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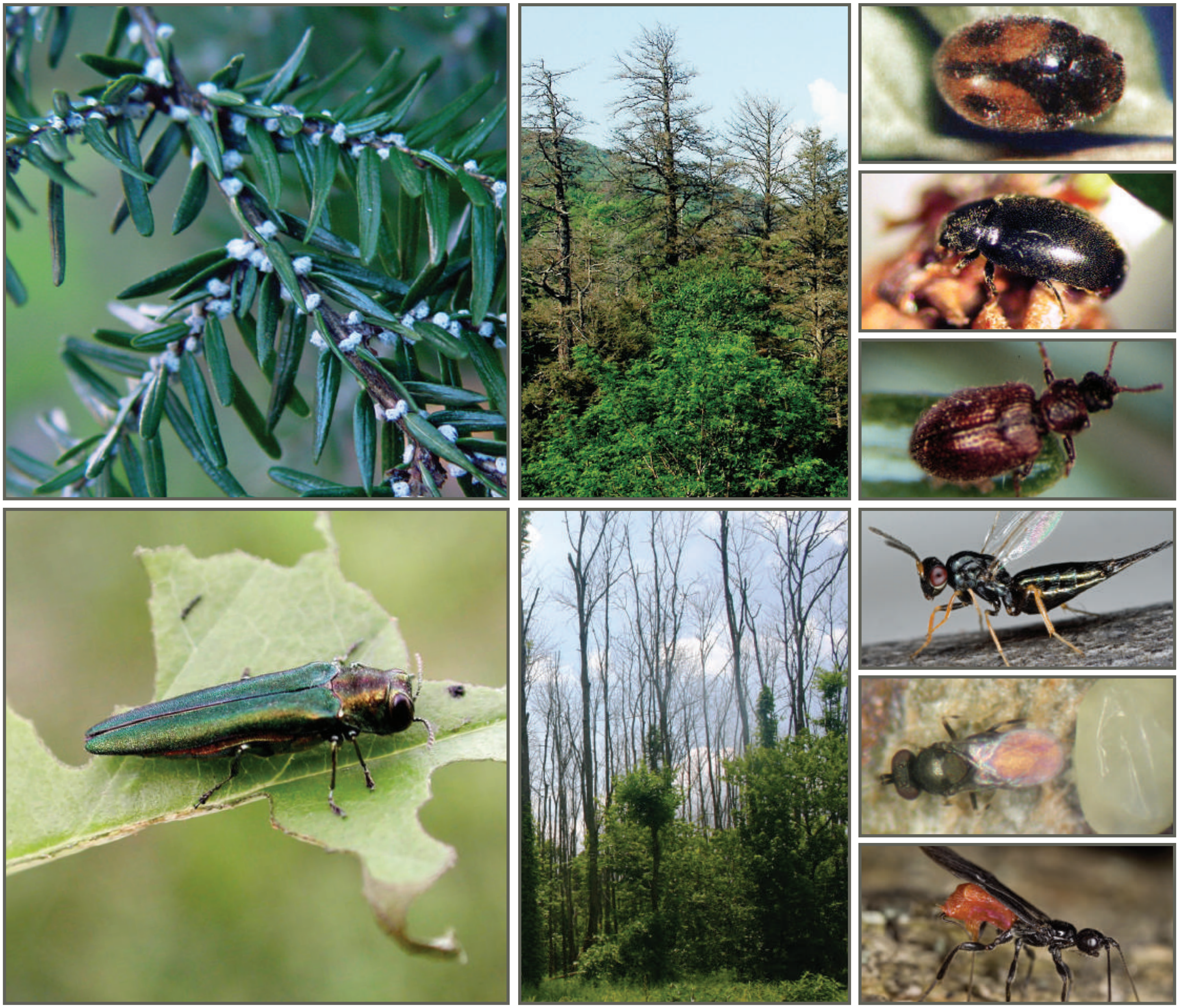
The Use of Classical Biological Control to Preserve Forests in North America

Edited by Roy Van Driesche and Richard Reardon



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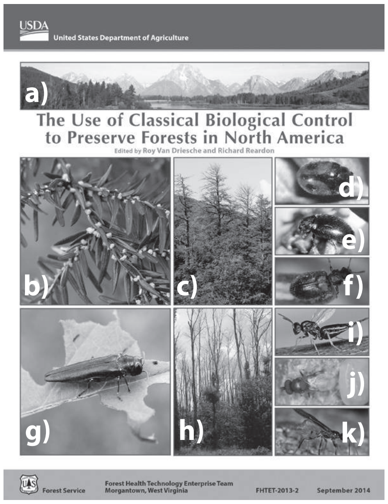

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Photos **a)** Grand Tetons. Brian Lockhart, USDA Forest Service, Bugwood.org. **b)** Hemlock woolly adelgid, *Adelges tsugae* infestation. Chris Evans, Illinois Wildlife Action Plan, Bugwood.org. **c)** Decline and mortality caused by hemlock woolly adelgid. William M. Ciesla, Forest Health Management International, Bugwood.org. **d)** *Scymnus ningshanensis*. Guangwu Li, Chinese Academy of Forestry. **e)** Lady beetle *Sasajiscymnus tsugae*. Carole Cheah, Connecticut Agricultural Experiment Station, Bugwood.org. **f)** Tooth-necked fungus beetle *Laricobius sp.* Tom McAvoy, Virginia Polytechnic Institute and State University, Bugwood.org. **g)** Emerald ash borer, *Agrilus planipennis*. David Cappaert, Michigan State University, Bugwood.org. **h)** Emerald ash borer damage. Christopher Asaro, Virginia Department of Forestry, Bugwood.org. **i)** Eulophid wasp, *Tetrastichus planipennisi*. David Cappaert, Michigan State University, Bugwood.org. **j)** Encyrtid wasp, *Oobius agrili*. Debbie Miller, USDA Forest Service, Bugwood.org. **k)** Braconid wasp, *Atanycolus cappaerti*. David Cappaert, Michigan State University, Bugwood.org.

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THE USE OF CLASSICAL BIOLOGICAL CONTROL TO PRESERVE FORESTS IN NORTH AMERICA

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I Introduction

Biological control of forest pests in North America: a reflection

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PREVIOUS RELATED PUBLICATIONS

This book is intended as an update of information in three booklets published by the Forest Health Technology Enterprise Team, USDA-FS (FHTET): Van Driesche et al. (1996) (FHTET–96–19), Frank and Foltz (1997) (FHTET–96–20), and Bellows et al. (1998) (FHTET–96–21), covering forest insect pests of the northeastern and north central United States, the southern region, and the western region, respectively. In this update, pest coverage has been restricted to just invasive species that either have been targeted for permanent suppression through the introductions of exotic natural enemies, or have potential for such work. Several new invasive pests now present in the United States, not discussed in these older booklets, have been added. Also discussed are several species of high concern that have not yet invaded the United States, but threaten to do so.

TYPES OF BIOLOGICAL CONTROL

Biological control can be used for forest pest management in four ways: **(1) Natural enemy conservation** For native insect pests, conservation of existing natural enemies can be important. Some natural enemies present in natural forests may be lost when trees are grown more intensely in simplified systems, such as on lands replanted to a single species following clear cut logging, or in plantations where fertilizers, herbicides, and insecticides are commonly used. In such systems, introducing more vegetative diversity may help conserve native parasitoids and predators, which then may slow pest population growth (see discussion in Van Driesche [2006]); **(2) Biopesticides** Preparations made from a pest's natural pathogens may be useful against species such as some eruptive sawflies and moths (native or invasive) that have highly specialized pathogens (e.g., the baculoviruses of many lepidoptera) that cause significant mortality. Some of these can be cultured in the laboratory and applied much like chemical pesticides (Bird, 1953); **(3) Augmentative releases** Insectary-reared natural enemies of insects or mites can be released in areas where temporary control is needed. This works best in smaller areas of high value plants, like those in greenhouses and tree nurseries, and is often used against spider mites, whiteflies, thrips and aphids; **(4) Classical biological control** Invasive insects may be permanently suppressed over large areas through the importation, release, and establishment of specialized natural enemies from the pest's native range (e.g., Casagrande et al., 2008). This approach is the only approach to biological control considered in this book.

CLASSICAL BIOLOGICAL CONTROL OF PESTS

The first successful use of an exotic natural enemy to suppress an invasive insect took place in the 1880s in California, where the specialized, imported, Australian lady bird *Rodolia cardinalis* Mulsant was released in citrus groves to control the invasive monophlebid scale *Icerya purchasi* Maskell (Caltagirone and Doutt, 1989). Over the ensuing 100 years, approximately 200 species of invasive insects have been suppressed through this approach (Van Driesche et al., 2008 and references therein). This approach is appropriate and potentially effective if the pest of concern is a non-native invader from another biogeographic region, separated from the invaded area by oceans or other natural barriers that prevent the free movement of insects. Invasive insects in some groups have frequently been suppressed through the introduction of their missing, specialized, natural enemies (e.g., scales, whiteflies, mealybugs, leafminers, and beetles or sawflies with externally feeding larvae). Other groups have been more difficult to control, because either they have fewer specialized natural enemies, or have immature stages that live in niches protected from all but their more specialized natural enemies (e.g., adelgids, borers, root feeding pests).

For classical biological control to have significant potential against an invasive forest pest, highly specialized natural enemies must be present in the pest's native range, but absent in its invaded range. Only surveys in both the invaded and native ranges can determine if this is the case. However, because invasives of native trees switch host trees during the invasion process, it is not easy to separate the effects of potentially lower host defenses in the new host tree from a lack of specialized natural enemies. For example, emerald ash borer (*Agrilus planipennis* Fairmaire) is native to northeast Asia and invasive in the eastern United States. Specialized parasitoids of this borer's eggs and larvae found in Asia were missing from the invaded range (until their introduction for biological control). As such, one might suppose that the lack of these species could explain the higher borer density in the invaded area. However, most North American ash are less resistant to this pest than are ash species native to Asia (see chapter in this book for details). Therefore, whether imported natural enemies of the borer from Asia will be able to sufficiently suppress the pest's density in North America is still an open question.

A further complication in controlling the damage of invasive insects is that some species are vectors or facilitators of tree-killing pathogens (e.g., Sirex woodwasp [*Sirex noctilio* F.], beech scale [*Cryptococcus fagisuga* Lindinger], walnut twig beetle (*Pityophthorus juglandis* Blackman), and redbay ambrosia beetle [*Xyleborus glabratus* Eichoff]) (see references in chapters in this book). If such pathogens are systemic in the tree, as is true for the pathogen spread by redbay ambrosia beetle, it is not likely that biological control of the vectoring insect, even if successful, would protect trees from the pathogen.

Projects of classical biological control of forest insects carried out in the first half of the 20th Century (1900–1950) were mostly undertaken for protection of tree species with high commercial value. Thus, biological control was carried out against pests such as invasive defoliating sawflies and moths attacking valuable trees like pines (*Pinus*), larch (*Larix*), and spruce (*Picea*), while pests affecting less desirable trees such as beech (*Fagus*) were not targeted. Since the 1990s, motivation for forest insect biological control has broadened and refocused on protecting forest health and preserving its biodiversity. Thus, current projects of classical biological control against forest pests are a form of ecological restoration whose goals must be framed in ecological terms. This implies commitment to a principle of minimizing nontarget effects from introduced biological control agents and using suppression of the invasive pests as means to return native forests to desired states similar to their original conditions. With this principle as our guide, we now consider the steps in any classical insect biological control project as background for the detailed discussions of particular cases in the chapters that follow.

THE PROCESS OF CLASSICAL BIOLOGICAL INSECT CONTROL

Choosing Targets and Setting Goals

Defining the goals of a classical biological control project begins with the decision to try to control a particular pest. Species chosen as targets for classical biological control are usually invasive species that cause significant damage to native species or communities. Project goals need to be established in consultation with conservation biologists, restoration ecologists, or others with insights or interests in the work and should be recorded for later reference to see if goals were met.

Financing for projects should be available for the life of the project, because unfinished projects or unevaluated releases damage public support for future work. Commitments in principle should be made at the beginning of the project to evaluate the impacts of all released natural enemies on both the target pest and relevant nontarget species. Finally, projects should evaluate both changes in pest density and resulting improvements in forest health.

Pest Identification

Authoritative identifications of the invasive species are essential to avoid misdirected efforts. DNA analyses should be made to establish a link between the invader and the putative species to which it is identified. In the absence of this approach, there is significant risk that the invader will be mistaken for some other similar species, especially if the invader is new to science, as happened in several past cases, e.g., lobate lac scale (*Paratachardina pseudolobata* Kondo & Gullan, Kerriidae) in Florida hardwood hammocks (Schroer et al., 2008), and cassava mealybug (*Phenacoccus manihoti* Matile-Ferrero) in Africa (see discussion in Cox and Williams [1981]). Such misidentification may lead to erroneous assumptions about the pest's true identity and native range, misdirecting the search for natural enemies.

The same concerns about correct identification also apply to natural enemies introduced in projects. Both adequate taxonomic support and DNA analyses are needed to avoid misidentifications, as has occurred, for example, in work on parasitoids of ambermarked birch leafminer (e.g., [*Profenusa thomsoni* {Konow}] in Alaska [Soper, 2012]).

