Forest Health Technology Enterprise Team

TECHNOLOGY TRANSFER

Biological Control

Biological Control of Arthropod Forest Pests of the Western United States:
A Review and Recommendations

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Cover Photo:

The larch casebearer, *Coleophora laricella* Hübner, was introduced into North America from Europe. Natural enemies from Europe were sought and introduced in the 1930's. Two parasitoids, *Agathis pumila* (Ratzeburg) and *Chrysocharis laricinellae* Ratzeburg established and soon relegated the larch casebearer to nonpest status. An adult female *C. laricinellae* (shown here) parasitizes a larch casebearer cocoon.

Biological Control of Arthropod Forest Pests of the Western United States:
A Review and Recommendations

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Introduction

The forests of western North America are a series of extensive habitats that make up one of our nation's largest natural resources. Much of this resource is managed for multiple objectives, which include renewable commercial harvesting, recreation, resource conservation, and wildlife management. Throughout the western forests are numerous insect pests which, when left unchecked, often conflict with one or more of the management objectives for these ecosystems. Managing these insect pests is a task of vast proportions, often involving millions of hectares of forest.

Biological control of pest insects and arthropods is an important technology for managing insect pests in forests. Although many insect pests have an abundance of natural enemies that affect their population dynamics, the degree to which natural enemies may be relied upon to suppress pest populations is often unknown. This publication summarizes the literature regarding the population biology and natural enemy relationships for the more serious pests of western forests, and presents the possibilities for enhancing the use of, or reliance on, natural enemies of these pests.

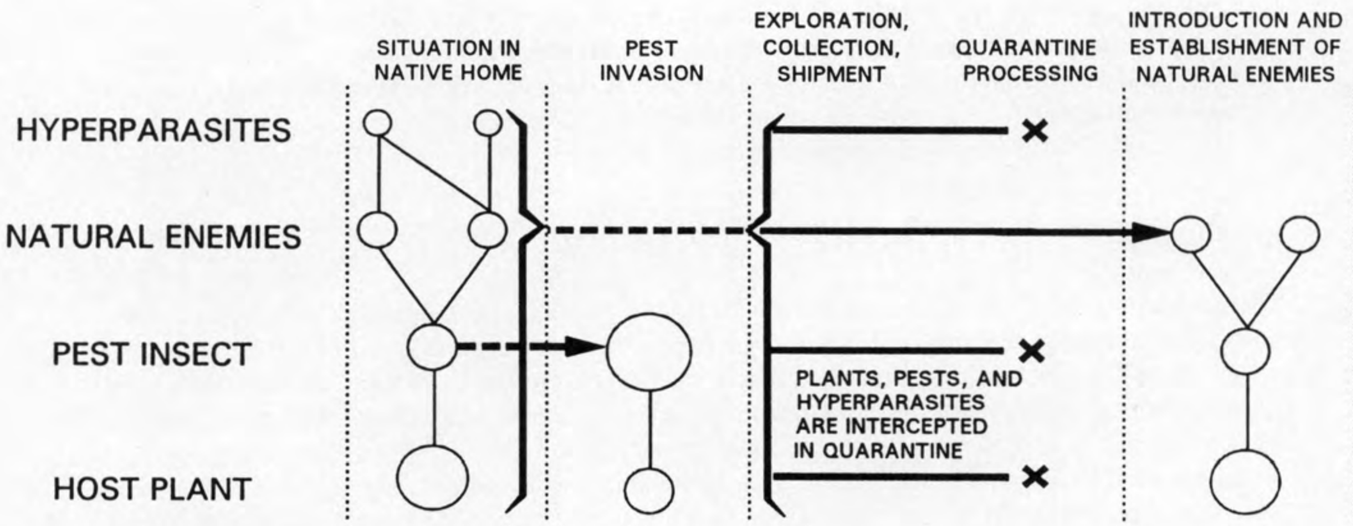
Biological Control in Forest Pest Management

Biological control is the management of arthropod or other pests using populations of other organisms (natural enemies) to limit the pest population's density and growth (Van Driesche and Bellows 1996). Natural enemies are organisms, such as predators, parasitoids, pathogens, and competitors, that suppress a pest population through such actions as killing, sterilizing, or otherwise reducing the potential for growth. Biological control is often only one component of pest management in forest systems. Important additional factors in maintaining high forest resistance to pest damage include maintenance of tree health and limiting breeding material for certain types of pests. Biological control generally integrates well with silvicultural and forest management practices to assist in suppressing insect populations. Barbosa and Wagner (1989) identified 22 biological control programs against forest pests around the world. Of these, 18 were described as successful, and four as unsuccessful. Two of these programs took place in the western United States, and one was successful.

There are three approaches to enhancing biological control of a particular pest species. These are (1) introduction of new natural enemy species, (2) conserving existing natural enemy populations, and (3) artificially augmenting natural enemy populations.

Introduce new natural enemy species: The significance of natural enemies in limiting pest population growth is most clearly seen when an insect or other pest enters a new environment where it has no natural enemies. Pest population growth is often explosive, and a severe forest condition results. The establishment of effective natural enemies to control the pest on a permanent, ongoing basis usually requires introducing new natural enemies into the system. This approach is termed biological control through introductions. The steps in this process are diagrammed in Figure 1. A crucial step in this approach is the use of quarantine facilities to screen imported material, thus ensuring the release of only desired organisms into the forest ecosystem.

Figure 1. Schematic diagram of the invasion of a pest species, followed by introduction of natural enemies and final reduction of pest population densities (after Van Driesche and Bellows 1996). The pest species is under natural control in its native home. The pest arrives in a new region without natural enemies, and the pest population explodes to damaging levels. Plant productivity is reduced. Natural enemies are sought through exploration and are processed through quarantine. Desirable natural enemy species are introduced and established into the new region, reducing pest population density by restoring natural balance to the pest population, and permitting renewed plant growth and productivity.



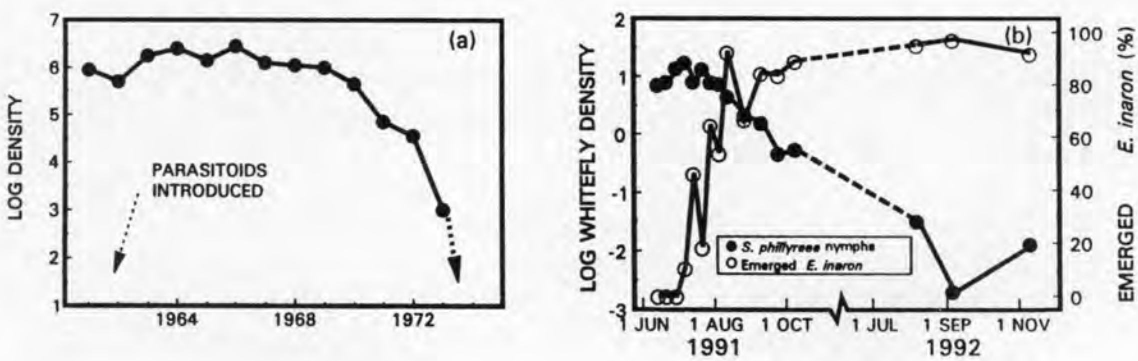
Biological control through introductions is applied typically to pests that become newly established in an area (adventive species). This approach has an overall success rate of about 60%. Complete control historically has been achieved in 17% of cases, with partial control achieved in an additional 43% of cases (Greathead and Greathead 1992).

The satin moth, *Leucoma salicis* (L.), is a case typical of many introduced insects. This moth was accidentally introduced into forests of the western United States and Canada in 1922. It is of Old World origin, extending in its native range from Europe eastward to Siberia and Japan (Clausen 1978). Its larvae feed on *Populus* spp. and *Salix* spp. Adult females lay up to 1000 eggs in a few batches of several hundred eggs each (Clausen 1978). When first introduced, it was considered a pest of economic importance (Furniss and Carolin 1977). Programs of natural enemy introductions were begun in both the United States and Canada. Ten natural enemies from Europe were released against this species in Washington, and four became established. Two of the natural enemy species were subsequently dominant in the control of the moth (Clausen 1978), which has now been relegated to nonpest status (Furniss and Carolin 1977).

This approach can also be applied to native pests (Drooz et al. 1977). In such cases, new natural enemies are sought from species related to the pest, in the hopes that these additional natural enemies might contribute to improved biological control. One oft-cited example is the use of the hymenopteran parasitoid *Telenomus alsophilae* Viereck of the North American fall cankerworm *Alsophilia pometaria* Harris. This parasitoid was used in a successful biological control program in South America against a native forest pest in the same family but in another genus *(Oxydia trychiata)* (Drooz et al. 1977). The success rate in such cases may be expected to be lower than for natural enemy introductions against adventive pests, but the approach may have value in forest ecosystems against native pest species.

The population reductions achieved by introducing new natural enemies against adventive pests are typically 1,000- to 10,000-fold (Bellows et al. 1992, Bellows 1993). Two examples of such reductions in pest densities, one for a pest of natural forests (a), and one for a pest of urban forests (b), are shown in Figure 2.

Figure 2. Examples of biological control of forest pest insects in North America. (a) Decline in larch sawfly, *Pristiphora erichsonii* Hartig, after introductions of *Olesiocampe benefactor* Hinz (after Ives 1976). (b) Decline in densities of *Siphoninus phillyreae,* a pest of ash trees (*Fraxinus* spp.), following the introduction in June 1991 of the parasitoid *Encarsia inaron* (Walker).



Conserve existing natural enemy populations: Many native insect species that are potential pests are already controlled by a wealth of natural enemies. Thus, biological control often consists of focusing management of the forest system in ways that preserve existing insect natural enemies and do not hinder or impair their activities. This approach to preserving the activities of existing natural enemies is referred to as biological control through conservation of natural enemies.

Augment natural enemy populations: Natural enemies can be added to a system in a periodic or on a continual basis, or otherwise manipulated, when their naturally occurring numbers are insufficient to provide control. These approaches are termed augmentative biological control. In large-scale systems such as western forests, such approaches may be limited by the cost of producing and delivering natural enemies over the large areas involved. There are two exceptions. The first is the use of a pathogen that can be mass produced relatively inexpensively (such as *Bacillus thuringiensis* Berliner). In such cases the pathogen can be employed in a manner similar to using an insecticide, and in fact is often termed a biopesticide or biological insecticide.

The second exception is manipulating populations of natural enemies already in the environment to concentrate their efforts in particular areas. Research on this approach in forests has been relatively limited, but may hold promise for some predators that are attracted to pheromones of their prey. These pheromones might be used to attract predators to specific places where their action is most needed.

Biological Control of Western Forest Pests

Most western forest pests are native to North America and are present in natural ecosystems over vast areas. The density of these insect populations, and consequently their pest status, are affected by two general ecological factors: the availability of resources for reproduction and the mortality in the populations. Biological control seeks to increase the amount of mortality experienced by a population to the point that it rarely, if ever, reaches pest status. Insect species in western forests are, however, often faced with an extraordinary surplus of resources available for reproduction. Consider, for example, the amount of breeding resource available to bark beetles after a large fire or windstorm which might weaken or kill trees. The resulting outbreak populations will spread into healthy trees and can cause serious damage unrelated to the lower density of populations throughout most of the forest. Thus management of forest insect pests often involves managing both natural enemy populations and breeding resources (through salvage harvesting of damaged timber, for example). In this context, biological control is a component of a larger scope of activities that comprise forest ecosystem management.

The three approaches to biological control (natural enemy introductions, conservation, or augmentation) have both advantages and limitations in management of insect pests over the vast forest ecosystems of western North America:

1. Introductions of exotic natural enemies against the few adventive pests of these forests has proved successful in many cases. These successes demonstrate the suitability of the approach to the stable, wide ranging ecosystems in which it has worked so well.

2. Introductions of exotic natural enemies against native pests has been reported as successful in at least one case (Drooz et al. 1977), but the success rate overall may be lower than for introductions of natural enemies against adventive pest species. Longer research and development times might be anticipated for this approach.

3. Conservation of natural enemies is an intrinsic part of most normal silvicultural practices, and this approach integrates well into forest management. Particular care can be taken, when necessary, to modify silvicultural and harvesting practices, such as timing the harvesting of infested trees, so as not to negatively influence the balance between natural enemy and pest populations.

4. Augmentation is costly on a per-area basis, and forest pests are often present over vast areas where the marginal economic return for management is small. Thus, augmentation likely will be most effective on high value plantation settings, or where the use of cost-effective or inexpensive microbial pathogens is possible.

Selection of Species for Review

Pest species reviewed here (Table 1) include those identified by Furniss and Carolin (1977) as consistent, serious pests of western forests. To these species we have added others that either occasionally reach severe pest status or are consistently moderate in their pest status. These species were selected primarily by reviewing the literature regarding forest insect pest damage (see also Furniss and Carolin 1977) and by reviewing the Forest Service's annual reports on pests and disease conditions in western forests (USDA 1983-1996).

For each pest species, the Review of Applied Entomology, Series A (agricultural and forestry pests) was reviewed for each year from 1913 to 1996. In addition, computer searches were made in the Agricola data base (1970-1996) and the CAB International data base (1987-1996). Abstracts were obtained for any paper containing a reference to the pest species, and these abstracts were reviewed for information pertinent either to the biology of the pest species or to its natural enemies. Copies of articles relevant to this review were then obtained. Reference to other published works on biological control and biology of these species was also made (e.g., Furniss and Carolin 1977, Clausen 1978, Barbosa and Wagner 1989, Kelleher and Hulme 1981). Information from all these sources was synthesized to provide the summaries in this work.

Table 1. Arthropods identified as frequent or severe forest pests in western North America by Furniss and Carolin (1977) and additional pests evaluated for biological control

PEST SPECIES
COLEOPTERA
Cerambicidae
Poplar butt borer, *Xylotrechus obliteratus* Leconte
Curculionidae
White pine weevil, *Pissodes strobi* (Peck)
Scolytidae
Sugar pine cone beetle, *Conophthorus lambertianae* Hopkins
Western pine beetle, *Dendroctonus brevicomis* LeConte
Jeffrey pine beetle, *Dendroctonus jeffreyi* Hopkins
Mountain pine beetle, *Dendroctonus ponderosae* Hopkins
Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins
Spruce beetle, *Dendroctonus rufipennis* Kirby
Pine engraver, *Ips pini* (Say)
Silver fir beetle, *Pseudohylesinus sericeus* (Mannerheim)
European elm bark beetle, *Scolytus multistriatus* (Marsham)
Fir engraver, *Scolytus ventralis* LeConte
Striped ambrosia beetle, *Trypodendron lineatum* (Olivier)
DIPTERA
Cecidomyiidae
Douglas-fir needle midge, *Contarinia pseudotsugae* Condrashoff
HOMOPTERA
Phylloxeridae
Balsam woolly aphid, *Adelges piceae* (Ratzeburg)
HYMENOPTERA
Diprionidae
Hemlock sawfly, *Neodiprion tsugae* Middleton
Tenthridinidae
Larch sawfly, *Pristiphora erichsonii* (Hartig)
LEPIDOPTERA
Coleophoridae
Larch casebearer, *Coleophora laricella* (Hübner)
Gelechiidae
Lodgepole needleminer, *Coleotechnites milleri* (Busck)
Geometridae
Greenstriped forest looper, *Melanolophia imitata* (Walker)
Saddleback looper, *Ectropis crepuscularia* (Denis and Schiffermüller)
Spearmarked black moth, *Rheumaptera hastata* (L.)
Bruce spanworm, *Operophtera bruceata* (Hulst)
Western hemlock looper, *Lambdina fiscellaria lugubrosa* (Hulst)
Lasiocampidae
Forest tent caterpillar, *Malacosoma disstria* Hübner
Lymantriidae
Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough)
Olethreutidae
Douglas-fir cone moth, *Barbara colfaxiana* (Kearfott)
Lodgepole cone moth, *Eucosma rescissoriana* Heinrich

Table 1. continued

Western pine shoot borer, *Eucosma sonomana* Kearfott
European pine shoot moth, *Rhyacionia buoliana* (Denis and Schiffermüller)
Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock)
Western pine tip moth, *Rhyacionia bushnelli* (Busck)
Southwestern pine tip moth, *Rhyacionia neomexicana* (Dyar)
Pieridae
Pine butterfly, *Neophasia menapia* (Felder and Felder)
Saturniidae
Pandora moth, *Coloradia pandora* Blake
Tortricidae
Western blackheaded budworm, *Acleris gloverana* (Walsingham)
Large aspen tortrix, *Choristoneura conflictana* (Walker)
Sugar pine tortrix, *Choristoneura lambertiana* (Busck)
Western spruce budworm, *Choristoneura occidentalis* Freeman
Yponomeutidae
Pine needle sheathminer, *Zelleria haimbachi* Busck
ACARIFORMES
Eriophyidae
***Trisetacus campnodus* Keifer and Saunders**
Tetranichidae
Spruce spider mite, *Oligonychus ununguis* (Jacobi)

The forests of western North American are botanically diverse and are dominated by conifers. Insect pests are responsible for damage on a variety of tree species of commercial and ecological importance. The tree species concerned are variously reported in the literature by common names or by Latin binomens. The principal tree species attacked by pests reviewed in this document, together with their usual common names, are listed in Table 2.

Table 2. Trees in the forests of western North America attacked by pests considered in this report

SPECIES	COMMON NAME
Abies spp.	Firs
Abies amabilis Dougl. ex Forbes	Pacific silver fir
Abies concolor (Gord. and Glend.) Hildebr.	True fir
Abies grandis (Dougl. ex D. Don) Lindl.	Grand fir
Abies lasiocarpa (Hook.) Nutt.	Subalpine fir
Abies magnifica A. Murr.	California red fir
Acer spp.	Maples and relatives
Alnus spp.	Alders
Alnus rugosa (Du Roi) Spreng.	Speckled alder
Betula spp.	Birches
Betula papyrifera Marsh.	Paper birch
Cupressus spp.	Cypresses
Juniperis spp.	Junipers
Larix spp.	Larches
Larix laricina (Du Rio) K. Koch	Tamarack, eastern larch
Larix lyallii Parl.	Subalpine larch

Table 2. continued

Larix occidentalis Nutt.	Western larch
Picea spp.	Spruces
Picea engelmannii Parry ex Engelm.	Engelmann spruce
Picea glauca (Moench) Voss	White spruce
Picea sitchensis (Bong.) Carr.	Sitka spruce
Pinus spp.	Pines
Pinus albicaulis Engelm.	Whitebark pine
Pinus banksiana Lamb.	Jack pine
Pinus contorta Doug. ex Loud.	Lodgepole pine
Pinus contorta var. *latifolia* Engelm.	Lodgepole pine
Pinus contorta var. *murrayana* (Grev. and Balf.) Engelm.	Sierra lodgepole pine
Pinus coulteri D. Don	Coulter pine
Pinus flexilis James	Limber pine
Pinus jeffreyi Grev. and Balf.	Jeffrey pine
Pinus lambertiana Dougl.	Sugar pine
Pinus monticola Dougl. ex D. Don	Western white pine
Pinus nigra Arnold	Austrian pine
Pinus ponderosa Dougl. ex Laws.	Ponderosa pine, yellow pine
Pinus radiata D. Don	Monterey pine
Pinus sylvestris L.	Scots pine
Populus spp.	Cottonwood and aspen relatives
Populus tremuloides Michx.	Quaking aspen
Prunus spp.	Cherry and plum relatives
Pseudotsuga menziesii (Mirb.) Franco	Douglas-fir
Salix spp.	Willows
Sequoia sempervirens (D. Don) Endl.	Redwood
Sequoiadendron giganteum (Lindl.) Buchholz	Giant sequoia
Thuja spp.	Cedars and relatives
Thuja plicata Donn ex D. Don	Western red cedar
Thuja occidentalis L.	Arborvitae
Tsuga spp.	Hemlocks
Tsuga heterophylla (Raf.) Sarg.	Western hemlock
Tsuga mertensiana (Bong.) Carr.	Mountain hemlock
Ulmus spp.	Elms
Ulmus americana L.	American elm
Ulmus parviflora Jacq.	Chinese elm
Ulmus procera Salisb.	English elm
Ulmus pumila L.	Siberian elm

Coleoptera

CERAMBICIDAE

POPLAR BUTT BORER, *Xylotrechus obliteratus* Leconte

Origin: North America.

Range in North America: Rocky Mountain region.

Plant hosts and damage: *Populus* spp., including *P. tremuloides.*

Natural Enemies: Spencer (1932) suggested, on fairly strong circumstantial evidence, that the nemestrinid dipteran *Rhyncocephalus sackeni* Williston parasitized larvae of *X. obliteratus.* No other natural enemies are reported.

Pest Status: This species is a serious pest in the Rocky Mountain Region, where the larvae work under bark and into the heartwood at the base of trees. Trees subject to repeated attacks may become so weak that they break off during wind or snow storms. Extensive areas of aspen above 2,130 m in Utah and Colorado have been killed by this species (Furniss and Carolin 1977).

Biological Control: No previous biological control work has been conducted on this species.

Recommendations: Very little is known about possible natural enemies of this pest. Studies to discover what predators, parasitoids, and pathogens exist for this species would be required before additional steps toward improved biological control could be taken. Because this species is a native cerambicid, there may be little that can be done to increase the numbers or the impact of natural enemies, but improved knowledge of the ecology of the pest might permit better understanding of the reasons why certain areas are severely affected. Such knowledge could lead to better options for management.

CURCULIONIDAE

WHITE PINE WEEVIL, *Pissodes strobi* (Peck)

Origin: Presumed North America.

Range in North America: Throughout North America.

Plant hosts and damage: Primary plant host varies with geographic range in North America. In western North America, this pest attacks *Picea sitchensis, Picea engelmannii,* and *Picea glauca* (Furniss and Carolin 1977, Kenis and Mills 1994). Eggs are laid in 1-year-old terminal internodes. Larval girdling of the intercortical tissues kills the growing tips, resulting in deformed and lower quality stands.

Natural Enemies: A number of studies have reported on the natural enemies associated with *P. strobi*. Several invertebrate predators and parasitoids are known from this species (Table 3). Predation by vertebrates is discussed briefly by Bellocq and Smith (1994). Streett et al. (1975) and Wilson (1984) report a microsporidian from *P. strobi*.

Table 3. Invertebrate predators and parasitoids of *Pissodes strobi*

NATURAL ENEMY SPECIES
Invertebrate Predators
Lonchaea corticus Taylor[1, 2]
Invertebrate Parasitoid
Allodorus crassigaster (Provancher)[2]
Allodorus sp.[2]
Bracon pini (Muesebeck)[1, 2]
Dolichomitus terebrans (Ratzeburg)[1, 2]
Eurytoma picea Bugbee[2]
Eurytoma pissodis Girault[1, 2]
Eurytoma sp.[2]
Mercetencyrtus sp.[2]
Rhopalicus pulchripennis (Crawford)[1, 2]

[1]VanderSar 1978
[2]Alfaro et al. 1985

Pest Status: This is the most injurious species attacking Sitka spruce in British Columbia, Washington, and Oregon. It is univoltine, with considerable overlapping of broods in each year. The adult female lays eggs in internodes of the previous year's growth. The larvae feed intercortically, girdling the leader, often killing it. The species attacks and seriously injures or kills the terminal shoots of trees from about 8 to 30 years old and up to 15 m tall. The killed leaders are replaced by laterals that compete for dominance, causing crooked or bushy, low-value trees (Kenis and Mills 1994). Damage to Sitka spruce has been so great that planting is much reduced (Furniss and Carolin 1977). Damage in eastern North America is similar in nature on white pine, *Pinus contorta*. Jaynes and MacAloney (1958) report effective control with insecticides, and also recommend planting susceptible trees under a light cover or overstory of previously established forest, because damage is less in such settings.

The species apparently suffers considerable mortality from natural factors (see below), but can still be responsible for significant damage. Damage is clearly most significant to commercially planted stands, and may be a consequence of resource concentration of evenly aged silviculture. Alfaro et al. (1995) report an integrated management program for this species, which emphasizes advances in genetic resistance in the host plant, silvicultural practices, and chemical control. The program also relies on consistent monitoring of populations and attack levels of the weevil.

Biological Control: *Pissodes strobi* is subject to attack by numerous natural enemies. Bellocq and Smith (1994) report predation by birds of 6-9% of the late larval and pupal stages. Overwintering mortality of adult weevils ranged from 76-92%, attributed in part to mammalian predators.

The dipteran predator *Lonchaea corticis* is widely reported attacking this weevil, and in two studies was the most abundant natural enemy recovered from infested shoots (VanderSar 1978, Alfaro et al. 1985). Hulme (1990) evaluated the impact of this predator in the field, and found the threshold for complete mortality of the weevils in a shoot was between two and four predators per weevil pupal cell.

A number of parasitoids are known from *P. strobi* (Table 3). The quantitative impact of these parasitoids has not been reported. Their cumulative impact is probably significant.

Recommendations: *Pissodes strobi* has a substantial fauna of natural enemies, capable of inflicting considerable mortality. The natural ecology of the species is probably one of seeking a host plant of limited age range in a mixed forest. In such an environment, the species would probably be at moderate to low density, limited by the time and energy required to locate suitable host material as well as by the action of natural enemies. In relatively evenly aged stands in exposed settings (without cover of a higher forest canopy), the time and energy required to locate hosts may be much less limiting, and favorable host material is concentrated. In these settings, the existing natural enemies do not suppress the population sufficiently to protect the maturing trees. The integrated management program described by Alfaro et al. (1995) responds to this change in the ecological interaction of the weevil and its host trees by monitoring population densities and treating as necessary to reduce populations.

Opportunities for increased use of natural enemies in these managed plantations may be limited. Two approaches may be considered. One approach, mass rearing of natural enemies and their release into the environment, could be evaluated for economic benefit. No rearing program for any of the principal natural enemies has been reported, so this approach might require considerable developmental research. The microsporidian of *P. strobi* (Wilson 1984) might be developed as a biological insecticide, although the limited market may be an economic restriction.

An alternative approach would be to attempt to establish additional natural enemies from related Palearctic weevils, a suggestion originally proposed by Taylor (1929). From surveys of natural enemies from Palearctic *Pissodes* species over a 10-year period, Kenis and Mills (1994) identified 18 parasitoids attacking five species of *Pissodes* in Europe, with ranges of parasitism from 1% to over 30%. The most common dominant parasitoids were members of the braconid genus *Eubazus*. Other common species included *Dolichomitus terebrans*, *Coeloides sordidator* (Ratzeburg), and three species of pteromalids. *Eubazus* spp. and *C. sordidator* were considered the best candidates for introduction against *P. strobi*. These species represent genera not present in North American *P. strobi* populations. This approach was tried on a small scale in 1950 (McGugan and Coppel 1962) and is being considered by Forestry Canada (Kenis and Mills 1994). For new plantings of susceptible tree species, establishing them under an overstory of existing trees may further reduce the impact of this pest (Jaynes and MacAloney 1958).

SCOLYTIDAE

The Scolytidae comprise the bark beetles and their relatives, and are the most destructive insects in western coniferous forests. The principal pest species are in three genera, *Dendroctonus*, *Ips*, and *Scolytus*. These beetles kill or destroy billions of board feet of sawtimber annually (USDA Forest Service 1958). Four species of *Dendroctonus* cause most of this damage.

Over the western region, most tree killing is dispersed among the forests and is the result of normal or endemic infestations that are continuously present in mature forests. This normal mortality is widely scattered, is usually greatest in undeveloped areas, and is occurs largely to trees that are predisposed to beetle attack. Factors that predispose trees to attack include being overmature, water stressed, or previously exposed to attack by other pests. In this context, beetle attack serves as natural thinning of these trees.

Under conditions favorable for the beetles, epidemics occasionally develop and spread over large areas, killing vast amounts of timber (Furniss and Carolin 1977), including trees that are healthy and normally would not be subject to attack. Many beetles also have associated fungi that stain the infected lumber, further reducing its value. These epidemics can set the stage for devastating fires. The end result is highly disruptive to orderly management of these forest areas.

For bark beetle attacks on healthy trees to be successful, the beetles must be present in sufficient numbers to overcome the natural defenses of the tree. Beetles use pheromones to communicate within and among populations, and beetle aggregations resulting from these pheromones serve to concentrate attacks on particular trees. A number of natural enemies also cue to these pheromones, using them as kairomones to locate their prey or hosts. As the pheromones can be quite specific among different bark beetle species, the responses of many of the predators and parasitoids to these pheromones can also be rather specific.

Most of the bark beetles currently in western North America are native, and have a native natural enemy fauna. Focus of biological control efforts will be most productive in working towards integrating knowledge of the biology and ecology of these species into an overall management program against the bark beetles. Thinning of potentially susceptible stands, harvesting susceptible trees, and using trap or bait trees to attract and then kill beetles (by insecticide or other means) (e.g., Payne and Billings 1988), may be beneficial in preventing or limiting the extent of outbreaks. Naturally occurring biological control is probably most valuable in limiting population densities in endemic situations, and this natural control is likely the principal use of biological control of these species for the present. Should a nonnative bark beetle establish in western North America, however, the importation of suitable exotic natural enemies should be pursued. Introducing natural enemies against an adventive bark beetle pest has shown promise in Australia against *Ips grandicollis* (Eichoff) (Berisford and Dahlsten 1989).

For native beetles, examination of exotic natural enemies may offer opportunities to increase natural mortality (Mills 1983, Mills and Krüger 1988), although in most cases these native beetles are already attacked by a widely diverse upper trophic level fauna. Biological control through introductions of exotic natural enemies against native bark beetles has not yet met with much success (Clausen 1978, Miller et al. 1987, Moser 1989, Van Driesche et al. 1996), but further work in this area may be warranted. At least one species of predaceous beetle, *Rhizophagus grandis* Gyllenhal from Europe, has shown attraction to pheromones from North American *Dendroctonus* spp. in laboratory trials (Miller et al. 1987).

A relatively undeveloped area is the potential for the use of nematodes, either inundatively or innoculatively, into populations of bark beetles. A large number of nematode associates of bark beetles have been described (Massey 1974), many of which are known or presumed to be parasitic on their hosts. Parasitism may lead to reduced fertility, sterility, or death of infected individuals.

Nematodes are omitted from many of the lists of natural enemies in the discussions which follow except where their life histories or associations with their host beetles are known to be parasitic.

SUGAR PINE CONE BEETLE, *Conophthorus lambertianae* Hopkins

Origin: North America.

Range in North America: California, Nevada, Oregon.

Plant hosts and damage: *Pinus lambertiana, Pinus monticola.* Several pine cone beetles are known from the West, many fairly specific to particular *Pinus* hosts (Furniss and Carolin 1977). The sugar pine cone beetle, *Conophthorus lambertianae* Hopkins, attacks primarily *P. lambertiana.* The adult beetle bores into the base or supporting stem of immature pine cones in spring. A small tunnel is projected along the axis of the cone in which the female deposits eggs. The larvae feed on the scales, seeds, and tissue of the withered cone. Development to the adult stage takes place in the dead cone during summer, and the adults usually overwinter in the cone.

Natural Enemies: The only natural enemies found reported from *C. lambertianae* were the predator *Enoclerus lecontei* Wolcott and the two parasitoids *Cephalonomia utahensis* Brues and *Tomicobia tibialis* Ashmead (Bedard 1968).

Pest Status: Among the Western pine cone beetles, *C. lambertianae* is the most destructive (Keen 1958). Cone crops of various pines periodically are severely damaged by *Conophthorus* spp. In some years, 25-50% of the sugar pine cones have been killed by *C. lambertianae* over large areas, increasing the difficulty and cost of collecting seeds for reforestation. In local areas, destruction often exceeds 90% (Bedard 1968). There is an increasing need to protect seed orchards and seed collecting areas from damage by *Conophthorus* spp., but practical measures have not yet been developed (Furniss and Carolin 1977).

Biological Control: Little is known of the natural enemies of *Conophthorus* spp. In the case of *C. lambertianae* (Bedard 1968), the wasp *Cephalonomia utahensis* parasitizes larvae in cones. The clerid *E. lecontei* may feed on beetle adults, which are also parasitized by *T. tibialis.* Significant mortality to the new broods of the cone beetle, attributed to the work of an undetermined entomophagous fungus, was recorded by Miller (1915). Miller reported mortality of up to 79% of broods in Oregon caused by this pathogen in 1914.

Recommendations: Too little is known to make immediate recommendations for the increased efficacy of natural enemies of this or other cone beetles. The report by Miller (1915) of a pathogenic fungus is worth pursuing, although it has not been mentioned in more recent literature. Region-wide application of natural enemies (including pathogens) would be expensive and probably not a viable option, particularly considering the annually variable nature of the cone crop set by sugar pines. Conservation of natural enemies of this species is probably already taking place, as there are no known silvicultural or harvesting practices that would destroy or remove major portions of the natural enemy population.

This pest species may be, as are other native pest species, a candidate for introduction of natural enemies from related species of beetles, in the "new association" paradigm of Pimentel and

Hokkanen (1989). Studies of the natural enemies of cone beetles in the Old World may provide candidates for consideration.

WESTERN PINE BEETLE, *Dendroctonus brevicomis* LeConte

Origin: North America.

Range in North America: Arizona, British Columbia, California, Colorado, Idaho, Montana, Nebraska, New Mexico, Oregon, Utah, Washington.

Plant hosts and damage: *Pinus ponderosa, Pinus coulteri.* Adults bore into bark, create egg galleries in the bark, and oviposit. Larvae feed between the bark and the wood. Heavy infestations kill the host tree.

Natural Enemies: Natural enemies known from *D. brevicomis* include vertebrate predators, invertebrate predators and parasitoids (Table 4).

Table 4. Natural enemies reported from *Dendroctonus brevicomis*

NATURAL ENEMY SPECIES
Vertebrate Predators
Dendrocopus albolarvatus[1]
Dendrocopus pubescens L.[1]
Dendrocopus villosus L.[1]
Dryocopus pileatus[1]
Invertebrate Predators
Aulonium longum LeConte[2]
Enoclerus lecontei Wolcott[2]
Enoclerus sphegeus (F.)[3]
Medetera aldrichii Wheeler[2]
Temnochila chlorodia (Mannerheim)[2, 3]
Invertebrate Parasitoids
Cecidostiba spp.[1]
Dinotiscus burkei Crawford[2]
Roptrocerus spp.[1]
Roptrocerus xylophagorum (Ratzeburg)[2, 4]

[1]Otvos 1965
[2]DeMars et al. 1986
[3]Goheen et al. 1985
[4]Stephen and Dahlsten 1976

Pest Status: In endemic populations this beetle breeds in overmature, windfall, or root-rotted trees (Keen and Salman 1942, Cobb et al. 1974), or in trees weakened by drought or fires. Under epidemic conditions, the species will attack and kill apparently vigorous trees of all ages, although trees under 15 cm diameter are seldom attacked. The beetle does not breed in limbs. Extensive damage of up to 90% of a forest stand has been recorded. From 1921-1937, 18.6 billion board feet of lumber were destroyed; this infestation was related to drought in the 1920's and 1930's.

Adults are active from late spring and early summer until the advent of cold weather. Females produce from one to three broods. There are from one to two generations annually in the northern part of this species' range, and from two to four in the southern portion of its range (Furniss and Carolin 1977). Attacked trees are often also attacked by other bark beetles, including *Ips* spp. and other *Dendroctonus* spp.

Management of this species has usually focused on reducing the impact of epidemics, usually by felling infested trees and either harvesting the lumber or destroying the brood in some other way.

Biological Control: *Dendroctonus brevicomis* is attacked by several invertebrate predators and parasitoids (Table 4), and ecotypically similar fauna make up the predatory and parasitic communities of bark beetles throughout the world. In California, over 90% of the predators feeding in broods of *D. brevicomis* were either *E. lecontei* or *Temnochila chlorodia* (Berryman 1967) A study of the laboratory biology of *E. lecontei,* the most common predator of this beetle, was conducted by Berryman (1967), who found 0.26 prey consumed per predator per day, a rate confirmed by field studies (Berryman 1967). Berryman (1966) reported a maximum oviposition by *E. lecontei* of over 1,000 eggs by a single female over 90 days.

Many of these natural enemies are attracted to infested trees (or to trees at high risk of infestation) as early as are the bark beetles (DeMars et al. 1986, Byers 1988). In a study by Stephen and Dahlsten (1976), predators that feed on adults and larvae arrived first, and parasitoids arrived later, coincident with the appearance of their later larval host stages. Attraction of predators to infested or at-risk trees is attributed to sensitivity to chemicals exuded either by the tree or by the attacking bark beetles. Sensitivity to various component chemicals of beetle aggregation pheromones have been examined in several predators (Tilden et al. 1983, Byers 1988, Payne 1989).

The impact of various management strategies on natural enemies of bark beetles can be considerable. Swezey and Dahlsten (1983) found, on logs treated with lindane, 89% reduction in emergence of predators and 80% reduction in the ratio of emerging predators to emerging bark beetles. In a comparative study of three insecticides, chlorpyrifos was equally toxic to *D. brevicomis, E. lecontei,* and *T. chlorodia;* lindane was more toxic to *E. lecontei* and *T. chlorodia* than to the bark beetle; and carbaryl was relatively nontoxic to *E. lecontei* compared with the other two species.

Removal of trap or bait trees can have a differential impact on pests and natural enemies, as natural enemies often emerge after the bark beetles. Removal of infested timber after the emergence of bark beetles but before the emergence of natural enemies could contribute to an imbalance in natural enemy and pest populations.

Vertebrate predators of this pest include birds. Otvos (1965) found, in decreasing order of importance, the woodpeckers *Dendrocopus villosus, Dendrocopus pubescens, Dendrocopus albolarvatus,* and *Dryocopus pileatus* preying on *D. brevicomis* (see also Berryman et al. 1970). Otvos (1965) noted additional bird species (creepers, nuthatches and flycatchers) thought likely to prey on this pest. Predation by woodpeckers reduced the population of *D. brevicomis* by direct consumption of 31.8% of the insects in the two generations studied. In addition, there was an increase in parasitoid densities by a factor of 3.85. This increase in parasitoid density was attributed to the removal of bark by the birds, so that parasitoids with short ovipositors (*Cecidostiba* spp. and *Roptrocerus* spp.) were more effective.

Recommendations: Natural variations in the density of this bark beetle in its principal host, *Pinus ponderosa,* appear more closely related to variations in tree stand health and vigor than to natural enemy action. The pest species is attacked by a diverse group of invertebrate predators and parasitoids and birds, which together appear likely to contribute considerable mortality to populations of the bark beetle in most situations. Conditions favorable to epidemics are often related to an increase in numbers of susceptible trees (such as through drought or windfall). During epidemics, sanitation may play an important role in removing or reducing populations of the beetle, but care must be taken not to differentially remove natural enemies.

Little additional biological control work appears practical at this time for this species. Some consideration might be given to the possible impact of predators of other bark beetles, but the potential for increasing the natural mortality of *D. brevicomis* may be limited. The introduction of exotic bark beetle predators against native bark beetles has been attempted, but has not yet proved successful (Moser 1989, Van Driesche et al. 1996).

JEFFREY PINE BEETLE, *Dendroctonus jeffreyi* Hopkins

Origin: North America.

Range in North America: California.

Plant hosts and damage: *Pinus jeffreyi.* The species is apparently monophagous on this pine. Damage is caused by adults boring into the bark and laying eggs in galleries between the bark and the wood, followed by larval feeding between the bark and the wood. Heavy infestations kill trees.

Natural Enemies: Little has been reported concerning natural enemies of *D. jeffreyi.* It is likely subject to clerid predation and hymenopteran parasitism as are other *Dendroctonus* species. The role of vertebrates, including woodpeckers, has not been reported.

