Forest Health Technology Enterprise Team

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Pathogens and Microbial Control of North American Forest Insect Pests

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Cover Photo

Walnut sphinx moth, Laothoe juglandis (J. E. Smith), killed by a fungus, Akanthomyces sp. (Photographed by G. J. Lenhard)

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Chapter 1

INTRODUCTION

Pathogens and Microbial Control of North American Forest Insect Pests

James R. Fuxa, Ramesh Ayyappath, Richard Goyer

Introduction

Systems of trees, insects, and entomopathogens are valuable for reasons ranging from the practical, such as resource protection, to the theoretical, such as ecological modeling. Studies of diseases of insects in trees or forests date back at least to the 1860's (Schwerdtfeger 1973), or to the 1830's (Steinhaus 1975) if one considers cultured silkworms, *Bombyx mori* (L.), to inhabit trees. The body of scientific literature concerning these systems, particularly including microbial control of forest pests, has increased greatly in recent years. So that scientists can concentrate on gaps in knowledge and select systems to study for microbial control or theoretical ecology, we reviewed the literature on tree, insect, and entomopathogen systems.

This paper gives the status of infectious diseases and microbial control of forest pests in North America and presents a system for researchers to use in prioritizing pathogen species for further study in microbial control.

Forest Entomology

Forest entomology was not as well studied in North America in the 1800s as other entomological disciplines, probably because forest resources were so vast that any insect damage was of relatively minor consequence (Schwerdtfeger 1973). This situation has changed as forests have become an increasingly valuable resource for recreation and ecosystem reserves as well as for lumber and other commercial products. The great majority of insects inhabiting these woodlands are either beneficial or innocuous; however, as the value of these lands increased, so too did the importance of insects as pests.

Insects are among the most destructive pests of forests and trees (Baker 1972). The relatively few insect species that are pests are the biggest competitors for wood fiber. They range from native species that usually occur in such low numbers as to be innocuous, to insects that are pests at their normal population levels, to introduced insects whose populations can explode to damaging numbers. Various pest species can attack virtually every part of the tree. Additionally, insect damage to trees can indirectly cause serious damage to the forest ecosystem, including increased fire hazard, destruction of watersheds and wildlife habitats, pollution of lakes and streams, and increased flooding.

In many cases biotic and abiotic factors in nature prevent pest populations from reaching damaging levels, but in other cases only intervention by man can reduce damage. Control practices have included regulatory means (preventing entry of new pests), altered silvicultural or management practices, physical or mechanical control methods, biological control, chemical control, and other methods (Baker 1972). Chemical controls have been effective to the point of being the major means of pest management, yet insecticides also have negative side effects. These side effects include human poisonings and chronic accumulations, acute and chronic effects on nontarget organisms, development of secondary pests, and resistance and resurgence in the target pest. Partly as a result of such drawbacks to chemical insecticides, the U.S. Department of Agriculture Forest Service adopted a policy of ecosystem management to emphasize the health of the nation's forests. This policy includes emphasis on development of technology in four areas, one of which is biological control of forest insects including microbial control.

Entomopathogens of Forest Insects

Insects, like humans and all other organisms, are susceptible to a variety of disease-causing microorganisms, or entomopathogens. These include viruses, bacteria, fungi, protozoa, and nematodes, among others. Insect diseases range from almost unnoticeable growths on the integument, to chronic diseases with sublethal effects, to virulent maladies that destroy the host.

The development of entomopathogens for insect control has been a subject of research since 1879 (Steinhaus 1975). Attempts at microbial control of tree pests began with fungi as early as the late 1800's (Cameron 1973), although disease epizootics in forest insects had been recorded as early as 1869 (Schwerdtfeger 1973). Attempts to control forest pests with viruses began in the 1920's, but the surge in the development of *Bacillus thuringiensis* in the 1960's (Schwerdtfeger 1973) probably was the catalyst in increasing interest in microbial control of forest pests.

Entomopathogens have both advantages and disadvantages for insect pest management. Currently, the primary reason for development of entomopathogens is environmental safety; due to their relatively narrow

host ranges, with few exceptions they are relatively safe to nontarget organisms. Other general advantages include persistence in terms of replicating or recycling, versatility in use and application techniques, relative compatibility with other control methods and management practices, and relatively low cost of development and registration. Their disadvantages in general include poor cost-competitiveness with chemical pesticides, host specificity which restricts market size for commercial products as well as activity against pest complexes, slow action, short persistence on surfaces particularly if exposed to sunlight, and perhaps inadequate delivery systems (Falcon 1985, Fuxa 1990, Khachatourians 1986). Certain of their strengths, such as the ability of many entomopathogens to spread and increase in numbers or to be improved through genetic engineering, can counteract many of their weaknesses. Microbial control has become a technology with successful examples and excellent potential for future development, although it still comprises only a small proportion of insecticide sales worldwide.

Forests have positive and negative characteristics as ecosystems with potential for microbial control of insect pests. For example, forests favor long-term approaches to microbial control, or those that require the pathogen to replicate and persist in the environment after release. Most of the successful examples of classical biological control with entomopathogens have been in forests (Fuxa 1997), probably due to habitat stability and diversity. Another positive feature is that a certain amount of damage to forest trees is tolerable in the great majority of forest situations. This is advantageous for microbial control, because many entomopathogens act slowly, allowing some feeding and damage by the pest before killing. On the other hand, the relatively inaccessible nature of forests restricts the options for application of entomopathogens, although inaccessibility is a problem for application of chemicals as well. Also, the height of tree canopies decreases the likelihood of natural epizootics when the entomopathogen persists in the soil and must be passively transported onto foliage where insects are feeding, which is often the case in the long-term approaches to microbial control.

Using This Book

In the first section of this book, criteria for selection of entomopathogens and pest-entomopathogen systems in which microbial control is likely to succeed are discussed. Three approaches to microbial control—short-term microbial insecticide, introduction and establishment, and seasonal colonization—are addressed. Criteria for a fourth approach—environmental manipulation—are discussed elsewhere (Fuxa 1998). Subsequent sections summarize characteristics of specific pests and review the available entomopathogen literature. The information in this book enables the reader access to prioritize pathogens and approaches for microbial control of each pest, or to identify gaps in knowledge that prevent such prioritization.

Insect List

Compiling a list of insect pests of North American forests turned out to be a somewhat subjective task. In general, our list includes insects with at least some significance in causing damage to trees of North American forests, even if those insects might be better known as pests of turf or trees in urban settings. We did not include annoyance pests that dwell in forests, such as mosquitoes, or orchard pests, unless they also attack forest trees. The list was organized first by insect order and second by type of damage or part of the tree that each pest attacks. It includes 165 species, although, in three cases, a group of species in one genus is treated as a single species. Our list was modified from a similar list developed by R. G. Van Driesche (Department of Entomology, University of Massachusetts).

Literature Search

The entomopathogen literature for forest insects was reviewed through several sources. Abstracts of publications were obtained through computer searches with DIALOG (Knight-Ridder International, Inc., Mountainview, CA), an electronic information access system which provides access to numerous online information databases. Our search included these databases: Agricola (National Agricultural Library, Beltsville, MD), AGRIS International (National Agricultural Library, Beltsville, MD), CAB Abstracts (CAB International, Slough, UK), BIOSIS (Biosciences Information service of Biological Abstracts, Philadelphia, PA), and Zoological Record Online (Biosciences Information Service of Biological Abstracts, Philadelphia, PA). Key words in the electronic searches included the insect genus and species names and the terms, "fungus," "bacterium," "virus," "protozoan," "nematode," "biological control," "microbial control," and "entomopathogen." These databases contained information published since the late 1960's. Literature before that time and until 1997 also was reviewed through books relating to insect pathology, as well as through a catalogue of entomopathogen literature maintained by the first author. The *Ecological Database of the World's Insect Pathogens on the World Wide Web* (http://insectweb.inhs.uiuc.edu), compiled by D. Onstad, was used to confirm that significant literature was not missed through the other literature research sources. Thus, the current review is based on information from abstracts, original publications, and literature reviews. In some cases, information in the abstracts was insufficient for our purposes; in these situations, we referred to the original publication whenever possible or used the sketchy information from the abstract when the original paper could not be obtained. The information for the Pest Situation sections was derived primarily from Furniss and Carolin (1977), U.S. Department of Agriculture Forest Service (1985), and Solomon (1995).

This literature search procedure revealed entomopathogen-related publications for 76 of the 165 species or groups in our list of forest insect pests. The 76 insect species with entomopathogen literature are included in the table of contents and in the main body of this document. The 89 insect species for which no entomopathogen literature was found are listed in the Appendix.

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Chapter 2

CRITERIA FOR CHOOSING ENTOMOPATHOGENS FOR MICROBIAL CONTROL OF INSECTS

Criteria for Choosing Entomopathogens for Microbial Control of Insects

Many, if not all, insect pests are susceptible to a variety of infectious diseases. This fact raises the question of how to choose species or even strains of entomopathogens to target for research and development in microbial control. This choice is not trivial, because the overall development cost for a bioinsecticide has been estimated at up to US$1 million to $10 million (Törmälä 1995).

Underlying the choice of entomopathogen is the approach with which it will be used. The choice of an entomopathogen for microbial control is then based on two major types of criteria: those related to the entomopathogen and those related to the target insect pest and host plant ecosystem. Criteria presented here are applicable to microbial control in row-crop agriculture and medical and veterinary entomology, as well as in forest entomology.

Approaches to Microbial Control of Insects

Microbial control can be defined simply as the use of microorganisms or their by-products by man to suppress insect pest populations.

This definition implies that the microorganism, almost always an entomopathogen, is subject to some sort of manipulation. There are four approaches to microbial control of insects: short-term insecticide, introduction and establishment, seasonal colonization, and environmental manipulation. Generally, commercial development is limited to the first two of these approaches. The four approaches differ fundamentally in the manner in which the entomopathogen is manipulated and in the expected results.

Short-term microbial insecticide — In the short-term insecticide approach, large numbers of entomopathogen units (the "microbial insecticide") are produced and released for relatively quick suppression of the pest population. The pathogen does not replicate or "recycle" in the environment sufficiently to suppress subsequent infestations of the pest. Thus, repeated applications are necessary, which is beneficial for commercial development. Entomopathogens generally are applied by means of technology developed for agricultural chemicals. They often, but not always, are formulated as aqueous concentrates or wettable powders and applied as sprays. Relatively rapid cessation of pest damage is often beneficial in this approach but is difficult to achieve with most entomopathogens.

Introduction and establishment — The introduction and establishment approach also is referred to as "classical biological control." An entomopathogen species or strain is released in an area where it did not previously occur. It becomes a permanent component of the ecosystem in which it is released, recycling and often spreading from the release site, resulting in permanent pest population suppression. Commercial development is virtually nonexistent, because the one-time release of pathogen units does not lead to monetary profit. This approach has unique advantages. Due to the one-time application and spread, the cost of production and application is a consideration but is not nearly as critical as with commercial approaches. This allows much more flexibility in the choice of the pathogen and release method. The entomopathogen does not necessarily have to kill the pest, only to reduce pest reproduction (e.g., the information on *Sirex noctilio* under Hymenoptera—Borers). Also, a release does not necessarily have to reduce pest populations below economic injury levels, for two reasons: first, multiple releases (of more than one entomopathogen species) are possible; second, if partial suppression even occasionally eliminates the need for application of a chemical insecticide, this still can be economically worthwhile because the permanent level of control is cost-free after the initial release.

Seasonal approach — The seasonal colonization approach can be thought of as a "booster shot" of an entomopathogen. The technology is usually similar to that for the short-term approach. Large numbers of pathogen units are produced as a microbial insecticide and usually applied by means of conventional agricultural technology. This approach usually, but not always, is a commercial venture. The difference from the short-term approach lies in the activity of the entomopathogen after its application. The pathogen again suppresses the target pest population, but in this approach it also recycles and significantly suppresses at least one subsequent generation of the pest insect. Population density of the entomopathogen eventually declines, however, necessitating additional applications of the microbial insecticide, usually once in each growing season. Since more than one pest generation is suppressed by one appli-

cation, this approach can be more cost competitive with chemical insecticides than are short-term microbial insecticides. On the other hand, seasonal colonization demands some capability for causing natural epizootics, which in turn requires some degree of pathogen replication, persistence, and efficient transmission in the target insect and ecosystem.

Environmental manipulation — The final approach is environmental manipulation, including conservation. This is the only approach that does not involve release of pathogen units, although it can be used to supplement the other three approaches. Instead, the usual agricultural or resource management practices are altered to conserve or create a more favorable environment for an entomopathogen population. This approach reduces the pest population without significantly interfering with management of the forest resource. Because this approach does not involve environmental application or release of an entomopathogen, it will not be discussed further in terms of criteria for microbial control.

Criteria for Choosing Entomopathogens

Criteria for choosing entomopathogens to develop for microbial control can be complex. These criteria differ somewhat for the short-term insecticide (Table 1), introduction and establishment (Table 2), and seasonal colonization (Table 3) approaches.

The first step in developing criteria was to create a list of characteristics of each approach. The criteria for each approach were then separated into three categories: criteria that are difficult to circumvent, characteristics that can be improved with research (this category was eliminated for introduction and establishment), and additional factors to consider. This categorization has an operational advantage in that the possible use of an entomopathogen against a particular pest can be evaluated quickly by the "criteria difficult to circumvent," because any negative responses in this category will weigh heavily against the development of microbial control. The criteria or factors are further subdivided into "pest and ecosystem" and "entomopathogen" characteristics. It is not possible to evaluate an entomopathogen for microbial control without doing so in the context of the target pest and ecosystem. The final category, "factors to consider," offers further criteria after the person considering development of microbial control has narrowed a list of candidate entomopathogens and requires more specific considerations.

The lists of criteria for the three approaches (Tables 1-3) represent some degree of personal opinion of the first author. The primary purpose here is to propose criteria as a foundation that can be further developed if necessary, and to reinforce the idea that criteria differ with the approach to using the entomopathogen. It is not only possible, but almost certain, that researchers considering microbial control of a particular pest will find that one or more criteria listed in categories II or III (Tables 1-3)

actually belong in category I, or vice versa, for a particular entomopathogen, pest, and ecosystem.

The next section of this chapter will offer brief explanations of the criteria in Tables 1-3. For the criteria difficult to circumvent (section I) in each list, a general decision-making guideline is also presented. The guideline will be presented in the form of "+," "0," or "–" scores for certain characteristics within that criterion. The 0 score may indicate either a lack of information for the entomopathogen or an intermediate score, neither distinctly + or –. The greater the number of "–" scores, the less likely the entomopathogen will succeed by the given approach in that particular pest and ecosystem. In many cases, even one "–" score might be decisive. Certain of these criteria and factors have been adapted from Burges (1981), Jutsum (1988), Barbosa and Segarra-Carmona (1993), and Fuxa (1995).

Criteria for Short-Term Microbial Insecticides

Criteria for short-term microbial insecticides, as well as the numbering system in the following text, correspond with the summary of points in Table 1.

I. Criteria Difficult to Circumvent

A. Pest and Ecosystem Characteristics

1 . *Direct or indirect pest* -- A direct pest damages parts of a resource that are used by man (e.g., tree fruit), whereas indirect pests damage parts with no inherent commercial value (e.g., tree twigs). This damage is of consequence due to the relatively slow speed, need for ingestion of the entomopathogen, or both. Microbial control generally has a higher success rate against indirect pests (+) than direct pests (–).

2. *Extent of damage* -- The short-term microbial insecticide generally enters final development as a commercial product, for which market size is of primary concern. Market size relates to a great degree to the extent of the pest problem: whether it must be treated every season, the extent of the geographic area of treatable damage, and whether multiple treatments are required each season. This is particularly true if the entomopathogen is host-specific to one or a very few insect pests. Thus, a large potential market (+) is preferable over a small one (–).

3. *Pest feeding and behavior* -- Entomopathogens differ in their portals of entry (sites where they invade or damage the host) and in how well they function in different components of the environment. Insects that chew (+) broad vegetative areas or that live in soil (+) usually offer more microbial control opportunities than aquatic insects (0) or those with sucking mouthparts (0); control of the latter is limited to fungi or nematodes. Insects that quickly bore (-)

into some substrate other than soil can be particularly difficult to target with a microbial insecticide, except for nematodes or perhaps those with unusual transmission.

4. *Member of a pest complex* -- In most cases, microbial insecticides are not likely to be successful for a pest of a crop or resource that has a complex (–) of pestiferous arthropods. The reason is host specificity. Even the more generalist pathogens usually are not virulent against insects outside one order. Users prefer a control agent that will suppress all pests in a complex. One exception might be a pest whose populations typically surpass economic injury levels (EIL) before the other pest(s) in the complex, such as *Helicoverpa zea* in U.S. cotton. The microbial can suppress the initial pest and allow parasitoids and predatory arthropods to delay the use of chemical insecticides on the other pests. Thus, a sole pest (+) on a crop or resource is advantageous.

5. *Economic injury level (EIL) not too low* -- The economic injury level (EIL) is the pest population density at which damage costs begin to exceed the costs of pest control. Due to the relatively slow speed or necessity for ingestion (and, thus, at least a small amount of feeding damage) of virtually all entomopathogens, crops or resources with a low EIL (–) (i.e., can tolerate little damage) are less likely to be conducive to microbial control than those with a moderate or high EIL (+) (can tolerate some degree of damage).

6. *Competing controls*-- There are numerous examples of microbial insecticides that were efficacious but not successful as commercial products, because - from the users' perspectives - they were not advantageous (–) over competing products. Host specificity (i.e., environmental safety) is a general advantage possessed by entomopathogens, but it usually is not enough to offset higher costs without government intervention. Thus, the microbial must have some advantage (+) over competing controls (primarily chemicals) to succeed in the insecticide market. Opportunites for microbials can arise when chemicals are unavailable for a crop or resource, are costly, fail (e.g., resistance), are restricted by the government, are not environmentally safe, or elicit adverse public opinion.

B. Entomopathogen Characteristics

1. *Host range* -- An entomopathogen with a relatively broad effective host range (+) is advantageous for commercial development over one with a narrow host range (–) due to potential market size and, perhaps, effectiveness in certain pest complexes. A broad host range can be something of a disadvantage, however,

in rare cases where a beneficial or endangered insect population might be affected.

2. *Virulence* -- For the short-term microbial insecticide approach, a high degree (+) of virulence (i.e., disease-producing power of an entomopathogen, measured in terms of degree or speed of damage to the insect) is virtually essential. Entomopathogens producing chronic disease or having low virulence (–) are unlikely to be successful in this approach, in terms of user acceptance as well as damage prevention.

3. *Cost of production* -- A major reason for failure in the pesticide market of certain, past microbial insecticides has been their cost-competitiveness with other pesticides, primarily chemicals. The obligate (–) pathogens (viruses and protozoa plus certain bacteria, fungi, and nematodes), which must be produced in living cells (at this time, this is equivalent to production in living insects), are more costly to produce than facultative pathogens (+).

4. *Speed of kill or damage cessation* -- A major weakness of most entomopathogens developed as microbial insecticides is the length of time required to kill the insect or at least terminate its damage-causing activity. The viruses, protozoa, fungi, and certain bacteria and nematodes mostly develop as parasites (–) in their hosts; they usually do not debilitate the insect for at least several days. Certain entomopathogens damage the insect very quickly (+), generally within 1 day and usually with toxins, symbiotic bacteria, or massive damage from invasion. Thus, the latter are more likely to prevent pest damage and be more acceptable to users who expect a "knockdown" action. It is difficult to achieve acceptable control with a slow pathogen against a pest in a crop with a low EIL. Genetic engineering is expected to improve certain of the "slow" entomopathogens.

5. *Reliably suppresses pest population below EIL* -- For a microbial insecticide to succeed (at least in terms of repeated usage), the entomopathogen must possess characteristics that enable it to reliably suppress the pest population below the EIL (+).

6. *Environmental safety* -- In view of public opinion, especially in recent years, environmental safety is essential. Fortunately, environmental safety (including humans, domestic animals, wildlife, plants) is the major strength of entomopathogens and the major rationale for developing them for insect control. Natural strains of entomopathogens are safe to nontarget organisms, although occasionally there is concern that a pathogen with a wide host range might harm an endangered insect species or upset an ecosystem by killing a nonpest species. There is

some concern about entomopathogens altered by recombinant-DNA techniques (–), but this is likely to decline as experience is gained with these new microorganisms.

7. *Cost effective* -- Cost effectiveness (+) encompasses more than just production cost versus damage reduction. It also includes environmental costs, infrastructure costs, and so on.

8. *Advantage over competing controls* -- The entomopathogen in a particular pest and ecosystem must not only be cost effective, it must have a relatively good degree of cost effectiveness (+) compared with other controls. Entomopathogens have an important, inherent advantage, namely, their environmental safety. However, this alone often is not sufficient to offset disadvantages such as high cost or unreliability in competition against chemicals (–). Thus environmental safety of an entomopathogen in a particular pest situation must supersede its lack of cost competitiveness. If it does not, then the pathogen must have additional advantages over competing methods of pest control.

9. *Patentable* -- Short-term microbial insecticides usually are developed by private industry, which in turn requires protection of its investment. Exclusive rights to a strain of an entomopathogen depend on a patent, which requires that the strain be novel in some respect and patentable (+). An entomopathogen that is not patentable (–) is at a serious disadvantage. The question still remains as to whether many patents recently obtained will be defensible in court.

10. *Registerable* -- The great majority of entomopathogens present no particular difficulty in meeting government guidelines for registration as a pesticide. The costs are low compared with those for chemicals; however, there are two problem areas. Although the costs are comparatively low, they are still prohibitive for a small company developing a microbial insecticide for a niche market. Registration also is still difficult for most recombinant entomopathogens, though this situation should improve as experience with these agents increases. Thus, registration is probably easiest for a new strain of *Bacillus thuringiensis* (+++) than for natural strains of most entomopathogens (++), with viruses (+) slightly more expensive, and recombinants (–) most expensive.

11. *Compatible* -- Another strength of entomopathogens is their compatibility with other insect controls and with agricultural and resource management practices in general. For example, the great majority of entomopathogens do not harm arthropods used in biological control and are not harmed by chemical pesticides (+). Occasionally there is concern that an entomopathogen with a relatively wide host range might harm a beneficial insect (0). Additionally,

entomopathogenic fungi usually are harmed by chemical fungicides used to control plant pathogens (–).

II. Characteristics That Can Be Improved With Research

A. Pest and Ecosystem Characteristics

1. *Pest population quality* -- Pest population quality mainly refers to insect resistance to a pesticide, although factors such as poor nutrition theoretically are possible. The threat of resistance can influence the pattern and extent of usage.

2. *Suitable environment* -- Entomopathogens generally do not persist for a few hours or, at best, days, when deposited on an exposed surface in the environment (e.g., sprayed onto a leaf). Thus, for example, treatment surfaces completely exposed to sunlight, leaf surfaces with pathogen-damaging pH when moist, dry areas, or polluted bodies of water might be prohibitively harmful to certain entomopathogens.

3. *Knowledge base* -- A good knowledge base of the pest, crop, and ecosystem, including effective interactions between users and extension personnel, are helpful for information distribution and user education as well as for research and development. For example, adapting an EIL for a chemical pesticide to a microbial insecticide generally requires less research than developing an EIL from scratch.

B. Entomopathogen Characteristics

1. *Amenable to genetic engineering* -- Genetic engineering simply increases the number of pathogen "strains" for possible development as insecticides. Furthermore, recombinant-DNA techniques can be used to combine different traits in a precise manner. For these purposes, "genetic engineering" can include classical techniques, such as strain selection, as well as use of recombinant-DNA. At this time, certain bacteria and viruses appear more amenable to recombinant-DNA research than fungi, nematodes, or protozoa.

2. *Persistence in storage* -- A certain time interval is necessary between the packaging of an insecticide and its application in the field. Most entomopathogens lose little efficacy over time in storage, as long as they are not exposed to excessive heat. For certain entomopathogens, most notably nematodes, inability to persist in storage is detrimental to their competitiveness in the insecticide market. Storage capacity of even nematodes, however, is being improved steadily with research.

3. *Persistence of pathogen units in the environment* -- Generally, there is a time interval between application of an entomopathogen and its invasion of or ingestion by the host insect. This time lag can create opportunities for serious problems. Almost all entomopathogens are killed quickly by sunlight. Many fungi and, especially, nematodes are inactivated by moisture deficiency. Persistence is another problem that can be alleviated by research into formulation, application, and strain selection.

4. *Amenable to appropriate formulation* -- Appropriate formulation can counteract certainly difficulties, such as lack of persistence or problems with application to a precise location. Most entomopathogens are not harmed by different types of formulation, although, for example, some perform better in oils than in aqueous sprays, or vice versa. Formulation has improved the performance of microbial insecticides, but it must do so at a low cost, or the product will not be competitive.

5. *Application with conventional equipment* -- It is beneficial if commonly used agricultural equipment can be used to apply an entomopathogen in an effective manner. Attempts to sell a product that would require additional capital outlay by the user probably would fail.

6. *Reliable efficacy* -- A microbial insecticide not only must be efficacious, but reliably efficacious. Under most circumstances, a user is not likely to repeatedly purchase a microbial insecticide that fails part of the time. This criterion implies that the microbial insecticide must be amenable to some form of product standardization.

III. Factors to Consider

A. Pest and Ecosystem Characteristics

1. *Severity of damage* -- Severity of damage can be either a positive or negative factor. If the damage to a crop or resource is costly, or if there is a severe problem with human contact or disease, opportunities can arise in terms of research and development funding and market potential. On the other hand, these conditions often also require that the insect control method be rapid-acting as well as efficacious.

2. *Pest population age structure* -- In the great majority of cases, insects exhibit maturation immunity to entomopathogens. In other words, larvae become increasingly refractive to infection in later instars. Thus, microbial insecticides generally are more efficacious when applied against pest populations consisting primarily of young

larvae in discrete generations. It can be difficult to achieve acceptable control if an entomopathogen must be applied against older insects or, at times, against a mixed-age population.

3. *Range of pest population density* -- Certain insects, particularly the so-called r-selected species, reproduce quickly and in high numbers, rapidly building dense populations. It can be difficult to achieve an acceptable level of control of such pests with many entomopathogens, particularly the slow-acting ones. On the other hand, such pests often require repeated application of a control agent, increasing the potential market size.

4. *Pest population distribution* -- The importance of pest population distribution or dispersion is not well understood; however, most application methods result in a somewhat widespread, indiscriminate, random distribution of entomopathogen units. Intuitively, this would seem to be disadvantageous against highly clumped pest populations.

5. *Pest rearing* -- Pest insect species vary greatly in their survival and reproduction in artificial settings. Some are easily reared on artificial diets, others require live host plants or animals, and still others cannot be reared at all. Research and development greatly benefits an entomopathogen if the pest can be reared in numbers sufficient for experimental and assay purposes. Rearing is a virtual necessity for entomopathogens that must be produced in living host insects.

6. *Pest of enclosed resource* -- A pest of a crop or resource that occurs in some sort of enclosed system, such as greenhouses, can provide a particularly attractive target for certain entomopathogens. Enclosed systems increase the possibilities for manipulating the environment to favor the entomopathogen. For example, a high level of relative humidity or moisture can enhance the activity of fungi and nematodes.

7. *Crop (resource) value* -- Intermediate-value or resource crops generally provide the best situation for short-term microbial insecticides; however, exceptions to this rule are numerous. Unless the cost of microbial insecticides is reduced, repeated application to low-value crops is not economically worthwhile. High-value crops often are associated with low EIL; direct pests of such crops often are not a good choice for microbial control, for reasons already discussed.

B. Entomopathogen Characteristics

1. *Subspecies or strains readily isolated* -- The ability to isolate strains of certain entomopathogens, most notably B. thuringiensis, has been an advantage, in most cases, in developing them for micro-

bial control. Strains increase the opportunity of discovering entomopathogens with different host ranges, greater virulence toward certain pests, increased persistence, source material for genetic engineering, and other characteristics. Strains with different biological characteristics generally are most readily isolated among bacteria and fungi, then nematodes and viruses. There has been limited work of this nature with the entomopathogenic protozoa.

2. *Portal of entry* -- For purposes of short-term microbial control, the portals of entry (i.e., routes of entry into the host insect) are primarily *per os* (oral) for bacteria, viruses, and protozoa, and penetration of cuticle or body openings for fungi and nematodes. Everything else being equal, cuticular penetration or "contact action" is an advantage because timing and placement of application are not as critical as for ingestion. Additionally, ingestion of microbial insecticides generally is not feasible for controlling insects with sucking mouth parts.

3. *Searching capability* -- The ability to actively seek a host insect is limited to certain nematodes and aquatic fungi among the entomopathogens. Even though this capability generally is limited in scope, it can be an important advantage to insect control in certain situations, especially when the pest insect burrows into its host plant or some other substrate.

4. *Efficacious outside North America* -- If an entomopathogen has been successfully developed for control of a pest somewhere other than North America, this success increases the probability that it will succeed through a similar approach in North America; however, caution is necessary. Numerous factors can hinder successful adaptation of a control agent to North America, including differences in the environment, regulatory oversight, and agricultural practices.

Criteria for Introduction and Establishment

Criteria for short-term microbial insecticides, as well as the numbering system in the following text, correspond with the summary of points in Table 2.

I. Criteria Difficult to Circumvent

A. Pest and Ecosystem Characteristics

1. *Pest origin* -- Pests introduced accidentally or purposely into new geographic areas, as well as migrant pests in some cases, often "escape" many of their natural enemies. In these situations a natural enemy that can significantly reduce the pest populations in the area of introduction may be found in the area of origin. Thus,

pests originally from outside North America (+) present a good opportunity for introduction and establishment. Introduction of a new species or strain of entomopathogen against an indigenous pest (0) may be possible. By definition, an entomopathogen strain indigenous to the area where the pest is to be controlled (–) cannot be used in this approach.

2. *Direct or indirect pest* -- See "Criteria for Short-Term Microbial Insecticides," section I.A.1.

3. Extent of damage -- The frequency of pest infestations can be important to the establishment of many entomopathogens. These microorganisms often persist well in the environment when no host insects are present. If there is too great a time period between availability of host insects, however, the host-specific pathogens can decline in population density to the extent that too few pathogen units remain to initiate epizootics.

4. *Pest feeding and behavior* -- See "Criteria for Short-Term Microbial Insecticides," section I.A.3.

5. *r or K pest* -- See "Criteria for Short-Term Microbial Insecticides," section III.A.3. It is not yet clear whether r- or K-selected species are more amenable to control by introduction and establishment of an entomopathogen. R pest populations can increase explosively, which should be a disadvantage for a relatively slow-acting microorganism, unless early instars become infected by pathogens "lying in wait." On the other hand, the high population densities of r pests in many cases can be conducive to entomopathogen transmission and epizootics (host density dependence), and some r pests are migrants that escape many of their natural controls. K-selected species provide advantages in having more consistent, nonexplosive populations; however, they also generally have more effective defenses against natural enemies than r-selected species do.

6. *Action thresholds in use* -- The action threshold, or economic threshold, is the pest population density at which a certain control action must be taken to prevent the pest population from reaching the EIL. If a control action is taken at an action threshold for a particular pest (+), it can reduce the requirements for success in introduction and establishment of an entomopathogen. In that situation, the entomopathogen can be successful if it only partially suppresses pest population density. It does not necessarily have to reduce pest numbers below the EIL, because there is no additional cost afer the initial release. For example, if the introduced entomopathogen causes sufficient mortality to prevent the pest population from reaching the action threshold only 25% of the time, this still constitutes "success" because there will be 25% fewer

pesticide applications with their associated monetary and environmental costs. Lack of action thresholds for a particular pest and resource (0) is not a disadvantage; in this situation, single-species introductions simply have criteria for success that are similar to the other approaches to microbial control.

7. *EIL not too low* -- See "Criteria for Short-Term Microbial Insecticides," section I.A.5.

8. *Crop (resource) biological characteristics* -- The resource biological characteristics that can affect microbial control include physical structure, growth characteristics, and chemistry. Plants that grow close to the ground (+) can be advantageous for entomopathogen transport from a soil reservoir to the pest's feeding substrate. In addition to transport from soil, slowly growing plants (+) can be advantageous because leaf growth does not as quickly reduce pathogen population density as in quickly growing or tall plants (–). The disadvantages of quick growth or tall plants can be counteracted by efficient entomopathogen transport, as can occur on air currents or in host insects.

9. *Habitat Stability* -- Classical biological control of insect pests with parasitoids or predators has a greater success rate in stable ecosystems, such as forests, than in ecosystems subject to frequent disturbances, such as in row-crop agriculture. Introduction and establishment of entomopathogens has not been as well studied, but indications are that this will be true for them as well, although there may be important exceptions, particularly in the case of baculoviruses. Until more is learned, the probability of entomopathogen success will be greater in stable ecosystems (+) than in unstable (–) or perennial (0) resources, except that the viruses in unstable ecosystems (0) also have some potential.

10. *Suitable environment* -- See "Criteria for Short-Term Microbial Insecticides," section II.A.2. In addition to persistence, the environment must be conducive to entomopathogen transport or transmission (+) for introduction and establishment to succeed. The presence or absence of just one environmental factor that breaks the life cycle of the entomopathogen (–) will eliminate the possibility of Introduction and Establishment, unless the environmental manipulation approach also can be taken to compensate for that factor.

11. *Impact of natural enemies already present* -- Virtually every insect pest, even introduced pests, has a cadre of natural enemies. If the pest population typically reaches the EIL despite high natural mortality (–), this situation often will not be ideal for an introduction. The introduced pathogen could replace part of the control component provided by another agent or agents, rather than increase the total

mortality. Introduced pests often do not have a high mortality rate due to natural enemies, particularly host-specific ones. This is one reason introduced pests present a somewhat greater opportunity than native pests for introduction and establishment.

