring from 1950 to 1962 after which the general collapse of the winter moth population made such measures unnecessary.

Since the collapse of the outbreak, a multi-million dollar hardboard manufacturing plant designed to use the low grade hardwoods in the area has been constructed. Ultimate consumption is expected to be 150,000 cords per year of which 70 per cent. will be hardwoods. In this area, an annual yield of 1 cord per acre on a 30-year rotation is expected from intolerant hardwood. This means that the value of oak, and the associated species on which the winter moth feeds, has been considerably increased (12). In addition, the importance of hardwood has increased throughout the Maritimes region with the construction of two hardwood pulp mills. The principal source of wood for these mills will be tolerant hardwoods, and although only a few stands of these hardwoods were eventually infested by the winter moth, damage was considerable. Sugar maple, white birch, yellow birch, and white ash all suffered mortality but less than that of red oak in the same area. Consequently, the spread of the winter moth constitutes a threat to similar stands inland, but the wide distribution of the parasites and the virus disease make it improbable that large outbreaks will occur.

Indirectly the winter moth had once posed an additional threat to a segment of the forest economy of the area. Oviposition occurs at the time when balsam fir Christmas trees were shipped to the United States, and the possibility of accidental introduction of winter moth into that country arose, although this did not occur during the years Christmas trees were exported and when severe outbreaks of the insect occurred. Quarantine regulations would have threatened the industry which in Lunenburg County alone is worth over one million dollars per year. After a thorough investigation the U.S. Bureau of Entomology and Plant Quarantine concluded that, along with other factors, the collapse of the winter moth population made quarantine measures unnecessary.

The winter moth is still a problem in apple orchards. Although it is easily controlled with insecticides, compounds such as DDT and Azinphos-methyl are toxic to predators, but not to phytophagous mites. Lead arsenate appears to be the most effective insecticide. It is only slightly toxic to both the phytophagous mites and predators but is effective against maturing winter moth larvae (17). In abandoned orchards parasitism by *C. albicans* and *A. flaveolatum* has exceeded 70 per cent. (13). Generation survival is possibly higher than in forested areas because winter moth hatching is well synchronized with flushing of apple foliage. However, the parasite population is generally low in commercial orchards possibly due to the effect of chemicals or to the low density of the winter moth (13).

RECOMMENDATIONS

Extensive winter moth outbreaks probably will not reoccur because outbreaks of exotic species, once under control, tend to fluctuate at lower, fairly static, levels (1). Moreover, since dispersion of the parasites appears to be as rapid as that of the winter moth, there is little likelihood of serious outbreaks arising in adjacent areas. In the event of an accidental introduction into a distant area, new releases could be made with much better initial chances of success than with the original ones because the behaviour of the parasites and host are better understood.

The background of academic studies by Varley and Gradwell, and recent work by Hassell (6), in England, and studies in Canada which are attempting to define the rôle of the parasites at low host populations, present a unique opportunity for thorough analyses of a successful biological control operation. There is an extremely good chance of producing the kind of information needed for the more sophisticated methods which will have to be employed in biological control programmes in the future. In this investigation we are in the process of explaining the various reasons why the combination of *C. albicans* and *A. flaveolatum* was successful in Canada. Analyses of the behaviour of the parasites under a variety of simulated conditions based on the mathematical models now being constructed, should define criteria for the selection of parasites and the planning of biological control operations against pests similar to the winter moth. If such investigations continue to be pursued as a part of biological control research, ultimately the selection of biological control agents and the manner in which they are to be manipulated, will be based on the results of simulation studies using standard mathematical models encompassing the prospective controlling agent and the ecosystem in which it is expected to act.

TABLE XXXI

Open releases and recoveries of parasites against *Operophtera brumata* (L.)

Species and Province	Year	Origin	Number	Year of recovery
Agrypon flaveolatum (Gravely)				
Nova Scotia	1959	Sweden	22	1961
	1961	Czechoslovakia, Germany, Austria	159	1965
	1962	Czechoslovakia	7	—
		Austria	87	—
Cyzenis albicans (Fallén)				
Nova Scotia	1959	Sweden	1349	1961
	1961	Czechoslovakia, Germany, Austria	3506	1961
	1962	Austria	597	1962
		Czechoslovakia, Austria	408	—
	1964	Nova Scotia *via* Europe	1126	—
	1965	Nova Scotia *via* Europe	226	—
New Brunswick	1963	Nova Scotia *via* Europe	77	—
Lypha dubia (Fallén)				
Nova Scotia	1961	Germany, Austria	263	—
	1962	Austria	158[1]	—
Phobocampe crassiuscula (Gravely)				
Nova Scotia	1961	Austria	150	—
	1962	Austria	51	—
Phorocera obscura (Fallén)				
Nova Scotia	1959	Sweden	85	—
	1961	Czechoslovakia, Germany, Austria	27	—
Pimpla contemplator Müller				
Nova Scotia	1964	France	11[1]	—

[1] Released in field cages.

LITERATURE CITED

1. Elton, C. S. (1958). The ecology of invasions by animals and plants. Methuen, London.
2. Embree, D. G. (1965). The population dynamics of the winter moth in Nova Scotia; 1954–62. *Mem. ent. Soc. Can.* No. 46, 57 pp.
3. Embree, D. G. (1966). The role of introduced parasites in the control of winter moth in Nova Scotia. *Can. Ent.* 98: 1159–68.
4. Embree, D. G. (1967). Effects of the winter moth on growth and mortality of red oak in Nova Scotia. *For. Sci.* 13: 295–9.
5. Graham, A. R. (1958). Recoveries of introduced species of parasites of the winter moth, *Operophtera brumata* (L.) (Lepidoptera: Geometridae), in Nova Scotia. *Can. Ent.* 90: 595–6.
6. Hassell, M. P. (1968). The behavioural response of a tachnid fly (*Cyzenis albicans* (Fall.)) to its host, the winter moth (*Operophtera brumata* (L.)). *J. Anim. Ecol.* 37: 627–39.
7. Jaques, R. P. (1961). Control of some lepidopterous pests of apple with commercial preparations of *Bacillus thuringiensis* Berliner. *J. Insect Path.*, 3: 167–82.
8. Jaques, R. P. (1965). The effect of *Bacillus thuringiensis* Berliner on the fauna of an apple orchard. *Can. Ent.* 97: 795–802.
9. Jaques, R. P. (1967). Mortality of five apple insects induced by the nematode DD–136. *J. econ. Ent.* 60: 741–3.
10. Jaques, R. P. & Fox, C. J. S. (1960). The influence of stickers on the effectiveness of sprays of *Bacillus thuringiensis* var. *thuringiensis* Berliner and *Bacillus entomocidus* var. *entomocidus* Heimpel and Angus. *J. Insect Pathol.* 2: 17–23.
11. Jaques, R. P., Stultz, H. T. & Huston, F. (1968). The mortality of the pale apple leafroller and winter moth by fungi and nematodes applied to soil. *Can. Ent.* 100: 813–8.
12. Johnson, R. S. (1967). A hardboard mill at East River, Lunenburg Co. Address to the Annual Meeting of the Nova Scotia Forest Technicians Association, Truro, N.S. 17 March.
13. MacPhee, A. W. (1967). The winter moth, *Operophtera brumata* (Lepidoptera: Geometridae), a new pest attacking apple orchards in Nova Scotia, and its coldhardiness. *Can. Ent.* 99: 829–34.
14. McGugan, B. M. & Coppell, H. C. (1962). Biological control of forest insects, 1910–1958. *In* A review of the biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol. Contr.* 2: 35–127.
15. Mesnil, L. P. (1967). History of a success in biological control: the winter moth project in Canada. *Tech. Bull., Commonw. Inst. biol. Contr.* 8: 1–6.
16. Neilson, M. M. (1964). A cytoplasmic polyhedrosis virus pathogenic for a number of lepidopterous hosts. *J. Insect Pathol.* 6: 41–52.
17. Sanford, K. B. & Hebert, H. J. (1966). The influence of spray programs on the fauna of apple orchards in Nova Scotia. XV. Chemical controls for winter moth, *Operophtera brumata* (L.), and their effects on phytophagous mite and predator populations. *Can. Ent.* 98: 991–9.
18. Thompson, W. R. (1946). A catalogue of the parasites and predators of insect pests. Sect. 1. Pt. 8. Parasites of the Lepidoptera. *Commonw. Inst. biol. Contr.*: 386–523.
19. Varley, G. C. and Gradwell, G. R. (1968). Population models for the winter moth. *Symp. R. ent. Soc. Lond.* 4: 132–42.
20. Wylie, H. G. (1960). Insect parasites of the winter moth, *Operophtera brumata* (L.) (Lepidoptera: Geometridae), in western Europe. *Entomophaga* 5: 111–29.

45. *PRISTIPHORA ERICHSONII* (HARTIG), LARCH SAWFLY (HYMENOPTERA: TENTHREDINIDAE)

W. J. Turnock and J. A. Muldrew

PEST STATUS

The larch sawfly, *Pristiphora erichsonii* (Hartig), is a major defoliator of larches in North America. It feeds on all three species of native larch; tamarack, *Larix laricina* (Du Roi) K. Koch, western larch, *L. occidentalis* Nutt. and alpine larch, *L. lyallii* Park., plus introduced European and Asian larch species and hybrids (4). In North America, the larch sawfly is probably present throughout the ranges of the native species of larch and it also occurs in plantations of these and other *Larix* species outside their natural range (Fig. 21). Its apparent absence from several northern areas reflects the incompleteness of surveys in this region.

Larch sawfly outbreaks have been recorded in Canada since 1882, in every province and in the Yukon and Northwest Territories. McGugan and Coppel (18) summarized the records of the distribution and duration of outbreaks prior to 1958 and information on the infestation pattern since

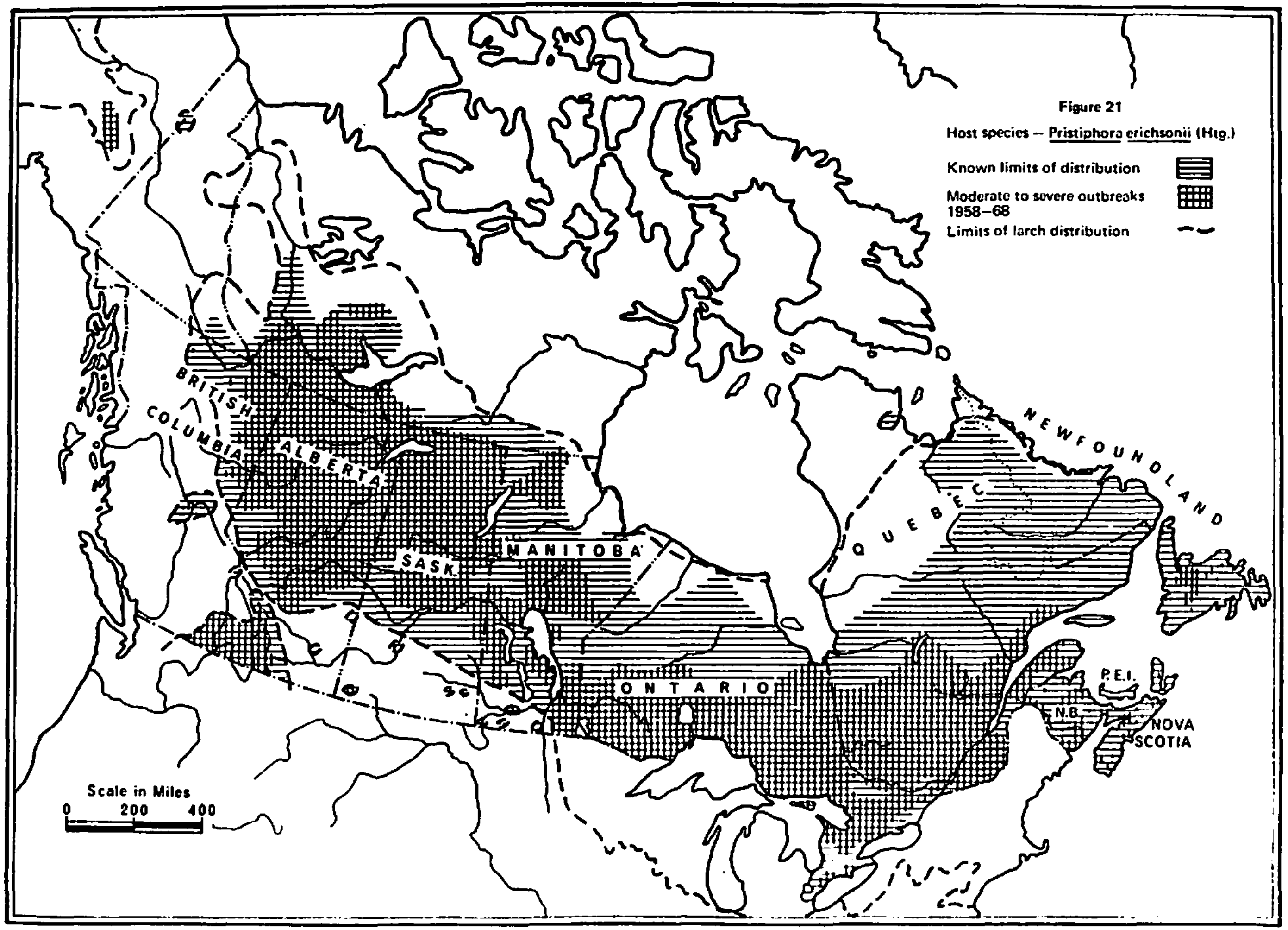

Figure 21

Host species -- *Pristiphora erichsonii* (Htg.)

then is given by the Annual Reports of the Forest Insect and Disease Survey, Department of Fisheries and Forestry, Ottawa, Canada. A summary of the infestation history since 1958 follows.

Populations on western larch in southern British Columbia increased from 1962 to 1964, caused moderate to heavy defoliation in most stands in 1965 and 1966, and declined in 1967. The intensive outbreak which was in process in the Prairie Provinces in 1958 continued to spread northwestward into northeastern British Columbia and the Yukon Territory until 1966. Populations in central Alberta declined in 1964 and the whole outbreak had subsided by 1967. In Saskatchewan and Manitoba large areas of moderate to severe defoliation occurred in 1959 and 1960, with less extensive outbreaks occurring annually since then. In Ontario and Quebec, the major outbreak in progress in 1958 continued through 1960. Populations declined from 1961 to 1965 although some areas were still heavily defoliated. A general resurgence was noted in 1966 and 1967, declining again in 1968. In New Brunswick, populations began to increase in 1960 and heavy defoliation was recorded from 1962 to 1968. In Nova Scotia and Newfoundland patches with moderate to severe defoliation occurred from 1958 to 1967.

The most severe and prolonged outbreaks are part of the series of infestations which began in Manitoba in 1938 and eventually extended from northeastern British Columbia to Nova Scotia. In some of these infestations, moderate to severe defoliation for 6 to 9 consecutive years has been recorded. The sawflies in these outbreak populations are resistant to the parasite *Mesoleius tenthredinis* Morley (20).

The foregoing discussion considered mainly moderate to severe outbreaks in which at least 40 per cent. of the foliage was consumed. Although most larch stands in outbreak areas were attacked, these stands are scattered and considerable variation in the level of infestation was common. In general, stands on the better sites were most heavily attacked, while slow-growing trees on very wet organic soils were protected by their paucity of new shoots (utilized for oviposition by the sawflies) and by high mortality of sawfly cocoons caused by wet soil conditions.

The effects of defoliation on growth and mortality of larch are difficult to ascertain. On western larch no mortality attributable to the larch sawfly has been reported, but growth suppression is common during outbreaks. Alpine larch has not been seriously defoliated. On tamarack, both growth suppression and mortality have been commonly observed but these effects, particularly mortality, are difficult to assign directly to the larch sawfly. As many of the affected stands were young and over-stocked at the beginning of the outbreak, it is difficult to separate normal losses due to suppression from those induced by defoliation.

In general, net growth has been negligible in tamarack stands that have been frequently defoliated in the past 20 years (22) and many of the surviving trees have decreased in height due to death of the upper part of the crown. Where additional stresses on defoliated stands such as flooding or attacks by the eastern larch beetle, *Dendroctonus simplex* Leconte, have occurred, the stand may be destroyed for commercial purposes (5). Growth loss and mortality have prevented existing tamarack stands from reaching the size and quality of the stands that were cut from 1880 to 1920. Present utilization of tamarack is primarily confined to fence posts and rails. In addition, the fear of attack by the larch sawfly has tended to prevent the use of larches in forest plantings.

The univoltine larch sawfly overwinters in cocoons in the duff with adult emergence occurring in spring and early summer (4, 28). Eggs are deposited in new shoots throughout the summer and the oviposition damage usually causes a characteristic curling. The larvae feed gregariously, then fall to the duff and spin cocoons.

Invertebrate predators and weather cause some mortality of eggs and feeding larvae but these do not have a measurable effect on population trends (13, 14, 15).

The parasite complex of the larch sawfly in North America, excluding rare or 'accidental' parasites, consists of four species, *Bessa harveyi* (Tnsd.), *Mesoleius tenthredinis*, *Eclytus ornatus* Holmgren and *Tritneptis klugii* (Ratzeburg). The first three attack feeding larvae and the last species attacks the cocoon stage of the host. Of these, only *B. harveyi* is a Nearctic species. It is the most abundant parasite of the larch sawfly in North America (29) and there is some evidence that parasitism by this species affects population trends in Manitoba (14).

Mesoleius tenthredinis was introduced from Europe from 1910 to 1913 and was credited with the control of several outbreaks (18). Since the appearance in Manitoba of a strain of larch sawfly capable of encapsulating the eggs of *M. tenthredinis* (19), and the subsequent spread of this strain across Canada (20), this parasite has become incapable of effecting control except in southern British Columbia (12).

E. ornatus is a widespread but unimportant parasite of larch sawfly in Europe and its limited distribution in eastern North America suggests that it was recently introduced. Parasitism reaches a maximum of 9 per cent. in Newfoundland (30), which is higher than in Europe.

T. klugii is widely distributed in both Europe and North America. It is an important control factor in British Columbia but elsewhere in North America it is rarely abundant and occurs only in drier larch stands.

The major mortality factors affecting sawfly cocoons are small mammals and flooding. These may kill a very high percentage but, except in specific instances, do not have a direct controlling influence on larch sawfly populations (2, 14). Avian predators on larch sawfly larvae and adults include many species (3) but these, like small mammals, do not show a significant controlling influence on population trends except under special circumstances.

Microorganisms are not generally important as natural control agents, although in some instances infections apparently kill many sawflies. *Entomophthora* (= *Empusa*) sp. occasionally causes high larval mortality in localized areas. In Ontario, mortality associated with bacterial infection was low and tests indicated that *Bacillus cereus* Fr. & Fr. was the only virulent species (9). In Quebec, a microsporidian, which affects reproduction, and a rickettsia, reported to be important in causing a larch sawfly population decline, have been isolated (26).

BACKGROUND

The decision, in 1957, to renew the biological control programme was influenced by the high larch sawfly numbers and paucity of parasite species in Canada, the success of the initial releases of *M. tenthredinis* in 1910–13 (18), and the belief that a study of parasitism in Europe would reveal species with a high potential for biological control in Canada.

Some estimate of the enormous difference in the density of larch sawflies in Europe and North America can be made by comparing the numbers collected per man-hour. In the best collecting areas of Europe since 1958, annual collecting rates have ranged from 3 to 17 per man-hour in Austria and from 22 to 180 per man-hour in the plantations of Bavaria (23). In contrast, collecting rates of 1,000 to 2,000 larvae per man-hour have been possible in southern Manitoba annually since 1946.

A separate decision was made to initiate a biological control programme against the larch sawfly in Newfoundland. Since the small mammal complex of this island was restricted and shrews were lacking, an introduction of the masked shrew, *Sorex cinereus cinereus* Kerr, was planned to augment the natural enemies of the larch sawfly (1).

STUDIES IN EUROPE AND JAPAN

Personnel of the European Station, Commonwealth Institute of Biological Control, began studies of the parasite complex of the larch sawfly in 1958 and continued until 1967. The results were presented in a series of interim reports which have been summarized in several papers (23, 6, 31, 24). These list the following species as parasites of the larch sawfly.

Europe		Japan
	LARVAL PARASITES	
	Ichneumonidae	
Mesoleius tenthredinis Morley[1]		*Mesoleius tenthredinis* Morley
Olesicampe benefactor Hinz[1]		
Hypamblys albopictus Gravenhorst[1]		
Polyblastus tener Habermehl		
Rhorus lapponicus Roman		
Eridolius hofferi Gregor		
Trematopygus sp.		
Eclytus ornatus Holmgren		
Erromenus sp. nr. *haemorrhoicus*		
	Tachinidae	
Myxexoristops stolida Stein[1]		*Vibrissina turrita* Meigen[1]
Hyalurgus lucidus Meigen[1]		*Bessa selecta* Meigen
Bessa selecta Meigen		*Drino bohemica* Mesnil
		Myxexoristops stolida Stein
	COCOON PARASITES	
	Ichneumonidae	
Pleolophus brachypterus Gravenhorst		*Pleolophus* sp.
Aptesis nigrocincta Gravenhorst		*Mastrus* sp.
	Pteromalidae	
Tritneptis klugii (Ratzeburg)		
	HYPERPARASITE	
	Ichneumonidae	
Mesochorus dimidiatus Holmgren		

[1] Considered to be important parasites.

In Europe, six species of larval parasites are important in terms of their distribution, constancy and abundance. The importance of parasites attacking host larvae just before or during the cocoon stage is underestimated because most collections were of younger larvae. The list of parasites from Japan is probably incomplete because it is based on only 4 years collecting in selected larch plantations on Hokkaido, outside the native range of Japanese larch.

M. tenthredinis and *O. benefactor* are known to be specific parasites of the larch sawfly while *M. stolida*, *H. lucidus* and *V. turrita* are polyphagous. *H. albopictus* is either a polymorphic, polyphagous species or a group of sibling species, one of which attacks the larch sawfly. These parasites are well-synchronized with the univoltine larch sawfly but *H. albopictus* may produce a partial second generation. Superparasitism is common with *M. tenthredinis* and *H. albopictus* but rare with *O. benefactor*.

Effective parasitism by *M. tenthredinis* is reduced by the encapsulation of its eggs by host larvae in many areas of Europe but not in larch plantations located north of the Alps to the North Sea. A hyperparasite, *M. dimidiatus*, attacks *O. benefactor* throughout its known range in Europe. Egg parasites of the larch sawfly have never been found. In Europe predators that attack the eggs were present but apparently of minor importance. Larval predation by ants (*Formica polyctena* group) was of much greater importance in Europe than in America, and the pentatomids *Picromerus bidens* L. and *Pinthaeus sanguinipes* F. were of occasional importance.

PREVIOUS BIOLOGICAL CONTROL ATTEMPTS

The larch sawfly has been the target of several parasite release programmes (18, 27). The various attempts were of three main types:

(1) Introduction of new parasite species from larch sawflies collected in other continents: *M. tenthredinis*, 1910–13; *Myxexoristops stolida* (= *Zenillia nox* Hall), 1935.

(2) Relocations of native parasites or introduced species already established in Canada: *M. tenthredinis*, 1927, 1929, 1934–45, 1947–52; *Bessa harveyi*, 1936–42; *Tritneptis klugii*, 1947–52.

(3) Introduction of parasites from hosts other than the larch sawfly: *Pleolophus* (=*Aptesis*) *basizonus*, 1949; *Drino bohemica*, 1948.

'With the exception of *M. tenthredinis*, the biological control programme against the larch sawfly was of little value' (18) but the attempts illustrate some generalities pertinent to biological control programmes:

(1) *M. tenthredinis* was successful only when it was introduced to areas where it did not occur: the original introductions to Manitoba and Quebec (1910–3); and relocations to Ontario (1929 and 1937–42), British Columbia (1934–42), New Brunswick (1935–8) and Nova Scotia (1937–42). In Newfoundland *M. tenthredinis* failed to become as abundant as elsewhere but the introduction was a partial success.

(2) The transfer of native parasites or established introduced species within their area of occurrence was a failure. The massive releases of *M. tenthredinis* and *T. klugii* (1947–52) and of *B. harveyi* (1936–42) failed because the released parasites were apparently genetically identical and thus were subject to the same limiting factors of the habitat. Subsequent studies indicated that these were the presence of the resistant host strain for *M. tenthredinis*, restricted physical requirements for *T. klugii*, and the latter plus poor synchronization for *B. harveyi*.

(3) The release of parasites which do not normally attack the target species were not successful (*P. basizonus* and *D. bohemica*).

Attempts at biological control using the fungus *Beauveria bassiana* (Bals.) Vuill. have not been successful: spraying host trees with spores gave only a temporary increase in the incidence of infection (17). Two factors may mitigate against microorganisms as effective control agents against the larch sawfly; the deciduous habit of larches, which prevents the overwintering of spores on the needles; and the uncertainty of optimal weather conditions for infection.

RELEASES AND RECOVERIES

PARASITES

Between 1959 and 1965 adults of 11 species of larch sawfly parasites were received in Canada and studied in the laboratories in Manitoba and Quebec (Table XXXV). Since comprehensive data from the donor countries were not available, the species selected for introduction were those primary parasites received in sufficient quantities to allow an initial release of at least 200 adults.

The chances of successful establishment were considered to be maximized by the release in an optimal environment of a large number of healthy, vigorous, female parasites that had previously mated and completed their pre-oviposition period. This environment should contain sufficient host larvae to allow maximum oviposition by the parasite but not so many as to exhaust the food supply and thus cause starvation. The presence of a food supply for parasite adults, particularly flowering plants for tachinids, and of alternate hosts for polyphagous parasites, was considered but little variation could be detected between otherwise suitable locations.

Nearly all the parasites used were reared to the adult stage at Belleville and shipped in a chilled condition to the regional laboratories at Winnipeg and Quebec. Shipments were made twice a week. Some parasite adults were reared at Winnipeg, from 1960 to 1962.

In Manitoba, parasite releases were made at weekly intervals mainly to allow time for mating before release. The release points selected in Manitoba generally satisfied the requirements mentioned above although host populations at the Pine Falls release point declined and parasitism by the native tachinid, *Bessa harveyi*, increased in the release year.

The initial release points, Pine Falls and Riverton, were adjacent to intensive study plots established by the larch sawfly population dynamics group of the Winnipeg laboratory. At these locations, annual estimates of the population density of several stages of the larch sawfly, estimates of sawfly mortality, the abundance of mortality agents and the monitoring of various aspects of site and weather are determined (16).

As many of the parasites were polyphagous in their native environment, a programme of collecting other possible hosts in Canada was undertaken by the Forest Insect and Disease Survey, Winnipeg.

Native parasites, but none of the introduced species released, were reared from the following sawflies: *Anoplonyx luteipes* Cresson from larch; *Pikonema alaskensis* Rohwer from spruce; *Neodiprion pratti banksianae* Rowher from jack pine; *Nematus* spp. from aspen; *Nematus limbatus* Cresson and *Pristiphora sycophanta* Walsh from willow; *Cimbex americana* Leach and *Hemichroa crocea* (Fourcroy) from alder. This limited evidence does not indicate the establishment of any of the released species on other potential hosts.

More detailed information on the laboratory studies, releases and establishment is given below for each species.

Cteniscus pedatorius Panzer (Hymenoptera: Ichneumonidae)

Although *C. pedatorius* was recently excluded from a listing of parasites of the larch sawfly in Europe (24) it was a suspected parasite at the time the shipments were received. The parasites were vigorous and active in test cages and some mating was observed. Larch sawfly larvae in the third to fifth instar were provided but parasitism did not occur.

Hyalurgus lucidus (Meigen) (Diptera: Tachinidae)

H. lucidus was the first parasite species received in Winnipeg. From 1960–2 the adults received from Belleville or reared at Winnipeg were unsatisfactory for study or release: vigour was low, survival poor and many adults were deformed. Suitable conditions for mating in the holding cages were not attained and even in 1964, when vigorous adults were available, mating was not common. Various flowers, including Umbelliferae, were placed in the cages as a food source but no improvement was noted. The best mating success was observed when newly-arrived females were kept with males over 5 days old at 23°C. and 55–60 per cent. relative humidity. In Quebec, *H. lucidus* mated in outdoor cages after rain when the sun came out in the late afternoon.[1] Attempts during 1960 to 1965 to obtain parasitism of larch sawfly larvae in both laboratory and large field cages were unsuccessful.

Despite these difficulties, 692 parasites in moderately good condition were released in Manitoba in 1963 and smaller numbers in good condition were released in Manitoba in 1964 and in Quebec in 1965. No evidence of the successful establishment of this species has been obtained. Although the vigour of the parasites used in early releases may have been too low, no explanation of the failure of the later releases can be given.

Hypamblys sp. (Hymenoptera: Ichneumonidae)

The parasites received from Europe included specimens reared from the larch sawfly (15 per cent.), *H. crocea* (85 per cent.) plus a single specimen from *Pteronidea* sp. The taxonomic position of these specimens remains poorly defined: Pschorn-Walcher and Zinnert (24) identify them as *H. albopictus* Gravenhorst, which they describe as a fairly polymorphic species that attacks a variety of nematine sawflies.

From 1961 to 1964, cage tests were conducted and parasitism of larch sawfly larvae was obtained. The 1964 tests indicated that adult females of *Hypamblys* sp. ex *P. erichsonii* and those ex *H. crocea* can parasitize Canadian larch sawfly larvae. There is some evidence that a greater number of attacks per female were made by those ex *P. erichsonii.*

In 1963, 214 adults, 12 per cent. of which had emerged from *P. erichsonii*, were released at Riverton, Manitoba. No recoveries were made.

Mesoleius tenthredinis Morley (Hymenoptera: Ichneumonidae)

The Bavarian strain of *M. tenthredinis* was introduced because it could overcome the host resistance of Canadian larch sawfly to a much greater degree than 'native' *M. tenthredinis*, and could pass this ability to the progeny of Bavarian X 'native' crosses.[2]

Vigorous, mated parasites of the Bavarian strain were released at two locations which differed markedly in the abundance of the native strain. At the release point on Hodgson Road, parasitism by

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[1] Quednau, F.W. Department of Fisheries and Forestry, Ste. Foy, Quebec 10, Quebec. Personal communication.

[2] Muldrew, J. A. Department of Fisheries and Forestry, Winnipeg, Manitoba. Unpublished data.

the native strain was high and the percentage encapsulation low while at the Rennie release point, *M. tenthredinis* appeared to be locally extinct.

The results of the releases reflect the difference in the status of the pre-release populations of the native strain. At the Hodgson Road location, dissections of cocoons collected at the release point and in a check plot 7 miles distant showed no consistent differences in the percentage of parasitism or encapsulation (Table XXXII). If the Bavarian strain is established, its abundance is so much lower than that of the native strain that its presence is undetectable.

At the Rennie plot, *M. tenthredinis* was reared from cocoons collected the year of release and its density has increased steadily. Dissections of cocoons since 1966 show the percentage of parasitism has been increasing and indicate a low level of encapsulation (Table XXXII). There seems little doubt that the Bavarian strain is established in this plot. No dispersal studies of the Bavarian strain have been made.

TABLE XXXII

Percentages of parasitism by *Mesoleius tenthredinis* Morley and of host resistance at release plots and a check plot following the release of the Bavarian strain

Year	Total	Effective	Resistant[1]	Total	Effective	Resistant[1]
		Hodgson Road Release Plot			Hodgson Road Check Plot[2]	
1963	12·1	5·8	52	9·0	2·2	75
1964	8·9	4·4	50	12·3	5·8	52
1965	15·5	9·5	39	8·8	3·2	64
1966	11·2	4·9	56	10·0	3·2	68
1967	4·7	1·6	75	7·5	3·2	57
1968	5·6	3·2	43	4·2	1·9	56
1969	41·2	29·4	29	5·0	3·0	60
		Rennie Release Plot				
1966	4·0	3·4	14			
1967	13·5	12·3	10			
1968	22·3	20·0	10			
1969	63·0	58·0	8			

[1] Resistant = (Hosts with encapsulated eggs/total parasitized hosts) 100.
[2] Data from Forest Insect and Disease Survey, Winnipeg, Manitoba.

Myxexoristops stolida (Robineau-Desvoidy) (Diptera: Tachinidae)

The parasite adults received in Winnipeg emerged from cocoons of a number of sawflies, but the larch sawfly was the major host. The adults received were quite vigorous and survival in the holding cages was fairly good. Mating was rarely observed and attempts to obtain parasitism of larch sawfly larvae in cages were unsuccessful.

Although the releases of *M. stolida* in 1962 were adequate in numbers and well synchronized with suitable host larvae, no evidence of establishment was found from this release nor from smaller releases in 1963 and 1964 at the same location. The failure of releases in Manitoba may be related to unfavourable conditions in the holding cages for mating and maintaining vigour while the Quebec release was not a fair test because only seven adults were released.

Olesicampe benefactor Hinz (Hymenoptera: Ichneumonidae)

From 1961 to 1964 *O. benefactor* adults were received at Winnipeg in excellent condition. Mating occurred freely in the holding cages and adult mortality was low. Releases of parasites reared from the European collections were made in Manitoba at Pine Falls in 1961, at Riverton in 1962 and 1963, and in Saskatchewan at Crutwell in 1964. Relocations of *O. benefactor* using adults emerging from collections made at Pine Falls and Riverton were also made at Crutwell, Saskatchewan (1965 and 1966), Manitoba (1967 and 1968), New Brunswick (1967), Nova Scotia (1967 and 1968) and Maine (1967) (Table XXXVII).

Both of the initial releases in Manitoba were successful (21) and the percentage parasitism has risen to very high levels (Table XXXIII). At Pine Falls, the small number of parasites released and the high level of parasitism in the release year by the native tachinid, *Bessa harveyi*, seems to have retarded the initial increase of *O. benefactor*. At Riverton, the rapid increase in parasitism was halted in 1966 by catastrophic mortality caused by flooding. Despite this loss, *O. benefactor* survived and a high level of parasitism was again recorded in 1963. At Crutwell, no recoveries were made following the release of parasites from European collection but *O. benefactor* was recovered following subsequent relocations from Pine Falls.

