Forest Health Technology Enterprise Team

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Biological Control

Biological Control of Arthropod Pests of the Northeastern and North Central Forests in the United States: *A Review and Recommendations*

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Cover Photo:

The hemlock woolly adelgid faces a challenge in the form of the newly-discovered exotic adelgid predator, *Pseudoscymnus tsugae* sp. nov. Laboratory and preliminary field experiments indicate this coccinellid's potential to be one of the more promising biological control agents this decade. Tiny but voracious, both the larva and adult (shown here) attack all stages of the adelgid.

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Biological Control of Arthropod Pests of the Northeastern and North Central Forests in the United States: *A Review and Recommendations*

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Introduction

Purpose. This report describes the potential for use of biological control against 94 forest pests in the northeastern and North Central regions of the United States. Biological control is considered to include (1) introduction of new species of natural enemies ("classical" biological control), (2) conservation of existing species of natural enemies through modification of stand conditions or silvicultural practices, (3) augmentative release of artificially reared natural enemies, and (4) application of pathogens as microbial pesticides. The use of pheromones, sterile insects, and plant breeding are not within the scope of this report.

This report includes the following:

(1) A convenient summary of the literature on population dynamics and natural enemies of each pest reviewed, i.e., how much is known about why each species occurs at densities that cause economic problems;

(2) Analysis of the existing knowledge about the effects of biological control agents on the population dynamics of each pest and whether such agents are important;

(3) Identification of opportunities in which investments of public funding in biological control of forest pests should be pursued, and, conversely, instances in which biological control would not be likely to succeed;

(4) Detailed recommendations, where appropriate, of how biological control might be used to control the specific pests.

Organization. Pests are arranged using a mixture of insect orders and feeding habits to define groups. Within these groups, species are not ordered. For each species, standard categories are used to organize information presented.

Selection of Species. Species considered pests to managed forests were identified based on four sources: (1) the second edition of *Eastern Forest Insects* (Drooz 1985); (2) mention more than once for the 9-year span, 1983-1991 in *Forest Insect and Disease Conditions in the United States;* (3) species of special interest (balsam woolly adelgid, pear thrips, hemlock woolly adelgid, larger pine shoot beetle, spruce bark beetle, nun moth, and steel blue wood wasp); and (4) comments from forest entomologists in Maine, Maryland, Kentucky and Wisconsin who reviewed a draft list.

Pests of urban landscape trees that are considered in this report were selected by the first author from a larger list developed by Roy G. Van Driesche, Michael Raupp, and John Davidson.

Literature Sources. For each pest, under all appropriate names, the Review of Applied Entomology, Series A (Agriculture and Forestry Pests) was reviewed for each year from 1913 to 1994. All abstracts concerning natural enemies, population dynamics, natural control, cultural control, and past biological control projects were noted. Articles of principal interest were obtained if in English, Spanish or French. All other materials were considered based on their English abstracts. Other sources included a variety of books, especially Drooz (1985), Clausen

(1978), the two volumes reviewing biological control projects in Canada (Anon. 1971, Kelleher and Hulme 1984), and books on forest insects or their population dynamics (Anderson and Kaya 1976, Barbosa and Schultz 1987, Berryman 1988, Kulhavy and Miller 1989, Solomon 1995). Host-parasitoid records for hymenopterous parasitoids also were taken in some cases from Krombein *et al.* (1979).

Changes in Scientific Names. In the course of the literature review of the selected pest species, the nomenclature of each pest species was reviewed such that the literature search was appropriately conducted to employ both the currently accepted name and, where dictated, earlier synonyms. At the beginning of the section on each pest, these earlier generic placements or synonyms are given to help readers clarify names encountered in older literature.

Names of natural enemies were updated if a comparison of early and later reports provided the necessary information. Names of natural enemies, however, were not reviewed comprehensively for current taxonomic correctness. Readers should be aware that older names may have changed.

Thysanoptera

1. PEAR THRIPS (*Taeniothrips inconsequens* [Uzel]) (Thysanoptera: Thripidae)

Origin: Pear thrips is not native to North America. It was first recorded in the United States in California about 1900, where it was observed as a pest of fruit trees (Bailey 1944).

Range in North America: The species is recorded from California (on fruit trees), and the northeastern United States and southern Canada, where it is occasionally damaging to sugar maples, sometimes over large acreages (Carey *et al.* 1992).

Damage: Pear thrips feed on buds and young leaves of hardwood trees, especially those of sugar maples. Feeding causes leaves to become distorted and tattered as buds develop.

Resident Natural Enemies: Natural enemies of thrips in general include fungal pathogens (e.g., Carl 1975, who records an *Entomophthora* sp. infection in *Thrips* spp.), various predators, including especially various phytoseiid mites (e.g., *Euseius hibisci* [Chant] on *Scirotothrips citri* [Moulton] in California, Tanigoshi *et al.* [1983]), and various hymenopterous parasitoids in the families Eulophidae, Trichogrammatidae, and Mymaridae, especially the first (see Loomans and van Lenteren 1995 for a review of thrips parasitoids).

Very few natural enemies have been recorded from *T. inconsequens*. Essig (1920) noted predation on pear thrips in California by such generalist feeders as *Hippodamia convergens* Guerin, *Chrysopa californica* Coq., and various species of *Hemerobius*. Fungal pathogens reported attacking pear thrips include *Verticillium lecanii* (Zimmerman) Viegas (which attacked up to 22% of pear thrips in soils in some locations in Vermont, Skinner *et al.* [1991]). Also noted from pear thrips in Europe by Carl *et al.* (1989) were *Entomophthora* nr. *parvispora*, *Hirsutella* sp., and *Metarhizium anisopliae*. Parasitoid species have not been

recorded attacking pear thrips. Ferriére's (1958) mention of *Ceranisus russelli* (Crawford) is apparently erroneous according to Loomans and van Lenteren (1995). Carl *et al.* (1989) reported 4% parasitism in samples of pear thrips in Europe, but the species was not identified.

Biological Control Attempts: Following widespread damage to sugar maples for several consecutive years in the northeastern United States at the end of the 1980s, the potential for suppression of pear thrips by importation of natural enemies from Europe was investigated, but useful natural enemies were not located in surveys in Germany, Switzerland, and France (Carl *et al.* 1989). Examples of successful use of parasitoids in classical biological control programs against thrips are rare, the best perhaps being work in California on greenhouse thrips. The eulophid *Thripobius semiluteus* Boucek was imported into California and released against the greenhouse thrips, *Heliothrips haemorrhoidalis* (Bouché). The parasitoid established and caused up to 63% parasitism of thrips in some sites (McMurtry and Badii 1991).

Reasons for Pest Status and Possibilities for Biological Control: The fundamental reasons for the occasional increase in damage from pear thrips in the eastern United States are unknown. While the species is not indigenous to North America, surveys for natural enemies in Europe (Carl *et al.* 1989) did not suggest that parasitoids or pathogens are suppressing pear thrips there. While pathogens or predators may act strongly in the soil against the pest during its long period of residence below ground (9-10 months per year), such generalist pathogens and predators are likely to be present in North America without need for introduction from Europe.

The possibility that deterioration of sugar maple health from such environmental factors as air pollution might stimulate thrips fecundity and lead to outbreaks has been examined (Carey *et al.* 1992); however, pear thrips fecundity was found to be higher on healthy, not declining, sugar maples.

A third mechanism governing the periodic outbreaks of damage has been postulated based on synchrony of pear thrips adults with bud break. Observations of pear thrips outbreaks document primarily increases in damage, with few direct estimates being available to document actual increases in thrips numbers *per se*. Damage may increase or decrease between years based on how well synchronized the emergence of pear thrips from soil in spring is with partly opened buds. Work of Kolb and Teulon (1991) confirm that buds in various stages of opening, if presented as feeding sites for thrips, receive different degrees of damage, with buds in early or late stages receiving the least damage. In a field test, Kolb and Teulon (1991) found that early-opening buds suffered greater damage than late-opening buds on maples in Pennsylvania. The vulnerable stage for the early-opening buds coincided better with pear thrips emergence than did that of late-opening buds.

Recommendations: No use of biological control is recommended. This species does not seem to have specialized natural enemies that would likely lower its population density in North America. Increases in damage levels that occasionally occur seem to be linked to variation in synchrony between thrips emergence and bud break of maples. Such weather driven events cannot be modified in natural forests. Should years of significant damage become more common, maple groves for sugar production might be protected by development of a temperature-based model to predict synchrony of pear thrips emergence and maple bud

burst to predict years of risk. Pesticides could then be applied to protect trees in these particular years. Recovery from damage seems to occur quickly. For the 1988-1990 period (covering a pear thrips outbreak and immediately thereafter) there was a noticeable improvement in the health of maple stands in the northeastern United States and southern Canada, within one year after an outbreak (Allen *et al.* 1992).

2. INTRODUCED BASSWOOD THRIPS (*Thrips calcaratus* Uzel) (Thysanoptera: Thripidae)

Origin: In North America, basswood thrips is an introduced species from Europe.

Range in North America: This species is recorded from New England and Quebec, westward through Pennsylvania, New York and the Great Lake States.

Damage: Damage has been reported only from Wisconsin (Raffa and Hall 1989, Raffa *et al.* 1992), where the only important host in the field is American basswood (*Tilia americana* Linnaeus) (Rieske and Raffa 1996).

Resident Natural Enemies: The black hunter thrips, *Leptothrips mali* (Fitch), a predacious thrips, has been found in significant numbers in association with introduced basswood thrips in Wisconsin. Fungal pathogens appear to be important during summer when thrips are in the soil (Raffa *et al.* 1992).

Biological Control Attempts: None to date.

Reasons for Pest Status and Possibilities for Biological Control: This species invaded North America and is not noted as causing damage to its hosts in its native range in Europe. As such, these factors would suggest the possibility that natural enemies might affect this species in Europe more strongly than in North America and that natural enemy introductions might be useful. Classical biological control programs have been conducted against several species of thrips, including the Cuban-laurel thrips, *Gynaikothrips ficorum* (Marchal); the cacao thrips, *Selenothrips rubrocinctus* (Giard); the onion thrips, *Thrips tabaci* Lindeman; and the greenhouse thrips, *Heliothrips haemorrhoidalis* (Bouché) (Clausen 1978, Hessein and McMurtry 1989). These projects have employed anthocorid predators, eulophid parasitoids of thrips nymphs and adults, and, in one case, an egg parasitoid. While these projects have resulted in establishment of some of the introduced natural enemies, evidence of thrips population suppression is generally lacking.

Nevertheless, several factors argue against the use of biological control introductions in the case of the introduced basswood thrips. First, most past projects against thrips have been directed against multivoltine species in warm to subtropical environments. Precedents for the successful use of biological control introductions against univoltine thrips in temperate climates are lacking, although some efforts were made in eastern North America against the exotic forest pest, the pear thrips, *Taeniothrips inconsequens* (Uzel). These efforts, while limited, suggested that parasitism levels of pear thrips larvae were very low, and that natural enemies, if they were important constraints on the pear thrips in Europe, were perhaps associated with the time larvae spent in the soil in summer and fall. This case is relevant to the introduced

basswood thrips case because the two species are similar in their overall biology and phenological relation to their host plants.

Damage from introduced basswood thrips to American basswood may relate to its being a new host, which occurs in concentrations greater than in Europe. Also, in Europe thrips feed on mature foliage, whereas in Wisconsin buds are attacked. Bud feeding amplifies damage and thus this shift in the phenological correspondence between the thrips and its new North American host may largely explain its greater effect on *T. americana* (Raffa *et al.* 1992). If this is the case, little value would result from natural enemy introductions.

Recommendations: A survey in Europe of natural enemies associated with *T. calcaratus* has not been conducted. If parasitism were found to be an important mortality factor, the responsible parasitoid could be imported. Mortality factors affecting thrips stages in the soil are likely to be generalist predators and fungal pathogens. Generalist predators are unlikely to be suitable for importation, and fungal pathogens are likely to be species already present in North America. These agents, therefore, would be unlikely to be useful for importation.

Homoptera

Adelgids (Adelgidae)

3. EASTERN SPRUCE GALL ADELGID (*Adelges abietis* [L.]) (Homoptera: Adelgidae)

Origin: Eastern spruce gall adelgid is not native to North America. It is found in Europe but whether this is its native range is not certain. A second closely related species, *Adelges viridis* (Ratzeburg), occurs in Europe, and in older literature these species were not recognized as separate species (Herrick and Tanaka 1926). Unlike *A. viridis*, *A. abietis* completes its whole life cycle on spruce, rather than having alternate cycles on larch (Wilford 1937).

Range in North America: Eastern spruce gall adelgid occurs in southern and eastern Canada, and in the eastern United States from New England through the Great Lake States.

Damage: This adelgid galls branches of the introduced tree Norway spruce (*Picea abies* [L.] Karsten), and various North American spruces, principally white spruce, *Picea glauca* (Moench). Damage is important in nurseries and Christmas tree plantations because galling and twig death reduce the aesthetic value of the plants.

Resident Natural Enemies: No reports on natural enemies in North America were found. In Switzerland, the syrphid *Cnemodon* sp. and the cecidomyiid *Aphidoletes abietis* (Kieff.) were found preying on the gallicolae stage within closed galls of this adelgid on Norway spruce (Mitchell and Maksymov 1977). A species of predacious dipteran, *Leucopis* sp., is reported as being partially effective for control of *Adelges nüsslini* (Börner) in the West Pontic Mountains of Turkey (Eichhorn 1969).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: In Europe, levels of infestation vary widely between trees. This is partly due to variation in the timing of bud opening. Buds that open either very early or late escape serious damage (Bischoff *et al.* 1969). Fertilization of forest stands or nursery plots was found not to significantly affect numbers of *A. abietis* galls (Thalenhorst 1972). No information exists on the importance of natural enemies in Europe in determining densities of this adelgid.

Recommendations: Efforts to locate natural enemies of this adelgid might be made in conjunction with work on balsam woolly adelgid. The cecidomyiid reported by Mitchell and Maksymov (1977), i.e., *Aphidoletes abietis*, could be relocated and imported for trials on its ability to reduce densities of *A. abietis* in North America.

4. BALSAM WOOLLY ADELGID (*Adelges piceae* [Ratzeburg]) (Homoptera: Adelgidae)

Notes: An annotated bibliography on *A. piceae* is provided by Schooley and Oldford (1981). Some species of *Adelges* in Europe are closely related to *A. piceae* and have in the past been confused with it. The biology and population dynamics of this species are reviewed by Hain (1988).

Origin: Balsam woolly adelgid first appeared in eastern North America around 1908 in Maine, most likely having been introduced on nursery stock (Balch 1952). *Adelges* spp. have complex life cycles, with several distinct morphological forms. Bryant (1974) lists and discusses eleven species of adelgids that infest true firs and discusses details of their taxonomy, biology, and interaction with host trees.

Adelges piceae occurs in central Europe (Germany, Austria, Switzerland, and the former Czechoslovakia, among others), and this area was the focus of all natural enemy collections made to provide predators for introduction to North America (Clark *et al.* 1971, Schooley *et al.* 1984), with the exception of collections made later in India, Pakistan, and Australia and one collection of *Leucopis* sp. from Turkey in 1967 (Amman and Speers 1971, Schooley *et al.* 1984).

It is not certain, however, that central Europe is the native range of *A. piceae*, but rather may be an area invaded at an earlier point, probably in the middle of the 19th century. The closely related species *Adelges nüsslini* (Börner) invaded central Europe around the middle of the 19th century and in 1903 Nüsslin proposed that *A. piceae* may be a *forma* that derived from *A. nüsslini* after it became separated from its primary tree host (Balch 1952). The native range of *A. nüsslini* is listed by Bach (1952) as the Caucasian region in Asia and by Bryant (1974) to be northwest Turkey. In either case, no natural enemies (with one minor exception of a *Leucopis* sp. collected from Turkey) were collected closer than within 1300 miles of these areas. Furthermore, these regions are ecologically separated from other forests with fir species by large areas unsuitable for firs by virtue of differences in elevation, rainfall, and agricultural use, or the presence of large seas. Also, the *forma* of *A. piceae* found in Canada is difficult to separate morphologically from *Adelges prelli* Francke-Grosmann, a species now

found in Europe but native to the Caucasus Mountains (Bryant 1974). While *A. prelli* is believed to be a distinct species, its closeness to *A. piceae* and its Caucasus origin both suggest the possibility that central Europe was not the native range of *A. piceae*.

Range in North America: There are three infested areas in North America: (1) eastern Canada and the northeastern United States — the area of greatest physical extent and where the pest has caused the greatest economic losses, on balsam fir, *Abies balsamea* (L.) Miller (Balch 1952), (2) higher elevation sites in the Appalachian Mountains, especially North Carolina where the species affected is Fraser fir, *Abies fraseri* (Pursh) Poir. (Amman 1966), and (3) the Pacific northwest States and British Columbia, where several species of native firs are attacked, including *Abies grandis* (Douglas) Lindl., *Abies amabilis* (Douglas) Forbes, and *Abies lasiocarpa* (Hooker) Nutt. (Mitchell and Wright 1967). These infestations are believed to derive from three separate invasions and may represent distinct subspecies or races of the pest (Foottit and Mackauer 1983).

Damage: On balsam fir, damage is of two types. In one type, large populations develop on trunks and kill host trees in one or two years. In another type, damage develops slowly, with distortion of wood growth ("gout" disease), and death occurs only after prolonged decline (10-20 years) (Bryant 1974). The area affected in the northeastern United States and eastern Canada is reported by Bryant (1974) as 13,000 square miles. Economic losses in this region have been large. The infested area in the western part of North America is smaller, estimated as 4000 square miles in southwestern British Columbia in 1958 (Clark *et al.* 1971, Bryant 1974). In the southern Appalachians, about 27,000 hectares are infested, with forest decline occurring in many areas, including Great Smoky Mountains National Park (Amman 1966, Dull *et al.* 1988).

Resident Natural Enemies: There are no known parasitoids of adelgids. Native species of predators consuming *A. piceae* in the field have been surveyed in both eastern Canada (Brown and Clark 1956) and the northwestern United States (Mitchell 1962). While a variety of species have been noted as occasional predators of this adelgid, none control the pest.

Biological Control Attempts: Over a 35-year period (1934-1969) a major effort to import natural enemies of this pest was undertaken by Canada, with subsequent importation into the United States of many of the same species of natural enemies (mostly importing material from Canada, but with direct importations from Europe or Asia in some cases). Work in Canada is reviewed in detail by Clark *et al.* (1971) and Schooley *et al.* (1984). For a discussion of the history of efforts in the United States, see Clausen (1978). Work in the United States included releases of various predators in all three infested areas (New England, North Carolina, and the Pacific Northwest).

Part of this effort involved extensive survey work to document the predator fauna in central Europe attacking various adelgids, especially those on fir (Pschorn-Walcher and Zwölfer 1956). Most work was done in Germany and Switzerland.

At least 13 species were released in eastern Canada and 23 in the United States (Tables 3 and 4, pp. 51 and 53 in Clausen 1978, and Mitchell and Wright 1967). Of the various species released, most efforts were focused on the following species (Smith 1958): (1) *Aphidecta obliterata* (Linnaeus) (Coleop.: Coccinellidae). (Wylie 1958, Witter 1969); (2) *Scymnus*

impexus (Mulsant) (Coleop.: Coccinellidae) (Delucchi 1954, Clark and Brown 1961); (3) *Laricobius erichsonii* (Rosenhauer) (Coleop.: Derodontidae) (Clark and Brown 1957, 1958, Franz 1958, Buffam 1962); (4) *Aphidoletes thompsoni* Möhn (Diptera: Cecidomyiidae) (Pschorn-Walcher 1956); (5) *Cremifania nigrocellulata* Czerny (Diptera: Chamaemyiidae) (Clark and Brown 1962); and (6) *Leucopis obscura* (Hal.) (Diptera: Chamaemyiidae) (Thomas 1968).

While perhaps eight species of natural enemies released against balsam woolly adelgid have established, none has provided control of the pest, in any of the geographic areas infested. Canada discontinued further efforts to obtain control with this set of natural enemies in 1969 and recommended that new species of potentially more effective predators were needed and could be sought in Europe on related species of adelgids. Additional surveys or importations, however, were not undertaken.

Reasons for Pest Status and Possibilities for Biological Control: The attainment of pest status by *A. piceae* in North America possibly can be explained by either of two mechanisms. One of these is the change in species of host trees attacked in North America versus Europe (where *A. piceae* exists but does not cause important damage to local tree species). The second explanation is that important natural enemies might occur in Europe but be missing in North America, permitting better survival of the pest, leading to higher densities and greater damage to the host trees.

Clearly the role of the change of tree hosts is important. This is borne out by the fact that importation of the principal predators of fir-attacking-adelgids found in central Europe has not reduced the problem in North America. This explanation is also supported by the fact that invasion of *A. nusslini* into North America has not been damaging, even though in Europe this species damages its hosts (tree species other than those attacked in North America). An additional piece of evidence that suggests that tree species may be an important factor is that early attempts at plantation use of balsam fir in the United Kingdom were abandoned, and failure of the species to thrive was attributed to attack by *A. piceae* (Baldon 1839). If this hypothesis is correct, it should be possible to verify it by planting plantations of balsam fir in locations in central Europe where populations of *A. piceae* are known to occur and observing whether damaging populations develop on balsam fir. If they do, in the presence of local predator populations that are apparently sufficient to suppress the pest on local tree species, then the difference could be attributed to tree species. Such a result would imply that balsam fir is intrinsically more susceptible to this adelgid and thus damage is explained on that basis. The role of host susceptibility is further emphasized by comparisons between North America species attacked by balsam woolly adelgid. Fraser fir in the Appalachian Mountains appears to be the least resistant host species and suffers the greatest injury.

An alternative hypothesis is that natural enemies are important but that Europe is not the native home of the pest. The failure of natural enemies collected in central Europe to suppress the pest in North America may imply that the wrong species or populations have been introduced. This hypothesis is tied to the possibility that central Europe may not be the pest's native home, but rather an area invaded in the previous century. If, as has been suggested in the literature, the native home is further east (Caucasus Mountains, or northwestern Turkey), then failure to obtain control in North America using collections of predators from central Europe would not disprove the possibility of suppressing this pest via predator introductions. The wrong predators may have been employed.

If central Europe is indeed an invaded area, then the natural enemies affecting the pest there may be local species that have crossed over from other adelgids and therefore are likely to be ineffective because they are not sufficiently well adapted to exploit the host at low densities. Alternatively these natural enemies may be species that migrated to central Europe along with the host from the native range. Such spread however, occurs reliably only when the host insect expands its range across a zone of continuous habitat. Such continuous spread seems unlikely in the case of fir-attacking adelgids, as continuous fir forests do not connect the Caucasus Mountains (or northwestern Turkey) to the Alps. Rather, these mountainous areas are ecological islands, isolated from each other by deserts, seas, and low elevation lands not supporting fir forests and largely employed for agriculture. A more likely link between these zones is human movement of nursery stock — a method likely to transport a rather sessile adelgid, but somewhat less likely to transport vagile predators.

If this reasoning is correct, then *A. piceae* could exist in the Caucasus Mountains or in Turkey and be suppressed there by natural enemies. From this homeland it may have later invaded first Europe and then North America through the human movement of trees. The differing levels of economic losses occasioned by these invasions may have resulted from the chance that in Europe local firs were relatively tolerant of the pest's feeding, while in North America, fir species were more sensitive. Under this hypothesis, local natural enemies in Europe do not control the pest, except perhaps partially as an adjunct to the plant resistance of the local fir species. This hypothesis can be tested by planting mixed fir plantations in Europe to observe the outcome of adelgid attacks when balsam fir is presented as a potential host.

In general, because suppression of the pest's population growth by natural enemies certainly interacts with the degree of host plant resistance shown by particular tree hosts, biological control is likely to be most difficult to achieve on very susceptible hosts such as Fraser fir.

Recommendations: Three actions are recommended:

1. Assess the tree species resistance hypothesis by planting balsam fir in areas in central Europe with *A. piceae* populations to determine whether local natural enemies suppress the adelgid on that tree species.

2. Employ molecular biological methods to compare the DNA of *P. piceae* populations in various parts of North America with that of populations in Europe and Asia. Comparisons should include balsam woolly adelgid populations in central Europe, the Caucasus Mountains, northeastern Turkey, and related adelgids such as *A. nüsslini* and *A. prelli*. These comparisons should help clarify the true origins of the pest, directing the search for natural enemies more accurately towards its the native home.

3. Initiate a comprehensive search for natural enemies in the Caucasus Mountains and northeastern Turkey. These regions were not examined in the earlier efforts. The Caucasus Mountains formerly were politically inaccessible, but now are potentially available for exploration. These regions are likely in the native range of the pest. Special efforts should be made to find local natural enemies attacking low density populations of *P. piceae*. Exposure of trap host populations on nursery grown and balled trees should be employed if encountering low density adelgid populations is difficult.

5. HEMLOCK WOOLLY ADELGID (*Adelges tsugae* Annand) (Homoptera: Adelgidae)

Origin: Hemlock woolly adelgid is not native to North America and is probably of Asian origin. The species is known to occur in Taiwan on *Tsuga chinensis* Pritzel and in Japan on *Tsuga sieboldii* Carriere and *Tsuga diversifolia* Masters (Takahashi 1937, McClure 1987a).

Range in North America: Two areas of the United States have been invaded by this pest. Northern California and Oregon were invaded in the 1920s, where *Tsuga heterophylla* Sargent and *Tsuga mertensiana* Carriere are the hosts (Annand 1924), but forest trees are rarely damaged. In the early 1950s, the pest appeared in Virginia and has since expanded northward along the coast to Massachusetts (McClure 1989, Salom *et al.* 1996).

Damage: Damage is unimportant on the two western hemlock species, but on eastern hemlock, *Tsuga canadensis* Carriere, and Carolina hemlock, *Tsuga caroliniana* Engelmann, damage is severe, both in natural forests and urban plantings (McClure 1991). Trees show reduced vigor and thinning canopies, and finally die. Expansion of the geographic area infested by the adelgid is continuing, aided by birds, deer, and wind (McClure 1990).

Resident Natural Enemies: There are no known parasitoids of adelgids. Specialized predators of adelgids have been introduced in the past for attempted control of balsam woolly adelgid (*Adelges piceae*). Interest exists in determining if any of these species (such as *Leucopis obscura* and *Laricobius erichsonii*) have any potential to control populations of hemlock woolly adelgid.

Biological Control Attempts: Extensive surveys have been conducted in Japan to locate predators for introduction into the eastern United States. Of the several predators that were found, the coccinellid *Pseudoscymnus* n. sp. has the greatest potential for biological control. The arboreal oribatid mite *Diapterobates humeralis* (Hermann) has also been identified as an important species affecting eggs of *A. tsugae* in Japan (McClure 1995). Another coccinellid (*Scymnus* sp.) is also currently being tested to determine its value for control. Surveys in China for additional natural enemies are being conducted by the USDA Forest Service.

Reasons for Pest Status and Possibilities for Biological Control: As with other cases of exotic adelgids, the fundamental reasons for the increased damage in North America compared to its native range are unclear. Since the pest is not native to eastern North America, lack of suitable predators may be an important factor favoring high densities. However, the tree species attacked in Japan and the eastern United States are different and therefore increased susceptibility of the eastern hemlock (compared to Asian hosts) could be a factor. Indeed North America hemlocks in Japan suffer greater damage than do native species.

Recommendations: Additional surveys in Asia are needed to locate the adelgid and collect predators from low density populations. Efforts should include focus on Taiwan and areas of mainland China where suitable tree hosts exist. Because of the continued spread of the pest into areas with increased concentrations of hemlock, such exploration is urgently needed.

6. COOLEY SPRUCE GALL ADELGID (*Adelges cooleyi* [Gillette]) (Homoptera: Adelgidae)

Origin: Cooley spruce gall adelgid is native to North America. It has invaded Europe, in conjunction with the use of North American conifer species, such as Sitka spruce, *Picea sitchensis,* and Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, for forestry and landscape purposes. This adelgid has also been reported from various parts of Europe, including the United Kingdom (Anon. 1921a), the Netherlands (van Poeteren 1929), Sweden (Witte 1947), and Italy (Covassi and Binazzi 1981), among others.

Range in North America: The native range of this insect appears to be the Rocky Mountain region of North America. It now occurs throughout North America wherever suitable hosts have been planted. It was first reported from Michigan in 1933 (McDaniel 1933).

Damage: In North America, concern is focused on aesthetic damage to landscape trees, or damage to plantation or shelterbelt trees (e.g., Cumming 1962). Economic losses have not been recorded in nonplantation forest stands. However, concern exists that adoption of forest stand fertilization practices might increase the pest status of this species. Application of 50-200 pounds of nitrogen per acre to 7-year-old Douglas-firs in Washington State increased adelgid fecundity 11-42% compared with that on untreated trees, as well as increasing winter survival (Mitchell and Paul 1974). However, differences between treated and control plots disappeared after two years. Further tests, however, showed that nitrogen applied as urea had no effect on adelgid densities, and that ammonium sulfate applications reduced adelgid densities (Johnson *et al.* 1977).

In the Scotland, the species has been of concern as a pest of plantation forests (Anon. 1947), and investigations have been conducted to determine what factors regulate pest numbers in that area (Parry 1978ab).

Resident Natural Enemies: Reports on natural enemies in the United States were not encountered. Several species have been reported as predators of this adelgid in studies from Scotland. These predators include the coccinellid *Aphidecta obliterata* (Linnaeus) (Parry 1978b, 1992), unspecified syrphids (Parry 1978b), and the brown lacewing *Hemerobius stigma* Steph. (Hemerobiidae) (Laidlaw 1936).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: This species has been spread internationally through the movement of nursery stock for ornamental and forestry purposes. It appears to have expanded its range greatly in North America via the same mechanism. Natural enemies have not been studied in the Rocky Mountain region (the native range). Some natural enemies might be present in the native range that could be of value in other parts of the pest's North American or international distribution.

Recommendations: A biological survey of natural enemies affecting this adelgid in the Rocky Mountain area would be useful. It should have as its goal both the compilation of names of species attacking the pest and the quantification of rates of survivorship for the pest in settings ranging from undisturbed forests to plantation plantings and urban trees.

7. PINE BARK ADELGID (*Pineus strobi* [Hartig]) (Homoptera: Adelgidae)

Origin: Pine bark adelgid is native to North America and also is present in Eurasia, where populations have been noted in France (Marchal 1913) and Ukraine (Dmitriev 1960), among other locations. In France, it is reported as having invaded the country from North America (Marchal 1913).

Range in North America: Pine bark adelgid occurs in most parts of the United States, wherever white pine (*Pinus strobus* Linnaeus) grows.

Damage: Pine bark adelgid populations are, at times, dense and strikingly visible, especially on trunks of trees in parks, planted landscapes, and nurseries. Little permanent damage is believed to occur, however, if trees are otherwise healthy (Drooz 1985). Heavy infestations on 2-yr-old white pines in plantations in North Carolina did not affect survival but did reduce growth, measured two years after planting (Rogers *et al.* 1984).

Resident Natural Enemies: Wilson (1938) investigated the natural enemies of *Pineus strobi* and the related species *Pineus pini* (*Gmel.*) (=*P. laevis* [Mask.]), looking for natural enemies suitable for introduction into Australia, where *P. pini* had invaded and become a pest on *Pinus radiata* D. Don.

As is true for all members of the family Adelgidae, there are no known parasitoids of *Pineus strobi*. A variety of predators were encountered in the United Kingdom by Wilson, of which the five he judged most important were the chamaemyiids *Leucopis obscura* Hal. and *Lestodiplosis pini* Barnes, the hemerobiids *Hemerobius stigma* Steph. and *Wesaelius concinnus* Steph. and the coccinellid *Exochomus quadripustulatus* Linnaeus. The chamaemyiid *Leucopis pinicola* Mall. has been noted in Ohio as feeding on *Pineus strobi* (Sluss and Foote 1973). Native natural enemies of *P. strobi*, such as the derodontid beetle *Laricobius rubidus* Leconte and *Leucopis pinicola,* have also been of interest as predators of exotic pest adelgids in North America such as the balsam woolly adelgid, *Adelges piceae* (Ratz.) (Clark and Brown 1957, 1960). Some species, such as *Leucopis obscura*, which were collected from Europe from various adelgids including *P. strobi* (Wilson 1938) and released in North America against *A. piceae*, have been reported feeding on *P. strobi* (Brown and Clark 1958).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: The damage caused by this insect is minor and biological control efforts against it in North America seem unwarranted.

Recommendations: This species is not a suitable target for natural enemy introductions for its own sake, both because of the minor nature of the damage it causes and its status as a native species. It is, however, of some interest as an alternate prey species for predators introduced against other exotic pest adelgids, including the balsam woolly adelgid, *Adelges piceae,* and the hemlock woolly adelgid, *Adelges tsugae.*

8. PINE LEAF ADELGID (*Pineus pinifoliae* [Fitch]) (Homoptera: Adelgidae)

Origin: Pine leaf adelgid is native to North America.

Range in North America: Pine leaf adelgid occurs widely throughout North America, coinciding with the ranges of its two primary hosts, red (*Picea rubens*) and black (*Picea mariana*) spruce (Drooz 1985)

Damage: The species has a complex life cycle that is divided between species of spruce on which it forms galls on tips of twigs, and white pine on which it feeds openly on needles (Balch and Underwood 1950). Galls on spruce are of no economic importance, except as a disfigurement on ornamental specimens. On white pine, however, populations can reduce growth, shorten internodes, and cause distortion (DeBoo *et al.* 1964). A prolonged outbreak of this species occurred in New York and New England from 1955 to 1964 (DeBoo *et al.* 1964). Methods for sampling various life stages on spruce (Howse and Dimond 1965) and white pine (Ford and Dimond 1973, Dimond and Allen 1974) have been developed.

Resident Natural Enemies: None are recorded.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Little or nothing is known of the determinants of population density in this species.

Recommendations: If economically warranted, comparisons of the intensity of natural enemy mortality in outbreak and non-outbreak areas, taking into account local spruce- white pine stand composition, might provide valuable insight as to whether natural enemies are an important mortality factor in this system.

True Aphids

9. WHITE PINE APHID (*Cinara strobi*) (Homoptera: Aphididae)

Notes: An earlier generic placement is *Dilachnus*.

Origin: White pine aphid is native to North America.

Range in North America: This aphid is found from New England through the Great Lakes States, in association with eastern white pine (*Pinus strob*us) (Drooz 1985).

Damage: Damage occasionally occurs to young trees and individual branches of larger trees when densities of this species are high.

Resident Natural Enemies: Muesebeck *et al.* (1979) lists two braconids as parasitoids of this species: *Pauesia bicolor* (Ashmead) and *Pauesia xanthothera* (Smith).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: This aphid appears to be a minor pest that only occasionally reaches densities sufficient to damage its host. Other species in the genus (e.g., *Cinara cupressi*) have become important pests of exotic pine plantations after invading new regions (Allard and Day 1994).

Recommendations: None.

10. WOOLLY ELM APHID (*Eriosoma americanum* [Riley]) (Homoptera: Aphididae)

Notes: Eastop (1987) provides a key to the subgenera of *Eriosoma*.

Origin: Woolly elm aphid is native to North America.

Range in North America: This species is found throughout eastern North America, wherever elms occur.

Damage: *Eriosoma americanum* is found on species of elms as primary hosts and *Amelanchier* spp. as alternate hosts. On elms, the aphids feed on the edges of young leaves, causing them to roll inward. Two other species in this genus are also found on elms. *Eriosoma lanigerum* (Hausmann), which is primarily a pest of apples, on elms feeds on new terminal leaves, causing them to form rosettes. *Eriosoma rileri* Thomas forms dense woolly clusters on the limbs and trunks of elms. Dense infestations can cause serious deformations (Drooz 1985).

Resident Natural Enemies: Predators found associated with *E. americanum* include the mirid *Saileria irrorata* Henry in Indiana (Henry 1976), the coccinellid *Scymnus brulleri*

Mulsant in Pennsylvania (Wheeler and Jubb 1979), and the coccinellid *Scynmus creperus* Mulsant in Massachusetts (Sweetman and Smith 1942). From related species of *Eriosoma* on elms in Europe, various species of predacious *Leucopis* (Diptera: Chamaemyiidae) have been recorded (Tanasijtshuk *et al.* 1976, Raspi 1988), as well as the parasitoid *Areopraon lepelleyi* Wtstn. (Starý 1976). The North American species, *E. lanigerum*, which has spread worldwide as a pest of apple, has been effectively controlled in a number of locations by introductions of the North American aphelinid parasitoid *Aphelinus mali* (Haldeman) (Clausen 1978).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: This species is of minor importance as a pest.

Recommendations: None.

11. WOOLLY BEECH APHID (*Phyllaphis fagi* [Linnaeus]) (Homoptera: Aphididae)

Origin: Woolly beech aphid is not native to North America. It occurs in Europe and may have invaded North America on nursery plants shipped from Europe. Whether Europe is the native home or was itself invaded at some earlier time, has not been determined. Outbreaks of this species occur occasionally in Europe, e.g., the former Czechoslovakia (Starý 1967) and Austria (Kurir 1947).

Range in North America: Woolly beech aphid is widely distributed in both eastern and western North America in association with its only host, European birch, *Fagus sylvatica* Linnaeus (Richards 1973).

Damage: Outbreaks occasionally occur in Europe (Starý 1967, Kurir 1947) and the aphid can cause damage in nurseries. In the United States, the aphid damages landscape specimens of European beech.

Resident Natural Enemies: No reports on natural enemies of this aphid in the United States were found. No parasitoids attacking this species are listed for North America in Krombein *et al.* (1979). The braconids *Praon flavinode* (Haliday) and *Trioxys phyllaphidis* Mackauer are reported attacking this aphid in the former Czechoslovakia (Starý 1967). Wobst (1990) records some parasitoids in Germany.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: The aphid's pest status in the United States is likely related to separation from key natural enemies due to invasion of new, disjunct geographical areas.

Recommendations: Importation of natural enemies, particularly specialized parasitoids, from the native home of the aphid is likely to be of value. A fuller review of the distribution of the aphid, its nearest relatives, and its host plant should be undertaken before importations to

determine whether Europe is the native home of the pest. If Europe is an area of earlier invasion, parasitoids from the true native home should be sought once this location has been determined.

12. TULIPTREE APHID (*Illinoia liriodendri* [Monell]) (Homoptera: Aphididae)

Notes: This species was known formerly as *Macrosiphum liriodendri.*

Origin: Tuliptree aphid is native to North America.

Range in North America: This species is native to the eastern United States. It has invaded northern California and other parts of the western United States where tuliptrees (*Liriodendron tulipifera* Linnaeus) have been introduced as shade trees.

Damage: In the eastern United States, the tuliptree aphid causes relatively little damage. Energy budget studies in Tennessee suggest that the aphid can remove up to 17% of the tree's nitrogen but only about 1% of its total photosynthate (Van Hook *et al.* 1980). In northern California, tuliptree aphid populations on urban tuliptrees are sufficiently high that honeydew contamination of parked cars is a nuisance (Dreistadt and Dahlsten 1988).

Resident Natural Enemies: In the eastern United States parasitoids attacking the tuliptree aphid include a *Praon* sp., *Ephedrus incompletus* Provancher, and *Aphidius polygonaphis* (Fitch) (formerly referred to as *Aphidius liriodendri*) (Zupark and Dahlsten 1993). Other species recorded as parasitizing tuliptree aphid in North America include *Aphidius nigripes* Ashmead and *Aphidius rosae* Haliday (Krombein *et al.* 1979).

Biological Control Attempts: To reduce honeydew production by tuliptree aphids on street trees in California, three species of parasitoids (a *Praon* sp., *Ephedrus incompletus*, and *Aphidius polygonaphis*) were collected at various locations in the eastern United States and released in northern California (Zupark and Dahlsten 1993). *Aphidius polygonaphis* has established and spread, and is now the most common parasitoid attacking the tuliptree aphid in California. While no quantitative assessments have compared aphid densities before and after establishment of this parasitoid, the aphid problem is clearly not yet fully resolved. The other two aphid parasitoids failed to establish. Tests of mass release of green lacewing eggs (*Chrysoperla* sp.) failed due to high ant predation on the eggs (Dreistadt *et al.* 1986).

Reasons for Pest Status and Possibilities for Biological Control: In the eastern United States, the species does not appear to be a pest, although population studies are lacking. Populations in the western United States appear to have increased in density and to reach pest status more regularly, perhaps because they have invaded a geographically isolated region outside the aphid's range and have thus escaped their natural enemies. Introductions of natural enemies from the aphid's native range in the eastern United States might reduce aphid densities in western invaded areas.

Recommendations: Initial efforts to reduce aphid numbers in California by introducing eastern species of parasitoids have been only partially successful. One of three known parasitoid species has established. Further efforts to collect and establish the *Praon* sp. and

Ephedrus incompletus should be made. These species were released in relatively small numbers (32 *Praon* sp. and 628 *E. incampletus*) (Zuparko and Dahlsten 1993), and thus the failure of these species to establish may not be biologically significant, but might merely reflect an insufficient effort.

13. NORWAY MAPLE APHID (*Periphyllus lyropictus* [Kessler]) (Homoptera: Aphididae)

Origin: Norway maple aphid is probably an exotic species that invaded the United States on nursery plants. It occurs in Europe and its principal host in the United States is Norway maple, *Acer platanoides*. The genus has been reviewed by Essig and Abernathy (1952).

Range in North America: This species appears to be widespread in the eastern United States, wherever Norway maple has been planted.

Damage: Dense populations of the aphid can defoliate Norway maple. In addition, honeydew from such populations would be a nuisance in cities to parked cars.

Resident Natural Enemies: Krombein *et al.* (1979) record two parasitoids in North America attacking this aphid: *Praon negundinis* Smith and *Euaphidius setiger* Mackauer. In Europe, Starý (1972) records three species of parasitoids attacking *P. lyropictus* in the former Czechoslovakia, *Aphidius setiger* Mackauer, *Trioxys falcatus* Mackauer, and *Praon silvestre* Starý, all of which are specialists on this aphid genus. (*Aphidius setiger* Mackauer and *Euaphidius setiger* Mackauer refer to the same species). In France, *Aphidius ribis* Haliday is reported as a parasitoid of this aphid (Paillot 1938). Wallace *et al.* (1928) in discussing natural enemies attacking Norway aphid in Illinois record various species of coccinellids, but no parasitoids.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: This aphid is believed to be an exotic species attacking principally the introduced tree *Acer platanoides*. The parasitoids reported in North America include only one of the three specialist species recorded by Starý (1972) in the former Czechoslovakia. The absence of important species of parasitoids from the aphid's homeland may be the reason for its ability to reach pest densities in North America.

Recommendations: The introduced status of this species should be confirmed by consultation with aphid taxonomists. A survey should be conducted to determine the extent of its pest status in selected States in the United States, and mummies collected to determine which species of parasitoids are attacking it in North America. Collections of additional species of parasitoids should be made in Europe and introduced to North America to further reduce the aphid's typical densities.

14. LINDEN APHID (*Eucallipterus tiliae* [L.]) (Homoptera: Aphididae)

Notes: Former generic placements include *Myzocallis* and *Callipterus*.

Origin: Linden aphid occurs as an exotic species in North America and is also found in Europe. Recently, the species has been recognized as occurring naturally in China and the Russian Far East (Zuparko and Dahlsten 1995). It was first recorded in the United States in Washington, D. C., in 1886, and in California about 1935 (Olkowski *et al.* 1982).

Range in North America: This species is found in both the eastern United States (Felt and Bromley 1937) and in California (Olkowski *et al.* 1982), and probably occurs wherever its host trees (*Tilia* spp.) occur. The linden aphid also occurs as an exotic pest in New Zealand, having first been recorded there in 1979 (Barlow 1982).

Damage: Large populations of the aphid develop on native and introduced species of *Tilia*, diverting energy from plant growth (Llewellyn 1972). When such trees are planted along city streets, honeydew dripping onto automobiles is a nuisance (Carter 1982, Zuparko and Dahlsten 1995).

Resident Natural Enemies: Information is available about the natural enemies of linden aphid principally from the United Kingdom, where it is called the lime aphid, and California, where it is exotic and has been the target of biological control introductions.

In the United Kingdom, the natural enemies that have received the most study are the predatory coccinellid *Adalia bipunctata* Linnaeus and the capsid bug *Blepharidopteris angulatus* (Fallén) (Dixon 1971; Glen 1973, 1975; Dixon and Barlow 1979; Glen and Barlow 1980; Mills 1982). Parasitoids have received little study, although Starý (1978) records *Trioxys tenuicaudus* Starý as a parasitoid of linden aphid in Europe.

In California, the braconid *Trioxys curvicaudatus* Mackauer has been imported from Europe and released in several locations as a biological control agent against linden aphid (Olkowski *et al.* 1982, Zuparko 1983, Zuparko and Dahlsten 1995). Evaluations of pre- and post-release aphid densities suggest that releases may have lowered aphid numbers, particularly in San José, although Zuparko and Dahlsten (1995) think that host plant resistance is more important in suppressing linden aphid in northern California than are parasitoids. Other parasitoids reared from linden aphid in northern California, apart from *Trioxys curvicaudatus*, include the braconids *Trioxys pallidus* (Haliday), *Trioxys tenuicaudus*, and an undescribed *Trioxys* sp.; and the aphelinids *Aphelinus subflavescens* (Westwood), *Aphelinus* sp. nr. *perpallidus* Gahan, and *Aphelinus automatus* Girault (Zuparko and Dahlsten 1995).

In Europe, studies suggest that the role of natural enemies is limited to causing mortality after aphid numbers have declined seasonally, causing aphid numbers to decrease to even lower levels (Dixon 1971). The fundamental cause of aphid population decline in the United Kingdom is believed to be decline in size and fecundity of aphids that develop in groups (Dixon 1971). Thus in years in which aphids are common at the start of the season, populations

quickly peak and crash and then are pushed to very low levels by generalist predators (Dixon and Barlow 1979). In contrast, if aphids are initially low in number, dense populations develop more gradually, and at the end of the year many oviparae are produced, leading to initially high numbers the following year. This alternating pattern of population size then repeats itself. Predators play important roles in this pattern in years when initial populations are high or medium, but not when aphids are initially scarce.

Biological Control Attempts: An attempt to suppress linden aphid in San Francisco, California, was begun in 1970. Several species of parasitoids were collected in Europe (Italy and France) and released, including a *Praon* sp., *Praon flavinode* (Haliday), an *Aphidius* sp., *Trioxys curvicaudus*, and *Aphelinus subflavescens* (Zuparko and Dahlsten 1995). Of these, the only parasitoid that established was *Trioxys curvicaudus*. While this species is credited with controlling the linden aphid in two cities, Berkeley (Olkowski *at al.* 1982) and San José (Zuparko 1983), the parasitoid has not been effective in Sacramento and other parts of northern California (Zuparko and Dahlsten 1995).

The degree of damage caused by linden aphid and its associated natural enemies appears not to have been studied in the eastern United States, other than a host record from New York noting the occurrence of both *Trioxys tenuicaudus* and *Aphelinus subflavescens* (Hajek 1986).

Reasons for Pest Status and Possibilities for Biological Control: Two different views are presented in the literature concerning the basic causes for the typical population densities of linden aphid. In the United Kingdom, Dixon (1971) views the aphid population cycle as driven predominately by an intraspecific competition effect of reduced size and fecundity of aphids reared in groups. Dixon views the role of natural enemies to be limited to exacerbating the crash phase of the population cycle, driving low, post-crash populations even lower, but not causing the crash itself. No particular importance was attached to parasitoids in the United Kingdom studies.

In contrast, work in California in the 1970s and 1980s was based on the premise that the aphid's population densities reflected its exotic status and lack of specific natural enemies. Control is asserted to have followed the introduction of one parasitoid species (Olkowski *et al.* 1982, Zuparko 1983).

Recommendations: The status of the linden aphid population and the importance of natural enemies in determining the species' typical density and population pattern could be investigated. Alternatively, a new line of investigation might be to search for additional natural enemies for importation from China and the Russian Far East, which recently have been recognized as part of the species' home range (Zuparko and Dahlsten 1995).

15. BEECH SCALE (*Cryptococcus fagisuga* Lindinger) (Homoptera: Eriococcidae)

Notes: Formerly this species has been cited in literature as both *Cryptococcus fagi* Douglas and *Cryptococcus fagi* (Baerensprung). A review of the biology and population dynamics of this species is provided by Wainhouse and Gate (1988).

Origin: In North America, beech scale is clearly an exotic invader, first recorded in Nova Scotia about 1890 (Hutchings 1926, Drooz 1985). This species also occurs in central and western Europe, where the scale is widespread but the disease is not (Wainhouse and Gate 1988). The possibility needs to be considered that Europe may not be the native range but merely a region invaded during an earlier period. Spread of the pest in some parts of Europe, e.g., Holland, is documented (Anon. 1921b). *Cryptococcus fagisuga* also occurs and causes damage in Iran (Adeli and Soleimani 1976). A map of its world distribution records the scale in much of Turkey and Europe, but not Greece, Spain, Russia (except the north coast area of the Black Sea), or Asia (Anon. 1979a). Its initial area of origin, if different from Europe, could not be determined from the literature.

Range in North America: The scale occurs in parts of eastern Canada, New England, New York, New Jersey and south into parts of the southern Appalachian Mountains (Drooz 1985, Houston 1994a). See Houston (1994a) for a map of both the scale and beech bark disease, which with the scale is associated. Houston (1983a, 1994a) discusses the history of the invasion of this scale into North America and its subsequent spread from Nova Scotia to other parts of Canada and the northeast United States.

Damage: Following its initial introduction, the scale was associated with a wave of mortality of older American beech (*Fagus grandifolia* Ehrhardt) trees as the scale invaded beech forests throughout the region (Houston 1983a). For example, Balch (1941) records that beech bark disease had by 1940 destroyed most of the mature beech stands in Nova Scotia. Damage is not due directly to the scale, but rather to associated fungal pathogens. In North America, two pathogens of beech are associated with beech scale, *Nectria coccinea* var. *faginata* Lohmman, Watson and Ayers and *Nectria galligena* Bres. (Felt 1934, Perrin 1983, Houston 1994b). Following initial mortality of beech after a new area is invaded by the scale, regrowth of sprouts from affected trees occurs. These stems are themselves subject to further attack (Houston 1975). Trees that are not killed produce wood of lower grade due to cankers (Houston 1983a, Burns and Houston 1987).

In Europe, European beech (*Fagus sylvatica*) is attacked by the scale and disease, but the combination appears to be less damaging to this host than to American beech (Ehrlich 1934, Wainhouse 1983), although losses may be significant in some areas (e.g., in France, Perrin 1979). In Germany over a 13-year period, 18% of European beech trees that were initially or heavily infested with beech scale died (Bogenshütz 1983).

In both Europe and the United States some beech trees show resistance to the scale (Houston 1983b, Houston and Houston 1987, Wainhouse and Howell 1983, Lunderstadt and Eisenwiener 1989).

Resident Natural Enemies: No parasitoids are known from this scale (Houston 1983a). Various coccinellids have been recorded as predators of beech scale, including *Chilocorus stigma* Say (Brown 1934, in the United States) and *Exochomus quadripustulatus* (L.) (Baylac 1980, in France). These predators, however, are believed to be of limited value in checking the population growth of the scale because of their dispersal from sites with declining scale densities and their selective feeding on only certain stages of the scale (Mayer and Allen 1983, Houston 1983a). A dipteran predator, *Lestodiplosis* sp. has also been noted in France (Baylac 1980). The life history of this dipteran predator has been studied in France, and it has been observed to increase too slowly to control the scale (Baylac 1986). The fungus *Verticillium lecanii* (Zimmerman) Viegas is a pathogen of beech scale (Lonsdale and Sherriff 1983).