12. *Competing controls* -- See "Criteria for Short-Term Microbial Insecticides," section I.A.6. Usually, classical biological control can outcompete any other type of control, because it has zero input or cost after the initial release. However, success of other types of control (–) is still a disadvantage for research and development of an entomopathogen for introduction.

B. Entomopathogen Characteristics

1. *Reliability in Causing Natural Epizootics*-- The ability to cause natural epizootics (+) is the most crucial characteristic for an entomopathogen used in introduction and establishment. The pathogen does not necessarily have to kill its host, but it must reliably occur at moderate to high prevalence rates. To produce epizootics, the entomopathogen must have some inherent means of reliable transmission. It must persist permanently in the ecosystem, either in the host insect or other reservoir, such as the soil. A high reproduction rate is beneficial, and the entire pathogen life cycle must be in synchrony with that of the host insect.

2. *Efficacy versus EIL and use of action thresholds* -- The entomopathogen obviously must be efficacious, although this requirement is not always as stringent for an introduction as for the other three approaches to microbial control (see section I.A.6.). Since introduction and establishment is long-term control, it need not necessarily induce rapid mortality of the pest. The primary requirement is that an introduction reduce pest reproduction (which, of course, does not preclude rapid mortality) and as a result reduce population density of subsequent pest generations (+). Additionally, if action thresholds are used, partial suppression of the pest population (+) can be successful (see section I.A.6.). If action thresholds are not used, however, the introduction usually is not successful if it does not permanently reduce pest numbers below the EIL (–), unless it is only one component in a multiple release (more than one species of natural enemy).

3. *Capability to spread* -- The capability to spread is not an absolute requirement. For example, a pathogen that spreads only a little from its release site can still be successful if it can be released in a wide-area spray. Nevertheless, the capability to spread (+) is advantageous in any situation against a particular pest, in terms of

reduced cost of release if nothing else, and is essential for entomopathogens that must be released by relatively expensive or laborious means over a limited area.

4. *Isolated from climatic region similar to that of the target ecosystem* -- Being from a climatic system similar to that of the target ecosystem (+) simply increases the probability that the entomopathogen will be suited to produce epizootics in its new ecosystem. An entomopathogen from a very different ecosystem (–) is less likely to establish.

5. *Density dependence versus long-term persistence* -- Populations of entomopathogens, like parasitoids and predators, are dependent on the host population's density. This dependence can be a problem, particularly in crops or resources with moderate-to-low EIL, because there generally is a "lag-time" after the host population increases before the natural enemy population can grow. Certain entomopathogens can counteract this problem in one of two ways. Explosive population growth (+) (rapid generation time and high reproductive rate) can greatly reduce the lag time. Additionally, entomopathogens that can persist in the environment (usually the soil) in high numbers for long time periods (+) exhibit a very delayed density dependence. Such a pathogen is basically "lying in wait" and is capable of causing epizootics even in low densities of the pest population. Entomopathogens without explosive growth or persistence (–) can be at a disadvantage in a low-EIL situation.

6. *Environmental safety* -- See "Criteria for Short-Term Microbial Insecticides," section I.B.6. Environmental safety is even more important in introduction and establishment than for short-term microbial insecticides, because the entomopathogen is intended to persist and spread, increasing the opportunity for exposure to any harmful effect.

II. Factors to Consider

A. Pest and Ecosystem Characteristics

1. *Range of pest population density* -- See "Criteria for Short-Term Microbial Insecticides," section III.A.3.

2. *Pest population distribution* -- See "Criteria for Short-Term Microbial Insecticides," section III.A.4. Pest population distribution also is not well understood in terms of natural epizootics. Clumped host populations should be conducive to entomopathogen transmission within clumps but might not be among clumps.

3. *Pest population quality* -- See "Criteria for Short-Term Microbial Insecticides," section II.A.1. Resistance is not expected to be as serious a problem in introduction and establishment, because the host and pathogen populations interact and coevolve. Thus, populations of pest insects quite likely will develop resistance if there is a continuously high level of mortality. Theoretically, however, host resistance should select for traits to increase virulence in the entomopathogen population.

4. *Pest generations per year* -- Compared with univoltine pests, multivoltine pests are probably better subjects for introduction and establishment because they generally provide the entomopathogen with opportunity for replication and transmission over a greater part of the year, and a shorter time is required for persistence outside the host. Numerous exceptions are likely, particularly with entomopathogens exhibiting good persistence. This criterion requires further research.

5. *Pest of enclosed resource* -- See "Criteria for Short-Term Microbial Insecticides," section III.A.6.

6. *Member of a pest complex* -- See "Criteria for Short-Term Microbial Insecticides," section I.A.4. The target pest being a member of a pest complex is not as serious a disadvantage for introduction and establishment as it is for short-term control, because the resource manager is not taking an action that affects only one pest; however, a pest complex is still something of a disadvantage for this approach. For example, if a complex is regularly treated with a chemical insecticide that also suppresses the target pest, then there will be less opportunity or need for classical biological control of one member of that complex.

7. *Pest rearing* -- See "Criteria for Short-Term Microbial Insecticides," section III.A.5. The ability to rear the pest is not as important as for short-term microbial insecticides that must be mass-produced in living host insects. Nevertheless, the ability to rear the insect in the laboratory is conducive to research and development.

8. *Severity of damage* -- See "Criteria for Short-Term Microbial Insecticides," section III.A.1.

9. *Crop (resource) value* -- See "Criteria for Short-Term Microbial Insecticides," section III.A.7. Valuable crops or resources associated with low EILs are disadvantageous to introduction and establishment as well as to microbial insecticides. Low-value crops or resources, however, present an excellent opportunity for classical biological control due to its low cost, due in turn to its permanence.

10. *Crop (resource) management practices* -- Resource management practices currently in use can improve the environment for an entomopathogen or have the opposite effect. It is an asset if such practices can be altered slightly to enhance the performance of a released pathogen.

11. *Infrastructure* -- It obviously is beneficial to a potential biological control project if a research and development infrastructure already exists, including elements such as personnel working with the pest, experts on the pathogen or related species, appropriate facilities, and an extension network.

B. Entomopathogen Characteristics

1. *Host range* -- The effects of a pathogen's host range on its success in introduction and establishment is not well understood. A host-specific entomopathogen might be more closely attuned to the host insect's life cycle than a pathogen with a broad host range might be. The latter might be more likely to infect non-target insects, but it also might reproduce in other insects, thereby increasing the probability of causing epizootics in the target pest.

2. *Subspecies or strains readily isolated* -- In addition to the considerations discussed in "Short-Term Microbial Insecticides," section III.B.1, strains raise interesting questions concerning introductions. If strains or subspecies with better characteristics for biological control than indigenous strains can be isolated, and if those strains or subspecies can compete with the indigenous strain for a niche in the ecosystem where released, then the number of opportunities for introduction and establishment will be greatly increased.

3. *Amenable to genetic engineering* -- See. "Criteria for Short-Term Microbial Insecticides," section II.B.1, as well as II.B.2 immediately above. Genetic engineering, particularly through recombinant DNA, of entomopathogens for introduction and establishment could eventually be the ultimate method of microbial control, if traits can be altered to improve capability for causing epizootics. The current regulatory climate, however, precludes any such development of a recombinant entomopathogen intended to persist and replicate in the environment. Additionally, lack of interest by private industry in this area will reduce funding opportunities.

4. *Virulence* -- Virulence is not necesarily as important for introduction and establishment of entomopathogens as it is for microbial insecticides. For example, pathogens have been successful in classical biological control by sterilizing host insects rather than killing them. Entomopathogens producing chronic diseases with sublethal effects can be effective in this long-term approach. There also is a hypothesis

that entomopathogens with moderate virulence are more likely to succeed in this approach than those with high virulence, which will contribute to long-term instability in the system.

5. *Searching capability* - See "Criteria for Short-Term Microbial Insecticides," section III.B.3.

6. *Cost of production*-- See "Criteria for Short-Term Microbial Insecticides," section I.B.3. Production costs are only a minor concern for introduction and establishment, unless it is difficult to produce any pathogen units at all. Since the entomopathogen is expected to spread outside the release site (in most cases) and to replicate in host insects virtually indefinitely after release, production costs are a factor for only a limited time.

7. *Method of application or release* -- As with production costs, introduction and establishment allows flexibility in application or release due to the lack of additional human input after the release. Low-cost application or release is an advantage, but methods that are costly in terms of money or effort do not preclude success.

Criteria for Seasonal Colonization Microbial Insecticides

Criteria for short-term microbial insecticides, as well as the numbering system in the following text, correspond with the summary of points in Table 3.

I. Criteria Difficult to Circumvent

A. Pest and Ecosystem Characteristics

1. *Direct or indirect pest* -- See "Criteria for Short-Term Microbial Insecticides," section I.A.1.

2. *Extent of damage* -- See "Criteria for Short-Term Microbial Insecticides," section I.A.2.; and "Criteria for Introduction and Establishment," section I.A.3.

3. *More than one pest generation per growing season* -- By definition, this criterion is almost essential to the seasonal colonization approach, although seasonal-colonization agents can function as short-term microbial insecticides if there occasionally are growing seasons with only one pest generation.

4. *Pest feeding and behavior* -- See "Criteria for Short-Term Microbial Insecticides," section I.A.3.

5. *Member of a pest complex* -- See "Criteria for Short-Term Microbial Insecticides," section I.A.4.

6. *EIL not too low* -- See "Criteria for Short-Term Microbial Insecticides," section I.A.5.

7. *Suitable environment* -- See "Criteria for Short-Term Microbial Insecticides," section II.A.2., and "Criteria for Introduction and Establishment," section I.A.10.

8. *Competing controls* -- See "Criteria for Short-Term Microbial Insecticides," section I.A.6. Seasonal-colonization microbial insecticides by definition have an inherent advantage over most chemical pesticides in that one application suppresses more than one pest generation.

B. Entomopathogen Characteristics

1. *Host range* -- See "Criteria for Short-Term Microbial Insecticides," section I.B.1., and "Criteria for Introduction and Establishment," section II.B.1.

2. *Virulence* -- The seasonal colonization approach requires a virulent pathogen—see "Criteria for Short-Term Microbial Insecticides," section I.B.2. This approach in most cases is not sufficiently long-term to make moderate virulence desirable, or chronic or sublethal diseases acceptable (see "Criteria for Introduction and Establishment," section II.B.4).

3. *Cost of production* -- See "Criteria for Short-Term Microbial Insecticides," section I.B.3.

4. *Speed of kill or damage cessation* -- See "Criteria for Short-Term Microbial Insecticides," section I.B.4.

5. *Suppresses pest population below EIL* -- See "Criteria for Short-Term Microbial Insecticides," section I.B.5.

6. *Reliability in causing natural epizootics* -- See "Criteria for Introduction and Establishment," section I.B.1.

7. *Environmental safety* -- See "Criteria for Short-Term Microbial Insecticides," section I.B.6, and "Criteria for Introduction and Establishment," section I.B.6.

8. *Cost effective* -- See "Criteria for Short-Term Microbial Insecticides," section I.B.7.

9. *Advantage over competing controls* -- See "Criteria for Short-Term Microbial Insecticides," section I.B.8. In addition to environmental safety, the seasonal colonization approach to microbial control has an advantage over most chemicals in that one application results in suppression of more than one pest generation.

10. *Patentable* -- See "Criteria for Short-Term Microbial Insecticides," section I.B.9.

11. *Registerable* -- See "Criteria for Short-Term Microbial Insecticides," section I.B.10.

12. *Compatible* -- See "Criteria for Short-Term Microbial Insecticides," section I.B.11.

II. Characteristics That Can Be Improved With Research

A. Pest and Ecosystem Characteristics

1. *Pest population quality* -- See "Criteria for Short-Term Microbial Insecticides," section II.A.1. Seasonal colonization is more similar to short-term microbial insecticides than to introduction and establishment in terms of insect resistance (see "Criteria for Introduction and Establishment," section II.A.3). The same pathogen isolate is released repeatedly, albeit at greater intervals than a short-term microbial insecticide would be, and thus cannot co-evolve with the host insect from a practical standpoint.

2. *Knowledge base* -- See "Criteria for Short-Term Microbial Insecticides," section II.A.3.

B. Entomopathogen Characteristics

1. *Amenable to genetic engineering* -- See "Criteria for Short-Term Microbial Insecticides," section II.B.1, and "Criteria for Introduction and Establishment," section II.B.3.

2. *Persistence in storage* -- See "Criteria for Short-Term Microbial Insecticides," section II.B.2.

3. *Persistence of pathogen units in the environment* -- See "Criteria for Short-Term Microbial Insecticides," section II.B.3.

4. *Amenable to appropriate formulation* -- See "Criteria for Short-Term Microbial Insecticides," section II.B.4.

5. *Application with conventional equipment* -- See "Criteria for Short-Term Microbial Insecticides," section II.B.5.

6. *Reliable efficacy* -- See "Criteria for Short-Term Microbial Insecticides," section II.B.6.

III. Factors to Consider

A. Pest and Ecosystem Characteristics

1. *Severity of damage* -- See "Criteria for Short-Term Microbial Insecticides," section III.A.1.

2. *Pest population age structure* -- See "Criteria for Short-Term Microbial Insecticides," section II.A.2.

3. *Range of pest population density* -- See "Criteria for Short-Term Microbial Insecticides," section III.A.3.

4. *Pest population distribution* -- See "Criteria for Short-Term Microbial Insecticides," section III.A.4, and "Criteria for Introduction and Establishment," section II.A.2.

5. *Pest of enclosed resource* -- See "Criteria for Short-Term Microbial Insecticides," section III.A.6.

6. Pest rearing -- See "Criteria for Short-Term Microbial Insecticides," section III.A.5.

7. *Crop (resource) value* -- See "Criteria for Short-Term Microbial Insecticides," section III.A.7.

8. *Crop (resource) management practices* -- See "Criteria for Introduction and Establishment," section II.A.10.

B. Entomopathogen Characteristics

1. *Subspecies or strains readily isolated* -- See "Criteria for Short-Term Microbial Insecticides," section III.B.1.

2. *Portal of entry* -- See "Criteria for Short-Term Microbial Insecticides," section III.B.2.

3. *Searching capability* -- See "Criteria for Short-Term Microbial Insecticides," section III.B.3.

4. *Efficacious outside North America* -- See "Criteria for Short-Term Microbial Insecticides," section III.B.4.

Prioritizing Entomopathogens

The criteria listed in this chapter can be used to prioritize entomopathogens for research and development against specific forest insect pests. Candidate entomopathogens can be screened initially with Category I criteria (those "difficult to circumvent"—Tables 1-3), with each pathogen's "score" tallied as the number of negative responses. For example, a list of simple +/0/– evaluations based on Category I.A (Tables 1-3) are scored here for *Lymantria dispar* as a candidate for the short-term microbial insecticide approach:

Lymantria dispar. I.A: +/+/+/0/+/+ = –0 (the number of negative responses)

Thus, from Table 1, I.A.1 is positive (indirect pest), I.A.2 is positive, and so on.

Similarly, for each pathogen species, the list of +/0/– scores based on Category I.B (Tables 1-3) can be tallied. For *L. dispar*, the nuclear polyhedrosis virus (LdNPV) and the fungus *Entomophaga maimaiga* as candidates for the microbial insecticide approach provide examples:

LdNPV. I.B: *–/+/–/–/+/+/0/+/0/+/+ = –3*

Entomophaga maimaiga. I.B: –/+/–/–/+/+/0/+/–?/+/+ = –4

Thus, the NPV, which scores fewer negatives than *E. maimaiga*, has more potential as a microbial insecticide. The minimal use of LdNPV as a microbial insecticide against *L. dispar* in North America does not invalidate this evaluation, for two reasons. First, the LdNPV was thought by experts for many years to have good potential as a microbial insecticide, based on the many years of research on LdNPV (see *Lymantria dispar* chapter). Second, the LdNPV did score three negatives, and, of course, it did fail to achieve widespread usage despite its registration as an insecticide with the U.S. Environmental Protection Agency.

The prioritizations based on Category I criteria can be used as a comprehensive yet rapid method to evaluate pest systems; more in-depth analyses can be based on Categories II and III (Tables 1-3). The proposed criteria (Tables 1-3) should provide a useful framework for initial prioritization of potential microbial control agents if sufficient information concerning the pest and the pathogen is available. If not, the Category I criteria, in particular, should identify key areas for further research.

Table 1 -- Criteria for choosing an entomopathogen to develop as a short-term microbial insecticide

I. Criteria difficult to circumvent
- **A.** Pest and ecosystem characteristics
  1. Direct or indirect pest
  2. Extent of damage
  3. Pest feeding and behavior
  4. Member of a pest complex
  5. Economic injury level (EIL) not too low
  6. Competing controls
- **B.** Entomopathogen characteristics
  1. Host range
  2. Virulence
  3. Cost of production
  4. Speed of kill or damage cessation
  5. Reliably suppresses pest population below EIL
  6. Environmental safety
  7. Cost effective
  8. Advantage over competing controls
  9. Patentable
  10. Registerable
  11. Compatible

II. Characteristics that can be improved with research
- **A.** Pest and ecosystem characteristics
  1. Pest population quality
  2. Suitable environment
  3. Knowledge base
- **B.** Entomopathogen characteristics
  1. Amenable to genetic engineering
  2. Persistence in storage
  3. Persistence of pathogen units in the environment
  4. Amenable to appropriate formulation
  5. Application with conventional equipment
  6. Reliable efficacy

III. Factors to consider
- **A.** Pest and ecosystem characteristics
  1. Severity of damage
  2. Pest population age structure
  3. Range of pest population density
  4. Pest population distribution
  5. Pest rearing
  6. Pest of enclosed resource
  7. Crop (resource) value
- **B.** Entomopathogen characteristics
  1. Subspecies or strains readily isolated
  2. Portal of entry
  3. Searching capability
  4. Efficacious outside North America

Table 2 -- Criteria for choosing an entomopathogen for introduction and establishment

- **I.** Criteria difficult to circumvent
  - **A.** Pest and ecosystem characteristics
    1. Pest origin
    2. Direct or indirect pest
    3. Extent of damage
    4. Pest feeding and behavior
    5. r or K pest
    6. Action thresholds in use
    7. EIL not too low
    8. Crop (resource) biological characteristics
    9. Habitat stability
    10. Suitable environment
    11. Impact of natural enemies already present
    12. Competing controls
  - **B.** Entomopathogen characteristics
    1. Reliability in causing natural epizootics
       - **a.** Efficient transmission
       - **b.** Persistence of pathogen population in the environment
       - **c.** High reproduction rate
       - **d.** Life cycle synchronous with host
    2. Efficacy versus EIL and use of action thresholds
    3. Capability to spread
    4. Isolated from climatic region similar to that of the target ecosystem
    5. Density dependence versus long-term persistence
    6. Environmental safety
- **II.** Factors to consider
  - **A.** Pest and ecosystem characteristics
    1. Range of pest population density
    2. Pest population distribution
    3. Pest population quality
    4. Pest generations per year
    5. Pest of enclosed resource
    6. Member of a pest complex
    7. Pest rearing
    8. Severity of damage
    9. Crop (resource) value
    10. Crop (resource) management practices
    11. Infrastructure
  - **B.** Entomopathogen characteristics
    1. Host range
    2. Subspecies or strains readily isolated
    3. Amenable to genetic engineering
    4. Virulence
    5. Searching capability
    6. Cost of production
    7. Method of application or release

Table 3 -- Criteria for choosing an entomopathogen as a seasonal colonization microbial insecticide

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I. Criteria difficult to circumvent
- **A.** Pest and ecosystem characteristics
  1. Direct or indirect pest
  2. Extent of damage
  3. More than one pest generation per growing season
  4. Pest feeding and behavior
  5. Member of a pest complex
  6. EIL not too low
  7. Suitable environment
  8. Competing controls
- **B.** Entomopathogen characteristics
  1. Host range
  2. Virulence
  3. Cost of production
  4. Speed of kill or damage cessation
  5. Suppresses pest population below EIL
  6. Reliability in causing natural epizootics
  7. Environmental safety
  8. Cost effective
  9. Advantage over competing controls
  10. Patentable
  11. Registerable
  12. Compatible

II. Characteristics that can be improved with research
- **A.** Pest and ecosystem characteristics
  1. Pest population quality
  2. Knowledge base
- **B.** Entomopathogen characteristics
  1. Amenable to genetic engineering
  2. Persistence in storage
  3. Persistence of pathogen units in the environment
  4. Amenable to appropriate formulation
  5. Application with conventional equipment
  6. Reliable efficacy

III. Factors to Consider
- **A.** Pest and ecosystem characteristics
  1. Severity of damage
  2. Pest population age structure
  3. Range of pest population density
  4. Pest population distribution
  5. Pest of enclosed resource
  6. Pest rearing
  7. Crop (resource) value
  8. Crop (resource) management practices
- **B.** Entomopathogen characteristics
  1. Subspecies or strains readily isolated
  2. Portal of entry
  3. Searching capability
  4. Efficacious outside North America

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Chapter 3

COLEOPTERA

Defoliating and Root-Feeding Beetles

- *Chrysomela scripta* F. – Cottonwood Leaf Beetle
- *Graphognathus* spp. – Whitefringed Beetles
- *Hylobius pales* (Herbst) – Pales Weevil
- *Otioryhynchus ovatus* (L.) – Strawberry Root Weevil
- *Otioryhynchus sulcatus* (F.) – Black Vine Weevil
- *Pachylobus picivorus* (Germar) – Pitch-Eating Weevil
- *Pissodes strobi* (Peck) – White Pine Weevil
- *Plagiodera versicolora* (Laicharting) – Imported Willow Leaf Beetle
- *Popillia japonica* Newman – Japanese Beetle
- *Pyrrhalta luteola* (Muller) – Elm Leaf Beetle

1. *Chrysomela scripta* (F.)

COTTONWOOD LEAF BEETLE

PEST SITUATION

- *Distributed throughout North America wherever cottonwood grows.*
- *Adults and larvae defoliate young trees in nurseries, plantings, and natural stands.*
- *Heavy and repeated defoliation reduces growth, deforms, and kills young trees.*
- *Economic injury level of two beetles per whip in nurseries, first-year plantings.*
- *Three generations per year in northern climates, up to seven generations per year in the southern United States.*
- *Feed in clumped distribution on trees, overwinter as adults in litter and under weeds.*
- *Could be reared on natural foliage in confinement.*
- *Resistant or tolerant cottonwood hybrids exist.*

PATHOGENS OF *CHRYSOMELA SCRIPTA*

A bacterium and protozoan are known pathogens of cottonwood leaf beetle. No reports of natural infection or microbial control of this insect were found.

Laboratory Experiments. Laboratory studies of pathogens of cottonwood leaf beetle have been limited to a bacterium and protozoan. The median lethal concentration (LC_{50}) of *Bacillus thuringiensis* var. *san diego* for second

instar cottonwood leaf beetle was 21,000 Colorado potato beetle international units (IU)/ml water. The LC_{50}s estimated for the third instars, fourth instars, and adults were 20-40 times higher than for second instars (Bauer 1990). Ultrastructural effects of *B. thuringiensis* var. *san diego* on midgut cells of the beetle include large cytoplasmic spaces, expansion of the basal labyrinth, disruption of rough endoplasmic reticulum, and apical displacement of nuclei (Bauer and Pankratz 1992). In laboratory bioassays, soluble protein extracted from *B. thuringiensis* isolate HD-290-1 was toxic to early larval instars of cottonwood leaf beetle. Susceptibility of the insect decreased with increasing age, and adult mortality did not exceed 30% at the highest dose of toxin tested (Ramachandran et al. 1993).

The microsporidium *Nosema scripta* infects the cottonwood leaf beetle. Both horizontal and vertical transmission have been demonstrated for this microsporidium in *C. scripta* in the laboratory (Bauer and Pankratz 1993).

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2. *Graphognathus* spp.

WHITEFRINGED BEETLES

PEST SITUATION

- *Introduced pests, primarily in the South, Virginia, Missouri, Florida.*
- *Adults feed on foliage of many plants, but damage by adults is of minor importance.*
- *Most injury is caused by larvae feeding on plant roots.*
- *Distribution is limited due to flightless condition.*
- *One generation per year, larvae overwinter.*
- *Long period in soil (eggs, larvae, pupae) subjects them to soil borne pathogens.*

PATHOGENS OF *GRAPHOGNATHUS* SPP.

Several species of nematodes, a protozoan, and a fungus are known pathogens of *Graphognathus* spp. Two or three nematodes and the protozoan have been detected in field-collected insects. Nematodes have been tested against this insect in the laboratory, and microbial control attempts have included a nematode and fungus.

Natural Infections. Field-collected *Graphognathus* spp. have been infected with nematodes and a protozoan. In Argentina, adults of *G. leucoloma* were infected with a microsporidium, *Nosema* sp. (Ahmad 1976). The nematode *Heterorhabditis* sp. caused 79% reduction in a natural population of *G. leucoloma* in Australia (Sexton and Williams 1981). *Neoaplectana (= Steinernema) bibionis* infected *G. leucoloma* in New Zealand (Wouts 1980), and *Heterorhabditis argentinensis* was isolated from *Graphognathus* sp. larvae in Argentina (Stock 1993).

Laboratory Experiments. Laboratory experiments have been limited to a nematode. *Graphognathus* sp. was moderately susceptible to the entomophilic nematode *Chromonema heliothidis (= Heterorhabditis bacteriophora)* under laboratory conditions (Khan et al. 1976).

Microbial Control. Nematodes and a fungus have been tried for the microbial control of *Graphognathus* spp. In Western Australia, an entomogenous fungus that can survive the winter in soil was described as having potential for microbial control of *Graphognathus* spp. (Ralph 1992). A population of white-fringed beetle (*G. peregrinus*) was reduced by 38% compared with controls 1 year after application of the nematode DD-136 (*Steinernema carpocapsae*) at 40,000 infective juveniles/0.093 m^2 (Harlan and Padgett 1969). Surface application of

Neoaplectana dutkyi (= Steinernema carpocapsae) at 430,000 nematodes/m^2 to a grassland field in Louisiana reduced a white-fringed beetle population by 38% 11 months after application (Harlan et al. 1971).

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3. *Hylobius pales* (Herbst)

Pales Weevil

Pest Situation

- *Widely distributed throughout North America east of the Great Plains and north to Ontario.*
- *Adults active at night feeding on bark of twigs or young conifer seedlings. Heavy bark scarring by adults girdles branches and kills small seedlings. Economic losses of 30-60% common in first year.*
- *Larvae feed in roots or root collar area and pupate in outer sapwood.*
- *One to two generations per year, depending upon location. Long life span of adults (up to 2 years). In the South, second generation in late summer and fall provides year round population of larvae and adults.*
- *Adult feeding is generally solitary, though larvae may be clumped in stumps.*
- *Long contact with soil by both adults and larvae leads to frequent infection.*
- *Cultural practice of delayed planting of seedlings reduces populations.*
- *Can be trapped and reared on conifer billets (chunky pieces of wood) in confinement.*

Pathogens of *Hylobius pales*

Infections by a nematode, two fungi, and a protozoan have been detected in field-collected pales weevils. Nematodes and fungi also have been tested against this insect in the laboratory. We found no attempts at microbial control of this weevil in the literature.

Natural Infections. Several pathogens of pales weevil have been detected in field samples. In Georgia, the fungus *Beauveria bassiana* caused approximately 15% mortality (Taylor and Franklin 1973). In North Carolina, several mite species possibly acted as phoretic carriers of the fungus *Metarhizium anisopliae* var. *major* to the beetles (Schabel 1982). Studies of these two species of fungi showed that moisture and temperature conditions in the habitat of the weevil are suitable for their development (Walstad et al. 1970). A protozoan, *Gregarina hylobii*, was identified in field-collected beetles from North Carolina. The prevalence of infection was higher in September than in March (Schabel and Taft 1988). Up to 30% of weevils sampled in North Carolina were infected with a nematode, *Neoaplectana (= Steinernema)* sp. (Thomas 1970). Severe endoparasitism by nematodes affected the reproductive organs and gametogenesis in beetles collected in North Carolina (Clark 1975).

Laboratory Experiments. Laboratory tests with entomopathogens have been limited to nematodes and fungi. Schabel (1976a) suggested that plants to be protected in the field might be dipped in suspensions of fungal spores at the time of planting, or the spores might be applied around the bases of the plants. Also, measures aimed at infecting larvae are more promising than those aimed at infecting adults. Germination and infection by *M. anisopliae* have been studied in *H. pales* (Schabel 1976a, 1976b, 1978). The nematodes *Neoaplectana (= Steinernema)* sp. (Jackson and Moore 1969) and *Bursaphelenchus xylophilus* (Tomminen and Akar 1990) were able to infect the beetle in the laboratory. *B. xylophilus* had lower infectivity, however, and produced fewer juveniles per beetle than did *Steinernema* sp. (Tomminen and Akar 1990).

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4. *Otiorhynchus ovatus* (L.)

STRAWBERRY ROOT WEEVIL

PEST SITUATION

- *Imported early in the 19th century.*
- *Distributed in northern United States, southern Canada, and Alaska. Arborvitae are the preferred host though larvae prefer roots of hemlock.*
- *Adults feed on leaves but cause little economic impact.*
- *Larvae, as with black vine weevil, are serious pests of nurseries and ornamental plantings but often are found as garden pests. Most damage to arborvitae and hemlock nursery stock.*
- *One generation is commonplace, but two generations per year may occur. Partially grown larvae overwinter in soil. Adults may invade homes during the summer, causing distress but no damage.*
- *Long life cycle in soil aids contact with soil pathogens. Moisture usually abundant in gardens and nurseries helps propagate pathogens.*

PATHOGENS OF *OTIORHYNCHUS OVATUS*

Strawberry root weevils have been found naturally infected by several species of fungi. Laboratory studies with entomopathogens have been limited to nematodes, and fungi and nematodes have been field tested against this insect.

Natural Infections. Infections by several species of fungi have been detected in field-collected larvae of strawberry root weevils. In Czechoslovakia, 8.5% of field-collected larvae and 2.5% of pupae, were infected with the fungus *Paecilomyces farinosus* (Srot 1979). In Poland, natural infections by *Paecilomyces fumosoroseus* resulted in 18% mortality of *O. ovatus* in winter. In eastern Poland, *Metarhizium anisopliae* was the dominant fungus infecting the strawberry root weevil at higher temperatures, while *Beauveria bassiana* occurred only sporadically (Mietkiewski et al. 1993).

Laboratory Experiments. A laboratory bioassay of larval and pupal strawberry root weevil resulted in 62% mortality from *Steinernema carpocapsae* and 51% mortality from *Heterorhabditis bacteriophora* (Simser and Roberts 1994).

Microbial Control. Microbial control studies were limited to fungi and nematodes. *M. anisopliae* was more virulent than *B. bassiana* toward strawberry root weevil, and it persisted for a longer period in the soil (Vainio and Hokkanen 1993). In the United States, applications of *S. carpocapsae* (A11 strain) or *H. bacteriophora* (NC-1) killed 32-38% of strawberry root weevils (Simser and Roberts 1994). Application at relatively high spray pressures of *S. carpocapsae* reduced *O. ovatus* numbers from 26.7 to 0.6 and of *H. bacteriophora* reduced numbers from 16.2 to 1.8 live larvae per sample (Simser and Roberts 1994).

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5. *Otiorhynchus sulcatus* (F.)

Black Vine Weevil

Pest Situation

- *Distributed throughout the northern portion of the United States and southern Canada. Imported in the early 19th century.*
- *Flightless adults are nocturnal feeders on leaves of many ornamentals, but do little economic damage.*
- *Larvae feed on roots of many ornamentals, leading to severe injury or death. Greenhouse plants and broadleaf evergreens sustain the greatest impact.*
- *There is one life cycle per year, with adults hiding in soil and litter and larvae spending their entire development in the soil.*
- *Distinguishing larvae of black vine weevil from other weevil species is impossible. Thus, this species and its close relative, the strawberry root weevil, may be joint targets of microbes in the soil.*
- *Well watered environments found in nurseries, greenhouses, and landscapes favor microbial control.*

Pathogens of *Otiorhynchus sulcatus*

Several pathogens of black vine weevil have been detected in field-collected samples. A bacterium and several species of fungi and nematodes have been tested against this insect in the laboratory. Microbial control attempts have been limited to a bacterium, fungus, and nematodes.

Natural Infections. In France, field-collected larvae of black vine weevil were infected with three species of nematodes from the order Rhabditida, one species of bacterium (*Bacillus cereus*), and five species of fungi imperfecti (*Metarhizium flavoviride, Metarhizium anisopliae, Paecilomyces fumosoroseus, Beauveria bassiana*, and *Beauveria brongniartii*) (Marchal 1977).

Laboratory Studies. Laboratory tests with black vine weevils have included fungi, nematodes, and a bacterium. In laboratory and field studies, *Bacillus thuringiensis* subsp. *tenebrionis* killed only 27.5% of *O. sulcatus* larvae and also was ineffective against adults, and its use as a biological control agent was not recommended (Landi 1990).