TABLE XXXIII

Host density per acre and percentage parasitism by *Olesicampe benefactor* Hinz. at Pine Falls and Riverton, Manitoba

	Pine Falls				Riverton			
	Host instar II		Host cocoons		Host instar II		Host cocoons	
Date	Density	Parasitism	Density	Parasitism	Density	Parasitism	Density	Parasitism
1961	216,400	—	25,900	—				
1962	125,700	—	73,400	<1	507,600	—	244,200	<1
1963	475,000	—	210,000	<1	145,400	—	60,800	<1
1964	537,100	—	507,300	8	57,500	—	32,500	36
1965	366,800	—	311,100	61	250,600	83	114,500	87
1966	693,200	71	333,900	93	65,100	76	8,500	77
1967	364,100	85	137,400	97	23,000	—	15,600	66
1968	368,300	86	122,000	95	196,300	68	32,000	98
1969	—	—	131,300	94	—	—	14,800	96

DISPERSAL. The initial dispersal of *O. benefactor* at Pine Falls and Riverton was very slow, the maximum distance of recovery in 1965 was 0·5 miles at Pine Falls and 1·0 miles at Riverton (21). In 1966, flooding of the Riverton release area reduced larch sawfly populations to a level where dispersal studies could not be continued but sampling of the Pine Falls area was repeated in 1966 and 1967. The known dispersal distance and the percentage parasitism increased significantly (Fig. 22). In 1968, the Forest Insect and Disease Survey continued the dispersal study and recovered *O. benefactor* up to 7·2 miles north and 8·3 miles south of the release point. The maximum dispersal recorded to date is 13·7 miles from the Riverton release plot by 1966 and 33 miles from the Pine Falls plot by 1969.

Muldrew (21) hypothesized that the slow initial dispersal of *O. benefactor* could be attributed to the abundance of larch sawfly in the release areas, because female parasites could find sufficient hosts for oviposition without dispersing. This is supported by the results; the greatest increase in the maximum recorded dispersal distance coincides with decreased host and parasite populations and high parasitism in the release area (Table XXXIII).

SURVIVAL AND RATE OF INCREASE. Survival ratios of the parasite during two intervals from hatching to adult emergence were calculated and compared to ratios for equivalent intervals in the host's life history (Table XXXIV). Hosts parasitized by *O. benefactor* had consistently higher survival ratios than unparasitized hosts during the host's larval feeding period, but lower survival ratios during the host's cocoon stage. The average survival ratios from the host's second instar to adult emergence was about the same for both. The higher survival rate of parasitized larvae may be related to their small size: either through lower food requirements or because they are less conspicuous to predators or other parasites. The reason for the lower survival rate of parasitized larvae during the cocoon stage may be similar to that described by Heron (10) for cocoons parasitized by *Bessa harveyi*: parasitized cocoons have a higher metabolic rate than unparasitized cocoons and are more likely to succumb to adverse physical conditions such as excess moisture.

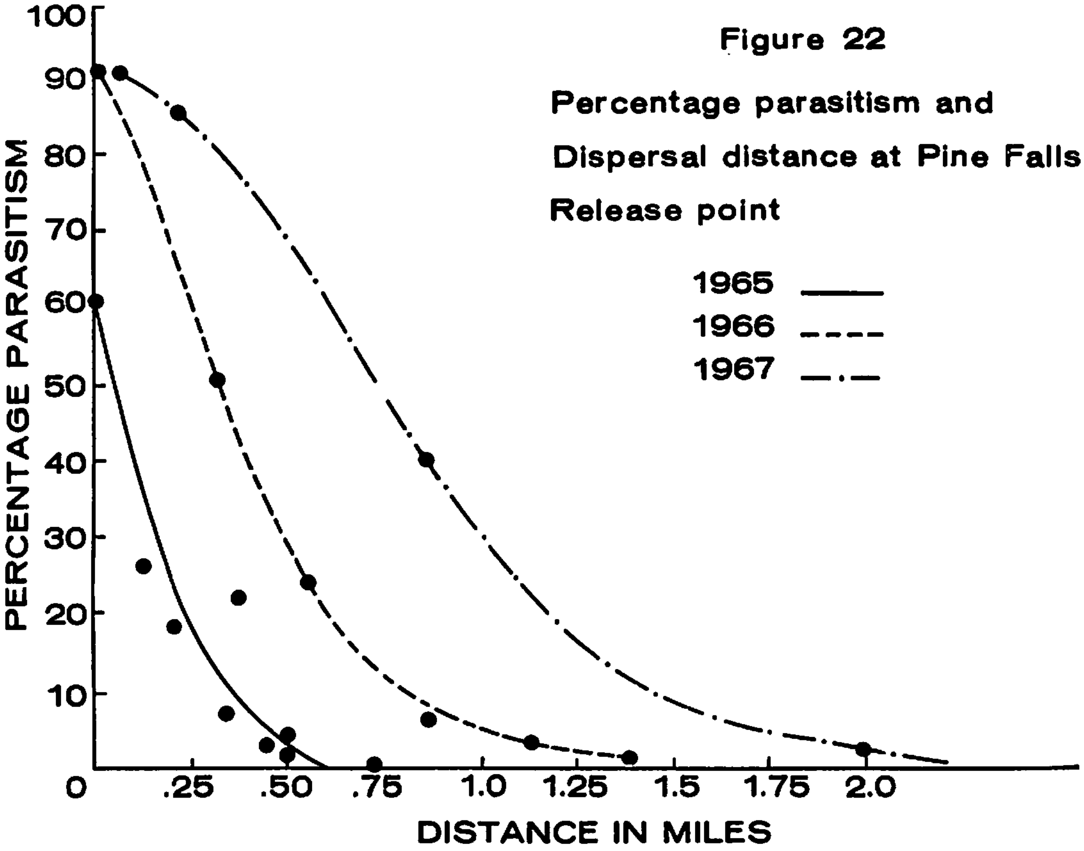

Figure 22

Percentage parasitism and Dispersal distance at Pine Falls Release point

TABLE XXXIV

Survival ratios for the larch sawfly and *Olesicampe benefactor* Hinz. Values calculated from data collected using techniques described by Ives *et al.* (1969)

		Host instar II to cocoon		Host cocoon to adult		Instar II to adult	
Plot	Year	Host	Parasite	Host	Parasite	Host	Parasite
Pine Falls	1964	—	—	·098	·064	—	—
	1965	—	—	·134	·137	—	—
	1966	·118	·626	·549	·109	·065	·068
	1967	·077	·438	·528	·045	·040	·020
	1968	·114	·468	—	—	—	—
Riverton	1964	—	—	·004	·013	—	—
	1965	·345	·480	0	·017	0	·008
	1966	·125	·132	0	0	0	0
	1967	—	—	·082	·042	—	—
	1968	·013	·297	—	—	—	—
Hodgson	1967	—	—	·026	·032	—	—
	1968	·271	·501	—	—	—	—
	Mean	·152	·421	·157	·051	·026	·024

Rate of increase of *O. benefactor* in the study plots has been rapid despite the generally low survival ratio and emigration from the plot area. At the Pine Falls release area, the estimated population of *O. benefactor* adults (based on adult emergence traps in the plot (16)) was 2,600 per acre in 1965: 26,600 in 1966, 33,800 in 1967, and 6,100 in 1968. The greatest increase, from 1965 to 1966, was over 10-fold. If we estimate survival for the 1965–6 generation of parasites to be equal to the mean value for the interval between the host's second instar and cocoon stage (·420, Table XXXIV) and use the observed survival rate to the adult stage (·137) the combined survival ratio is ·058, more than twice the mean of ·024. If emigration and adult mortality are excluded, each of the 1,300 females emerging in 1965 would have to have laid 353 eggs to produce a population of 26,600 adults in 1966.

The reproductive capacity of the larch sawfly in Manitoba varies between 60 and 80 (11) but the mean number of eggs actually laid per female is usually less than 20 (unpublished data). Reproductive advantage appears to have been the major factor allowing this parasite to overtake host populations.

Hyperparasitism. Heavy losses of *O. benefactor* through hyperparasitism by *Mesochorus dimidiatus* in Europe were known before *O. benefactor* was released and extreme care was taken to prevent the introduction of the hyperparasite. Hyperparasites were recovered, however, from the Pine Falls area 5 years after the release of *O. benefactor*. These hyperparasites were found to be conspecific with *M. dimidiatus* collected in Europe.[1,2] Subsequently, specimens of *M. dimidiatus* have been reared from larch sawfly cocoons collected at the following *O. benefactor* release points: Hodgson and Riverton, Manitoba (1968); Grand Manan and St. Stephen, New Brunswick (1969). Specimens of *M. dimidiatus* in the Canadian National Collection,[1,3] from unknown hosts collected in Alberta (1924) and the Northwest Territories (1949) and ex *Neodiprion abietis* collected in Nova Scotia (1961), indicate that *M. dimidiatus* is a Holarctic species with a wide distribution in Canada.

The incidence of *M. dimidiatus* at Pine Falls rose rapidly from 0·4 per cent. of the hosts parasitized by *O. benefactor* in 1966 to 8 per cent. in 1967 and 61 per cent. in 1968. At Riverton and Hodgson, 13 and 4 per cent. were attacked by *M. dimidiatus* in 1968, while its incidence in New Brunswick is still very low.

In the five transfers of *M. dimidiatus* from native hosts to *O. benefactor* that have occurred, the first recoveries of the hyperparasite were made close to the parasite release points. This is probably

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[1] Dasch, C. E. Muskingum College, New Concord, Ohio. Personal communication.

[2] Schwenke, W. Institut für angewandte Zoologie, Munich, West Germany. Personal communication.

[3] Mason, W. R. M. Entomology Research Institute, Canada Department of Agriculture, Ottawa, Ontario. Personal communication.

because *M. dimidiatus* transferred when *O. benefactor* still occupied a limited range and the build-up and dispersal of the former lags behind that of the latter. At Pine Falls, where *O. benefactor* had spread up to 8·3 miles by 1968, *M. dimidiatus* was found at maximum distances of 1·3 miles south and 0·5 miles north of the release point.

Polyblastus tener Habermehl (Hymenoptera: Ichneumonidae)

The three specimens received at Winnipeg were caged with larch sawfly larvae but no parasitism was recorded. Since it prefers solitary-feeding sawflies in Europe it will not be considered for future releases.

Rhorus lapponicus Roman (Hymenoptera: Ichnemonidae)

In Winnipeg, adults of *R. lapponicus* ex *P. erichsonii*, were used in 1962 and 1963 for cage studies. The adults were active and some mating was observed. Cage studies were negative, probably because the preference of ovipositing females for very young host larvae was unknown to us.

Vibrissina turrita (Meigen) (Diptera: Tachinidae)

Adults of *V. turrita* from Japanese larch sawfly were received from 1962–5 in good condition. Although it probably has other hosts in Japan and does not attack the larch sawfly in Europe, its abundance in Japanese collections made it a reasonable prospect for release. Mating was not observed in cages and attempts to obtain cage parasitism of larch sawfly larvae in 1962 and 1964 were unsuccessful.

In 1964, the release of 521 adults in Manitoba was well-synchronized with preferred larval instars. The numbers released in Manitoba in 1963 and Quebec in 1965 were small but were equally well-synchronized. No explanation of the failure of the releases can be given unless, like other tachinid species, suitable conditions for mating and egg maturation were not provided.

PREDATORS

Sorex cinereus cinereus Kerr (Insectivora: Soricidae)

The introduction of the masked shrew into Newfoundland appears to be a unique venture in biological control. Although the larch sawfly was the target species, it was recognized that the predator could influence a wide range of species. Since no insectivores and few small fossorial mammals occurred on the Island, a largely unoccupied niche was available to the colonists.

A major problem in attempting to release shrews was their excitability and susceptibility to death at the time of capture or subsequently. Masked shrews were trapped in northern New Brunswick in 1958 and 22 (12 females and 10 males) were released near St. George's, Newfoundland (1). The release point was selected to provide an appropriate habitat and was semi-isolated to prevent dispersal loss before establishment.

At least half of the animals released survived the first winter and from this small colony the masked shrew increased and spread rapidly. Populations increased rapidly and reached very high levels in the years immediately following their invasion of a new area. They then decreased but have maintained higher population levels and have occupied a wider variety of habitats than is characteristic of continental Canada. Dispersal from the original release and two relocations have extended the range of the masked shrew over much of western and central Newfoundland by 1964 (1) and by 1968 nearly two thirds of the island was occupied.

EVALUATION

PARASITES

Selection of species for release

The information now available on larch sawfly parasites generally confirms our selection of *M. tenthredinis*, *O. benefactor*, *M. stolida* and the exclusion of less effective species. The release of

H. albopictus is justified if the adults released represent a single, polymorphic, polyphagous species as described by Pschorn-Walcher and Zinnert (24). The selection of *V. turrita* and exclusion of other species from Japan seems justified by the rather limited information now available.

The simultaneous release of several parasite species, rather than sequential releases in order of estimated potential for exerting control appears justified. European studies do not indicate that competition between the parasitic species released reduced their effectiveness. In addition, had releases been delayed until sufficient information was available to select a single most-promising species, the brief period of relative abundance of larch sawfly in Europe would have been past, and obtaining sufficient material for release at a later date would have been expensive if not impossible.

Pre-release handling

The use of holding cages under rearing room conditions to allow mating, to equalize sex ratios, and to reduce the number of trips for releases worked well with *O. benefactor* but poorly for the tachinids and possibly some other species. In retrospect, we underestimated the necessity of preliminary studies to determine optimum conditions for mating and pre-oviposition survival. Synchronization was not a problem since adult emergence of the host occurs over a period of nearly two months in Manitoba and the larval stages overlap (28).

Quality and genetic composition

The number of parasite adults released does not appear to have been a major influence on the establishment of the released species. In the case of *O. benefactor*, the initial release of only 158 females at Pine Falls, Manitoba, in 1961, was successful but with larger releases the rate of parasite-increase was more rapid. At Pine Falls, parasitism reached 90 per cent. in the sixth generation after release. At Riverton, following a small release in 1962 and a large one in 1963, parasitism reached 87 per cent. in the third generation after the initial release.

Evidence that the relocations of *O. benefactor* to the Maritimes were successfully established was obtained in the year of release, despite the relatively small numbers of adults in the colonies, 149 to 388 mated females per location.[1] The quick establishment of these relocations might be related to the favourability of the Maritime environment but may also indicate that a strain of *O. benefactor* better adapted to North American conditions had developed in Manitoba. If so, this would be an example of an improved 'inherent host-finding efficiency' and a 'much greater rate of increase' of established progeny relative to the imported stock (8).

Remington (25) recommended that establishment would be improved by introducing 'a closely spaced succession of samples collected from several source populations from various environments similar to the area of intended colonization'. The full range of *O. benefactor* is unknown but the introduced colonies were derived from many small scattered populations in alpine areas of Austria and Switzerland and from much larger populations in subalpine Bavaria. The colonies released thus appear to have had a satisfactory degree of genetic diversity.

Impact on host populations

Only tentative conclusions on the impact of *O. benefactor* and the Bavarian strain of *M. tenthredinis* can be made at this time. In the latter case, effective parasitism increased to 58 per cent. at Rennie in 1969. However, the total population of *M. tenthredinis* is still small in relation to the host population and there is no evidence that this parasite is affecting the population trend of the host (Fig. 23).

In contrast, evidence suggests that *O. benefactor* has caused a reduction in larch sawfly populations at Pine Falls. At this plot, larch sawfly populations declined in 1966 and 1967 (Fig. 23) while populations in similar sites in southeastern Manitoba increased. For example, the number of larch sawfly adults per acre in the Rennie plot increased 20-fold from 1965 to 1967 (Fig. 23). Some idea of

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[1] Embree, D. G. & Underwood, G. R. Department of Fisheries and Forestry, Fredericton New Brunswick. Unpublished data.

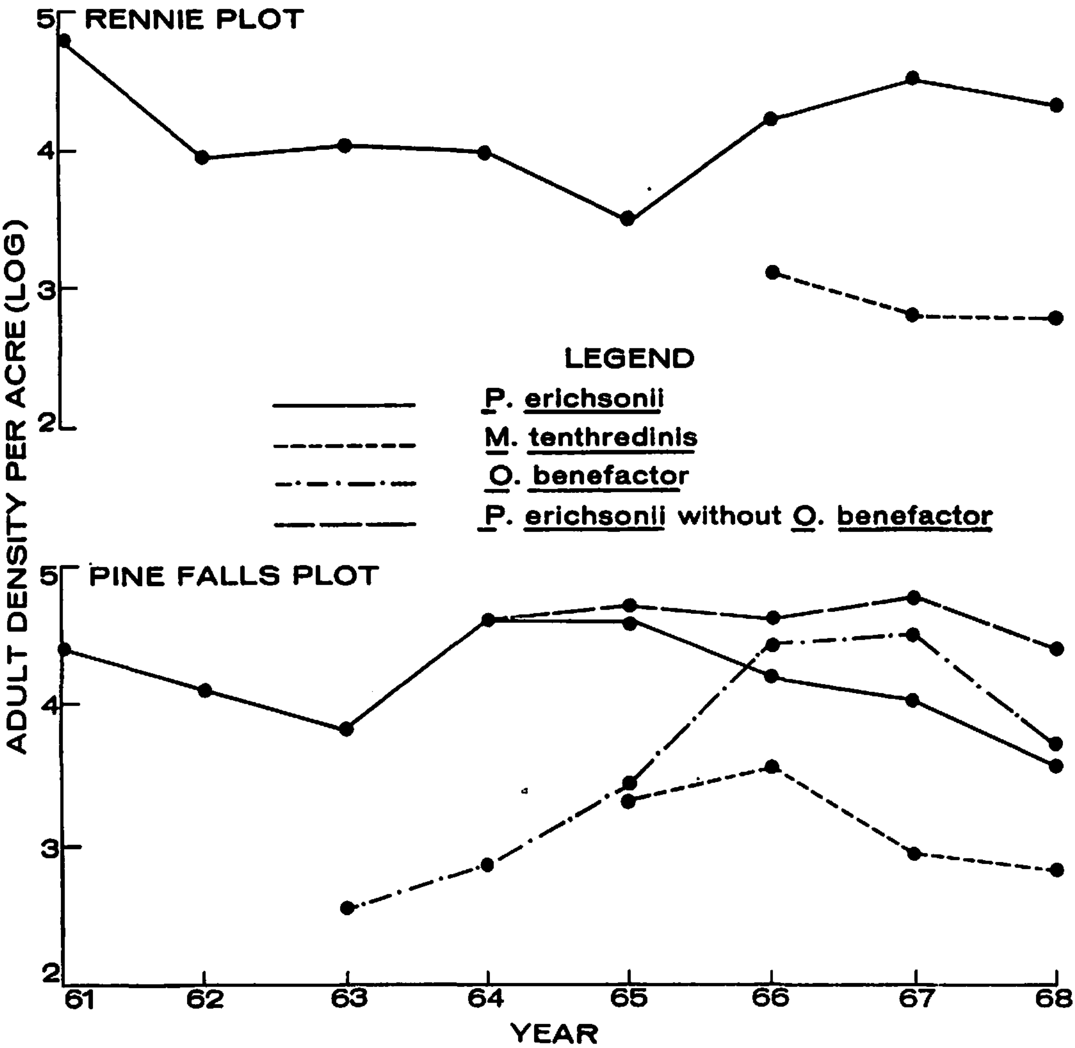

Figure 23

Numbers of adult *P. erichsonii*, *O. benefactor* and *M. tenthredinis* estimated from emergence traps, 1961 - 1968. No adult parasites were caught in years where points are absent.

the impact of *O. benefactor* on the host populations at Pine Falls can be gained by simulating population changes in the absence of the parasite. The number of larch sawfly adults per acre was calculated assuming that all the *O. benefactor* adults were larch sawfly adults and that these adults produced the same number of eggs per female and their progeny had the same survival ratio as was recorded for the appropriate larch sawfly generation. Mortality affecting larch sawflies after parasitism by *O. benefactor* is non-compensatory because the parasitized larvae remain in the population. These calculations indicate that *O. benefactor* did not appreciably affect host population trends until 1966 (Table XXXIII) when 61 per cent. of the cocoons in the previous host generation were parasitized. The data for the Riverton plot tend to support this conclusion, but the effects of flooding in 1966 make interpretation difficult.

The parasitism of second-instar larvae and cocoons by *O. benefactor* has risen to very high levels but successful emergence of adults is much lower. In the larch sawfly generation of 1966–7 at Pine Falls, the second-instar parasitism was 71 per cent. and cocoon parasitism 93 per cent. (Table XXXIII) but *O. benefactor* adults successfully emerged from only 10 per cent. of the cocoons. In this example, larch sawfly adult populations would have been four times greater in the absence of *O. benefactor*, despite the heavy parasite losses due to overlapping mortality. A high percentage of initial parasitism guarantees that total larch sawfly mortality will be less affected by erratic fluctuations in the losses caused by succeeding mortality factors.

The introduction of *O. benefactor* can be described as successful. Its dispersal rate is satisfactory and defoliation of larch should be substantially reduced. The presence of the hyperparasite, *Mesochorus dimidiatus*, in Canada, poses a threat to effective control by *O. benefactor*. However, the hyperparasite has not prevented the initial build-up of *O. benefactor* in release areas and the European situation suggests that high rates of hyperparasitism do not markedly reduce the effectiveness of *O. benefactor*. This is consistent with Flanders (7) hypothesis that hyperparasitism may stabilize the relation between a highly effective parasite and its host.

PREDATORS

The masked shrew has been successfully established in Newfoundland and is filling a formerly unoccupied niche. Buckner (1) notes that in the absence of competition from other insectivores and with only limited competition from other small fossorial mammals, it is likely that it will occupy a wide spectrum of habitats and exert an influence on a number of prey species. He cites an observation that slug populations at the St. George's release site have apparently declined since the masked shrew became established.

Predation on larch sawfly cocoons is considerably higher than that caused previously by predators in the absence of the masked shrew.[1] Predation by invertebrates has declined since the shrew introduction, possibly because these predators are preyed on by the shrew.

This introduction can be tentatively classed as successful, in that it has apparently increased average mortality of the target species. This should lead to a depression of the average abundance of the larch sawfly and the strong functional response of the masked shrew to prey density should help it maintain these lower prey densities.

General assessment of results

The usefulness of a successful biological control programme against the larch sawfly in Canada is difficult to evaluate in economic terms. In the stands of western larch in British Columbia, the reduction or elimination of increment losses would certainly be of some value, but larch sawfly outbreaks have been neither so frequent nor so prolonged as to make these losses a major problem for the industry. In the rest of Canada, both increment loss and tree mortality in tamarack stands have been high but the utilization of this species has been very low. If these losses are eliminated, economic returns can be expected because: (1) the existing stands of tamarack will more rapidly reach merchantable size and (2) larch species, both native and exotic, may be included in forest plantings where their

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[1] Warren, G. L. Department of Fisheries and Forestry, St. John's, Newfoundland. Unpublished data.

rapid growth will be an advantage. In addition, the ability of tamarack to grow on sites too wet for other tree species, if coupled with freedom from larch sawfly attack, provides a means of producing a tree crop on the extensive areas of wet lands in many parts of Canada.

Evaluation of the biological control programme against the larch sawfly suggests the following points, pertinent to this and other programmes:

1. As the larch sawfly in North America had very few parasites the initial lack of detailed information on the relative effectiveness of natural enemies in the donor countries does not seem to have been critical. The criteria of primary parasitism and abundance led to the release of the species causing the highest and most consistent mortality to the host in the donor area and excluded hyperparasites and species which occurred rarely or sporadically.
2. More information on the biology of the species selected for introduction would have aided in the development of better pre-release handling methods. Tachinid species in particular require very careful handling to avoid losses during the rearing, mating and pre-oviposition periods. Experimental studies of the physical and other requirements (e.g. food) for mating and adult vigour should be made very early in a biological control programme.
3. The effects of the introduction of a relatively few individuals of a parasitic species into an abundant host population will be difficult to document until several years have elapsed. In this programme, 7 years after the initial release, sufficient information is not available to fully assess the rôle of *O. benefactor* in reducing host populations. This time-period might be reduced by increasing the number of colonists, but this solution is impractical when host material is scarce in the donor country and propagation of the control agent difficult and expensive.
4. The introduction of a polyphagous insectivore may have as great an effect on other invertebrates as on the target species. Assessment of the total impact of such a predator in the environment is desirable.

RECOMMENDATIONS

The biological control programme against the larch sawfly promises to reduce larch sawfly populations and damage to larch. The studies of the establishment, increase, and rôle of the introduced species in regulating host numbers are also contributing to the understanding of the regulation of pest populations and to the elucidation of biological control. Returns from the investment in this programme would be maximized by:

1. completing the evaluation of the effectiveness of the biological agents already established—*O. benefactor*, Bavarian strain of *M. tenthredinis* and the masked shrew, *S.c. cinereus*.
2. developing and using *O. benefactor* as a control agent, with emphasis on relocation within climatic and geographical areas where it is already established, experimental releases in other parts of Canada, and experiments with massive releases of *O. benefactor* for quick control of larch sawfly in small but valuable larch stands.

If *O. benefactor* does not achieve a satisfactory level of control in all parts of Canada, the following alternative biological control programmes could be considered:

(a) relocation of the Bavarian strain of *M. tenthredinis* from Manitoba, of *E. ornatus* from eastern Canada, and disease organisms from Quebec.

(b) re-introduction of European parasites for which life history data is known. *H. lucidus*, with its native boreoalpine distribution, seems more promising for continental Canada while *M. stolida* seems better adapted to a Maritime climate and might prove a useful addition to the parasitic fauna of Newfoundland. *R. lapponicus* attacks a number of larch feeding sawflies in Europe but in Canada it may act as a specific parasite of larch sawfly.

(c) initiation of a new search for natural enemies of the larch sawfly in the Palearctic region. In Europe, emphasis should be placed on cocoon collections to evaluate *Eridolius hofferi* (Grégor) and parasites that attack sawfly cocoons. In Japan, studies are needed of larval and cocoon parasites on Honshu where larch is native. In northeast Asia, the parasite complex and distribution of larch sawfly are unknown and this could be a fruitful source of new parasites.

ACKNOWLEDGMENTS

We are pleased to acknowledge the great assistance given to us by the following persons and organizations: Dr. H. Pschorn-Walcher and his colleagues at the European Station, C.I.B.C. for permission to use data from unpublished reports; Dr. J. S. Kelleher, Research Institute, Belleville; Drs. D. G. Embree and F. W. Quednau and Messrs. Warren, Ives and Underwood for permission to cite unpublished data and the Regional Heads of the Forest Insect and Disease Survey for permission to use unpublished reports to establish the distribution of larch sawfly and define outbreak areas.

TABLE XXXV

Cage releases and laboratory studies of parasites against *Pristiphora erichsonii* (Hartig)

Species and Province	Year	Origin	Number
Cteniscus pedatorius Panzer			
Manitoba	1963	Austria	449
	1964	Austria	167
Hyalurgus lucidus (Meigen)			
Quebec	1965	Austria	6
Manitoba	1960	Austria	16
	1961	Austria	69
	1962	Austria	9
	1964	Austria	8
Hypamblys spp.			
Quebec	1965	Austria	26
Manitoba	1961	Germany	28
	1962	Austria,	13
		Germany	15
	1963	Austria, Germany	502
	1964	Austria, Germany	289
Mesoleius aulicus Gravenhorst			
Manitoba	1962	Austria	66
Mesoleius opticus Gravenhorst			
Manitoba	1962	Austria	7
Mesoleius tenthredinis Morley			
Manitoba	1959	Austria	28
	1961	Austria	234
		Germany	909
	1962	Austria	285
		Germany	1141
		Japan	34
	1963	Japan	316
		Germany	50
		Austria	43
		Switzerland	34
	1964	Germany	56
		Austria	37
Myxexoristops stolida (Robineau-Desvoidy)			
Quebec	1965	Austria	1
Manitoba	1961	Germany	28
	1962	Germany, Austria	111
	1964	Austria, Germany	1
Olesicampe benefactor Hinz.			
Manitoba	1963	Germany, Austria	64
Saskatchewan	1964	Germany	4
Polyblastus tener Habermehl			
Manitoba	1964	Austria	3

TABLE XXXV (continued)

Species and Province	Year	Origin	Number
Rhorus lapponicus Roman			
Manitoba	1962	Germany	20
	1963	Germany	127
Vibrissina turrita (Meigen)			
Quebec	1965	Japan	26
Manitoba	1962	Japan	134
	1964	Japan	83

TABLE XXXVI

Open releases and recoveries of parasites against *Pristiphora erichsonii* (Hartig)

Species and Province	Year	Origin	Numbers released		Total	Year of recovery
			♂	♀		
Hyalurgus lucidus (Meigen)						
Quebec	1965	Austria	—	—	734	—
Manitoba	1961	Austria	62	121	183	—
	1962	Austria	48	60	108	—
	1963	Austria, Germany			692	—
	1964	Austria			462	—
Hypamblys spp.						
Manitoba	1963	Austria, Germany	80	134	214	—
Mesoleius tenthredinis Morley						
Manitoba	1963	Germany	1151	1870	3021	1963
	1964	Germany	331	485	816	1964
Myxexoristops stolida (Robineau-Desvoidy)						
Quebec	1965	Austria	—	—	7	—
Manitoba	1962	Austria	66	143	281	—
	1963	Germany, Austria	—	—	77	—
	1964	Germany, Austria	16	13	29	—
Olesicampe benefactor Hinz.						
New Brunswick	1967	Manitoba (Europe)	751	537	1288	1967
	1968	Manitoba (Europe)	2052	1436	3488	1968
Nova Scotia	1967	Manitoba (Europe)	352	286	638	1967
Manitoba	1961	Austria, Germany	56	158	214	1962
	1962	Austria, Germany	65	152	217	1962
	1963	Germany, Austria, Switzerland	910	1245	2155	1963
	1967	Manitoba (Europe)	385	447	832	1967
	1968	Manitoba (Europe)	694	737	1431	1968
Saskatchewan	1964	Germany, Austria	18	21	39	1966
	1965	Manitoba (Europe)	16	24	40	—
	1966	Manitoba (Europe)	202	346	548	1966
Vibrissina turrita Meigen						
Quebec	1965	Japan	—	—	50	—
Manitoba	1963	Japan	52	52	149	—
	1964	Japan	155	164	521	—

TABLE XXXVII

Location of release points of larch sawfly parasites and the masked shrew, *Sorex cinereus cinereus* Kerr

Location		Nearest named place	Lat.	Long.	Species released
Number	Province				
1	Manitoba	Pine Falls	50°41′	96°05′	*Hyalurgus lucidus*, *Olesicampe benefactor*
2		Hodgson	51°15′	97°18′	*Hyalurgus lucidus*, *Hypamblys* spp., *Mesoleius tenthredinis*, *Myxexoristops stolida*, *Olesicampe benefactor*, *Vibrissina turrita*
3		Rennie	49°49′	95°31′	*Mesoleius tenthredinis*
4		Winnipeg	49°53′	97°09′	*Olesicampe benefactor*
5		The Pas	53°51′	101°19′	*Olesicampe benefactor*
6	Saskatchewan	Crutwell	53°15′	106°06′	*Olesicampe benefactor*
7	Quebec	Ste. Hilarion	47°27′	70°30′	*Hyalurgus lucidus*, *Myxexoristops stolida*, *Vibrissina turrita*
8	Nova Scotia	Chignecto Game Sanctuary	45°31′	64°29′	*Olesicampe benefactor*
9	New Brunswick	North Head	44°44′	66°46′	*Olesicampe benefactor*
10		St. Stephen	45°12′	67°20′	*Olesicampe benefactor*
11		Beulah	45°37′	66°00′	*Olesicampe benefactor*
12	Maine, U.S.A.	Greenbush	45°07′	68°37′	*Olesicampe benefactor*
13		Mariaville	44°48′	68°22′	*Olesicampe benefactor*
14	Newfoundland	St. George's	48°30′	58°20′	*Sorex c. cinereus*
15		Exploits Dam	48°46′	56°35′	*Sorex c. cinereus*
16		Halls Bay	49°25′	56°04′	*Sorex c. cinereus*

LITERATURE CITED

1. Buckner, C. H. (1966). The role of vertebrate predators in the biological control of forest insects. *A. Rev. Ent.* **11**: 449–70.
2. Buckner, C. H. (1967). Avian and mammalian predators of forest insects. *Entomophaga* **12**: 491–501.
3. Buckner, C. H. & Turnock, W. J. (1965). Avian predation on the larch sawfly, *Pristiphora erichsonii* (Htg.) (Hymenoptera: Tenthredinidae). *Ecology* **46**: 223–36.
4. Drooz, A. T. (1960). The larch sawfly, its biology and control. *Tech. Bull. U.S. Dep. Agric.* **1212**, 52 pp.
5. Drouin, J. A. & Turnock, W. J. (1967). Occurrence of the eastern larch beetle in Manitoba and Saskatchewan. *Manitoba Ent.* **1**: 18–20.
6. Eichhorn, O. (1965). Uber einige Lärchenschädlinge und ihre Parasiten in Japan, Europa und Kanada. *Beitr. Ent.* **15**: 111–26.
7. Flanders, S. E. (1963). Hyperparasitism, a mutualistic phenomenon. *Can. Ent.* **95**: 716–20.
8. Flanders, S. E. (1966). Herbert D. Smith's observations on citrus blackfly parasites in India and Mexico and the correlated circumstances. *Can. Ent.* **101**: 467–80.
9. Heimpel, A. M. (1954). A strain of *Bacillus cereus* Fr. and Fr. pathogenic for the larch sawfly, *Pristiphora erichsonii* (Htg.). *Can. Ent.* **86**: 73–7.
10. Heron, R. J. (1961). A note on temperature and post-diapause development of the larch sawfly and its parasite *Bessa harveyi* (Tnsd.). *Can. Ent.* **93**: 431–3.
11. Heron, R. J. (1966). The reproductive capacity of the larch sawfly and some factors of concern in its measurements. *Can. Ent.* **98**: 566–78.
12. Hopping, G. R., Leech, H. B. & Morgan, C. V. G. (1943). The larch sawfly, *Pristiphora erichsonii* (Hartig) in British Columbia, with special reference to the cocoon parasites *Mesoleius tenthredinis* Morley and *Tritneptis klugii* (Ratzeburg). *Sci. Agric.* **24**: 53–63.
13. Ives, W. G. H. (1967). Relation between invertebrate predators and prey associated with larch sawfly eggs and larvae on tamarack. *Can. Ent.* **99**: 607–22.
14. Ives, W. G. H. (1967). Determination of premature larval drop and other causes of larch sawfly mortality. *Can. Ent.* **99**: 1121–31.
15. Ives, W. G. H. (1968). Weather and larch sawfly survival. Inf. Rep. MS-X-11. Forest Research Laboratory, Winnipeg, Manitoba, 28 pp.
16. Ives, W. G. H., Turnock, W. J., Buckner, C. H., Heron, R. J. & Muldrew, J. A. (1968). Larch sawfly population dynamics: techniques. *Manitoba Ent.* **2**: 5–36.
17. MacLeod, D. M. and Heimpel, A. M. (1955). Fungal and bacterial pathogens of the larch sawfly. *Can. Ent.* **87**: 128–31.