Natural enemies of the beech bark disease pathogens have also been recorded. The *Nectria* fungi are attacked by the mycoparasite *Nematogonum ferrugineum* (Pers.) Hughes (=*Gonatorrhodiella higlei* A. L. Smith) (Perrin 1977 Houston 1983c). Houston (1983a) also records a *Fusarium* sp. as an antagonist of *Nectria* sp.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: At high densities, beech scale, when attacking American beech, and to a lesser degree when attacking European beech, increases pathogen invasion because of bark cracking. American beech is a new host for this scale which colonized this tree species after invading North America. Whether the scale also invaded Europe is less clear. If so, damage from the scale in both locations would be attributable to high scale densities after movement to new regions, due to some mix of colonizing more sensitive host trees and loss of natural enemies present in the scale's native range. Without a better understanding of the original hosts of the scale in its native range, the degree of importance of increased susceptibility of new tree hosts in newly invaded regions is hard to judge. However, variation of host plant resistance with American beech is clearly an important factor determining degree of damage between trees.

Recommendations: It is not certain whether Europe is the native range of this scale. If Europe is the native home, then there would appear to be relatively little prospect for control of the scale through importation of natural enemies, as studies in Europe have found neither parasitoids nor important predators. Under this scenario, the greater damage in North America would be attributable to greater sensitivity of American beech to either the scale (more bark cracking) or the pathogen (less resistance to infection), or both.

An alternative hypothesis is that Europe is not the native home, but rather an area of earlier invasion. If this is the case, efforts to locate the area of origin might lead to discovery of more effective natural enemies of the scale.

Europe and any other region that might be suspected as a native home of the scale should be surveyed for antagonistic or mycoparasitic fungi capable of suppressing the pathogen.

Barring success in either of these approaches, efforts might be made in North America to propagate beech trees that show natural resistance to the disease. Use of herbicides to kill regrowth of susceptible beeches might be used to favor the resistant individuals (Ostrofsky and McCormack 1986).

16. RED PINE SCALE (*Matsucoccus resinosae* Bean and Godwin) (Homoptera: Margarodidae)

Notes: *Matsucoccus resinosae* may be a synonym of *Matsucoccus matsumurae* (Kuwana) (McClure 1983a). Evidence for synonymy includes cross attraction of pheromones from the two populations (Young *et al.* 1984).

Origin: Red pine scale is believed to be native to Japan and to have invaded both eastern North America (Bean and Godwin 1955) and China (McClure 1983a).

Range in North America: The scale's range in North America is currently restricted to red pine (*Pinus resinosa* Ait.) plantations south of the natural range of red pine, mostly in Connecticut, Long Island, New York, New Jersey, and Pennsylvania (Bean and Godwin 1955, Stimmel 1981, Drooz 1985). The infested area continues to expand at a slow rate.

Damage: Of trees native to North America, damage is limited to red pine. Six other pines, of Asian origin, are known to be suitable hosts (McClure 1983a). On red pine, damage is severe; in some instances entire plantations are killed over a number of years (McClure 1983b).

Resident Natural Enemies: Native natural enemies reported feeding on this scale in North America include the cecidomyiid *Lestodiplosis* sp. nr *grassator* (Fyles) (McClure 1983b) and the predacious anthocorid bug *Xanotrachelliella inimica* D. and H. (Bean and Godwin 1955). However, neither of these agents cause sufficient mortality to be of any importance in regulating the density of the pest. An Asian coccinellid, *Harmonia yedoensis* (given as *Harmonia axyridis* Pallas in McClure 1983c), feeds on this scale, and is believed to be capable of suppressing the pest (McClure 1983c). This predator is credited with controlling the scale in China, another area the scale is believed to have invaded (McClure 1983a,c), and is reported to be an important natural enemy of the scale in Japan (McClure 1986a).

Biological Control Attempts: Natural enemies of this scale have been studied in Japan (McClure 1986a,b) and China (Cheng and Ming 1979, McClure 1983c). Studies of the potential of *Harmonia axyridis* as a predator of red pine scale have been conducted in Connecticut (McClure 1983c). At the time of this later study, it was uncertain whether this coccinellid could successfully overwinter in New England. This species has since spread naturally northward and has become abundant in southern New England.

Reasons for Pest Status and Possibilities for Biological Control: Red pine scale is most likely a pest in North America because it has invaded the region and is insufficiently suppressed by North American natural enemies. Introduction of natural enemies appears to have controlled the scale in China, another area invaded by the pest, and would be the obvious approach to pursue in North America. Work of McClure (1983a,c) has pursued this possibility. To date, the only candidates identified have been *Harmonia yedoensis and H.*

axyridis). *Harmonia axyridis* has now become established in the northeast throughout the area infested by red pine scale, and studies should be made of its impact, if any, on red pine scale densities.

Recommendations: Field studies are needed to determine the degree of impact that *H. axyridis* is having (since about 1994) on red pine scale. Further explorations in Japan (the native home of the pest) and China to discover additional natural enemies of promise would also be useful. Should *H. axyridis* prove ineffective, *H. yedoensis* should be considered provided it can be shown not to compete with native coccinellids and not to aggregate in buildings.

17. TULIPTREE SCALE (*Toumeyella liriodendri* [Gmelin]) (Homoptera: Coccidae)

Origin: Tuliptree scale is native to North America.

Range in North America: This scale is found from Connecticut through southern Illinois and Tennessee, and in some parts of Florida. See Burns and Donley (1970) for a distribution map.

Damage: This scale damages tuliptree, also known as yellow-poplar, (*Liriodendron tulipifera* Linnaeus), and various species of magnolia.(*Magnolia* spp.) (Drooz 1985). Scale infestations can kill seedling trees (2-4 years old); kill leaders, causing crooked trees; kill leaders and laterals, causing bushy trees; and cause loss of vigor of whole trees (Burns 1970).

Resident Natural Enemies: In Tennessee, Simpson and Lambdin (1983) found that up to 74% of second stage male scales were parasitized by a set of species including *Aphidius* sp., *Metaphycus flavus* (Howard), *Coccophagus* sp., and *Syntomosphyrum* sp. Female scales were parasitized by the syrphid *Baccha costata* (Say), with rates of parasitism up to 98%. Predators noted included larvae of the pyralid moth *Laetilia coccidivora* (Comstock) and the coccinellids *Adalia bipunctata* (Linnaeus), *Chilocorus stigma* (Say), *Cyoneda* sp., and *Hyperaspis signata* Olivier. In Pennsylvania, Burns (1973) recorded the presence of *Hyperaspis proba proba* (Say), the pyralid *Laetilia coccidivora* (Comstock), and the syrphid *Baccha costata* (Say). At this location, however, levels of parasitism by *B. costata* were less than 1%. Other natural enemies associated with this scale species include the fungal pathogen *Aschersonia cubensis* Berkeley and Curtis and the encyrtid parasitoid *Anicetus toumeyella* (Milliron) (Burns and Donley 1970). *Anicetus toumeyella* was first described in association with a tuliptree scale outbreak that occurred in the 1950s in Delaware (Milliron 1959).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: This species is reported as frequently being abundant (Drooz 1985). One potential explanation for this condition is the frequent tending of this scale by ants (Burns 1973, Simpson and Lambdin 1983). Studies have shown that scale survivorship increases markedly (from 8 to 47%) when

scales are tended by ants, presumably because at least some species of the natural enemies are hampered by ants (Burns 1973).

Recommendations: Should tuliptree scale populations occur at damaging levels in plantations, the site should be checked to determine if ant species tending scales are abundant and if so, trials focused on ant suppression should be conducted to see if scale densities decline when ant numbers are minimized with baits or tree bands. Care should be taken not to induce scale outbreaks by use of broadcast pesticide applications that would themselves suppress natural enemies of the scale.

18. PINE TORTOISE SCALE (*Toumeyella parvicornis* [Cockerell]) (Homoptera: Coccidae)

Origin: Pine tortoise scale is native to North America.

Range in North America: Pine tortoise scale is found throughout the eastern United States, westward to the Dakotas. It is found on various pines, especially Scotch (*Pinus sylvestris* Linnaeus), but also jack (*Pinus banksiana* Lamb.) and Virginia (*Pinus virginiana*), among others (Drooz 1985).

Damage: In most settings, scale populations are suppressed by natural enemies to harmless levels. Damage occurs when natural enemy action is reduced by ant-tending (e.g., Wilkenson and Chellman 1979) or in intensively managed settings such as seed orchards (Clarke *et al.* 1992) and Christmas tree plantations (Nielsen 1990).

Resident Natural Enemies: Krombein *et al.* (1979) list four parasitoids as using pine tortoise scale as hosts: *Coccophagus albicoxa* Howard, *Coccophagus immaculatus* Howard, *Coccophagus quaestor* Girault, and *Microterys fuscicornis* (Howard).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Pest status is attained when native natural enemies are suppressed by factors such as dust, ant-tending, or pesticide use. Prevention of these conditions can aid in the conservation of natural enemies of this scale. In seed orchards or Christmas tree plantations, pesticide applications for other pests, should be selected (in terms of chemicals chosen, and manner and time of application) so as to minimize effects on natural enemies of the scale. If ant-tending causes outbreaks, chemical suppression of ants may be necessary.

Recommendations: Studies on methods to conserve natural enemies of this scale in seed orchards and Christmas tree plantations would be useful in defining the best management methods.

19. ELONGATE HEMLOCK SCALE (*Fiorinia externa* Ferris) (Homoptera: Diaspididae)

Notes: A review of the biology and population dynamics of this species is provided by McClure (1988).

Origin: Elongate hemlock scale is of Japanese origin (McClure 1978a). It has also invaded other locations in addition to North America, such as the United Kingdom (Williams 1988).

Range in North America: This scale is now found from Connecticut to Georgia, and west to Ohio (Drooz 1985).

Damage: This scale can reproduce on over 40 species of conifers, but is most commonly found on eastern hemlock (*Tsuga canadensis*) (McClure 1978a). This scale is one of three exotic Homoptera (the others being *Tsugaspidiotus tsugae* [Marl.] [now *Nuculaspis tsugae*], and *Adelges tsugae*) currently attacking eastern hemlock in eastern North America (McClure 1978a). Collectively these species pose a serious threat to the continued existence of eastern hemlock as an important component of the eastern deciduous forest.

Resident Natural Enemies: An aphelinid, *Aspidiotiphagus citrinus* (Crawford), was found attacking this scale in Connecticut at levels that varied from 5-48%; the percentage of parasitism was positively correlated to scale density (McClure 1977a). In Connecticut this species is not well synchronized with *F. externa*, which is univoltine in Connecticut, in contrast to the parasitoid, which is mulitivoltine. As a consequence, this parasitoid cannot regulate this scale in Connecticut (McClure 1978b).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: The pest status of this scale is likely due to its having escaped important natural enemies in the process of invading eastern North America. A shift to new host plant species, however, is a complicating factor that might also be important, as the hemlock species attacked in eastern North America is a different host than that attacked in Asia. In Connecticut, elongate hemlock scale populations are ultimately self-regulated (at high densities) because developmental rates, survival rates and fecundity decline with increasing density (McClure 1979). However, the densities at which populations are self-regulated are sufficiently high to damage, and sometimes kill hemlocks. Life tables of *F. externa* and another exotic scale on eastern hemlock, *Nuculaspis tsugae*, for co-existing and separate populations, show that *F. externa* is the superior competitor (by virtue of earlier emergence) (McClure 1981). In addition, their shared parasitoid *Aspiotiphagus citrinus* in fall has a disproportionate effect on *N. tsugae*, which in Connecticut is bivoltine.

These studies emphasize that the details of the seasonal life history of each host are important in determining the importance of specific parasitoids as sources of mortality and potential population regulators. These features vary by location, as illustrated by Stimmel's (1980) record that *F. externa* is multivoltine, not univoltine, in southern Pennsylvania. Fertilization may play some (probably small) role in the development of pest populations in nurseries and

urban landscapes, as fertilization increases survival of the immature stages of the scale (McClure 1977b). Information on the relationships between these parasitoids and their hosts in the native range (Japan) of these pest scales is given by McClure (1986c).

Recommendations: This species is a good target for a classical biological control project. Additional species of parasitoids should be imported from its home range in Japan and other parts of Asia. Special attention should be paid to selecting parasitoid populations that will be well synchronized with the scale in each particular release location. Parasitoids of each species may have to be collected at several locations to adequately match the range of areas where the scale is a pest but may have different numbers of generations per year.

20. OYSTERSHELL SCALE (*Lepidosaphes ulmi* [Linnaeus]) (Homoptera: Diaspididae)

Origin: Oystershell scale is known to be invasive in North America, Australia, New Zealand, and Japan (Tothill 1918, Kaburaki 1934, Hill 1989). It is widespread in Europe, North Africa, the Middle East, Russia, and the Far East (Clausen 1978). Its native range has not been determined and has been obscured by widespread movement of the scale on apple nursery stock.

Range in North America: The species is found throughout the United States and southern Canada (Drooz 1985).

Damage: This species has been of concern primarily as a pest of apple. However, this scale is polyphagous and attacks a wide variety of ornamental and forest trees, especially species of ash, willow, and poplar (Drooz 1985). It has potential to become a pest in poplar plantations (Masutti 1982). It has also been observed in India to vector a plant disorder ("little leaf" of *Angelonic grandiflora*) that is believed to be caused by a mycoplasma-like organism (Hedge *et al.* 1977). This observation suggests some risk for a future increase in damage from this scale should pathogens it can transmit be introduced into North America.

Resident Natural Enemies: The literature on natural enemies of oystershell scale refers most often to two species, the predacious mite *Hemisarcoptes malus* (Shimer) and the aphelinid parasitoid *Aphytis mytilaspidis* (Le Baron). Each of these are found in both Europe and North America and are believed to have invaded North America together with the pest.

Hemisarcoptes malus. This species was first studied in North America, but was later also observed in Europe. In North America, this mite was found to be an important predator of eggs, nymphs, and adults of oystershell scale in medium to high density scale populations. It was found to be active even at relatively low temperatures and has been recorded as the most important natural enemy of this scale in Ontario (Tothill 1918). This species was later introduced to British Columbia and is credited with controlling the scale in some locations in that province (Venables 1923). Analysis of lifetables developed by Samarasinghe and LeRoux (1964, 1966) showed this predator to be the key factor controlling this scale on apple in Quebec.

Aphytis mytilaspidis. Imms (1916) describes the biology of this parasitoid (under the name *Aphelinus mytilaspidis*) on oystershell scale on apple in Britain. Imms notes that

this wasp was the most common parasitoid of the scale in Britain, but levels of parasitism were low (around 7%) and other measures were required for control of the scale on apple. *A. mytilaspidis* was also the most important parasitoid in Ontario (Tothill 1919). The biology and early literature on this species are discussed by Griswold (1925). Lord and MacPhee (1953) found that larvae of this parasitoid (in parasitized scale) were less tolerant of extremes of winter cold than eggs of the scale, leading to great variation in this parasitoid's importance in various parts of eastern Canada. This parasitoid is also recorded from oystershell scale from Italy and the Netherlands (Monti 1956, Karsemeijer 1973).

Other natural enemies. Several other parasitoids have been reared from oystershell scale in various parts of the world. In Ontario, Tothill (1919) noted the presence of *Aspidiotiphagus citrinus* (now *Encarsia citrina*). In Italy, *Apterencyrtus microphagus* (Mayr), *Physcus testaceus* Masi, and *Anabrolepis* (now placed in *Epitetracnemus*) *zetterstedtii* (Westwood) have been reared from oystershell scale from poplar (Monti 1956). *Apterencyrtus microphagus*, *Anabrolepis zetterstedtii*, and *Aphytis proclia* (Walker) have been reared from this scale in the Netherlands (Karsemeijer 1973). Saakyan-Baranova and Dergunova (1978) provide information on species of parasitoids reared from oystershell scale from various host plants in the central Asian portion of the former U.S.S.R. Of these parasitoids, *Aphytis proclia* has been observed in Quebec (Parent 1973), and *Physcus testaceus* was released (from collections from Europe) in California but not recovered (Flanders 1942).

Little mention is made in the literature of diseases or other predators of oystershell scale.

Biological Control Attempts: Relatively little work has been done on the biological control of this scale. The predacious mite *Hemisarcoptes malus* was moved from eastern to western Canada and is believed to have controlled the scale in that location (Venables 1923, Lord 1971, Clausen 1978). Hill (1989) notes the need to introduce this species to New Zealand.

Virtually no parasitoid introductions have been made against this scale, with the exception of *Physcus testaceus*, which was moved from Europe to California (Flanders 1942). The target for this species, however, was largely a different scale, *Lepidosaphes ficus* Sign.

The effects of sulfur and other pesticides on natural enemies of oystershell scale have been studied on apple in eastern Canada (Lathrop and Hilborn 1950, Pickett and Patterson 1953). Sulfur was found to be more damaging than copper fungicides or ferbam.

Reasons for Pest Status and Possibilities for Biological Control: Oystershell scale is a diaspid scale of uncertain origin (perhaps from Central Asia or the Russian Far East) that has spread around the temperate parts of the world on nursery stock. Its pest status in much of its range is likely related to a lack of key natural enemies, together with the low tolerance for this pest in the key crop, apples. Biological control of this pest has received only local attention, focusing on the effects of local natural enemies on the scale and on the effects of climate and pesticides on the natural enemies. This lack of interest in biological control for oystershell scale with a world perspective stems from the frequent application of pesticides in apple orchards and the zero tolerance for scale on fruit grown for the export market (Hill 1989). Opportunities do exist, however, to employ biological control against this species, particularly on shade trees and in poplar plantations.

Recommendations: Once the site for biological control of oystershell scale is seen not as apple orchards but in other contexts (shade trees, poplar plantations, etc.) in which a low level of scale would be acceptable, opportunities for increased biological control efforts may be identified.

First, surveys need to be conducted to identify the various natural enemies attacking the scale in central Asia and the Russian Far East, areas which are likely to be the pest's native range. To date, nearly all efforts have focused on two species of natural enemies that by accident accompanied the scale in its spread. Perhaps better species exist in the native range. This possibility needs to be thoroughly explored.

Second, it has been shown that in some parts of the North American range of the pest, the parasitoid *Aphytis mytilaspidis* is insufficiently cold tolerant for its population to have high overwintering survival (Lord and MacPhee 1953). Collections of new populations of this same parasitoid from northern areas of the Russian Far East, or perhaps other species of parasitoids from the same climatic area, should be made to correct this lack of cold tolerance.

Third, Gharib (1978) has shown that races of oystershell scale found on poplar versus apple maintain their distinct biologies even when reared on the same host (watermelon). This result suggests that more than one biological entity may be involved. A molecular biology study should be conducted to clarify what races of this scale exist in North America. This would aid in the location of the native ranges of each race. Each race of scale should then be viewed as a distinct pest and pursued in whatever location seems most likely to be its native range. To assume that the same natural enemies would be optimal for all races of the pest would be an error that might lead to overlooking some valuable natural enemy species or races.

21. SAN JOSÉ SCALE (*Quadraspidiotus perniciosus* [Comstock]) (Homoptera: Diaspididae)

Notes: An old generic name for this species is *Aspidiotus*. Some recent papers refer to this species as *Comstockapsis perniciosus* (Comstock) (e.g., Bower 1989).

Origin: San José scale is native to Asia, including the Russian Far East (Sakhalin Island), northern China and Korea (Chumakova 1964, Pilipyuk 1971, Aksyutova and Gul'dyaeva 1977, Caltagirone 1981).

Range in North America: San José scale is found throughout North America as a pest of cultivated apple and various ornamental shrubs and trees, especial ones in the Rosaceae. It is not reported as a forest or forest nursery pest. It was first noticed in North America in California in 1870 and later spread eastward (Caltagirone 1981). San José scale has been transported on fruit tree stock or fruit to various parts of the world including Europe, the Black Sea region of the former U.S.S.R., Chile, and parts of Africa, Australia, and New Zealand (Jarvis 1927, Richards 1960, van der Merve 1962, Clausen 1978, González 1981). A map of this species' world distribution is available (CAB 1986).

Damage: Damage in North America formerly was severe on many hosts, especially in the decades first following the invasion of the pest. Subsequently, this scale has been attacked by native parasitoids and other species which were either intentionally or accidentally introduced (Flanders 1960, Clausen 1978, Caltagirone 1981). The most important species ultimately proved to be two native North American parasitoids, *Aphytis* (formerly *Aphelinus*) *diaspidis* (Howard) and *Aphytis mytilaspidis* (LeBaron), and two Chinese species, *Encarsia* (formerly *Prospaltella*) *perniciosi* (Tower) and *Coccophagoides kuwanae* (Silvestri). Both *E. perniciosi* and *C. kuwanae* were found in the United States before any deliberate introductions, but each was later also introduced from various sources. Currently the pest is no longer damaging in the eastern and middle regions of North America, except in situations where pesticide use destroys these parasitoids, such as pesticide-treated apple orchards.

Resident Natural Enemies: Parasitoids attacking *Q. perniciosus* in New York were studied by Hodgkiss and Parrott (1914), who found that the three most important species were *Encarsia perniciosi*, *Aphelinus fuscipennis* Howard, and *Aphelinus diaspidis*. *Encarsia perniciosi* was thought to be of greatest significance. It is of Asian origin but was first described from Massachusetts (Tower 1913), apparently having invaded eastern North America on its own. Quaintance (1915) lists several natural enemies known to attack San José scale in the United States, including the predators *Chilocorus bivulnerus* and *Microwesia misella*, six parasitoids, and one fungal pathogen. A further list of 10 species of parasitoids from San José scale in Michigan is provided by McDaniel (1919) and a list of 6 species in Maryland by Siegler and Baker (1924). Rice (1937) provides information on natural enemies of San José scale in Ohio. *Encarsia perniciosi* is identified as an important parasitoid of this pest in all of these areas. Cox (1942) records 41% parasitism of San José scale in an unsprayed fruit orchard in Virginia. San José scale was collected in the United States in 1961-1962 to obtain parasitoids to send to Germany. Samples from Connecticut had up to 95% parasitism; samples from Wisconsin had 90-92% parasitism, compared with only 7-13% parasitism in Germany (Neuffer 1964a). Most parasitism in U.S. samples was due to *E. perniciosi*.

In the native range of San José scale in the Russian Far East, China, and Korea, a different set of parasitoids are present than in North America, except for *E. perniciosi*, which is important in both areas. In Korea, *Coccidencyrtus steinbergi* Chumakova and Tryapitsyn and *Euussuria shutovae* are reported (Tryapitsyn 1963, Myartseva 1978). On the island of Sakhalin in the Russian Far East, *E. shutovae* is also present, together with *E. perniciosi*, *Pteroptrix wanhsiensis* (Comp.), *Thomsonisca typica* (Merc.), *Coccophagoides* sp., and *Aphytis proclia* (Wlk.) (Chumakova 1967, Pilipyuk 1971). *Chilocorus kuwanae* Silvestri is an important predator of San José scale on Sakhalin (Pilipyuk 1971). Parasitism levels of San José scale in the mainland areas of the Russian Far East are given by Chumakova (1964), who notes that *E. pernciosi* was the most abundant parasitoid and *E. wanhsiensis*, the second most important.

Tree species on which this scale can be found in the Russian Far East are recorded by Pilipyuk (1971) who found the scale on flat-leafed birch (*Betula platyphylla*) and hawthorne (*Crataegus* sp.) on Sakhalin, and by Chumakova (1964) who found the scale on *Malus manshurica* on the mainland.

Studies of local natural enemies that attack San José scale have also been conducted in India and Pakistan, the Black Sea coast and Caucasus Mountains regions of the former U.S.S.R., and Europe.

In India and Pakistan, the major natural enemies of this scale (other than exotic parasitoid species introduced to the region), have been various species of coccinellids in the genus *Chilocorus* (Nagaraja and Hussainy 1967) and some local parasitoids, including *Aspidiotiphagus* sp. (Fotidar and Raina 1936). These agents, however, are not generally able to prevent increase of the scale to damaging levels (Fotidar and Raina 1936).

In addition to the Russian Far East (where San José scale is a native species), this scale is also found in the Black Sea coast and Caucasus Mountains regions of the former U.S.S.R. (presumably as an invader). Several studies document the natural enemies that attack the scale in this region. The predators of greatest importance in these areas are several species of *Chilocorus*, including *C. renipustulatus* (Scriba) and *C. bipustulatus* (L.) (Murashevskaya 1969). Species of parasitoids in the region which attack the scale include *Encarsia perniciosi*, *Aphytis proclia*, *Aphytis mytilaspidis*, *Aspidotiphagus citrinus* (Craw.), *Thysanus ater* (Wlk.), and *Pteroptrix chinensis* (How.) (Popova 1976). Of these, most studies have concerned *E. perniciosi*, of which several strains from different areas exist which differ in their biology and effectiveness against this pest scale.

Following the invasion of Europe by San José scale, the scale became attacked by a variety of native parasitoids, which have been identified in several locations, including Italy (Goidanich 1945), the former Yugoslavia (Tadíc 1960, 1961), and Germany (Neuffer 1966). In Greece, native predators proved to be an important complement to the introduced aphelinid *E. perniciosi*, especially the cybocephalid beetle *Cybocephalus fodori* Enrody-Younga and the coccinellid *Chilocorus bipustulatus* L. (Katsoyannos and Argyriou 1985).

Biological Control Attempts: To enhance the mortality to San José scale provided by local natural enemies, one species of exotic aphelinid, *Encarsia perniciosi*, has been introduced into many areas, including California (Clausen 1978), Germany (Neuffer 1964b), Austria (Böhm 1965), France (Bénassy and Burgerjon 1955), Greece (Argyriou 1981), and parts of the Black Sea coast and Caucasus Mountains region of the former U.S.S.R. (Goryunova 1964). Significant drops in scale density are reported in some locations after introduction of *E. perniciosi*, as for example, in Switzerland, where scale populations collapsed within 1½-3½ years after parasitoids were introduced (Mathys and Guignard 1967). Strains used for introductions have been collected in many locations and in some sites, multiple strains have been introduced (Goryunova 1964). In the Black Sea coast and Caucasus Mountains region, several other species of natural enemies have also been introduced, including *Chilocorus bijugus* Mulsant to the Adzharia region from India (Chanyuvadze 1976), and strains of *Aphytis proclia* Wlk. (Goryunova 1965).

Reasons for Pest Status and Possibilities for Biological Control: Pest status of San José scale in nearly all parts of the world is related to a lack of effective natural enemies, due to the pest's invasion of new areas, or local destruction of natural enemies by pesticides. Control of the scale by various natural enemies has been reported in some countries. In the Himachal Pradesch region of India, two introduced coccinellids, *Chilocorus bijugus* and *Paraoscymnus flexibilis* Mulsant, reduced the incidence of scale from 30-100% before

introduction to 10-39% after establishment (Rawat *et al.* 1988). In the Hebei Province of China, the coccinellid *Chilocorus kuwanae* reduced San José scale density by 60-87% (Zhang 1983). The reduction in level of infestation by San José scale in orchards in Germany from 1960 (100%) to 1989 (4%) is credited to the introduction of *E. perniciosi* (Neuffer 1990). Finally, in Sicily, the predacious mite *Hemisarcoptes malus* is reported as killing 70% of adult females of this scale on apple and pear (Vacante 1985).

Recommendations: In the eastern United States in areas where pesticides are not applied, native parasitoids plus *E. perniciosi* appear to suppress San José scale to acceptable levels. Problems occur in sprayed environments due to natural enemy destruction, but these must be resolved by changes within the pest management systems of the crops concerned. If other regions are identified in which biological control is insufficient, introduction of *E. perniciosi* is recommended, following consideration of which source population of the parasitoid would be best adapted to local conditions.

Should further control be needed, comprehensive study of the natural enemies of San José scale in the Russian Far East (its native range) is recommended. The opportunity to find potentially useful new parasitoids of this scale in that area is good.

Other Homoptera

22. SARATOGA SPITTLEBUG (*Aphrophora saratogensis* [Fitch]) (Homoptera: Cercopidae)

Origin: Saratoga spittlebug is native to North America.

Range in North America: The Saratoga spittlebug is found in southeastern Canada and in the United States from Maine to the Great Lakes States. The pest is particularly important in red pine (*Pinus resinosa* Ait.) plantations in Michigan and Wisconsin.

Damage: Damage is done exclusively by the adults. Nymphs feed on various woody or herbaceous plants in the understory of pine plantations rather than on the pines themselves. The list of nymphal hosts is extensive (see Wilson 1971), but the most important is sweet fern (*Comptonia peregrina* [Linnaeus] Coulter) (Secrest 1944, Wilson 1971). Adults extract sap from pine shoots and inject toxic saliva. This leads to the formation of necrotic pockets in phloem and xylem tissues. Extensive feeding kills branches, stunts and deforms shoots, and can kill entire trees (Drooz 1985). Saratoga spittlebug is considered to be one of the more serious pests of red pine plantations.

Resident Natural Enemies: Ewan (1961) reported two parasitoids attacking eggs of this spittlebug, both at low levels (1-5%): the mymarid *Ooctonus aphrophorae* Milliron and the aphelinid *Tumidiscapus cercopiphagus* Milliron. More importantly, an unidentified pipunculid fly parasitized up to 50-65% of adult spittlebugs at sampled sites. This pipunculid might have been *Verrallia virginica* Banks, which was subsequently noted as attacking Saratoga spittlebugs in Maine (Linnane and Osgood 1977).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: One requirement for populations of this spittlebug to reach pest densities is abundant growth of suitable host plants for nymphs in the plantation understory. Counts of nymphs are the best means to predict future risks of damage, and survey methods have been defined to conduct such estimations (Ewan 1961, Wilson 1990). The risk of spittlebug damage at specific sites can also be assessed by determining the percentage of ground covered by sweet fern or other nymphal host plants (Kennedy and Wilson 1971a, Wilson 1971). Suppression of sweet fern and other nymphal hosts, either mechanically or with herbicides (Heyd *et al.* 1987), coupled with factors (fertile sites, good planting stock) promoting fast growth of pines able to suppress other vegetation, are silviculture methods to control Saratoga spittlebug.

Natural enemies may also be important factors affecting spittlebug populations. Of greatest likely importance may be the pipunculid fly attacking the adult. Another pinpunculid (*Verralia aucta* Fallén) has been shown to be a critical factor influencing populations of another cercopid, the meadow spittlebug *Philaenus spumarius* (Linnaeus) (Whittaker 1969, 1973). The effectiveness of *V. aucta* against *P. spumarius*, the high percentage of pipunculid parasitism of *A. saratogensis* observed by Ewan (1961), and the observation that *Verralia virginica* attacks *A. saratogensis* together suggest that more information should be gathered on the importance of this pipunculid as a parasitoid of Saratoga spittlebug.

Recommendations: A population dynamics study should be conducted to determine the level of mortality of adult spittlebugs due to pipunculid parasitism, the impact of parasitism on trends in spittlebug densities, and identification of vegetation or site factors affecting the level of parasitism.

Coleoptera

Defoliating and Root-Feeding Beetles

23. COTTONWOOD LEAF BEETLE (*Chrysomela scripta* Fabricius) (Coleoptera: Chrysomelidae)

Notes: Former generic placements include *Melasoma* and *Lina.*

Origin: Cottonwood leaf beetle is native to North America.

Range in North America: The cottonwood leaf beetle is found throughout the United States and Canada (Drooz 1985).

Damage: This leaf beetle feeds on various species of poplar, willow, and alder, but is most damaging to hybrid poplars. It has been of economic concern in various areas. It is reported as a nursery pest, e.g., in Minnesota (Washburn 1914), a pest in prairie windbreaks and shade trees (e.g., Severin 1922), and in the southern United States where intensive culture of cottonwoods is of interest (Head and Neel 1973). Cottonwood clones vary in susceptibility to defoliation from cottonwood leaf beetle; same season height growth of susceptible clones can be reduced up to 80% by defoliation by this beetle (Caldbeck *et al.* 1978).

Resident Natural Enemies: Few reports exist on the natural enemies of this leaf beetle. In Mississippi the main predators of the species are pentatomid bugs and coccinellid beetles, especially *Coleomegilla maculata* (De Geer) (Head *et al.* 1977). Parasitoids of the species in Mississippi included the pteromalid *Schizonotus latus* (Wlk.) and an unidentified tachinid. In Wisconsin, *C. maculata* was again an important predator of this leaf beetle, eating 25% of the eggs; and *S. latus* was an important parasitoid, attacking 26% of the pupae (Burkot and Benjamin 1979). The pathogen *Nosema scripta* Bauer and Pankratz has been described from *C. scripta* in Michigan (Bauer and Pankratz 1993).

Biological Control Attempts: Efforts to augment numbers of the coccinellid *Coleomegilla maculata* De Geer in cottonwood plantations by collecting wild adult beetles and releasing them at desired locations increased the number of beetles per tree from 0.35 to 5.1, but numbers returned to original levels within two weeks (Neel and Solomon 1985). The efficacy of strains of *Bacillus thuringiensis* active against Coleoptera has also been examined (Ramachandran *et al.* 1993).

Reasons for Pest Status and Possibilities for Biological Control: Only one study was found that examined the population dynamics of cottonwood leaf beetle (Burkot and Benjamin 1979). That report provides life tables for populations during one year at a study site in Wisconsin, showing that natural enemies and other factors increased in intensity within a season, across the four generations of the pest, progressively lowering population growth from a 25-fold rate of increase to 19, 8 and 0.75 across succeeding generations. Causes of population change between years were not studied. Among the factors needing careful examination is potentially increased susceptibility of new cultivars of hybrid poplars compared to native aspens.

Recommendations: This insect has exposed life stages susceptible to attack by many sorts of natural enemies. Investigation into its population dynamics and the effectiveness of its natural enemies in natural stands would be useful because they might suggest ways to make key natural enemies more effective in plantations. Such studies would need to account for cultivar effects to correctly make forest versus plantation comparisons. Transplant experiments would be useful in separating such cultivar effects from site effects.

24. PALES WEEVIL (*Hylobius pales* [Herbst]) (Coleoptera: Curculionidae)

Origin: Pales weevil is a native North American species, first noted as a pest around 1914 (Peirson 1921). A bibliography of the literature on this species has been assembled by Lynch (1984).

Range in North America: Pales weevil is found throughout the United States east of the Great Plains, and north to Ontario (Drooz 1985).

Damage: Adults of this species are serious pests of young seedling pines in both cutover lands undergoing natural regeneration and in recently planted plantations (either for pulp or Christmas tree production). Losses of 30-60% of first year pine seedlings are not uncommon (Drooz 1985). Damage is most serious in intensely managed pine plantations. Adults breed in stumps and roots of newly cut trees and emerging adults later feed on bark of young trees

(Lynch and Hedden 1984). In Christmas tree plantations, continuous harvest over several years in a given locality creates good conditions for population increases of pales weevil by providing an even supply of stumps suitable for breeding (Corneil and Wilson 1984). Additionally, evidence suggests that pales weevil can transmit some pathogens of pines such as the fungus that causes procerum root disease (Klepzig *et al.* 1991, Nevill and Alexander 1992). All species of native pines in the eastern United States are attacked, as well as various other conifers (Drooz 1985).

Resident Natural Enemies: Very few natural enemies have been recorded attacking pales weevil (Nord *et al.* 1984, Schabel and Raffa 1991). Two fungi (*Metarhizium anisopliae* and *Beauveria bassiana*), both species with broad host ranges, infect pales weevil in the laboratory (Walstead and Anderson 1971). *Beauveria bassiana* infection rates of adult pales weevils arising from naturally occurring inoculum have been observed to reach 15% in Georgia (Taylor and Franklin 1973). Attempts to use these fungi in the field have shown that uneconomically high application rates of spores are needed to infect weevils. It has been suggested that this might be partially overcome by dipping seedlings in fungal spore solutions instead of applying treatments to the whole field after planting (Schabel 1976).

Other than fungal pathogens, only one other natural enemy is reported for this species, the euphorine braconid *Microctonus pachylobii* Muesebeck, which has been reared from the adult stage (Rieske *et al.* 1989).

Biological Control Attempts: Nematodes, while very virulent to this pest in the laboratory, have been relatively ineffective in field trials, in part because pest infestations occur on droughty, sandy soils.

Reasons for Pest Status and Possibilities for Biological Control: Damage arises in natural stands because adults are attracted to stumps of recently cut trees, breed in them, and then the following year new adults are locally abundant and inflict high mortality on new seedling pines at the site. In plantations, the way in which stumps are treated and the timing of replanting determine the abundance of breeding sites for pales weevil. If, for example, stumps are produced continuously in Christmas tree plantations over various years by partial cutting within stands or cutting of adjacent stands sequentially, pales weevil populations can increase in response to greater availability of breeding sites and then damage blocks as they are replanted. Damage can be reduced either by eliminating breeding sites, or by delaying replanting of blocks in the vicinity of recently cut areas for one year, by which time most stump-bred weevils will have left and stumps will have deteriorated as breeding sites. Delayed planting imposes costs equal to one year's growth and may be unacceptable. Stumps may be rendered unsuitable for pales weevil breeding either by insecticide application to the stump, mechanical destruction of the stump, or keeping the stump alive (by leaving one whorl of live branches at harvest: Corneil and Wilson 1981).

Recommendations: No important role for biological control of this pest species was identified. Nematode applications might prove effective for use on sites with non-sandy soils. Prevention of pest buildup by treating stumps after harvest in ways that make them unsuitable for breeding appears to be the best method for management of the species.

25. PINE ROOT COLLAR WEEVIL (*Hylobius radicis* Buchanan) (Coleoptera: Curculionidae)

Origin: Pine root collar weevil is native to eastern North America.

Range in North America: Pine root collar weevil is found from Newfoundland south to Virginia, and west to Minnesota and Manitoba (Drooz 1985).

Damage: This species is not damaging to natural reproduction of native trees (Schaffner and McIntyre 1944). Damage is nearly always concentrated in plantations of native and exotic pines (Wilson and Schmiege 1970). The pine attacked most often is Scotch pine (*Pinus sylvestris*) (e.g., Finnegan 1962), followed by red pine (*Pinus resinosa*) (e.g., Kennedy and Wilson 1971b). Healthy trees are used for oviposition, in the root collar zone. Young trees may be killed and older trees become badly stressed (Rieske and Raffa 1993). *Hylobius radicis* is one of several wood-feeding insects associated with several fungi in a syndrome termed red pine decline (Klepzig *et al.* 1991). Silvicultural methods to reduce damage include pruning of lower branches and removal of litter and soil around the base of trunks (Wilson 1973). This method often suppresses damage long enough to last until crown closure.

Resident Natural Enemies: Very few natural enemies have been recorded attacking pine root collar weevil (Schabel and Raffa 1991). One species of parasitoid, the braconid *Bracon radicis* Shenefelt and Miller, has been recovered from *H. radicis* (Shenefelt and Millers 1960).

Biological Control Attempts: Nematodes, while very virulent to this pest in the laboratory, have been relatively ineffective in field trials, in part because pest infestations occur on droughty, sandy soils.

Reasons for Pest Status and Possibilities for Biological Control: The reasons why this species is a pest in plantations but not in natural forests are unknown but may relate to the species' weak dispersal behaviors and its preference for sites prior to canopy closure. Both of these features favor population increase in plantations where resources are concentrated in a favorable physical environment. The importance of biological control agents, in plantations and natural forests, is unknown.

Recommendations: A study comparing reproduction and mortality rates of *H. radicis* at plantation and natural forest sites, in both native and exotic tree species at each habitat, could be conducted. Such a study might indicate whether the differences between pest levels in natural forests and plantations are caused by unfavorable conditions in plantations for native parasitoids and predators, differences in tree species or resource concentration favoring the pest. Some opportunities to employ nematode applications may exist at sites with soil moisture levels adequate for nematode survival.

26. PINE ROOT TIP WEEVIL (*Hylobius rhizophagus* Millers, Benjamin, and Warner) (Coleoptera: Curculionidae)

Notes: The generally recognized description of this species was written by Millers *et al.* (1963). However, *Hylobius assimilis* Boheman has recently been found to be a valid senior synonym (O'Brien and Wibner 1986) and should be the name used in the future.

Origin: Pine root tip weevil is native to North America.

Range in North America: This species is primarily of importance in the Great Lakes region of the United States (Drooz 1985).

Damage: *Hylobius rhizophagus* feeds on the tips of roots of various pines, especially jack, red and Scotch pine in plantation settings (Kearby and Benjamin 1969, Mosher and Wilson 1977). It is part of a complex of root-feeding insects associated with tree decline in pine plantations (Mosher and Wilson 1977). In jack pine, decline appears to be associated with both insect feeding and the presence of a pathogenic fungus, *Leptographium terebrantis*, whose incidence may be enhanced by insect feeding (Raffa and Smalley 1988). Damage in jack pine in Wisconsin is especially likely on poor sites (Kearby and Benjamin 1969).

Resident Natural Enemies: The only natural enemy reported for this species is *Microctonus pachylobii*, a euphorine braconid that parasitizes the adult stage of the pest (Rieske *et al.* 1989). The fungal pathogens *Metarhizium anisopliae* and *Beauveria bassiana* have been observed attacking this weevil, but only at very low levels (1%) (Goyer and Benjamin 1971).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Reasons for the pest status of this species are unknown. No population dynamics studies have been conducted on the species, and the role natural enemies play in determining its average density is unknown. Damage occurs in plantations rather than natural stands, suggesting that some feature of plantations favors population increase in this weevil. Control measures recommended focus on reducing available susceptible hosts by planting less susceptible species like red pine, locating plantations on sites where the pest is locally known not to occur, and avoiding recropping Christmas trees from the stumps of earlier crops (Mosher and Wilson 1977).

Recommendations: Basic research would be required to determine why stand declines occur in some areas but not others. Such studies would have to answer several questions, including: (1) whether variation in intensity of pine decline is driven by variation between sites in beetle density or in suitability for associated fungal pathogens, (2) whether natural enemies, such as the *Microctonus* species observed, significantly suppresses the species' density, and (3) which conditions in plantations promote decline.

27. PITCH-EATING WEEVIL (*Pachylobius picivorus* [Germar]) (Coleoptera: Curculionidae)

Origin: Pitch-eating weevil is native to North America.

Range in North America: This weevil occurs throughout the eastern United States and is most common in the southern region (Drooz 1985).

Damage: This weevil breeds in stumps. Adults feed on bark of young trees, causing extensive seedling mortality (50% or more under some conditions). Damage is greatest to pine seedlings planted within one year after cutting. Seedlings planted soon after felling can be protected by dipping in insecticides before planting (Walstad *et al.* 1973). Damage is important in both pine plantations (e.g., Thatcher 1960) and Christmas tree farms. This weevil is one of several beetles associated with red pine decline and is believed to transmit several fungi associated with this condition (Klepzig *et al.* 1991).

Resident Natural Enemies: Few natural enemies of this species have been reported (Schabel and Raffa 1991). The braconid *Microctonus pachylobii* Muesebeck has been noted attacking adult weevils (Muesebeck *et al.* 1979). Up to 15% of adults may be naturally infected in the field with the fungal pathogen *Beauveria bassiana* (Taylor and Franklin 1973). A gregarine, *Gregarina hylobii*, has also been found in association with this weevil (Schabel and Taft 1988).

Biological Control Attempts: Nematodes, while very virulent to this pest in the laboratory, have been relatively ineffective in field trials, in part because pest infestations occur on droughty, sandy soils.

Reasons for Pest Status and Possibilities for Biological Control: Damage results from increased densities of this species that develop under conditions of intensive pine culture. Suppression of breeding by stump management, delay of replanting, or chemical protection of seedlings are current options for control. Little or no role appears to exist for biological control of this pest, based on existing research.

Recommendations: Nematode applications may have same potential for use at sites with soils favorable to nematode survival.

28. MAY AND JUNE BEETLES (White Grubs) (*Phyllophaga* spp.) (Coleoptera: Scarabaeidae)

Notes: In the older literature, the genus *Lachnosterna* was employed, until it was recognized as a junior synonym of *Phyllophaga* by Glasgow (1916). Lim *et al.* (1980) provide a bibliography for *Phyllophaga anxia* (LeConte), a species of importance in Quebec.

Origin: Species in the genus *Phyllophaga* are native to North America.

Range in North America: *Phyllophaga* species are widespread in North America. There are more than 100 species in the United States and Canada (Luginbill and Painter 1953) and 254 in Mexico (Morón 1986). Böving (1942) discusses the classification and recognition of adults and larvae of *Phyllophaga* spp.

Damage: In some years *Phyllophaga* spp. populations have occurred at densities high enough to devastate crops and strip foliage from woodlots (Davis 1913, 1918). Damage to forest nurseries can be severe at times (Anon. 1937), as can be damage to young plantations (Schwardt 1942, Stone and Schwardt 1943). Fowler and Wilson (1971) quantified the mortality rates of red pine seedlings in plantations in Michigan and Wisconsin in relation to white grub densities in the soil and found that as few as 0.75 grubs per cubic foot of soil resulted in 15-45% mortality. The economic consequences of such levels of mortality were found to depend on the stocking rate of the stand. In overstocked stands (more than 1000 seedlings per acre) thinning by white grubs could be beneficial provided it does not reduce the stocking rate at maturity below 500 trees per acre, as this rate produces the maximum volume of timber (Fowler and Wilson 1975).

Resident Natural Enemies: Davis (1913, 1916, 1919) records natural enemies of various *Phyllophaga* spp., especially those in Indiana. These include various parasitoids, such as five species of *Tiphia* (especially *Tiphia inornata* [Say]) and five species of *Elis,* such as *Elis 5-cincta,* and various tachinids, such as *Microphthalma disjuncta* Wiedman. Larvae of the asilid fly *Promachus vertebratus* Say (as well as other species in the genus) are predacious on *Phyllophaga* larvae. Petch and Hammond (1926) studied the natural enemies of *P. anxia* in Quebec and found that *Tiphia inornata* and *Microphthalma michiganensis* Townsend were important species. The biology of one of the *Tiphia* species, *Tiphia bebereti* Allen, has been studied in some detail (Berberet and Helms 1970). Lim *et al.* (1981) surveyed the natural enemies of *P. anxia* in Quebec and found 16 species of parasitoids or predators and four of pathogens. Poprawski (1994) conducted another survey in Quebec over a four year period and found *P. anxia* to be attacked by 29 species of parasitoids or predators. Parasitism was greatest (8%) for adult females, but in general it was concluded that natural enemies have only a small impact on this species.

Several pathogens have been noted causing disease in species of *Phyllophaga.* Milky spore diseases caused by *Bacillus* spp. were reported in *P. anxia* in New York (Tashiro and Steinkraus 1966). Berberet and Helms (1969) found two eugregarines in *P. anxia* in Nebraska. Yule and Poprawski (1983) surveyed the field infection rates of bacterial and viral pathogens of *Phyllophaga* spp. in Quebec and found an overall infection rate of 16% in larvae. Other pathogens that have been observed in *Phyllophaga* include various bacteria (Poprawski and Yule 1990a), an iridescent virus (Poprawski and Yule 1990b), and a diplogasterid nematode, *Chroniodiplogaster aerivora* (Cobb), which was found in 1-7% of larvae of *P. anxia* in Quebec (Poprawski and Yule 1991a).

Biological Control Attempts: Biological control attempts against *Phyllophaga* spp. have consisted of trials of various nematodes and fungi as bioinsecticides. Kard *et al.* (1988) tested two species of nematodes (*Steinernema feltiae* [Filipjev] and *Heterorhabditis heliothidis* [=*bacteriophora*] Poinar) against white grubs in pastures in North Carolina but obtained inconsistent results. Velásquez (1990) achieved substantial reductions in white grubs in field trials in Guatemala with applications of the fungi *Beauveria* sp. and *Spicaria* sp., and an

unnamed diplogasterid nematode. Poprawski and Yule (1991b), in laboratory trials, confirmed the susceptibility of *P. anxia* to the fungi *Beauveria bassiana* and *Metarhizium anisopliae.*

Reasons for Pest Status and Possibilities for Biological Control: No studies were found that addressed the population dynamics of *Phyllophaga* spp. In part this may be due to their 3-year life cycle. Consequently little can be said about the underlying reasons for the characteristic densities of these species. Kard and Hains (1987) examined the possibility that weed control practices, such as the use of herbicides, might be affecting pest abundance in Christmas tree plantations, but found that pest numbers increased when herbicides were not used, suggesting that leaving sodded areas favored the pest by providing food resources.

Recommendations: The line of research that seems most likely to provide biological control methods for these species would seem to be continued efforts to develop nematodes, bacteria, and fungi as bioinsecticides. Key to this process will be screening of naturally infected beetles and larvae to detect pathogen species or strains that are highly effective but can be reared economically.

29. A WHITE GRUB (*Polyphylla variolosa* Hentz) (Coleoptera: Scarabaeidae)

Origin: The white grub *Polyphylla variolosa* is native to North America.

Range in North America: This species is reported from the northeastern United States, including New York, New Jersey, and Indiana.

Damage: Damage by this species to seedlings in forest nurseries has been reported in New Jersey and New York (Headlee 1916, Heit and Henry 1940).

Resident Natural Enemies: None reported.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Damage appears to be due to population increases in response to the favorable conditions of forest nurseries in which suitable hosts are concentrated.

Recommendations: While no trials of the ability of steinernematid or heterorhabditid nematodes to control this species have been conducted, it likely could be controlled in this manner because many soils are a favorable habitat for nematodes. Other white grubs have been controlled with nematode applications (e.g., turf pests), and the high value of forest nurseries would make the use of nematodes economically possible. Commercial products marketed for control of various turf and cranberry weevils and scarabaeids should be tested for their effectiveness against this species.

30. BLACK VINE WEEVIL (*Otiorhynchus sulcatus* [Fabricius]) (Coleoptera: Curculionidae)

Notes: A former generic placement is *Brachyrhinus.*

Origin: Black vine weevil occurs throughout Europe, including European Russia, but is recorded in Asia only from Japan, which it invaded. Other regions of the world where the black vine weevil occurs include southern Australia, New Zealand, the southern part of South America, and parts of western and eastern North America, all areas that the species invaded. The mechanism for such invasions has been transport in balled nursery stock (e.g., Sasscer 1922). Whether the weevil is native to all of Europe or invaded the area at an earlier period is not known. See Moorhouse *et al.* (1992) for a world map of the species' distribution.

Range in North America: In eastern North America, the black vine weevil is found in southern Canada and the northeastern and northcentral United States. A separate infested area extends from southern Alaska through California (Moorhouse *et al.* 1992).

Damage: Larvae of this species damage both woody and other plants by feeding on their roots. Damage is a concern in strawberries, nursery, such greenhouse crops as *Taxis*, hemlock, rhododendron, cyclamen, and others. Black vine weevils can be damaging to forest nurseries and it is in this context that they are relevant to this report.

Resident Natural Enemies: Few reports exist concerning parasitoids or predators of black vine weevil. Evenhuis (1983) reports that numbers of this species increased in strawberry fields treated with insecticides that were ineffective against black vine weevil. The author attributed this increase to destruction of predacious carabid beetles, which he felt at least partially suppressed numbers of black vine weevil. No parasitoids are listed by Krombein *et al.* (1979) as attacking black vine weevil, although one species, the braconid *Triaspis kurtogaster* Martin, is listed as a parasitoid of the closely related species *Otiorhychus ovatus* (L.).

Two groups of natural enemies have been extensively studied as potential biological control agents of the black vine weevil by means of augmentative applications: pathogenic fungi and nematodes. Species of fungi tested include *Metarhizium flavoviride* Gams and Rosyzpal, *Metarhizium anisopliae* (Metchnikoff) Sorokin, *Paecilomyces fumosoroseus, Beauveria bassiana* (Balsamo) Vuillemin, *Beauveria brongniartii* (Saccardo) Petch (Marchal 1977), and *Verticillium lecanii* (Zimmerman) Viegas (Landi 1990).

Nematodes tested for control of black vine weevil come from the two families of entomopathogenic nematodes for which commercial mass-production techniques exist, i.e., the Steinernematidae and Heterorhabditidae. Nematodes used in tests are often not identified to species, being designated only by generic names and strain numbers. Where species have been identified, they most often have been *Heterorhabditis heliothidis* (e.g., Kahn, Brooks, and Hirschmann) (Bedding and Miller 1981), *Heterorhabditis bacteriophora* Poinar (Barratt *et al.* 1989), *Steinernema carpocapsae* (Weiser), *Steinernema glaseri* (Steiner) (Georgis and Poinar 1984), and *Steinernema feltiae* (Filipjev) (Dorschner *et al.* 1989).

In addition to these pathogens, one trial of the bacterium *Bacillus thuringiensis* subsp. *tenebrionis* was found (Landi 1990).