Pest Status: This is the most destructive bark beetle attacking *P. jeffreyi.* It normally breeds in scattered individual mature or overmature trees with retarded growth rates, or in lightning-struck or windthrown trees. It does not breed in slash. During the period 1930-1970, it destroyed 55 million board feet of lumber annually in California (Furniss and Carolin 1977).

Biological Control: No previous efforts at biological control of this species have been reported.

Recommendations: The impact of this beetle on its principal host, *P. jeffreyi,* appears related to variations in tree health and vigor. Biological control may be able to play only a limited role in affecting the damage attributed to this pest. Harvesting high-risk trees before infestation may help to retard or eliminate outbreaks. During epidemics, sanitation may play an important role in removing or reducing populations of the beetle, but care must be taken not to differentially remove natural enemies.

Knowledge of this species' natural enemy fauna and its impact is sparse. Quantitative research will be important before additional recommendations can be made regarding the potential role of natural enemies in affecting or limiting the damage caused by this beetle.

MOUNTAIN PINE BEETLE, *Dendroctonus ponderosae* Hopkins

Origin: North America.

Range in North America: Throughout the pine forests of Alberta, British Columbia, the western United States, and Mexico.

Plant hosts and damage: Principal hosts: *Pinus albicaulis, Pinus contorta* var. *latifolia, Pinus lambertiana, Pinus monticola, Pinus nigra, Pinus ponderosa, Pinus sylvestris.* Other pines are also recorded as hosts. Adults bore into bark, create egg galleries between the bark and the wood, and oviposit. Larvae feed between the bark and the wood. Heavy infestations kill the host tree.

Natural Enemies: Natural enemies of this species include woodpeckers, predaceous and parasitic insects (Table 5), and nematodes (Reid 1963, Rasmussen 1976).

Table 5. Invertebrate natural enemies of *Dendroctonus ponderosae*

NATURAL ENEMY SPECIES
Invertebrate Predators
Enoclerus sphegeus (F.)[1]
Laphria gilva (L.)[2]
Lonchaea sp.[1]
Medetera aldrichii Wheeler[1]
Temnochila chlorodia (Mannerheim)[3]
Thanasimus undatulus (Say)[1]
Xylophagus sp.[1]
Invertebrate Parasitoids
Coeloides dendroctoni Cushman[1]
Dinotiscus burkei Crawford[1]
Roptrocerus eccoptogastri (Ratzeburg)[1]

[1]Rasmussen 1976
[2]Schmid 1969
[3]Furniss and Carolin 1977

Pest Status: This beetle ranks first in destructiveness among the bark beetles in the western United States (Furniss and Carolin 1977). It was responsible for tremendous losses in several outbreaks in the 20th century, including the loss of 15 billion board feet in Idaho and Montana from 1911 to 1935. In lodgepole pine, this species infests mature forests, often over large areas. In ponderosa, western white, and sugar pines, group killing often on a large scale can occur in both mature forests and in young overstocked stands. This beetle is epidemic almost continuously somewhere in the West on one or more of its principal hosts. During endemic infestations, the beetle tends to attack weaker, less vigorous trees. During epidemic infestations, healthy trees are also attacked. Over most of its range, the beetle is univoltine. In the more northerly regions, it may require 2 years to complete a single generation. In parts of California, two or more generations may develop in a single year.

Natural factors that affect the abundance of this species include subzero winter temperatures, nematodes, and various natural enemies. As stand susceptibility to the beetle increases, the suppression by natural controls is overcome by beetle reproduction, and outbreaks may develop. Harvesting susceptible stands before outbreaks or relieving stand stress (as by thinning) may be of value in preventing an outbreak. Control before an outbreak begins is important because of the large areas over which measures must be applied once an outbreak is underway. Direct control measures against outbreaks, such as felling, burning, and related approaches, are considered uneconomical. The development of pheromone traps may assist in control or at least detection of incipient outbreaks.

Spacing within stands may have considerable bearing on the susceptibility of trees to this pest. Cochran and Barrett (1993) demonstrated marked increases in pine mortality due to this beetle as stand density increased. Wide spacings increased average tree volumes, increased mean diameters, and reduced the probability of mortality without sacrificing gross cubic volume potential.

Biological Control: Survival of this pest and the role of natural enemies have been evaluated in both endemic and epidemic populations. Beetle survival was significantly greater in endemic (3.7%) than in epidemic (1.4%) or post-epidemic (0.5%) infestations (Amman 1984). Parasitoids and predators accounted for 8% of beetle mortality in endemic populations, 33% in epidemic populations, and 4% in post-epidemic populations. The dolichopodid predator *Medetera aldrichii* (13%) and woodpeckers (15%) accounted for the greatest amount of predation in endemic populations in that study.

Schmid, in a series of studies, evaluated the role of several predators on this beetle. The asillid fly *Laphria gilva* took 1% of adults (Schmid 1969). The clerid beetle *Enoclerus sphegeus* fed on *D. ponderosae* in the laboratory (Schmid 1970). Each clerid adult killed about one adult of *D. ponderosae* per day, and each larval clerid killed about 25 larvae, pupae or teneral adults of *D. ponderosae* during development. It was estimated that adult clerids consumed less than 1% of the adult bark beetle population and that the larvae killed 5-11% of the brood. Larval *M. aldrichii* entered galleries of the bark beetle through the entrance holes made by the adult scolytids (Schmid 1971), and probably caused a major part of the bark beetle mortality between August and the following May. Amman (1972) concluded from laboratory studies of the clerid *Thanasimus undatulus* that each clerid larva would consume between 18 and 43 larvae of the scolytid, depending on the size and abundance of the prey.

The natural enemies known for this species are likely most important in limiting or controlling populations in the endemic phase. In outbreak phase, natural enemies appear less able to exert sufficient limits on the population.

Recommendations: The opportunities for enhancing biological control of this species may be limited. There is a diverse natural enemy fauna already attacking this species. Biological control by augmentation has been suggested as a possible tactic against this beetle. Research into the possibility of rearing some of the more common predaceous beetles that attack bark beetles may lead to alternative approaches to management of incipient infestations. Following studies of spot infestations of this beetle, Borden (1993) suggested that spot infestations can be depended upon to expand and form subsequent outbreaks if not treated before adult beetles emerge. In an unrelated report, Moeck and Safranyik (1983) suggested that the main tactic for increasing biological control of this pest should be inundative releases of native clerids against low intensity outbreaks. Employing inundation against spot infestations may prove successful, but no studies have been reported. The major hurdles to overcome will be the cost of production and release, and the technology of mass rearing numbers sufficient to treat the areas involved.

Many management options are available during bark beetle infestations. Among these are various forms of harvesting, destruction, or removal of the infested or at-risk trees. Care should be exercised to conduct such operations with a clear understanding of the biology of the natural enemies involved. Many natural enemies of bark beetles use kairomonal cues to locate their hosts or prey (Chatelain and Schenk 1984), and will attack beetle infestations in trees and logs. Untimely removal of infested trees and logs could remove large numbers of natural enemies from the system. Similarly, pheromone traps can attract and kill large numbers of natural enemies that are using these chemical cues to locate host-infested trees. Careful integration of management options, based on the status of the forest stands at risk, the biology of the pest species, and the responses of the natural enemies, will be necessary to optimize the reduction of the beetle population while retaining the beneficial effect of the natural enemy populations (Nebeker 1989).

DOUGLAS-FIR BEETLE, *Dendroctonus pseudotsugae* Hopkins

Origin: North America.

Range in North America: Throughout the range of *Pseudotsuga menziesii* in western North America, along the Pacific Coast through to the Rocky Mountains.

Plant hosts and damage: Primarily *Pseudotsuga menziesii*, but also recorded from *Larix occidentalis*, *Tsuga heterophylla*. Adults bore into bark, create egg galleries, and oviposit. Larvae feed between the bark and the wood. Heavy infestations kill the host tree.

Natural Enemies: Both vertebrate and invertebrate natural enemies are reported from *D. pseudotsugae* (Table 6). Nematode associates of this beetle have been reported by Thong and Webster (1983), but the nature of the associations for those species is not clear.

Table 6. Natural enemies of *Dendroctonus pseudotsugae*

NATURAL ENEMY SPECIES	REFERENCE
Vertebrate Predators	
woodpeckers	Swaine 1925
Pathogens	
Aphelenchoides sp.	Furniss 1967
Chytridiopsis typographi	Weiser 1970
Contortylenchus reversus Thorne	Furniss 1967, Thong and Webster 1975
Ektaphelenchus obtusus	Furniss 1967
Micoletzkya sp.	Furniss 1967
Nosema dendroctoni Weiser	Weiser 1970
Ophryocystis dendroctoni Weiser	Weiser 1970
Parasitorhabditis obtusa	Furniss 1967

Table 6. continued

Sphaerulariopsis dendroctoni	Furniss 1967
Invertebrate Predators	
Enoclerus sphegeus (F.)	Marsden et al. 1981
Enoclerus sphegeus var. *arachnodes* Klug	Furniss and Cibrián Tovar 1980
Medetera aldrichii Wheeler	Nagel and Fitzgerald 1975
Medetera spp.	Marsden et al. 1981
Thanasimus undatulus Say	Furniss et al. 1974
Invertebrate Parasitoids	
Coeloides vancouverensis (D.T.)	Furniss and Cibrián Tovar 1980, Marsden et al. 1981
Coeloides brunneri Viereck	Richerson and Borden 1972
Karpinskiella paratomicobia Hagen and Caltagironi	Furniss 1968

Pest Status: This species is the most important bark beetle attacking Douglas-fir throughout the range of this tree in North America. The beetle usually breeds in felled, injured or diseased trees. Damage from endemic populations of this beetle is considerable but widely scattered. Outbreaks also occur, during which healthy trees are killed over extensive areas. Outbreaks are sporadic and of short duration along the Pacific coastal region from British Columbia to California, but kill large amounts of timber. These outbreaks usually follow extensive windthrow or fire, which provides abundant breeding resource for the beetle. In the Rocky Mountain region outbreaks also develop in trees felled by wind or snow or affected by drought, and are of longer duration.

In coastal Douglas-fir, outbreaks usually subside abruptly. Resistance of the host tree evidently keeps the beetle under control, as the beetles do not thrive in green timber. In interior areas tree stress is an important factor affecting the extent and duration of an outbreak.

Direct control of the Douglas-fir beetle has seldom been attempted. Salvage of at-risk trees in coastal areas is practical. In inland forests, prevention is practiced by thinning and harvesting.

Biological Control: Several studies have evaluated the role of natural enemies in populations of *D. pseudotsugae.* Rust (1933) notes the presence of predaceous mites in *Ips* spp. populations, and suggests that they are probably the cause of 63% egg mortality observed in *D. pseudotsugae.* Marsden et al. (1981) attributed 58% preimaginal mortality to entomophagous insects, including the predators *Medetera* spp. and *Enoclerus sphegeus* and the parasitoid *Coeloides vancouverensis.* The predator *Medetera aldrichii* consumed an average of 14.7 immature beetles in the laboratory (Nagel and Fitzgerald 1975). Infection of adult female beetles by the nematode *Contortylenchus reversus* resulted in lowered levels of protein in the haemolymph and a 20% reduction in the size of oocytes (Thong and Webster 1975). The abundance of larvae of the predators *E. sphegeus* and *Thanasimus undatulus* was significantly correlated with the abundance of attacks by *D. pseudotsugae* (Furniss et al. 1974). *Karpinskiella paratomicobia* parasitized adult *D. pseudotsugae,* causing a 67% reduction in fertility (Furniss 1968). Furniss (1967) reported six parasitic nematodes in adult beetles in Idaho and Utah. The report states that 93% of the beetles were infected, but the impact of the infection was not quantified. Hopping (1948) reports on the effectiveness of *Medetera aldrichii* as a predator of the beetle, and notes that only one other natural enemy, *E. sphegeus,* seems to be as effective.

Recommendations: As this beetle is a native pest, the introduction of additional natural enemies would have to be made from other species of related beetles. Some studies toward this end have been initiated against other *Dendroctonus* spp. (Miller et al. 1987), particularly focused around European or Asian species of clerid predators. None has yet met with success. *Enoclerus sphegeus* var. *arachnodes* preyed on the beetle in Chihuahua, Mexico, but not in Idaho, where the beetle was preyed on by *Enoclerus sphegeus* (Furniss and Cibrián Tovar 1980). The common braconid larval parasitoid *Coeloides pseudotsugae* was absent in Mexico, and might be profitably introduced there (Furniss and Cibrián Tovar 1980). This pest might be a suitable target to test the idea of introducing exotic natural enemies against native bark beetle pests (as might *D. brevicomis* or *D. ponderosae*).

Integrating knowledge of the biology and ecology of the predators with forest sanitation practices holds promise for integrating biological and cultural control. Ryan and Rudinsky (1962) described the field biology of the braconid parasitoid *Coeloides brunneri*, and discussed how the removal of infested logs from the forest, particularly late in the season, would remove overwintering parasitoids. They proposed felling small diameter trees late in the flight season of the beetle to favor late infestation as a means to promote populations of the parasitoid.

SPRUCE BEETLE, *Dendroctonus rufipennis* Kirby

Origin: North America.

Range in North America: Throughout the range of *Picea* spp. (spruces).

Plant hosts and damage: In the West, primarily *Picea engelmannii, Picea glauca,* and *Picea sitchensis.* Adults bore into bark, create egg galleries between the bark and the wood, and oviposit. Larvae feed between the bark and the wood. Heavy infestations kill the host tree.

Natural Enemies: Vertebrate predators are known to include woodpeckers. The parasitic nematodes *Sphaerularia dendroctoni* Massey and *Contortylenchus reversus* Thorne infect adult beetles, but the impact of such infection on the beetles is unknown. In one study such nematode infection did not reduce adult fertility (McCambridge and Knight 1972). Fewer studies of the natural enemies of *D. rufipennis* have been reported than for other members of the genus (Table 7). A few studies have reported a number of predaceous or parasitic invertebrates associated with wood infested with *D. rufipennis.* These records may be viewed as tentative or possible natural enemies of this species. These association records include *Dinotiscus dendroctoni* (Ashmead), *Dinotiscus eupterus* (Walker), *Medetera signaticornis* Loew., *Roptrocerus xylophagorum* (Ratzeburg) and *Rhyzophagus* spp. (Gara et al. 1995), and *Rhyzophagus dimidiatus* (Massey and Wygant 1954). *Thanasimus dubius* Fab. is attracted to the *D. rufipennis* aggregation pheromone (Lindgren 1992), indicating a possible predatory relationship.

Table 7. Natural enemies of *Dendroctonus rufipennis*

NATURAL ENEMY SPECIES
Vertebrate Predators
Dendrocarpus pubescens L.[1]
Dendrocarpus villosus L.[1]
Hylocichla guttata Pellas[1]
Picoides tridactylus L.1
Invertebrate Predators
Medetera aldrichii Wheeler[1]
Invertebrate Parasitoids
Coeloides dendroctoni Cushman[1]
Coeloides rufovariegatus (Provancher)[2]
Xylophagus sp.[2]
Xylophagus abdominalis Loew.[2]

[1]McCambridge and Knight 1972
[2]Gara et al. 1995

Pest Status: The beetle is normally present in small numbers in weakened or windthrown trees (Furniss and Carolin 1977). Outbreaks can occur, and cause extensive damage. In Colorado from 1942 to 1948, 3.8 billion board feet of spruce were killed by this beetle (Wygant and Nelson 1949). The life cycle varies, requiring a single year in coastal populations, 2 years in the main distribution of *P. engelmannii,* and 3 years at high elevations. Harvesting stands of overmature spruce is effective in preventing the development of outbreaks. Other silvicultural measures are discussed by Furniss and Carolin (1977).

Biological Control: No biological control program has been mounted against this species. Spruce beetle populations are normally kept at low levels by a combination of factors, which include predation by woodpeckers, insect predators and parasitoids, and possibly parasitic nematodes.

Recommendations: The start of an outbreak is difficult to detect in this species. Direct control can be costly, and management should be focused on prevention of outbreaks. Such management should include sanitation, timely harvesting, and monitoring for infestations. Natural enemies are little known for this species. Additional research into the impact of natural enemies and their ability to respond to population increases of their hosts may prove beneficial in defining practices that would more effectively utilize natural control.

IPS BARK BEETLES

The genus *Ips* contains 25 species recognized in the western United States, and these form the second most destructive group among the western bark beetles. The species are multivoltine (from two to five generations per year, occasionally univoltine at high latitudes). They typically attack windfalls, cut trees, slash, or trees weakened or predisposed to attack of drought or attack of other bark beetles. While *Ips* spp. have a number of predaceous and parasitic natural enemies, densities of *Ips* species appear to be largely limited by the quantity of available host material. In a quantity of freshly cut slash or windfall, a large beetle population can develop. This population usually does not remain at high densities once the breeding material is exhausted. Direct control of these beetles has rarely been practiced, because of the brevity and focused nature of these outbreaks. Management practices focus on limiting breeding material during logging operations, and on harvesting or salvaging windthrown timber. Direct control by felling infested trees and treating felled timber can be employed on extensively used areas, such as recreation areas.

The 25 species of *Ips* in North America are all native and have similar ecological contexts regarding the possibilities for biological control. We will examine *Ips pini*, the principal western species, as typical of this group.

PINE ENGRAVER, *Ips pini* (Say)

Origin: North America.

Range in North America: Throughout North America.

Plant hosts and damage: *Pinus* spp., commonly in *P. jeffreyi, P. ponderosa, P. contorta*. The adults bore into the bark, and construct an oviposition chamber between the bark and the wood, on limbs or the bole of the tree. The larvae feed between the bark and the wood, killing limbs or tree tops. Severe infestations can kill trees.

Natural Enemies: Natural enemy associations are very poorly understood for *Ips pini* (and other *Ips* spp.). Predators, pathogens, and parasitoids have been reported either associated with or parasitizing *I. pini* (Table 8).

Table 8. Natural enemies associated with or reported from Ips pini

NATURAL ENEMY SPECIES	REFERENCE
Vertebrate Predators	
woodpeckers	Sartwell et al. 1971
Pathogens	
Contortylenchus reversus Thorne	Choo et al. 1987
Contortylenchus spp.	Choo et al. 1987
Parasitaphelenchus sp.	Choo et al. 1987
Parasitilenchus ipini	Choo et al. 1987
Parasitylenchus ovarius	Choo et al. 1987
Invertebrate Predators	
Corticeus parallelus Melsh	Raffa 1991
Cylistix cylindrica (Paykull)	Raffa 1991
Thanasimus dubius (F.)	Raffa 1991
Invertebrate Parasitoids	
Tomicobia tibialis Ashmead	Senger and Roitberg 1992

Pest Status: *Ips pini* is one of the most common bark beetles in North America, and at times becomes a serious pest. Large populations can develop in the tops or limbs of trees killed by *Dendroctonus* spp. or in slash from logging. When populations become large, they become aggressive and attack healthy trees. Outbreaks are usually of short duration and seldom last more than one season (Furniss and Carolin 1977). There may be from one to five generations per year, depending on locality and length of season.

Biological Control: Very little is known about the role of natural enemies in the population dynamics of Ips spp., including *I. pini.* Raffa (1991) and coworkers have identified predaceous beetles that are attracted to *I. pini* pheromone (ipsdienol). These beetles are known to prey upon other bark beetles and are likely predators of *I. pini.* A number of nematodes, some with parasitic life cycles, are known from *I. pini*. Choo et al. (1987) reported up to 99% infection in some populations of *I. pini*, but the impact of such parasitism on beetle population biology is unknown. Senger and Roitberg (1992) demonstrated reduced fecundity in adult *I. pini* parasitized by the pteromalid wasp *Tomicobia tibialis.* Parasitized adults produced only half the number of progeny of nonparasitized adults. The absolute or relative abundance of natural enemies in *Ips* populations is not well documented.

Recommendations: Outbreaks of this species are self-limiting and usually of short duration. The species has a extant upper trophic level of predators and parasitic natural enemies, and usually reaches serious levels only in the presence of large amounts of breeding material. Therefore, management options should focus on limiting the availability of this breeding material. Control practices with pheromones have been proposed and evaluated (Raffa 1991 and references therein), but the pheromones also act as kairomones to many predators. If pheromones are used in trapping, technologies should be developed so as not to unduly trap natural enemies and harm the balance of natural enemies to pests. Some natural enemies may be reared or collectable in large numbers, but the scale of application necessary to employ them in augmentation programs is likely prohibitive. Additional biological control actions do not appear warranted at this time. Should additional interest in biological control arise, the first needs to be addressed would be quantitative research into the roles of natural enemies in endemic and epidemic beetle populations.

SILVER FIR BEETLE, *Pseudohylesinus sericeus* (Mannerheim)

Origin: North America.

Range in North America: Alaska, British Columbia, California, Idaho, Montana, Oregon, Washington.

Plant hosts and damage: *Abies* spp., *Tsuga heterophylla, Pseudotsuga menziesii.* Adults bore into the bark, and excavate egg galleries between the bark and wood, where the larvae then feed. Attack is usually on windthrown, felled, injured or weakened trees. Extensive attacks can kill otherwise healthy trees.

Natural Enemies: Only one report (McGheney and Nagel 1969) identifies natural enemies of this species (Table 9).

Table 9. Natural enemies reported from *Pseudohylesinus sericeus* (after McGheney and Nagel 1969)

NATURAL ENEMY SPECIES
Invertebrate Predators
Medetera aldrichii Wheeler
Invertebrate Parasitoids
Bracon pini (Muesebeck)
Coeloides brunneri Viereck
Cecidostiba acuta (Provancher)
Roptrocerus sp.

Pest Status: This beetle generally attacks predisposed or weakened trees. However, during 1947-1958 this beetle, together with *Pseudohylesinus granulatus,* killed 528 million board feet of commercial grade Pacific silver fir, mostly in Washington (Thomas and Wright 1961). It has also attacked young-growth stands of *Tsuga heterophylla* (McGheney and Nagel 1969).

Biological Control: Little is known of the natural enemies of this species. McGheney and Nagel (1969) reported parasitism by *Cecidostiba acuta* as a likely major mortality factor. Woodpeckers have also been reported feeding on this species (Thomas and Wright 1961). No diseases are reported.

Recommendations: This beetle has a demonstrated potential for serious infestations of firs. Our knowledge of its population biology is limited, and further studies of its ecology, particularly with reference to the role of natural enemies, and its host-plant relationships, are necessary before recommendations can be made.

EUROPEAN ELM BARK BEETLE, *Scolytus multistriatus* (Marsham)

Origin: Old World. The species is known from Europe, the Middle East, and northern Africa (CAB 1975).

Range in North America: Throughout North America on *Ulmus* spp.

Plant hosts and damage: *Ulmus alata, Ulmus americana, Ulmus pumila, Ulmus procera, Ulmus parvifolia,* and other *Ulmus* spp. Overwintering adults of this species feed on twigs and, if the adults are carrying infective stages of the Dutch elm disease pathogen, *Ceratocystis ulmi,* the tree is usually infected by this feeding. Adults then fly to a new host tree to bore into the bark (Wood 1982). Egg galleries are excavated between the bark and the wood. Larvae feed on the intercortex tissues. Severe infestations can kill trees, usually those under water stress, in the absence of Dutch elm disease (Brown and Eads 1966). Trees are usually killed by the fungal disease.

Natural Enemies: Pathogens, predators and parasitoids have been reported from this species (Table 10). Additional parasitoids are known in Europe (Thompson 1943, Herting 1973).

Table 10. Principal species of natural enemies reared from, or associated with, *Scolytus multistriatus*

NATURAL ENEMY SPECIES	REFERENCE
Pathogens	
Beauveria bassiana (Bals.) Vuill.	Doberski 1981 (record from *Scolytus scolytus*), Houle et al. 1987
Cordyceps militarius	Houle et al. 1987
Heterorhabditis bacteriophora Poinar	Poinar and Deschamps 1981
Hirsutella thompsonii Fisher	Houle et al. 1987
Metarhizium anisopliae (Metchnikoff) Sorokin	Doberski 1981 (record from *Scolytus scolytus*), Houle et al. 1987
Neoaplectana carpocapsae	Poinar and Deschamps 1981, Mazzone and Peacock 1985
Nomureae rileyi (Farlow)	Houle et al. 1987
Nosema scolytii Lipa	Lipa 1968
Paecilomyces farinosus	Doberski 1981 (record from *Scolytus scolytus*)
Paecilomyces fumosoroseus	Houle et al. 1987
Parasitilenchus scolyti Oldham	Oldham 1930
Scytalidium lingnicola	Jassim et al. 1990
Stempella scolytii (Weiser)	Lipa 1968
Trichoderma harzianum Rifai	Jassim et al. 1990
Trichoderma polysporum	Jassim et al. 1990
Verticillum lecanii	Houle et al. 1987
Invertebrate Predators	
Acari	
Histiogaster sp.[1]	Hajek and Dahlsten 1985
Insecta	
Agulla sp.[2]	Hajek and Dahlsten 1985
Axinopalpus bipalgiatus (Dejean)[1]	Hajek and Dahlsten 1985
Corticeus substriatus (LeConte)[1]	Hajek and Dahlsten 1985
Dufouriellus ater (Dufour)[1]	Hajek and Dahlsten 1985
Lonchaea sp.[1]	Hajek and Dahlsten 1985
Proctolaelaps scolytii Evans[1]	Hajek and Dahlsten 1985
Temnochila chlorodia (Mannerheim)[2]	Hajek and Dahlsten 1985
Invertebrate Parasitoids	
Acari	
Pyemotes scolytii (Oudemans)	Hajek and Dahlsten 1985
Insecta	
Cerocephala eccoptogastri Masi[1]	Hajek and Dahlsten 1985
Cheiropachus quadrum (F.)[3]	Merlin 1984, Hajek and Dahlsten 1985
Coeloides scolyticida Wesm	Fransen 1931
Dendrosoter protuberans (Nees)[3]	Merlin 1984, Hajek and Dahlsten 1985, Maksimovic 1986
Ecphylus silesicacus (Ratzeburg)	Maksimovic 1986
Entedon ergias (=*leucogramma* Ratzeburg) Walker[3]	Merlin 1984, Hajek and Dahlsten 1985, Maksimovic 1986
Rhaphitelus maculatus Walker	Hajek and Dahlsten 1985
Spathius benefactor Matthews	Hanula and Berisford 1984
Spathius canadensis (Ashmead)	Kennedy 1970
Theocolaxia pityophthori (Ashmead)[1]	Hajek and Dahlsten 1985

[1]Reared in association with *S. multistriatus*

[2]Laboratory record

[3]Reared from infestations of *S. multistriatus* together with two other *Scolytus species*

Pest Status: There may be up to three generations per year in the United States (Hanula and Berisford 1984). This bark beetle is most renowned as a vector of Dutch elm disease, a fungus of Old World origin that can kill otherwise healthy elm trees. Trees become infected when beetles carrying infective stages of the fungus feed on twigs, before boring into the bark to reproduce. Many strains of the disease-causing fungus are known. Some fungal strains are more virulent than others, and many lead to death of the tree. Different species of *Ulmus* have different susceptibilities to infection. The greatest significance of this pest in North America is in the urban landscape, where many *Ulmus* spp. have been widely used as shade and ornamental trees.

This beetle species was accidentally introduced into eastern North America early in the 20th century. Populations eventually spread to the West Coast. In California, populations initially did not vector Dutch elm disease (Brown and Eads 1966, the causative agent is presumed to have been absent at that time). Nonetheless, these populations were still of sufficient intensity that concentrated attack on water-stressed trees could lead to tree death.

The disease-causing pathogen has become widespread and is a major cause of damage to elms. Trees are infected widely throughout the continent, but quantitative estimates of regional losses were not located. Westwood (1991) reports on management costs and losses in Manitoba, and equates a small percentage loss of elm trees in the region to Can$43 million. Cost of management in Manitoba averaged Can$1.5 million annually since 1981. Interest in control has focused both on controlling the vector *(S. multistriatus)* and on controlling the fungal disease.

Biological Control: Natural enemy introductions into North America were initiated in 1965 (Clausen 1978), when the braconid *Dendrosoter protuberans* was introduced from Europe. Millions of individuals were released in infested areas, and the species is widely established. The pest beetle is also attacked by other natural enemies (Table 10) in Europe. The species is susceptible in the laboratory to many different pathogenic fungi and nematodes. In laboratory and field studies, pathogenic nematodes are capable of killing all stages of the beetle (Poinar and Deschamps 1981). Adult beetles can be sterilized by some species of nematode (Oldham 1930).

Although several pathogens are reported as infective against *S. multistriatus* and other *Scolytus* species, Mazzone and Peacock (1985) consider that efforts to find effective pathogens of this pest have been essentially futile. Investigations by Jassim et al. (1990) demonstrated pathogenicity by certain fungi, but these authors thought it unlikely that treating elm trees with these pathogens would reduce larval populations through mycotic infections.

The few field studies that have been conducted have identified braconids, either *Coeloides scolyticida* (Fransen 1931) or *D. protuberans* (Maksimovic 1979, Schröder 1974a) as the principal parasitoids in Europe. Parasitism of 73% was noted in Yugoslavia in 1972-1973 (Maksimovic 1986). Hajek and Dahlsten (1985) found total mortality of about 80% in California populations, with parasitism contributing 2% mortality.

Recommendations: While *S. multistriatus* is clearly a species of major importance, our knowledge of its population dynamics of is very limited. Quantitative studies on factors affecting population rates of increase are lacking, so determining the significance of natural enemies relative to other biotic (host-plant health) and abiotic factors remains difficult. Population studies in both the United States and areas where the beetle is native are needed to determine whether mortality caused by natural enemies is still lacking in the United States. If this is the case, additional natural enemies should be sought and released. The area evaluated for seeking additional natural enemies should include populations of the beetle in the Middle East. If population dynamics and mortality (related to natural enemies) on the two continents are equivalent, other strategies for control should be applied.

Among the possible strategies for control are the augmentation or application of pathogenic fungi or nematodes (Finney and Walker 1977) to elm trees in high value areas. Sanitation and related practices will continue to be important in limiting losses to the beetle and to Dutch elm disease (Westwood 1991). Biological control of the pathogen could be pursued, either through seeking antagonists to the pathogen (Gemma et al. 1984, 1985) or through efforts to reduce its virulence (Brasier and Gibbs 1975, Pusey and Wilson 1979). Genetic engineering of genus *Ulmus* has been proposed to improve disease resistance (Mazzone and Peacock 1985).

FIR ENGRAVER, *Scolytus ventralis* LeConte

Origin: North America.

Range in North America: Arizona, British Columbia, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, Wyoming (Stevens 1956).

Plant hosts and damage: *Abies grandis, Abies concolor, Abies magnifica,* and occasionally *Pseudotsuga menziesii, Tsuga* spp. and *Picea* spp. Adults and larvae mine the cambium. Repeated or heavy attacks can lead to tree death.

Natural Enemies: Few natural enemies are reported in the literature. These include (Table 16) clerid predators, insect parasitoids, woodpeckers, and a mite (Stevens 1956). Other parasitoids or pathogens probably await discovery or reporting.

Table 11. Invertebrate natural enemies of *Scolytus ventralis* (after Stevens 1956)

NATURAL ENEMY SPECIES
Invertebrate Predators
Acari
Pediculoides ventricosus Newport
Insecta
Enoclerus lecontei Wolcott
Enoclerus sphegeus (F.)
Invertebrate Parasitoids
Coeloides brunneri Viereck
Coeloides scolyti Cushman

Pest Status: Of the 18 species of *Scolytus* in western North America, *Scolytus ventralis* is the only pest of major significance in the management of western forests (Furniss and Carolin 1977). The other *Scolytus* species are primarily secondary attackers of trees weakened or killed by other insect species or other causes (Furniss and Carolin 1977). This species is responsible for losses of 450 million board feet annually in California alone, and outbreaks cause greater losses.

This species is univoltine throughout much of its range, but semivoltine (requires 2 years to complete one generation) in northern latitudes (Furniss and Carolin 1977). Adults bore directly into the bark on the bole, from the base to the top of the tree. Eggs are laid in transverse galleries, which can deeply score the wood. Subsequent larval feeding causes mines in the cambium that are usually with the growing grain of the tree. Pupation takes place in the inner bark.

Scolytus ventralis primarily attacks firs. Populations of this species are widespread in western forests, and are found in healthy as well as weakened or dying trees. Minor or modest infestations in healthy trees are not invariably fatal, as these trees often survive and continue to grow. Heavy infestations can lead to tree death. Because of the sporadic character of outbreaks and the prevalence of healthy broods in living trees, direct control measures are generally impractical. On intensively used areas, prompt removal or treatment of infested trees may protect remaining trees from immediate risk. In such areas, however, the best practice is to prevent tree stress by minimizing soil compaction and other adverse conditions (Furniss and Carolin 1977). Trees infected with the root rot fungus *Fomes annosus* are at greater risk of beetle infestation (Cobb et al. 1974, see also Filip and Goheen 1982). Outbreaks often follow droughts (Furniss and Carolin 1977). In the forest, stand sanitation together with measures to promote tree vigor are the most practical means for minimizing losses to this species.

Biological Control: No biological control program has been mounted against this species. The few natural enemies known are general predators of many species of bark beetles. Of the braconid parasitoids known, *C. brunneri* is also known from other bark beetles.

Recommendations: Although this species of beetle is responsible for major losses in western forests, the potential for enhanced biological control appears somewhat limited. The primary factors predisposing trees to attack appear to be related to forest health and tree vigor, not lack of natural enemies of the beetle. Additional natural enemies of *Scolytus* spp. from other related environments (e.g. Europe) might be considered for importation. Although the principal niches for natural enemy impact (predators, parasitoids) are currently represented in North America, other species could conceivably increase natural mortality. Additional studies should be conducted on life tables for this pest species, with special reference to the role of natural enemies in population demography, particularly pathogens (which are not represented in the literature for this species), before future programs for enhancing biological control are undertaken.

STRIPED AMBROSIA BEETLE, *Trypodendron lineatum* (Olivier)

Origin: Holarctic.

Range in North America: Throughout North America, from Alaska and Newfoundland south to New Mexico and North Carolina.

Plant hosts and damage: Most species of *Abies, Larix, Picea, Pinus, Pseudotsuga, Thuja, Tsuga.* Damage is usually limited to felled, injured, or weakened trees.

Natural Enemies: Few natural enemies have been reported directly from this species. The predaceous clerid *Thanasimus formicarius* (L.) is attracted to the pheromone of *T. lineatum* (Tommeras 1988). This predator is attracted to pheromones of other bark beetles on which it is known to prey, and its attraction to *T. lineatum* pheromone indicates that it may be a predator of that species also. The fungus *Beauveria bassiana* (Bals.) Vuill., when sprayed on logs or soil, will infect adults of *T. lineatum,* causing up to 100% mortality (Prazak 1991).

Pest Status: *Trypodendron lineatum* is the most damaging of the ambrosia beetles in the West (Dyer and Wright 1967, Furniss and Carolin 1977). Damage is usually in felled or stored timber, or in weakened or damaged trees. Populations can also build up on slash. The larval galleries degrade the lumber value of infested timber.

Biological Control: No projects targeting this species have been reported. Few natural enemies have been reported.

Recommendations: Controlling damage by this species is usually a matter of processing felled timber in a timely manner. Felled trees can be protected by chemical treatments with insecticides (Furniss and Carolin 1977), pine oil (Dubbel 1992), or pathogenic fungi (Prazak 1991). Biological control probably plays an important role in limiting natural populations, as with other bark beetles, but in such favorable situations as stored logs and felled trees populations can increase and cause damage. Opportunities for enhancing biological control in these situations appears limited, except perhaps by spraying with the pathogenic fungi *B. bassiana.*

Diptera

CECIDOMYIIDAE

DOUGLAS-FIR NEEDLE MIDGE, *Contarinia pseudotsugae* Condrashoff

Origin: North America.

Range in North America: British Columbia, California, Idaho, Montana, Oregon, Washington.

Plant hosts and damage: *Pseudotsuga menziesii.* The larvae mine the needles, causing discoloration and needle death.

Natural Enemies: Condrashoff (1962) notes the following parasitoids of larvae: *Platygaster* sp., *Tetrasticus* sp., *Tridymus* sp.

Pest Status: This midge is a pest of limited concern to forests, but has been a serious pest to commercial Christmas tree farms (Condrashoff 1962).

Biological Control: No programs for biological control of this pest have been reported.

Recommendations: This pest appears to be native, and can encapsulate eggs of one of its primary parasitoids (Condrashoff 1962). Little is known about its population dynamics or factors affecting its abundance. Basic research in these areas is needed and may help determine if natural enemies can be manipulated or augmented to improve biological control.

Homoptera

ADELGIDAE

BALSAM WOOLLY ADELGID, *Adelges piceae* (Ratzeburg)

Origin: Europe or Asia.

Range in North America: Northeastern United States, Canada, Pacific Northwest.

Plant hosts and damage: *Abies amabilis, Abies lasiocarpa, Abies grandis.* The aphid feeds on all aerial parts of the tree except needles. Feeding causes hypertrophy of plant cells, resulting in a condition known as "gouting" of the limbs and twigs. Feeding resulting in gouting causes tree decline and tree death over a period of 10-20 years. Intense feeding on the trunk results in more immediate damage to the tree, leading to death in a few years.

Natural Enemies: No insect parasitoids are known from adelgid aphids. Predators of this group are known from many continents. Several insect predators have been studied in Europe. Some of these have been introduced into North America against this pest species (Table 12).

Table 12. Insect predators of *Adelges piceae* released in the western United States

INSECT PREDATORS	
Adalia luteopicta Mulsant[1]	*Laricobius erichsonii* Rosenhall[1]
Adalia tetraspilota bispilota Weise[1]	*Leis dimidiata* (F.)[1]
Aphidecta obliterata (L.)[1]	*Leucopis atratula* (Ratzeburg)[2]
Aphidoletes thompsoni Möhn[1]	*Leucopis* n. sp. nr. *obscura*[1]
Balia eucharis Mulsant[1]	*Leucopis obscura* Hal.[1]
Chilocorus kuwanae Silvestri[1]	*Scymnus impexus* (Mulsant)[1]
Chrysopa sp.[1]	*Scymnus pumilio* Weise[1]
Cremifania nigrocellulata Czerny[1]	*Synharmonia conglabata* (L.)[1]
Exochomus lituratus Corh.[1]	*Tetraphleps* sp.[1]
Exochomus uropygialis Mulsant[1]	
Harmonia breiti Mader[1]	

[1]Clausen 1978
[2]Humble 1994

Pest Status: This aphid is a major destructive pest on true firs in the northeastern United States, Canada, and in the Pacific Northwest. During the late 1950's, an outbreak in southwestern Washington killed an estimated 1.5 billion board feet of timber, much of which could not be salvaged (Johnson et al. 1963). The insect affects both forests and ornamental plantings.

The insect feeds on the stem, branches and twigs, as well as the bole. Salivary injections cause gall-like formations on twigs and branches. Bole infestations may be very heavy, and usually kill the trees in a few years. There are two to four generations in the West each year, all on *Abies* spp. Distribution is apparently by wind during the first instar stage. All individuals are females. Alates (winged individuals) appear rarely.

Biological Control: This insect is adventive to North America, and has been the subject of biological control programs in both Canada and the United States. Several predators have been sought from Europe (where this species and related forms occur) and from India and Pakistan, during the period 1933-1963.