18. McGugan, B. M. & Coppel, H. C. (1962). Biological control of forest insects, 1910–1958. *In* A review of the biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol Contr.* **2**: 35–127.
19. Muldrew, J. A. (1953). The natural immunity of the larch sawfly (*Pristiphora erichsonii* (Htg.)) to the introduced parasite (*Mesoleius tenthredinis* Morley), in Manitoba and Saskatchewan. *Can. J. Zool.* **31**: 313–32.
20. Muldrew, J. A. (1964). The biological control program against the larch sawfly. *Proc. ent. Soc. Man.* **20**: 63.
21. Muldrew, J. A. (1967). Biology and initial dispersal of *Olesicampe* (*Holocremnus*) sp. nr. *nematorum* (Hymenoptera: Ichneumonidae), a parasite of the larch sawfly recently established in Manitoba. *Can. Ent.* **99**: 312–21.
22. Nairn, L. D., Reeks, W. A., Webb, F. E. and Hildahl, V. (1962). History of larch sawfly outbreaks and their effect on tamarack stands in Manitoba and Saskatchewan. *Can. Ent.* **94**: 242–55.
23. Pschorn-Walcher, H. & Eichhorn, O. (1963). Investigations on the ecology and natural control of the larch sawfly (*Pristiphora erichsonii* (Htg.) Hym. Tenthredinidae) in central Europe. Part I. Abundance, life-history and ecology of *P. erichsonii* and other sawflies on larch. *Tech. Bull., Commonw. Inst. biol. Contr.* **3**: 51–82.
24. Pschorn-Walcher, H. & Zinnert, K. D. (1971). Investigations on the ecology and natural control of the larch sawfly (*Pristiphora erichsonii* Htg., Hym. Tenthredinidae) in central Europe. Part II—Natural enemies: their biology and ecology, and their role as mortality factors in P. erichsonii. *Tech. Bull. Commonw. Inst. biol. Contr.* **14**: (In press).
25. Remington, C. L. (1968). The population genetics of insect introduction. *Rev. Ent.* **13**: 415–26.
26. Smirnoff, W. A. (1968). Diseases of the larch sawfly *Pristiphora erichsonii* in Quebec. *J. Invert. Pathol.* **10**: 417–24.
27. Turnbull, A. L. and Chant, D. A. (1961). The practice and theory of biological control of insects in Canada. *Can. J. Zool.* **39**: 697–753.
28. Turnock, W. J. (1960). Ecological life history of the larch sawfly *Pristiphora erichsonii* (Hymenoptera: Tenthredinidae) in Manitoba and Saskatchewan. *Can. Ent.* **92**: 500–16.
29. Turnock, W. J. and Melvin, J. C. E. (1936). The status of *Bessa harveyi* (Tnsd.) (Diptera: Tachinidae). *Can. Ent.* **95**: 646–54.
30. Warren, G. L. & Pardy, K. W. (1968). Parasite complex of the larch sawfly (*Pristiphora erichsonii* (Htg.)) in Newfoundland. *Bi-mon. Res. Notes, Can. Dep. For. Rural Dev.* **24** (1): 5.
31. Zinnert, K. D. (1968). Vergleichende Untersuchungen zur Morphologie und Biologie der Larvenparasiten (*Hymenoptera : Ichneumonidae, Braconidae*) mitteleuropäischer Blattwespen aus der Subfamilie Nematinae (*Hymenoptera : Tenthredinidae*). Doctoral Thesis, Albert-Ludwigs Universität zu Freiburg in Breisgau. 155 pp.

46. *RHYACIONIA BUOLIANA* (SCHIFF.), EUROPEAN PINE SHOOT MOTH (LEPIDOPTERA: OLETHREUTIDAE)

Paul D. Syme

PEST STATUS

Rhyacionia buoliana (Schiff.) has been a destructive pest of hard pine plantations in North America since it was discovered in 1914 (5). Its history and biology have been the subjects of extensive studies and are well summarized by McGugan and Coppel (28), Pointing and Green (36) and Miller (31). Also, the status of *R. buoliana* has been under continual surveillance and has been recorded regularly in the Annual Reports of the Forest Insect and Disease Survey.

The shoot moth has one generation per year and adults appear in the field over a 4-week period that begins from the first to the third week in June. Single eggs or small groups are laid on the twigs or needle sheaths of the new growth. Incubation requires 2 weeks. First- and second-instar larvae mine needle bases on the new growth. Later, they migrate to the new buds where they feed before over-wintering as half-grown larvae within the bud. Feeding is resumed in the spring and is extended to additional buds before pupation takes place in May.

The shoot moth is primarily a pest of pine plantations. In North America, red pine is most seriously damaged. Scots, Austrian, ponderosa and ornamental mugho pines are moderately susceptible, whereas pitch, Virginia, jack and eastern white pines are relatively resistant. The needle-mining larvae cause a browning of the foliage, but this has little effect on the vigour of the host. Feeding on the terminal bud causes serious injury to the main stem and repeated destruction of the entire terminal cluster during the summer months initially causes profusion of shoot growth (witch's broom) and eventually a spike top when the leader dies. Various degrees of crookedness result from lateral branches or buds assuming dominance over terminal shoots. Attack becomes less serious as trees increase in height.

In Canada, the shoot moth is an important pest of pine plantations in southern Ontario, but it exists also in southern Quebec primarily on ornamentals (4). In British Columbia, it is presently confined to nursery and ornamental stock, but potential danger to natural stands and to plantations has resulted in regulations to prevent the movement of infested stock to uninfested areas (16). The pine shoot moth was first found in the Maritimes at Bear River, Nova Scotia, in 1925 (38). It was considered primarily a pest of ornamentals until recently, when it became more serious in Scots pine plantations in Nova Scotia.

In Ontario, attack declined after 1958, partly due to the severe winter mortality experienced in 1959, greater than 90 per cent. in some areas (39). Local fluctuations occurred, but generally the populations declined to extinction in the main study plots in southwestern Ontario during the period 1962–8. During this period, virtually no red pine was planted within the range of the shoot moth in Ontario, and as existing plantations closed, shoot moth populations declined. Recovery of severely damaged plantations after closure has been encouraging (36). Indications are, however, that residual populations in many areas may lead to severe damage and high populations on recently established red pine plantations in southern Ontario.

In absolute terms, Miller (31) indicates that 163 insects per tree (4 to 7 feet tall) is a record population. However, at Dorcas Bay, Ontario, in 1960, red pine trees averaging 5·7 feet tall supported a shoot moth larval population of 601·8 insects per tree. This population is now extinct. The history of distribution of the shoot moth in North America suggests that shipping of infested nursery stock has contributed strongly to the wide dispersal of this pest. This has resulted in spotty distribution, which has changed little since 1958. The Forest Insect and Disease Survey has reported no increase in the distribution of the persistent population in the Maritime Provinces and Newfoundland, whereas in Quebec, there has been a constant decline since 1961. In Ontario, the northern limit of continuous distribution appears to be holding as predicted (12), at about the — 20°F isotherm (37). Two persistent populations on red pine have been recorded on Manitoulin and Cockburn islands, in the North Channel of Lake Huron. Both of these are within the — 20°F isotherm limit but are westward extensions of range. They have persisted since their discovery, but are now rapidly decreasing in numbers.

The major parasites,[1] both introduced and indigenous, are more widespread than before 1959 (4, 30, 21). Judd (17) reported no parasites in a collection of 127 infested shoots from Austrian pine at Hamilton in 1951. Miller (30) suggests that the presence of *Orgilus obscurator* (Nees) in the eastern part of Michigan, where it had not been released, indicates that it probably spread from Ontario, whereas Watson and Arthur (47) suggest that the movement of infested nursery stock plays an important rôle in the spread of parasites. Changes in distribution will be discussed under each species in following sections. A recent excellent annotated bibliography of the parasites of *Rhyacionia* is presented by Yates (48) and includes keys to the parasite species.

BACKGROUND

Considerable work has been done on various aspects of the European pine shoot moth since 1958 and the literature is voluminous. The history, distribution, biology, ecology, behaviour, damage and control have been summarized (36, 37, 31). Many studies have been made of the distribution, and biology and behaviour, of parasites of the shoot moth, and of the effects of various environmental factors on them (48), but little work has been published on the impact of parasites on shoot moth dynamics (4, 33). Predators have received little attention (20, 41), the only really quantitative study,

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[1] Watson, W. Y. Laurentian University, Sudbury, Ontario. Unpublished data.

by Pointing (35), indicates that the spider studied had no significant impact on shoot moth mortality. The bacterium, *Bacillus thuringiensis* Berliner, was shown by Pointing (34) to be lethal to shoot moth larvae, but ineffective in the field because of the larval behaviour.

Studies in Canada are continuing on the quantitative effects of parasites on the population dynamics of the shoot moth, and on the behavioural and ecological factors affecting parasite effectiveness. Flowering plants, as food for adult parasites, increase longevity and fecundity and the suitability of many of these is being investigated, as is the interaction between those parasites showing the most potential for impact on shoot moth dynamics. A cooperative programme by the staff of the Commonwealth Institute of Biological Control in Europe has involved the study of the competition between European species of parasites under field conditions, to elucidate their potential for importation into Canada, and the study of the biology and behaviour of the potentially useful parasite *Lypha dubia* (Fallén) in its native habitat. Details are given in the following sections.

RELEASES AND RECOVERIES

The following discussion, by species, includes not only open (Table XXXVIII) and cage (Table XXXIX) releases since 1958, but also recoveries or significant range extensions of species released prior to 1958. All locations mentioned are in Ontario, unless otherwise stated. Species mentioned by McGugan and Coppel (28) and not mentioned here have not been released or recovered since 1958.

Actia nudibasis Stein (Diptera: Tachinidae)

Two hundred and forty adults of this species were released at Elmira from 1955 to 1958. No recoveries have been made.

Eulimneria rufifemur (Thom.) (Hymenoptera: Ichneumonidae)

E. rufifemur was released prior to 1959 at Toronto, Niagara Falls and Elmira (28), but has not been released since. All recoveries since release have been through dissection of field-collected host larvae and, therefore, have not been confirmed through identification of adult specimens. However, this species, or one very similar to it,[1] has been recovered from shoot moth (and always in association with *O. obscurator*) from Elmira, 1962, 1964, 1966–8; St. Williams, 1962; Clear Creek, 1964; Mansfield 1962, 1963; and Port Elgin, in 1964 and 1966. It has extended its range significantly to the west of the release points (Fig. 24). It was most abundant at Mansfield in 1962 where it parasitized 17 per cent. of living host larvae in the fall. Despite its ability to achieve significant levels of parasitization, this species interacts with *O. obscurator* to the latter's detriment. In view of the relatively greater importance of *O. obscurator*, it is unfortunate that *E. rufifemur* was introduced.

Lypha dubia (Fallén) (Diptera: Tachinidae)

This species was described in 1810 from Sweden (40) and is recorded from many species of Lepidoptera in Europe (44). It is a primary larval parasite that deposits living larvae on twigs or foliage near host larvae. The wide range of host habitats suggests an unresolved synonymy. Small numbers were released in Nova Scotia against the winter moth, *Operophtera brumata* (Linnaeus), but none were recovered (28).

L. dubia attacks late-instar shoot moth larvae, and after rather rapid development within the host, the parasite larva drops to the ground to pupate. It spends most of the summer and all winter in the ground as a fully developed adult and the adults emerge at about the time the shoot moth commences feeding in the spring. There is a preoviposition period of about 4 weeks. Studies in Europe show that there is no serious interference by this species with *O. obscurator*, the most effective introduced parasite in Ontario, and that *L. dubia* is one of the more effective parasites in northern

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[1] Some authorities feel that this univoltine (18) species is conspecific with multivoltine *E. alkae* (Ell. and Sacht.) (Sailer, R. L. Entomology Research Division, United States Department of Agriculture, Beltsville, Maryland, U.S.A. Personal communication) which has been released against the European corn borer, *Ostrinia nubilalis* (Hbn.) (29).

Germany[1] (1). The parasite has been released against the shoot moth in the United States in the years 1933–8, and again in 1962 and 1963, but has not been recovered (8).

In 1966 and 1967 a technique was developed at Elmira for liberating the flies from the puparium stage. During the summer of 1968, 1,217 puparia were set out in the field at Elmira and in the spring of 1969, adults emerged from approximately 90 per cent. of them. As *L. dubia* attacks a late larval stage, and does not seriously interfere with the established *O. obscurator*, it shows promise as a major parasite. It is generally conceded that a change in mortality rate at a late stage in host development is frequently more important than a change in earlier stages (27, 32). The results of the Elmira release will be followed closely in future studies.

Orgilus obscurator (Nees) (Hymenoptera: Braconidae)

O. obscurator is an internal solitary parasite that attacks first-instar larvae. Its life history has been described by Juillet (19). Early introduction of the parasite and movement of shoot moth-infested nursery stock resulted in a wide distribution of *O. obscurator* in Ontario (28). This spread has continued to date (47, 4) and the species now occurs virtually throughout the range of shoot moth in Ontario (Fig. 25).

Small experimental releases were made at Elmira in 1959 and 1961; at Dorcas Bay in 1960; and on Cockburn Island in Lake Huron in 1966.

In 1960, 133 female *O. obscurator* were released at Dorcas Bay in a red pine plantation of about 600 6-foot trees supporting a record population of 601 shoot moth larvae per tree. By October, 1961, parasitism by *O. obscurator* had reached 21 per cent. and the shoot moth population had declined to 61 larvae per tree. In 1962, the host population increased to 105 larvae per tree and parasitism reached 53 per cent. In 1963 parasitism increased to 79 per cent. and the host population declined to 22 larvae per tree. This trend continued until 1964, when 92 per cent. of a total population of 2·8 hosts per tree were parasitized. Since 1965, the shoot moth has not been recorded from this plantation. This was a case unique in the history of the European pine shoot moth in North America, both in host density and rate of parasitism reached by *O. obscurator*. It has been argued, Syme (42), that the presence of wild carrot (*Daucus carota* L.) in abundance in this particular location provided a food source for *O. obscurator* and contributed to the longevity and increased fecundity of the parasite and hence to the decline and eventual collapse of the *R. buoliana* population in that area.

On Cockburn Island in 1966, 148 female *O. obscurator* were released in a shoot moth infested red pine plantation where a unique opportunity presented itself to study the effectiveness of *O. obscurator* in the absence of any competing internal parasites. Although establishment was obtained and the parasite population has persisted at low levels in this plantation, the host population is rapidly decreasing because of other factors and the results from this experiment are, therefore, inconclusive.

On a broader basis, recoveries of *O. obscurator* since 1959 have indicated a substantial change in distribution. It is well established in Quebec (4) and has recently been recovered in the Maritimes (Forbes, pers. comm.) and also in Michigan where it had not been released (30). The pattern of spread suggests that this species is easily dispersed through the planting of infested nursery stock (28). Recoveries throughout southern Ontario during the 1960's have consistently yielded rates of parasitism between 20 to 50 per cent., considerably above those recorded in the 1950's from the same area (6, 47). In fact, total parasitism peaked in 1953 at 10 per cent. at Hamilton and Niagara Falls (6), whereas parasitism by *O. obscurator* alone in 1959 was about 10 per cent. in southern Ontario generally, with a maximum of 32 per cent. at St. Williams. Since then, rates have increased generally throughout southern Ontario, levelling off at about 20–50 per cent., except for the 92 per cent. recorded at Dorcas Bay.

O. obscurator is currently the most common, widespread and most effective introduced parasite of the European pine shoot moth in North America.

Pristomerus sp. (Hymenoptera: Ichneumonidae)

Two small lots of this internal larval parasite were released in small numbers at Elmira prior to

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[1] Schröder, D. Commonwealth Institute of Biological Control, Delémont, Switzerland. Personal communication.

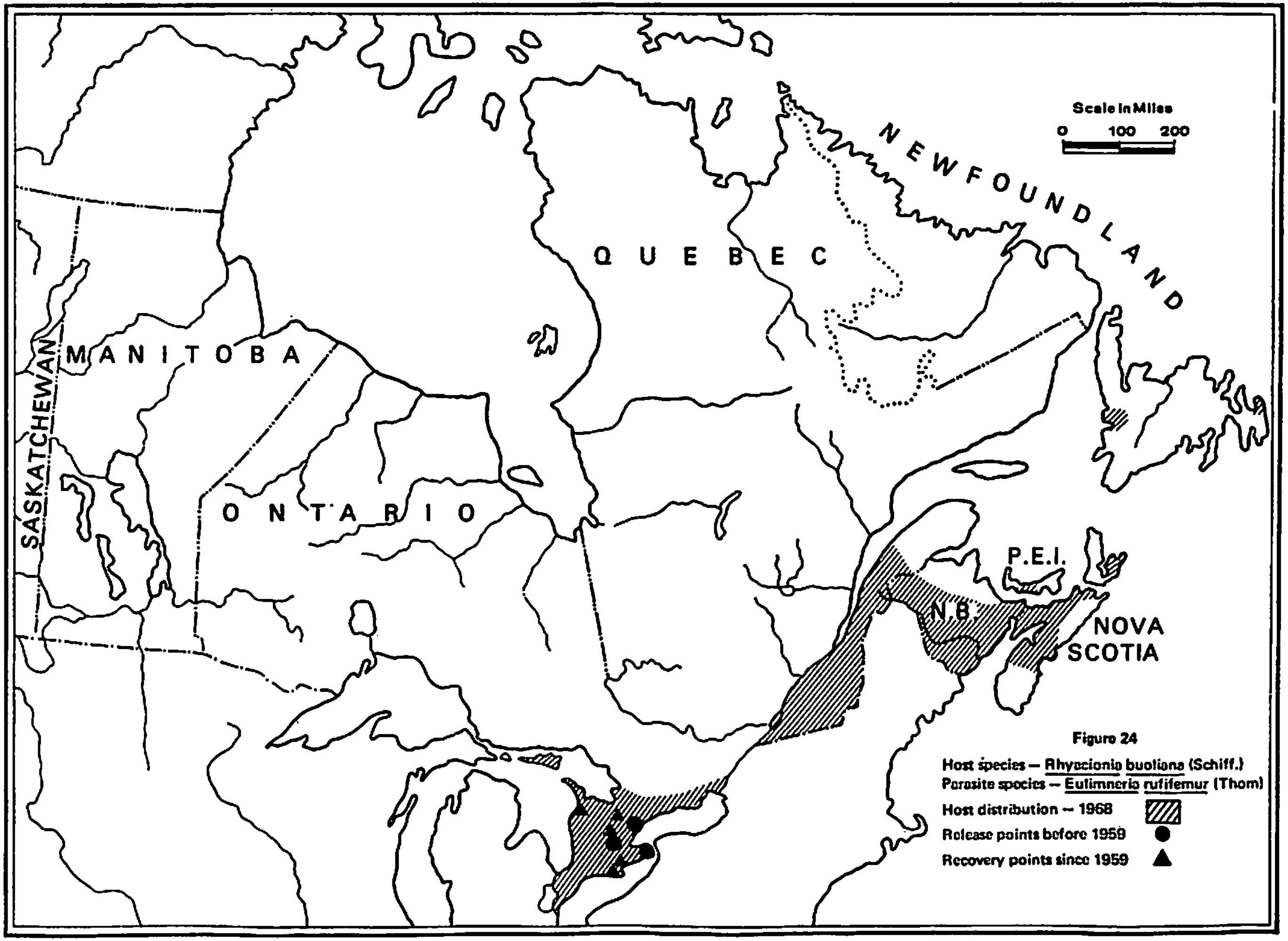

Figure 24

Host species — Rhyacionia buoliana (Schiff.)
Parasite species — Eulimneria rufifemur (Thom)

1958 (28) but it has never been recovered. Recent cage studies of the competition of *Pristomerus* with *O. obscurator* have indicated cleptoparasitic habits[1] (43). Therefore no future releases of *Pristomerus* are planned.

Temelucha interruptor (Gravenhorst) (Hymenoptera: Ichneumonidae)

This primary internal larval parasite of various Microlepidoptera was also released prior to 1958 (28), and its spread has been supplemented through parasites being distributed with infested trees. Attempts to re-establish it after a decline due to severe winters were apparently unsuccessful and it was not recovered in surveys from 1954 to 1956 (28). Watson and Arthur (47) reported that the distribution suggests that *T. interruptor* was limited to areas where the minimum winter temperature rarely falls below 0°F; however, it has been recovered consistently, although in small numbers, at Elmira since 1963, and once in 1962 at Dorcas Bay (Fig. 26), where the mean minimum winter temperatures are −10°F.

Early observations suggested, and Arthur, Stainer and Turnbull (3) confirmed that *T. interruptor* is a cleptoparasite. It competes to the detriment of *O. obscurator* and consequently has not been released since 1961.

Tetrastichus turionum (Hartig) (Hymenoptera: Eulophidae)

This species is an internal, gregarious, pupal parasite. The larvae overwinter within the remains of the host and pupate the following spring. Its biology has been described by Juillet (18) and its potential as a biological control agent by Arthur and Juillet (2). They considered it a potentially valuable control agent, but Schröder[1] has found it to be hyperparasitic on other parasites in Europe. It had been released at Kingsville, Elmira and Clear Creek prior to 1959 and was recovered in 1953 in the Kingsville area (28). However, since then no recoveries have been made despite intensive searching at both Elmira and Clear Creek.

EVALUATION OF CONTROL ATTEMPTS

Evaluation of the impact of biological control agents on the European pine shoot moth is difficult because, as so aptly described by Turnbull and Chant (45), young plantations are usually infested most heavily and as these plantations mature the levels of infestation decline. To add to this inherent difficulty, the severe shoot moth infestations in southwestern Ontario in the 1950's resulted in the curtailment of red pine planting within the distribution of the pest. Consequently, no young plantations have existed for many years and evaluations of the impact of biological control agents have had to be made on declining host populations on older trees. In addition, shoot moth populations are not particularly amendable to biological control since relatively low populations of the pest can cause disproportionate damage to the trees because of a propensity to attack leading shoots. Therefore, it is not surprising that biological control attempts against the European pine shoot moth have not met with complete success in North America.

Earlier work on biological control of the shoot moth in North America was concerned mainly with the release of a broad spectrum of species which attained high population levels in Europe. Inadequate concern was given to their potential interaction with other introduced or native parasites (see comments under *E. rufifemur*, *Pristomerus* sp., *T. interruptor* and *T. turionum*) and some undesirable species were introduced into the North American complex. Investigations since 1958 have emphasized critical evaluation of candidate parasites in terms of hyperparasitic activity, the origin and quality of the candidate species and their interaction with other parasites that may be present. Although satisfactory biological control of the shoot moth has not been attained, investigations since 1958 have provided some hope for the future.

It is now evident that red pine in particular is able to outgrow rather extensive shoot moth damage

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[1] Schröder, D. Commonwealth Institute of Biological Control, Delémont, Switzerland. Unpublished data.

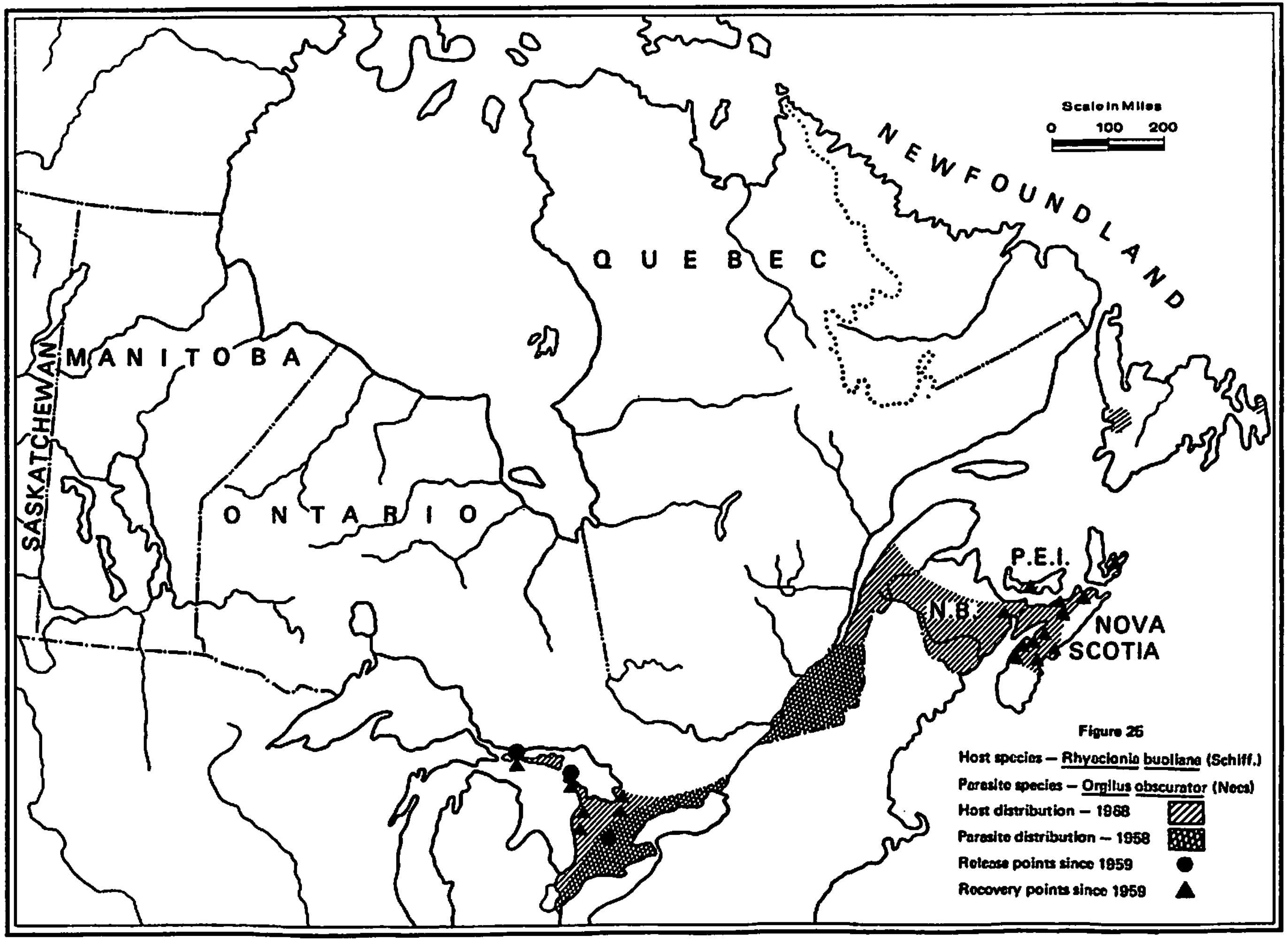

Figure 26

Host species — Rhyacionia buoliana (Schiff.)

Parasite species — Orgilus obscurator (Nees) and that the level of control required may not be as critical as once supposed. Certain elements of the native parasite complex (*e.g. Hyssopus thymus* (Girault), *Exeristes comstockii* (Cresson) and *Agathis binominata* (Muesebeck)) have established themselves in shoot moth populations and significantly reduced generation survival of the pest. Our data show *O. obscurator* to be an extremely effective parasite. It is an efficient searcher at low host densities. It has parasitized up to 92 per cent. of the host population at Dorcas Bay and was probably a major factor in the complete collapse of that host population in the next generation. In addition, recent studies (42) on the effect of wild carrot on the longevity of *O. obscurator* strongly suggest that this parasite's effectiveness, and probably that of other species also, can be increased significantly with cultural practices that favour growth of certain flowering plants in pine plantations. Another species, *L. dubia*, seems to be a potentially significant addition to the North American complex. It attacks a stage of the shoot moth that is presently only occasionally attacked by the native parasite *E. comstockii*. It does not seriously interfere with *O. obscurator* and is one of the most important parasites of the European pine shoot moth in northern Germany. It can overwinter successfully under southern Ontario conditions, but its potential as a control agent has yet to be confirmed.

In summary, it can be stated that a satisfactory level of biological control has not been achieved against the European pine shoot moth in North America, but there is some promise of success.

RECOMMENDATIONS

Fortunately, most of the undesirable parasites introduced in earlier biological control attempts were unsuccessful. Pine plantations, occurring on sandy soils, are generally relatively sterile habitats for flowering plants other than grasses, and are therefore generally poor sites for the establishment of parasitic species which require nutritive sources other than their hosts. Many workers (9, 10, 11, 13, 14, 15, 22, 23, 24, 25, 26, 46) have stressed the importance of having nectar- and pollen-bearing plants present where parasites are to be introduced or encouraged. DeBach (7) cites many examples where this practice has been suggested or employed. Apparently, little effort has been made along these lines with respect to parasites of the shoot moth. Recent studies (42) on the effect of wild carrot on the longevity of *O. obscurator*, and the fact that this plant was absent from most of the plots under study, except at Dorcas Bay, already cited, strongly suggests that the presence of this plant could increase the effectiveness of the parasite. More trials are needed to establish whether this cultural approach to biological control is feasible. Preliminary results encourage our confidence in the scheme.

TABLE XXXVIII

Open releases and recoveries of parasites against *Rhyacionia buoliana* (Schiff.)

Species and Province	Year	Origin	Number	Year of recovery
Lypha dubia (Fallén)				
Ontario	1968	Germany	1217	
Orgilus obscurator (Nees)				
Ontario	1959	England	2603	1961–8
	1960	Sweden	52	1961–4
		Czechoslovakia	279	
	1961	Sweden	89	1962–8
		Austria	385	
		Czechoslovakia	408	
	1966	Germany	228	1966–8
Temelucha interruptor (Gravenhorst)				
Ontario	1959	England	1459	1963–8
	1961	Czechoslovakia	191	
		Austria	767	
		Sweden	6	

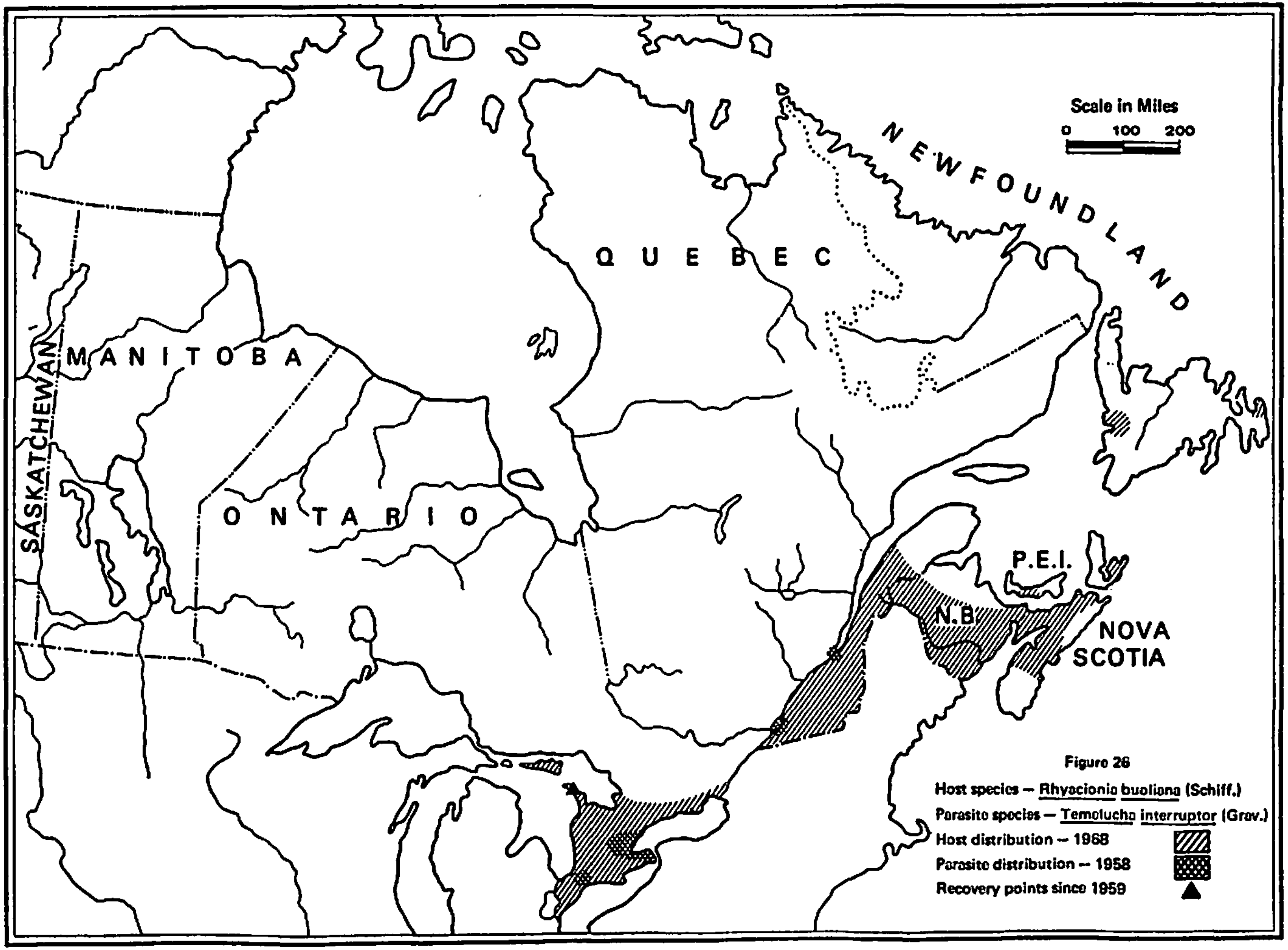

Figure 26

Host species — Rhyacionia buoliana (Schiff.)