Biological Control Attempts: Biological control attempts directed at black vine weevil have consisted of screening programs to identify species or strains of fungi or nematodes able to kill a high percentage of the pest. Such screening efforts have sought to identify agents that (1) are effective on the target crop, of which there are a large number; (2) kill a high percentage (70% or more) of the pest's eggs and larvae, including both young and old stages; (3) achieve these levels of pest mortality at the lowest possible application rates (to reduce costs); and (4) are effective at temperatures as low as 8-12 °C.

Fungi of several species have been considered for black vine weevil control on strawberries, including *Metarhizium flavoviride*, *M. anisopliae*, *Paecilomyces fumosoroseus*, *Beauveria bassiana*, *B. brongniartii* (Marchal 1977). On potted plants in greenhouse trials, *M. anisopliae* was one of the most effective species, with control being achieved at rates as low as 1 X 10^5 spores per cm^3 (Prado 1980, Zimmermann 1981). Screening programs have been carried out seeking strains of *M. anisopliae* with high effectiveness against black vine weevil larvae (Soares *et al.* 1983, Moorhouse *et al.* 1993a). Some fungi, such as *M. flavoviride*, have been noted to infect eggs as well as larvae of black vine weevils (Poprawski *et al.* 1985). Outdoor tests in Italy with *V. lecanii* found this fungus to be ineffective (Landi 1990). In contrast, *M. anisopliae* has been produced commercially for use in outdoor nurseries on crops such as rhododendrons (Reinecke *et al.* 1990), both as a conidia-based product and a mycelial granule (Stenzel *et al.* 1992). Levels of control in the range of 74-82% have been reported (Stenzel *et al.* 1992). Tests in the United Kingdom with *M. anisopliae* products gave variable results, depending on the plant species treated and the manner of application. In those tests, prophylactic treatments were more effective than curative ones (Moorhouse *et al.* 1993b).

Nematodes tested for control of black vine weevil have included *Heterorhabditis heliothidis*, *H. bacteriophora*, *Steinernema carpocapsae*, *S. glaseri*, and *S. feltiae*. Trials in Australia found *H. heliothidis* to be effective on crops such as yew, raspberries, and grape (Bedding and Miller 1981). Trials in Holland with an unnamed *Heterorhabditis* sp. gave variable results (Simons 1981). When applied to the soil surface, *H. heliothidis* was the most effective of three species tested against young black vine weevil larvae, but against older larvae, *H. heliothidis*, *S. carpocapsae*, and *S. glaseri* gave equal results (Georgis and Poinar 1994). When nematodes were injected 20 cm into the soil, *S. glaseri* was best for control of older larvae, but if injected only 5 cm, the three species again gave similar results. In pots in greenhouses, *H. heliothidis* was better than *S. carpocapsae* against older larvae, but was difficult to store (Stimmann *et al.* 1985). Conversely, relatively high application rates of *S. carpocapsae* were needed for control (30,000 per pot). In outdoor trials on lodgepole pine, *H. heliothidis* at 500-5,000 nematodes per liter of soil gave better control than did Diazinon® (Rutherford *et al.* 1987).

One of the reasons advanced to explain reduced control outdoors (compared to control in greenhouses) is the presence of lower temperatures during outdoor applications made early in the season. Efforts have been made to find more cold-adapted strains of nematodes. In Holland, Westerman and van Zeeland (1989) have isolated a strain of *Heterorhabditis* that provided 100% control at temperatures as low as 8-10 °C.

The degree of control achieved from nematode applications is also affected by the manner of application, with injection or heavy watering often improving control (Curran 1992). While *Heterorhabditis* spp. are often found to be more effective than *Steinernema* spp., the former are, as a group, harder to mass-produce and have shorter persistence under field conditions (Moorhouse *et al.* 1992). Consequently, efforts to find an effective *Steinernema* sp. have continued. Of three strains tested by Mracek *et al.* (1993) in the Czech Republic, the *S. feltiae* strain Hyl provided the best control.

Few studies have compared fungi to nematodes. Barratt *et al.* (1989) found that in bagged rhododendrons in a nursery, *H. bacteriophora* provided 93% control, compared with only 32% for *M. anisopliae* and 39% for *B. bassiana* two weeks after treatment.
One trial was found that tested the efficacy of *Bacillus thuringiensis* subsp. *tenebrionis*. This microbe caused 70% mortality under a constant temperature of 20 °C, but only 28% under greenhouse conditions (Landi 1990).

Reasons for Pest Status and Possibilities for Biological Control: No studies of the population dynamics of the black vine weevil were located. Basic causes of its typical density are unknown. Whether the weevil is more abundant in recently invaded areas than in Europe is not known.

Recommendations: As a forest pest, the black vine weevil is of interest only in nurseries. In these sites, management by use of nematodes or fungi as microbial insecticides is potentially economically feasible. Development of effective products is likely to occur due to demand in strawberries and other crops. Testing of the efficacy of commercial products in forest nurseries is recommended on a periodic basis as new formulations or species become commercially available.

31. STRAWBERRY ROOT WEEVIL (*Otiorhynchus ovatus* [Linnaeus]) (Coleoptera: Curculionidae)

Origin: In North America, strawberry root weevil is an exotic species (Drooz 1985).

Range in North America: This species is found throughout the United States and Canada (Drooz 1985).

Damage: Adult beetles feed on foliage, especially of arborvitae. The larvae feed on the roots of hemlock and various conifers, and other crops (Drooz 1985). High densities of this species have occurred in forest nurseries, causing considerable mortality of seedlings, e.g., in Sweden (Spessivtseff 1923), New York (Gambrell 1938), and the former Czechoslovakia (Srot 1979).

Resident Natural Enemies: Krombein *et al.* (1979) record only one parasitoid of this species in North America, the braconid *Triaspis kurtogaster* Martin. Naturally occurring infestations of several pathogenic fungi have been noted in field-collected specimens, including *Paecilomyces farinosus* in the former Czechoslovakia (Srot 1979) and *Paecilomyces fumosoroseus* and *Metarhizium anisopliae* in Poland (Mietkiewski *et al.* 1993)

Biological Control Attempts: The only sustained efforts to employ biological control against this species have been through the augmentative application of nematodes and fungal pathogens, mostly the former. Rutherford *et al.* (1987) describe trials in forest nurseries in British Columbia which employed several species of nematodes, under both greenhouse and field conditions. Of the three nematodes tested under greenhouse conditions on potted Douglas-fir seedlings, the nematode *Heterorhabditis* sp. (NC 447) gave the best control of strawberry root weevil larvae. Under outdoor conditions in a forest nursery, control was not satisfactory, which the authors attributed to unusually cool (average 11°C), wet conditions during the test. Nielsen (1989) also expresses the view that control is often better on potted stock than under field conditions.

In cranberries in Massachusetts, *Steinernema carpocapsae* (Weiser) and *Heterorhabditis bacteriophora* (HP88 strain), when applied with high pressure, caused 74% and 59% mortality of larvae respectively (Simser and Roberts 1994). Klein (1990) summarizes studies on efficacy of nematodes against the closely related species, *Otiorhyncus sulcatus* (Fabricius), the black vine weevil. Control is generally rated as better in potted stock than under field conditions, and the reduction of control caused by cold temperatures is noted. Efforts to locate a new strain more effective under cool temperature (11-14 °C) are underway. *Heterorhabditis bacteriophora* appears to be the most promising species.

Reasons for Pest Status and Possibilities for Biological Control: No ecological studies were found that provided any understanding of basic causes of this insect's characteristic density.

Recommendations: Because this pest is of concern to forestry only in nurseries, augmentative use of nematodes or fungi would be the logical way to use biological control against this species.

32. JAPANESE BEETLE (*Popillia japonica* Newman) (Coleoptera: Scarabaeidae)

Origin: Japanese beetle is native to the various Japanese islands (but not mainland Asia) and invaded North America, in the area of New Jersey, around 1916 (Clausen 1978).

Range in North America: The Japanese beetle's range in North America is still expanding as it invades new areas. Currently the beetle is found in most states east of the Mississippi River, Wisconsin, and Minnesota (Drooz 1985).

Damage: Larvae consume roots of grass and are important turf pests. Adults defoliate a wide range of plants including grapes, roses, and important shade and fruit trees.

Resident Natural Enemies: Natural enemies of Japanese beetle that now occur in the United States include parasitic wasps, pathogens, and nematodes. In the 1920s and 1930s, parasitoids of scarabs in Asia were sought for use against Japanese beetle in the eastern United States. Collections were made in Japan, Korea, and to a lesser extent in parts of China and India (Assam). In addition, pathogens and nematodes of Japanese beetle that were encountered in the United States were mass reared and redistributed to expand their ranges.

These efforts are reviewed in detail by Fleming (1968) and Clausen (1978) and are discussed below.

Parasitoids and predators. Among parasitoids and predators affecting Japanese beetle in the United States, native species have been of little importance, although some generalist predators have been noted as consuming eggs or larvae of the pest (Terry *et al.* 1993). Introduced parasitoids from Asia have, in contrast, been the object of extensive effort. Fourteen species have been introduced from Asia to North America (for a list, see Clausen 1978), and five originally became established. These established species include two species of tiphiid wasps (*Tiphia popilliavora* Rohwer and *Tiphia vernalis* Rohwer) and three tachinids (*Istocheta aldrichi* [Mesnil], *Prosena siberita* [Fabricius], and *Dexilla ventralis* [Aldrich]). *Istocheta aldrichi* is referred to in older literature as *Centeter cinerea*, or later as *Hyperecteina aldrichi*. For discussions of the biologies of these various species (both established and not) see Clausen *et al.* (1932, 1933), Gardner and Parker (1940), Fleming (1963, 1968), and Clausen (1978). Effects of these biological control releases in the United States are summarized in the next section.

Pathogens. Pathogens that have been found infecting Japanese beetle include bacteria, microsporidia, and fungi. The pathogen that has received the most attention has been *Bacillus popilliae* Dutky, which along with *Bacillus lentimorbus* Dutky, was found causing a milky spore disease of larvae (Dutky 1940). Whether this species is native to North America is debated. Rearing of this species (in living hosts) led to production of inoculum that was used to spread the pathogen on a large scale to new areas in the eastern United States (White and Dutky 1940, Polivka 1956). However, in field trials in small turf plots in Kentucky, application of *in vivo*-reared *B. popilliae* spores failed to either increase disease rates in Japanese beetle larval populations or to reduce larval densities (Redmond and Potter 1995). Klein *et al.* (1976) provide a bibliography of articles on milky spore disease of Japanese beetle.

A subspecies of *Bacillus thuringiensis, B.t. japonensis,* has been found infecting Japanese beetle in Japan (Ohba *et al.* 1992). This discovery is of considerable interest because spores of this species can be reared effectively in fermentation media, which is not the case for *B. popilliae* (Stahly and Klein 1992). Another pathogen found attacking the Japanese beetle is the microsporidian *Ovavesicula popilliae* Anreadis and Hanula. This species has been found to be common in Japanese beetle populations in Connecticut and to reduce the beetle's fecundity and delay adult emergence (Hanula and Anreadis 1988, Hanula 1990). Fungi reported as infecting Japanese beetles include *Metarhizium anisopliae*, *Metarhizium glutinosum* Pope, and *Isaria densa* Auct. (Fleming 1963).

Nematodes. The nematode *Steinernema glaseri* (Steiner) was found attacking Japanese beetle in southwestern New Jersey (Glaser and Fox 1930) and appears to be native to North America (Gaugler *et al.* 1992). Studies of the rearing and biology of this species at the time of discovery suggested that it could be released into new locations and permanently establish (Glaser *et al.* 1940). Based on these facts, a large scale rearing program was initiated, and the nematode was inoculated into soils at over 500 sites in New Jersey. Other nematodes that also have been found infecting naturally occurring Japanese beetle grubs include *Steinernema carpocapsae* (Weiser) (reported as *Neoaplectana chresima*, Fleming 1963) and *Heterorhabditis megidis* Poinar, Jackson and Klein (Poinar *et al.* 1987). Additional species of nematodes have been tested as

augmentative biological controls for Japanese beetles and these efforts are discussed below under Biological Control Attempts/Nematodes.

Biological Control Attempts:

Parasitoids. Extensive efforts to collect and ship parasitoids attacking the Japanese beetle, other species of *Popillia*, and more distantly related scarabids were made in Japan and Korea in the 1920s and 1930s. Less extensive efforts were made in China and India (Assam). Outside of Japan, collections were made from related species, as *P. japonica* is restricted to Japan in its distribution. Documentation of these collection efforts, and notes on the biologies, phenologies, and hosts of the various parasitoid species collected are given in a series of papers. Clausen and King (1924) review early work in Japan and Korea, identifying three species attacking adult beetles and three attacking larvae. Notes on collections in Japan, Korea, and China are given by Illingworth (1926). Burrell (1931) reviews collection of *Dexilla ventralis* (Aldrich) in Korea and Clausen *et al.* (1933) review work during 1924-1928 in Japan, Korea, China and India (Assam). Work from 1929 to 1933 is summarized by Gardner and Parker (1940). Summary accounts are provided by Fleming (1968) and Clausen (1978).

Information on work in the United States with these parasitoids (releases, establishment, levels of parasitism) are provided by various authors. King *et al.* (1927) records the establishment of *Istocheta aldrichi*, as well as releases of other species. King and Holloway (1930ab) discuss establishment of *Tiphia popilliavora* in New Jersey and its field collection and redistribution. Establishment of *Tiphia vernalis* in Pennsylvania, as well as its biology and method of colonization, are discussed by Balock (1934). Krombein (1948) summarizes liberations of *Tiphia* spp. in the United States and their results.

Outcomes of releases of the various parasitoids in the United States were recorded at various times and locations, but a coordinated evaluation over the whole period of the project was not conducted. Records include establishment at release sites, numbers of parasitoid adults (*Tiphia* spp.) that could be successfully collected at such sites for use in colonization of additional sites, and in some cases levels of parasitism in grub collections. Studies discussing changes in grub densities before and after parasitoid releases were not found. A quantitative evaluation of the impact, if any, of these introduced parasitoids on densities of Japanese beetle could not be made based on the literature. Some authors do, however, assert that beetles did decline in number following the biological control efforts (including those with pathogens) made against the species (e.g., Hadley 1939).

Of the five parasitoid species that were successfully established in the United States, the following summaries can be given:

1. *Tiphia vernalis* has exhibited good synchrony with its host, but is limited by the adult wasp's need for plant nectar or insect honeydew. Close to such resources, rates of parasitism may be relatively high (47-62%) (Gardner 1938). Ladd and McCabe (1966), however, were only able to relocate this parasitoid in 1963 in one of 29 sites at which it had been released previously. R. McDonald (personal communication, North Carolina Department of Agriculture), however, has found this species to continue to be of local importance in parts of North Carolina and sees

opportunities to establish it on golf courses where Japanese beetles occur by planting tulip poplar trees as nectar sources.

2. *Tiphia popilliavora* has been less effective. This ineffectiveness is believed to be related to poor synchrony with its host. Of the three biotypes (Japan, Korea and China) of this parasitoid originally collected in Asia and released in the United States, the collection from Japan is believed to be the one that became established. This strain emerges the earliest of the three strains (Clausen 1978). *Tiphia popilliavora* in the United States emerges when Japanese beetle larvae are only in their second instar. In this instar, only 6% of parasitoid offspring are female compared with 67% in third instar larvae (Brunson 1934, 1938). As a consequence, this parasitoid's population is limited by an unfavorable sex ratio in its progeny. No recoveries of this species have been made in the United States since the 1960s and is believed to have died out in North America.

3. *Istocheta aldrichi* also is reduced in effectiveness by poor synchrony with its host, the adult beetle. The strain collected from northern Japan has established in the northeastern United States, but emerges too early relative to the emergence of adult beetles (Holloway 1960).

4. *Dexilla ventralis* is multibrooded and hence depends for some generations on hosts other than Japanese beetle. This species has persisted at only one site in the United States (Clausen 1978).

5. *Prosena siberita*'s current status is not reported, but this species is not known to be of any importance in the United States.

Currently, new efforts are being made by Richard McDonald of the North Carolina Department of Agriculture in cooperation with the U.S. Department of Agriculture to revisit the biological control of Japanese beetle. These activities include the following objectives:

- To locally enhance the effectiveness of *Tiphia vernalis* by planting tulip poplar trees as nectar sources at golf courses and other areas with chronic Japanese beetle problems.

- To explore in China for new natural enemy species, conducting searches on the many species of *Popillia* that exist in the region (some 57).

- To locate in China additional species of *Tiphia* from *Popillia* spp. that might also attack *Popillia japonica* (not found in China). Over 50 species of *Tiphia* occur in the region, only a few of which have been studied for this purpose.

- To use pheromone traps to collect adult Japanese beetles in various localities in central Japan at times corresponding to flight periods of adult Japanese beetles in

the United States. These collections will then be examined for immature stages of *Istocheta aldrichi* to obtain a population of this parasitoid that emerges late enough to be in synchrony with adult beetles in the United States.

- To collect a new strain of *Tiphia popilliavora* from China that emerges late enough to have good synchrony with third instar larvae in the fall in the United States.

- To collect other parasites that would be suited to climates of areas invaded by the Japanese beetle since the work in the 1930s and 1940s (such as the southeastern and north central United States).

Pathogens. Following the recognition of milky spore disease in Japanese beetle populations in the United States, the causative agent (*Bacillus popilliae*) was mass produced. In the 1940s a series of sites were inoculated with the agent. The intent was to establish the pathogen over the range of the pest to achieve permanent reductions in pest density (White and Dutky 1940). The long term effectiveness of these releases has been investigated in Ohio, New Jersey, and Delaware.

In Ohio, sites were inoculated with the pathogen in 1941-1945. Data from eight counties in 1951 revealed rates of milky disease from 1 to 35%, but rates were reduced by averaging samples from different dates, not all of which were properly timed seasonally to observe the full extent of disease (Polivka 1956).

In New Jersey, in 1963, twenty three years after initial distribution of the pathogen in the State, most sites at which inoculum had been released against a high density grub population (27 or more larvae per square foot) still had larval infection rates of 25-50% (Ladd and McCabe 1967). Sites that initially had a low grub population (6 or fewer per square foot) had lower infection rates (10-25%).

In Delaware in 1972, a survey was conducted of eight untreated sites and six sites treated with *Bacillus popilliae* in the 1940s. Densities of both summer grubs (3.4 per square foot versus 10.8) and fall grubs (1.4 versus 3.8) were lower at formerly treated sites than at untreated sites. Infection rates observed in the 1972 survey were 25% for the treated sites and 4% for untreated locations (Hutton and Burbutis 1974). These studies suggest that this pathogen has persisted in many areas that were inoculated and that the pathogen contributes to the beetle's mortality and lowers grub density to some degree.

Results of field trials with *B.t. japonensis* were not located, but likely have been or are being conducted. Tests of the fungal pathogen *Metarhizium anisopliae* have given inconsistent results, which are partly explained by grub avoidance of pathogen-contaminated soil (Villani *et al.* 1994).

Nematodes. Following the discovery of *Steinernema glaseri* infecting Japanese beetle grubs, the species was mass reared and used to inoculate over five hundred sites throughout New Jersey with the intent of permanently establishing the species at the sites. These releases generally failed to establish the species, as documented in a 1991 survey by Gaugler *et al.* (1992), that examined ecologically diverse habitats at or near as many of

the 1939-1942 sites as could be relocated. Of 304 sites examined, only 14 were found to have *S. glaseri* present, and all of these sites were in southern New Jersey. The authors attribute the failure of these nematode releases to two factors. One, the climatic tolerance of the nematode may be limiting, as this species is believed to be a subtropical species that reaches the northern limit of its distribution in southern New Jersey. Two, nematodes used for parts of the release program (the later phase, when the largest number of sites were treated) were reared in media to which antimicrobial materials had been added. Researchers were unaware at the time of the key role played by symbiotic bacteria in the biology of these families of nematodes. Symbiotic bacteria kill hosts penetrated by nematodes and are important in facilitating nematode reproduction in grubs.

More recently, efforts have been made to develop augmentative nematode applications for suppression of Japanese beetle grubs. Klein and Georgis (1992) found that effectiveness of augmentative nematode applications continued to increase for up to a year after initial application. Selvan *et al.* (1994) showed that a genetically modified strain of *S. glaseri* gave better control that the wild type nematode. Tests in the Azores found that *S. glaseri* and *Heterorhabditis bacteriophora* gave better control than *Steinernema carpocapsae*; but at soil temperatures below 15°C, only *S. glaseri* was effective (Simões *et al.* 1993). Immediate watering in of nematodes following application on turf can also improve control significantly (Downing 1994).

Reasons for Pest Status and Possibilities for Biological Control: The high densities of Japanese beetle grubs and adults in North America are presumed to be due to its status as an invading species since its density is sufficiently low in its native range that it is not considered a pest. Work to import natural enemies from Japan and other parts of Asia was based on the further presumption that this difference in densities was due in an important way to the absence of natural enemies in North America. These assumptions are still likely to be true. However, actual numerical comparisons of beetle densities between Japan and the eastern United States were not located. Such observations likely exist in the field notes of early explorers, but this report has not examined such sources of information. Furthermore, at least part of the difference in densities of Japanese beetle between Japan and the United States may be related to the extent of the area devoted to sod, which is relatively scarce in Japan. In parts of Japan where the area in sod is increasing, densities of Japanese beetle are higher (Ando 1986).

Recommendations: The work currently being undertaken by Richard McDonald (see above section, Biological Control Attempts/Parasitoids, for details) needs to be expanded and conducted more aggressively with more resources. Substantial opportunity clearly exists to increase the level of biological control of Japanese beetle by collecting new parasitoids and better populations of existing ones. These efforts should be coordinated at the national level and adequately funded rather than being conducted as a small project stimulated by the initiative of one State. These new efforts should also pay considerable attention to quantitatively evaluating the densities of Japanese beetles before and after additional agents are released. Comparisons should also be made between Japanese beetle densities in the eastern United States and Japan. Lifetables for Japanese beetle do not exist and would provide an effective framework to organize information about mortality, and to make contrasts between sites with and without various natural enemies.

33. IMPORTED WILLOW LEAF BEETLE (*Plagiodera versicolora* [Laicharting]) (Coleoptera: Chrysomelidae)

Origin: Imported willow leaf beetle is an exotic species from Eurasia, first detected in North America in New York in 1915 (Drooz 1985).

Range in North America: This species is now found throughout the eastern United States, southern Canada, and parts of Alaska (Drooz 1985).

Damage: Larvae and adults of this leaf beetle skeletonize leaves of willow (*Salix*) and poplar (*Populus*), causing extensive defoliation of willows in both landscape plantings and natural willow stands. Defoliation of native willows in wetlands, combined with disease caused by an exotic scab fungus, killed large numbers of willows in New York in the 1930s (Felt 1935).

Resident Natural Enemies: Parasitoids recorded in North America include *Schizonotus rotundiventris* (Girault) (Girault 1916, Krombein *et al.* 1979) and *Schizonotus latus* (Walker) (Jones 1933, Krombein *et al.* 1979). This second species was erroneously identified in the original literature as *Schizonotus sieboldi* Ratz., a Holoarctic species now known not to occur in North America. The biology of *S. latus* as a parasitoid of *P. versicolora* in North America is discussed by Dowden (1939). In Italy, the tachinid *Ptilopsina nigrisquamata* (Zett.) is also recorded as a parasitoid of this species (Mellini 1973). In North America, the coccinellid *Neoharmonia venusta* (Melsheimer) is reported as a specialized predator of *P. versicolora*. This coccinellid is unique in its ability to overcome the chemical defenses of the larvae and pupae (Whitehead and Duffied 1982). The *tenebrionis* subspecies of *Bacillus thuringiensis* is effective against larvae but not adults of this species, and can be used to provide foliage protection at particular sites (Bauer 1992).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Because this species is not native to the United States, its pest status is likely to be related to separation from controlling natural enemies. The world distribution of this species is comprised of three areas: (1) eastern North America, (2) Europe and the Middle East, and (3) China and Japan (Balcells Rocamora 1946). The second and third areas are separated by a large geographic area where the pest does not occur. *Plagiodera versicolora* is reported as a pest in Europe. These facts suggest the possibility that China is the area of origin, and that Europe and the Middle East are areas of secondary invasion. This view suggests that China, not Europe, would be the appropriate location to search for natural enemies. This species is reported as a pest of willow in China (Xu and Wan 1990), but it is not clear whether outbreaks are pesticide-induced or reflect a lack of effective natural enemies in the region.

Recommendations: Potential exists to control this species by means of introductions of natural enemies from its native range, presumably some part of China. The impact of this species on native willows in wetlands, and various willows in landscapes, suggest that biological control of this pest would serve a public need. Before undertaking natural enemy collections two actions are recommended. First, a survey of the existing natural enemies in North America should be made to verify the list of species present and to obtain an

approximate estimate of parasitism rates and the degree to which natural enemies lower pest density. Second, Chinese entomologists should be contacted to determine in more detail the history of movement of the species, if any, in China to determine if a likely area of original distribution can be identified.

34. ELM LEAF BEETLE (*Xanthogaleruca lutelola* [Müller] (Coleoptera: Chrysomelidae)

Notes: Elm leaf beetle was formerly known in the literature as *Galerucella xanthomelaena* (Schrank). Alternate generic placements have been in *Galerucella* and *Pyrrhalta.*

Origin: This species invaded North America in the 1830s (Dreistadt and Dahlsten 1990), apparently from Europe. Its range in Eurasia includes a wide zone from Spain through Russia. Its occurrence, however, as a pest in such locations as Italy (Goidanich 1983) and Russia (Movsesyan 1980), suggests that its true area of origin may be more restricted, and that perhaps western Europe is only an area of earlier invasion. However, information on this speculation is lacking and confirmation would require more intensive efforts to define the species' range in greater detail (e.g., examination of collection localities for specimens in museum collections throughout the world).

Range in North America: The species invaded the northeastern United States in the 1830s and by the 1920s had reached California. It is currently found widely throughout the United States and southern Canada, wherever elms occur naturally or have been planted. The spread of this species to new regions continues, as shown by its invasion in the 1980s of Australia (Osmelak 1990).

Damage: Larvae and adults feed on elm foliage, skeletonizing leaves. Multiple generations of the pest occur in most locations and dense populations cause defoliation. Defoliation weakens trees, predisposing them to bark beetle attack and Dutch elm disease.

Resident Natural Enemies: Other than generalist predators (e.g., Eikenbary and Raney 1968), only one species of natural enemy native to North America has been of any importance against this pest: the eulophid *Tetrastichus brevistigma* Gahan (Gahan 1936). Prior association of this species with native North American insects as hosts is presumed but not recorded (Clausen 1978). Eggs of the parasitoid are laid in host pupae or prepupae. In the northeastern United States, levels of parasitism are high (10-47%, Jones 1933). This species was purposefully introduced into California, where it established but has remained rare and is of no practical importance (Dreistadt and Dahlsten 1990, 1991). Laboratory rearing of this species is described by Hamerski *et al.* (1990).

Biological Control Attempts: Several species of parasitoids have been introduced into North America against the elm leaf beetle. Parasitoids were introduced into the eastern United States from 1911 through the 1930s. In California, introductions occurred in the 1930s and again during 1974-1989 (Dreistadt and Dahlsten 1991).

The principal parasitoid species introduced in these efforts were the eulophid egg parasitoid *Tetrastichus gallerucae* (Fonscolmbe), the tachinid larval parasitoid *Erynniopsis antennata* (Rondani), and a unidentified eulophid egg parasitoid, *Tetrastichus* sp., from Japan.

The egg parasitoid *Tetrastichus gallerucae* (=*Tetrastichus xanthomelaenae*) was collected in Europe and released in both the eastern United States and California (Howard 1917, Clausen 1978). Establishment has been confirmed only in Ohio and California (Clausen 1978, Dahlsten *et al.* 1985). In California, the parasitoid is scarce and does not suppress the pest (Dreistadt and Dahlsten 1991). The status of this parasitoid in the eastern United States is uncertain. Laboratory rearing of this species is described by Clair *et al.* (1987).

The tachinid larval parasitoid *Erynniopsis antennata* (=*Erynnia nitida* R.-D. and *Anachaetopsis nitudula* Vill.), a parasitoid of the elm leaf beetle in Europe (Howard 1925), was released in New England and California in the 1930s. Establishment was observed in California, but not in New England (Clausen 1978). This species is currently of moderate importance in California (Dreistadt and Dahlsten 1991), except where its hyperparasitoid, *Tetrastichus erynniae* Domenichini, suppresses it.

The unidentified eulophid egg parasitoid, *Tetrastichus* sp., introduced into California from Japan in the 1930s, (collected from a related species, *Galerucella maculicollis* Mots.) did not establish (Flanders 1936, Clausen 1978).

Other parasitoids noted from elm leaf beetle, include *Tetrastichus celtidis* and *Medina collaris*, recovered in California (Dahlsten *et al.* 1985) and *Aplomyiopsis galerucellae*, noted in Oregon (Villenueve De Janti 1933). European species of *Tetrastichus* associated with *Xanthogaleruca luteola* and *Galeruca* spp. have been revised and keyed, providing useful information for the selection of additional parasitoids for introduction (Graham 1985).

Pathogens attacking elm leaf beetle include the fungus *Beauveria bassiana*, which caused 70-87% mortality to overwintering adults at study sites in Italy (Triggiani 1986); the microsporidian *Nosema galerucellae*, which has been observed in France (Tonguebaye and Bouix 1989); and the "San Diego" isolate of *Bacillus thuringiensis*, which has been found to provide control of larvae and adults when used as a bioinsecticide (Cranshaw *et al.* 1989).

Reasons for Pest Status and Possibilities for Biological Control: The fundamental reason for the pest status of this species appears to be separation from key natural enemies, following its invasion of new regions.

Recommendations: Control of this pest should be possible through introduction of appropriate species and strains of natural enemies. Past efforts to date have been unsuccessful. This suggests that more careful studies are needed to define which natural enemies most strongly affect the pest in areas in Eurasia where it is held at harmless levels. Additional efforts are needed to define what the climatic or other requirements are of key parasitoids in these areas. Topics that may require attention include determination of how parasitoids overwinter, to help select collection locations from which strains well adapted to the release area could be obtained. For example, in other systems it has been noted that strains of parasitoids from northeast Asia can sometimes be better adapted to the climate and photoperiod seasonality of the northeastern United States than the same species from western Europe.

After population dynamics studies have been conducted in the area of origin, new parasitoids should be collected and imported from Europe, Russia, China, and Japan. An analysis is also needed of the climatic compatibility between the various possible collection and release areas. Attention should also be given to the overwintering needs of each introduced species.

35. NATIVE ELM BARK BEETLE (*Hylurgopinus rufipes* [Eichhoff]) (Coleoptera: Scolytidae)

Notes: Former generic placements include *Hylastes*. Based on an examination of type specimens and exact publication dates, Wood (1979) proposed that the name *Hylurgopinus opacus* (LeConte) has priority over *H. rufipes*, even though the latter has been the name used during most of the last century.

Origin: Native elm bark beetle is native to North America.

Range in North America: *H. rufipes*' native range originally included southern Canada and the eastern United States (Drooz 1985). A map of this distribution is available (Anon. 1975a). Some displacement of *H. rufipes* has occurred due to competition from the introduced smaller European elm bark beetle, *Scolytus multistriatus* (Marsham), except in the more northern parts of *H. rufipes*' range where overwintering survival of *S. multistriatus* is low (Drooz 1985).

Damage: By itself this bark beetle is of little importance, breeding as it does in dead and dying trees or recently cut logs. As a vector, however, it has importance in promoting the spread of Dutch elm disease. Transmission occurs when adults emerge from dead trees and fly to healthy trees into which they burrow to feed or hibernate (Drooz 1985).

Resident Natural Enemies: In a study of natural enemies of *H. rufipes* in Connecticut, Kaston (1939) found the main predator to be the clerid *Enoclerus nigripes* Say. Other predators noted were the histerid *Platysoma coarctatum* LeConte and the dipteran *Lonchaea polita* Say. The principal parasitoid was *Spathius canadensis* Ashmead, which attacked 5-10% of the larvae. Occasional parasitism by *Spathius benefactor* Matthews has also been recorded (Gardiner 1976) and it also appears from laboratory studies that the introduced species *Dendrosoter protuberans* (Nees) (released against *Scolytus multistriatus*) is able to develop on *H. rufipes* (Gardiner 1976). The aphelenchoidid nematode *Parasitaphelenchus oldhami* (Rühm) was noted in Manitoba parasitizing *H. rufipes* (Tomalak *et al.* 1988).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: This native bark beetle has achieved importance as a pest because it transmits an exotic pathogen causing Dutch elm disease.

Recommendations: Biological control of this bark beetle is inappropriate since it is not the major vector of Dutch elm disease and its suppression alone would not prevent disease transmission. Effort might be better directed at suppression of the pathogen directly rather than at the vectors (see Stillwell 1977 for a discussion of this idea).

36. SMALLER EUROPEAN ELM BARK BEETLE (*Scolytus multistriatus* [Marsham]) (Coleoptera: Scolytidae)

Notes: Former generic placements include *Eccoptogaster*.

Origin: Smaller elm bark beetle is of European origin and invaded the United States on unbarked elm logs imported from Europe (Knull 1934). The species is found throughout Europe, Iran, and parts of Egypt (Anon. 1975b).

Range in North America: In North America, *S. multistriatus* is found throughout most of the United States except some parts of Florida and Maine (Anon. 1975b).

Damage: This species transmits *Ceratocystis ulmi* (Buisman) Moreau, the pathogen that causes Dutch elm disease (Betrem 1929-30, Collins *et al.* 1936, Kaston and Riggs 1938). For historical information on the elm disease epidemics in Europe and North America, see Readio (1935), Sinclair and Campana (1978), and Campana and Stipes (1981). Losses from Dutch elm disease are discussed by Campana and Stipes (1981), but quantitative data are lacking. General reviews of options for control of Dutch elm disease, including the role of biological control, are given by Mazzone and Peacock (1985).

Resident Natural Enemies: Studies of natural enemies of this species have been conducted in both Europe and North America. Some European species occur in North America, apparently having accompanied their host during its invasion. Others have been deliberately introduced. A summary of information concerning these natural enemies follows.

Parasitoids. The pteromalids *Cheiropachus quadrum* (Fabricius) (mistakenly listed as *Cheiropachus colon* L.) and *Rhaphitelus ladenbergi* Ratz. are recorded from *S. multistriatus* in Spain and Poland, respectively (Mercet 1926-28, Sitowski 1930). In Holland, nine species of parasitoids were noted by Fransen (1931), of which the most important was the braconid *Coeloides scolyticida* Wesm., which parasitized up to 89% of the larvae. In the former Yugoslavia, that the main parasitoids of *S. multistriatus* and other Dutch elm disease vectors were the braconid *Dendrosoter protuberans* (Nees), *Ecphylus silesicacus* (Ratzbug), *C. scolyticida*, and *Entedon leucogramma* (Ratzburg) (Maksimovic 1979). Schröder (1974) found *D. protuberans* to be the most significant parasitoid of *S. multistriatus* larvae in Austria. Merlin (1984) lists parasitoids found in a survey of *S. multistriatus* in Belgium. The parasitic mite *Pyemotes scolyti* Oud. has been recorded attacking *S. multistriatus* in England (Beaver 1967).

In the United States, the egg-larval eulophid parasitoid *E. leucogramma* was found by Galford (1967), apparently having invaded the United States naturally together with its host. Other species recorded from North America include the native braconid *Spathius canadensis* (Ashmead), the European pteromalid *C. quadrum,* and the introduced braconid *D. protuberans* (Kennedy 1970). Kennedy (1970) discusses the biology of *D. protuberans*. Hajek and Dahlsten (1985a) list the parasitoids and predators found attacking *S. multistriatus* in California.

Predators. The most effective predator of *S. multistriatus* in Austria was the dolichopodid fly *Medetera nitida* (Macq.) (Schröder 1974).

Pathogens. Various nematodes have been recorded from *S. multistriatus*. *Rhabditolaimus leuckarti* was found in larvae in Holland (Fransen 1931). In the United Kingdom up to 60% of adults were found infected by *Parasitylenchus scolyti* Oldham (Oldham 1930). Of infected beetles, 40% were sterile. Nematodes found in *S. multistriatus* in Wisconsin are given by Saunders and Norris (1961). Hunt and Hague (1974) reported 24-68% infection rates of adults of *S. multistriatus* by *Parasitaphelenchus oldhami* Rühm, but found no detrimental effects on the host from infection by this nematode.

The microsporidia *Stempellia scolytii* (Weiser) and *Nosema scolytii* Lipa were found infecting 32% of larvae, pupae, and adults of *S. multistriatus* in Poland by Lipa (1968).

Infectivity rates of eight species of fungal pathogens have been assessed against *S. multistriatus* (Houle *et al.* 1987).

Antagonists of Dutch elm pathogen. *Trichothecium roseum* (Pers.) Link has been recorded as an antagonist of *C. ulmi* (Richards 1988). In artificial rearing systems, addition of the antagonistic fungi *Trichoderma harzianum* Rifai, *Trichoderma polysporum*, and *Scytalidium lignicola* increased mortality rates of *S. multistriatus* larvae from 21% to over 80% (Jassim *et al.* 1990).

Overall mortality estimates from natural enemy complexes. In California, Hajek and Dahlsten (1985b) found overall mortality of *S. multistriatus* brood to be 49-86%, but concluded that natural enemies were of little or no importance. In Austria, Schröder (1974) found mortality of brood to be 75-85%. No experimental, quantitative evaluations of the importance of natural enemies were located.

Biological Control Attempts: In Europe, some early attention was given to mass rearing parasitoids of *S. multistriatus* (Roepke 1934).

In North America, several species of European parasitoids have been imported to attempt to suppress *S. multistriatus*. *Dendrosoter protuberans* and *Ecphylus silesicacus* were imported into Ohio. *Coeloides scolyticida*, together with the first two species, was sent from Europe to Michigan (Greathead 1976). Work in Ohio with *D. protuberans* is reviewed by Kennedy (1970), work in Michigan by Truchan (1970), and in Ontario by Gardiner (1976). A technique for mass rearing *D. protuberans* has been developed (Kennedy and Galford 1972). Later, work with this species was also conducted in Colorado, where it established. Poor overwinter survival of this parasitoid has limited its impact in areas such as Colorado that have cold winters (Hostetler and Brewer 1976). This same parasitoid has been recovered from California, although it was not released in that State (Hajek and Dahlsten 1981).

Reasons for Pest Status and Possibilities for Biological Control: Since densities of this bark beetle have not been quantitatively compared between Europe and North America, it is not certain whether densities in North America are higher. Importations of natural enemies that have been made to date are based on the assumptions that the bark beetle's densities are

higher in North America and that establishing European natural enemies of *S. multistriatus* would lower the beetle's density.

Recommendations: Work with European natural enemies could be continued, especially with species that have not yet established or were never tried. For example, the microsporidia reported in Europe by Lipa (1968) and the sterilizing nematode from England (Oldham 1930) might merit consideration for importation.

Alternatively, it might be more productive to focus work on a search for the native range of the Dutch elm pathogen and examine that region for antagonists of the pathogen that might be suitable for introduction into North America (see Mazzone and Peacock 1985 for a discussion of this option).

37. SPRUCE BEETLE (*Dendroctonus rufipennis* [Kirby]) (Coleoptera: Scolytidae)

Notes: Prior to 1969, six different names were applied to spruce beetle: (1) *Dendroctonus engelmanni* Hopk., (2) *D. rufipennis* (Kirby), (3) *D. obesus* (Mannerheim), (4) *D. piceaperda* Hopk., (5) *D. similis* Le Conte, and (6) *D. borealis* Hopk. These were synonymized in 1963 and *D. rufipennis* was established as the correct name in 1969 (Linton and Safranyik 1988). An annotated bibliography for the species is provided by Linton and Safranyik (1988).

Origin: Spruce beetle is native to North America.

Range in North America: The spruce beetle is found throughout the spruce forests of North America (Drooz 1985).

Damage: The spruce beetle has in some years reached high densities over wide areas. While the species normally breeds in wind thrown, overmature, or weakened trees at endemic levels, during outbreaks trees are attacked and killed regardless of size or vigor (Drooz 1985). Morris (1958) provides notes on the history of spruce beetle outbreaks in the Canadian Maritime provinces. A hazard rating system estimating which trees are at greatest risk from attack by spruce beetle has been developed by Hard *et al.* (1983) for white spruce in Alaska. In general, old, slow growing trees in denser stands were at greatest risk.

Resident Natural Enemies: Mills (1983) tabulates arthropod natural enemies of spruce beetle from the literature. He records five parasitoids: the braconids *Coeloides rufovariegatus* (Prov.) and *Coeloides vancouverensis* (D.T.); the pteromalids *Dinotiscus burkei* (Crawford) and *Roptrocerus xylophagorum* (Ratz.); and the cleonymid *Heydenia unica* Cook and Davis. He also records three predacious clerids: *Enoclerus lecontei* (Wolc.), *Enoclerus sphegeus* (F.), and *Thanasimus undulatus* (Say). Knight (1958) records *Coeloides dendroctoni* Cushman as a parasitoid of this beetle, and *Medetera aldrichii* Wheeler and *Thanasimus nigriventris* Le Conte as predators. The life history of *Coeloides dendroctoni* has been studied by Ostmark (1957). A quantitative understanding of the importance of invertebrate natural enemies to the population dynamics of spruce beetle, however, is not available.

In contrast to the absence of studies on the contribution of invertebrate natural enemies to the population dynamics of this pest species, the influence of avian predators— mainly woodpeckers—has been researched extensively, using experimental cage exclusion methods under a variety of habitat and beetle population conditions. Collectively these studies demonstrate that woodpeckers are an important mortality source for spruce beetle.

Knight (1958) used cage exclusion methods to demonstrate that woodpeckers caused 45-98% mortality to brood of spruce beetle in Colorado. Baldwin (1968a) identified the three-toed woodpecker, *Picoides tridactylus*, as the most important species of woodpecker attacking spruce beetles in Colorado, and provides a lifetable for the beetle showing 59-88% larval mortality in various larval stages. Woodpecker predation was greatest in declining populations (33-56%) and less in increasing (28-26%) or static (24-42%) populations (Baldwin 1968a). The percentage mortality from woodpecker predation increased over a range of beetle densities from 0.0 to 0.2 million larvae per acre and then, as predators became saturated, the percentage predation declined at higher host densities. Baldwin (1968b) found 70-79% mortality to spruce beetle brood from three-toed woodpeckers in logs on the ground in Colorado. Shook and Baldwin (1970) contrasted woodpecker predation rates in various habitats and found that there was no predation in open meadows, 52% mortality in dense forests, 71% in open forest and 83% in semi-open forest.

Koplin (1967) states that woodpecker predation increases in small outbreaks, rising from 28% in endemic beetle populations to 84% in epidemic populations, but declines to 53% in outbreaks that cover large areas. This difference appears to be based on the ability of three-toed woodpecker populations to increase in number in local areas with high spruce beetle concentrations, as demonstrated by Koplin (1969). A model describing the effectiveness of woodpeckers as predators of spruce beetles has been developed (Koplin 1972).

Biological Control Attempts: Few attempts to actively increase the level of biological control of spruce beetle have been made. In the 1930s, one predator, *Rhizophagus* sp., and one larval parasitoid, *Rhopalicus tutela* (Wilkr.), were imported from England and released in Quebec against spruce beetle, but no recoveries were made (Clausen 1978).

Werner *et al.* (1983) compared the relative toxicities of three insecticides (chlorpyrifos, fenitrothion, and permethrin) to spruce beetles and their natural enemies. Use of pesticides to protect high value trees would cause less harm to natural enemies of spruce beetle if selective compounds were available.

Reasons for Pest Status and Possibilities for Biological Control: No specific studies have attempted to identify forces that control the release of this species from endemic to epidemic levels. Initiation of an outbreak is believed to be caused by a local discrete increase in the quantity of available breeding material, particularly wind thrown trees after storms, but also stumps after harvest and logs after thinning (Safranyik 1978, Safranyik *et al.* 1983). Experimental data demonstrating this release mechanism, however, are not available. Some potential causes of collapse of outbreak populations have been studied. Most attention has focused on the role of predation by woodpeckers (see above discussion on Resident Natural Enemies).

Recommendations: There seems to be no obvious means by which biological control could be enhanced to increase the current level of control of this species. Introduction of exotic natural enemies from related *Dendroctonus* spp. in Europe has been suggested (Mills 1983) but not effectively pursued.

38. BLACK TURPENTINE BEETLE (*Dendroctonus terebrans* [Olivier]) (Coleoptera: Scolytidae)

Origin: Black turpentine beetle is native to North America.

Range in North America: This species occurs from the coastal areas of southern New England, south to Florida, and west to Missouri and Texas (Drooz 1985).

Damage: Before 1949 this species was considered to be of little importance, limited to breeding in stumps or killing, at most, bark patches on healthy trees (Drooz 1985). More recently, however, stands of healthy trees have been killed by this species. Losses have occurred in pulpwood stands, seed orchards, resin plantations, and landscape plantings of specimen trees.

Resident Natural Enemies: No articles were located on natural enemies of this species, although a detailed analysis of the natural enemy complexes affecting other *Dendroctonus* spp. attacking conifers in Europe is given by Mills (1983).

Biological Control Attempts: The predatory rhizophagid beetle *Rhizophagus grandis* Gyllenhal is a specific predator of the spruce bark beetle, *Dendroctonus micans* (Kugelann) and has been used in western Europe via inoculative releases to combat the spread of *D. micans* (Evans and King 1989). *Rhizophagus grandis* locates its prey by attraction to chemicals in host frass. Studies have indicated that this predator is also attracted to chemicals in frass of other *Dendroctonus* spp., including *D. terebrans* and *D. frontalis* (Miller *et al.* 1987, Moser 1989). This led to the suggestion that this predator might be useful for introduction into the United States for control of *D. terebrans* and *Dendroctonus frontalis* Zimmermann. Limited numbers (500-1000) of *R. grandis* were released in 1988 at one site in Louisiana, but the predator has not been recovered (Moser 1989). No further efforts have been made to establish this species in North America.

Reasons for Pest Status and Possibilities for Biological Control: This species attacks stumps and injured trees. Populations are likely to increase when breeding sites become common because of management or storm damage. The role of biological control agents in the population dynamics of this species is poorly understood.

Recommendation for Biological Control Actions: Introduction of exotic natural enemies against the native black turpentine beetle (mainly the predator *R. grandis*) has been attempted but is controversial and is not recommended.

39. EASTERN LARCH BEETLE (*Dendroctonus simplex* LeConte) (Coleoptera: Scolytidae)

Origin: Eastern larch beetle is native to North America.

Range in North America: The eastern larch beetle is found in the United States from New England south to West Virginia, and west to Minnesota. It occurs from coast to coast in Canada, and also in Alaska (Drooz 1985).

Damage: This bark beetle is generally not regarded as an aggressive species, attacking only dying or recently felled trees. However, during outbreaks apparently healthy trees may also be attacked and killed (Drooz 1985). Its only host of importance is tamarack, *Larix laricina* (Du Roi) K. Koch. The literature on the species is listed in Langor and Raske (1988a).

Resident Natural Enemies: Mills (1983) summarizes the literature records of parasitoids and predators attacking various species of *Dendroctonus*, including *D. simplex*. Langor (1991) documents in detail the arthropod and nematode associates of *D. simplex* at two study sites in Newfoundland and notes that the most important predators were the dolichopodid *Medetera gaspensis* Bickel and the rhizophagid *Rhizophagus dimidiatus* Mannerheim. The main parasitoids were the braconid *Spathius canadensis* Ashmead and the pteromalids *Rhopalicus tutela* (Walker) and *Roptrocerus xylophagorum* (Ratzburg). Earlier literature records are also noted and discussed. At one of the study sites, larval parasitism reached 30%, and was more common at mid and upper positions on the trunk than near the bole. Life tables developed for *D. simplex* by Langor and Raske (1988b) record overall mortality levels of 79% and 82% for the first and second broods of the pest, with pathogens being important to the egg, second instar, and pupal stages; resinosis to the first instar larvae; and parasitism to the third and fourth instar larvae. In Alaska, Werner (1986) recorded overall mortality levels of 87-98%. Bushing (1965) provides further information on host-parasitoid records within the Scolytidae in North America.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Langor and Raske (1989) discuss the history of *D. simplex* outbreaks in North America. They point out that while the antecedents of eastern larch beetle outbreaks are not proven, outbreaks have often followed stress from fires, floods, drought, or outbreaks of defoliating insects. Commenting on the details of the major outbreaks in various States and provinces, Langor and Raske (1989) point out that many outbreaks followed outbreaks of defoliation by the larch sawfly, *Pristiphora erichsonii* (Hartig). Outbreaks of this sawfly often cause the death of a significant percentage of larch in an area, providing considerable breeding material for *D. simplex*.

Recommendations: *Dendroctonus simplex* is a native insect that appears to have a well developed parasitoid and predator complex associated with it (Langor and Raske 1988b, Langor 1991). Nevertheless, Mills (1983) has included this species as one for which natural enemy introductions from related European scolytids might be considered.

An alternate approach might be to focus on reducing the frequency of the predisposing stresses, particularly outbreaks of the larch sawfly. This species is believed to be an exotic native species in North America. Efforts to introduce effective natural enemies against this species have been made, but have been only partially successful, with continued outbreaks in some locations. Further work on biological control of larch sawfly might be especially beneficial, as it has potential to provide control both of larch sawfly and the eastern larch beetle.

40. ENGRAVER BEETLE (*Ips typographus* [Linnaeus]) (Coleoptera: Scolytidae)

Notes: The biology and population dynamics of engraver beetle are reviewed by Christiansen and Bakke (1988).

Origin: This beetle is native to Europe and is not yet known to occur in North America, but is a potential exotic invader of concern. Laidlaw (1947) records finding live *I. typographus* brood in poorly barked logs being imported into Britain (where this bark beetle is not present). Risk of movement of the pest in logs to new parts of the world remains an important quarantine concern.

Range in North America: This species does not yet occur in North America. It is found throughout much of western and central Europe; see Anon. (1976) for a map of its world distribution.

Damage: *Ips typographus* is the most damaging bark beetle in Europe, and a series of outbreaks of wide geographic extent and long duration have occurred over the last 200 years. See Christiansen and Bakke (1988) for a description of several of the largest of these outbreaks. Attacks on living trees are facilitated by mass attack and beetle-inoculation of tree tissues with a pathogenic fungus, *Ceratocystis polonica* (Horntvedt *et al.* 1983, Christiansen 1985). Beetles are preferentially attracted to volatile odors from trees infected by wood rot fungi such as *Armillaria mellea* (Madziara-Borusiewicz and Strzelecka 1977).

Resident Natural Enemies: The natural enemies attacking *Ips typographus* have been studied in many locations. For a review of natural enemies of *I. typographus* through 1988, see Mills and Schlup (1989).

Parasitoids. Mokrzecki (1922-23) recorded four species as parasitoids of *I. typographus* in a study in Poland: *Bracon flavator* F., *Roptrocerus xylophagorum* Ratz., *Pimpla alternans* Grav., and *Dendrosoter middendorfi* Ratz. Parasitoids noted in Austria include *Tomicobia seitneri* (Ruschka), *Rhopalicus suspensus* Ratz., *Rhoptrocerus xylophagorum* Ratx., *Coeliodes bostrychorum* Giraud, and *Rhopalophorus claviornis* (Wesm.) (Seitner 1922). In Germany, adults of *I. typographus* were parasitized by *Rhopalophorus clavicornis*, *Cosmophorus klugi* Ratz., and *Tomicobia seitneri*, and larvae were killed by *Coeloides bostrichorum*, *Bracon stabilis* Wesm., *Spathius brevicaudis* Ratz., *Dendrosoter middendorffi*, *Pachyceras xylophagorum* Ratz., *Rhopalicus tutela* (Wlk.), *Cheriopachus colon* (L.), *Eurytoma arctica* Thoms., and *Eurytoma morio* Boh (Sachtleben 1952). The biologies

of three *I. typographus* parasitoids, *Coeloides bostrichorum*, *Dendrosoter middendorffii*, and *Rhopalicus tutela*, have been studied (Krüger and Mills 1990).