Several fungi have been tested against *O. sulcatus*. The fungi *M. anisopliae* var. *anisopliae, M. flavoviride, Paecilomyces farinosus*, and *P. fumosoroseus* were infectious to both eggs and larvae of the black vine weevil. For *M. flavoviride*

the LD_{50} was 1 $\infty 10^1$ spores/ml and the median lethal time (LT_{50}) was 6.6 days at 10^8 conidia/ml (Poprawski et al. 1985). In Sweden, larvae treated with *B. bassiana* and *M. anisopliae* had LD_{50}s of 4 $\infty 10^6$ and 1 $\infty 10^5$ spores/cm^3, respectively (Prado 1980). A suspension of *M. anisopliae* containing 5 $\infty 10^7$ spores/ml killed 80-100% of black vine weevil larvae in a greenhouse experiment (Zimmermann 1985). In Germany, susceptibility to *M. anisopliae* decreased as age of eggs increased; the mean infection rates were 84%, 12%, and 4% for 1-, 6-, and 8-day old eggs, respectively (Zimmermann 1982). In Belgium, various strains of *B. bassiana* and *Beauveria brongniartii* were virulent toward the larvae of black vine weevils (Coremans-Pelseneer and Nef 1986). This was confirmed in greenhouse studies, wherein application of *B. brongniartii* spores at 2.1 conidia/liter of soil resulted in 89% mortality of the curculionid larvae in 21 days (Tillemans and Coremanns-Pelseneer 1987). Black vine weevil larvae were tested for susceptibility to 19 isolates of *Metarhizium*. Strains of *M. anisopliae* var. *majus* were pathogenic to the larvae but were less virulent than strains of *M. anisopliae* var. *anisopliae*, whereas all the *M. flavoviride* and *Metarhizium album* strains were either only slightly virulent or nonpathogenic (Moorhouse et al. 1993). BIO 1020, a granular formulation of *M. anisopliae* (strain DSM 3884), at 1.0 g/liter of soil, reduced larval numbers by 80% (Stenzel et al. 1992).

Several nematodes can infect the black vine weevil. *Heterorhabditis heliothidis (= bacteriophora)*, isolate T327, killed up to 100% of black vine weevil larvae in freshly potted yew, raspberries, and grapes, and over 87% in cyclamens and strawberries in Australia (Bedding and Miller 1981). In New Zealand, *Heterorhabditis bacteriophora* killed 93% of black vine weevil larvae when applied to planter bags containing Rhododendron plants (Barratt et al. 1989). In Italy, application of *Heterorhabditis* sp. in pots resulted in 100% infection of *O. sulcatus* (Deseo and Costanzi 1987). The nematodes *Steinernema carpocapsae, Steinernema feltiae,* and *H. bacteriophora* (strains C1 and HP 88) were capable of moving to the bottom of 20-cm soil columns at a moisture content typical of the field to infect larvae of black vine weevil. Under field conditions, however, only *S. carpocapsae* infected larvae at that depth; *S. feltiae* and *H. bacteriophora* could not infect larvae below 17.5 and 12.5 cm, respectively (Hanula 1993). Isolates of *Heterorhabditis* spp. (*H. bacteriophora, Heterorhabditis megidis, Heterorhabditis zealandica*, and unidentified *Heterorhabditis* species) were studied in a systems analytical approach with *S. carpocapsae* and *S. feltiae* included for comparison (Westerman 1997). Laboratory experiments on nematode movement, accumulation near host insects, host penetration, and temperature effects, in conjunction with the modeling, indicated that control of *O. sulcatus* by *Heterorhabditis* spp. could be enhanced through improved production and storage of the nematodes to increase and stabilize the proportion of infectious nematodes.

Microbial Control. Microbial control attempts have been limited to a bacterium, fungus, and nematodes. Commercially available strains of *Heterorhabditis* sp. (Terbiot) and *Steinernema* sp. (Pianbiot), *B. thuringiensis*

subsp. *tenebrionis,* and *Verticillium lecanii* have been tested against the black vine weevil. The nematodes killed 70-90% of black vine weevil larvae in March and October but only 27-33% in February, while the bacteria and the fungus did not control the larvae (Landi 1990).

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6. *Pachylobius picivorus* (Germar)

PITCH-EATING WEEVIL

PEST SITUATION

- *Distributed throughout eastern United States, but is most common in the south.*
- *Adults feed on small twigs and bark of seedlings resulting in girdling and seedling death. Similar in damage characteristics to pales weevil. Feed mostly at night.*
- *Larvae bore in roots of recently cut or killed pines. Can be clumped in recently cutover areas. May coexist with pales weevils.*
- *Generally, one generation occurs annually, but life stages may overlap due to long life span of adults.*

- *Long contact with soil by both larvae and adults results in exposure to soil-borne pathogens.*
- *Can be cultured on pine billets in confinement.*

Pathogens of *Pachylobius picivorus*

Infections by a fungus and a protozoan have been detected in field-collected *P. picivorus*. No reports of other entomopathogens infecting this insect were found.

Natural Infections. In the United States, 15% of field-collected *P. picivorus* were infected with *Beauveria bassiana* (Taylor and Franklin 1973). A protozoan, *Gregarina hylobii*, also infects *P. picivorus* in the United States, and the prevalence of infection was higher in September than in March (Schabel and Taft 1988).

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7. *Pissodes strobi* (Peck)

White Pine Weevil (Also called Sitka Spruce Weevil and Engelmann Spruce Weevil)

Pest Situation

- *Distributed from coast to coast, but primarily a pest of eastern white pine.*
- *Adults feed on cambial tissue of the main stems of host trees.*
- *Larvae feed on cambium, under the bark of pine and spruce terminals. Larvae feeding can kill stems or entire seedlings. Usually, forked stems result from damage by larvae.*
- *One generation per year with adults overwintering in the litter. Larvae often clumped in stems.*

- *Weevils prefer moist sites with a hardpan.*
- *Overwinter mortality of adults in soil due to climatic factors and pathogens are of key importance to population dynamics.*

Pathogens of *Pissodes strobi*

Infections by a microsporidium have been detected in field-collected larvae of *P. strobi*. No reports of other entomopathogens infecting this insect were found.

Natural Infections. In Canada, 9-16% of field-collected *P. strobi* were infected with a microsporidium believed to be a species of *Nosema* (Wilson 1984).

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8. Plagiodera versicolora (Laicharting)

Imported Willow Leaf Beetle

Pest Situation

- *Distributed in the eastern United States and Canada, westward to Michigan. Imported into New York in 1915.*
- *Adults feed on most species of willow. Larvae feed gregariously and skeletonize leaves. Often a severe pest of ornamental willows.*
- *Three to four generations in North Carolina and Virginia, with two or three in other parts of its range.*
- *Adults overwinter under the bark, in debris or grass around bases of trees.*
- *Trees subjected to excessive ozone seem to be preferred.*
- *An imported pupal parasite is widely used to reduce populations.*

Pathogens of *Plagiodera versicolora*

Laboratory studies with entomopathogens have been limited to a bacterium and several species of nematodes. No reports of other entomopathogens infecting this insect were found.

Laboratory Experiments. A bacterium and several species of nematodes have been tested against this insect in the laboratory. The toxicity of M-One (*Bacillus thuringiensis* subsp. *san diego*) to larvae and adults of *P. versicolora* reared either on poplar or willow foliage was determined with leaf-dip bioassays. The LC_{50} estimates were up to threefold higher for *P. versicolora* reared on poplar than on willow (Bauer 1992). *P. versicolora* is susceptible to infection by the mermithid nematodes *Mermis gigantea, Hexamermis albicans, Hexamermis parastepposis,* and *Octomermis lisicovae* (Siddikov et al. 1989).

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9. *Popillia japonica* Newman

Japanese Beetle

Pest Situation

- *Imported into New Jersey in 1916.*
- *Distributed through many northeastern states from New Hampshire to Georgia and Ohio. Occasionally found in Canada from Ontario to Nova Scotia.*
- *Adult beetles feed on foliage, flowers, and fruits of a wide variety of plants. Ornamental trees are often attacked. Trees (and other plants) can be totally defoliated. Often gregarious feeders.*
- *Larvae damage roots, and damage can go unnoticed until plants are beyond recovery. Grasses appear to be the choice food source, but ornamental nursery stock can be affected.*

- *There may be two generations per year in the southern portion of the species range. Farther north, 2 years may be required to complete development.*
- *Moist loamy soil under grass is a favorite oviposition site, leading to ideal conditions for bacterium propagation and infection.*
- *Usually not an economic pest of industrial forests.*

Pathogens of *Popillia japonica*

Members of all five major groups of entomopathogens have been detected in field-collected Japanese beetles. Bacteria, fungi, protozoa, and nematodes have been tested against this insect in the laboratory. Microbial control attempts have been limited to entomopathogenic nematodes and a bacterium.

Natural Infections. Field sampling of Japanese beetles has detected infections by several types of entomopathogens. In Portugal, a blue iridovirus infected a very low percentage (0.01%) of field-collected Japanese beetle larvae (Lacey and Adams 1994). *Bacillus popilliae* caused heavy natural mortality among early larval stages of Japanese beetles at various sites in New Jersey (White 1941). Larvae of Japanese beetles collected from turf in North Carolina were infected with three nematodes eugregarine protozoan, and the bacterium *Bacillus lentimorbus* (Regniere and Brooks 1978). In another survey, entomopathogens isolated from field-collected Japanese beetle larvae in the United States included the protozoa *Ovavesicula popilliae* and cephaline eugregarines, the bacteria *B. popilliae* and *B. lentimorbus*, and the fungus *Metarhizum anisopliae* (Hanula and Andreadis 1988).

Laboratory Studies. Laboratory tests with Japanese beetle have included bacteria, fungi, protozoa, and nematodes.

There have been several studies of *B. popilliae*, the causative agent of milky disease in larvae of the Japanese beetles. Tashiro (1987) examined field-collected larvae from Connecticut in laboratory bioassays and concluded that resistance to *B. popilliae* was not causing low levels of infectivity of Japanese beetle observed in Connecticut. The deleterious effects of 14 pesticides on *B. popilliae* were tested. All of the pesticides reduced levels of spore viability, spore germination, and vegetative cell growth when they were tested over a range of concentrations from 0 to 1,000 ppm of active ingredient (Dingman 1994).

Temperature limitations on the efficacy of *B. popilliae* are a concern worldwide. The length of time before disease symptoms appear after injection of *B.* popilliae spores into Japanese beetle larvae increases as the temperature decreases (Dutky 1940). A temperature range of 15.5 to 36°C limited disease development in Japanese beetle when the temperature of the assay was kept constant (Dutky 1963). When soil temperature fluctuated, however, a range of 13 to 23°C did not restrict the development of disease caused by *B.*

popilliae subsp. *rhopaea*. Infected larvae died before the bacteria sporulated only in conditions of high temperatures (>25°C) and heavy doses of inoculum (Milner et al. 1980).

Fewer studies were conducted on *Bacillus thuringiensis* infecting Japanese beetles. *B. thuringiensis* serovar *japonensis* (flagellar antigen 23), isolated from Japanese soil, exhibited high larvicidal activity against the Japanese beetle (Ohba et al. 1992). Sharpe (1976) demonstrated that *B. thuringiensis* var. *galleriae* NRRL B-4027 invaded the hemocoel of Japanese beetle larvae.

The Japanese beetle is susceptible to several fungi. The LC_{50}s of *M. anisopliae* and *Beauveria bassiana* were 0.7 and 0.026 mg of conidia/100 adults, respectively, at 22-24°C (Lacey et al. 1994). The efficacy of two types of *M. anisopliae* propagules against third-instar larvae of the Japanese beetle was studied in the laboratory. Mortality was significantly quicker in mycelia-inoculated soil compared with conidia-inoculated soil, but total mortality did not differ between the two types of inoculum (Krueger et al. 1992). A coelomycete, *Entoderma colletosporium*, was able to invade the cuticle of the Japanese beetle (Hanula and Andreadis 1991). Other entomopathogenic fungi able to infect the larvae of Japanese beetle include *M. anisopliae* var. *anisopliae* and *Paecilomyces fumosoroseus* (Humber 1992).

Several protozoa have been tested against the Japanese beetle. In infections by *O. popilliae*, the normally transparent Malphighian tubules of larvae were hypertrophied and white when infected with the protozoan, which also infected the fat body, epidermis, and pericardial cells (Hanula and Andreadis 1990). Larvae of Japanese beetle also have been infected with *Actinocephalus* sp. and *Adelina* sp. (Hanula and Andreadis 1992).

Nematodes might include candidates for microbial control of Japanese beetle, based on laboratory experiments. *Heterorhabditis bacteriophora* 'Oswego' strain was capable of dispersing to all sections of experimental flats, but this nematode dispersed more rapidly within flats infested with Japanese beetle grubs than in flats not infested with grubs (Schroeder et al. 1993). In another study, steinernematids infected Japanese beetle grubs through the mouth or anus, but not through the spiracles or cuticle; *Steinernema glaseri* had higher infection rates than *Steinernema carpocapsae*. The overall results of this study indicated that *S. carpocapsae* is not as well adapted to parasitizing Japanese beetle larvae as is *S. glaseri* (Cui et al. 1993). Endophyte-induced starvation of Japanese beetle reduced vigor of larvae and rendered them more susceptible to entomopathogenic nematodes (Grewal et al. 1995).

Microbial Control. Attempts at microbial control of Japanese beetles have included a bacterium and nematodes.

B. popilliae is one of the primary agents used for the biological suppression of the Japanese beetle. This milky disease bacterium was the first registered microbial insecticide in the United States and has been used for the control of

Japanese beetle for more than 50 years (Klein 1989, 1992). Both Lacey and Harper (1986) and Fuxa (1987) considered the use of milky disease bacteria against the Japanese beetle as an example of suppression of a pest by the introduction and establishment of an entomopathogen. White (1940) placed infected larvae in the soil and showed that spores of *B. popilliae* were able to withstand soil temperatures that were fatal to Japanese beetle larvae and could remain active in the soil until larval populations returned. Beard (1945) found no infection by *B. popilliae* 2 months after application of $1.25\text{-}5 \infty 10^{10}$ spores/m^2 to plots with 30 larvae/m^2. With 180 and 480 larvae/m^2, however, the rates of infection were 11-15% and 28-37%, respectively.

A resurgence in Japanese beetle populations in Connecticut and New York has been observed. Attenuation of *B. popilliae* and resistance of the larvae to the disease is likely (Dunbar and Beard 1975).

There have been numerous attempts at microbial control of this insect with nematodes. Preliminary field studies with *Steinernema (Neoaplectana)* spp. isolated from a soil sample in Japan indicated that the minimal effective dose for the control of the beetle was $1 \infty 10^6$ infective juveniles/m^2 (Kushida et al. 1987). Applications of *Neoaplectana (= Steinernema) carpocapsae* and *Heterorhabditis heliothidis (= bacteriophora)*, followed by irrigation to provide moderate soil moisture, produced 53% and 73% control of Japanese beetle, respectively, in turf (Shetlar et al. 1988). *H. bacteriophora* (C1 strain) at 1.25-5.0 billion nematodes/ha killed more than 80% of Japanese beetles when experimental plots were irrigated before treatment and within 24 hours after treatment (Downing 1994). In potted Japanese yew, *Heterorhabditis* sp. ('Holland' strain) and *H. heliothidis (= bacteriophora)* at 92 and 192 nematodes/cm^2, respectively, killed 90% of Japanese beetles, whereas *S. glaseri* and *Steinernema feltiae*, both at 385 nematodes/cm^2, killed 58% and 29%, respectively (Wright et al. 1988). Of various entomopathogenic nematodes tried against Japanese beetles, *S. glaseri* at 24.7×10^9 nematodes/ha was the most effective, killing 71% of the Japanese beetle larvae (Alm et al. 1992). Two species and four strains of entomopathogenic nematodes, *H. bacteriophora* (HP88 and NJ-2) and *S. glaseri* (NC and NJ-43), killed 51.0%, 71.6%, 50.4%, and 70.1% of Japanese beetle larvae (Selvan et al. 1993). In Portugal, *S. glaseri* and *S. carpocapsae* applied at the rate of 10^6 nematodes/m^2 in September reduced Japanese beetle larval populations by 91 and 44%, respectively. When they were applied in April, however, *S. glaseri* reduced numbers of larvae by 31%, but *S. carpocapsae* was ineffective (Simoes et al. 1993).

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10. *Pyrrhalta luteola* (Müller)

Elm Leaf Beetle

Pest Situation

- *Distributed throughout most of the United States.*
- *Introduced pest, early 19th century at Baltimore, Maryland.*
- *Adult elm leaf beetles overwinter in sheltered dry places, often hibernating in houses, barns, and sheds. Adults produce minor injury in the spring before oviposition.*
- *Larvae are gregarious feeders on elms and serious injury occurs when repeatedly defoliated. Branch mortality is prevalent, though whole trees occasionally die.*
- *Up to three or four generations can occur in the West, while two generations occur commonly elsewhere in the United States*
- *Pupates in bark crevices at base of tree or openly on ground.*
- *Brief contact with soil and dry habitat of overwintering adults can limit infection by pathogens.*
- *Insect parasites and predators used to aid population reduction.*

Pathogens of *Pyrrhalta luteola*

Pathogenic fungi and a protozoan have been detected in field-collected elm leaf beetles. Laboratory studies with entomopathogens have included bacteria, nematodes, and a fungus. The two major reports of microbial control research included a bacterium and a nematode.

Natural Infections. There have been two studies of naturally occurring diseases in elm leaf beetles. In Italy, mortality in overwintering adults was due to the fungus *Beauveria bassiana* (Triggiani 1986). In France, field-collected elm leaf beetles were infected with the fungi *B. bassiana, Paecilomyces farinosus, Paecilomyces fumosoroseus,* and *Verticillium lecanii* (Humber 1992), and with a protozoan, *Nosema galerucellae* (Tonguebaye and Bouix 1989).

Laboratory Studies. There have been several laboratory studies of bacteria infecting elm leaf beetles. Dose response curves from a laboratory bioassay of *Bacillus thuringiensis* subsp. *tenebrionis* indicated that the mortality of first- and third-instar elm leaf beetles increased with increasing dosage, and a minimum tenfold increase in dosage in third instars was required to cause the same level of mortality as in first instars (Wells et al. 1994). In another study, *B. thuringiensis* subsp. *tenebrionis* at 3, 6, 9, 12, 15, and 18 ml/liter of

water (International units were not provided) resulted in greater than 50% mortality of elm leaf beetle larvae as compared with 24% mortality in controls. First and second instars of the beetle were more susceptible than third instars were (Francardi 1990). In the United States, *B. thuringiensis* subsp. *tenebrionis* and *B. thuringiensis* subsp. *san diego* (later found to be identical to *B. thuringiensis* subsp. *tenebrionis* [Krieg et al. 1987]) were virulent towards larvae and adults of *P. luteola*; however, persistence of the formulations on foliage was short, indicating that correct timing of treatment is important (Cranshaw et al. 1989).

There has been one study of bacterium-nematode interactions in *P. luteola*. In a laboratory bioassay, the development of *Neoaplectana (= Steinernema) carpocapsae* and *Heterorhabditis heliothidis (= bacteriophora)* was reduced by *B. thuringiensis* subsp. *san diego*, when elm leaf beetle larvae were simultaneously exposed to one nematode species and the bacterium. When the larvae were inoculated with the nematodes 24 hours before inoculation with *B. thuringiensis* subsp. *kurstaki*, however, their development was almost normal (Poinar et al. 1990).

Healthy elm leaf beetles became infected with *B. bassiana* 10 days after exposure, and most of the exposed adults were dead within 35 days (Triggiani 1986).

Microbial Control. Microbial control attempts have been limited to a bacterium and a nematode. In Australia, application of *B. thuringiensis* var. *tenebrionis* to an elm leaf beetle population resulted in 56.5 -67.2% mortality (Wells et al. 1994). The nematode *S. carpocapsae* applied in 2% aqueous Volck oil did not reduce numbers of elm leaf beetle in California, probably due to desiccation of the nematodes. Significant population reduction resulted, however, when the nematodes were applied to *P. luteola* pupae in litter (Kaya et al. 1981).

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Chapter 4

COLEOPTERA

Borers and Bark Beetles

- *Curculio caryae* (Horn) – Pecan Weevil
- *Dendroctonus brevicomis* LeConte – Western Pine Beetle
- *Dendroctonus frontalis* (Zimmermann) – Southern Pine Beetle
- *Dendroctonus ponderosae* Hopkins – Mountain Pine Beetle
- *Dendroctonus pseudotsugae* Hopkins – Douglas-fir Beetle
- *Dendroctonus rufipennis* Kirby – Spruce Beetle
- *Hylurgopinus rufipes* (Eichhoff) – Native Elm Bark Beetle
- *Ips avulsus* (Eichhoff) – Small Southern Pine Engraver
- *Ips calligraphus* (Germar) – Sixspined Ips
- *Ips grandicollis* (Eichhoff) – Eastern Fivespined Ips
- *Ips paraconfusus* Lanier – California Fivespined Ips
- *Ips pini* Say – Pine Engraver
- *Ips typographus* L. – Engraver Beetle
- *Plectrodera scalator* (F.) – Cottonwood Borer
- *Scolytus multistriatus* (Marsham) – European Elm Bark Beetle

11. *Curculio caryae* (Horn)

PECAN WEEWIL

PEST SITUATION

- *Distributed throughout the range of hickory and pecan.*
- *A serious pest of commercial pecan orchards. Many orchardists rely upon insecticidal control.*
- *Though adults are present and attack nuts each year, many individuals require 2 or more years to pupate in fallen nuts or soil.*
- *Prolonged prepupal period in nuts or in ground litter favors pathogen infections.*
- *Potential to culture in lab on or in nuts.*

PATHOGENS OF *CURCULIO CARYAE* (HORN)

Field collected pecan weevils have been infected with bacteria, fungi, and nematodes. Laboratory experiments and microbial control have been limited to studies of fungi and nematodes.

Natural Infections. Pecan weevils have been infected with several species of fungi and nematodes in nature. In the United States, pecan weevils were infected in the field by a strain of *Beauveria bassiana* that occurred naturally in the soil (Campbell et al. 1979). Pecan weevil larvae collected in Mississippi and Arkansas were infected with *Metarhizium anisopliae*, *B. bassiana*, *Pseudomonas aeruginosa*, and *Serratia marcescens* (Sri-Arunotal et al. 1975). In Texas, the fungus *Synnematium* sp. and the nematode *Neoaplectana (= Steinernema)* sp. were de-

tected in fourth instars of pecan weevil (Harp and Van Cleave 1976). Infections by the nematode *Heterorhabditis bacteriophora* have been detected in field collected larvae in the United States (Nyczepir et al. 1992). A strain of the nematode *Heterorhabditis heliothidis (= bacteriophora)* showed promise as a possible biological control agent against pecan weevil (Sanchez 1989).

Laboratory Experiments. Laboratory tests with entomopathogens have been limited to fungi and nematodes. Fourth-instar larvae and adults of pecan weevil were tested for their susceptibility to seven isolates of *B. bassiana*. The larvae and adults were most susceptible to isolates ARSEF-738 and CCGI (Harrison et al. 1993). Five different mutant strains of *B. bassiana* exhibited different degrees of virulence for pecan weevil larvae (Champlin et al. 1981). *In vitro* inhibition of the two entomopathogenic fungi by six fungicides used in pecan culture revealed that fentin hydroxide was the most toxic to both pathogens followed by benomyl, zineb, and dodine. Sulfur and dinocap were the least toxic (Tedders 1981).

The nematode *H. bacteriophora* caused 20-34% mortality of pecan weevil larvae, and the nematode killed larvae for at least 5 days after application to a soil surface (Nyczepir et al. 1992).

Microbial Control. Fungi and nematodes have been tested for microbial control of pecan weevils. Field tests with three isolates of *B. bassiana* (isolates AF-4, CCGI, and ARSEF-252) resulted in 23, 34, and 2% mortality of pecan weevil larvae, respectively (Harrison et al. 1993). In field and greenhouse trials, *B. bassiana* and *M. anisopliae* inocula killed 72 and 50% of adult pecan weevils and 30 and 6% of larvae, respectively (Gottwald and Tedders 1983). *B. bassiana* and *M. anisopliae* significantly increased mortality of larvae in field experiments within 20 days after soil treatment (Tedders et al. 1973). *Neoaplectana dutkyi (= Steinernema carpocapsae)* caused larval mortality within 20 days after soil treatment (Tedders et al. 1973).

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12. *Dendroctonus brevicomis* LeConte

Western Pine Beetle

Pest Situation

- *Distributed from British Columbia southward to Arizona and New Mexico.*
- *Ponderosa pine appears to be the predominant host tree attacked.*
- *Epidemics can be extremely damaging and vigorous trees of all ages having phloem thick enough to support development can be attacked and killed.*
- *Heaviest outbreaks in California, Oregon, and Washington, with lesser losses in the northern and southern extremes of its range.*
- *There are three distinct broods often overlapping throughout much of the beetles range, with continuous activity.*

Pathogens of *Dendroctonus brevicomis*

Infections by a nematode have been detected in field-collected D. *brevicomis*. There were no reports of other entomopathogens infecting this insect.

Natural Infections. In British Columbia, 17-32% of *D. brevicomis* were infected with *Contortylenchus brevicomi* (Thong 1974). All beetles had *Ektaphelenchus* sp. immatures under the elytra and *Parasitorhabditis obtusa* immatures in their gut (Thong 1974).

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13. *Dendroctonus frontalis* Zimmermann

Southern Pine Beetle

Pest Situation

- *Distributed from Maryland throughout the southeastern United States and westward to eastern Texas. Also occurs in Mexico, Guatemala, and Honduras.*
- *Attacks and kills all species of yellow pine in its range. Eastern white, red, and spruce pines plus red and Norway spruces are occasionally attacked.*
- *One of the most destructive, tree-killing forest insects. Kills healthy trees during frequent epidemics causing losses worth hundreds of millions of dollars in the United States.*
- *Up to eight overlapping generations in the southern portion of its range.*
- *Nearly impossible to culture in the laboratory.*

Pathogens of *Dendroctonus frontalis*

Infections by bacteria, fungi, protozoa, and nematodes have been detected in field-collected *D. frontalis*. These entomopathogens have been tested against this insect in the laboratory, but microbial control attempts have been limited to nematodes.

Natural Infections. Many entomopathogens are known to infect southern pine beetles in nature. In Mississippi and Alabama, the bacteria *Pseudomonas* spp. and *Serratia marcescens* infected 1.5 and 0.2% of southern pine beetles. In North Carolina, 22.3% of southern pine beetles collected were diseased. Bacteria isolated from dead beetles included *S. marcescens, Pseudomonas aeruginosa, Bacillus thuringiensis* var. *thuringiensis, Flavobacterium* spp., and several other pathogenic species. Fungi isolated were *Fusarium solani, Beauveria bassiana, Aspergillus flavus*, and four other pathogenic species (Moore 1971). In Mississippi and Alabama, the beetles were infected with *A. flavus, B. bassiana, Cephalosporium* sp., *Entomophthora* sp., *Metarhiziium anisopliae, Paecilomyces viridis*, and *Paecilomyces* sp. The percent infection ranged from 0.01 to 7.5% (Sikorowski et al. 1979).

Adults of southern pine beetle collected in Florida had 66.9 to 79.3% infection by a protozoan, *Unikaryon minutum;* collections from Georgia had only 2% infection (Atkinson and Wilkinson 1979). In another study, 62 populations of southern pine beetle were sampled, and the percentage of beetles infected with the protozoan *U. minutum* ranged from 2.3 to 70.3% in 1983 and from 0 to 41.9% in 1984 (Bridges 1987). *U. minutum* and an unknown microsporidium were isolated from southern pine beetles collected in Mississippi and Alabama (Sikorowski et al. 1979). The nematode *Contortylenchus* sp. infected a high proportion of southern pine beetles attacking pine trees in the southeastern United States (Joye and Perry 1976). Samples of southern pine beetles collected from Arkansas and Louisiana were infected with *Contortylenchus brevicomi.* Beetles emerging from the lower and middle sections of infested boles usually had a higher prevalence of infection by the nematode than did beetles emerging from the upper bole (Kinn and Stephen 1981). *Contortylenchus* sp. infected 7.3% of the southern pine beetles collected in Mississippi and Alabama (Sikorowski et al. 1979).

Laboratory Studies. Laboratory tests with entomopathogens have included bacteria, fungi, protozoa, and nematodes. Ten strains of bacteria were tested for their virulence to larvae of southern pine beetle. *Bacillus* spp. (*B. cereus, B. thuringiensis* var. *thuringiensis,* and *B. thuringiensis* var. *kenyae*) as well as *P. aeruginosa, Pseudomonas fluorescens,* and *S. marcescens,* all isolated from diseased beetles, were pathogenic to the southern pine beetle (Moore 1972a). The virulence of *B. bassiana, A. flavus, Penicillium* sp., and an entomogenous strain of *Fusarium solani* was tested against southern pine beetles. All inoculated beetles died in 6-10 days when held at ambient temperatures and 95% humidity (Moore 1970a).

Southern pine beetles were susceptible to three entomogenous fungi, *P. viridis, B. bassiana,* and *M. anisopliae,* in another study. Their LD_{50}s and LD_{90}s (in numbers of conidia per larva) after topical application of conidia were $1.2\infty10^3$ and $2.2\infty10^4$, respectively for *B. bassiana*, $1.5\infty10^3$ and $2.2\infty10^4$ for *P. viridis*, and $7.2\infty10^3$ and $1.1\infty10^5$ for *M. anisopliae* (Pabst and Sikorowski 1980). *Aerobacter aerogenes, Alcaligenes faecalis,* and *S. marcescens* were the principal

species of bacteria, and *Aspergillus* and *Penicillium* the principal genera of fungi recovered from the alimentary canals of healthy southern pine beetles. Seven of the species recovered were identical with facultative or conditioned pathogens recovered from diseased beetles in other studies (Moore 1972b). The nematode *C. brevicomi* and the microsporidium *U. minutum* infected 25% and 65% of southern pine beetles, respectively. Nematode-infected females produced fewer eggs and shorter galleries than did uninfected females (Macguidwin and Smart 1979). The phoretic mite *Dendrolaelaps neodisetus* (Hurlbutt), sometimes found in association with southern pine beetle, feeds on *C. brevicomi* (Kinn 1982). Beetles harboring the mite had less endoparasitism by the entomopathogenic nematode (Kinn 1980).

Microbial Control. Only nematodes have been tested for microbial control of southern pine beetle. A formulation of 100 ml 0.1% formalin with a wetting agent, containing 31,000 infective second-stage nematodes (*Neoaplectana [= Steinernema] carpocapsae* strain DD-136), sprayed on bolts of shortleaf pine (*Pinus echinata*) resulted in 44% mortality of *D. frontalis*. The nematodes parasitized mature larvae, but rarely young larvae or adults and never pupae (Moore 1970b).

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14. *Dendroctonus ponderosae* Hopkins

Mountain Pine Beetle

Pest Situation

- *Distributed throughout the West from British Columbia into Mexico.*
- *Host species include most pines, with lodgepole and ponderosa pine being most severely affected.*
- *Kills extensive areas of mature-overmature lodgepole and ponderosa pines with thick phloem being preferred.*
- *Up to 2 years may be required to complete a life cycle in the coldest portions of its range, while two or three generations occur per year in parts of California.*
- *Not easily cultured.*

Pathogens of *Dendroctonus ponderosae*

There have been no reports of natural infections or microbial control of mountain pine beetle. Laboratory studies with entomopathogens have been limited to nematodes.

Laboratory Experiments. *D. ponderosae* has been infected with nematodes in the laboratory. All stages of the mountain pine beetle are susceptible to *Neoaplectana (=Steinernema) carpocapsae*, with rates of infection ranging from 10-66%. The adults are least susceptible to the nematodes (MacVean and Brewer 1981). In greenhouse trials, dauers of the nematode could be recovered alive from frass in beetle-infested pine bolts several weeks after spraying with a water-plus-antidesiccant suspension of infective nematodes (MacVean and Brewer 1981).

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15. *Dendroctonus pseudotsugae* Hopkins

Douglas-fir Beetle

Pest Situation

- *Distributed throughout the range of Douglas-fir in western North America.*
- *Hosts, primarily Douglas-fir but can breed in downed western larch.*
- *One generation per year with adults and large larvae overwintering.*
- *Though ubiquitous in Douglas-fir, most severe problems are in the Rocky Mountains.*
- *Can breed in fire-killed, wind-thrown trees.*
- *Outbreaks short lived in coastal forests (though severe) and may limit slow acting biological controls.*

Pathogens of *Dendroctonus pseudotsugae*

Infections by protozoa, a fungus, and a nematode have been detected in field-collected Douglas fir beetles. Laboratory experiments have been limited to nematodes, and no reports of microbial control of this insect were found.

Natural Infections. Sampling of naturally occurring pathogens of *D. pseudotsugae* has been limited to British Columbia. *Beauveria bassiana* infections were detected in adults (Weiser 1970). Protozoa sampled included *Nosema dendroctoni*, *Ophryocystis dendroctoni*, and *Chytridiopsis typographi* (Weiser 1970). Additionally, 50% of *D. pseudotsugae* were infected with the nematode *Contortylenchus reversus* (Thong 1974).

Laboratory Experiments. Laboratory tests with entomopathogens have been limited to nematodes. The morphology and post-embryonic development of the bark beetle nematode *C. reversus* were described by Thong and Webster (1973). Infection by *C. reversus* did not affect hemolymph trehalose levels. Total protein levels decreased during maturation of parasitized female beetles from the callow adult state, reducing the size of oocytes by 20%. There was no difference in total amino-acid levels between control and infected Douglas-fir beetles (Thong and Webster 1975a). Infection by the same nematode caused 25, 28, and 27% reduction in length of the primary egg galleries; and 50, 33, and 45% fewer eggs were oviposited by infected versus healthy females at 7, 14, and 23 days, respectively. Gallery shape and egg viability were not affected by infection (Thong and Webster 1975b).

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16. *Dendroctonus rufipennis* Kirby

Spruce Beetle

Pest Situation

- *Distributed transcontinentally throughout the range of spruce in North America.*
- *Breeds in all native spruces infesting weakened or windthrown trees, large pieces of slash, or fresh stumps.*
- *Life cycle varies based on latitude, elevation, and climate. At higher elevations up to 3 years may be required for one generation while a 2-year life cycle is usual elsewhere.*
- *Small larvae feed gregariously.*
- *Nematodes significantly reduce the egg-laying capacity of infected females.*

Pathogens of *Dendroctonus rufipennis*

Infections by nematodes have been detected in field-collected *D. rufipennis* in the United States and Canada. No reports of other entomopathogens infecting this insect were found.