Parasite species — Temelucha interruptor (Grav.)

Host distribution — 1968 ▨

Parasite distribution — 1958 ▩

Recovery points since 1959 ▲

TABLE XXXIX

Cage releases and laboratory studies of parasites against *Rhyacionia buoliana* (Schiff.)

Species and Provinces	Year	Origin	Number
Lypha dubia (Fallén)			
Ontario	1964	Germany	116
	1965	Germany	1188
	1966	Germany	600
	1967	Germany	810
	1968	Germany	775
Orgilus obscurator (Nees)			
Ontario	1961	Czechoslovakia	275
		Sweden	58
	1962	Austria	179
	1964	Germany	126
		Austria	78
	1965	Germany	454
	1966	Germany	185
	1967	Germany	505
	1968	Austria	69
Pristomerus sp.			
Ontario	1960	Czechoslovakia	36
	1961	Sweden	11
	1963	Germany	355
	1964	Germany	1246
Temelucha interruptor (Gravenhorst)			
Ontario	1960	Czechoslovakia	42
	1961	Czechoslovakia	67
		Austria	8
Tetrastichus turionum (Hartig)			
Ontario	1961	Czechoslovakia	1445
		Sweden	65
	1962	Austria	216
		Yugoslavia	53
		Sweden	31
		Czechoslovakia	12
	1963	Germany	241
		Austria	165
	1964	Germany	2923
	1965	Austria	220

LITERATURE CITED

1. Adlung, K. G. & Sailer, R. I. (1963). Forest entomological studies in German afforestation areas, with special regard to pine shoot moth parasites of *Rhyacionia buoliana* (Schiff.). *Allgem. Forst. U. Jagdzeit.* **134**: 229–38. (English and French summaries.)
2. Arthur, A. P. & Juillet, J. A. (1961). The introduced parasites of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae), with a critical evaluation of their usefulness as control agents. *Can. Ent.* **93**: 297–312.
3. Arthur, A. P., Stainer, J. E. R. & Turnbull, A. L. (1964). The interaction between *Orgilus obscurator* (Nees) (Hymenoptera: Braconidae) and *Temelucha interruptor* (Grav.) (Hymenoptera: Ichneumonidae), parasites of the pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae). *Can. Ent.* **96**: 1030–4.
4. Béique, R. (1960). The importance of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) in Quebec City and vicinity. *Can. Ent.* **92**: 858–62.
5. Busck, A. (1914). A destructive pine moth introduced from Europe. *J. econ. Ent.* **7**: 340–1.
6. Coppel, H. C. & Arthur, A. P. (1954). Notes on introduced parasites on the European pine shoot moth *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Torticidae), in Ontario. *A. Rep. ent. Soc. Ont.* **84**: 55–8.
7. DeBach, P. [ed.] (1964). Biological control of insect pests and weeds. Chapman and Hall, London.
8. Dowden, P. B. (1962). Parasites and predators of forest insects liberated in the United States through 1960. *Handb. U.S. Dep. Agric.* 226, 70 pp.
9. Emden, H. F. van (1963). A preliminary study of insect numbers in field and hedgerow. *Entomologist's mon. Mag.* **98**: 255–9.
10. Emden, H. F. van (1963). Observations on the effect of flowers on the activity of parasitic hymenoptera. *Entomologist's mon. Mag.* **98** 265–70.

11. Emden, H. F. van (1964). The role of uncultivated land in the biology of crop pests and beneficial insects. *Sci. Hort.* **17**: 121–36.
12. Green, G. W. (1962). Low winter temperatures and the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) in Ontario. *Can. Ent.* **94**: 314–36.
13. Gulii, V. V. (1963). Increasing the effectiveness of parasites of the European pine shoot moth, *Evetria buoliana* Schiff. in pine stands on the northern slopes of the central Caucasus. *Zool. Z. Moskva.* **42**: 1414–5.
14. Györfi, J. (1951). Die Schlupfwespen und der Unterwinchs des Waldes. *Z. angew. Ent.* **33**: 32–47.
15. Györfi, J. (1962). Der Einfluss der Waldpflanzen auf die Vermehrung der Schlupwespen. *Anz. Schädlingsk.* **35**: 20–2.
16. Harris, J. W. E. & Wood, R. O. (1967). The European pine shoot moth, *Rhyacionia buoliana* (Lepidoptera: Olethreutidae), another introduced forest pest. *J. ent. Soc. Brit. Columb.* **64**: 14–7.
17. Judd, W. W. (1951). The European pine shoot moth, *Rhyacionia buoliana* (Schiff.) on Austrian pine at Hamilton, Ontario. *J.N.Y. ent. Soc.* **59**: 241–3.
18. Juillet, J. A. (1959). Morphology of immature stages, life history, and behaviour of three hymenopterous parasites of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae). *Can. Ent.* **91**: 709–19.
19. Juillet, J. A. (1960). Immature stages, life histories, and behaviour of two hymenopterous parasites of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.). (Lepidoptera: Olethreutidae). *Can. Ent.* **92**: 342–6.
20. Juillet, J. A. (1961). Observations on arthropod predators of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae), in Ontario. *Can. Ent.* **93**: 195–8.
21. Kulman, H. M. (1966). Distribution of the European pine shoot moth, its parasites, and associated insects in red pine trees and stands. *A. ent. Soc. Am.* **59**: 34–9.
22. Leius, K. (1960). Attractiveness of different foods and flowers to the adults of some hymenopterous parasites. *Can. Ent.* **92**: 369–76.
23. Leius, K. (1961). Influence of food on fecundity and longevity of adults of *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae). *Can. Ent.* **93**: 771–80.
24. Leius, K. (1961). Influence of various foods on fecundity and longevity of adults of *Scambus buolianae* (Htg.) (Hymenoptera: Ichneumonidae). *Can. Ent.* **93**: 1079–84.
25. Leius, K. (1963). Effects of pollens on fecundity and longevity of adult *Scambus buolianae* (Htg.) (Hymenoptera: Ichneumonidae). *Can. Ent.* **95**: 202–7.
26. Leius, K. (1967). Food sources and preferences of adults of a parasite, *Scambus buolianae* (Hymenoptera: Ichneumonidae). *Can. Ent.* **99**: 865–71.
27. Leroux, E. J. *et al.* (1963). Population dynamics of agricultural and forest insect pests. *Mem. ent. Soc. Can.* **32**, 102 pp.
28. McGugan, B. M. & Coppel, H. C. (1962). Biological control of forest insects, 1910–1958. *In* A review of the biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol. Contr.* **2**: 35–127.
29. McLeod, J. H. (1962). Biological control of pests of crops, fruit trees, ornamentals and weeds in Canada up to 1959. *In* A review of the biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol. Contr.* **2**: 1–33.
30. Miller, W. E. (1960). Discovery in Michigan of *Orgilus obscurator* (Nees), a foreign parasite of the European pine shoot moth. *J. econ. Ent.* **53**: 318.
31. Miller, W. E. (1967). The European pine shoot moth—Ecology and control in the Lake States. *For. Sci. Monogr.* **14**, 72 pp.
32. Morris, R. F. (1957). The interpretation of mortality date in studies on population dynamics. *Can. Ent.* **89**: 49–69.
33. Pierrard, G. & Baurant, R. (1961). Note sur la parasitisme de *Rhyacionia buoliana* Schiff. Microl. Eucosmidae. *Bull. Inst. agron. et Stat. Rech., Gembloux* **29**: 102–4.
34. Pointing, P. J. (1962). The effectiveness of a microbial insecticide against larvae of the European pine shoot moth, *Rhyacionia buoliana* (Schiffermüller). *J. Insect Path.* 4: 484–97.
35. Pointing, P. J. (1966). A quantitative field study of predation by the sheet-web spider, *Frontinella communis*, on European pine shoot moth (*Rhyacionia buoliana*) adults. *Can. J. Zool.* **44**: 265–73.
36. Pointing, P. J. & Green, G. W. (1962). A review of the history and biology of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae) in Ontario. *Proc. ent. Soc. Ont.* **92**: 58–69.
37. Pointing, P. J. & Miller, W. E. (1967). European pine shoot moth, pp. 162–6. *In* Important forest insects and diseases of mutual concern to Canada, the United States and Mexico. *Publ. Can. Dep. For. Rural. Dev.* **1180**, 248 pp.
38. Reeks, W. A., Forbes, R. S. & Cuming F. G. (1951). *Rep. Forest Insect Dis. Surv. Can.* 1950: 5–20.
39. Sippell, W. L., MacDonald, J. E. & Rose, A. H. (1960). *A. Rep. Forest. Insect Dis. Surv. Can.* 1959: 44–62.
40. Stone, A., Sabrosky, C. W., Wirth, W. W., Foote, R. H. & Coulson, J. R. (1965). A catalogue of the diptera of America, north of Mexico. *Handb. U.S. Dep. Agric.* **276**, 1696 pp.
41. Syme, P. D. (1965). Nocturnal and diurnal fluctuations in abundance of some predaceous insects on red pine. *Bi-mon. Prog. Rep., Can. Dep. For.* **21** (4): 1–2.
42. Syme, P. D. (1966). The effect of wild carrot on a common parasite of the European pine shoot moth. *Bi-mon. Res. Notes, Can. Dep. For.* **22** (4): 3.
43. Syme, P. D. (1969). Interaction between *Pristomerus* sp. and *Orgilus obscurator*, two parasites of the European pine shoot moth. *Bi-mon. Res. Notes, Can. Dep. Fish. For.* **25**: 30–1.

44. Thompson, W. R. (1951). A catalogue of the parasites and predators of insect pests. Sect. 2, Pt. 1. Hosts of the Coleoptera and Diptera. *Commonw. Inst. biol. Contr.*: 1–147.
45. Turnbull, A. L. & Chant, D. A. (1961). The practice and theory of biological control of insects in Canada. *Can. J. Zool.* 39: 697–753.
46. Voûte, A. D. (1946). Toegepaste entomologie en verrijking of verarming der fauna. *Tijdschr. PlZiekt.* 52: 150–7.
47. Watson, W. Y. & Arthur, A. P. (1959). Parasites of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) in Ontario. *Can. Ent.* 91: 478–84.
48. Yates, H. O. III (1967). Key to nearctic parasites of the genus *Rhyacionia* with species annotations. *South. For. Exp. Sta., U.S. Dep. Agric.*, Asheville, N.C.

47. *STILPNOTIA SALICIS* (L.), SATIN MOTH (LEPIDOPTERA: LIPARIDAE)

R. S. Forbes and D. A. Ross

PEST STATUS

The early spread and status of the satin moth, *Stilpnotia salicis* (L.), and the effectiveness of introduced parasites in Canada to 1958 have been reviewed (7). Since then evaluations have been made of the rôle of native and introduced parasites of the satin moth in British Columbia (6), and of the programme of introducing parasites to that Province (10).

Unlike most of the other major insects treated in this bulletin, the satin moth has not received close attention during the period under review. The only work done was by regional Forest Insect and Disease Survey units whose work programmes emphasize problems of high or potentially economic import. The satin moth fits in the latter category, and work has been concerned mainly with surveys to detect and monitor infestations and the rearing with material collected when the pressures of other work allowed. Emphasis has varied greatly in each region as shown by the number of rearing records: Newfoundland 8; Maritimes 242; Quebec 12; and British Columbia 67.

The accompanying map (Fig. 27) shows the known distribution of the satin moth in Canada. In the past, the distribution in Newfoundland and the Maritime Provinces was mostly confined to areas where poplars are planted as ornamental or shade trees. In recent years, however, the insect has been found over wider areas and now occurs wherever introduced and native poplars and willows are common. The patchy distribution shown for Quebec may be attributed either to sporadic host-tree distribution or less intensive surveys for infestations, or both. The range of the insect in British Columbia, confined to southern and eastern Vancouver Island, lower coast mainland and southern interior, has not changed appreciably since 1965.

Favoured host trees are silver poplar, *Populus alba* L.; Carolina poplar, *P. eugenei* Simon-Louis; trembling aspen, *P. tremuloides* Michx.; Lombardy poplar, *P. nigra* L. var *italica* Muench; eastern cottonwood, *P. deltoides* Marsh.; black cottonwood, *P. trichocarpa* Torr. & Gray; balsam poplar, *P. balsamifera* L.; largetooth aspen, *P. grandidentata* Michx.; and willow, *Salix* sp.

The satin moth has a history of host adaptations and the list of hosts has grown ever since its introduction. Also, up to 1925 this insect was thought of primarily as a pest of ornamental and shade trees but infestations in woodland areas are becoming more common. For example, in New Brunswick infestations before 1967 were confined to single and small groups of shade and ornamental trees, mostly exotics. In 1967, however, severe defoliation of stands of native poplars was observed in six areas of New Brunswick ranging from 10 to 260 acres (2). In 1968, four of these continued and five additional outbreaks occurred in poplar stands over areas varying from 1 to 1,000 acres (3). Similarly in Maine, near Mt. Katahdin, small areas of largetooth aspen attacked in 1967, were enlarged in 1968 to include some 10,000 acres of moderate to severe infestation.[1] In Quebec, attacks to date have been severe, usually confined to exotic poplars, eastern cottonwood and willow shade trees, and always localized. In British Columbia, the satin moth is at times a spectacular defoliator of exotics in coastal areas and of both exotic and native trees in the Interior. It persists in sometimes widely fluctuating densities and generally defoliation has been most severe in new centres along the advancing edge of the insect's range.

Observations since 1958 show that outbreaks usually lasted 2 years in Newfoundland, 2 years and occasionally 3 in the Maritimes, 1 year in Quebec, and usually 2 years in British Columbia. These outbreaks were of much shorter duration than those observed in the Maritimes prior to 1958, which lasted 4 to 9 years (9). In the Maritimes the period between outbreaks has varied from 1 to 6 years.

Dispersion and rate of spread depends on many factors but adult flights seem to be most important. The catches of adult satin moths at Ashton Hill fire tower near Newcastle, N.B., from 1962 to 1967 were: 1962—38; 1963—68; 1964—128; 1965—129; 1966—387; and 1967—2,187. These figures suggest a build-up of populations leading to the first recorded attacks in natural stands of aspen in New Brunswick in 1967.

McGugan and Coppel (7) state that '—defoliation is rarely complete and hence the satin moth is not considered a serious economic pest—.' A careful review of the literature and of infestation records since 1958 indicates that defoliation is often complete. The satin moth has not been considered a serious economic pest not so much because defoliation is partial or complete, but rather because outbreaks rarely last more than 2 years and records of widespread tree mortality are scarce. Except for mortality of young cottonwoods over sizeable areas in the lower Fraser River Valley in the 1920's (4) and more recently of some poplars in the arid portions of the interior of British Columbia, damage in Canada has been confined mainly to twig and branch mortality. The insect has been generally considered as an annoying pest by resort owners and communities where shade trees are valued. However, if the insect continues to adapt its attack from ornamental exotics to native poplars in forest stands, its economic impact in the future may be considerably greater than in the past.

The satin moth is known to be the host for 35 primary parasite species. Despite the large number of primary parasites parasitism by native species is low. The tachinid *Exorista mella* Wlkr., appears to be the most common native parasite, killing as many as 5 per cent. (based on parasite emergence) of host larvae in New Brunswick, 4 per cent. in Nova Scotia, and 17 per cent. in British Columbia. The next most important native parasite in British Columbia was the tachinid, *Tachinomyia similis* Will., which killed up to 2 per cent. of the host larvae.

Hyperparasites are an important part of the biological complex. The introduced parasite, *Apanteles solitarius* (Ratz.), is host to 19 of these, which could affect its effectiveness as a control agent. In the Maritimes, *A. solitarius*, is host to 11 of 15 of the hyperparasites, and in British Columbia to 14 of 18. In British Columbia another introduced parasite, *Meteorus versicolor* (Wesm.), is host to 12 of these 18.

Except for very recent data on the incidence of a cytoplasmic polyhedrosis virus in New Brunswick very little is known of the pathogens of the satin moth in Canada. Bacteria were observed in dead larvae as early as 1952 and fungi in 1953 but it is not known whether they were primary or secondary. A microsporidian was first discovered in the satin moth in New Brunswick in 1954 but this parasite has always been rare. The polyhedrosis virus in this insect has been known in the Maritime Provinces and Newfoundland since the early 1950's (9) but was not identified as a cytoplasmic disease until 1967. More recent and detailed studies on the incidence of this disease in populations in natural

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[1] Nash, Robley W. Maine Forest Service, Augusta, Maine, U.S.A. Personal communication.

stands in New Brunswick show that up to 67 per cent. of the larvae may be infected, and infection rate seems to depend upon population density as well as time of collection. The disease was recorded in Quebec in 1968 but so far has not been reported in British Columbia.

RELEASES AND RECOVERIES

No releases of introduced parasites were made against the satin moth in Canada from 1959 to 1968, but there are additional records on the distribution and behaviour of native parasites and species introduced prior to the decade under review.

PARASITES

Apanteles solitarius (Ratz.) (Hymenoptera: Braconidae)

The distribution and spread of *A. solitarius* in eastern Canada appears to be closely related to the location of main trunk highways and the direction of prevailing winds. *A. solitarius* was released in the Maritimes only in southeastern New Brunswick and although it has spread in all directions dispersal has been mainly to the east and southeast. This species was first found in Quebec in 1941 (1) but has not been collected there since 1956. In British Columbia, the parasite has spread through the major portion of the host's range (Fig. 27) and has accompanied its advancing periphery.

Condensation of larval rearing data presents a conservative view of mortality from parasitism (Table XL). For example, in a localized infestation in Nova Scotia, which reached its peak in 1965, the percentage parasitism by *A. solitarius* in 1966 was as high as 88 per cent. and was undoubtedly a major factor in ending the outbreak in 1967. Collections of host larvae in this and nearby areas in 1969, after 2 years of very low populations, showed about 86 per cent. parasitism, mostly by *A. solitarius*, indicating that the parasite is able to maintain itself at low host population levels and continue as an important control factor. Again, in an infestation in a wooded area of New Brunswick in 1968 about 90 per cent. of the overwintering satin moth larvae were parasitized, *Apanteles* predominating. However, its effectiveness may be reduced by hyperparasites, whose incidence can reach 70 per cent.

On the basis of only a few rearings of host larvae in British Columbia parasitism by *A. solitarius* seems low (Table XL). However, most collections of satin moth larvae taken since 1959 were made after the *Apanteles* larvae had emerged. Observations on the abundance of parasite cocoons in several infestations along the coast and in the Interior indicate higher mortality of host larvae due to this parasite than is demonstrated in the rearing data, and provide good evidence that the parasite is playing an effective rôle in reducing the severity and spread of satin moth infestations.

Compsilura concinnata Meig. (Diptera: Tachinidae)

This parasite was found on the satin moth only in the Maritimes and British Columbia from 1959 to 1968. It was not recorded in Prince Edward Island from 1959 to 1968, and was reared from

TABLE XL

Parasitism of satin moth larvae by *Apanteles solitarius* (Ratz.) by Provinces, 1959–68

	Host larvae		
Province	Reared	Parasitized	%
Newfoundland	474	78	16·5
Nova Scotia	754	350	46·4
New Brunswick	98	32	32·7
Prince Edward Island	71	41	57·7
Quebec	463	0	0
British Columbia	2248	122	5·4

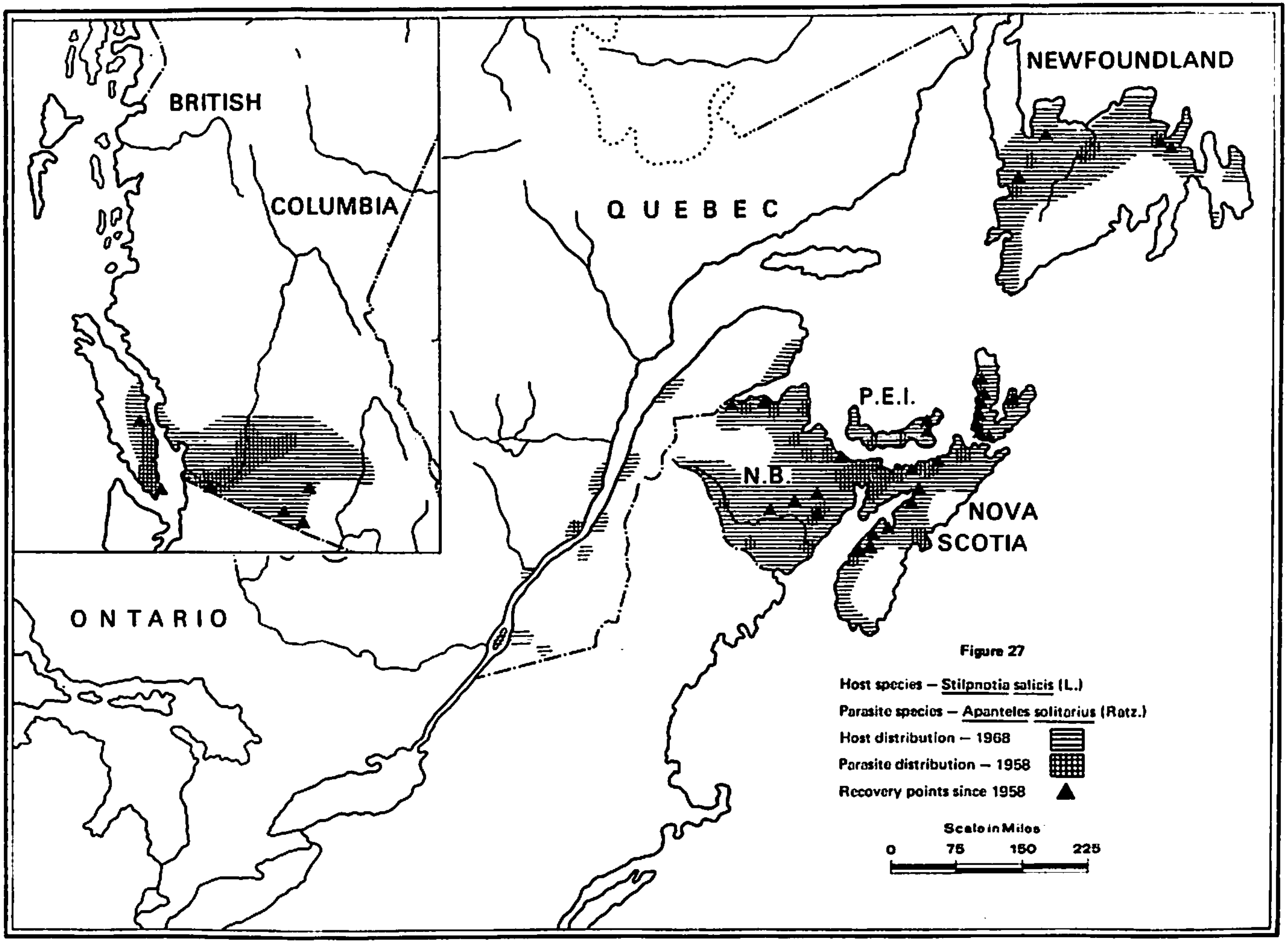

Figure 27

Host species — *Stilpnotia salicis* (L.)

Parasite species — *Apanteles solitarius* (Ratz.)

Host distribution — 1968 ▤

Parasite distribution — 1958 ▦

Recovery points since 1958 ▲

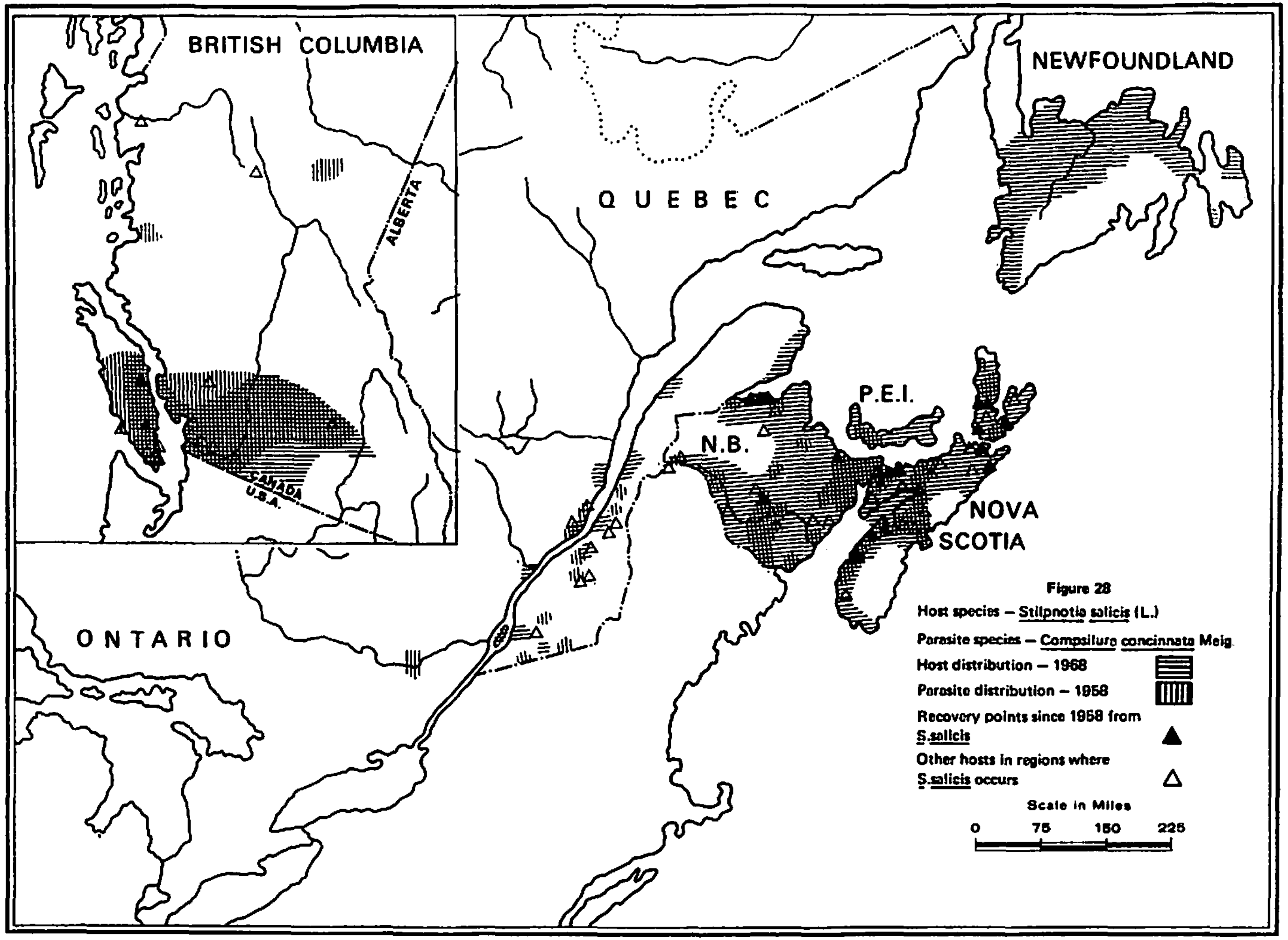

Figure 28

Host species – *Stilpnotia salicis* (L.)

Parasite species – *Compsilura concinnata* Meig.

the satin moth in New Brunswick and Nova Scotia from only a few new areas. It has been collected in Nova Scotia, New Brunswick and Quebec on miscellaneous hosts, sometimes beyond the known range of the satin moth. In British Columbia, *C. concinnata* has spread slowly through the Interior even though it attacks and develops successfully on a number of lepidopterous hosts. It was reared from lepidopterous larvae collected considerably north of the range of the satin moth (Fig. 28).

This parasite effected considerably less control of the satin moth than *A. solitarius*, despite its long establishment, wide distribution, and multitude of hosts (Table XLI). In the Maritimes, its effectiveness seems to vary considerably in time and place with percentage parasitism in individual collections ranging from 2–77. It cannot overwinter in hibernating satin moth larvae but does so in pupae of other hibernating Lepidoptera. Therefore, its effectiveness as a parasite of the satin moth depends on the abundance of alternate hosts. Another limiting factor may be associated with the tendency of *C. concinnata* to attack, in a mixed population of suitable hosts, the first host to make its appearance (11), thus reducing its capacity to attack later appearing hosts. Therefore, in areas where earlier, alternate hosts predominate the parasite's effectiveness on the satin moth might be greatly reduced. Superparasitism of host larvae by *C. concinnata* is common in the Maritimes. No more than one parasite larva was observed to issue from a host pupa, suggesting that hosts with more than one parasite larva cannot pupate. In British Columbia rearing data are insufficient for an adequate assessment of the effectiveness of *C. concinnata*. It has spread slowly and is not common in collections.

TABLE XLI

Parasitism of satin moth larvae by *Compsilura concinnata* Meig. by Provinces, 1959–68

	Host larvae		
Provinces	Reared	Parasitized	%
Nova Scotia	331	54	16·3
New Brunswick	61	12	2·0
British Columbia	378	36	9·5

Eupteromalus nidulans (Thoms.) (Hymenoptera: Pteromalidae)

No recent recoveries of this parasite have been made from satin moth in Canada.

Meteorus versicolor (Wesm.) (Hymenoptera: Braconidae)

No specimens of this parasite were recovered in eastern Canada from 1959 to 1968. Its distribution in British Columbia is shown in Fig. 29. *M. versicolor* seems less numerous than *A. solitarius* but, like it, has spread quickly into newly infested areas.

EVALUATION OF CONTROL ATTEMPTS

The extensive methods of collecting and rearing used by the Forest Insect and Disease Survey, in contrast to the life-table approach used for some forest insects, provide only partial assessment of the effect of parasites and hyperparasites on satin moth populations. Normally the field staff take collections only where defoliation is noticed, that is when population levels are high and often when larvae are mature. Thus few collections are taken of eggs, hibernating and other early-instar larvae, and pupae, each of which is subject to attack by different parasite species. For this reason the rearing of satin moth material provides information only on the incidence of the second generation of *A. solitarius* and *M. versicolor*, but reasonably complete information on the population levels of *C. concinnata* which issues from late-instar larvae and from pupae. Despite these shortcomings the use of the same methods of collecting each year shows that the range of the satin moth is increasing and that it is becoming more important on native poplars in woodland areas. The level of control by

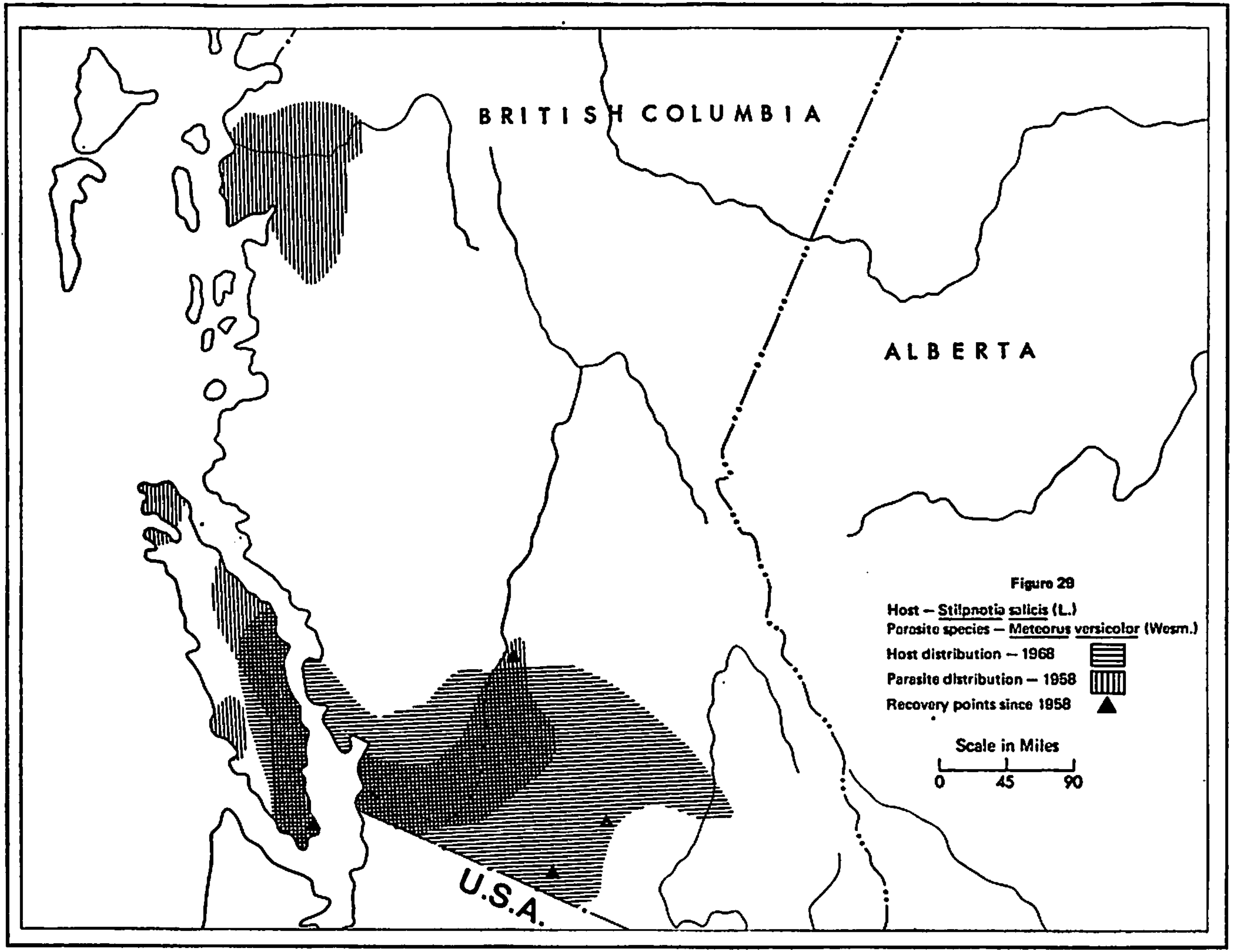

Figure 29

Host – *Stilpnotia salicis* (L.)