Many of these predators became established in their release locations. Effectiveness was variable, and somewhat limited. Mitchell and Wright (1967) considered *Laricobius erichsonii* the most promising of the introduced predators to exert a measurable degree of control in the Pacific Northwest. Two or three years may be required to bring about a significant degree of control by this species, and some tree species such as subalpine fir cannot withstand long infestations. *Cremifania nigrocellulata* and *Leucopis obscura* are found mostly in trees with heavy infestations, and the infested trees usually die in spite of the presence of these predators. In Canada, however, extremely heavy stem infestations became very rare following the establishment of *L. obscura* (Balch et al. 1958).

Five predators are considered established in the western United States: *Aphidoletes thompsoni, Scymnus impexus, L. erichsonii, C. nigrocellulata,* and *L. obscura.* Although Clausen (1978) comments that, as a whole, there is little promise they will contribute any appreciable suppression of the aphid, studies by Clark and Brown (1958) showed that the presence of *L. erichsonii* and *L. obscura* together considerably decreased the upward population trend between the first and second generation of the aphid. Humble (1994) further documents the presence of these natural enemies in British Columbia, as well as the presence of *A. obliterata* and *Leucopis atratula* (Ratzeburg).

Recommendations: The possible reasons behind the current pest status of this species in the United States must be examined. The aphid is known from Europe, where it is not a severe pest. This may be because it attacks different species of host trees in Europe than in North America, and the North American hosts may be more susceptible to the damaging effects of the salivary secretions. If this is the case, management strategies may need to include tactics in addition to biological control to reduce the damage caused by this species.

Another possibility is that the natural enemies thus far accumulated in North America are unsuited to control this pest in its new environment. There is some evidence that the aphid may not be of European origin, but rather may have originated farther east, perhaps in the Caucasus (Van Driesche et al. 1996). Other related aphid species are known from that area (Balch 1952) and have been introduced into Europe in the last century.

The first step in unraveling this problem should be research focused at obtaining basic knowledge about the precise systematic position of the pest species in this country. Genomic analysis of the strains here, in Europe, and in the Caucasus and related areas could provide important information about the origin of the species and strains present in these various geographic regions. Identification of the species present here should be confirmed against possible similar species from Europe, the Caucasus region, and perhaps related areas where firs occur. This step will answer the questions of what species or strains are in North America, and where the closest relatives are.

The next step in seeking a biological control solution should be quantitative studies on the life cycle and demography of the pest, and on the role of natural enemies, for the species in its native home. Artificial plantings of some North American firs in its native home could also be incorporated, and comparative studies on the survival and reproduction of the aphids on native (European or Asian) firs and North American firs could be conducted. Results of these studies could demonstrate whether in the natural setting the predators and other enemies of this pest are capable of preventing population growth to damaging levels, on both naturally occurring fir species and on firs found in North America.

The results of these studies will provide the basis for additional recommendations regarding the suitability of a biological control solution. If a native home for the pest species is identified from which natural enemies have not been previously sought, and studies demonstrate that natural enemies there are capable of controlling it, then new natural enemies from these locations should be imported and established into pest populations on this continent. If native natural enemies cannot prevent damaging levels on North American fir species in natural settings, then other options will have to be sought.

Hymenoptera

DIPRIONIDAE

The conifer sawflies (Diprionidae) are represented in western North America by about 16 species (Ross 1955), all native. They rarely reach pest status, but a few have been recorded at outbreak densities, occasionally defoliating their hosts. The sawflies feed on older foliage and tend to reduce growth rather than kill trees outright. Outbreaks, when they have been recorded, last 1 or 2 years and subside suddenly due to natural causes (Furniss and Carolin 1977). We consider here the hemlock sawfly, *Neodiprion tsugae* Middleton, as representative of this native group. It is the most consistently important of the western species, noted as an important defoliator of hemlock and other conifers (Furniss and Carolin 1977).

The family Diprionidae includes other species that are significant pests of conifers, particularly when they are introduced or adventive to new regions without their native natural enemies. These include three Old World sawflies, *Diprion hercyniae* (Hartig), *Diprion similis* (Hartig), and *Neodiprion sertifer* (Goeffroy), each of which has been introduced unintentionally to eastern North America. These species are potential invaders of western forests. Biological control efforts against these species have been generally successful (Van Driesche et al. 1996), and natural enemies for them are well known. Should they become established in the West, similar programs would also likely be successful.

HEMLOCK SAWFLY, *Neodiprion tsugae* Middleton

Origin: North America.

Range in North America: Alaska, British Columbia, Idaho, Montana, Oregon, Washington.

Plant hosts and damage: Primarily *Tsuga heterophylla,* although *Tsuga mertensiana* and *Abies amabilis* are also recorded as hosts (Downing 1959, Furniss and Carolin 1977). The larvae feed on old needles. Damage is usually confined to reduced tree growth.

Natural Enemies: Several studies have reported invertebrate parasitoids of this sawfly (Table 13). In addition, one study (Hard 1976) reports considerable mortality caused by the fungus *Entomophthora sphaerosperma* Fres., particularly in wet years. Predation by birds was not mentioned in the reviewed literature. Mammals are credited with consuming up to 50% of the pupal cocoons in the forest litter (Furniss and Dowden 1941, Downing 1959). No reference to invertebrate predators was found in the reviewed literature.

Table 13. Invertebrate parasitoids recorded from *Neodiprion tsugae*

PARASITOID SPECIES	REFERENCE
Aptesis tsugae Cushman	Furniss and Dowden 1941
Delomerista japonica diprionis Cushman	Furniss and Dowden 1941, Downing 1959, Torgersen 1968, Torgersen 1969, Hard 1976
Delomerista sp.	Hopping and Leech 1936
Diadegma sp.	Torgersen 1968
Diplostichus sellersi Hall	Hall 1939, Furniss and Dowden 1941
Euceros fasciens Davis	Furniss and Dowden 1941
Exenterus tsugae Cushman	Cushman 1940, Furniss and Dowden 1941
Itoplectis quadricingulatus (Provancher)	Furniss and Dowden 1941, Downing 1959, Torgersen 1968, Torgersen 1969, Hard 1976
Lamachus spp.	Torgersen 1968, Torgersen 1969
Lamachus oregon Cushman	Furniss and Dowden 1941
Lamachus tsugae Cushman	Furniss and Dowden 1941
Mastrus spp.	Torgersen 1968, Torgersen 1969
Mastrus neodiprioni Viereck	Furniss and Dowden 1941
Olesicampe sp.	Hopping and Leech 1936
Oresbius tsugae tsugae (Cushman)	Furniss and Dowden 1941, Torgersen 1968, Hard 1976
Pezoporus sp.	Hopping and Leech 1936
Phaeogenes arcticus Cushman	Hopping and Leech 1936
Phaeogenes hariolus (Cresson)	Hopping and Leech 1936
Pseudischnus oregonensis (Cushman)	Furniss and Dowden 1941, Walkley 1954
Rhorus sp.	Torgersen 1968, Torgersen 1969
Scambus (Scambus) nucum (Ratzeburg)	Torgersen 1968
Spilocryptus neodiprionis Cushman	Furniss and Dowden 1941
Stylocryptus subclavatus (Say)	Furniss and Dowden 1941
Tritneptis klugii (Ratzeburg)	Furniss and Dowden 1941
Tsugaea nox Hall	Hall 1939, Furniss and Dowden 1941

Pest Status: The species is generally univoltine, although some individuals remain in pupal diapause for more than one season. The adults are usually present in late summer, and eggs are laid singly in slits cut in the needle by the ovipositor. Needles usually carry a single egg, although sometimes 2-5 eggs will be laid in a single needle (Hopping and Leech 1936). Larvae hatch in spring, feeding gregariously during the first few instars on year-old foliage, then singly in later instars. New foliage is eaten only when old foliage is largely consumed (Furniss and Dowden 1941, Hard 1976). Pupation takes place in cocoons, usually in litter on the forest floor, but also among twigs or needles of the host tree (Hopping and Leech 1936), or on the bark. Fecundity is about 72 eggs per female except from collapsing populations, where fecundity is lower (49 eggs per female, Hard 1976). The cause of this reduced fecundity is unknown, but may be related to poor nutrition of larvae in defoliated areas.

Extensive outbreaks have been recorded on *T. heterophylla* in natural forests in Alaska, British Columbia, and Oregon. Hopping and Leech (1936) report substantial tree kill from an outbreak of this sawfly covering about 12,000 ha on the Queen Charlotte Islands during 1931-1933. In Oregon, 30,000 ha were infested in 1934, with about 5,000 ha heavily defoliated, in an outbreak that spanned 1933-1936. Noticeable defoliation occurred every year except 1957 in southeast Alaska during the period 1952-1974 (Hard 1976). Damage is usually limited to reduced growth, and most trees in an infested stand survive even substantial outbreak populations (Hard 1976, Furniss and Carolin 1977). Risk of pest status is considered greatest when this species occurs together with populations of pests that prefer young foliage (Furniss and Dowden 1941, Furniss and Carolin 1977).

Biological Control: No biological control program has been directed at this species. More than 20 parasitic species are known from this native sawfly (Table 13). *Delomerista japonica diprionis* was one of the most important parasitoid species in Oregon in 1933-1936 (Furniss and Dowden 1941); *Itoplectis quadricingulatus, Exenterus tsugae, Aptesis tsugae,* and *Stylocryptus subclavatus* were also common. The ichneumonid *I. quadricingulatis* parasitized several species of sawfly in the laboratory (Furniss and Dowden 1941). In Alaska in 1964-1966 the most common natural enemy was *Oresbius tsugae tsugae* (Torgersen 1968). In sawfly populations from Alaska during 1969-1971, the most prominent natural enemies were the fungus *Entomophthora sphaerosperma* and the parasitoids *D. japonica diprionis, O. tsugae tsugae,* and *I. quadricingulatus* (Hard 1976).

In Oregon, mortality of pupae was 87% in 1935 and 72% in 1936 (Furniss and Dowden 1941). Based on dissections of pupae, Furniss and Dowden (1941) estimated that parasitism of pupae was 61% in 1936. In Alaska in 1964-1966, parasitism of cocoons ranged from 3% to 40% (Torgersen 1968). Cocoon samples from a population in 1945 on Vancouver Island contained 18% adult sawflies, 14% parasitoids, 11% opened by predators, and 57% with larvae killed by fungal infection (Hard 1976). Hard (1976) also reported lethal infection of larvae in 1972 and 1973 in southern Alaska by *E. sphaerosperma,* but did not give rates of infection of larvae before they spun cocoons. Rates of infection (mortality) in cocoons ranged from 20% to near 100%. Wetter than normal conditions were associated with higher infection rates.

Recommendations: No action is necessary at this time regarding biological control of this species. The native natural enemy fauna caused considerable mortality in all the studied populations, although the faunal composition of the natural enemies varied in different locations. Population outbreaks are generally short-lived, and damage is limited. Infested stands generally recover with little loss to tree death.

TENTHRIDINIDAE

LARCH SAWFLY, *Pristiphora erichsonii* (Hartig)

Origin: The species currently is Holarctic in distribution (CAB 1959), with at least five known strains (Wong 1974). Four strains are present in North America. Of these four, at least two appear to have been introduced. The remaining two are either native in North America or were introduced before collections were recorded. Turnock (1972) presents evidence that the species is native to Europe, where it is generally rare, and outbreaks are local and do not lead to widespread defoliation. Biological control programs have traditionally treated this species as adventive in North America. The response of the populations to introduced natural enemies (e.g., Figure 2, p. 3) argues for adventive status of this species.

Range in North America: This species occurs throughout North America on its host trees. In western North America, this includes Alaska, Idaho, Montana, North Dakota, Oregon, Washington, Alberta, British Columbia, and Saskatchewan (Drooz 1960, Furniss and Carolin 1977). Its range of distribution is delimited north of about the 38th parallel to just north of the 60th parallel (Drooz 1960).

Plant hosts and damage: This species feeds solely on larch, *Larix* spp. It is the most destructive insect feeding on *Larix laricina* in the eastern portion of North America. In the West, is feeds on *Larix occidentalis* in Montana, Idaho, Washington, Oregon, and British Columbia and on *Larix lyallii* in Alberta (Furniss and Carolin 1977). The larvae of this species feed on needles and, at outbreak levels, can defoliate trees.

Natural Enemies: The species has been widely studied in concert with biological control programs aimed against it, and a variety of natural enemies are known (Table 14). It has numerous natural enemies in Europe, its presumed native range. It has no specific egg or pupal parasitoids native to North America.

Table 14. Natural enemies of *Pristiphora erichsonii*

NATURAL ENEMY SPECIES

Vertebrate Predators
Clethrionomys gapperi[1]
Microtus agrestis Flemming[1]
Microtus pennsylvanicus[1]
Peromyscus maniculatus (Wagner)[1]
Rana pipiens[1]
Rana sylvatica[1]
Sorex arcticus[1]
Sorex cinereus[1]
numerous bird species[1]

Pathogens
Bacillus sp.[1]
Beauveria bassiana (Bals.) Vuill.[1]
Beauveria flobulifera (Specg.) Pic.[1]
Isaria farinosa (Dicks.) Fr.[1]
Spicaria sp.[1]

Invertebrate Predators
Arachnida
Balaustrum sp.[2]
Neoscona arabesca (Walckenaer)[2]
Insecta
Apateticus bracteatus Fitch[1]
Ctenicera sp.[1]
Deraeocoris laricicola Knight[1]
Euschistus sp.[1]
Formica whymperi adamsi Wheeler[1]
Ludius lutescens Fall.[1]
Phytocoris neglectus Knight3

Table 14. continued

Ludius lutescens Fall.[1]
Phytocoris neglectus Knight[1]
Plaziognathus repeticus Knight[1]
Podisus modestus Dall.[1]
Podisus spp.[1]
Tetraphelps sp.[1]
Vespula sp.[1]

Invertebrate Parasitoids
Diptera
Argyrophylax bimaculata Hartig[1]
Bessa harveyi (Townsend)[1]
Exorista spp.[1]
Muscina stabulans (Fall.)[1]
Neophoracera hamata (A. and W.)[1]
Spathimeigenia aurifrons Curran[1]
Zenilla pexops B. and B.[1]
Hymenoptera
Agrothereutes sp. nr. similaris (Provancher)[1]
Aptesis indistincta (Provancher)[1]
Aptesis nigrocinctor Förster[1]
Aptesis sp. nr. *basizonia* (Gravenhorst)[1]
Aptesis sp.[1]
Coelichneumon fuscipes Gravenhorst[1]
Cratichneumon annulator F.[1]
Cryptus minator Gravenhorst[1]
Ctenochira sp.[1]
Dahlbominus fuscipennis (Zett.)[1]
Dusona sp.[1]
Eclytus ornatus Holmg.[1]
Endasys pubescens (Provancher)[1]
Endasys sp.[1]
Endasys subclavatus (Say)[1]
Euceros frigidus Cresson[1]
Euceros sp.[1]
Euceros thoracicus Cresson[1]
Hyalurgus licidus (Meig.)[3]
Hypamblys albopictus (Gravenhorst)[3]
Ichneutes bicolor Cresson[1]
Macrocentrus uniformis Provancher[1]
Mastrus spp.[1]
Mesoleius sp.[1]
Mesoleius tenthredinis Morley[1]
Microcryptus labralis Gravenhorst[1]
Myxexoristops stolidus (Stein)[3]
Olesicampe benefactor Hinz[4]
Perilampus sp.[1]
Phygadeuon sp.[1]
Smicroplectrus velox Wall.[1]
Spilocryptus incubitor Strom[1]
Tritneptis klugii (Ratzeburg)[1]
Vibrissina turrita (Meig.)[3]

1Drooz 1960
[2]Turnock 1953
[3]Clausen 1978
[4]Drooz et al. 1985

Pest Status: The pest is univoltine, although some individuals remain in cocoons for more than 1 year. Reproduction is by parthenogenesis. Eggs (up to 100 per female) are laid in spring in new shoots. Young larvae feed along the edges of needles on new shoots, before moving back to feed on needle clusters on older twigs. Mature larvae drop to the forest floor, where they spin cocoons in the litter and overwinter as prepupal larvae.

This species was originally recognized in North America in Massachusetts in 1880, and then in Quebec in 1882. It was first reported in western North America in 1930 in British Columbia. Populations can reach defoliating levels and can kill trees. Outbreaks have occurred repeatedly in North America since this species' initial discovery here. Damage has been most severe in the Lake States, where populations have killed large amounts of *L. laricina.* On *L. occidentalis,* it has slowed tree growth by repeated defoliation but has not killed trees extensively, except in stands stressed from other factors (Furniss and Carolin 1977). The species attacks all types and ages of larch, thus the prospects for control through stand management or silvicultural practices appear limited.

Biological Control: This species has a lengthy history of biological control work in North America. Reviews of this work are presented by Clausen (1978) and Van Driesche et al. (1996). Importation of natural enemies was begun in 1910, and initially concentrated on the parasitoid *Mesoleius tenthredinis.* Cocoons were obtained from England from 1910-1913. Adult parasitoids from early shipments were reared, and adults of *M. tenthredinis* were released. Cocoons from later shipments were placed directly in the field. Early reports showed rapid increases in parasitism, from zero to 66% in the 7 years after release (Criddle 1928). This parasitoid was shipped from Quebec to British Columbia, after the pest's discovery there, during 1934-1942. These shipments resulted in ready establishment and rapid increase of parasitoid populations (McLeod 1954). The Holarctic tachinid parasitoid *Bessa harveyi* was introduced to British Columbia and became established, but not abundant (McLeod 1954). In later programs additional parasitoids were introduced, primarily into eastern North America. These included *Myxexoristops stolidus* and *Vibrissina turrita* from Japan, and *Hyalurgus lucidus, M. stolidus, Olesicampe benefactor, Hypamblys albopictus,* and *M. tenthredinis* from Europe (Clausen 1978).

Of the early natural enemies introduced, *M. tenthredinis* was the most effective parasitoid. By the late 1930's, however, parasitism by this species had dropped to nearly zero in several locations (e.g., Drooz 1960). Muldrew (1953, 1955) investigated this phenomenon and determined that larvae of *P. erichsonii* were encapsulating eggs or young larvae of the parasitoid. Multiple strains of the pest were recognized, some of which were susceptible to the parasitoid and could not encapsulate the eggs, and at least one strain which was "resistant" to the parasitoid via its ability to encapsulate eggs. The origin of this resistant strain may have been the wholesale release of cocoons earlier in the century, which may have included healthy cocoons of sawflies as well as parasitized cocoons. This development serves to emphasize the importance of the modern practice of processing all released material through a quarantine screening process, ensuring that only beneficial natural enemies are released into a new environment.

The presence of the resistant strain led to continued outbreaks of the pest in eastern North America; the resistant strain is apparently not present in the West. Populations of *M. tenthredinis* collected from central Europe were not subject to encapsulation by the "resistant" strain of the pest, and material from these collections was introduced into Canada and the United States (Kulman et al. 1974). Evidence of establishment of this strain of *M. tenthredinis* has not been reported (Thompson et al. 1977). The introduction of *O. benefactor,* however, appears to have been successful in reducing pest populations in areas where populations were persistently at outbreak levels (Ives 1976) (see also Figure 2, p. 3).

Recommendations: The natural enemies that have been most important in limiting infestations in North America have been *Mesoleius tenthredinis, Olesicampe benefactor,* and *Bessa harveyi.* Where infestations of this pest occur in the West without these natural enemies, they should be introduced (particularly *O. benefactor*) in sufficient numbers to establish. Pest populations should continue to be monitored regionally, and where populations arise or increase and the natural enemies are absent, they should be introduced into these populations.

The historical record indicates that damage to *L. occidentalis* will be limited, and the experience in eastern North America indicates that these natural enemies should provide substantial benefit in reducing pest population densities. The combination of the naturally limited damage on this host plant, together with the suppression of populations from the action of these natural enemies, should provide considerable protection to larch in western forests.

Lepidoptera

COLEOPHORIDAE

LARCH CASEBEARER, *Coleophora laricella* Hübner

Origin: Europe.

Range in North America: Throughout North America, coincident with the range of *Larix* spp.

Plant hosts and damage: *Larix laricina* in the East, and *Larix occidentalis* in the West.

Natural Enemies: Few natural enemies of this species were recorded in North America before parasitoids were imported from Europe (Table 15). Birds were noted as an important group of natural enemies of this pest in New Brunswick (Baird 1922).

Table 15. Natural enemies of *Coleophora laricella* introduced to the United States from Europe (after Clausen 1978)

INVERTEBRATE PARASITOIDS
Agathis pumila (Ratzeburg)
Chrysocharis laricinellae Ratzeburg
Diadegma laricinellae (Strobl.)
Diadegma nana (Gravenhorst)
Dicladocerus westwoodii Westwood

Pest Status: *Coleophora laricella* was, after its introduction to North America in 1886, a serious defoliating pest of larch. The species is univoltine, and eggs are laid in midsummer. First instar larvae mine needles and later emerge to feed on foliage more generally. The larvae overwinter in the case, complete feeding in spring, and pupate in the case attached to foliage or twigs.

This pest was initially limited to eastern forests, but invaded the range of western larch in 1957 and spread rapidly (Ryan et al. 1974). In both areas of North America, damage was largely limited to reduction in growth of host trees. Damage is also occasionally reported in Europe.

Biological Control: Natural enemies from Europe were sought and introduced into the eastern United States during the infestation that began in the 1930's (Thorpe 1933, Dowden 1934). Five species of parasitoid were released (Clausen 1978), and two of these proved significant: *Agathis pumila* and *Chrysocharis laricinellae.* Both established in the eastern United States and Canada in the 1930's and 1940's, but *Agathis pumila* spread more rapidly than *C. laricinellae*. *Coleophora laricella* was soon relegated to nonpest status throughout most of the region (Webb and Quednau 1971).

Following the discovery of *C. laricella* in western larch forests in 1957, the two natural enemies *A. pumila* and *C. laricinellae* were introduced from eastern North America. Eight additional parasitoids were also imported from Europe and Japan (Ryan 1980). *Agathis pumila* and *C. laricinellae* eventually proved to be effective in western forests, and larch casebearer larval densities declined from 52.6 to 0.8 cases per 100 buds (Ryan 1990). The species is no longer considered a pest in the West.

Recommendations: No further action appears necessary at this time. The biological control program appears to have proved successful.

GELECHIIDAE

LODGEPOLE NEEDLEMINER, *Coleotechnites milleri* (Busck)

Origin: Presumed North America.

Range in North America: California.

Plant hosts and damage: *Pinus contorta* var. *murrayana*. Larvae of all ages mine needles.

Natural Enemies: No vertebrate predators are reported from this species. A native granulosis virus is reported by Struble and Martignoni (1959), who also report that insect parasitoids were responsible for greater mortality than was the virus. Struble (1967) reports predation from a few groups of invertebrate generalist predators, and states that they were few, occurred only infrequently, and had minimal impact. Struble (1967) reports a diverse collection of insect parasitoids reared from larvae and pupae (Table 16).

Table 16. Parasitoids reared from *Coleotechnites milleri* (after Struble 1967)

PARASITOID SPECIES	
Parasitoids reared from larvae	**Parasitoids reared from pupae**
Apanteles californicus Muesebeck	*Aethecerus pinifolii* Mason
Copidosoma decepter Miller	*Dicladocerus* sp.
Copidosoma sp.	*Eriplatys* sp.
Decladocerus sp.	*Itoplectis behrensii* (Cresson)
Diglyphus sp.	*Scambus aplopappi* (Ashmead)
Hypoteromalus sp.	*Spilochalcis albifrons* (Walsh)
Sympiesis sp.	*Spilochalcis sanguiniventris* (Cresson)
Meterorus pinifolii Mason	*Spilochalcis side* (Walker)
Zagrammosoma multilineatum (Ashmead)	

Luck (1976) reports on the biology of a univoltine *Coleotechnites* species in *Pinus jeffreyi* in southern California. In addition to some of the parasitoids listed in Table 22, Luck (1976) reports *Haltichella rhyacioniae* Gahan as a parasitoid of this *Coleotechnites* species.

Pest Status: This species is a renowned forest pest because of its repeated and sustained outbreaks in Yosemite National Park during 1903-1921, 1933-1941, and 1947-1963. In these outbreaks, trees were killed over extensive areas through repeated defoliation. Feeding damage primarily results in slowed growth, resulting in lengthened rotation periods (Amman 1975). Outbreaks are most severe in mature lodgepole pine, the principal host. During epidemics, the species may also feed on other pines, red fir, and mountain hemlock.

The adults are active between mid-July and mid-August in odd numbered years. The species is semivoltine, requiring 2 years to complete a single generation. Eggs are laid in late summer, and upon hatching the first instar larvae mine individual needles near the growing tip, where they overwinter. The following season they develop to fourth instars, feeding in several needles. The subsequent spring they develop into fifth instar larvae, feed heavily, and then pupate in mined needles. Adults emerge 1 month later. A related univoltine species periodically defoliates lodgepole pine in central Oregon.

Biological Control: A large complex of natural enemies is known from this species (Struble 1967, Table 16). This collection was made during the decline of an outbreak in California. This diversity includes some groups known as generalist parasitoids of leafminers. These parasitoids together caused 28-46% parasitism in the 1963 generation (Struble 1967). Struble also recorded the presence of hyperparasitoids, and suggested that the effectiveness of the natural enemies was hindered by the hyperparasitoids.

Recommendations: This species poses some research questions before recommendations can be made. This species may not be native to Western North America (California in particular), although several facets of its biology indicate that it could be. It feeds primarily on a single host species that is native to the region, its distribution is limited to high-altitude stands of this host, and it has a diverse set of natural enemies. It is unusual for a native species to remain at outbreak levels for more than a few generations, as natural biotic factors tend to respond and limit infestations. For this semivoltine species, outbreaks of 5-10 generations span 10-20 years. This may be a natural cycle for this species. Such cycles are common in other lepidopteran forest defoliators. The factors driving such cycles are not well understood. They may be related to time lags in the relationship between the insect pest and disease processes (such as the virus disease known from this pest), or may be related to changes in host plant susceptibility related to tree age or other factors.

In the absence of specific knowledge about the relationship of parasitoids and the viral disease to the dynamics of this species, the best recommendation would be to study it in both endemic and epidemic phases, and to quantify differences in factors affecting its population dynamics. When these factors are identified, additional recommendations about the roles of natural enemies, either through augmentation or conservation, could be made.

GEOMETRIDAE

GREENSTRIPED FOREST LOOPER, *Melanolophia imitata* (Walker)

Origin: Presumed North America.

Range in North America: Pacific coast, from British Columbia (and probably adjoining Alaska) south to Los Angeles, California, and inland to eastern Oregon and western Nevada (Evans 1962).

Plant hosts and damage: The species is polyphagous. Evans (1962) reports principal host trees, in order of preference, to include *Pseudotsuga menziesii, Tsuga heterophylla, Thuja plicata, Abies amabilis, Picea sitchensis, Abies grandis, Picea engelmannii, Pinus monticola, Larix occidentalis.* Larvae feed on foliage of all ages, preferring 1-year-old foliage.

Natural Enemies: Vertebrate predation has not been reported, but predation of larvae by birds and of pupae (in the soil) by insectivorous mammals might be expected. Morris (1983) reports recovering *Entomophthora* sp., *Verticilium* sp., a nuclear polyhedrosis virus, *Bacillus* spp., and a microsporidian from larvae of this looper. Parasitoids of this species are reported by Evans (1962) (Table 17).

Table 17. Parasitoids reared from *Melanolophia imitata* (after Evans 1962)

PARASITOID SPECIES
Actia inturrupta Curran
Casinaria geometrae occidentalis Walley
Casinaria melanolophiae Walley
Compsilura concinnata Meigan
Dusome pilosa (Walley)
Euplectrus melipes Provancher
Eusisyropa virilis (Aldrich and Webber)
Glypta fumiferanae (Viereck)
Gravenhorstia alaskensis (Ashmead)
Horogenes eureka (Ashmead)
Ictericophyta tibialis Curran
Meteorus hyphantriae Riley
Meteorus versicolor (Wesmael)
Phobocampe sp.

Pest Status: *Melanolophia imitata* was not recognized as a significant forest pest until 1960-1961, when an epidemic of this species killed 2.4 million cubic feet of lumber on Vancouver Island. Two other outbreaks were recorded in the 1960's on the Pacific coastal islands. All three outbreaks subsided abruptly from natural causes (Furniss and Carolin 1977). When not at epidemic levels, this species is generally widespread and common in coastal forests, preferring humid areas.

Biological Control: No biological control program has been developed against this species. Shepherd (1994) placed this looper in his "fast-cycling" defoliator group — defoliators whose outbreaks are brief (1-4 years) and naturally limited in duration. The quantitative role of natural enemies has not been clearly defined in these outbreaks or in endemic populations. Evans (1962) reported parasitism to vary from 4% to 35%. Morris (1983) reported recovering five different pathogens from this species, but did not report infection rates.

Recommendations: Available information about the ecological causes of outbreaks and the roles of natural enemies in this species' population dynamics is insufficient to evaluate the possibility of improving biological control. It is apparently native, present commonly throughout much of its range, and has a diverse natural enemy fauna. Reasons leading to the outbreaks are not well understood. Outbreaks have been limited in duration, but destructive when they occurred. Initial research should focus on determining the quantitative roles of natural enemies in both endemic and epidemic populations, and defining the ecological reasons leading to outbreaks, before additional recommendations can be made.

SADDLEBACK LOOPER, *Ectropis crepuscularia* (Denis and Schiffermüller)

Origin: North America.

Range in North America: Throughout North America. In the West, it occurs along the Pacific coast from Oregon to Alaska.

Plant hosts and damage: In the West, *Tsuga heterophylla* is preferred, and other principal hosts include *Pseudotsuga menziesii*, *Thuja plicata*, *Abies* spp., and *Picea* spp. Larvae feed on foliage and at outbreak densities can cause significant damage.

Natural Enemies: No significant reports of natural enemy activity on this species were found. One report of a parasitic or phoretic mite, *Callidosoma droozi* Treat (Treat 1985), and one report of larval predation by the sphecid *Ammophila mediata* Cresson (O'Brien and O'Brien 1988) were located.

Pest Status: Before 1951 this species was considered economically inconsequential (Furniss and Carolin 1977). Outbreaks in 1951-1953 and 1960-1961 in British Columbia, and in 1969 in Alaska were significant, and warrant pest status for this species (Furniss and Carolin 1977).

Biological Control: No biological control program has been proposed for this species. Little is known about its natural enemies. No information on the quantitative population biology of the pest or on the impact of natural enemies was located.

Recommendations: This species is one for which little quantitative population biology is known, and no demographic information on its natural enemies was found. Its restricted pest status in the past may indicate that the outbreaks in the middle portion of the 20th century were a result of favorable conditions, and that natural enemies and host-plant relationships generally relegate this species to only moderate pest status. The abrupt termination of the outbreaks argues for the action of natural enemies, probably invertebrates or pathogens. Study of the species' population biology, with particular reference to natural enemies, would be the first priority for an evaluation of this species as a candidate for biological control actions.

SPEARMARKED BLACK MOTH, *Rheumaptera hastata* (L.)

Origin: This species is circumpolar in distribution (Holland 1903, Werner 1977). We treat it as native to North America.

Range in North America: McGuffin (1973) reports it to be widespread in North America from Alaska east to Labrador and Newfoundland, south to northern California, New Mexico, and North Carolina. Outbreaks are recorded from Alaska, British Columbia, and South Dakota (Furniss and Carolin 1977).

Plant hosts and damage: In Alaska the preferred host is *Betula papyrifera,* but the larvae also feed on *Alnus* spp., *Salix* spp. and *Rosa* spp. (Werner 1978). Larvae tie leaves into shelters and skeletonize them. Pupae overwinter in the soil.

Natural Enemies: Natural enemies of this species have been reported by Werner (1977) (Table 18). Werner (1977) also reports birds (*Junca hyemalis, Acanthis* sp., and *Parus* sp.) feeding on adults, *Sorex obscurus obscurus* feeding on pupae, and larvae of the carabid *Calosoma* sp. feeding on larvae.

Table 18. Natural enemies of *Rheumaptera hastata* (after Werner 1977)

NATURAL ENEMY SPECIES
Pathogens
Entomophthora sp.
Nosema sp.
Granulosis virus
Invertebrate Parasitoids
Aoplus ruficeps vagans (Provancher)
Coccygomimus aquilonius aquilonius (Cresson)
Coccygomimus pedalis (Cresson)
Cratichneumon sp.
Mesochorus sp.
Meteorus niveitarsis (Cresson)

Pest Status: Outbreaks on birch have been extensive, one covering nearly 3 million ha in central Alaska in 1957, and in the same area nearly 1.3 million ha were defoliated in 1974-1975. The impact of these outbreaks, accompanied by defoliation of the host trees, has not been reported. Additional outbreaks have occurred in South Dakota and in British Columbia (Furniss and Carolin 1977).

Biological Control: The decline of both of the outbreaks recorded in Alaska was rapid, and was attributed to the action of diseases and parasitoids. In 1975, parasitoids accounted for about 90% mortality in pupal populations, and pathogens contributed a 95% reduction in larval populations (Werner 1977).

Recommendations: We do not have sufficient information on the dynamics of this species to make any recommendations at this time. Birch trees in Alaska, in response to defoliation, have changes in leaf nutritional quality (to immature insects) for several years after defoliation (Bryant et al. 1993). Such time-delayed responses could induce long-term cycles in linked populations such as the birch-*R. hastata* system, and thus cyclical outbreaks could be a natural dynamical pattern for this system. Research into the conditions leading to outbreaks should be conducted. Particular attention should be given to the role of natural enemies and host plant-insect interactions in the population dynamics of this pest. With such information, recommendations regarding the appropriate steps for enhancing biological control of this species could be made.

BRUCE SPANWORM, *Operophtera bruceata* (Hulst)

Origin: North America.

Range in North America: Alaska, California, Colorado, Idaho, Minnesota, Oregon, Washington, Wisconsin, and throughout Canada (Troubridge and Fitzpatrick 1993).

Plant hosts and damage: *Populus tremuloides, Salix* spp., *Alnus* spp., *Acer* spp., *Betula* spp. (Brown 1962). Larvae feed on foliage. Extensive outbreaks can occur (Furniss and Carolin 1977), leading to defoliation of host trees.

Natural Enemies: Few studies of natural enemies of this species have been reported. Martineau and Monnier (1966) noted predation by birds during an outbreak population. Smirnoff (1964) and Ives and Cunningham (1980) reported infection by a nuclear polyhedrosis virus. Several invertebrate parasitoids known from this species (Table 19).

Table 19. Invertebrate parasitoids of *Operophtera bruceata*

PARASITOID SPECIES
Apanteles sp.[1]
Buathra dorsicarinata (Pratt)[2]
Campopletis sp.[1]
Coccigomimus hesperus Townes and Townes[2]
Cratichneumon sp.[2]
Eulophus sp.[1]
Horogenes oculus (Viereck)[1]
Triclistus creassus (Townes and Townes)[1]

[1]Brown 1962
[2]Humble 1985

Pest Status: The larvae of this univoltine species emerge from overwintering eggs in spring or early summer. First stage larvae spin silken threads and disperse on the wind (Brown 1962). Larvae feed on broadleaved trees, particularly *P. tremuloides* and *Salix* spp. in the West. The Bruce spanworm occasionally reaches outbreak densities, leading to defoliation of host trees. Outbreaks have occurred in Alberta, for example, in 1903, 1913, and 1957-1959, the last covering 15 million ha (Furniss and Carolin 1977). The outbreaks have been of short duration. Quantification of host production loss has not been reported.

Operophtera brumata (L.), a European species, has been unintentionally introduced into Canada, including British Columbia, and is also recorded from Washington (Troubridge and Fitzpatrick 1993). Adult males with characters intermediate between *O. brumata* and *O. bruceata* have been reported (Fitzpatrick et al. 1991) in British Columbia. Troubridge and Fitzpatrick (1993) suggest that hybridization between these species could occur between males of *O. bruceata* and females of *O. brumata,* but not vice versa.

Biological Control: No biological control program has been mounted against this species. It is attacked naturally by several parasitoids (Table 19) and by a nuclear polyhedrosis virus (Ives and Cunningham 1980). Termination of outbreaks of this moth in Quebec in 1964 were credited to the virus (Forbes et al. 1964, Ives and Cunningham 1980). Ives and Cunningham (1980) also reported the mass rearing of the virus in 5,000 larvae of this moth, and the application of the resulting virus polyhedra onto *P. tremuloides.* The treated trees were subject to less defoliation than untreated trees. Larval mortality in the treated trees ranged from 80%-100% higher than in control plots.

Recommendations: This species is native, and its infrequent outbreaks suggest the presence of effective natural enemies. The reasons for the outbreaks have not been reported. They are short-lived and self-limiting, perhaps because of epizootics of a native virus. Mass production of the virus could be considered, but might be costly if *O. bruceata* was used as the rearing host. Ives and Cunningham (1980) suggested seeking an alternate, larger facultative host for rearing the virus. Alternatively, commercially available viruses might be tested against this species. The impact of natural enemies introduced against *O. brumata* on this species is unknown. Unless the species becomes a more frequent pest, opportunities to determine whether biological control can play an enhanced role appear limited.

WESTERN HEMLOCK LOOPER, *Lambdina fiscellaria lugubrosa* (Hulst)

Origin: North America.

Range in North America: Alaska, British Columbia, Idaho, Montana, Oregon, Washington.

Plant hosts and damage: Primarily *Tsuga heterophylla,* but also *Picea sitchensis, Abies amabilis, Pseudotsuga menziesii.* Larvae feed indiscriminately on needles, causing needle death and tree defoliation. Repeated attacks can lead to tree death.

Natural Enemies: Natural enemies of this species include nine species of birds (Hopping 1934), together with pathogens and invertebrate parasitoids (Table 20).

Table 20. Natural enemies reported from *Lambdina fiscellaria lugubrosa*

NATURAL ENEMY SPECIES	REFERENCE
Pathogens	
Erynia rhizospora	Hopping 1934
Nuclear polyhedrosis virus	Sager 1957
Invertebrate Parasitoids	
Aoplus velox occidentalis (Harrington)	Torgersen 1971
Apechthis ontario (Cresson)	Hopping 1934
Chaetophlepsis nasellensis Reinhard	Medley and Carolin 1977
Cratichneumon ashmeadi (Schulz)	Torgersen 1971
Itoplectis quadricingulatus (Provancher)	Torgersen 1971
Mastrus laplantei Mason	Torgersen 1971
Pimpla aquilonia Cresson	Torgersen 1971
Pimpla hesperus (Townes)	Torgersen 1971
Pimpla pedalis Cresson	Torgersen 1971
Telonomus sp.	Hopping 1934
Winthemia occidentis (Hopping)	Hopping 1934

Pest Status: *Lambdina fiscellaria fiscellaria* and *L. f. lugubrosa* attack primarily hemlock in the eastern and western portions of North America, respectively. Both species' population dynamics are characterized by alternating endemic and epidemic densities.

Recorded outbreaks of the *L. f. lugubros*a have occurred in Oregon, Washington, and British Columbia, and generally have been limited to 2-3 years duration (Furniss and Carolin 1977). Outbreaks have been localized, generally covering several thousand hectares. Losses have been substantial in some outbreaks, estimated at 500 million board feet of timber in 1918-1921, 200 million board feet in 1929-1932, and 500 million board feet in 1944-1946. Losses to later outbreaks were minimized by prompt treatment with insecticides and intensive salvage harvesting (Furniss and Carolin 1977).

The causes of population outbreaks have not been determined. The cause of the collapse of at least one of the outbreaks was a viral epizootic (Sager 1957). Cyclical population dynamics of this type are typical of many forest defoliators, and have been theoretically related to the presence of diseases, overcompensatory density dependence, and the action of invertebrate natural enemies.