Natural Infections. Several entomopathogenic nematodes infect *D. rufipennis* in nature. In 1957, a decline in field populations of *D. rufipennis* in Colorado was caused by unidentified nematodes (McCambridge and Knight 1972). Natural infection of *D. rufipennis* by a nematode was reported by Schmidt and Beckwith (1975). In British Columbia 13.6-45.5% of *D. rufipennis* were infected with *Sphaerulariopsis dendroctoni* or *Contortylenchus brevicomi* (Thong 1974). A survey of nematode parasites of bark beetles in British Columbia revealed that *Parasitorhabditis obtusa, C. reversus,* and *S. dendroctoni* were infecting the guts and hemocoels of *D. rufipennis* (Thong and Webster 1983).

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17. *Hylurgopinus rufipes* (Eichhoff)

Native Elm Bark Beetle

Pest Situation

- *Distributed throughout the eastern United States north of Alabama and Mississippi west to Nebraska and North Dakota. Also in Canada from New Brunswick to Manitoba.*
- *Elm is the major host, but basswood, ash, and wild cherry are attacked on occasion.*

- *Responsible for transmitting Dutch elm disease when broods emerge from infected hosts.*
- *Two generations per year in the southern portion of its range, and one to one and a half per year in the North.*
- *Susceptible to parasites and predators.*
- *Can be cultured in dead wood.*

Pathogens of *Hylurgopinus rufipes*

Laboratory experiments with pathogens of *H. rufipes* included a bacterium and nematodes. There have been no reports of natural infections or microbial control of this insect.

Laboratory Experiments. Laboratory studies have been limited to a bacterium and nematodes. This bark beetle has been infected with a gram-negative, rod-shaped bacterium, mostly found in the fat body, the cytoplasm of the tropharia of the ovaries, and later in the developing eggs (Tomalak et al. 1988). A concurrent infection by this bacterium and a nematode, *Parasitaphelenchus oldhami*, led to the rupture of cell membranes by the nematodes and bacterial dispersal throughout the hemocoel. A substantial reduction in the prevalence and intensity of nematode infections in adult bark beetles was observed prior to and during hibernation (Tomalak et al. 1988). The DD-136 strain of the nematode *Neoaplectana (= Steinernema) carpocapsae* was effective against *H. rufipes* in the laboratory. Larvae of *H. rufipes* were more susceptible to the nematode than pupae or adults (Tomalak and Welch 1982).

References

Tomalak, M.; Welch, H. E. 1982. *Neoaplectana carpocapsae* dd-136 as a potential biological agent for control of *Hylurgopinus rufipes* (Eichhoff). *In:* E. S. Kondo, Y. Hiratsuka, and B. G. Denyer, eds. Proceedings of the Dutch Elm Disease Symposium and Workshop; 1981 Oct. 5-9; Winnipeg, MB. Manitoba Department of Natural Resources; 14-23.

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18. *Ips avulsus* (Eichhoff)

Small Southern Pine Engraver

Pest Situation

- *Distributed from southern Pennsylvania to Florida and westward to Texas.*
- *Hosts are the southern yellow pines, and occasionally pitch pine.*
- *Thin-barked limbs, tops of logging debris, or storm-damaged trees, as well as the tops of standing trees stressed by other agents are infested. Often associated with other engravers or* ***Dendroctonus*** *infestations.*
- *Many generations (average of eight) per year depending on geographic location.*
- *Easily cultured in natural or artificial medium in the laboratory.*
- *Responds to pheromones.*

Pathogens of *Ips avulsus*

Infections by nematodes have been detected in field-collected larvae of *I. avulsus*. No reports of other entomopathogens infecting this insect were found.

Natural Infections. In Louisiana, populations of this bark beetle have been infected with *Neoparasitylenchus avulsi* and *Parasitaphelenchus* sp. A higher prevalence of disease was observed in late winter than in summer, and male beetles had a higher prevalence than females (Kinn 1984). In Texas, field-collected *I. avulsus* were infected with *Parasitylenchus avulsi*; 50-58% of adults were infected during July and August, whereas only 20-30% were infected in January and February (Hoffard and Coster 1976).

References

Hoffard, W. H.; Coster, J. E. 1976. Endoparasitic nematodes of *Ips* bark beetles in eastern Texas. Environmental Entomology 5: 128-132.

Kinn, D. N. 1984. Incidence of endoparasitic nematodes in *Ips* engraver beetles in central Louisiana, USA. Journal of Georgia Entomological Society 19: 322-326.

19. *Ips calligraphus* (Germar)

SIXSPINED IPS

PEST SITUATION

- *Distributed throughout eastern North America, though its distribution in the Northeast is limited to that of pitch pine.*
- *Breeds in all species of southern yellow pines as well as pitch pine.*
- *Trunks, stumps, and large limbs of recently felled trees are attacked as well as trunks of standing live trees in the Southeast. Of the engravers, I. calligraphus is most likely to kill green trees.*
- *Often found in association with other Ips or Dendroctonus species.*
- *Up to six generations per year in the southern United States.*
- *Fairly easy to culture in the laboratory.*
- *Also introduced into the western United States (California) where ponderosa pines are attacked. Occasionally subspecies designations are used to separate the eastern and western populations (**I. c. c.** in the East and **I. c. ponderosae** in the West).*

PATHOGENS OF *IPS CALLIGRAPHUS*

Infections by nematodes have been detected in field-collected larvae of *I. calligraphus*. No reports of other entomopathogens infecting this insect were found.

Natural Infections. In Louisiana, members of a population of the bark beetle *I. calligraphus* were infected with *Contortylenchus elongatus* and *Contortylenchus grandicolli*. The prevalence of infection was greater in late winter than in summer, and male beetles had a higher prevalence of disease than females (Kinn 1984). In Texas, field-collected *I. calligraphus* were infected with *C. elongatus* and *Parasitaphelenchus* sp. In this study, 50-58% of the adult insects were infected during July and August, whereas only 20-30% infection was observed in January and February (Hoffard and Coster 1976).

REFERENCES

Hoffard, W. H.; Coster, J. E. 1976. Endoparasitic nematodes of *Ips* bark beetles in eastern Texas. Environmental Entomology 5: 128-132.

Kinn, D. N. 1984. Incidence of endoparasitic nematodes in *Ips* engraver beetles in central Louisiana, USA. Journal of Georgia Entomological Society 19: 322-326.

20. *Ips grandicollis* (Eichhoff)

EASTERN FIVESPINED IPS

PEST SITUATION

- *Distributed in eastern Canada and in the United States from Massachusetts to Minnesota and southward to Florida to Texas.*
- *Hosts are, primarily, southern yellow pines. North of the southern pine region occurrence is coincident with presence of pitch pine.*
- *Attacks recently downed pines and large populations can affect (and kill) living pines in the vicinity. Spot-kills are common.*
- *Associated closely with other* ***Ips*** *and* ***Dendroctonus*** *species, often cohabiting with one or more of these species.*
- *Six or more generations per year in the South, fewer in the North.*
- *Can be cultured in living or semiartificial medium.*

PATHOGENS OF *IPS GRANDICOLLIS*

Infections by nematodes have been detected in field-collected larvae of *I. grandicollis*. No reports of other entomopathogens infecting this insect were found.

Natural Infections. In Louisiana, members of a population of *I. grandicollis* were infected with *Contortylenchus elongatus* and *Contortylenchus grandicolli*. The prevalence of infection was greater in late winter than in summer, and male beetles had a higher prevalence of disease than did females (Kinn 1984). In Australia, *C. grandicolli* was recovered from *I. grandicollis* attacking *Pinus taeda* (Stone 1990).

REFERENCES

Kinn, D. N. 1984. Incidence of endoparasitic nematodes in *Ips* engraver beetles in central Louisiana, USA. Journal of Georgia Entomological Society 19: 322-326.

Stone, C. 1990. Parasitic and phoretic nematodes associated with *Ips grandicollis* (Coleoptera: Scolytidae) in New South Wales, Australia. Nematologica 36: 478-480.

21. *Ips paraconfusus* Lanier

California Fivespined Ips

Pest Situation

- *Distributed from southern Oregon west of the Cascades and throughout California west of the Sierra Nevada.*
- *All species of pines in the region are attacked with ponderosa pine being most seriously affected.*
- *Taxonomically close to* ***I. confusus****, and much early literature used that species name to refer to* ***I. paraconfusus****.*
- *Kills saplings, poles, and young trees and is found in the tops of larger trees. Breeds in slash in spring.*
- *Two generations per year at higher elevations and three to five per year in southern California.*
- *In some cases, overpopulation of individual trees may prevent brood survival.*

Pathogens of *Ips paraconfusus*

Infections by nematodes have been detected in field-collected larvae of *I. paraconfusus*. There have been no reports of other entomopathogens infecting this insect.

Natural Infections. In California, *I. paraconfusus* from ponderosa pine were infected with undescribed species of *Parasitaphelenchus* and *Parasitorhabditis*. They also were infected with *Contortylenchus elongatus, Contortylenchus reversus,* and *Contortylenchus brevicomi* (Choo et al. 1987).

References

Choo, H. Y.; Kaya, H. K.; Shea, P.; Noffsinger, E. M. 1987. Ecological study of nematode parasitism in *Ips* beetles from California and Idaho, USA. Journal of Nematology 19: 495-502.

22. *Ips pini* Say

Pine Engraver

Pest Situation

- *Distributed throughout most of the coniferous forests of North America except the Pacific Coast, the southern pine forests, and Mexico.*
- *Breeds in all species of pine and spruce within its range.*
- *Long known as* ***I. oregonis*** *in the West.*
- *Breeds in slash, windfalls, and dying trees. Nearby healthy trees are then attacked and killed. Effects of tree killing similar to that by the mountain pine beetle.*
- *One to five generations per year depending upon the locality and length of growing season.*
- *Adults overwinter in bark or forest litter aiding infection by pathogens.*

Pathogens of *Ips pini*

Infections by nematodes have been detected in field-collected larvae of *I. pini*. There were no reports of other entomopathogens infecting this insect.

Natural Infections. Field-collected *I. pini* were infected with an undescribed *Parasitaphelenchus* sp., two undescribed *Contortylenchus* spp., *Contortylenchus reversus, Parasitylenchus (= Neoparasitylenchus) ovarius*, and *Parasitorhabditis ipini*. *Parasitaphelenchus* sp. was found in 99% and 45% of the beetles from Idaho and California, respectively (Choo et al. 1987). Of 1000 *I. pini* collected from Idaho and California, 157 were parasitized by *Contortylenchus* sp. or *P. ovarius* (Choo et al. 1987).

References

Choo, H. Y.; Kaya, H. K.; Shea, P.; Noffsinger, E. M. 1987. Ecological study of nematode parasitism in *Ips* beetles from California and Idaho, USA. Journal of Nematology 19: 495-502.

23. *Ips typographus* L.

Engraver Beetle

Pest Situation

- *Distributed in the British Isles, Scandinavia, throughout Europe and eastward into Siberia and to Manchuria.*
- *Infests all pine species within its range, occasionally other conifers.*
- *Not a serious problem in North America.*

Pathogens of *Ips typographus* (L.)

A virus, protozoan, and several species of nematodes are known pathogens of the bark beetle *I. typographus*. Laboratory research has included a bacterium, protozoa, and nematodes. Attempts at microbial control of this insect have been limited to fungi.

Natural Infections. A virus, protozoan, and several species of nematodes have been detected in field samples. An entomopoxvirus was isolated from 0.3-1.1% of *I. typographus* attacking spruce in Austria (Wegensteiner and Weiser 1995). In Germany, *I. typographus* were infected with a protozoan, *Gregarina typographi* (Purrini 1978). In France, *Tylaphelenchus* sp. and *Parasitorhabditis bellifonti* were isolated from field-collected bark beetles (Lieutier and Laumond 1978). Eight nematodes were isolated from *I. typographus* in the USSR: *Parasitorhabditis obtusa, Contortylenchus diplogaster, Bursaphelenchus eidmanni, Devibursaphelenchus typographi, Ektaphelenchus typographi, Cryptaphelenchus macrogaster, Neoditylenchus major,* and *Mikoletzkya buetschli* (Kakuliya 1971).

Laboratory Experiments. Laboratory tests with entomopathogens have included a bacterium, protozoa, and nematodes. Studies of the chemical and serological characteristics of different isolates of *Bacillus thuringiensis* var. *thuringiensis* Serotype I isolated from *I. typographus* indicated that one isolate was promising for microbial control because of its production of thermostable toxin (Imnadze 1978). Brief notes on the morphology, distribution, and systematics of the protozoan *G. typographi* infecting *I. typographus* were reported by Purrini (1978). Also, Purrini and Weiser (1985) reported an ultrastructural study of the microsporidium *Chytridiopis typographi* infecting this bark beetle. Lieutier and Laumond (1978) reported brief morphological and biological data on *Tylaphelenchus christinae* and *Parasitorhabditis ipsophila* attacking *I. typographus* in France. In another study, the nematode *Neoaplectana (= Steinernema) carpocapsae agriotos* did not infect *I. typographus*

as they failed to develop and were destroyed when the host was carrying tylenchids (Ivanova 1976). Parasitic nematodes (mainly *C. diplogaster*) had no significant effect on the flight duration of *I. typographus* when studied in the laboratory in a flight mill (Forsse 1987).

Microbial Control. Microbial control experiments have been limited to fungi. A formulation containing *Beauveria bassiana* and *Verticillium lecanii* applied to *I. typographus* during the period of bark penetration did not cause significant infection (Cichonska and Swiezynska 1993).

References

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Forsse, E. 1987. Flight duration in *Ips typographus* L.: insensitivity to nematode infection. Journal of Applied Entomology 104: 326-328.

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Purrini, K.; Weiser, J. 1985. Ultrastructural study of the microsporidian *Chytridiopsis typographi* (Chytridiopsida: Microspora) infecting the bark beetle, *Ips typographus* (Scolytidae: Coleoptera), with new data on spore dimorphism. Journal of Invertebrate Pathology 45: 66-74.

Wegensteiner, R.; Weiser, J. 1995. A new Entomopoxvirus in the bark beetle *Ips typographus* (Coleoptera: Scolytidae). Journal of Invertebrate Pathology 65: 203-205.

24. *Plectrodera scalator* (F.)

COTTONWOOD BORER

PEST SITUATION

- *Distributed from New York to Georgia and west to Texas, New Mexico and northward to Montana. Most common in the Great Plains and Mississippi River Valley regions.*
- *Eastern cottonwood is the preferred host, followed by other poplars; willows are attacked on occasion.*
- *Both adults and larvae cause damage to trees. Larvae are particularly damaging to cottonwood nursery stock. Shelterbelt plantings in the Great Plains have been severely damaged by borers also.*
- *A 2-year life cycle is common in large trees, while nursery saplings in Mississippi Harbor populations that develop in 1 year.*
- *Where most damaging, larvae are exposed to prolonged periods of moisture near or below the root collar potentially aiding pathogens.*

PATHOGENS OF *PLECTRODERA SCALATOR*

Microbial control of *P. scalator* has been attempted with a fungus. There have been no reports of other entomopathogens infecting this insect.

Microbial Control. A commercial conidial formulation of *Beauveria bassiana* (AGB 6178) applied at $2\infty10^9$, $2\infty10^{10}$, and $1\infty10^{11}$ conidia/m^2 as a soil drench in a cottonwood nursery resulted in 60% infection of *P. scalator* adults (Forschler and Nordin 1989).

REFERENCES

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25. *Scolytus multistriatus* (Marsham)

European Elm Bark Beetle

Pest Situation

- *An exotic pest presently distributed transcontinentally in southern Canada and in all States, except Alaska and Hawaii.*
- *All native and introduced elms are hosts.*
- *Responsible for being a primary vector of Dutch elm disease in many cities and suburbs of the United States and Canada. Millions of dollars are spent to control spread of Dutch elm disease.*
- *Two or three generations develop per year.*
- *Pheromones useful in detection, monitoring, and in timing other potential control activities.*

Pathogens of *Scolytus multistriatus*

Only nematodes have been detected in field-collected *S. multistriatus*. Laboratory studies with entomopathogens have included bacteria, fungi, and nematodes. There apparently have been no attempts at microbial control.

Natural Infections. In England, 44-55% of *S. multistriatus* were infected with *Parasitaphelenchus oldhami* with means of 10-12 nematodes per beetle; however, there were no pathological effects on the beetles (Hunt and Hague 1974).

Laboratory Studies. Bacteria, fungi, and nematodes have been tested against this insect in the laboratory. *Bacillus thuringiensis* ser 3a and 3b caused 80% mortality of *S. multistriatus* larvae, compared with 20% mortality in control insects. The mortality was dose dependent, with an LC_{50} of $2.2 \infty 10^3$ spores/ml (Jassim et al. 1990a). *Bacillus alvei* and *Bacillus cereus* also were pathogenic to the beetle (Jassim et al. 1990a). The fungi *Trichoderma harzianum, Trichoderma polysporum,* and *Scytalidium lignicola* killed 80% of *S. multistriatus* larvae (Jassim et al. 1990b). Infections of *S. multistriatus* with *Neoaplectana (=Steinernema) carpocapsae* and *Heterorhabditis bacteriophora* resulted in death of larvae, pupae, and adults (Poinar and Deschamps 1981) . Each beetle larva produced approximately 4131 infective-stage juveniles of *S. carpocapsae* and 4238 juveniles of *H. bacteriophora*, equivalent to 1620 and 1659 juveniles per milligram of host larval tissue, respectively.

References

Hunt, D. J.; Hague, N. G. M. 1974. The distribution and abundance of *Parasitaphelenchus oldhami*, a nematode parasite of *Scolytus scolytus* and *S. multistriatus*, the bark beetle vectors of Dutch elm disease. Plant Pathology 23: 133-135.

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Chapter 5

HEMIPTERA

Cone and Seed Feeders

- *Leptoglossus corculus* (Say) – Leaffooted Pine Seed Bug
- *Tetyra bipunctata* (Herrich-Schäffer) -- Shieldbacked Pine Seed Bug

26. *Leptoglossus corculus* (Say)

Leaffooted Pine Seed Bug

Pest Situation

- *Distributed throughout the eastern and southern United States.*
- *All species of pines grown in seed orchards are hosts.*
- *Both nymphs and adults feed on the embryos of developing pine seeds, resulting in their nonviability.*
- *Damage to female flowers in early spring can result in mortality (abortion) of conelets.*
- *Several generations per year in the South.*
- *Adults overwinter in debris, litter, and old cones.*
- *Early nymphal stages are gregarious.*

Pathogens of *Leptoglossus corculus*

Microbial control attempts for *L. corculus* have been limited to a bacterium. There were no reports of natural infections or labora tory experiments with entomopathogens for this insect.

Microbial Control. In Texas, *Bacillus thuringiensis* applied at biweekly intervals did not reduce the damage caused by *L. corculus* in a loblolly seed orchard (Cameron 1989).

References

Cameron, R. S. 1989. Promising new pesticides for cone and seed insect control in the southern United States. In: Proceedings of the 3rd cone and seed insects working party conference; 1988 June 26-30; Victoria, British Columbia: Pacific Forestry Centre, Forestry Canada, Victoria, British Columbia; 193-202.

27. *Tetyra bipunctata* (Herrich-Schäffer)

Shieldbacked Pine Seed Bug

Pest Situation

- *Distributed throughout the South and Lake States.*
- *Hosts include all major (commercial) pine species.*
- *Both nymphs and adults feed on developing pine seeds (embryos) resulting in reduced viability. Feeding can result in abortion of conelets.*
- *One generation per year. Overwinters as adults in litter.*
- *Young nymphs feed gregariously.*
- *Long exposure to soil-borne pathogens while overwintering in litter.*

Pathogens of *Tetyra bipunctata*

The only pathological research on *T. bipunctata* has been a microbial control attempt with a bacterium.

Microbial Control. In the United States, *Bacillus thuringiensis* applied 11 times at biweekly intervals did not significantly reduce the damage caused by this pentatomid in loblolly pine (Cameron 1989).

References

Cameron, R. S. 1989. Promising new pesticides for cone and seed insect control in the southern United States. In: Proceedings of the 3rd Cone and Seed Insects Working Party Conference; 1988 June 26-30; Victoria, BC. Pacific Forestry Centre; 193-202.

Chapter 6

HOMOPTERA

Gall Formers

- *Adelges piceae* (Ratzeburg) – Balsam Woolly Adelgid
- *Adelges tsugae* Annand – Hemlock Woolly Adelgid

28. *Adelges piceae (Ratzeburg)*

Balsam Woolly Adelgid

Pest Situation

- *An introduced species in Maritime Canada and the eastern United States as far south as the Appalachians.*
- *Hosts are balsam and Fraser firs.*
- *Two to three generations per year.*
- *Galls, dieback, and mortality of firs can be extensive. Often acts in concert with pollution effects to worsen impact to high elevation forests.*
- *Low temperatures in the northern part of the range and silvicultural controls to reduce the fir content of stands can help control infestations.*
- *The rapid buildup of populations causes irreversible damage to trees. Thus, short-term control with pathogens may be effective if topically applied.*

Pathogens of *Adelges piceae*

Infections by several species of fungi have been detected in field-collected balsam woolly adelgid in many countries. No reports of other groups of entomopathogens infecting this aphid were found.

Natural Infections. Several fungal pathogens of balsam woolly aphid have been detected in field samples. An unidentified fungus was found in Canada (Balch 1952) and Austria (Schremmer 1956) on dead *A. piceae,* but was not confirmed as the primary cause of death. Many fungi were identified from

diseased *A. piceae* in Canada, Germany, Switzerland, and Turkey (Smirnoff 1971). They included *Fusarium larvarum, Cephalosporium coccorum, Cladosporium* sp., *Beauveria* sp., *Paecilomyces farinosus, Entomophthora* sp., and *Cucurbidothis* sp. *F. larvarum* was the most widespread fungal pathogen of *A. piceae*. Also, Fusarium nivale killed 45% of the aphids in a sample in North Carolina (Fedde 1971).

Microbial Control. Microbial control studies have been limited to a fungus. Field tests with *F. larvarum* in Canada and Germany resulted in insignificant control of aphid populations. Combinations of the fungus with sublethal doses of chemical insecticides, however, were effective (Smirnoff 1971). This fungus possibly was accidentally introduced and established with populations of the aphid in North America (Smirnoff 1971).

References

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29. *Adelges tsugae* Annand

Hemlock Woolly Adelgid

Pest Situation

- *Distributed throughout the range of western hemlock and in the East on eastern hemlock. Hosts are eastern and western hemlock. Alternate hosts are* ***Picea*** *spp.*
- *Twigs and needles are frequently affected, with most severe damage confined to ornamental trees.*
- *Multiple generations (three) occur annually, with wind dispersal of crawlers being important. Spruce may harbor an autumn and winter generation in some areas.*
- *Not considered a serious pest in western forests, but recent outbreaks in the East are of major concern.*
- *Predators and parasites show promise as introduced biological control agents.*

Pathogens of *Adelges tsugae*

Numerous fungi have been isolated from the hemlock woolly adelgid, and other fungi have been studied in laboratory bioassays. No other type of pathogen has been studied in this insect.

Natural Infections. Numerous fungi have been isolated from field-collected A. tsugae, including members of four genera that include insect pathogens (listed in descending order of prevalence): *Paecilomyces* sp., *Beauveria bassiana, Verticillium lecanii,* and *Acremonium* sp. (Gouli et al. 1997).

Laboratory Studies. Five fungal species were bioassayed against *A. tsugae* (Gouli et al. 1997). *Scopulariopsis* sp. was the most virulent pathogen of this insect, and *V. lecanii, B. bassiana, Paecilomyces farinosus,* and *Fusarium* sp. also were pathogenic to the hemlock woolly adelgid.

References

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Chapter 7

HOMOPTERA

Sap Feeders

- *Chrysomphalus aonidum* (L) – Florida Red Scale
- *Quadraspidiotus perniciosus* (Comstock) – San Jose Scale

30. *Chrysomphalus aonidum* (L.)

Florida Red Scale

Pest Situation

- *Apparently introduced into the South, with Florida being the focus of severe infestations. Hosts are many, but holly, citrus, and palms are most commonly infested.*
- *At least four generations occur in Florida, and five or six have been reported on occasion.*
- *Leaf drop and damage to fruit occur when populations are high.*
- *Parasites and predators provide adequate natural control in ornamental settings where direct damage to fruit is not a concern.*

Pathogens of *Chrysomphalus aonidum*

Infections by several fungi have been detected in field-collected *C. aonidium*. No reports of other entomopathogens infecting this scale insect were found.

Natural Infections. Numerous fungi are known to infect *C. aonidium* in nature. An outbreak of fungal diseases occurred among populations of *C. aonidum* in Taiwan. The fungal species isolated were *Podonectria coccicola*, *Pseudomicrocera henningsii*, and *Sphaerostilbe aurantiicola* (Yen and Tsai 1969). In India, the fungus *Podonectria sp.* was isolated from *C. aonidum*; the high natural rate of infection and mortality of scales indicated that this fungus could be used as a biological control agent for *C. aonidum* (Rao 1979). The fungus *Fusarium coccidicola* also was isolated from this scale insect in India (Barua 1983).

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31. *Quadraspidiotus perniciosus* (Comstock)

San Jose Scale

Pest Situation

- *Distributed throughout the United States, though of Asian origin*
- *Hosts are many species of shade, ornamental, and fruit trees.*
- *Fruit, twigs, or stems can be damaged. Heavy populations kill entire trees. The most destructive of scale insects in the United States.*
- *Up to five generations occur annually, but, due to asynchronous development, all life stages may occur simultaneously and throughout the season.*
- *A large number of natural enemies including introduced species often are effective controls.*

Pathogens of *Quadraspidiotus perniciosus*

Fungal infections have been detected in field-collected *Q. perniciosus*, and many fungi have been tested against this insect in laboratory. Apparently, microbial control of this scale insect has not been attempted.

Natural Infections. In the United States, field-collected *Q. perniciosus* were infected with the fungi *Fusarium coccophilum* and *Nectria flammea* (Evans and Prior 1990).

Laboratory Studies. Several pathogenic fungi have been tested against this insect in diverse locations. This scale insect has been susceptible to infection by *Nectria aurantiicola* and *Fusarium larvarum* in the United States, *Nectria diploa* and *Fusarium juruanum* in Japan, *Myrangium duriaei* in Taiwan and in the United States, *Fusarium sp.* in Syria, and *Peziotrichum saccardinum* in Argentina (Evans and Prior 1990).

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Chapter 8

HOMOPTERA

Root Feeders

- *Magicicada septendecim* (L.) -- Periodical Cicada

32. *Magicicada septendecim* (L.)

Periodical Cicada

Pest Situation

- *Widely distributed throughout the eastern United States.*
- *Lays eggs in more than 70 species of trees, but primarily oaks.*
- *Damage is due, primarily, to egg laying scars on twigs. Females may cause severe damage to young trees, nurseries, or orchards during years of emergence.*
- *Long life span (up to 17 years) of immature cicadas in the soil.*

Pathogens of *Magicicada septendecim*

A fungus infects *M. septendecim* nymphs in the field and also has been tested against this insect in the laboratory. The insect's life cycle probably has precluded any attempts at microbial control.

Natural Infections. The fungus *Massospora cicadina* has been one of the major natural mortality factors for *M. septendecim*, causing 15.7-27.1% mortality in the United States (Maier 1982).

Laboratory Studies. Laboratory tests with entomopathogens have been limited to *M. cicadina*. The fungus invaded only the abdomen of the cicadas, producing conidia that infected other cicadas (Speare 1921). Individuals secondarily infected by conidia developed resting spores in their abdomen, which eventually washed into the soil and remained viable for several years (Soper et al. 1976). It has been hypothesized that *M. cicadina* is the only host-density-dependent mortality agent for periodical cicadas (White et al. 1979).

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Chapter 9

HYMENOPTERA

Defoliators and Leaf Miners

- *Diprion similis* (Hartig) -- Introduced Pine Sawfly
- *Neodiprion excitans* Rohwer -- Blackheaded Pine Sawfly
- *Neodiprion lecontei* (Fitch) -- Redheaded Pine Sawfly
- *Neodiprion sertifer* (Geoffroy) -- European Pine Sawfly
- *Neodiprion swainei* Middleton -- Swaine Jack Pine Sawfly
- *Neodiprion taedae tsugae* Ross -- Hemlock Sawfly
- *Pikonema alaskensis* (Rohwer) -- Yellowheaded Spruce Sawfly
- *Pristiphora erichsonii* (Hartig) -- Larch Sawfly

33. *Diprion similis* (Hartig)

Introduced Pine Sawfly

Pest Situation

- *Introduced initially into Connecticut, now occurs from Maine to North Carolina, in the Central and Lake States, and in southern Ontario and Quebec.*
- *Hosts are eastern white pine and Scotch, Jack, and red pines.*
- *Severe defoliation, in the absence of natural parasites and predators if it occurs late in the season when buds are formed, can result in branch or tree death.*
- *One and a partial second generation occur. Larvae diapause in cocoons overwinter.*
- *Cocoons are subject to considerable parasitism or predation.*
- *Larvae are easily reared on host tree material.*

Pathogens of *Diprion similis*

A virus, bacteria, and several fungi have been detected in field-collected D. *similis*. There have been no reports on microbial control of this insect.

Natural Infections. A virus, bacteria, and fungi infect *D. similis* in nature. The virus *Birdiavirus diprionis* was isolated from *D. similis* in Siberia and the Soviet Far East (Gulii 1971). In Poland, *Enterobacter aerogenes* and *Pseudomonas sp.* killed 22-28% of insects in the genus *Diprion* (Glowacka-Pilot 1983). Field-collected *D. similis* in Wisconsin were infected with *Entomophthora tenthredinis* (Klein and Coppel 1973). In Poland, this fungus caused 86% mortality in *D. similis* (Swiezynska and Gornas 1976). Other pathogenic fungi

infecting *D. similis* were *Aspergillus parasiticus, Beauveria bassiana, Cephalosporium lecanii, Fusarium sp., Paecilomyces farinosus, Scopulariopsis brevicaulis*, and *Trichothecium roseum* (Swiezynska and Gornas 1976).

Laboratory Experiments. Laboratory experiments have included one virus and two bacteria. *D. similis* was not susceptible to an isolate of the European sawfly SNPV (Lobinger and *Skatulla 1989). Enterobacter cloacae* and *Streptococcus* sp. isolated from field collected *D. similis* produced 50-60% mortality in *Diprion* spp. (Glowacka-Pilot 1983).

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34. *Neodiprion excitans* Rohwer

Blackheaded Pine Sawfly

Pest Situation

- *Distributed from Virginia to Florida and westward to Arkansas and Texas.*
- *Loblolly and shortleaf pines are preferred, while longleaf, slash, spruce, and sand pines can be attacked.*
- *Defoliation in fall in dense sawtimber stands results in growth loss and increased susceptibility to bark beetles and borers.*

- *Outbreaks usually subside after one or two seasons.*
- *There are three or four generations per year in the Gulf Coast region.*
- *Cocoons are subject to considerable parasitism and predation.*
- *Controls are normally not necessary in natural forests.*

Pathogens of *Neodiprion excitans*

Infections by fungi have been detected in field-collected larvae of *N. excitans*. There have been no reports of other entomopathogens infecting this insect.

Natural Infections. In Central America, field-collected *N. excitans* have been found infected with the fungi *Aspergillus* sp., *Scopulariopsis* sp., *Penicillium* sp., *Beauveria bassiana, Fusarium* sp., and *Cladosporium* sp. (Wilkinson and Drooz 1979).

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35. *Neodiprion lecontei* (Fitch)

Redheaded Pine Sawfly

Pest Situation

- *Distributed in southeastern Canada and throughout the eastern United States, westward to Texas.*
- *Preferred hosts are jack, red, shortleaf, loblolly, slash, longleaf, and pitch pines. Other conifers may also be defoliated, especially when growing near preferred hosts.*
- *Probably the most widespread and destructive of the pine sawflies. Any stress from climate or competition furthers susceptibility to infestation, defoliation, and damage. Outbreaks occur frequently throughout the range.*
- *In the South there are at least three and in the North one generation per year.*
- *Preventive practices reduce hazard in managed pine plantations.*
- *Egg parasites and other beneficial insects reduce natural population levels.*

Pathogens of *Neodiprion lecontei*

Naturally occurring entomopathogens have not been reported for the redheaded pine sawfly, and laboratory studies have been limited to a protozoan. There have been numerous attempts, however, at microbial control of this insect with a virus.

Natural Infections. Presumably, *N. lecontei* nuclear polyhedrosis virus (NPV) must naturally infect pineheaded sawfly populations, because this virus has been isolated (Groot et al. 1979).

Laboratory Studies. In Canada, the microsporidium *Thelohania pristiphorae* was transmitted orally to larvae of *N. lecontei* feeding on *Pinus strobus* (Smirnoff 1974).

Microbial Control. Microbial control attempts have been limited to viruses. In the United States, application of Lecontvirus (an *N. lecontei* NPV) at $5 \infty 10^6$ polyhedral inclusion bodies per hectare (PIB/ha) eliminated a redheaded pine sawfly larval population in 2 weeks. Additionally, larval populations were reduced by more than 96% even at a low dosage of 10^6 PIB/ha (Podgwaite et al. 1986). In Canada, Lecontvirus at $5 \infty 10^9$ PIB/ha in volumes ranging from 2.4 to 9.4 l/ha resulted in excellent control of redheaded pine sawfly (Cunningham et al. 1987). In Canada, an NPV isolated from *N. lecontei* was applied at $5 \infty 10^6$ PIB/ha at a rate of 9.4 l/ha; the virus killed 90% of larval colonies 16 days after application (Groot et al. 1979). Similar results have been reported by Kaupp et al. (1978) and Groot and Cunningham (1985). Application of insect virus with a Leco ultra-low volume (ULV) cold fog generator model HD, with a droplet spectrum of 15-30 nm and densities of more than $5000/cm^2$ (at the nozzle) and $390/cm^2$ (22 m away from nozzle), killed 72% of redheaded pine sawfly larvae, as compared to 9% mortality in controls (Johnson et al. 1978).