Predators. Mokrzecki (1922-23) recorded three species as predators of *I. typographus* in Poland: the anthocorid *Piezostethus cursitans* Fallén, larvae of *Lonchaea laticornis* Mg., and larvae of *Lonchaea parvicornis* Mg. In Austria, Seitner (1922) recorded the clerid *Thanasimus formicarius* (L.) and the Diptera *Medetera signaticornis* Lw., *Palloptera usta* Mg., and *Lonchaea fugax* Beck. as predators of *I. typographus*. Rudinsky *et al.* (1971) found that three species of predators were attracted to the pheromone of *I. typographus*: *Thanasimus formicarius*, *Medetera signaticornis* Lw., and *Epuraea pygmaea* (Gylh.). Laboratory tests have been conducted to determine the relative preference of various *I. typographus* predators for either *I. typographus* brood or the immature stages of other natural enemies found in *I. typographus* galleries (Ounap 1992).

Mites found to be predacious on various stages of this bark beetle include *Iponemus gaebleri* (Schaarschmidt), which attacks the eggs (Balazy and Kielczewski 1965), as well as *Paracarophenax ipidarius* (Redikortsev), also an egg predator, and *Pyemotes dryas* (Vitz.), a brood predator (Moser and Bogenschütz 1984).

Pathogens. In the Bavarian Alps, Purrini (1978) noted infections of the protozoa *Gregarina typographi* in *I. typographus*. Lieutier (1979) lists 14 species of nematodes that are associated with this bark beetle, either for phoresy or as pathogens. Kurashvili *et al.* (1981) note that an unspecified species of "tylenchid" nematode [no longer used as a family designation] was effective in regulating the numbers of *I. typographus* in southern and western Georgia in the former U.S.S.R. Wegensteiner and Weiser (1995) report the occurrence of an entomopoxvirus from adults of *I. typographus* in Austria.

Rates of Mortality Observed.

Rates of mortality to brood. Balazy (1968) compared rates of mortality of *I. typographus* brood among a variety of habitats and found that natural enemies caused four times as much mortality in wild forest sites as in plantations. In the Archangel area of Russia, natural enemies caused relatively little mortality to brood of *I. typographus*, except when bark beetle densities were low (Ogibin 1974). At higher population densities, Ogibin felt that most brood mortality was related to intraspecific competition, not the action of natural enemies. In Bavaria, the most important predator of *I. typographus* was the clerid *T. formicarius*, which killed 18% of the brood (Mills 1985). However, Mill notes that overall brood mortality was 81%, with most mortality due to factors other than natural enemies (mainly intraspecific competition). Parasitism by braconids of older larvae was, however, relatively important (19-48%) in the upper 60% of the trunks of beetle-infested trees, and less important (3-11% parasitism) in the lower 40% of the trunks (Mills 1986).

Weslien and Regnander (1992) used cages to compare the number of progeny that beetles produced per gallery in spruce bolts that were either allowed to become naturally infested in a Swedish spruce stand (uncaged treatment) or were infested at the field site with 200 beetles per cage (the caged treatments). The study was conducted in the final year of an *I. typographus* outbreak, which collapsed the following year. The level of bark beetle infestation in the bolts achieved by the two infestation methods was similar, as measured

by egg galleries per m^2, numbers of nuptial chambers per m^2, and egg gallery length. Brood in various treatments had, therefore, similar initial densities and thus were subjected to the same potential levels of intraspecific competition. Levels of offspring production, however, showed a strong effect of caging that could be attributed to natural enemy presence or absence. In uncaged bolts in the forest, which were exposed to the full force of natural enemies, only 0.9 new adults emerged per gallery. In contrast, 4.5 adults emerged from caged bolts, indicating that natural enemies caused 80% mortality. Cages to which clerid adults (*Thanasimus formicarius*) were added produced only 2.45 adults per gallery, indicating that this predator could account for a little less than half the mortality from the whole natural enemy complex. In a separate experiment Weslien (1992) caged bolts sequentially at 0, 1, 4, or 8 weeks. The "0 weeks" exposure bolts were infested by introducing beetles into cages placed at the field site. Bolts in the other treatments were caged after 1, 4 or 8 weeks of exposure at field sites after the first *I. typographus* attacks at the field site were observed. The breeding density of brood (as egg galleries per m^2) was similar in all treatments (range 420-496), showing approximately equal levels of initial intraspecific competition. Rates of offspring production, however, were again very different, with an 82% reduction in brood by 8 weeks exposure to natural enemies compared with no exposure.

Rates of mortality to adult beetles. Rates of mortality or sterility of adult beetles that remain in galleries can reach 50-80% (Balazy *et al.* 1967). Such mortality is caused by various agents, including the braconid *Rhopalophorus clavicornis*, the pteromalid *Tomicobia seitneri*, fungal pathogens such as *Beauveria bassiana* and *Paecilomyces farinosus*, and predators such as *Lonchaea* spp. and *Medetera* spp.

Biological Control Attempts: No natural enemies have been moved to new locations in attempts to suppress this bark beetle. Conservation of existing natural enemies by manipulation of site characteristics that would favor natural enemy abundance has not been attempted, although observations suggest that rates of natural enemy attack are substantially lower in managed plantations than in natural forests (Balazy 1968). The reasons for these differences have not been determined. Artificial rearing of the natural enemies of *I. typographus* has been considered but not implemented (Kolubajiv 1958).

Reasons for Pest Status and Possibilities for Biological Control: Berryman *et al.* (1987) present the view that *I. typographus* populations are little affected by natural enemies. They postulate that at low population densities beetle populations are limited by high levels of mortality from intraspecific competition within galleries. This occurs because the population is concentrated in a limited number of available breeding sites (Ogibin 1974, Anderbrant *et al.* 1985, Mills 1986). This limit is removed when sudden events (like storms or logging damage) increase the number of damaged or downed trees suitable for breeding or if tree resistance to bark beetle attack declines because of stand aging, drought (especially in stands planted on dry sites), air pollution or other forms of stress (Kautsch 1927, Popovic 1931, Baltensweiler 1985). With increased numbers of breeding sites available, the population becomes less concentrated and intraspecific competition decreases, leading to increased numbers of beetles being produced. This increase in the number of beetles in a stand allows beetles to engage in mass attack on healthy or less stressed trees, resulting in a self-sustaining process that continues until beetle density again saturates available hosts and intraspecific mortality increases, causing the number of beetles to decline. A qualitative model of these processes has been presented by Berryman and Stenseth (1989). In general, any process that increases

breeding material abundance has potential to trigger an outbreak. Such processes include drought, selective felling of mature stands (if, as is often the case, this results in increased numbers of wind thrown trees), failure to remove downed logs promptly after a storm, and abandonment of the practice of debarking logs in the forest.

According to this view, mortality caused by natural enemies is unimportant and would largely be compensated for by reduced levels of intraspecific mortality. This view, however, has been made less convincing by the experiments of Weslien (1992) and Weslien and Regnander (1992), who demonstrated via cage exclusion methods that natural enemies were important and were able to reduce the number of beetle offspring by as much as 82%.

Other methods proposed for control of this species have included the use of trap logs (used to focus beetle oviposition into logs that are later destroyed) (Marié 1924) and mass trapping with pheromone baits (Vité 1989).

Recommendations: Because of the highly damaging nature of this species in European forests, every effort should be made to prevent its transport to North America. Should the species become established, importation of natural enemies should be undertaken, based on the work of Weslien (1992) and Weslien and Regnander (1992), which document the importance of natural enemies.

41. PINE ENGRAVER (*Ips pini* [Say]) (Coleoptera: Scolytidae)

Notes: For a list of synonymies and alternate generic placements before 1916, see Clemens (1916).

Origin: Pine engraver is native to North America.

Range in North America: *Ips pini* is found throughout the coniferous forests of North America, except in the Pacific coastal forests, the southern pine forests of the United States, and in Mexico (Drooz 1985)

Damage: In natural forests, this bark beetle is of little importance. Slash from logging or thinning, however, provides suitable breeding material in which populations of this beetle are able to increase. After such increase, healthy trees in the local area may be attacked and killed, causing economic damage (Thomas 1961, Ciesla and Bell 1968, Sartwell 1970, Drooz 1985). Population increases may also occur after storms uproot trees or drought, defoliation, or root diseases weaken living trees. *Ips pini* is considered the most important bark beetle attacking red pine in the Great Lakes States (Raffa 1991).

Resident Natural Enemies: The parasitoids and predators that attack *Ips pini* are varied, and many also attack a variety of other bark beetles. Studies by Kudon and Berisford (1980) provide some perspective on the interlocking and flexible nature of these host/natural enemy relationships. Many of the predators of *Ips pini* are attracted to beetle-infested trees by ipsdienol, a chemical associated with the beetle-host plant complex during mass attack (Miller and Borden 1990, Raffa 1991).

Lists of predators or parasitoids reared from or found associated with *Ips pini* are given by various authors. One of the earliest such list is that of Clemens (1916). Schenk and Benjamin (1969) record natural enemies of *I. pini* from jack pine forests in Wisconsin, and state that, among the predators, *Thanasimus dubius* (Fabricius) was the most abundant. In Alberta, Reid (1957a) lists the clerid *Enoclerus sphegeus* Fabricius as the dominant predator and records predation by larvae of this clerid on young brood and predation by the adult clerids on adult bark beetles. The same study noted the pyemotid mite *Pygmephorus* sp. as being the main predator of *I. pini* eggs. In Wisconsin, Raffa (1991) notes predation on *I. pini* by the clerid *Thanasimus dubius*, the histerid *Cylistix cylindrica* (Paykull), the tenebrionid *Corticeus parallelus* Melsch, and the trogositid *Tenebriodes collaris* (Sturm).

Also in Alberta, Reid (1957b) recorded a variety of parasitoids from *I. pini*, including the braconid *Coeloides dendronctoni* Cushman, and the three pteromalids *Pachyceras xylophagorum* Ratz., *Rhopalicus pulchripennis* (Crawford), and *Tomicobia tibialis* Ahmead. *Tomicobia tibialis* parasitizes adult beetles, reducing their fecundity by 50% (Senger and Roitberg 1992). Berisford *et al.* (1970) describe the parasitoid complex associated with various species of *Ips* beetles on standing and felled loblolly pine (*Pineus taeda* Linnaeus) and white pine in Virginia. From *I. pini*, Berisford *et al.* (1970) record eleven species of parasitoids.

Few pathogens have been associated with *I. pini*, but Choo *et al.* (1987) record various nematodes found in this bark beetle.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: The reason commonly given in the literature for the development of damaging *I. pini* populations is a local increase in the availability of breeding sites, after thinning of stands or storms. While a variety of natural enemies have been recorded as attacking *I. pini*, no quantitative or experimental understanding of their significance in the population dynamics of *I. pini* has been developed.

Recommendations: The most likely method for damage avoidance would appear to be chipping or otherwise removing, poisoning, or destroying slash from thinnings in commercial stands. Experiments might be conducted to determine whether beetle increase is proportional to quantities of slash or there are thresholds below which slash increase does not promote beetle population increases. The existence of such thresholds would indicate that natural enemies are able to suppress beetles in certain density ranges, but become saturated at higher host densities. Another approach might consist in manipulating pheromone blends used in bark beetle trapping programs, or the timing of trap deployment, to reduce catch of bark beetle natural enemies while maximizing catch of bark beetles (Raffa and Klepzig 1989, Raffa and Dahlsten 1995). Such a strategy might favorably influence the resulting natural enemy/pest ratio.

42. SPRUCE BUDWORM (*Choristoneura fumiferana* [Clemens]) (Lepidoptera: Tortricidae)

Notes: Former generic placements include *Harmologa*, *Cacoecia,* and *Archips*. Assignment to *Choristoneura* was by Freeman (1947). Several other North American budworm populations that are now are considered full species were formerly considered to be subspecies of the spruce budworm. As a consequence, older literature on these species (e.g., *Choristoneura pinus* and others) appears under the name of *fumiferana*, in various generic placements. Several bibliographies of studies of North American *Choristoneura* species have been compiled, with emphasis on spruce budworm (e.g., Jennings *et al.* 1979, Volney 1989, Hudak 1991).

Origin: Spruce budworm is native to North America (Miller 1984).

Range in North America: Spruce budworm is found throughout the spruce-fir forests of the eastern United States and Canada. Areas where important outbreaks of this species have been most frequent are New Brunswick, Nova Scotia, Newfoundland, Quebec, Ontario, Maine, and the Great Lake States region (Mattson *et al.* 1988).

Damage: Economic losses from spruce budworm are enormous during outbreaks. For example, the average annual loss of wood volume due to tree mortality and growth reduction in eastern Canada during the outbreak of 1978-1982 was 42.5 million cubic meters, which is equal to two thirds the total annual harvest of softwoods in Canada (Mattson *et al.* 1988). Peirson (1923) records that an outbreak in Maine destroyed 40% of the merchantable fir and spruce timber in Maine at that time. In the 20th century, there have been three major outbreaks, beginning approximately in 1915, 1933, and 1960 (Miller 1984). Blais (1965) discusses a 300-year record of spruce budworm outbreaks in a nature reserve (Laurentide Park) in Quebec. Damage occurs to balsam fir and various species of spruce. Mature balsam fir trees are killed after three to four years of severe defoliation. At the peak of the 1960-1980 outbreak, 19 million ha were defoliated (Miller 1984)

Resident Natural Enemies: This section gives a brief sketch of the natural enemies that exist in North America, and attempts to understand their contribution to the population dynamics of spruce budworm. In the next section on Biological Control Attempts, manipulative attempts to employ these agents in various ways to suppress spruce budworm populations are discussed.

Parasitoids. More than 90 species of parasitoids are known to attack spruce budworm in Canada (Clausen 1978). Most studies have been of outbreak or collapsing populations, but see Miller and Renault (1976).

In general, the most common parasitoids, by host life stages they attack are these (Mattson *et al.* 1988):

- egg parasitoid
  Trichogramma minutum Riley
- small-larvae parasitoids
  Apanteles fumiferanae Viereck
  Glypta fumiferanae (Viereck)
  Synetaeris tenuifemur Walley
- large-larvae parasitoids
  Meteorus trachynotus
  Actia interrupta
  Aplomya caesar
  Phryxe pecosensis
- pupal parasitoids
  Agria housei Shewell

The life histories and effects on spruce budworm populations of some of these parasitoids have been studied in detail, e.g., *Apanteles fumiferanae* (Brown 1946, Miller 1959), *Glypta fumiferanae* (Brown 1947, Miller 1960), *Meteorus trachynotus* (Thireau and Régnière 1995), and *Agria housei* (Coppel *et al.* 1959, given in this article as *Agria affinis*). Numerous studies have listed the composition of parasitoid complexes found in particular locations (e.g., Dowden *et al.* 1948, for a population in the Adirondack Mountains in New York; Miller and Renault 1976, for a population in New Brunswick).

Various methodologies have been developed to more accurately score the mortality caused by parasitoids and to estimate the importance of this mortality in the population dynamics of spruce budworm (e.g., Jaynes and Drooz 1952, Morris and Miller 1954, Miller 1955, Lewis 1960, Royama 1984).

Relatively few studies have assessed mortality factors affecting low density, endemic spruce budworm populations. In one such study, the most common parasitoid at low host density was *Synetaeris tenuifemur*, a species not common at high host densities (Miller and Renault 1976).

Predators. Birds are the group of predators believed to be of greatest importance attacking spruce budworm. Several studies have attempted to exclude birds from plots to observe the effects of the absence of birds on spruce budworm larval and pupal survival (Dowden *et al.* 1953, Crawford and Jennings 1989). A study of the closely related western spruce budworm, *Choristoneura occidentalis* Freeman, provides particularly clear evidence of the significance of predation from birds on budworm populations (Torgerson and Campbell 1982). Other groups of predators have received relatively little attention.

Pathogens. Some 15 species of pathogens in several groups have been recognized in natural spruce budworm populations (Mattson *et al.* 1988). Five viruses (one nuclear polyhedrosis virus, one granulosis virus, one cytoplasmic virus, one entomopoxvirus, and

one crichet paralysis virus) have been found infecting spruce budworm stages in nature, but natural epidemics of these agents do not occur (Cunningham and Howse 1984). Other pathogens observed in natural spruce budworm populations include the microsporidian *Nosema fumiferanae* and the fungal pathogens *Zoophthora radicans* (Brefeld) A. Bakto and *Entomphthora egressa* MacLeod (Wilson *et al.* 1984). However, no pathogen of any group causes much mortality in spruce budworm populations under natural conditions.

Hypotheses about causes of population fluctuations. A large data set from studies in New Brunswick ("the Green River Project") has served as the basis for much of the analysis of the population dynamics of spruce budworm populations in eastern Canada (Morris 1963, Royama 1984).

At least two hypotheses of spruce budworm population behavior have been formulated (Mattson *et al.* 1988). The **double equilibrium theory** postulates that populations may be stable for long periods at low densities, during which time they are regulated by natural enemies, and at other times populations may rise to high levels (following release events, perhaps favorable weather) which persist for a while before collapsing. Collapses are brought about by dramatic reduction in the food resource rather than by natural enemies in this theory. The alternative hypothesis, advanced by Royama (1984) is the **continuous oscillation theory**, which states that there is long-term population oscillation driven by parasitoids, disease, and an unknown mortality factor affecting large larvae. These factors drive the population in long cycles about which random fluctuations occur due to dispersal of fecund moths among sites.

Why spruce budworm populations reach high densities is debated. Conditions associated with outbreaks include the increasing area of forest occupied by mature stands of balsam fir (Tothill 1922, Mattson *et al.* 1988). Stands with spike-topped trees above the canopy, stands on wet or dry sites, areas downwind from current outbreaks, and areas below 700 m elevation and below latitude 50 °N have been recognized as being at increased risk of spruce budworm outbreaks (Mattson *et al.* 1988). According to the continuous oscillation theory, spruce budworm population fluctuations are caused by the time lags with which important sources of mortality from natural enemies and an important unknown factor affecting older larvae act. Under the double equilibrium theory, favorable events occasionally allow densities to rise to levels that saturate natural enemies, permitting budworm populations to escape the controlling action of their natural enemies.

Factors that might trigger population escape (as per the double equilibrium hypothesis) have been postulated to include the action of weather, in that several warm, dry years have sometimes preceded outbreaks (Greenbank 1957, Pilon and Blais 1961). The link between weather and different rates of spruce budworm survival might be in the area of weather's effect on the relative synchrony between budbreak and arrival of dispersing overwintered second instar larvae at tree branches. Mortality during dispersal has been shown to be one of the largest categories of mortality in spruce budworm populations (Mattson *et al.* 1988). If bud break is early, dispersing larvae can enter buds directly; alternatively (if bud break is neither early nor late), dispersing second instar larvae feed as miners in older needles and later third instar larvae enter and feed on the more nutritious foliage of newly opened buds. If bud break is late, when young third instar larvae emerge

from older needles (in which they fed as miners in their second instar) they must disperse to look for open buds, exposing themselves to increased mortality.

Biological Control Attempts: Efforts to employ biological control to suppress spruce budworm populations have been made in three areas: (1) importation of parasitoids, (2) development of inundative releases of the egg parasitoid *Trichogramma minutum*, and (3) use of pathogens as microbial insecticides.

Importation of parasitoids.

(1) Parasitoids imported from British Columbia. Studies of budworm populations in western North America led to the realization that a number of parasitoids were found in western North America that had not been recorded in the eastern part of the continent. Movement of these parasitoids from west to east was undertaken to see if they might improve control in the eastern region. From 1944 to 1953, two species of tachinids (*Ceromasia auricaudata* Towns. and *Phorocera incrassata* Smith), one sarcophagid (*Agria housei*, known earlier as *Pseudosarcophaga affinis*), and one ichneumonid (*Phytodietus fumiferanae* Rohw.) found parasitizing western spruce budworm (*C. occidentalis*) in British Columbia were collected and released into eastern Canada (Wilkes 1946). None established, however (Clausen 1978, Varty 1984).

(2) Parasitoids imported from Europe or Japan. Comparative studies between budworm populations in various parts of the world were undertaken to see if parasitoids might exist that would be of potential value if imported into North America (Franz 1952, Bucher 1953, Zwölfer 1961, Kamijo 1973, Mills and Kenis 1991). From 1948 to 1953, twelve species of ichneumonids from European species of conifer-feeding budworms (especially *Choristoneura muriana* [Hb.]) were imported from France, Germany, and the former Czechoslovakia and released in small numbers in Ontario and Quebec (see Clausen 1978 for a list of species). No establishments occurred (Varty 1984). In the 1960s, three species of ichnuemonids were imported from *C. muriana*, but again none established. In the late 1960s and early 1970s, parasitoids from Japanese budworms (especially, *C. diversana* [Hb]) were imported and released with few recoveries and no permanent establishments. Notes are given by Varty (1984) on four of the species of parasitoids involved in these releases, including *Cephaloglyta laricis* Momoi, *Cephaloglypta murinanae* Bauer, *Lissonata* sp. (all ichneumonids), and the sarcophagid *Agria housei*. More recently renewed attempts to established parasitoids of European budworms in North America have begun again with the release in 1990 of *Apanteles murinana*.

***Trichogramma minutum* as an agent of mass release**. A major effort has been made to develop mass releases of the egg parasitoid *Trichogramma minutum* Riley for control of spruce budworm populations (see Carrow 1990 for an overview of this effort). These efforts included attention to development and testing of an aerial release system (Hope *et al.* 1990) and evaluation of the resulting control (Smith *et al.* 1990). Small scale field efficacy trials showed that two parasitoid releases, one week apart, early in the pest oviposition period, increased the parasitism rate by 14-83%, reducing larval populations by 42-82%. Combinations of parasitoid releases with applications of *Bacillus thuringiensis* also were tested and found to provide good control (Smith *et al.* 1990). Operational implementation of this system has not yet occurred.

Application of pathogens as microbial insecticides.
(1) ***Bacillus thuringiensis***. A long concerted effort has been made to develop the application of *Bacillus thuringiensis* preparations for protection of conifer forests from defoliation by spruce budworm. Much of this work has been conducted by researchers in eastern Canada and is reviewed by Smirnoff and Morris (1984). Many technical issues affect the degree of pest mortality and foliage protection achieved, including the strain tested, the formulation and various additives employed to enhance deposition or coverage, and the mechanical and operational systems used to make or guide applications. Conditions associated with successful control were these: (1) budworm larval densities of fewer than 28 larvae per 45-cm branch tip before application, (2) applications timed to coincide with occurrence of the fourth larval instar, (3) applications made when bud flushing was 80-100% complete (except on red spruce), (4) application rates of 20-40 billion I.U. per ha in one or two applications, (5) depositions of more than 25 droplets per cm^2, (6) applications made when relative humidity was higher than 65%, and (7) good weather immediately after application (Smirnoff and Morris 1984).

Using these approaches, *Bacillus thuringiensis* applications were finally considered in 1984 to be a viable alternative to chemical pesticide applications in terms of efficacy, but to be two to three times more expensive. Further efforts to improve the use of this material and thus reduce costs were recommended. Valéro (1989) reports that three commercial formulations of *B. thuringiensis* subsp. *kurstaki* in Quebec, applied at 22-25 billion I.U. per ha against spruce budworm larval populations with densities of 0.06-0.16 larvae per bud, caused 90-100% mortality of larvae and reduced defoliation levels from 59-83% in the controls to 2-16% in the treated areas. New strains (e.g., "Biodart") continue to be developed and tested (Bernier *et al.* 1990). Studies have also been conducted on the integration of *Bacillus thuringiensis* applications with naturally occurring parasitoids (Nealis *et al.* 1992).

(2) ***Viruses***. Efforts have also been made to develop several of the five viruses found infecting spruce budworm larvae for use as microbial insecticides. These have been reviewed in detail by Cunningham and Howse (1984). Various field trials have been conducted since 1971. Early efforts with nuclear polyhedrosis viruses were more promising than those with entomopoxviruses and so work has been concentrated on these viruses. Applications of virus were found not to initiate spreading epidemics. Control of larvae in areas treated in various trials has been highly variable and, as of 1984, viruses were not considered a practical solution for spruce budworm control. More recent trials of spruce budworm viruses as microbial insecticides have also been ineffective (e.g., Kaupp *et al.* 1989).

(3) ***Microsporidia and fungi.*** As with viruses, interest exists in developing microsporidia and fungi as microbial pesticides for control of spruce budworm larvae. Microsporidia are debilitating agents that reduce fertility, but cause relatively low levels of mortality (Bauer and Nordin 1989). Fungi have potential to cause epidemics and directly kill affected individuals, but are sensitive to environmental conditions. A few field trials of microsporidia have been conducted against spruce budworm. These trials showed that it is possible to increase infection rates in field budworm populations via applications of laboratory reared microsporidia (Wilson *et al.* 1984). However, microsporidia applications are not yet an effective control method.

Reasons for Pest Status and Possibilities for Biological Control: The root causes for the periodic eruption of spruce budworm in North America, where it is a native insect, are not fully understood. One view (double equilibrium hypothesis) holds that eruptions are associated with extensive stands of nature conifer forest and periodic favorable weather patterns which result in higher population growth rates to which natural enemies are unable to respond with sufficient speed to check incipient outbreaks.

Approaches that have been considered as methods to enhance biological control include introduction of better parasitoids from related hosts, mass release of egg parasitoids, and application of microbial insecticides. Potentially each of these approaches might play an important role. To date, success has been most nearly achieved with the development of *Bacillus thuringiensis* as a microbial insecticide.

Problems exist with each approach. Introduction of new parasitoids from related budworm species is attractive in that it offers the prospect of a permanent control without the need for repeated intervention. In practice, it is uncertain whether a parasitoid species exists with the necessary properties. No clear way to chose appropriate species exists, but comparisons between parasitoid complexes (as in Mills and Kenis 1991) have identified some possibilities.

Mass release of egg parasitoids appears to be biologically feasible, but is strongly affected by economic issues. Also, since *Trichogramma* spp. are relatively polyphagous, mass releases over the large areas that would need to be treated to protect forests against budworm outbreaks might pose risks to nontarget species of native Lepidoptera (Andow *et al.* 1995).

Microbial pesticide development appears feasible for *Bacillus thuringiensis*, but unlikely for other pathogens, which are less effective under field conditions.

Recommendations: The control method of greatest importance is the use of *Bacillus thuringiensis* as a microbial pesticide. Improving the consistency of *B.t.* applications is the most important area for future spruce budworm control studies in Canada.

Governments will need to provide economic incentives or legal restriction to promote the use of *B. thuringiensis.* While new importations of exotic parasitoids have been advocated, careful attention will be needed to assess likely host ranges (relative to safety to nontarget Lepidoptera of interest) of the candidate species with the highest potential to be effective.

43. JACK PINE BUDWORM (*Choristoneura pinus pinus* Freeman) (Lepidoptera: Tortricidae)

Notes: Recognition of jack pine budworm as distinct from the spruce budworm as (*Choristoneura fumiferana*) was suggested by Brown and McKay (1943) who thought the form feeding on jack pine in the Great Lakes region must be at least a distinct subspecies. Freeman (1953) later described this population as a separate species. Species within the genus *Choristoneura* may be separated based on male genitalia using a key provided by Dang (1985). Literature on this species before 1953 refers to it as *Choristoneura fumiferana,* and it may be recognized as *C. pinus pinus* by its range and host plant.

Origin: Jack pine budworm is native to North America.

Range in North America: This species occurs in Canada in Nova Scotia, New Brunswick, Quebec Ontario, Manitoba and Saskatchewan. In the United States it occurs in the Great Lake States and parts of New England (Drooz 1985).

Damage: At irregular intervals, this species reaches densities that defoliate jack pine stands. Older trees are rarely killed outright, but tops of trees may die and suppressed trees may be killed (Drooz 1985). Temporary decreases in growth, however, can be large, with estimates of 56-75% reduction in the year after a severe defoliation (Gross 1992).

Resident Natural Enemies: Following the recognition of jack pine budworm as a separate species, considerable attention was devoted to understanding the natural control factors affecting the species in a search for fundamental reasons for its periodic outbreaks. Natural enemies attacking the various sub-adult life stages were documented in a series of studies in the Great Lakes region:

State or Province	# of Parasitoid Species	Study
Ontario, Manitoba	13	Walley 1953
Michigan	15	Benjamin and Drooz 1954
Michigan (Upper Peninsula)	14	Drooz and Benjamin 1956
Michigan	26	Allen *et al.* 1969
Minnesota	29	Kulman and Hodson 1961
Wisconsin	46	Dixon and Benjamin 1963

The species often accounting for the largest portion of the mortality in samples were the larval parasitoids *Apanteles fumiferanae* Viereck (Braconidae) and *Glypta fumiferanae* (Viereck) (Ichneumonidae), and the pupal parasitoid *Itoplectis conquisitor* (Say) (Ichneumonidae) (Allen *et al.* 1969). Zwölfer (1963) in studies of other *Choristoneura* spp. also found parasitoid complexes with many species, of which only two or three species could be considered specialists. He thought that large parasitoid complexes diminished the suppressing effect of these specialists. Nealis (1991) compared parasitoid complexes between sustained and collapsing populations in Ontario. As in earlier studies, just a few species dominated the parasitoid complexes and one of the few differences between parasitism of sustained and collapsing populations was the relatively high levels of parasitism by the braconid *Meteorus trachynotus* Viereck and the tachinid *Lypha setifacies* (West.) in collapsing populations.

Only a few studies have considered the role of predators in the population dynamics of jack pine budworm. Allen *et al.* (1970) recorded invertebrate species, especially spiders, found in association with an outbreak population of jack pine budworm in Michigan. They concluded that while these predators' effects seemed limited, the species of greatest potential importance was the pentatomid bug *Podisus serieventris* Uhler. Jennings (1971) found six species of ants in Minnesota preying on jack pine budworm larvae which had fallen to the soil.

Pathogens of jack pine budworm include a microsporidian, *Nosema fumiferanae* (Thompson 1959) and the same nuclear polyhedrosis virus that attacks spruce budworm (*Choristoneura fumiferana*) (Stairs 1960).

Biological Control Attempts: While many studies have noted which natural enemies are associated with jack pine budworm populations (see list of studies in previous section), or have used population dynamics analysis methods to discover their importance (see section entitled Reasons for Pest Status and Possibilities for Biological Control below for a discussion of these studies), few attempts have been made to use biological control methods to increase control over that provided by nature. The introduction of new parasitoids from other *Choristoneura* species from Europe or Japan to control *Choristoneura* species in North America has been suggested (Mills and Kenis 1991). This work has focused on spruce budworm as the target pest, but applies as well to jack pine budworm, as both species share many parasitoids in North America. Field releases of one species, the braconid *Apanteles murinanae* (Capek and Zwölfer), which was collected in Europe from *Choristorneura murinana* Hübner, began in Ontario in 1990 (Mills and Kenis 1991). Translocations of parasitoids from western spruce budworm (*Choristoneura occidentalis*) to spruce budworm in eastern Canada have been made, but had no noticeable effect (Clausen 1978).

Another approach to biological control has focused on discovering methods to integrate the use of pesticides with existing parasitoids (see below for discussion).

Reasons for Pest Status and Possibilities for Biological Control: Graham (1935) was one of the first authors to discuss factors promoting outbreaks of jack pine budworm. Stands with trees producing male flowers appeared to be favorable to jack pine budworm outbreaks, presumably by providing high quality feeding sites for the second instar larvae dispersing onto trees from overwintering sites in the spring. Since suppressed or open-grown trees produce more male flowers, Graham (1935) recommended their removal as a form of control. Hodson and Zehngraff (1946) also emphasized the apparent connection between abundant male flowers and outbreaks of jack pine budworms. They thought that the mechanism by which abundant male flowers promoted outbreaks was by enhancing survival of larvae by providing an excellent diet for the larvae. Nealis (1990), however, found that larvae, once established on tips, did not enjoy higher survival on tips with male flowers than on tips without pollen cones, suggesting that given a chance to eat either newly emerged foliage or flower cones, larvae survived well on either food. However, Nealis (1990) also observed that more larvae successfully established on trees with abundant male flowers and that losses due to dispersal were lower.

Earlier work by Foltz *et al.* (1972) and Batzer and Jennings (1980) identified losses between egg hatch (in the fall) and establishment of second instar larvae (the following spring) as being large and variable between years and thus contributing most to variation in population size between years. Incorporated into this period are two cycles of dispersal, one in the fall by first instar larvae which move from egg masses on foliage to overwintering sites on trunks, and one in the spring when second instar larvae return to branch tips to initiate feeding. Life tables by Batzer and Jennings (1980) suggest that losses in the first dispersal are small (5%) compared with losses in the spring dispersal period (90%).

Batzer and Jennings (1980) used a very powerful technique for experimental analysis of populations (paired life tables), constructing life tables for stands with both high and low stocking rates (trees per hectare). Competition between trees in densely stocked stands was greater and led to more abundant production of male flowers on trees. Life tables for budworms in stands with high stocking rates showed that losses during spring dispersal were lower than in stands with lower stocking rates, which had fewer trees with abundant male flowers. Differential survival during spring dispersal thus appears to be the mechanism by which male flower cone densities affect jack pine budworm populations. The importance of male flowers in reducing losses of second instar larvae during spring dispersal was further confirmed by direct measurement by Nealis and Lomic (1994) who found dispersal losses to be negatively related to male flower density.

The role of male flower cones is to provide a favorable site at which dispersing larvae can establish and begin feeding (later, these larvae also feed on foliage). The flower cones are critical to jack pine budworm survival because in many years the number of foliage buds that have opened (and thus become available as feeding sites) by the date dispersing larvae arrive on the tips may be too small to accommodate all dispersing larvae arriving on branches. Male flower cones are particularly important in years in which dispersing larvae arrive early relative to foliage bud break. In such years, flower cones, which typically are acceptable before foliage buds, are a limiting, early-season resource determining the number of larvae likely to survive. Factors that lead to abundant production of male flower cones will, therefore, tend to favor increase in jack pine budworm population densities. Male flower production is most abundant on suppressed or open-grown trees. Thinning of overstocked stands and removal of open-grown trees to achieve an optimal stand density are thus measures that can be taken to prevent development of outbreaks.

Nealis and Lomic (1994) also proposed that the abundance of male flower cones plays a role in ending outbreaks because few male flower cones are produced in stands following a year of defoliation. This lack of male flower cones then causes a sharp increase in larval mortality during the spring dispersal period in the next year. This reduction in larval numbers also causes the relative level of mortality from parasitism to increase sharply in the year after defoliation. This occurs because the reduced number of jack pine budworm larvae increases the parasitoid/host ratio. Indeed, relatively high levels of parasitism have been observed, particularly of pupae, during the decline of jack pine budworm outbreaks (Dixon and Benjamin 1963, Benjamin 1964, Allen *et al.* 1969, Batzer and Jennings 1980, Nealis 1991).

Perspective on the relative importance of the various sources of mortality affecting jack pine budworm populations is given by life tables from the studies of Allen *et al.* (1969), Fotz *et al.* (1972), and Batzer and Jennings (1980).

Weather patterns have also been explored as a potential cause of jack pine budworm outbreaks (Clancy *et al.* 1980), using models that consider a variety of temperature and precipitation variables. Models used were able to explain 64-70% of the variation in density of some jack pine budworm life stages. A model by Nyrop *et al.* (1983) organizes information into an economic model for foresters which helps maximize profits from jack pine stands.

Recommendations: Three categories of action can be undertaken to suppress jack pine budworm populations and enhance their natural enemies: (a) silviculture methods to made

stands less favorable to outbreaks, (b) methods to reduce harm to parasitoids from use of other controls such as chemical pesticides, and (c) introductions of new species of parasitoids.

Silviculture options for suppression of jack pine budworm outbreaks consist primarily of thinning and other methods to reduce the number of suppressed or open-grown trees in stands, both of which produce large numbers of male flower cones.

Conservation methods to preserve parasitoids from the harmful effects of pesticides are based on timing, choice of *Bacillus thuringiensis* pesticides, and identification of areas with high levels of parasitism. Pesticide applications made to third or fourth instar larvae do not affect adult parasitoids of species such as *Apanteles fumiferanae* or *Glypta fumiferanae* because their adult stages are not present at that time of the year (Blais 1977). Mortality of immature parasitoids can be reduced by taking advantage of the fact that *Apanteles fumiferanae* larvae in budworms complete development and form cocoons before healthy budworm larvae pupate. Day degree models of Lysyk and Nealis (1988) can be used to time pesticide applications for this purpose. A sampling plan developed by Nealis and Lysyk (1988) can be used earlier in the season to measure both the density of overwintering second instar jack pine budworm larvae and the proportion that are parasitized. This information can be useful in suggesting whether pesticide treatment is likely to be needed, and if needed, whether or not application timing should be adjusted to conserve parasitoids. Similar integration of *Bacillus thuringiensis* sprays (reasonably effective for jack pine budworm control, see Cadogan *et al.* 1986 and Cadogan 1993 for results of field trials) with parasitoids is possible, particularly if applications are timed to coincide with older (fourth instar) larvae (Nealis and van Frankenhuyzen 1990, Nealis *et al.* 1992).

Importations of new species of parasitoids for jack pine budworm are not presently being undertaken directly, but species being introduced for suppression of spruce budworm are likely also to affect jack pine budworm (Mills and Kenis 1991) and should be evaluated for their effects on this species.

44. LARGE ASPEN TORTRIX (*Choristoneura conflictana* [Walker]) (Lepidoptera: Tortricidae)

Notes: Before placement in *Choristoneura* by Prentice (1955), large aspen tortrix had been placed in various other genera, including *Tortrix*, *Heterognomon*, *Cacoecia*, and *Archips*.

Origin: Large aspen tortrix is native to North America.

Range in North America: The large aspen tortrix occurs throughout most of the range of its preferred host, quaking aspen (*Populus tremuloides* Michx.), in Canada and the United States (Drooz 1985).

Damage: In some years, densities of this species increase to levels that cause defoliation of aspen. Such defoliation may occur over wide geographic areas. Prentice (1955) records the history of such outbreaks in Canada. Outbreaks have also occurred in various parts of the United States, including California (Wickman 1963) and Alaska (Beckwith 1968), as well as in the northeastern United States and the Great Lakes region.

Resident Natural Enemies: Prentice (1955) lists 21 species of parasitoids reared from large aspen tortrix in Canada. Of these, the more common larval parasitoids were *Glypta fumiferanae* (Viereck), *Apanteles* sp., *Macrocentrus iridescens* French, *Microgaster canadensis* Muesbeck, *Zenillia* (*Eumea*) *caesar* Ald., *Winthemia* (*Omotoma*) *fumiferana* Tothill, and *Actia interrupta* Curr. Important pupal parasitoids included *Itoplectis conquisitor* Say and *Agria* (*Pseudosarcophaga*) *affinis* Fallén. (Note, the identity of this last species is probably *Agria housei* Shewell, see Shewell 1971). In California, the parasitoid of greatest importance was recorded as *Gypta* sp. nr. *fumiferanae* (Wickman 1963). Torgersen and Beckwith (1974) record 24 species of parasitoids from the large aspen tortrix in Alaska, providing a key for their separation and notes on their appearance and habits. In Alberta, the most important larval parasitoids are given as *Macrocentrus iridescens* French, *Glypta inversa* Cresson, and *Agathis annulipes* (Cresson), with larval parasitism rates up to 50% (Wong 1979).

Pathogens recorded from the large aspen tortrix include the microsporidian *Nosema thomsoni* Wilson and Burke (Wilson and Burke 1971) and an entomopoxvirus (Cunningham *et al.* 1973), both in Ontario. Other pathogens are recorded by Burke and Percy (1982). *Bacillus thuringiensis* applications have been found to control large aspen tortrix under field conditions in Alaska (Holsten and Hard 1985).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Relatively little work on the population dynamics of this species has been done. However, its biology is similar to that of both spruce budworm and jack pine budworm, with which it is congeneric. Comparisons of studies on these species to studies on *C. conflictana* suggest possible reasons for outbreaks. For example, aspen clones with the earliest bud break had up to six times as many established second instar larvae on them as clones breaking bud about ten days later (Witter and Waisanen 1978). It is possible that synchrony between bud break and bud colonization by dispersing, overwintered second instar larvae of this species may be critical. Year-to-year variation in such synchrony may cause average survival rates of young larvae to vary strongly between years. Such a process seems important in determining outbreaks of jack pine budworm, and may also be involved with the large aspen tortrix.

Recommendations: Investigation into the fundamental reasons for variation in the species' numbers, particularly the bud break and larval dispersal synchrony hypothesis outlined above, would be valuable. Should this hypothesis be correct, then the role of biological control agents may be limited to a reactive one, as in jack pine budworm. In such a case, the existence of ways to employ biological control agents to suppress outbreaks would be unlikely.

45. FALL CANKERWORM (*Alsophila pometaria* [Harris]) (Lepidoptera: Geometridae)

Origin: Fall cankerworm is native to North America.

Range in North America: Fall cankerworm occurs across southern Canada from the Maritimes to Alberta, and throughout the eastern United States from New England to Georgia and west to Missouri and Montana (Drooz 1985).

Damage: Periodically, high density populations of fall cankerworm arise and defoliate various species of hardwood trees (elm, apple, hickory, maple, ash, and others). While frequent and sometimes severe, these outbreaks are local and brief (Fedde *et al.* 1973).

Resident Natural Enemies: Relatively few parasitoids have been noted attacking the various life stages of fall cankerworm. Among these are the braconid *Meteorus autographae* (Muesebeck 1923) and the scelionid egg parasitoid *Telenomus alsophilae* Viereck (Viereck 1924). Parasitism by *T. alsophilae* is recorded by various authors (Rauschenberger and Talerico 1967, Fedde *et al.* 1973), and this parasitoid is reputed to be the most important species attacking fall cankerworm. Parasitism levels are reported in the 15-20% range by some authors (Rauschenberger and Talerico 1967). This egg parasitoid appears to have a broad host range, attacking twelve species of geometrids and two noctuids under laboratory conditions (Fedde 1977). *Telenomus alsophilae* was exported from North America to Colombia, where it is credited with suppressing outbreaks of a native conifer-feeding geometrid, *Oxydia trychiata*, in plantations of exotic conifer species (Bustillo and Drooz 1977). A method to estimate parasitism based on emergence holes and other features such as parasitoid meconia has been developed (Fedde 1979).

Other natural enemies known to affect fall cankerworm populations include the nuclear polyhedrosis virus from *Autographica californica* (Kaya 1977) and some strains of *Bacillus thuringiensis* (Harper 1974), both of which might be used augmentatively as biopesticides.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: The basic causes of outbreaks of fall cankerworm appear not to have been investigated. Fall cankerworm is a polyphagous species specialized to feed on young foliage (Futuyma and Wasserman 1980). As such, it is synchronized to hatch near the period of bud break of one or several possible hosts, such as scarlet oak (*Quercus coccinea*) (Futuyma and Wasserman 1980). Life tables for the species were not found, but poor synchrony with major hosts is likely to be an important factor determining survival. In years of poor synchrony mortality is likely to increase, due to a need to await bud break of the preferred host, to disperse to alternate host species, or to feed on older, less suitable foliage of species breaking bud substantially earlier.

Recommendations: Construction of life tables for populations over a series of years, to measure losses from both dispersal and parasitism in years of varying synchrony, might be helpful in developing a more basic understanding of the dynamics of outbreaks of this species. If variation in synchrony is fundamental to fluctuation in population densities, there may be little opportunity to enhance the controlling effects of natural biological control by existing natural enemies. Further studies of natural enemies of larval and pupal stages might also be valuable, as little information is available.

46. BRUCE SPANWORM (*Operophtera bruceata* [Hulst.] (Lepidoptera: Geometridae)

Origin: Bruce Spanworm is native to North America (Troubridge and Fitzpatrick 1993).

Range in North America: The bruce spanworm is found coast to coast in Canada and in the United States from New England to the Great Lake States (Drooz 1985). It also is found in Greenland (Koponen 1978).

Damage: This species periodically reaches densities sufficient to defoliate stands of various hardwood species, including sugar maple, beech, quaking aspen, and willow (Drooz 1985). An outbreak in eastern Quebec in the 1960s defoliated sugar maple and beech over a 15,000 square mile area (Martineau and Monnier 1966).

Resident Natural Enemies: Various parasitoids have been recorded attacking pupae or other stages of bruce spanworm, although these have not been studied in any detail. Brown (1962) noted the following parasitoids attacking bruce spanworm: *Apanteles* sp., *Campoletis* sp., *Cratichneumon* sp., *Eulophus* sp., *Horogenes oculus* (Viereck), *Triclistus crassus* (Tow. and Tow.). Marineau and Monnier (1966) reported egg parasitism by a *Telenomus* sp. and larval parasitism by a *Nythobia* (=*Horogenes*) sp. Bruce spanworm is also attacked by *Cyzenis albicans* Fallén, an ichneumonid introduced into Canada against the closely related species, the winter moth, *Operophtera brumata* (Linnaeus) (Embree 1966). Separation of immature stages of these two species is discussed by Eidt and Embree (1968), and of the adults by Troubridge and Fitzpatrick (1993).

A nuclear polyhedrosis virus attacks larvae of this species (Smirnoff 1964), and virus infection rates of up to 95% were associated with collapsing populations of bruce spanworm in Quebec (Martineau and Monnier 1966).

Predation by birds has also been noted in outbreak populations (Martineau and Monnier 1966).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities Biological Control: The reasons for outbreaks of this species have not been investigated. Because it is a native species, separation from controlling natural enemies is not a likely cause.

Recommendations: Because this species is closely related to winter moth, it would be of interest to examine bruce spanworm populations to see if parasitoids and predators affecting the pupal stage are similar to those that have been demonstrated to control winter moth populations, both in terms of the species of natural enemies involved and the levels of mortality they cause.

The nuclear polyhedrosis virus of the species might be developed for augmentative use. Costs for efficacy trials, registration, and production of a viral insecticide would likely have to be borne publicly, as there would be no commercial market for a virus specific to this pest.

Alternatively, broad spectrum viruses currently under development for other pests, could be tested for use against this species as well.

47. SPRING CANKERWORM (*Paleacrita vernata* [Peck]) (Lepidoptera: Geometridae)

Notes: *Anisopteryx sericeiferata* Walker is a synonym; previous generic placements, using *vernata*, include *Phalaena* and *Geometra* (Porter and Alden 1924) .

Origin: Spring cankerworm is native to North America.

Range in North America: This species is found throughout the northeast and northcentral United States, and parts of California. See Porter and Alden (1924) for a distribution map.

Damage: This species periodically reaches high densities and defoliates various species of deciduous trees, with apple and elm being of special importance (Stein 1974, Drooz 1985).

Resident Natural Enemies: Krombein *et al.* (1979) list five species of parasitoids as attacking spring cankerworm. These include three braconids, *Rogas geometrae* Ashmead, *Apanteles paleacritae* Riley, and *Meteorus hyphantriae* Riley, and two ichneumonids, *Phobocampe geometrae* (Ashmead) and *Hyposoter fuscitarsis* (Viereck). *Bacillus thuringiensis* has been considered as a microbial insecticide for suppression of this species (Harper 1974).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: This species is of concern because it periodically experiences high populations that defoliate valuable trees. No studies have addressed the reasons behind such outbreaks.

Recommendations: Insufficient information was found on this species to determine either its current status or the reasons why outbreaks occur. No action is recommended until such time that outbreaks become widespread and damaging. Should this occur, long term study plots should be established to determine what factors cause outbreaks and determine if these are subject to manipulation.

48. EASTERN HEMLOCK LOOPER (*Lambdina fiscellaria fiscellaria* Guenée) (Lepidoptera: Geometridae)

Notes: An earlier generic placement for eastern hemlock looper was in *Ellopia*. Closely related loopers include the western hemlock looper, *Lambdina fiscellaria lugubrosa* (Hulst) and the western oak looper *Lambdina fiscellaria somniaria* (Hulst) in western North America (Cunningham 1970). In eastern North America, closely related loopers are the eastern pine looper, *Lambdina pellucidaria* (Grote and Robinson) and *Lambdina fervidaria athasaria* (Walker) (Drooz 1985).

Origin: Eastern hemlock looper is a native species to North America.

Range in North America: The eastern hemlock looper is found from Newfoundland to Alberta, and throughout the eastern United States as far south as Georgia (Drooz 1985).

Damage: In the northern part of its range (Canada), eastern hemlock looper attacks older stands of eastern hemlock (*Tsuga canadensis*) or mature stands of balsam fir (*Abies balsamae*) — either pure stands or ones mixed with white spruce (*Picea glauca*). In more southern areas (United States), it is mostly associated with hemlock (Schedl 1931, Drooz 1985). Damage results from periodic high density populations that defoliate stands, killing trees. Outbreaks in Michigan and Wisconsin from 1921-1925 killed extensive areas of hemlock (Graham 1943). Outbreaks have occurred periodically in Newfoundland (Carroll 1956, Otvos *et al.* 1973, Otvos *et al.* 1979) and Quebec (Benoit and Desaulniers 1972). Six outbreaks were recorded in each of these areas between 1912 and 1979.

Resident Natural Enemies: A review of the natural enemies recorded from eastern hemlock looper in Newfoundland and Ontario, and from western hemlock looper in British Columbia and Alberta, is given by Mills and Räther (1990). Reports of parasitoids or pathogens associated with outbreaks are available from Ontario (Schedl 1931, 11 species of parasitoids), Quebec (Smirnoff and Jobin 1973, 12 species of parasitoids), and Newfoundland (Carroll 1956, 13 species of parasitoids; Otvos *et al.* 1973, two species of fungal pathogens).

Of the various parasitoids recorded attacking this host before 1950, the most commonly reared larval parasitoid was *Apanteles* sp. nr. *flavovariatus* Muesbeck (Mills and Räther 1990). This changed after the tachinid *Winthemia occidentis* Reinhard, an important parasitoid of the western hemlock looper (Hopping 1934), was transferred from British Columbia to eastern Canada in the 1949-1951 period, and recovered in 1969 (Otvos 1973). The pupal parasitoids of eastern hemlock looper are mostly polyphagous, except for *Aoplus velox* (Cresson), which sometimes parasitizes up to 32% of the pupae (Mills and Räther 1990).

Pathogens of eastern hemlock looper include a nuclear polyhedrosis virus (Cunningham 1970), two species of *Entomophthora* (Otvos *et al.* 1973), *Entomophaga aulicae* (Murrin and Nolan 1989), and (as an augmentative agent) *Bacillus thuringiensis* (Raske *et al.* 1986, West *et al.* 1989). In their review, Mills and Räther (1990) also list the fungal pathogens, *Zoophthora radicans* and *Erynia rhizospora*.

Predators appear to be of little recorded importance, although bird consumption of larvae has been noted.

Biological Control Attempts: Because this insect is a native species, related species from other locations have been considered as possible sources of parasitoids for introduction. To date, only one species seems to have been moved in this manner, the tachinid *Winthemia occidentis*, which was collected from western hemlock looper in British Columbia and released in eastern Canada (Otvos 1973). This species has established (Otvos 1973) and is now said to be the dominant larval parasitoid (Mills and Räther 1990).

In addition, the parasitoid complexes of related geometrid moths in Europe (five species of Ennominae and three of Larentiinae) have been studied with the proposition of identifying candidates for further importations (Mills and Räther 1990). These authors, however, conclude that while such importations merit consideration, too little information is currently available on these parasitoids to evaluate their potential.

For broader perspective on the task, it can be noted that parasitoid importations have been used successfully to provide biological control of two other forest defoliators in the family Geometridae: winter moth (*Operophtera brumata*), an exotic pest in North America, and *Oxydia trychiata*, a native pest of exotic pine plantations in Colombia. The first was controlled by importations from Europe of some of winter moth's coevolved parasitoids. The second was controlled by the scelionid *Telenomus alsophilae* from Virginia, previously not associated with the target pest in Colombia.

Reasons for Pest Status and Possibilities for Biological Control: Basic reasons for outbreaks of eastern hemlock looper are uncertain. Factors associated with the collapse of high density populations have included starvation (after defoliation), disease, and parasitism (Carroll 1956). Sites with an abundance of mature or overmature balsam fir, or pure stands of old (80 years or more) hemlock were associated with greater risk of outbreaks (Carroll 1956). Outbreaks are reported to be very localized geographically. Otvos (1977) analyzed the history of outbreaks in Newfoundland and concluded that outbreaks were preceded by two or more years that were warmer and dryer than average, and that outbreaks ended in cool wet years. These conclusions have not been confirmed by other analyses elsewhere. In their review, Mills and Räther (1990) do not comment on reasons behind outbreaks.