Biological Control: The natural enemies of *L. f. lugubrosa* have been reported by Hopping (1934), Sager (1957), and Torgersen (1971), and partially reviewed by Mills and Räther (1990). A large number of invertebrate parasitoids are known from this insect, and it is also subject to bird predation. Larval parasitism is dominated by *Winthemia occidentis* (Hopping 1934), and pupal parasitism by *Aoplex velox occidentalis* (Torgersen 1971). The nuclear polyhedrosis virus (Sager 1957) is the most virulent pathogen known from this insect, and was responsible (at least in part) for the collapse of the 1946-1947 epidemic. Steinhaus (1945) also reported a disease of this species, but did not describe the causative agent.

Recommendations: Potential recommendations for biological control of forest defoliators can span an array of options, and in the case of this species several options are available.

One option is to presume that the natural enemy fauna needs no amendments, and that it is fairly efficient in its present structure. The short duration of the outbreaks and their abrupt conclusions suggest that natural enemies may be responding successfully in one or perhaps two generations (leading to 2- or 3-year outbreaks). Additional natural enemies might not be expected to respond with any greater efficiency or rapidity. Whether additional natural enemies could prevent endemic populations from reaching epidemic levels is unknown.

Another option is to consider introducing natural enemies of other species of lepidopterans, possibly from Europe (Mills and Räther 1990). Part of the impetus behind this idea is the reported successful control of a South American lepidopteran in its native habitat following the introduction of a North American egg parasitoid (Drooz et al. 1977). Several candidate natural enemies have been identified from European fauna by Mills and Räther (1990), but current knowledge of the ecology and host relationships is insufficient to permit selection of suitable candidates. Additional information, from both laboratory assessments concerning physiological and behavioral relationships between candidate natural enemies and their putative new host, and from additional field research, would be required to fully appraise the potential for new natural enemy introductions. Additional candidates might also be sought in Asia, or even South America. The impact of additional natural enemies could only be fully measured by conducting introductions and following them with quantitative field studies in both endemic and epidemic populations. The amount of investment and research could be large in this approach, and the potential return is unknown.

Other options include augmenting existing natural enemy populations, perhaps the nuclear polyhedrosis virus, 1 year earlier than would naturally occur, to shorten outbreaks to a single year (Shepherd 1994). The economic suitability of such an option would depend on the cost of such augmentation, versus the possible cost of timber loss after a second year of attack by this species.

LASIOCAMPIDAE

FOREST TENT CATERPILLAR, *Malacosoma disstria* Hübner

Origin: North America.

Range in North America: Throughout North America, including Canada but not Alaska.

Plant hosts and damage: The preferred host is *Populus tremuloides,* but larvae also feed on other species of *Populus, Salix, Alnus, Betula, Prunus,* and other deciduous trees. In outbreaks characterized by repeated defoliation for several years, tree death can occur, but reduced growth and branch killing are the usual extent of damage (Furniss and Carolin 1977).

Natural Enemies: Natural enemies for this widespread species have been studied by many authors, usually during outbreak populations. The parasitoid complex is diverse over the range of this species. Two studies addressing its natural enemies in the West represent the diversity of its natural enemies (Table 21). In addition to these invertebrates, birds have been recorded in several studies feeding on *M. disstria* larvae. Pathogens recovered from *M. disstria* include nuclear polyhedrosis viruses, entomopathogenic fungi, and bacteria.

Table 21. Predators and parasitoids from selected studies on *Malacosoma disstria*

NATURAL ENEMY SPECIES
Invertebrate Predators
Hemiptera
Podisus placidus Uhler[1]
Zelus exsanguis (Stal)[1]
Invertebrate Parasitoids
Hymenoptera
Ableris clisiocampae (Ashmead)[1]
Agathus annulipes (Cresson)[2]
Bracon xanthonotus Ashmead[1]
Campopletis sp.[2]
Coccygomimus pedalis (Cresson)[1]
Coccygomimus sanguinipes erythropus (Viereck)[1]
Cotesia atalantae (Pack.)[1]
Gambrus canadensis canadensis (Provancher)[2]
Hyposoter annulipes (Cresson)[2]
Hyposoter fugivitus fugivitus (Say)[2]
Iseropus stercorator orgyiae (Ashmead)[2]
Itoplectis conquisitor (Say)[1,2]
Itoplectis vidulata (Gravenhorst)[1]
Macrocentrus iridescens French[1]
Macrocentrus sp.[2]
Meteorus sp.[2]
Ooencyrtus clisiocampae (Ashmead)[1, 2]
Phobocampae clisiocampae (Weed)[2]
Pimpla pedalis Cresson[2]
Rogas sp.[2]
Scambus hispae (Harris)[2]
Scambus nigrifrons (Viereck)2
Sympiesis sp.[2]
Syntomoshipyrum esurus (Riley)[2]
Telenomus clisiocampae Riley[1, 2]
Telenomus sp.[1]
Tetrastichus silvaticus Gahan[2]
Tetrastichus sp.[1]
Theronia atalantae fulvescens (Cresson)[1, 2]
Trichonotous analis (Say)[2]
Diptera
Archytas lateralis (Macquart)[1]
Euclytia flava (Townsend)[2]
Euexorista futilis (Osten Sacken)[2]
Exorista mella (Walker)[1, 2]
Leschenaultia exul (Townsend)[2]
Lespesia archippivora (Riley)[1]
Lespesia flavifrons Bens.[1]
Lespesia frenchii (Williston)[2]
Patelloa pachypyga (Aldrich and Whebber)[2]
Sarcophaga aldrichi Parker[2]
Spoggossia sp.[1]

[1]Knight et al. 1991
[2]Witter and Kulman 1979

Pest Status: *Malacosoma disstria* is the most widely distributed and destructive tent caterpillar in North America (Furniss and Carolin 1977). Its dynamics are characterized by aperiodic increases in population densities to outbreak levels. Populations remain at outbreak levels for 3-6 years, and then decline rapidly. The species remains at endemic levels for 6-16 years (Witter et al. 1972) between outbreaks. This type of dynamic behavior appears typical of this genus, and is demonstrated by the five other North American species of tent caterpillar and also by Palearctic species of this genus. Outbreaks in the West typically last 2-3 years and cover up to 60,000 ha (Furniss and Carolin 1977), although in western Canada some outbreaks have persisted up to 6 years and defoliation occurred over 22 million ha (Furniss and Carolin 1977). Repeated defoliation can cause up to 90% reduction in annual growth in *P. tremuloides* (Batzer and Waters 1956).

A number of authors have evaluated factors affecting the population dynamics of this species. Weather appears to play a dominant role in the overall survival of populations, and thus population increases or decreases (while at endemic levels) are at least in part due to variations in weather patterns. Oviposition occurs in late summer or autumn, and larvae develop inside the eggs at that time. Larvae overwinter inside the eggs. The impact of weather on survival is most significant to these overwintering larvae. The most favorable pattern is a cool autumn, followed by a cold winter and a warm spring (Martinat 1987). This combination maintains larvae inside the egg throughout the winter and permits successful establishment of the larvae at feeding sites in the spring. Warm winters followed by cold springs are detrimental to early larval survival. Ives (1973) correlated patterns in weather with population trends for this species in Canada and found that increases in population density were related to a single season with a cool winter and warm spring 2-4 years prior to the outbreak. Witter et al. (1972) suggested that unfavorable weather patterns lead to deaths of pharate larvae before hatch or to deaths of first instar larvae after hatch. Such unfavorable weather patterns are two of the three causes of population decline that they suggest are responsible for termination of population outbreaks.

Biological Control: No program of biological control has been mounted against this species. When abundant, the species is subject to attack by numerous natural enemies (e.g., Witter and Kulman 1979, Knight et al. 1991). These natural enemies probably play a significant role in limiting population dynamics to, on average, little or no population increase. Natural enemies, however, do not respond with sufficient rapidity to increasing populations to prevent outbreaks. This dynamic pattern would be expected for univoltine systems, where increases in reproduction or survival of the host would lead to population increases, which would be followed by increases in the natural enemy populations one or two generations (i.e., years) later. High density populations of this pest species are subject to high levels of parasitism and also to disease. Thus natural enemies probably play either a causal role in the collapse of outbreak populations or a role complementary to unfavorable weather patterns. In either case, the result is an outbreaks of short duration with a rapid decline.

Recommendations: Addition of natural enemy species from other tent caterpillars elsewhere in the world does not hold significant promise for reducing the occurrence of population outbreaks. The reasoning behind this assessment is twofold: *M. disstria* has a diverse natural enemy fauna, and its variable population dynamics appears to be typical of all tent caterpillars. Thus, the roles of natural enemies in the population dynamics of these different pest species is probably similar to the roles of the native natural enemies present in populations of *M. disstria* here. If the hypotheses of Ives (1973) and Witter et al. (1972) regarding the role of weather in population dynamics of this species are correct, then there may be little room for additional suppression of this species by natural enemies. This pest species is susceptible to nuclear polyhedrosis viral diseases and other viral diseases, and the use of such viruses as a biological insecticide could be highly selective, but the cost of production might be high. This pest is also susceptible to *Bacillus thuringiensis,* which could be used when necessary.

LYMANTRIIDAE

DOUGLAS-FIR TUSSOCK MOTH, *Orgyia pseudotsugata* (McDunnough)

Origin: North America.

Range in North America: Arizona, British Columbia, California, Idaho, Montana, New Mexico, Oregon, Utah, Washington.

Plant hosts and damage: *Pseudotsuga menziesii, Abies concolor, Abies grandis, Pinus ponderosa.* Larvae feed on needles (both new and old foliage). Defoliation can occur, and during outbreaks this species can cause extensive tree death.

Natural Enemies: Natural enemies known from this species in North America include vertebrate predators, pathogens, and invertebrate predators and parasitoids (Table 22).

Table 22. Natural enemies reported from *Orgyia pseudotsugae*

NATURAL ENEMY SPECIES	REFERENCE
Vertebrate Predators	
Junco hyemalis (L.)	Torgersen et al. 1983, Torgersen and Mason 1987
Parus gambeli Ridgeway	Torgersen et al. 1983
Sitta canadensis L.	Torgersen et al. 1983, Torgersen and Mason 1987
Vermivora ruficapilla (Wilson)	Torgersen and Mason 1987
Pathogens	
Multicapsid baculovirus	Stelzer et al. 1977
Nuclear polyhedrosis virus	Morris 1963
Nuclear polyhedrosis virus of *Autographa californica* (Speyer)	Martignoni et al. 1982
Invertebrate Predators	
Araneae	
Anyphaena pacifica (Banks)	Mason and Torgersen 1983, Swezey et al. 1991 (laboratory study)
Apollophanes margareta Lowrie and Gertsch	Mason and Torgersen 1983, Swezey et al. 1991 (laboratory study)
Araneus spp.	Swezey et al. 1991 (laboratory study)
Araniella displicata (Hentz)	Swezey et al. 1991 (laboratory study)
Clubiona sp.	Mason and Torgersen 1983
Dictyna chitina Chamberlin and Gertsch	Mason and Torgersen 1983
Euryopis formosa Banks	Mason and Torgersen 1983
Mallos pallidus Banks	Mason and Torgersen 1983
Metaphidippus aeneolus (Curtis)	Mason and Paul 1988
Metaphidippus harfordi (Peckham)	Swezey et al. 1991 (laboratory study)
Metaphidippus sp. nr. *insignis* (Banks)	Mason and Torgersen 1983

Table 22. continued

Metaphidippus sp. nr. *montanus* (Emerton)	Mason and Torgersen 1983
Misumenops lepidus (Thorell)	Swezey et al. 1991 (laboratory study)
Neoscona arabesca Walkenaer	Mason and Torgersen 1983
Nodocion voluntarius (Chamberlin)	Mason and Torgersen 1983
Novalena intermedia Chamberlin and Gertsch	Mason and Torgersen 1983
Philodromus spectabilis Keyserling	Swezey et al. 1991 (laboratory study)
Philodromus oneida Levi	Mason and Torgersen 1983
Philodromus quercicola Schick	Mason and Torgersen 1983
Philodromus rufus Walckenaer	Mason and Torgersen 1983, Swezey et al. 1991 (laboratory study)
Philodromus speciosus Gertsch	Swezey et al. 1991 (laboratory study)
Pityohyphantes costatus (Hentz)	Mason and Torgersen 1983
Pityohyphantes sp.	Swezey et al. 1991 (laboratory study)
Poecilochroa sp.	Mason and Torgersen 1983
Prolinyphia sp.	Swezey et al. 1991 (laboratory study)
Steatoda hespera Chamberlin and Ivie	Mason and Torgersen 1983
Tetragnatha versicolor Walckenaer	Mason and Torgersen 1983
Theridion lawrencei Gertsch and Archer	Mason and Torgersen 1983
Theridion murarium Emerton	Mason and Torgersen 1983
Theridion neomexicanum (Banks)	Mason and Torgersen 1983, Swezey et al. 1991 (laboratory study)
Xysticus locuples Keyserling	Mason and Torgersen 1983, Swezey et al. 1991 (laboratory study)
Insecta	
Agula occidentis Carpenter	Mason and Torgersen 1983
Agulla unicolor Carpenter	Mason and Torgersen 1983
Anatis rathvoni LeConte	Dahlsten et al. 1977, Mason and Torgersen 1983
Camponotus herculeanus (L.)	Mason and Torgersen 1983
Camponotus laevigatus (F. Smith)	Mason and Torgersen 1983
Camponotus sp. nr. *modoc* Wheeler	Torgersen et al. 1983
Camponotus vicinus Mayr	Mason and Torgersen 1983
Formica accreta Francoeur	Mason and Torgersen 1983
Formica neorufibarbis Emery	Mason and Torgersen 1983
Formica subnuda Emery	Mason and Torgersen 1983
Lasius pallitarsis (Provancher)	Mason and Torgersen 1983
Neomysia subvittata (Mulsant)	Dahlsten et al. 1977, Mason and Torgersen 1983
Podisus serieventris Uhler	Dahlsten et al. 1977
Tapinoma sessile (Say)	Mason and Torgersen 1983
Invertebrate Parasitoids	
Insecta	
Agria housei Shewell	Mason 1976
Apanteles sp.	Dahlsten et al. 1977, Mason et al. 1983, Mason and Torgersen 1987
Brachymeria ovata ovata (Provancher)	Mason et al. 1983, Mason and Torgersen 1987
Bracon xanthonotus Ashmead	Dahlsten et al. 1977, Mason et al. 1983,

Table 22. continued

Carcelia yalensis Sellers	Dahlsten et al. 1977, Mason et al. 1983, Mason and Torgersen 1987
Coccygomimus sanguinipes erythropus (Viereck)	Dahlsten et al. 1977
Elachertus cidariae Ashmead	Mason et al. 1983
Ephialtes componotus (Davis)	Dahlsten et al. 1977, Mason et al. 1983, Mason and Torgersen 1987
Exorista mella (Walker)	Mason et al. 1983
Gambrus canadensis burkei (Viereck)	Dahlsten et al. 1977
Hyposoter fugitivus (Say)	Dahlsten et al. 1977, Mason et al. 1983, Mason and Torgersen 1987
Hyposoter masoni Torgersen	Torgersen 1985, Mason and Torgersen 1987
Itoplectis quadricingulatus (Provancher)	Dahlsten et al. 1977, Mason and Torgersen 1987
Itoplectis viduata (Gravenhorst)	Dahlsten et al. 1977, Mason et al. 1983, Mason and Torgersen 1987
Meteorus tersus Muesebeck	Mason et al. 1983, Mason and Torgersen 1987
Phobocampe pallipes (Provancher)	Mason et al. 1983, Mason and Torgersen 1987
Telenomus californicus Ashmead	Dahlsten et al. 1977, Mason et al. 1983, Torgersen and Mason 1985, Mason and Torgersen 1987
Tetrastichus sp.	Dahlsten et al. 1977, Mason et al. 1983
Theronia atalantae fulvescens (Cresson)	Dahlsten et al. 1977, Mason et al. 1983
Trichogramma californica Nagarkatti and Nagaraja	Dahlsten et al. 1977
Trichogramma minutum Riley	Dahlsten et al. 1977

Pest Status: This species is a defoliator of major importance in interior Douglas-fir and true fir forests of western North America (Furniss and Carolin 1977). Outbreaks develop explosively and, after about 3 years, subside abruptly. When at endemic population levels, this insect is seldom seen. The first reported outbreak was in 1916 in British Columbia. Since then, eight additional outbreaks have occurred in the Pacific Northwest, and 17 outbreaks have been recorded elsewhere in the West (Pettinger 1985). Cumulative losses exceed 1.3 billion board feet of timber (Furniss and Carolin 1977). Extensive outbreaks create major problems in salvage, forest regeneration, and fire prevention.

Pettinger (1978) describes the cycle of a typical outbreak for this species in four phases. During Phase I the population increases rapidly to outbreak levels, and defoliation is light and spotty. During Phase II the population is at maximum density and activity, and damage is greatest. During Phase III, the decline phase, the population collapses rapidly. Decline typically occurs after feeding for that season is completed, and defoliation can occur during this phase. The postdecline phase, Phase IV, is when remnants of the population can still be found. Defoliation is seldom seen during this phase. The outbreak cycles typically last 3-4 years in forested areas, but may be extended and last several years in urban areas. In forests defoliation can lead to tree death, while in urban areas defoliation is less common.

The species has been widely studied, both at epidemic and endemic levels, in many parts of its range. At endemic levels, it suffers considerable attack by natural enemies, with predation and parasitism (of all preimaginal stages) dominating the life tables (Dahlsten et al. 1977, Mason et al. 1983). In endemic populations, natural mortality factors such as predation, parasitism, abiotic mortality, and early larval dispersal combine to suppress population growth to near unity, so that the population is replaced but does not grow substantially between generations. Natural enemies apparently play a significant, if not determinative, role in suppressing these populations.

At epidemic levels, population processes are clearly different during both the buildup and collapse phases than they are at endemic levels. Factors that influence population increase to epidemic levels are not clearly understood, but may be related to random events leading to higher than usual preimaginal survival, or possibly to abiotic events leading to aggregations of dispersing larvae in a particular area. The collapse of epidemic populations usually has been associated with an epizootic of a nuclear polyhedrosis virus (Dahlsten and Thomas 1969, Mason and Thompson 1971). After trees are defoliated, larvae may be stressed for food (Mason 1981). Egg masses laid by females in declining populations have fewer eggs than those from females in populations not stressed by abiotic factors or food resources (Dahlsten et al. 1977, Mason 1981).

Biological Control: Natural enemies for this species are common throughout its range. No program of biological control has been mounted against this species, although reliance on natural enemies forms the basis for much of the management of this species, particularly in endemic populations. Parasitism and predation were higher in thinned than in unthinned stands of *Abies concolor* in Oregon; hence, silvicultural practices may have impacts on the effectiveness of natural enemies (Wickman and Torgersen 1987).

Recommendations: Direct control treatments against this species were among the earliest attempted in forest ecosystems (Furniss and Carolin 1977) and have proven effective in reducing epidemics and tree losses. The use of biological control during epidemics appears limited, as epidemics develop and decline so rapidly that response time for augmentation (of, for example, an egg parasitoid) is limited. The use of the nuclear polyhedrosis virus products TM-Biocontrol and Virtus have been demonstrated in the field as a biological insecticide against this species (Morris 1963, Stelzer et al. 1977). The commercially available baculovirus of *Autographa californica* appears equally effective (Martignoni et al. 1982), and may provide a more readily available alternative for early treatment against increasing populations.

Additional natural enemies for this species could be sought elsewhere. In the existing system, natural enemies generally appear to control endemic populations successfully. Consequently, the potential role of new natural enemies in the system would be to prevent populations from increasing to outbreak numbers. Whether such natural enemies exist is a matter for conjecture at this point. A priority for research on this species should be quantitative investigations into why populations increase from endemic to epidemic proportions, and the role natural enemies play during that transition. Research into optimal stand conditions (such as plant density) for natural enemy effectiveness should also be pursued.

DOUGLAS-FIR CONE MOTH, *Barbara colfaxiana* (Kearfott)

Origin: North America.

Range in North America: British Columbia, California, Colorado, Idaho, Montana, Oregon, Washington.

Plant hosts and damage: *Pseudotsuga menziesii*, *Abies* spp. Larvae mine through the cone scales and seeds, seriously damaging the cones.

Natural Enemies: Hedlin (1960) reported rearing several primary parasitoids from *B. colfaxiana.* All were listed as "rare" except *Glypta evetriae* Cushman, which was noted as "very common." Nebeker (1977) noted several natural enemies, including an undiagnosed disease. A summary of the invertebrate natural enemies is given in Table 23.

Table 23. Invertebrate predators and parasitoids reported from *Barbara colfaxiana*

INVERTEBRATE NATURAL ENEMIES
Invertebrate Predators
Agulla sp.[1]
Enoclerus sp.[1]
Hemerobius sp.[1]
Lestodiplosis sp.[1]
Invertebrate Parasitoids
Apanteles sp.[2]
Bracon sp.[1]
Elachertus pini Gahan[1]
Elachertus sp.[2]
Glypta evetriae Cushman[2]
Itoplectis evetriae Viereck[1]
Perilampus fulvicornis Ashmead[1]
Platymesopus sp.[2]
Pseudoeribia sp.[2]
Tetrastichus barbarae Burks[1]
Tetrastichus strobilus Burks[2,3]
Trichogramma sp.[1]

[1]Nebeker 1977
[2]Hedlin 1960
[3]possibly a hyperparasitoid (Bringuel 1968)

Pest Status: *Barbara colfaxiana* larvae feed on the cone scales and seeds of Douglas-fir and true firs. It is most often reported as a pest of Douglas-fir. Clark et al. (1963) reported averages of 38% and 44% of cones infested in 1958 and 1959, with ranges of 8-88%. Seed losses vary among years, from slight to nearly 100% (Hedlin 1960). The species is univoltine, with some pupae remaining in diapause for 1-3 years (Furniss and Carolin 1977). The causes of population fluctuations among years are unknown.

Biological Control: Several natural enemies of this species have been reported. The ichneumonid *Glypta evetriae* Cushman is widely reported parasitizing this pest (Townes and Townes 1951, Keen 1958, Hedlin 1960). In one study, 55-90% of the pest larvae which survived to pupate were parasitized by this species (Hedlin 1960). Nebeker (1977) reports that earwigs (*Forficula auricularia* L.) may cause mortality in the egg and early larval stages. An undescribed species of *Pyemotes* mite has been reported feeding on eggs of this pest (Moser et al. 1986). One preliminary study evaluated the possibility of employing *Trichogramma minutum* against this pest (Hulme and Miller 1988). About 3 million eggs of *Sitotroga cerealella* (a common laboratory rearing host for *T. minutum*) parasitized by this natural enemy were released in 19 trees in Ontario. Of the eggs of *B. colfaxiana* sampled, 2-4% were parasitized by *T. minutum*. Thus, the potential for this augmentative approach appears limited.

Recommendations: Because this moth is native, the potential role of exotic natural enemies is more limited than for introduced pests. The variable amount of damage caused by populations of this moth from year to year (Hedlin 1964) makes the development of augmentation programs difficult, as the demand for natural enemies would vary from year to year. The opportunity to enhance control of this moth with predators and parasitoids may be limited. Investigations into the possible use of commercially available pathogens may be the most appropriate next step for consideration.

LODGEPOLE CONE MOTH, *Eucosma rescissoriana* Heinrich

Origin: North America.

Range in North America: Alberta, California, Idaho, Oregon, Washington.

Plant hosts and damage: Primarily *Pinus monticola* (Ollieu and Schenk 1966) but also *Pinus contorta* and other pines (Furniss and Carolin 1977).

Natural Enemies: Several insect parasitoids are known from this moth, and these records are summarized by Goyer and Schenk (1969, 1970) (Table 24).

Table 24. Parasitoids of *Eucosma rescissoriana* reported by Goyer and Schenk (1969, 1970).

INVERTEBRATE PARASITOIDS
Apanteles starki Mason
Bracon rhyacioniae (Meusebeck)
Camploplex sp.
Chelonus petrovae McComb
Coelichneumon brunneri (Rohwer)
Elachertus proteoteratis (Howard)
Eubadizion sp.
Habrocytus phycidis Ashmead
Pimplopterus sp.
Zacalochlora milleri Crawford

Pest Status: This species can be highly destructive to cones and seeds of *P. monticola.* Reports of losses vary from 15% to 90% of cones (Goyer and Schenk 1969).

Biological Control: No previous programs have been reported against this species.

Recommendations: Natural enemies appear to be operating in every location where this native species is reported. Goyer and Schenk (1969) report parasitism rates of up to 41% during a 3-year study. Opportunities for enhancing this natural control appear limited, and no general recommendations can be made at this time. The parasitic fauna of this species is diverse, and probably capable of exerting considerable pressure on the moth populations. If areas are found that lack elements of this fauna, specific introductions could be made to add natural enemies to those areas.

WESTERN PINE SHOOT BORER, *Eucosma sonomana* Kearfott

Origin: Presumed North America.

Range in North America: Arizona, British Columbia, California, Colorado, Michigan, Minnesota, Montana, Oregon, Wisconsin.

Plant hosts and damage: Primarily *Pinus ponderosa,* but also *Pinus contorta* and *Picea engelmannii.* Larvae of this moth bore down the center of terminal shoots, stunting growth.

Natural Enemies: Butcher and Hodson (1949) report 19 of 80 pupae yielding a species of Glypta parasitoid. This is the only record of a natural enemy for this species.

Pest Status: This pest is unusual in that the damage it causes is chronic, causing up to 25% loss of tree elongation growth per annum. Awareness of this pest has increased in the last two decades, perhaps in relation to the continued development of managed forests. A pheromone has been used to bait traps for sampling and to reduce population densities with some success (Sower and Mitchell 1994).

Biological Control: None has been attempted.

Recommendations: The paucity of natural enemies reported for this species, compared for example with the natural enemy diversity on *Eucosma rescissoriana,* prompts the question of its origin. Studies on its taxonomic position and geographic origin, together with studies on its natural enemies and on natural enemies of other related species elsewhere, would be an important first step in developing biological control for this species.

EUROPEAN PINE SHOOT MOTH, *Rhyacionia buoliana* (Denis and Schiffermüller)

Origin: Europe.

Range in North America: British Columbia, Oregon, Washington, eastern North America.

Plant hosts and damage: *Pinus* spp. in eastern North America are attacked. In the West, ornamental pines (mugo, Scots, Japanese red, lodgepole) are heavily attacked, and naturally growing lodgepole and ponderosa pines are susceptible to damage (Mathers and Olds 1940, Furniss and Carolin 1977). Young larvae mine the base of needles, and older larvae mine buds and then the bases of elongating shoots, deforming the growing shoots and the leader of the plant. Damage results in deformed trees and reduced growth. Damage in Europe is reported to be more severe in plantations (particularly in open, even-aged stands) than in natural forests.

Natural Enemies: This species is reported from North America, South America, Europe (where it is native), and Japan (CAB 1978). It has been studied in many locations. Several studies in each location list native and introduced natural enemies of this species. Table 25 lists some of the more commonly mentioned species in North America and elsewhere. In addition, Adlung (1962) mentions birds as predators of this species.

Table 25. Partial listing of natural enemies of *Rhyacionia buoliana*

NATURAL ENEMY SPECIES	REFERENCE
Pathogens	
Granulosis virus	Harris 1960
Paecilomyces farinosus (Dicks ex Fr.) Brown and Smith	Harris 1960
Neoaplectana sp. DD-136	Burke and Percy 1983
Invertebrate Predators	
Araneae	
Frontinella communis (Hentz)	Pointing 1966
Insecta	
Coccinella bipunctata (L.)	Butovitsch 1936
Dromius linearis (Ol.)	Adlung 1962
Invertebrate Parasitoids	
Insecta	
Actia nubibasis Stein*	Schindler 1960
Actia pilipennis Fall.	Tempel 1925
Alegina sp.	Watson and Arthur 1959
Apanteles epinotiae Viereck	Harman and Kulman 1962
Apanteles pastrana Blanchard	Blanchard 1960
Atrometrus clavipes (Davis)	Watson and Arthur 1959
Bracon brevicornis Wesm.	Filipescu et al. 1970
Bracon gelechiae Ashmead	Watson and Arthur 1959
Bradysia sp.	Harman and Kulman 1962
Calliephialtes nubilipennis (Viereck)	Watson and Arthur 1959
Campoplex borealis (Zett.)*	Thorpe 1930
Campoplex mutabilis (Holmb.)*	Clausen 1978
Campoplex ramidulus (Brisch)	Gulii 1963
Campoplex rufifemur (Thomson)*	Juillet 1959, Harris 1960, Schindler 1960
Campoplex submarginatus	Tsankov 1988
Campoplex sp.	Watson and Arthur 1959

Table 25. continued

Chremylus elaphus Hal.	DeSantis and DeSantis 1960
Coccygomimus fuscipes	Lanfranco and Cerda 1986
Copidosoma geniculatum Dalman*	Ruschka 1924, Marlatt 1933
Cremastus confluens Gravenhorst	Schindler 1960
Diapetimorpha venturii (Schrott.)	DeSantis and DeSantis 1960
Elachertus spp.	Watson and Arthur 1959
Ephialtes comstockii (Cresson)	Watson and Arthur 1959, Harman and Kulman 1962
Euderus subopacus (Gahan)	Watson and Arthur 1959
Eulimneria crassifemur Ths.	Smits van Burgst 1919
Eupelmella vesicularis (Retz.)	Watson and Arthur 1959
Eupelmus cyaniceps Ashmead	Harman and Kulman 1962
Eupelmus elgans Blanch.	DeSantis and DeSantis 1960
Eurytoma sp.	Watson and Arthur 1959
Exeristes roborator (F.)*	Maksimovic and Schindler 1969
Exeristes ruficollis (Gravenhorst)*	Juillet 1959
Gelis sp.	Watson and Arthur 1959
Gelis teneluus (Say)	DeSantis and DeSantis 1960
Glypta resinana Hartig	Smits van Burgst 1919
Habrocytus sp.	Watson and Arthur 1959
Habrocytus thyridopterigis Howard	Harman and Kulman 1962
Haltichella xanticles Walker	Swenk 1927
Horogenus sp.	Watson and Arthur 1959
Hyssopus thymus Girault	Watson and Arthur 1959, Harman and Kulman 1962
Idemum sp.	Watson and Arthur 1959
Itoplectus conquisitor (Say)	Watson and Arthur 1959, Harman and Kulman 1962
Itoplectus evetriae Viereck	Watson and Arthur 1959
Lissonota boulianae Hartig	Smits van Burgst 1919
Lissonota humerella Ths.	Smits van Burgst 1919
Lypha dubia (Fall.)*	Schröder 1969
Meteorus sp.	Harman and Kulman 1962
Monodontomerus minor (Ratzeburg)	Harman and Kulman 1962
Oedemopsis scabricula (Gravenhorst)	Loan and Doganlar 1980
Omorgus ensator Gravenhorst	Thorpe 1930
Omorgus mutabilis Holmg.	Thorpe 1930
Omorgus ramidulus Brischke	Smits van Burgst 1919
Orgilus obscurator (Nees)*	Smits van Burgst 1919, Watson and Arthur 1959, Harris 1960, Schindler 1960, Harman and Kulman 1962
Orgilus punctulator (Nees)	Filipescu et al. 1970
Parasierola nigrifemur (Ashmead)	de Escudero et al. 1979
Perilampus canadensis Crawford	Harman and Kulman 1962
Perilampus fulvicornis Ashmead	Harman and Kulman 1962
Perisierola nigrifemur (Ashmead)	Ogloblin 1960
Phaeogenes sp.	Watson and Arthur 1959
Pimpla aequalis Provancher	Watson and Arthur 1959
Pimpla alternans F.	Smits van Burgst 1919

Table 25. continued

Pimpla brevicornis Gravenhorst	Smits van Burgst 1919
Pimpla boulianae Hartig	Smits van Burgst 1919
Pimpla detrita Hübner	Tempel 1925
Pimpla examinator F.	Smits van Burgst 1919, Tempel 1925, Thorpe 1930
Pimpla inquisitor Sc.	Smits van Burgst 1919
Pimpla obesa Cushman	Mathers and Olds 1940
Pimpla ruficollis Granvenhorst	Smits van Burgst 1919
Pimpla sagax Hartig	Smits van Burgst 1919
Pimpla tomyris (Sel.)	DeSantis and DeSantis 1961
Pimpla turionellae (L.)*	Smits van Burgst 1919, Berry 1939, Watson and Arthur 1959
Pristomerus orbitalis (Hlmgr.)	Schindler 1960
Pristomerus sp.	Clausen 1978
Pristomerus vulnerator Panz.*	Smits van Burgst 1919
Pseudoperichaeta roseanae (Br. and Berg.)	Schindler 1960, Maksimovic and Schindler 1969
Scambus buolianae (Hartig)*	Leius 1967
Scambus hispae Harris	Watson and Arthur 1959
Scambus sagax (Hartig)*	Harris 1960
Scambus sp.	Watson and Arthur 1959
Scambus tecumseh Viereck	Harman and Kulman 1962
Sympiesis guttatipennis Girault	Harman and Kulman 1962
Temelucha arenosa (Szépl.)	Fitton and Gauld 1980
Temelucha interruptor (Gravenhorst)*	Watson and Arthur 1959, Harris 1960, Fitton and Gauld 1980
Temelucha minor (Cushman)	Watson and Arthur 1959
Temelucha sp.	Watson and Arthur 1959
Temelucha turionum (Hartig)*	Clausen 1978
Tetrastichus pseudoceticola Blanch.	DeSantis and DeSantis 1961
Tetrastichus turionum (Hg.)*	Watson and Arthur 1959, Juillet 1959
Trichogramma evanescens Westwood	Evans 1930, Tkachenko and Danilyuk 1974
Trichogramma minutum Riley	Kulman 1965

*Species has been introduced into North America

Pest Status: This is a much-studied species, and its pest status is reported widely in the literature. In many countries it attacks various species of pines in natural forests; pines used in reforestation, plantations, or silviculture; and pines used in ornamental settings. It is an enigma because it reaches pest status commonly in Europe, where it is presumed to be native and has a substantial natural enemy fauna. Zethner and Bejer-Petersen (1972) reported significant damage in Denmark in 1937, 1948, 1961, and 1967. Other countries in Europe recognize this species as a significant pest, from Sweden to Spain and east to Russia.

The species is univoltine. Eggs are laid in midsummer on twigs, buds and needles. The small larva mines the bases of needles and later bores into a bud. The partially grown larva overwinters either in the mined bud or under the resultant crust of dried pitch. The following spring, the larva mines another bud and the bases of elongating shoots. Pupation takes place in a mined shoot. This feeding results in deformation of the pine and is particularly damaging when the leader is killed. Even-aged, young stands are most susceptible. Older pines (20 years or more) are less susceptible, either because they are attacked less or because they have greater resistance to attack.

Biological Control: The species has been subject to a variety of biological control activities. The two most extensive were the introduction of natural enemies into Canada (1928-1958) and the United States (1931-1938), as discussed by Clausen (1978). Most of this work was targeted at reducing the pest status of this species in eastern Canada and the United States, where the moth was a concern. Some 15 species of natural enemies were introduced, and three established (Schröder 1974b, Clausen 1978).

Despite these establishments, there was little reduction in pest status of the moth (Turnbull and Chant 1961, Dowden 1962, Arthur and Juillet 1961). Arthur and Juillet (1961) suggested reasons for the failure of several natural enemy species to establish, including poor release conditions, lack of alternate hosts (which appear obligatory for some of the European parasitoids), absence of suitable food plants for the adult parasitoids (which live longer and have greater fecundity when permitted access to flowering plants, Syme 1975), and the presence of large areas of even-aged monoculture of *Pinus* spp. Each of these conditions could contribute either to restricting the activity of the natural enemies or to providing unlimited reproductive resources to the moth, and combinations of these conditions would contribute to pest status.

Where this species has been introduced, it is universally attacked by native parasitoids of other lepidopteran hosts (e.g., Coppel and Arthur 1954, DeSantis and DeSantis 1958, 1960, 1961). Some of these native parasitoids can be significant. In North America, a widespread native parasitoid attacking larvae of this moth is *Hyssopus thymus* (Syme 1971). Native parasitism in Europe is reportedly highly variable, ranging from 10% to 80% in different studies. Egg parasitism is variously reported, from insignificant to as high as 98% (Tkachenko and Danilyuk 1974).

Of the parasitoids introduced to North America, the braconid *Orgilus obscurator* (Nees) has become widely established. This is the most abundant of any parasitoid found in Europe. This univoltine parasitoid attacks a number of other lepidopteran species. Parasitism of *R. buoliana* (due almost entirely to *O. obscurator*) in Quebec increased from 9% to 66% after this parasitoid was released there (Beique 1960). This parasitism is in part responsible for the noneconomic status of the moth in that region (Clausen 1978). The ichneumonid *Temelucha interruptor* preferentially attacks host larvae that have been previously parasitized by *O. obscurator*. In this context, it is a cleptoparasitoid or a facultative hyperparasitoid. Other cleptoparasitoids and hyperparasitoids are known for this moth in Europe. Arthur (1961) reports that *Eurytoma pini* acts as a cleptoparasitoid.

Two natural enemies of this pest species have been introduced from North America to Europe: *H. thymus* and *Itoplectis conquisitor*. Their impact there is unknown, and they may not have established (Biermann 1973, Altenkirch 1976).

Recommendations: Of the many studies on *R. buoliana* and its natural enemies, most consist of reports of damage or lists of natural enemies and their relative abundance. There have been no quantitative long-term studies on the factors affecting its population dynamics, either in its native range or in North America. Thus, the roles that various natural enemies play and the interactions between the moth population and its pine hosts are not well understood. The moth is clearly a more significant problem in even-aged, young pine plantations than in a naturally maturing forest. This likely represents the response of the moth population to a concentration of optimal resources - the shoots and needles of young pines. In these cases, natural enemies may not be able to suppress the population below economic levels.

There are studies indicating that host plants are more susceptible on drier sites, and the level of moisture available to the plants and their overall general health may also play a role in pest status. Stressed plants may be better resources for reproduction than healthy plants because they may be less able to ward off attack by the moths. Across a forest ecosystem, the diversity of plant ages and health, together with the action of natural enemies, probably leads to limited damage. Silvicultural practices for uniform reforestation or the use of marginal sites for plantations may lead to more damage than is natural.

Hypotheses such as these could be best tested in a long-term study on the relationships between the moth, its plant hosts, and its natural enemies. Such a study could be set up in a factorial design as suggested by Van Driesche et al. (1996), with various factors such as the presence of flowering plants for adult parasitoid food, and the age and species composition of the plantation, as factors. Different pine species differ in their susceptibility, and the tree species chosen for such a study should be selected to span a range of susceptibilities. Host plant monocultures and diverse plantings may also differ in their susceptibility, and could be evaluated in such an study. Quantitative information gathered in these settings could then allow effective comparisons between the impacts of native natural enemy fauna in Europe and the United States, for example, or between eastern and western North American populations.

There are certainly many additional parasitoids and predators, in Europe and elsewhere, that could be imported into the United States against this pest. The failure of several species to establish earlier in the 20th century does not argue against further introductions, but rather indicates that some careful preparatory and follow-up studies would be appropriate for new introductions. Such studies might reveal the reasons behind establishment or failure to establish, and provide quantitative knowledge of the role natural enemies play in this pest's life history. This better understanding can then be the basis for effective management programs that take advantage of biological control integrated together with stand management and reforestation cultural practices.