Parasite species – *Meteorus versicolor* (Wesm.)

introduced parasites achieved through early releases and subsequent spread has generally been maintained. *A. solitarius* now occurs through much of the host's range and is the most important introduced agent with parasitism reaching 90 per cent. in some localized infestations. It is a major factor in reducing the severity and the duration of outbreaks, which rarely last more than 2 or 3 years, and thus helps to reduce the mortality of poplars. However, it is sometimes heavily attacked by secondary parasites which may lower its effectiveness. *C. concinnata*, which has spread more slowly, can reach a high incidence but it seems to be generally a less effective control agent than *A. solitarius*. The multitude of widely distributed hosts of *C. concinnata* helps to provide a reservoir of material. However, the abundance, and early seasonal appearance of some of these hosts and its overwintering requirements may limit its potential as a control agent of the satin moth. The impact of *M. versicolor*, which occurs only in British Columbia, is less well known; it spreads rapidly and helps reduce spread of the host.

To summarize, in its early years in Canada the satin moth was primarily a pest of exotic ornamental poplars but recently attacks have also become common on native poplars in woodland areas. The reasons for this trend are not well understood but it could have serious economic implications in the future. There is also a trend towards reduced duration of outbreaks, at least in eastern Canada, from 4 to 9 years previously to no more than 3 years in the past decade. Associated with this is reduced damage confined largely to twig and branch mortality and annoyance to owners of high value trees. For helping to shorten outbreak periods and thus reducing damage, introduced parasites must receive major credit. Thus, it is clear that the programme of introducing biological agents of control against the satin moth has not been completely effective, but outbreaks have been shortened and damage reduced, and so considerable success, economic and biologic, is claimed.

RECOMMENDATIONS

As aesthetic and economic value of poplar increases the need for effective control agents will increase. Recent studies in Canada and Europe (8, 5) show effective control by the bacterium, *Bacillus thuringiensis* Berliner, has been achieved in the laboratory. If reported results can be extended to field conditions, control of the satin moth with this organism may be realized. This work seems worth investigating, especially in view of hazards in the use of broad-spectrum chemical agents. Also, further studies are recommended on the occurrence and effectiveness in control by the polyhedrosis virus in eastern Canada with ancillary studies on methods of artificial dissemination.

LITERATURE CITED

1. Beaulne, J. I. (1948). Notes sur quelques predateurs et parasites d'importance economique. 13th *Rep. Quebec Soc. Prot. Pl.*: 206–9.
2. Forbes, R. S., Underwood, G. R. & Van Sickle, G. A (1968). Maritimes Region. *Rep. Forest Insect Dis. Surv. Can.* 1967: 17–23.
3. Forbes, R. S., Underwood, G. R. & Van Sickle, G. A. (1969). Maritimes Region. *Rep. Forest Insect Dis. Surv. Can.* 1968: 18–34.
4. Glendenning, R. (1932). The satin moth in British Columbia. *Pamphl., Ent. Br., Can. Dep. Agric.* 50: (revd.) (new series), 15 pp.
5. Kudler, J. & Lysenko, P. (1963). [Tests with micro-organisms for the control of *Stilpnotia salicis*.]—Lesn. Ces. 9 pt. 9 pp. 787–98, 4 figs., 13 refs. Prague, 1963 (with summaries in Russian and English). (Cited in *Rev. appl. Ent.* 54, 1966, p. 8).
6. Lejeune, R. R. & Silver, G. T. (1961). Parasites and hyperparasites of the satin moth, *Stilpnotia salicis* Linnaeus, (Lymantriidae) in British Columbia. *Can. Ent.* 93: 456–67.
7. McGugan, B. M. & Coppel, H. C. (1962). Biological control of forest insects, 1910–1958. *In* A review of the biological control attempts against insects and weeds in Canada. *Tech. Commun. Commw. Inst. biol. Contr.* 2: 35–127.
8. Morris, O. N. (1963). Pathogenicity of three commercial preparations of *Bacillus thuringiensis* Berliner for some forest insects. *J. Insect Path.* 5: 361–7.
9. Reeks, W. A. & Smith, C. C. (1956). The satin moth, *Stilpnotia salicis* (L.) in the Maritime Provinces and observations on its control by parasites and spraying. *Can. Ent.* 88: 565–79.
10. Turnbull, A. L. & Chant, D. A. (1961). The practice and theory of biological control of insects in Canada. *Can. J. Zool.* 39: 697–753.
11. Webber, R. T. & Schaffner, J. V. (1926). Host relations of *Compsilura concinnata* Meig., an important tachinid parasite of the gypsy moth and browntail moth. *Bull. U.S. Dep. Agric.* 1363, 32 pp.

PART IV
BIOLOGICAL CONTROL IN CANADA, 1959-1968: SYNOPSIS

48. STATUS AND POTENTIAL OF BIOLOGICAL CONTROL IN CANADA

E. G. Munroe

The form of this section of the *Review* is somewhat different from what I anticipated when I began work on it. I expected to be concerned mainly with principles and scientific interpretations, somewhat less with specific operations, and only incidentally with organization. Instead the report deals primarily with organization, and discusses the science and technology of biological control secondarily, as it relates to an effective operational system. There are several reasons for this evolution. Some of them should perhaps have been obvious at the outset.

First, biological control is a complex and highly detailed subject. The variety of resources, pests, natural enemies, environments and cultural and economic practices concerned is very large. The operations are sometimes straightforward and predictable, but more often they involve subtleties of handling, evaluation and management in which experience and flair may be more important than theory. In my opinion it is both inappropriate and unfeasible for a person without first-hand familiarity with the field to comment on the specifics of biological control operations. On the other hand the overall shape, objectives and systems design of programmes may be criticized from a management point of view by an individual with only general knowledge.

Second, even the theory of biological control is a subject for experts. Complexity of practical situations is reflected in complexity of theoretical models. Simple theories have usually turned out to be provocative rather than useful. The day of the dilettante in biological control theory is over. Progress will be made on the one hand by acquiring *and formulating* detailed practical experience of real problems and on the other hand by constructing *and testing in real situations* increasingly comprehensive dynamic, ecological, econometric and management models, using increasingly realistic inputs. Answers will be found by cooperation, not warfare, between practitioners and theoreticians. Positive steps are needed to bring about the required degree of cooperation. Meanwhile armchair theorizing by an amateur is unlikely to yield convincing or useful results.

Third, in every area where biological control has been seriously tried, including Canada, it has had major successes, sufficient to repay manyfold all the resources expended. This does not mean that every individual project has been successful, but serious major national programmes have generally been highly successful. The question therefore is not whether biological control should be undertaken, but how our resources can most effectively be used in developing it.

Fourth, there is at present very strong pressure to find reliable alternatives to substantial classes of chemical control. The answers are specific to Canada and, unlike those of chemical control technology, will not be provided readily by foreign or industrial research. Canadian programmes to develop biological control must therefore have a high priority.

Fifth, it is obvious that, although our research related to biological control, our international search and import programmes for natural enemies and certain of our initiatives at the field operations level have been excellent, our systems for concentrating expertise and resources in the solution of specific control problems have been defective, and are far inferior to those developed by, or in cooperation with, industry for the deployment and marketing of chemical control.

Therefore the main theme of my report has been the improvement of organization to supply biological control knowledge and materials promptly and effectively wherever they are needed in the field. This is not a recommendation against research—we need more research, not less. It is not a recommendation against local planning—we need local planning with the best knowledge and materials at its disposal. *It is a recommendation for a planning and delivery system that will apply the best knowledge and the most suitable materials effectively when and where they are required.* The details of the recommendations are arguable but the principle is not. We will never have adequate alternatives to chemical control until our formulation, supply, application and information services are at least as effective for the alternatives as they are for chemical control at the present time.

CONCLUSIONS AND RECOMMENDATIONS

Biological control is a practical and desirable approach to the control of many pest species. It has achieved important successes in Canada, and indeed wherever it has been seriously undertaken. Its value includes not only continuous, self-maintaining suppression of pest species to non-economic levels, but also: partial suppression, so that damage is less frequent or severe or expenditures on control are less; replacement of other methods of control that have undesirable features, such as residues, non-specificity or development of resistance—for instance by inundation or inoculation with doses of biotic agents sufficient to substitute for poisoning with chemical materials—and contribution to integrated programmes that have desirable characteristics such as stability, permanence and economy.

Canada's capacity and standing in the biological control field have been high on both theoretical and operational sides. Since 1958 they have tended to decline, because of priority given to other objectives, because of underemphasis on operational effectiveness, and because of departure of expert personnel.

In the next 10 years several factors will work to reverse this downward trend. Among these are: pressure for alternatives to chemical control; increased emphasis on mission-oriented work; development of the integrated control concept; and emphasis on rational and integrated management of renewable and other resources.

If the response to these pressures is adequate, biological control can be a very important component of Canada's resource protection programme (and perhaps also a field for effective foreign aid). However, there is a danger that the response will be inadequate. Among specific points of danger are: that there will be insufficient attention to operational effectiveness; that biological control will be regarded as an end in itself or a dangerous rival to chemical control, rather than as a component of a total programme; that the key importance of selection of suitable personnel for different biological control tasks will not be recognized; that the complexity and individuality of biological control problems will be underestimated; that research both on principles of biological control and on the variety, sources, biological characteristics and management of biological control agents will receive insufficient support or will not be effectively coupled with practical planning and operations; and that budgetary economies will force cutback of the effort in this field below the level of effectiveness.

The following recommendations are presented with the object of improving the effectiveness of biological control and of its integration with other aspects of pest control and related activities in Canada.

(1) *It is recommended that* an Operational and Advisory Centre for Biological Control be established, with the following responsibilities:

—Acting as a centre of expertise on the practice, theory and background data of biological control of pests and weeds.

—Participating in central planning of biological and of integrated control operations and policies, in the Departments of Agriculture, of Fisheries and Forestry, and other relevant agencies.

—Distributing state-of-the-art summaries and bulletins for use by regional and local planning and control centres or personnel.

—Providing experts on request to assist in planning regional and local biological control programmes and operations.

—Providing task forces or individuals on request to give expert operational help in regional and local control activities.

—Importing, screening, propagating and distributing all biological control agents of foreign origin.

—In consultation with the appropriate departments and agencies, maintaining liaison with foreign and international biological control organizations.

—Conducting, participating in, supporting, or maintaining liaison with research programmes on:

  —selection, handling and improvement of biological control agents.

  —principles and practice of predicting and managing the fluctuations and interactions of pests and their biotic enemies.

  —identification, sources, geographical ranges, variability, host relationships and biological characteristics of potential biological control agents.

  —systems management and integration of biological control in a rational control programme.

—Developing standards and procedures for, and providing expert assistance in the process of monitoring the results of biological or integrated control programmes.

A single centre would have the greatest potential strength, but if necessary separate departmental centres would be operable.

(2) *It is recommended that* general policies and plans for biological control be developed as part of an overall strategy of pest control for each major crop or resource area, and that such planning include economic evaluation at a competent professional level and consideration of environmental-quality and resource-management implications in consultation with representatives of appropriate agencies and interest-groups. The Operational and Advisory Centre should be a source of operational and technological advice in this planning.

(3) *It is recommended that* actual biological control programmes should normally, as now, be initiated regionally, and that this should be done as part of general or integrated regional control planning. However, the Operational and Advisory Centre should provide information, comparable to that available for pesticide use, to help preliminary planning, and should where necessary provide expert assistance in detailed planning and subsequent operations. It should also take the initiative in calling the attention of regional centres to promising opportunities for biological control. Though the initiative should remain with the region, the relationship with the Operational and Advisory Centre must be much closer and more dynamic than has existed with the parasite- or pathogen-distributing agencies in the recent past. Central policy and direction should actively foster a receptive and constructive attitude in regional centres.

(4) *It is recommended that* the Canadian Government should support the Commonwealth Institute of Biological Control (C.I.B.C.) on a modestly larger scale than it now does, and that the added support should take the form of additional or extended contracts for the conduct of search for and field investigation of biotic agents for use against specific pests, rather than an increase in general grants.

(5) *It is recommended that* this form of support be supplemented by the more frequent secondment of Canadian personnel abroad to participate in the search for useful natural enemies and to study their biology in the field. Such secondment should normally be directed towards a particular problem or group of problems, and the seconded officer should preferably be one directly associated before and after his secondment with the control programme in which the natural enemies are to be used. Typically the officer should be seconded to work with the local C.I.B.C. station or other appropriate agency, but should have some independent operating funds and discretion to follow what is in his judgment the best programme. Continuity of experience from field study abroad to employment

of biotic agents in the control programme in Canada is essential. There is also room for occasional, more general, exploratory surveys provided they are closely integrated with actual biological control investigations (Recommendation 8).

(6) *It is recommended that* monitoring of the results of biological control programmes be greatly improved, both in extent and depth. Principles, procedures and interpretation all require development. No programme should be undertaken without reasonable provision for assessment of the results. This specific monitoring function, directly related to following up the course of active control projects, should be clearly distinguished from the general pest surveillance function of the Forest Insect Survey, which is not under criticism here. Specific monitoring at a meaningful level should be an integral part of each control activity. It would be better, if necessary, to make fewer control attempts than to continue a larger number blindly, without knowing whether they are beneficial, useless or harmful.

(7) *It is recommended that* research in population dynamics and mathematical models be more strongly and generally supported than in the recent past and that it be more directly and extensively applied in biological and integrated control operations. In particular, verification by field trials and interchange of concepts and data between modelling and operational groups should as a matter of urgency be vigorously encouraged. The most practical way of doing this appears to be by the development of grants, contracts, and cooperative programmes directed towards university groups now engaged in such research. Such research should be directed to non-biological and integrated control and to integrated resource management as well as to biological control.

(8) *It is recommended that* research on background information related to the characteristics, identification, establishment and sources of potential biological control agents be broadened, intensified and more closely integrated with the control programme. A much larger spectrum of natural enemies is available than is being used, and both taxonomic and biological knowledge are fragmentary for most groups. Predators and non-European sources have been more seriously neglected than European parasites, but even for the latter much better knowledge is needed. The three most important areas for research are: specific, practical biological knowledge related to handling, establishment and effectiveness; capacity to make good identifications; and full exploration of the potential range of natural enemies. *Such research should take priority over research on chemical control,* as it is more specific to Canadian conditions as well as much less readily available from industrial and foreign sources. Much of this research could best be developed from the base of in-house facilities, in fact every aspect of the programme—taxonomic, biological, and exploratory—should be carried out in close liaison with the Operational and Advisory Centre and/or field control programmes.

(9) *It is recommended that* much more emphasis be placed on the propagation of predators, parasites and pathogens, and of enemies of weeds. Adequate and controlled supplies of biotic agents permit a more flexible and more effective programme of introductions, and also permit research and development directed to the improvement of agents and of handling methods.

(10) *It is recommended that* the development and utilization of genetic knowledge of pests and their natural enemies be made a specific objective, and that either contracts or in-house programmes should be initiated as soon as resources permit. The goals should be: (a) improvement and diversification by selective breeding of natural enemies considered to have high control potential, and (b) development of methods of controlling the density of pests or increasing the effectiveness of other control methods by understanding and altering the genetic composition of wild populations. Such research should at least in part be associated with the propagation programme recommended above (Recommendation 9).

DEFINITION OF BIOLOGICAL CONTROL

A number of definitions of biological control are possible. In this section biological control is taken to mean:

Planned reduction or regulation of pest populations by (a) the use of predators, parasites, pathogens, herbivores, competitors or other natural enemies.

or (b) interference with the genetic fitness or reproductive potential of pest populations by the introduction of sterile or genetically different individuals. Use of chemicals such as pheromones or hormones is excluded.

OBJECTIVES OF BIOLOGICAL CONTROL

The objectives of biological control are to prevent or reduce direct or indirect losses from pests by:

(a) regulating pest populations so that harmful densities are not attained;
(b) limiting or reducing such densities if they do occur;
(c) reducing damage at a given density by altering the action or the distribution in space or time of the pests; or
(d) contributing to the effectiveness, economy or social acceptability of a total control programme.

The criteria of success are always technological, economic and social. A high level of technological success, such as establishment of a control agent that automatically prevents the recurrence of harmful pest densities, is often considered the ideal; but it is not necessarily a feasible solution, or the best one. The value of a control must be judged by social and economic criteria as well as by technological ones. There is a wide variety of levels and kinds of success above the minimum threshold where some marginal gain in economy, effectiveness, social acceptability or operational flexibility is achieved. Success may be achieved by varied methods, for instance, establishment of a complex biosystem, introduction of an exotic control agent, cultural encouragement of a native one, or periodic inundation with an agent used as a biological insecticide. Biological control may be used alone or in an integrated programme with other control methods. The planning stage should consider a variety of methods and their possible integration. Biological control should be adopted only after comparison with other possible choices.

PLACE IN THE PEST CONTROL PROGRAMME

Biological control is one of several major classes of methods available for control of pests. Beirne (3) distinguishes nine bases for the classification of control methods, and contrasts biological with chemical and physical controls. Stapley and Gayner (23) distinguish five main classes: use of resistant varieties; cultural methods; biological control; government action, such as quarantines; and application of pesticides. Other classifications are possible.

On any classification biological control is an alternative to other control methods. There is a tendency for emotionalism to centre on this antithesis, both among entomologists, many of whom tend to favour or oppose biological control for disciplinary or organizational reasons, and in the community at large, where different interests tend also to take one side or the other because of business affiliations, economic or operational considerations, concern for the environment, and other reasons. In the broader view such polarization is undesirable and probably largely unnecessary. Biological and non-biological controls and the problems they are designed to meet have so many different specific forms that a general judgment as to their relative values is rarely possible or useful. On the contrary, biological control is one of several approaches, all of which have to be considered in planning a solution to any particular pest problem (4). In some cases successful biological control is a pre-emptive alternative to other methods, as when introduction of control agents results in permanent regulation of the pest population at subeconomic levels. In others it may complement chemical or other controls, for instance in special environments or to redress a disturbed predator-pest balance. Or it may be complemented by chemical control, as when a normally effective biological control permits occasional outbreaks. Shorter-term inundative methods may be direct alternatives to chemical treatment in specific circumstances, as when the use of chemicals is considered harmful or where resistance to them has developed.

Rational selection and combination of biological and non-biological elements in a harmonious control programme is a normal objective of planning (2, 3, 14). More formal combination in an interlocking programme designed to minimize use of chemicals and maximize self-perpetuating elements of the control complex has been called *integrated control* (18, 22).

Integrated control was pioneered by Pickett (16, 17, 18) but has been highly developed in California and elsewhere, and has been the subject of two FAO symposia (7, 8). The FAO Panel of Experts has endorsed the following sequential points in its guidelines for integrated control procedure (7):

(a) Evaluate natural control
(b) Determine economic injury levels
(c) Determine mortality of natural enemies caused by insecticides and other control measures
(d) Establish pest surveillance and prediction
(e) Promote ecological diversity
(f) Maintain minimum levels of pests (dirty-field technique)
  to (i) maintain natural enemies
    (ii) prevent substitute pests from appearing
(g) Use interdisciplinary approach
(h) Plan host sequence
(i) Use cultural controls
(j) Use selective pesticides
(k) Use resistant plant varieties
(l) Establish effective training and extension programmes
(m) Maintain efficient administration of crop protection.

From the standpoint of biological control, the following elements are important: emphasis on use of biotic agents; combination with other methods to permit use of minimum quantities and selective kinds of pesticides; integration in an interdisciplinary, managed system; importance of monitoring pests, controls and damage; and importance of effective training, extension and administration.

EVALUATION OF PEST CONTROL

Pest control is an activity undertaken to achieve a benefit—reduction of the harmful effects of pests. It is therefore subject to evaluation on three general counts: technological (does it work?); economic (is it worth the price?); and social (are its side-effects acceptable?). As the first criterion is the most easily measured, it usually receives the most attention, though the second and third are in the last analysis more important.

TECHNOLOGICAL EVALUATION

This is a well-developed aspect of economic entomology. Earlier measures tended to focus on the number or proportion of insects killed, or the densities remaining after treatment. Attention is now shifting to damage control—already a partly economic measure. However, the technologist must often plan and monitor pest control on the basis of density. Trends in density may be observable long before the degree of damage is apparent; indeed direct estimation of damage is often difficult or impossible until it is too late for successful control. Biological control of populations rests to a considerable extent on density-dependent, or at the very least density-related, processes. Population density is therefore a natural measure in such operations. But for density-based measures to be meaningful they must be related to a measure or forecast of damage, and to a damage tolerance level. Such relationships have been developed, mostly on a rule-of-thumb basis, for certain pests and crops.

Another approach, requiring much less refined monitoring, depends on regular suppression of pests to levels at which damage will never occur, whether or not there is an actual threat at any particular time. Though such policies are widespread, Smith and van den Bosch (22) emphasize their bankruptcy. They have characteristically led to overexpenditure on pesticides, to suppression of beneficial insects and upset of ecosystems, to poisoning of the environment, and to the generation of resistant pests. Typically they have created more problems than they have solved. Smith concludes that measures of damage in tolerance are essential to a well-ordered pest control programme, which will be characterized by minimal, integrated controls.

For biological control, understanding of the dynamics of the ecosystem is almost equally important. Observations of pest or parasite density are of little value if we cannot use them to predict the risk of damage a few weeks later. Both monitoring and prediction must be carried out at a level of accuracy that will permit timely adjustment of the control programme. If only coarse adjustment is needed, then rough estimates and generalized predictions may suffice. Where exact values are critical, more sophisticated sampling and modelling procedures are required.

Technological evaluation concerns not only quantitative effectiveness of methods, but also many other factors, for example: dependability, simplicity and acceptability of procedures; compatibility with other operations; availability, safety and stability of materials. For biological control, complexity, incompatibility, unavailability and perishability are ever-present problems. Only by careful planning, expert supervision and thoughtful integration with other programmes can they be overcome.

ECONOMIC EVALUATION

Although the economic evaluation of pest control is simple in principle, neither the theory nor the practice is as far advanced as we could wish. The basic question the resource manager should ask himself is: will the marginal benefit gained from a given marginal expenditure on a control programme be greater or less than that from an equal marginal expenditure on any other object? Risks, externalities, lack of information, and the complexity of the decision matrix usually make it impossible to answer this question in its general form, either at the individual or the social level. Normally a decision is made first as to whether pest control is required, and then as to the most suitable method. In this decision cost and the expected level of control are important elements. The latter includes a judgment of the amount of resource likely to be saved and of its expected value. If the time between applying the control and marketing the product is long, interest or discount rates have to be considered as well as risk factors. These weigh against long-term programmes, especially at times when markets are changing and interest rates are high. Externalities are also important: the costs and benefits to the individual producer may be quite different from those to the community as a whole.

It is not surprising that definite solutions to these problems are rarely available for particular cases. It is more surprising, first that pest control research and even operations are often conducted with so little attention to comparative costs and benefits, and second that the advice of professional economists is so seldom sought in evaluating pest control problems. No commercial manufacturing enterprise would consider running for a day with as little economic information as is available for the typical pest control programme. At least part of the difficulty arises from the concept that work done on a non-profit basis and from motives of public service necessarily justifies the cost—that services provided by the government are somehow cost-free; part unfortunately also stems from organizational disjunction between economists and technologists, both in government and in the private sector. Whatever the cause, pest control programmes will never be properly evaluated until economics plays a larger part in the process than it generally has in the past.

SOCIAL EVALUATION

Social evaluation is never wholly separable from economic evaluation. Every social action has an economic cost and may have an economic benefit as well; also every social cost or benefit has at least a theoretical economic measure in terms of an alternative. Nonetheless many actions are taken or avoided for reasons that are primarily social rather than economic. More loosely, economic externalities may also be considered social benefits. Avoidance of economic damage by pollution or of the costs of remedial action is an economic benefit to the community, though it may be a social benefit and an economic cost from the standpoint of the individual manufacturer or farmer. On the other hand, preservation of the aesthetic values of the rural environment is primarily a social rather than an economic benefit, though it may have an economic measure in the aggregate of what people are willing to spend on it.

Social costs and benefits have a very real significance in connection with biological control and with pest control generally, because of the close association of chemical pesticides with actual or possible pollution, and because of the potential effects of all classes of pest control on important or pleasing features of the ecosystem. Because of current public concern with pollution, these considerations are weighing heavily against pesticides. Social issues when they reach the political level are always fraught with emotionalism. The emotionalism towards chemical controls might be less had social considerations entered more effectively into past decisions or more visibly into current ones, and if more hard data were available on the actual, rather than the possible, effects of pesticidal pollutants. More reasonable alternatives might be offered if we had a more varied and more reliable array of non-chemical controls.

However, it would be a delusion to suppose that only chemical controls can have a harmful effect on the environment. Cultural controls may have drastic local or general effects on climate, vegetation or other environmental components. In biological control, parasites, predators and pathogens are often highly specific, but their specificity varies widely, and is potentially mutable, though little is known of the mechanisms or frequency of change. Biological pollution by non-specific or mutant natural enemies cannot be completely discounted, and the possibility needs more attention than it has generally received. Indeed it is customarily considered in weed control, because so many weed species are related to useful plants; but it is usually ignored in controlling insect pests. In the use of micro-organisms, risks to health of man and animals are within the bounds of possibility, though perhaps not very probable. Rickettsiae, for example, are poorly understood and some of them cause dangerous diseases of man. Viruses seem to be highly specific, but not enough is known about what makes them so, or about the relationships of different groups of viruses to one another. Certainly some viruses live in man and insects as alternate hosts.

From a broader point of view, the effects on the environment as a whole of indiscriminate introduction of pesticidal species have not been adequately considered. Radical reduction of the level and perhaps the variety of phytophagous insects might have unforeseen effects on pollination and on ecological balance, as well as on the attractiveness and interest-value of our environment. This may perhaps become a concern only when biological control is much more successful than it is at present, but of course our primary object is to make it more successful. The possible consequences of doing so ought not to be absent from our minds.

The moral appears to be that representatives of the public interest, and particularly of those aspects of it that may be threatened by pest control measures, should participate in the decision process, at the technological as well as at the political level. Hard data on levels of undesirable side-effects of pest control will be essential if rational decisions on social costs and benefits are to be reached.

TECHNOLOGY OF BIOLOGICAL CONTROL

The technology of biological control can conveniently be considered under two headings: first, materials and parameters, and second, methods. Materials include hosts, pests and agents. Parameters include environment, sources of agents, interactions, reliability and side-effects. Methods include inoculation, regulation, inundation, management of environment, handling of agents, improvement of agents, genetic control, and methods involving combination or integration of different approaches.

MATERIALS AND PARAMETERS

The nature and success of biological control methods are profoundly influenced by the nature of the organisms concerned, by their environments, and by interactions of these components. These factors are so varied as to make each control situation unique; nonetheless certain generalizations are possible.

Resource or product threatened

Most commonly this is a living organism—an ornamental, a crop or forage plant, a tree, a domestic animal, or man himself; but it may be a stored product, such as grain, or non-food material, such as fibre or structural timber. The nature of the resource or product affects the problem of protection in three important ways: it determines the kinds of pests that will be important; it determines the conditions under which control can be attempted; and under given economic conditions it determines the level of damage that is tolerable and the urgency and the acceptable cost of control efforts.

The *kinds of pests* that attack any particular plant or animal species or any susceptible product are restricted in number, and characteristic in identity. The numbers vary from host to host—oaks and poplars in North America are attacked by thousands of species of insects, whereas buckeyes (*Aesculus* spp.) are attacked by few. They vary with the region—termites of many species are ubiquitous enemies of timber in warm climates, but only a few species are important, and only under special conditions in Canada. Pests important in one region are often prevented by geographic barriers from reaching another. More subtle influences of the natural or cultural environment further affect the array of pests found in any particular time and place. Most host species have a relatively small number of recurrent, dangerous pests, such as the codling moth, *Carpocapsa pomonella* (L.), for apple, and a larger number of minor pests. Some of the latter regularly cause minor damage; others become important either sporadically or under special conditions, such as upset of predator balance by use of insecticides. The kinds of pests to be feared in any particular situation can therefore be predicted with a degree of accuracy. The predictability is greater for widely grown crops than for specialized ones, greater for monocultures than for mixed stands, and greater for major pests than for minor ones. In particular, major pests missing from a particular growing area can be identified, and precautions can be taken against an upset in control practices should they appear. Failure to do so may lead to serious consequences, as in the recent upset of integrated control of cotton pests in California following the introduction of the pink bollworm, *Pectinophora gossypiella* (Saunders) (21).

The nature of the resource or product imposes a more general ecological pattern on the pest array as well as the taxonomic one already discussed. Species or products are susceptible to damage only in certain ways—trees, for example, by root, trunk, twig, subcortical or seed borers, by defoliators, leaf miners, flower and fruit feeders, sap suckers, root feeders, *etc.* This may have considerable influence on the kinds of pests that are important—bark beetles for forest trees, stem borers for grain crops, and the like.

The *conditions under which control can be attempted* are affected by the physical nature of the resource or product, by its cultural environment, and particularly by its distribution in space and time. Protection of bulk products in warehouses, of plants in greenhouses, of field crops, of orchards, of shade trees and of forests, for example, present completely different problems of introduction and application of control agents. In highly regulated environments, such as greenhouses and warehouses, simple methods may have relatively predictable results, whereas the variation in mixed outdoor environments is much greater, and weather and biotic interactions may have unforeseen effects. Automatic, self-perpetuating controls are favoured by continuity of the environment over time. They can most easily be established in forests or orchards, or in areas where the crop pattern does not change much or where there are substantial uncultivated areas to maintain reservoir populations (13).

This type of control may be impractical where there is major disjunction of crops by cultivation and rotation regimes. Other biological control methods, depending on inundation, on introduction of agents with quick build-up characteristics, or on attraction of natural enemies from surrounding areas, may, however, be feasible in these temporary environments. In areas of monoculture it has sometimes proved necessary deliberately to provide refuge areas for predators and parasites. Woodlots, hedgerows or even artificial shelters have been used.

Damage tolerance also depends on the type of product, and in turn is related to the suitability and nature of biological control. Automatic biological controls rarely suppress pests uniformly to extremely low densities; therefore, when damage tolerance is low, for example if there is a requirement for blemish-free fruit or insect-free bulk products, this kind of control is insufficient, though integrated or inundative methods may prove satisfactory. The characteristics of the pest enter this problem also (see the distinction between direct and indirect pests, below).

Pests

Pest species, like the species they attack, have relatively restricted lists of natural enemies. Some of these are highly specific, others are moderately so and still others attack a wide range of species. Lists of natural enemies of the same pest may be very different in separate areas because of environmental differences, or because geographic barriers have prevented the spread of some natural enemies. The latter case points to a very important distinction in biological control, that between *introduced* and *native* pests. Many of the successes of biological control have been achieved by bringing in missing enemies to control a pest species introduced into a country without its natural controlling agents. Practitioners of biological control have tended to be pessimistic about controlling native pests by biological means, on the ground that the best-adapted natural enemies should already exist in the native habitat. This seems too simplistic a view. First, it ignores the possibility of managing native enemies so as to bolster their concentrations at critical places and times. Second, it ignores the very real difficulty of deciding whether pests in one country are really the same as in another—time after time earlier judgments have been fallacious, as in the case of the corn earworm, *Heliothis zea* (Boddie). Third, it ignores the fact that 'native' and 'foreign' are relative terms, and that even relatively small intra-continental distances may be serious obstacles for some kinds of natural enemies. Fourth, it is hard to understand why, if introduced pests can be destructive to native crops and trees, introduced parasites, predators and diseases may not be equally destructive to native pests (19).

The distribution in space and time of pests, and particularly their pattern of build-up in relation to that of biological control agents and in relation to the incidence of damage, are factors of crucial importance. The spread of natural enemies is easier in continuous dense host populations than in discontinuous or sparse ones; continuity and density must be judged in terms of the area of search and range of dispersal of the enemies concerned, attributes which may be very different for different enemies. Host populations that build up rapidly or hosts that readily establish new colonies at a distance from the parent population are apt to escape from natural control agents unless the latter can build up even more quickly, or can search out distant colonies efficiently. Artificial reinforcement may of course supplement natural capacities in these directions. The degree of control required to prevent effective damage, the stage of the life cycle at which damage is done, and the relationship of the damage cycle to the pest, control agent and seasonal cycle are extremely significant. Turnbull and Chant (24) have emphasized the first of these factors. They distinguish between *direct pests*, 'relatively small populations of which by directly attacking produce immediately destroy a significant part of its value'; and *indirect pests*, which 'attack produce and cause economically significant damage only by intensive or extended infestations'. They point out that relatively high populations of indirect pests can be tolerated, whereas direct pests must be controlled almost to the point of extinction. They conclude that indirect pests are much more suitable subjects for biological control than are direct ones. Although it is easy to think of qualifications and exceptions to this generalization, which may not apply at all, for instance, to inundative techniques, Canadian experience in general supports it.

Agents

The biotic agents used to control insect pests comprise predators, parasites, pathogens, and sterilized or otherwise modified individuals of the same species. Also, phytophagous insects may be used to control weeds. *Predators* tend to be voracious and mobile, and to concentrate in response to increases in host density. These positive characteristics tend to be offset by non-specificity and by inefficiency at low host densities. *Parasites* tend to be specific, as to both host and ecological niche, though these characters vary with the group. Many have the capacity for rapid build-up in numbers and many are relatively easily propagated and handled. Some are hard to establish; their taxonomy is difficult; there are often unfavourable interactions between species. *Pathogens* propagate rapidly and are often highly lethal. Many can be handled relatively easily in the laboratory, and many can be dispersed in the field by mechanical methods, like those used for pesticides. Many are highly specific. Some are persistent over long periods. On the negative side, micro-organisms and viruses need special techniques for study and propagation. Their identification is difficult and their effectiveness often unpredictable. Their specificity is sometimes unreliable and their possible effects on man are sometimes in doubt, or at least give rise to public anxiety. *Genetically altered individuals* can be very effective in depressing reproduction of pests, temporarily and perhaps over long periods. They are expensive to produce, and their management is not yet free from pitfalls.