Surveys for Natural Enemies in Invaded Areas

Concurrent with the development of plans for natural-enemy surveys in the native range of the pest, it is common and necessary to run similar surveys in the range the pest invades. In some cases, as for example with emerald ash borer, native parasitoids may attack the invader and sometimes such species cause significant mortality. Surveys can show if any of the parasitoids or predators attacking the pest in the native range have co-invaded with the pest. Information from such surveys can help prevent accidental introductions of species already present, and can indicate if markers might be needed to separate or distinguish any newly introduced natural enemies from pre-existing ones.

Identifying the Pest's Native Range

After a pest has been correctly identified, its native range must be located, either from historical records or by other means such as the area with the greatest genetic diversity of the pest (e.g., Gwiazdowski et al., 2006) or the highest natural enemy diversity, etc. If there are many areas where the pest is known to occur, the exact source of an invading population can be identified by genetic matching of the invasive population to the various native populations (e.g., in such a process hemlock woolly adelgid [*Adelges tsugae* Annand], invasive in the eastern United States, was determined to be from Japan and not the western United States or China [Havill et al., 2006]). In many programs, several areas may be searched for natural enemies, choosing areas that are climatically matched to intended areas of introduction (e.g., Mausel et al., 2011). Collecting Natural enemies may require a series of trips over a number of years.

Collecting Natural Enemies in Native Range

Before investing in the study of natural enemies under quarantine conditions in the invaded country, it is useful to gain as much information as possible from studies in the native range. Such surveys typically cover a range of places where the pest is known to be present, filtered somewhat by comparative climatic analyses (e.g., Climex [Baker et al., 2002]). Surveys should be both comparative among locations and times of year, and quantitative (to estimate the amount of mortality to the pest caused by each candidate natural enemy). Widespread species causing higher levels of mortality should be preferred for introduction. In addition to providing a list of candidate natural enemies, surveys also provide some estimate of which species are more likely to be effective, although this is not something that is easily or accurately predicted. Also, collections of other species found in the pest's native range that are either related to the pest taxonomically or ecologically, or share the same host plant, can help determine if any of the candidate natural enemies are plausibly specific to the pest. If a local cooperator is available, data from field surveys conducted in the native range can be combined with data from laboratory experiments.

Quarantine Studies

Establishing quarantine colonies Once seemingly specialized parasitoids or predators of the target invasive insect have been collected in the native range (following the exclusion of any obviously non-specialized species based on data collected in the native range country), individuals of the natural enemy are shipped to a quarantine laboratory, usually in the invaded country, and used to establish a colony for further study. Also during this process, any contaminants, hyperparasitoids, or unwanted infectious agents are removed from the group of individuals used to start the natural enemy colony. Colony maintenance requires that the supporting food chain be in place, including a rearing system for the target pest and a suitable host plant. Sometimes, as in the case of borers, this can be quite difficult; in other cases, for example, foliage feeders, laboratory colonies of the pest can be established using in-season foliage harvested or collected locally or shipped in if out of season. More effort is required for insects requiring stems, especially large stems. For example, to rear emerald ash borer in the laboratory, tropical ash (*Fraxinus uhdei* [Wenzig] Lingelsh) produced in greenhouses was used with hand-insertion of field-collected larvae (Jian Duan, pers. com.).

For very small parasitoids, as for example those of scales, cross contamination between cultures is a potential risk, requiring several layers of containment or even rearing in separate quarantine laboratories.

Estimating host ranges Using parasitoids or predators from the quarantine colony, the oviposition (or for predators, also feeding) behavior of adult females is studied when they are offered different potential hosts or prey. For groups that are easily reared, such as aphids, individuals of nontarget species may be obtained from laboratory colonies; for species that are difficult or expensive to rear continuously in laboratory colonies, such as borers, individuals must be field-collected. Each project poses its own opportunities and limitations, based on the biology of the species required for tests.

Data collected from these tests will include a list of species that the candidate natural enemy either oviposits in or attacks, as well as a record of the frequency of successful development of the natural enemy's offspring in each nontarget species. Tests commonly used employ either "no choice" or "choice" designs and may focus on oviposition, feeding, or survival, and development of immature stages as outcomes. For parasitoid oviposition tests, sequential choice tests in which a nontarget species is presented first to naïve females, followed by presentation of the target pest to the same female, is a design with many advantages. (See Van Driesche and Murray (2004) for discussion of test designs.)

Deciding which native species to test can be based on phylogenetic relatedness to the target pest (same subgenus, genus, subfamily, family, etc) or if phylogenetic trees are available for the group containing the target pest, they can be used to identify species of decreasing relatedness.

For parasitoids (and some predators) that attack herbivores that have narrow host plant ranges, volatiles from the pest's host plant may be attractive to natural enemies. If the target pest is specialized to feed on a limited group of plants, and if a natural enemy of the pest is strongly attracted only to volatiles of those plants, then that behavior is a filter narrowing the natural enemy's host range, and study of such relationships in quarantine can help define the host range. This approach is particularly useful when the target pest's genus is large, with many species attacking many groups of plants. This is the case, for example with emerald ash borer, in which the North American fauna of the genus *Agrilus* is a very large (174 species), but with nearly all of these species attacking trees other than ash. In such a case, attraction of a parasitoid to ash volatiles suggests specificity to those borers that feed on ash (e.g., Yang et al., 2008)

Petitioning for release permits Once experiments on host range have been run, data on the pest, its damage, natural enemies, biology, and host range are assembled in a petition requesting permission to release the natural enemy into the environment. In the United States, the petition is submitted to both the Animal and Plant Health Inspection Service (APHIS) and to the North American Plant Protection Organization (NAPPO) for review. If the petition is viewed favorably by both groups, permission is granted to release the natural enemy into the field.

Release of the Natural Enemy and Monitoring Outcomes

Once a parasitoid or predator has been approved for release, individuals from laboratory colonies are released at field sites where it is hoped they will establish permanent populations. Following one or several releases at a site, recovery sampling is done to detect offspring of the released individuals. Recovery of the released species one full year (or better, two years) after the last release of the species at a site, is considered reasonable evidence of establishment. Similar sampling done at increasing distance from the release point can be used to document the spread of the natural enemy.

At sites where the new natural enemy has become established, further sampling can be done to determine the degree to which the new biological control agent both increases mortality to the pest and reduces the pest's density (see Van Driesche et al., 2008 for discussion of methods for determining impacts). Monitoring is sometimes based on experimental plots having and lacking the natural enemy (created by various means, including timing or location of releases or use of cages or insecticides to create plots lacking natural enemies) (Calderón et al., 2012). In other cases, life tables of natural populations or artificially established cohorts may be used to measure mortality caused by the natural enemy, relative to other sources of mortality affecting the pest (e.g., Duan et al., 2010; Abell and Van Driesche, 2011). Depending on results of releases of initially chosen natural enemies, the project may be considered finished, or a need may be identified to return to the native range to collect additional species for further releases.

In addition to determining if the released natural enemy attacks the target pest, sampling efforts should be made to determine if any nontarget hosts attacked in laboratory tests are actually attacked in the field, and if so, to what degree (e.g., Barratt et al., 1997).

PESTS COVERED IN THIS BOOK

Past Projects

Past projects of biological control against 14 invasive insects are discussed. While details are presented in chapters that follow, we can broadly state that three projects clearly failed: balsam woolly adelgid (*Adelges piceae* [Ratzeburg]), smaller European elm bark beetle (*Scolytus multistriatus* [Marsham]), and larch sawfly (*Pristiphora erichsonii* [Hartig]). Three others were extremely complicated in the sense that many poorly studied agents, with host ranges that included several pests, were introduced whose effects were volatile over time, regionally variable, and hard to interpret, today. These projects are best classified as having little proven effect on their targets: European pine tip moth (*Rhyacionia buoliana* [Denis and Schiffermüller]), introduced pine sawfly (*Diprion similis* [Hartig]), and European pine sawfly (*Neodiprion sertifer* [Geoffroy]) (although, an effective biopesticide was discovered for the latter). One project (birch casebearer, *Coleophora serratella* [L.]) was terminated before the released parasitoids were evaluated and so the project's outcomes cannot be evaluated.

The other seven projects in this section effectively controlled their pests to a substantial degree. Four of these involved only a few relevant agents and field data demonstrating suppression are convincing: browntail moth (*Euproctis chrysorrhoea* [L.]), larch casebearer (*Coelophora laricella* [Hübner]), mountain ash sawfly (*Pristiphora geniculata* [Hartig]), and birch leafminer (*Fenusa pumila* Leach). Of the three remaining projects that appear to have suppressed their targets, two did so by inadvertent or accidental introduction of key pathogens, which seem to provide control in conjunction with the deliberately introduced parasitoids, which also play some role: gypsy moth (*Lymantria dispar* [L.]) and European spruce sawfly (*Gilpinia hercyniae* [Hartig]). The final successful project, against elm leaf beetle (*Xanthogaleruca luteola* [Müller]), appears to have suppressed the target insect gradually over long time periods when few or no observations were made. We can thus record a maximal success rate here of 50% (7/14), although classification of outcomes is somewhat subjective and others may score projects differently.

Ongoing Projects

Projects against seven pests were considered to be active in 2012 and their outcomes could not be scored. However, two of these targeted pests, winter moth (*Operophtera brumata* [Hulst]) in Massachusetts and the chestnut gall wasp (*Dryocosmus kuriphilus*) in the southern United States, have been successfully controlled elsewhere (Canada and Japan, respectively) with classical biological control. Other ongoing projects are engaged in various stages of natural-enemy survey, introduction, and evaluation. These projects include two species of buprestid borers, emerald ash borer (*A. planipennis*) and gold spotted oak borer (*Agrilus auroguttatus* Schaeffer); hemlock woolly adelgid (*A. tsugae*); and two invasive sawflies, ambermarked birch leafminer (*Profenusa thomsoni* [Konow]) and the pine false webworm (*Acantholyda erythrocephala* [L.]). Only two of these, emerald ash borer and hemlock woolly adelgid, are large projects with many scientists and continuing resources. The remaining five are much smaller projects, largely based around one or two research groups.

Possible Future Targets

Ten invasive species are discussed in this book as potential targets of new biological control projects. Of these, some are regional threats to specific trees, such as soapberry borer (*Agrilus prionurus* Chevrolat) in Texas, pine blast scale (*Matsucoccus matsumurae* [Kuwana]) in the northeastern United States, and introduced basswood thrips (*Thrips calcaratus* Uzel) in the northern parts of the Great Lakes States. Each of these predominately affects a single tree species, in one or a few adjacent states. Another tier of pests of wider importance includes the aspen/

willow scale (*Diaspidiotus gigas* [Thiem and Gerneck]) in the Rocky Mountain area, elongate hemlock scale (*Fiorinia externa* Ferris) on two species of hemlock, and green spruce aphid (*Elatobium abeitinum* [Walker]). Still more widespread and highly damaging (at least potentially) are the final four species: Sirex woodwasp (*S. noctilio*), beech scale (*C. fagisuga*), redbay ambrosia beetle (*X. glabratus*), and walnut twig beetle (*P. juglandis*).

Of these ten pests, a project against soapberry borer might be feasible because of experience gained from two ongoing projects against congeners (emerald ash borer, gold spotted oak borer) with similar biology, as would a project against the Sirex woodwasp, based on projects in the Southern Hemisphere. The aspen/willow scale also might be a good choice, because of the many cases of successful control of diaspidid scales and the widespread importance of the pest. Potential also exists for biological control of beech scale and elongate hemlock—especially for elongate hemlock scale, for which natural enemies in the native range (Japan) have been identified (Abell, 2010). Potential for control of green spruce aphid needs to be evaluated.

Four of the species in this group, beech scale, Sirex woodwasp, redbay ambrosia beetle, and walnut twig beetle, are vectors of fungal pathogens. Two of these pests, redbay ambrosia beetle and Sirex woodwasp, are associated with systemic pathogens. While the biology of the species associated with Sirex woodwasp has allowed for its biological control in plantations, there seems to be little hope of biological control against redbay ambrosia beetle, because a single inoculation (one beetle-feeding event) is sufficient to a kill tree.

In contrast, for two of these pests, beech scale and walnut twig beetle, the pathogen's effect is dependent on the pest insect's density. As a consequence, these species may be suitable targets for biological control. Surveys for natural enemies of beech scale in its native range are underway (see chapter in book). Investigating the natural enemies of walnut twig beetle in its native range in Arizona should be a high priority, given the threat it poses to black walnut (*Juglans nigra* L.) in deciduous forests elsewhere in the eastern United States.

Potential Future Invaders

In the final section of this book, five pests are discussed that either have yet to invade North America, or, as in the case of Asian longhorned beetle (*Anoplophora glabripennis* [Motschulsky]), have done so in limited areas where eradication is being attempted. Work against Asian longhorned beetle should be pursued through surveys of natural enemies in China. This work would allow an assessment of the potential for biological control of this borer if eradication fails.

Other species in this group include a cerambycid beetle (Japanese pine sawyer, *Monochamus alternatus* Hope) able to vector pine wilt nematodes, and three Asian lymantriid moths (Asian pink moth, *Lymantria mathura* [Moore]; nun moth, *Lymantria monarcha* [L.], and Siberian moth, *Dendrolimus sibiricus* [Chetverikov]) able to defoliate a broad range of trees. None of these species is a particularly good target for biological control. The three lymantriids have large native ranges and enormous natural-enemy guilds, many members of which require alternative hosts. The only potential avenue for suppression of these species may be their adoption as hosts by gypsy moth parasitoids already introduced and established.