Recommendations: Before importing new species of parasitoids against eastern hemlock looper, studies should be conducted to better clarify the current situation. Specifically, basic population dynamics studies are needed, based on life tables to try to identify causes of transitions from low density to high density populations. These studies should examine populations both at sites where outbreaks have occurred in the past and sites where the pest occurs but outbreaks have not been recorded. Population studies should be conducted for a series of years, starting at low population levels and following the same populations until outbreaks occur.

This approach will be useful in formulating hypotheses about events that trigger outbreaks, which is the key process about which information is needed. Studies of the factors that cause outbreak populations to decline should be reduced. Long term, comparative studies will better reveal the composition of the current parasitoid complex and how it varies with host density. Structuring studies in this way will be more productive than conducting reactive studies after outbreaks are in progress.

49. FOREST TENT CATERPILLAR (*Malacosoma disstria* Hübner) (Lepidoptera: Lasiocampidae)

Notes: Stehr and Cook (1968) provide a revision of the species of *Malacosoma* in North America.

Origin: Forest tent caterpillar is native to North America.

Range in North America: Forest tent caterpillar is found throughout most of the United States and Canada (Drooz 1985).

Damage: In some years, this species reaches densities that cause widespread defoliation of aspen or other species. For example, ten such outbreaks occurred in Ontario between 1867

and 1960 (Sippell 1962). These outbreaks have occurred at intervals of 6-16 years and have lasted from 3-6 years before collapsing (Witter *et al.* 1972). In addition to damaging northern aspen stands (e.g., Witter 1979), forest tent caterpillar defoliates stands of deciduous tree species in southern river bottom swamps (e.g., Harper and Hyland 1981).

Defoliation during outbreaks causes a variety of harmful effects on trees. For example, Duncan and Hodson (1958) report a reduction of 58% in basal growth of defoliated aspen trees in Minnesota when losses were averaged over the several years of outbreak and pest population collapse. Growth reduction in individual years reached 90%. Kulman (1971) reviews studies on growth losses after defoliation by forest tent caterpillar, distinguishing different degrees and yearly patterns of defoliation and effects on different tree species.

Resident Natural Enemies: In the course of outbreaks of this species, natural enemies of the various life stages have been studied in many locations. Witter and Kulman (1972) review the parasitoids and predators of *Malacosoma* spp. in North America.

The eggs of forest tent caterpillar are laid in groups, and egg mass architecture protects many eggs from exposure to parasitism. Consequently, parasitism of eggs is generally low (e.g., 2-8%, Hodson 1939a, Witter and Kulman 1972, Frye and Ramse 1975, Witter and Kulman 1979), even though most egg masses (39-73%, Hodson 1939a) may have at least some eggs that are parasitized. Egg parasitism of forest tent caterpillar in Louisiana appears to be higher (15-34%) than in northern areas (Smith and Goyer 1985). Commonly encountered egg parasitoids include *Ooencrytus clisiocampae* Ashmead, *Tetrastichus silvaticus* Gahan, and *Telenomus clisiocampae* Ashmead (Hodson 1939a, Witter and Kulman 1972). Egg parasitism of a Holoarctic species, *Malacosoma neustria* (L.), is reported to be higher than the above figures for forest tent caterpillar in North America, reaching 80-90% of the eggs in some locations in Ukraine (Romanova and Lozinskii 1958). In this study, the dominant parasitoid was the scelionid *Telenomus laeviusculus* (Ratz.).

Literature records of parasitoids of larvae and pupae of forest tent caterpillar are reviewed by Witter and Kulman (1972). Sippell (1957) lists 45 species recorded from the literature as parasitoids of forest tent caterpillar, 34 of which were reared from this host in Ontario. A list of parasitoids from a study in Minnesota is given by Witter and Kulman (1979) and for North Dakota by Frye and Ramse (1975). Parasitoids attacking forest tent caterpillar in southern swamp forests are listed by Stark and Harper (1982). Eggen (1987) compares the New York parasitoid complexes of forest tent caterpillar and gypsy moth.

Larval parasitism of forest tent caterpillar is most often lower than pupal parasitism. Life tables for forest tent caterpillar in Minnesota showed larval parasitism rates to be only 2-10%, in contrast to pupal parasitism rates of 50-74% (Witter *et al.* 1972). The braconid wasp *Rogas* sp. is the only important parasitoid of young larvae (Witter *et al.* 1972, Witter and Kulman 1979). Older larvae are attacked by tachinids and ichneumonids, the most important of which in North Dakota was the ichneumonid *Theronia atalantae fulvescens* (Cresson) (Frye and Ramse 1975); and in Minnesota were the three tachinids *Patelloa pachypyga* (Aldrich and Webber), *Leschenaultia exul* (Townsend), and *Lespesia frenchii* (Williston), and the ichneumonid *Trichonotus analis* (Say) (Witter and Kulman 1979). Levels of parasitism of larvae reported by Frye and Ramse (1975) in North Dakota were higher (33%) than in studies in Minnesota.

Parasitism of pupae is overwhelmingly due to the sarcophagid *Sarcophaga aldrichi* Parker. The level of parasitism by this fly is high and increases from year to year during forest tent caterpillar outbreaks. Hodson (1939b) recorded levels of parasitism by this fly of 30-80%, 60-100%, and 90-100% for the three years of the 1936-1938 outbreak in Minnesota. Witter and Kulman (1972) recorded levels of parasitism by this species of 24, 36, 48, 75, and 78% across the 1950-1955 outbreak in Minnesota. Life tables by Witter *et al.* (1972) list pupal parasitism levels of 50-74% and attribute this parasitism mostly to *S. aldrichi.* This tachinid is also recorded as the dominant parasitoid attacking forest tent caterpillar pupae in the 1964-1972 outbreak in Minnesota (Witter and Kulman 1979). The only situation in which this sarcophagid does not dominate the pupal parasitoid guild of forest tent caterpillar is in southern swamp forests, where *Sarcophaga houghi* Aldrich and the tachinid *Hyphantrophaga euchaetiae* (Sellers) are listed as important (Stark and Harper 1982).

Predators of forest tent caterpillar have received little attention. Green and Sullivan (1950) record predation on larvae in Ontario by the ants *Camponotus herculeanus ligniperdus* (Latr.) and *Formica fusca* L.

Several pathogens have been noted as attacking forest tent caterpillar larvae, including the microsporidia *Pleistophora schubergi* and *Nosema disstriae* (Wilson 1977), the fungus *Entomophthora crustosa* MacLeod and Tyrrell (MacLeod and Tyrrell 1979), and two viruses — a cytoplasmic polyhedrosis virus and a nuclear polyhedrosis virus (Bird 1969). Viruses and fungi are believed sometimes to be important agents in terminating outbreaks of forest tent caterpillar, although this has not been extensively documented. See Stairs (1972) for a discussion of existing information on this point. Forest tent caterpillar can also be controlled by forest applications of *Bacillus thuringiensis* spores and toxins (Wallner 1971), and efforts have been made to identify strains of *B. thuringiensis* with high efficacy against this species (Pinkham *et al.* 1984).

Biological Control Attempts: Documentation of natural control during outbreaks has been extensive, but this has not included suggestions for actions to enhance natural biological control. Considerable efforts have been made to develop the use of *Bacillus thuringiensis* applications for forest tent caterpillar suppression and this approach now has potential for operational use.

Reasons for Pest Status and Possibilities for Biological Control: Weather conditions appear to strongly affect the survival of forest tent caterpillar larvae, and to contribute to both the release of low density populations and the collapse of high density ones. The mechanisms involved vary (Martinat 1987). Because forest tent caterpillars overwinter as pharate larvae inside eggs, the most favorable weather pattern, according to Martinat (1987), is a cool fall, followed by a cold winter and warm spring. If falls are warm, pharate larvae may emerge in fall and die. Cold winters keep pharate larvae inactive and prevent early emergence once diapause is broken, which occurs after about three months of exposure to cold (Martinat 1987). Warm springs promote successful establishment of newly emerged larvae at feeding sites.

Ives (1973) correlated weather variables in various locations across Canada with population trends of forest tent caterpillar and found that sites with increasing populations were characterized by a single year with a relatively cool winter and an unusually warm spring that occurred 2-4 years prior to each outbreak. Most population collapses occurred in years with a

cool spring or warm winter. Ives (1973) further suggested that forest tent caterpillar populations that begin to increase in density after a year of unusually favorable weather continue to increase because natural enemies acting on these low density populations are scarce. Such natural enemies, however, eventually increase to higher levels, causing populations to collapse, perhaps in combination with weather unfavorable for survival of young larvae.

Witter *et al.* (1972) provide life tables for two generations of forest tent caterpillar in Minnesota. Factors that in their opinion, might vary strongly enough to explain collapse of outbreaks include: (1) deaths of pharate larvae in eggs due to warm weather in spring, followed by a cold period, (2) deaths of first instar larvae, after hatching, due to frost or effects of frost on foliage, or (3) high rates of parasitism of pupae by *S. aldrichi.* Witter (1979) presents a table in which he summarizes the presumed causes for the collapse a variety of outbreaks of forest tent caterpillar in various years and locations. Of fifteen outbreaks discussed, eleven appeared to be terminated by weather factors — mostly cold temperatures acting on pharate larvae in eggs and small larvae. One outbreak was ended by a virus epidemic, three were ended by the combination of starvation and pupal parasitism, and one by pupal parasitism alone.

Population models have been built for both northern (Harmsen *et al.* 1976) and southern swamp forest (Rejmánek *et al.* 1987) populations of forest tent caterpillar.

In addition to the preceding work on temporal variation across years in weather and rates of natural enemy attack, other studies suggest that spatial factors might affect population trends. Some habitats may act as refuges for forest tent caterpillar populations. In Ontario in years between outbreaks, forest tent caterpillars are too scarce to collect in dry upland habitats, but can be found in wet habitats (Harmsen and Rose 1983). This difference is related to lower rates of parasitism in wet habitats. Smith and Goyer (1986) found a similar relationship between wet and dry southern habitats, with lower rates of parasitism in wet habitats, which they interpreted as being due to unfavorable conditions in wet soils for the survival of parasitoid puparia.

Recommendation: Forest tent caterpillar periodically reaches damaging densities over large areas of natural forest, defoliates trees, and causes significant losses in tree growth. Population fluctuations, however, appear fundamentally to be related to occasional periods of weather that by chance are more favorable than average to survival of forest tent caterpillar larvae. Outbreaks appear to be terminated by the combined effects of less favorable weather and increasing levels of mortality from natural enemies, particularly the pupal parasitoid *Sarcophaga aldrichi.* There is no obvious method to enhance natural control to end outbreaks more rapidly, or to prevent their occurrence. In areas with especially high economic losses, augmentative intervention with microbial pesticides during the early phase of population increase might be beneficial. Aerial applications of *Bacillus thuringiensis* might be a method to reduce damage. However, widespread application of any pesticide, including *Bacillus thuringiensis*, over large regions of forest would also reduce native Lepidoptera of non-target species and this cost would have to be considered.

50. EASTERN TENT CATERPILLAR (*Malacosoma americanum* [Fabricius]) (Lepidoptera: Lasiocampidae)

Notes: Early records refer to eastern tent caterpillar as *Masacosoma americana.*

Origin: Eastern tent caterpillar is native to North America (Stene 1914).

Range in North America: The eastern tent caterpillar is found throughout southeastern Canada and the eastern United States. Its principal hosts are cherry, apple, and other broadleaf trees (Drooz 1985).

Damage: Most damage from this species is to roadside trees of little economic value. As a forest pest, eastern tent caterpillar is of occasional interest when it defoliates stands of cherry grown for furniture wood. Principally, it is a pest of landscape trees, especially ornamental crabapple and cherry.

Resident Natural Enemies: This species is showy and common, and hence many studies have been conducted on aspects of its biology and ecology. However, almost no studies of this species' population dynamics have been carried out. Consequently most of what is known of the natural enemies of eastern tent caterpillar consists of recognition of various parasitoids and pathogens as being associated with the pest. A quantitative understanding of the influence of these agents on the long term trends of eastern tent caterpillar density is not available.

A variety of parasitoids have been reared from the eastern tent caterpillar's various life stages. Parasitoids of the eggs include the aphelinid *Ablerus clisiocampae* Ashmead, the scelionid *Telenomus clisiocampae*, the encyrtid *Ooencyrtus clisiocampae* Ashmead, a *Tetrastichus* sp., and *Aphycoideus io* Girault (Williams 1916). The *Tetrastichus* sp. reared by Williams (1916) may have been *Tetrastichus malacosomae* Girault (Girault 1916). Rates of egg parasitism, however, are low (Sweetman 1940, Stacey *et al.* 1975). This low percentage arises in part from the protection provided by the shape of the egg mass, parasitism of marginal eggs being dramatically higher (23%) than that of interior eggs (1%) (Darling and Johnson 1982).

Larval parasitoids include the tachinids *Cartocometes io* Aldrich (Aldrich 1929) and *Leschenaultia exul* Townsend (Bess 1936). The biology of *L. exul* is described by Bess (1936), who records its egg laying habit as one of egg deposition on foliage likely to be eaten by hosts. Other larval parasitoids include the ichneumonids *Coccygomimus pedalis* (Cresson) and *Pimpla coelebs* Walsh (Felt and Bromley 1937); *Monodontomerus subobsoletus* (Gahan 1941); *Muscina stabulans* Fabricius (Curran 1942); *Meteorus hyphantriae* Riley, *Hyposoter fugitivus* Say, and *Phobocampe clisiocampe* Weed (Warren and Tadic 1963); and *Rogas malacosomatos* Mason (Mason 1979). Kulman (1965a) records 23 species of parasitoids in West Virginia and Pennsylvania, the most important of which were *Itoplectis conquisitor* and *Theronia atalantae fulvescens.* Ravlin and Haynes (1987) have developed a model of the field population interactions of eastern tent caterpillar and one

of its parasitoids, *Hyposoter fugitivus*, in Michigan. Leius (1967) found that parasitism of eastern tent caterpillar larvae in unsprayed apple orchards increased in relation to increases in the floristic richness of the orchard floor. He interpreted this to be caused by increasing nectar resources for adult parasitoids.

Predators of eastern tent caterpillar include ants of various species (Ayre and Hitchon 1968) and various species of predacious pentatomids (*Podisus* spp.) (Evans 1982, 1983). Both of these reports stress that these generalist predators are effective only in warm springs when temperatures permit their foraging activities early enough to encounter eastern tent caterpillars that are still small (first two larval instars). Larger larvae are too big for these predators to easily subdue. In cooler springs, tent caterpillars are able continue to feed and develop at rates higher than expected based on air temperature, which is possible because they have several behaviors (group resting and tent construction) that provide them with elevated temperature environments. Measurements have shown that inside tents, air temperatures on sunny days are at least 4 °C above outside temperatures (Joos *et al.* 1988).

Pathogens of eastern tent caterpillar are varied and are believed to be important in reducing densities of the species. A nuclear polyhedrosis virus (NPV) is known to affect the larvae (Glaser and Chapman 1916), and vertical transmission through the egg has been suggested (Glaser 1927). Epizootics of NPV infections are believed to be important in ending eastern tent caterpillar outbreaks (Felt and Bromley 1937, Sweetman 1940, Smirnoff 1968). The host ranges of this NPV and those of related tent caterpillars have been compared (Stairs 1964). A second NPV, that of *Autographa californica*, while it does not occur in eastern tent caterpillar populations naturally, does infect the species, suggesting the potential to control larvae by use of microbial pesticides based on this virus (Kaya 1977). A similar potential for augmentative use also exists with the bacteria *Bacillus thuringiensis* (Jaques 1961), *Clostridium brevifaciens,* and *Clostridium malacosomae* (Bucher 1961), all of which infect eastern tent caterpillar larvae if artificially applied. Other pathogens that affect eastern tent caterpillar naturally include two microsporidia, *Nosema disstria* and *Pleistophora* sp. (Nordin 1974). Field studies showed that cumulative mortality through the second instar increased from 13% in disease-free colonies to 46% in colonies in which *Nosema* infections were present (Nordin 1976).

Biological Control Attempts: The only attempts to employ biological control methods against this species have been tests of augmentatively-applied pathogens such as *Bacillus thuringiensis.*

Reasons for Pest Status and Possibilities for Biological Control: Despite the many studies on eastern tent caterpillar, few provide reliable information concerning the reasons for changes in population density over time. Outbreaks of the species have been observed to occur periodically; e.g., Britton (1935) recorded outbreaks in Connecticut in 1913, 1924, and 1935. Many studies have observed the kinds and severity of various mortality agents in collapsing populations and have suggested which factors are typically associated with declines of this species. Blackman (1918) thought that year-to-year declines were mainly due to weather, not parasitoids. Felt and Bromley (1937) stated that mortality in 1935, the year of collapse of an outbreak in Connecticut, consisted of deaths from diseases (30%), parasitism (25%), and starvation plus predation (20%). Sweetman (1940) stated that outbreaks lasted 2-4 years and occurred at 9-12 year intervals. Smirnoff (1968) also thought that NPV disease was at least sometimes responsible for ending populations outbreaks of this species.

In summary, while a variety of observations have been made on single-year population changes in eastern tent caterpillar, no study has spanned a series of generations and none has tried to experimentally manipulate sources of mortality to understand their effects, with the noticeable exception of a study on the role of *Nosema* infection (Nordin 1976).

Recommendations: This species is of minor concern as a forest pest, and thus a detailed investigation of its dynamics cannot be justified on that basis. As an ornamentals pest, more direct management with chemicals, *Bacillus thuringiensis*, and hand removal of tents seem adequate. No actions are recommended.

51. GYPSY MOTH (*Lymantria dispar* [Linnaeus]) (Lepidoptera: Lymantriidae)

Notes: Earlier generic placements of gypsy moth include *Porthetria.*

Origin: Gypsy moth is an exotic species in North America, found widely in the Palearctic region.

Range in North America: Gypsy moth was introduced to New England and its range has expanded west to the Great Lakes States, south to North Carolina, and north into parts of Canada (Drooz 1985). Isolated infestations have been detected in western States (Dreistadt and Dalhstein 1989).

Damage: This species periodically reaches high densities that defoliate hardwood forest species, especially oaks, over large areas. The area subject to defoliation has increased significantly in the last ten years as the range of the pest has expanded west and south.

Resident Natural Enemies:

Parasitoids: In the course of the century-long effort to discover and import natural enemies capable of suppressing this pest in North America, a large number of parasitoids and a lesser number of predators have been found and studied. Of these, the species that have established and become most common are the encyrtid egg parasitoid *Ooencyrtus kuvanae* (Howard), the braconid *Cotesia melanoscela* (Ratzeburg) and the tachinids *Compsilura concinnata* (Meigen), *Blepharipa pratensis* (Meigen), and *Parasetigena silvestris* (Robineau-Desvoidy), all of which attack larvae, and the chalcidid *Brachymeria intermedia* (Nees) which attacks pupae (Montgomery and Wallner 1988). Recently, one additional pupal parasitoid, the ichneumonid *Coccygomimus disparis* (Viereck), has also established in North America after its release (Coulson *et al.* 1986).

Clausen (1978), Doane and McManus (1981), and Elkinton and Liebhold (1990) provide notes on the biology and importance of these species. Also, for *Ooencyrtus kuvanae* see Brown (1984), for *Cotesia melanoscela* see Crossman (1922), for *Compsilura concinnata* see Culver (1919), for *Parasetigena silvestris* see Prell (1915), and for *Blepharipa pratensis* see Shields (1976) and ODell and Godwin (1984).

Predators: Rodents and other predators of gypsy moth larvae and pupae are believed to be important in suppressing the population increase of low density populations

(Montgomery and Wallner 1988, Elkinton and Liebhold 1990). The carabid beetle *Calosoma sycophanta*, as both adult and larva, is an important specific predator of gypsy moth pupae, consuming as many as 40% of the pupae at some sites (Weseloh 1985). Ants are believed to be important predators of young larvae (Weseloh 1994). Bird predation is an important source of mortality of egg masses, with 67-89% of all egg masses being at least partially eaten at some sites (Cooper and Smith 1995).

Pathogens: High density populations of gypsy moths are frequently greatly reduced by epizootics of a nuclear polyhedrosis virus. The dynamics of this pathogen in nature have been modeled by Elkinton *et al.* (1995). This virus has been reared *in vivo* and tested for use as microbial insecticide (Cunningham and Kaupp 1991, Podgwaite *et al.* 1992), but has not been commercially accepted, in part because of problems related to lack of economical virus production methods.

Since 1989 epizootics of a second pathogen, the fungus *Entomophaga maimaiga,* have become an important additional source of mortality of gypsy moth larvae in the northeastern United States (Elkinton and Liebhold 1990, Hajek *et al.* 1993). Although introduced from Japan at the beginning of this century, this pathogen was not noted in the field until 1989, and has been common ever since. This long lag raises the questions as to whether the pathogen currently causing epizootics stems from the early introduction or from some other more recent source.

The bacterial pathogen *Bacillus thuringiensis* kills young gypsy moth larvae when ingested, and its use as a microbial pesticide for control of this pest has been investigated (DuBois *et al.* 1988, 1993). Commercial *Bacillus thuringiensis* products have been developed for control of gypsy moth. Reardon *et al.* (1994) review the use of this pathogen for gypsy moth control.

In Europe, studies have noted the existence of microsporidia that appear to have important suppressive effects on gypsy moth populations (Weiser and Novotný 1987), and their introduction into North America has been proposed.

Biological Control Attempts:

Efforts: The history of the nearly 100 year effort to obtain biological control of gypsy moth in North America has been summarized by Clausen (1978), Reardon (1981), and Griffiths and Quednau (1984). Over the course of these efforts, some 80 species of parasitoids have been imported into North America, with the establishment of ten species. Of these, six have become common (*Ooencyrtus kuvanae, Cotesia melanoscela, Compsilura concinnata, Parasetigena silvestris, Blepharipa pratensis,* and *Brachymeria intermedia*). Another four species have either remained too rare to be significant, or have established too recently (the braconid *Rogas indiscretus* and *Coccygomimus disparis*) for their impact to be clear.

More recent efforts to import parasitoids have focused on two tachinids that have been found attacking low density gypsy moth populations in Europe but have not yet been established in North America, i.e., *Ceranthia samarensis* and *Blepharipa schineri.* Attention has also been devoted to the exploration of new geographic areas, especially China (Schaefer *et al.* 1984) and the Russian Far East (Kolomeits (1987). Schaefer *et*

al. (1986) provides an annotated bibliography of the natural enemies of gypsy moth in Japan and other parts of Asia.

Results: Whether introduced natural enemies have reduced the average density of the pest or lengthened the period between outbreaks is difficult to determine. The extended periods of time needed for such studies and the wide variation in gypsy moth numbers between sites and years have made assessment difficult. Literature on the population dynamics of the gypsy moth is voluminous and has been reviewed by Doane and McManus (1981), Montgomery and Wallner (1988), and Elkinton and Liebhold (1990). Only a few data sets cover a sufficient period to determine if the new agents have modified the pest's average density. A study in Melrose, Massachusetts from 1910 to 1930 spans the period over which the initial group of parasitoids established. At this site, the numbers of egg masses per hectare was very high (about 7000) from 1910 to 1921, and later declined, remaining at 100-1000 egg masses per hectare from 1922 to 1930, which was the last year of the study (as discussed in Montgomery and Wallner 1988). This decline suggests some partial reduction in density that correlates in time to the introductions of exotic natural enemies.

Field studies have shown parasitoids to be important sources of gypsy moth mortality (Doane 1971, Barbosa *et al.* 1975), although the importance of *Cotesia melanoscela* is limited by problems of host-parasitoid synchrony (Weseloh 1976) and hyperparasitism. Long term summaries of the action of parasitoids at fixed study plots have shown that the egg parasitoid *Ooencrytus kuvanae* provides about 26% mortality (data for 19 years in 17 plots, in New Jersey, Williams *et al.* 1990). Data for larval parasitoids from the same plots are summarized by Williams *et al.* (1992). New methods to measure parasitism levels have been assessed by Gould *et al.* (1992). Because of the formidable difficulties in sampling gypsy moth populations, complete life table data are rare. Campbell (1981) presents life tables for some stable, rising, and collapsing populations.

Experimental manipulations to assess the role of various mortality factors have been based on the artificial deployment of gypsy moths to either create cohorts for study, or to raise the density of local populations to observe the natural enemy response. Fukuyama *et al.* (1990) studied how the species of parasitoids and levels of parasitism of gypsy moths varied when cohorts of the host were artificially established in different habitats. In grasslands, a habitat not normally used by this host, natural enemies were found to be absent. In Massachusetts, experimental deployment of large numbers of egg masses to create abnormally high populations (relative to the prevailing levels in the surrounding area) was found to include spatial aggregation of tachinids that resulted in the virtual annihilation of the gypsy moth population (Liebhold and Elkinton 1989, Ferguson *et al.* 1994).

Reasons for Pest Status and Possibilities for Biological Control: Gypsy moth is an exotic species in North America and the biological control project directed against it has explicitly assumed that the frequency and intensity of defoliation events is higher in North America than elsewhere because important natural enemies were missing. Introduction of these natural enemies apparently has partially reduced the damage from this pest. The species is also a pest in eastern Europe and Asia, suggesting that complete suppression of the

species may not be feasible, or may be limited to only certain areas. Some areas in Europe are known, however, in which outbreak populations of this species rarely or never occur.

Recommendations: A comprehensive review of the present knowledge of the population dynamics of this species and of the opportunities to obtain new, more effective natural enemies either from low density populations in previously explored areas or in areas from which few natural enemies have previously been obtained (Russian Far East, China) should be made. This review should specifically assess the likelihood that such efforts might be productive.

For operational control of gypsy moth populations, use of *Bacillus thuringiensis* and the gypsy moth nuclear polyhedrosis viral pathogen as formulated insecticides is recommended. Improvements are needed for these products to enhance field efficacy, and for virus, to lower production costs.

52. NUN MOTH (*Lymantria monacha* [Linnaeus]) (Lepidoptera: Lymantriidae)

Notes: Synonyms for Nun moth include *Liparis monacha* and *Porthetria monacha*. Biology and population dynamics are reviewed by Bejer (1988).

Origin: Nun moth is widely distributed in Eurasia from eastern Siberia through western Europe. It has not yet successfully invaded North America. Periodic outbreaks of this species have occurred in various parts of central Europe. Outbreaks are reported from the Baltic states (Rodzianko 1915), Russia (Kapper 1915), Sweden (Trägårdh 1920), the former Czechoslovakia (Loos 1920/21), Poland (Sitowski 1928), Austria (Kurir 1946), Macedonia (Karaman 1956), and the Amur region of eastern Siberia (Nakonechnyi, undated).

Range in North America: This species is not yet present in North America. A risk exists of accidental importation of this pest on logs from Siberia.

Damage: Stands of Norway spruce (*Picea abies*) in southern Moravia (in the former Czechoslovakia) which had experienced two successive years of defoliation showed a loss of growth directly proportional to defoliation; e.g., a 30% defoliation resulted in 30% less wood growth (Vins and Svestka 1973).

Resident Natural Enemies: Natural enemies attacking nun moth in Europe include many parasitoids (mostly tachinid and sarcophagid flies, and some braconids), a predaceous carabid, and a nuclear polyhedrosis virus. While species differ, the general structure of the natural enemy complex attacking nun moth resembles that associated with the gypsy moth, *Lymantria dispar* (Linnaeus). One important difference is the greater rate of transovarial transmission of the baculovirus of nun moth.

Kolubajiv (1937) lists 52 species of parasitoids from nun moth in Czechoslovakia. Of these, the most important are considered to be the tachinid *Parasetigena silvestris* (Robineau-Devoidy) (Loos 1915/16, Rebel 1921, Komárek 1931, Kolubajiv 1937), the sarcophagid *Sarcophaga affinis* Fallén (Sitowski 1928), and the braconid *Apanteles solitarius* Ratzeburg (=*Cotesia melanoscela* [Ratzeburg]) (Komárek 1931). Many of these parasitoids require

alternate hosts for overwintering and are often not found in sites, such as dense spruce stands, which lack necessary alternate hosts (Kolubajiv 1937). Lists of alternative hosts for the various species of parasitoids are given by Fahringer (1941), together with keys for parasitoid identification. Outbreaks are typically ended by some combination of dipteran parasitism and disease from a nuclear polyhedrosis virus (e.g., Schedl 1949). The same agents are operative in eastern Siberia, although outbreaks are not viewed by foresters as extremely damaging to stands in that area (Nakonechnyi, undated). Various pupal parasitoids have been reported, but appear to be less abundant and, at least some species are polyphagous in nature (e.g., Führer 1975).

Few predators have been recorded as being of any importance as mortality agents of nun moth. The most important include the carabid *Calosoma sycophanta* Linnaeus (Nolte 1938) and the ant *Formica rufa* Linnaeus (Prell 1925).

A nuclear polyhedrosis virus attacks nun moth (Paillot 1913/1915), being transovarially transmitted (Roegner-Aust 1949ab, Larionov and Bakhvalov 1974, Nakonechnyi, undated), and frequently causing the collapse of nun moth outbreaks (Komárek 1921, Schedl 1949, Karaman 1956). This virus has been cultured in live hosts and the resulting viral preparations applied to suppress outbreaks, with mixed results (in Denmark, Zethner 1976; in Russia, Atanasov 1979; in Sweden, Olofsson 1980; and in Poland, Glowacka-Pilot 1983). Applications of the virus may be more effective in controlling damage if the treatments are made when pest numbers are at moderate rather than defoliating levels (Glowack-Pilot 1982). The virus is closely related to, but distinct from, the baculovirus attacking the gypsy moth (Zethner *et al.* 1979).

Biological Control Attempts: Efforts in Europe have centered on the culture and dissemination of the baculovirus of nun moth as a biopesticide.

Reasons for Pest Status and Possibilities for Biological Control: No experimental evidence exists as to the cause of nun moth outbreaks in Europe or Asia. At least three explanations have been advanced. The first of these is that outbreaks are triggered by random occurrences of weather patterns that promote higher than average levels of larval survival. Survival is enhanced by good synchrony of early larvae with their food resource, with best survival occurring when nun moth eggs hatch late and shoot growth is early (Knoche 1929, Svestka 1971). The importance of weather under this hypothesis is its influence on the existence of a food supply of acceptable quality for the young nun moth caterpillars (Komárek 1931). Only one attempt has been made to determine if correlations exist between weather patterns and nun moth outbreaks (Bejer 1985). An analysis of eight outbreaks from 1971 to 1979 in Denmark, plus three earlier ones (1848, 1856, and 1902) found that the pattern of outbreaks could not be explained by overall climate, nor by site or stand factors. The data suggested that outbreaks occurred only on sites with poor sandy soils and followed sets of 3 to 4 years with high summer temperatures and low summer rainfall, preceded by low spring temperatures (Bejer 1985).

The second explanation for outbreak cycles relates to the influence of the nuclear polyhedrosis virus. This virus is commonly observed to end outbreaks (Komárek 1921, Schedl 1949, Karaman 1957). Such disease epizootics have been postulated, in some insect population models, to have the ability to induce periodical cycles in insect populations.

The third explanation for outbreaks attributes them to silvicultural techniques that employ intensively managed spruce monocultures, often in locations outside the natural habitat of spruce forests (Mangin 1921, Wilke 1931, Komárek 1931). The contrary view, that natural spruce stands were affected more than plantations outside the normal range of spruce, was held by Ruzicka (1931) for nun moth outbreaks in Bohemia. The mechanisms through which these silvicultural practices influence nun moth survival are not discussed. However, Kolubajiv (1937) observed that the hymenopteran parasitoids of nun moth and some of its tachinid parasitoids require alternate host species for overwintering. These hosts are generally absent in spruce monocultures. Parasitoid abundance is reduced in such stands, permitting the nun moth population to increase rapidly when weather and host plant conditions are favorable.

Recommendations: This species has the potential to be to conifers a pest of a similar nature and magnitude as the gypsy moth currently is to oak forests. Strict quarantine measures to exclude the pest are extremely important. Importation of raw conifer logs, especially with intact bark, from infested areas such as eastern Siberia are a likely method of importation. Measures restricting the movement of such logs from central Europe into France were contemplated as a quarantine measure in the early part of this century (Anon 1921c).

Should nun moth invade the United States, eradication would be desirable if the species is detected early. For this reason, ongoing surveys of forested areas around high risk ports of entry should be conducted using pheromone lures.

Should the species invade and establish over a region too great to effect eradication, some of the enemies already imported for gypsy moth biological control, especially *Parasetigena silvestris* and *Cotesia melanoscela*, would also attack nun moth. Should a natural enemy introduction program be conducted, efforts should be made to determine whether the species exists anywhere in central Asia in a stable nonoutbreak condition, or if it is an outbreak pest throughout its range. Because the species is clearly an outbreak pest in central Europe, that region is not a particularly likely area in which to encounter natural enemies capable of suppressing outbreaks, and should be given a low priority as a search area.

53. PINE WEBWORM (*Tetralopha robustella* Zeller) (Lepidoptera: Pyralidae)

Origin: Pine webworm is native to North America.

Range in North America: Pine webworm occurs in southern Canada and throughout most of the eastern half of the United States (Drooz 1985).

Damage: Young larvae mine in pine needles. Older larvae feed externally, building webs around groups of needles and frass. Various species of pines are attacked, in particular slash, red, and jack pines (Drooz 1985). In southern slash pine (*Pinus elliottii* Engelman) plantations, defoliation by pine webworm can cause some mortality to young pines, but only in the first season after planting. Thereafter, pines are too large to be defoliated given typical densities of this pest (Hertel and Benjamin 1977). In the Great Lakes States, damage occurs in red and jack pine plantations (Wallesz and Benjamin 1960). Injury is largely related to loss of quality in pines grown for the Christmas tree market, due to unsightliness of webbed limbs.

Resident Natural Enemies: Hertel and Benjamin (1979) list eleven species of parasitoids reared from this species in northeast Florida, but do not discuss their importance as control agents of the pest. Of the species mentioned, the most frequently reared species was the ichneumonid *Syzeuctus elegans* (Cresson). Eight species of parasitoids have been reported by Wallesz and Benjamin (1960) in Wisconsin, but no quantitative data are given on the importance of these in suppressing the numbers of the pest.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Hertel and Benjamin (1977) examined the impact of various site preparation methods in slash pine plantations on the density of this pest in Georgia, but concluded that the pest was of minor importance and that site preparation methods had only limited effect on pest densities. No studies were discovered on the population dynamics of this pest in the northern United States.

Recommendations: The only logical avenue by which biological control of this pest might be enhanced would be changes in silviculture practices to enhance natural enemies. This would be justified only if pest damage were high, since choice of silviculture methods is likely to be constrained by needs to maximize growth rates. Since injury is aesthetic and of concern only in the year of harvest, a more economical approach is likely to be pesticide application to prevent infestation, but only in the year of intended harvest. A test might be conducted to determine if some form of *Bacillus thuringiensis* might be commercially available that would provide acceptable pest suppression. If this material were used, it would not reduce levels of natural enemies of the pest.

54. ZIMMERMAN PINE MOTH (*Dioryctria zimmermani* [Grote]) (Lepidoptera: Pyralidae)

Notes: Earlier generic placements for Zimmerman pine moth include *Pinipestis* and *Nephopteryx* (Munroe 1959). *Dioryctria zimmermani* was not well distinguished from related species until the work of Mutuura (1982). As a consequence, care must be taken in interpreting whether earlier records refer to this species. Munroe (1959) placed *Retinia austriana* Cosens and *Salebria delectella* Hulst in synonymy with *D. zimmermani*. Mutuura (1982) concurs with the first, but not the second of these synonymies. Mutuura divided what he saw as the part of the "*D. zimmermani* group" that occurred in eastern Canada into three species: *Dioryctria zimmermani*, *Dioryctria resinosella* Mutuura, and *Dioryctria banksiella* Mutuura and Munroe. Additional species occur in the *D. zimmermani* group in the western part of North America. Furthermore, Mutuura (1982) records *D. zimmermani* as feeding only on the bark of stems, not on cones. This observation suggests that earlier records of "*D. zimmermani*" as a cone feeding pest (Coulson and Franklin 1970) refer to other species.

Origin: Zimmerman pine moth is native to North America.

Range in North America: Mutuura (1982), following his narrowed redefinition of *D. zimmermani*, gives the distribution of *D. zimmermani* as southeastern Canada and northeastern United States as far west as Minnesota, corresponding with the range of white pine.

Damage: Members of the genus *Dioryctria* are cone feeders, or twig or trunk cambial feeders, or both. *Dioryctria zimmermani* is reported in the literature to feed on cones (Coulson and Franklin 1970), but the species as Mutuura (1982) defined it appears to be limited to feeding in the cambial layer of trunks and branches, including terminal shoots. Losses have been noted in Scotch pine Christmas tree plantations due to deformity from death of terminal shoots (Butcher and Carlson 1962, Yonker and Schuder 1987).

Resident Natural Enemies: Cameron (1962) lists seven species of North American parasitoids recorded in the literature from *Dioryctria* spp. that he considered as potentially significant as biological control agents for this pest. Carlson and Butcher (1967) record *Hyssopus rhyacioniae* Gahan and *Elachertus pini* Gahan as important parasitoids of older *D. zimmermani* larvae, with parasitism reaching 51-57% between the two parasitoids at two study sites in Michigan. Rennels (1960) in Indiana also recorded *H. rhyacioniae* as the most important larval parasitoid, with other species noted being *Melittobia chalybii* Ashmead, *Elachertus pini*, *Ephialtes comstockii* Cresson, and *Eurytoma pini* Bugbee. Total parasitism, however, did not exceed 5%.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Fundamental reasons for the typical densities of this species are unknown, as no population dynamics studies have been conducted. Whether any of the observed parasitoids are significant factors regulating the pest is unknown.

Recommendations: None.

55. SPRUCE BUD MOTH (*Zeiraphera canadensis* Mutuura and Freeman) (Lepidoptera: Tortricidae)

Origin: Spruce bud moth, while formerly believed to be of European origin, is now considered to be distinct from European forms and to be native to North America (Drooz 1985).

Range in North America: Spruce bud moth is found throughout the northern United States and Canada, wherever spruce occurs (Drooz 1985).

Damage: This species damages the shoots of spruce. Such damage leads to immediate reductions in height growth of white spruce (*Picea glauca*) in plantations, but 60% or more of the shoots must be damaged yearly for two or three consecutive years before total wood growth is reduced (Carroll *et al.* 1993). Damage from this species has become of economic concern only since the development of plantation spruce production in the 1980s in eastern Canada, e.g., in New Brunswick (Mills 1993).

Resident Natural Enemies: Specific studies on the natural enemies of this species were not encountered. Pilon (1977) reported on the natural enemies of *Zeiraphera fortunana* Kft., a closely related species, in Quebec. Eggs of this species were attacked by *Trichogramma minutum* (up to 29% by natural parasitoids). Up to 41% of the larvae were parasitized by various species, including *Scambus brevicornis* (Grav.), *Itoplectis conquisitor* (Say),

Triclistus podagricus (Grav.), *Diadegma* sp. and *Apanteles* sp. Mills (1993) studied the parasitoids of conifer bud moths in Europe, analyzing the parasitoid complexes and the biologies of various species for possible importation to Canada against *Z. canadensis.*

Biological Control Attempts: Importation of European species of parasitoids from related conifer bud moths has been proposed (Mills 1993). Among the species identified by Mills (1993) for study as possible candidates for introduction are the pupal parasitoid *Phaeogenes osculator* (Thunberg) and the European ecotypes of the holarctic species of *Triclistus* sp., *Chorinaeus funebris* (Gravenhorst), *Chorinaeus cristator* (Gravenhorst) and *Phytodietus* spp. Studies are needed on host ranges of candidate parasitoids, confirming their acceptance of *Z. canadensis* as a host. In addition, *Z. canadensis* has been considered as a possible target for augmentative releases of *Trichogramma minutum.*

Reasons for Pest Status and Possibilities for Biological Control: No studies on the population dynamics of this species were encountered. Information on factors determining the typical densities of this species, either in natural forests or spruce plantations, is lacking.

Recommendations: Before undertaking importations of new species of parasitoids from Europe, it is recommended that basic population dynamics studies be conducted, using life tables, on the roles of various mortality factors. Such studies should compare the mortality from native parasitoids with that from other factors. Studies should be conducted in both natural spruce stands and spruce plantations to see if any factors might be reducing the effectiveness of parasitoids in plantations.

56. BAGWORM (*Thyridopteryx ephemeraeformis* [Haworth]) (Lepidoptera: Psychidae)

Origin: Bagworm is native to North America (Howard and Chittenden 1916).

Range in North America: Bagworm is widely distributed across the eastern half of North America (Drooz 1985).

Damage: The host range of this species is very broad. Dense populations defoliate cedars, arborvitae, other conifers, and some hardwoods.

Resident Natural Enemies: Because larvae in bags are highly visible, slow moving, and easy to collect, this species has attracted attention for study in several states. Consequently, numerous studies exist which document the parasitoids that can be bred from late stage larvae or pupae in bags.

The parasitoid complexes in most areas are dominated by ichneumonids, the most common of which is *Itoplectis conquisitor* (Say), and chalcidoids, many of which are hyperparasitic, at least facultatively. Balduf (1937) reviews previous parasitism records from the literature, and notes that among the primary parasitoids affecting this bagworm are the ichneumonoids *Itoplectis conquisitor*, *Epiurus indagator* (Cresson), and *Hemiteles* (*Allocota*) *thyridopterigis* Riley; the eupelmid *Eupelmus cyaniceps amicus* Girault; and the chacidids *Spilochalcis mariae* Riley and *Brachymeria ovata* Say. Kulman (1965b) lists 25 species of parasitoids associated with common bagworm, in part from studies in West Virginia on black

locust and in part from literature records. Overall, 25% of the bagworms collected were parasitized, of which the majority of parasitism was due to the ichneumonid *I. conquisitor*. In Kansas, bagworms from a variety of host plants exhibited an average of 12% parasitism, about equally divided between larval and pupal parasitism (Barrows and Gordh 1974). Most parasitism was caused by various ichneumonids, including *I. conquisitor*. Similarly, in Ohio, bagworm populations on arborvitae (*Thuja occidentalis* Linnaeus) and juniper (*Juniperus virginiana*) were attacked by eleven species of primary or secondary parasitoids, but the majority of the parasitism was due to *I. conquisitor* (Sheppard and Stairs 1976). Berisford and Tsao (1975a) report that parasitism of bagworms on *Juniperus* sp. and *Thuja orientalis* Georgia varied from 10% to 46%, with more parasitism in dry years. Parasitism and mortality from fungal pathogens were inversely related, with 13-51% mortality from fungi, mostly in wet years. Eight species of primary parasitoids are reported by Berisford and Tsao (1975a), among which the most important were the ichneumonids *Calliephialtes grapholithae* (Cresson) and *I. conquisitor*.

Difference in parasitism rates between the sexes of bagworms and for different heights within host plants have been examined. In Maryland, female bagworm larvae selected higher positions within host plants for pupation than did male larvae (Gross and Fitz 1982). This difference was believed to explain the observation that rates of parasitism on male pupae were higher, parasitism being believed to occur more frequently within the lower parts of the host plant. (However, a later explanation was based on bag size.) As in previous studies, a complex of several parasitoids occurred, with *I. conquisitor* being the most numerous. The importance of pupation location within the host plant in determining parasitism rates was not supported by later studies (Cronin 1989, Cronin and Gill 1989), which found that position within the host plant had no effect on parasitism rates of male bagworms and for females was actually somewhat higher at elevated positions. The difference in parasitism rates between the sexes was instead related to bag size, with rates of parasitism in females being lower (10%) than in males (61%) (Cronin 1989). Ovipositor length of the principal parasitoid, *I. conquisitor*, limited successful attack of hosts in very large bags (mostly females).

Fungal pathogens of bagworms have been examined carefully less often than parasitoids. Berisford and Tsao (1975b) identified ten species of pathogenic fungi associated with bagworms in Georgia, among which the most important were judged to be *Aspergillus parasiticus* Speare, *Beauveria bassiana* (Bals.) Vuill., and *Paecilomyces lanosum* Westling.

The bacterial pathogen *Bacillus thuringiensis*, applied augmentatively, has been noted to provide control of bagworm (Kearby *et al.* 1972).

Most predators attacking bagworms are generalists, including birds and larger wasps. A more unusual case is presented by the pyralid *Dicymolomia julianalis* Walker, which has a complex relationship with bagworm. This pyralid is both a scavenger and egg predator, and an endoparasitoid of larvae and pupae, attacking up to 20% of bagworms in undisturbed locations in Oklahoma (Kaufmann 1985).

Studies designed to develop a quantitative understanding of changes in densities of bagworm populations have been less common than those simply documenting mortality sources. In a 3-year study of a bagworm population in Kansas, mortality rates of bagworms from unknown factors other than parasitism and predation varied significantly by host plant (Barrows 1974).

Indirect evidence suggested that bagworm larvae escaped parasitism by migrating to new host plants after egg hatch. Dispersal is achieved by aerial ballooning of young larvae, most of which have small bags at the time (Cox and Potter 1986), and larvae are able to disperse up to 245 feet by this mechanism (Cox and Potter 1990). Horn and Sheppard (1979) followed two bagworm populations over a 5- to 6-year period, observing each to decline in density from outbreak to innocuous levels. Over the study period, increases in overall mortality at one site was best correlated with increases in predation, indicated by torn bags, believed to be the result of attack by birds. Other mortality factors killed larger percentages of bagworms but were either constant or declining in intensity. As in earlier studies, the most important parasitoid was the ichneumonid *I. conquisitor*. At the other site, decline was associated with a large shift in sex ratio toward males, for unknown reasons.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Fluctuations in densities of local bagworm populations are not understood, but may relate to variation in predation or sex ratio of bagworm pupae. Locally, bagworms may escape some mortality agents by dispersing and colonizing new host plants. Our knowledge of the mechanisms behind changes in densities of bagworms is insufficient to explain outbreaks and these are likely related to local conditions.

Recommendations: None.

57. MIMOSA WEBWORM (*Homadaula anisocentra* Meyrick) (Lepidoptera: family given alternatively as Plutellidae or Yponomeutidae)

Notes: The original description of mimosa webworm in North America was as *Homadaula albizziae* Clarke, which was later recognized as a synonym of *Homadaula anisocentra* (Clarke 1968).

Origin: Mimosa webworm is an exotic species from the Indo-Australian region (Clarke 1943), that was first recorded in North America in Washington, D.C. in 1940.

Range in North America: This moth occurs from New Jersey and Pennsylvania, south to Florida, and west to Mississippi, Kansas, and Nebraska (Drooz 1985).

Damage: Larvae feed on flowers and foliage of the silktree (mimosa) (*Albizia jubibrissin*) and honeylocust (*Gleditsia triacanthos*). Larvae web together areas they feed upon.

Resident Natural Enemies: Miller *et al.* (1987) recorded the ichneumonid *Parania geniculata* and the eulophid *Elasmus albizziae* as pupal parasitoids of mimosa webworm in Illinois, but at very low levels of parasitism (2-4%). One of these, *E. albizziae*, was noted in Iowa causing high levels (39-47%) of parasitism (Bastian and Hart 1989).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Since this is an exotic lepidopteran with free-feeding larvae, it is reasonable to suppose that it has escaped association with a variety of parasitoids affecting it in Asia or Australia. Biologically, this species is a likely target for biological control introductions of parasitoids from its home range. The economic justification for such efforts would have to be verified, based on current economic costs of pesticide control and plant damage. No such estimates were encountered in the literature.

Recommendations: A survey could be conducted to ascertain which species of parasitoids are currently associated with this insect in North America. The list of such species could be compared with literature records, such as might exist in insect collections, in Asia or Australia. This comparison would help identify candidate species to collect for introduction to North America.

58. BIRCH CASEBEARER (*Coleophora serratella* [L.]) (Lepidoptera: Coleophoridae)

Notes: The synonymy of birch casebearer is complicated and affects the interpretation of the literature (see Coshan 1974). The species was originally described by Linnaeus in 1761 as *Coleophora serratella*, but until the early 1970s the species was referred to in the literature by a synonym, *Coleophora fuscedinella* Zeller. When the name *C. serratella* was revived (Benander 1939, Toll 1962), it was misapplied to another species (*C. cerasivorella*). The name *C. serratella* was later restored to the correct species by Kloet and Hincks (1972). Because of this misapplication of the name, literature citing the name *C. serratella* in the period from 1938 to 1972 is likely not to refer to the true *C. serratella*.

For example, McDunnough (1957) used the name *C. serratella* in this incorrect sense and further synonymized it with several species, including *C. nigricella* (Steph.), *C. cerasivorella* Pack., and *C. fletcherella* Fernald. In general, the host plants referred to in studies from this period provide some partial warning, with species on apple and other members of the rose family not being the true *C. serratella*, which typically feeds on species of birch and alder. Specifically, the references by LeRoux *et al.* (1963) and LeRoux (1971) to *C. serratella* on apple being controlled by *Chrysocharis laricinellae* (previously imported for control of larch casebearer, *Coleophora laricellae*) actually refer to the pistol casebearer, *Coleophora malivorella* Riley (Paradis and LeRoux 1971).

Origin: Birch casebearer is an exotic species in North America that is believed to have invaded Maine about 1927 (Drooz 1985). Its status as an invader is further confirmed by the clear pattern of range expansion recorded in the literature, northward from Maine into Newfoundland and also westward (Raske 1984). The species is found throughout much of Europe (Coshan 1974).

Range in North America: The birch casebearer is found from Newfoundland to southern Ontario and in the northeastern States (Drooz 1985).

Damage: *Coleophora serratella* feeds on birches, alders, and elms (Coshan 1974). High density populations defoliate birches in parts of both North America and Europe, and the

species is considered the most important pest of birch in some areas (e.g., Newfoundland, Raske 1973).

Resident Natural Enemies: Twenty five species of parasitoids attack *C. serratella* in central Europe (Gepp 1975). Pschorn-Walcher (1980) analyzes the effect of habitat type on the composition of birch casebearer parasitoid complexes. Hawkins (1988) provides a list of parasitoids of this casebearer in the United Kingdom and notes parasitism rates for each species for two years. In this United Kingdom study, parasitism rates, summed over all species, averaged 21-36%. In another study in the United Kingdom, 55% of overwintered larvae collected in the spring were parasitized (Coshan 1974). References from Europe to *C. serratella* as a fruit tree pest probably refer to different species (see the introductory note on taxonomy).

In North America, a variety of native parasitoids have adopted the birch casebearer as a host. Guèvremont and Juillet (1975) list 38 species of parasitoids reared from this casebearer in the Sherbrooke region of Quebec. The three most common were *Agathis cincta* (Cresson), *Orgilus coleophorae* Muesebeck, and *Orgilus scaber* Muesebeck, all of which emerge from pupae. In life tables for the study site over three successive years, rates of parasitism of fifth instar larvae were 6-16% and of pupae were 31-51% (Guèvremont and Juillet 1974). Surveys of parasitoids of birch casebearer in Newfoundland before introduction of exotic species were conducted by Raske (1978), who reared 19 species from this host. Most of these were not host-specific. The most commonly reared species were *Itoplectis quadricingulatus* (Prov.), *Cirrospilus cinctithorax* (Girault), and *Habrocytus semotus* (Wlk.). Parasitism levels, however, were low, averaging only 5-16% when summed over all species.

Predators associated with this casebearer in North America include the mite *Triophtydeus triophthalmus* (Oudm.), which was sufficiently abundant at some locations in Newfoundland to cause high levels of mortality to the eggs of this casebearer (Raske 1974).

Biological Control Attempts: Parasitoids of birch casebearer were collected in Europe and released in Newfoundland from 1971 to 1975 (Raske 1977). In contrast to European parasitoid guilds attacking birch casebearer, which are dominated by species of *Apanteles* and *Campoplex*, parasitoid guilds of birch casebearer in Newfoundland lacked species in these genera (Raske 1978). Consequently, parasitoid introductions to North America have focused on these groups, including *Campoplex borealis* (Zett.), *Campoplex* sp., *Apanteles coleophorae* (Wilk.), *Apanteles mesoxanthus* Ruschka, and *Apanteles corvinus* Reinh. (Raske 1984). The outcome of these releases has not been determined. No recoveries had been made at release sites as of 1984, nine years after the last releases.