Among *predators* some of the more important groups are vertebrates, insects, spiders and mites. Vertebrate predators are useful because of their intelligence, mobility and high food intake, and sometimes their close ecological association with particular pests. They have a good functional response to high densities of pests, and they may be relatively easy to encourage by management techniques. Their non-specificity and adaptability make them less effective at low densities. In Canada, birds and small mammals are the most important vertebrate predators of insects in terrestrial environments. Many groups of insects are predatory on arthropod pests. These include a number of families of beetles (*e.g.* Carabidae and many Staphylinidae); flies—both adults (*e.g.* Asilidae) and larvae (*e.g.* Syriphidae, Chamaemyiidae); Hymenoptera (*e.g.* many wasps and ants); Neuroptera (*e.g. Chrysopa* spp.); Heteroptera of many families; and a number of other orders. Many of the insect predators are rather general in their host or habitat preference; others are highly specific. Spiders are almost exclusively predatory, though the economic potential of different species and groups varies widely. Many species and groups of mites are predators; some are of considerable practical importance in control.

There have been a number of attempts to use predators in control of Canadian pests. Results have been varied. In general, predators have received less attention in biological control and supporting research than have parasites. There may be room for intensification of work in this direction in Canada, especially in certain crop situations.

The parasites useful in biological control can be divided into *parasitoids*, which characteristically kill the host, and *parasites in the restricted sense*, which usually do not kill the host, though they may reduce its vigour and fecundity. In general, parasitoids have been more widely used and are more effective than are true parasites, though the latter have had some value. The most important parasitoids are certain Diptera, especially Tachinidae, certain Hymenoptera, especially Ichneumonoidea, Braconoidea and Chalcidoidea, and certain Nematoda.

Among pathogens, bacteria, fungi, protozoa and viruses have all shown promise in particular situations. The bacterium *Bacillus thuringiensis* Berliner has been used in the control of a variety of caterpillar pests, and is being commercially produced in the U.S.A. Its effects appear to be due largely to the toxin that accompanies the spore, and it seems to have shown little tendency to multiply and spread under field conditions. It can only marginally be classed as a biological control agent, and its use is primarily inundative. Viruses have in general been the most promising group of pathogens. The high infectivity, pathogenicity and specificity of many viruses make them effective control agents and they are relatively easy to store and apply. A virus is considered to be the chief factor in the persistent automatic control of the spruce sawfly, *Diprion hercyniae* (Hartig) (Chapter 39, p. 136). Viruses show promise for local inoculative or inundative control of the cabbage looper, *Trichoplusia ni* (Hübner) (Chapter 26, p. 59) and of certain pine sawflies (Chapters 41 and 42, pp. 148 and 150).

Inundation with sterile males has had conspicuous success in regional eradication of a few pest species in the U.S.A., where the method has been energetically developed. The possible use of sterile males to control codling moth is under investigation in British Columbia (Chapter 4, p. 12). The method shows promise, but there have been production difficulties, and economic evaluation is not yet possible. Mathematical models suggest that there are critical factors of density and timing and that paradoxical results may be obtained at high densities of males.[1]

A wide variety of phytophagous species is available for weed control. Among the main problems are specificity (it is important to avoid infestation of useful plants), ease of establishment, and capacity to spread and to reach a desirable equilibrium with the weed. Successes against several weed species have been reported.

Environments

Environments depend partly on the nature of the resource and on the regime of managing it. These factors have been discussed on p. 221. They depend also on physical and general biotic aspects of the environment. These may be important to successful biological control. Biological control agents may have highly specific environmental requirements. Soils, climate, general vegetation pattern and biotic interactions may all be important. A single species may vary strongly in genetic make-up and environmental response from one part of its range to another. To search for potential agents in environments that resemble those in which control is being tried seems to be a good rule. Yet species have been established repeatedly in substantially different environments; so the rule is not infallible.

Biotic gradients also appear to exist. Continental species have become established in islands much more often than island species on continents. Species from Europe and temperate Asia have colonized North America more frequently than American temperate species have invaded the Old World. Such gradients, too, are purely statistical, and there are conspicuous exceptions.

Another aspect of the environment is the extreme specificity of some species in their habitat requirements. Tachinid parasitoids, for example, seem to require particular configurations of topography and plant forms to serve as mating stations. These differ for different species.[2] Knowledge of such requirements is needed for efficient establishment procedures.

Sources

In general the most promising source areas for biological control agents are, first, the presumed source areas of introduced pests, and second, regions climatically and biotically like the infested area, but where there are substantial numbers of different species. On both grounds the cooler parts of Europe and temperate Asia form the primary area of search for control agents to be used in Canada. Faunistically, too, Eurasia appears to be a dominant area, with a high proportion of hardy, aggressive species and a considerable number that have successfully adapted to habitats disturbed by man. Within this area, Central Europe has been rather frequently explored for natural enemies, Scandinavia somewhat less so, and Japan sporadically. The U.S.S.R. has been explored to some degree, but few parasites have been exported; China has been explored hardly at all. Since Japan has one of the richest faunas of parasitic Hymenoptera known,[3] and since the fauna of Central Asia and Siberia is phenomenally rich in cold-adapted species, inattention to these areas is a serious omission. Search in China appears to be ruled out at present, but obstacles to work in the U.S.S.R. would probably not be insuperable. Work in Japan would be relatively easy. Several temperate areas fringing the Central Asian heartland are also readily accessible. These include Turkey, with many mountain ranges, Iran, with the rich Elburz Mountains, Afghanistan, with high though largely dry mountains, and the Himalayan areas of Pakistan and India, with strong temperate elements in their biota. The C.I.B.C. already has permanent stations near the last two areas.

[1] Conway, G. R. Imperial College, Field Station, Sunninghill, Ascot, Berks, U.K. Personal communication.

[2] Wood, D. M. Entomology Research Institute, Canada Department of Agriculture, Ottawa, Ontario. Personal communication.

[3] Mason, W. R. M. Entomology Research Institute, Canada Department of Agriculture, Ottawa, Ontario. Personal communication.

In second place are the temperate and high-mountain areas of Central and South America, and particularly Mexico, where the presence has been shown of a rich biota related to, but with many different species from, our own boreal and cordilleran biotas. Sawflies, bark-beetles, cone-borers and other species related to our own have been found, but no serious attempt has been made to introduce parasites to Canada.

Interactions

Possible interactions between different natural enemies have been considered by a number of authors, from both theoretical and practical standpoints (10, 11, 24, 26). Synergistic effects are possible, as when a parasite helps to spread a virus (Chapters 42, 43, pp. 150, 162), but attention has focused on interference. The principle is that when two natural enemies attack the same prey, either both may fail to reproduce or the species with less destructive potential may be a more successful competitor. If the average lowering of destructive potential by competition exceeds the additional destructive potential generated by the presence of the less destructive species, then it would have been better to have had the more destructive species alone.

The theoretical argument is complex. It depends on incidence and degree of overlap of attack, on remote as well as proximate population effects, on spatial and temporal distribution, and on the capacity of the organisms to evolve adaptively. Practical experience suggests that, while interference is a possibility, it may have been overestimated as a danger (11). Multiple introductions do not usually seem to have led to bad effects in the past, and it is usually impossible to wait until every significant characteristic of the various potential agents has been measured and compared. However, in the broader sense Turnbull and Chant (24) are very wise in recommending that each introduction be studied carefully before and after it is made, and that the lessons be applied in future work. It is only by such rational study that a wide enough spectrum of manageable agents will be developed to permit reasonably flexible and effective control.

Reliability

Beirne (4) among others points out that biological control, depending as it does on complex organisms strongly influenced by changes in the environment, will not always have the degree of predictability found in simple physical or chemical systems. This is especially true of controls which depend on complicated interactions and balances, where disturbance of any element may upset the whole. Nonetheless there are many examples of control systems that have proved highly reliable over extended periods of time. For example, the European spruce sawfly, with its two-component control system, has not been a serious problem since 1942 (Chapter 39, p. 136). The greater variability of biological systems may well be offset in some cases by greater adaptability and homeostatic properties.

Side-effects

The dangers of unwanted side-effects were mentioned on p. 220. They are reiterated briefly here. Although one of the advantages of many biological control agents is specificity, this specificity is often only relative, and its degree is not always well known. Many parasitoids, for example, have a moderately wide host range, extending across several families or even to different orders of insect hosts. Diseases, too, may be more or less specific. The possibility of mutation or modification, even in highly specific forms, must be considered. The two main classes of dangers are, first, that attack will be transferred from pest species to beneficial species, and, in the case of diseases, perhaps even to man; and, second, that too massive loading with parasites, predators and pathogens may exert harmful pressures on the ecosystem. Though biological agents are more selective than chemical and physical ones, the possibility of biological pollution must not be discounted.

METHODS

Inoculation

This is the classical procedure of biological control. The idea is to introduce an exotic control agent at one or more selected points in the area where control is desired in such a way that it will establish itself, spread, multiply and effect control. The method has been tried with many variants and many degrees of success. The characteristics of individual situations are very different, but certain generalizations seem possible. Selection of a suitable strain for establishment and care in making the inoculation are important. The organism must be in good condition, be at the right life stage and be released in a suitable micro-environment. There is no substitute for careful observation and thorough understanding of the organism in determining these factors. Genetic studies show theoretical promise in improving performance in colonization (1, 20), but there have not been extensive practical applications as yet. Many species undergo a phase of severe adverse selection during a few generations after establishment (see Chapter 28, p. 67). If this is passed successfully, then the species may multiply rapidly. Size and distribution of the releases are important. Mortality, dispersion and density-fecundity relationships are significant factors. Larger introductions have in general more chance of succeeding than have smaller ones, but of course they are more costly. Slowly-spreading agents and hosts with dispersed ranges are indicators for multiple inoculations. Harris (Chapter 28, p. 67) emphasizes the need for understanding the causes of mortality if establishment is to be successful. Often important sources of mortality can be avoided in the critical early stage if they are identified.

These and similar considerations underline the importance of selecting the right people to carry out introductions. They should be individuals with a demonstrated ability to perceive and cope with the many biological and environmental variables that determine success or failure. Talent and experience are required, and an effective inoculation programme will not be developed without them.

Regulation

It is the hope in most biological control attempts that persistent automatic regulation will be achieved. This hope has been realized in a certain number of cases, sometimes by using single agents, sometimes by using a combination. The European spruce sawfly and the larch sawfly, *Pristiphora erichsonii* (Hartig), are among a number of Canadian examples of pests that have been so controlled. The latter is interesting in that after a period of successful control the pest developed resistance to its main parasite, and this resistance was overcome in one area by introduction of a new strain of the same species of parasite (Chapter 46, p. 194).

Regulation is not always as successful as this: it may depress pest levels but not to the point of eliminating damage, or it may be uneven, permitting occasional or local outbreaks of damage. Reinforcement by various means can often convert such partial successes into fully successful, though not fully automatic, controls. With accurate knowledge it may be possible to reinforce populations of control agents at critical times or to make timely inoculations at the sites of potential outbreaks. Or the answer may lie in an integrated programme using chemical or other non-biological means.

Local regulation over limited periods of time is a less ambitious goal, requiring repeated inoculations, but capitalizing on the ability of biological agents to multiply and to seek out their pest hosts. It is suitable for use in single-season crops over a long growing season, for protection of a multiple-season crop on a periodic rotation cycle, and to combat long-cycle outbreaks of rather scattered occurrence. Early inoculation and rapid build-up are important factors in this type of regulation.

Inundation

Inundation is the massive release of biological control agents, with emphasis on their immediate lethal or antifecundity effects rather than on their capacity to multiply and perpetuate themselves, at least beyond the limits of one growing season. It is used in the sterile-male technique, and it is no doubt adaptable to other strategies directed against the mating system. It is also used for biological control agents that are easily distributed and have high lethality and specificity, but low multiplication potential or persistence. *Bacillus thuringiensis* and many viruses, also *Trichogramma* and other small parasitoids, fall into this category.

Since saturation is possible and there is no need for a persistent residual population, inundation methods can be used for eradication. The first success of the sterile-male technique used this approach. However inundation is also a component of the integrated-control repertoire, and can replace pesticides under certain conditions.

Standardization and large-scale production makes this a suitable field for industrial operation. *Trichogramma* and *Bacillus thuringiensis* are both being produced and applied commercially at the present time.

Management of environment

This comprises a potentially important class of auxiliary methods, which has not always received the attention it merits. Van den Bosch and Telford (25) discuss under this heading artificial structures, supplementary food for natural enemies, alternative hosts, improvement of synchronization of pests and control agents, control of honey-dew-feeding ants, and modification of adverse agricultural practices. To these could be added the use of aggregation methods and various other behaviour-oriented techniques. Pioneer work on supplementary food for parasites was done at Belleville, but it is only beginning to be followed up. The Nova Scotia integrated control programme has made use of reservoir areas to maintain stocks of biological control agents to attack orchard pests.

Handling of agents

At least four elements are important in this connection: to have pure materials, *i.e.*, accurately identified, hyperparasite- and disease-free stock; to have materials in adequate quantity at the right time; to have materials in suitable condition, both as to general quality and specific life stage at the time of release; and to release materials under circumstances where they have a good chance of surviving and propagating.

Pure materials might seem an obvious requirement. Indeed quarantine and screening procedures are standard practice at most laboratories. However, clean cultures seem hard to maintain, and the standards at several parasite rearing facilities appear to the author to leave something to be desired, except for potentially dangerous quarantined materials, which usually are kept under rather rigid control. I have seen loose parasites and hosts, mixed cultures and open connecting doors at a number of insectaries. Similar standards would certainly not be tolerated in a bacteriological laboratory and they must lower the reliability of material used in control efforts. These comments are not directed at any particular institution in or outside Canada; they seem to reflect a general lack of emphasis in the parasite-rearing community.

The importance of facilities for mass propagation is very high. Mass propagation is needed not only for inundation techniques; it also permits multiple releases according to plan instead of accidents of availability of material, and it permits inoculative releases to be made on a sufficient scale. It also provides an adequate base for selection and improvement of stocks and for related genetic and biological research.

Improvement of agents

This has been tried in a limited way, by selection for climatic adaptation in California, for host preference in the C.I.B.C. and California, and for more specific characters such as sex ratio and DDT-resistance at Belleville. The work has been exploratory and the full power of modern scientific breeding techniques has certainly not been applied. Facultative parthenogenesis and polyembryony may make some hymenopterous parasites particularly suitable subjects for genetic work. Breeding for particular desirable characteristics is an approach that seems worth an energetic try.

Genetic control

Massive distribution of sterile males is an extreme example of control by disturbance of population fitness, of which other forms are also possible, in theory at least. There are three possible approaches: eradication, by complete destruction of fitness—this is the objective of the sterile-male techniques; regulation of pest populations at lower average densities by changing the population genotype; and improving the self-regulating characteristics of populations so that outbreaks do not occur, even though normal density levels may not change much. Both inoculative and inundative methods can theoretically be used, but considerable research to understand the basic genetic structure of selected pest populations would be a prerequisite.

Compound methods

No attempt will be made to elaborate these. Some have been mentioned elsewhere in this report. Two basic principles are repeated: first, biological control is not an end in itself—it should be used in competition and in the most suitable combination with other methods; second, a planned and integrated control programme can be more economical, more effective and less harmful then either a massive single-method programme or an unplanned mixture of methods.

POTENTIAL OF BIOLOGICAL CONTROL

Although a general assessment of the potential of biological control is needed as a guide for policy, actual forecasting is a highly specific undertaking for each problem. Organisms and circumstances vary widely; the number of case histories is limited; the reasons for success or failure are not always understood or agreed upon. Generalizations therefore tend to be diffuse and subjective. Biological control in some form is worth considering in every pest control problem. Whether it is practical will be determined by the species and environments concerned, by costs, by the availability of skills and materials, by acceptability to the proprietors and technologists concerned, and by evaluation of benefits, direct and indirect. The decision must be made individually for each problem, and must be re-examined from time to time. In the present chapter a brief general evaluation is given, followed by an assessment of Canadian experience. These will support the organizational recommendations made elsewhere in this section, and they will provide a very rough guide to some of the opportunities and pitfalls that should be considered in Canadian projects in the short-term future.

GENERAL

The main types of successful biological control to date have been: inoculation with agents which have spread to achieve automatic regulation; planned limitation of applications of chemical pesticides to encourage natural enemies in an integrated programme; and inundation with massive numbers of parasites, pathogens or sterile males in a restricted area. More elaborate integrated programmes show promise, as do techniques involving encouragement of biological control agents by providing food, shelter or other amenities.

REGULATION FOLLOWING INOCULATION

This is the classical approach to biological control. The great success against the cottony cushion scale, which first triggered popular interest in the use of natural enemies, set a pattern which was emulated in many subsequent control attempts. In some respects this may have been detrimental, partly because it generated cost-benefit expectations that were hard to realize, and partly because it diverted attention from more flexible limited-objective control methods that are practical in many situations where automatic regulation is not fully successful.

De Bach (5, table 12) lists a number of successful or partly successful biological control attempts, the majority of which are of this type. Certain features of this table are summarized here (Tables XLII to XLIV). De Bach (5, pp. 690–5) also calls attention to some general conclusions arising from these data.

TABLE XLII

Successful or partly successful biological control attempts classified by geographical region[1]

Region	Number of successful introductions	Rank in richness of species
Oceanic Islands	48	9
Nearctic	45	5
Australia	15	6
Tropical America	14	1
New Zealand	10	7
Palaearctic	8	4
Tropical Asia	7	2
Africa	6	3

[1] Source: DeBach (5, Table 12).

TABLE XLIII

Successful or partly successful biological control attempts classified by taxonomic grouping of pest species[1]

Group	Number of species successfully controlled	Rank in richness of species
Homoptera	42	6
Lepidoptera	21	4
Coleoptera	18	1
Diptera	7	3
Orthoptera	5	7
Hymenoptera	3	2
Dermaptera	1	8
Heteroptera	1	5

[1] Source: DeBach (5, Table 12).

TABLE XLIV

Successful or partly successful biological control attempts classified by crop type and climate[1]

	Crop type				
Climate	Forest and shade trees	Orchards and plantations	Ornamentals	Field crops	Household pests
Tropical	3	27	4	20	0
Subtropical	2	14	0	1	1
Temperate	17	13	2	12	1

[1] Source: DeBach (5, Table 12).

It is no surprise that the data are dominated by the very different scales of biological control work in different areas. The relatively large number of successes in the Nearctic region (Table XLII), for instance, reflects an intensive and continued programme especially in California. Similarly, half the successes in oceanic islands were in Hawaii, where there has been a vigorous interest in biological control. De Bach's conclusion that 'over a period of time, the number of successes attained will be proportional to the amount of research and importation work carried out' may be stated too simply, but there is no question that in experience up to the present there has been a general correlation. On the broad scale, success has rewarded effort.

Of course, such a statement represents a purely technological judgment. De Bach's book (6) devotes only five pages out of over 800 to economic evaluation. This limited material suggests a massive dollar return for expenditures on biological control in the State of California. The estimated savings ascribed to biological control of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), in the year 1958 alone exceeded the cumulative budget for all work on biological control of all pests in the State for the years 1923 to 1959. Such estimates are open to criticism, first through not being certified as having been subjected to professional economic analysis, and second through having been prepared by persons with a strong professional commitment to the biological control programme. Nonetheless the cost-benefit ratio for California appears so highly favourable that it seems unlikely that the most sophisticated analysis would upset it. No comparison is given with costs and benefits of other control approaches, and particularly with those of chemical controls. Such comparison is of course necessary at the level of directly alternative controls for a true economic evaluation, though the external considerations weighing against chemical control might at present justify the use of biological methods even at substantial added cost.

De Bach's data give strong evidence of at least a qualitative proportionality between the scale of biological control efforts and the number of successes obtained. A quantitative proportionality has not been shown; indeed, such a trend would almost certainly be obscured by other variables in the small number of examples. In principle, one might expect the law of diminishing returns to operate: as better control is achieved, diminishing marginal gains would be obtained for comparable marginal expenditures. The relatively small proportion of pests yet controlled and of natural enemies yet in use suggest that the point of significantly diminishing returns has probably not been closely approached. It should be noted, too, that the law of diminishing returns is considerably softened in management of biosystems, because these systems can change so radically. First, additional species or changed environments are likely to alter the basic characteristics of the system; second, the organisms themselves may adapt so as to alter the system without change in the physical environment or the species composition, as in the development of DDT-resistance. In open-ended systems of this kind the need to adapt management systems may prove to be open-ended too.

We can accept, then, that many of the apparent geographical and ecological regularities in the distribution of successful biological control attempts reflect only the distribution of total effort. However, a core of apparently significant observations remains. In discussing these, de Bach notes 11 theses that have been proposed at one time or another. These have varying degrees of validity, but most have at least some conspicuous exceptions. These 11 theses, with de Bach's evaluations, are as follows:

(i) *Biological control works better on islands.*
This is doubtful. There have been more successes on continents and over much larger average areas.

(ii) *Parasites are better than predators* (*or* vice versa).
Parasites have produced control about four times as often as predators, but predators have provided outstandingly successful control in some cases.

(iii) *Monophagous enemies are better than polyphagous enemies* (*or* vice versa).
Monophagous or oligophagous species are usually best, but there have been exceptions.

(iv) *Many species of enemies attacking a single host are better than one.*
Probably untrue: usually control has been ascribed to a single enemy.

(v) *Egg parasites acting alone are ineffective.*
Untrue: there are cases of successful control by egg parasites.

(vi) *Complete biological control following introduction will occur rapidly* (*within three years or three generations*) *if at all.*
There are exceptions, as with *Gonipterus* in South Africa.

(vii) *Biological control is most likely to be successful on trees or long-lived perennials.*
Biological control has been obtained in all kinds of plant environments.

(viii) *Sedentary hosts, especially Coccidae, are more amenable to biological control than other types.*
Statistically true, but the reasons bear examination (see below).

(ix) *The natural enemy should come from the same host in the country of origin.*
Doubtful: there have been striking successes with natural enemies from other hosts.

(x) *Natural enemies should be imported from countries ecologically analogous to the area of introduction.*
Doubtful: there have been striking successes with natural enemies from ecologically different areas.

(xi) *Immigrant pests offer the best opportunities for biological control.*
Doubtful: native pests have been controlled by imported enemies.

De Bach concludes that, after the effects of intensity of effort have been allowed for, the following additional factors have to be considered:

(i) About 40 per cent. of the species controlled have been coccids, with Lepidoptera and Coleoptera next in order (Table XLIII). The disproportion is increased if the relative richness of the groups in species is considered. De Bach notes that coccids are easily transported, and therefore among the most common of accidentally introduced pests, that they have often occurred on expensive crops and have defined easy chemical control, that early successes have given an historical impetus to biological control work on scales, especially citrus, and that the biological attributes of scales may give them above-average susceptibility to control by natural enemies.

(ii) Most instances of control have been ascribed to one dominant natural enemy (the European spruce sawfly is an exception).

(iii) Parasites have produced control about four times as often as predators.

(iv) Successes have been numerous in temperate as well as tropical and subtropical areas (Table XLIV).

The most significant and best-founded conclusions are that temperate continental areas provide a suitable theatre for biological control, and that successes in biological control are more numerous where efforts are more intensive. These conclusions are in accord with Canadian experience. Almost all other points are subject to too many uncertainties or exceptions to make them a reliable guide to action.

PLANNED LIMITATION OF APPLICATIONS OF PESTICIDES IN AN INTEGRATED CONTROL PROGRAMME

Some of the most striking work in this field has been done in Canadian fruit orchards, especially in Nova Scotia (18). The details are well known, and will not be discussed here. There have been a number of successful examples in California and elsewhere. As Turnbull and Chant (24) emphasize, the damage tolerance in the crop or resource to be protected is a critical factor, though not the only one. It seems likely that in a large majority of pest control programmes for high value crops too much pesticide is being applied. The amount can be reduced safely given certain conditions: that suitable natural enemies exist in the area or can be introduced to maintain a reasonable degree of control; that means are available to supplement this automatic control at critical times by suppressing threatened outbreaks; and that planning, monitoring and extension systems are able to permit timely action in meeting such threats.

Integrated control is under intensive study in California and internationally. It is referred to elsewhere in this volume and is not discussed further here.

INUNDATION METHODS

The relative importance of inundation methods has increased in the last 10 years, partly because the range of agents has been widened, partly because of improved production systems, and partly because of successful application of the principles of population dynamics.

The three kinds of agents that have been used have been small, rapidly multiplying parasites, such as *Trichogramma* spp.; micro-organisms, such as polyhedral viruses and *Bacillus thuringiensis*; and sterile males of the pest species. The first two are used as biological pesticides, the last as a biological sterilant. The use of parasites is relatively old, but recent studies (12) and technological and commercial developments may improve the efficiency of their use considerably. Micro-organisms, too, have been used for many years, but the success and commercial production of *Bacillus thuringiensis* and the discovery of new viruses and progress in culturing and application technology have made this an active and promising field. The main problems at present seem to be costs—which can probably be reduced by large-scale standardized production methods—and difficulties of certification. It is not yet certain how serious the latter will be.

The use of sterile males has been well publicized. Other, related methods based on the population dynamics of fecundity and on altering the genetic structure of pest populations are likely to extend the potential of this method very considerably. Projects on the interaction between fecundity and population dynamics were begun at Belleville in 1968.

The main use of parasite and micro-organism inundation has been in replacement of pesticides in periodic control programmes by selective and non-toxic alternatives. The main use of sterile males has been in attempts at regional eradication. It is most likely that genetic alteration of populations would be directed at regulation rather than at eradication or temporary control, but inundation methods might be important in launching genetic alteration programmes.

PROVISION OF AMENITIES

Research suggests increasingly that the performance of control agents can often be improved significantly if critical amenities are supplied at the right time and in suitable places. Supplies of natural or distributed food may improve attack rates and fecundity of parasites or fecundity of predators (see Chapters 45 and 46, pp. 175 and 194). The action may be a general one, improving the condition of the organism, or a specific one, providing a prerequisite for oviposition. Shelters and reservoir habitats may be essential for concentrating and ensuring survival of adequate numbers of control agents. Specific kinds of mating sites may be needed for establishment and perpetuation of some species, and may have to be identified and located if they are scarce, or supplied if they are absent.

This general aspect of management of natural enemies needs intimate knowledge of the biological characteristics of each species. One species of green lacewing is attracted to yeast suspensions which provide food essential for oviposition; a second species can use the suspensions in the same way but is not attracted to them; a third is not attracted to the suspension and does not need them.[1] The importance of providing amenities is beginning to be appreciated, but knowledge and practical application are in their infancy.

THE CANADIAN EXPERIENCE

To 1958

Canadian biological control experience to the end of 1958 is summarized in two important digests (15, 24). The assessments made in those publications are summarized in Tables XLV to XLVII. Attempts were made to control 24 agricultural insect pests, with partial or full success in 10 cases, 25 forest insect pests, with partial or full success in 9 cases, and two weed species, with success not assessed by 1962. All the attempts were by inoculation, and success was judged complete if automatic regulation at sub-economic levels was obtained. Some work on integrated control of orchard pests was done during this period, especially on orchard pests in Nova Scotia, but it was not reported in either of the reviews considered.

The most conspicuous successes in the agricultural category were against woolly apple aphid *Eriosoma lanigerum* (Hausmann), apple mealybug, *Phenacoccus aceris* (Signoret), and oystershell

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[1] Hagen, K. S. Department of Biological Control, University of California, Albany, California. Personal communication.

TABLE XLV

Attempted biological control of agricultural arthropod pests up to 1959[1]

Pest	Degree of success[2]	Establishment[3]	Remarks
Bruchus pisorum L. Pea weevil	F	O	
Carpocapsa pomonella (L.) Codling moth (C)[4]	F	X	
Cephus cinctus Nort. Wheat stem sawfly	F	O	
Ceutorhynchus assimilis (Payk.) Cabbage seedpod weevil	P?	X	
Coccus hesperidum (L.) Soft scale	F	O	
Eriosoma lanigerum (Hausmann) Woolly apple aphid	S	X	
Forficula auricularia L. European earwig (C)	(S)[5] P	X	
Grapholitha molesta (Busck) Oriental fruit moth	P	X	
Heliothrips haemorrhoidalis (Bouché) Greenhouse thrips		?	Not assessed
Hylemya spp. Root maggots (C)	F	X	
Hypera postica Gyll. Alfalfa weevil (C)		?	Not assessed, but see Table I, p. 2
Laspeyresia nigricana (Steph.) Pea moth	P	X	
Lepidosaphes ulmi (L.) Oystershell scale (C)	(S) P	X	
Melanoplus spp. Grasshoppers	F	O	
Myzus persicae (Sulzer) Green peach aphid	S	G	
Ostrinia nubilalis (Hbn.) European corn borer	P (F)	X	
Panonychus ulmi (Koch) European red mite (C)	F	X	
Phenacoccus aceris (Sign.) Apple mealybug	S	X	
Phytomyza ilicis (Curt.) Holly leaf miner	(S) P (F)		Success on ornamentals; failure in orchards
Planococcus citri (Risso) Citrus mealybug	S	G	
Pseudococcus comstocki (Kuw.) Comstock mealybug		?	Not assessed
Pseudococcus maritimus (Ehrh.) Grape mealybug	F	G	
Psila rosae (F.) Carrot rust fly	F	X	
Trialeurodes vaporariorum (Westwood) Greenhouse whitefly (C)	S	G	

[1] Sources: McLeod, McGugan and Coppel (15) and Turnbull and Chant (24). All attempts were by inoculation.

[2] Degree of success:
S Success
P Partial success
F Failure.

[3] Establishment:
X Established
O No evidence of establishment
G Greenhouse pest, with local inoculation.

[4] (C) indicates that attempts were continued after 1959.

[5] Evaluations in parentheses are those of Turnbull and Chant (24) where these differ from those based on McLeod, McGugan and Coppel (26).

TABLE XLVI

Attempted biological control of weeds up to 1959[1]

Weed	Status of attempt
Hypericum perforatum L. St. John's wort, and *Linaria vulgaris* Mill. Yellow toadflax	Promising herbivores introduced; not yet assessed by 1961; project was continued

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[1] Source: McLeod, McGugan and Coppel (15).

TABLE XLVII

Attempted biological control of forest insect pests up to 1959[1]

Pest	Degree of success[2]	Establishment[3]	Remarks
Adelges piceae (Ratz.) Balsam woolly aphid (C)[4]	P	X	
Carulaspis visci (Schrank) Juniper scale	F	O	
Choristoneura fumiferana (Clemens) Spruce budworm (C)	F	X	
Coleophora laricella (Hübner) Larch casebearer (C)	(S)[5] P	X	
Dendroctonus piceaperda Hopk. Eastern spruce beetle	F	O	
Diprion frutetorum (F.) Nursery pine sawfly	F	X	
Diprion hercyniae (Hartig) European spruce sawfly (C)	S	X	
Diprion similis (Hartig) Introduced pine sawfly	S	X	
Evagora starki Free. Lodgepole needle miner	X	?	
Exotelia pinifoliella (Chamb.) Pine needle miner			Not a serious attempt
Hemichroa crocea (Fourc.) Striped alder sawfly	S	X	
Lambdina fiscellaria (Guen.) Eastern hemlock looper	F	O	
Lambdina somniaria Hulst Oak looper	F	O	
Laspeyresia youngana Kearf. Spruce seed moth	F	?	
Lecanium tiliae L. Lecanium scale	F	?	
Malacosoma disstria Hübner Forest tent caterpillar (C)	F	O	
Neodiprion sertifer (Geoff.) European pine sawfly	P	X	
Nygmia phaeorrhoea (Donov.) Brown-tail moth	S? (F)	X	
Operophtera brumata (L.) Winter moth (C)			Not assessed, but see Table XXXI, p. 169
Pineus strobi (Hartig) Pine bark aphid			Not a serious attempt
Pissodes strobi (Peck) White pine weevil			Not a serious attempt
Pristiphora erichsonii (Hartig) Larch sawfly (C)	(S) P	X	
Pristiphora geniculata (Hartig) Mountain-ash sawfly			Not a serious attempt

TABLE XLVII (continued)

Pest	Degree of success[2]	Establishment[3]	Remarks
Rhyacionia buoliana (Schiff.) European pine shoot moth (C)	F	X	
Stilpnotia salicis (L.) Satin moth (C)	(S)	X	

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[1] Sources: McLeod, McGugan and Coppel (15) and Turnbull and Chant (24). All attempts were by inoculation.

[2] Degree of success:

S Success
P Partial success
F Failure.

[3] Establishment:

X Established
O No evidence of establishment
G Greenhouse pest, with local inoculation.

[4] (C) indicates that attempts were continued after 1959.

[5] Evaluations in parentheses are those of Turnbull and Chant (24) where these differ from those based on McLeod, McGugan and Coppel (26).

scale, *Lepidosaphes ulmi* (L.), in orchards; and against green peach aphid, *Myzus persicae* (Sulzer), citrus mealybug, *Pseudococcus citrae* (Risso), and greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), in greenhouses. All are Homoptera and all are indirect pests. In the forest category the most conspicuous successes were against satin moth, *Stilpnotia salicis* (L.), brown-tail moth, *Nygmia phaeorrhoea* (Donovan) (somewhat doubtful), larch casebearer, *Coleophora laricella* (Hübner), European spruce sawfly and larch sawfly. These are Lepidoptera (three species) and sawflies (two species); all are external defoliators, and all are indirect pests.

The majority of successful control agents were parasitic Hymenoptera, but the list included tachinid flies, predatory mites and a virus. The last achieved the most spectacular success, the virtually complete control of the European spruce sawfly. A virus was also considered to show promise against the European pine sawfly, *Neodiprion sertifer* (Geoff.), but subsequent work suggests that the main use of this will be in inundation. It is uncertain whether the predominant position of hymenopterous parasites should be ascribed to greater biological effectiveness, or to the larger number of introductions. In agricultural programmes 65 out of 86 species and 54·3 million out of 54·8 million individuals released were Hymenoptera. In forest programmes 74 out of 104 species released were Hymenoptera, but the establishment rate was higher for Diptera (8 out of 20 species, *versus* 25 out of 74 species of Hymenoptera).