CONCLUSION

The purpose of assembling this detailed retrospective analysis of past forest biological control projects carried out in North America has been to provide guidance for future work. This takes place in the broader context of the need to bridge the gap between biological-control scientists and conservation biologists. The coming together of these two groups is a logical outcome of the shift in thinking, from an exclusive focus on resource protection to a broader consideration of forest health and protection of the biodiversity of the affected forest communities, within forest biological control projects. Details in the following chapters suggest that a shift in this direction began in the 1960s and 1970s. Projects as carried out in the 1920s to 1950s, based on parasitoid importation on a massive scale involving many poorly known species with limited host specialization, would not be considered today. That said, the need to protect forests from destructive invasive insects has never been greater, and projects such as those against hemlock woolly adelgid and emerald ash borer illustrate both the need for such work and the care exerted in biological control today. Funding is never adequate and the future is not particularly encouraging in this regard. Classical biological control is necessarily a public-works activity: therefore, both strong political support for the activity and strong institutions staffed by skilled scientists are essential. Efforts to maintain and expand those resources are fundamental if the biodiversity and productivity of American forests are to be preserved and protected against the inadvertent but certain, continued arrival, through international travel and trade, of highly damaging invasive insects.

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II Balsam Woolly Adelgid

(*Adelges piceae* [Ratzeburg]) (Hemiptera: Adelgidae)

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DESCRIPTION OF PEST

Taxonomy

Figure 1 Slide-mounted balsam woolly adelgid adult collected in Bourrignon, Switzerland.

Balsam woolly adelgid (Fig. 1) is a common name for *Adelges piceae* (Ratzeburg), introduced by Balch (1952), which in Europe is known as the "silver fir Adelges" (referring to its native host, *Abies alba* Miller [Varty, 1956]. Initially, Ratzeburg described as *Chermes piceae* in 1884 and Boerner renamed *Dreyfusia piceae* in 1908. The combination *Adelges piceae* proposed by Annand in 1928 is now widely accepted, but the genus *Dreyfusia* is still sometimes used, especially in Europe.

Adelges piceae is part of a group of morphologically similar species of *Adelges* that includes *A. nebrodensis* (Binazzi and Covazzi), *A. schneideri* (Börner), *A. nordmannianae* (Eckstein) (= *nusslini* Boerner), *A. merkeri* Eichhorn, and *A. prelli* (Grossmann). The latter three species are holocyclic, alternating between *Picea* and *Abies,* and the remaining species are anholocyclic, completing their life cycles only on *Abies*. The holocyclic species are thought to be ancestral to the group (Havill and Foottit, 2007), and the Caucasus Mountains are considered the ancestral geographic range of the group, because the primary host, *Picea orientalis* (L.) Link, is native to this region. The morphological differences distinguishing the species in this group are subtle and difficult to interpret (Mantovani et al., 2001; Havill and Foottit, 2007), and based on molecular evidence, there is some question about how many species should be recognized (Havill et al., 2007; Toenshoff et al., 2011).

Three subspecies of *A. piceae* have been identified in North America: *Adelges piceae piceae* in the southeastern United States (North Carolina, Tennessee, Virginia) and Pacific northwest (Oregon, Washington); *Adelges piceae occidentalis* in British Columbia, Canada; and *Adelges piceae canadensis* in Quebec and the northeastern United States (Foottit and Mackauer, 1983).

Distribution

The balsam woolly adelgid is considered native in Europe and was first reported in North America in Maine in 1908, in California in 1928, in Virginia in 1957, and in Idaho in 1983 (Livingston et al., 2000). Currently, it is found where its fir hosts grow in western and eastern North America, but is absent in central Canada and the Great Lakes region.

Damage

Type In North America, BWA most frequently attacks *Abies balsamea* (L.), *A. fraseri* (Pursh) Poir., *A. lasiocarpa* (Hooker) Nuttall, *A. amabilis* Douglas ex J. Forbes, and *A. grandis* (Doug.) Lindl. (Ragenovich and Mitchell, 2006). Silver fir, *A. alba*, is its principal host in Europe.

In Europe, BWA causes little damage to native firs, but North American fir species have hypersensitive responses to the adelgid's feeding that disrupt the trees' metabolism, damage the vascular system, and reduce radial growth, which can kill the trees (Balch, 1952; Balch et al., 1964). There are two symptoms of attack: gouting and formation of red wood (Balch, 1952). Gouting, which occurs on all North American firs, is a stunting of terminal growth with conspicuous swelling at the branch nodes (Fig. 2). This injury causes loss of branch growth and slow decline, which may persist for several years. Formation of red wood ("Rotholz," German for red wood) is a result of mass infestation of the main stem (Fig. 3). The wood beneath the bark develops a reddish-brown color and cell division is abnormal, producing thickened walls, large parenchyma cells, and decreasing water flow in the sapwood (Puritch, 1971). External symptoms are not visible until the tree is dying, which often occurs after 2 or 3 years of heavy stem infestation.

Extent BWA continues to be a serious pest of balsam fir in Maritime Canada, 100 years after its introduction (Quiring et al., 2008). In western North America, BWA is causing the slow disappearance of fir from some ecosystems (Ragenovich and Mitchell, 2006). Severe infestations of older grand fir (*A. grandis*) at low elevations result in a gradual decline in crown health and complete lack of fertile seed set. BWA is eliminating subalpine fir (*A. lasiocarpa*) from high altitude areas where the cone crops of this pioneer tree are an important food source for birds and other animals. In the southeastern United States, BWA-caused mortality of mature Fraser fir (*A. fraseri*) is over 80%, although there is still significant regeneration in some infested stands (McManamay et al., 2011). The considerable impacts on understory flora and fauna may result in permanent ecosystem changes, including loss of the spruce-fir moss spider (*Microhexura montivaga* Crosby and Bishop (U.S. Fish and Wildlife Service, 1995) and other endemic flora and fauna associated with Fraser fir (Houk, 1993). BWA is also a severe pest in Christmas tree plantations, especially in the southeastern United States where Fraser fir is the most common species planted (Potter et al., 2005).

Biology

A good review of the insect's biology in its native environment is provided by Varty (1956) and in its introduced environment by Balch (1952). *Adelges piceae* is strictly parthenogenetic on its secondary host (*Abies* spp.) and does not have a sexual generation on spruce (Balch, 1952. It has two to four sistens (diapausing) generations per year, depending on climate, and a single, rare progrediens (non-diapausing) generation that has little significance in the population dynamics of the adelgid (Marchal, 1913; Balch, 1952; Varty, 1956; Mitchell et al., 1961. Typically,

Figure 2 Infestation of terminals by balsam woolly adelgid causes swelling of nodes or gouting. Dawn Dailey O'Brien, Cornell University, Bugwood.org.

Figure 3 Balsam wooly adelgid infestations on the trunk of a fir tree. Scott Tunnock, USDA Forest Service, Bugwood.org.

BWA overwinters as a first instar and reaches the adult stage in March with egg-laying beginning in April and peaking in May. The crawlers that hatch from these eggs settle on twigs or the trunk, insert their stylets, become sclerotized, and aestivate for 3–6 weeks, followed by rapid development and production of another batch of eggs in mid-summer. This is followed by a third generation that produces eggs in October, which hatch, settle, and overwinter as hiemosistens.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

The number of adelgid species in the United States is about 17, of which about 9 are native (Blackman and Eastop, 1994; Havill and Foottit, 2007). The exact number is uncertain because the taxonomy of the Adelgidae needs revision.

The most widespread native species in the western United States are *Adelges cooleyi* (Gillette) on Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco), *A. tsugae* Annand on hemlock (*Tsuga* spp.), and *Pineus coloradensis* (Gillette) and *P. similis* (Gillette) on *Pinus* spp.

There are no native *Adelges* species in the eastern United States, but *A. cooleyi* and *A. tsugae* are established. *Adelges tsugae* in the eastern United States was introduced from Japan, and is distinct from the western North American lineage (Havill et al., 2006). *Pineus* species native to the eastern United States include *P. strobi* (Hartig), *P. pinifoliae* (Fitch), and *P. floccus* (Patch). Nearly all of the species present in the western states are present in the eastern states and vice-versa.

Native Natural Enemies Affecting the Pest

There are several native predators in North America that attack adelgids, but adelgids have no known parasitoid. Specialist predators of the family Adelgidae are in the beetle genus *Laricobius* (Derodontidae), the fly family Chamaemyiidae, and the lady beetle genus *Scymnus*. The native derodontids *Laricobius laticollis* Fall., *L. nigrinus* Fender, and *L. rubidus* (LeConte) are specialists on *A. cooleyi, A. tsugae,* and *P. strobi*, respectively, but can be found on other adelgid species. *Laricobius nigrinus* and *L. rubidus* have been recovered occasionally from *A. piceae* (Mitchell, 1962; Clark et al., 1971; Zilahi-Balogh et al., 2002). Native chamaemyiid species, which prey primarily on pine adelgids, that have been recovered from *A. piceae*, include *Neoleucopis pinicola* Malloch, *N. ancilla* McAlpine, *Leucopis piniperda* Malloch, *L. americana* Malloch, and *L. argenticollis* Zetterstedt (Brown and Clark, 1956; Mitchell, 1962; McAlpine, 1971; McAlpine and Tanasijtshuk, 1972; Tanasijtshuk, 2002).

Native generalist predators seem to have a greater impact on *A. piceae* than the native adelgid specialists. Mitchell (1962) recorded six species of Syrphidae, two Cecidomyiidae, one Hemerobiidae, two Chrysopidae, one Coccinellidae, one Anthocoridae, and two Acarina on *A. piceae* in Oregon and Washington. Syrphids were the most abundant predators, but because of poor synchrony with the adelgid, they, as well as the other predators, were regarded as opportunistic and ineffective. The predator complex, which peaked in July at 0.8 individuals/100 cm^2, reduced unprotected *A. piceae* populations of 2,500/100 cm^2 by 40%, compared to populations protected by enclosures; however, as fall approached the predator population declined and the unprotected populations quickly recovered (Mitchell, 1962). In British Columbia, the red velvet mite, *Allothrombium mitchelli* Davis, with up to 500 individuals per linear meter of trunk, was the most abundant of several generalist predators (Harris and Dawson, 1979). Other abundant generalist predators included brown and green lacewings, syrphids, and the lady beetle, *Scymnus* (*Scymnus*) *nebulosus* LeConte (*S. phelpsii* in article. In eastern Canada, Brown and Clark (1956) reported 19 native arthropods preying on *A. piceae*. Only four were common: the brown lacewing, *Hemerobius humulinus* L., *Syrphus torvus* Osten Sacken, *N. pinicola,* and *L. americana*. In Newfoundland, *Tetraphleps canadensis* Provancher, fed voraciously on *A. piceae*, but it did not substantially reduce the density of the adelgid. In Maine, Brower (1947) observed several larvae of the harvester butterfly, *Feniseca tarquinius* (F.), preying on *A. piceae*. In North Carolina, Amman (1970) counted predators weekly on the trunks of ten trees. Similar to British Columbia, the most abundant predators were mites, with *Anystis* sp., *Leptus* sp., and *A. mitchelli* comprising 75–92% of the total number of predators. The syrphid *A. torvus* was next in abundance. Predation was primarily on the egg stage, but accounted for only a small portion of the total egg mortality (Amman, 1970). In sum, although many of native specialists and generalists were observed to prey on the balsam woolly adelgid, their combined impact was limited.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Europe is regarded as the origin of the balsam woolly adelgid found in the United States. It is not clear whether the morphological variation observed in North American is evidence of multiple introductions or of divergence after introduction (Foottit and Mackauer, 1980).

Areas Surveyed for Natural Enemies

The first surveys were done in Great Britain on pines infested with adelgids in the genus *Pineu*s. Later, extensive surveys for natural enemies attacking *A. piceae* and related species on silver fir were made in Germany, France, Switzerland, and Austria, and these were the sources of many natural-enemy importation. Additional work on the survey and study of other *Adelges* species and the collection of their natural enemies were carried out in India, Pakistan, and Japan. At the end of the program, a survey was done of natural enemies in the Caucasus Mountains region of Turkey, but no predators were exported.