Reasons for Pest Status and Possibilities for Biological Control: Birch casebearer in North America has attained pest status because it has become separated from important natural enemies in Europe and as such it is a good candidate for further parasitoid importations (Raske 1984). The species sometimes defoliates birches in Switzerland, Scandinavia, and Estonia (Coshan 1974). Quantitative comparisons between pest densities and defoliation levels in North America and Europe were not found in the literature. Reasons why this species sometimes reaches damaging levels in Europe were not found.

Recommendations: The problem in North America could likely be reduced by further importations of parasitoids from Europe, including those imported previously that did not establish. Failure of these earlier releases may well be due to release of inadequate numbers. Before resuming importations, surveys should be conducted in the original release areas to determine if any released species can be detected.

59. LARCH CASEBEARER (*Coleophora laricella* [Hübner]) (Lepidoptera: Coleophoridae)

Origin: In North America, larch casebearer is an exotic species believed to be of European origin. It was first recorded in North America in Massachusetts in 1886 and is believed to have invaded on imported nursery stock (Otvos and Quednau 1984).

Range in North America: *Coleophora laricella* is found in the Atlantic maritime provinces of Canada, southern Quebec, Ontario, westward to British Columbia. In the United States, the species occurs from New England west to Minnesota and, separately, in the Pacific Northwest States, especially Idaho and Oregon (Drooz 1985). This distribution follows the distribution of the two principal hosts, *Larix laricina* in the east and *Larix occidentalis* Nuttl. in western North America. See Otvos and Quednau (1984) for a map of the distribution in Canada.

Damage: Outbreaks of this species occurred in eastern North America early in this century (e.g., Felt and Bromley 1932) before the widespread establishment of European parasitoids that were used successfully to suppress the species. Currently, outbreaks are local and brief. The last prolonged, widespread outbreaks in eastern Canada occurred in the 1940s and 1950s (Webb and Quednau 1971). Outbreaks in the 1950s occurred in central Ontario in areas that had not yet been colonized by European parasitoids.

A separate successful use of biological control in the part of the western United States (Idaho and Oregon) was achieved after the invasion of that region in 1957 (Ryan *et al.* 1974, Ryan 1990). Before suppression in that region by imported biological control agents, *C. laricella* was rated as one of the top two pests of western larch (Schmidt *et al.* 1976).

Damage from larch casebearer is due to a reduction in tree growth, rather than tree mortality. Growth reduction of 80% is recorded for stands of western larch in northern Idaho subject to repeated defoliation by larch casebearer (Long 1988). The same author also documents complete return to normal growth rates after the successful termination, by introduced parasitoids, of defoliating outbreaks of the pest.

In some parts of northeastern Ontario, larch casebearer is still listed as an important pest (Constable *et al.* 1991). Whether this reflects climatic limitations on the effectiveness of the imported parasitoids or greater concern over small outbreaks (now that large ones no longer occur) is not known.

Damage also is recorded from Europe (Kadocsa 1917, Malenotti 1924, Schönwiese 1937, Eidmann 1965). Why these outbreaks occur is not clear (see Reasons for Pest Status and Possibilities for Biological Control for possible explanations). Damage is also reported from China (Li *et al.* 1989).

Resident Natural Enemies: In Europe, the resident natural enemy complexes have been investigated by European entomologists out of concern over local damage from the pest and by North American entomologists seeking natural enemies for importation. Thorpe (1933) studied parasitoids of larch casebearer in the United Kingdom. While both parasitoid species that ultimately controlled the pest in North America, *Agathis pumila* (Ratzburg) and *Chrysocharis laricinellae* Ratzburg, were present in the United Kingdom, they were rare. *Agathis pumila* is, however, abundant in southern France. The most common parasitoid in Thorpe's (1933) study was *Angitia nana* Gravenhorst. Collections made by Dowden (1934) in Austria included both *Chrysocharis laricinellae* and *Agathis pumila*. In Austria, *C. laricinellae* was the main parasitoid associated with the subsidence of an outbreak of larch casebearer (Schönwiese 1937). In Sweden, the main parasitoid recorded by Eidmann (1965) was listed as *Chrysocharis nitetis* (Wlk.), but this is a synonym of *Chrysocharis laricinellae* (Ryan and Yoshimoto 1976). Jagsch (1973) analyzed the dynamics of larch casebearer in Austria and reported parasitoids to be relatively unimportant, even though the two species later found to be important in North America (*A. pumila* and *C. laricinellae*, the latter recorded by Jagsch [1973] under the synonym *C. novellus* [Wlk.]) were both present. Similarly in Poland, parasitism rates were very low (1-3%) (Skrzypczynska 1978).

In North America, the native parasitoids attacking larch casebearer have been recorded in several locations. This work has typically been done as part of studies leading to or following up on importations of parasitoid species from Europe or Japan. In New Brunswick before parasitoid importations, birds were one of the more important groups of natural enemies of larch casebearer and parasitoids were rare (Baird 1922). A similar finding was made in Wisconsin by Sloan and Coppel (1968). Studies in Idaho, Minnesota, and Washington by Bousfield and Lood (1973) record 20 species of parasitoids attacking larch casebearer. Miller and Finlayson (1974) recovered 32 species of parasitoids from larch casebearer in British Columbia.

Biological Control Attempts: Larch casebearer has been the successful object of biological control programs twice in North America, first in eastern and later in western North America.

As early as 1922, interest existed in importing parasitoids of larch casebearer from Europe (Baird 1922). Surveys of European parasitoids were conducted in the 1930s (e.g., Thorpe 1933), followed immediately by introductions (e.g., Dowden 1934, Clausen 1978). The history of this project in Canada is given by Webb and Quednau (1971). Ultimately, four parasitoids were released, but only two, *Agathis pumila* and *Chrysocharis laricinellae*, proved significant. Released and established in eastern Canada and the United States in the 1930s and early 1940s, *A. pumila* spread more rapidly than *C. laricinellae* (Graham 1958). Following the establishment of these two parasitoids, their life histories were investigated in depth (Quednau 1966, 1967, 1970a). This in turn lead to evaluations of the interaction of these two species in the field in efforts to account for successful control of the pest (Quednau 1970b). While not as extensively documented as was later to be the case in the western United States, this first biological control project against larch casebearer is rated as a complete success (Webb and Quednau 1971). Whereas outbreaks in eastern Canada before the 1930s were long and widespread, after introduced parasitoids became well distributed in the late 1940s, outbreaks were reduced in extent and duration.

The second biological control project in North America against larch casebearer followed the invasion of the pest in the western larch forests of Idaho, Oregon, and surrounding States about 1957. These forests are disjunct from the larch forests in the east. Consequently, the pest arrived without its parasitoids and quickly reached damaging levels, causing sustained defoliating outbreaks. Importations of *Agathis pumila* from eastern North America were made into this western region, with redistribution, in the 1960s. *Chrysocharis laricinellae* was later collected in Wisconsin, England, Austria, and Sweden and released in Oregon (Ryan and Yoshimoto 1976). These releases were followed between 1972 and 1980 by importations of additional parasitoids, including seven species from Europe and one from Japan (Ryan 1980). Ultimately, the same species providing control in eastern North America (*A. pumila* and *C. laricinellae*) proved effective in western forests as well. Studies in Oregon documented reductions of larch casebearer larval densities from 52.6 to 0.8 insect cases per 100 buds (Ryan 1990). Results of these releases were extensively documented, including the creation of a long series of life tables, both before and after parasitoid introductions (Ryan *et al.* 1978; Long 1988, 1990; Ryan 1990).

Reasons for Pest Status and Possibilities for Biological Control: The fundamental cause of defoliating outbreaks of larch casebearer populations in North America was the absence in North America of effective parasitoids. This is demonstrated by the elimination of damaging outbreaks, in both eastern and western North America, following the introduction of European parasitoids.

A more complex question is why the pest is still considered damaging in Europe. Possible explanations include these:

- Greater damage in very northerly areas like Sweden may be due to reduced effectiveness of parasitoids caused by climatic effects on host-parasitoid synchrony.
- Greater damage may occur if larch plantations are planted beyond the tree species' natural range.
- Efficacy of large parasitoid complexes may be reduced by competition between parasitoid species.
- Foresters in North America and Europe may differ in their perspectives, with small outbreaks seeming relatively more important in Europe.

Recommendations: Because this pest has already been successfully controlled, no further action is needed. The project has many features that could be a model for how to conduct other biological control projects.

60. OAK LEAF ROLLER (*Archips semiferanus* (Walker) (Lepidoptera: Tortricidae)

Origin: Oak leaf roller is native to North America.

Range in North America: This species is found throughout eastern and central North America.

Damage: Periodic outbreaks of this species have occurred in oak forests in North America since the 1960s. In Pennsylvania and Michigan, hundreds of thousands of acres have been

defoliated in various years, with substantial tree mortality and economic loss (Mumma and Zettle 1977). Wilson (1972) describes the general biology of species, conducting his study in the decline phase of an outbreak in Michigan in 1969-1970.

Resident Natural Enemies: Natural enemies of this species have been studied in few cases. Mumma *et al.* (1974) reported on pupal parasitism in Pennsylvania, noting that two ichneumonids, *Itoplectis conquistor* (Say) and *Phaeogenes gilvilabris* Allen, together attacked about 6% of the pupae. Other surveys in Pennsylvania (Mumma and Zettle 1977) found higher levels of parasitism (18-63% for larvae; 4-35% for pupae), with most larval parasitism being caused by tachinids and most pupal parasitism being caused by Hymenoptera. The principal larval parasitoid was *Lypha setifacies* (West), and the most common pupal parasitoid was *Itoplectis conquisitor*. *Itoplectis conquisitor* is a polyphagous parasitoid reported from more than 75 host species (Krombein *et al.* 1979).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: The reasons for the periodic pest outbreaks of this species are unknown and have not been investigated.

Recommendations: In view of the native status of this species and the intermittent nature of its outbreaks, importations of new species of natural enemies is not recommended. Studies of populations might be conducted to determine the causes of outbreaks. However, should the cause of the outbreaks be related to either weather or population cycles driven by disease epizootics, understanding of these causes are not likely to lead to useful options to manage populations.

61. SADDLED PROMINENT (*Heterocampa guttivitta* [Walker]) (Lepidoptera: Notodontidae)

Origin: Saddled prominent is a moth that is native to North America.

Range in North America: This species is found in southeastern Canada and the eastern United States from New England south to Florida and west to the Great Lakes states. Some populations occur farther west (Texas, Colorado, Nebraska), but outbreaks are limited to New England and the Great Lakes States.

Damage: This species periodically reaches densities high enough to defoliate forest stands of preferred hosts (beech, birch, maple). Outbreaks were first recorded in 1907 and have reoccurred in New England approximately every 10-12 years (Collins 1926; Martinat and Allen 1987, 1988). Following two or more years of consecutive defoliation, tree mortality may occur (Drooz 1985).

Resident Natural Enemies: Allen (1972) lists parasitoids reared from saddled prominent eggs, larvae, and pupae from samples taken in New York and New England during the 1968-1971 outbreak, and summarizes previous records from the literature (e.g., Collins 1926, Fisher 1970). Thirty-four species are listed from New York and New England, of which only three occurred consistently in significant numbers: the egg parasitoids *Telenomus coelodasidis* Ashmead (Hymenoptera: Scelionidae) and *Trichogramma minutum* Riley (Hymenoptera:

Trichogrammaditidae), and the pupal parasitoid *Cratichneumon sublatus* (Hymenoptera: Ichneumonidae). Larvae and adults of the carabid *Calosoma frigidum* Kirby have been observed preying on saddled prominent larvae during outbreaks in Michigan (Loesch 1977) and other locations (Collins 1926, Fisher 1970). The biology of the most important egg parasitoid, *Telenomus coelodasidis,* has been studied by Ticehurst and Allen (1973).

A fungal pathogen in the *Entomophaga aulicae* group has been recorded from saddled prominent larvae and has been observed to caused epidemics in outbreak populations (Hajek *et al.* 1991). An unidentified virus has also been reported from saddled prominent populations in Michigan (Loesch and Foran 1979). This virus, together with parasitoids, is believed to have reduced larval population of this lepidopteran. A nuclear polyhedrosis virus and fungus are reported to have caused the collapse of populations of a related species, *Heterocampa manteo* (Doubleday), in Maryland (Staines 1977).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Reasons for outbreaks of this insect are unknown. Weather variation (excess or deficiency of rainfall) was considered as a possible cause by Martinat and Allen (1987), but statistical analysis failed to demonstrate any significant differences between rainfall in the presumed years of release (immediately before outbreaks) and other years for a set of nineteen independent outbreaks between 1907 and 1979. Pathogen-induced cycling is another general potential mechanism for insect outbreaks (Ewald 1987) that may apply to this species, but which has not been studied.

Recommendations: Because this species is native to North America and reaches pest densities only periodically, no importations of natural enemies are recommended. It is possible that outbreaks are rooted in disease cycles. Studies could be undertaken to investigate this possibility. Such knowledge would be valuable in that it would increase our understanding of the origin of the outbreaks, but seems unlikely to lead to management options. Monitoring sites with histories of outbreaks might be employed for prediction of future outbreaks. Intervention through forest applications of chemical pesticides, *Bacillus thuringiensis,* or baculoviruses might be of value at sites where tree mortality is likely (sites defoliated in previous year), if these are of sufficient value to justify the cost of the treatment (perhaps, sugar maple stands used for sugaring).

62. BALSAM GALL MIDGE (*Paradiplosis tumifex* Gagné) (Diptera: Cecidomyiidae)

Origin: Balsam gall midge is apparently native to North America.

Range in North America: This species is probably found in North America throughout the range of its hosts, balsam fir (*Abies balsamea*) and Fraser fir (*Abies fraseri*) (Drooz 1985).

Damage: This species is of concern in Christmas tree plantations. Needles that are galled by this pest fall off trees in late October. Heavy infestations make trees unsaleable as Christmas trees. Older literature mistakenly credits gall formation to another midge, *Dasineura balsamicola* (Lintner), which is now known to be an inquiline that invades the gall, feeding on gall tissue and subsequently killing the gallmaker (Osgood and Gagné 1978, Shorthouse and West 1986).

Resident Natural Enemies: Recent studies have clarified which natural enemies associated with these needle galls are parasitoids of the gallmaker and which attack the inquiline. The encyrtids *Pseudoencyrtus borealis* MacGown, *Tetrastichus cecidivorus* MacGowan (MacGown 1979) and *Tetrastichus marcovitchi* (Crawford), *Tetrastichus whitmani* (Girault), and the platygasterids *Platygaster abicollis* MacGown and Osgood and *Playtgaster mainensis* MacGown and Osgood (Connor and Osgood 1979) are now known to be parasitoids of *P. tumifex*. The biologies of these parasitoids are reviewed by Räther and Mills (1989).

Another source of mortality affecting the needle gallmaker is the leaf rust fungus *Uredinopsis mirabilis*, which causes early needle abscission and results in the death of the gallmaker when galled needles are affected (Bergdahl and Mazzola, 1985).

Biological Control Attempts: The importation of parasitoids from related gall midge species in Europe has been proposed. The redistribution of the North American inquiline (*Dasineura balsamicola*) to plantations where it does not occur has also been suggested (Räther and Mills 1989). Neither of these steps have been taken.

Reasons for Pest Status and Possibilities for Biological Control: Too little is known about this species to identify potential reasons for its typical population levels.

Recommendations: Studies of this species' population dynamics in Christmas tree plantations, especially with regard to effects of common silvicultural practices, would be useful.

63. PINE FALSE WEBWORM (*Acantholyda erythrocephala* [Linnaeus]) (Hymenoptera: Pamphiliidae)

Notes: A former generic placement of pine false webworm is in *Lyda*.

Origin: Pine false webworm is an exotic species in North America that occurs in Europe and various parts of Russia. Early notes on the invasion of the species into North America are given by Rohwer (1927) and Griswold (1939). For a short synopsis, see Lyons (1995).

Range in North America: In North America, this species is found in Connecticut, New Jersey, New York, Pennsylvania, the Great Lake States, and Ontario, Newfoundland and Alberta (Drooz 1985, Lyons 1995).

Damage: In North America, local outbreaks defoliate plantations of the species' preferred hosts, red and white pines. This species is listed as the most important defoliating insect pest of red pine plantations in southern Ontario (Lyons 1994). In Europe, outbreaks also are reported in various locations such as Germany (Schwerdtfeger 1941, Austria (Jahn 1967), and Russia (Galkin 1979).

Resident Natural Enemies: In Europe the tachinid *Myxexoristops hertingi* Mesnil and the ichneumonid *Xenoschesis fulvipes* attack this sawfly (Schwerdtfeger 1944, Herting 1957) and are credited with causing the collapse of an outbreak in Germany (Rumphort and Goossen 1960). In Austria, a nuclear polyhedrosis virus has been noted attacking this sawfly (Jahn 1967). Laboratory studies suggest that this species is susceptible to the microsporidian *Pleistophora schubergi* (Wilson 1984a). Reports on natural enemies of this sawfly in North America were not found.

Biological Control Attempts: Tests of the efficacy of releases of *Trichogramma minutum* have been conducted.

Reasons for Pest Status and Possibilities for Biological Control: This species is a pest in pine plantations in both Europe and North America. Comparative data were not found to evaluate whether the pest is a greater problem in North America than in Europe. Potentially, this species may be damaging in plantations in all areas simply because conditions there favor the pest and are unfavorable for natural enemies of the pest. Opportunities exist to import natural enemies of this species from Europe into North America. These may be of value, or their efficacy may be limited if plantation conditions are inherently unsuitable for these natural enemies.

Recommendations: Comparative studies need to be conducted in Europe on population dynamics, to define the parasitoid complex and the magnitude of mortality it causes, in both plantations and natural forest stands. These results would allow a determination as to whether importations of European natural enemies of this sawfly would have potential to provide control in North America under plantation conditions.

64. RED-HEADED PINE SAWFLY (*Neodiprion lecontei* [Fitch]) (Hymenoptera: Diprionidae)

Notes: Former generic placements of red-headed pine sawfly include *Diprion* and *Lophyrus*. The genus *Neodiprion* was erected by Benson (1939), with *lecontei* being designated as the type species. Atwood (1961) reviews species of Diprionidae in Ontario.

Origin: Red-headed pine sawfly is native to North America.

Range in North America: Red-headed pine sawfly is found in southeastern Canada and throughout the eastern United States (Drooz 1985).

Damage: Periodic high density populations of this species defoliate species of pines, especially jack, red, and short-leaf pines (Beal 1942, Drooz 1985). Benjamin (1955) lists outbreaks that have occurred in the eastern United States.

Resident Natural Enemies: A list of 58 species recorded from the literature as attacking red-headed pine sawfly is given by Benjamin (1955). Species recorded by Benjamin (1955) as being important in Illinois include the egg parasitoid *Closterocerus cinctipennis* Ashmead and the larval parasitoids *Spathimeigenia spinigera* Townsend and *Phorocera hamata* Aldrich and Webber. Baldwin and Coppel (1949) discuss the details of the biology of the tachinid *P. hamata*, which parasitized 11% of the larvae in a study in Ontario. Another species, *Perilampus hyalinus* Say, was noted to be an important parasitoid in Ontario (Riodan 1963). This species, sometimes recorded as a hyperparasitoid, is generally a primary parasitoid in sawflies (Bird 1971). Bird (1971) lists four egg and four larval parasitoids. Some of the parasitoids that attack this species, together with other sawflies, include *Pleolophus basizonus* (Grav.) (Price 1970) and *Dahlbominus fuliginosus* (Nees) (Smirnoff 1971). Parasitoids noted from this sawfly in the southern part of its range, in Florida, include *Spathimeigenia* spp. and *Diplostichus lophyri* (Tns.) (Drooz *et al.* 1977). Keys to classify remains of parasitoids found in association with *N. lecontei* in Ontario are given Finlayson (1963).

The above articles indicate which species of parasitoids are most often associated with red-headed pine sawflies. Very little information exists, however, about the quantitative importance of these parasitoids as causes of population fluctuations or average density of this sawfly.

Most research on natural enemies of red-headed pine sawfly has focused on pathogens. This species is susceptible to a highly virulent nuclear polyhedrosis virus that is transmitted both vertically in the eggs, and horizontally between larvae (Bird 1961). The first successful use of this virus for sawfly suppression in the field was achieved by Kaupp and Cunningham (1977). Field trials of this pathogen (called Leconte virus) showed that applications of five billion polyhedral inclusion bodies per hectare gave 100% control within two weeks in trials in Michigan and Wisconsin (Podgwaite *et al.* 1986). Methods to produce the virus are described by Cunningham and McPhee (1986). Efforts to develop Leconte virus for commercial use through aerial application are reviewed by Cunningham and De Groot (1984) and Cunningham

et al. (1986). While highly effective biologically, demand for Leconte virus has been too small to justify the cost of production of this virus and its registration as a pesticide.

In contrast, little work has been done with *Bacillus thuringiensis*, other than to determine that this sawfly is susceptible to some strains of this pathogen (Shaikh and Morrison 1965). The same is true for the microsporidian *Thelohania pristiphorae*, which has been shown in laboratory trials to be able to infect *N. lecontei* larvae in feeding trials (Smirnoff 1974).

Biological Control Attempts: The only attempt to control red-headed pine sawfly through biological control has been the development of Leconte virus as an augmentative biopesticide, as discussed above.

Reasons for Pest Status and Possibilities for Biological Control: Because the principal effort to suppress this pest sawfly has been directed at the development of the Leconte virus as a biopesticide, relatively little work has been done on the population dynamics of this species. Consequently, little is known about reasons for the periodic outbreaks of the species. Bird (1971) attributes increased problems with this species in Canada since the 1930s to increased planting of pure pine plantations.

Recommendations: Leconte virus as a biopesticide is highly effective biologically. Its current lack of use is due to the small demand for control of this species. Should problems from this species increase significantly, the economic feasibility of the use of Leconte virus should also increase. For this reason, no new efforts to develop biological control methods against red-headed pine sawfly are needed.

65. SWAINE JACK PINE SAWFLY (*Neodiprion swainei* [Middleton]) (Hymenoptera: Driprionidae)

Notes: Former generic placements of Swaine jack pine sawfly include *Diprion* and *Lophyrus*.

Origin: Swaine jack pine sawfly is apparently native to North America, and was originally described from specimens collected in Quebec (Middleton 1931).

Range in North America: This species is present in Minnesota, Michigan, Wisconsin Ontario, and Quebec (Becker and Benjamin 1964, Drooz 1985).

Damage: The preferred host is jack pine (*Pinus banksiana* Lamb.). Outbreaks have been reported at about 8-year intervals in jack pine stands in Quebec and Ontario, especially in stands on sandy sites (Drooz 1985). The species is considered one of the more important forest pests in Quebec in recent years (Anon. 1991). Becker and Benjamin (1964) discuss the biology and seasonal history of the species in Wisconsin.

Resident Natural Enemies: Natural enemies reported attacking *N. swainei* include parasitoids, predators, and pathogens.

All the immature stages of *N. swainei* are attacked by parasitoids in North America. Egg parasitoids include *Closterocerus cinctipennis* Ashmead and *Tetrastichus silvaticus* Gahan

(Lyons 1962). Laval parasitoids include the perilampid *Perilampus hyalinus* Say (Tripp 1962a) and the ichneumonid *Exenterus amictorius* (Panzer) (McLeod 1972), both of which are native; and the introduced European ichneumonids *Exenterus amictorius* (Panzer) (McLeod 1972) and *Pleolophus basizonus* (Grav.) (Price 1970), both of which were imported for control of other exotic diprionids in Canada. Becker and Benjamin (1964b) report on the parasitoids attacking this sawfly in Wisconsin.

The important groups of predators are those that prey on cocoons of the sawfly on the ground. These include carabids (Tostowaryk 1972) and small mammals, such as species of *Sorex* (MacLeod 1966).

Pathogens affecting *N. swainei* include a nuclear polyhedrosis virus (Smirnoff 1959, 1961), which has been used successfully as a biopesticide to suppress this sawfly in forest stands (Smirnoff *et al.* 1962). The microsporidian *Thelohania pristiphorae* has been shown in laboratory tests to also attack *Neodiprion swainei* (Smirnoff 1974a). In Quebec, the flagellate protozoa *Herpetomonas swainei* Smirnoff is found infecting *N. swainei* and reduces adult emergence from 55% for uninfected cocoons to 20% (Smirnoff 1974b).

Quantitative considerations of the mortality caused by natural enemies to *N. swainei* populations are limited. Price and Tripp (1972) quantified sources of mortality for an *N. swainei* population in Quebec and concluded that, while unable to prevent occasional outbreaks, parasitoids attacking *N. swainei* cocoons were beneficial and important. Mortality of cocoons from parasitism at the site studied by Price and Tripp (1972) reduced the overwintering cocoon population by 66%. Life tables for a population of *N. swainei* in Quebec over a 12-year period were developed by McLeod (1975). These showed a cyclic trend in levels of mortality from parasitism.

Biological Control Attempts: The artificial employment of the nuclear polyhedrosis virus of this species has been tested and found successful under field conditions, but is not in commercial use at this time. No parasitoid introductions have been targeted against this sawfly, but parasitoids introduced for other diprionids have included this species in their host range and become important sources of mortality for the species.

Reasons for Pest Status and Possibilities for Biological Control: The periodic outbreaks of this sawfly are attributed by Tripp (1965) to weather, site, and stand conditions that favor early emergence of adult sawflies, followed by rapid development of the immature stages. Such early and rapid development permits cocoon formation to be completed earlier when weather conditions are more favorable (in northwestern Quebec, the study site) for spinning of cocoons. Dense stands of jack pine typically do not present these conditions, explaining the observation that outbreaks are concentrated in warmer, more open habitats such as windbreaks, plantations, and stands on poor, sandy soils (Tripp 1965).

Fluctuations in fecundity of sawflies is also indicated as an important factor affecting population trends. Adults that were poorly fed as larvae, or that were parasitized but encapsulated the parasitoid, or that passed two winters in diapause, all exhibited reduced fecundity (Tripp 1962b, Lyons 1970). While a nuclear polyhedrosis virus has been noted attacking the species, there are no indications in the literature whether population outbreaks are related to host-pathogen cycles.

Recommendations: Because this species remains at nonpest levels at most sites, suppression tactics need not be broad based, but rather should be targeted to those locations prone to damage. Importation of parasitoids is not recommended, but rather the development of a government-assisted system to employ the nuclear polyhedrosis virus. Market considerations make it unlikely that this virus will be commercially attractive for development. Consequently, virus preparations would be applicable only if a broad spectrum virus (developed for other, larger markets) could be used effectively. At present this is not the case. As an alternative, government efforts to produce, store, and provide the specific virus attacking *N. swainei* should be considered. Such a process would require reduction in the costs to register such products for use (through altered registration standards for such viruses by the U.S. Environmental Protection Agency), and government commitment to produce and store virus against future needs, as they might arise.

Interactions with management on lands surrounding pine stands may also affect the likelihood of sawfly outbreaks. Conversion of lands in Quebec to blueberry production increased *N. swainei* numbers on adjacent pine stands (Smirnoff 1971b). This increase occurred because scattered pines left in blueberry fields to protect bumblebee nesting areas to promote pollination were highly favorable to this sawfly, which does well in full sun.

66. VIRGINIA PINE SAWFLY *(Neodiprion pratti pratti* [Dyar]) (Hymenoptera: Diprionidae)

Origin: Virginia pine sawfly is native to North America (Rennels 1973).

Range in North America: This species has been recorded from New Jersey to North Carolina, and west to Illinois (Drooz 1985).

Damage: This species is typically of little importance, but at times densities increase to levels that cause defoliation of various pines, especially Virginia pine, *Pinus virginiana.* An outbreak in Virginia in 1957-1960 covered 5.6 million acres (Bobb 1965, Droz 1985).

Resident Natural Enemies: Under outbreak conditions, Bobb (1965) reported parasitism of larvae of *N. pratti pratti* in Virginia to be very low (1-3%), but parasitism of noncocooned prepupae on the ground to be high (40-56%). Most parasitism was caused by the ichneumonid *Exenterus nigrifrons* Rohwer which was referred to erroneously in this article as *E. canadensis* Provancher, a different species. Cocooned prepupae were attacked at significant levels by the fungus *Beauveria bassiana* and various species of predacious ants, as well as a variety of parasitoids. Among the parasitoids was *Dahlbominus fuscipennis*, an introduced parasitoid moved secondarily from New Jersey to Virginia (Bobb 1964a, 1965). Other natural enemies that have been noted attacking this species include the eulophid egg parasitoid, *Closterocerus cinctipennis* Ashmead (Morris and Schroeder 1966) and a nuclear polyhedrosis virus (McIntyre and Dutky 1961). Application of this virus as a microbial pesticide killed 90% of larvae under field conditions (McIntyre and Dutky 1961).

Biological Control Attempts: The parasitoid *Dahlbominus fuscipennis*, introduced into North America for control of other pest sawflies, was moved from New Jersey to Virginia for control of *N. pratti pratti.* It established and causes some mortality to this pest sawfly (Bobb 1965).

Reasons for Pest Status and Possibilities for Biological Control: No suggestions have been made as to why outbreaks of this native sawfly sometimes occur. Similarly, causes of the collapse of outbreaks are poorly defined. While mortality of the cocooned stages exceeded 80% during the collapse of the Virginia outbreak of 1957-1960, this was felt to be insufficient to have been the sole cause of the collapse (Bobb 1963). Rather, collapse was felt to be due largely to a sharp decrease in mating success of female sawflies during the outbreak, with a subsequent drop in population fecundity levels (Bobb 1963, 1964b). No fundamental explanation, however, has been advanced for this drop in mating success.

Recommendations: Outbreaks of this species appear to be infrequent. As such, no action is needed. Should outbreaks become more frequent or widespread, efforts to manage the species would require the development of information on the factors determining patterns of mortality and fecundity during nonoutbreak years to identify the mechanism that permits population outbreaks to be initiated. Should forest managers need a nonchemical tool to suppress outbreaks, use of this species' nuclear polyhedrosis virus would appear to be feasible biologically. The feasibility of this approach economically would depend on reducing the cost of production and registration of the virus.

67. INTRODUCED PINE SAWFLY (*Diprion similis* [Hartig]) (Hymenoptera: Diprionidae)

Notes: Other names for introduced pine sawfly cited in the literature are *Lophyrus simile* and *Diprion simile.*

Origin: Introduced pine sawfly is not native to North America. It occurs in Europe and Asia, including Norway (Schíyen 1915), Finland (Kangas 1963), Poland (Finlayson and Finlayson 1958), Germany (Scheidter 1926), Italy (Casale and Currado 1977/1979), Ukraine (Shiperovich 1927), western Siberia (Kolomiets 1966), the Cisbaikalia region of Siberia (Verzhutski 1965), eastern Siberia (Gulii 1971), and China (Xiao *et al.* 1983).

Range in North America: This species was first recorded in North America in Connecticut in 1914 (Britton 1915). Currently it is found in the United States from Maine through Minnesota, south to North Carolina, Tennessee, and Virginia, and in Canada, in southern Ontario, Quebec (Drooz 1985), and, most recently, parts of Manitoba (Wong and Tidsburg 1983).

Damage: Dense populations may defoliate various species of pines, especially eastern white pine (*Pinus strobus*).

Resident Natural Enemies: Diprionid sawflies of several species have been observed to share parasitoids with *Diprion similis*, both in Europe and North America. Observations on the natural enemies of *D. similis* in Europe have been made principally in Poland, largely in connection with efforts to obtain parasitoids for introduction either into Canada against other adventive diprionid pest species, or into the United States against the gypsy moth. Nineteen species of parasitoids have been reared from *D. similis* in Poland (Hardy 1936, Finlayson and Finlayson 1958). Parasitoid species reported by both of the above cited studies include *Aptesis subguttatus* (Grav.), *Aptesis basizonia* (Grav.), *Exenterus amictorius* (Panzer), *Exenterus adspersus* Hartig., *Palexorista inconspicua* (Meigen), *Hypsantyx impressus*

(Grav.), and *Monodontomerus dentipes* (Dalman). *Palexorista* (also given as *Sturmia* or *Drino*) *inconspicua* is stated by Webber (1932) to be the most important tachinid parasitoid of *D. similis* in Europe. Hardy (1936) analyzes mortality from predation, disease, and parasitism and concludes that, after allowances for hosts subject to two or more mortality factors, parasitoids accounted for 16% to 31% of the mortality of *D. similis* cocoons, with mortality from parasitism being lowest in April, and increasing thereafter. One parasitoid, *Dahlbominus fuscipennis* (Zetterstedt), was mass reared in Poland and released into pine forests for sawfly control (Szmidt 1959).

Biological Control Attempts: Some European species of parasitoids that attack *D. similis* have been introduced and established in North America. These were, for the most part, directed against other species, such as other exotic diprionids or the gypsy moth. Effects of these introduced parasitoids are documented in studies from the northeastern United States, the Great Lakes States, North Carolina, and Canada.

In the northeastern United States, nearly 50% of *D. similis* larvae in Connecticut were parasitized by a complex of eight parasitoid species, especially *Monodontomerus dentipes* (Britton and Zappe 1917). *Monodontomerus dentipes* was later recorded as one of the most important parasitoids of *D. similis* in Pennsylvania and New Jersey (Hartley 1923).

Surveys of parasitoids that can be reared from cocoons of *D. similis* have been conducted in Minnesota and Wisconsin. In Minnesota, the most common species have proved to be *Exenterus amictorius* (a European species), *Monodontomerus dentipes*, and *Delomerista japonica* Cushman (Thompson *et al.* 1977a). Of these, the most prevalent, *E. amictorius*, caused up to 44% mortality in some cases. Parasitism by the later two species was higher in the second generation. Parasitism was greater in cocoons collected from foliage than in those extracted from the duff beneath trees (Weber 1977). Work on this pest sawfly in Wisconsin has resulted in the preparation of a key to separate the various parasitoid species reared from *D. similis* (Mertins and Coppel 1971), as well as a literature review on *D. similis* (Coppel *et al.* 1974)

Diprion similis did not invade the southern United States until the 1970s (Drooz *et al.* 1985a), and in that region, few parasitoid species were found attacking the pest. Several species of cocoon and egg parasitoids were collected in Wisconsin and introduced into North Carolina (Drooz *et al.* 1985a), among which was *Monodontomerus dentipes*. This species became abundant and is credited with controlling the pest in North Carolina (Ghent *et al.* 1982). Its biology is reviewed by Fedde (1974).

In Canada, releases of *Monodotomerus dentipes* were made against *D. similis* in Quebec (Finlayson and Reeks 1936). In addition, the ichneumonid *Pleolophus basizonus* (Grav.), originally released in Canada for control of other sawflies, has been recorded as parasitizing *D. similis* in Quebec (Price 1970).

Reasons for Pest Status and Possibilities for Biological Control: In Europe and Asia, *D. similis* is recorded occasionally as a pest, but of minor importance. In the United States, it is recorded as a pest of what appears to be a more intense or frequent nature, although not devastating. It is affected in the United States by a series of parasitoids, some native and some introduced from Europe. Population suppression following liberations of parasitoids to

newly infested areas (e.g., North Carolina) reinforce the view that pest status is reached where effective parasitoids are absent.

Recommendations: The currently established set of parasitoids that parasitize *D. similis* in the United States appear to suppress the pest adequately in many areas. Should the pest invade new parts of the United States by long distance disjunct movement (as on nursery plants), interstate shipment of parasitoids is recommended. Introduction of the tachinid *Palexorista inconspicua* to the southern United States may also be of value. If outbreaks are observed in regions in which the parasitoid species that generally control the pest are already established, outbreak populations should be sampled to determine if the key parasitoids are present locally at the outbreak sites. If key parasitoids are not present, the silvicultural practices employed at the site should be evaluated to determine their effects on key parasitoids and their alternate hosts.

68. EUROPEAN SPRUCE SAWFLY (*Gilpinia hercyniae* [Hartig]) (Hymemoptera: Diprionidae)

Notes: Earlier generic placements of European spruce sawfly include *Lophyrus* and *Diprion* (Enslin 1916). *Gilpinia* was erected by Benson (1939), who made *G. polytomus* Hartig the type species. The European spruce sawfly in North America was originally thought to be the same as *G. polytomus* in Europe and much of the early literature is under this name. Balch suggested that the population in Canada might be distinct from that in Europe, based on differences in biology and chromosome number and the Canadian population was later described as a distinct species, *G. hercyniae*, by Balch *et al.* (1941). *Gilpinia hercyniae* is a different species from *G. polytoma*, but is identical to a previously unrecognized thelytokous strain in Europe, from which the Canadian population is believed to have come. Confirmation of the distinctness of *G. hercyniae* from *G. polytoma* was confirmed by Forster (1949) by examination of Hartig's type specimens. An annotated bibliography for *G. hercyniae* is provided by Adams and Entwistle (1981).

Origin: The European spruce sawfly in North America is an exotic species from Europe (Balch *et al.* 1941). It was first noted in small numbers in North America in 1922 in Ontario (Clausen 1978). By 1932 a defoliating outbreak in the Gaspe Peninsula of eastern Canada covered 2000 square miles and was expanding rapidly (Balch and Simpson 1932).

Range in North America: A world map of *G. hercyniae*'s range is provided by Anon. (1953), and a map of the Canadian distribution by Magasi and Syme (1984). In North America, this sawfly is found in southern Canada from the Maritimes, west to the beginning of the prairie provinces. In the United States, *G. hercyniae* is present in the northeastern States, west to the Great Lake States (Drooz 1985).

Damage: The history of damage from this species in North America consists of one large outbreak that started in the Gaspe Peninsula in Quebec in the early 1930s (Balch and Simpson 1932) and spread rapidly west, north, and south. By 1932, the pest was recorded from the State of Maine in the United States (Anon 1932). The Gaspe Peninsula infestation expanded rapidly from 2000 square miles in 1932, to 4000 in 1934, and 6000 in 1935. It later reached 140,000 square miles, with about 25,000 square miles of this in the United States (Balch and Simpson 1932; Balch 1934, 1935). By 1940, an introduced disease and several

species of parasitoids initiated the start of the collapse of this outbreak (Balch 1942), as discussed under Biological Control Attempts. Minor outbreaks continued to occur for some years on the edge of the species' range. In these areas, the pest temporarily outpaced the expansion of the ranges of the virus and parasitoids. Reeks and Barter (1951) review the economic losses from the 1930-1942 outbreak in Canada and note that in the Gaspe Peninsula, where damage was greatest, some 11,400,000 cords of spruce wood was lost.

Resident Natural Enemies: Native parasitoids rarely attack this exotic sawfly, causing less than 1% mortality (Balch 1935, Reeks 1938). Native predacious mammals, however, readily adopted this sawfly into their prey range, causing up to 50% mortality (Morris 1942, Dirks 1944).

Biological Control Attempts: Importations of parasitoids from Europe against the European spruce sawfly were begun immediately after detection of the Gaspe outbreak and were carried out on a massive scale. Literally millions of sawfly cocoons and eggs were collected in Europe and their parasitoids reared and shipped to Canada. In Canada, certain species were mass reared to provide larger numbers for release. Finlayson and Reeks (1936) record the early collections, which were made largely in Germany and Czechoslovakia, from which over 3.5 million parasitoids were obtained for release in Quebec and New Brunswick in 1935 and 1936. Some 12 species were included in these early releases. By 1937, some 28 million parasitized cocoons or eggs had been collected and shipped to Canada (Morris *et al.* 1937). Parasitoids were collected from a variety of diprionid sawflies and, in the early part of the project, the true target pest was not recognized. The closely rated species *G. polytoma* was often the closest species from which collections were made.

Overall, some 30 species of parasitoids were collected from Europe and Japan, and introduced into Canada. Tables documenting the species, countries of origin and fate of these species are given by Finlayson and Finlayson (1958), Clausen (1978), and Neilson *et al.* (1971). Biological notes on some 27 species of sawfly parasitoids encountered in Europe for potential introduction to Canada are given by Morris *et al.* (1937).

Of the European parasitoids introduced to Canada that were mass reared, the species reared most extensively was *Dahlbominus fuscipennis* (Zett.) (referred to in the early literature as *Microplectron fuscipenne*). More than 392 million of this species were produced and released (Lambert 1941). Notes on the biology of this species are provided by Morris and Cameron (1935).

At least seven of the introduced species established (Bird and Elgee 1957), of which the first was *D. fuscipennis* in Quebec (Reeks 1937), followed by several species of *Exenterus*. Early literature on the *Exenterus* species that were released in Canada contains some misidentifications which were noted and corrected by Reeks (1952). The dominant species of introduced parasitoids attacking European spruce sawfly in North America changed as the sawfly's densities declined over the course of the biological control project against *G. hercyniae*. While sawfly densities were high, the dominant parasitoids were *Dahlbominus fuscipennis* and *Exenterus claripennis* (Thoms.). Later, when sawfly densities had declined by 90-95%, the dominant species became *Exenterus vellicatus* Cushman and the tachinid *Palexorista bohemia* (Mesnil) (Bird and Elgee 1957). This tachinid is referred to in much of the literature from the period of this project as *Sturmia bohemia* or *Drino bohemia*.

Evaluation of the effect of the introduction of these parasitoids on *G. hercyniae*'s densities in North America is complicated by the simultaneous accidental introduction of a viral disease of the pest. The first examples of larvae of European spruce sawfly in North America dying of a viral disease were noted in 1937 in Vermont and New Hampshire. By 1938 the disease had become common in the area and by 1939 was found throughout the region (Dowden 1940). The disease was first noted in the Gaspe Peninsula in 1939 (Lambert 1941), and by 1940 the disease was spreading and reducing sawfly populations in some areas (Balch 1941).

The virus continued to spread and cause high levels of mortality over an increasingly large area, particularly warm regions such as central New Brunswick (Balch 1942). By 1943, *G. hercyniae* populations were in marked decline, and the viral disease was identified as the most important cause (Brown 1943). Artificial inoculation of the disease into new areas was achieved by application of water extracts of moribund larvae from areas undergoing epidemics, resulting in self-sustaining epidemics in the new locations (Balch and Hawboldt 1943, Bird and Burk 1961). By 1946, epidemics of this viral disease had declined as sawfly populations were reduced in most areas. The disease continued to be present and, together with the introduced parasitoids, continued to suppress the pest (Balch and Reeks 1946). Morris (1949), using frass collectors to measure sawfly larval density, showed that mortality from virus was higher in areas with higher sawfly densities.

The virus is transmitted when healthy larvae consume foliage contaminated by virus from cadavers of diseased larvae. Longer range spread of the virus can also occur through parasitoid oviposition (Bird 1961) or defecation of birds which have eaten diseased larvae (Entwistle *et al.* 1977). Survival of the virus over the winter was thought by Bird (1961) to be based on transovarial transmission (inside eggs of sublethally infected survivors), but this was later questioned by Neilson and Elgee (1968) who thought that virus survived externally on contaminated females. In the United Kingdom it has been shown that infective virus can survive the winter on foliage (Entwistle and Adams 1977).

How the virus arrived in North America is not explicitly known. The virus is thought to have been accidentally imported together with the large number of sawfly parasitoids brought in from Europe in the course of this biological control project, and then to have been spread by infected parasitoids as these were reared and released (Balch and Bird 1944).

Together, the parasitoid introductions and accidental introduction of the viral disease resulted in a widespread reduction of *G. hercyniae* of 90-95%. Mortality from disease has fluctuated, with levels of 60-90% in some years (Dirks 1944) and declines in mortality from virus following collapses of sawfly populations. Quantitative data documenting the decline of the sawfly are provided by Bird and Elgee (1957). In their study plots cocoon densities fell from 1.5 to 0.1 per square feet from 1932 to 1942. Data are also provided on the proportion of larvae killed by parasitoids and disease in each generation from 1944 to 1954, documenting the fluctuating importance of each source of mortality. The continued importance of parasitoids in this system is confirmed by the observed termination of the 1952 outbreak in this study by parasitoids, not disease. A long term analysis of population dynamics of this species, suggests that a permanent, stable reduction of over 90% in the density of this pest was achieved. Both disease and parasitoids remain important sources of mortality, with parasitoids acting at low densities and virus acting at higher densities (Neilson and Morris 1964).

Reasons for Pest Status and Possibilities for Biological Control: The outbreak of this sawfly that began in North America in the 1930s was without doubt caused by this species' invasion of a favorable new habitat with ample suitable host plants, favorable climate, and no effective parasitoids or diseases. This is confirmed by the subsequent permanent reduction in sawfly density that occurred after the establishment in North America of various parasitoids and a viral disease affecting the sawfly in Europe (Neilson and Morris 1964).

Recommendations: Biological control of this pest has been achieved, and no further action against it is needed. An opportunity might exist to increase understanding of the interaction of parasitoids and pathogens for control of forest insects by comparing the quantitative spatial and temporal rates of disease and parasitism in spruce sawfly to those in the gypsy moth. Gypsy moth has many similarities to spruce sawfly, but instead of stable reductions in the pest, population collapses of gypsy moth from virus are followed by unstable rebounds to high densities.

69. LARCH SAWFLY (*Pristiphora erichsonii* [Hartig]) (Hymenoptera: Tenthredinidae)

Notes: Early literature also refers to larch sawfly as *Nematus erichsonii* or *Lygaeonematus erichsonii* or with the specific epitaph spelled *erichsoni*.

Origin: The origin of larch sawfly, and indeed whether a single entity or several are present in North America, has been debated extensively, without conclusive resolution (Coppel and Leius 1955, Jardon *et al.* 1994). Evidence that the species might be an exotic species that had invaded North America consists of the observation that the species was not recorded with certainty in North America before 1880, and that records appeared to support a pattern of westward spread, especially invasion of British Columbia (Hopping *et al.* 1943, Ives and Muldrew 1984). Further support for this belief comes from Pschorn-Walcher's (1963) analysis of the relative richness of natural enemy complexes affecting the pest in various countries versus the depauperate fauna in North America, which suggests that the species is an invader.

Evidence for native status is principally as follows:

(1) The species was not recorded in Europe until 1840, an area where it clearly is native. Therefore the absence of records in North America before 1880 could have been due to a lack of economic interest in the swampy habitat in which the insect occurred.

(2) Tree ring analysis suggests that larches in North America have suffered growth reductions before 1880 that are consistent with the observed effects of defoliation (Graham 1929). This evidence, however, is inconclusive because growth reduction from defoliation cannot be separated from that due to drought or other climatic events.

(3) Direct observations of defoliated larch stands that were seen by travelers before 1880 and a pre-1880 record in North America of a species later declared a synonym of *P. erichsonii*.

Ultimately, a morphological study of larch sawflies from various countries and locations concluded that more than a single strain of the larch sawfly existed (Wong 1974). This study asserted that five strains (termed Aweme, Fernie, Ambleside, Thirlmire, and Salzburg) existed which could be distinguished based on morphological details previously overlooked. Wong (1974) classified available museum specimens of larch sawfly from different locations and years (into his morphological strains) and studied the actions taken by Hewitt (1917) and Criddle (1928), who released in Canada live sawfly cocoons that had been collected in Europe. Based on these efforts, he stated that the five morphological strains represented populations with different origins, histories, and biological properties.

The Aweme and Fernie strains were strains present in North America before 1900. Their origins (native or introduced accidentally at some earlier time) could not be determined. The Ambleside and Thirlmire strains were introduced into North America as cocoons collected in the United Kingdom by Hewitt and transported to Canada for parasitoid release without any quarantine to exclude viable individuals of the host species (which was believed to already occur in Canada, and so thought not to be dangerous). While both from Europe, the Ambleside and Thirlmire strains differed biologically in their ability to encapsulate a key parasitoid. The Salzberg strain is another population present in Europe, not found in North America.

Furthermore, because the strains present in North America by 1920 differed in their ability to encapsulate the ichneumonid parasitoid *Mesoleius tenthredinis* Morley, the presence of this parasitoid after 1920 caused the relative dominance of larch sawfly strains to change. The Ambleside strain showed resistance to this parasitoid (via encapsulation) and gradually increased in abundance with respect to the other strains from 1940 to 1972 (Wong 1974). However the current dominance of the Ambleside strain that effectively encapsulates the strain of *M. tenthredinis* introduced from the United Kingdom by Hewitt may change. Such a shift may occur because a second strain of this parasitoid which is able to defeat the encapsulation abilities of the Ambleside strain of larch sawfly was later introduced from Bavaria (Eichhorn *et al.* 1965).

Range in North America: Larch sawfly occurs in all Canadian provinces, Alaska, all the northern tier of U.S. States, as well as Maryland, North Carolina, and West Virginia (Drooz 1985); however, distributions of individual sawfly strains differ. It is these strain-specific distributions that are critical in understanding the biological properties of larch sawfly in any particular region (see Drooz 1975).

Damage: Outbreaks of this species have occurred periodically in North America, affecting various species of larch, including eastern larch (*Larix laricina*), western larch (*Larix occidentalis* Nutt), and alpine larch (*Larix lyallii* Parl.). These outbreaks have been extremely damaging, killing a high proportion (up to 30%) of mature larch trees over vast areas (Beeson 1918, Ives and Muldrew 1984). In addition, dead or weakened trees that result from defoliation of larch stands by the sawfly appear to initiate outbreaks of the native bark beetle, the eastern larch beetle, *Dendroctonus simplex* LeConte.

Resident Natural Enemies: Natural enemies, now resident in North America, that are important to the population dynamics of larch sawfly include a tachinid (*Bessa harveyi*), a guild of native small mammals, and two introduced ichneumonid parasitoids, *Mesoleius tenthredinis* and *Olesicampe benefactor*.

(1) ***Bessa harveyi* (Townsend).** The native tachinid *Bessa harveyi* was formerly confused with a European species, *Bessa selecta* (Meigan), such that early North American literature refers to *B. selecta* when it means *B. harveyi* (Turnock and Melvin 1963). This tachinid has frequently been reported as being an important source of mortality (up to 44% of larvae) in larch sawfly populations, but seems incapable of suppressing outbreaks, showing no positively density dependent response (Hawboldt 1947, Ives and Muldrew 1984). Methods for its study have been developed (Ives and Prentice 1959).

(2) **Native small mammals.** A guild of native small mammals are important predators of sawfly cocoons in the soil (Graham 1921). Small mammals alone, however, appear to be unable to control sawfly populations. Direct manipulation of small mammals for sawfly control has not been attempted with one exception, the introduction and establishment of the masked shrew (*Sorex cincereus* Kerr) in Newfoundland in 1958 (Warren 1971).

(3) ***Mesoleius tenthredinis* Morley.** Of the various parasitoids that have been imported to combat the larch sawfly in North America (see Clausen 1978 for a list), two ichneumonids, *Mesoleius tenthredinis* and *Olesicampe benefactor*, have been of greatest importance. *Mesoleius tenthredinis* has been imported into North America twice. The first importation was from the United Kingdom into Quebec and Manitoba by Hewitt (1917), and later by Criddle (1928). This strain of the parasitoid was effective in parasitizing the Aweme and Fernie strains of the sawfly and appeared to suppress larch sawfly in eastern Canada from 1920 to approximately 1940 (Graham 1931, Ives and Muldrew 1984). After that time, however, effectiveness declined due to increased rates of encapsulation by the host (LeJeune 1948, Drooz 1952).

The increase in encapsulation was not due, as first thought (Muldrew 1955), to development of resistance by the original sawfly population, but rather by the selective replacement of the original sawfly strains (Aweme and Fernie) in Canada by a newly introduced strain (Ambleside), which already had the ability to encapsulate this parasitoid. This sawfly strain gained entrance to Canada, as noted above, because live larch sawflies from Europe (inside cocoons) were released in the field in Canada along with the imported parasitoids. The U.K. strain of *M. tenthredinis* remained effective longer in British Columbia, presumably because the resistant Ambleside strain had not moved yet from Manitoba to British Columbia (McLeod 1954).