Turnbull and Chant (24) have discussed some general implications of this work. Their main conclusions were that direct pests were unsuitable targets for biological control by automatic regulation, that careful study would make better selection and more effective introduction of natural enemies possible, and that introduction of a single, carefully selected, natural enemy was likely to give better results than introduction of a number of species, which by interfering with one another might give less effective control. The detailed argument that Turnbull and Chant devoted to the last point has tended to overshadow their wise strictures on the many factors to be considered in undertaking introductions in a rational way. They emphasize that, whereas there are no certain criteria for preselection of effective natural enemies, intelligent consideration and good knowledge of biology will greatly improve chances of success. They emphasize a point echoed in the present report, that where possible the same person should be involved in foreign exploration and domestic introduction programmes related to a particular pest. At the very least there should be close and direct liaison between the two. Turnbull and Chant's conclusions were undoubtedly a healthy criticism of the massive but often somewhat mechanical programme of releases in the years they reviewed. With this programme as a background they may well have overemphasized selectivity and caution. In particular, they may have attached too much weight to interference of co-existing parasites as a practical danger. Such authors as Huffaker and Kennett (11) point out that too cautious an approach may lead to paralysis of action and avoidable economic loss. However, the California programmes have characteristically been accompanied by careful theoretical analysis, close study of the biology of host and agent and detailed tactical planning and monitoring. They have therefore been relatively free of some of the faults to which Turnbull and Chant were reacting.

To summarize, Canadian experience up to 1958 was characterized by massive introduction capacity, vigorous though often unselective efforts to establish automatic regulative control, and by a number of successes, some dramatic, and probably sufficient in the aggregate to outweigh by far the costs of the programme.

1959 to 1968

Tables XLVIII to L summarize the work done in the period 1959–68 and dealt with in the present volume. Several changes have taken place since 1958. The rôle of the Belleville Institute was changed from that of an active control agency with national responsibility to a responsive introduction, quarantine and liaison agency with an overshadowing mission in 'basic applied' research. The great success of chemical pesticides considerably lessened the demand for biological control in high-value agricultural crops. Belleville's rôle is again in process of change, but up to the present more in the direction of particulate, limited-objective, mission-oriented research projects than in the direction of integrated research or operational programmes. The present functions of Belleville are therefore for the most part not those of an Operational and Advisory Centre as here conceived. During the same period the rôle of the Sault Ste. Marie Institute remained relatively unchanged.

Inoculative programmes were continued, but on a somewhat reduced scale. In *agriculture* the rate of success in such programmes declined. Programmes were continued against four pests that had been worked on previously. In three instances there was no success. Technological success with the greenhouse whitefly was unchanged but there was a decline in use of biological control, because of improved alternatives. Attempts were made against 10 additional pests, with eight failures or inconclusive cases, one partial success and one full success, against the pistol casebearer, but this success was considered to be an unforeseen by-product of a successful programme against a forest pest, the larch casebearer. In *forestry* the record was better: among seven pests for which pre-1959 programmes were continued there was partial or complete success against five. This included control of the larch casebearer in the east, and partial control with a good outlook for improvement in the west, probably re-establishment of control of the larch sawfly, and an important success against the winter moth, *Operophtera brumata* (L.). New programmes against two species of pine sawflies showed success or possible partial success.

New methods or emphases are conspicuous in the programme and show a somewhat brighter picture than the continuation of old work. There are several examples in *agriculture* of successful fostering of natural enemies in a programme in which minimal and selective pesticide applications are featured. Inundation with microbial materials—*Bacillus thuringiensis*, viruses and others—has been technologically successful in a variety of situations in both *agriculture* and *forestry*. Costs and certification are problems in most of these cases. A determined effort is being made to use sterilized males in the control of codling moth in British Columbia. Fostering of natural enemies by suitable management techniques has been tried in one or two instances, but is probably not being used to its full potential.

The relative success in forestry programmes in this period almost certainly reflects greater interest, partly at least because of the relatively high cost-benefit ratio of chemical pesticide application for most forest uses. As a result, forestry programmes have been directed to active control attempts against major pests, whereas most biological control efforts in agriculture during this period have been against marginal pests or on a pilot scale. The relatively passive rôle assigned to Belleville appears to have weakened the operational effectiveness of the biological control effort as a whole, but it has not

TABLE XLVIII

Attempted biological control of agricultural arthropod pests, 1959–68[1]

Pest (and agent)	Degree of success[2]	Establishment[3]	Remarks
By inoculation; (a) continuation of pre-1959 programme			
Coleophora malivorella Riley Pistol casebearer[4]	S	X	
Forficula auricularia L. European earwig (Newfoundland)	F	X	
Panonychus ulmi (Koch) European red mite (Ontario)	F	O	
Sitona cylindricollis Fåhr. Sweetclover weevil	F	X	
Spilonota ocellana (D. & S.) Eye-spotted bud moth	P	X	
Trialeurodes vaporariorum (Westwood) Greenhouse whitefly		G	Decline in use since 1958
(b) new programmes			
Acyrthosiphon pisum (Harris) Pea aphid	F	O	
Argyrotaenia velutinana (Walker) Red-banded leaf roller	F	O	
Psylla pyricola Förster Pear psylla	F	X	
Rhagoletis pomonella (Walsh) Apple maggot			Preliminary studies only
Swammerdamia lutarea (Haworth) A hawthorn defoliator	F	O	
Tetranychus urticae (Koch) Two-spotted spider mite		G	Shows promise
Thymelicus lineola (Ochs.) Introduced skipper			Preliminary studies only
Tipula paludosa Meigen European crane fly	F	O	
By inundation; new programmes			
Agriotes obscurus (L.) An elaterid wireworm (fungus)	F		
Alsophila pometaria (Harris) Fall cankerworm (Bt)[5]	T		
Carpocapsa pomonella (L.) Codling moth (sterile males)	D		
Euxoa messoria (Harris) Dark-sided cutworm (virus)	T		
Heliothis zea (Boddie) Corn earworm (polyhedrosis; Bt)	D		
Malacosoma americanum (Fabricius) Eastern tent caterpillar (*Clostridium*; Bt)	T		
Panonychus ulmi (Koch) European red mite (virus; Bt)	D		
Pieris rapae (L.) Imported cabbageworm (granulosis; Bt; DD–136)	D		
Pseudexentera mali (Freeman) Pale apple leafroller (fungi; DD–136)	D		
Spilonota ocellana (D. & S.) Eye-spotted bud moth (Bt)	T		

TABLE XLVIII (continued)

Attempted biological contol of agricultural arthropod pests, 1959-68[1]

Pest (and agent)	Degree of success[2]	Establishment[3]	Remarks
Thymelicus lineola (Ochs.) Introduced skipper (Bt)	T		
Tipula paludosa (Meig.) European crane fly (virus)	D?		
Trichoplusia ni (Hübner) Cabbage looper (polyhedrosis; Bt)	T		Success with Bt uncertain
By natural enemies in integrated control programmes;			
(a) continuation of pre-1959 programmes			
Hylemya brassicae (Bouché) Cabbage maggot (Newfoundland)	P?		
Lecanium tiliae L. Lecanium scale	S		A secondary pest in DDT-treated orchards
Lepidosaphes ulmi (L.) Oystershell scale	S		Effective when wide-spectrum insecticides avoided
Panonychus ulmi (Koch) European red mite (Nova Scotia)	S		Predators are effective under integrated control
(b) new programme			
Psylla mali (Schmidberger) Apple sucker (Nova Scotia)	S		Avoidance of captan fungicide permits natural control by fungi
By management of natural enemies;			
(a) continuation of pre-1959 programme			
Carpocapsa pomonella (L.) Codling moth (Nova Scotia)	P?		Woodpeckers and other predators
(b) new programme			
Rhopalosiphum maidis (Fitch) Corn leaf aphid	P?		Shows some promise

[1] Source: Part I of this *Review*; evaluations are based on E.G.M.'s interpretation of individual chapters.

[2] Degree or kind of success:

S Success — E Economic success
P Partial success — T Technological success
F Failure — D With potential for development.

[3] Establishment:

X Established
O No evidence of establishment
G Greenhouse pest, with local inoculation.

[4] Results are attributed to *Chrysocharis laricinellae* (Ratz.), a parasite introduced against a forest pest, *Coleophora laricella* (Hübner), the larch casebearer.

[5] Bt *Bacillus thuringiensis* Berliner.

TABLE XLIX

Attempted biological control of weeds, 1959–68[1]

Weed	Degree of success[2]	Establishment[3]	Remarks
By inoculation;			
(a) continuation of pre-1959 programmes			
Hypericum perforatum L. St. John's wort	S	X	

TABLE XLIX (continued)

Weed	Degree of success[2]	Establishment[3]	Remarks
Linaria vulgaris Mill. and *L. dalmatica* (L.) Yellow and broad-leafed toadflax		X	Not yet evaluated
(b) new programmes			
Carduus acanthoides L. and *C. nutans* L. Welted and nodding thistle		X[4]	Not yet evaluated
Cirsium arvense (L.) Scop. Canada thistle		X	Not yet evaluated
Euphorbia esula L. and *E. cyparissias* L. Leafy and cypress spurge	F	X[4]	
Senecio jacobaea L. Tansy ragwort	P?	X	Outlook promising

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[1] Source: Part II of this *Review*; evaluations are based on E.G.M.'s interpretation of individual chapters.

[2] Degree of success:
S Success
P Partial success
F Failure.

[3] Establishment:
X Established
O No evidence of establishment.

[4] Required confirmation up to 1968.

TABLE L

Attempted biological control of forest insect pests, 1959–68[1]

Pest (and agent)	Degree of success[2]	Establishment[3]	Remarks
By inoculation: (a) continuation of pre-1959 programmes			
Adelges piceae (Ratz.) Balsam woolly aphid	P?	X	
Coleophora laricella (Hübner) Larch casebearer (E)	S	X	
Coleophora laricella (Hübner) Larch casebearer (W)	P	X	Outlook favourable
Diprion hercyniae (Hartig) European spruce sawfly	S	X	Earlier control maintained
Operophtera brumata (L.) Winter moth	S	X	Control achieved since 1959
Pristiphora erichsonii (Hartig) Larch sawfly	P	X	Earlier control regressed through development of host resistance; new introductions show promise
Rhyacionia buoliana (Schiff.) European pine shoot moth	F	X	Management may improve control
Stilpnotia salicis (L.) Satin moth	P	X	Control may be slowly regressing
(b) New programmes			
Neodiprion lecontei (Fitch) Red-headed pine sawfly	S	X	Repeated local inoculations probably needed
Neodiprion swainei Midd. Swaine jack pine sawfly	P?	X	

TABLE L continued

Pest (and agent)	Degree of success[2]	Establishment[3]	Remarks
By inundation;			
(a) continuation of pre-1959 programme			
Choristoneura fumiferana (Clemens) Spruce budworm (Bt)[4]	D? F		
Malacosoma disstria Hübner Forest tent caterpillar (polyhedrosis)	D		
Neodiprion sertifer (Geoff.) European pine sawfly (nuclear polyhedrosis)	T		Economic success expected in certain areas
(b) new programmes			
Neodiprion lecontei (Fitch) Red-headed pine sawfly (Bt)	E? T		
Neodiprion swainei Midd. Swaine jack pine sawfly (polyhedrosis)	D		

[1] Source: Part III of this *Review*; evaluations are based on E.G.M.'s interpretation of individual chapters.

[2] Degree or kind of success:

S Success
P Partial success
F Failure
E Economic success
T Technological success
D With potential for development.

[3] Establishment:

X Established
O No evidence of establishment.

[4] Bt *Bacillus thuringiensis* Berliner.

completely blocked it. Where there have been strong local initiatives, successful or at least promising biological control programmes have been sustained. This is very creditable to the officers concerned, but the organizational and promotional responsibility placed on individuals has been far too high. The lack of an active source of initiatives, advice and support for biological control has weighed strongly against achievement of a balanced programme in the face of the dynamic and well-endowed supply and information organization that supports chemical control efforts.

There is in general, as in so many other fields, a gap in the development zone of the research and development spectrum. Good research with important potential applications is being done, but it is not feeding effectively enough into operational control programmes. The defect lies in awareness and interest on the operations side and in communication on the research side. Bridges have to be built. It is urged in this report that the need is for an effective and informed operational and advisory agency.

A conspicuous exception is found in the programme on biological control of weeds (Table XLIX). Although this has been a small-scale operation it has preserved an excellent balance and continuity of exploration, research, development and actual control attempts. Two programmes initiated before 1959 are still under way—that on St. John's Wort, *Hypericum perforatum* L., has been partly successful, and that on toadflax, *Linaria* spp., is still not evaluated. Of four new projects, one on tansy ragwort shows promise, one on spurge has so far failed, and two on thistles have not yet reached the stage of evaluation. The operational flow of this programme and its good liaison with field stations is to be commended, though of course these might be more difficult to maintain with a larger and less intimate working group.

STRATEGY OF BIOLOGICAL CONTROL

INTEGRATION INTO GENERAL PROGRAMMES

Biological control is not an end in itself. It is one of several approaches to controlling pests. The decision to use this or any other form of control is part of the general resource management process. In this process three kinds of question have to be answered. First: is pest control feasible and economic from the standpoint of the resource threatened? Second: do external considerations—costs, benefits, risks, possibilities of combining operations related to other resources—alter the balance determined by the directly threatened resource? Third: are feasibility and economic status altered by administrative and political considerations, and if so how does this affect planning?

Resource management has been very loosely organized in the past, but both pressures and techniques for closer integration are developing. It is likely that within a very few years programmes in agriculture and forestry will be compared not only among themselves, but against a wide range of alternatives over the whole resource spectrum. This has two implications. First, the economic and social values of programmes will have to be much more explicitly visualized and defined than has usually been done in the past, with external as well as internal values being taken into consideration. Second, the need for, and benefits from, long-term programmes will have to be clarified and vigorously supported. Economic analysis based on commercial investment at high interest and discount rates is almost inevitably loaded against long-term benefits such as automatic control of pests, indirect returns from basic research, and conservation of resources for future generations. Also, external benefits, such as prevention of pollution, or contribution to international technology, and diffuse benefits, such as those arising from education or from long-term or basic research, are less easily defined than direct cash and social returns within a particular industry or community. Unless there is better definition and defence of these elements they will be gravely prejudiced in at least the first attempts at integrated resource analysis.

Strategic consideration of biological control must begin, then, with identification of the technological strengths and weaknesses and the economic and social costs and benefits of biological control, in its various forms, as it fits into the general resource management picture. So far as possible these should be quantified, or at least ranked or estimated. On the positive side, automatic regulation, once established, may be cheaper than other forms of control; the target-seeking ability of organisms may make them effective where chemicals are not; the selectivity of certain natural enemies and their freedom from toxic materials may make them relatively safe for use in the specific and general environments. The capacity of organisms for self-regulation makes them useful in integrated, self-balancing management programmes. On the negative side, the complexity of biological materials may make them unpredictable and hard to manage; density-dependent characteristics may lower their effectiveness at low densities; special rearing and handling requirements may make them costly; delayed, indirect and preventive modes of action may lower the visibility of even highly effective control, thus interfering with its salability; and the complex nature of biological interactions makes a relatively costly and sophisticated research effort necessary, and increases the difficulty of developing concepts to a practically applicable stage.

Such considerations translated into specific terms may recommend or disqualify biological control for a particular problem. More typically they may simply relegate the decision to a technological level within the problem area. However, the merits of biological control ought to be considered explicitly at the strategic level first. Otherwise the judgment as to whether it should be used will be made on too narrow a ground; it will not take adequate account of externalities and it will perhaps be negative and over-defensive towards them. The machinery for this level of consultation has hardly been developed yet: it transcends existing departments, industries and sectors; but it is sure to develop with time, and planners for pest control must be prepared for it.

There is of course a danger, often a serious one, that planning structures intended to meet such needs may have a stultifying rather than a stimulating effect. Over-organization, factionalism, undue preoccupation with political, administrative or technological criteria to the exclusion of others, and inadequate communication among different operational and interest groups can lead to paralysis of planning, which is more harmful the greater the area of responsibility. Careful selection of planners and managers and frequent review of performance may go some way towards minimizing this danger. However, practical experience suggests that while general planning is important in setting frameworks and guidelines, there is no substitute for local and individual initiatives in solving operational problems. Successful resource planning will have to reconcile this dilemma by some system that preserves particulate operational responsibility while encouraging effective consultative planning.

SELECTION OF OBJECTIVES

The importance of technological, economic and social criteria in selection of objectives has already been emphasized. In good planning these criteria must be applied at every level of decision, so far as information permits. Using them, it is possible to make a rational selection of objectives in a given situation. This selection will ordinarily have three phases, though with some feedback and interaction. These are the selection of resources to be protected, of pests to be attacked and of types of control to be considered.

RESOURCES

The value of the resource to be protected, the cost of preventable damage by pests, the degree of satisfaction with existing control practices, and forecasts of future trends of all these factors, are among the elements that have to be considered. They are important in determining the priority of control efforts and the permissible level of expenditures. The pattern of damage is also important. Unpredictable damage and locally concentrated damage tend to be more disturbing than foreseen and widely dispersed damage of the same aggregate value. The structure of the industry, the patterns of operation, and the nature of the crop or resource itself are all important factors. Systems of financing and delivery may be just as significant as technology in developing practical control.

For biological control the possibility of achieving large savings by protection makes more sophisticated control and monitoring possible, but high cash values may impose a low damage tolerance and confer an economic advantage on high-kill methods. The latter, whether chemical or biological, carry with them the danger of built-in resistance. Perennial crops maintained over substantial areas offer the greatest possibilities for automatic regulative control. The maintenance cost of such control may be low or negligible, but to initiate it may require intensive and costly efforts.

These are only a few of the considerations that have been mentioned elsewhere in this chapter. Every problem has to be decided on its own merits. What is important is that the decisions should consider not only technological feasibility, but also the economic and social context of the resource.

PESTS

Selection of pests to be controlled by biological means involves at least three judgments: the need for control, the technological feasibility of biological control, and a comparison of biological with other means. The need for control is an economic judgment. Technological feasibility has been discussed in other chapters, where it was seen that although some general rules appeared to be useful, the specifics of particular cases were much more important in determining the possibilities of control.

TYPES OF CONTROL

Types of control can be selected to some degree at the strategic level. The influence of the nature of the crop was discussed above. Substantial areas under continuing commitment to a perennial crop provide a good environment for automatic regulation. More erratic cultivation patterns might require periodic inoculation or inundation. Inundative methods have been used in eradication and in rapid control or prevention of damage to valuable crops. Established patterns of chemical control or the requirement for very intensive or reliable control may indicate that integrated programmes are the best. Again the specifics of each situation are important and will influence the final decision.

INFORMATION GATHERING

At the strategic level this is primarily a question of setting up systems that will ensure effective information to guide programmes, both initially and as the programme continues.

Information is needed at the beginning of the programme to identify promising kinds and sources of natural enemies. Assembly of information will begin with search of literature and canvassing of information agencies. This will indicate the biology and probably the origin of the pest and may provide a list of enemies known to be effective in other countries. Commonly such lists will prove to be very incomplete.

Background research will almost certainly be required to provide adequate information on the full range of natural enemies and on the ecological factors that will determine successful control. Study of the pest and its enemies in foreign and domestic habitats will give insights into approaches to control that cannot be developed in any other way. Wherever possible, direct continuity of personnel from foreign search to domestic control operations is the best means of transferring detailed ecological information from source to point of application.

Monitoring at an adequate level of accuracy is essential to follow the progress of the work that is under way and to show the need for a changed approach if the initial one is not successful. To be useful, monitoring must be based on appropriate sampling procedures and must be statistically evaluated to determine the level of confidence at which it can be used.

Arrangements for surveys of information, for background research and for effective monitoring are, then, essential strategic requirements for intelligent selection of materials and methods.

THE RÔLE OF RESEARCH

Research has sometimes seemed to be the tail that wagged the dog in biological control work, yet the right kinds of research in sufficient quantity and depth are absolutely necessary if biological control is to be successful. Zeal for operational effectiveness must not lead to downgrading of the research function, or failure to develop adequate interchange between research and operational arms.

For biological control, research in several areas is very important. Among these are: identity, sources, host preferences and natural characteristics of potential biological control agents; basic biological characteristics of selected agents that will permit them to be used and managed most effectively; quantitative population dynamics as applied to principles and methods of biological control; principles and practice of integrated control; and economic and social aspects of biological control as a component of resource management. These different areas of research involve different disciplines and different discipline mixes. They will not all be done in the same way or probably at the same institution or kind of institution. However, it is very important that they all be effective in themselves and that they all have effective interfaces with the organization or organizations responsible for operational biological control. This organization must be of a professional standard such that it can absorb the latest advances from first-class research establishments and adapt them to a progressive and energetic control programme. It must have arrangements and incentives that will ensure effective flow and use of such information, and effective presentation of current and urgent problems to appropriate research groups. Quality, scale, direction, communication, and use of research are each important. Arrangements for ensuring them are discussed in the next chapter.

ORGANIZATIONAL PROBLEMS

The primary problem of biological control in Canada is organizational. The technological and practical promise of biological control is great, if suitable methods are used in integrated approaches to pest problems. Research and development are required, but the pre-emptive need is for effective and well-deployed operational capacity. This must be planned and directed so that it will make full use of existing and new technology. It must be supported by research into general principles and detailed biological data, by effective information links with Canadian research centres and foreign sources of data and technology, and by first-class facilities for identifying, collecting, propagating and handling varied biological control agents. It must have effective and flexible inputs into planning and conduct of control operations; it must be able both to respond to the needs expressed by control programmes and to call attention to problems and approaches that might otherwise be overlooked.

These functions can best be served by a single, central, operationally oriented organization. This should constitute a centre for information, advice and technological expertise on biological control. It should procure, propagate and distribute biological control materials, when necessary co-ordinating, supporting or conducting field operations. It should participate in central and regional planning, both routinely and in response to special requests. It should provide planning and operational specialists for temporary support of particular regional operations. It should co-ordinate, collate, support and in part perform research related to biological control.

Two points are of particular importance. First, the proposed organization should be a component of the general pest control structure. It must be integrated at the planning level with the general programme and responsive at the operational level to regional needs. An insulated discipline-oriented group will not be adequate. Information, extension and liaison will be primary concerns in an effective organization. Second, the selection of personnel for different functions will be of critical importance. Not only should the management be dynamic and have a record of success in biological control operations, but also many of the specialized functions require rare or highly specific personal qualities. Only a few people, for example, have the talents and experience for real success in detecting, propagating and especially establishing parasites and predators. Quite another type of person may be required to organize and co-ordinate programmes, another yet for successful liaison, and still another to perform, direct or interpret research. Individual performance in the complex and specialized tasks of biological control will spell the difference between success and failure.

The need for and characteristics of a biological control organization, here called an Operational and Advisory Centre for Biological Control, are discussed in greater detail in the following subsections.

BIOLOGICAL CONTROL IN THE CONTROL PROGRAMME

There is no magical significance in biological control. It is emphasized throughout this chapter that biological control is only one of the classes of methods that must be considered in any rational control programme. For a particular operation it may be used alone, it may be integrated with other methods, or it may be rejected. It is important, first, that this choice be based on an informed and unbiased evaluation of the facts; second, that if integration is necessary it should be rationally planned; and third, that organizationally it should be possible to mobilize adequate technology if the use of biological control is indicated.

It is doubtful that these conditions have generally existed in Canada in recent years. There have been difficulties at the decision level, at the planning level, and at the level of mobilizing technology. These do not reflect any sinister tendency, nor do they imply stupidity or incompetence on anyone's part. They result from defects of organization of overall systems that are correctable once recognized.

Difficulties at the decision level arise from two sources: the relatively strong inputs related to chemical control as compared to other types of control, and the relatively unsophisticated level of some components of evaluation procedure.

At the input stage, information on chemical insecticides and on methods and problems of applying them is readily available from a variety of governmental, educational and commercial sources. The grower and economic entomologist are accustomed to chemical methods and are equipped to use them. They are under active and competitive persuasion from sales representatives to use chemical products and application machinery. This is not discreditable. It is a tribute to a well-organized, active and self-supporting industry. However, equally vigorous and effective organization for non-chemical control is needed if balanced decisions are to be made. There must be both practical, well-digested information and the capacity to back it up with effective action. Otherwise chemical control will continue to be the necessary choice in most circumstances, whatever the broader economic and social costs.

At the evaluation stage, there have been a number of weaknesses in the past. These are now widely recognized in principle, but methods are only beginning to be developed to correct them in practice. The most characteristic faults are: poor definition of the problem; rigidity or unselectivity of response; preoccupation with immediate or short-term damage and remedies; preoccupation with technology rather than economics; and failure to give adequate consideration to externalities, *e.g.* pollution and development of resistance. These affect the whole pest control programme, and indeed range far beyond it. They will be discussed here very briefly and only as they relate to the biological control component.

Poor definition of problems results partly from the difficulty of diagnosis. It is impossible to have a network of specialists sufficient to detect every incipient outbreak. The onus rests largely on the farmer and the forester, and secondarily on agronomists or entomologists with very general training and responsibilities. On the one hand important outbreaks may be detected only when it is too late to prevent damage; on the other hand the presence of a few pests may cause needless alarm. In general, this aspect of the problem has been better dealt with for forest pests than for agricultural ones, partly because of the existence of a relatively sophisticated Forest Insect Survey with the function of monitoring the general and local abundance of harmful and beneficial species. Accurate evaluation of damage, both in terms of physical product and in terms of economic value, requires extensive sampling and difficult analysis. Development in this area is badly needed.

Many control operations, particularly in agriculture, are based on rough evaluation before and after the fact, and are carried out by non-specialists. This already predisposes to rigidity of response. Not unnaturally the operator tends towards prevention and suppression by visible, simple means, and towards massive response to any sign of trouble. The presence of the pesticide salesman and of prepared spray schedules and formulations influences the pattern of his operations. He may be well aware that more selective measures would save him money and perhaps work, as well as undesired side-effects, but this knowledge is useless to him unless definite, reliable programmes, instructions and facilities are available conveniently and at a cost he can afford.

It follows that selective, integrated, and economically and socially rationalized control operations are difficult or impossible for the individual operator or local authority to plan or initiate, though local initiative may be essential to adapting and implementing a well-designed general or regional plan. Planning itself, however, must be done at a level where: (a) general and longer-term as well as specific and short-term problems and remedies can be considered; (b) programmes in the same area can be made harmonious, and conflicts arising from lack of planning or communication can be minimized; (c) an adequate level of expertise can be brought in to develop good advice on each phase of the problem; (d) fully professional technical and economic analysis can be applied; and (e) externalities, such as preservation of the environment, can be brought into the discussion as well as the direct concerns of a particular industry.

Often, at least, this type of planning is best done at the regional level, by a cooperative effort on the part of some regional centre in conjunction with individual and local operators, proprietors and authorities. Planning and problem-solving at this level is the rationale for the present regional laboratories in the Agriculture and Forestry Departments. In a complex field such as biological control their planning function would be strengthened if they could draw at appropriate times on the services of top experts in the field. Such experts could well come from the proposed Operational and Advisory Centre, not only giving experienced and technologically sophisticated advice, but also giving first-hand insight into the problems and a sense of participation in planning, to the benefit of subsequent operational support by the Centre. Information on the kinds and level of available operational support would also be a direct input into the planning process under this arrangement.

Difficulties in mobilizing technology have arisen from lack of interest or facilities at various stages of the operational chain and lack of an operational group equipped to give full support to local or regional initiatives. At one time, under the old divisional organization, Belleville was administered as such an operational centre, though without the level of interdisciplinary expertise and the systems orientation that would be considered desirable today. In recent years Belleville has tended to diverge into a passive parasite-supply function on the one hand and to a research function on the other, neither intended for active, integrated participation in field programmes. Though this approach is now being modified, new interactions to date have been mainly at the single-project level, and Belleville has no mandate to intervene effectively in central or regional planning and programmes. As a result, successful field operations in biological control have generally depended on exceptional interest and drive on the part of a regional entomologist. Although the successes have been gratifying, a system that made regional success less dependent on such unusual levels of local initiative would be more reliable. An effective system would provide not only expert advice, but also operational reinforcement at critical times, and a prompt, flexible and dependable source of biotic agents well adapted to special requirements.

NEED FOR A BIOLOGICAL CONTROL CENTRE

It has already been stated that biological control should be considered as a component or alternative in every pest control programme, that biological control expertise should be brought in at every level of planning, that back-up teams of operational experts should be available to strengthen biological control projects at critical times, that research and information flow from source to application point should be strengthened and co-ordinated, and that strong facilities for the location, collection, characterization, screening, improvement, propagation and distribution of biological control agents are essential for a fully effective programme. It has been recommended that a large part of these functions be assigned to a single Operational and Advisory Centre for Biological Control. What are the pros and cons of this proposal?

The reasons favouring it are the following:

(i) Biological control as a whole and many of the individual functions require a high level of technological or research expertise. Persons with the required abilities will be scarce, and should be deployed economically.

(ii) The operations themselves are complex and interdependent. Large parts of them depend on integrated planning and on the smooth flow of complicated information and delicate and unstable living material. A unified organization can best meet these needs.

(iii) The need for biological control expertise at any particular site of operations will fluctuate, and will tend to have peaks at critical points in the decision or operation. It would be uneconomical to maintain regional teams capable of dealing with such peaks, but it would be more logical to dispatch teams from the Operational and Advisory Centre to reinforce the local team at critical times.

(iv) Efficient biological control depends on collation of research results of different kinds from many sources. For example, population dynamic models are important for planning and evaluating control, but it is essential that their development should interact with pragmatic control experience. A wide variety of specific taxonomic, biological and distributional information is needed to develop a good arsenal of biological control agents. Unless there is a central co-ordinating, evaluating and information-processing group, the results of research will remain unfocussed. With such a group it will be possible to make best use of existing information and to perform or to encourage or support the performance of research on important gaps in knowledge.

(v) Many biological control agents are of foreign origin, and all introductions are of continental as well as national significance. Liaison with international and foreign organizations, such as is now very effectively performed by Belleville, will therefore remain essential. This liaison has to be carried out in a unified way and at a level where technological as well as political considerations can be given due weight. The Operational and Advisory Centre would be a reasonable place for this liaison function, but the excellent existing arrangements should not be disrupted without the prospect of definite advantage from the change.

(vi) The introduction of foreign biological control agents requires quarantine, screening and propagation facilities which should continue to be centralized at least to a considerable degree, for uniformity of policy and economy of operation. A facility for large-scale propagation of selected organisms would make possible more flexible programmes for release and improvement of biological control agents, and could well be combined with the introduction and screening facility.

(vii) Chemical control information, though often simpler technologically, is propagated by an active and effective system of commercial and public information channels. It is important that comparable channels be developed for biological control information. The proposed Operational and Advisory Centre can be an important element in the development of an effective information distributing system.

(viii) The best means of transmitting information and know-how from one stage of a biological control operation to another is often by moving people. In particular it is valuable if those responsible for controlling an introduced pest have had an opportunity of studying it in its native environment abroad. An Operational and Advisory Centre could provide a convenient administrative focus for arranging suitable temporary assignments of personnel.

The arguments *against* concentrating responsibility in an Operational and Advisory Centre relate mainly to the potential vices of centralization. They are as follows:

(i) Whereas an efficient centre may greatly assist effective use of biological control, inefficiency in a centralized organization would be much more serious than local inefficiency in a decentralized one. The answer to this is good management and effective supervision of management. The biological control organization will not be effective unless pest control management as a whole is effective.

(ii) Concentration of biological control work may lead to over-specialization, partisan advocacy, isolation from other control approaches, and unresponsiveness to regional needs. The answers lie again partly in effective and operationally oriented management, but also in good terms of reference, effective procedures for participation in central and regional planning, responsibility and flexibility for responding to national or regional requirements, and in good quality and orientation of staff.

(iii) Empire-building and monopoly of resources may stultify research and operational development in other centres. This is a real danger, which again can be countered partly by good management, but also by good organizational and scientific arrangements, including: defined areas of responsibility for operations and in-house research; defined responsibilities and policies for coordination and encouragement of cognate research in other establishments; substantial separate funds earmarked for grants and contracts in support of at least partly defined fields of research in non-government laboratories; a secondary and responsive rôle in planning regional operations, counter-balanced by regular participation in central planning and policy-making; and frequent interchange of personnel with other establishments by secondment and transfer related to particular activities.

(iv) It may also be argued that establishment of a government centre with these wide responsibilities constitutes unwarranted competition with industrial interests and responsibilities, particularly in chemical control. However, there are several arguments against this view. First, there is no intention to compete with industry as such, but rather to present viable alternatives or complements to chemical control. Such alternatives are very much in the public interest at the present time. Second, the problems of biological control are much more dependent on the specific environments and faunistics of Canada than are those of chemical control, and demand indigenous research as well as complex technical supervision. It seems unlikely that any commercial organization would have the resources or be able to take the financial risks to get the required programmes off the ground. Once an effective control organization is developed, of course, it is likely that industry can play an increasing rôle in supplying materials and services in support of biological control, as it now does for chemical control. Such development should be encouraged.

NEED FOR RESEARCH SUPPORT

As there is a danger that giving priority to operational effectiveness might lead to downgrading of research support for biological control, a special section is devoted to this requirement. Biological control is inherently a complex procedure. Even where the methods themselves are comparatively simple, as in inundation with micro-organisms for short-term control, the basic dynamics of the populations must be understood, the characteristics of a variety of possible control agents must be known for the best selection to be made, and the possibilities must be considered of mutant or variable behaviour, of sensitive reaction to environmental conditions and of other complexities inherent in biological material. In more complex ecosystems and longer-term regulation, the problems are multiplied. Our knowledge of theory and of background information is far from adequate for the most efficient use of biological control. Five main areas of research must be considered: theoretical; inventory; taxonomic; behavioural and methodological; and genetic.

Theoretical research

This is concerned mainly with population interactions: relations of pests to their hosts, relations of natural enemies to pests, and the effects of numbers, densities and biological characteristics on damage, control, stability, persistence and other technological and economic measures. Quantitative understanding of such relationships provides a powerful tool for management and monitoring, and also for comparing the effects of biological control with those of other methods of pest management. The rise of applied mathematics and computer science have permitted rapid advance into realms of measurement, modelling and management that were only theoretical possibilities a few years ago.

So far work along these lines has followed two major channels. Theoretical model builders have tended to investigate more and more complex situations by modelling and computer simulation, whereas practical statisticians and resource managers have tended to develop fairly sophisticated sampling and measurement systems in concrete environments. Model builders are now tending increasingly to test their models against practical situations, but the main impetus for such development at the moment is coming from resource and environment management. Mathematical ecologists who received their training in pest management are being diverted increasingly into those fields.