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36. *Neodiprion sertifer* (Geoffroy)

European Pine Sawfly

Pest Situation

- *A widely distributed introduced pest occurring from New England to Missouri and South Dakota.*
- *Hosts include Scotch, red, jack, and other pines.*
- *Defoliation, even when severe, rarely results in tree mortality since the larvae avoid new foliage.*
- *Damage is most severe in Scotch pine Christmas tree plantations where cosmetics are important.*
- *There is one generation per year and eggs (in needles) overwinter.*
- *Several parasites have been released to provide some population control.*

Pathogens of *Neodiprion sertifer*

Viral and fungal infections have been detected in European pine sawfly populations, and viruses and a nematode have been tested against this insect in the laboratory. There have been numerous attempts at microbial control of this insect, primarily with viruses.

Natural Infections. Viruses and fungi are known pathogens of European pine sawfly in nature. A virus, *Birdiavirus diprionis*,was isolated from field-collected European pine sawfly in Siberia (Gulii 1971) and the USSR (Supatashvili and Chkhubianishvili 1982). A nuclear polyhedrosis virus (NPV) caused epizootics in *N. sertifer* populations in Britain, producing up to $2\text{-}3\infty10^{15}$ PIB/ha (Kaupp 1983). The NPV occurred naturally in soil from different sites in Great Britain (Kaupp 1989a) and caused natural epizootics that were dependent on population densities of the NPV and of *N. sertifer* (Kaupp 1989b). The entomopathogenic fungi *Beauveria bassiana, Metarhiziium anisopliae, Paecilomyces farinosus*, and *Paecilomyces fumoso-roseus* also have been isolated from *N. sertifer* (Kalvish et al. 1991).

Laboratory Studies. Laboratory experiments have included viruses and a nematode. Virox, an NPV preparation, was effective against *N. sertifer* with an LC_{50} of $6.9\infty10^2$ PIB/ml for the first and second instars (Glowacka et al. 1987). In Sweden, soil extracts contained 10^5 and $7\infty10^2$ PIB/ml soil of *N. sertifer* NPV 1 year and 9 years after a viral application and epizootic, respectively (Olofsson 1988a). The nematode Heterorhabditis heliothidis (= bacteriophora) killed 100% of late-instar European pine sawflies at 15°C (Finney and Bennett 1983).

Microbial Control. Microbial control experiments with N. sertifer have included viruses and a bacterium.

Attempts at microbial control of N. sertifer have primarily involved viruses. *N. sertifer* NPV at $2.5\infty10^9$ PIB/ha controlled the European pine sawfly in a plantation with moderate to dense populations of the insect (Podgwaite et al. 1984). The 'Latvian' strain of NPV killed 80-100% of European pine sawfly within 13-17 days after application (Zarin and Augstkalnin 1976). Application of high and low doses of Neocheck-S (an N. sertifer NPV product) reduced larval populations by 90% in all sprayed plots within 28 days (Podgwaite et al. 1984). Virox, another preparation of NPV, when sprayed on young pine trees at 0.1 l/ha, killed 100% of European pine sawflies (Glowacka et al. 1987). Virin-Diprion (another N. sertifer NPV preparation) was 91% effective against *N. sertifer* in the USSR (Kulikovskii 1984). A 0.05-0.1% copper sulphate adjuvant shortened the incubation period of NPV and increased its effectiveness against European pine sawfly even under unfavorable field conditions in West Germany (Wellenstein 1973).

Certain microbial control experiments with viruses have included aspects of viral persistence and spread, as well as host-insect susceptibility. Application of *N. sertifer* NPV against European pine sawflies infesting red pine resulted in viral recycling, and the average number of PIB accumulated was inversely related to larval density (Mohamed et al. 1983). In Wisconsin, rapid field release of adults of the parasitoid *Lophyroplectus oblongopunctatus* sprayed with NPV successfully transmitted the virus to feeding European pine sawfly larval populations in red pine (Mohamed et al. 1981). In Sweden, *N. sertifer* NPV did not persist and spread sufficiently in field trials for control of a European pine sawfly outbreak (Olofsson 1988b). In Finland, acid rain might have reduced the susceptibility of *N. sertifer* to the NPV due to changes in the quality of pine foliage (Neuvonen et al. 1990).

Two control experiements have included *Bacillus thuringiensis*. In Austria, Dipel *(B. thuringiensis HD-1)* was not effective against the European pine sawfly (Donaubauer and Schmutzenhofer 1973). In Russia, an aqueous suspension of *N. sertifer* NPV was more effective against European pine sawfly than Entobakterin (a *B. thuringiensis* preparation) (Gulii 1972).

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37. *Neodiprion swainei* Middleton

SWAINE JACK PINE SAWFLY

PEST SITUATION

- *Distributed throughout eastern Canada and the Great Lakes States.*
- *The preferred host is jack pine, but red, Scotch, and eastern white pines growing in close proximity to infested jack pines are subject to defoliation by dispersing larvae.*
- *Outbreaks have occurred at approximately 8-year intervals in jack pine stands in Ontario and Quebec.*
- *Tree mortality occurs on sandy plains after successive years of defoliation. Surviving trees may display considerable variation in crown dieback.*
- *There is one generation per year with prepupae in cocoons overwintering in the litter on topsoil.*

PATHOGENS OF *NEODIPRION SWAINEI*

A protozoan and virus have been detected in field-collected larvae of *N. swainei.* Two species of protozoa and a virus have been tested against this insect in the laboratory.

Natural Infections. Field-collected larvae of *N. swainei* have been infected with a protozoan, Herpetomonas swainei, in Canada. Mortality of *N. swainei*infected by this protozoan in the early stage of development of the larvae was 20% (Smirnoff and Jipa 1970).

Laboratory Studies. Laboratory studies with entomopathogens have been limited to a virus and protozoa. *N. sertifer* nuclear polyhedrosis virus (NPV) was 50% inactivated after exposure to sunlight for 150 h (Smirnoff 1971). *Herpetomonas swainei* reduced the proportion of sawfly adults emerging from cocoons to 20% compared with 55% among healthy insects (Smirnoff 1974a).

The microsporidium *Thelohania pristiphorae* was transmitted orally to larvae of *N. swainei* feeding on *Pinus strobus* (Smirnoff 1974b).

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38. *Neodiprion taedae linearis* Ross

Loblolly Pine Sawfly

Pest Situation

- *Distributed throughout Arkansas, Louisiana, eastern Texas, Mississippi, South Carolina, and northward to Ohio and Illinois.*
- *Loblolly and shortleaf pines are the only hosts.*
- *Severe outbreaks can occur resulting in severe temporary losses in radial growth. Mortality is not commonplace even during prolonged outbreaks.*
- *There is one generation per year, with eggs overwintering in needles.*
- *Naturally occurring parasites and cold weather in spring are effective control factors.*
- *Direct control is usually not necessary except in high-value plantings.*

Pathogens of *Neodiprion taedae linearis*

Loblolly pine sawfly larvae are known to be susceptible to infection by a virus, which also has been tested in the field against this insect. There have been no reports of other entomopathogens infecting the loblolly pine sawfly.

Natural Infections. Larvae of loblolly pine sawfly collected in Arkansas were infected with a nuclear polyhedrosis virus (NPV) (Young et al. 1972).

Microbial Control. Microbial control studies have been limited to the *N. taedae linearis* NPV. Application of NPV at 10^7 polyhedral inclusion bodies PIB/ml to eggs and surrounding foliage significantly increased the mortality of the loblolly pine sawfly compared with an untreated check (Young and Yearian 1986). Aerial application of NPV at $5 \infty 10^7$ PIB/ml reduced sawfly populations in Arkansas (Yearian et al. 1973). Larval susceptibility decreased as the stage of the insect increased (Young and Yearian 1984). In Arkansas, there was 37-98% secondary transmission of the NPV from primary infected larvae. Intercolony secondary transmission was lower than intracolony transmission (Young and Yearian 1987). Mortality in untreated colonies was greatest when the treated and untreated colonies were located in the upper canopy of trees and when small larvae were treated with the virus (Young and Yearian 1989).

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39. *Neodiprion taedae tsugae* Ross

HEMLOCK SAWFLY

PEST SITUATION

- *Distributed throughout West Coast States and Provinces from Oregon to Alaska. Also found in interior forests of Idaho and Montana.*
- *The preferred host is western hemlock.*
- *Damage, through defoliation and growth loss, is evident on trees with severe defoliation.*
- *Larvae feed on old needles only, leaving new growth to sustain trees, even during outbreaks.*
- *There is one generation per year, and cocoons overwinter in the duff layer.*
- *Direct control often is not warranted because only old needles are consumed.*

PATHOGENS OF *NEODIPRION TSUGAE*

Infections by a fungus have been detected in field-collected larvae of hemlock sawfly. No reports of other entomopathogens infecting this insect were found.

Natural Infections. One of the most important biotic agents limiting populations of hemlock sawfly in Alaska was the fungus *Entomophthora sphaerosperma* (Hard 1976, Hard and Schmiege 1968).

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40. *Pikonema alaskensis* (Rohwer)

Yellowheaded Spruce Sawfly

Pest Situation

- *Distributed from Wyoming to Alaska.*
- *Hosts are Engelmann, white, blue, and black spruces.*
- *Most severe damage and mortality occur in ornamental and shelterbelt plantings.*
- *There is one generation per year with cocoons overwintering in the duff or topsoil.*
- *Like many sawflies, natural controls are usually sufficient to preclude direct control measures.*

Pathogens of *Pikonema alaskensis*

Laboratory studies with entomopathogens have been limited to a protozoan. There were no reports on other entomopathogens infecting this insect.

Laboratory Studies. *Thelohania pristiphorae,* a microsporidium that infects larvae of *Pristiphora erichsonii,* could be transmitted orally to larvae of *P. alaskensis* feeding on *Picea* spp. (Smirnoff 1974).

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41. *Pristiphora erichsonii* (Hartig)

LARCH SAWFLY

PEST SITUATION

- *Distributed throughout the range of eastern and western larch in the northern United States, including Alaska and Canada.*
- *Hosts are native as well as exotic larches (tamarack).*
- *Heavily defoliated trees often refoliate after a few weeks; however, repeated defoliations result in dieback and, after 6-9 years, in tree mortality.*
- *Mortality to western larch has been confined to areas under stress from other factors.*
- *There is one generation per year, with cocoons overwintering on or in the ground.*
- *Parasites, both native and introduced, have provided effective control, although sawflies developed immunity to at least one imported ichneumonid.*

PATHOGENS OF *PRISTIPHORA ERICHSONII*

A pathogenic protozoan has been detected in field-collected larch sawfly, and laboratory experiments similarly have been limited to protozoa. A bacterium, fungus, protozoan, and nematodes have been tried for the microbial control of this insect.

Natural Infections. In Canada, 25% of natural populations of larch sawfly contained insects that were infected with a microsporidium, *Pleistophora sp.* (Percy et al. 1982).

Laboratory Studies. The protozoan *Cystosoporogenes pristiphorae*, a conspecific of *Thelohania pristiphorae* and *Pleistophora* sp., infected larvae of larch sawfly after laboratory inoculation (Darwish et al. 1992). *Pleistophora schubergi* at $4 \infty 10^6$ and $4 \infty 10^8$ spores/ml infected 45.5 and 65.6%, respectively, of larch sawfly larvae (Wilson 1981). An infection with an unidentified microsporidium reduced the degree of lipid unsaturation in larvae of larch sawfly (Smirnoff 1971).

Microbial Control. Several entomopathogens have been tested for microbial control of this insect. In China, applications of *Bacillus thuringiensis, Beauveria* sp., and entomopathogenic nematodes killed 5-27%, 28-52%, and 80-100% of larch sawfly larvae, respectively (Zhou et al. 1995). An aqueous suspension of *P. schubergi* containing $5 \infty 10^8$ spores/ml and 30 g/l of the sunlight protectant IMC 90-001 was applied to branches of larch in Canada, resulting in 40% infection in treated branches as compared with 10% in controls (Wilson 1981). In a nematode

experiment, addition of a water thickener (Gelgard M at 0.13%), an evaporation retardant (Folicote 351 at 0.2%), and a surfactant (Arlatone T at 0.1%) to a suspension of *Steinernema carpocapsae* increased mortality of sawfly larvae from 24 to 90% (Webster and Bronskill 1968).

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Chapter 10

HYMENOPTERA

Borers

- *Sirex* spp., *Sirex noctilio* F. -- Horntails

42. *Sirex* spp., *Sirex noctilio* F.

HORNTAILS

PEST SITUATION

- *Several species distributed throughout North America.* ***Sirex noctilio*** *is a severe problem in plantations of Australia, New Zealand, and Brazil.*
- *Larvae bore in stems of stressed or recently felled trees.*
- *Many species have symbiotic fungi required for larval feeding.*
- *Long life cycle—up to several years in wood—favors introduction into new hosts and habitats.*
- *Larvae can be exposed to pathogens in dead, moist wood over a long developmental period.*
- *Not easily cultured in the laboratory.*

PATHOGENS OF *SIREX NOCTILIO*

Entomopathogenic nematodes are known to infect *S. noctilio* in nature, and nematodes have been tested for microbial control. No reports of other entomopathogens infecting this insect were found.

Natural Infections. Nematodes are important natural control agents for *S. noctilio*. More than 95% of horntail larvae collected in New Zealand were infected with a nematode, which was later identified as *Deladenus* sp. (Zondag 1969). Adult females can be sterilized by infections with these nematodes; however, in Auckland, a benign strain of *Deladenus siricidicola* was isolated, that does not sterilize the female *S. noctilio* (Zondag 1975). Bedding (1974) described five new species of *Deladenus* parasitizing *S. noctilio* in North Africa, Japan, Canada, the United States, India, Pakistan, New Zealand, and in most European countries.

Microbial Control. An important example of introduction-establishment involves a nematode pathogen of *S. noctilio*. The introduction of *D. siricidicola* into *S. noctilio* populations in Australia has resulted in classical biological control of this insect (Bedding 1984). After introduction, the nematodes were found in 37% of Sirex-infested trees, increasing to 70% after 2 years. Over 90% of the Sirex emerging from the trees were infected with the nematode (Bedding 1984). In another study, release of nematode-infected *S. noctilio* and inoculation of trees with nematodes resulted in rapid spread of the nematode and 90% infection of the emerging horntails (Pinnock 1976). In another method of introduction, Sirex-attacked trees were felled, holes were punched with a Gould hammer every 30 cm along the bole of a tree, and these holes were filled with a 12% gelatin foam containing the nematodes (ca. 2000 nematodes/hole). This resulted in 95% parasitism of emerging *S. noctilio* (Bedding and Akhurst 1974). In 1985-88, artificial inoculation of radiata pines with the nematode resulted in less than 30% parasitization of the emerging S. noctilio (Haugen and Underdown 1993). Microbial control of the horntails with *D. siricidicola* was attempted in Brazil, and the initial results were promising (Vibrans 1991).

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Chapter 11

LEPIDOPTERA

Defoliators and Budworms

- *Acleris gloverana* (Walsingham) -- Western Blackheaded Budworm
- *Alsophila pometaria* (Harris) – Fall Cankerworm
- *Anisota senatoria* (J.E. Smith) – Orangestriped Oakworm
- *Archips argyrospila* (Walker) – Fruittree Leafroller
- *Argyresthia thuiella* (Packard) – Arborvitae Leafminer
- *Choristoneura conflictana* (Walker) – Large Aspen Tortrix
- *Choristoneura fumiferana* (Clemens) – Spruce Budworm
- *Choristoneura occidentalis* Freeman – Western Spruce Budworm
- *Coloradia pandora* Blake – Pandora Moth
- *Datana integerrima* Grote and Robinson -- Walnut Caterpillar
- *Dioryctria abietivorella* (Grote) -- Fir Coneworm
- *Dioryctria amatella* (Hulst) -- Southern Pine Coneworm
- *Ennomos subsignaria* (Hübner) -- Elm Spanworm
- *Hemileuca maia* (Drury) -- Buck Moth
- *Heterocampa guttivitta* (Walker) -- Saddled Prominent
- *Lochmaeus manteo* Doubleday -- Variable Oakleaf Caterpillar
- *Hyphantria cunea* (Drury) -- Fall Webworm
- *Lambdina fiscellaria fiscellaria* (Guenée) -- Hemlock Looper
- *Lambdina fiscellaria lugubrosa* (Hulst) -- Western Hemlock Looper
- *Lambdina fiscellaria somniaria* (Hulst) -- Western Oak Looper
- *Lymantria dispar* (L.) -- Gypsy Moth
- *Malacosoma americanum* (F.) -- Eastern Tent Caterpillar
- *Malacosoma disstria* Hübner -- Forest Tent Caterpillar
- *Orgyia leucostigma* (J. E. Smith) -- Whitemarked Tussock Moth
- *Orgyia pseudotsugata* (McDunnough) -- Douglas-fir Tussock Moth
- *Paleacrita vernata* (Peck) -- Spring Cankerworm
- *Thyridopteryx ephemeraeformis* (Haworth) -- Bagworm
- *Zeiraphera canadensis* Mutuura and Freeman -- Spruce Bud Moth

43. *Acleris gloverana* (Walsingham)

Western Blackheaded Budworm

Pest Situation

- *Distributed from northern California to western Montana and northward into the Yukon and Northwest Territories of Canada.*
- *Hosts are various species of firs, western hemlock, and Engelmann, sitka, and white spruces.*
- *Extensive outbreaks in British Columbia and southern Alaska resulted in considerable tree mortality.*
- *There is one generation per year, with eggs on the undersides of needles being the overwintering stage.*
- *Can be cultured in the laboratory on natural foliage or artificial media.*

Pathogens of *Acleris gloverana*

Infections by a virus have been detected in field-collected larvae and pupae of western blackheaded budworm. There were no reports of other entomopathogens infecting this insect.

Natural Infections. In British Columbia, a nuclear polyhedrosis virus (NPV) infected a small percentage of the larvae and pupae in a population of *A. gloverana* which was increasing to outbreak status (Smirnoff 1972).

References

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44. *Alsophila pometaria* (Harris)

FALL CANKERWORM

PEST SITUATION

- *Distributed from the Maritime Provinces to Alberta in southern Canada, and throughout the eastern United States as far south as Georgia and as far west as Montana.*
- *Hosts are elm, apple, hickory, maple, beech, cherry, various oaks, and other forest and shade trees.*
- *Defoliation occurs periodically over large, forested areas. Shade trees in urban and suburbanareas are subject to heavy infestation and may be severely damaged.*
- *There is one generation per year with pupae overwintering in the soil.*
- *A parasitoid is a major factor in the decline of cankerworm populations.*

PATHOGENS OF *ALSOPHILA POMETARIA*

Viruses and a bacterium are known pathogens of fall cankerworm. Two strains of *Bacillus thuringiensis* also have been tested against this insect in the laboratory. There have been few attempts at microbial control.

Natural Infections. Infections by a nuclear polyhedrosis virus and a cytoplasmic polyhedrosis virus have been detected in field samples of fall cankerworm (Martignoni and Iwai 1981). Apparently, there has been no other research of these viruses.

Laboratory Experiments. Laboratory tests with entomopathogens have been limited to a bacterium. *A. pometaria* has been infected with *B. thuringiensis* var. *thuringiensis* and *B. thuringiensis* var. *galleriae*. *B. thuringiensis* var. *thuringiensis* was 30-60% more virulent than *B. thuringiensis* var. *galleriae* based on LD_{50}s, and the former had an efficacy level that should be sufficient for economic pest control (Larson and Ignoffo 1971).

Microbial Control. Microbial control experiments have been limited to *B. thuringiensis*. Foliar sprays of *B. thuringiensis* gave excellent control of the larvae on American linden (*Tilia americana*) in Illinois (Appleby et al. 1975). *B. thuringiensis* applied with hydraulic sprayer or fogger controlled *A. pometaria* on Siberian elm (*Ulmus pumila*) in North Dakota (Frye et al. 1976). Spraying *B. thuringiensis* var. *alesti* (Dipel R) in late May or early June was recommended for control of *A. pometaria* infesting hardwoods in the United States and Canada (Hildahl and Peterson 1974).

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45. *Anisota senatoria* (J. E. Smith)

Orangestriped Oakworm

Pest Situation

- *Distributed from eastern Canada to Georgia and westward to Minnesota, Iowa, and Texas, rare in the Southeast.*
- *Various species of oaks throughout the range of the insect serve as hosts. No single species is preferred.*
- *Gregarious feeders consume all but leaf veins. Solitary feeding by older larvae occurs also.*
- *Defoliation, though often extensive, occurs late in summer or fall and, thus, has little impact on tree growth.*
- *There is one generation (one or two in Southeast) per year with pupae overwintering in the soil.*

Pathogens of *Anisota senatoria*

Orangestriped oakworm larvae are known to be susceptible to infection by a virus, bacterium, and protozoan. These entomopathogens have been tested against this insect in the laboratory. No reports of nematode or fungal infections in *A. senatoria* were found.

Natural Infections. Only one protozoan, *Pleistophora schubergi*, has been found infecting the orangestriped oakworm in nature (Henry 1981). There have been no reports of natural infection by other group of entomopathogens.

Laboratory Experiments. Laboratory tests with entomopathogens have been limited to a virus, bacterium, and protozoan. A nuclear polyhedrosis virus isolated from *Autographa californica* infected larvae of *A. senatoria* (Kaya 1977). Larvae were also susceptible to a liquid formulation of *Bacillus thuringiensis* var. *alesti*, with an LC_{50} of $2.2 \infty 10^3$IU /ml per gram of insect (Ignoffo et al. 1973). When various formulations of *B. thuringiensis* var. *alesti* were evaluated, dust formulations were least effective against the larvae (Kaya 1974). The protozoan *P. schubergi* is also pathogenic to larvae; infected larvae were smaller and less vigorous than uninfected insects (Kaya 1973).

Microbial Control. Bacteria and protozoa were tested for the microbial control of *A. senatoria* larvae. The *B. thuringiensis* product Thuricide HPC at $1.80 \infty 10^9$ IU/100 gal gave good control of the second and third instars (Kaya 1974). Spores of *P. schubergi* applied at $2 \infty 10^8$ spores/ml with an ultraviolet protectant infected 88% of *A. senatoria* larvae (Kaya 1975).

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46. *Archips argyrospila* (Walker)

FRUITTREE LEAFROLLER

PEST SITUATION

- *Distributed throughout the United States and from coast to coast in southern Canada.*
- *Hosts include many fruit treees and forest and shade trees such as ash, elm, oaks, citrus in California, and baldcypress in Louisiana.*
- *Varying degrees of defoliation result in growth loss in timber species. Destruction of vegetative tips can reduce fruit production. In certain orchard species, direct damage to fruit can result in heavy commercial loss. Baldcypress trees in Louisiana are heavily damaged in permanently flooded landscapes.*
- *There is one generation per year throughout the range, and eggs overwinter.*
- *Not easily reared.*

PATHOGENS OF *ARCHIPS ARGYROSPILA*

Viral infections have been detected in fruit tree leafroller, and a bacte rium and virus have been field tested against this insect. No reports of other entomopathogens infecting *A. argyrospila* were found.

Natural Infections. A granulosis virus was found infecting the fruittree leafroller in the United States and Canada (Martignoni and Iwai 1986, Zimmermann and Weiser 1991).

Microbial Control. A bacterium and virus have been used for microbial control of *A. argyrospila* larvae. A granulosis virus applied at $1.4 \infty 10^9$ granules/ml caused 50% mortality of fifth instars (Pinnock and Milstead 1978). Early season control of fruittree leafroller on pear was attempted with *Bacillus thuringiensis* applied with Microgen or handgun. Both application methods suppressed the number of rolled leaves and early fruit damage compared to the control (Sorensen and Falcon 1980). *B. thuringiensis* applied at the pink stage of apple blossom development gave adequate control of fruit tree leafroller in Canada and was suggested as the control material for commercial orchards (Vakenti et al. 1984). In another trial, *B. thuringiensis*

serotype III at 192 and $80 \infty 10^6$ IU/liter was effective against field populations of this insect (Pinnock and Milstead 1978). However, the *B. thuringiensis* product Dipel at 1.1 kg/ha was ineffective against the larvae (Madsen et al. 1977).

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47. *Argyresthia thuiella* (Packard)

Arborvitae Leafminer

Pest Situation

- *Distributed throughout the range of northern white cedar (eastern Canada, south and west to the Mid-Atlantic States and Missouri).*
- *Hosts are northern white and red cedars.*
- *Damage to ornamentals and nursery seedlings often is serious, and heavily defoliated trees may die.*
- *One generation per year with larvae overwintering in leaf mines.*
- *Protected in leaf mines throughout most of their life cycle.*

Pathogens of *Argyresthia thuiella*

Microbial control of Arborvitae leafminer has been attempted with *Bacillus thuringiensis*. No reports of other entomopathogens infecting *A. thuiella* were found.

Microbial Control. Field trials in the German Federal Republic determined that at least five applications of Dipel (*B. thuringiensis* var. *kurstaki*) were required for effective control of *A. thuiella* (Langenbruch 1984).

References

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48. *Choristoneura conflictana* (Walker)

LARGE ASPEN TORTRIX

PEST SITUATION

- *Distributed from the Atlantic Coast to Alaska, California, Arizona, New Mexico, and throughout the range of quaking aspen.*
- *The principal host is quaking aspen, though several other hardwoods such as balsam poplar, big tooth aspen, paper birch, willow, and alder are also damaged.*
- *Epidemics have occurred sporadically in extensive stands of aspen in the western Provinces of Canada and in the eastern United States. Trees may be defoliated for 2 or 3 years during outbreaks, but they normally recover after only growth loss.*
- *One generation per year, with second instars overwintering in hibernacula in bark crevices.*
- *Starvation of larvae is considered to be the likely cause of decline of outbreaks.*
- *Large, contiguous, pure stands of aspen lead to large populations of the insect.*

PATHOGENS OF *CHORISTONEURA CONFLICTANA*

Pathogenic viruses, fungi, and a protozoan have been detected in field-collected *C. conflictana* larvae. Only *Bacillus thuringiensis* has been tested for microbial control of this insect.

Natural Infections. Numerous pathogens are known to infect *C. conflictana* in nature. A previously undescribed entomopoxvirus was isolated from larvae of *C. conflictana* in Canada (Cunningham et al. 1973). *C. conflictana* also has been infected by entomopoxvirus, nuclear polyhedrosis virus, and cytoplasmic polyhedrosis virus (Martignoni and Iwai 1986, Zimmermann and Weiser 1991). Prevalence rates in *C. conflictana* populations in Canada ranged as high as 18.1% infection by granulosis virus, 44.4 % by microsporidia, 10.6% by entomopoxvirus, 0.5% by *Entomophthora* sp., and 16.7% by multiple infections with two or three of the pathogens (Burke and Percy 1982). Burke (1985) reported several microorganisms infecting *C. conflictana*, including granulosis virus, entomopox virus, three species of microsporidia, three species of fungi, and mixed infections of two or three microorganisms.

Microbial Control. The efficacy of *B. thuringiensis* was evaluated against the large aspen tortrix. Treatments with Dipel 4L and Thuricide 32LV resulted in population reductions of 69% and 76%, respectively (Holsten and Hard 1985).

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49. *Choristoneura fumiferana* (Clemens)

Spruce Budworm

Pest Situation

- *Distributed from Virginia to Labrador and westward to the Mackenzie River Valley in the Yukon.*
- *Preferred host is balsam fir. White, red, and black spruces; larches, pines, and western firs also are infested.*
- *Forms occurring in western Canada and the United States have been considered a different species (**C. occidentalis**).*

- *Defoliation results in growth loss and, when repeated for several years, can lead to widespread mortality. Overmature stands with a majority component of balsam fir have traditionally been most severely impacted.*
- *One of the most widespread and damaging forest insect pests in North America.*
- *One generation per year with second instars overwintering in hibernacula in needles.*

Pathogens of *Choristoneura fumiferana*

Infections by different types of viruses, fungi, and protozoa have been detected in field-collected spruce budworm. Various groups of entomopathogens have been tested against this insect in the laboratory, and there have been numerous attempts at microbial control.

Natural Infections. Nuclear polyhedrosis virus (NPV), cytoplasmic polyhedrosis virus (CPV), granulosis virus (GV), and entomopox virus (EPV) have been isolated from the spruce budworm (Martignoni and Iwai 1986, Zimmermann and Weiser 1991). Two EPV strains, which could exist separately or together, were isolated in Canada (Arif et al. 1980).

Field sampling of spruce budworm larvae has detected infections by several fungal pathogens. *Entomophthora sphaerosperma*, *Entomophthora egressa*, and a species of *Conidiobolus* were isolated in the United States (Vandenberg and Soper 1978). In New Brunswick, the fungi *Hirsutella longicolla* var. *cornuta* and *Hirsutella nodulosa* were found infecting larvae (Strongman et al. 1990a). In Ontario, *Beauveria* sp. and *Cephalosporium sphaerosperma* infected insects in the field but caused less than 2% mortality (Harvey and Burke 1974). Also, *Erynia* sp. (Humber 1986), *Hirsutella gigantea* (Humber 1992), *Tolypocladium nivem* (Humber 1992), *Entomophthora egressa* (=*Entomophaga aulicae*) (Zimmermann and Weiser 1991, Humber 1992) and *Zoophthora* (=*Erynia*) *radicans* (Zimmermann and Weiser 1991, Humber 1992) were isolated from field collected larvae in the United States and Canada.

Protozoan pathogens are commonly found in field-collected *C. fumiferana*. In Canada, 50.6, 41.6, and 82.0% of spruce budworm larvae were infected with *Nosema fumiferanae* in 1972, 1973, and 1974, respectively (Wilson 1973). Spruce budworm larvae collected in Canada over a 6-year period indicated that infections by *N. fumiferanae* increased from 35.9% in 1973 to 69.0% in 1978 (Wilson 1978a). Prevalence rates of *N. fumiferanae* also have been observed in other field studies of spruce budworm in Canada and the United States (Canning 1981, Henry 1981, Zimmermann and Weiser 1991). Other protozoa that infect the spruce budworm are *Nosema cerasivoranae*, *Nosema cacoeciae*, *Nosema thomsonii*, *Thelohania* sp., and *Pleistophora schubergi fumiferanae* (Zimmermann and Weiser 1991).

Laboratory Experiments. Laboratory tests with spruce budworm have included all five entomopathogen groups.

Spruce budworm has been infected with NPV, GV, and CPV in the laboratory. The LC_{50}s of NPV and GV against fifth instars were 483 polyhedral inclusion bodies (PIB)/mm^2 of diet and 14,652 capsules/mm^2 of diet, respectively (Cunningham et al. 1983a). *C. fumiferana* larvae developed resistance to both NPV and CPV. The resistance developed more rapidly and to a greater degree against NPV than against CPV (Bird 1969). An NPV isolated from the larvae of *Archips cerasvoranus* (Fitch) in Canada caused 100% mortality of spruce budworm in 25-65 days (Smirnoff 1971). NPV from spruce budworm changed its production and virulence after passage in *Trichoplusia ni* (Hübner) and *Galleria mellonella* (L.) (Stairs et al. 1981).

The virulence of several varieties of *Bacillus thuringiensis* was tested in spruce budworm. The varieties *alesti, berliner, entomocidus, sotto,* and *galleriae* were highly to moderately virulent; the variety *kenyae* was less virulent; and the variety *finitimus* was only slightly virulent to the spruce budworm (Yamvrias and Angus 1970). Van Frankenhuyzen (1989a) found no significant differences in virulence between the HD-1 and NRD-12 strains of *B. thuringiensis* var. *kurstaki*. One strain of *B. thuringiensis* was more effective than HD-1 was against spruce budworm, both under laboratory and field operational conditions (Dubois 1985). Non-crystalliferous strains of *B. thuringiensis* and *Bacillus cereus* were as virulent to budworm larvae as a crystalliferous strain of *B. thuringiensis* (Smirnoff 1977).

Several studies of this pest have been directed at improving the efficacy of *B. thuringiensis*. Van Frankenhuyzen and Payne (1993) presented theoretical calculations of droplet sizes and product potencies required to deliver a lethal dose of *B. thuringiensis* in one droplet to larvae in aerial spray applications. Payne and Van Frankenhuyzen (1995) suggested that the efficacy of spruce budworm sprays might be improved by increasing the product potency and active ingredient application rate. Infection with *N. fumiferanae* increased spruce budworn susceptibility to *B. thuringiensis* (Bauer and Nordin 1989a). There was a strong correlation between enhanced spruce budworm mortality and an increase in chitinase titre among *B. thuringiensis* strains (Gunner et al. 1985). *B. thuringiensis* virulence to *C. fumiferana* was greater at higher than at lower temperatures due to proliferation of vegetative cells in the infected larvae (Van Frankenhuyzen 1994). *B. thuringiensis* inhibited feeding of spruce budworm larvae at sublethal concentrations (Retnakaran et al. 1983). Finally, sixth-instar spruce budworms were force-fed purified *B. thuringiensis* crystals, purified *B. thuringiensis* spores, and mixtures of both. The spores played little or no role in mortality (Fast 1977).

The fungi might include candidates for spruce budworm control, based on laboratory experiments. Spruce budworm has been infected by *Fusarium sporotrichioides* (Strongman et al. 1990b), *E. aulicae* (Tyrrell 1990), and *Z. radicans* (Soper and Ward 1981). *F. sporotrichioides* produces a mycotoxin which was toxic to spruce budworm (Strongman et al. 1990b), but no evidence for toxin production was found in *E. aulicae* culture (Tyrrell 1990).