On a historical note, this species is the impetus behind one of the early records recommending the augmentation of bats as natural enemies of insect pests. In response to possible infestation by *R. buoliana,* Jolyet (1918) proposed the breeding of bats and their encouragement and protection in or near pine woods, and describes the construction and placement of refuges for them.

NANTUCKET PINE TIP MOTH, *Rhyacionia frustrana* (Comstock)

Origin: Eastern North America.

Range in North America: Before this moth was unintentionally introduced to California in the 1970's, its range included principally the range of *Pinus* spp. in the eastern United States, from Texas and Missouri to Florida and north to Massachusetts.

Plant hosts and damage: In the West, this moth attacks 23 species of *Pinus* (Scriven and Luck 1980). In particular, it is a pest of *Pinus radiata* in Christmas tree plantations and in ornamental plantings

(Scriven and Luck 1978). The larvae feed on growing tips and shoots, deforming the trees and reducing their suitability for market (Scriven and Luck 1978). Van Driesche et al. (1996) review its status in the eastern United States.

Natural Enemies: The species has been widely studied, and numerous natural enemies are known (Table 26).

Table 26. Invertebrate predators and parasitoids of *Rhyacionia frustrana*

NATURAL ENEMY SPECIES	REFERENCE
Invertebrate Predators	
Araneae	
Allepeira conferta (Hentz)	Eikenbary and Fox 1968a, Bosworth et al. 1970
Argiope aurauntia (Lucas)	Eikenbary and Fox 1968a, Bosworth et al. 1970
Cyclosa conica (Pallas)	Bosworth et al. 1970
Frontinella communis (Hentz)	Eikenbary and Fox 1968a, Bosworth et al. 1970
Mangora gibberosa (Hentz)	Eikenbary and Fox 1968a, Bosworth et al. 1970
Metaphidippus galathea (Walckenaer)	Eikenbary and Fox 1968a
Misumenops asperatus (Hentz)	Eikenbary and Fox 1968a
Neoscona sp.	Bosworth et al. 1970
Peucetia viridans (Hentz)	Eikenbary and Fox 1968a
Insecta	
Apiomerus crassipes (F.)	Eikenbary and Fox 1968a
Chrysopa plorabunda (Fitch)	Eikenbary and Fox 1968a
Coccinella novemnotata Herbst	Eikenbary and Fox 1968a
Cryptothrips pini (Watson)	Eikenbary and Fox 1968a
Enoclerus sp.	Eikenbary and Fox 1968a
Formica integra Nylander	Eikenbary and Fox 1968a, Wilkinson et al. 1978
Formica schaufussi dolosa Wheeler	Eikenbary and Fox 1968a
Hyppodamia convergens Guérin-Méneville	Eikenbary and Fox 1968a
Phyllobaenus lecontei (Wolcott)	Eikenbary and Fox 1968a
Phyllobaenus singularis (Wolcott)	Eikenbary and Fox 1968a
Pogonomyrmex badius (Latreille)	Eikenbary and Fox 1968a
Sinea diadema (F.)	Eikenbary and Fox 1968a
Solenopsis saevissima richteri Forel	Wilson and Oliver 1970
Invertebrate Parasitoids (Insecta)	
Agathis acrobasidis (Cushman)	Eikenbary and Fox 1965, Kearby and Taylor 1975, Warren 1985
Agathis binominata Muesebeck	Lewis et al. 1970, Warren 1985
Agathis pini (Muesebeck)	Warren 1985
Agienaspis sp.	Freeman and Berisford 1979
Apanteles petrovae Walley	Eikenbary and Fox 1965, Mason 1974, Kearby and Taylor 1975, Warren 1985

Table 26. coninued

Atrometus clavipes (Davis)	Lewis et al. 1970
Bassus bicolor (Provancher)	Underhill 1943
Bassus pini Muesebeck	Muesebeck 1940
Brachymeria molesta Burks	Eikenbary and Fox 1965
Bracon cushmani (Muesebeck)	Warren 1985
Bracon gelechiae Ashmead	Eikenbary and Fox 1965, Lewis et al. 1970, Kearby and Taylor 1975, Freeman and Berisford 1979, Warren 1985
Bracon gemmaecola (Cushman)	Eikenbary and Fox 1965, Warren 1985
Bracon mellitor Say	Eikenbary and Fox 1965, Lewis et al. 1970, Freeman and Berisford 1979, Warren 1985
Calliephialtes comstockii (Cresson)	Cushman 1927a, Cushman 1927b, Underhill 1943
Calliephialtes grapholithae (Cresson)	Freeman and Berisford 1979
Campoplex frustranae Cushman	Cushman 1927a, Cushman 1927b, Underhill 1943, Eikenbary and Fox 1965, Eikenbarry and Fox 1968b, Lewis et al. 1970, Kearby and Taylor 1975, Freeman and Berisford 1979, Lashomb and Steinhauer 1982a, Lashomb and Steinhauer 1982b, Warren 1985
Catolaccus aeneoviridis Girault	Underhill 1943
Copidosoma geniculatum (Dalman)	Warren 1985
Cremastus epagoges Cushman	Cushman 1927a, Underhill 1943
Dibrachys sp.	Underhill 1943
Elachertus pini Gahan	Cushman 1927a, Gahan 1927, Warren 1985
Epiurus indagator (Cresson)	Cushman 1927a, Underhill 1943
Euderus argyresthiae (Crawford)	Eikenbary and Fox 1965, Warren 1985
Euderus subopacus (Gahan)	Warren 1985,
Eupelmus cyaniceps amicus Girault	Underhill 1943, Warren 1985
Eupelmus cyaniceps cyaniceps Ashmead	Cushman 1927a, Eikenbary and Fox 1965, Lewis et al. 1970, Kearby and Taylor 1975, Freeman and Berisford 1979, Warren 1985
Euplectrus sp. nr. *catocalae*	Freeman and Berisford 1979
Eurytoma extremitatis Bugbee	Lewis et al. 1970, Warren 1985
Eurytoma pini Bugbee	Eikenbary and Fox 1965, Lewis et al. 1970, Kearby and Taylor 1975, Lashomb and Steinhauer 1982a, Lashomb and Steinhauer 1982b, Warren 1985
Eurytoma tylodermatis Ashmead	Cushman 1927a, Underhill 1943
Exeristes comstockii (Cresson)	Eikenbary and Fox 1965, Lewis et al. 1970, Kearby and Taylor 1975, Freeman and Berisford 1979, Warren 1985
Glypta rhyacioniae Walley and Barron	Walley and Barron 1977
Glypta rufiscutellaris Cresson	Warren 1985
Glypta sp.	Lewis et al. 1970
Glypta varipes Cresson	Cushman 1927a, Warren 1985
Goniozus colombianus Ashmead	Warren 1985
Goniozus electus Fouts	Eikenbary and Fox 1965, Warren 1985

Table 26. continued

Goniozus longiceps Kieffer	Cushman 1927a, Warren 1985
Goniozus sp.	Lewis et al. 1970, Kearby and Taylor 1975, Freeman and Berisford 1979
Habrocytus phycidis Ashmead	Eikenbary and Fox 1965, Warren 1985
Habrocytus thyridopterigis Howard	Cushman 1927a, Eikenbary and Fox 1965, Lewis et al. 1970, Kearby and Taylor 1975, Warren 1985
Haltichella rhyacioniae Gahan	Cushman 1927a, Gahan 1927, Underhill 1943, Eikenbary and Fox 1965, Lewis et al. 1970, Kearby and Taylor 1975, Freeman and Berisford 1979, Warren 1985
Hockeria micra Halstead	Halstead 1990
Horismanus sp.	Freeman and Berisford 1979
Hyssopus rhyacioniae Gahan	Cushman 1927a, Gahan 1927, Underhill 1943, Eikenbary and Fox 1965, Freeman and Berisford 1979, Warren 1985
Hyssopus thymus Girault	Cushman 1927a, Eikenbary and Fox 1965, Lewis et al. 1970, Kearby and Taylor 1975, Warren 1985
Itoplectis conquisitor (Say)	Cushman 1927a, Underhill 1943, Eikenbary and Fox 1965, Lewis et al. 1970, Kearby and Taylor 1975, Warren 1985
Itoplectis evetriae Viereck	Freeman and Berisford 1979, Warren 1985
Lixophaga mediocris Aldrich	Cushman 1927a, Underhill 1943, Eikenbary and Fox 1965, Kearby and Taylor 1975, Freeman and Berisford 1979, Lashomb and Steinhauer 1982a, Lashomb and Steinhauer 1982b
Lixophaga plumbea Aldrich	Cushman 1927a, Underhill 1943
Macrocentrus ancylivorus Rohwer	Eikenbary and Fox 1965, Kearby and Taylor 1975, Freeman and Berisford 1979, Warren 1985
Macrocentrus instabilis Muesebeck	Eikenbary and Fox 1965, Warren 1985
Microbracon gelechiae (Ashmead)	Cushman 1927a, Underhill 1943
Microbracon gemmaecola Cushman	Cushman 1927a, Cushman 1927b, Underhill 1943
Microbracon mellitor (Say)	Cushman 1927a, Underhill 1943
Microgaster epagoges Gahan	Warren 1985
Neocatolaccus sp.	Freeman and Berisford 1979
Ooencyrtus sp.	Underhill 1943
Parania geniculata (Holmgreen)	Warren 1985
Paraolinx taedae Miller	Warren 1985
Pauesia gilletei (Gahan)	Eikenbary and Fox 1965
Pauesia sp.	Eikenbary and Fox 1965
Perilampus fulvicornis Ashmead	Underhill 1943, Eikenbary and Fox 1965, Lewis et al. 1970, Kearby and Taylor 1975, Freeman and Berisford 1979, Warren 1985
Phaeogenes walshiae Ashmead	Warren 1985

Table 26. continued

Phaneratoma rhyacioniae Cushman	Cushman 1927a, Cushman 1927b, Underhill 1943, Freeman and Berisford 1979, Warren 1985
Pristomerus austrinus Townes and Townes	Kearby and Taylor 1975, Warren 1985
Scambus hispae (Harris)	Lewis et al. 1970, Kearby and Taylor 1975, Freeman and Berisford 1979, Warren 1985
Scambus tecumseh Viereck	Lewis et al. 1970
Secodella subopaca (Gahan)	Cushman 1927a, Gahan 1927, Underhill 1943
Spilochalcis flavopicta (Cresson)	Eikenbary and Fox 1965, Freeman and Berisford 1979, Warren 1985
Spilochalcis leptis Burks	Eikenbary and Fox 1965, Warren 1985
Sympiesis stigmatipennis Girault	Warren 1985
Temelucha epagages (Cushman)	Eikenbary and Fox 1965, Kearby and Taylor 1975, Warren 1985
Temelucha minor (Cushman)	Lewis et al. 1970, Warren 1985
Tetrastichus cuneiformis Girault	Underhill 1943
Tetrastichus marylandensis (Girault)	Warren 1985
Tetrastichus varicornis (Girault)	Warren 1985
Trichogramma minutum Riley	Yates 1966, Warren 1985
Zethus spinipes Say	Lashomb and Steinhauer 1975

Pest Status: The early records of this species included the form now known as *Rhyacionia bushnelli* Miller (1967). Thus, the early literature, particularly near the plains or Rocky Mountain areas, may refer to *R. bushnelli*, or to mixed populations.

This species was introduced into California, which is its only record in the West. Infestations in *Pinus radiata* in Christmas tree plantations and in urban ornamental settings led to deformed growth. The species is multivoltine in southern California. Management has relied heavily on repeated insecticide treatments.

Biological Control: Scriven and Luck (1978) report on the biological control program against this moth in California. Two natural enemies, widely reported as dominant in natural enemy complexes in the native range of the pest in eastern North America, were introduced: *Campoplex frustrana* Cushman and *Lixophaga mediocris* Aldrich. *Campoplex frustrana* established, and increased parasitism from 10% (by local parasitoids) to 50%. This species established widely throughout infested urban areas, adjacent to commercial Christmas tree orchards. The proportion of infested tips declined (Scriven and Luck 1978), and infestations began later in the season. Insecticide use for management in commercial orchards declined by 25%.

Recommendations: Assessing the potential value of further introductions of natural enemies from the eastern United States is difficult. Even though there is a great diversity of natural enemies of this species known from the eastern United States, young pines are still subject to attack in that region and some damage occurs. Previous studies on this species have focused on surveys of natural enemies and their relative abundance, and not on factors that determine pest abundance, so the impact of natural enemies relative to other mortality factors is difficult to assess. Egg parasitism has been reported to be substantial in one study (Yates 1966).

Introduction of additional parasitoids could possibly lead to further population reductions in the West. However, the degree to which populations will decline in the presence of additional natural enemy species will only be clear following their introductions, and predictions cannot be made based on existing information. Good candidates for introduction might be one or both of the two *Lixophaga* species reported from this moth, both of which are dominant in many studies of parasitoid complexes, but neither of which is established in the West. When spraying for management is necessary, use of selective insecticides may be advantageous. Applications of either Bacillus thuringiensis or Metarhizium anisopliae provided some control in field trials (Menendez et al. 1986, Duarte et al. 1992).

WESTERN PINE TIP MOTH, *Rhyacionia bushnelli* (Busck)

Origin: North America.

Range in North America: Arizona, Kansas, Montana, Nebraska, New Mexico, North Dakota, South Dakota, Texas.

Plant hosts and damage: *Pinus ponderosa.* The species occurs naturally on young ponderosa pines in Montana, the Dakotas and Nebraska. It also occurs in New Mexico and Arizona, presumably by introduction (Furniss and Carolin 1977). The larvae mine growing tips, including leaders, resulting in deformed trees and reduced growth.

Natural Enemies: Before 1967, *R. bushnelli* was included in *R. frustrana,* and some records of natural enemies of *R. frustrana* may refer to this species. The primary natural enemies of *R. bushnelli* reported in the literature are insect parasitoids (Table 27).

Table 27. Invertebrate parasitoids of *Rhyacionia bushnelli*

INVERTEBRATE PARASITOIDS	
Apanteles bushnelli Muesebeck[1,2]	*Habrocytus* sp.[1]
Apanteles epinotiae Viereck[1]	*Haltichella rhyacioniae* (Gahan)[1]
Bracon gelechiae Ashmead[1]	*Itoplectis conquisitor* (Say)[1]
Bracon gemmaecola (Cushman)[1]	*Lixophaga mediocris* Aldrich[1]
Bracon mellitor Say[1]	*Lixophaga plumbea* Aldrich[1]
Bracon rhyacioniae (Muesebeck)[1]	*Macrocentrus ancylivorus* Rohwer[1]
Campoplex frustranae (Cushman)[1]	*Perilampus fulvicornis* Ashmead[1]
Catolaccus aeneoviridis (Girault)[1]	*Phaeogenes walshiae australis* (Cushman)[1]
Chelonus petrovae McComb[1]	*Scambus hispae* (Harris)[1]
Diadegma sp.[1]	*Spilochalcis albifrons* (Walsh.)[1]
Eurytoma pini Bugbee[1]	*Temelucha epagoges* (Cushman)[1]
Exeristes comstockii (Cresson)[1]	
Goniozus longinervis Fouts[3]	

[1]McKnight 1973
[2]Muesebeck 1933
[3]Fouts 1928

Pest Status: This species has been variously placed taxonomically, recognized as a species in the early part of the century (Busck 1914), then considered a type of *Rhyacionia frustrana,* and more recently placed as a species distinct from *R. frustrana* (Miller 1967). Introduced between 1902 and 1909 into plantations in the Nebraska National Forest, it seriously stunted and deformed *P. ponderosa* there. *Rhyacionia bushnelli* spread extensively in shelterbelt plantings of *P. ponderosa* in the Central Plains states. This species is univoltine in the Black Hills of South Dakota and bivoltine in Nebraska. The larvae feed on growing tips and on leaders, seriously deforming the pines. Damage has been a serious deterrent to planting *P. ponderosa* in some locations (Furniss and Carolin 1977).

Biological Control: There is a diverse natural enemy fauna known from this species and from the related *R. frustrana.* Some natural enemies may have occurred naturally in the range of *R. bushnelli* before the accidental introduction of this moth into Nebraska. A biological control project was mounted against this species shortly after its appearance in Nebraska. Collections were made of *R. frustrana* in Virginia in 1925 and in Massachusetts in 1926 to obtain parasitoids for release in Nebraska. Releases at Halsey, Nebraska comprised 369 *Campoplex frustranae,* 1,437 *Eurytoma pini,* 254 *Haltichella rhyacioniae,* and small numbers of other parasitoids. *Campoplex frustrana* established (Dowden 1962).

Following these introductions, *C. frustrana* soon attained a high percentage of parasitism and appeared to bring the pest under control. Parasitism reached 80% in a few years, infestations were greatly reduced, and planting of *P. ponderosa* resumed (Cushman 1932). Infestation of shoots declined from 90% to 15%; however, parasitism then declined and moth population densities rose (Baumhofer 1932). At the same time, populations of *Rhyacionia neomexicana* Dyar, a species not subject to attack by *C. frustrana,* increased rapidly (Graham 1956). Whether this increase was coincidental or constituted replacement of one moth species by the other is not known. The result, to forestry concerns, was that the pest situation remained unchanged, with infestation by *Rhyacionia* spp. again an economic problem. This situation was not permanent, and *R. bushnelli* again became the dominant *Rhyacionia* species (Clausen 1978).

Recommendations: This species attacks pine trees usually less than 3 m in height. The concentration of breeding resource represented by young trees in plantations may be responsible in part for the damage level reached by this species in the Great Plains region. Natural enemies will likely need to play a role in an integrated management program for this species, which might include early protection by insecticides, cultural management by planting various pine species in mixed stands, or selecting nonhost plants for new plantings. Possible beneficial effects of planting under a overstory have not been reported.

On the whole, natural enemies for this species appear widely distributed throughout its range. Where natural enemies are lacking (as might be the case in new plantings), they should be introduced as soon as infestations are discovered. Parasitized moth larvae and pupae should be reared, and only adult natural enemies should be released into affected plantations.

Additional research on the natural ecology of this species, and on its relationship to *R. neomexicana,* would provide information that would be helpful in developing a management program. Proper taxonomic diagnosis of infestations will be crucial in defining future strategies. If natural enemies appear lacking or ineffective in an area, research should be conducted to determine the species of moth is involved, what natural enemies are present, and what species or strains of natural enemies might be added to the system to reduce moth population densities.

SOUTHWESTERN PINE TIP MOTH, *Rhyacionia neomexicana* Dyar

Origin: North America.

Range in North America: Arizona, Colorado, Montana, Nebraska, New Mexico, North Dakota, South Dakota.

Plant hosts and damage: Primarily *Pinus ponderosa,* but also *Pinus sylvestris, Pinus banksiana, Pinus nigra.* Larvae mine the growing tips and buds, killing the tips and deforming the tree.

Natural Enemies: In addition to the natural enemies listed in Table 28, Jennings (1975) reports mites feeding on eggs. No pathogens were recovered during his study. No other studies identifying natural enemies of this species were found.

Table 28. Natural enemies of *Rhyacionia neomexicana* (after Jennings 1975)

NATURAL ENEMY
Vertebrate Predators
Loxia curvirostra L.
Oporonis tolmiei (Townsend)
Peromyscus maniculatus (Wagner)
Invertebrate Predators
Aranaea
Phidippus sp.
Theridion goodnightorum Levi
Insecta
Apiomerus crassipes (F.)
Athous sp. nr. *scapularis* (Say)
Camponotus laevigatus (F. Smith)
Formica fusca L.
Formica rasilis densiventris Viereck
Liometopum apiculatum Mayr
Liometopum occidentale luctuosum Wheeler
Melanotus sp.
Monomorium viridum peninsulatum Gregg.
Sinea diadema (F.)
Invertebrate Parasitoids
Insecta
Agathis sp.
Apanteles sp.
Blondelia sp.
Bracon gemmaecola (Cushman)
Bracon sp.
Bracon sp. nr. *hobomok* (Viereck)
Erynnia tortricis (Cresson)
Eubadizon sp.
Eurytoma pini Bugbee
Exeristes comstockii (Cresson)
Geron albarius Painter
Habrocytus phycidis Ashmead
Hyssopus novus (Girault)
Itoplectis sp.
Lissonata conocola Roh.
Lissonata sp.
Lordotus gibbus striatus Painter
Macrocentrus sp.
Madremyia saundersii (Williston)
Microplitis autographae Muesebeck
Nemorilla pyste (Walker)
Parania geniculata geniculata (Holm)
Psalidopteryx sp. nr. *grandis* Burks
Psalidopteryx sp. nr. *psilocorsiphaga* Burks
Scambus (Scambus) aplopappi (Ashmead)
Sinophorus sp.
Spilochalcis leptis Burks
Telenomus sp.
Trichogramma minutum Riley
Trichogramma semifumatum (Perkins)

Pest Status: The species is univoltine. Both naturally growing and planted trees are attacked. From 1966 to 1971, this insect infested 50,000 ha in Arizona. Seedlings on poor sites were most seriously damaged. Growth loss was not serious enough to justify the costs of direct controls (Furniss and Carolin 1977).

Continued attack results in accumulated growth loss (Long and Wagner 1992). Attack is concentrated on trees younger than 20 years or shorter than 4 m (Spiegel and Price 1996). Seedlings are also attacked (Jennings 1975). Repeated attacks lead to distorted trees and retarded growth.

Biological Control: No biological control program has been mounted against this species. A diverse fauna of natural enemies, including both vertebrate and invertebrate species, is known from this pest (Jennings 1975). Natural enemies are recorded from every life stage.

Recommendations: It is difficult to determine how natural enemies can be manipulated to enhance the biological control of this species. The principal cause for concern is reforestation of southwestern regions with *P. ponderosa*. *Rhyacionia neomexicana* appears to respond to the abundance of young trees, and intense attacks by these larger populations on growing shoots can lead to substantial damage. In natural conditions, annual variations in seed production and seedling establishment would lead to widely dispersed resources of varying ages, and probably more limited attack. Restructuring the planting of seedlings, on several-year rotations for a particular area, may lead to lower populations of the pest at a level at which they can be maintained by extant natural enemies.

PIERIDAE

PINE BUTTERFLY, *Neophasia menapia* (Felder and Felder)

Origin: Presumed North America.

Range in North America: British Columbia, California, Idaho, Montana, Oregon, Washington.

Plant hosts and damage: Principally *Pinus ponderosa*. During outbreaks, intermixed *Pseudotsuga menziesii*, *Pinus monticola*, *Pinus contorta*, and *Larix* spp. are also fed upon. Larvae feed on old and new needles, weakening or killing trees.

Natural Enemies: No vertebrate predators of this species are recorded, although the habit of the larvae of pupating near the ground would invite predation by insectivorous rodents. A nuclear polyhedrosis virus is reported by Hughes (1977). Morris (1983) reports recovering a nuclear polyhedrosis virus, microsporidia, and *Bacillus thuringiensis* from larvae, but did not give rates of infection. Few invertebrate natural enemies have been reported. These include the predators *Podisus placidus* Uhler (Evenden 1926) and *Mesuminops* sp. (Jennings and Toliver 1976), and the parasitoids *Theronia fulvescens* Cresson (Evenden 1926) and *Agria housei* Shewell (Shewell 1971).

Pest Status: This species is one of the most destructive pests of *P. ponderosa* in the northwestern United States. Outbreaks have been recorded since 1892 in British Columbia, Washington, Oregon, and Idaho. From 1893 to 1895 this species, augmented by bark beetles, killed nearly 1 billion board feet of timber on 75,000 ha infested in Washington. In 1953, 80,000 ha were heavily infested in Idaho;

aerial spraying the following year prevented heavy losses. The species is univoltine, with stages overlapping during the summer. Eggs overwinter on mature needles.

Biological Control: No biological control programs have targeted this species. Reports of outbreaks indicate that they are generally short-lived, typically lasting 2 years. Evenden (1926) attributes the collapse in the second year of a widespread outbreak in Idaho to the action of natural enemies, primarily parasitism by the ichneumonid *T. fulvescens,* with possible contributions by the predatory bug *P. placidus.* Parasitism in the second year was extensive, and butterfly larvae were rare in the area the following year. The common reports of the short duration of outbreaks indicate that this scenario may be duplicated elsewhere (Evenden 1926). Jennings and Toliver (1976) report a single incident of crab spider predation on a male adult butterfly on a flower of goldenrod, *Solidago rigida* L. The sarcophagid *Agria housei* is also reported from larvae of this butterfly (Shewell 1971), but no quantitative information on its impact is available.

Recommendations: There is insufficient information to make recommendations toward enhancing the action of natural enemies against this native species. Outbreaks appear to be limited naturally within one or two generations by the action of native parasitoids. Mortality of trees has been extensive after an outbreak of two successive years, presumably due to the cumulative effects of successive defoliation, but outbreaks usually collapse at that point The conditions leading to outbreaks have not been studied, nor have the roles of natural enemies in the population dynamics of this pest been quantified. When outbreaks are extensive, direct control during the first year of an outbreak has been successful in limiting damage (Cole 1961). Research into the causes of outbreaks might permit preemptive actions and help prevent future losses. Because action in the first year of an outbreak prevents losses, and because outbreaks appear to be limited naturally after approximately 2 years, such additional research may not be a high priority for western forestry concerns.

SATURNIIDAE

PANDORA MOTH, *Coloradia pandora* Blake

Origin: Presumed North America.

Range in North America: Arizona, California, Colorado, Oregon, Utah, Wyoming.

Plant hosts and damage: *Pinus contorta* var. *latifolia, Pinus jeffreyi, Pinus ponderosa.* This species is a foliage feeder, feeding directly on needles in all larval stages.

Natural Enemies: Little is known of the natural enemies of this species. Early work reported predation by vertebrates (but not birds), and a few parasitoids. Larvae in dense outbreak populations also exhibit infection of a wilt disease, possibly of viral origin (Patterson 1929, Wygant 1941). A summary of natural enemies known from this species is given in Table 29.

Table 29. Natural enemies of *Coloradia pandora.*

NATURAL ENEMY SPECIES	REFERENCE
Vertebrate Predators	
ground squirrels (*Callospermophilus* spp.)	Engelhardt (1924), Schmid and Bennett (1988)
Pathogens	
wilt disease, probably of viral origin	Engelhardt (1924), Patterson (1929), Wygant (1941), Schmid and Bennett (1988)
Parasitoids	
Apanteles sp.	Wygant (1941)
Blepharipeza adusta Loew.	Engelhardt (1924)
Cratichneumon unifasciatorius (Cresson)	Schmid and Bennett (1988)
Hemiteles tenellus Say	Engelhardt (1924)
Telonomus sp.	Schmid and Bennett (1988)
Tetrastichus sp.	Engelhardt (1924)
Trichogramma minutum Riley	Engelhardt (1924)

Pest Status: *Coloradia pandora* is an important defoliator of western forests (Furniss and Carolin 1977). Outbreaks have been recorded in the 20th century, the most widely studied in 1918-1925 when thousands of hectares of *P. ponderosa* were defoliated in Oregon (Engelhardt 1924, Patterson 1929). The species historically has occurred at epidemic levels at intervals of 20 to 30 years, with populations at high levels for 6 to 8 years (Patterson 1929). Outbreaks occurred in 1937-1940 in Colorado (Wygant 1941), in 1959-1966 in Oregon, California, Utah, Wyoming, and Colorado (Furniss and Carolin 1977), and in Arizona in 1978-1984 (Schmid and Bennett 1988). During periods of abundance feeding may be severe and defoliation may occur, with consequent loss to timber growth. Tree death occurred widely in the 1937-1940 outbreak. Weakened trees are susceptible to bark beetle infestation.

The species is primarily semivoltine, taking 2 years to complete its life cycle. Eggs are laid in late summer and hatch in August. Early larvae feed in groups on new foliage and overwinter in clusters at the base of needles. Larvae resume feeding the following spring. When mature, they crawl down trees and pupate in the soil. Typically, the pupal stage lasts for 1 year, and most of the population is biennial. Pupae can remain in diapause up to 5 years (Wygant 1941, Furniss and Carolin 1977).

Biological Control: No previous biological control program has been reported. Little is known about the natural enemies of this species. Engelhardt (1924) reported that approximately 50% of pupae had been killed by parasitoids and bacterial diseases in 1923 in the outbreak in Oregon. Schmidt and Bennett (1988) found a viral disease in the Arizona outbreak in 1979-1984. The incidence of this disease increased during the outbreak, and they hypothesize that the increasing prevalence of the disease was responsible for the decline of the outbreak. Schmidt and Bennett (1988) also reported an egg parasitoid (*Telonomus* sp.) attacking egg masses, with parasitism rates increasing during the outbreak. One unidentified tachinid fly was infrequently reared from late instar larvae, and the ichneumon *Cratichneumon unifasciatorius* (Cresson) emerged from pupae, causing less than 1% mortality (Schmidt and Bennett 1988). Kaibob squirrels consumed pupae (Schmidt and Bennett 1988).

Recommendations: Outbreaks of this species appear to be self-limiting but can lead to large losses of timber. The role of biological control in possibly preventing or in limiting outbreaks is unknown, and research is needed to better define the direction in which biological control should proceed. First, some attention should be given to defining the native range of this species and to determining the population ecology and role of natural enemies in that region. Further study of the population biology and natural enemies of the species when not at outbreak levels could be very valuable in defining the role of natural enemies in this system. The wilt disease may be a candidate for augmentation at the early phases of an outbreak, where augmenting the innoculum in the environment might induce widespread disease and prevent outbreak.

TORTRICIDAE

WESTERN BLACKHEADED BUDWORM, *Acleris gloverana* (Walsingham)

Origin: North America.

Range in North America: Alaska, California, Colorado, Idaho, Montana, Oregon, Utah, Washington, Wyoming, western Canada.

Plant hosts and damage: *Tsuga heterophylla, Tsuga mertensiana, Picea sitchensis, Picea engelmannii, Picea glauca, Abies* spp., and *Pseudotsuga menziesii.* Larvae defoliate these conifers. Trees of all ages may be killed, top killed, or severely weakened.

Natural Enemies: Smirnoff (1972) records a nucleopolyhedrosis virus from larvae and pupae. Birds may play some role as predators (McCambridge and Downing 1960). Torgersen (1970, 1973) and Gray and Shepherd (1993) report hymenopteran parasitoids from this species (Table 30), and also report substantial parasitism by dipteran larvae, but were unable to determine the species. Torgersen (1970) cites an unpublished report identifying 48 parasitoids reared from this pest in British Columbia. *Acleris gloverana* is susceptible to commercial *Bacillus thuringiensis* preparations (Morris 1962).

Table 30. Parasitoids recorded from *Acleris gloverana*

PARASITOID SPECIES	REFERENCE
Actia interrupta Curran	Torgersen 1970
Actia sp.	Torgersen 1970
Amblymerus verditer (Norton)	Torgersen 1970
Apanteles sp.	Torgersen 1970
Ascogaster provancheri Dalla Torre	Gray and Shepherd 1993
Ascogaster sp.	Torgersen 1970
Campoplex sp.	Gray and Shepherd 1993
Charman extensor (Linne)	Gray and Shepherd 1993
Chorinaeus californicus Ashmead	Torgersen 1973
Elachertus aeneoniger (Girault)	Torgersen 1969, Torgersen 1970
Erynnia tortricis (Coquillet)	Torgersen 1970
Exochus decoratus hebes Townes	Torgersen 1970
Gelis (=Alegina) apantelis Cushman	Torgersen 1973

Table 30. continued

Habrocytis sp.	Gray and Shepherd 1993
Itoplectis quadricingulatus (Provancher)	Torgersen 1970, Gray and Shepherd 1993
Mastrus laplantei Mason	Torgersen 1973
Mesocharis sylvarum (Curtis)	Gray and Shepherd 1993
Mesocharus pictilis (Holmg.)	Gray and Shepherd 1993
Mesopolobus sp.	Gray and Shepherd 1993
Meteorus argyrotaeniae Johansen	Torgersen 1970, Gray and Shepherd 1993
Microgaster peroneae Walley	Torgersen 1970, Gray and Shepherd 1993
Phaeogenes arcticus Cushman	Torgersen 1970, Gray and Shepherd 1993
Phaeogenes hariolus (Cresson)	Gray and Shepherd 1993
Scambus decorus Walley	Torgersen 1973
Trichogramma minutum Riley	Torgersen 1970
Triclistus pallipes Holmg.	Torgersen 1970

Pest Status: This species, originally described as *Lophoderus gloveranus* by Walsingham (1879), was for many years considered a western form of *Acleris variana* (Fernald). Early literature may be sought under this name. Powell (1962) redescribed both species, and they have since been considered separate.

This species occurs over much of the western portion of the continent (CAB 1989). The most serious outbreaks have been in the coastal regions. Extensive outbreaks occurred in British Columbia during the 1940's and 1950's, involving millions of hectares and causing considerable tree mortality (McCambridge and Downing 1960, Furniss and Carolin 1977). Minor population increases have occurred in interior forests, sometimes over wide areas, but have subsided without causing appreciable damage. Outbreaks are characterized by population increases for 2-3 years, then high population levels for 2-3 years, and then decline, which often is abrupt (Furniss and Carolin 1977). Direct control is sometimes needed to prevent serious economic damage.

Considerable research has been done relating phases of population increase or decrease to climate and weather patterns. Silver (1960, 1963) relates increases to drier-than-normal summers, and decreases to wetter-than-normal summers, in British Columbia. Hard (1974) analyzed population cycles in Alaska, and demonstrated convincing relationships between higher-than-average temperatures and population increases, and between lower-than-average temperatures and population declines. Colder summers and autumns were associated with slow larval and pupal development, delaying adult emergence in the autumn as much as 30 days or more, and probably resulting in poor population reproduction. The same mechanism may be reflected both by Silva's and by Hard's findings, as wetter summers may have generally lower temperatures, and vice versa. Biotic factors (such as natural enemies), which might be at low levels at the beginning of an outbreak, have opportunity to increase during an outbreak, and thus can contribute to the decline of an outbreak. Natural factors affecting populations at the end of outbreaks include starvation, but also increases in parasitism, and diseases (Graham 1954).

Biological Control: No biological control program has been mounted against this species. It appears to be in approximate equilibrium with its average abiotic environment, with natural enemies playing a normal role in mortality of populations. Variation among years in the abiotic environment leads to variation in pest population survival and reproductive success. Several favorable years in series can lead to population increases, and unfavorable years contribute to the catastrophic population declines typical of the end of an outbreak.

Recommendations: The factors leading to outbreaks of this species appear to be variation in abiotic parameters. In this context, natural enemies can respond to (and hasten the decline of), but probably not prevent, outbreaks. The addition of new natural enemies is unlikely to alter this fundamental feature of this pest's dynamics. Augmentation of natural enemies following years when reproductive success is higher than average could hasten the impact of natural enemies, but would be expensive to conduct. Use of the biological insecticide *Bacillus thuringiensis* provides a relatively selective treatment against this pest, with limited impact on its natural enemies.

In the natural forests of North America, the impact of *A. gloverana* is limited, and affected stands of conifers recover naturally (Hard 1974). The principal concern is outbreaks in managed forests, where protection against defoliation may be more important. The best available solution at this time is consistent monitoring of populations combined with intervention (such as spraying) to protect forest stands where the economic benefit of treatment can be justified. There appears to be limited scope for economically improving the role of natural control in preventing outbreaks.

LARGE ASPEN TORTRIX, *Choristoneura conflictana* (Walker)

Origin: North America.

Range in North America: Throughout the continent, usually associated with its principal host, *Populus tremuloides.*

Plant hosts and damage: *Abies grandis, Alnus rugosa, Betula papyrifera, Populus balsamifera, Populus tremuloides, Prunus virginiana, Pseudotsuga menziesii, Salix* spp. This insect species feeds on buds and foliage, and during outbreaks can defoliate its hosts. Second instar larvae overwinter. They feed on buds early in the following season, and can defoliate hosts before budbreak (Furniss and Carolin 1977). Older larvae roll leaves into shelters in which they feed and pupate.

Natural Enemies: *Choristoneura conflictana* has numerous natural enemies in North America, including birds, diseases, and invertebrate predators and parasitoids (Table 31).

Table 31. Natural enemies of *Choristoneura conflictana*

NATURAL ENEMY SPECIES	REFERENCE
Vertebrate Predators	
downy woodpecker	Prentice 1955
red-eyed vireo	Prentice 1955
Pathogens	
Granulosis virus	Burke and Percy 1982
Entomopox virus	Cunningham et al. 1973
Nosema thomsoni	Wilson and Burke 1971
Entomophthora sp.	Burke and Percy 1982
Invertebrate Predators	
Formica fusca L.	Prentice 1955

Table 31. continued

Formica sanguinea subnuda Emery	Prentice 1955
Invertebrate Parasitoids	
Actia interrupta Curran	Prentice 1955, Carolin and Coulter 1971
Actis diffidens Curran	Prentice 1955
Agathis annulipes (Cresson)	Prentice 1955, Torgersen and Beckwith 1974
Agria housei Shewell	Shewell 1971
Agrypon provancheri (Dalla Torre)	Torgersen and Beckwith 1974
Amblymerus sp.	Prentice 1955
Amblymerus verditer (Norton)	Torgersen and Beckwith 1974
Apanteles fumiferanae Viereck	Carolin and Coulter 1971
Apanteles polychrosidis Viereck	Torgersen and Beckwith 1974
Apanteles sp.	Prentice 1955, Carolin and Coulter 1971
Aplomya crassiseta (A. and W.)	Prentice 1955
Bracon politiventris (Cushman)	Carolin and Coulter 1971
Catolaccus aeneoviridis (Girault)	Prentice 1955
Ceromasia auricaudata Townsend	Carolin and Coulter 1971
Chaetophlepsis sp.	Prentice 1955
Coccygomimus pedalis (Cresson)	Torgersen and Beckwith 1974
Elachertus cacoeciae Howard	Carolin and Coulter 1971
Ephialtes ontario (Cresson)	Prentice 1955, Torgersen and Beckwith 1974
Ephialtes picticornis (Cresson)	Prentice 1955, Torgersen and Beckwith 1974
Euderus cushmani (Crawford)	Torgersen and Beckwith 1974
Eumea caesar (Aldrich)	Prentice 1955
Exochus sp.	Prentice 1955
Exochus washingtonensis (Davis)	Torgersen and Beckwith 1974
Glypta fumiferanae (Viereck)	Carolin and Coulter 1971
Glypta inversa Cresson	Torgersen and Beckwith 1974
Glypta sp. nr. *fumiferanae* (Viereck)	Wickman 1963
Gravenhorstia sp.	Prentice 1955
Habrocytus phycidis Ashmead	Prentice 1955, Torgersen and Beckwith 1974
Horogenes spp.	Prentice 1955, Carolin and Coulter 1971
Hyposoter annulipes (Cresson)	Torgersen and Beckwith 1974
Ischnus sp.	Prentice 1955
Ischnus sp. nr. *atricollaris*	Prentice 1955
Itoplectis conquisitor (Say)	Prentice 1955
Itoplectis quadricingulatus (Provancher)	Carolin and Coulter 1971, Torgersen and Beckwith 1974
Labrorhychus sp.	Carolin and Coulter 1971
Lypha fumipennis Brooks	Carolin and Coulter 1971
Lypha setifacies (West.)	Prentice 1955
Macrocentrus iridescens French	Prentice 1955
Macrocentrus sp. nr. *pyraustae*	Prentice 1955
Madremyia saundersii (Williston)	Prentice 1955, Carolin and Coulter 1971
Mesochorus sylvarum Curt.	Torgersen and Beckwith 1974
Meteorus dimidiatus (Cresson)	Torgersen and Beckwith 1974
Meteorus trachynotus Viereck	Carolin and Coulter 1971
Microgaster canadensis Muesbeck	Prentice 1955
Nemorilla sp.	Torgersen and Beckwith 1974

Omotoma fumiferanae Tothill	Prentice 1955, Carolin and Coulter 1971, Torgersen and Beckwith 1974
Phaeogenes cacoeciae Viereck	Prentice 1955, Torgersen and Beckwith 1974
Phaeogenes hariolus (Cresson)	Carolin and Coulter 1971, Torgersen and Beckwith 1974
Phorocera incrassata Smith	Carolin and Coulter 1971
Phryxe pecosensis Townsend	Prentice 1955
Phryxe vulgaris (Fall.)	Torgersen and Beckwith 1974
Phytodietus burgessi (Cresson)	Prentice 1955
Phytodietus fumiferanae Rohwer	Carolin and Coulter 1971
Phytodietus vulgaris Cresson	Prentice 1955, Torgersen and Beckwith 1974
Pseudosarcophaga affinis (Fall.)	Prentice 1955, Carolin and Coulter 1971
Psychophagus tortricis (Brues.)	Prentice 1955
Scambus canadensis Walley	Torgersen and Beckwith 1974
Scambus hispae Harris	Prentice 1955
Scambus sp. nr. *pterophori*	Prentice 1955
Sympiesis sp.	Prentice 1955
Tranosema interrupta pterophorae (Ashmead)	Torgersen and Beckwith 1974
Trichogramma minutum Riley	Torgersen and Beckwith 1974

Pest status: This species causes little or no discernible damage at low population levels. It is most commonly associated with *P. tremuloides,* but at outbreak levels will feed on other broadleaved trees. Outbreaks normally decline after 2 or 3 years. Outbreaks have been recorded in California (Wickman 1963) and Alaska (Beckwith 1968). Affected plants, even those defoliated for 1 or 2 years, normally recover with only growth loss (Furniss and Carolin 1977). Reasons leading to outbreak levels might include synchrony of bud break with appearance of overwintering larvae in some years, providing greater survival and hence greater population growth (Witter and Waisanen 1978). Starvation of larvae has been suggested as a possible cause of outbreak decline, although the role of natural enemies has not been determined.