Natural Enemies Found

The first predators imported to North America for biological control of *A. piceae* were collected in England from adelgids on pines (Wilson, 1938). Of the ten species found, six were introduced. The predators considered most important were *Neoleucopis obscura* Haliday, *Lestodiplosis pini* Barnes, and *Hemerobius stigma* Stephens. Surveys of *A. piceae* on silver fir in Switzerland, Germany, and France identified ten species as important predators (Delucchi, 1954): (1) Coleoptera–*Pullus* (= *Scymnus*) *impexus* (Mulsant); (2) *Aphidecta obliterata* (L.); (3) *Laricobius erichsonii* Rosenhauer; (4) Diptera–*N. obscura*; (5) *Leucopis griseola* (Fallén) (= *Leucopis hennigrata* McAlpine); (6) *Cremifania nigrocellulata* Czerny; (7) *Cnemodon latitarsis* Eggleston (= *Heringa vitripennis* [Meigen]); (8) *Syrphus arcuatus* (Fallén) (= *Dasysyrphus venustus* [Meigen]); (9) *Aphidoletes thompsoni* Moehn, and; (10) Neuroptera–*Chrysopa* (= *Dichochrysa*) *ventralis* Curtis. All ten predators were present and ovipositing when *A. piceae* oviposition was at its peak in the spring, but only the species of Diptera were numerous in the fall. The author believed it was the combined predation of all the predators in the spring that was responsible for the reduction of *A. piceae* to a low level. In Sweden, *N. obscura*, *A. obliterata* and *Chrysopa* (= *Dichochrysa*) *prasina* Burmeister were the most abundant predators; *L. erichsonii* and *S. impexus* were absent (Pschorn-Walcher and Kraus, 1956). In Turkey, *A. piceae* attacks mostly the twigs rather than the bole of the fir tree, which is the primary site of attack in western Europe. The most abundant and effective predator was an unidentified species of *Leucopis* followed by *Syrphus lapponicus* Zett. (Eichhorn 1969a).

Host Range Test Results

The host specificity of important predators was based on field survey rather than laboratory choice tests. Pschorn-Walcher and Zwoelfer (1956) scored the relative abundance of predators on seven adelgids and the predators relative attack rate on different life stages of *A. piceae*. Adelgid eggs were preferred by all of the predator. The least host specific predators were *A. obliterata* and *N. obscura*; *L. erichsonii* was intermediate; and *S. impexus* and *C. nigrocellulata* were the most specific to *A. piceae*. Many of the predators shipped from India and Pakistan were also observed feeding on aphids and scale insects (Rao and Ghani, 1972).

Releases Made

More than 700,000 individuals representing about 33 predator species were released in five areas of the United States and Canada from 1933–1969 (The major species are listed in Table 1). The first releases (1933–1947) came from the Imperial Institute of Entomology, Farnham Royal, England (Smith and Coppel, 1957). During this period, there were six species released in the Maritime Provinces of Canada (1,710 *A. obliterata*, 23,377 *Exochomus quadripustulatus* L., 110 *Hemerobius nitidulus* F., 4,913 *H. stigma*, 3 *Lipoleucopis praecox* de Meijere, and 6,656 *Neoleucopis obscura*), and one species (559 *N. obscura*) was released in New Hampshire, USA. Fifteen species of predators imported from India and Pakistan were released between 1960–1965 (Amman and Speers, 1971; Clark et al. 1971). The others listed in Table 1 were released from 1951–1969 and most of these were supplied by the Commonwealth Institute of Biological Control, Delémont, Switzerland.

Table 1 Predators released (1933–1969) in North America for biological control of *Adelges piceae*[1]

Species	Origin	OR, WA[7]	BC[7]	Maritime Canada	New England	NC[7]	Status in NA[6]
Adalia ronina (Lewis)	Japan			1,004			E[?]
Aphidecta obliterata (L.)	Europe	2,237	7,133	17,818		1,730	E4
Aphidoletes thompsoni (Moehn)	Europe	36,413	8,721	164,818		8,089	E[?]
Ballia eucharis Mulsant	India	85		163		279	NR
Cremifania nigrocellulata Czerney	Europe	1,374	941	351			E[4]
Exochomus lituratus Gorham	Pakistan	93					NR
Exochomus quadripustulatus (L.)	Europe			23,377			E*
Exochomus uropygialis Mulsant	Pakistan	5,426		14,656			NR
Harmonia breiti Mader	India/ Pakistan	83		173		131	NR
Hemerobius nitidulus F.	Europe			110			NR
Hemerobius stigma Stephens	Europe			4,915			E*[5]
Laricobius erichsonii Rosenhauer	Europe	13,968	10,879	127,410	16,193	1,719	E[?]
Leucopis atratula Ratzburg	Europe			385			E*[4]
Leucopis hennigrata McAlpine[3]	Europe		2,273	1,607	3,259	126	E[5]
Neoleucopis obscura Haliday	Europe[2]	2,785		6,941	559	1,366	E[?]
Scymnus (Pullus) impexus (Mulsant)	Europe	1,342	25,649	124,548	268	290	E[?]
Scymnus (= *Diomus*) *pumilio* Weise	Australia	2,859	2,930	22,563		3,300	E*
Tetraphleps spp.	India/Pak.	98	1,276	7,430		782	NR

[1] Compiled from Smith and Coppel (1957), Dowden (1962), Amman and Speers (1964, 1971), Mitchell and Wright (1967), Clausen (1978), Harris and Dawson (1979), and Schooley et al. (1984); these references contain 15 additional species not recovered after release.

[2] Collected mostly in Great Britian from *Pineus pini* and *P. strobi*; releases in New Brunswick spread to Maine, which was the source of releases in North Carolina, Oregon and Washington, but identity uncertain.

[3] Released as *L. griseola* and *L.* sp. nr. *melanopus*, and in part, *L. obscura*

[4] Recovered in 1991, Victoria, British Columbia (Humble, 1994)

[5] May be endemic to North America.

[6] E = established; NR = not recovered.

[7] OR = Oregon; WA = Washington; NC = North Carolina; BC = British Columbia

*Reported as not established after biological control release, but has been recovered in non-release areas.

? Reported established after release for biological control, but not reported in North America after 1978.

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

About twelve of the predators released for biological control of *A. piceae* either were reported as established or are now known to be established in North America (Table 1). *Diomus pumilio* Weise and *Exochomus quadripustulatus*, which feed on psyllids and scale insects, respectively, did not establish on *A. piceae* but occur in California, probably from other introductions (Gordon, 1985). The species reported at the end of the program to be established in both Canada and the United States were *Aphidecta obliterata*, *Aphidoletes thompsoni*, *Cremifania nigrocellulata*, *Laricobius erichsonii*, *Neoleucopis obscura,* and *Scymnus impexus* (Schooley et al., 1984; Clausen, 1978. A later taxonomic study of vouchers indicates that *Leucopis hennigrata* (released as *Leucopis melanopus* and *L.* n. sp. nr. *melanopus*) and *L. atratula* had been established during the program in Maritime Canada, but that the only recovery of *L. obscura* was in the year of its release (McAlpine, 1971). In British Columbia, *A. obliterata*, *L. atratula*, and *C. nigrocellulata* have been verified to have established (Humble, 1994).

Many of the imported species reported to have established might have been confused with native species. The brown lacewing *Hemerobius stigma* was reported to not have established, but the native *Hemerobius stigmaterus* Fitch was recovered and later recognized as a junior synonym of *H. stigm*a. *Aphidoletes thompsoni* is likely a junior synonym of *Aphidoletes abietis* (Kieffer), a common, widespread species considered native to North America (Gagne, 2010). *Aphidoletes abietis* was reported in New York State (Felt, 1917) and has been collected recently from *A. piceae* in Canada and the United States (Gagne, 2010), and from *A. tsugae* in the eastern United States (Wallace and Hain, 2000). On the other hand, *A. thompsoni* was described in 1954 in conjunction with the balsam woolly adelgid biological control program and its only collection is associated with that program. *Laricobius erichsonii*, which is very similar in appearance to the native *L. rubidus*, was reported to be widely established and spreading in the years following release in North Carolina (Amman and Speers, 1964); however, post-release recovery of *L. erichsonii* in the eastern United States is not supported by vouchers (Montgomery pers. obs.). The report of *L. erichsonii* in British Columbia 15 years following its release (Harris and Dawson, 1979) is supported by vouchers (Lee Humble, *in litt.*), but it has not since been collected in North America. Clark et al. (1971) regarded the *Leucopis* and *Neoleucopis* released in North America as a mixture of five species, two of which may be confused with native North American species. When the European *N. obscura* was released in New Brunswick, it was reported to have spread rapidly, including to neighboring Maine. Subsequently, field recoveries from Maine were relocated to North Carolina and Oregon, where it also quickly established. However, the reports of this remarkable establishment and spread did not mention the similar native species *N. pinicola* and *L. piniperda*, which also feed on *A. piceae*. Furthermore, it was later determined from vouchers that *L. hennigrata* and *L. atratula* were also released in the Maritimes, with the latter recovered at several locations from 1933–1968 (McAlpine, 1971). Although it is unclear which species were moved from Maine, *L. piniperda*, *L. hennigrata,* and *L. atratula* now occur in western North America (McAlpine, 1978; Humble, 1994; Tanasijshuk, 2002; Ross et al., 2011)

Nontarget Effects

Neoleucopis obscura was reported to have displaced the native predator *L. americana* in New Brunswick and Newfoundland (Balch, 1952; Bryant, 1963); however, uncertainty in the identification of *Leucopis*/*Neoleucopis* makes it difficult to verify this. The types of *L. americana* and associated specimens collected in Illinois were determined by Tanasijshuk (2002) to be indistinguishable from *L. glyphinivora* Tanasijtshuk, a cosmopolitan species that feeds on aphids. A field identification guide (Brown and Clark, 1956) provided characters to separate larva, pupa and adult stages of *N. obscura* and *L. americana*, but did not include *L. atrulata* and *L. piniperda*, the species most represented in museums from field collections made during the program (McAlpine, 1971; Tanasijshuk, 2002). Until a good study of voucher specimens and existing predators is made, it will remain unclear if an introduced predator has displaced native predators or if native predators made a host shift to a new prey, *A. piceae*.

Recovery of Affected Tree Species or Ecosystems

There is no evidence that biological control resulted in enough of a reduction in balsam woolly adelgid populations to improve tree survival. In Washington and Oregon there is concern about impacts of the pest on grand fir and subalpine fir, with continued gradual elimination of these species in many habitats (Mitchell and Buffam, 2001). In eastern North America, many stands that were originally severely damaged are regenerating, but are still infested and damage to these young trees is expected to increase as they mature (Raganovich and Mitchell, 2006). In recent years, populations of BWA have increased in Maine and the Canadian Maritime Provinces, perhaps as a result of milder winter temperatures (Quiring et al., 2008).

Broad Assessment of Factors Affecting Success or Failure of Project

Biological control of adelgid pests is especially challenging because there are no known parasitoids attacking any adelgid species, and there are only a few specialist predators. Therefore, the strategy was to introduce an array of natural enemies with little information about their host ranges. None of the species from non-European countries established on *A. piceae*: these species were from areas with a poor climatic match to the target areas and the species imported were mostly generalist predators associated with fir trees. The first importations of natural enemies from Europe were from Great Britain, from adelgids on pine, and only one of these six species was specific to adelgids. None of the species imported from India and Pakistan were reported to have established: many of these were released in small numbers and did not prey specifically on adelgids.

The importations made later through the Commonwealth Agricultural Bureau International (CABI) biological control laboratory in Switzerland are an example of a well-run classical biological control program; the natural enemy complex on the target host was studied and the most promising species exported in large numbers. However, none of these species established well enough to provide effective control (Clark et al., 1971; Schooley et al., 1984. This outcome should not be surprising, because in Europe the population dynamic of the entire predator complex was inversely density-dependent and not regulative (Eichhorn, 1969b), and both tree resistance and weather were strong influences on the pest's population dynamics (Franz, 1956; Pschorn-Walcher and Zwolfer, 1956).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Laricobius erichsonii

The biology of *L. erichsonii* was thoroughly studied by Franz (1958). Its biology is similar to that of *L. nigrinus*, a native predator of *A. tsugae* in the United States, except that *L. erichsonii* adults emerge in early summer rather than the fall after pupating in the soil, feed for a few weeks and then re-enter the soil (Franz, 1958). Adults deposit their eggs in mid-April, after adelgids have started laying eggs. It has been suggested that its development indicates that it is not adapted specifically to *A. piceae* as compared with real specific predators like *Pullus impexus* (Franz, 1958). Although *L. erichsonii* was the most promising predator introduced in the Pacific northwestern United States, its effectiveness was limited because it attacked only high density adelgid populations (Mitchell and Wright, 1967) and preferred adelgids feeding on stems rather than twigs (Harris and Dawson, 1979). In the Canadian Maritimes, it was considered more effective than *N. obscura* (Clark and Brown, 1958), but it seldom reached population levels that suppressed the adelgid (Clark et al., 1971). The suggestion that low winter temperatures may have affected *L. erichsonii* survival was dismissed by Harris and Dawson (1979), but its survival might have been affected by soil moisture levels (Smith and Coppel, 1957).

Chamaemyiidae (Silver Flies)

There are 28 genera of silver flies comprised of more than 330 described species (Gaimari, 2010). This group of flies has been considered a promising source for biological control of adelgids, because species specialize on particular groups of sternorrhynchous Hemiptera (Gaimari, 1991). Species of *Neoleucopis, Anchioleucopis, Cremifania,* and some *Leucopis* seem to specialize on adelgids (Gaimari, 2010). Ross et al. (2011) summarize the biology of adelgid-feeding silver flies. The larvae feed on all stages of adelgids. They pupate on the host trees of their adelgid prey, with the puparia often found within the adelgid colony. They have 1–3 generations per year, and overwinter as larvae or puparia. In Europe, both immature beetle and fly predators are present and when *A. piceae* is laying eggs in the spring, but only fly predators are present in the fall (Pschorn-

Walcher and Zwolfer, 1956). The order of appearance of the predators in the spring was first *Leucopis*, then *Scymnus*, *Laricobius*, and *Cremifania*, with *Aphidoletes* appearing last. The Diptera were prevalent when adelgid populations were high, coating the trunk with white wax. Although *C. nigrocellulata* and *L. obscura* spread rapidly in the United States, they seldom developed large populations and were found only on trees with heavy adelgid populations; trees that soon died (Mitchell and Wright, 1967). In Maritime Canada, the lack of effective control was attributed to limited searching ability and appearing too late in the season (Balch et al. 1958; Clark et al., 1971).