Entomophthoralean fungi were not compatible with other pathogens of spruce budworm, indicating that the spread of this fungus might be inhibited by the presence of other pathogens (Soper and Ignatowicz 1986).

Certain microsporidia have features that could make them useful for the introduction and establishment or seasonal colonization approaches to microbial control of *C. fumiferana*. *N. fumiferanae* and *P. schubergi* had LD_{50}s of $2.81 \infty 10^6$ spores/larva (Wilson 1985a) and $6.3 \infty 10^4$ spores/larva (Wilson 1985b), respectively. Susceptibility to both protozoans decreased with increasing larval age (Wilson 1974, 1982), but high concentrations of *N. fumiferanae* spores fed to larvae resulted in 100% infection of the adults (Wilson 1974). *N. fumiferanae* was transmitted transovarially to 100% of the progeny of infected adults; diseased progeny died as larvae, and surviving progeny were approximately 25% smaller and took 17% longer to complete development than did healthy insects (Bauer and Nordin 1989b). *N. fumiferanae* and *P. schubergi* are not transmitted congenitally through the male. Mating of infected males and healthy females did not reduce fecundity or egg viability; however, the fecundity of females infected with *P. schubergi* was reduced (Wilson 1984). Also, female larvae inoculated with the LD_{50} of *N. fumiferanae* exhibited significant reductions in consumptive index, nitrogen consumptive index, relative growth rate, and gross and net production efficiencies compared with microsporidium-free larvae (Bauer and Nordin 1988). The microsporidium *Vairimorpha necatrix* killed 100% of overwintered larvae when administered orally at the relatively low dose of $5 \infty 10^4$ spores/insect (Wilson 1986).

Spruce budworm is susceptible to a nematode, *Heterorhabditis heliothidis (= bacteriophora)*, which killed 100% of fourth to sixth instars (Finney et al. 1982) and pupae (Moyle and Kaya 1981). The nematode also kills the first and second instars but cannot penetrate the protective webbing of their hibernaculum. Therefore, the nematode is not likely to be useful against first and second instars in the field (Finney and Bennett 1984).

Microbial Control. Attempts at microbial control of spruce budworm have included viruses, bacteria, a fungus, and protozoa.

An NPV and a GV have shown promise for microbial control. In Canada, both viruses were able to infect the larvae after field application (Bird et al. 1973). However, initiation and maintenance of epizootics were better with the GV (Cunningham et al. 1983b). Viral infection and larval mortality were unsatisfactory in Canada when second instars were treated with NPV (Kaupp et al. 1978). Also, the results of aerial sprays of NPV, GV, CPV, and EPV were inconsistent and unsatisfactory in Canada (Cunningham 1985). NPV, applied either as a single application at the emergence of second instars or as two applications with the second applied at pest population outbreak, did not significantly reduce the insect population or protect foliage. A disease epizootic was not initiated even after introduction of $5.74 \infty 10^{12}$ PIB/ha (Kaupp et al. 1989). Hydraulic applications of two baculovirus preparations

(NPV and GV), however, provided 35% protection of foliage in a trial in the United States (Stelzer and Scott 1985). A combination of NPV and a low dose of fenitrothion suppressed spruce budworm population density on balsam fir for 3 years (Morris 1977).

B. thuringiensis effectively controlled spruce budworm in Canada (Green 1981), and the beneficial effects can last 1 or 2 years (Smirnoff 1974). Larval biomass was significantly reduced after applications of commercial *B. thuringiensis* (Thuricide 16B, 24B and 32BX and Dipel 85) in Canadian forests (Morris and Moore 1983). In one case, effective control resulted when the bacterium was formulated with chitinase, an antievaporant, and a sticker, and applied at 16.8-20.0 BIU/ha in a final volume of 4.7 liters/ha when third instars were at a peak (Smirnoff 1980). Aerial sprays of Dipel or Thuricide applied at 8 billion IU/acre under favorable conditions controlled spruce budworm on balsam fir and Douglas-fir (Walton and Lewis 1982). Applications of *B. thuringiensis* with sublethal doses of fenitrothion or Orthene resulted in low spruce budworm survival (Morris 1975, Morris and Armstrong 1975). The insecticide Foray 48B (*B. thuringiensis* var. *kurstaki*) at 30 BIU/ha, timed to correspond with the flushing of black spruce, was more efficacious in controlling spruce budworm than was a spray applied to newly flushed balsam fir (Cadogan and Scharbach 1993). A *B. thuringiensis* formula called Futura killed 70-90% of larvae in a test in Canada (Smirnoff 1985). Also, BIODART, a novel and indigenous Canadian *B. thuringiensis* strain (A20), was successful in controlling spruce budworm larvae in Canada (Bernier et al. 1990). Residual toxicity of one *B. thuringiensis* formulation, Thuricide 48LV, was reduced on foliage by rain (Frankenhuyzen 1989b).

The fungus *E. radicans* was investigated for several years as a possible alternative to chemical control of the spruce budworm (Soper 1985).

Protozoa have been tested for the microbial control of spruce budworm. In Canada, *N. fumiferanae* infections in a spruce budworm population persisted 2 years after application. Thus, once introduced, *N. fumiferanae* can perpetuate itself in the pest population. Even if *N. fumiferanae* does not kill large numbers of spruce budworms due to its low virulence, it might contribute to integrated pest management by weakening the pest population (Wilson 1981). Prevalence of *P. schubergi* after spraying initially was high but decreased greatly before the end of the year (Wilson 1978b). Persistence studies of *N. fumiferanae* and *P. schubergi* in populations of spruce budworm revealed that *N. fumiferanae* persisted for about 3 years, whereas *P. schubergi* did not exhibit any carry-over effect (Wilson 1980).

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50. *Choristoneura occidentalis* Freeman

Western Spruce Budworm

Pest Situation

- *Often considered a form of the spruce budworm, **C. fumiferana**, though species status has been attained more recently.*
- *Distributed throughout the western United States and Canada into the Yukon.*
- *The primary host in the west is Douglas-fir, though spruces and the true firs are also infested.*
- *Damage and most characteristics of its life cycle are similar to those of **C. fumiferana**.*

Pathogens of *Choristoneura occidentalis*

Viruses, bacteria, and a nematode have been the subjects of laboratory experiments with *C. occidentalis*, and there have been numerous attempts at microbial control. No reports of natural infections in *C. occidentalis* populations were found.

Laboratory Experiments. Laboratory tests with entomopathogens have been limited to viruses, bacteria, and a nematode. The LC_{50} of nuclear polyhedrosis virus (NPV) isolated from *C. fumiferana* and granulosis virus (GV) isolated from *C. occidentalis* were 0.22 polyhedral inclusion bodies (PIB)/mm^2 of diet and 8.46 capsules/mm^2, respectively, for fifth-instar *C. occidentalis* (Cunningham et al. 1983a). The virulence of NPV to larvae of western spruce budworm increased as temperature increased (Reichenbach 1985). The HD-1 and NRD-12 strains of *Bacillus thuringiensis* did not differ significantly in virulence toward western spruce budworm (Van Frankenhuyzen and Fast 1989). Western spruce budworm larvae were susceptible to the nematode *Neoaplectana (= Steinernema) carpocapsae* under laboratory conditions (Kaya et al. 1981).

Microbial Control. An NPV and GV have been field-tested against *C. occidentalis*. Aerial application of NPV in Canada had a significant impact on tortricid numbers for 1 year after treatment (Shepherd et al. 1982). Field tests with NPV and GV in Canada indicated that the GV might be a better candidate than NPV for initiating and maintaining an epizootic in populations of *C. occidentalis* (Cunningham et al. 1983b). In another field study in Canada, GV and NPV treatments caused 34.6% and 51.8% population reduction, respectively, in the first year after treatment. The epizootics were not sufficiently intense, however, to control *C. occidentalis* in subsequent years (Otvos et al. 1989). Three 20-ha plots of Douglas-fir in British Columbia infested with fifth instars of western spruce budworm were aerially treated with 750 billion PIB/ha of NPV. Viral

prevalence in the treated area was 25, 55, and 87%, and population reduction was 0, 26, and 48% after 15 days (Hodgkinson et al. 1979).

B. thuringiensis has been tested frequently against this pest. Application of *B. thuringiensis* at 12 billion IU/gal/acre resulted in 81% reduction in the emergence of adult western spruce budworm moths (Bousfield et al. 1987). In Canada, Thuricide HPC (*B. thuringiensis* var. *kurstaki*) was not effective in seed orchards, but it was suggested that multiple applications might improve its efficacy (Summers et al. 1989). Four 40-ha plots of Douglas-fir in Canada were treated with *B. thuringiensis* at a rate of 20 billion IU/ha, with population reductions of 32, 66, 79, and 91% (Hodgkinson et al. 1979). The persistence of two *B. thuringiensis* formulations, measured in terms of the number of days before spray residues declined to 50% of original activity, varied with dosage. One *B. thuringiensis* control program depended on initial larval mortality rather than on the persistence of the bacterium (Beckwith and Stelzer 1987). Two formulations of *B. thuringiensis*, Thuricide 32LV and SAN-415 32LV, did not differ in control of western spruce budworm. A dosage of 30 billion IU per ha provided good western spruce budworm population control (Stelzer and Beckwith 1988).

B. thuringiensis has exhibited minor affects against certain nontarget organisms in field tests against *C. occidentalis*. The bacterium was toxic to certain nontarget lepidopterans for at least 30 days after a spray (Johnson et al. 1995). *Glypta fumiferanae* (Viereck), *Apanteles fumiferanae* Viereck, and *Phytodietus fumiferanae* Rohwer, parasites of western spruce budworm, contained *B. thuringiensis*. The occurrence of parasites contaminated with *B. thuringiensis*, however, was extremely low (Niwa et al. 1987).

Entomopathogenic nematodes were not effective in controlling *C. occidentalis*. Field application of *S. carpocapsae* did not significantly reduce populations of western spruce budworm when compared with controls; desiccation of the infective nematodes probably was a factor in their ineffectiveness (Kaya et al. 1981, 1982). Various spray additives did not increase the persistence of the nematode (Kaya and Reardon 1982).

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51. *Coloradia pandora* Blake

PANDORA MOTH

PEST SITUATION

- *Distributed throughout the Rocky Mountains and westward except Idaho and Washington.*
- *Principal hosts are ponderosa and lodgepole pines.*
- *Periodic outbreaks have resulted in severe defoliation of host trees. Serious consequences of defoliation are minimal since the terminal buds are not eaten and the 2-year life cycle permits recovery.*
- *Both hibernating larvae (first year) and pupae overwinter, with extended pupal diapause commonly observed (up to 5 years).*
- *In earlier times, and to a lesser extent recently, Indians sought larvae for food, reducing population numbers.*

Pathogens of *Coloradia pandora*

No reports of natural infection or microbial control of *C. pandora* were found. Pathology has been limited to one laboratory experiment.

Laboratory Experiments. Laboratory research has been limited to a virus. The morphology of a nuclear polyhedrosis virus isolated from *C. pandora* was described by Hughes (1977).

References

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52. *Datana integerrima* Grote and Robinson

Walnut Caterpillar

Pest Situation

- *Distributed throughout the eastern United States and into southern Ontario.*
- *A wide variety of deciduous trees are hosts, but walnut, pecan, and hickory are preferred.*
- *Walnut trees defoliated 2 years or more in succession are seriously injured or killed. Isolated trees or small groups of trees often are subject to heavy defoliation.*
- *One or two generations per year depending upon locality. Pupae overwinter in the duff and upper layers of soil.*
- *The scattered nature of infestations can reduce the importance of applied controls.*

Pathogens of *Datana integerrima*

Walnut caterpillars are susceptible to a protozoan in nature. Microbial control studies of entomopathogens have been limited to bacteria. There were no reports of other entomopathogens infecting *D. integerrima*.

Natural Infections. A microsporidium caused mortality in fifth instars of walnut caterpillars in Illinois and Texas (Farris and Appleby 1979).

Microbial Control. Control studies with entomopathogens have been limited to *Bacillus thuringiensis*. In Georgia, application of an isolate of *B. thuringiensis* in a pecan orchard gave 93% control of *D. integerrima* (Kaniuka 1985). In Illinois, application of *B. thuringiensis* var. *kurstaki* (Dipel) WP at 0.5 lb/100 gal resulted in 100% mortality of walnut caterpillars on treated branches (Farris and Appleby 1980). Aerial sprays of Dipel at 6.05g formulation per liter effectively controlled *D. integerrima* on shade and ornamental pecan trees (Tedders and Ellis 1977). *B. thuringiensis* also was effective against *D. integerrima* (Polles 1974, Polles and Payne 1975).

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53. *Dioryctria abietivorella* (Grote)

Fir Coneworm

Pest Situation

- *Distributed across Canada and the adjoining eastern and western United States.*
- *Hosts are eastern spruces and firs as well as certain eastern and western pines.*
- *Principal damage is to cones of firs and pines, as well as buds, twigs, and subcuticular areas of host trees.*

- *In general, only one generation per year, though some larvae mature and moths may emerge in late summer.*
- *Eggs and larvae are exposed to direct control agents for only a short time.*

Pathogens of *Dioryctria abietivorella*

A bacterium has been the only pathogen tested against *D. abietivorella*.

Laboratory Experiments. The HD-1 strain of *Bacillus thuringiensis* was toxic to fir coneworm larvae. First, third, and fifth instars did not differ significantly in their susceptibility to the bacterium (Trudel et al. 1997).

References

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54. *Dioryctria amatella* (Hulst)

Southern Pine Coneworm

Pest Situation

- *Distributed throughout the southeastern United States from Virginia to Florida and westward to Texas.*
- *All species of yellow pines are potential hosts.*
- *Pine cones and flowers, galls caused by fusiform rust, and injured tree stems are infested. The greatest economic loss arises from infestations in pine seed orchards and seed production areas.*
- *Several overlapping generations occur annually in the southern United States, and pupation and overwintering occur within infested host materials.*
- *Can be reared in culture on semiartificial media.*

Pathogens of *Dioryctria amatella*

Laboratory studies and microbial control of *D. amatella* have been limited to bacteria. No reports of other entomopathogens infecting this insect were found.

Laboratory Experiments. Laboratory tests with *D. amatella* have been limited to *Bacillus thuringiensis*. First instars of *D. amatella* were most susceptible with an LC_{50} value of 0.64 IU/ml diet. Older larvae were less susceptible, but died quickly (McLeod et al. 1982). Persistence of *B. thuringiensis* on second-year loblolly pine was determined by bioassays with second-instar southern pine coneworm, in which 81, 47, and 14% of the original activity remained at 4, 7, and 14 days after application, respectively (McLeod et al. 1983).

Microbial Control. Microbial control of *D. amatella* has been attempted with *B. thuringiensis*. Applications of *B. thuringiensis* (formulated as Thuricide HP or Dipel) at $7.7 \infty 10^4$ IU/ml of spray, 1 week after the detection of *D. amatella* adults, significantly reduced cone damage. Insect control was comparable to or better than that achieved with 0.2% sprays of azinphos-methyl (McLeod et al. 1984).

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55. *Ennomos subsignaria* (Hübner)

Elm Spanworm

Pest Situation

- *Distributed from southern Ontario and throughout the eastern United States westward to Wisconsin, Colorado, and Texas.*
- *Preferred hosts are hickory, oak, red maple, and ash, but a large number of hardwoods are also attacked.*
- *Large areas of mixed hardwoods can be defoliated during periodic outbreaks. Growth loss is the primary impact.*
- *One generation per year with eggs overwintering.*
- *Several parasitoids are responsible for assisting population crashes, especially after several years of outbreak conditions.*
- *A more serious pest historically (100 years ago) than at present.*

Pathogens of *Ennomos subsignaria*

A viral infection was detected in field-collected elm spanworm larvae. A virus also has been tested against this insect in the laboratory. Microbial control of *E. subsignarius* has been attempted with a bacterium.

Natural Infections. In New York, a nuclear polyhedrosis virus (NPV) was responsible for rapid decline in populations of *E. subsignarius* (Karpel 1973). No reports of other entomopathogens infecting this insect in nature were found.

Laboratory Experiments. Laboratory studies with entomopathogens have been limited to viruses. Elm spanworms are susceptible to an NPV (Martignoni and Iwai 1981). An NPV isolated from larvae of *Autographa californica* (Speyer) was able to infect *E. subsignarius* (Kaya 1977).

Microbial Control. Microbial control experiments have been limited to *Bacillus thuringiensis*. In Connecticut, Biotrol XK, Dipel, and Thuricide HPC effectively controlled third and fourth instars of elm spanworm (Dunbar and Kaya 1972).

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56. *Hemileuca maia* (Drury)

BUCK MOTH

PEST SITUATION

- *Distributed from Maine and Wisconsin to Florida, Louisiana, and Texas.*
- *Hosts apparently are various species of oaks, especially live oak in the South.*
- *Defoliation of oaks in the forest ecosystem is not a severe problem. In urban areas where oaks predominate, outbreaks can severely stress trees. Urbanization stresses coupled with defoliation can lead to dieback or tree death.*
- *One generation per year; however, there are two dormant periods, with pupae spending the summer months in the duff layer and eggs overwintering.*
- *Spotty infestations make coordinated suppression activities difficult.*

PATHOGENS OF *HEMILEUCA MAIA*

Infections by a virus have been detected in field populations of *H. maia*. No reports of other entomopathogens infecting this insect or of attempts at microbial control were found.

Natural Infections. In Texas, a nuclear polyhedrosis virus (NPV) killed 10% of a field population of *H. maia* larvae 2 weeks before they pupated (Wangberg 1984).

Laboratory Experiments. Laboratory experiments with entomopathogens have been limited to a virus. An NPV was isolated from *H. maia* feeding on foliage that was naturally contaminated with the virus in the field. Infected larvae exhibited classical virus symptoms and died in 3-6 days (Mitchell et al. 1985).

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57. *Heterocampa guttivitta* (Walker)

Saddled Prominent

Pest Situation

- *Distributed from southeastern Canada throughout most of the eastern United States.*
- *Preferred hosts are beech, yellow birch, and sugar maple.*
- *Outbreaks can result in severe defoliation over large forested areas. After two consecutive years of defoliation, considerable tree mortality can occur. Surviving trees display death of portions of the canopy.*
- *In general, one generation per year with pupae overwintering in the duff beneath defoliated trees.*

Pathogens of *Heterocampa guttivitta*

A virus and a fungus have caused mortality of saddled prominent in field populations, and *Bacillus thuringiensis* has been tested for control of this insect.

Natural Infections. Infections by a virus and fungus have been observed in field-collected saddled prominent. In Michigan, a virus infecting larvae of *H. guttivitta* caused population reduction of the pest (Loesch and Foran 1979). An unidentified member of the *Entomophaga aulicae* species complex was responsible for *H. guttivitta* mortality in Vermont (Hajek et al. 1991).

Microbial Control. Attempts at microbial control of *H. guttivitta* have been limited to *B. thuringiensis*. In Michigan, dilute sprays of *B. thuringiensis* var. *thuringiensis* and *B. thuringiensis* var. *kurstaki* did not control the saddled prominent (Wallner 1971).

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58. *Lochmaeus manteo* Doubleday

Variable Oakleaf Caterpillar

Pest Situation

- *Distributed throughout the eastern provinces of Canada from western Ontario through the eastern United States to Texas.*
- *White oak is the preferred host, but all oaks are attacked as are several other hardwood species.*
- *Trees of all sizes are attacked, and heavy defoliation may occur anywhere within the insect's range. Larger trees appear to withstand several years of defoliation.*
- *Two generations in the southern parts of its range and one in the northern parts. Prepupae overwinter, and pupae spin cocoons in the topsoil.*
- *Despite severe defoliation of large acreages, tree mortality has been relatively minor, and usage of applied controls may be restricted.*

Pathogens of *Lochmaeus manteo*

Viral and fungal infections have been detected in field-collected variable oakleaf caterpillar, and *Bacillus thuringiensis* has been tested against this insect in the laboratory.

Natural Infections. In Maryland, infections by a nuclear polyhedrosis virus and a fungus (probably *Cordyceps* sp.) were detected in larvae of variable oakleaf caterpillar (Staines 1977).

Laboratory Experiments. Laboratory experiments with entomopathogens have been limited to *B. thuringiensis*. The variable oakleaf caterpillar was susceptible to a commercial forumulation of *B. thuringiensis* var. *alesti*. The LC_{50} was $8.6 \infty 10^3$ IU/ml/g of insect (Ignoffo et al. 1973).

References

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59. *Hyphantria cunea* (Drury)

Fall Webworm

Pest Situation

- *Distributed throughout much of southern Canada and the United States.*
- *Hosts include more than 100 species of forest and shade trees.*
- *The damage to forestry is not of great importance, because the fall webworm usually attacks understory weed species of little economic value.*
- *There is one generation in the North and up to four in the South. There are two distinct races—orange-headed and black-headed. Pupae overwinter in the duff beneath infested trees.*

Pathogens of *Hyphantria cunea*

Infections by several viruses, protozoa, and one bacterium have been detected in field-collected fall webworm. Various groups of entompathogens have been tested against this insect in the laboratory, and there have been numerous attempts at microbial control.

Natural Infections. Numerous pathogens are known to infect *H. cunea* in nature. Field-collected fall webworm larvae have been infected with a nuclear polyhedrosis virus (NPV) and a species of *Bacillus* (Park and Cho 1982). In Japan, the degree of viral contamination of the soil surface in an area where the viral disease had occurred naturally in host populations was estimated to be as high

as the IC_{50} (median infectious concentration) (Hukuhara 1973). In Korea, an inclusion-forming virus was isolated from fall webworm and was later identified as NPV (Im et al. 1979). A granulosis virus (GV) caused 2-31% mortality of the fall webworm in Yugoslavia (Injac 1973). Fall webworms from field samples were infected with cytoplasmic polyhedrosis virus (CPV) and GV in Japan and China, respectively (Kunimi 1993).

Several protozoa have been found in field studies of *H. cunea*. *Nosema necatrix*, *Pleistophora schubergi*, and an unidentified *Nosema* species were recovered from field-collected larvae in Illinois (Nordin and Maddox 1974). In Japan, field populations of *H. cunea* have been infected with *Microsporidium hyphantriae*, *P. schubergi*, *Nosema mesnili*, *Nosema bombycis*, *Nosema trichoplusiae*, *and Vairimorpha necatrix* (Kunimi 1993).

Laboratory Studies. Laboratory tests with entomopathogens have included four pathogen groups, the viruses, bacteria, fungi, and protozoa.

Laboratory research of viruses has identified promising candidates for microbial control of *H. cunea*. Fall webworm larvae were susceptible to a GV and an NPV, but this susceptibility decreased as the larvae matured (Boucias and Nordin 1977a). The LD_{50} of a GV isolated from *Diacrisia virginica* (F.) in fall webworm larvae was $7.9 \infty 10^5$ capsules per larva (Boucias and Nordin 1977b). In Canada, an NPV isolated from *Thymelicus* sp. was infective to larvae of *H. cunea*, killing 100% of the second instars (Smirnoff 1976). An NPV isolated from *H. cunea* in Korea killed 70.6% of fall webworm larvae (Park and Cho 1982). Methoprene treatment was antagonistic to the natural development of NPV in populations of *H. cunea*. This might be useful in the laboratory to increase larval biomass for greater production of viruses or other pathogens for microbial control (Boucias and Nordin 1980). A CPV isolated from *Isia isabella* (J. E. Smith) also infected larvae of *H. cunea* (Boucias and Nordin 1978).

Numerous commercial formulations of *Bacillus thuringiensis*, as well as unknown species of *Bacillus*, have been tested against the fall webworm. Laboratory tests indicated that commercial formulations of *B. thuringiensis* (Thuricide 90TS, Thuricide S7-150, and Plantibac 701) were virulent to *H. cunea* (Morris 1969). Dipel at 0.1% caused 100% mortality of second to fifth instars, and 65.6-71.2% mortality of seventh instar fall webworm larvae (Zivanovic and Stamenkovic 1976). In Italy, Bactuspeine, Thuricide, and Bactucide at 1.5g/l killed 45-100% of fall webworm larvae (Montermini et al. 1985). The LC_{50} of *B. thuringiensis* Cry1A(a) toxin for first instars was 0.1 g engineered *Escherichia coli* protein extract per milliliter diet (Ramachandran et al. 1993a). The soluble protein extracted from *B. thuringiensis* HD-290-1, however, was not toxic to first instars of fall webworm (Ramachandran et al. 1993b). The serotype 3 *B. thuringiensis* isolated from the wheat bug, *Eurygaster austriaca* Schrk., was effective against *H. cunea* (Sidor et al. 1986). A strain of *B. thuringiensis* (AF 101) was toxic to *H. cunea* in Japan (Aizawa 1975). A species of *Bacillus* isolated from *H. cunea* in Korea caused 49.5% mortality when tested against healthy fall webworm larvae (Park and Cho 1982).

Certain laboratory studies of *H. cunea* have involved more than one type of entomopathogen. Simultaneous infections by an NPV and a microsporidium were studied in larvae of fall webworm. Total mortality in treatments with the virus, *Nosema* sp., and a combination of virus plus *Nosema* sp. was 97%, 21%, and 70%, respectively (Nordin and Maddox 1972). In China, larvae of the fall webworm were infected with NPV, the fungus *Beauveria globulifera*, and certain bacteria (Shu and Yu 1985).

Fungi might include candidates for fall webworm control, based on laboratory experiments. *Beauveria bassiana* and *Metarhizium anisopliae* at 10g/l (1009 conidia/g) killed 83-100% of fall webworm larvae in a test in Italy (Montermini et al. 1985). In Japan, the entomogenous fungus *Erynia neopyralidarum* infected laboratory-reared *H. cunea* larvae (Pena et al. 1990).

Laboratory experiments with *H. cunea* have included several protozoa. The fall webworm has been infected with *Pleistophora schubergi hyphantriae* and *Microsporidium necatrix* (Sprague 1977). A microsporidium isolated from *Spodoptera litura* (F.) was infectious to larvae of fall webworm (Watanabe 1976). *H. cunea* also was susceptible to *Nosema antheraeae* (Simchuk et al. 1979). A microsporidium isolated from *H. cunea* in the USSR underwent two types of development in *H. cunea*, with characteristics of both *Nosema* and *Thelohania* (Simchuk 1982). Infection of *H. cunea* larvae with a *Thelohania* sp. was not successful (Wilson 1975).

Microbial Control. Attempts at microbial control of fall webworm have included viruses, bacteria, nematodes, and a fungus.

Two viruses have shown promise for microbial control. Vertical transmission is a phenomenon potentially useful to long-term approaches to microbial control. The NPV of fall webworm was vertically transmitted under both field and laboratory conditions when female moths were treated with viral paste, viral suspension, or a mixture of viral dust and Vaseline. The prevalence of NPV in progeny was higher in the field than in the laboratory (Kunimi 1982). A GV isolated from fall webworm, when applied in the field, resulted in 20%, 47%, and 85% mortality of fall webworm larvae at 5, 10, and 15 days post-treatment, respectively (Lappa and Krasnitskaya 1976). A formulated *H. cunea* NPV product (spreader, sticker, and ultraviolet protector) and an aqueous *H. cunea* NPV suspension were tested for their persistence under field conditions. The aqueous viral suspension was completely inactivated by the fifth day after application, while the formulated viral product still was active at 20 days (Jin et al. 1987).

Various isolates and formulations of *B. thuringiensis* have been evaluated for microbial control of fall webworm. Aerial application of Dipel (HD-1 isolate of *B. thuringiensis* var. *kurstaki*) at 6.05 g formulation per liter water effectively controlled fall webworm larvae on shade and ornamental pecan trees in Georgia (Tedders and Ellis 1977). Application of DiBeta 1.5EC (the *B. thuringiensis* toxin thuringiensin) reduced infestation by fall webworms on

persimmon trees in Alabama (Williams et al. 1987). Dipel at 0.1% killed 100% of third- to fifth-instar fall webworms (Zivanovic and Stamenkovic 1976).

In the USSR, Dendrobacillin (*B. thuringiensis* subsp. *dendrolimus*) at 1.5 kg/ha, Gomelin (*B. thuringiensis*), and Lepidocide (*B. thuringiensis* subsp. *kurstaki*) killed 98-99%, 6-98%, and 97-99% of fall webworm, respectively (Sikura et al. 1988a). In a similar experiment, a majority of a wide range of *B. thuringiensis* preparations tested in the USSR killed 95% of third and fourth instars of the fall webworm (Sikura et al. 1988b). Entobakterin (*B. thuringiensis* subsp. *galleriae*), Bitoxibacillin, and Dipel killed 100% of fall webworms and persisted in the subsequent generation (Kondrya et al. 1980, Sikura and Simchuk 1981). Preliminary field tests in Italy with Bactuspeine, Thuricide, and Bactucide at 100-150 g/l killed 60-91% of fall webworm larvae (Montermini et al. 1985). *B. thuringiensis* has been used in urban areas in Yugoslavia for the control of *H. cunea* (Maceljski 1985). Dipel sprays at 0.2-0.3% effectively and rapidly killed fall webworms in Austria (Arthofer and Kaplan 1976).

B. thuringiensis has been field-tested in combination with chemical pesticides and a virus. In Romania, mixtures of Thuricide, Thuringin, and pyrethroids (fenvalerate, deltamethrin, and cypermethrin) were compatible for 18 h after dilution in water at low concentrations and were effective against the fall webworm (Baicu and Hussein 1984). Combinations of 0.2% Entobakterin with 0.002% trichlorphon or with a polyhedrosis virus suspension resulted in 85.3% and 100% mortality of fall webworm larvae, respectively (Sikura et al. 1971).

Attempts at control of *H. cunea* with nematodes and fungi have been limited. Preliminary field tests in Italy with *B. bassiana* resulted in only 23% mortality of fall webworm larvae (Montermini et al. 1985). The nematodes *Complexomermis* sp. and *Complexomermis elegans* parasitized 21.0-27.7% of *H. cunea* larvae when applied under maple trees in China (Wei and Wu 1984).

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60. *Lambdina fiscellaria fiscellaria* (Guenée)

Hemlock Looper

Pest Situation

- *Distributed from Newfoundland to Alberta in Canada and south to Georgia in the eastern United States.*
- *Preferred hosts are balsam fir, white spruce, and eastern hemlock. During outbreaks many associated tree species are consumed.*
- *One generation per year with eggs as the overwintering stage.*
- *Looper outbreaks develop very suddenly in mature and overmature stands of balsam fir and hemlock.*

Pathogens of *Lambdina fiscellaria fiscellaria*

A nuclear polyhedrosis virus (NPV) is the only pathogen reported for the hemlock looper.

Laboratory Experiments. The DNA of an NPV isolated from *L. fiscellaria fiscellaria* was characterized. This NPV was more similar to that from *Lambdina fiscellaria lugubrosa* (Hulst) than to NPV isolates from *Lambdina fiscellaria somniaria* (Hulst) (Levin et al. 1997).

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61. *Lambdina fiscellaria lugubrosa* (Hulst)

Western Hemlock Looper

Pest Situation

- *Distributed throughout the west coastal States, Alaska, and British Columbia. Occasionally destructive in the interior forests of Idaho and Montana.*
- *Preferred host is western hemlock. Sitka spruce, Douglas-fir, and associated trees, vines, and shrubs can be affected.*
- *Principal damage is defoliation and mortality of western hemlock in coastal states and British Columbia.*
- *One generation per year, with eggs overwintering. Outbreaks often last 3 years.*

Pathogens of *Lambdina fiscellaria lugubrosa*

No reports of entomopathogens infecting this insect in nature were found. Laboratory studies have been limited to a virus, and a bacterium has been tested for microbial control of this insect.

Laboratory Studies. The morphology of a nuclear polyhedrosis virus isolated from *L. fiscellaria somniaria* was described by Hughes (1977), and the DNA of this NPV was characterized by Levin et al. (1997).

Microbial Control. In the United States, *Bacillus thuringiensis* (Thuricide 90-T) in 1 US gal water per acre killed larvae of *L. fiscellaria lugubrosa* but not did not adequately control an infestation. The material retained effectiveness for 9 days, which was too short a period to result in high levels of mortality (Carolin and Thompson 1967).

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62. *Lambdina fiscellaria somniaria* (Hulst)

Western Oak Looper

Pest Situation

- *Distributed primarily in Oregon, Washington, and British Columbia.*
- *The preferred host is Oregon white oak. Other oaks are utilized during outbreak situations.*
- *The life cycle is similar to the western hemlock looper with one generation per year and eggs as the overwintering stage.*
- *Damage is of minor consequence due to short duration of outbreaks and to the ability of oaks to refoliate.*

Pathogens of *Lambdina fiscellaria somniaria*

No reports of entomopathogens infecting this insect in nature were found. Laboratory studies have been limited to viruses, and a bacterium has been tested for microbial control of this insect.

Laboratory Studies. Laboratory research has been limited to nuclear polyhedrosis viruses (NPV). The morphology of an NPV isolated from *L. fiscellaria somniaria* was described by Hughes (1977). Precocious development of antennae and mouthparts, adult-type forelegs, and partial fusing of ocelli have been observed in larvae of western oak looper infected with a homologous NPV (Morris 1970). Exposure of western oak looper NPV to sunlight reduced the mortality of larvae subsequently ingesting it, but exposure of the preparation to an artificial source of ultraviolet radiation or to gamma radiation had little apparent effect on pathogenicity (Morris 1971). Additionally, incubation of the virus at 45°C for up to 200 h affected the LT_{50} but not the final percentage mortality of treated larvae (Morris 1971). NPV isolated from western oak looper on Douglas-fir trees had different restriction enzyme patterns from NPV from insects on Garry oak trees (Levin et al. 1997).