It seems unlikely in present circumstances that the former high relative competence of government agencies in theoretical research can be completely restored. A level of in-house research should certainly be encouraged that will permit ready adaptation and application of the main results of modern quantitative ecology. However, it seems more practical to stimulate relevant sectors of fundamental research by a policy of substantial grants, contracts and cooperative programmes directed to appropriate existing university centres, to ensure that their programmes continue or expand in the desired directions. This should benefit both theoretical and practical sides by providing practical tests for models as well as theoretical models for practical situations.

Inventory research

This kind of research is urgently needed. Our knowledge of natural enemies of insect pests and their ranges and host specificities is extremely fragmentary. Of some 2,000 agricultural pest species in Canada, Graham (9) found information on any natural enemies for only about 500 (25 per cent.). The majority of natural enemies he listed are parasites, and the lists for most species are obviously far from complete. Predators and pathogens have had even less complete treatment. The predators listed are mostly arthropods. Vertebrate predators are almost ignored, and spiders and beetles among others are obviously under-represented. The search for foreign natural enemies has followed very restricted channels of taxonomy, geography and ecology. Altogether it seems likely that, simply through absence of information, only a very small segment of potential biological control agents are being utilized. No discredit is intended to past and present work by the Forest Insect and Disease Survey, the Commonwealth Institute of Biological Control and other agencies. The task is a very large one which deserves the application of continued and intensified effort.

Taxonomic research

Here this is taken to mean research on the identities and classification of natural enemies whose presence is known in a general way. To this must be added research on the identities and classification of pest organisms, which are often less well understood than has sometimes been supposed, as witness recent subdivision of the corn earworm and European corn borer complexes, among many others. Resolution of such host complexes or demonstration of unsuspected relationship patterns can shed completely new light on possibilities of parasite introduction.

The level of taxonomic understanding of natural enemies varies considerably, but is in general low. New parasitic Hymenoptera are being discovered in considerable numbers even in Great Britain, which has by far the best-known fauna of any part of the world. Most parasitic insect groups are very imperfectly known, especially at the species level. Among predators some groups are better known than others: carabid beetles are comparatively well known, and staphylinids comparatively poorly. Vertebrate predators are relatively well known taxonomically, though their relationships to insect prey are seldom well understood. In general, a large amount of work remains to be done on the taxonomy of insects, arachnids and pathogenic fungi and micro-organisms.

Behavioural and methodological research

These are potentially very large fields, as each natural enemy, once recognized, has complex behavioural and biological characteristics which affect its manageability, and these in turn interact with similar characteristics of crop, pest and environment. In practice it seems necessary to concentrate, first on forms that show particular facets to best advantage, and second, on species that show real promise as biological control agents. Within this context the array of problems is very wide, comprising many different properties that determine the effectiveness and specific action of organisms. These lead directly into developmental research on the specifics of establishing and managing control agents.

Such behavioural and methodological research tends to break into discrete problems, and for this reason it lends itself to dispersal. Nonetheless, a substantial body of it should be associated with the Operational and Advisory Centre, first because it can be directed and applied to problems of current priority or of strategic importance, second because it will tend to stimulate and update tactical planning, and third because the importation and propagation facility will provide the best source of material for many kinds of experiments. On the other hand, many projects of this kind may well be dispersed at regional operational centres, related to work on other non-biological control methods, or supported by grants or contracts at graduate schools.

Genetic research

This field has been seriously neglected in biological control work. Selection and improvement are considered a normal technique in managing crops and domestic animals. Extensive breeding programmes are even undertaken to develop resistance to insect pests. For some reason comparable efforts to improve biological control agents have been few and mostly primitive, though parasitic Hymenoptera in particular would provide easy genetic material. Genetic research would be important not only in improving the effectiveness of predators, parasites and pathogens; it might also contribute to refinement of the use of sterile males and related techniques. The importance of both host and parasite genetics is underlined by the experience with the spread of the encapsulating strain of the larch sawfly and the differential success of different strains of *Mesoleius tenthredinis* Morley in controlling it (Chapter 45, p. 175). It is hard to understand why, when so much genetic work has been based on insects, so little attempt has been made to apply our knowledge of individual and population genetics to economic problems. Work in this direction should be encouraged and efforts should be made to apply it in the biological control programme.

Relationship of biological control research to research on other non-chemical controls

This has not been considered specifically in the present report. There are obvious points of contact, but much depends on the operational framework in which the controls are to be applied. There is also a danger of dilution or under-support of biological control work if it is carried out as part of too varied a programme in one centre. These observations point out problems for consideration but should not be taken as expressing settled judgments.

NEED TO STRENGTHEN SEARCH AND SUPPLY NETWORK

The performance of Canadian and Commonwealth Institute of Biological Control personnel in searching for and supplying biological control agents has in general been extremely creditable.

Limitation of resources has imposed some difficulties, which will become severe if, as seems likely, there is an increased demand for biological control. The main points of constraint appear to be: limited resources for specific search and field study operations; absence of any serious general exploration for potential natural enemies; and absence of a serious propagating operation in Canada.

Constraint on specific search and field study can be relieved in two ways. First, somewhat larger funds can be devoted to this object, and larger sums specifically earmarked for particular operations. For a serious control operation a couple of weeks' search can hardly be considered adequate. Concentrated study of the biology and major enemies of the pest, followed by collection of the most promising enemies from a variety of suitable locations seems a more effective approach, and has proved its value in some actual cases. Such concentrated efforts can be facilitated by (a) earmarking sufficient supplementary funds, preferably in contract form, to ensure that C.I.B.C. can mount an effort on an adequate scale and (b) seconding Canadian personnel to work cooperatively with C.I.B.C., while ensuring that normally they would have sufficient discretionary funds to follow their independent judgment should this prove advisable. The second course has the strong advantage that the same person can carry direct field experience from the country of origin over to the subsequent control operation in Canada. However, personal, financial or logistical difficulties may prevent its adoption in certain cases.

General exploration for natural enemies appears to have been inadequate in the past. This point has already been touched on above (p. 224). A substantial element of this exploration is provided by primarily taxonomic and faunistic research. The assistance of the taxonomic community should be actively co-opted in exploration for natural enemies, but this in itself will not provide adequate results, because unsupplemented taxonomic surveys tend to diffuse their efforts into other objectives: they rarely go into sufficient biological depth, and special arrangements must be made to receive materials and avoid wastage of effort. The most effective plan would appear to be a systematic programme of exploratory surveys directed to particular host groups and emphasizing neglected taxonomic, ecological or geographical divisions. These surveys should be conducted by persons with a primary interest in biological control, though the latter could benefit greatly from association with taxonomists or ecologists, either Canadian or local, in the country being surveyed. Biological and taxonomic surveys of Canadian natural enemies are also badly needed, and a systematic programme in this area is desirable.

Finally, the facilities for receipt and handling of natural enemies in Canada (at Belleville and Sault Ste. Marie) are excellent, but they have not been fully utilized in recent years. In particular, propagation on the scale needed for substantial and well and flexibly distributed introductions has rarely been undertaken during this time; expert assistance in establishment and inoculation has not always been either readily available or enthusiastically sought; and in some cases material procured with great effort from abroad has been lost through lack of co-ordinated planning between establishments. More emphasis on the propagating function, more active participation in the release and establishment of biotic agents, and better co-ordination with field activities will improve this aspect of the programme.

NEED FOR EXTENSION, SERVICE, SUPPLY AND MONITORING ARRANGEMENTS

Biological control programmes or integrated control programmes involving biological control are complex and easily upset. Good communications, good logistics and good monitoring are necessary if they are to succeed. The cooperation of a large number of individual operators, growers, proprietors and officials is required, and it is essential that they be well disposed and well informed. They must not only be informed of the principles and merits of proposed programmes; they must have detailed information on what they should and should not do, and they need prompt, sensitive, active monitoring of the progress of infestations and controls.

The California experience has shown that there is no substitute for detailed, conscientious, tireless and imaginative extension, and an organization that is effective in bringing all levels of the community into contact in a cooperative approach to pest control. Responsiveness is the keynote of an effective control operation, but political responsiveness at the expense of technological downgrading is not adequate. The objective is to bring a high level of technology to the producer and manager in terms that he can understand and accept.

NEED TO INVOLVE INDUSTRY

One of the curious characteristics of pest control is that a large part of the operational phase is performed by what are ostensibly research organizations and is paid for out of research funds. The reasons lie partly in the structure of the renewable resource industries, and partly in the complexity of biological interactions, which makes many control situations into research problems *sui generis*. The whole tenor of this chapter is that for biological control to be carried out effectively it must be, at least initially, the responsibility of an operating and advisory agency of the Federal Government. It seems completely impracticable at this stage for single producers, or for companies, associations or provinces to initiate and co-ordinate biological control at the level needed to make it effective. On the other hand, where biological and integrated control programmes are well established there will often be a need for substantial production and distribution of biological control agents. In part these may be required for repeated or widespread introductions in an inoculative programme, but much larger and steadier production will be needed to support inundative releases of parasites, predators or micro-organisms.

Production of these agents by industry might well be encouraged. Chemical companies with insecticide experience, makers and operators of application machinery, and firms specializing in biological materials, such as pharmaceutical houses and breweries, might well undertake the commercial production of biological control agents. One good way of encouraging industrial involvement is by letting of contracts for developmental research. In doing the research, the companies build up experience that can be used in commercial production should this prove economic.

Another promising area for commercial involvement is in the actual management on a contract basis of biological or integrated control for producers in a particular region. 'Supervised control operators' have already achieved some degree of success in California, applying approved methods under the advice and inspection of State-employed entomologists. With the increasing size of farm units and with improving knowledge of management methods, such enterprises are likely to become more important in future.

On the whole it seems desirable to put as much of the biological control programme as possible on a self-sustaining basis. Although progress in commercial involvement may be slow at first, a programme of development contracts, perhaps supplemented by other forms of assistance, would help to expedite it.

RELATIONSHIPS TO EXISTING ORGANIZATIONS

It is not intended here to recommend a detailed plan for restructuring existing organizations in the Federal Government or elsewhere. Such recommendations would be inappropriate in a publication of the present type. However, a few observations seem desirable, either to reiterate basic principles or to prevent certain unintended inferences from being drawn.

Federal Departments of Agriculture and of Fisheries and Forestry

The administrative relationships of these sectors have varied in the past and no doubt will continue to change from time to time. Cooperation of agricultural and forest entomologists has been a source of great strength in supply of biological control materials, in development of principles of control and in a number of aspects of research. Although pooling of resources presents certain administrative difficulties, it appears to be desirable in the interests of economy and operational effectiveness. Indeed, in the more basic fields of population theory and resource management, sharing of resources with other biological sectors such as fisheries and wildlife management might be advantageous.

Canada Department of Agriculture, Research Institute, Belleville

Though a number of individual research projects link directly with specific control operations, the Belleville Institute is in its terms of reference a research establishment, and its main organized operational function at present is importation. Even this is a passive responsibility, dependent on demand from operational agencies. The recommendations of the present report are for a much stronger operational centre, with broadened functions. However, these recommendations do not contemplate dismantling the research functions now carried by Belleville. On the contrary these should be strengthened, perhaps especially on the systems side, and be coupled with more active co-ordination and development of cognate research done elsewhere. The relationship of operational, research and international co-ordination functions is an administrative question with several possible solutions. It is deliberately excluded from the present report.

Canada Department of Fisheries and Forestry, Insect Pathology Research Institute, Sault Ste. Marie

This Institute has over a period of years maintained a research programme of a very high standard with strong emphasis on practical problems. This kind of programme should not be permitted to deteriorate for lack of support. The Institute will obviously be an important component of an effective and well-integrated biological control organization. For this to be achieved it will be necessary to develop easier input from the Institute to practical control programmes and more effective interchange with research and development activities in other establishments and departments. The key to accomplishing this appears to lie more at the level of departmental and interdepartmental organization than within the Institute itself.

Provinces

With so much emphasis on regional involvement, extension and information it seems obvious that effective biological control will require active cooperation with appropriate provincial organizations. Circumstances will obviously differ in different provinces. Ultimately, some provinces at least may be expected to assume a substantial share of the research and operational load.

Universities

Although Canadian universities are much less closely involved with practical economic entomology than are those of the U.S.A., and particularly the land-grant colleges, nonetheless, it has been emphasized at several places in this chapter and is repeated here that the universities can play an important part in biological control research. This rôle can be encouraged, expanded and to some extent guided in directions of current practical interest, by judicious support through grants, contracts and fellowships. University participation has particular promise in at least three situations:

(a) where there is a centre of excellence, *e.g.* in population dynamics, resource management, or pestology, that can give expert attention to strategic problems;

(b) where an agricultural or forestry faculty has a special interest or competence in regional problems; and

(c) where the work lends itself to subdivision into unit projects of a size suitable for thesis problems, as is the case with many problems of the biology and host relationships of particular predators, parasites and diseases.

Such programmes can effectively increase the amount and scope of research related to departmental responsibilities, without adding to the already large total of in-house government research.

International and foreign agencies

The importance of cooperation with agencies outside Canada has already been noted. These will include international agencies, among which Canada has had a particularly close association with the Commonwealth Institute of Biological Control, and national agencies, of which the association with the United States Department of Agriculture is the most intimate because of geographic proximity. The framework of international and national organizations is changing, and will continue to change from time to time. Canada's pattern of contribution and cooperation will change correspondingly. Geography, the nature of current problems, and the operational effectiveness of the various organizations will all influence the selection. A pragmatic approach would appear best. Those organizations which appear best able to serve Canadian needs or implement Canadian policies at any particular time should receive the most support.

Scale of support

Without detailed study the exact scale of resources needed to implement the recommendations of this report cannot be forecast with any accuracy. It seems likely that, for in-house activities, redistribution rather than reinforcement of existing staff may be the most important need, at least initially. In particular, grouping of persons of demonstrated executive or operational ability in the biological control field in such a way that their abilities will have the most effective possible application would seem to be a prime requisite. Some kinds of background research may well need to be strengthened; perhaps this would best be deferred until the operational needs are defined. However, genetic research, directed to both hosts and control agents, and exploration for and investigation of potential control agents appear to be areas that need added in-house capacity. Additional grant and contract funds to support specific outside activities, particularly in the universities, are probably essential. In particular it seems that this may be the best way of developing an adequate base of theory and an effective integration of theory and practice in the quantitative population dynamics of biological control, and in the evaluation and planning of biological control methods in terms of the economic and social objectives of integrated resource planning.

ACKNOWLEDGMENTS

I take great pleasure in acknowledging the advice and assistance of the many experts in biological control and related fields who were kind enough to spend some of their time with me while I was preparing this evaluation. Without their help it would have been impossible for me to complete the task assigned to me. It is hard to single out everyone who made a significant contribution, but at least the following should be mentioned: Dr. P. S. Corbet, Dr. J. S. Kelleher, Dr. T. Burnett, Dr. H. L. House, Dr. G. E. Bucher, Dr. P. Harris, Dr. A. P. Arthur, Dr. G. K. Bracken, Dr. C. C. Loan, Mr. M. G. Maw, Mr. L. G. Monteith, Dr. D. P. Peschken, Mr. B. C. Smith and Dr. H. G. Wylie, all of the Canada Department of Agriculture, Research Institute, Belleville; Mr. W. A. Reeks, and Mr. R. M. Prentice, Department of Fisheries and Forestry, Ottawa; Dr. B. B. Migicovsky, Dr. E. J. LeRoux, Dr. R. A. Ludwig, Dr. J. J. Cartier, Dr. H. Hurtig, Mr. D. G. Peterson, Dr. W. B. Mountain, Dr. W. R. M. Mason, Dr. D. M. Wood, Dr. A. Wilkes, Dr. G. P. Holland, all of Canada Department of Agriculture, Research Branch, Ottawa; Dr. G. M. Carman, Canada Department of Agriculture, Information Division, Ottawa; Dr. C. D. F. Miller, of the Canada Department of Agriculture, Research Station, Harrow, Ontario; Mr. G. T. McColm, Science Secretariat, Privy Council Office, Ottawa; Dr. B. M. McGugan, Treasury Board, Ottawa; Dr. J. W. MacBain Cameron, Dr. T. A. Angus, Dr. F. T. Bird, Dr. D. M. McLeod, Dr. R. Ishihara, Department of Fisheries and Forestry, Insect Pathology Research Institute, Sault Ste. Marie, Ontario; Mr. L. A. Smithers, Dr. G. W. Green, Mr. W. L. Sippell, Dr. C. R. Sullivan, Dr. G. T. Harvey, Dr. P. D. Syme, Dr. P. J. Griffiths, Dr. J. C. Sanders, Dr. A. H. Rose, Department of Fisheries and Forestry, Regional Laboratory, Sault Ste. Marie, Dr. W. J. Turnock, Dr. H. R. Wong, Mr. W. G. Ives, Dr. C. H. Buckner, Mr. J. A. Muldrew, Dr. R. J. Heron, Mr. L. D. Nairn among others at Department of Fisheries and Forestry, Regional Laboratory, Winnipeg, Manitoba [since disbanded], Dr. A. E. Hannah, Canada Department of Agriculture, Research Station, Winnipeg; Dean L. Shebeski, Prof. H. E. Welch, Prof. J. Ansel Anderson, University of Manitoba, Winnipeg; Prof. B. P. Beirne, Prof. A. L. Turnbull, Dr. J. Weiser, Prof. M. Mackauer, Mrs. T. Finlayson, Simon Fraser University, Burnaby, B.C.; Prof. C. S. Holling, Prof. G. G. E. Scudder, University of British Columbia, Vancouver; Dean E. Gorton Linsley, Prof. Ray F. Smith, Dr. J. E. Swift, Prof. Carl B. Huffaker, Prof. Paul D. Hurd, Jr., Prof.

D. D. Jensen; Prof. P. S. Messenger, Prof. W. W. Middlekauff, Prof. R. W. Stark, Prof. Robert van den Bosch, Dr. Howell V. Daly, Jr., Dr. D. L. Wood, Dr. W. W. Allen, Dr. L. A. Falcon, Prof. K. S. Hagen, Dr. J. A. Powell, Dr. L. E. Caltagirone, Prof. R. L. Doutt, Dr. C. E. Kennett, Dr. R. Garcia, Prof. E. I. Schlinger, all at the University of California, Berkeley; Dr. L. A. Andres, U.S.D.A., Albany; Prof. K. E. F. Watt, Dr. Gordon R. Conway[1], University of California, Davis; Prof. H. T. Reynolds, Dr. E. C. Bay, Mr. Harold Compere, Prof. I. M. Hall, Dr. B. R. Bartlett, Mr. Stan Warner, Prof. C. A. Fleschner, Dr. R. D. Goeden, Dr. D. Gonzalez, Dr. J. A. McMurtry, Dr. E. F. Legner, Prof. C. P. Clausen, University of California, Riverside; Mr. B. Puttler, Dr. Frank Parker, Dr. G. Thomas, Mr. J. D. Hoffman, Dr. K. D. Biever, Dr. N. Marston, Mr. D. Hostetter, Mr. R. K. Morrison and Mr. J. B. Brown, U.S. Department of Agriculture, Biological Control Investigations Laboratory, Columbia, Missouri; Dr. Reece I. Sailer, Dr. R. H. Foote, U.S. Department of Agriculture, Beltsville, Maryland; and Dr. C. W. Sabrosky, U.S. Department of Agriculture, Washington, D.C.; Dr. M. L. Prebble, Department of Fisheries and Forestry, Ottawa, Dr. J. R. Weir, Fisheries Research Board, Ottawa, and Dr. R. Glen, Scientific Secretary to the Commonwealth Secretary, London, England, though they were not consulted directly in the preparation of the present summary, strongly influenced my general thinking in this subject area, as did many of my former associates in the Science Secretariat and the Science Council of Canada. To all these, and to those whom I have not mentioned by name because of *lacunae* in my notes or my memory, I express my warmest thanks. It would be unfair, of course, to saddle my advisers with responsibility for the statements and opinions expressed here. Though I have benefited greatly from the advice I received, few people other than the compilers of this *Review* have read the final draft. The conclusions and recommendations are mine alone and would not necessarily be endorsed by those who have advised me.

[1] Now at Imperial College Field Station, Sunninghill, Ascot, Berks, U.K.

LITERATURE CITED

1. Baker, H. G. & Stebbins, G. L. (eds.) (1965). The genetics of colonizing species. Academic Press, New York and London.
2. Beirne, B. P. (1962). Integration of biological and chemical control: desirable attributes of biotic agents. *Bull. ent. Soc. Am.* 8: 189–91.
3. Beirne, B. P. (1967). Pest management. Leonard Hill, London.
4. Beirne, B. P. (1967). Biological control and its potential. *Wld Rev. Pest Control* 6: 7–19.
5. DeBach, P. (1964). Successes, trends, and future possibilities, pp. 673–713. *In* P. DeBach (ed.), Biological control of insect pests and weeds. Chapman & Hall, London.
6. DeBach, P. (ed.) (1964). Biological control of insect pests and weeds. Chapman & Hall, London.
7. FAO (1966). Proceedings of the FAO symposium on integrated pest control, Parts 1–3. Food & Agriculture Organization of the United Nations, Rome.
8. FAO (1968). Report of second session of FAO panel of experts on integrated pest control. Rome, 19–24 Sept., 1968. Meeting Report No. PL/1968/M/3. Food and Agriculture Organization of the United Nations, Rome.
9. Graham, A. R. (1965). A preliminary list of the natural enemies of Canadian agricultural pests. *Inf. Bull. Can. Dep. Agric., Belleville, Ontario* 4, 179 pp.
10. Griffiths, K. J. & Holling, C. S. (1969). A competition submodel for parasites and predators. *Can. Ent.* 101: 785–818.
11. Huffaker, C. B. & Kennett, C. E. (1969). Some aspects of assessing efficiency of natural enemies. *Can. Ent.* 101: 425–47.
12. Knipling, E. F. & McGuire, J. V. (1968). Population models to appraise the limitations and potentialities of *Trichogramma* in managing host insect populations. *Tech. Bull. U.S. Dep. Agric.* 1387, 44 pp.
13. Lloyd, D. C. (1960). The significance of the type of host plant crop in successful biological control of insect pests. *Nature, Lond.* 187: 430–1.
14. Ludwig, R. A. (1965). The role of chemicals in the biological control of soil-borne plant pathogens, pp. 471–7. *In* K. F. Baker and W. C. Snyder (eds.), Ecology of soil-borne plant pathogens, prelude to biological control. University of California press.
15. McLeod, J. H., McGugan, B. M. & Coppel, H. C. (1962). A review of the biological control attempts against insects and weeds in Canada. *Tech. Commun. Commonw. Inst. biol. Control* 2, 216 pp.
16. Pickett, A. D. (1949). The philosophy of orchard insect control. *79th Rep. ent. Soc. Ont.* 1949: 37–41.
17. Pickett, A. D. (1949). A critique on insect chemical control methods. *Can. Ent.* 81: 67–76.
18. Pickett, A. D. & MacPhee, A. W. (1965). Twenty years' experience with integrated control programs in Nova Scotia apple and pear orchards. *Proc. 12th Int. Congr. Ent., London:* 597.
19. Pimentel, D. (1963). Introducing parasites and predators to control native pests. *Can. Ent.* 95: 785–92.
20. Remington, C. L. (1968). The population genetics of insect introduction. *A. Rev. Ent.* 13: 415–26.

21. Smith, R. F. & Reynolds, H. T. (1968). Effects of manipulation of cotton agro-ecosystems on insect pest populations. Conference on the ecological aspects of international development, Airlie House, Warrenton, Virginia, 9–11 Dec., 1968. University of California, Berkeley. 36 pp. (duplicated).
22. Smith, R. F. & van den Bosch, R. (1967). Integrated control. pp. 295–340. *In* W. W. Kilgore & R. L. Doutt (eds.), Pest control. Academic Press, New York.
23. Stapley, J. H. & Gayner, F. C. H. (1969). World crop protection. Vol. 1, Pests and diseases. CRC Press, Cleveland, Ohio.
24. Turnbull, A. L. & Chant, D. A. (1961). The practice and theory of biological control of insects in Canada. *Can. J. Zool.* 39: 697–753.
25. van den Bosch, R. & Telford, A. D. (1964). Environmental modification and biological control, pp. 459–88. *In* P. DeBach (ed.), Biological control of insect pests and weeds. Chapman & Hall, London.
26. Watt, K. E. F. (1965). Community stability and the strategy of biological control. *Can. Ent.* 97: 887–95.

OTHER LITERATURE CONSULTED

Beirne, B. P. (1962). Trends in applied biological control of insects. *A. Rev. Ent.* 7: 387–400.

Clausen, C. P. (1956). Biological control of insect pests in the Continental United States. *Tech. Bull. U.S. Dep. Agric.* 1139, 151 pp.

Cramer, H. H. (1967). Plant protection and world crop production. *Pflanzenschütz-Nachrichten 'Bayer', Leverkusen* 20, 524 pp.

Embree, D. G. (1965). The population dynamics of the winter moth in Nova Scotia, 1954–1962. *Mem. ent. Soc. Can.* 46, 57 pp.

Embree, D. G. (1966). The role of introduced parasites in the control of the winter moth in Nova Scotia. *Can. Ent.* 98: 1159–67.

Flanders, S. E. (1955). The organization of biological control and its historical development. *Meded. LandbHoogesch. OpzoekStns Gent* 20: 257–70.

Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. ent. Soc. Can.* 45, 60 pp.

Kilgore, W. W. & Doutt, R. L. (eds.) (1967). Pest control. Academic Press, New York and London.

LeRoux, E. J. *et al.* (1963). Population dynamics of agricultural and forest insect pests. *Mem. ent. Soc. Can.* 32, 102 pp.

McGugan, B. M. (1960). Biological control of forest insects: the role of parasites and predators. *Proc. 5th Wld For. Congr., Seattle* 2: 935–40.

Morris, R. F. (ed.) (1963). The dynamics of epidemic spruce budworm populations. *Mem. ent. Soc. Can.* 31, 332 pp.

National Academy of Sciences (1969). Principles of plant and animal pest control. Vol. 2, Weed control. National Academy of Sciences, Washington, Publ. 1597, 471 pp.

National Academy of Sciences (1969). Principles of plant and animal pest control. Vol. 3, Insect-pest management and control. National Academy of Sciences, Washington, Publ. 1695, 508 pp.

Raizenne, H. (1952). Forest Lepidoptera of southern Ontario and their parasites. Can. Dep. Agric., Sci. Serv., Div. For. Biol., Ottawa.

Rothman, H. (1969). The changing pattern of economic entomology. *Sci. World* 13: 11–6.

Simmonds, F. J. (1948). Some difficulties in determining by means of field samples the true value of parasitic control. *Bull. ent. Res.* 39: 435–40.

Swift, J. E. (1969). Unexpected effects from substitute pest control methods. University of California, Berkeley. 16 pp. (duplicated).

APPENDIX
ADDRESSES OF CONTRIBUTORS

Alex, J., Department of Botany, University of Guelph, Guelph, Ontario.
Angus, T. A., Insect Pathology Research Institute, Department of Fisheries and Forestry, Box 490, Sault Ste. Marie, Ontario.
Arthur, A. P., Research Institute, Canada Department of Agriculture, Box 367, Belleville, Ontario.
Bird, F. T., Insect Pathology Research Institute, Department of Fisheries and Forestry, Box 490, Sault Ste. Marie, Ontario.
Bryant, D. G., Forest Research Laboratory, Department of Fisheries and Forestry, Box 304, St. John's, Newfoundland.
Bucher, G. E., Research Institute, Canada Department of Agriculture, Box 367, Belleville, Ontario.
Cameron, J. M., Insect Pathology Research Institute, Department of Fisheries and Forestry, Box 490, Sault Ste. Marie, Ontario.
Carder, A. C., (Retired) Research Station, Canada Department of Agriculture, Beaverlodge, Alberta.
Clarke, R. C., Forest Research Laboratory, Department of Fisheries and Forestry, Box 304, St. John's, Newfoundland.
Corbet, P. S., Research Institute, Canada Department of Agriculture, Box 367, Belleville, Ontario.
Downing, R. S., Research Station, Canada Department of Agriculture, Summerland, British Columbia.
Embree, D. G., Forest Research Laboratory, Department of Fisheries and Forestry, Box 4000, Fredericton, New Brunswick.
Forbes, R. S., Forest Research Laboratory, Department of Fisheries and Forestry, Box 4000, Fredericton, New Brunswick.
Greenbank, D. O., Forest Research Laboratory, Department of Fisheries and Forestry, Box 4000, Fredericton, New Brunswick.
Griffiths, K. J., Forest Research Laboratory, Department of Fisheries and Forestry, Box 490, Sault Ste. Marie, Ontario.
Harris, J. W. E., Forest Research Laboratory, Department of Fisheries and Forestry, 506 West Burnside Road, Victoria, British Columbia.
Harris, P., Research Institute, Canada Department of Agriculture, Box 367, Belleville, Ontario.
Hikichi, A., Ontario Department of Agriculture and Food, Simcoe, Ontario.
Jaques, R. P., Research Station, Canada Department of Agriculture, Box 370, Harrow, Ontario.
Kelleher, J. S., Research Institute, Canada Department of Agriculture, Box 367, Belleville, Ontario.
LeRoux, E. J., Research Branch, Canada Department of Agriculture, Ottawa, Ontario.
Loan, C. C., Research Institute, Canada Department of Agriculture, Box 367, Belleville, Ontario.
Lord, F. T., Research Station, Canada Department of Agriculture, Kentville, Nova Scotia.
Mackauer, M., Department of Biological Sciences, Simon Fraser University, Burnaby 2, British Columbia.
MacLellan, C. R., Research Station, Canada Department of Agriculture, Kentville, Nova Scotia.
MacPhee, A. W., Research Station, Canada Department of Agriculture, Kentville, Nova Scotia.
Martineau, R., Forest Research Laboratory, Department of Fisheries and Forestry, Box 3800, Ste. Foy, Quebec.
McClanahan, R. J., Research Station, Canada Department of Agriculture, Box 370, Harrow, Ontario.
McLeod, J. M., Forest Research Laboratory, Department of Fisheries and Forestry, Box 3800, Ste. Foy, Quebec.
McMullen, R. D., Research Station, Canada Department of Agriculture, Summerland, British Columbia.
Miller, C. A., Forest Research Laboratory, Department of Fisheries and Forestry, Box 4000, Fredericton, New Brunswick.
Monteith, L. G., Research Institute, Canada Department of Agriculture, Box 367, Belleville, Ontario.

Morris, R. F., Research Station, Canada Department of Agriculture, Box 7098, St. John's West, Newfoundland.

Muldrew, J. A., Forest Research Laboratory, Department of Fisheries and Forestry, 5320–122 Street, Edmonton, Alberta.

Munroe, E. G., Entomology Research Institute, Canada Department of Agriculture, Ottawa, Ontario.

Neary, M. E., Zoology Department, Nova Scotia Agricultural College, Truro, Nova Scotia.

Neilson, M. M., Forest Research Laboratory, Department of Fisheries and Forestry, Box 4000, Fredericton, New Brunswick.

Paradis, R. O., Research Station, Canada Department of Agriculture, Box 457, St. Jean, Quebec.

Parent, B., Research Station, Canada Department of Agriculture, Box 457, St. Jean, Quebec.

Peschken, D. P., Research Institute, Canada Department of Agriculture, Box 367, Belleville, Ontario.

Prentice, R. M., Program Coordination Branch, Department of Fisheries and Forestry, Ottawa, Ontario.

Proverbs, M. D., Research Station, Canada Department of Agriculture, Summerland, British Columbia.

Putman, W. L., (Retired) Research Station, Canada Department of Agriculture, Box 185, Vineland Station, Ontario.

Quednau, F. W., Forest Research Laboratory, Department of Fisheries and Forestry, Box 3800, Ste. Foy, Quebec.

Read, D. C., Research Station, Canada Department of Agriculture, Box 1210, Charlottetown, Prince Edward Island.

Reeks, W. A., Programme Coordination Branch, Department of Fisheries and Forestry, Ottawa, Ontario.

Rose, A. H., Forest Research Laboratory, Department of Fisheries and Forestry, Box 490, Sault Ste. Marie, Ontario.

Ross, D. A., Forest Research Laboratory, Department of Fisheries and Forestry, 506 West Burnside Road, Victoria, British Columbia.

Sanford, K. H., Research Station, Canada Department of Agriculture, Kentville, Nova Scotia.

Smirnoff, W. A., Forest Research Laboratory, Department of Fisheries and Forestry, Box 3800, Ste. Foy, Quebec.

Smith, B. C., Research Institute, Canada Department of Agriculture, Box 367, Belleville, Ontario.

Syme, P. D., Forest Research Laboratory, Department of Fisheries and Forestry, Box 490, Sault Ste. Marie, Ontario.

Thompson, L. S., Research Station, Canada Department of Agriculture, Box 1210, Charlottetown, Prince Edward Island.

Turnock, W. J., Science Secretariat, Privy Council Office, East Block Parliament Buildings, Ottawa, Canada.

Webb, F. E., Forest Research Laboratory, Department of Fisheries and Forestry, Box 4000, Fredericton, New Brunswick.

Welch, H. E., Department of Zoology, University of Manitoba, Winnipeg, Manitoba.

Wilde, W. H. A., Department of Zoology, University of Guelph, Guelph, Ontario.

Wilkinson, A. T. S., Research Station, Canada Department of Agriculture, 6660 N.W. Marine Drive, Vancouver 8, British Columbia.

Williamson, G. D., Research Institute, Canada Department of Agriculture, Box 367, Belleville, Ontario.

Zwölfer, H., European Station, Commonwealth Institute of Biological Control, Chemin des Grillons, 2800 Delémont, Switzerland.

INDEX TO SPECIES

The only vascular plants indexed are weeds; these are grouped separately. Other organisms indexed are pests, biotic agents, and other species likely to be of ecological significance in control programmes.
Where used in the text, common names of species are those listed in the *Bulletin of the Entomological Society of America* **11**: 287–320 (1965). A species mentioned in the text, whether by its common or scientific name, will (if indexed) be found only under the scientific name; entries are given for both generic and trivial names, but only the former entry contains a page number. Subspecific names are not included. The citation appears in bold type if the entry constitutes the main subject of a chapter, or a section of a chapter.

WEEDS