RECOMMENDATIONS FOR FURTHER WORK

A prerequisite for any additional work would be to use modern morphological and molecular methods to definitively identify the native and previously introduced fauna of natural enemies. It would be worthwhile to specifically assess the occurrence of *C. nigrocellulata*, and other chamaemyiids that are already present in North America. This has not been attempted in recent decades. Species feeding on *A. piceae* and on other adelgid species in North America should be systematically documented. This will provide important baseline information to document the geographic and host ranges of the native and introduced species already present with which to compare establishment and impact of any new introductions. Also, it will help clarify the role of *A. piceae* as an alternate prey for biological control agents of the hemlock woolly adelgid, such as the Japanese lady beetle *Sasajiscymnus tsugae* (Sasaji and McClure), which has been shown in the lab to complete development on *A. piceae* (Jetton et al., 2011).

At the end of the balsam woolly adelgid biological control program, the Caucasus Mountains were explored for natural enemies, as it was felt that this may be the ancestral home of *A. piceae* (Eichhorn, 1969a, b.) Indeed, if the holocyclic species *A. nordmannianae* is ancestral to *A. piceae*, then the natural enemies in this region may have a longer association with this lineage of adelgids than those in Europe. Eichhorn 1969a,b suggested that an unidentified *Leucopis* species was the most promising predator from the Caucasus. This was later described as a new species, *L. hennigrata*, that had been imported to North America in 1959–1968 and based on its collection in 1960 in Banff, Alberta is considered native to North America (McAlpine, 1978). Also, a recent survey of sites in Turkey, Georgia, and Russia showed that *L. hennigrata* was abundant and appears to be having an impact on *A. nordmannianae* populations (Ravn et al., 2012). There is also a *Laricobius* species endemic to the Caucasus, *L. caucasicus* Rost (Leschen, 2011), but the impact of this species on fir adelgids in the Caucasus is not known. Future work could focus on evaluating these two species for importation to North America.

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III Elm Leaf Beetle

(*Xanthogaleruca luteola* [Müller]) (Coleoptera: Chrysomelidae)

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DESCRIPTION OF PEST

Taxonomy

Elm leaf beetle, *Xanthogaleruca luteola* (Müller), originally was described as *Chrysomela luteola* Müller, 1766. This species also has been known as *Galerucella xanthomelaenae* Schrank, 1781, and *Pyrrhalta luteola* (Müller) Weise, 1886. It is now placed in the subfamily Galerucinae Latreille, 1802, tribe Galerucini Laboissiére, 1921, and genus *Xanthogaleruca* Laboissiére, 1934, although Wilcox (1965) considered *Xanthogaleruca* to be a subgenus.

Distribution

Xanthogaleruca luteola occurs in Europe, North Africa, Asia Minor, Central Asia east to at least Afghanistan, and in Siberia (Aslan et al., 2000) and China (Zhenya et al., 2001). It was introduced into the northeastern United States in the 1830s and into California by the 1920s. It now occurs in much of the world where elms occur naturally or have been planted, including southern Canada, Mexico, Argentina, Chile, Australia, and New Zealand.

Damage

Type Elm leaf beetle feeds on elms (*Ulmus* spp.) and occasionally on *Zelkova serrata* (Thunberg). Larvae skeletonize the underside of leaves. Adults chew small holes through leaves, resembling damage to elms from the more recently introduced European flea weevil, *Orchestes alni* (L.). Extensive foliar damage causes premature leaf drop, and high elm leaf beetle populations can defoliate large trees entirely, sometimes twice in a single season. Defoliation weakens trees, predisposing them to attack by bark beetles (*Scolytus* spp.) that vector *Ophiostoma* spp. fungi, which in turn leads to the tree-killing Dutch elm disease. Elm leaf beetle damage alone is a nuisance and the loss of summer shade and costs of repeated control efforts can be significant.

Extent Historically, elm leaf beetle was among the top five urban forest insect pests in the United States, including western states, according to surveys of tree managers (Kielbaso and Kennedy, 1983; Wu et al., 1991). In California, it has been the most important pest of *Ulmus* spp. (Luck and Scriven, 1976; Dahlsten et al., 1993) and the only elm tree pest that is commonly treated with pesticides. However, according to many extension entomologists' informal field observations and the lack of public inquiries received on this pest, elm leaf beetle has not been a significant, widespread problem in most of the United States since about 1990 or 2000 (varying by location). Classical biological control in at least some locations is a likely but undocumented cause of elm leaf beetle's population decline and current non-pest status.

Biology of Pest

Adults (Fig. 1) commonly overwinter in bark crevices, litter, woodpiles, or in buildings. In spring, beetles fly to foliage to feed and lay eggs. Females deposit a double-row cluster of 5–25 eggs, mostly on the underside of elm leaves. Larvae chew foliage for several weeks, and develop through three instars. Late third instars move downward to pupate, often on soil or in litter around the tree trunk, sometimes together in great numbers. After about 10 days, adults emerge and fly to the canopy to feed and (during spring and summer, before diapause induction) lay eggs.

Elm leaf beetle has about two annual generations in much of its range, but this varies with weather and location.

Figure 1 An elm leaf beetle adult, egg mass, and first instar. Jack Kelly Clark, courtesy University of California Statewide IPM Program.

For example, typically there is only one complete generation a year in northeastern California, while up to three generations can occur in central and southern California. A degree-day model can predict the overwintering emergence of adults and timing of each life stage in the field in northern California (Dreistadt and Dahlsten, 1990a).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

About 1,500 species and 175 genera of Chrysomelidae occur in North America. The Galerucinae subfamily includes over 200 species in Canada and the United States and about 5,800 species worldwide. *Xanthogaleruca* is a Palearctic genus of about a dozen species mostly limited to eastern Asia (Löbl and Smetana, 2010). No other *Xanthogaleruca* species are reported in North America, although that genus name and others have been used for *Galerucella nymphaeae* (L.), an introduced Eurasian species that feeds on water lilies (*Nymphaeae* spp.). Other *Ulmus*-feeding chrysomelids include *Xanthogaleruca (=Pyrrhalta) maculicollis* (Motschulsky) and *Xanthogaleruca (=Altica =Pyrrhalta) aenescens* (Weise), both reported only from eastern Asia.

The name *Pyrrhalta,* still used by some, is not a guide for biological relatedness and whether nontarget chrysomelids might also be hosts for specialized natural enemies of *X. luteola*. *Pyrrhalta* is a diverse, paraphyletic group of uncertain affinity and includes at least 55 species in the Palearctic and 17 species in the Neotropics (Park and Lee, 2004). No other *Ulmus*-feeding *Pyrrhalta* species are reported in the United States or Europe.

Other Galerucinae in the United States include the introduced larger elm leaf beetle, *Monocesta coryli* (Say), which feeds mostly on the leaves of elms, but occasionally on other plants including black birch (*Betula nigra* L.), hawthorn (*Crataegus* spp.), hazel *(Corylus* spp.), and pecan (*Carya illinoinensis* Koch). *Pyrrhalta viburni* (Paykull), introduced from Europe, feeds on about 150 plants in the genus *Viburnum* and is a major ornamental plant pest in the eastern and northwestern United States.

Native Natural Enemies Affecting the Pest

Barbosa et al. (1997) review the European and American reports of elm leaf beetle predators, of which there are many. For example, at least a dozen generalist predators are reported to feed on elm leaf beetle in Oklahoma (Eikenbary and Raney, 1968). We found few studies on pathogens and no studies evaluating the importance of predation on elm leaf beetle populations. Our review focuses on parasitism.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Xanthogaleruca luteola is of Palearctic origin, likely within the region from Asia Minor through Central Asia to the Far East. Its *Ulmus* spp. hosts originated in Central Asia and spread over much of the Northern Hemisphere during prehistoric times. By the 1800s, elms were widely planted in Australasia, Europe, North America, and South America.

Areas Surveyed for Natural Enemies

The first detailed publication on elm leaf beetle natural enemies was by Silvestri (1910) in Italy. He illustrates and discusses two primary parasitoids, one secondary parasitoid, and several predators. Silvestri (1910) also refers to this pest in Austria and France and cites the first report (Howard, 1908) of the introduction to the United States of the egg parasitoid *Oomyzus gallerucae* (Fonscolombe) (given as *Tetrastichus xanthomelaenae*).

It was originally believed that *X. luteola* "is of European origin," and from 1908–1939 all reported surveys and imported collections of *X. luteola* natural enemies were from France, other European countries (Clausen, 1978), or the United States. Collection (or survey) locations during the 1970s–1990s that were sources of introductions into the United States included Algeria, France, Greece, Iran, Israel, Morocco, Romania, and Spain (Fig. 2, Table 1). Some of these reports are not formally published and this list is probably incomplete. After the early surveys, the European species of *Aprostocetus* and *Oomyzus* associated with *X. luteola* and *Galeruca* spp. were revised and keyed (as *Tetrastichus* spp.) by Graham (1985), who clarified that only two Hymenopteran primary parasitoids, *O. gallerucae* and *Aprostocetus* (=*Geniocerus* =*Tetrastichus*) *celtidis* (Eros), were associated with elm leaf beetle in Europe.

Figure 2 California sites of release of *Oomyzus gallerucae* adults totaling over 400,000 individuals during 1984–1998 (Dahlsten et al. 1998).

Table 1 Parasitoid introductions in central and southern California for the biological control of *Xanthogaleruca luteola*, 1933–1983.

Year	Source	Release Location(s)	Reference
1933–36	Europe, Japan[a]	Fresno	Berry, 1938[b]; Clausen, 1978; Flanders, 1936
1934	Eastern United States[b]	Fresno, Orangevale, Port Costa, Visalia	Berry, 1938[a]
1939	Europe[c]	Stockton	Clausen, 1978
1971–83	France, Iran, Morocco, Spain	Southern California, including: Bishop, Hesperia, Landcaster, N. Hollywood, Redlands, Riverside, Temecula, Thurman Flt., Yucaipa	Luck and Scriven, 1984
1974–80	Iran, Greece	Davis, Modesto, San Jose, St. Helena, Winters	Olkowski et al., 1986
1977	Iran[b]	Stanislaus,d Yolod	van den Bosch, 1977
1981–83	Israel, Morocco	Chico, Davis, Dixon, Fresno, Marysville, Merced, Modesto, Sacramento, Stockton, Winters, Woodland	Bugg and Ehler, undated

All introductions were of *Oomyzus gallerucae*, except as noted.

[a]Unidentified *Tetrastichus* sp. from *Xanthogaleruca* (=*Pyrrhalta*) *maculicollis* from Japan; [b]*Baryscapus brevistigma;* [c]*Erynniopsis antennata;* [d]County names, all other release locations are cities.

Natural Enemies Found

Various predators, parasitoids, and pathogens of elm leaf beetle are reported from Asia, Europe, and the United States. Generalist predators of *X. luteola* in Italy mentioned by Silvestri (1910) include *Anisolabis moesta* (Serv.) (Dermaptera: Forficulidae), *Zicrona coerulea* (L.) (Hemiptera: Pentatomidae), *Lebia scapularis* (Fourcroy) (Coleoptera: Carabidae), and *Coccinella lycenea* Olive. (Coleoptera: Coccinellidae). *Lebia scapularis* "from Europe" was reportedly introduced into Massachusetts (Clausen, 1978), but no recoveries were reported. There are three primary parasitoids and one secondary parasitoid of *X. luteola* that are definitely established in the United States: (1) *Baryscapus brevistigma* (Gahan) (Hymenoptera: Eulophidae), a gregarious prepupal-pupal endoparasitoid*;* (2) *Erynniopsis antennata* (Rondani) (Diptera: Tachinidae), a solitary endoparasitic larval-prepupal and larval-adult parasitoid*;* (3) *Baryscapus erynniae* (Domenichini) (Eulophidae)*,* a gregarious secondary endoparasitoid of *E. antennata;* and (4) *Oomyzus gallerucae* (Fonscolombe) (Hymenoptera: Eulophidae), a solitary endoparasitoid of eggs. Silvestri (1910) from Italy provides the first detailed account of the parasitoids *O. gallerucae* (as *Tetrastichus xanthomelaenae), E. antennata* (as *Erynnia nitida),* and the secondary parasitoid *B. erynniae* (as *Tetrastichus rapo).* Silvestri does not mention *B. brevistigma.*

Baryscapus brevistigma The prepupal-pupal parasitoid *B. brevistigma* originally was described from collections in Massachusetts (Gahan, 1936) and also was collected in at least another seven northeastern states. "It would seem to be native to the United States as no records of its attacking elm leaf beetle pupae have been made in other countries," according to Berry (1938a) and other American entomologists, who by then had accumulated over 25 years of contact with Europeans working on elm leaf beetle. Subsequently, *B. brevistigma* was reported from *X. luteola* in Iran (van den Bosch, 1977; Azmayesh-Fard and Esmaili, 1981) and probably is native to that part of the world.