Microbial Control. Application of a commercial formulation of *Bacillus thuringiensis* killed 50% of *L. fiscellaria somniaria* 6-7 days after treatment (Morris 1962).

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63. *Lymantria dispar* (L.)

Gypsy Moth

Pest Situation

- *An introduced pest of unsurpassed importance, the gypsy moth has demonstrated classic population increase.*
- *Now widely distributed in New England, southward into Virginia and North Carolina, westward through New York, Pennsylvania, and into Ohio and Michigan. Isolated infestations have occurred recently in Arkansas, Tennessee, and Georgia. Utah, Oregon, Idaho, and nearby western states also have reported populations.*
- *Most species of hardwoods are suitable hosts, and larvae feed on pines as well. Oaks and fruit trees are traditional hosts, especially where they grow on thin, rocky soils.*
- *Severe defoliation can persist along the advancing front of the ever-expanding range of the gypsy moth. It has long been considered one of the most important forest pests, and enormous sums of money have been spent to eradicate, suppress, and slow its spread.*
- *One generation per year throughout the range of the gypsy moth, with eggs overwintering.*
- *An extensive effort to import, culture, and apply various biological control organisms has met with repeated success. Several parasites, predators, and diseases are known to be important in reducing populations.*

PATHOGENS OF *LYMANTRIA DISPAR*

Infections by viruses, bacteria, fungi, protozoa, and a nematode have been detected in field-collected gypsy moth larvae. Various entomopathogens have been tested against this insect in the laboratory, and there have been numerous attempts at microbial control.

Natural Infections. Field sampling of gypsy moth larvae has detected infections by several viruses. Karpov et al. (1977) reported that carriers of latent infections of nuclear polyhedrosis virus (NPV) were widely distributed in some populations of gypsy moth larvae in the USSR. In Southern Italy, a baculovirus of subgroup A caused 5-28% mortality among gypsy moth larvae (Triggiani 1982a). A small proportion of gypsy moth larvae collected in Italy were infected by a polyhedrosis virus characterized by large, cubic polyhedra causing nuclear hypertrophy within the haemocytes (Skatulla 1977). In Iran, 85% of gypsy moth larvae were killed by virus and a microsporidium, *Nosema* sp. (Herard et al. 1979). In Yugoslavia, 5.4% to 43.6% of gypsy moth larvae were infected with NPV in a false acacia (*Robinia pseudoacacia*) forest (Sidor and Jodal 1990). Viruses were isolated from field-collected gypsy moth larvae in China (Weseloh 1983), where NPV caused 13% mortality (Yue et al. 1989). In Algeria, 8.0% of first to third instars and 98.2% of fourth to sixth instars were infected with NPV (Khous et al. 1991). In the United States, 19.5% to 22.8% of gypsy moth larvae collected from a hardwood forest were parasitized and more than 70% of the parasitised larvae were also infected with *L. dispar* NPV (LdNPV) (White and Webb 1994). Densonucleosis virus, entomopoxvirus (EPV), iridescent virus, and cytoplasmic polyhedrosis virus were isolated from field-collected gypsy moth larvae in Japan (Kunimi 1993).

Bacteria are commonly found in field collected gypsy moth larvae. Bacilli from natural epizootics in old Yugoslavian mills were identified as *Bacillus thuringiensis* var. *thuringiensis*, *B. thuringiensis* var. *morrisoni*, *B. thuringiensis* var. *kurstaki*, and *Bacillus cereus* (Vankova and Purrini 1979). In Bulgaria, field-collected larvae of gypsy moth were infected with *Streptococcus faecalis* (Grigorova et al. 1982). A natural population of gypsy moth in Connecticut was infected with *S. faecalis*, *B. cereus*, *B. thuringiensis*, Group C Enterobacter types, and *Pseudomonas* spp. (Podgwaite and Campbell 1973).

Several fungal pathogens of gypsy moth have been detected in field samples. In North America, a fungus causing epizootics in populations of the gypsy moth was identified as *Entomophaga maimaiga*, which caused 60% to 88% mortality of late instars (Hajek et al. 1990). Screen cage studies to determine the distribution of cadavers of third and fifth instars of gypsy moth killed by *E. maimaiga* on red oak revealed that the dead larvae were distributed at the same heights within trees as were healthy larvae (Hajek and Soper 1991). Overwintering resting spores of the fungus infect young larvae, producing sufficient conidia to cause epizootics in older larvae (Shimazu et al. 1987).

Rainfall is very important in causing epizootics of the fungus. In areas where overwintering resting spores of the fungus were abundant, the most important determinant of fungal effectiveness was rainfall amount and pattern (Weseloh and Andreadis 1992).

Fusarium sambucinum and *Fusarium polyphialidicum* were identified in field-collected gypsy moth larvae in the eastern United States (Hajek et al. 1993a). Mixed infections of gypsy moth larvae by *Entomophthora aulicae* and *Paecilomyces canadensis* have been observed in a larch forest in Japan (Aoki 1974). In Poland, *Entomophthora* sp. played an important role in regulation of natural gypsy moth populations (Glowacka-Pilot 1983). Approximately 9% to 55% of gypsy moth eggs collected from various sites in Connecticut were infected with *Paecilomyces farinosus*, and most of the eggs infected had been parasitized by *Ooencyrtus kuwanai* (Dunbar et al. 1972).

Other fungi that were found infecting eggs and larvae of gypsy moth in the field include *Mortierella hyalina, Mortierella claussenii, F. polyphialidicum, F. sambucinum, Fusarium avenaceum, Fusarium merismoides, Aspergillus flavus, Penicillium thomii, Scopulariopsis* sp., *Verticillium* sp., *Acrodontum crateriforme, Aphanocladium album, Filobasidiella arachnophila, Humicola* sp., *Philophora malorum, Phoma cava, Verticillium coccosporum, Verticillium fungicola, Trichothecium roseum,* and *Acremonium berkeleyanum* (Humber 1992).

Several protozoa infect gypsy moth larvae. Larvae of gypsy moth collected during an outbreak in forests in Sardinia were infected with *Nosema lymantriae,* resulting in 14% and 60% mortality in 1976 and 1977, respectively (Purrini and Skatulla 1978). In the Ukraine, *N. lymantriae, Nosema serbica, Thelohania disparis,* and *Pleistophora schubergi* infected larvae of gypsy moth attacking tree plantations (Zelinskaya 1980). In Poland, *N. lymantriae* played an important role in regulation of natural gypsy moth populations (Glowacka-Pilot 1983). Other protozoa infecting gypsy moth include *Thelohania similis, Nosema muscularis,* and *Vairimorpha lymantriae* (Kunimi 1993).

One nematode species has been detected in field samples. In Japan, *Hexamermis* sp. caused 61-100% mortality in natural populations of the gypsy moth (Schaefer and Ikebe 1982).

Laboratory Experiments. Laboratory tests with gypsy moth have included all five entomopathogen groups.

There have been numerous laboratory studies of the viral diseases of gypsy moth. Cell cultures of gypsy moth were successfully infected with an EPV of *Amsacta moorei* (Bltr.) (Quiot et al. 1975). The NPV of *Mamestra brassicae* was reproduced in cultivated cells of the gypsy moth. The viral inclusion bodies were polyhedral, and their virulence remained constant for 15 passages or replication cycles in host insects and then decreased (Miloserdova et al. 1980).

The NPV is the most frequently studied virus of *L. dispar*. The LD_{50} of an American isolate of gypsy moth NPV to the third instars was 72 polyhedral

inclusion bodies (PIB) per milligram of larval body weight (Magnoler 1974a). The LD_{50} for second instars reared on an artificial diet contaminated with NPV was $1.8 \infty 10^4$ PIB/ml diet (Yendol 1975). Based on LC_{50}s, first instars were approximately 2, 3, 23, and 111 times as susceptible to the NPV as were second, third, fourth and fifth instars (Shapiro et al. 1986). NPV-infected neonate larvae of the gypsy moth were significantly smaller than uninfected control larvae. In late instars, virus infection slowed weight gain, delayed the onset of apolysis, inhibited molting, and blocked pupation (Burand and Park 1992). In one study some gypsy moth larvae recovered from NPV infection, and there was no difference in fecundity between adults obtained from infected and uninfected larvae (Bakhvalov et al. 1982). Females of the gypsy moth were more vulnerable than males to infection by NPV and *Streptococcus faecalis*, resulting in a sex ratio of 71:29 compared with 52:48 in an untreated control (Mirchev 1987).

Possible adjuvants for field application have been investigated for *L. dispar* NPV. The fluorescent brightener, Tinopal LPW, acted synergistically with *L. dispar* NPV and lowered the LC_{50} by a factor of 1,000 (Sheppard and Shapiro 1994). After inoculation with virus and 1% Tinopal, many virions were detected in columnar cell nuclei in the tissues of the midgut, but no virions were detected in control larvae (Adams et al. 1994). Boric acid enhances viral activity, expressed as increased mortality in treated larvae. Boric acid at 0.5% doubled gypsy moth NPV virulence, and 1.0% boric acid enhanced activity by a factor of 11. Time until death also was reduced by the addition of boric acid (Shapiro and Bell 1982). Larvae consuming virus on diets with additional casein, salts, or condensed or hydrolyzable tannins, or diets that were acidic, were one-fourth as susceptible to the virus (Keating et al. 1989). Suspension of gypsy moth NPV in 1.0% Congo red provided significant protection from ultraviolet radiation, with 100% of original viral activity remaining after 60 min of exposure (Shapiro 1989). Gypsy moth NPV fed to *L. dispar* larvae in combination with the triterpene azadirachtin reduced the NPV lethal dose and lethal time (Cook et al. 1996).

Shapiro et al. (1981a) developed efficient methods for mass production of gypsy moth NPV. For large-scale in vivo production, a wheat germ diet was the most suitable and cost-effective (Shapiro et al. 1981b). Inoculation of fourth instars produced more NPV than fifth instars (Shapiro et al. 1986). Virus yields increased to $2 \infty 10^9$ PIB/larva during the first 11 days after inoculation and then remained constant (Shapiro and Bell 1981). Suspensions of viral PIB retained their potency for 5 years under refrigeration and for 2 years at room temperature, and an air-dried powder stored at 4°C lasted for a year before losing potency (Lewis and Rollinson 1978). Prolonged storage of the virus at room temperature in a dry form caused structural changes in some of the inclusion bodies and virions (Bakhvalov and Larionov 1987).

In China, comparative bioassay of viral strains isolated from the gypsy moth indicated that the U.S. Hamden standard isolate was more virulent than Chinese isolates (Lewis et al. 1984). In the German Federal Republic, a strain of NPV with

cuboid inclusion bodies was more virulent than a strain with spherical polyhedra (Skatulla 1986). Studies of different strains of NPV in Yugoslavia revealed that mixed viral preparations may be more effective than preparations of virus from a single source in controlling the gypsy moth (Ruperez 1973). In one study, gypsy moth originating from six different countries were tested for their susceptibility to NPV. Comparative mortality rates ranged from 90% in gypsy moth populations from Iran, Hungary, and Sardinia, to 75% in Greece, 62% and 38% in Germany, and 26 % in Austria (Skatulla 1987). Natural variability in virulence of different isolates of gypsy moth NPV varied from an LC_{50} of 0.17 ± 0.19 PIB/mm^2 (Abington, Massachusetts isolate) to 17.4 ± 13.5 PIB/mm^2 (Dalmatia, Yugoslavia) (Shapiro and Robertson 1991).

Bacteria also have been subjects of laboratory studies with gypsy moth. Dosage-mortality studies revealed that 0.02 gal ($4 \infty 10^6$ IU/acre) of *Bacillus thuringiensis* (Dipel) (with molasses) might give economic control of first to second instars of gypsy moth (Morris 1973). Two bacterial preparations, Insektin-2 (*B. thuringiensis*) and Tuverin-2 (*Bacillus tuviensis*), killed gypsy moth larvae, pupae, and adults (Mashanov et al. 1980). A strain of *B. thuringiensis* (T83016) killed more than 80% of gypsy moth larvae (Dai et al. 1989). Studies of 25 strains of *B. thuringiensis* revealed that phospholipase C of some strains had entomopathogenic properties, causing 75-100% mortality of gypsy moth larvae (Ivanov et al. 1990). Adhesiveness to the leaf surface and resistance to precipitation can influence the effectiveness of *B. thuringiensis*. The adhesive Atplus 240 did not provide complete adherence of *B. thuringiensis* spores to the leaves of trees at localities with high precipitation (Svestka et al. 1988).

The insect's host plant can affect *B. thuringiensis* activity against gypsy moth. The activity of nine strains of *B. thuringiensis* was tested in the laboratory on larvae of *L. dispar* reared on cork oak *(Quercus suber)* and poplar *(Populus nigra). B. thuringiensis* var. *morrisoni, B. thuringiensis* var. *kenyae* and *B. thuringiensis* var. *subtoxicus* were effective against larvae on cork oak, and *B. thuringiensis* var. *thuringiensis* was more effective against larvae on poplar trees (Cabral 1973). In another study, *B. thuringiensis* var. *morrisoni* at 4 grams/liter caused 86.8%, 71.5%, and 1.2% mortality of gypsy moth larvae feeding on *Populus nigra, Ulmus scabra,* and *Quercus coccifera,* respectively (Cabral 1978). Differences of more than 10 times (Farrar et al. 1996) to 100 times (Hwang et al. 1995) were observed in *B. thuringiensis* toxicity among gypsy moth larvae reared on different host plants. Chemical analyses of leaves revealed that condensed tannins and phenolic glycosides affect the toxicity of *B. thuringiensis* (Hwang et al. 1995).

Another bacterium also has been studied. The ED_{50}s of a strain of *Serratia marcescens* to third and fourth instars of gypsy moth were 7.5 and 14.5 viable cells, respectively. Histological and biological studies revealed that this bacterium might not be very effective as a conventional microbial insecticide (Podgwaite and Cosenza 1976).

Synergism between various agents has been studied in gypsy moth. Synergism has been demonstrated between beta exotoxin and *B. thuringiensis* ssp. *kurstaki* HD-1. Addition of 0.001% beta-exotoxin significantly increased gypsy moth larval susceptibility to *B. thuringiensis* (Dubois 1986). The LD_{50} of *B. thuringiensis* var. *kurstaki* and a subgroup A baculovirus combined was significantly lower than the LD_{50}s of each applied separately, indicating that the virus and bacterium had a synergistic action (Triggiani 1982b). Synergism also has been reported between *B. thuringiensis* and a parasitoid. The retarding effect of *B. thuringiensis* infection kept larvae of gypsy moth small enough to permit female parasitoids to parasitize relatively large numbers of larvae (Weseloh et al. 1983).

The fungi might include candidates for gypsy moth control. The virulence of 20 fungi was tested against eggs of the gypsy moth, and *Beauveria bassiana, Paecilomyces farinosus, Spicaria coccospora,* and *Verticillium lecanii* were consistently virulent (Carroll 1988). Gypsy moth larvae were resistant to infections by *B. bassiana,* with lethal times of 11 and 20 days for first and second and third instars, respectively (Markova and Samshinyakova 1990). Exposure of second instars to sporulating cultures of *Nomuraea rileyi* resulted in 100% mortality at 48 h post-inoculation (Wasti and Hartmann 1978). An isolate of *B. bassiana* (isolate 0200) and three isolates of *P. farinosus* (isolates 0500, 0501, and 0502) caused 79.3%, 93%, 67%, and 74% mortality of third instars, respectively (Majchrowicz and Yendol 1973).

Larvae also have been infected by *Metarhizium anisopliae* and *Paecilomyces fumosoroseus*. Viscera of infected larvae completely disintegrated within 95 and 120 h after inoculation with *M. anisopliae* and *P. fumosoroseus,* respectively (Wasti et al. 1980). Fourth instars of gypsy moth have been infected by *Conidiobolus coronatus;* the signs of infection were lightening of color, flaccidity, shrinking, and desiccation (Hartmann and Wasti 1974). Larvae of the gypsy moth were infected with sporulating cultures of *Entomophthora virulenta,* with penetration of integument and conidiophore production occurring 24 and 72 h after infection (Hartmann and Wasti 1976).

One of the most promising fungi for microbial control of the gypsy moth is *E. maimaiga*. Among isolates of *E. maimaiga* from Japan, ARSEF 1400 caused 90-95% mortality among third instars of gypsy moth (Soper et al. 1987). Second instars had a greater tendency to induce conidia formation than did third or fourth instars, possibly because of their different water content (Shimazu 1987). Fifth instars infected with *E. maimaiga* ate less food and gained less weight than healthy larvae did (Hajek 1989). Successful infection by conidia required a median time of 8.7 h at 25 °C, and the pathogen could not develop below 5 °C or above 30 °C (Hajek et al. 1993b). Incorporation of *Quercus rubra* foliage into artificial diet of gypsy moth inhibits the development of *E. maimaiga* (Hajek and Renwick 1993). The fungus can be detected in infected gypsy moth larvae with an indirect enzyme-linked immunosorbent assay (ELISA) (Hajek et al. 1991).

Certain microsporidia have features that could make them useful for the introduction and establishment or seasonal colonization approaches to microbial control of the gypsy moth. A species of *Nosema* infected the silk glands of gypsy moth, and spores were frequently found in the silk produced by the infected larvae, which could lead to horizontal transmission of the microsporidium in the field (Jeffords et al. 1987). In China, *Nosema furnacalis* infected gypsy moth larvae under laboratory conditions (Wen and Sun 1988). The morphology and development of *N. serbica* infecting the gypsy moth have been described (Pilarska and Vavra 1991). *N. lymantriae* fed to young larvae caused 90-100% mortality at the end of larval development, whereas larvae of middle age suffered 70-85% mortality (Novotny 1991a). A sporozoan was antagonistic with the NPV (Saftoiu and Caloianu-Iordachel 1978).

There have been few laboratory experiments with nematodes and the gypsy moth. *Steinernema feltiae* and *Steinernema bibionis* caused 93-95% mortality of gypsy moth larvae in petri dishes (Reardon et al. 1986). Spraying of *Neoaplectana (= Steinernema) carpocapsae* onto adults of gypsy moth resulted in 80% mortality in 2 days and prevented oviposition (Triggiani undated).

Microbial Control. Attempts at microbial control of gypsy moth have included viruses, bacteria, protozoa and a fungus.

L. dispar NPV has been registered for control of the gypsy moth (Shapiro and Dougherty 1985). In Canada, aerial sprays with Disparvirus (an isolate of *L.dispar* NPV) at $2.2 \infty 10^{12}$ and $2.7 \infty 10^{11}$ PIB/ha resulted in 46.7% and 66.5% larval infection, respectively (Kaupp et al. 1988). A double application of Disparvirus at $1.25 \infty 10^{12}$ PIB/ha, giving a total of $2.5 \infty 10^{12}$ PIB/ha, resulted in a corrected population reduction of 84-92% (Cunningham and Kaupp 1991). Gypchek (an *L. dispar* NPV product) and Disparvirus at 5 l/ha resulted in 87-92% and 87-95% reductions in gypsy moth populations in red and white oaks respectively (Cunningham et al. 1991). In the Soviet Union, an exceptionally virulent experimental strain (S 11p) of NPV gave excellent control of an outbreak in a forest area (Orlovskaya 1970). In Maryland, Gypchek applied at 378 liters and $2.5 \infty 10^{12}$ PIB/ha reduced numbers of egg masses by 81% compared with control plots (Podgwaite 1991). Similar treatments to lower halves of trees in homeowner-sized plots resulted in a significant increase in mortality of gypsy moth larvae (Webb et al. 1990). In Czechoslovakia, both the American and local strain of LdNPV reduced gypsy moth populations to 95% and 93%, respectively, and hence did not differ in their effects on European populations of the gypsy moth (Novotny 1991b).

In the USSR, application of Virin-ENS (*L. dispar* NPV) at 0.1 l/ha killed 93% of second and third instars of gypsy moth in pistachio and other nut plantations (Tanabaev 1984). Also, treatment of egg masses with Virin-ENS at $5 \infty 10^{6}$ PIB/ml immediately after oviposition caused high mortality of first instars (Orlovskaya and Meshkova 1984). In the United States, however, treatment of egg masses with sprays of NPV did not even temporarily control the insect (Campbell 1983). In the USSR, the virus preparation Virin-ENS resulted in 80%, 68.6% and 56.6% mortality of the gypsy moth when applied at

concentrations of 1:10, 1:15 and 1:25, respectively (Romanenko 1982). The two virus preparations Virin-ENS and Gypchek at 300g/ha in 300 l of working liquid were equally effective in controlling the first and second instars of the gypsy moth; and the viruses had spread outside release plots 1 year after the initial treatments (Timchenko and Meshkova 1985). In the Ukraine, Virin-ENS treatment reduced egg and larval numbers by over 80% and by 6.5% in 1982 and 1983, respectively (Meshkova 1985). In Romania, NPV at $1 \infty 10^{13}$ PIB/ha caused 59.6-66.8% mortality of gypsy moth larvae at 25 and 35 days after treatment, respectively (Mihalache et al. 1978). In China, spraying NPV at $0.6 \infty 10^{7}$ PIB/ml killed 85% of gypsy moth larvae (Yue et al. 1984).

Adjuvants and formulations to improve the efficacy of NPV against gypsy moth larvae have been sought. Addition of neem extract to NPV resulted in faster virus-caused mortality among gypsy moth larvae (Shapiro et al. 1994). The incubation period of the virus was shortened by the addition of chemicals such as 0.05-0.1% copper sulfate to the virus suspension (Wellenstein 1973). Shielding substances such as LOVO 192 and Amelozan were effective in protecting NPV from solar radiation and in preventing the virus from being washed from foliage by rain (Vasiljevic and Injac 1975). Twenty-three fluorescent brighteners were tested as radiation protectants for LdNPV; eight protectants (Intrawite CF, Leucopor BS, Leucophor BSB, Phorwite AR, Phorwite BRU, Phorwite BKL, Phorwite CL, and Tinopal LPW) at 1% concentration gave complete protection with 100% original activity remaining (Shapiro 1992). Plots treated with *L. dispar* NPV plus Blankophor BBH (a stilbene disulfonic additive) had significantly more larval mortality and shorter lethal times than did plots treated with NPV alone (Webb et al. 1994). A molasses formulation containing the viral product Gypchek was more effective when applied with Becomist nozzles, while Pro-tec formulations were more effective when applied with Flat Fan 8006 nozzles (Lewis et al. 1979).

Interactions occasionally are investigated between LdNPV and other biotic agents. Prevalence of the NPV was positively correlated with prevalence of parasitism by *Cotesia [Apanteles] melanoscela* and *Parasetigena silvestris* (Reardon and Podgwaite 1976). Aerial application of NPV had no short-term adverse effect on birds that contacted the virus during its application or that subsequently fed on NPV-infected gypsy moth or other NPV-contaminated food sources (Lautenschlager et al. 1979). These birds and mammals can passively transport infectious gypsy moth NPV in the wild (Lautenschlager et al. 1980).

B. thuringiensis is a bacterial candidate for microbial control of the gypsy moth. In the United States, a single aerial application of *B. thuringiensis* at 12 or 16 BIU/0.4 ha significantly reduced gypsy moth larval density resulting in only 4% net defoliation, which was equivalent to the control achieved with two weekly applications at 8 BIU/0.4 ha (Andreadis et al. 1983). Thuricide HPC at $16 \infty 10^{9}$ and $8 \infty 10^{9}$ IU/acre was effective in controlling gypsy moth larvae in the eastern United *States (Yendol et al. 1973).* The estimated defoliation at both rates did not exceed 30%, as compared with 50-95% in controls

(Yendol and Hedlund 1972). Dipel *(B. thuringiensis subsp. kurstaki)* and Thuricide HPC at $8 \infty 10^9$ IU/acre applied twice at a 10-day interval did not reduce a population of gypsy moth larvae in the eastern United States, probably due to unfavorable weather and excessive size of spray droplets (Lewis et al. 1974). In oak trees, gypsy moth larvae caused only 18% defoliation after being sprayed with Dipel (Moore 1982). Reardon et al. (1994) reviewed aspects of *B. thuringiensis* application against *L. dispar,* primarily in the United States, including effects on nontarget organisms.

Application of Foray 4B at 31.75 BIU/ha and Bactucide S at 56 BIU/ha resulted in 85% and 80% mortality of gypsy moth larvae in a cork oak forest in northern Sardinia (Luciano et al. 1992). In Yugoslavia, Dipel TM (*B. thuringiensis* var. *alesti*) at 700 and 1000g/ha was effective in preventing defoliation, in killing the gypsy moth larvae, and in reducing the number of pupae (Vasiljevic and Injac 1973). In Italy, a single aerial application of Thuricide HPSC at 0.5kg/ha resulted in heavy mortality of the gypsy moth (Barbone 1976). A commercial preparation of *B. thuringiensis* var. *kurstaki* containing $4 \infty 10^6$ viable spores/mg at 100-400 g/ha when applied to branches of macedonian oak resulted in 64-93% mortality of second and third instars (Triggiani 1979). In Romania, aerial application of Dipel at 1 kg/ha in a 40- to 50-year-old mixed hardwood stand was effective against gypsy moth larvae (Mihalache et al. 1972). Larval susceptibility depended not only on the concentration of the *B. thuringiensis* suspensions but also on the age of the larvae and length of time the infested site had been occupied by the gypsy moth (Mihalache et al. 1969).

In the USSR, commercial preparations of *B. thuringiensis* caused 94% mortality of *L. dispar* (Kondrya et al. 1980). Application of 2% Gomelin (*B. thuringiensis*) caused 40-60% mortality even at low temperatures (Lazareva et al. 1980). Treatment of black-fruited rowan with Lepidocide (*B. thuringiensis* subsp. *kurstaki*) at 1.2 and 1.5 kg/ha during flowering gave 77-90% control of gypsy moth larvae in the Ukraine (Zurabova et al. 1986). Gomelin, Dendrobacillin *(B. thuringiensis* subsp. *dendrolimus*), and Bitoxibacillin (*B. thuringiensis* subsp. *thuringiensis*) at 3 kg/ha have been recommended for gyspy moth control in Central Asia (Guzeev 1986). In the USSR, Entobakterin (*B. thuringiensis* var. *galleriae*) and Dendrobacillin *(B. thuringiensis* var. *dendrolimus*) at 0.5-2.0% were sprayed in forest stands against gypsy moth larvae. Entobakterin was more effective than Dendrobacillin; peak mortality occurred on the ninth day after treatment, and the infection spread from treated to untreated areas (Akimtseva 1975).

In Canada, application of undiluted formulations of *B. thuringiensis* containing 16.9 BIU/l in 1.8 l water/ha have been recommended for the control of gypsy moth larvae (Van Frankenhuyzen et al. 1989). An aerially sprayed Czechoslovak bacterial preparation, Bathurin 82 (*B. thuringiensis* var. *kurstaki*), killed 31-88% of larvae, depending on the weather (Novotny 1987). In Bulgaria, strains of *B. thuringiensis* (including *B. thuringiensis* subsp.

dendrolimus [Dendrobacillin] and *B. thuringiensis* subsp. *thuringiensis* [Bactospeine]) at 0.5 kg/ha reduced an infestation of gypsy moth by 2.2-19.8% on oak and 2.1-19.3% on apple (Ovcharov 1982). In Romania, Dipel and Turingin applied to oak forests killed 90-98% of gypsy moth larvae (Pasovici et al. 1978). In Canada, BIODART (*B. thuringiensis* strain A20) was effective in controlling a gypsy moth larval population and significantly reducing defoliation (Bernier et al. 1990). Bitoxibacillin (BTB-202) (a biopreparation of unstated composition) caused 97.1% mortality of gypsy moth larvae on oak (Okhotnikov 1975) and was recommended for large-scale control of insect defoliators of oak in the Ukraine (Okhotnikov 1978). Bactospeine Creme, a commercial formulation of *B. thuringiensis*, resulted in only 33% mortality of second and third instars in Sardinia (Magnoler 1974b)

Interactions of *B. thuringiensis* occasionally have been tested. Bacterial suspensions were synergistic with pyrethrins at 0.02 mg active ingredient per milliliter against early instars of the gypsy moth (Kudler and Lysenko 1976). Dipel mixed with low doses of tetrachlorvinphos (Gardona) has been effective against third instars of gypsy moth in Bulgaria (Videnova 1980). Entobakterin (*B. thuringiensis* var. *galleriae*), Dendrobacillin (*B. thuringiensis* var. *dendrolimus*), and BIP (*B. thuringiensis* var. *alesti*) at 50g/10 l of water, each in combination with a low dosage of trichlorfon (1g/10 l water), effectively controlled gypsy moth larvae (Linskii 1983). A mixture of Dipel at 1 kg in 100 l water/ha plus an emulsion concentrate containing 25% permethrin applied at 0.6-3 ml/ha caused 97-100% mortality of gypsy moth larvae in Czechoslovakia (Kudler and Lysenko 1984).

Streptococcus faecalis is the only other bacterium investigated for control of *L. dispar*. Application of *S. faecalis* by mistblower to apple trees induced disease among the second and third instars of gypsy moth, thereby reducing defoliation (Doane 1971). Aerial spraying of *S. faecalis* on second and third instars resulted in 45.6% mortality of larvae in Bulgaria (Grigorova and Mirchev 1992).

During 1910-1911, a fungus now believed to be *E. maimaiga* was imported from Japan via infected gypsy moths and subsequently was released at several locations near Boston (Speare and Colley 1912). The fungus was thought to have failed to establish, and was never recovered. The epizootic potential of this fungus in Japan was well known (Koyama 1954, Aoki 1974, Yanbe 1976). In 1989 and 1990, however, *E. maimaiga* spontaneously caused extensive epizootics in gypsy moth larval populations in 10 adjacent States in the northeastern United States (Andreadis and Weseloh 1990, Hajek et al. 1990). Although no definitive information is available on the source of infection, it was presumed that the epizootic in the northeastern United States was initiated via resting spores (Andreadis and Weseloh 1990). It is doubtful whether the 1910-1911 releases resulted in epozootics 80 years later, but there is no question that *E. maimaiga* can establish after release, spread rapidly, and cause epizootics (Reardon and Hajek 1993). When resting spores were applied at the bases of oak trees in Maryland, Pennsylvania, Virginia,

and West Virginia (34 plots in 1991 and 7 plots in 1992), the fungus spread up to 350 m from plots in 1991 and was detected in 1992 in 40 of the 41 plots at a mean prevalence rate of 72% (Hajek et al. 1996).

Protozoa have been tested for microbial control of gypsy moth. Two European species of microsporidia, *Nosema* sp. and *Vavraia* sp., were introduced into woodlots in Maryland by placing contaminated gypsy moth egg masses on centrally located trees. Sampling revealed that 10.5% and 21.1% of first instars, and 7.8% and 16.9% of second instars, were infected by *Nosema* sp. and *Vavraia* sp., respectively (Jeffords et al. 1988). *Nosema* sp., but not *Vavraia* sp., was able to overwinter after a field release and infect up to 10% of gypsy moth larvae during the subsequent year, a prevalence rate about the same as during the first year. *Nosema* is transovarially transmitted while *Vavraia* is not, which might account for observed overwintering success of *Nosema* sp. (Jeffords et al. 1989). Both microsporidia can be introduced into gypsy moth populations by inoculative release of contaminated egg masses (Jeffords et al. 1989).

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64. *Malacosoma americanum* (F.)

EASTERN TENT CATERPILLAR

PEST SITUATION

- *Distributed widely throughout the eastern half of the United States and southern Canada.*
- *Preferred hosts are cherry and apple, although a wide variety of forest, shade, and fruit trees are attacked.*
- *The major impact comes from the disfigured canopies of trees in parks, recreational areas, and suburban areas.*
- *One generation per year, with eggs overwintering as bands encircling small twigs.*

- *During most years and in most places, the eastern tent caterpillar is controlled satisfactorily by natural enemies.*

Pathogens of *Malacosoma americanum*

Infections by a virus, two fungi, and three protozoa have been de tected in field-collected eastern tent caterpillars. Viruses, bacteria, and protozoa also have been tested against this insect in the laboratory. However, there apparently have been no attempts at microbial control of *M. americanum*.

Natural Infections. Several pathogens of eastern tent caterpillar have been detected in field samples. Field-collected larvae of *M. americanum* in Kentucky were infected with a nuclear polyhedrosis virus (NPV) (Nordin 1974). The fungi *Beauveria bassiana* and *Paecilomyces farinosus* also have been isolated from this insect (Humber 1992). The microsporidia *Nosema disstria* and *Pleistophora* sp. were isolated from field-collected larvae in Kentucky, with *N. disstria* accounting for 92% of the cases of infection (Nordin 1974). Embryos in 56-90% of egg masses of *M. americanum* were infected with *Nosema* sp. (Nordin 1975). The proportions of hatched and surviving larvae recovered at the end of the experiment in the infected colonies were 79% and 54% as compared with 92% and 73% in the uninfected colonies, respectively (Nordin 1976).

Laboratory Studies. Laboratory tests with entomopathogens have been limited to viruses, bacteria, and protozoa. The *Autographa californica* (Speyer) NPV can infect larvae of *M. americanum* (Kaya 1977). The eastern tent caterpillar has also been infected by cytoplasmic polyhedrosis virus (Martignoni and Iwai 1981). Five strains of *Bacillus thuringiensis* (ARSEF 283, 1775, NRRL 3108, 20699, and 20700) killed eastern tent caterpillars within 4 days (Leathers and Gupta 1993). *M. americanum* has been successfully infected with *Thelohania pristiphorae*, a microsporidian pathogen of *Pristiphora erichsonii* (Hartig) (Smirnoff 1975). The eastern tent caterpillar also has been infected with *Pleistophora schubergi schubergi* (Sprague 1977).