To correct the problem of the failure of the U.K. strain of *M. tenthredinis* to continue to control the Ambleside strain of the sawfly, studies of the parasitoid complexes associated with larch sawfly in Europe and Japan were undertaken (Eichhorn *et al.* 1965, Pschorn-Walcher and Zinnert 1971). One of the consequences of this effort was the introduction of a second strain of *M. tenthredinis*, collected in Bavaria (Germany), that was not susceptible to encapsulation by the Ambleside strain of the pest (Eichhorn *et al.* 1965). This strain was introduced into Canada and subsequently into the United States (Minnesota) (Kulman *et al.* 1974). Evidence for the establishment of this strain, however, is lacking (Thompson *et al.* 1977b).

(4) ***Olesicampe benefactor* Hinz.** The fourth important natural enemy of larch sawfly in North America is the ichneumonid *Olesicampe benefactor* (Hinz 1969, known earlier as *Olesicampe* sp. nr. *nematorum*). This parasitoid was first released in Manitoba

(Muldrew 1967) and later the United States (Embree and Underwood 1972). The species established and increased rapidly, causing high levels of parasitism (up to 59%) (Thompson *et al.* 1977b, Muldrew and Ives 1984, Drooz *et al.* 1985b). However, a previously established European hyperparasitoid, *Mesochorus globulator* (Thunberg) (=*Mesochorus dimidiatus* Holmgren), (Drooz *et al.* 1985b) increased in number and parasitized up to 70% of *O. benefactor*, whose parasitism rate then fell to much lower levels (Muldrew and Ives 1984).

Biological Control Attempts: Considerable effort has been made to understand the population dynamics of the larch sawfly and to suppress the pest through parasitoid introductions from Europe.

Natural enemy introductions occurred mainly in two periods. In the early part of this century (starting in 1910), Hewitt (1917) introduced *Mesoleius tenthredinis* from the United Kingdom to Quebec and Manitoba. It established and suppressed the sawfly. Subsequent appearance of damaging sawfly populations in British Columbia in the 1930s led to the redistribution of this species to that province. Details of these efforts, as well as notes on the introduction of the additional species, are given by Clausen (1978) and Ives and Muldrew (1984).

From about 1940, a second period of damaging sawfly outbreaks began. These were of the Ambleside strain that had been introduced accidentally by Hewitt (1917) and was able to encapsulate the eggs of *M. tenthredinis*. To combat this strain, a series of comprehensive surveys of the pest and its parasitoids in Europe were conducted starting about 1960 (Pschorn-Walcher and Eichhorn 1963, Pschorn-Walcher 1963, Pschorn-Walcher and Zinnert 1971). These surveys led to the introduction into Canada of a Bavarian strain of *M. tenthredinis* that was resistant to encapsulation by the Ambleside that stain of the sawfly (Eichhorn *et al.* 1965). Another parasitoid, *Olesicampe benefactor*, was also introduced (Muldrew 1967).

Coupled with these efforts, an extensive set of investigations were conducted to develop an in depth understanding of the population dynamics of the larch sawfly in North America (Graham 1921, Ives and Prentice 1959, Ives *et al.* 1968, Turnock 1972, Ives 1976). These investigations have provided life table analyses of the pest, as well as a series of sampling techniques for the estimation of densities of various stages of the pest, and estimation of death rates caused by various mortality factors.

Reasons for Pest Status and Possibilities for Biological Control: The root cause of the outbreaks of the larch sawfly in North America has been shown to be a depauperate parasitoid fauna. This certainly relates in part to some strains of the sawfly being exotic (e.g., the Ambleside and Thirlmire strains). Other strains (Fernie and Aweme) may be native or exotic (no clear way to decide), but in either case, they lack a well developed parasitoid complex. The control achieved by the subsequent introduction of parasitoids proves that lack of such parasitoids was the reason for the outbreaks and that parasitoid introductions would be valuable in permanently reducing outbreaks.

Recommendations: While a great deal has been achieved through previous natural enemy introductions, three points need to be made. First, harm was apparently done in the early

parasitoid introductions because quarantine measures were not followed, leading to the introduction of new, harmful strains of the sawfly. If the parasitoid-resistant strain of the sawfly had not been introduced, the early introduction of *M. tenthredinis* would likely have prevented further major outbreaks of larch sawfly.

Second, the establishment of the Bavarian strain of *M. tenthredinis*, needed to suppress the Ambleside strain of the sawfly, has not been confirmed (Ives and Muldrew 1984). New collections of this parasitoid in Bavaria should be made, and genetic markers sought that would make it possible to distinguish this strain from the earlier strain from the United Kingdom. Such markers would allow documentation of establishment and spread of the Bavarian strain.

Third, genetic marking methods now available offer a tremendous opportunity to reexamine Wong's (1974) interpretation of the strains of larch sawfly. This would be a valuable undertaking because the accurate recognition of all pest strains is critical to correctly understand the species and its biology relative to the biological control efforts that have been made. Such methods might also be able to settle the question concerning the origins of the Aweme and Fernie strains.

70. YELLOW-HEADED SPRUCE SAWFLY (*Pikonema alaskensis* [Rohwer]) (Hymenoptera: Tenthredinidae)

Notes: Before 1938, yellow-headed spruce sawfly was known as either *Pachynematus piceae* or *Pachynematus alaskensis* (Rose 1938).

Origin: Yellow-headed spruce sawfly is native to North America (Houseweart *et al.* 1984).

Range in North America: This sawfly occurs throughout the range of its principal host, white spruce (*Picea glauca*), in all of southern Canada, and from the northeastern United States to Idaho (Houseweart *et al.* 1984, Drooz 1985).

Damage: High densities of this species often occur in spruce plantations or sites of natural spruce regeneration, causing defoliation and reducing growth. Little damage occurs in stands with closed canopies (Houseweart *et al.* 1984). Trends in levels of defoliation can be forecast using traps baited with sawfly and parasitoid pheromones (Morse and Kulman 1985). Stand location and site characteristics can be used in a hazard rating system to predict risk of defoliation in specific spruce plantations (Morse and Kulman 1986). Silvicultural practices that reduce shading increase risk of defoliation by yellow-headed spruce sawfly. Risk of defoliation was increased sixfold by removal of competing vegetation in young spruce stands in Minnesota (Morse and Kulman 1984). Fertilization of plantations can also stimulate increases in sawfly densities (Popp *et al.* 1986).

Resident Natural Enemies: At least 32 hymenopteran and nine dipteran species have been recorded as primary parasitoids of yellow-headed sawfly in North America (Houseweart *et al.* 1984). Of these, the most common is the tachinid *Bessa harveyi* (Townsend) (Valovage and Kulman 1983). This tachinid was formerly confused with a European species, *Bessa selecta* (Meigan) (Turnock and Melvin 1963). The parasitoid complexes in Maine and Nova

Scotia are discussed by Thompson and Kulman (1980) and compared to that in Minnesota. The parasitoid complexes in these regions are very similar, and no opportunities for interregional transfer of parasitoids were identified.

The contribution of natural enemies to the regulation of population dynamics of the yellow-headed sawfly have been considered by Houseweart and Kulman (1976) who developed life tables for populations in Minnesota over a 3-year period. These tables show that eggs were not subject to any parasitism, that late larvae suffered from 2-20% mortality from parasitism, and that cocooned stages experienced high levels of mortality (67%) from predation by small mammals and insects. In a later study, Schoenfelder *et al.* (1978) used selective exclosures to separately estimate predation rates on cocooned stages due to small mammals and due to insects, and found that 45% of cocoons were consumed by small mammals and 20% by predacious insects.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Densities of yellow-headed sawfly are not reported to reach pest levels in stands with closed canopies. In addition, the parasitoid complex and predator guild attacking this sawfly in North America are rich in species and cause considerable mortality to sawfly populations. Damage appears to occur chiefly in sunny areas of spruce regeneration or in young plantations. From these observations, it can be hypothesized that natural enemies are less effective at these sorts of sunny sites or that sawflies are able to realize a higher level of fecundity, or both.

Recommendations: Studies should be conducted to compare life tables of yellow-headed sawfly at sunny sites (including both plantations and sites of natural spruce reproduction) where defoliation is known to occur, with sites with closed canopies where defoliation is not observed. These studies should compare rates of reproductive success of sawflies at each type of site, lists of species of natural enemies present at each type of site, and rates of mortality caused in each sawfly life stage by natural enemies. In addition, a review of the literature concerning parasitoids of other species of sawflies should be conducted to identify parasitoids from Europe or Asia that are effective in causing mortality in plantations and other sunny sites. These parasitoids should then be tested to identify species that are capable of attacking yellow-headed sawflies, particularly stages (eggs, young larvae) that are little attacked by the existing natural enemies in North America (Houseweart and Kulman 1976).

71. STEEL BLUE WOOD WASP (*Sirex noctilio* [Fabricius]) (Hymenoptera: Siricidae)

Notes: A former generic placement for steel blue wood wasp is *Paururus*. The early literature from New Zealand refers to *Sirex juvencus*, which is a separate valid species with which this sawfly was initially confused after its discovery in New Zealand (see Clark 1932). A key to the world genera of this family and the European species of *Sirex* is given by Benson (1943). Kirk (1974) discusses the native species of *Sirex* in the southeastern United States. A review of the bionomics of the Siricidae is given by Morgan (1968). Madden (1988) discusses the biology and population dynamics of this species in Australia.

Origin: Steel blue wood wasp is a European species (see Chrystal 1928, Benson 1943) that invaded New Zealand (Tillyard 1927), and later Australia (Mucha 1967, Bedding and Akhurst 1974, Morgan 1989), Brazil (Iede *et al.* 1988), and Argentina and Uruguay (Aguilar and Lanfranco 1988), and is likely to soon be found in Chile.

Range in North America: One record was found of *Sirex noctilio* in North America (Ontario, Benson 1943), however, this species is not mentioned further in North America. Either the record is an error, or the species failed to establish. International movement of *Sirex* spp. in timber shipments occurs periodically (e.g., Duffield 1927), however, and exotic siricids have established in the United States, e.g., the Formosan horntail (*Eriotremex formosanus* [Matsumura]) (Drooz 1985).

Damage: In general, damage from *Sirex* species is minor because most species attack mechanically damaged, suppressed, stressed, or dying trees (Clark 1932, Schimitschek 1968, Morgan 1968), not healthy ones. In the northern hemisphere, damage from siricids has been localized and of limited importance. In contrast, in the southern hemisphere in plantations of *Pinus radiata*, more extensive outbreaks have occurred following invasions of *Sirex noctilio.* During these outbreaks, young trees in a healthy condition have been attacked and killed (Cameron 1965, Haugen and Underdown 1990a, Bedding 1993).

The ability of *Sirex noctilio* to kill healthy trees seems linked to its production of copious amounts of a phytotoxic mucous, which is injected into the sapwood by ovipositing wood wasps and which interferes with the transport of water and starch (Coutts 1969). Other European wood wasps studied by Spradbery (1977) did not possess mucous that was as phytotoxic. Compounding the harmful effect of this mucous on the plant's transportation of water and nutrients is the growth in the wood of the symbiotic fungus (*Amylostereum areolatum*) (see Gaut 1969 for identity of the fungus) that is inoculated into the tree by the oviposting wood wasps (Clark 1933, Francke-Grosmann 1939, Vaartaja and King 1964, Bedding 1968, Coutts 1969). However, even in New Zealand and Australia, where losses have been large, overstocking and drought stress are still considered important contributing factors promoting tree susceptibility to this wood wasp (Nuttall 1989, Morgan 1989).

Resident Natural Enemies: Following the invasion of New Zealand by *S. noctilio* and the subsequent damage in pine plantations, studies were begun on the natural enemies of this wood wasp. Surveys to locate candidate natural enemies were conducted in Europe, the United States, and the Himalaya Mountains. Studies were later conducted in New Zealand and Australia on the biologies of these parasitoids and, after their field release, the effects they had on the target pest. A nematode of uncertain origin, first observed in New Zealand but likely native to somewhere else, was also studied. Relatively few reports of predators or pathogens (other than nematodes) were found. In this section, the key natural enemies are listed and references cited that concern their biology. In the following section on Biological Control Attempts, the history of the importations of these agents and the results are discussed.

Parasitoids. The ichneumonid *Rhyssa persuasoria* (L.) was reported attacking *S. noctilio* in Germany (Scheidter 1923). Following the invasion of this wood wasp into New Zealand, studies of its natural enemies were begun. *Rhyssa persuasoria* and *Ibalia leucospoides* Hochenwald were found in a study of this wood wasp in the United Kingdom (Chrystal and Myers 1928), and this report gives some details of the biologies and life cycles of these parasitoids. *Rhyssa persuasoria* has three generations for each

generation of its host, and was believed to be more important than *I. leucospoides* (Hanson 1939). Reviews of the *Sirex* programs in New Zealand (Taylor 1976, Nuttall 1989) and Australia (Taylor 1976, 1978; Morgan 1989) summarize the various species of parasitoids that were imported. In New Zealand, the parasitoids that established most readily and caused the greatest mortality to the wood wasp were *Ibalia leucospoides* and *Megarhyssa nortoni nortoni* (Nuttall 1989). In Tasmania, the parasitoids causing the greatest impact on the pest were *Megarhyssa nortoni* (Cresson) and *Rhyssa persuasoria* (Taylor 1978). Clausen (1978) discusses the biologies of *Ibalia leucospoides* and *Rhyssa persuasoria*. A key to the species of *Ibalia* found in North America is provided by Liu and Nordlander (1992).

Predators. While *Sirex noctilio* populations are undoubtedly subject to attack by predators, these have not been studied.

Nematodes and other pathogens. Zondag (1965) mentioned the occurrence of a nematode that was observed to be killing wood wasp larvae in several pine stands in the North Island of New Zealand. Following the collapse of the wood wasp populations in these areas, the nematode was suspected as being the responsible factor. The life cycle of this nematode, later named *Beddingia siricidicola* (Bedding) (earlier given as *Deladenus siricidicola* Bedding), proved complex, consisting of both a phase feeding on fungus and a phase parasitizing *Sirex* stages (Anon. 1967; Bedding 1968, 1993). The key to the nematode's effect on the wood wasp was the nematode's sterilizing action on adult females. For a discussion of the biology of the nematode's life cycles, see Bedding (1993). This sterilization effect was reported by Morgan (1989) to result in a 92% reduction in the wood wasp population's fecundity and to be the most important factor in the pest's life table. While discovered in New Zealand, this nematode may or may not be native to New Zealand. Nematodes were found in five siricid species and in three of the parasitoid species imported from Europe and India (Bedding 1968). However, *B. siricidicola* is not the same species as the nematode that was introduced in a parasitoid from the Himalaya Mountains (Zondag 1969). It is possible that the nematode was accidentally introduced in some other collection of wood wasps or their parasitoids, but no proof of this was located.

In addition to the nematode *B. siricidicola*, on which most attention has been focused, another pathogen reported as attacking *Sirex noctilio* in Germany is a cytoplasmic polyhedrosis virus (Schimitschek and Jahn 1967).

Biological Control Attempts: In broad outlines, the program of biological control against *Sirex noctilio* started in New Zealand and was based on the importation of parasitoids from Europe, India, and later the United States. The nematode *Beddingia siricidicola* was first observed in New Zealand and later moved to Australia, as were the more promising parasitoids. Eventually the impact of the nematode was large enough to overshadow that of the parasitoids, particularly in Australia.

Sirex noctilio invaded New Zealand in the late 19th century (Nuttall 1989) but was not considered important until the 1920s when tree mortality attributed to it began in pine plantations (Tillyard 1927). Shortly thereafter, parasitoid studies began in the United Kingdom, and the parasitoids *Ryssa persuasoria* and *Ibalia leucospoides* were found (Chrystal and

Myers 1928). Shipments of wood wasp parasitoids to New Zealand began soon thereafter (Myers 1928), and recoveries were made after releases (Miller and Clark 1937, Zondag 1959). Collections were also made in the Himalayas (Dharmadhikari and Achan 1965) and California (Zondag 1965). Details of the various collection locations, parasitoid species, and numbers of parasitoids released against *S. noctilio* in New Zealand from 1928-1968 are given by Nuttall (1989). By 1963-1964, wood wasps in the field infected with a previously undescribed nematode were reported in New Zealand (Zondag 1965). Nuttall (1989) and Clausen (1978) provide reviews of the *Sirex* biological control project in New Zealand. Evaluations of the outcome of work in New Zealand are limited. Levels of parasitism by *I. leucospoides* are usually 25-30% and can be as high as 55%. Total parasitism (all species) can reach 70% in local areas (Nuttall 1989). Information on the current importance of the nematode in New Zealand was not found.

By the early 1950s, *Sirex noctilio* had invaded Tasmania, and by the beginning of the 1960s had reached mainland Australia (Bedding 1993). Parasitoids from New Zealand were introduced to Tasmania by 1957 (Clausen 1978). Taylor (1976) lists the species of wood wasp parasitoids introduced to Australia and notes that five species had established: *Ibalia leucospoides*, *Megarhyssa nortoni*, *Rhyssa persuasoria*, *Ibalia rufipes* subsp. *drewseni* Borries, and *Schlettererius cinctipes* (Cress.). Parasitoids were redistributed to various parts of Australia by moving bolts cut from trees bearing parasitized hosts (Haugen and Underdown 1990b). Releases of the nematode *Beddingia siricidicola* were also made, both in Tasmania (Bedding and Akhurst 1974) and later in other pine-producing parts of Australia.

Taylor (1980) provides an analysis of the separate impact of the parasitoids in Tasmania, made before the nematode was introduced. Some part of the decline in wood wasp densities observed must be attributed to changing composition of the pine stands (proportion of susceptible trees) as well as to the action of the parasitoids. Taylor (1976) Morgan (1989), and Bedding (1993) provide historical reviews of the *Sirex* biological control program in Australia. Spradbery and Kirk (1978) summarize information on European species of *Sirex* and their associated parasitoids.

In Australia, the biological control of *Sirex noctilio* relied heavily on inoculation of susceptible pine stands with the nematode *B. siricidicola*, which was widely distributed in infested areas. To support inoculations of forest stands with the nematode, methods were developed to mass rear the nematode on autoclaved wheat inoculated with the wood wasp's fungal symbiont (*Amylostereum areolatum* for *S. noctilio*, but *A. chaillettii* for most other *Sirex* species). Using this system, the nematode was propagated in its fungal-feeding phase (Bedding 1993). Herbicides were used to kill trees to provide sample points to detect wood wasps in forest stands (Neumann *et al.* 1982). The abundance of the nematode in particular stands could then be assessed by cutting wood chips from 20 such *Sirex*-infested trees. The number of nematodes in such samples could then be used to estimate the proportions of *Sirex* larvae infected by nematodes using a predictive equation developed by Haugen and Underdown (1991).

This system for wood wasp suppression remained effective for several decades. However, eventually the infectivity of the laboratory nematode strain (reared for some 20 years in its non-parasitic, fungal-feeding form) to wood wasp larvae, declined to low levels. The laboratory strain then failed to provide control of the wood wasp in Australian pine plantations. Damaging field populations of the wood wasp developed in some areas (Bedding 1993). To suppress the wood wasp, it was necessary to again isolate from nature an effective parasitic strain to reinoculate areas that no longer had effective nematode populations.

To ensure future maintenance of this new strain's infectivity, stock cultures have been placed in liquid nitrogen, and new production batches are initiated yearly from this stock culture. To separate the infective strain from the former, now ineffective strain, DNA probes are being sought that will be specific to the new strain (Bedding 1993).

Reasons for Pest Status and Possibilities for Biological Control: The wood wasp *S. noctilio* became a serious pest in Australia and New Zealand, following its invasion of these areas. The wood wasp's pest status in these regions was facilitated by several factors, including the species' possession of a more phytotoxic mucous (compared with that of other members of the genus), escape from natural enemies, and extensive monocultures of Monterey pine under climatic and silvicultural conditions (overstocking of stands and periodic drought stress) that increased tree susceptibility to the pest. Biological control, in this setting, played a key role in suppressing the pest. Use of the nematode has provided sustained, effective control within stands following initial inoculation of the stand with the nematode. Movement of the nematode between forest stands, however, is unreliable and so mass rearing of the nematode and initial (but not repeated) inoculation is a critical feature of this biological control program. Parasitoids also play an important, but secondary, role as classical biological control agents not needing reinoculation.

Recommendations: The project in Australia has demonstrated the successful suppression of *S. noctilio* in Monterey pine plantations in mild climates. As *S. noctilio* invades new areas with similar climate and pine plantations, the nematode and parasitoids effective in Australia should be logical first choices for control. *Beddingia siricidicola* has, for example, recently been released in Brazil to suppress *S. noctilio* there (Vibrans 1991). Similar efforts in the future are likely to be needed in Argentina and Chile, and perhaps in parts of Africa. Success in new areas, however, may vary due to differences in climatic conditions and careful monitoring of initial results will be important.

A second lesson from this project is the importance of periodic assessment of the quality of reared natural enemies held in long term rearing programs. Loss of infectivity of the nematode reared for several decades as a fungal feeder shows that such processes are real and can have serious consequences unless controlled by periodic assessment.

Applicability of these results to the northern hemisphere is uncertain. Should *S. noctilio* invade the United States, many silvicultural and climatic conditions would be very different from those in Australia. It cannot be predicted how serious a pest *S. noctilio* would be in the United States or how effective the agents employed in Australia would be.

72. TWO-LINED CHESTNUT BORER (*Agrilus bilineatus* [Weber]) (Coleoptera: Buprestidae)

Origin: The two-lined chestnut borer is native to North America.

Range in North America: This species occurs throughout southeastern Canada and the eastern and central United States (Drooz 1985, Solomon 1995).

Damage: This borer attacks dying trees, mainly chestnut and several species of oaks (for an exact list, see Solomon 1995), starting at the tops of trees and progressing downward for two to three years until the tree is killed (Haack and Benjamin 1982). Proof that attacks are focused on dying trees, or trees in poor states of health has come from both correlation studies and manipulative experiments. Haack and Benjamin (1982) observed more attacks on trees in classification categories indicative of poor than good health. Cote and Allen (1980) observed higher arrival and attack rates of beetles on girdled trees than on healthy ones. Phloem-girdled trees remained attractive to beetles longer that xylem-girdled trees, which died too rapidly for beetles to successfully reproduce. Attraction appears to be mediated by volatile chemicals emitted by wounded trees (Dunn *et al.* 1986). Previous injuries, such as defoliation of oaks by gypsy moth (*Lymantria dispar*), increase attacks by this borer (Felt and Bromley 1944). After outbreaks of gypsy moth, two-lined chestnut borer attacks may cause significant mortality to defoliated oaks (18-79% in Connecticut, Dunbar and Stephens 1975). This borer, together with the fungal root pathogen *Armillaria mellea* (Vahl.), are important causes of decline in oaks (Wargo *et al.* 1983). While this pathogen is usually a saprophyte living on stumps and previously was thought not to attack living trees (Dunbar and Stephens 1975), it does attack roots of stressed trees and thus is a contributing factor to oak decline (Wargo *et al.* 1983).

Resident Natural Enemies: The literature on this species is reviewed by Smith and McManus (1968), and its biology, distribution, and control are discussed by Dunbar and Stephens (1976). A few parasitoids have been reared from the species, including the braconid *Atanycolus* sp. (Ruggles 1914) (probably *A. simplex* [Cresson], Kombein *et al.* 1979), and the braconids *Doryctes anatolikus* Marshall and *Spathius simillimus* Ashmead (Kombein *et al.* 1979). The most abundant parasitoid is reported to be the chalcidid *Phasgonophora sulcata* Westwood (Cote and Allen 1980, Haack *et al.* 1981), that attacks up to 10% of the borer population. See Solomon (1995) for a few additional records from the literature.

Predators associated with this borer include the trogositid *Tenebroides corticalis* (Melsh.) and the clerids *Phyllobaenus verticalis* (Say), *Phyllobaenus* sp., and *Cymatodera bicolor* (Say) (Cote and Allen 1980). Predation by woodpeckers sometimes causes high levels of mortality (up to 78%) (Cote and Allen 1980).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: None of the above mentioned studies examined the fundamental reasons for the characteristic densities of this

species, and the studies provide only a very limited sense of the quantitative importance of the various natural enemies recorded.

Recommendations: Management of this borer in landscape settings focuses on prevention of stresses of all sorts, including defoliation, that weaken trees and stimulate attacks. No management involving biological control has been recommended, and there is no obvious way to employ biological control against this pest.

73. BRONZE BIRCH BORER (*Agrilus anxius* Gory; Coleoptera: Buprestidae)

Notes: In the literature before 1950, the bronze birch borer was not distinguished from the aspen borer. Both were jointly referred to as *Agrilus anxius*.

Origin: Bronze birch borer is native to North America.

Range in North America: This species is found across Canada from Newfoundland to British Columbia, south to New Jersey, Ohio, and Colorado, where it bores in weakened trees of various species of birch (*Betula*) (Barter 1957).

Damage: This species is considered the most serious pest of paper birch (Peirson 1927), and in 1939 during an outbreak in New Brunswick this insect caused a loss of 981 million cubic feet of wood, the greatest for any single species that year in Canada (Brown 1940). The larvae of this species tunnel in the limbs and trunks of birch trees, mechanically wounding and girdling them. While originally considered primarily an urban tree pest (e.g., Hutchings 1917), it is now recognized as an important forest pest as well.

Widespread damage in birch stands in New Brunswick in the 1930s (Balch and Prebble 1940) was attributed to the overmature status of stands, together with stresses such as defoliation from other insects. Whether this species is "aggressive" (i.e., prone to attack and kill healthy trees) or "secondary" (i.e., attacking principally trees in decline from other stresses) is a critical and debated point. Balch and Prebble (1940), while attributing the 1930s outbreak in New Brunswick to poor tree condition in general, recorded some instances of apparently healthy trees being attacked and killed. Work of Anderson (1944) on borer attack in aspen, while reported as being a study of *Agrilus anxius*, was really a study of the aspen borer, *Agrilus liragus* Barter and Brown, which was not distinguished as a separate species until later (Barter and Brown 1949). In the study on aspen borer by Anderson (1944), trees of various health status were created by topping or girdling. Aspen borer attack occurred principally in girdled trees, indicating the species to be nonaggressive. This was, however, a different borer species. Bronze birch borer, while it apparently attacks mainly stressed trees, does attack some healthy trees during outbreaks (Barter 1957). Damage appears to be most frequent to trees in understocked stands, trees left isolated after selective logging, trees on the edges of clearings, or ornamental trees planted in open sites (Peirson 1927). Attempts have been made to identify the early stages of tree stress using electrical resistance in stems (Ball and Simmons 1984), as a means of predicting susceptibility of individual trees to bronze birch borer.

Resident Natural Enemies: Surveys have quantified the effect of natural enemies on bronze birch borer populations in New Brunswick and Pennsylvania, with somewhat different results. In New Brunswick (Barter 1957) egg parasitism was approximately 50% at most sites, and was considered important. Major parasitoids were the signiphorid *Thysanus* sp. and the encyrtid *Coccidencyrtus* sp. Important larval parasitoids included the braconid *Atanycolus charus* (Riley) and the chalcidid *Phasgonophora sulcata* Westwood, which together parasitized an average of 18% of the larvae (Barter 1957). In Pennsylvania, on European white birch (*Betula pendula* Roth) planted to reforest strip mines, egg parasitism was lower (7%) and mainly due to the encyrtids *Avertianella* sp. and *Ooencyrtus* sp. (Loerch and Cameron 1983). Larval parasitism (18%) was similar to the level to New Brunswick, with the most common species being a eulophid, *Tetrastichus* sp.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: The causes of pest outbreaks in forests are unknown, but are presumed to be stimulated by the occurrence of an abundance of breeding material, produced when stands of birch decline in health for other reasons.

Recommendations: Management of birch stands can minimize losses from bronze birch borers by minimizing stresses from other factors. Cutting practices should not leave lightly stocked birch stands (Peirson 1927) or isolated birches on cutover land or at forest edges. No recommendations for biological control can be made based on the available information. Birch trees in urban areas should be managed in ways that reduce stress from drought, defoliation, and mechanical damage.

74. RED OAK BORER (*Enaphalodes rufulus* [Haldeman]) (Coleoptera: Cerambycidae)

Origin: Red oak borer is native to North America.

Range in North America: This species occurs on oaks throughout southern Canada and the eastern United States (Drooz 1985).

Damage: This species is an important pest of various oaks, including black (*Quercus velutina*), northern red (*Q. rubra*), and scarlet (*Q. coccinea*) oaks. Damage results in the downgrading of lumber found to contain larval tunnels upon harvest, resulting in about a 40% loss in value compared with top quality grades (Drooz 1985). By volume about 38% of oak lumber is downgraded because of borers (Drooz 1985).

Resident Natural Enemies: No parasitoids of this species were mentioned in the literature encountered, nor in Krombein *et al.* (1979). Because the 2-year life cycle of borers in each generation is synchronized (Hay 1969) and because the survival of larvae in tunnels can be monitored by catching ejected frass in traps (Hay 1974a), survival of cohorts of larvae can be estimated. Overall larval mortality was found to be 81-87%. Two sources of mortality were recorded by Hay (1974a). In younger larvae, predation by woodpeckers caused about 40% mortality, and in larger larvae invasion of borer tunnels by other insects attracted to sap

exudates caused about 51% mortality. Because woodpeckers kill young larvae before they penetrate deeply into the wood (Hay 1972), such predation effectively reduces both damage and the number of emerging adult borers (Galford 1985).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Because as few as one larva per tree can be economically important, the natural population densities of this species are considered harmful. The importance of woodpeckers as predators has been demonstrated, and so the conservation of these birds in forest stands is of value. In particular, this predation is likely to be important in combination with selective felling of "brood trees" (Hay 1974a; Donley 1981, 1983). This control system is based on the preference of this borer to oviposit in smaller trees (less than 29 cm in diameter), especially ones showing slow growth (less than 5 mm in diameter per year) (Hay 1974a). Because such brood trees are preferred, oviposition is concentrated and removal of as little as 1% of an oak stand (i.e., the brood trees) can suppress the density of the borers in the next generation by 63-68% (Donley 1983). Inspection of all oaks in stands allows brood trees to be identified and removed. Once suppressed by this treatment, borer densities remain low for extended periods (Donley 1981). The reason for the failure of populations to return over time to higher densities is unclear, but is likely related either to lower success in beetle mating or higher predation rates on larvae. Regardless, the persistence of this effect makes this silvicultural technique economically successful.

Recommendations: Woodpecker conservation is important for continued control of red oak borer. Stand management practices should be evaluated to assure that woodpecker populations are conserved. Direct provision of nesting boxes might be of value in locations lacking sufficient natural sites.

75. POPLAR BORER (*Saperda calcarata* Say) (Coleoptera: Cerambycidae)

Origin: Poplar borer is native to North America.

Range in North America: *Saperda calcarata* is found throughout Canada and North America, wherever poplar trees occur (Drooz 1985).

Damage: This borer attacks both healthy and injured live poplar and willow.

Resident Natural Enemies: Drouin and Wong (1976) list thirteen parasitoids as having been reared from *S. calcarata* larvae in western Canada: two dipteran odiniids, *Odinia* sp. and *Odinia* poss. *boletina* (Zetterstedt); two tachinids, *Eutheresia* sp. and *Ptilodexia canescens* (Walker); three braconids, *Bracon* sp., *Atanycolus* sp., and *Atanycolus charus* Riley; one gasteruptiid, *Pristaulacus rufitarsis* (Cresson); and five ichneumonids, *Pimpla* sp., *Pimpla messor perlongus* (Cresson), *Gambrus canadensis* (Provancher), *Lampronota* sp., and *Phygadeuon* sp.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: No information is available on the population dynamics of this species. It is a native species whose effects are considered damaging even at low population levels. No obvious role for biological control is suggested based on past research. The nature of its galleries (having an open tunnel near ground level through which frass is ejected) suggests that nematode applications might prove effective against this pest.

Recommendations: Nematode products used for other borers should be tested to determine their effectiveness against this species in landscape and plantation poplars.

76. COTTONWOOD BORER (*Plectrodera scalator* [Fabricius]) (Coleoptera: Cerambycidae)

Origin: Cottonwood borer is native to North America.

Range in North America: The cottonwood borer is found from New York to Montana and south to Texas. It is of greatest concern in the southern United States (Drooz 1985).

Damage: This borer breeds in the bases and roots of living cottonwoods, poplars, and willows. It attacks trees of all sizes, and does most damage in nurseries, plantations, and young stands on sandy soils (Drooz 1985).

Resident Natural Enemies: Hungerford (1915) records parasitism by the sarcophagid *Sarcophaga vericauda*.

Biological Control Attempts: Forschler and Nordin (1989) conducted trials which indicated that soil applications of *Beauveria bassiana* were partially effective against adult borers, and at the highest dosage application of this fungus reduced the number of larvae recruited in the treatment year by approximately 50%.

Reasons for Pest Status and Possibilities for Biological Control: No studies have been conducted on the population dynamics of this species. It is a native species whose typical densities are considered damaging. The role of native natural enemies has not been investigated. Introduction of exotic natural enemies has not been considered and does not seem to have value given the native status of the pest.

Recommendations: Tests could be conducted to determine if applications of commercially available nematode species might be effective against this borer.

77. FLATHEADED APPLE TREE BORER (*Chrysobothris femorata* [Olivier]) (Coleoptera: Buprestidae)

Origin: Flatheaded apple tree borer is native to North America.

Range in North America: This species is found throughout most of Canada and the United States (Drooz 1985).

Damage: Larvae tunnel in the sapwood, girdling trees and sometimes killing them. Newly transplanted young trees and trees under environmental stress, such as drought, are most frequently attacked (Wygant 1938). Vigorous, established trees are usually not injured.

Resident Natural Enemies: Twelve parasitoid species have been reared from this host, including three *Spathius* or *Atanycolus* braconids, two ichneumonids (in *Lebena* and *Xorides*), three chalcidids (in *Trigonura* and *Phasgonophora*), one eupelmid (in *Metapelma*), and two eulophids (in *Tetrastichus* and *Horismenus*) (Leiby 1925, Fenton 1942, Krombein *et al.* 1979). Also two clerids, *Chariessa pilosa* Forester and *Chariessa pilosa onusta* Say have been recorded as predators of the larvae of this species (Fenton 1942). No studies, however, provide quantitative information on the degree of mortality these agents cause to populations of the borer.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: This species' typical population densities are damaging to some classes of trees.

Recommendations: Wrapping of tree trunks with paper or burlap is recommended to prevent borer oviposition and reduce risk to newly transplanted trees (Baerg and Isely 1938, Solomon 1995). Practices that maintain tree vigor are recommended to minimize damage. Active attempts to apply biological control are not recommended.

78. LOCUST BORER (*Megacyllene robiniae* [Forster]) (Coleoptera: Cerambycidae)

Origin: Locust borer is native to North America.

Range in North America: Originally this beetle occurred only in the native range of its one host, black locust (*Robinia pseudoacacia* L.), in the Allegheny Mountains from Pennsylvania to Georgia and in the Ozark Mountains in Arkansas (Galford 1984). Black locust, however, grows well on poor sites and has been introduced widely to such areas across the United States and parts of Canada and the beetle now has a much wider distribution in the United States and eastern Canada (Drooz 1985).

Damage: Larvae bore in young black locust trees and in older trees that are overtopped or drought-stressed. Trees are most susceptible to attack on poor sites, during droughts. Pest

attack rates increase as the proportion of black locust in a stand increases (Harman *et al.* 1985a), and larval to adult survival increases as attack rate increases (Harman *et al.* 1985b). Attack rates are higher on strip-mined sites, than on undisturbed sites (Harman *et al.* 1985b).

Resident Natural Enemies: No information was located on parasitoids or predators of this species. The susceptibility of locust borer larvae to nematodes under laboratory conditions has been investigated and the species was found to be highly susceptible to some nematode species, especially *Steinernema carpocapsae* (Weiser) (Forschler and Nordin 1988a).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Too little information is available to determine the reasons for observed levels of pest populations; however, planting black locust on poor sites increases densities of physiologically susceptible trees, and increases borer survival rates.

Recommendations: Life table studies of borer populations at sites within the native range and on poor sites outside the native range of the tree host would be valuable to define which parasitoids or other mortality factors most strongly affect the pest and how these factors vary by site. It would be of special interest to see if important natural enemies occurred in the native range that did not occur at poor quality sites, especially ones outside the native range of black locust.

Conservation of tree health on poor sites is desirable, but will often not be feasible because of the nature of the sites. Nematode applications might provide control, but may be economically unjustified on poor sites.

79. WHITE OAK BORER (*Goes tigrinus* [De Geer]) (Coleoptera: Cerambycidae)

Origin: White oak borer is native to North America.

Range in North America: White oak borer occurs throughout the eastern United States from New York to Florida, westward to Louisiana and Michigan (Drooz 1985).

Damage: This borer is considered to be a very important pest of white oak (*Quercus alba*) and, in the southern United States, of overcup oak (*Quercus lyrata*). In Ohio, it is considered to be the pest causing the greatest injury to white oak wood produced for cooperage. Damage is most severe to smaller trees (Solomon and Donley 1983). Borer tunneling promotes additional losses by promoting entry of decay organisms into tree trunks (Berry 1978).

Resident Natural Enemies: None reported.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Solomon and Donley (1983) discuss the biology and life history of this species. Little, however, is known about its

population dynamics. Infestations in oak stands appear to be sustained by the occurrence of "brood" trees in which borer reproduction is concentrated. Removal of such trees can reduce stand infestation levels with relatively small percentages of the basal area of the stand being cut (Solomon and Donley 1983).

Recommendations: As a native insect capable of causing damage at relatively low population levels, this insect is a poor target for biological control methods.

80. WHITESPOTTED SAWYER (*Monochamus scutellatus* [Say]) (Coleoptera: Cerambycidae)

Origin: Whitespotted sawyer is native to North America.

Range in North America: The whitespotted sawyer is found from Newfoundland south to North Carolina, and westward through the Great Lake States, Canada, and Alaska (Drooz 1985).

Damage: This borer attacks dying or recently dead trees that have dried out somewhat but are not heavily attacked by other wood-feeding insects. It attacks a variety of conifers, but is especially important as a pest of white pine. Logs left in the forest untended over a summer season are especially suitable for attack by this borer. The whitespotted sawyer is also able to vector the Asian plant-parasitic nematode *Bursaphelenchus xylophilus* (Steiner and Buhrer), which causes pine-wilt disease in Minnesota and Wisconsin (Wingfield and Blanchette 1983).

Damage can be minimized by cutting timber in fall and winter, with removal the next year before late June — the breeding period of the beetle (Raske 1973, Drooz 1985). Pulpwood may be partially protected by piling logs in shade, or covering them with slash ((Wilson 1962). At processing sites, sprinkling water on logs helps reduce infestation rates (Gray and Mol 1969).

Resident Natural Enemies: Natural enemies of this sawyer are reported to be rare (Rose 1957), but include tachinids in the genus *Eutheresia* and ichneumonids in the genera *Rhyssa* and *Dolichomitus* (Parmelee 1941, Soper and Olson 1963). Their quantitative importance has not been determined.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Little is known of the population dynamics of this species. Damage increases when fire or storm-damaged timber cannot be harvested and removed from forested areas before summer when beetles breed.

Recommendations: Whitespotted sawyer seems an unlikely candidate for biological control by parasitoids or predators because ovipositing adults appear to be present in sufficient numbers to cause damaging larval densities wherever suitable dead timber becomes available.

81. CARPENTERWORM (*Prionoxystus robiniae* [Peck]) (Lepidoptera: Cossidae)

Origin: Carpenterworm is native to North America (Lindegren *et al.* 1981).

Range in North America: Carpenterworms are widely distributed in the eastern United States and southern Canada (Drooz 1985).

Damage: This borer breeds in various hardwoods, especially oaks in the red oak group and green ash. It rarely kills trees. Economic damage occurs due to downgrading of lumber from logs with borer tunnels present (Drooz 1985). In Ohio this species affected 34% of the oaks examined, causing 25% of all losses from borers, and in Kentucky it affected 30% of the oaks, causing 9% of losses (Donley 1974).

Resident Natural Enemies: Unlike many bark beetles and some other borers, for this species woodpecker predation appears to be of little importance (Munro 1931). Because larvae must eject frass to the outside as they tunnel, a hole to the outside is maintained (Lindegren *et al.* 1981). This creates the possibility of injecting nematodes into such holes, which migrate along the moist tunnel, encounter larvae, and kill them. Injection of nematodes into borer tunnels at the rate of 10,000 to 100,000 per milliliter was found to give 80% control of larvae (Lindegren *et al.* 1981). Comparison of control from nematode injection versus application of a nematode spray to the tree bark showed bark sprays to give 47-85% control (Forschler and Nordin 1988b). The ichneumonid *Amersibia prionoxysti* Rohwer has been recorded as a parasitoid of this borer (Munroe and Fox 1934).

Biological Control Attempts: The only biological control approach that has been explored has been the application of nematodes as a curative spray.

Reasons for Pest Status and Possibilities for Biological Control: This native pest naturally occurs at levels that are economically damaging.

Recommendations: Further development of the use of nematodes against this pest is recommended.

82. BANDED ASH CLEARWING (*Podosesia aureocincta* Purrington and Nielson) (Lepidoptera: Sesiidae)

Notes: Before 1975, banded ash clearwing was not recognized, but was thought to be a race or second brood of the lilac borer *Podosesia syringae* (Harris). Status as a separate species has been confirmed based on differences in flight periods and biology (Nielsen and Purrington 1974) and structure of male genitalia (Purrington and Nielsen 1979). In literature before 1975, *P. aureocincta* may be recognized either by designation as *Podosesia syringae fraxini* Lugg., or by mention of late season emergence (September), or emergence from ash.

Origin: Banded ash clearwing is native to North America.

Range in North America: This borer is widely distributed in the eastern and middle parts of North America, from New York to Florida, and west to Oklahoma (Drooz 1985).

Damage: The banded ash clearwing tunnels in various species of ash (*Fraxinus*), especially green ash (*Fraxinus pennsylvanica* Marsh.), and damages both trees grown for timber and for use as ornamentals. In the southern United States the moth is important as a timber pest (Soloman 1975), and in the prairie States it is damaging to trees in shelterbelts (McKnight and Tunnock 1973).

Resident Natural Enemies: Natural enemies of this species have received little attention. Solomon (1975) records predation by woodpeckers as being the largest observed source of mortality to immature stages (67-81% in two years), and notes the emergence of small numbers of three species of parasitoids (*Phorocera signata*, *Apanteles* sp., and *Lissonota* sp.) from infested logs held in the laboratory. *Bracon sanninoideae* (Gahan) is listed as a parasitoid of this species by Krombein *et al.* (1979).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Little is known of the determinants of population density in this species. Wounding is believed to predispose individual trees to selection for oviposition by adult clearwings. No options for enhancing biological control have been suggested.

Recommendations: None.

83. COLUMBIAN TIMBER BEETLE (*Corthylus columbianus* Hopkins) (Coleoptera: Scolytidae)

Origin: Columbian timber beetle is native to North America.

Range in North America: This borer is found from Massachusetts to Georgia and west to Michigan and Missouri (see Kabir and Giese 1966 for a map of the known distribution).

Damage: The Columbian timber beetle is an ambrosia beetle, one of a large group that tunnel in the wood of trees, inoculate their galleries with symbiotic fungi, and then feed on the resulting fungal mycelia. Unlike many ambrosia beetles, the Columbian timber beetle attacks healthy trees, rather than dead, dying, or recently cut trees. Many hardwood species are attacked, including various oaks and maples, sycamore, poplar, elms, beech, and others (Drooz 1985). Attacks increase over time as new generations of the beetle are produced either in a single season, or across several years. Trees, however, are not killed. Galleries are filled with callus after beetle feeding has ceased. Damage consists in reduction of the grade of lumber cut from attacked trees because infested wood retains visible signs of former tunnels, callus wood, and associated staining. Loss of quality can be economically significant (Donley 1974, Hay 1974b).

Resident Natural Enemies: Because Columbian timber beetle galleries remain as clear features in formerly infested wood, studies have quantified some aspects of Columbian timber beetle population dynamics based on counts of such features as egg chambers, larval tunnels, and other signs in wood of various ages (e.g., Milne and Giese 1969, 1970). In spite of such careful observations, virtually no parasitoids and almost no predators of this beetle have been recorded (Nord 1972). One dipteran, *Odinia meijerei* Collin, has been recorded as a predator (Milne and Giese 1969), although this observation has not been confirmed by other studies.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Population studies of this species exist, but only as retrospective descriptions based on galleries in wood of various ages in trees in study stands. No predictive hypotheses have been formulated or tested about the determinants of average population density in this species. No evidence has been obtained suggesting any important role for biological control agents in the population dynamics of this beetle.

Recommendations: None

Shoot, Twig, Or Cone Borers

84. EUROPEAN PINE TIP MOTH (*Rhyacionia buoliana* [Denis and Schiffermüller] (Lepidoptera: Tortricidae)

Notes: A former generic placement for European pine tip moth was in *Evetria.*

Origin: European pine tip moth is known from Europe, the eastern end of the Mediterranean Sea (Israel and surrounding area), and Japan. It also occurs in parts of North and South America, areas it is known to have invaded within the last 100 years (CAB 1978a). The most recent area of invasion has been Chile (Espiñoza Zuniga *et al.* 1986). The species was first recorded in the United States in 1914, and is believed to have invaded by means of infested nursery stock on Long Island (New York) and other locations (Busck 1914).

Range in North America: In eastern North America, the moth occurs in southern Canada from Newfoundland to the Great Lakes and in the United States south to Maryland and Illinois. A separate area of infestation exists in British Columbia, Oregon, and Washington (CAB 1978a).

Damage: Young larvae feed on needles, and older larvae enter and feed on the buds, especially the leaders, of hard pines such as red pine (*Pinus resinosa*). Buds of branches are also attacked. Damage results from death of leaders, which leads to deformed, bushy trees (Drooz 1985). In some areas, red pine is no longer recommended for use in new plantations because of damage from this species (Kulman 1966). In Chile, infestations of 23-32% of trees in *Pinus radiata* plantations have caused growth losses of 9-15% (Araya and de Ramirez 1989).

Resident Natural Enemies: More than a hundred species of parasitoids have been recorded attacking *R. buoliana*. Many studies have described the parasitoids that can be reared from larvae and pupae of European pine tip moth in various locations, tree hosts, and tree heights. At the world level these have been summarized by Harman and Kulman (1973). A key to the Nearctic species is provided by Yates (1967).

In Europe, this tip moth has been of interest as a pest in Scots pine plantations, as well as a source of parasitoids for importation into North America. Early parasitoid surveys from this host in Europe include those of Smits van Burgst (1919, 18 spp. recorded), Feytaud (1921, 16 spp.), Tempel (1925, 6 spp. in Saxony, in Germany), and Thorpe (1930, 28 spp. in the United Kingdom). Studies conducted in Germany in the 1950s and 1960s found larval and pupal parasitism of this species to be in the 28-65% range in pine plantations in the coastal areas of Germany (Schindler 1960, 1965). The most common parasitoids observed were the ichneumonid *Cremastus confluens* Grav. and the braconid *Orgilus obscurator* Nees. In pine plantations in eastern Germany, Fankhänel (1963) recorded 16 species of parasitoids of larvae and pupae, with half of all parasitism being due to the *O. obscurator*. In Serbia, Vasic (1967) found 17 species of parasitoids, with parasitism rates of 12-57%. The most important species were *Temelucha* (formerly *Cremastus*) *interruptor* and *Orgilus obscurator*. In Europe, *O. obscurator* is in many locations the most effective parasitoid of European pine tip moth, but its action is stated to be reduced by competition from other parasitoids, such as *T. interruptor*, which attack hosts previously parasitized by *O. obscurator*. Other damaging factors include the hyperparasitoid *Perilampus tristis* Mayr. (Bogenschütz 1969). Studies in Poland (Kolk 1984) also record high levels (55%) of parasitism of larvae, particularly in pine plantations near areas of natural woody vegetation. The most common parasitoid species in Poland was *O. obscurator*. In contrast to many other sites, in the United Kingdom *Eulimneria rufifermur* was cited as the most efficient parasitoid, even at low host densities (Brooks and Brown 1936). Many of the earlier records from Europe are summarized by Arthur and Juillet (1961).

Similarly, many studies document the native or introduced parasitoid species recovered from European pine tip moth in North America, including Friend and West (1933, 7 native species in Connecticut), Coppel and Arthur (1953, 8 native and 3 introduced species in Ontario), Watson and Arthur (1959, Ontario), and Kulman (1966, 20 species of parasitoids or associated organisms in West Virginia and Maryland).

Biological Control Attempts: Attempts to suppress European pine tip moth in North America have been made in both Canada and the United States. In Canada 13 species of parasitoids were released in two periods, 1928-1938 and 1954-1958 (Clausen 1978). In the United States, 15 species were introduced between 1931 and 1937. Clausen (1978) documents the history of these releases, providing tables of parasitoid species released, years released, and total numbers released. Efforts in Canada are summarized by Syme (1971a, 1984). Arthur and Juillet (1961) provide an analysis of work in Canada, pointing out which species of introduced parasitoids are most likely to be successful and which, such as *Ephialtes ruficollis* and *Exeristes roborator* F., might merit further investigation. This paper, plus those of Syme (1971a, 1984) provide excellent summaries of the many studies conducted as part of the attempt at biological control of this pest.

While many papers have been published as part of this biological control project, most concern themselves with parasitoid collection, rearing, release, recovery and survey efforts, and

parasitoid biology. Few studies address the population dynamics of the pest. Of the many parasitoid species released, only a few have become established. Of these, only one, *Orgilus obscurator*, appears to be widespread and of some importance. Some species that were released early in this biological control project and that have completely or nearly died out, such as *Temelucha interruptor*, are now considered facultative hyperparasitoids of the best species (*O. obscurator*). In the United States, the two species of greatest importance among the introduced parasitoids appear to be *O. obscurator* and the tachinid *Lypha dubia* Fallén (Drooz 1985).

Of the many native species of parasitoids attacking European pine tip moth in North America, *Hyssopus thymus* Girault is said to be the most important in many areas (Friend *et al.* 1938, Syme 1971b), followed by others such as *Ephialtes comstockii* (Cresson) and *Eurytoma pini* Bugbee (Watson and Arthur 1959). Parasitism rates of larvae by native species in North America are often about 10% (Watson and Arthur 1959, Torgersen and Coppel 1969), although higher rates have been reported in some studies (e.g., in West Virginia and Maryland, 14-39%, Kulman 1966).

Broadly, releases of European parasitoids in North America have had limited effect in most areas, although in some specific restricted sites greater suppression appears to have resulted after the introduction of *O. obscurator* (Beiqué 1960; Syme 1971a, 1984). Reasons for this are discussed in the following section.

Because *R. buoliana* is also considered a pest in Europe, at least two species of North American parasitoids attacking the pest have been collected and released in Europe, although neither is reported to have established. These include *H. thymus* and *Itoplectis conquisitor* (Biermann 1973, Altenkirch 1976).

Reasons for Pest Status and Possibilities for Biological Control: The underlying reasons for the population levels of this species seen in Europe and North America, and the relations of pest densities in each location to biological control agents, are complex and poorly studied. In Europe the species is considered a pest, showing that the complex of natural enemies present is not fully able to suppress the pest to noneconomic levels. Outbreaks of this species in Europe are reported to occur periodically (e.g., in 1805-1807, 1937, 1948, 1961, and 1967 in Denmark, Zethner and Bejer-Petersen 1972). Causes of outbreaks are not known, but a correlation was detected between outbreaks in Denmark and warmer, drier weather in July and August in the two years preceding outbreaks (Bejer-Petersen 1972).

While parasitoids do not completely prevent outbreaks in Europe, they are credited with providing substantial levels of control. In Denmark, studies in lodgepole pine plantations (*Pinus contorta* var. *latifolia*) have shown parasitism to be 51-75%, several fold higher than reported by most studies in North America (Esbjerg 1972). Furthermore, Miller (1962), summarizing literature on *R. buoliana* densities in North America and Europe, concluded that the pest was eightfold more abundant in North America. The underlying reasons for this difference were unclear. Possible reasons suggested by the author included greater rates of predation in Europe, higher host plant resistance in the European species of pine studied (Scots pine) compared with that of the host tree in North America (red pine), and the absence in North America of several species of internal parasitoids believed to be important in Europe.