Biological control: No program focused on improving biological control of this species has been reported. The abundant natural enemy fauna, particularly invertebrate parasitoids, indicate that there is a well-developed upper trophic level feeding on this species.

Recommendations: Outbreaks of this species are relatively short-lived, and the reasons for their appearance is not clear. Additional research could determine if these outbreaks are cyclical and intrinsic to the moth populations, or if outbreaks are a result of some outside interaction, such as synchrony of bud break to emergence of overwintering larvae. This information would permit assessing the role of natural enemies in the dynamics of this pest. At present, no specific action can be recommended other than this additional research. Normal forestry practices do not appear to be detrimental to resident natural enemies. When spraying is necessary in regions at risk from this pest, the use of selective insecticides might conserve natural enemies attacking this species. *Bacillus thuringiensis* formulations affected control in Alaska (Holsten and Hard 1985) and would be selective to most natural enemies.

SUGAR PINE TORTRIX, *Choristoneura lambertiana* Busck

Origin: North America.

Range in North America: California, Colorado, Idaho, Montana, Oregon, Wyoming.

Plant hosts and damage: *Pinus contorta, Pinus flexilis, Pinus ponderosa, Pseudotsuga menziesii, Juniperis* spp. Larvae mine needle sheaths and staminate cones.

Natural Enemies: *Choristoneura lambertiana* is likely subject to bird predation and diseases, as are its near relatives. The natural enemies known from this species are primarily insect parasitoids (Table 32).

Table 32. Natural enemies of *Choristoneura lambertiana*

NATURAL ENEMIES
Invertebrate Predators
Deraeocoris barberi Knight[1]
Invertebrate Parasitoids
Actia interrupta Curran[1]
Amblymerus verditer (Norton)[1]
Apanteles fumiferanae Viereck[1, 2]
Apanteles spp.[1]
Casinaria sp.[1]
Ceromasia auricaudata Ins.[1]
Coccygomimus aequalis (Provancher)[2]
Elasmus atratus Howard[1]
Exochus nigripalpus tectulum Townes[2]
Glypta fumiferanae (Viereck)[1, 2]
Itoplectis conquisitor (Say)[2]
Itoplectis quadricingulatus (Provancher)[1]
Madreymia saundersii (Williston)[1, 2]
Meteorus trachynotus Viereck[1]
Nemorilla pyste (Walker)[1]
Pachyneuron allograptae Ashmead[1]
Parania geniculatus geniculatus Holmgren[2]
Phaeogenes sp.[1, 2]
Phytodietus hariolus (Cresson)[2]
Phytodietus sp.[2]
Pseudoperichaeta erecta (Coquillet)[1]
Pteromalini sp.[1]

[1]McGregor 1970
[2]Stevens et al. 1977

Pest status: This species contains many different forms or races. Some of these have previously been considered species but are now usually considered forms of *C. lambertiana.* Adults of this moth are active in July and August, and oviposit on host plants. The first instar larvae overwinter in silken hibernaculae. The following spring the larvae mine needle sheaths and staminate cones. The species will also damage new buds and pollen bodies of sugar pine. McGregor (1970) reported treetops of lodgepole pine killed in Idaho and Montana in 1965-1968. Stevens et al. (1977) reported *C. lambertiana ponderosana* Obraztsov infesting *P. ponderosa* in Colorado.

Biological control: There have been no reports of biological control programs targeted at this pest.

Recommendations: This pest is native, and has a large complex of natural enemies already associated with it. Its pest status is due to large populations and, as for many forest insects, little is known about the factors leading to outbreaks. While additional natural enemies could be sought from related species elsewhere, at this point a more fruitful endeavor would be to study the effects of abiotic factors, host plants, and natural enemies on the dynamics of this species. Such knowledge would permit a better evaluation of the potential role additional natural enemies might play. Normal forestry practices do not appear to affect natural enemies. Spraying, when necessary, should conserve natural enemies as far as possible.

WESTERN SPRUCE BUDWORM, *Choristoneura occidentalis* Freeman

Origin: North America.

Range in North America: British Columbia, Colorado, Idaho, Montana, New Mexico, Oregon, Washington.

Plant hosts and damage: *Abies concolor, Abies grandis, Abies lasiocarpa, Larix occidentalis, Picea engelmannii, Picea glauca, Pseudotsuga menziesii.* Damage is to the buds and needles, by mining and general feeding. Epidemics can cause decreased growth, tree deformity, top killing, and tree death over extensive areas.

Natural Enemies: Many natural enemies are known for this species, including vertebrate predators (mostly birds), pathogens, and invertebrate predators and parasitoids (Table 33).

Table 33. Natural enemies of *Choristoneura occidentalis*

NATURAL ENEMY SPECIES	REFERENCE
Vertebrate Predators	
Hesperiphona vespertina	Torgersen and Campbell 1982, Campbell et al. 1983, Takekawa and Garton 1984
Junco hyemalis L.	Torgersen and Campbell 1982, Campbell et al. 1983
Piranga ludoviciana	Torgersen and Campbell 1982, Campbell et al. 1983
Spinus pinus	Torgersen and Campbell 1982, Campbell et al. 1983
Spizella passerina	Torgersen and Campbell 1982, Campbell et al. 1983

Table 33. continued

Pathogens	
Bacillus thuringiensis var. *kurstaki*	Van Frankenhuyzen and Fast 1989
Granulosis virus	Stelzer and Scott 1985
Neoaplectana carpocapsae	Kaya et al. 1981, Kaya and Reardon 1982
Nosema fumiferanae	Sweeney and McLean 1987
Nuclear polyhedrosis virus	Stelzer and Scott 1985
Thelona sp.	Harris and Dawson 1979
Invertebrate Predators	
Camponotus herculeanus (L.)	Youngs and Campbell 1984
Camponotus laevigatus (F. Smith)	Campbell and Torgersen 1982, Campbell et al. 1983, Youngs and Campbell 1984, Murphy and Croft 1990
Camponotus modoc (Wheeler)	Youngs and Campbell 1984, Murphy and Croft 1990
Camponotus vicinus Mayr	Campbell and Torgersen 1982, Campbell et al. 1983, Youngs and Campbell 1984, Murphy and Croft 1990
Dioryctria pseudotsugella Munroe	Doganlar and Beirne 1978
Dioryctria reniculelloides Mutuura and Monroe	McKnight 1968
Formica accreta Francoeur	Murphy and Croft 1990, Youngs and Campbell 1984
Formica argentea Wheeler	Youngs and Campbell 1984
Formica criniventris Wheeler	Youngs and Campbell 1984
Formica hewitii Wheeler	Youngs and Campbell 1984
Formica lasioides Emery	Youngs and Campbell 1984
Formica neorufibarbis Emery	Youngs and Campbell 1984
Formica obscuripes Forel	Youngs and Campbell 1984
Formica podzolica Francoeur	Youngs and Campbell 1984, Murphy and Croft 1990
Formica sp. (*microgyna* group)	Youngs and Campbell 1984, Murphy and Croft 1990
Formica subnuda Emery	Youngs and Campbell 1984
Invertebrate Parasitoids	
Actia interrupta Curran	McKnight 1974, Harris and Dawson 1979, Shea et al. 1984
Agathis acrobasidis (Cushman)	McKnight 1974
Agathis sp.	Shea et al. 1984
Agria housei Shewell	McKnight 1974, Hamel 1977, Harris and Dawson 1979
Amblymerus verditer (Norton)	McKnight 1974
Ancistrocerus antilope (Panzer)	Evans 1987
Aoplus sp. nr. *vagans* (Provancher)	Williams et al. 1969
Apanteles absonus Muesebeck	McKnight 1974, Shea et al. 1984
Apanteles aristoteliae Viereck	McKnight 1974
Apanteles fumiferanae Viereck	Williams et al. 1969, McKnight 1974, Hamel 1977, Harris and Dawson 1979, Schmid 1981, Shea et al. 1984

Table 33. continued

Apanteles petrovae Walley	McKnight 1974
Apechthis ontario (Cresson)	McKnight 1974, Hamel 1977, Harris and Dawson 1979
Aplomya caesar Aldrich	McKnight 1974, Hamel 1977, Harris and Dawson 1979, Shea et al. 1984
Bracon politiventris (Cushman)	McKnight 1974
Campoplex sp.	McKnight 1974, Harris and Dawson 1979, Shea et al. 1984
Ceromasia auricaudata Townsend	McKnight 1974, Hamel 1977, Harris and Dawson 1979, Schmid 1981, Shea et al. 1984, Evans 1987
Clinocentrus sp.	McKnight 1974
Coccygomimus (=Pimpla) pedalis (Cresson)	McKnight 1974
Diadegma sp.	Harris and Dawson 1979
Enytus eureka (Ashmead)	Shea et al. 1984
Enytus montanus (Ashmead)	Shea et al. 1984
Euphorocera sp	McKnight 1974
Exochus nigripalpis tectulum Townes	Hamel 1977
Glypta fumiferanae (Viereck)	Williams et al. 1969, McKnight 1974,\ Hamel 1977, Harris and Dawson 1979, Schmid 1981, Shea et al. 1984
Goniozus gracilicornis (Kieffer)	Evans 1987
Habronyx sp. nr. *aclerivorus* Rohwer	Schmid 1981
Hemisturmia tortricis Coquillet	Harris and Dawson 1979
Hyposoter sp.	McKnight 1974
Itoplectis conquisitor Say	McKnight 1974, Harris and Dawson 1979
Itoplectis quadricingulatus (Provancher)	Harris and Dawson 1979, Campbell and Torgersen 1982, Shea et al. 1984
Itoplectis vesca Townes	McKnight 1974
Macrocentrus iridescens French	McKnight 1974
Madremyia saundersii (Williston)	McKnight 1974, Hamel 1977, Harris and Dawson 1979, Schmid 1981, Shea et al. 1984
Meteorus campestris Viereck	Hamel 1977
Meteorus sp.	Hamel 1977
Meteorus trachynotus Viereck	Williams et al. 1969, McKnight 1974, Schmid 1981, Shea et al. 1984
Nemorilla pyste (Walker)	McKnight 1974
Omotoma fumiferanae (Tothill)	McKnight 1974
Perilissus coloradensis (Ashmead)	McKnight 1974
Phaeogenes hariolus (Cresson)	Williams et al. 1969, Hamel 1977, Harris and Dawson 1979, Shea et al. 1984
Phaeogenes maculicornis hariolus (Cresson)	McKnight 1974, Schmid 1981, Shea et al. 1984
Phryxe pecosensis (Townsend)	McKnight 1974, Harris and Dawson 1979, Shea et al. 1984
Phytodietus fumiferanae Rohwer	McKnight 1974, Hamel 1977, Schmid 1981, Stein 1981, Shea et al. 1984
Pristomerus sp.	McKnight 1974
Pseudoperichaeta erecta Coquillet	Harris and Dawson 1979, Shea et al. 1984

Psychophagus tortricis (Brues.)	McKnight 1974
Scambus hispae (Harris)	McKnight 1974
Scambus sp. nr. *aplopappi* (Ashmead)	Schmid 1981
Sinophorus sp.	Hamel 1977, Shea et al. 1984
Temelucha evetriae (Cushman)	Schmid 1981, Shea et al. 1984
Temelucha rhyacioniae (Cushman)	Shea et al. 1984
Timavia fumiferanae (Tothill)	Schmid 1981, Shea et al. 1984
Tranosema arenicola Thomson	McKnight 1974
Tranosema rostrale rostrale (Brischke)	Stein 1981, Shea et al. 1984
Trichogramma minutum Riley	McKnight 1974, Hamel 1977, Harris and Dawson 1979
Winthemia fumiferanae Tothill	Doganlar and Bierne 1978, Harris and Dawson 1979

Pest status: The larval stage of this lepidopteran is probably the most destructive forest defoliator in western North America (Furniss and Carolin 1977). Earlier records considered this species and near relatives as strains of *Choristoneura fumiferana* (Clemens), and early information on this species appears under that name (Freeman 1967, McKnight 1968). The species occurs primarily on Douglas-fir and true firs in the Pacific coast regions and in the Rocky Mountains. Eggs are laid in late summer, first instar larvae do not feed but overwinter, and feed the following year primarily on buds and new needles. The species is univoltine, with adults appearing in late summer.

Outbreaks of this species have occurred several times since the first recorded outbreak in 1909. Some of these subsided naturally in a few years, while others have lasted up to 20 years (Furniss and Carolin 1977).

Biological control: This budworm, like most forest defoliators, is affected by natural enemies as well as by abiotic factors and host plant quality and availability. It is native to western North America and has numerous natural enemies (Table 33). Of the more than 40 species of insect parasitoids that attack it, approximately 10 exert significant natural control (Carolin and Coulter 1959). When outbreaks have occurred despite natural controls, aerial spraying has been used to limit losses. The species is subject to infection by *Bacillus thuringiensis,* and the use of this pathogen offers an option for biological control by augmentation.

Recommendations: The cyclic occurrence of outbreaks of forest defoliators appears intrinsic to their population dynamics, and likely is related to interaction with host tree age or stand health. *Choristoneura occidentalis* is native to western North America, with a highly diverse upper trophic level feeding upon it. The introduction of natural enemies of related species or of ecological homologues from other regions may prove beneficial, but the degree of success might also be very limited, considering the extensive resident fauna already feeding on this species. Normal forestry practices do not appear to be detrimental to the conservation of existing natural enemies, so there are no particular practices to avoid. Spraying of insecticides (against this pest or others), when necessary, should be conducted with selective materials when possible, to preserve natural enemies. In general, there appears to be little opportunity for enhancing the natural control of this species.

YPONOMEUTIDAE

PINE NEEDLE SHEATHMINER, *Zelleria haimbachi* Busck

Origin: Unknown.

Range in North America: Throughout North America.

Plant hosts and damage: Many two- and three-needle species of *Pinus*, especially *P. ponderosa* and *P. jeffreyi.* Eggs are laid in summer. First instar larvae mine needles and spend winter in the needles. The following spring, larvae emerge from the needles and migrate to the base of the needle cluster, where they feed within the sheath and kill the needles. The species is univoltine.

Natural Enemies: The chalcid *Spilochalcis leptis* Burks is the only reported natural enemy of this species (Burks 1940).

Pest Status: When the pest is abundant, it has caused appreciable damage in plantings and plantations in California and Oregon.

Biological Control: No information was found regarding biological control of this species.

Recommendations: The paucity of information regarding natural enemies of this species may indicate that it has few natural enemy species in North America and perhaps is not native to this region. Alternatively, the lack of information may indicate that little research has been conducted. In either case, a study on the dynamics of the pest and its natural enemy fauna would help clarify these issues. If the species is not native to western North America, natural enemies could be sought from its native home which could reduce its populations here.

Acariformes

ERIOPHYIDAE

A MITE, *Trisetacus campnodus* Keifer and Saunders

Origin: Unknown.

Range in North America: Pacific Northwest.

Plant hosts and damage: *Pinus sylvestris.* The mite attacks pine needle bases under the needle sheath, causing chlorosis, stunting, and distortion of the needles. Damage to Christmas tree plantations can be severe.

Natural Enemies: None is known.

Pest Status: Bud mites in the genus *Trisetacus* are minute (about 300 nm) and difficult to see inside the buds or beneath the needle sheaths where they occur. Feeding on plant tissues by large populations can cause the destruction of the entire needle base. The needle becomes necrotic, brown, and callused. The conditions are accompanied by chlorosis, stunting, and deformation of the needle. Needle length growth may be reduced 70%. Mites are active throughout the year (Keifer and Saunders 1972).

Biological Control: Few biological control programs have been undertaken against bud mites in the family Eriophyidae, in part because they are so difficult to work with because of their small size. The origin of this species is unknown, although it has relatives in Europe and elsewhere in North America. No biological control program has been conducted against this species, and no natural enemies of it have been reported.

Recommendations: Because so little is known about this species, and because relatively little has been done in the past on eriophyids, it is difficult to estimate the impact that natural enemies, either by introduction or by augmentation, might have on this pest. The initial work that should be conducted includes a taxonomic survey of the group, with efforts focusing on determining the native range of this species, a survey of natural enemies (if any) currently attacking this species, and a survey of natural enemies attacking related species elsewhere. If natural enemies are lacking in western North America, they could be introduced. Additional recommendations regarding augmentation or conservation would need to await the outcome of the survey for natural enemies.

TETRANICHIDAE

SPRUCE SPIDER MITE, *Oligonychus ununguis* (Jacobi)

Origin: Unknown.

Range in North America: Throughout most of North America, widespread with its hosts. Overall range is worldwide.

Plant hosts and damage: Species of *Abies, Cupressus, Picea, Pinus, Pseudotsuga, Sequoia, Sequoiadendron, Thuja, Tsuga,* and Chinese chestnut *(Castanea mollisima)* (Wheeler et al. 1973, Furniss and Carolin 1977). Mites of all feeding stages attack needles. The mite is a common pest of ornamentals and sometimes becomes epidemic in the forest.

Natural Enemies: Little information is known about the quantitative impact or role of natural enemies of this mite. Many natural enemies have been reported, primarily from Europe and North America (Table 34). Several mite predators have also been studied in laboratory trials as possible augmentation agents (Mangini and Hain 1991). Two species of *Typhlodromus* and one of *Amblyseis* have been reported as associated with *O. ununguis* in Christmas tree plantings. Kramer and Hain (1989) suggest that hot, dry weather may favor development of populations of *O. ununguis* more than those of the predator *Neoseiulus fallacis,* possibly leading to higher populations of the pest mite. Mangini and Hain (1991) suggest that *Metaseiulus occidentalis* (Nesbitt) may be a suitable predator of *O. ununguis,* particularly in more arid climates.

Table 34. Pathogens and predators associated with *Oligonychus ununguis*

NATURAL ENEMY SPECIES	REFERENCE
Pathogens	
Entomophthora sp.	Löyttyniemi 1970
Predators	
Amblyseis andersoni	West and DeAngelis 1993
Anystis baccarum L.	von Scheller 1962
Atractotomus magnicornis (Fall.)	Thalenhorst 1962
Conwentzia pineticola End.	von Scheller 1962
Neoseiulus collegae (DeLeon)	Mizell and Schiffhauer 1991
Neoseiulus fallacis (Garman)	Boyne and Hain 1983, Kramer and Hain 1989, Mangini and Hain 1991
Stethorus punctillum Weise	Putman 1955, Wheeler et al. 1973
Typhlodromus spp.	Thalenhorst 1962
Typhlodromus bakeri (Garman)	Thalenhorst 1962, von Scheller 1962
Typhlodromus americanus Chant and Yoshida-Shaul	West and DeAngelis 1993
Typhlodromus rhenanoides	West and DeAngelis 1993
Typhlodromus rhenanus (Oudm.)	Thalenhorst 1962, von Scheller 1962
Typlodromus pyri Scheuten	Thalenhorst 1962, von Scheller 1962

Pest Status: This species is multivoltine, with as many as seven generations annually (Johnson 1958, Doidge and Marshall 1971). Outbreaks can occur, and usually develop and subside in a single year (Furniss and Carolin 1977). The species thrives under hot and dry conditions. Poor tree vigor may promote population growth. The largest recorded outbreak of this species occurred in Montana in 1957, affecting 400,000 hectares of Douglas-fir, following aerial spraying against another pest. This suggests that spraying may promote outbreaks. Insecticide treatments in other systems are known to lead to outbreaks of related spider mites (Van Driesche and Bellows 1996), but the mechanisms are not always simple. Destruction of the natural enemies can be an important causal factor. In addition, there may be effects from spraying on either the host plant (such as induced higher foliar nitrogen levels) or on the pest itself (hormolygotic effects causing increased reproductive rates) that could increase population growth. Thalenhorst (1962) suggests that soil fertilization to increase nitrogen content favors the mite population.

Biological Control: No biological control programs directed against this pest have been reported. Several studies have determined what natural enemies are associated with this pest in different countries, but the specific impact of these natural enemies has not been measured (Wheeler et al. 1973, Gutierrez et al. 1986, West and DeAngelis 1993). These predators generally are credited with providing important control of mite populations (e.g., Thalenhorst 1962), but few quantitative data are available. Laboratory studies have reported the impact of abiotic parameters on the development and survival of several predators under different conditions (Putman 1955, Kramer and Hain 1989, Mangini and Hain 1991). In the laboratory, *Neoseiulus fallacis* severely limited population growth of *O. ununguis* (Boyne and Hain 1983).

Recommendations: Research directed at determining the native home for this mite would be beneficial to determining the correct biological control action. Taxonomic and biogeographic research should be directed toward this end. Research should then be directed toward evaluating the natural enemy fauna of this species in its native range, and also toward importing and evaluating these natural enemies in North America.

Spider mites in this family have been successfully managed with biological control in other systems, so this pest species is a good candidate for biological control, particularly as it has natural enemies elsewhere in the world. Many natural enemies of this species are known that are not reported from North America. A good candidate for introduction might be *Anystis baccarum* from Europe. The impact of insecticide spraying in the forest on outbreaks of this species also should be evaluated. Until the impact of such treatments is known, future treatments of areas at risk from this species should be made with a selective insecticide.

Summary

We treat here 42 serious pests of western North American forests. These western forests are dominated by conifers, and the principal pests are bark beetles, defoliators, and cone or twig borers. Of these 42 species, 26 are considered native to the region (Table 35). Five species are adventive or introduced to the region, and evidence for one additional species indicates that it is also best treated here as adventive. Seven species are presumed native to western North America, but evidence is limited as to their precise origin; three species are of unknown origin.

Table 35. Regions of origin for 42 pests of western North American forests

SPECIES	STATUS IN WESTERN NORTH AMERICA
COLEOPTERA	
Xylotrechus obliteratus	native
Pissodes strobi	presumed native
Conophthorus lambertianae	native
Dendroctonus brevicomis	native
Dendroctonus jeffreyi	native
Dendroctonus ponderosae	native
Dendroctonus pseudotsugae	native
Dendroctonus rufipennis	native
Ips pini	native
Pseudohylesinus sericeus	native
Scolytus multistriatus	adventive, *ex* Old World
Scolytus ventralis	native
Trypodendron lineatum	presumed native
DIPTERA	
Contarinia pseudotsugae	native
HOMOPTERA	
Adelges piceae	adventive, *ex* Europe
HYMENOPTERA	
Neodiprion tsugae	native
Pristiphora erichsonii	presumed adventive, *ex* Europe

Table 35. continued

LEPIDOPTERA	
Coleophora laricella	adventive, *ex* Europe
Coleotechnites milleri	presumed native
Melanolophia imitata	presumed native
Ectropis crepuscularia	native
Rheumaptera hastata	native
Operophtera bruceata	native
Lambdina fiscellaria lugubrosa	native
Malacosoma disstria	native
Orgyia pseudotsugata	native
Barbara colfaxiana	native
Eucosma rescissoriana	native
Eucosma sonomana	presumed native
Rhyacionia buoliana	adventive, *ex* Europe
Rhyacionia frustrana	adventive, *ex* eastern North America
Rhyacionia bushnelli	native
Rhyacionia neomexicana	native
Neophasia menapia	presumed native
Coloradia pandora	presumed native
Acleris gloverana	native
Choristoneura conflictana	native
Choristoneura lambertiana	native
Choristoneura occidentalis	native
Zelleria haimbachi	unknown
ACARIFORMES	
Trisetacus campnodus	unknown
Oligonychus ununguis	unknown

The opportunities for enhanced biological control of these species may be grouped into four strategies (Table 36):

1. Introduce new natural enemies of the pest species. This strategy will be most applicable to species adventive to the region.
2. Introduce new natural enemies of related species.
3. Augment existing natural enemy populations (including use of pathogens as biological insecticides).
4. Promote silvicultural practices that favor natural enemy impact.

Research would be needed for development of any appropriate strategy for a particular pest species. For some of the pests, we recognize a fifth category of action, that of fundamental research. This category applies to those pests for which insufficient information is available to make a well-founded recommendation to pursue any particular strategy of biological control. Finally, there are also some pests for which our assessment is that there is little opportunity for enhancing the role of biological control in western forests. One adventive species, the larch casebearer *(Coleophora laricella)*, is currently under satisfactory biological control and no actions directed against it are necessary; this species is omitted from Table 36.

Recommendations

Introduce natural enemies of the pest species. This strategy is the best approach for six of the pest species currently present in western forests (Table 36). For *Pristiphora erichsonii, Rhyacionia buoliana, Rhyacionia frustrana,* and *Oligonychus ununguis,* there is evidence of effective natural enemies known outside western North America, and the introduction and establishment of these natural enemies would likely bring about a reduction in pest status. For *Scolytus multistriatus* and *Adelges piceae,* we suggest that the introduction of new natural enemies should be beneficial, but in these cases additional research into the fundamental relationships between the pests and their native natural enemy faunas will be important prior to new introductions, as the precise direction that introductions should take is less well defined. The specific issues requiring further investigation are noted in the discussions under each species name.

Introduce natural enemies of related species. This strategy is discussed in the body of the text as a possibility for several native species. We are cautious about this strategy, however, as it is less well tested than introductions against adventive pests. It consequently may require more investment in research and development than the introduction of natural enemies of an adventive species, and quantitative research will be crucial to understanding the roles of new natural enemies in natural ecosystems. One possible approach might be to pursue this strategy first with one or two taxa representative of groups where it might apply (perhaps a bark beetle or a defoliator, or both). This strategy could then be reevaluated based on the results of these test species.

While this strategy could be said to be applicable to any native insect, there is some preliminary research points to particular groups as at least more suitable candidates (Table 36). Among these we identify *Pissodes strobi, Lambdina fiscellaria lugubrosa,* and one or more of the scolytid bark beetles (perhaps *Dendroctonus ponderosae* or *Scolytus ventralis*) as possible targets. In each case, evidence exists (see papers cited under each species) that there are natural enemies of ecological homologues elsewhere (in Europe, in these cases), that may possibly attack one of these western pests. Attempting to implement this strategy to reduce the pest status of these species would provide some definitive evidence on this strategy's future suitability in the western forests. Considerable time must be anticipated before a quantitative answer will emerge, as most of these species are univoltine, and any additions of natural enemies to the system would require several generations (i.e., years) before their quantitative impact might be recognized.

Augment existing natural enemy populations. Augmentation of invertebrate natural enemies (predators and parasitoids) of forest pests is a major undertaking and, considering the marginal economic value of protection obtained and the vast areas that must be covered in a release or augmentation program, may only rarely be economically viable. Two possible applications of this technique, however, may be important to forest pest management.

One application is the use of pathogens as augmented natural enemies. Several pests of western forests are susceptible to *Bacillus thuringiensis* or to various viral or fungal pathogens which may be commercially available. In such cases, the use of pathogen formulations as biological insecticides still incurs considerable expense for procurement of the material and its application. Such an approach may be much less expensive than rearing parasitoids or predators, and would provide the further benefit of protecting existing natural enemies from the direct harm of general broad-spectrum insecticides.

For pests which undergo relatively short epidemic cycles, early detection and treatment with biological insecticides may limit the impact of an epidemic to a single year of damage. Use of pathogens as biological insecticides on longer-cycling pests may also hasten the collapse of an epidemic. Among the pests to which this strategy (employing pathogens) may apply (Table 36) are *Acleris gloverana, Choristoneura conflictana, Choristoneura occidentalis, Malacosoma disstria, Operophtera bruceata, Orgyia pseudotsugata,* and *Pissodes strobi.*

The other application of augmentation that has been suggested is the inundative release of predators, specifically native clerids, for increasing biological control of *Dendroctonus ponderosae* (Moeck and Safranyik 1983). These authors propose releases of native clerids against low density populations of this pest species, but a mass rearing program for the predators has not been evaluated for economic viability.

Promote silvicultural practices to favor natural enemy impact. In a few cases (Table 36), the pest status of a species appears related to silvicultural practices, particularly plantation plantings of uniformly aged trees. In such settings, forest insect species that would normally be constrained by a combination of limited resource and the action of natural enemies reach pest status, apparently because of the concentration of suitable reproductive resource in the plantation or replant area. In such cases, natural enemies are still active, but do not provide enough suppression to limit damage to trees. Among these species are *Pissodes strobi* and *Rhyacionia neomexicana,* species that preferentially attack younger (up to 3 m tall) pines. Modifying replant strategies to diversify the ages of plants may help limit pest infestation by reducing concentrations of optimally aged trees. Limiting plantings to habitats with sufficient water and nutrients may help the trees' natural defenses ward off limited pest attack. In such settings of suitable habitat and diversified tree ages, natural enemies may be able to maintain pest populations under control. For *Orgyia pseudotsugata,* predation and parasitism was greater in thinned stands (Wickman and Torgersen 1987), and studies on optimal stand density for enhancing biological control could prove beneficial for management of this species.

Limited opportunity for enhancing biological control. There are 5 species for which no clear opportunity for enhancing biological control could be identified (Table 36). These include one of the western bark beetles, a native defoliator, one of the native tip moths, and two of the native cone moths.

Need for additional research. For several of these western pest species, additional research will be needed to undertake any of the recommendations proposed in Table 36, and such research should shape the direction taken for a biological control strategy for those species. For some species, however, we lack even enough basic information about the population ecology of the pest and their natural enemies to make a recommendation as to an appropriate strategy. These species include several of the borers and defoliators (Table 36). The research areas requiring investigation for these and other species are indicated in Table 37. Details concerning the applicability of the different strategies, together with more detailed analyses of the research needs, are given in the body of the text for each species.

Table 36. Recommended actions for pursuing biological control of western forest insect and mite pests.

Species	Introduce Natural Enemies of the Pest	Introduce Natural Enemies of Related Species	Augment Existing Natural Enemies	Silvicultural Practices that Favor Natural Enemy Action	Need for Fundamental Research	Little Opportunity for Enhanced Biological Control in Western Forests
COLEOPTERA						
Xylotrechus obliteratus					X	
Pissodes strobi		X	X	X		
Conophthorus lambertianae					X	
Dendroctonus brevicomis						X
Dendroctonus jeffreyi					X	
Dendroctonus ponderosae		X	X			
Dendroctonus pseudotsugae		X				
Dendroctonus rufipennis					X	
Ips pini					X	
Pseudohylesinus sericeus					X	
Scolytus multistriatus	X					
Scolytus ventralis		X				
Trypodendron lineatum			X[1]			
DIPTERA						
Contarinia pseudotsugae					X	
HOMOPTERA						
Adelges piceae	X					
HYMENOPTERA						
Neodiprion tsugae						X

Table 36. Continued.

Pristiphora erichsonii	X					
LEPIDOPTERA						
Coleotechnites milleri					X	
Melanolophia imitata					X	
Ectropis crepuscularia					X	
Rheumaptera hastata					X	
Operophtera bruceata			X			
Lambdina fiscellaria lugubrosa		X				
Malacosoma disstria			X[2]			
Orgyia pseudotsugata			X[3]	X		
Barbara colfaxiana						X
Eucosma rescissoriana						X
Eucosma sonomana					X	
Rhyacionia buoliana	X					
Rhyacionia frustrana	X					
Rhyacionia bushnelli						X
Rhyacionia neomexicana				X		
Neophasia menapia					X	
Coloradia pandora					X	
Acleris gloverana			X[2]			
Choristoneura conflictana			X[2]			
Choristoneura lambertiana					X	
Choristoneura occidentalis			X[2]			
Zelleria haimbachi					X	
ACARIFORMES						
Trisetacus campnodus					X	
Oligonychus ununguis	X					

[1]Use of *Beauveria bassiana* has been demonstrated to protect cut lumber

[2]Species is susceptible to use of *Bacillus thuringiensis* in forest ecosystems

[3]Species is susceptible to baculovirus of *Autographa californica*

Table 37. Pests of western forests for which additional information is needed to guide research and development of biological control as a pest management strategy

SPECIES	INFORMATION NEEDED
COLEOPTERA	
Xylotrechus obliteratus	Basic information on natural enemy fauna
Conophthorus lambertianae	Basic information on natural enemies of this and related species; investigate the fungal pathogen
Dendroctonus jeffreyi	Basic and quantitative information on natural enemies
Dendroctonus rufipennis	Basic information on natural enemies
Ips pini	Quantitative impact of natural enemies in endemic and epidemic populations
Pseudohylesinus sericeus	Basic ecological studies, with particular reference to natural enemies
Scolytus multistriatus	Quantitative population dynamics; role of natural enemies in native and adventive populations
Scolytus ventralis	Basic life-table studies
DIPTERA	
Contarinia pseudotsugae	Basic ecological studies
HOMOPTERA	
Adelges piceae	Quantitative studies of natural enemy impact in native populations; study variations in host plant susceptibility
LEPIDOPTERA	
Coleotechnites milleri	Geographic origin; population dynamics; impact of natural enemies in endemic and epidemic populations
Melanolophia imitata	Causes of outbreaks; impact of natural enemies in endemic and epidemic populations
Ectropis crepuscularia	Basic ecological studies
Rheumaptera hastata	Causes of outbreaks; roles of natural enemies; host plant-insect biochemical interactions
Lambdina fiscellaria lugubrosa	Possible test species for introduction of natural enemies of related Lepidoptera from Europe
Orgyia pseudotsugata	Causes of outbreaks; role of natural enemies in endemic and epidemic populations
Barbara colfaxiana	Possible impact of augmented pathogens
Eucosma sonomana	Geographic origin; natural enemies of this and related species
Neophasia menapia	Causes of outbreaks; role of natural enemies
Rhyacionia buoliana	Factors affecting population dynamics; quantitative roles of natural enemies
Coloradia pandora	Role of natural enemies in endemic populations; wilt disease
Choristoneura conflictana	Role of natural enemies in endemic and epidemic populations; causes of outbreaks
Choristoneura lambertiana	Causes of outbreaks; effects of abiotic factors, host plants, and natural enemies on dynamics
Zelleria haimbachi	Geographic origin; natural enemies; population dynamics
ACARI	
Trisetacus campnodus	Basic taxonomic and biogeographic information; basic information on natural enemies of this and related species
Oligonychus ununguis	Geographic origin; impact of natural enemies

References Cited

Adlung, K. G. 1962. Beobachtungen zum Auftreten *Tetrastichus turionum* Hg. (Hym. Euloph.), einem Parasiten von *Rhyacionia buoliana* Schiff. (Lep. Tortric.). *Zeitschrift für angewandte Entomologie* 50 (4): 455-462.

Alfaro, R. I.; Hulme, M. A.; Harris, J. W. E. 1985. Insects associated with the Sitka spruce weevil, *Pissodes strobi* (Col.: Curculionidae) on Sitka spruce, *Picea sitchensis* in British Columbia. *The Canadian Entomologist* 30 (4): 415-418.

Alfaro, R. I.; Borden, J. H.; Fraser, R. G.; Yanchuk, A. 1995. The white pine weevil in British Columbia: basis for an integrated pest management system. *Forestry Chronicle* 71 (1): 66-73.

Altenkirch, W. 1976. Experiments on the mass rearing and release of *Elachertus (Hyssopus) thymus* Girault (Hym., Chalcidoidea, Eulophidae). *Zeitschrift fur Pflanzenkrankheiten und Pflanzenschutz* 83: 1-15.

Amman, G. D. 1972. Prey consumption and development of *Thanasimus undatulus,* a predator of the mountain pine beetle. *Environmental Entomology* 1 (4): 528-530.

Amman, G. D. 1975. Insects affecting lodgepole pine productivity. In: Baumgartner, D. M. (ed.). *Management of Lodgepole Pine Ecosystem Symposium Proceedings.* Pullman, WA: Washington State University Cooperative Extension Service. U.S. Department of Agriculture, Forest Service, Ogden, Utah: Intermountain Forest and Range Experiment Station; 310-314.

Amman, G. D. 1984. Mountain pine beetle (Coleoptera: Scolytidae) mortality in three types of infestations. *Environmental Entomology* 13 (1): 184-191.

Arthur, A. P. 1961. The cleptoparasitic habits and the immature stages of *Eurytoma pini* Bugbee (Hymenoptera: Chalcidae), a parasite of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae). *The Canadian Entomologist* 93 (8): 655-660.

Arthur, A. P.; Juillet, J. A. 1961. The introduced parasites of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae), with a critical evaluation of their usefulness as control agents. *The Canadian Entomologist* 93 (4): 297-312.

Baird, A. B. 1922. Some notes on the natural control of the larch sawfly and larch casebearer in New Brunswick in 1922. *Proceedings of the Acadian Entomological Society* 8: 158-171.

Balch, R. E. 1952. Studies of the balsam woolly aphid, *Adelges piceae* (Ratz.) (Homoptera: Phylloxeridae) and its effects on balsam fir, *Abies balsamea* (L.) Mill. Ottawa: *Canada Department of Agriculture, Publication No. 867;* 76 p.

Balch, R. E.; Clark, R. C.; Brown, N. R. 1958. *Adelges picea* (Ratz.) in Canada with reference to biological control. *Proceedings of the 10th International Congress of Entomology (1956)* 4: 807-818.

Barbosa, P.; Wagner, M. R. 1989. *Introduction to Forest and Shade Tree Insects.* New York: Academic Press, Inc.; 639 p.

Batzer, H. O.; Waters, W. E. 1956. Forest Tent Caterpillar. *U.S. Department of Agriculture Forest Pest Leaflet 9;* 4 p.

Baumhofer, L. G. 1932. Biological control of the pine tip moth in Nebraska. *Proceedings of the Entomological Society of Washington 34:* 28.