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65. *Malacosoma disstria* Hübner

FOREST TENT CATERPILLAR

PEST SITUATION

- *Distributed transcontinentally throughout Canada and the United States.*
- *In the North and West, aspen is the preferred host, while water tupelo, sweetgum, and oaks are heavily defoliated in the South.*
- *An important pest of forest, orchard, and shade trees. Outbreaks have occurred both periodically and often persistently in portions of its range. Western Canada and the forested wetlands in the South have been repeatedly defoliated. Radial growth losses of 90% are not uncommon during outbreaks.*
- *Populations often collapse from natural controls and weather before tree mortality is extensive.*
- *One generation per year with eggs overwintering on twigs.*
- *Parasitoids are responsible for extensive larval and pupal mortality in nature.*

Pathogens of *Malacosoma disstria*

Infections by a virus and two species of fungi have been detected in field-collected forest tent caterpillars. Viruses and a protozoan have been investigated in the laboratory, and a virus has been field tested for microbial control.

Natural Infections. In North America, a nuclear polyhedrosis virus (NPV) caused epizootics in forest tent caterpillar populations, resulting in their rapid decline (Myers 1993). In Canada, six isolates of NPV were recovered from this insect (Ebling and Kaupp 1995). The fungi *Entomophthora crustosa* and *Entomophaga aulicae* are naturally occurring pathogens of forest tent caterpillar in North America (McLeod and Tyrell 1979, Humber 1992).

Laboratory Experiments. Laboratory experiments have been limited to viruses and a protozoan. Quantitative differences in susceptibility to NPV have been observed among larval instars of the forest tent caterpillar. Some fourth instars survived dosages two billion times greater than those required to kill first instars (Stairs 1965). NPV isolates from other species of *Malacosoma* also infect *M. disstria* (Stairs 1964a). Isolates of NPV have been characterized from *M. disstria* populations in Alberta (Keddie and Erlandson 1995), and bioassays of six isolates of NPV recovered from the forest tent caterpillar in Ontario indicated that those isolates differed in their infectivity to *M. disstria* (Ebling and Kaupp 1995). One isolate, 7-21, was more virulent than others tested; this isolate could improve the results of microbial control tests in the field (Ebling and Kaupp 1997). The microsporidium *Thelohania pristiphorae* has infected this insect under laboratory conditions (Smirnoff 1968).

Microbial Control. Microbial control studies with *M. disstria* have been limited to NPV. In Canada, *M. disstria* adults infected with NPV transmitted the virus from generation to generation (Stairs 1966). Application of *M. disstria* NPV in dosages ranging from $1 \infty 10^5$ polyhedral inclusion bodies (PIB)/ml to $1 \infty 10^8$ PIB/ml to second, third, and fourth instars of forest tent caterpillars with ground based equipment resulted in mortality as high as 100% after 10 days (Stairs 1964b, Ives and Muldrew 1978). Aerial application of NPV at $1.8 \infty 10^{13}$ PIB/ha resulted in 36-97% mortality of early instars of forest tent caterpillar (Ives et al. 1982).

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66. *Orgyia leucostigma* (J. E. Smith)

WHITEMARKED TUSSOCK MOTH

PEST SITUATION

- *Distributed throughout the eastern United States and eastern Canada.*
- *Preferred hosts are apple, basswood, elm, poplar, maple, sycamore birch, and balsam fir. A wide variety of other deciduous and conifer trees also are attacked.*
- *Primarily a pest of shade trees in cities and towns, with minor damage in forested areas.*
- *Two generations per year, with eggs overwintering on or near the pupal cocoons.*
- *There appears to be little economic justification for applied controls in most forest settings.*

PATHOGENS OF *ORGYIA LEUCOSTIGMA*

Injections by a virus and a fungus have been detected in field-collected larvae of *O. leucostigma*. Viruses and a bacterium have been tested against white-marked tussock moth in the laboratory and for microbial control.

Natural Infections. In Canada, field-collected larvae of *O. leucostigma* were infected with a single-enveloped nuclear polyhedrosis virus (NPV) (Hughes and Cunningham 1976). In India, *O. leucostigma* collected from the leaves of mango, *Cassia fistula*, and from *Terminalia arjuna* were infected with the fungus *Fusarium solani* (Maharaj and Patil 1986).

Laboratory Studies. Laboratory tests with entomopathogens have included viruses and a bacterium. Larvae of *O. leucostigma* were susceptible to NPV isolated from *Orgyia pseudotsugata* (McDunnough) and from *Orgyia antiqua* (L.). First instars were very susceptible to the viruses, whereas fourth instars were refractive to infection. A suitable application rate for aerial spraying of NPV was estimated at 10^8 polyhedral inclusion bodies (PIB)/ml at 2.5 US gal/acre (Cunningham 1972). Larvae of *O. leucostigma* also were susceptible to activated toxin solutions from the HD-1 and NRD-12 isolates of *Bacillus thuringiensis* (Van Frankenhuyzen et al. 1993). Dosage-mortality studies with Dipel (*B. thuringiensis)* indicated that a deposit rate of $2 \infty 10^6$ IU/acre might give good control of second to fifth instars (Morris 1973). Both the HD-1 and NRD-1 strains of *B. thuringiensis* subsp. *kurstaki* were equally toxic to larvae of *O. leucostigma* (Van Frankenhuyzen et al. 1992).

Microbial Control. A virus and a bacterium were tested for microbial control of this insect. In Canada, the viral insecticide Virtuss, at $2.5 \infty 10^{11}$ PIB/ha, killed 91%

of larvae in a treated plot as compared with 69% in a nearby control plot (West et al. 1989). The *O. leucostigma* NPV, when deposited naturally or artificially on foliage of *Abies balsamea* in summer, retained its activity throughout the winter to kill at least some white-marked tussock moth larvae the next season (Elgee 1975). Combinations of low concentrations of insecticides and low to moderate concentrations of *B. thuringiensis* caused high mortality of the larvae of *O. leucostigma*. A dosage of *B. thuringiensis* that produced 20-60% mortality combined with a fenitrothion dosage causing 15-50% mortality or with a sublethal dosage of tetrachlorvinphos resulted in low rates of survival of *O. leucostigma* (Morris 1975).

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67. *Orgyia pseudotsugata* (McDunnough)

Douglas-fir Tussock Moth

Pest Situation

- *Distributed from southern British Columbia through the eastern half of the Pacific Coast States and through the Rocky Mountain States to Arizona and New Mexico.*
- *Douglas-fir, grand, white, and subalpine firs are the preferred hosts, although associated conifer species are attacked when intermixed with firs.*
- *Outbreaks appear and end suddenly, and between outbreaks the insects cannot be seen easily. Much timber is killed, and growth loss and mortality have affected billions of board feet of lumber.*
- *One generation per year, with eggs overwintering on cocoons.*

Pathogens of *Orgyia pseudotsugata*

Pathogenic viruses have been detected in field-collected Douglas-fir tussock moth larvae. Laboratory studies with entomopthogens have been limited to viruses and a fungus, and there have been field tests with viruses and a bacterium.

Natural Infections. A nuclear polyhedrosis virus (NPV) was the major cause of collapse of an outbreak of *O. pseudotsugata* in a forest of *Pinus ponderosa* in California (Mason and Thompson 1971). Two types of NPV have been isolated from Douglas-fir tussock moth larvae collected from various sites in the United States, a single-nucleocapsid NPV (OpSNPV) and a multinucleocapsid NPV (OpMNPV) (Hughes and Addison 1970). Studies of the production and prevalence of NPV of Douglas-fir tussock moth have indicated that low prevalence rates of NPV in populations with early instars can lead to mortality of older instars, ultimately resulting in greater production and persistence of polyhedra in the forest ecosystem (Thompson and Scott 1977).

Laboratory Studies. Viruses and a fungus have been tested against this insect in the laboratory. An NPV isolated from *Autographa californica* (Speyer)

was virulent toward the Douglas-fir tussock moth but was less virulent than NPV isolated from *O. pseudotsugata* (Martignoni et al. 1983). In studies of viral interactions, the OpMNPV had a tendency to predominate over the OpSNPV, particularly in massive doses (Hughes 1979). ARSEF 1400, an isolate of *Entomophaga maimaiga*, was an effective pathogen of *O. pseudotsugata*, killing 92.5% of the larvae tested (Soper et al. 1988).

Microbial Control. Microbial control attempts have been limited to viruses and a bacterium. An NPV isolated from *O. leucostigma*, when applied aerially at $2.2 \infty 10^{11}$ polyhedral inclusion bodies (PIB) in 11.3 l/ha, killed 77-100% of Douglas-fir tussock moth larvae 5-8 weeks after treatment. Ground-spray applications at $2.4 \infty 10^{10}$ PIB in 4.5 l/tree killed 83-85% of the larvae 8 weeks after treatment (Shepherd et al. 1984). The *O. leucostigma* NPV preparation Virtuss, at $2.5 \infty 10^{11}$, $8.3 \infty 10^{10}$, and $1.6 \infty 10^{10}$ PIB/ha applied with a fixed-wing aircraft fitted with boom and nozzle calibrated to deliver 9.4 l/ha, reduced *O. pseudotsugata* numbers by 65% in plots that received the lowest concentration and by 87-100% at the higher concentrations (Otvos et al. 1987b). The NPV spread from the treated plots to adjoining areas within 1-2 years after application (Otvos et al. 1987a). Spraying of *O. pseudotsugata* NPV (TM-Biocontrol-1) at 10^{11} PIB/acre in 25% molasses or 25% molasses formulation of Dipel (*Bacillus thuringiensis*) at 1 lb/acre resulted in 95% reduction of a larval population 35 days after spraying (Stelzer et al. 1975). In Canada, spray applications of the same formulations with or without molasses, at 10^{11} PIB/acre in 1 or 2 US gal water, resulted in excellent foliage protection, with mortality rates of 60-87% 5 days after treatment (Stelzer et al. 1977). In the early 1990s, aerial spraying of TM-Biocontrol-1 against Douglas-fir tussock moth larvae in Idaho was not successful; therefore, the stock of TM-Biocontrol-1 is being bioassayed using the laboratory strain (Goose Lake) and wild strains.[1]

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[1] ***Reardon, Richard C. 1998.*** *Program Manager, USDA Forest Service, Morgantown, WV. Conversation with Imre Otvos at informal working group meeting, Portland, OR, March 10-11,1998*

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68. *Paleacrita vernata* (Peck)

Spring Cankerworm

Pest Situation

- *Distributed from the Maritime provinces southwest to Texas and west to Colorado and California.*
- *Apple and elm appear to be preferred hosts, but hickory, maple, ash, beech, cherry, and several oaks also are infested.*
- *Outbreaks have occurred over large areas, but shade trees in and near urban areas are most affected.*
- *One generation per year with larvae overwintering in earthen cells.*

Pathogens of *Paleacrita vernata*

Microbial control of spring cankerworm has been attempted with several commercial preparations of *Bacillus thuringiensis*, and an entomopathogenic nematode has been studied in the laboratory. No reports of other entomopathogens infecting this insect were found.

Laboratory Studies. Various strains of *Steinernema* have been tested in the laboratory for virulence to spring cankerworm. *Steinernema feltiae* All was highly virulent for spring cankerworm at 96 h after exposure. *S. feltiae* Breton and *Steinernema bibionis* were moderately virulent, and *Steinernema glaseri* and *S. feltiae* Mexican were weakly virulent at 48 and 96 h after exposure (Morris et al. 1990).

Microbial Control. *B. thuringiensis*, serotypes I and III at 4 BIU/acre, killed 85-95 % of spring cankerworm (Harper 1974). Thuricide 16B at 0.946 l/acre sprayed through a hydraulic sprayer or cold fogger also controlled this insect (Frye et al. 1976). Dipel, Thuricide, and Biotrol effectively controlled spring cankerworm in North Dakota (Frye et al. 1977).

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69. *Thyridopteryx ephemeraeformis* (Haworth)

BAGWORM

PEST SITUATION

- *Distributed widely throughout the eastern and southern United States.*
- *Cedar, pine, baldcypress, poplar, willow, and maple are commonly attacked along with several other hardwood as well as conifer species.*
- *Primarily a pest of ornamentals and shade trees, with occasional outbreaks on baldcypress, can result in crown dieback and tree mortality when repeated defoliation occurs in midsummer.*
- *One generation per year, with eggs overwintering in the bags of the wingless females.*
- *A difficult defoliator to control because of the protection afforded by the bags.*
- *Spotty infestations hamper widespread control efforts.*

PATHOGENS OF *THYRIDOPTERYX EPHEMERAEFORMIS*

Representatives of several groups of entomopathogens have been detected in field populations of bagworms. Bacteria, fungi, and nematodes have been field tested against this insect.

Natural Infections. Pathogens isolated from field-collected bagworm larvae in Georgia included bacilliform bacteria, a polyhedrosis virus, and fungi belonging to the genera *Aspergillus, Penicillium, Geotrichum, Paecilomyces, Hirsutella, Beauveria, Cordyceps, Scopulariopsis,* and *Pestalotia* (Berisford and Tsao 1975a). Fungal diseases were the most prevalent among these pathogens, ranging from 13% infection during one year to 51% during another. An inverse relationship existed between the levels of fungal disease and parasitoids in bagworm larval populations (Berisford and Tsao 1975a).

Microbial Control. Microbial control attempts have included bacteria, fungi, and nematodes. Biotrol XK ($3.4 \infty 10^9$ IU/lb) (a wettable powder formulation of *Bacillus thuringiensis* var. *kurstaki*) at 4, 2, 1, and 0.5 lb/100 gal water significantly reduced bagworm populations (Bishop et al. 1973). Aerial application of Dipel at 0.5 lb/acre resulted in 95% control of bagworm larvae attacking *Pinus sylvestris* in Missouri (Kearby et al. 1975). Thuricide HPC (a liquid formulation of spores and crystals of *B. thuringiensis* var. *alesti*) effectively controlled bagworm larvae, especially in nursery stocks (Kearby et al. 1972). In field tests, the fungi *Aspergillus parasiticus* and *Beauveria bassiana* killed 53-91% of bagworms (Berisford and Tsao 1975b). Formulations of the nematodes *Steinernema carpocapsae* and *Steinernema feltiae*, either alone or with oil or antidesiccant additives, killed 91-100% of bagworm larvae (Gill and Raupp 1994).

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70. *Zeiraphera canadensis* Mutuura and Freeman

Spruce Bud Moth

Pest Situation

- *Distributed throughout the range of spruce in the northern United States and Canada.*
- *Spruces are the preferred hosts, but several other conifers including balsam fir are attacked.*
- *Damage is generally confined to opening buds or to tender needles. Younger trees are especially hard hit.*
- *One generation per year, and winter is spent in the egg stage. Pupae are found in the soil.*
- *Larvae habitually wander extensively before dropping to the ground to pupate.*

Pathogens of *Zeiraphera canadensis*

Laboratory studies with entomopathogens have been limited to a nematode. A bacterium and a nematode have been field tested against this insect.

Laboratory Studies. The spruce bud moth has been infected with *Heterorhabditis heliothidis (= bacteriophora)* under laboratory conditions. Infection rates were greatly reduced, however, when the nematodes were applied to the foliage of potted trees (Turgeon and Finney-Crawley 1991).

Microbial Control. Microbial control attempts have been limited to a bacterium and a nematode. Foliar applications of a mixture of Futura (a commercial *Bacillus thuringiensis* formulation) and a suspension of *Steinernema carpocapsae* at 9,785 viable infective juvenile nematodes per liter resulted in 82% reduction in a bud moth population. Mortality was attributed primarily to the nematodes. Soil drench treatments also have been encouraging and may be feasible for microbial control (Eidt and Dunphy 1991).

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Chapter 12

LEPIDOPTERA

Shoot Borers

- *Hypsipyla grandella* (Zeller) -- Mahogany Shoot Borer
- *Prionoxystus robiniae* (Peck) -- Carpenterworm
- *Rhyacionia buoliana* (Denis and Schiffermüller) -- European Pine Shoot Moth
- *Rhyacionia frustrana* (Comstock) -- Nantucket Pine Tip Moth

71. *Hypsipyla grandella* (Zeller)

Mahogany Shoot Borer

Pest Situation

- *Distributed in southern Florida and throughout the tropics wherever its hosts grow.*
- *Preferred host is mahogany, but Spanish cedar also is attacked.*
- *Shoot growth is reduced, and small seedlings and saplings are killed where populations are prevalent. The shoot borer is a serious obstacle in growing mahogany.*
- *Two generations per year in Florida.*
- *Some insects pupate in the wood while some pupate in the soil.*

Pathogens of *Hypsipyla grandella*

A fungus and one or more nematodes are known natural pathogens of mahogany shootborer. Various strains of *Bacillus thuringiensis* and three fungi have been tested against this insect in the laboratory. No attempts at microbial control were found.

Natural Infections. Field-collected mahogany shootborers have been infected with a fungus and possibly two nematodes. An unidentified, parasitic nematode and the fungus *Beauveria* sp. were isolated from *H. grandella* in the Amazon (Yamazaki et al. 1990). Larvae of mahogany shootborer collected from Costa Rica were parasitized by *Hexamermis albicans*. Mortality of the larvae due to this nematode was 25% during the wettest season and 5% at the end of the dry season (Nickle and Grijpma 1974).

Laboratory Experiments. Laboratory experiments with entomopathogens have involved bacteria and fungi. *B. thuringiensis* var. *sotto* caused high levels of mortality among first instars of mahogany shootborer (Salvatierra 1973). Also, *H. grandella* was susceptible to both *B. thuringiensis* var. *thuringiensis* and *B. thuringiensis* var. *entomocidus*, with 96% mortality of first instars at the highest concentration tested (Salvatierra and Palm 1972). Fifth-instars were the most susceptible of the instars tested to the fungus *Metarhizium anisopliae*, with an LC_{50} of $3.6 \infty 10^7$ spores/ml, followed by the sixth and seventh instars (Salvatierra et al. 1972). Radiation-induced mutants of *M. anisopliae* proved more virulent to *H. grandella* than wild strains (Salvatierra 1973). Larvae of the mahogany shootborer, when immersed for 1 min in a suspension of *Beauveria bassiana* at $1.4 \infty 10^6$ viable spores/ml or in *Beauveria tenella* at $2.9 \infty 10^6$ viable spores/ml, suffered 13.9% and 12.7% mortality, respectively. The highest mortality by *B. bassiana* occurred at 8 days and by *B. tenella* at 10 days after infection (Berrios and Salvatierra 1971).

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72. *Prionoxystus robiniae* (Peck)

CARPENTERWORM

PEST SITUATION

- *Distributed widely throughout the United States and southern Canada.*
- *Hosts are oak, elm, willow, poplar, ash, black locust, sycamore, and sugarberry.*
- *A major contributor to quality loss in hardwood timber, the carpenterworm honeycombs wood causing breakage in wind, but directly causes little mortality.*
- *Life cycle requires 1-2 years in the South and 2-4 years in the North.*

PATHOGENS OF *PRIONOXYSTUS ROBINIAE*

Laboratory studies with entomopathogens have been limited to nematodes. A bacterium and nematodes have been tested for microbial control of this insect, and field populations have not been surveyed for naturally occurring entomopathogens.

Laboratory Studies. Pathogenic nematodes have been tested against *P. robiniae*. The nematodes *Neoaplectana (= Steinernema) carpocapsae* and *Steinernema bibionis* were pathogenic to the larvae of *P. robiniae*. *S. carpocapsae* was the most virulent, however, based on LD_{50}s, which were 1.5 and 3.7 nematodes per larva for *S. carpocapsae* and *S. bibionis*, respectively (Forschler and Nordin 1988a). The vulnerability of *P. robinae* to infection by *S. bibionis* decreased during the fifth and sixth instars. (Forschler and Nordin 1988a).

Microbial Control. Attempts at microbial control have included a bacterium and nematodes. *Bacillus thuringiensis* was ineffective in controlling larvae of the carpenterworms even at a very high dosage (Solomon 1985). Injection of *Steinernema feltiae* and *S. bibionis* into galleries resulted in 70-100% mortality of fifth and sixth instar carpenterworms. Bark surface treatments around gallery entrances with *S. feltiae* at $2.9 \infty 10^4$ nematodes per gallery resulted in 85% mortality (Forschler and Nordin 1988b). A suspension of *S. carpocapsae* at 9,000 nematodes per carpenterworm gallery killed 100% of carpenterworms (Anonymous 1987).

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73. *Rhyacionia buoliana* (Denis and Schiffermüller)

European Pine Shoot Moth

Pest Situation

- *An introduced species widely distributed in the northeastern United States and southernCanada. Isolated infestations have been noted in Washington, Oregon, and British Columbia.*
- *Hosts include Scotch, red, ponderosa, eastern white, jack, pitch, longleaf, and Virginia pines.*
- *Spring feeding kills terminal and lateral buds resulting in bushy, dense growth. Damage is most important in younger trees before crown closure.*
- *One generation per year with larvae overwintering within burrowed shoots.*
- *Climate is an important factor in regulating abundance. Warm, dry summers and winters favor survival.*

Pathogens of *Rhyacionia buoliana*

A pathogenic virus has been detected in field-collected *R. buoliana*, and laboratory studies with entomopathogens have been limited to a virus and a fungus. No reports of other entomopathogens infecting this tortricid or of attempts at microbial control were found.

Natural Infections. In Canada, field-collected *R. buoliana* were infected with a granulosis virus (GV) (Burke and Percy 1983).

Laboratory Studies. A virus and a fungus have been tested against *R. buoliana* in the laboratory. *R. buoliana* is susceptible to a GV isolated from *Cydia (= Laspeyresia) pomonella* (L.). After infection per os (oral), larvae caused negligible feeding damage before death (Dickler and Huber 1986). The fungus *Paecilomyces farinosus* also can infect this tortricid (Zimmermann and Weiser 1991).

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74. *Rhyacionia frustrana* (Comstock)

Nantucket Pine Tip Moth

Pest Situation

- *Distributed widely in the eastern, central, and southern United States and elsewhere.*
- *Hosts are nearly all species of pine except eastern white and longleaf pines. Slash pine is attacked only occasionally.*
- *A major pest of young pines, the larvae cause stunting, forked, or crooked stems and, occasionally, death to young seedlings on poor sites. Attacks can damage and reduce flower and conelet production in pine seed orchards in the South.*
- *Three or four generations per year in the South and two in Pennsylvania and Ohio. Pupation occurs both in shoots and in the soil beneath infested trees.*
- *Pupae overwinter in the soil duff layer.*

Pathogens of *Rhyacionia frustrana*

A pathogenic virus has been detected in field-collected *R. frustrana*, and microbial control attempts have been limited to a virus and a bacterium. No reports of other entomopathogens infecting this insect were found.

Natural Infections. Infections by a granulosis virus (GV) have been detected in larvae of *R. frustrana* (Martignoni and Iwai 1986, Zimermann and Weiser 1991).

Microbial Control. Microbial control attempts have included a virus and a bacterium. In the United States, *Cydia (= Laspeyresia) pomonella* (L.) GV sprayed at $2.5 \infty 10^{13}$ granules/ha in 93.5 l of water controlled populations of *R. frustrana* (McLeod et al. 1983). Sprays of SAN 406 I (a wettable powder formulation of *C. pomonella* GV containing $2.5 \infty 10^{11}$ capsules/g) at $1 \infty 10^{7}$, $1 \infty 10^{8}$, and $1 \infty 10^{9}$ capsules per milliliter effectively reduced larval densities on loblolly pines (Stephen et al. 1982). Applications of Biotrol XK (a formulation of *Bacillus thuringiensis*) were ineffective against the Nantucket pine tip moth in the United States (Dupree and Davis 1975).

References

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Chapter 13

ORTHOPTERA

Defoliators

- *Diapheromera femorata* (Say) -- Walkingstick

75. *Diapheromera femorata* (Say)

WALKINGSTICK

PEST SITUATION

- *Distributed throughout southern Canada and the eastern United States west to the Great Plains and Texas.*
- *Preferred hosts are black and red oaks, basswood, elm, black locust, and cherry. It also feeds on white oak, aspen, ash, dogwood, and hickory.*
- *Nymphs and adults defoliate host trees. Severe outbreaks have occurred in the Lake States, but occasionally severe damage is noted from Nebraska eastward to Delaware.*
- *Trees defoliated twice in the same season are most affected. Trees repeatedly defoliated may die.*
- *Only one generation per year, but the nymphal feeding period is prolonged.*
- *Subject to considerable predation.*
- *Eggs overwinter free on the ground surface.*
- *Widely sporadic outbreaks deter active control efforts.*

PATHOGENS OF *DIAPHEROMERA FEMORATA*

No reports of natural infections or microbial control of *D. femorata* were found. This insect was susceptible to a bacterium under laboratory conditions.

Laboratory Experiments. Only one laboratory experiment with *D. femorata* was reported. This insect was susceptible to *Bacillus thuringiensis* var. *alesti*, with an LC_{50} of $6150 \infty 10^3$ IU/ml/gm of insect (Ignoffo et al. 1973).

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Chapter 14

THYSANOPTERA

Raspers

- *Taeniothrips inconsequens* (Uzel) -- Pear Thrips

76. *Taeniothrips inconsequens* (Uzel)

PEAR THRIPS

PEST SITUATION

- *Distributed in most of the northwestern quadrant of the United States; also in Pacific Coast States and British Columbia.*
- *Larvae and adults rasp surfaces of flowers and leaves, resulting in distorted, chlorotic, dwarfed, or defoliated plants.*
- *Shade and forest trees such as maple, birch, beech, ash, pear, plum, and cherry.*
- *One generation per year. Larvae in spring until June. Pupation occurs on the ground beneath host trees.*
- *Pupae overwinter in soil, where they are exposed to soil-borne pathogens.*
- *Culturing larvae on host material is possible.*

PATHOGENS OF *TAENIOTHRIPS INCONSEQUENS*

Field-collected pear thrips have been infected with a fungus. No reports of other entomopathogens infecting this insect were found.

Natural Infections. The fungus *Verticillium lecanii* was isolated from 12-22% of field-collected pear thrips in the northeastern United States. This fungus might prove to be an effective part of an integrated pear thrips management program in forest habitats (Skinner et al. 1991).

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Chapter 15

RECOMMENDATIONS

RECOMMENDATIONS

The primary area for further research on most North American insect pests of forests is surveying for entomopathogens that occur naturally in each insect host. Ideally, such surveys would include observational studies in epizootiology to provide some understanding of the system and ideas for experimental research in microbial control (Fuxa 1987). This is an obvious first step for the 89 insect species for which there is no entomopathogen literature (Appendix). It is impossible to recommend agents to develop for microbial control without knowledge of naturally occurring entomopathogens already present in various populations of a pest species.

Research on most of the 76 insect species for which there is some pathogen literature also would benefit from survey sampling for entomopathogens. Sampling of populations of all these species should be undertaken with the cooperation of a pathologist skilled in identifying a broad range of infectious disease organisms. Representative ecological settings should be sampled on a regular basis for at least two or three growing seasons, with sampling timed to detect entomopathogens in the early, middle, and late parts of the insect's growing season, to determine prevalence of various diseases at different times of year. Sampling in the geographical area of origin for those pest insects that have been introduced into North America should create possibilities for all four approaches to microbial control. Observational research in epizootiology of native insect species also could benefit the microbial insecticide, seasonal colonization, or environmental manipulation approaches.

Once there is a basic understanding of the natural enemy complex of a particular pest species, researchers can begin to select one or more entomopathogens for further study. None of the four approaches to microbial control should be ignored in these early phases. Previous chapters have demonstrated that introduction and establishment can succeed in forest ecosystems in North America, sometimes when the microbial insecticide approach has not worked well (e.g., see *Entomophaga maimaiga* in the *Lymantria dispar* chapter). It also is important to remember in early phases of choosing entomopathogens for research that the introduction and establishment approach, due to its permanence, sometimes can succeed with agents that do not always reduce the pest population below economic injury levels or with those that produce chronic or sublethal diseases (e.g., see *Deladenus siricidicola* in the *Sirex* spp. chapter). Even environmental manipulation of entomopathogens should not be ignored. This approach, which is rarely researched, has been a component of control of at least one tree pest outside North America (Zelazny et al. 1992).

This paper should prove useful in identifying gaps in knowledge as targets for further research. Along with basic pathology and epizootiology information on pest insects, this review also should provide information that can be applied to the criteria in tables 1-3 to select pathogens of a given pest for research and development for microbial control.

References

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Appendix

APPENDIX

North American forest insect pests, for which no scientific papers about entomopathogens were found by means of the searches outlined in the Introduction, are listed here.

Coleoptera—Defoliating and Root-Feeding Beetles

Hylobius radicis Buchanan, Pine Root Collar Weevil
Hylobius wareni Wood
Monocesta coryli (Say), Larger Elm Leaf Beetle
Phyllophaga spp.
Pissodes nemorensis Germer, Eastern Pine Weevil

Coleoptera—Borers and Bark Beetles

Agrilus anxius Gory, Bronze Birch Borer
Agrilus bilineatus (Weber), Twolined Chestnut Borer
Chrysobothris femorata (Olivier), Flatheaded Appletree Borer
Chrysobothris mali Horn, Pacific Flatheaded Borer
Conophthorus coniperda (Schwarz), White Pine Cone Beetle
Conophthorus ponderosae Hopkins, Ponderosa Pine Cone Beetle
Corthylus columbianus Hopkins, Columbian Timber Beetle
Cylindrocopturus furnissi Buchanan, Douglas-Fir Twig Weevil
Dendroctonus adjunctus Blandford, Roundheaded Pine Beetle
Dendroctonus jeffreyi Hopkins, Jeffrey Pine Beetle
Dendroctonus simplex LeConte, Eastern Larch Beetle
Dendroctonus terebrans (Olivier), Black Turpentine Beetle
Enaphalodes rufulus (Haldeman), Red Oak Borer
Glycobius speciosus (Say), Sugar Maple Borer
Goes tigrinus (De Geer), White Oak Borer

Ips confusus (LeConte)
Ips emarginatus (LeConte)
Ips lecontei Swaine
Knulliana cincta (Drury), Banded Hickory Borer
Megacyclene robiniae (Forster), Locust Borer
Melanophila californica Van Dyke, California Flatheaded Borer
Monochamus notatus (Drury), Northeastern Sawyer
Monochamus scutellatus (Say), Whitespotted Sawyer
Odontopus calceatus (Say)
Saperda calcarata Say, Poplar Borer
Tomicus piniperda L., Pine Shoot Beetle
Xyleborus sp.
Xylosandrus compactus (Eichhoff), Black Twig Borer
Xylotrechus obliteratus LeConte

Diptera—Gall Formers

Contarinia oregonensis Foote
Contarinia pseudotsugae Condrashoff

Homoptera—Gall Formers

Adelges abietis (L.), Eastern Spruce Gall Adelgid
Adelges cooleyi (Gillette), Cooley Spruce Gall Adelgid
Adelges oregonensis Annand
Pineus pinifoliae (Fitch), Pine Leaf Adelgid
Pineus strobi (Hartig), Pine Bark Adelgid

Homoptera—Sap Feeders

Aphrophora parallel (Say)
Aphrophora saratogensis (Fitch), Saratoga Spittlebug
Cinara strobi (Fitch), White Pine Aphid
Laspeyresia piperana Kearfott
Lepidosaphes ulmi (L.), Oystershell Scale
Lopholeucaspis japonica Cockerell
Matsucoccus resinosae Bean and Godwin, Red Pine Scale
Phenacaspis pinifoliae (Fitch)
Physokermes insignicola (Craw)
Physokermes piceae (Schrank), Spruce Bud Scale
Pulvinaria innumerabilis (Rathvon), Cottony Maple Scale
Toumeyella liriodendri (Gmelin), Tuliptree Scale
Toumeyella parvicornis (Cockerell), Pine Tortoise Scale
Toumeyella piniperdia

Hymenoptera—Defoliators and Leaf Miners

Atta texana (Buckley), Texas Leafcutting Ant
Fenusa pusilla (Lepeletier), Birch Leafminer
Gilipinia hercyniae (Hartig), European Spruce Sawfly

Neodiprion menapia
Neodiprion merkeli Ross, Slash Pine Sawfly
Neodiprion pratti pratti (Dyar), Virginia Pine Sawfly
Neodiprion warreni Ross

Hymenoptera—Seed Feeders

Megastigmus spermotrophus Wacht

Lepidoptera—Defoliators and Bud Worms

Bucculatrix ainsliella Murtfeldt, Oak Skeletonizer
Bucculatrix canadensisella Chambers, Birch Skeletonizer
Choristoneura pinus Freeman, Jack Pine Budworm
Coleophora laricella (Hübner), Larch Casebearer
Coleotechnites milleri (Busck), Lodgepole Needleminer
Dasychira pinicola (Dyar), Pine Tussock Moth
Dioryctria clarioralis (Walker), Blister Coneworm
Dioryctria merkeli Mutuura and Munroe
Dioryctria zimmermani (Grote), Zimmerman Pine Moth
Ichthyura inclusa (Hübner)
Lambdina pellucidaria (Grote and Robinson), Eastern Pine Looper
Lymantria matheura
Neophasia menapia (Felder and Felder), Pine Butterfly
Symmerista leucitys Franclemont, Orangehumped Mapleworm
Tetralopha robustella Zeller

Lepidoptera—Shoot Borers

Barbara colfaxiana (Kearfott), Douglas-fir Cone Moth
Epinotia meritana Heinrich, White Fir Needleminer
Eucosoma gloriola Heinrich, Eastern Pine Shoot Borer
Eucosoma rescissoriana Heinrich
Eucosoma sonomana Kearfott, Western Pine Shoot Borer
Rhyacionia rigidana (Fernald), Pitch Pine Tip Moth
Rhyacionia subtropica Miller, Subtropical Pine Tip Moth
Rhyacionia zozana (Kearfott), Ponderosa Pine Tip Moth

Thysanoptera

Gnophothrips fruscus (Morgan), Slash Pine Flower Thrips

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