Oomyzus gallerucae The egg parasitoid *O. gallerucae* (Fig. 3) occurs in Europe, Iran, China, and elsewhere (Table 1). It is unlikely that *O. gallerucae* is native to Europe,

Figure 3 Whitish eggs from which elm leaf beetle larvae emerged and darker eggs (bottom) that were parasitized by *Oomyzus gallerucae*. Jack Kelly Clark, courtesy University of California Statewide IPM Program.

and the newness of the first Chinese report (Zhenya et al., 2001) may indicate *O. gallerucae* has been introduced at least in the Far East. The Chinese report makes use of the old name, *Tetrastichus gallerucae*, for *O. gallerucae*, illustrating the challenges of discerning distribution and host range, given the many synonymies and multilingual literature.

Other egg parasitoids During the initial importation into Massachusetts and subsequent laboratory rearing of *O. gallerucae* (as *T. xanthomelaenae*), Berry (1938b) observed a second egg parasitoid, given only as *Tetrastichus* sp., which was distinguishable morphologically and by its different fecundity and development time. That report likely refers to the polyphagous eulophid egg parasitoid *Aprostocetus celtidis*, known from other European species of *Pyrrhalta* and at least one lepidopteran, the gracillariid *Lithocolletis lantanella* Matsumura. Among a large number of eulophids reared from European *X. luteola* eggs, Graham (1985) found that nearly all were *O. gallerucae*, and only a few were *A. celtidis*.

Tachinids In addition to *E. antennata,* which is reported from Europe and recently from Turkmenistan (Middle Asia), at least one other tachinid (*Medina collaris* Fallén) has been reported from *X. luteola* in Europe (Dahlsten et al., 1985). Males of the Neotropical tachinid *Euthelyconychia* (=*Aplomyiopsis*) *galerucellae* (Villeneuve) are reported having been reared from *X. luteola* larvae in the 1930s from Medford, Oregon and Stockton, California (Flanders, 1940). We found no subsequent reports of *E. galerucellae* associated with *X. luteola*.

Pathogens The fungus *Beauveria bassiana* (Balsamo) Vuillemin (=*Sporotrichum globuliferum*) has been reported as an important mortality factor for elm leaf beetle under the moist conditions in Europe, California, the northeastern United States (Britton, 1907), and Minnesota (Krischik, 2007). The microsporidian *Nosema galerucellae* Tonguebaye and Bouix occurs in elm leaf beetles, at least in France (Tonguebaye and Bouix, 1989). The nematode *Steinernema (=Neoaplectana) carpocapsae* Weiser applied to pupae (Kaya et al., 1981) and larvae (Thurston, 1998) and *Bacillus thuringiensis tenebrionis* (Krieg) when eaten by larvae (Cranshaw et al., 1989; Thurston, 1998) kill a large proportion of treated elm leaf beetles.

Host Range Test Results

We found no reports of host range testing before the last reported parasitoid introductions in the United States in the late 1990s. Although many publications mention *O. gallerucae,* this parasitoid has been reported in the field only from *X. luteola* (Graham, 1985); thus, it appears to be specialized on *X. luteola* eggs. In laboratory cage studies, an *Oomyzus* sp. parasitized the eggs of both elm leaf beetle and introduced species of *Diorhabda* (Brown et al., unpublished). However, given the species-specific chemical stimuli involved in *O. gallerucae* host-habitat location, host finding, and host acceptance (Meiners and Hilker, 1997) and the parasitoid's discrimination between non-host leaf beetle eggs and eggs of *X. luteola* (Meiners et al., 2000) (summarized below), *O. gallerucae* is unlikely to parasitize other hosts in the field.

Oomyzus gallerucae is attracted to *Ulmus* by tree volatiles (synomones), whose release is induced by egg deposition of *X. luteola,* but is not attracted to elm leaves carrying eggs of the chrysomelid *Galeruca tanaceti* L., a polyphagous European chrysomelid that is attacked by the egg parasitoid *Oomyzus galerucivorus* (Hedqvist). An elicitor chemical from the oviduct secretion of *X. luteola*, used to glue eggs to leaves, triggers the release of elm volatiles that specifically attract *O. gallerucae* before the occurrence of any actual herbivory. *Oomyzus gallerucae* is attracted by the volatile kairomones from the feces of *X. luteola* feeding on elms, but is not attracted by the larval feces of a lepidopteran (*Opisthograptis luteolata* L.) feeding on elms. The antennal responses of *O. gallerucae* are stimulated by contact kairomones extractable from the egg shells of *X. luteola*. Comparison of the duration of antennal drumming on chrysomelid eggs showed that *O. gallerucae* clearly differentiates between eggs of *X. luteola* and the chrysomelid *Galerucella lineola* L., and strongly preferred the former (Meiners et al., 2000).

Releases Made and Resulting Establishment

Four exotic parasitoid species of elm leaf beetle (three primary, one secondary) have definitely established in the United States. Two of these, the primary parasitoid *B. brevistigma* and the secondary parasitoid *B. erynniae*, appear to have invaded on their own, along with their host, rather than having been deliberately introduced as biological control agents.

Baryscapus brevistigma This self-invading parasitoid of elm leaf beetle was first reported in the United States in Massachusetts, but was subsequently intentionally spread to new areas, such as California, with elm leaf beetle infestations. After pre-introduction surveys did not detect *B. brevistigma* in California, about 6,600 *B. brevistigma* individuals, collected from the eastern United States, were released in 1934 in four central California counties across a distance of about 250 miles. This eulophid readily established (Berry, 1938a; Clausen, 1978).

Erynniopsis antennata This tachinid (Figs. 4, 5) readily established in California after a single release of 31 European females in Stockton in 1938 (Flanders, 1940), and it now also occurs in Oregon. Except from California and Oregon, we found no original reports that *E. antennata* has been collected from the field in other parts of North America, even though at least 1,121 adults of this tachinid, from several European countries, were released in Massachusetts and Connecticut from 1934 to 1936. Also, flies collected in California were released in at least Arkansas, Idaho, Maryland, Nevada, Pennsylvania, and Virginia (Clausen, 1978). *Erynniopsis antennata* is known not to occur in Missouri (Puttler and Bailey, 2003) and also was not found in about 1,000 larvae of elm leaf beetle and 340 prepupae collected in Maryland (Barbosa et al., 1997).

Baryscapus erynniae This secondary parasitoid has been known in Europe since at least 1839 and was discussed at length by Silvestri (1910), based on work in Italy (Figs. 6, 7). The first report we found of *B. erynniae* in the United States was from southern California by Luck and Scriven (1976), 40 years after its tachinid host had established in California. *Baryscapus erynniae* could not have been introduced during the 1938 introduction and establishment of its tachinid host because *E. antennata* was

Figure 4 An adult *Erynniopsis antennata* and two second instar elm leaf beetles. Jack Kelly Clark, courtesy University of California Statewide IPM Program.

FIgure 5 A close-up of elm leaf beetle prepupae (left) and pupae (center) and pupae of *Erynniopsis antennata* (right). Jack Kelly Clark, courtesy University of California Statewide IPM Program.

Figure 6 The secondary parasitoid *Baryscapus erynniae* on a third-instar elm leaf beetle that may be parasitized by *Erynniopsis antennata*. Jack Kelly Clark, courtesy University of California Statewide IPM Program.

Figure 7 *Baryscapus erynniae* dissected from *Erynniopsis antennata*. Jack Kelly Clark, courtesy University of California Statewide IPM Program.

imported as a single "shipment of parasitized adults of the elm leaf beetle...sent to the Citrus Experiment Station at Riverside, California from Hyères, France..." (Flanders, 1940) and when it is inside of adult elm leaf beetles, this tachinid is not parasitized by *B. erynniae* (Luck and Scriven, 1976). The French importation was received in California the first week of May, after which the adult tachinids emerged. *Baryscapus erynniae* is believed to oviposit in tachinid-parasitized elm leaf beetles only during the beetle's last instar, and the shipment was likely too early in the season for host larvae susceptible to *B. erynniae* oviposition to have been present in France.

Unpublished introductions of its tachinid host, under the names *Erynnia nitida* and *Erynniopsis rondani,* were made in California between 1955 and 1972 (Dahlsten and Dreistadt, 1995). Contamination with *B. erynniae* during these introductions of *E. antennata* may be the source of this secondary parasitoid's introduction into California. In addition to parasitizing *E. antennata,* some state that *B. erynniae* also is a primary parasitoid of *X. luteola* (Gates et al., 2005).

Oomyzus gallerucae This egg parasitoid was initially collected in Europe, and from 1908 to 1935 over 28,000 adults were released at sites from Massachusetts south to Virginia and west to Ohio, and about 7,000 adults were released in California (Berry, 1938b). Although there were recoveries in the year of release, no establishment was reported (Clausen, 1978). Unpublished attempts to establish *O. gallerucae* in California occurred during the 1950s and 1960s, apparently without success (Luck and Scriven, 1984; Dahlsten and Dreistadt, 1995). In the late 1970s, R. F. Luck and G. T. Scriven introduced *O. gallerucae* from Morocco into southern California. They recovered successfully overwintered populations in Snow Creek Village, Riverside County, 1981–1984 (Luck and Scriven, 1984), which is the first documented, deliberate establishment of *O. gallerucae* in the United States. In the 1980s, collections from Israel and southern California were released in central California (Table 1) and establishment was documented in at least three locations, the most northern of which was Stockton (Ehler et al., 1987; Dahlsten and Dreistadt, 1995). From 1984 to 1998, approximately 400,000 individuals of *O. gallerucae,* representing at least six strains from several European sources plus the Stockton, California strain (believed to be from Morocco), were released in 28 locations in central and northern California (Fig. 2), and sporadic recoveries were made in subsequent years at locations including Cloverdale, Marysville, and Princeton (Dreistadt and Dahlsten, 1991). These releases included a strain of *O. gallerucae* from Grenada, Spain that was released between 1995 and 1999 in Sacramento, California, and although recoveries were made within the release year (with parasitism up to 55%), no overwintering establishment of *O. gallerucae* was detected (Lawson, 2000). A complete list of sites where *O. gallerucae* is definitely established in California and quantification of its impact has not been published, largely due to the death of the project's leader, Donald L. Dahlsten, in 2003.

The first published report of establishment of *O. gallerucae* in the United States was by Hall and Johnson (1983). They collected *O. gallerucae* in Ohio, apparently from the 1930s introductions. Puttler and Bailey (2003) reported that between 1999 and 2000, *O. gallerucae* was present in Missouri and five adjacent states, from Illinois to Oklahoma, none of which were recorded as release locations of *O. gallerucae*. In New Mexico, *O. gallerucae* established after release of parasitoids shipped from California in the 1990s.

Additionally an unidentified "*Tetrastichus* sp." reared from *Xanthogaleruca* (=*Pyrrhalta*) *maculicollis* (Motschulsky) in Japan was introduced into California between 1934 and 1936. but was never reported as recovered (Flanders, 1936; Clausen, 1978).

Current Work

No current elm leaf beetle biological control efforts in the United States are known to the authors. However, parasitoids were collected from *X. luteola* in California and exported for potential introduction elsewhere as recently as 2006.

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

Establishment of elm leaf beetle parasitoids released for biological control and information about releases in the United States are discussed above. Four exotic parasitoid species of elm leaf beetle (three primary, one secondary) have definitely established in the United States: *B. brevistigma, E. antennata, B. erynniae,* and *O. gallerucae.* The effect of these parasitoids on population levels of elm leaf beetle has not been adequately assessed. Biological control may be responsible for the elm leaf beetle's current non-pest status in at least California, Missouri and adjacent states, but there are no controlled field studies demonstrating this.

Baryscapus brevistigma The prepupal-pupal parasitoid *B. brevistigma* is reportedly important in Iran (Azmayesh-Fard and Esmaili, 1981) and is the most important elm leaf beetle parasitoid in the eastern United States, with reported apparent parasitism rates of 10–47% (Jones, 1933) and 50–80% (Berry, 1938a). The reported parasitism rate was much lower in Ohio (Hamerski et al., 1990), and although *B. brevistigma* occurs throughout much of northern California it is of little apparent importance there, being present at 7 of 12 California sites, with a maximum apparent parasitism of 22% and a seasonal average of just 1% for all sites pooled (Dreistadt and Dahlsten, 1990b). However, *B. brevistigma* can be laboratory-reared in large numbers and cold-stored for several weeks, creating some interest in its use for inundative biological control (Hamerski et al., 1990).

Erynniopsis antennata The larval-prepupal and larval-adult tachinid parasitoid *E. antennata* is apparently of moderate importance in southern California (Luck and Scriven, 1976) and northern California. Its effectiveness is reduced by early season life cycle asynchrony with its hosts and because of hyperparasitism by *B. erynniae*. At 11 of 12 northern California sample sites, apparent parasitism of *X. luteola* by *E. antennata* was sometimes over 40% (Dreistadt and Dahlsten, 1990b).

Oomyzus gallerucae The egg parasitoid *O. gallerucae* is believed to be important in Europe (Marchal, 1905; Howard, 1908), Iran (Azmayesh-Fard and Esmaili, 1981), the U.S. state of Missouri and adjacent states (Puttler and Bailey, 2003), and in southern California (Luck and Scriven 1976). Except for its establishment in Ohio, we found no assessment of *O. gallerucae*'s importance in the eastern United States.