Beckwith, R. C. 1968. The large aspen tortrix, *Choristoneura conflictana* (Wlkr.) in interior Alaska. *U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station,* Research Notes PNW-81.

Bedard, W. D. 1968. The sugar pine cone beetle. *U.S. Department of Agriculture Forest Pest Leaflet* 112; 6 p.

Beique, R. 1960. The importance of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) in Quebec City and vicinity. *The Canadian Entomologist* 92: 858-862.

Bellocq, M. I.; Smith, S. M. 1994. Predation and overwintering mortality of the white pine weevil, *Pissodes strobi,* in planted and seeded Jack pine. *Canadian Journal of Forest Research* 24 (7): 1426-1433.

Bellows, T. S., Jr. 1993. Introduction of natural enemies for suppression of arthropod pests. *In:* Lumsden, R. D.; Vaughn, J. L. (eds.). *Pest Management Biologically Based Technologies.* Washington, D.C.: American Chemical Society; 82-89.

Bellows, T. S., Jr.; Paine, T. D.; Gould, J. R.; Bezark, L. G.; Ball, J. C.; Bentley, W.; Coviello, R.; Downer, J.; Elam, P.; Flaherty, D.; Gouveia, P.; Koehler, C.; Molinar, R.; O'Connell, N.; Perry, E.; Vogel, G. 1992. Biological control of ash whitefly: a success in progress. *California Agriculture* 46 (1): 24, 27-28.

Berisford, C. W.; Dahlsten, D. L. 1989. Biological control of *Ips grandicollis* (Eichhoff) (Coleoptera: Scolytidae) in Australia- a preliminary evaluation. *In:* Kulhavy, D.L. and Miller, M. C. (eds.). *Potential for Biological Control of* Dendroctonus *and* Ips *Bark Beetles:* Nacogdoches, TX: Center for Applied Studies, School of Forestry, Stephen F. Austin State University; 81-93.

Berry, P. A. 1939. Biology and habits of *Ephialtes turionellae* (L.), a pupal parasite of the European pine shoot moth. *Journal of Economic Entomology* 32 (5): 717-721.

Berryman, A. A. 1966. Factors influencing oviposition, and the effect of temperature on development and survival of *Enoclerus lecontei* (Wolcott) eggs. *The Canadian Entomologist* 98 (6): 579-585.

Berryman, A. A. 1967. Estimation of *Dendroctonus brevicomis* (Coleoptera: Scolytidae) mortality caused by insect predators. *The Canadian Entomologist* 99 (10): 1009-1014.

Berryman, A. A.; Otvos, I. S.; Dahlsten, D. L.; Stark, R. W. 1970. Interactions and effects of the insect parasite, insect predator, and avian predator complex. *In:* Stark, R.W.; D. L. Dahlsten (eds.). *Studies on Population Dynamics of Western Pine Beetle,* Dendroctonus brevicomis *LeConte (Coleoptera: Scolytidae).* University of California, Division of Agricultural Sciences; 147-154.

Biermann, G. M. 1973. Investigations on the establishment of the North American pimpline *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae) as a parasite of *Rhyacionia buoliana* Den. Schiff. (Lepidoptera: Olethreutidae) in northwest Germany. Gottingen, German Federal Republic: Georg. August. Universitat; 133 p. Thesis.

Blanchard, E. E. 1960. Un *Apanteles* parasito de *Evetria buoliana* (Schiff.) (Hymenoptera, Braconidae). [An *Apanteles* parasitic on Rhyacionia buoliana.] *Revista de investigaciones agricolas* 14 (1): 31-33

Borden, J. H. 1993. Uncertain fate of spot infestations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins. *The Canadian Entomologist* 125 (1): 167-169.

Bosworth, A. B.; Raney, H. G.; Eikenbary, R. D.; Flora, N. W. 1970. Nocturnal observations of spiders in loblolly pines at Haworth, Oklahoma. *Journal of Economic Entomology* 63: 297-298.

Boyne, J. V.; Hain, F. P. 1983. Responses of *Neoseiulus fallacis* (Acarina: Phytoseiidae) to different prey densities of *Oligonychus ununguis* (Acarina: Tetranychidae) and to different relative humidity regimes. *The Canadian Entomologist* 115: 1607-1614.

Brasier, C. M.; Gibbs, J. N. 1975. Variation of *Ceratocystis ulmi:* Significance of the aggressive and nonagressive strains. *In: Dutch Elm Disease; Proceedings of the IUFRO Conference,* September 1973, Minneapolis-St. Paul, Minnesota; 53-66.

Bringuel, G. J. 1968. Two new parasites of the Douglas-fir gall midge, *Contarinia oregonensis* Foote (Diptera: Cecidomyiidae). *The Pan-Pacific Entomologist* 44: 339-340.

Brown, C. E. 1962. The life history and dispersal of the Bruce spanworm, *Operophtera bruceata* (Hulst), (Lepidoptera: Geometridae). *The Canadian Entomologist* 94: 1103-1107.

Brown, L. R.; Eads, C. O. 1966. A technical study of insects affecting the elm tree in southern California. *California Agricultural Experiment Station Bulletin* 821; 16-20.

Bryant, J. P.; Reichardt, P. B.; Clausen, T. P.; Werner, R. A. 1993. Effects of mineral nutrition on delayed inducible resistance in Alaska paper birch. *Ecology* 74 (7): 2072-2084.

Burke, J.; Percy, J. 1982. Survey of pathogens in the large aspen tortrix, *Choristoneura conflictana* (Lepidoptera: Tortricidae), in Ontario and British Columbia with particular reference to granulosis virus. *The Canadian Entomologist* 114: 457-459.

Burke, J.; Percy, J. 1983. Viruses infecting five species of Lepidoptera. *Canadian Forestry Service Research Notes.* 3(1): 1-2.

Burks, B. D. 1940. Revision of the Chalcid-flies of the Tribe Chalcidini in America, north of Mexico. *Proceedings of the United States National Museum* 88 (3082): 237-354.

Busck, A. 1914. Description of new microlepidoptera of forest trees. *Proceedings of the Entomological Society of Washington* 16 (4): 143-149.

Butcher, J. W.; Hodson, A. C. 1949. Biological and ecological studies on some lepidopterous bud and shoot insects of Jack pine (Lepidoptera-Olethreutidae). *The Canadian Entomologist* 81: 161-173

Butovitsch, V. 1936. Studies in the pine shoot tortrix, *Rhyacionia buoliana.* Part I. Stockholm: *Meddelanden fran Statens Skogsforsoksanstalt* 29 (5): 471-556.

Byers, J. A. 1988. Novel diffusion-dilution method for release of semiochemicals: testing pheromone component ratios on western pine beetle. *Journal of Chemical Ecology* 14: 199-212.

CAB (Commonwealth Agricultural Bureaux). 1959. *Distribution maps of pests, Series A (Agricultural),* No. 97. London, United Kingdom: Commonwealth Institute of Entomology.

CAB (Commonwealth Agricultural Bureaux). 1975. *Distribution maps of pests, Series A (Agricultural),* No. 347. London, United Kingdom: Commonwealth Institute of Entomology.

CAB (Commonwealth Agricultural Bureaux). 1978. *Distribution maps of pests, Series A (Agricultural),* No. 387. London, United Kingdom: Commonwealth Institute of Entomology.

CAB (Commonwealth Agricultural Bureaux). 1989. *Distribution maps of pests, Series A (Agricultural),* No. 507. London, United Kingdom: International Institute of Entomology.

Campbell, R. W.; Torgersen, T. R. 1982. Some effects of predaceous ants on western spruce budworm pupae in north central Washington. *Environmental Entomology* 11(1): 111-114.

Campbell, R. W.; Torgersen, T. R.; Srivastava, N. 1983. A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. *Forest Science* 29(4): 779-790.

Carolin, V. M.; Coulter, W. K. 1959. The occurrence of insect parasites of *Choristoneura fumiferana* (Clem.), in Oregon. *Journal of Economic Entomology* 52: 550-555.

Carolin, V. M.; Coulter, W. K. 1971. Trends of western spruce budworm and associated insects in Pacific Northwest forests sprayed with DDT. *Journal of Economic Entomology* 64(1): 291-297.

Chatelain, M. P.; Schenk, J. A. 1984. Evaluation of frontalin and exo-brevicomin as kairomones to control mountain pine beetle (Coleoptera: Scolytidae) in lodgepole pine. *Environmental Entomology* 13 (6): 1666-1674.

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

Clark, R. C.; Brown, N. R. 1958. Studies of predators of the balsam woolly aphid, *Adelges piceae* (Ratz.) (Homoptera: Adelgidae), V. *Laricobius erichsonii* Rosen. (Coleoptera: Derodontidae), an introduced predator in eastern Canada. *The Canadian Entomologist* 90 (11): 657-672.

Clark, R. C.; Schenk, J. A.; Williamson, D. L. 1963. The cone-infesting moth *Barbara colfaxiana* as a pest of Douglas-fir in northern Idaho. *Annals of the Entomological Society of America* 56: 246-250.

Clausen, C. P. (ed.) 1978. *Introduced Parasites and Predators of Arthropod Pests and Weeds: A World Review.* Washington, D.C: Agriculture Handbook No. 480, U.S. Department of Agriculture, Forest Service; 545 p.

Cobb, F. W., Jr.; Parmeter, J. R.; Wood, D. L.; Stark, R. W. 1974. Root pathogens as agents predisposing ponderosa pine and white fir to bark beetles. Int. Union For. Res. Organ. *In:* Proceedings 4th International *Fomes annosus* Conference (Sect. 24). Asheville, N.C: U.S. Department of Agriculture, Forest Service; 8-15.

Cochran, P. H.; Barrett, J. W. 1993. Long-term response of planted ponderosa pine to thinning in Oregon's Blue Mountains. *Western Journal of Applied Forestry* 8 (4): 126-132.

Cole, W. E. 1961. Pine butterfly. *U.S. Department of Agriculture Forest Pest Leaflet 66;* 1p.

Condrashoff, S. F. 1962. Bionomics of three closely related species of *Contarinia* Rond. (Diptera: Cecidomyiidae) from Douglas-fir needles. *The Canadian Entomologist* 94: 376-394.

Coppel, H. C.; Arthur, A. P. 1954. Notes in introduced parasites of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Tortricidae), in Ontario. *84th Report of the Entomological Society of Ontario;* 55-58.

Criddle, N. 1928. The introduction and establishment of the larch sawfly parasite *Mesoleius tenthredinis* Morley, into southern Manitoba (Hymen.). *The Canadian Entomologist* 60: 51-53.

Cunningham, J. C.; Burke, J. M.; Arif, B. M. 1973. An entomopoxvirus found in populations of the large aspen tortrix, *Choristoneura conflictana* (Lepidoptera: Tortricidae) in Ontario. *The Canadian Entomologist* 105: 767-773.

Cushman, R. A. 1927a. The parasites of the pine tip moth, *Rhyacionia frustrana* (Comstock). *Journal of Agricultural Research* 34: 615-622.

Cushman, R. A. 1927b. Three new hymenopterous parasites of the pine tip moth, *Rhyacionia frustrana* (Comstock). *Journal of Agricultural Research* 34: 739-741.

Cushman, R. A. 1932. Note on biological control of the pine tip moth in Nebraska. *Proceedings of the Entomological Society of Washington* 34: 28.

Cushman, R. A. 1940. A review of the parasitic wasps of the ichneumonid genus *Exenterus* Hartig. *Washington, D.C.: United States Department of Agriculture, Miscellaneous Publication* 354; 14 p.

Dahlsten, D. L.; Thomas, G. M. 1969. A nucleopolyhedrosis virus in populations of the Douglas-fir tussock moth, *Hemerocampa pseudotsugata,* in California. *Journal of Invertebrate Pathology* 13: 264-271.

Dahlsten, D. L.; Luck R. F.; Schlinger, E. I.; Wenz, J. M.; Copper, W. A. 1977. Parasitoids and predators of the Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae) in low to moderate populations in central California. *The Canadian Entomologist* 109: 727-746.

de Escudero, G. S.; Arenas, E.C.; Rudenbacher, M. C. 1979. *Acción de Parasierola nigrifemur* (Ash.) (Hym. Bethylidae) sobre *Rhyacionia buoliana* (Den. Schiff.) (Lep. Tortricidae) en pinares artificiales. I. Período 1976-1977. [Action of *Parasierola nigrifemur* (Ash.) (Hym. Bethylidae) on *Rhyacionia buoliana* (Den. and Schiff.) (Lep. Tortricidae) in pine plantations. I. Period 1976-1977.] *Acta Zoologica Lilloana* 35: 777-784.

DeMars, C. J., Jr.; Dahlsten, D. L.; Sharpnack, N. X.; Rowney, D. L. 1986. Tree utilization and density of attacking and emerging populations of the western pine beetle (Coleoptera: Scolytidae) and its natural enemies, Bass Lake, California, 1970-1971. *The Canadian Entomologist* 118: 881-900.

DeSantis, Millan de E.; DeSantis, L. 1958. Himenopteros parasitos de Evetria buoliana en las Republicas del Plata. [Hymenopterous parasites of *Rhyacionia buoliana* in the Plata Republics.] *Revista de investigaciones agricolas* 12 (1): 105-110.

DeSantis, Millan de E.; DeSantis, L. 1960. Himenopteros parasitos de *Evetria buoliana* (Schiff.) en la Republica Argentina. Segunda contribucion. [Hymenopterous parasites of Rhyacionia buoliana in the Argentine Republic. Second contribution.] *Revista de investigaciones agricolas* 14 (1): 25-29.

DeSantis, Millan de E.; DeSantis, L. 1961. Himenopteros parasitos de *Evetria buoliana* en la Republica Argentina. Tercera contribucion. [Hymenopterous parasites of *Rhyacionia buoliana* in the Argentine Republic. Third contribution.] *Revista de investigaciones agricolas* 15 (3): 461-464.

Doberski, J. W. 1981. Comparative laboratory studies on three fungal pathogens of the elm bark beetle *Scolytus scolytus:* Pathogenicity of *Beauvaria bassiana, Metarhizium anisopliae* and *Paecilomyces farinosus* to larvae and adults of *S. scolytus. Journal of Invertebrate Pathology* 37: 188-194.

Doganlar, M.; Beirne, B. P. 1978. Natural enemies of budworms, *Choristoneura* spp. (Lepidoptera: Tortricidae), on Douglas-fir near Yale, British Columbia, in 1977. *Journal of the Entomological Society of British Columbia* 75: 25-26.

Doidge, D. F.; Marshall, V. G. 1971. Spruce spider mite in British Columbia. Canadian Forest Service, *Forest Insect and Disease Survey Pest Leaflet 33.* Victoria, British Columbia: Forest Reserve Laboratory; 3 p.

Dowden, P. B. 1934. Recently introduced parasites of three important forest insects. *Annals of the Entomological Society of America* 27: 599-603.

Dowden, P. B. 1962. Parasites and predators of forest insects liberated in the United States through 1960. U.S. Department of Agriculture, *Agricultural Handbook* 226; 70 p.

Downing, G. L. 1959. Hemlock Sawfly. *U.S. Department of Agriculture Forest Pest Leaflet* 31; 4 p.

Drooz, A. T. 1960. The Larch Sawfly - Its Biology and Control. *U.S. Department of Agriculture Technical Bulletin No. 1212;* 52 p.

Drooz, A. T.; Bustillo, A. E.; Fedde, G. F.; Fedde, V. H. 1977. North American egg parasite successfully controls a difficult host genus in South America. *Science* 197: 390-391.

Drooz, A. T.; Quimby, J. W.; Thompson, L. C.; Kulman, H. M. 1985. Introduction and establishment of *Olesicampe benefactor* Hinz (Hymenoptera: Ichneumonidae), a parasite of the larch sawfly, *Pristiphora erichsonii* (Hartig) (Hymenoptera: Tenthredinidae), in Pennsylvania. *Environmental Entomology* 14 (4): 420-422.

Duarte, A.; Menendez, J. M.; Martinez, J. 1992. Use of a biopreparation of *Metarhizium anisopliae* strain Nina Bonita in plantations of *Pinus caribaea* for control of *Rhyacionia frustrana. Revista Forestal Baracoa* 22: 17-23.

Dubbel, V. 1992. The effectiveness of pine oil as a repellent against the striped ambrosia beetle *Trypodendron lineatum* (Col., Scolytidae). *Journal of Applied Entomology* 114 (1): 91-97.

Dyer, E. D. A.; Wright, K. H. 1967. Striped ambrosia beetle, *Trypodendron lineatum* (Oliv.). *In*: Davidson, A. G.; Prentice, R. M. (eds.). *Important Forest Insects and Diseases of Mutual Concern to Canada, the United States, and Mexico.* Ottawa: Canadian Department of Forestry and Rural Development; 27-30.

Eikenbary, R. D.; Fox, R. C. 1965. The parasites of the Nantucket pine tip moth in South Carolina. *Technical Bulletin of South Carolina Agricultural Experiment Station* 1017; 9p.

Eikenbary, R. D.; Fox, R. C. 1968a. Arthropod predators of the Nantucket pine tip moth, *Rhyacionia frustrana. Annals of the Entomological Society of America* 61(5): 1218-1221.

Eikenbary, R. D.; Fox, R. C. 1968b. Investigations of *Campoplex frustranae,* a parasite of the Nantucket pine tip moth. *Annals of the Entomological Society of America* 61(6): 1430-1433.

Engelhardt, G. P. 1924. The Saturniid moth, *Coloradia pandora,* a menace to pine forests and a source of food to Indians in eastern Oregon. *Bulletin of the Brooklyn Entomological Society* 19: 35-37.

Evans, D. 1962. Descriptions and life history of *Melanolophia imitata* (Walker) (Lepidoptera: Geometridae). *The Canadian Entomologist* 94: 594-605.

Evans, H. 1987. Observations on natural enemies of western spruce budworm (*Choristoneura occidentalis* Freeman) (Lepidoptera, Tortricidae) in the Rocky Mountain area. *Great Basin Naturalist* 47(2): 319-321.

Evans, J. W. 1930. The control of the codling moth in Australia. Notes on the possible utilization of *Trichogramma* (Hymenoptera: Chalcidoidea). *Journal of the Council for Scientific and Industrial Research* 3(2): 106-116.

Evenden, J. C. 1926. The pine butterfly, *Neophasia menapia* Felder. *Journal of Agricultural Research* 33: 339-344.

Filip, G. M.; Goheen, D. J. 1982. Tree mortality caused by root pathogen complex in Deschutes National Forest, Oregon. *Plant Disease* 66 (3): 240-243.

Filipescu, C.; Tudor, I.; Marcu, O. 1970. Braconidae (Hymenoptera) parasitic in pupae of *Evetria buoliana* Schiff. (Lepidoptera: Tortricidae). *Communicari de Zoologie* (1970): 121-126.

Finney, J. R.; Walker, C. 1977. The DD-136 strain of *Neoaplectana* as a potential biological control agent for the European bark beetle, *Scolytus scolytus. Journal of Invertebrate Pathology* 29: 7-9.

Fitton, M. G.; Gauld, I. D. 1980. A review of the British Cremastinae (Hymenoptera: Ichneumonidae), with keys to the species. *Entomologist's Gazette* 31 (1): 63-71.

Fitzpatrick, S. M.; Troubridge, J. T.; Peterson, B. 1991. Distribution of European winter moth, *Operophtera brumata* (L.), and Bruce spanworm, *O. bruceata* (Hulst), in the lower Fraser Valley, British Columbia. *Journal of the Entomological Society of British Columbia* 88: 39-45.

Forbes, R. S.; Underwood, G. R.; Cuming, F. G. 1964. Maritime Provinces. Forest insect conditions. In: *A Report of Forest Insect and Disease Survey,* 1963. Ottawa: Forest Entomological Pathology, British Department Forestry, 21-32.

Fouts, R. 1928. Notes on the Bethylinae with descriptions of one new Cuban and twelve new North American species (Hym.). *Proceedings of the Entomological Society of Washington* 30(7): 121-132.

Fransen, J. J. 1931. Some data on the spread by the cambium beetles, *Scolytus scolytus* F. and S. *multistriatus* Marsh. of the elm disease due to *G. ulmi* in connection with the control of the disease. *Tijdschrift over Plantenziekten* 37: 49-62.

Freeman, B. L.; Berisford, C. W. 1979. Abundance and parasitic habits of some parasitoids of the Nantucket pine tip moth (Lepidoptera: Tortricidae). *The Canadian Entomologist* 111: 509-514.

Freeman, T. N. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. 1. Some new forms of *Choristoneura* allied to *C. fumiferana*. *The Canadian Entomologist* 99 (5): 449-455.

Furniss, M. M. 1967. Nematode parasites of the Douglas-fir beetle in Idaho and Utah. *Journal of Economic Entomology* 60 (5): 1323-1326.

Furniss, M. M. 1968. Notes on the biology and effectiveness of *Karpinskiella paratomicobia* parasitizing adults of *Dendroctonus pseudotsugae*. *Annals of the Entomological Society of America* 61 (6): 1384-1389.

Furniss, M. M.; Cibrián Tovar, D. 1980. Reproductive compatibility and insects associated with *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae) from Chihuahua, Mexico and Idaho, USA. *Folia Entomologica Mexicana* 44: 129-142.

Furniss, R. L.; Carolin, V. M. 1977. Western Forest Insects, *Miscellaneous Publication No. 1339.* U.S. Department of Agriculture, Forest Service; 654 p.

Furniss, R. L.; Dowden, P. B. 1941. Western hemlock sawfly, *Neodiprion tsugae* Middleton, and its parasites in Oregon. *Journal of Economic Entomology* 34: 46-52.

Furniss, M. M.; Daterman, G.E.; Kline, L. N.; McGregor, M.D.; Trostle, G.C.; Pettinger, L. F.; Rudinsky, J. A. 1974 Effectiveness of the Douglas-fir beetle antiaggregative pheromone methylcyclohexenone at three concentrations and spacing around felled host trees. *The Canadian Entomologist* 106 (4): 381-392.

Gahan, A. B. 1927. Four new Chalcidoid parasites of the pine tip moth, *Rhyacionia frustrana* (Comstock). *Journal of Agricultural Research* 34 (6): 545-548.

Gara, R. I.; Werner, R. A.; Whitmore, M. C.; Holsten, E. H. 1995. Arthropod associates of the spruce beetle, *Dendroctonus rufipennis* (Kirby) (Col., Scolytidae) in spruce strands of south-central and interior Alaska. *Journal of Applied Entomology* 119: 585-590.

Gemma, J. N.; Hartmann, G. C.; Wasti, S. S. 1984. Inhibitory interactions between the Dutch elm fungus, *Ceratocystis ulmi* and several species of entomogenous fungi. *Mycologia* 76: 256-260.

Gemma, J. N.; Wasti, S. S.; Hartmann, G. C. 1985. Antagonism of entomogenous fungal extracts to the Dutch elm disease fungus, *Ceratocystis ulmi*. *Journal of the New York Entomological Society* 93: 1109-1112.

Goheen, D. J.; Cobb, F. W., Jr.; Rowney, D. L. 1985. Visitation frequencies of some insect species on *Ceratocystis wagneri* infected and apparently healthy ponderosa pines. *The Canadian Entomologist* 117: 1535-1543.

Goyer, R. A.; Schenk, J. A. 1969. Parasitism of the cone moth, *Eucosma rescissoriana* (Lepidoptera: Olethreutidae), in northern Idaho. *The Canadian Entomologist* 101: 1063-1069.

Goyer, R. A.; Schenk, J. A. 1970. Notes on the biology and habits of insect parasites associated with *Eucosma rescissoriana* (Lepidoptera: Olethreutidae) in northern Idaho. *The Canadian Entomologist* 102: 1546-1553.

Graham, K. 1954. Notes on a polyhedral disease of black-headed budworm. *The Canadian Entomologist* 86 (12): 546-548.

Graham, S. A. 1956. Forest insects and the law of natural compensations. *The Canadian Entomologist* 88: 45-55.

Gray, T.; Shepherd, R. 1993. Hymenopterous parasites of the blackheaded budworm, *Acleris gloverana* on Vancouver Island, British Columbia, 1970-1974. *Journal of the Entomological Society of British Columbia* 90: 11-13.

Greathead, D. J.; Greathead, A. H. 1992. Biological control of insect pests by parasitoids and predators: The BIOCAT database. *Biocontrol News and Information* 13 (4): 61N-68N.

Gulii, V. V. 1963. Increasing the effectiveness of parasites of the pine-shoot moth (*Evetria buoliana* Schiff.) in pine stands on the northern slopes of the Central Caucasus. *Zoologicheskii Institut (Akademia nauk SSSR) Zhivotnyi mir SSSR* 42 (9): 1414-1415.

Gutierrez, J.; Kreiter, S.; Brian, F.; Cotton, D. 1986. Mites, little-known pests of cypress. *Phytoma* (376): 47-48.

Hajek, A. E.; Dahlsten, D. L. 1985. Insect and Mite Associates of *Scolytus multistriatus* (Coleoptera: Scolytidae) in California. *The Canadian Entomologist* 117: 409-421.

Hall, D. G. 1939. Two new species of Tachinidae parasitic upon hemlock sawfly larvae in North America (Diptera: Tachinidae). *Proceedings of the Entomological Society of Washington* 41: 239-243.

Halstead, J. A. 1990. New Hosts for *Cephalonomia utahensis* Brues (Hymenoptera: Bethylidae). *Pan-Pacific Entomologist* 66: 170-171.

Hamel, D. R. 1977. The effects of *Bacillus thuringiensis* on parasitoids of the western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), and the spruce coneworm, *Dioryctria reniculelloides* (Lepidoptera: Pyralidae), in Montana. *The Canadian Entomologist* 109(11): 1409-1415.

Hanula, J. L.; Berisford, W. C. 1984. Seasonal flight activity of the smaller European elm bark beetle, *Scolytus multistriatus* (Coleoptera: Scolytidae), and associates in Georgia. *The Canadian Entomologist* 116: 1251-1258.

Hard, J. S. 1974. Budworm in coastal Alaska. *Journal of Forestry* 72 (1): 26-31.

Hard, J. S. 1976. Natural control of hemlock sawfly, *Neodiprion tsugae* (Hymenoptera: Diprionidae), populations in southeast Alaska. *The Canadian Entomologist* 108: 485-498.

Harman, D. M.; Kulman, H. M. 1962. Parasites of the European pine shoot moth, *Rhyacionia buoliana. Journal of Economic Entomology* 55 (6): 1007-1008.

Harris, J. W. E.; Dawson, A. F. 1979. Parasitoids of the western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in British Columbia. *Journal of the Entomological Society of British Columbia* 76: 30-38.

Harris, P. 1960. Natural mortality of the pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae), in England. *Canadian Journal of Zoology* 38: 755-768.

Hedlin, A. F. 1960. On the life history of the Douglas-fir cone moth, *Barbara colfaxiana* (Kft.) (Lepidoptera: Olethreutidae), and one of its parasites, *Glypta evetriae* Cush. (Hymenoptera: Ichneumonidae). *The Canadian Entomologist* 92: 826-834.

Hedlin, A. F. 1964. A six-year plot study on Douglas-fir cone insect population fluctuations. *Forest Science* 10: 124-128.

Herting, B. 1973. *A Catalogue of Parasites and Predators of Terrestrial Arthropods. Section A: Host or Prey Enemy. Vol. III. Coleoptera to Strepsiptera.* Farnham Royal, England: Commonwealth Institute of Biological Control; 185 p.

Holland, W. J. 1903. *The Moth Book: A popular guide to a knowledge of the moths of North America.* New York: Doubleday, Page, and Co.; 479 p.

Holsten, E. H.; Hard, J. 1985. Efficacy of *Bacillus thuringiensis* Berliner for suppressing populations of large aspen tortrix in Alaska. *The Canadian Entomologist* 117: 587-591.

Hopping, G. R. 1934. An account of the western hemlock looper, *Ellopia somniaria* Hulst, on conifers in British Columbia. *Scientific Agriculture* 15: 12-29.

Hopping, G. R. 1948. Notes on the seasonal development of *Medetera aldrichii* Wheeler (Diptera: Dolichopidae) as a predator of the Douglas-fir bark beetle, *Dendroctonus pseudotsugae* Hopkins. *The Canadian Entomologist* 79 (7-8): 150-153.

Hopping, G. R.; Leech, H. B. 1936. Sawfly biology. I. *Neodiprion tsugae* Middleton. *The Canadian Entomologist* 68: 71-79.

Houle, C.; Hartmann, G. C.; Wasti, S. S. 1987. Infectivity of eight species of entomogenous fungi to the larvae of the elm bark beetle, *Scolytus multistriatus* (Marsham). *Journal of the New York Entomological Society* 95: 14-18.

Hughes, K. M. 1977. Observations on the morphology of nuclear polyhedrosis viruses from six forest insects. *The Canadian Entomologist* 109 (5): 759-762.

Hulme, M. A. 1990. Field assessment of predation by *Lonchaea corticis* (Diptera: Lonchaeidae) on *Pissodes strobi* (Coleoptera: Curculionidae) in *Picea sitchensis. Environmental Entomology* 19 (1): 54-58.

Hulme, M. A.; Miller, G. E. 1988. Potential for control of *Barbara colfaxiana* (Kearfott): (Lepidoptera: Olethreutidae) using *Trichogramma* sp. *Colloques de l'INRA* No. 43 *In: Trichogramma and other egg parasites.* Victoria, BC: Pacific Forest Centre; 438-488.

Humble, L. M. 1985. Seasonal activity of ichneumonid pupal parasitoids of *Operophtera* spp. (Lepidoptera: Geometridae). *Journal of the Entomological Society of British Columbia* 82: 44-46.

Humble, L. M. 1994. Recovery of additional exotic predators of balsam woolly adelgid, *Adelges piceae* (Ratzeburg) (Homoptera: Adelgidae), in British Columbia. *The Canadian Entomologist* 126: 1101-1103.

Ives, W. G. H. 1973. Heat units and outbreaks of the forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae). *The Canadian Entomologist* 105: 529-543.

Ives, W. G. H. 1976. The dynamics of larch sawfly (Hymenoptera: Tenthredinidae) populations in southeastern Manitoba. *The Canadian Entomologist* 108: 701-730.

Ives, W. G. H.; Cunningham, J. C. 1980. Application of nuclear polyhedrosis virus to control Bruce spanworm (Lepidoptera: Geometridae). *The Canadian Entomologist* 112: 741-744.

Jassim, H. K.; Foster, H. A.; Fairhurst, C. P. 1990. Biological control of Dutch elm disease: Larvicidal activity of *Trichoderma harzianum, T. polysporum* and *Scytalidium lignicola* in *Scolytus scolytus* and *S. multistriatus* reared in artificial culture. *Annals of Applied Biology* 117: 187-196.

Jaynes, H. A.; MacAloney, H. J. 1958. White pine weevil. *U.S. Department of Agriculture Forest Pest Leaflet* 21, 7 p.

Jennings, D. T. 1975. Life history and habits of the southwestern pine tip moth, *Rhyacionia neomexicana* (Dyar) (Lepidoptera: Olethreutidae). *Annals of the Entomological Society of America* 68: 597-606

Jennings, D. T. ; Toliver, M. E. 1976. Crab spider preys on *Neophasia menapia* (Peiridae). *Journal of the Lepidopterists' Society* 30 (3): 236-237.

Johnson, N. E.; Mitchell, R. G.; Wright, K. H. 1963. Mortality and damage to Pacific silver fir by the balsam woolly aphid in southwestern Washington. *Washington Journal of Forestry* 61: 854-860.

Johnson, P. C. 1958. Spruce spider mite infestations in northern Rocky Mountain Douglas-fir forests. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, *Research Paper 55,* Jolyet, A. 1918. The use of bats in the control of insects especially Tortricidae, injurious to pine woods. *Revue des Eaux et Forets,* Paris 56 (6): 121-216.

Juillet, J. A. 1959. Morphology of immature stages, life-history, and behaviour of three hymenopterous parasites of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae). *The Canadian Entomologist* 91(11): 709-719.

Kaya, H. K.; Reardon, R. C. 1982. Evaluation of *Neoaplectana carpocapsae* for biological control of the western spruce budworm, *Choristoneura occidentalis:* ineffectiveness and persistence of tank mixes. *Journal of Nematology* 14(4): 595-597.

Kaya, H. K.; Hara, A. H.; Reardon, R. C. 1981. Laboratory and field evaluation of *Neoaplectana carpocapsae* (Rhabditida: Steinernematidae) against the elm leaf beetle (Coleoptera: Chrysomelidae) and the western spruce budworm (Lepidoptera: Tortricidae). *The Canadian Entomologist* 113: 787-793.

Kearby, W. H.; Taylor, B. 1975. Larval and pupal parasites reared from tip moths of the genus *Rhyacionia* in Missouri (Lepidoptera: Olethreutidae). *Journal of the Kansas Entomological Society* 48: 206-211.

Keen, F. P. 1958. *Cone and seed insects of western forest trees.* U.S. Department of Agriculture Technical Bulletin 1169; 168 p.

Keen, F. P.; Salman, K. A. 1942. Progress in pine beetle control through tree selection. *Journal of Forestry* 40 (11): 854-858.

Keifer, H. H.; Saunders, J. L. 1972. *Trisetacus campnodus,* n. sp. (Acarina: Eriophyidae), attacking *Pinus sylvestris. Annals of the Entomological Society of America* 65: 46-49.

Kelleher, J. S.; Hulme, M. A. (eds.). 1981. *Biological control programmes against insects and weeds in Canada 1969-1980.* Farnham Royal, U.K: Commonwealth Agricultural Bureaux; 410 p.

Kenis, M.; Mills, N. J. 1994. Parasitoids of European species of the genus *Pissodes* (Col: Curculionidae) and their potential for the biological control of *Pissodes strobi* (Peck) in Canada. *Biological Control* 4: 14-21.

Kennedy, B. H. 1970. *Dendrosoter protuberans* (Hymenoptera: Braconidae), an introduced larval parasite of *Scolytus multistriatus. Annals of the Entomological Society of America* 63: 351-358.

Knight, G. A.; Lavigne, R. J.; Pogue, M. G. 1991. The parasitoid complex of forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae), in eastern Wyoming shelterbelts. *The Great Lakes Entomologist* 24 (4): 255-261.

Kramer, D. A.; Hain, F. P. 1989. Effect of constant and variable humidity and temperature regimes on the survival and developmental periods of *Oligonychus ununguis* (Acarina: Tetranychidae) and *Neoseiulus fallacis* (Acarina: Phytoseiidae). *Environmental Entomology* 18: 741-746.

Kulman, H. M. 1965. Oviposition habits of *Trichogramma minutum* on artificial concentrations of eggs of the European pine shoot moth. *Annals of the Entomological Society of America* 58 (2): 241-243.

Kulman, H. M.; Thompson, L. C.; Witter, J. A. 1974. Introduction of parasites of the larch sawfly in Minnesota. *Great Lakes Entomologist* 7: 23-25.

Lanfranco, D.; Cerda, L. 1986. *Coccygomimus fuscipes,* an indigenous ichneumon parasite of the budworm *Rhyacionia buoliana. Bosque* 7 (1): 36-37.

Lashomb, J. H.; Steinhauer, A. L. 1975. Observations of *Zethus spinipes* Say (Hymenoptera: Eumenidae). *Proceedings of the Entomological Society of Washington* 77: 164.

Lashomb, J. H.; Steinhauer, A. L. 1982a. Within-tree response of Nantucket pine tip moth, *Rhyacionia frustrana* (Lep.: Tortricidae) parasitoids to varying host densities. *Entomophaga* 27: 277-282.

Lashomb, J. H.; Steinhauer, A. L. 1982b. Association of three Nantucket pine tip moth parasitoids within the crown of loblolly pine. *Journal of the Georgia Entomological Society* 17: 287-291.

Leius, K. 1967. Food sources and preferences of adults of a parasite, *Scambus buolianae* (Hym.: Ichn.), and their consequences. *The Canadian Entomologist* 99: 865-871.

Lewis, K. R.; Kulman, H. M.; Heikkenen, H. J. 1970. Parasites of the Nantucket pine tip moth in Virginia with notes on ecological relationships. *Journal of Economic Entomology* 63: 1135-1139.

Lindgren, B. S. 1992. Attraction of Douglas-fir beetle, spruce beetle and a bark beetle predator (Coleoptera: Scolytidae and Cleridae) to enantiomers of frontalin. *Journal of the Entomological Society of British Columbia* 89: 13-17.

Lipa, J. J. 1968. *Stempellia scolyti* (Weiser) comb. nov. and *Nosema scolyti* sp. n., microsporidian parasites of four species of *Scolytus* (Coleoptera). *Acta Protozoologica* 6: 69-78.

Loan, C.; Doganlar, D. 1980. *Oedemopsis scabricular* in British Columbia (Hymenoptera: Ichneumonidae, Tryphoninae). *Naturaliste Canadien* 107 (1): 11-14.

Long, D. W.; Wagner, M. R. 1992. Effects of southwestern pine tip moth and vegetation competition on ponderosa pine growth. *Forest Science* 38: 173-186.

Löyttyniemi, K. 1970. On the biology of the conifer spider mite (*Oligonychus ununguis*) in Finland. *Acta Entomologica Fennica* 27; 64 p.

Luck, R. F. 1976. Bionomics and parasites of a needle miner, *Coleotechnites* sp., infesting Jeffrey pine in southern California. *Environmental Entomology* 5 (5): 937-942.

Maksimovic, M. 1979. Influence of the density of bark beetles and their parasites on dieback of elm in some woods of Yugoslavia. *Zeitschrift fur Angewandte Entomologie* 88: 283-295

Maksimovic, M. 1986. Laboratory investigations on the parasites of elm bark beetles. *Zastita Bilja* 37 (1): 5-20.

Maksimovic, M.; Schindler, U. 1969. Investigations on the pine shoot moth Rhyacionia (Evetria) buoliana Schiff. and its parasites in Serbia. Zeitschrift fur Angewandte Entomologie 64 (1): 86-103.

Mangini, Jr., A. C.; Hain, F. P. 1991. Vapor pressure deficit differentially affects laboratory populations of *Metaseiulus occidentalis* and *Neoseiulus fallacis* (Acarina: Phytoseiidae) reared together. *Environmental Entomology* 20: 823-831.

Marlatt, C. L. 1933. *Report of the Chief of the Bureau of Entomology,* 1933. Washington D.C.: U.S. Department of Agriculture; 47 p.

Marsden, M. A.; Furniss, M. M.; Kline, L. N. 1981. *Modeling seasonal abundance of Douglas-fir beetle in relation to entomophagous insects and location in trees.* U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station General Technical Report 111; 23 p.

Martignoni, M. E.; Stelzer, M. J.; Iwai, P. J. 1982. Baculovirus of *Autographa californica* (Lepidoptera: Noctuidae): a candidate biological control agent for Douglas-fir tussock moth (Lepidoptera: Lymantriidae). *Journal of Economic Entomology* 74: 1120-1124.

Martinat, P. J. 1987. The role of climatic variation and weather in forest insect outbreaks. In: Barbosa, P.; Schultz, J.C., (eds.). *Insect Outbreaks.* New York: Academic Press; 241-268.

Martineau, R.; Monnier, C. 1966. Recent outbreak of the Bruce spanworm in Quebec. *Bi-monthly Research Notes of the Department of Forest Canada* 22: 5.

Mason, R. R. 1976. Life tables for a declining population of the Douglas-fir tussock moth in northeastern Oregon. *Annals of the Entomological Society of America* 69: 948-958.

Mason, R. R. 1981. Numerical analysis of the causes of population collapse in a severe outbreak of the Douglas-fir tussock moth. *Annals of the Entomological Society of America* 74: 51-57.