Possible explanations for the lack of success in using biological control introductions to suppress European pine tip moth in North America include reduced vegetational diversity in North American pine plantations and a need to import additional species of parasitoids from Europe. In Europe, pine plantations have greater vegetational diversity than do plantations in North America where the moth is of concern. Reduced vegetational diversity could potentially be reducing natural enemy numbers or diversity in two ways. First, many of the European parasitoid species need alternate hosts, which are often species of Lepidoptera not found in pine monocultures. Second, some parasitoids, such as *O. obscurator,* do better at sites with flowering Umbelliferaceae species such as wild carrot (*Daucas carota* L.), which provide nectar resources to adult parasitoids.

It is also possible that additional species of parasitoids need to be imported from Europe to achieve biological control of this pest in North America. There are many more species of parasitoids of this pest in Europe than have been collected and released to date. Some of these untied species could be beneficial in North America. Some of these European parasitoids are considered undesirable because they attack hosts already parasitized by *O. obscurator* or other primary parasitoids. While it may be valid to hold this view, examples to the contrary need to be recalled. For example, larch casebearer (*Coleophora laricella*) was controlled in North America by the combined action of two parasitoids, the braconid *Agathis pumila* and the eulophid *Chrysocharis laricinellae*, even though the latter is sometimes a facultative hyperparasitoid of the former.

Little basic work has been done on the population dynamics of this moth and its parasitoids, in either Europe or North America. Causes of population changes have been addressed only once, by Harris (1960) in the United Kingdom, in a study lasting only three generations. He found parasitism rates to be high but constant, and failure of third instar larvae to successfully establish in buds to be the most variable source of mortality. Establishment in buds was better in warm than cool years. A single short term study, however, is insufficient to determine what is typical in the population dynamics of this species.

Basic studies in both Europe and North America would provide a firmer foundation to judge whether further parasitoid importations from Europe would be helpful, and, if so, which species would be most promising. Simply releasing all the primary parasitoids encountered is unsatisfactory because when it fails, it is unclear if the species released were biologically wanting or were used incorrectly (too few released, poorly timed, etc.). Also some facultative hyperparasitoids might be useful and could be considered.

Work on this pest is made more difficult by the fact that it prefers to attack young red pines, such that as plantations age, the moth density declines because the trees become less attractive for oviposition. This confounds long term population studies, unless special research sites are prepared in which trees are subject to periodic partial replanting to maintain tree patches of favorable ages. The general reduction in use of red pine in North America (at least in part because of problems with this pest) reduces the availability of research sites. Also, because the leader is the preferred site of attack, damage decreases more slowly than does population density. As populations decrease fewer side branches, but not necessarily fewer leaders, are attacked.

Recommendations: The present pest status of European pine tip moth should be determined by surveying plantations and ornamental plantings of susceptible pines to estimate pest density and rates and species of parasitoids attacking larvae and pupae. If such surveys find the pest not to be under biological control, studies of population dynamics should be started at two sites, one in the United States in the center of the area of greatest concern, and one in Europe in a region with winters of equal severity to those of the generally infested area in the United States. These studies should last 7-10 years and be designed to produce life tables and other data on the basic factors determining the population dynamics of the pest in both locations. Study sites in both Europe and North America must consist of the same tree species (red pine) and should both be managed by rotation planting to maintain a population of young trees, in ages highly attractive for oviposition by the pest. Sites should be divided into two large blocks and one managed as a pine monoculture and the other sown with cover crops of wild carrot. This will allow an experimental assessment to be made of the relative controlling power of parasitoids in Europe compared with those in the United States, without confounding effects of tree species, tree age, or variation in vegetation diversity.

85. NANTUCKET PINE TIP MOTH *(Rhyacionia frustrana* [Comstock]) (Lepidoptera: Tortricidae)

Notes: Miller (1967) revised the group of North American *Rhyacionia* species closely related to *Rhyacionia frustrana* and elevated a prairie population, known previously as *R. frustrana bushnelli*, to full species status as *Rhyacionia bushnelli* Miller. Infestations of *R. bushnelli* in the National Forests of Nebraska, which consist solely of planted pine plantations, previously were thought to be an *R. frustrana* population that had been accidentally introduced from the eastern United States. Because of this error, interest existed for some period in translocating parasitoids of *R. frustrana* from the eastern United States to these parts of Nebraska (Cushman 1927a). Berisford (1988) reviews the taxonomy, biology, natural enemies, population behavior, and management of this species.

Origin: Nantucket pine tip moth is native to North America.

Range in North America: Nantucket pine tip moth's range extends from eastern Texas to Florida, north to Missouri, and east to Massachusetts. The species is also found in Central America (Miller 1967).

Damage: Larvae of Nantucket pine tip moth bore into and kill leaders of pines, both reducing overall increase in wood volume and deforming the tree. The species was recognized early as a pest of various southern pines in plantations and areas of natural reproduction (Wakeley 1929). Some species such as shortleaf (*Pinus echinata*) and loblolly (*Pinus taeda*) pines are more severely affected than others, for example longleaf (*Pinus palustris*) and slash (*P. elliotti*) pines, which are relatively resistant (Yates 1966a). The proportion of tips infested by this pest decreases after trees reach 3-4 meters in height (Lashomb *et al.* 1980).

Resident Natural Enemies: Because of the concern over damage to pine reproduction and plantations caused by this pest, many studies have been conducted to determine which natural enemies attack Nantucket pine tip moth. Nearly all of these studies, however, have been surveys that identified species of natural enemies and rates of mortality seen in samples, but

did not experimentally examine the population dynamics that determine the average density of the species in particular habitats or management systems.

Among the surveys documenting parasitoid complexes associated with Nantucket pine tip moth in various parts of the United States are these: (1) Cushman (1927a), who reared 21 species of Hymenoptera and two tachinids from hosts collected in Virginia; (2) Eikenbary and Fox (1965), who recorded 35 species of parasitoids from Nantucket pine tip moth in the Piedmont of South Carolina; (3) Freeman and Berisford (1979), who reared 27 species from this tip moth in Georgia; and (4) Lashomb *et al.* (1980), who found 24 parasitoid species from this host in Maryland.

Of the various larval parasitoids noted, the species that are consistently of greatest importance in nearly all studies have been, in order of importance, the ichneumonid *Campoplex frustranae* Cushman (Cushman 1927b), the tachinid *Lixophaga mediocris* Aldrich (Aldrich 1925), and the eurytomid *Eurytoma pini* Bugbee (Lashomb *et al.* 1980). The biology of *C. frustranae* has been studied by Eikenbary and Fox (1968a), who found that this species accounted for 18-47% of all the larval parasitism of Nantucket pine tip moth in the Piedmont area of South Carolina. In Georgia, 42% of Nantucket pine tip moth larvae were parasitized, and of this parasitism, *C. frustranae* and *L. mediocris* accounted for two thirds (Freeman and Berisford 1979).

Egg parasitism has occasionally been reported to be of significance. Yates (1966b) in Georgia found 65% of Nantucket pine tip moth eggs to be naturally parasitized by the trichogrammatid *Trichogramma minutum* Riley.

Predators of Nantucket pine tip moth have received less attention than parasitoids. Eikenbary and Fox (1968b), in the Piedmont of South Carolina, recorded fourteen species of insects and seven of spiders as predators of this tip moth. The clerids *Phyllobaenus singularis* (Wolc.) and *Phyllobaenus lecontei* (Wolc.) were important predators of larvae and pupae. The biology of *P. singularis* is given by Wingfield and Warren (1968).

Articles discussing pathogens of Nantucket pine tip moth under natural conditions were not encountered. Artificial applications of pathogens as microbial insecticides have been tested against this tip moth in Cuba. Application of either *Bacillus thuringiensis* or the fungus *Metarhizium anisopliae* has both been found to provide some control under field conditions (Menendez *et al.* 1986, Duarte *et al.* 1992).

Few attempts have been made to build on the preceding descriptive information about these natural enemies to develop a quantitative understanding of the forces determining the population dynamics of this tip moth. One exception is a study by Gargiullo and Berisford (1983) in which life tables for six generations of *R. frustrana* in loblolly pine plantations in Georgia were constructed and analyzed via k-factor analysis. Variation in levels of egg and pupal mortality were found to best reflect variation in total mortality across these generations. In Maryland, the level of parasitism in the overwintering generation of tip moth larvae was low (3%), suggesting that this may be an important limitation on the importance of parasitoids in the life system of this host in that State (Staines *et al.* 1984). Berisford (1988) synthesizes knowledge of the population dynamics of Nantucket pine tip moth. Pine plantations are rapidly colonized by the pest, but decline in suitability as crown closure begins. Parasitoids, initially rare or absent, colonize stands after the host, and are influenced by associated vegetation in the stand.

Biological Control Attempts: One biological control attempt via natural enemy introduction has been conducted against *R. frustrana*. This species invaded southern California (most likely in infested nursery stock) and was found infesting *Pinus radiata* in urban areas. Two parasitoids from the eastern United States, *C. frustranae* and *L. mediocris*, were introduced. Only the former established. This species caused pupal parasitism to increase from 10% (by local native parasitoids) to 50% in three years. The proportion of infested tips subsequently declined (Scriven and Luck 1978).

In the eastern United States, because this tip moth is a native species, introduction of new natural enemies has not been proposed. Some consideration, however, has been paid to the effects of the silvicultural practices employed in southern pine plantations on parasitism levels. Herbicide use to suppress competing vegetation in pine plantations in Georgia increased tip moth densities for the first two years after planting (Ross *et al.* 1990). However, growth increases from the reduction in competition from other vegetation more than offset these growth losses and herbicide use was, on balance, favorable to tree growth.

Reasons for Pest Status and Possibilities for Biological Control: In southern California, Nantucket pine tip moth became a pest because it was an invasive species that, before natural enemy introductions, lacked locally effective natural enemies. In its native range, many natural enemies attack Nantucket pine tip moth. Nevertheless, in pine plantations, populations reach levels that reduce tree growth rates. Comparative studies of survivorship rates of Nantucket pine tip moth in natural and managed pine stands were not found in the literature. Similarly, few studies were found on effects of silvicultural practices on the population dynamics of *R. frustrana* or its natural enemies.

Recommendations: Studies should be conducted on the survivorship of Nantucket pine tip moth life stages in natural pine stands and managed plantations to determine if managed stands promote higher densities of tip moth either (1) directly by enhancing resources for tip moths or reducing mortality from dispersal or lost fecundity, or (2) indirectly because plantation conditions are unfavorable to tip moth natural enemies.

86. EASTERN PINE SHOOT BORER (*Eucosma gloriola* Heinrich) (Lepidoptera: Tortricidae)

Origin: Eastern shoot borer is native to North America.

Range in North America: This shoot borer is found from the northeastern United States to the Great Lake States, and in southern Canada (Drooz 1985). A map of the species' distribution is given by DeBoo *et al.* 1971).

Damage: Larvae tunnel in new shoots, killing them. Damage arises from deformity of the trunk when the terminal leader is killed. DeBoo *et al.* (1971) report that the species is rare in natural stands, but is more common in plantations and artificially reforested areas. In plantations, 7-41% of shoots and up to 10% of terminal leaders may be infested (DeBoo *et al.* 1971). McKeague and Simmons (1978) report only 2% of trees in Christmas tree plantations as having their terminal leaders killed by this pest, and did not recommend control.

Resident Natural Enemies: Five species of natural enemies have been reported, based on surveys in Pennsylvania, New York, Ontario, and Manitoba: *Glypta* sp., *Rhorus* sp. *Bracon rhyacioniae* (Muesebeck), *Elachertus cidariae* Ashmead, and *Habrocytus* sp. (DeBoo *et al.* 1971). Of these, *Glypta* sp. was the most important species in the survey by Deboo *et al.* (1971). In a separate study by Drooz (1960), *Glypta* sp. was reported as parasitizing 56-61% of larvae sampled. This *Glypta* sp. would appear to be *Glypta eucosmae* Walley and Baron, based on Walley and Baron's (1971) review of the genus.

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: The biology of this species is discussed by DeBoo *et al.* (1971). However, little is known of the population dynamics or ecology of this shoot borer. Parasitoids appear to be potentially important mortality factors, and pest problems under plantation conditions appear to be greater than in forests.

Recommendations: A population study should be conducted comparing pest densities and levels of mortality from various natural enemies, especially larval parasitoids, in monoculture plantations, weedy plantations and natural forests. This study could be patterned after current work by Berisford on effects of vegetational diversification in southern pine plantations on Nantucket pine tip moth (*Rhyacionia frustrana* [Comstock]) and its natural enemies. Such a study would indicate whether or not stand management might be manipulated in ways acceptable to producers that would enhance shoot borer natural enemies sufficiently to reduce damage to acceptable levels.

87. COTTONWOOD TWIG BORER (*Gypsonoma haimbachiana* [Kearfott]) (Lepidoptera: Tortricidae)

Notes: Earlier generic placements of cottonwood twig borer include *Epinotia*, *Enharmonia*, and *Hedya* (Morris 1967).

Origin: Cottonwood twig borer is native to North America.

Range in North America: This species occurs throughout the eastern United States and Ontario (Drooz 1985). It is common in the southern United States (Morris 1967) and occurs west to Texas (Stewart and Payne 1972).

Damage: This is one of the most destructive pests of young eastern cottonwood trees (*Populus deltoides* Bartr.). Damage is of economic importance mainly in cottonwood plantations (Morris 1967, Stewart and Payne 1972).

Resident Natural Enemies: Morris (1967) mentions as natural enemies of cottonwood twig borer in Mississippi, Louisiana, and Arkansas, various Hymenoptera including the parasitoids *Bracon mellitor* Say, *Bracon* sp., *Apanteles clavatus* (Provancher), *Agathis* sp., and *Trichogramma minutum*, and the predacious potter wasps (*Eumenes* spp.). In Texas, Stewart and Payne (1972) note egg parasitism by *Trichogramma* spp. up to 61% in samples,

and record various larval or pupal parasitoids, including *Apanteles* sp., *Phanerotoma* sp., *Coccygomimus*, and *Itoplectis conquisitor* (Say). Other records from the literature are summarized by Morris (1978).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: No studies were found on the causes of either the fundamental population levels of this species, or effects of different habitats (such as plantations versus natural cottonwood stands).

Recommendations: Too little information is available to assess the potential for biological control to contribute to the management of this species in plantation forestry. A comparative study of the population dynamics and natural enemies of this species in both natural stands and plantations, using life tables to organize and quantify data, might be conducted. This type of study would increase understanding of the role natural enemies play and would reveal if management options in plantations provide the means to enhance biological control above current levels or not.

88. WHITE PINE WEEVIL (*Pissodes strobi* [Peck]) (Coleoptera: Curculionidae)

Notes: Western populations of white pine weevil from Engelmann (*Picea engelmanni* Hopkins) and sitka spruce (*Picea sitchensis* [Bong.] Carr.) were believed to be distinct species (*Pissodes engelmanni* Hopk. and *Pissodes sitchensis* Hopk.) until cross breeding experiments showed they were interfertile with the eastern population (Smith and Sugden 1969). As a consequence, *P. engelmanni* and *P. sitchensis* were declared junior synonyms of *P. strobi* by Warner (1971). O'Brien (1989) provides a handbook covering the taxonomy and food plants of *Pissodes* species of North America north of Mexico. Wallace and Sullivan (1985) review the behavior and other biological features of *P. strobi*.

Origin: *Pissodes strobi* is native to North America. The genus *Pissodes* contains numerous species, with members in Europe, Russia, and Japan, among other locations.

Range in North America: *Pissodes strobi* is found widely in both the eastern and western United States and Canada in the range of its principal hosts—white and jack pine and sitka, white, Norway, and Engelmann spruce.

Damage: Larvae tunnel in terminal leaders, killing them. This greatly reduces height growth of the tree and causes crooked trunks, reducing the value of the log for lumber. Younger trees that are attacked are at increased risk of death. Waters (1969) constructed a tree lifetable in a white pine stand and found that white pine weevil killed 40% of the trees in the 3 to 20-year-old class. The species is generally considered the most serious pest of regenerating white pine.

Resident Natural Enemies: Taylor (1929-1930) found that the most important natural enemies of this species in the eastern United States were, in order of importance, the eurytomid parasitoid *Eurytoma pissodes* Girault, the lonchaeid predator *Lonchaea corticis* Taylor, and the braconid parasitoid *Microbracon* (now *Bracon*) *pini* Muesebeck. For a

population of *P. strobi* on Engelmann spruce in Alberta, Stevenson (1967) found the most important natural enemies to be the ichneumonid *Dolichomitus terrebrans nubilipennis* (Viereck), *Eurytoma pissodes*, and *Lonchaea corticis*. In Virginia, Harmon and Kulman (1968) found fifteen common insect associates of white pine weevil in terminals, of which the most important natural enemies were *Lonchaea corticis*, *Bracon pini*, and the braconid *Coeloides pissodes* (Ashmead). Alfaro *et al.* (1985) in a study of white pine weevils in terminals of sitka spruce in British Columbia found the most common natural enemies to be *Lonchaea corticis* and the braconid *Allodorus crassigaster* (Provancher). Mills and Fischer (1986) review the literature on natural enemies of *P. strobi* in North America and record a total of nine parasitoids and two predators. They compare this list of natural enemies to those of three species of *Pissodes* in Europe. Kenis and Mills (1994) review the parasitoids associated with species of *Pissodes* in Europe.

Whether *Lonchaea corticis* was a scavenger or true predator of white pine weevil (and if a predator, of what life stages) was initially uncertain. Clear proof of its role as a predator of white pine weevil pupae was obtained by Hulme (1989, 1990) and colleagues (Hulme and Harris 1989).

Few reports exist of disease among white pine weevil life stages. Wilson (1984b) noted that 16% of larvae and 9% of adults were infected by a *Nosema* sp. in Ontario.

Evaluations of the importance of these various natural enemies in the population dynamics of white pine weevil are scarce. Taylor (1929-1930) estimated total mortality to white pine weevil larvae from parasitism and predation in Maine to be 19%. Dixon and Houseweart (1982) used exclusion cages to construct life tables for cohorts of white pine weevil immatures either subject to or protected from the action of natural enemies. They found that the overall contribution of natural enemies was to lower the rate of population growth between generations by two thirds. Harman and Kulman (1968) compared parasitism rates in white pine weevil immatures in stands of different ages, in open versus closed stands, and natural stands versus plantations. They found that the numbers of *Lonchaea corticis* emerging in relation to white pine weevil adults was highest in plantations with closed canopies and in natural stands with a hardwood overstory—conditions that are less favorable to white pine weevil than more open sites.

Biological Control Attempts: No attempts have been made to employ biological control against this species. It has been suggested, however, that natural enemies attacking *Pissodes* species in Europe might be of value (Taylor 1929-1930). Mills and Fischer (1986) evaluated the literature on three species of *Pissodes* from Europe and suggested that the European species of parasitoids with the greatest potential to increase mortality of *P. strobi* in North America would be the parasitoids *Eubazus atricornis* (Ratz.) and *Coeloides sordidator* Ratz. Information on *C. sordidator* (an ectoparasitoid of second and third instar larvae), as a parasitoid of *P. notatus* (=*P. castaneus*) Fabricius in France, is given by Alauzet (1987, 1990). Haeselbarth (1962) records that *Brachistes* (now *Eubazus*?) *atricornis* caused up to 40% parasitism of eggs of *Pissodes piceae* (Ill.) in Germany. This species oviposits in host eggs but emerges from host prepupae. Kenis and Mills (1994) recommended the diapausing biotype of *Eubazus semirugosus* as the most likely candidate for introduction to North America from Europe.

Silvicultural methods of control of white pine weevil have been examined and consist of use of a protective overstory to provide shade during the years after seedling establishment. Such conditions appear to reduce attacks by white pine weevil adults and to favor the predator *Lonchaea corticis* (Harman and Kulman 1968). Clearance of hardwood competitors for release of young pines appears to increase white pine weevil attacks and to be counterproductive in the long run (Patterson and Aizen 1989). The effects of other silvicultural practices on the white pine weevil, either directly or indirectly through effects on the pest's natural enemies, have been considered by Bellocq and Smith (1994) but found to be of limited importance.

Reasons for Pest Status and Possibilities for Biological Control: White pine weevil is a native species that is significantly reduced in population growth potential by natural enemies, but whose usual densities are nevertheless damaging to forestry interests. Opportunities to use biological control against this species would appear to consist mainly of trying to increase mortality caused by natural enemies by introducing new species from other *Pissodes* in other parts of the world. Studies have been conducted relative to European *Pissodes* species that have identified some parasitoids as possible candidates for introduction (Mills and Fischer 1986, Kenis and Mills 1994).

Recommendations: Introduction of European species of parasitoids of other *Pissodes* species as recommended by Mills and Fischer (1986) and Kenis and Mills (1994) is possible. Such introductions would first require more detailed study of the various candidate species to clarify their biology and confirm their ability to attack *P. strobi* (Kenis *et al.* 1996). In addition, further life table studies of the type conducted by Dixon and Houseweart (1982) should be conducted to document the amount of suppression of white pine weevil population growth rates caused by existing natural enemies.

89. NORTHERN PINE WEEVIL (*Pissodes approximatus* Hopkins) (Coleoptera: Curculionidae)

Notes: *Pissodes approximatus* and *Pissodes nemorensis* were considered separate species until Phillips *et al.* (1987) showed these populations to be part of a single species, with *Pissodes nemorensis* being the name with priority. This review concerns only the northern population, formerly known as *P. approximatus*.

Origin: Northern pine weevil is native to North America.

Range in North America: The range of the northern form of *Pissodes nemorensis* (formerly known as *Pissodes approximatus*) extends from the Atlantic coast to Manitoba and south to North Carolina and Minnesota (Drooz 1985).

Damage: This species breeds in dying trees of various species of pines, especially red pine (*Pinus resinosa*) and Scots pine (*Pinus sylvestris*), attacking the roots, trunk, and major and minor branches. The weevil does not breed successfully in healthy trees. In natural forests it remains at low densities. In plantations, it breeds in stumps of cut trees and reaches densities sufficiently high that feeding by adults on live trees is considered to cause economic loss (Finnegan 1958).

Resident Natural Enemies: Up to 35% of the larvae of the northern form have been recorded as parasitized by *Coeloides* sp. (Finnegan 1958), and 22% of the southern form (*P. nemorensis*) have been observed to be parasitized by *Coeloides pissodis* (Ashmead) (Atkinson *et al.* 1988). Sapsuckers and woodpeckers, which are believed to be important in natural forests, do not attack the pest when it breeds in stumps in plantations (Finnegan 1958).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: This species reaches pest levels only in Christmas tree plantations. This appears to be related to increased breeding material in the form of stumps.

Recommendations: Reduction of breeding material in plantations by stump removal, mechanical destruction, or poisoning is recommended as a way to control increases of this species in such plantations. No biological control actions are recommended.

90. LARGER PINE SHOOT BEETLE (*Tomicus piniperda* [Linnaeus]) (Coleoptera: Scolytidae)

Notes: Former generic placements of larger pine shoot beetle include *Myelophilus* and *Blastophagus*.

Origin: Larger pine shoot beetle is native to Eurasia (see Anon 1972 for a map of its distribution), but has recently established in North America.

Range in North America: In North America, this species is currently limited in its distribution to the area around the Great Lakes.

Damage: Larvae of this species develop in branches and under bark of smaller, often suppressed or fallen, trees as well as in stumps. Adults are the more damaging stage because they feed by tunneling in the living shoots and leaders of healthy trees, reducing growth and deforming tree shape, which causes important losses in Christmas tree production (Trägårdh 1921, Hanson 1937).

Tomicus piniperda is also reported to be associated with a pine pathogen, the fungus *Gremmeniella abietina* (Anon. 1979b) and to transmit *Ophiostoma minus* in France (Piou and Lieutier 1989), as well as various blue-stain fungi such as *Leptographium* spp. (Gibbs and Inmans 1991).

Simulation of damage (by shoot removal) suggests that, for stands of Scots pine under 20 years in age, there is less reduction in growth than previously thought (Ericsson *et al.* 1985). However, in older stands (60 years), damage was higher (Langstrom *et al.* 1990).

Resident Natural Enemies: A variety of organisms have been mentioned in the literature as attacking this species. Feytaud (1927) summarizes the early literature, listing eight species of predators and twelve of parasitic Hymenoptera.

Parasitoids recorded from this shoot beetle include the pteromalid wasp *Rhopalicus suspensus* Ratz., which is widely distributed in Poland and attacks up to 84% of the larvae (Nunberg 1930). The same species (under the synonym *T. tutela* Wlk.) was found by Hanson (1937) to be the most important parasitoid of this shoot beetle in the United Kingdom, being widely distributed and accounting for the vast majority of parasitism in field samples. Hanson (1937) lists nine other species of parasitoids encountered in lesser numbers. Other records of parasitoids are given by Lovázy (1941) and Nuorteva and Nuroteva (1968) in Finland. In western Siberia, the main parasitoids of larvae of this pine beetle are *Coeloides abdominalis* (Zett.), *Coeloides bostrichorum* Girault, and *Rhopalicus brevicornis* Thoms. (Bogdanova 1982). In Japan, *Atanycholus initiator* (Fabricius) has been recorded from this shoot beetle (Urano and Hiui 1991).

Predators reported as attacking the larger pine shoot beetle include the clerid *Thanasimus formicarius* in Sweden (Kemner 1913). In Europe, this clerid is reported as killing up to one third of the beetle's eggs and 72% of its larvae and pupae, at a study site where overall survival of the shoot beetle was only 18-19% (Butovitsch 1925). The value of this clerid has been debated, with some authors finding it more or less valuable in their areas (e.g., Nechleba 1929 in the former Czechoslovakia and Hanson 1940 in the United Kingdom). In Russia, the histerid *Platysoma oblongum* Fabricius is reported to be effective in suppressing this pest in pine stands, but not in mixed pine and fir areas (Stark 1926). In the United Kingdom, the predators of greatest importance according to Hanson (1937) were the cybocephalid *Pityophagus ferrugineus* Fabricius and the rhizophagid *Rhizophagus ferrugineus* Pk.; other species of lesser importance are also listed. Laidlaw (1941) provides notes on species of *Rhizophagus* important in Scotland as predators of shoot beetles. The snakefly *Rhaphidia ophiopsis* Linnaeus is recorded as an important predator of *T. piniperda* larvae under thick bark in pine plantations in the former U.S.S.R. (Pishchik 1979).

Pathogens noted infecting this beetle include nematodes, some species of which were found in Belarus to attack the reproductive organs of up to 25% of the pupae and adults (Yatzentkovskii [Jazentkovsky] 1924). The fungus *Beauveria bassiana* was found to cause 71-100% mortality of beetles in log piles that were sprayed with the fungus and then wrapped in a plastic tarp (Lutyk and Swiezynska 1984).

Biological Control Attempts: In Europe, conservation of the natural enemies of this species of shoot beetle has been attempted by using several silvicultural methods, such as destruction of bark on half of the stumps after cutting, to concentrate brood and increase natural enemy attack (Stark 1926). Hanson (1937) conducted large block field tests to measure the effect of leaving different quantities and kinds of slash and thinnings on beetle reproduction and levels of natural enemies. He concluded that a small, continuous supply of breeding material best conserved natural enemies. Sudden increases in quantities of larger diameter, rough barked limbs or trunks favored outbreaks of the beetle because brood experienced lower competition, and natural enemies were less able to attack larvae under rough bark. Hanson (1940) claimed that excessively clean forestry is counterproductive, and recommended leaving smaller diameter, thin-barked limbs in the stand rather than collecting and burning them.

Natural enemies are being introduced into the United States to combat this new pest. The predacious clerid *Thanasimus formicarius* is being reared by USDA scientists to develop a colony sufficient to support releases.

Reasons for Pest Status and Possibilities for Biological Control: In Europe, the pest status of this species is driven by sudden increases of breeding resources (Bevan 1921). Conservation of natural enemies by modification of silvicultural methods to dispose of branches and small-diameter downed trees is also recommended. An important release mechanism seems to be the large reduction in intraspecific competition by brood that follows a surge in available breeding resources (Nuorteva 1964).

Lack of European species of natural enemies will be an obvious suspect should highly damaging populations become typical in North America. Natural enemies have been reported as being important in various places in Europe. However, these statements are largely based on just the observed level of commonness of a natural enemy in field samples. The only life table developed for this species, that of Hui and Zhimo (1995) in China, shows natural enemies to be only minor sources of mortality under the study conditions.

Recommendations: Two routes for use of biological control of this beetle are available: classical biological control and conservation. Classical biological control could be employed by releasing the more important European natural enemies of this species in North America. However, prior to any releases of exotic natural enemies against *T. piniperda* in North America, studies in Europe should be conducted to determine which natural enemy species are of greatest value and to quantify experimentally their contribution to mortality, using a life table approach. Furthermore, the economic damage from the pest in North America should be determined to see if control efforts would be economically justified.

Conservation of natural enemies is suggested as a means of control by the work of Hanson (1937). Silvacultural practices that result in a steady addition of a small quantity of wood favorable for beetle reproduction might conserve natural enemy populations. How such practices might interact with a sudden surge in availability of breeding material should be tested by artificially creating such a surge of breeding material by felling and leaving trees in areas under each of the two management systems — maintenance of steady, low input of breeding material versus rigorous suppression of breeding material, i.e., "clean forestry"). Eidmann (1985) describes some of the potential interactions that would need to be considered.

91. WHITE PINE CONE BEETLE (*Conophthorus coniperda* [Schwarz] (Coleoptera: Scolytidae)

Origin: White pine cone beetle is native to North America.

Range in North America: This beetle is found throughout the range of its host, white pine.

Damage: Adult beetles deposit eggs inside immature cones. Heavy populations can reduce seed crops by 50% or more.

Resident Natural Enemies: The parasitic Hymenoptera *Cephalonomia hyalinipennis* Ahmead and *Spathius* sp. and the predacious clerid *Enoclerus* sp. attack immature stages of white pine cone beetle (Godwin and Odell 1965).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: Too little is known about this species to identify potential reasons for its typical population levels, and consequent pattern of damage.

Recommendations: If this beetle is identified as an important constraint in seed orchards, a study of its typical densities and levels of mortality due to natural enemies might be useful to see if these are affected by common seed orchard management practices. However, even this type of study might be economically unjustifiable if the affected acreage is small and existing chemical controls are effective.

Leafminers

92. ARBORVITAE LEAFMINER (*Argyresthia thuiella* [Packard]) (Lepidopera: Argresthiidae)

Notes: Some recent literature refers to arbovitae leafminer as *Blastotere thuiella* or *Blastotere thujella.*

Origin: Arborvitae leafminer is a native species in North America. In Europe, this species is an invasive pest that was first detected in Holland in the early 1970s (van Frankenhuyzen 1974), and subsequently extended its range to Germany (Plate and Köllner 1977), Austria (Kurir 1983), and the former Czechoslovakia (Povolny and Zacha 1990).

Range in North America: Arborvitae leafminer is found in Quebec, Ontario, and the northern parts of the eastern United States (Maine) where its host, eastern white cedar (*Thuja occidentalis* Linnaeus), occurs (Laviolette and Juillet 1976, Bazinet and Sears 1979, Drooz 1985).

Damage: In Europe, this species is considered an important pest of ornamentals, damaging hedges (van Frankenhuyzen 1974) and other plants. Chemical controls are employed against it (Köllner and Plate 1983). *Bacillus thuringiensis* is ineffective because of the long period of larval emergence (Langenbruch 1984).

In North America, this leafminer is a forest pest as well as a pest of ornamentals, with occasional outbreaks in stands of eastern white cedar in Maine (Drooz 1985) and Canada (Biggs *et al.* 1991). It is the most important of the several species of leafminers that feed on arbovitae (Brower 1935). Damage from this species may be distinguished from that of other leafminers on arborvitae by keys of Laviolette and Juillet (1976).

Resident Natural Enemies: Britton and Zappe (1922) record two species of parasitoids, *Pentacnemus bucculatricis* Howard and *Apanteles bedelliae* Viereck, from this leafminer in Connecticut. In Quebec, Juillet (1972) records 26 species of parasitoids that collectively destroyed up to 50% of larvae of several species of arborvitae leafminers, including *Argresthia thuiella.* Life tables for one population of arborvitae leafminers in Guelph,

Ontario, showed parasitism by a set of seven parasitoids to cause 9-18% mortality of larvae (Bazinet and Sears 1979). Among the parasitoids of arborvitae leafminer, the species of greatest distribution and importance is said to be *Pentacnemus bucculatricis* (Anon. 1983).

In Europe native parasitoids cause 12-14% mortality of larvae in Germany (Köllner and Plate 1983) and up to 16% parasitism was observed from a *Necremnus* sp. in Austria (Kurir 1983).

Biological Control Attempts: None.

Reasons for Pest Status and Possibilities for Biological Control: In Europe the pest status of this species is likely related to its status an exotic invader. In North America, the basic causes for the occasional outbreaks in forests have not been investigated.

Recommendations: In Europe, importations of parasitoids from eastern North America could be made to help suppress the pest. In North America, basic studies of the species would increase understanding of its population dynamics. Before such studies are initiated, the economic importance of the pest should be evaluated to assess whether investment of resources is warranted.

93. BIRCH LEAFMINER (*Fenusa pusilla* [Lepeletier]) (Hymenoptera: Tenthredinidae

Origin: Birch leafminer is an exotic species in North America.

Range in North America: This European species, first recorded in North America in Connecticut in 1923 (Friend 1933), now occurs from Newfoundland south to Maryland, and west to Alberta, the Great Lake States, and Iowa, with populations also in Washington and Oregon (Drooz 1985, and personnel communication from David Langor of the Northern Forestry Centre in Edmonton, Alberta). In addition, *F. pusilla* has also invaded Turkey (Özbek 1986).

Damage: Damage appears to be solely aesthetic. No studies were found supporting the idea that this species is a stressing agent that predisposes trees to attack by the bronze birch borer, *Agrilus anxius*.

Resident Natural Enemies: Some seventeen species of parasitoids have been recorded attacking *F. pusilla* in North America, most of them eulophids (Cheng and LeRoux 1969), and life tables for the species have been constructed for populations in Quebec (Cheng and LeRoux 1965). These native parasitoids, however, attack only a small percentage (less than 5%) of the larvae and are not considered important sources of mortality (Cheng and LeRoux 1970).

Biological Control Attempts: Two European ichneumonids (*Lathrolestes nigricollis* [Thompson] and *Grypocentrus albipes* Ruthe) and one eulophid (*Chrysocharis nitetis* [Walker]) have been introduced into North America in various locations, including Quebec (Guèvremont and Quednau 1977), Newfoundland (Raske and Jones 1975), Pennsylvania and New Jersey (Fuester *et al.* 1984), and Massachusetts and Rhode Island (Van Driesche *et al.*, in press). *Lathrolestes nigricollis* has become established in each of these regions (Raske

and Jones 1975, Guèvremont and Quednau 1977, Fuester *et al.* 1984, Van Driesche *et al.*, in press) and become widely distributed in some areas (Van Driesche *et al.*, in press). *Grypocentrus albipes*, in contrast, while established in a few locations has been recovered much less frequently. Quantitative evaluation of the impact of *L. nigricollis* on leafminer densities suggests the introduction of this species has been beneficial, but has not completely resolved the problem (Van Driesche *et al.*, in press).

Reasons for Pest Status and Possibilities for Biological Control: Studies of birch leafminer populations in central Europe reveal significantly higher levels of mortality from parasitoids (Eichhorn and Pschorn-Walcher 1973) compared with those in North America (Cheng and LeRoux 1970). This observation suggests that the higher pest densities noted in North America are related to separation of this herbivore from its specific natural enemies. Post-introduction evaluation of the effect of *L. nigricollis* on *F. pusilla* populations in New England further support this view (Van Driesche *et al.*, in press). Introductions made to date, however, have only partially resolved the problem as leafminer populations remain high in some locations even after the establishment of *L. nigricollis*.

Recommendations: Further parasitoid introductions are recommended to provide additional suppression of this pest. Specifically, new releases of *G. albipes* and *C. nitetis* would be desirable.

Mites

94. SPRUCE SPIDER MITE (*Oligonychus ununguis* [Jacobi]) (Acari: Tetranychidae)

Notes: In early literature spruce spider mite is referred to as *Paratetranychus ununguis*. Tetranychid mites associated with conifers are reviewed by Mitrofanov *et al.* (1975).

Origin: Spruce spider mite is of cosmopolitan distribution and uncertain origin (Jeppson *et al.* 1975). It has been reported from Brazil (Finilli and Flechtmann 1990), Sweden (Brammanis 1956), Germany (von Scheller 1962), the United States (Fellin 1968), New Zealand (Dumbleton 1932), and Japan (Akita 1971, Gotoh 1984), among other locations. Its occurrence in regions without native conifers (e.g., New Zealand) suggests that part of its current distribution is likely due to invasions via transport of nursery stock.

Range in North America: This spider mite is widely distributed throughout the United States and Canada.

Damage: Dense populations cause chlorotic foliage (bronzing), loss of nutrients from removal of plant sap, and webbing on various conifers (Jeppson *et al.* 1975). Spruce spider mite is also reported from Japan as feeding on chestnut (*Castanea crenata*), a non-coniferous host (Gotoh 1984).

Resident Natural Enemies: As with all mites, parasitoids are unknown, but a variety of predators, especially predacious mites, have been reported feeding on spruce mite. These include the predacious mites *Neoseiulus fallacis* (Garman) in North Carolina on Fraser fir

(*Abies fraseri*) (Kramer and Hain 1989); *Typhlodromus americanus* Chant and Yoshida-Shaul in mixed conifer Christmas tree plantations in Oregon (West and DeAngelis 1993); *Neoseiulus collegae* (De Leon) in nurseries in Florida (Mizell and Schiffhauer 1991); and *Anystis baccarum* (Linnaeus) (von Scheller 1962), *Typhlodromus pyri* Scheuten, *Typhlodromus rhenanus* (Oudm.), and *Typhlodromus bakeri* (Garman), in Germany (Thalenhorst 1962, von Scheller 1962). These predacious mites are all phytoseiids, with the exception of *Anystis baccarum*, which is in the Anystidae (Gerson and Smiley 1990).

Other natural enemies recorded attacking spruce mite include the coniopterygid *Conwentzia pineticola* End. from Finland (Löyttyniemi 1970) and Germany (von Scheller 1962), the fungal pathogen *Entomophthora* sp. in Finland (Löyttyniemi 1970), and the coccinellid *Stethorus punctillum* Weise in Pennsylvania (Wheeler *et al.* 1973).

Biological Control Attempts: No efforts at biological control of spruce mite have been made directly. However, conservation of existing natural enemies (presumably local predators, especially phytoseiids and other predacious mites) has been recognized as important because outbreaks of spruce mite have been observed to follow pesticide applications in forests and nurseries. In Montana, applications of DDT in 1956-1957 for control of western spruce budworm (*Choristoneura occidentalis* Freeman) were followed by outbreaks of spruce mite over nearly one million acres of forest (Fellin 1968). Similar outbreaks have been noted after pesticide applications in European larch forests to control thrips (von Scheller 1962), and in pesticide-treated Douglas-fir seed orchards in Oregon (Sandquist *et al.* 1993).

The anystid *Anystis baccarum* was thought to be the most important predator of spruce mite by von Scheller (1962) in Germany. This species is not reported from the United States as a predator of spruce mite. This, plus the fact that a related species, *Anystis salicinus* (Linnaeus), was successfully moved from France to Australia where it controlled the exotic pest mite *Halotydeus destructor* (Tucker) (Wallace 1981), suggests the possibility of reducing spruce mite in North America through introduction of *Anystis baccarum*.

Reasons for Pest Status and Possibilities for Biological Control: In some locations, pest populations of spruce spider mite developed after pesticides were applied for other pests (e.g., von Scheller 1962, Fellin 1968, Sandquist *et al.* 1993), suggesting destruction of natural enemies as a possible causal mechanism for the outbreaks.

In other cases, outbreaks may have been promoted by forest or nursery fertilization practices, as higher plant nitrogen levels appear to increase the reproductive success of the mite (Thalenhorst 1963, Löyttyniemi and Heliövaara 1991).

Separation of the spruce mite from controlling predators in an original homeland may have contributed in part to spruce mite's pest status in some areas. This is somewhat uncertain because the origin of the spruce mite in North America, whether native or invasive, could not be determined. However, the presence of the mite in countries without native conifers suggests it can be spread by movement of nursery stock. This, combined with the observation that in several sites in Europe the most important predator of spruce mite is *Anystis baccarum* (a species not reported attacking spruce mite in North America), suggests that lack of specific predators might be part of the reason for the pest status of spruce mite in North America.

Recommendations: Outbreaks of spruce mite in seed orchards, nurseries, and Christmas tree plantations can be avoided by eliminating or minimizing the use of miticides and insecticides likely to destroy phytoseiids and other spruce mite predators. For sites of limited acreage, augmentative releases of reared phytoseiids such as *Amblyseius fallacis* might be of value. This approach has been effective for other tetranychid pest mites in strawberry fields and fan palm nurseries and so might be effective on conifers as well, although specific tests assessing this are lacking.

Importation of predators from Europe, especially the anystid *Anystis baccarum*, might enhance control in North America. This possibility should be investigated, first confirming that the species is not already present in North America.

Phytoseiids associated with spruce mite in different countries vary by species. However, given the wide host ranges of many phytoseiids, there is no reason to believe that European species would be more effective against spruce mite than North American species, and so there appears to be no reason to consider their importation.

Summary of Recommendations

Of the 94 species reviewed in this report, 61 (65%) are native to North America. Of these, 3 species (Cooley spruce gall adelgid, Nantucket pine tip moth, and tuliptree aphid) have spread into regions of North America outside their original ranges, and thus occur as non-native species in some areas of the United States. Twenty eight species (30%) are exotic pests currently found in North America, and three species (3%) (the engraver beetle, the steel blue wood wasp, and the nun moth) are not yet found in North America, but are of concern as potential invaders. Two species (spruce spider mite and larch sawfly) are of uncertain or disputed origin.

Recommendations on how biological control might be used to control these pests are divided into categories that correspond to the ways in which biological control can be employed (*Tables 1 - 4*): (1) introductions of natural enemy, (2) augmentations of natural enemies, through artificial propagation and release, (3) studies of population dynamics to clarify importance of natural enemies or to identify modifications of silvicultural practices that enhance effects of existing natural enemies at production sites, and (4) no role for biological control. These tables of necessity omit much information presented in the test of this report. The following tables are intended only to help orient the reader to the test and its broad conclusions. These tables, if viewed in isolation, may fail to present a balanced picture and their use in this manner is not recommended.

Introduction of Natural Enemies. Of the 28 species of exotic pests reviewed, 26 were judged to provide opportunities for their control via natural enemy introductions (*Table 1*). (See Pschorn-Walcher [1977] and Van Driesche and Bellows [1996] for overviews of how natural enemy introduction programs may be organized and conducted.) In addition, included in Table 1 are 6 species of native insects which are exotic in some parts of the United States (Cooley spruce gall adelgid, tuliptree aphid, and Nantucket pine tip moth) or have been proposed as targets for introduction of natural enemies of congeneric European species (white pine weevil, spruce budworm, black turpentine beetle). Also included is one species of uncertain origin (larch sawfly). Natural enemy introduction offers opportunities against all of these species as well, for a total of 34 species listed in Table 1. In some cases, these species have never been targets of natural enemy importations (e.g., beech scale, mimosa webworm, eastern spruce gall adelgid) or present opportunities for work additional to that done in the past. An example of an opportunity for additional work would be searching new regions not considered or accessible in the past, e.g., the Caucasus Mountains for predators of the balsam woolly adelgid.

Some species in this category have already been successfully controlled through natural enemy introductions (e.g., larch casebearer, European spruce sawfly, introduced pine sawfly, and Nantucket pine tip moth in California).

For the species that have invaded North America from abroad, it is important to identify the native homeland, which may be different from the area from which the pest came to North America. Many species, for example, appear to have moved from Russia or Asia to Europe and then to North America. In such cases, the species may lack important natural enemies in Europe as well as in North America, and Europe would thus be an inappropriate location in which to seek natural enemies able to suppress the pest.

Augmentation of Natural Enemies. For pests of high value sites (forest nurseries, shade trees, Christmas tree plantations), use of more expensive biological control products such as nematodes, predacious mites, or formulated pathogens is possible. Fourteen species were identified for which studies on the effectiveness of augmentative biological control through artificial propagation of pathogens or other natural enemies seem useful (*Table 2*). Examples include the development of nematodes for the control of white grubs in forest nurseries, the use of *Bacillus thuringiensis* for control of defoliating Lepidoptera, and the use of nuclear polyhedrosis viruses for control of some species of sawflies.

Basic Studies and Conservation of Natural Enemies. For some pests, insufficient information was found to judge the importance of natural enemies in the population dynamics of the species. In some cases there were needs to compare the importance of natural enemies between habitats such as natural stands versus managed plantations or between North America and the native range. A need for population dynamics studies of these sorts was identified for 20 species (*Table 3*). Examples include the need to clarify the importance of pipinculid parasitoids attacking the Saratoga spittlebug, a need to study the effect of different slash management practices on natural enemies of pine engraver and larger pine shoot beetle, and studies of effects of vegetational diversity on various shoot borers.

No Role for Biological Control. For 32 species (*Table 4*), no role for manipulative biological control was identified. These species were predominantly native (30) insects, for which natural enemy introductions were not likely to be relevant and for which augmentative biological control methods were too expensive in view of the nature and distribution of the damage. While natural control by unmanipulated natural enemies is undoubtedly a factor to some degree in the population dynamics of these species, opportunities to intentionally employ silvicultural practices to increase biological control were not identified. It is important to recognize, however, that future research might reveal new ways to better conserve or manipulate native natural enemies of such species.

Table 1. *Species for which introductions of new species of natural enemies are needed or have previously controlled the pest.*

Species	Number in this report	Pest Origin	Natural Enemy Needed, or Area to be Explored
Eastern spruce gall adelgid	3	E[1]	*Aphidoletes abietis*
Balsam woolly adelgid	4	E	Explore Caucasus Mts.
Hemlock woolly adelgid	5	E	Explore China and Japan
Cooley spruce gall adelgid	6	N[2] (but E in eastern N.A)	Explore Colorado
Woolly beech aphid	11	E	Determine native range
Tuliptree aphid	12	N (but E in CA)	Explore eastern United States
Norway maple aphid	13	E	Explore Europe
Linden aphid	14	E	Explore China
Beech scale	15	E	Determine native range
Red pine scale	16	E	*Harmonia yedoensis* in Japan
Elongate hemlock scale	19	E	Explore Japan and China for parasitoids with better synchrony
Oystershell scale	20	E	Explore Russian Far East
San José scale	21	E	Explore Russian Far East
Japanese beetle	32	E	Explore China and Japan for parasitoids
Imported willow leaf beetle	33	E	Explore China
Elm leaf beetle	34	E	Explore Europe and Asia
Smaller European elm bark beetle	36	E	Collect nematodes and microsporidia from Europe
Black turpentine beetle	38	N	Re-release *Rhizophagis grandis*
Engraver beetle	40	E	Collect in Europe, when needed

Table 1. *(Cont.)*

Species	Number in this report	Pest Origin	Natural Enemy Needed, or Area to be Explored
Spruce budworm	42	N	Collect in Europe and Japan from congeneric species
Gypsy moth	51	E	Explore Russia and China, but prepare detailed evaluation first
Nun moth	52	E	Collect in Europe, when needed
Mimosa webworm	57	E	Explore Asia and Australia
Birch casebearer	58	E	Explore Europe
Larch casebearer	59	E	Already controlled through natural enemy introductions
Pine false webworm	63	E	Compare status in Europe and North America
Introduced pine sawfly	67	E	Already controlled through natural enemy introductions
European spruce sawfly	68	E	Already controlled through natural enemy introductions
Larch sawfly	69	uncertain	Continue work in Europe on encapsulation-resistant parasitoids
European pine tip moth	84	E	Reassess pest levels in North America, then explore in Europe
Nantucket pine tip moth	85	N (but E in CA)	Already controlled in CA by natural enemy introductions
White pine weevil	88	N	Collect in Europe from congeneric species
Birch leafminer	93	E	Collect in Europe
Steel blue woodwasp	71	E	No action needed yet

[1,2]*E=exotic, N=native*

Table 2. *Species for which development of augmentative use of natural enemies is recommended.*

Species	Number in this report	Pest Origin	Type of Natural Enemy
May and June beetles	28	N[1]	Nematodes and fungi
A white grub (*Polyphylla variolosa*)	29	N	Nematodes and fungi
Black vine weevil	30	E[2]	Nematodes and fungi
Strawberry root weevil	31	E	Nematodes and fungi
Japanese beetle	32	E	Nematodes and fungi
Spruce budworm	42	N	*Bacillus thuringiensis*
Bruce spanworm	46	N	Nuclear polyhedrosis virus
Gypsy moth	51	E	*Bacillus thuringiensis* or NPV
Red-headed pine sawfly	64	N	Nuclear polyhedrosis virus
Swaine jack pine sawfly	65	N	Nuclear polyhedrosis virus
Poplar borer	75	N	nematodes
Cottonwood borer	76	N	nematodes
Carpenterworm	81	N	nematodes
Spruce spider mite	94	?	predaceous mites

[1,2]*E=exotic, N=native*

Table 3. *Species which need basic studies of their population dynamics to clarify reasons for typical population densities, or to determine if modifications of silvicultural practices can enhance natural enemy effectiveness.*

Species	Number in this report	Pest Origin	Aspect Needing Study
Tuliptree scale	17	N[1]	Effects of ants on outbreaks
Saratoga spittlebug	22	N	Effect of pipinculid parasitoids
Cottonwood leaf beetle	23	N	Population dynamics in natural stands vs. plantations
Pine root collar weevil	25	N	Population dynamics in natural stands vs. plantations
Pine root tip weevil	26	N	Relation between beetle and stand decline
Pine engraver	41	N	Effect of slash management on natural enemies
Jack pine budworm	43	N	Effects of stand conditions on natural enemies
Large aspen tortrix	44	N	Basic population study
Fall cankerworm	45	N	Basic population study
Bruce spanworm	46	N	Basic population study
Eastern hemlock looper	48	N	Basic population study
Spruce bud moth	55	N	Basic population study
Balsam gall midge	62	N	Effects of Christmas tree plantation silvicultural practices on natural enemies
Yellow-headed spruce sawfly	70	N	Comparison of natural enemies in open versus shady sites
Red oak borer	74	N	Woodpecker conservation methods
European pine tip moth	84	E[2]	Comparison of effects of stand age and vegetational diversity in Europe and North America

Table 3. (*Cont.*)

Species	Number in this report	Pest Origin	Aspect Needing Study
Nantucket pine tip moth	85	N	Effect of vegetational diversity on natural enemies
Eastern pine shoot borer	86	N	Effect of vegetational diversity on natural enemies
Cottonwood twig borer	87	N	Importance of natural enemies in natural stands versus plantations
Larger pine shoot beetle	90	E	Effects on natural enemies of slash management practices

[1,2]E=exotic, N=native

Table 4. *Species for which no important role was identified for biological control.*

Species	Number in this report	Pest Origin
Pear thrips	1	E
Introduced basswood thrips	2	E
Pine bark adelgid	7	N
Pine leaf adelgid	8	N
White pine aphid	9	N
Woolly elm aphid	10	N
Pine tortoise scale	18	N
Pales weevil	24	N
Pitch-eating weevil	27	N
Native elm bark beetle	35	N
Spruce beetle	37	N
Eastern larch beetle	39	N
Spring cankerworm	47	N
Forest tent caterpillar	49	N
Eastern tent caterpillar	50	N
Pine webworm	53	N
Zimmerman pine moth	54	N
Bagworm	56	N
Oak leaf roller	60	N
Saddled prominent	61	N
Virginia pine sawfly	66	N
Two-lined chestnut borer	72	N
Bronze birch borer	73	N
Flatheaded apple tree borer	77	N
Locust borer	78	N
White oak borer	79	N
Whitespotted sawyer	80	N
Banded ash clearwing	82	N
Columbian timber beetle	83	N
Northern pine weevil	89	N
White pine cone beetle	91	N
Arborvitae leafminer	92	N

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