In Missouri, parasitism (ave. 38%) and associated host feeding by *O. gallerucae* apparently suppressed damage to elm foliage. Elm leaf beetle is now uncommon in Missouri and *O. gallerucae* is the only known, new biotic agent that could have caused this pest's precipitous decline. Severe defoliation from elm leaf beetle was frequently reported throughout Missouri from the 1950s through 1980s (USDA, 1950–1980). Missouri University Extension Entomology personnel received no public inquiries about this pest from the early 1990s through at least 2002 (Puttler and Bailey, 2003) and few if any since then. Elm leaf beetle eggs are now difficult to find and no obvious foliage damage from it has occurred in at least the Columbia area for the last 18 years. This marked change in elm leaf beetle pest status coincided with the discovery that *O. gallerucae* was widely established and parasitized a substantial proportion of host eggs in Missouri and neighboring states. *Oomyzus gallerucae*'s control of elm leaf beetle in Missouri appears to be a previously unrecognized case of successful classical biological control.

Unlike in Missouri, in northern California rates of egg parasitism in the first host generation were low-to-undetectable in spring during the 1980s through the late 1990s, even though sometimes there had been up to 50–90% parasitism at the same sites during fall of the previous years (Dahlsten and Dreistadt, 1995). However, since the introduction in the late 1990s of *O. gallerucae* populations from new geographic locations (ones believed to be better climatic matches for California [Fig. 2]), elm leaf beetle populations have apparently remained low throughout the season in much of California.

Laboratory study of the host response behavior of *O. gallerucae* suggests that this egg parasitoid could be an effective agent for augmentative biological control (Ehler et al., 1987). Elm leaf beetle populations apparently were suppressed by early season inundative release of large numbers of laboratory-reared *O. gallerucae* in northern California (Dreistadt et al., 1992), but rearing *O. gallerucae* is labor-intensive and therefore inundative releases are expensive.

Nontarget Effects

Erynniopsis antennata was first introduced into the United States in the 1930s and was long thought to be a monophagous parasitoid of *X. luteola*. Tomov (1974) reported *E. antennata* emerging from third instars of the tamarisk beetle, *Diorhabda elongata* (Brullé), in Bulgaria. This report may have been unknown to American workers until cited by Richter and Myartseva (1996) in their report of *E. antennata* from *D. elongata* in Middle Asia (Turkmenistan). *Diorhabda elongata* was then being investigated for importation into the United States for the biological control of invasive saltcedars (*Tamarix* spp.). Tracy and Robbins (2009) questioned the Turkmenistan record because "*Diorhabda elongata* does not occur in Turkmenistan and this record [of *E. antennata* emergence] probably should refer to *D. carinata* (Faldermann), which is generally much more abundant than *D. carinulata* in Ashgabat [Turkmenistan]". Subsequent shipments of *D. elongata* from Crete and Greece, and *D. carinulata* from Fukang, China, were cleared of *E. antennata* during quarantine in the United States (Herr et al., 2009). *Diorhabda carinulata* and *D. elongata* were released into the open field in the western United States beginning in 2001, are established at various locations, and are susceptible to parasitism by *E. antennata*.

Recovery of Affected Tree Species or Ecosystems

The number of elms in American forests and landscapes has declined precipitously since the 1930s, because of the introduction in the eastern United States of Dutch elm disease (DED), which is caused by a complex of fungi including *Ophiostoma* (=*Ceratocystis*) *ulmi* (Buisman) and *O. novo-ulmi* Brasier. Millions of elms were killed and few were planted for decades. Similar decline occurred in mature American elm trees (*Ulmus americana* L.) growing naturally in riparian areas, although the species survives, because young trees reproduce before the disease kills them. In California from 1947 to about 1989, the sale of elms was generally prohibited and their planting discouraged. However, more recently, after decades of resistance selection in the eastern United States, elm cultivars resistant to Dutch elm disease are now available. Recent results of the National Elm Trial at 18 locations nationwide demonstrate that many of these Dutch elm disease-resistant elms have desirable horticultural characteristics and are also resistant to elm leaf beetle. For example, among 15 cultivars planted in Davis, California, Accolade, Emerald Sunshine, and Frontier (hybrids or selections of several Eurasian *Ulmus* spp.) were pest-resistant and had low pruning requirements (McPherson et al., 2009). Pest-resistant elms are available in commercial nurseries and are increasingly being planted in America's urban forests. Elm restoration in native habitats is also underway, with planting of resistant American elms in natural habitats along the Connecticut River starting in 2011.

Broad Assessment of Factors Affecting Success or Failure of Project

Some factors making implementation of this biological control program difficult have been (1) The virtual inability to detect *O. gallerucae* throughout at least most of its reported range across the United States during most of the year; (2) an apparent range limitation (California and Oregon only) of *E. antennata* and its complex life history that permits it to parasitize a range of host's life stages from the second instar through adult; (3) the difficulty in studying overwintering of these insects, about which virtually nothing is known; (4) introduction of exotic *Ophiostoma* spp. fungi causing Dutch elm disease that has reduced *Ulmus* spp. to relatively minor status in European landscapes and killed millions of elm trees in the United States; and (5) the difficulty American workers have in accessing foreign literature and the region from Iran through Middle Asia to China, which is the likely area of origin for *X. luteola* and its parasitoids.

Biological control efforts are not anticipated in the near future for reasons that include (1) an apparent absence of high elm leaf beetle populations in at least most of its range during recent years; (2) availability and widespread use of highly effective systemic insecticides; (3) availability of elm leaf beetle-resistant elms and a declining number of older, pest-susceptible elms, including the native *U. americana* and European *Ulmus* spp. planted mostly during the 1800s to early 1900s; (4) significant classical biological control efforts that have been made over several decades for control of this pest; and (5) shrinking budgets of government agencies and universities that conduct this work.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

The biology and life history of several elm leaf beetle natural enemies have been described, including (1) *E. antennata* in Italy (Silvestri, 1910) and California (Luck and Scriven, 1976; Dreistadt and Dahlsten, 1990b); (2) *O. gallerucae* from France (Marchal, 1905; Howard, 1908), Italy (Silvestri, 1910), and laboratory studies in the United States (Berry, 1938a; Clair et al., 1987; Hamerski and Hall, 1988, 1989); and (3) *B. brevistigma* from the eastern United States (Berry, 1938a), Ohio (Hamerski et al., 1990), and California (Dreistadt and Dahlsten 1990b).

Most of what is known is from laboratory studies and qualitative observations in the field, and not much is reported on the field ecology of any of these species. Very little is reported on the secondary parasitoid *B. erynniae*.

Baryscapus brevistigma

This is a gregarious larval-pupal endoparasitoid that overwinters as mature larvae in host pupae. It apparently has the same number of generations as *X. luteola,* i.e., two generations per year in most locations.

Oomyzus gallerucae

This species is a solitary endoparasitoid reported in the field only from the eggs of *X. luteola* and unlikely to parasitize other species as described above in *Host Range Test Results*. Females generally mate only once while males mate repeatedly and are aggressive toward other males and near parasitized egg masses (Hamerski and Hall, 1989). Females on average oviposit in about half or more of the eggs in a parasitized egg mass, and they kill other eggs through host feeding before starting to oviposit (Ehler et al., 1987; Hamerski and Hall, 1988). From oviposition to adult emergence requires about 2 weeks at 27°C and six or more generations may occur in warmer locations of California. Some authors believe *O. gallerucae* overwinters as adults (Hall and Johnson, 1983), but the overwintering method is not known. When eggs parasitized in the fall were buried in leaf litter and left to overwinter at sites in northern California, only a tiny fraction produced live adult parasitoids when new host eggs appeared in spring (Dreistadt and Dahlsten, 1991). Overwintering may occur as mature larvae in host eggs, but winter survival is very poor. Winter temperatures in California are generally warmer than those in Europe, so that the host-free period in California exceeds most individuals' life span (Dreistadt and Dahlsten, 1991). Even when apparent parasitism in northern California was >50–90% during fall (Clair et al., 1997; Dahlsten and Dreistadt, 1995; Lawson, 2000), *O. gallerucae* populations the next spring were very low or undetectable.

Erynniopsis antennata

This species is a larval-prepupal or larval-adult parasitoid, depending on the time of year and host development stage. If oviposition is into second or third instars during spring to mid-summer, *E. antennata* immature stages complete their development and adults emerge that same season from host prepupae. If oviposition occurs later in the season, *E. antennata* larvae overwinter inside adult hosts and emerge from adult beetles the following spring. Generation time apparently varies from about one month during spring to early summer to about six months if flies overwinter as immature stages.

Baryscapus erynniae

This hyperparasitoid is a gregarious larval-pupal parasitoid of the primary elm leaf beetle parasitoid *E. antennata*. *Baryscapus erynniae* overwinters in the pupal case of *E. antennata*, which normally (when unparasitized) is not present during winter because the last (late-summer or fall) generation of *E. antennata* overwinters as larvae inside adult leaf beetles and do not pupate until the next spring.

RECOMMENDATIONS FOR FURTHER WORK

Elm leaf beetle has not been a significant pest throughout most of its range across the United States during recent years. The introduced parasitoid *O. gallerucae* occurs in much of the United States. *Baryscapus brevistigma* occurs in California and throughout a large part of the northeast United Sates. *Erynniopsis antennata* is common in California. No further elm leaf beetle natural enemy introductions seem warranted unless the damage from this beetle increases. The recent recognition that *E. antenna* is not monophagous means that this species should not be redistributed through introduction to areas where it does not currently occur.

The first steps in classical biological control are to determine the origin of the introduced pest and then to collect and study appropriate natural enemies associated with it and closely related species. Except for collections from Iran made in the 1970–80s, there apparently have been no importation-related surveys for specialized natural enemies in Asia, which is now believed to be the native range of *X. luteola*. Systematic work since the early collections and improved access to foreign literature reveals that there are several elm-feeding chrysomelids related to *X. luteola* in Asia. Since the parasitoids introduced to North America were collected mostly from Europe, a region to which they probably were not native, and since researchers in parts of the native range (Iran and China) have recently collected elm leaf beetle parasitoids (Hesami et al., 2010; Zhenya et al., 2001), there appears to be an opportunity to obtain potentially better parasitoids from the unexplored native range.

There is little Palearctic literature on the ecology of elm leaf beetle and its natural enemies. From both the Nearctic and Palearctic, relatively little is known about host-parasitoid interactions in the field, parasitoid population dynamics and overwintering, or the quantitative impact of natural enemies on this pest. However, the most promising locations for foreign exploration for elm leaf beetle natural enemies are largely unexplored as sources of biological control agents of this beetle.

Due to the elm leaf beetle's diminished status as a pest, other introduced pests are more deserving of the increasingly limited resources for biological control. If there is further work it should include (1) controlled field studies of the elm leaf beetle natural enemies and quantification of the impact of biological control agents already present in the United States; (2) host collections and rearing for parasitoids from throughout south and east Asia; (3) field studies of the ecology of key natural enemies in their native range, including determination of the overwintering biology of the species already established in the United States; (4) authoritative species identification and voucher-specimen retention of any introduction candidates; (5) a thorough search of the literature on any introduction candidates including synonymies; and (6) pre-importation host-range testing.

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IV SMALLER EUROPEAN ELM BARK BEETLE

(*Scolytus multistriatus* [Marsham]) (Coleoptera: Curculionidae: Scolytinae)

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DESCRIPTION OF PEST

Taxonomy

The smaller European elm bark beetle, *Scolytus multistriatus* (Marsham), is one of over 140 named species in the genus *Scolytus* (Petrov and Mandelshtam, 2010). There are no synonyms for this species, but former generic assignments include *Eccoptogaster* (Blackman, 1934).

Distribution

Native to Europe, the Middle East, and northern Africa (Bellows et al., 1998), the smaller European elm bark beetle (Fig. 1) is an invasive species that was first recorded at Cambridge, Mass-achusetts, in 1909 (Chapman, 1910) and is believed to have been in-troduced either in burl elm logs sent to veneer plants or in elm crates used to carry cargo (Whitten, 1960). To date, it has spread throughout the United States (except for Alaska and Hawaii), southern Canada, and parts of northern Mexico (Ciesla, 2011). This wide distribution reflects the fact that the beetle can develop in all native and introduced species of elm (*Ulmus* spp.) as well as Japanese zelkova (*Zelkova serrata* [Thunb.] Makino) (Solomon, 1995). An on-line map of the beetle's world distribution is available at: http://www.plantwise.org/default.aspx?site=234&page=4393&speciesID=39118&dsID=49212

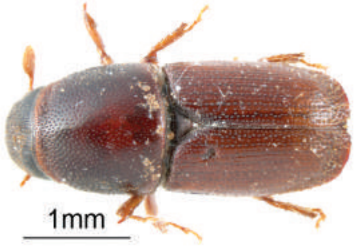

Figure 1 Adult smaller European elm bark beetle, *Scolytus multistriatus*. (Photo credit: Pest and Diseases Image Library, Bugwood.org)

Damage

Type The enormous importance of this pest results not so much from direct injury to the trees, but from the rolL the beetles play as vectors of the fungal species that cause the highly destructive disease known as Dutch elm disease (DED). Though severe infestations of the beetle can kill trees, especially ones under water stress, in the absence of Dutch elm disease (Brown and Eads, 1966), trees usually are not killed by the beetle alone. A native elm bark beetle, *Hylurgopinus rufipes* (Eichhoff), also can vector this disease: however, in most regions of North America, *S. multistriatus* is by far the more common vector, because it is highly competitive and usually displaces the native elm bark beetles. A closely related species, the banded elm bark beetle (*Scolytus schevyrewi* Semenov) also attacks twigs and branches of elms and has been listed as a possible DED vector in Asia (Webber, 2000). This species has been discovered in the United States, and may be an effective vector of the disease (Negrón et al., 2005; Lee et al., 2011). To further complicate the matter, there is some evidence that *S. schevyrewi* might be competitively displacing *S. multistriatus* in some areas where the two species are sympatric (Lee et al., 2009, 2010).