Mason, R. R.; Paul, H. G. 1988. Predation on larvae of Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae), by *Metaphidippus aeneolus* (Araneae: Salticidae). *The Pan-Pacific Entomologist* 64: 258-260.

Mason, R. R.; Thompson, C. G. 1971. Collapse of an outbreak population of the Douglas-fir tussock moth, *Hemerocampa pseudotsugata* (Lepidoptera: Lymantriidae). U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station *Research Note* 139; 10 p.

Mason, R. R.; Torgersen, T. R. 1983. Mortality of larvae in stocked cohorts of the Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae). *The Canadian Entomologist* 115: 1119-1127.

Mason, R. R.; Torgersen, T. R. 1987. Dynamics of a non-outbreak population of the Douglas-fir tussock moth (Lepidoptera: Lymantriidae) in southern Oregon. *Environmental Entomology* 16: 1217-1227.

Mason, R. R.; Torgersen, T. R.; Wickman, B. E.; Paul, H. G. 1983. Natural regulation of a Douglas-fir tussock moth (Lepidoptera: Lymantriidae) population in the Sierra Nevada. *Environmental Entomology* 12: 587-594.

Mason, W. R. M. 1974. The Apanteles species (Hymenoptera: Braconidae) attacking Lepidoptera in the micro-habitat of the spruce budworm (Lepidoptera: Tortricidae). *The Canadian Entomologist* 106: 1087-1102.

Massey, C. L. 1974. Biology and taxonomy of nematode parasites and associates of bark beetles in the United States. *Agriculture Handbook* No. 446. Washington, D.C.; U.S. Department of Agriculture, Forest Service; 233 p.

Massey, C. L.; Wygant, N. D. 1954. Biology and control of the Engelmann spruce beetle in Colorado. *U.S. Department of Agriculture, Forest Service Circular No. 944*; 35 p.

Mathers, W. G.; Olds, H. F. 1940. The European pine shoot moth in British Columbia. *Journal of Economic Entomology* 33 (6): 941.

Mazzone, H. M.; Peacock, J. W. 1985. Prospects for control of Dutch elm disease - biological considerations. *Journal of Arboriculture* 11: 285-292.

McCambridge, W. F.; Downing, G. L. 1960. Black-headed budworm. U.S. Department of Agriculture, Forest Service, *Forest Pest Leaflet* 45; 4 p.

McCambridge, W. F.; Knight, F. B. 1972. Factors affecting spruce beetles during a small outbreak. *Ecology* 53: 830-839.

McGheney, J. H.; Nagel, W. P. 1969. The biologies of *Pseudohylesinus tsugae* and *P. grandis* (Coleoptera: Scolytidae) in western hemlock. *The Canadian Entomologist* 101: 269-279.

McGregor, M. D. 1970. Biological observations on the life history and habits of *Choristoneura lambertiana* (Lepidoptera: Tortricidae) on lodgepole pine in southeastern Idaho and western Montana. *The Canadian Entomologist* 102: 1201-1208.

McGuffin, W.C. 1973. The *Rheumaptera* of North America. *The Canadian Entomologist* 105: 383-398.

McGugan, B.M.; Coppel, H.C. 1962. Biological control of forest insects, 1910-1958. In: "A Review of the Biological Control Attempts against Insects and Weeds in Canada." *Commonwealth Institute of Biological Control Technical Communication* 2: 35-127.

McKnight, M.E. 1968. Natural mortality factors of western budworm in Colorado. *Proceedings of the North Carolina Branch of the American Association of Economic Entomology* 23: 45-46.

McKnight, M.E. 1973. Parasitoids reared from collections of Rhyacionia bushnelli from the Great Plains. *Journal of the Kansas Entomological Society* 46: 139-143.

McKnight, M.E. 1974. Parasitoids of the western spruce budworm in Colorado. *Environmental Entomology* 3(1): 186-187.

McLeod, J. H. 1954. Statuses of some introduced parasites and their hosts in British Columbia. *Proceedings of the Entomological Society of British Columbia* 50: 19-27.

Medley, R. D.; Carolin, V. M., Jr. 1977. *Chaetophlepsis nasellensis,* a dipterous parasitoid of the western hemlock looper (Lepidoptera: Geometridae). *The Canadian Entomologist* 109: 1121-1128.

Menendez, J. M.; Echevarria, E.; Garcia, A.; Berrios, C.; Fernandez, C.; Valdes, H.; Ramos, R. 1986. Use of *Bacillus thuringiensis* in the control of *Rhyacionia frustrana. Revista Forestal Baracoa* 16: 101-111.

Merlin, J. 1984. Elm bark beetles and their main parasitoids in Belgium: emergence and some aspects of their ecological relations. *Mededelingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent.* 49 (3a): 857-865.

Miller, J. M. 1915. Cone beetles: injury to sugar pine and western yellow pine. *United States Department of Agriculture Bulletin No. 243*; 12 p.

Miller, W. E. 1967. Taxonomic review of the *Rhyacionia frustrana* group of pine-tip moths, with description of a new species (Olethreutidae). *The Canadian Entomologist* 99: 590-596.

Miller, M. C.; Moser, J.C.; McGregor, M.; Gregoire, J. C.; Baisier, M.; Dahlsten, D. L.; Werner, R. A. 1987. Potential for biological control of native North American *Dendroctonus* beetles (Coleoptera: Scolytidae). *Annals of the Entomological Society of America* 80: 417-428.

Mills, N. J. 1983. The natural enemies of Scolytids infesting conifer bark in Europe in relation to the biological control of *Dendroctonus* spp. in Canada. *Biocontrol News and Information* 4 (4): 303-326.

Mills, N. J.; Krüger, K. 1988. Host location: An important factor in the use of exotic natural enemies for the biocontrol of native Scolytids. In: Payne, T. L.; Saarenmaa, H. (eds.) *Integrated Control of Scolytid Bark Beetles.* Blacksburg, VA: College of Agriculture and Life Sciences, Virginia Polytechnic Institute and State University; 321-328.

Mills, N. J.; Räther, M. 1990. Hemlock loopers in Canada; biology, pest status and potential for biological control. *Biocontrol News and Information* 11: 209-221.

Mitchell, R. G.; Wright, K. H. 1967. Foreign predator introductions for control of the balsam woolly aphid in the Pacific Northwest. *Journal of Economic Entomology* 60: 140-147.

Mizell, R. F.; Schiffhauer, D. E. 1991. Kairomone response, pesticide tolerance and field efficacy of the predatory mite, *Neoseiulus collegae* (De Leon). *Journal of Environmental Horticulture* 9: 155-159.

Moeck, H. A.; Safranyik, L. 1983. Assessment of predator and parasitoid control of bark beetles. Canada: Pacific Forest Research Center, *Information Report No. BC-X-248;* 24 p.

Morris, O. N. 1962. Comparative susceptibility of four forest insects to a commercial preparation of Bacillus thuringiensis (Berliner). The Canadian Entomologist 94: 686-690.

Morris, O. N. 1963. The natural and artificial control of the Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough, by a nuclear-polyhedrosis virus. *Journal of Insect Pathology* 5: 401-414.

Morris, O. N. 1983. Microorganisms isolated from forest insects of British Columbia. *Journal of the Entomological Society of British Columbia* 80: 29-36.

Moser, J. C. 1989. Inoculative release of an exotic predator for the biological control of the black turpentine beetle. *In*: Kulhavy, D.L.; Miller, M.C., (eds.). *Potential for Biological Control of Dendroctonus* and *Ips* Bark Beetles. Nacogdoches, TX: Center for Applied Studies, School of Forestry, Stephen F. Austin State University; 189-200.

Moser, J. C.; Smiley, R. L.; Otvos, I. S.; Lorio, P. L. 1986. Pyemotes n. sp. (Acari: Pyemotidae) a potential biological control agent for cone and seed insects. *In*: Roques, A. (ed.) *Proceedings of the 2nd Conference of the Cone and Seed Insects Working Party S2.07-01. September 3-5, 1986* Olivet, France: Station de Zoologie Forestiere. Pineville, LA: U.S. Department of Agriculture, Forest Service; 307-310.

Muesebeck, C. F. W. 1933. Seven new species of reared Braconidae (Hymenoptera). *Proceedings of the Entomological Society of Washington* 35(9): 193-200.

Muesebeck, C. F. W. 1940. Two new reared species of *Bassus* (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Washington* 42(4): 91-93.

Muldrew, J. A. 1953. The natural immunity of the larch sawfly (*Pristiphora erichsonii* HTG.) to the introduced parasite *Mesoleius tenthredinis* Morley in Manitoba and Saskatchewan. *Canadian Journal of Zoology* 31: 313-332.

Muldrew, J. A. 1955. Parasites and insect predators of the larch sawfly. *The Canadian Entomologist* 87: 117-120.

Murphy, C. F.; Croft, B. A. 1990. Forest ant composition and foraging following aerial spraying of carbaryl to suppress western spruce budworm. *The Canadian Entomologist* 122: 595-606.

Nagel, W. P.; Fitzgerald, T. D. 1975. *Medetera aldrichii* larval feeding behavior and prey consumption (Diptera: Dolichopodidae). *Entomophaga* 20 (1): 121-127.

Nebeker, T. E. 1977. A partial life table for the Douglas-fir cone moth, *Barbara colfaxiana* (Lepidoptera: Olethreutidae). *The Canadian Entomologist* 109: 943-951.

Nebeker, T. E. 1989. Bark beetles, natural enemies, management selection interactions. In: Kulhavy, D.L.; Miller, M.C., (eds.). *Potential for Biological Control of Dendroctonus and* Ips *Bark Beetles.* Nacogdoches, TX: Center for Applied Studies, School of Forestry, Stephen F. Austin State University; 71-80.

O'Brien, M. F.; O'Brien, A. M. 1988. Biology of *Ammophila evansi* and *A. mediata* in northern Michigan (Hymenoptera: Sphecidae). *Pan-Pacific Entomologist* 64 (1): 73-79.

Ogloblin, A. 1960. Un betilido parasito de la *Evetria buoliana* (Schiff.) (Hymenoptera, Bethylidae). [A Bethylid parasite of *Rhyacionia buoliana.*]. *Revista de investigaciones agricolas* 14 (1): 35-40.

Oldham, J. N. 1930. On the infestation of elm bark beetles (Scolytidae) by a nematode, *Parasitylenchus scolyti* n. sp. Journal of *Helminthology* 8: 239-248.

Ollieu, M. M.; Schenk, J. A. 1966. The biology of *Eucosma rescissoriana* Heinrich in western white pine in Idaho (Lepidoptera: Olethreutidae). *The Canadian Entomologist* 98: 268-274.

Otvos, I. S. 1965. Studies on avian predators of *Dendroctonus brevicomis* LeConte (Coleoptera: Scolytidae) with special reference to Picidae. *The Canadian Entomologist* 97 (11): 1184-1199.

Patterson, J. E. 1929. The Pandora moth, a periodic pest of western pine forests. *U.S. Department of Agriculture Technical Bulletin No. 137;* 99 p.

Payne, T. L. 1989. Olfactory basis for insect enemies of allied species. *In*: Kulhavy, D.L.; Miller, M.C., (eds.). *Potential for Biological Control of Dendroctonus and* Ips *Bark Beetles.* Nacogdoches, TX: Center for Applied Studies, School of Forestry, Stephen F. Austin State University; 55-69.

Payne, T. L.; Billings, R. F. 1988. Effect of pheromone and pheromone plus tree cutting on suppression of southern pine beetle infestations. *In*: Payne, T. L.; Saarenmaa, H. (eds.) *Integrated Control of Scolytid Bark Beetles.* Blacksburg, VA: College of Agriculture and Life Sciences, Virginia Polytechnic Institute and State University; 267-274.

Pettinger, L. F. 1978. On the downswing. *In*: Brooks, M. H.; Stark, R. W.; Campbell, R. W. (eds.). *The Douglas-fir tussock moth:* a synthesis. U.S. Department of Agriculture, Forest Service Technical Bulletin 1585; 2-7.

Pettinger, L. F. 1985. Douglas-fir tussock moth. *In: Insect and Disease Conditions in the United States* 1979-83. General Technical Report WO-46, U.S. Department of Agriculture, Forest Service; 2-7.

Pimentel, D.; Hokkanen, H. 1989. Alternative for successful biological control in theory and practice. *In*: Kulhavy, D.L.; Miller, M.C., (eds.). *Potential for Biological Control of Dendroctonus and Ips Bark Beetles.* Nacogdoches, TX: Center for Applied Studies, School of Forestry, Stephen F. Austin State University; 21-51.

Poinar, G. O., Jr.; Deschamps, H. 1981. Susceptibility of *Scolytus multistriatus* to neoaplectanid and heterorhabditid nematodes. *Environmental Entomology* 10: 85-87.

Pointing, P. J. 1966. A quantitative field study of predation by the sheet-web spider, *Frontinella communis,* on European pine shoot moth adults. *Canadian Journal of Zoology* 44 (2): 265-273.

Powell, J. A. 1962. Taxonomic studies on the *Acleris gloverana-variana* complex, the black-headed budworms (Lepidoptera: Tortricidae). *The Canadian Entomologist* 94: 833-840.

Prazak, R. 1991. Studies on indirect infection of *Trypodendron lineatum* Oliv. with *Beauveria bassiana* (Bals.) Vuill. *Journal of Applied Entomology* 111: 431-441.

Prentice, R. M. 1955. The life history and some aspects of the ecology of the large aspen tortrix, *Choristoneura conflictana* (Wlkr.) (n. comb.) (Lepidoptera: Tortricidae). *The Canadian Entomologist* 11: 461-473.

Pusey, P. L.; Wilson, C. L. 1979. Double-stranded RNA in *Ceratocystis ulmi. Phytopathology* 69: 542.

Putman, W. L. 1955. Bionomics of *Stethorus punctillum* Weise (Coleoptera: Coccinellidae) in Ontario. *The Canadian Entomologist* 87: 9-33.

Raffa, K. F. 1991. Temporal and spatial disparities among bark beetles, predators, and associates responding to synthetic bark beetle pheromones: *Ips pini* (Coleoptera: Scolytidae) in Wisconsin. *Environmental Entomology* 20 (6): 1665-1679.

Rasmussen, L. A. 1976. Keys to common parasites and predators of the mountain pine beetle. Ogden, UT: *U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station General Technical Report* 29; 4 p.

Reid, R. W. 1963. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay region of British Columbia. III. Interaction between the beetle and its host, with emphasis on brood mortality and survival. *The Canadian Entomologist* 95 (3): 225-238.

Richerson, J. V.; Borden, J. H. 1972. Host finding behavior of *Coeloides brunneri* (Hymenoptera: Braconidae). *The Canadian Entomologist* 104 (8): 1235-1250.

Ross, H. H. 1955. The taxonomy and evolution of the sawfly genus *Neodiprion. Forest Science* 1 (3): 196-209.

Ruschka, F. 1924. Minor contributions to the knowledge of the forest chalcids and proctotrupids of Sweden. *Entomologisk Tidskftri* 45 (1): 6-16.

Rust, H. J. 1933. Many bark beetles destroyed by predacious mite. *Journal of Economic Entomology* 26 (3): 732-733.

Ryan, R. B. 1980. Rearing methods and biological notes for seven species of European and Japanese parasites of the larch casebearer (Lepidoptera: Coleophoridae). *The Canadian Entomologist* 112: 1239-1248.

Ryan, R. B. 1990. Evaluation of biological control: introduced parasites of larch casebearer (Lepidoptera: Coleophoridae) in Oregon. *Environmental Entomology* 19: 1873-1881.

Ryan, R. B.; Rudinsky, J. A. 1962. Biology and habits of the Douglas-fir beetle parasite, *Coeloides brunneri* Viereck (Hymenoptera: Braconidae), in western Oregon. *The Canadian Entomologist* 97 (7): 748-763.

Ryan, R. B.; Bousfield, W. E.; Miller, G. E.; Finlayson, T. 1974. Presence of *Chrysocharis laricinellae,* a parasite of the larch casebearer [*Coleophora laricella*], in the Pacific Northwest. *Journal of Economic Entomology* 67 (6): 805.

Sager, S. M. 1957. A virus disease of western hemlock looper, *Lambdina fiscellaria lugubrosa* (Hulst) (Lepidoptera: Geometridae). *Canadian Journal of Microbiology* 3: 799-803.

Sartwell, C.; Schmitz, R. F.; Buckhorn, W. J. 1971. Pine engraver, *Ips pini,* in the Western States. U.S. *Department of Agriculture Forest Pest Leaflet* 122; 5 p.

Schindler, U. 1960. Zur Parasitierung von Evetria buoliana Schiff. in Westdeutschlands Kustenregion und dem Montanen Gebiet Serbiens [On the parasitism of *Rhyacionia buoliana* in the coastal region of western Germany and the mountain region of Serbia]. *Internationaler Kongress fur Entomologie, Wien, 17. bis 25. August 1960. Verhandlungen. Band II (Sektion VII bis XIV). Sektion VIII. Forstentomologie.* [Proceedings of the Eleventh International Congress of Entomology, Vienna, 17th-25th August 1960. Volume II (Sections VII - XIV). Section VIII. Forest Entomology.] II: 173-178.

Schmid, J. M. 1969. *Laphria gilva* (Diptera: Asilidae), a predator of *Dendroctonus ponderosae* in the Black Hills of South Dakota. *Annals of the Entomological Society of America* 62 (6): 1237-1241.

Schmid, J. M. 1970. *Enoclerus sphegeus* (Coleoptera: Cleridae), a predator of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in the Black Hills. *The Canadian Entomologist* 102 (8): 969-977.

Schmid, J. M. 1971. *Medetera aldrichii* (Diptera: Dolichopodidae) in the Black Hills. II. Biology and densities of the immature stages. *The Canadian Entomologist* 103 (6): 848-853.

Schmid, J. M. 1981. Distribution of western spruce budworm (Lepidoptera: Tortricidae) insect parasites in the crowns of host trees. *The Canadian Entomologist* 113: 1101-1106.

Schmid, J. M.; Bennett, D. D. 1988. The north Kaibab pandora moth outbreak 1978-1984. Fort Collins, CO: *U.S. Department of Agriculture, Forest Service General Technical Report RM-153;* 18 p.

Schröder, D. 1969. *Lypha dubia* (Fall.) (Dip.: Tachinidae) as a parasite of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lep.: Eucosmidae) in Europe. Delemont, Switzerland: *Technical Bulletin, Commonwealth Institute of Biological Control* No. 12; 43-60.

Schröder, D. 1974a. Untersuchungen über die Aussichten einer biologischen Bekaempfung von Scolytiden and Ulmen als Mittel zur Einschraenking des Ulmensterbens. (Investigations on the prospects for biological control of scolytids on elms as a means of reducing Dutch elm disease.) *Zeitschrift fur Angewandte Entomologie* 76: 150-159.

Schröder, D. 1974b. A study of the interaction between the internal larval parasites of *Rhyacionia buoliana* (Lepidoptera: Olethreutidae). *Entomophaga* 19 (2): 145-171.

Scriven, G. T.; Luck, R. F. 1978. Natural enemy promises control of Nantucket pine tip moth. *California Agriculture* 32(10): 19-20.

Scriven, G. T.; Luck, R. F. 1980. Susceptibility of pines to attack by the Nantucket pine tip moth in southern California. *Journal of Economic Entomology* 73: 318-320.

Senger, S. E.; Roitberg, B. D. 1992. Effects of parasitism by *Tomicobia tibialis* Ashmead (Hymenoptera: Pteromalidae) on reproductive parameters of female pine engravers, *Ips pini* (Say). *The Canadian Entomologist* 124: 509-513.

Shea, P. J.; Johnson, D. R.; Nakamoto, R. 1984. Effects of five insecticides on two primary parasites of the western spruce budworm, *Choristoneura occidentalis* (Freeman) (Lepidoptera: Tortricidae). *Protection Ecology* 7: 259-268.

Shepherd, R. F. 1994. Management strategies for forest insect defoliators in British Columbia. *Forest Ecology and Management* 68: 303-324.

Shewell, G. E. 1971. On the type of Agria, with description of a new nearctic species (Diptera: Sarcophagidae). *The Canadian Entomologist* 103: 1179-1191.

Silver, G. T. 1960. The relation of weather to population trends of the black-headed budworm *Acleris variana* (Fern.) (Lepidoptera: Tortricidae). *The Canadian Entomologist* 92(6): 401-410.

Silver, G. T. 1963. A further note in the relation of weather to population trends of the black-headed budworm, *Acleris variana* (Fern.) (Lepidoptera: Tortricidae). *The Canadian Entomologist* 95: 58-61.

Smirnoff, W. A. 1964. A nucleopolyhedrosis of *Operophtera bruceata* (Hulst) (Lepidoptera: Geometridae). *Journal of Insect Pathology* 6: 384-386.

Smirnoff, W. A. 1972. Energy resources of a diseased *Acleris gloverana* (Wals.) in British Columbia. Canadian Forestry Service *Bi-Monthly Research Notes* 28(2/3): 11.

Smits van Burgst, C. A. L. 1919. Parasitic Hymenoptera bred from *Rhyacionia (Evetria) buoliana; Perilampus batavus*, sp.n. *Tijdschrift voor Entomologie, The Hague* 61(3-4): 143-146.

Sower, L. L.;Mitchell, R. G. 1994. Mating disruption of western pine shoot borer (Lepidoptera: Olethreutidae) in lodgepole pine. *Journal of Economic Entomology* 87 (1): 144-147.

Spencer, G. J. 1932. Further notes on *Rhyncocephalus sackeni* Will. (Diptera, Nemestinidae). *Proceedings of the Entomological Society of British Columbia* 29: 25-27.

Spiegel, Lia H.; Price, Peter W. 1996. Plant aging and the distribution of *Rhyacionia neomexicana* (Lepidoptera: Tortricidae). *Population Ecology* 25 (2): 359-365.

Stein, J. D. 1981. Notes on the biology of the western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae) in north central Washington. *Pacific Insects* 23: 101-106.

Steinhuas, E. A. 1945. Insect pathology and biological control. *Journal of Economic Entomology* 38: 591-596.

Stelzer, M. J.; Scott, D.W. 1985. Evaluation of hydraulically applied baculovirus preparations to control western spruce budworm (Lepidoptera: Tortricidae) on Grand Fir. *Journal of Economic Entomology* 78: 1105-1108.

Stelzer, M.; Neisess, J.; Cunningham, J. G.; McPhee, J. R. 1977. Field evaluation of baculovirus stocks against Douglas-fir tussock moth in British Columbia. *Journal of Economic Entomology* 70: 243-246.

Stephen, F. M.; Dahlsten, D. L. 1976. The arrival sequence of the arthropod complex following attack by *Dendroctonus brevicomis* (Coleoptera: Scolytidae) in ponderosa pine. *The Canadian Entomologist* 108 (3): 283-304.

Stevens, R. E. 1956. Fir engraver beetle. *U. S. Department of Agriculture Forest Pest Leaflet 13;* 7 p.

Stevens, R. E.; Borg, T.K.; Thatcher, T.O. 1977. Notes on a pine-feeding budworm, *Choristoneura lambertiana ponderosana* (Lepidoptera: Tortricidae), in the Colorado Rockies. *The Canadian Entomologist* 109: 1269-1274.

Streett, D.A.; Sprague, V.; Harman, D.M. 1975. Brief study of microsporidian pathogens in the white pine weevil, *Pissodes strobi. Chesapeake Science* 16:32-38.

Struble, G. R. 1967. Insect enemies in the natural control of the lodgepole needle miner. *Journal of Economic Entomology* 60: 225-228.

Struble, G.R.; Martignoni, M.E. 1959. Role of parasites and disease in controlling *Recurvaria milleri* Busck. *Journal of Economic Entomology* 52(3): 531-532.

Swaine, J.M. 1925. The factors determining the distribution of North American bark-beetles. *The Canadian Entomologist* 57(11): 261-266.

Sweeney, J.D.; McLean, J.A. 1987. Effect of sublethal infection levels of Nosema sp. on the pheromone-mediated behavior of the western spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae). *The Canadian Entomologist* 119: 587-594.

Swenk, M. H. 1927. The pine tip moth in the Nebraska National Forest. *Nebraska Agricultural Experiment Station Research Bulletin 40;* 50 p.

Swezey, S. L.; Dahlsten, D. L. 1983. Effects of remedial application of lindane on emergence of natural enemies of the western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Scolytidae). *Environmental Entomology* 12 (1): 210-214.

Swezey, S. L.; Dahlsten, D. L.; Schlinger, E. I.; Tait, S. M. 1991. Predation on Douglas-fir tussock moth (Lepidoptera: Lymantriidae) and white fir sawfly (Hymenoptera: Diprionidae) larvae by captive spiders from white fir in California. *The Pan-Pacific Entomologist* 67: 243-250.

Syme, P. D. 1971. The life history and biology of *Hyssopus thymus* (Hymenoptera: Eulophidae), a parasite of the European pine shoot moth (Lepidoptera: Olethreutidae) in Ontario. *The Canadian Entomologist* 103 (12): 1691-1696.

Syme, P. D. 1975. The effects of flowers on the longevity and fecundity of two native parasites of the European pine shoot moth in Ontario. *Environmental Entomology* 4 (2): 337-346.

Takekawa, J. Y.; Garton, E. O. 1984. How much is an evening grosbeak worth? *Journal of Forestry* 82: 426-428.

Taylor, R. L. 1929. The biology of the white pine weevil, *Pissodes strobi* (Peck), and a study of its insect parasites from an economic viewpoint. *Entomologica Americana* 9: 167-246; 10: 1-86.

Tempel, W. 1925. The pine shoot moth, *Rhyacionia buoliana. Die kranke Pflanze,* ii (8): 166-167.

Thalenhorst, W. 1962. Occurrence, population dynamics and control of *Oligonychus ununguis* (Jacobi). *Der Forst und Holzwirt* 17 (15): 6.

Thomas, G. M.; Wright, K. H. 1961. Silver fir beetles. *U.S. Department of Agriculture Forest Pest Leaflet* 60; 7 p.

Thompson, W. R. 1943. *A Catalogue of the Parasites and Predators of Insect Pests. Section I: Parasite Host Catalogue. Part I: Parasites of the Arachnida and Coleoptera.* Belleville, Ontario: Imperial Agricultural Bureaux; 151 p.

Thompson, L. C.; Kulman, H. M.; Witter, J. A. 1977. Introduction, establishment, and dispersal of exotic parasites of larch sawfly in Minnesota. *Environmental Entomology* 6: 549-556.

Thong, C. H. S.; Webster, J. M. 1975. Effects on *Contortylenchus reversus* (Nematoda: Sphaerulariidae) on hemolymph composition and oocyte development in the beetle *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *Journal of Invertebrate Pathology* 26: 91-98.

Thong, C. H. S.; Webster, J. M. 1983. Nematode parasites and associates of *Dendroctonus* spp. and *Trypodendron lineatum* (Coleoptera: Scolytidae), with a description of *Bursaphelenchus varicauda* n. sp. *Journal of Nematology* 15 (2): 312-318.

Thorpe, W. H. 1930. Observations on the parasites of the pine-shoot moth, *Rhyacionia buoliana* Schiff. *Bulletin of Entomological Research* 21: 387-412.

Thorpe, W. H. 1933. Notes on the natural control of *Coleophora laricella,* the larch casebearer. *Bulletin of Entomological Research* 24: 271-291.

Tilden, P. E.; Bedard, W. D.; Lindahl, K. Q., Jr.; Wood, D. L. 1983. Trapping *Dendroctonus brevicomis:* changes in attractant release rate, dispersion of attractant, and silhouette. *Journal of Chemical Ecology* 9 (3): 311-321.

Tkachenko, A. K.; Danilyuk, A. A. 1974. *Trichogramma* in the control of pine budworms. *Zashchita Rastenii* 1: 45-46.

Tommeras, B. A. 1988. The clerid beetle, *Thanasimus formicarius,* is attracted to the pheromone of the ambrosia beetle, *Trypodendron lineatum. Experientia* 44 (6): 536-537.

Torgersen, T. R. 1968. Parasites of the hemlock sawfly, *Neodiprion tsugae,* in coastal Alaska. *Annals of the Entomological Society of America* 61: 1155-1158.

Torgersen, T. R. 1969. Hymenopterous parasites of the hemlock sawfly, *Neodiprion tsugae* Middleton, in southeast Alaska, with a key to larval remains. *Journal of the Entomological Society of British Columbia* 66: 53-62.

Torgersen, T. R. 1970. Parasites of the black-headed budworm, *Acleris gloverana* (Lepidoptera: Tortricidae), in southeast Alaska. *The Canadian Entomologist* 102: 1294-1299.

Torgersen, T. R. 1971. Parasites of the western hemlock looper, *Lambdina fiscellaria lugubrosa* (Hulst), in southern Alaska. *The Pan-Pacific Entomologist* 47: 215-219.

Torgersen, T. R. 1973. New parasite-host records for North American Ichneumonidae (Hymenoptera) in Alaska. *The Canadian Entomologist* 105: 997-998.

Torgersen, T. R. 1985. A new *Hyposoter* (Hymenoptera: Ichneumonidae) from *Orgyia pseudotsugata* (Mcd.) (Lepidoptera: Lymantriidae). *The Canadian Entomologist* 117: 941-947.

Torgersen, T. R.; Beckwith, R. C. 1974. Parasitoids associated with the large aspen tortrix, *Choristoneura conflictana* (Lepidoptera: Tortricidae), in interior Alaska. *Canadian Entomologist* 106: 1247-1265.

Torgersen, T. R.; Campbell, R. W. 1982. Some effects of avian predators on the western spruce budworm in north central Washington. *Environmental Entomology* 11: 429-431.

Torgersen, T. R.; Mason, R. R. 1985. Characteristics of egg parasitization of Douglas-fir tussock moth, *Orgyia pseudotsugata* (McD.) (Lepidoptera: Lymantriidae), by *Telenomus californicus* Ash. (Hymenoptera: Scelionidae). *Environmental Entomology* 14: 323-328.

Torgersen, T. R.; Mason, R. R. 1987. Predation on egg masses of the Douglas-fir tussock moth (Lepidoptera: Lymantriidae). *Environmental Entomology* 16: 90-93.

Torgersen, T. R.; Mason, R. R.; Paul, H.G. 1983. Predation on pupae of Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough) (Lepidoptera: Lymantriidae). *Environmental Entomology* 12: 1678-1682.

Townes, H.; Townes, M. 1951. Family Ichneumonidae. In: Muesebeck, C.F.W.; Krombein, K.V.; Townes, H.K. *Hymenoptera of America, north of Mexico - synoptic catalog.* U.S. Department of Agriculture Monograph 2; 184-409.

Treat, A. E. 1985. Larval *Callidosoma* (Acari, Erythraeidae): new records and a new rearing from the Americas. *International Journal of Acarology* 11 (2): 93-123.

Troubridge, J. T.; Fitzpatrick, S. M. 1993. A revision of the North American *Operophtera* (Lepidoptera: Geometridae). *The Canadian Entomologist* 125: 379-397.

Tsankov, G. 1988. The ichneumonoid parasites of the European pine shoot moth caterpillars in Bulgaria (Hymenoptera: Ichneumonoidea). *Advances in Parasitic Hymenoptera Research: Proceedings of the II Conference on the Taxonomy and Biology of Parasitic Hymenoptera.* Sofia Bulgaria: Forest Research Institute, Bulgarian Academy of Sciences; 391-394.

Turnbull, A. L.; Chant, D. A. 1961. The practice and theory of biological control of insects in Canada. *Canadian Journal of Zoology* 39 (5): 697-753.

Turnock, W. J. 1953. Some aspects of the life history and ecology of the pitch nodule maker, *Petrova albicapitana* (Busck) (Lepidoptera-Olethreutidae). *The Canadian Entomologist* 85: 233-243.

Turnock, W. J. 1972. Geographical and historical variability in population patterns and life systems of the larch sawfly (Hymenoptera: Tenthredinidae). *The Canadian Entomologist* 104: 1883-1900.

U.S. Department of Agriculture, Forest Service. 1958. Timber resources for America's future. *Forest Resource Report No. 14;* 713 p.

U.S. Department of Agriculture, Forest Service. 1983-1996. *Forest Insect and Disease Conditions in the United States* [1983-1996]. Washington, D.C.

Underhill, G. W. 1943. Some insect pests of ornamental plants. *Bulletin of Virginia Agricultural Experiment Station* 349; 38 p.

Van Driesche, R. G.; Bellows, T. S., Jr. 1996. Biological Control. New York: Chapman and Hall; 539 p.

Van Driesche, R. G.; Healy, S.; Reardon, R. 1996. *Biological Control of Arthropod Pests of the Northeastern and North Central Forests in the United States: A Review and Recommendations.* FHTET-96-19. Morgantown, WV: U.S. Department of Agriculture, Forest Service, Northeastern Area State and Private Forestry; 150 p.

Van Frankenhuyzen, K.; Fast, P. 1989. Susceptibility of three coniferophagous *Choristoneura* species (Lepidoptera: Tortricidae) to *Bacillus thuringiensis* var. *kurstaki. Journal of Economic Entomology* 82(1): 193-196.

VanderSar, T. J. D. 1978. Emergence of predator and parasites of the white pine weevil, *Pissodes strobi* (Coleoptera: Curculionidae) from Englemann spruce. *Journal of the Entomological Society of British Columbia* 75: 14-18.

von Scheller, H. D. 1962. On the bionomics and injuriousness of *Oligonychus ununguis* and of *Rhopalosiphum abietinum.* Part I. *O. ununguis. Zeitschrift für Angewandte Entomologie* 51: 69-85.

Walkley, L. M. 1954. A new cryptine genus of economic interest (Hymenoptera: Ichneumonidae). *Journal of the Washington Academy of Sciences* 44: 219-220.

Walley, G. S.; Barron, J. R. 1977. Nearctic *Glypta* parasites (Hymenoptera: Ichneumonidae) of conifer feeding Olethreutidae (Lepidoptera). *Entomological News* 88(7 and 8): 177-184.

Walsingham, Lord Thos. de Grey. 1879. *Illustrations of typical specimens of Lepidoptera Heterocera in the collection of the British Museum. Part IV. North American Tortricidae.* London: Department of Zoology, British Museum..

Warren, L. O. 1985. Primary hymenopterous parasites of Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock). *Journal of Entomological Science* 20: 383-389.

Watson, W. Y.; Arthur, A. P. 1959. Parasites of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.), in Ontario. *The Canadian Entomology* 91 (8): 478-484.

Webb, F. E.; Quednau, F. W. 1971. *Coleophora laricella* (Hübner), larch casebearer (Lepidoptera: Coleophoridae). In: *Biological Control Programmes against Insects and Weeds in Canada,* 1959-1968. Slough, England: Commonwealth Agricultural Bureaux, Farnham Royal; 131-136.

Weiser, J. 1970. Three new pathogens of the Douglas-fir beetle, *Dendroctonus pseudotsugae: Nosema dendroctoni* n. sp., *Ophryocystis dendroctoni* n. sp., and *Chytridiopsis typographi* n. comb. *Journal of Invertebrate Pathology* 16 (3): 436-441.

Werner, R. A. 1977. Biology and behavior of the spear-marked black moth, *Rheumaptera hastata,* in interior Alaska. *Annals of the Entomological Society of America* 70 (3): 328-336.

Werner, R. A. 1978. Overwinter survival of spear-marked black moth, *Rheumaptera hastata* (Lepidoptera: Geometridae), pupae in interior Alaska. *The Canadian Entomologist* 110: 877-882.

West, K. J.; DeAngelis, J. D. 1993. *Typhlodromus americanus* Chant and Yosida-Shaul, a predator of the spruce spider mite. *International Journal of Acarology* 19 (2): 193-194.

Westwood, A. R. 1991. A cost benefit analysis of Manitoba's integrated Dutch elm disease management program 1975-1990. *Proceedings of the Entomological Society of Manitoba* 47: 44-59.

Wheeler, A. G., Jr.; Colburn, R. B.; Lehman, R. D. 1973. *Stethorus punctillum* associated with spruce spider mite on ornamentals. *Environmental Entomology* 2: 718-720.

Wickman, B. E. 1963. The large aspen tortrix, *Choristoneura conflictana,* in California (Lepidoptera: Tortricidae). *Journal of Economic Entomology* 56: 593-596.

Wickman, B. E.; Torgersen, T. R. 1987. Phenology of Douglas-fir tussock moth, *Orgyia pseudotsugata,* egg eclosion and mortality in a thinned and unthinned stand (Lepidoptera: Lymantriidae). *The Pan-Pacific Entomologist* 63: 218-223.

Wilkinson, R. C.; Bhatkar, A. P.; Kloft, W. J.; Whitcomb, W. H.; Kloft, E. S. 1978. *Formica integra* 2. feeding, trophallaxis, and interspecific confrontation behavior. *The Florida Entomologist* 61: 179-187.

Williams, C. B., Jr.; Walton, G. S.; Tiernan, C. F. 1969. Zectran and Naled affect incidence of parasitism of the budworm *Choristoneura occidentalis* in Montana. *Journal of Economic Entomology* 62: 310-312.

Wilson, G. G. 1984. Observations of a microsporidian parasite in the white pine weevil *Pissodes strobi* (Peck) (Coleoptera: Curculionidae). *Canadian Forestry Service Research Notes* 4 (3): 33-35.

Wilson, G. G.; Burke, J. M. 1971. *Nosema thomsoni* n. sp., a microsporidian from *Choristoneura conflictana* (Lepidoptera: Tortricidae). *Canadian Journal of Zoology* 49: 786-788.

Wilson, N. L.; Oliver, A. D. 1970. Relationship of the imported fire ant to Nantucket pine tip moth infestations. *Journal of Economic Entomology* 63: 1250-1252.

Witter, J. A.; Kulman, H. M. 1979. The parasite complex of the forest tent caterpillar in northern Minnesota. *Environmental Entomology* 8: 723-731.

Witter, J. A.; Waisanen, L. A. 1978. The effect of different flushing times among trembling aspen clones on tortricid caterpillar populations. *Environmental Entomology* 7: 139-143.

Witter, J. A.; Kulman, H. M.; Hodson, A. C. 1972. Life tables for the forest tent caterpillar. *Annals of the Entomological Society of America* 65: 25-31.

Wong, H. R. 1974. The identification and origin of the strains of the larch sawfly, *Pristiphora erichsonii* (Hymenoptera: Tenthredinidae), in North America. *The Canadian Entomologist* 106: 1121-1131.

Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Provo, UT: *Great Basin Naturalist Memoirs,* No. 6, Brigham Young University.

Wygant, N. D. 1941. An infestation of the Pandora moth, *Coloradia pandora* Blake, in lodgepole pine in Colorado. *Journal of Economic Entomology* 34: 697-702.

Wygant, N. D.; Nelson, A. L. 1949. Four billion feet of beetle-killed spruce. Washington D.C.: *U.S.Department of Agriculture, Yearbook of Agriculture* 1949; 417-422.

Yates, H. O. III. 1966. *Rhyacionia* egg parasitism by *Trichogramma minutum* Riley. *Journal of Economic Entomology* 59(4): 967-969.

Youngs, L. C.; Campbell, R. W. 1984. Ants preying on pupae of the western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in eastern Oregon and western Montana. *The Canadian Entomologist* 116: 1665-1669.

Zethner, O.; Bejer-Petersen, B. 1972. Outbreak years of the pine shoot moth (*Rhyacionia buoliana* Schiff.) known from Denmark. *Forstige Forsogsvaesen i Danmakr* 33: 33-38.