The causal agent of Dutch elm disease, *Ophiostoma ulmi* (Buisman) Moreau, is a highly lethal fungal pathogen that has killed an enormous number of elms both in Europe and North America (Gibbs, 1978). More recent studies have shown that more pathogenic or aggressive races have emerged, causing the original agent to be replaced by a new fungal pathogen, *Ophiostoma novo-ulmi* Brasier (Brasier, 1991). Though all elm species can be attacked to some extent, the North American species are more susceptible than those of Asian and European origin. The American elm, *Ulmus americana* L., has been severely affected. This highly valued shade tree, greatly prized for its characteristic vase-like crown, once graced the streets of many U.S. cities, its high-arching branches providing shade to pedestrians and parked cars (Fig. 2). Chemicals in healthy elm bark elicit a broad array of biological activities in elm bark beetles including short-range orientation, feeding incitation, and feeding stimulation (Baker and Norris, 1968). Adult beetles emerging from trees killed by the fungus or from fungus-infested logs carry the fungal spores on their bodies, inoculating new elm trees at beetle feeding sites made in twig crotches (Baker, 1972). Twigs infested with the fungal spores develop symptoms of Dutch elm disease: wilting, drying, yellowing, and browning of foliage, generally referred to as "flagging" (Fig. 3). Defoliation and death of the tree usually follow (Schreiber and Peacock, 1979).

Figure 2 Street lined with American elms, forming a virtual monoculture of trees highly susceptible to Dutch elm disease. Joseph O'Brien, USDA Forest Service, Bugwood.org.

Extent DED apparently originated in Asia, but was first described from the Netherlands in 1919 (Peace, 1960), from which it spread rapidly and by 1934 had become widely distributed in Europe (Gibbs, 1978). The earliest records from the United States were in Ohio (1930) and somewhat later in New York (1933). By the 1950s, the disease had been reported from many midwestern states, and was reported from Oregon in 1973 (Gibbs, 1978). By 1976 only 34 million of the estimated 77 million elms present in urban locations before introduction of the DED pathogen remained, and far fewer are still present today (USDA, 2003).

Figure 3 Elm tree exhibiting "flagging," an early symptom of Dutch elm disease. Fred Baker, Utah State University, Bugwood.org)

Biology of Pest

Most of the following details are taken from Whitten (1960), Baker (1972), and Solomon (1995). The life history of *S. multistriatus* parallels that of many other bark beetles. Mature larvae (Fig. 4) pass the winter in their galleries in the bark, pupate in the spring in cells in the outer bark, and the adult beetles emerge from under the bark of elm trees in early spring and start to feed on the bark of twigs, usually at the crotches in the upper canopy (Rabaglia and Lanier,

Figure 4 Mature larvae of *S. multistriatus*. Thérèse Arcand, Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre.

1984). After several weeks of feeding, adult females bore into the bark of unhealthy or dead elm trees. They chew through the cambium, forming an oviposition gallery (Fig. 5) parallel to the wood grain that is about 5–7 cm long, and deposit 80–100 eggs along the sides of each gallery.

Figure 5 Oviposition gallery of *S. multistriatu*s. Joseph O'Brien, USDA Forest Service, Bugwood.org.

The eggs hatch and larvae feed on the inner bark, making tunnels perpendicular to the egg gallery. The number of generations per year varies with latitude: in Canada there is typically one generation per year, whereas two generations occur each year in the northeastern United States, with up to three per year in southern states (Hanula and Beresford, 1984).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

No analysis was made of North American *Scolytus* species and other bark beetles to see if any indigenous species might be within the host range of the European parasitoid introduced for control of this pest. With regard to the introduced parasitoid that eventually became established, *Dendrosoter protuberans* Nees (Hymenoptera: Braconidae) (Fig. 6), it was known to attack other bark beetles in Europe (Thompson, 1943) and has been reported from a few other species in North America (see "Nontarget Effects" below).

Figure 6 Adult of *Dendrosoter protuberans*. Gabor Keresztes, Debrećen, Hungary.

Native Natural Enemies Affecting the Pest

Before attempts to use classical biological control against this invasive bark beetle, only a few species had been reported attacking the pest in North America. With respect to parasitoids, Hoffman (1942) recorded two braconids from this bark beetle, *Spathius laflammei* Provancher (mistakenly listed as *Spathius canadensis* Ashmead, a synonym of *S. sequoiae* Ashmead), which primarily attacks bark beetles on conifers (Marsh and Strazanac, 2009, and *Eubadizon magdalis* (Cresson). Three chalcidoids were also noted: *Eupelmus cyaniceps* var. *amicus* (Gir.) (Hymenoptera: Eupelmidae), *Entedon ergias* Walker (= *Entedon leucogramma* Ratzeburg) (Hymenoptera: Eulophidae), and *Cheiropachus quadrum* (Fabricius), mistakenly listed as *Cheiropachus colon* L., (Hymenoptera: Pteromalidae). Of these, *S. laflammei*, is also a parasitoid of *H. rufipes* (Kaston, 1939). Burks (1959) listed *S. multistriatus* among the hosts of *Trigonura elegans* Provancher (Hymenoptera: Chalcididae) but considered the host record of questionable status, because members of the genus typically attack Buprestidae and xylophagous true snout weevils (e.g., *Pissodes, Magdalis*). Nevertheless, both *S. multistriatus* and *Magdalis armicollis* Say (red elm weevil) can occur under the bark of dying or dead elm branhes and trees (Hoffman, 1942), so accidental attacks on the former seem possible. In any case, the synoptic list of North American scolytid parasitoids published by Bushing (1965) also considered this host record to be questionable. Thus, at the time explorations for natural enemies of *S. multistriatus* in Europe were commencing, there were five parasitoids (and a possible sixth) known to attack the pest in North America, two of which, *E.*

ergias and *C. quadrum,* were known to occur in Europe (Mercet, 1926–1928; Russo, 1938), respectively, and could have entered the United States along with their host *S. multistriatus* (Van Driesche et al*.,* 1996). Moreover, there were no quantitative studies on the impact of the resident complex of parasitoids (indigenous or accidentally introduced), and it was assumed that they didn't have much effect on this introduced bark beetle. When *D. protuberans* was first released for establishment in Ohio and Missouri, the native parasitoid *S. laflammei* was the dominant species in the complex, but the European species *E. ergias* and *C. quadrum* were also present (Kennedy, 1970). The following species have also been listed as parasitoids of the smaller European elm bark beetle in North America: (1) *Xorides albopictus* (Cresson) (Hymenoptera: Ichneumonidae) (Carlson, 1979) (validity of record doubtful; (2) *Rhaphitelus maculatus* Walker (Hymenoptera: Pteromalidae) (Burks, 1979); and (3) *Eurytoma abatos* (Walker) (Hymenoptera: Eurytomidae) (Burks, 1979.).

Hanula and Berisford (1984) reported *S. laflammei* and *E. ergias*, attacking the smaller European elm bark beetle in Georgia. In California, Hajek and Dahlsten (1985a) reared the following species from *S. multistriatus*: *E. ergias, C. quadrum,* and *R. maculatus,* and the pteromalids *Neocalosoter pityophthori* (Ashmead) and *Cerocephala eccoptogastri* Masi (the latter being a facultative hyperparasitoid [Grissell, 1981]). In addition, Hajek and Dahlsten (I981) recovered *D. protuberans*, which was noteworthy because the westernmost releases had been made in Colorado.

Among the North American predators noted attacking the smaller European elm bark beetle, Hoffman (1942) reported the two checkered beetles (Coleoptera: Cleridae) *Neichnea laticornis* (Say) and *Cariessa pilosa* (Forster). Hanula and Berisford (1984) reared the clerid *Enoclerus nigripes* Say and the bark-gnawing beetle *Temnochila virescens* (F.) (Coleoptera: Trogositidae) from *S. multistriatus*-infested logs. Hajek and Dahlsten (1985a) noted that predators of *S. multistriatus* were uncommon in California but stated that larvae of *Temnochila chlorodia* (Mannerheim) and a snakefly, *Agulla* sp. (Raphidioptera: Raphidiidae), fed on larvae of the smaller European elm bark beetle in the laboratory. No quantitative estimates were made of predation levels in these studies.

In field studies, Pathogens have been noted infecting *S. multistriatus* in both North America and Europes. These have included nematodes and fungi. Saunders and Norris (1961) found twelve genera of nematodes associated with *S. multistriatus,* but only one species, *Parasitylenchus scolyti* Oldham (Tylenchida: Allantonematidae), appeared to be parasitic. Doane (1959) found the entomopathogenic fungus *Beauveria bassiana* (Balsamo) Vuillemin in galleries of *S. multistriatus* in Connecticut, where it was the most frequently encountered pathogen, infecting over 90% of the beetle larvae in a shady grove. However, overall, levels of mortality were less than 10%. Laboratory tests showed that pupae and adults of the beetle also were susceptible to this fungus.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Europe is the region of origin of the smaller European elm bark beetle.

Areas Surveyed for Natural Enemies

Areas in Europe where natural enemies of this bark beetle have been studied include Spain, Poland, Holland, Belgium, Austria, the UK, and the former Yugoslavia.

Natural Enemies Found

Parasitoids In Europe, the resident natural enemy complexes were investigated by entomologists concerned with vectors of Dutch elm disease and by North American biological control scientists seeking natural enemies for importation. For the most part, the latter explorations for natural enemies of the smaller European elm bark beetle were conducted by personnel of the USDA Agricultural Research Service (then Entomology Research Division, European Parasite Laboratory, Nanterre, France and Gif-sur-Yvette, France) under the leadership of Reece Sailer and Richard Dysarg, 1963–1968. In addition, projects in the former Yugoslavia were also used to collect, identify and ship parasitoids of smaller European elm bark beetle to the United States. Moreover, studies on behalf of Canada and Michigan State University were performed by CABI (then Commonwealth Institute of Biological Control, European Station, Délémont, Switzerland) scientists.

Before the U.S.-funded work, studies by European entomologists had been conducted in Spain (Bolivar-

Pieltain, 1926; Mercet, 1926–1928), Poland (Sitowski, 1930), and Holland (Fransen, 1931; Roepke, 1934; the principal parasitoid species attacking *S. multistriatus* were *C. quadrum* (Spain), *R. maculatus* (Poland) (reported as *Rhaphitelus ladenburgii* Ratzeburg [Hymenoptera: Pteromalidae]), and *Coeloides scolyticida* Wesmael (Hymenoptera: Braconidae) (Hollandy. Another parasitoid found by early investigators attacking the smaller European elm bark beetle was *Eusandalum* (= *Polymoria*) *merceti* (Bolivar-Pieltain) (Hymenoptera: Eupelmidae) in Spain (Bolivar-Pieltain, 1926). USDA scientists working primarily in France (and to a lesser extent in Germany and Holland) found *D. protuberans* to be the dominant primary parasitoid of *S. multistriatus* larvae, followed by *Ecphylus silesiacus* (Ratzeburg) (Hymenoptera: Braconidae), *C. quadrum*, *E. ergias*, and *C. scolyticida*. Schröder (1974), working in Austria, likewise found *D. protuberans* to be the dominant primary parasitoid of *S. multistriatus* and also recovered the braconids *C. scolyticida, E. silesiacus* and *Spathius rubidus* Rossi, as well as the chalcidoids *C. quadrum, E. ergias, Cerocephala cornigera* Westwood*, Dinotiscus aponius* (Walker)*, Eurytoma arctica* Thomson, and *Eurytoma morio* Boheman. The last four species also can function as hyperparasitoids or cleptoparasites (Kenis, et al. 2004), and so are of limited interest for biological control purposes. Maksimović (1979) concluded that *D. protuberans*, followed by *E. silesiacus*, *C. scolyticida,* and *E. ergias,* were the most important parasitoids. Beaver (1967) observed the parasitic mite *Pyemotes scolyti* Oudemans (Acari: Pyemotidae) in galleries of *S. multistriatus* in elm logs in the United Kingdom. Where found, this mite had destroyed a high percentage of the bark beetle brood, but the mite's biological control potential was compromised by its limited survival and dispersal ability. Lipa and Chmielewski (1977) observed the same mite attacking *S. multistriatus* and other species of *Scolytus* in Poland.

Predators Schröder (1974) concluded that *Medetera nitida* (Macquart) (Diptera: Dolichopodidae) was the most effective predator of *S. multistriatus* in eastern Austria. Woodpeckers were observed attacking many bark beetles, including *S. multistriatus* (Kirby and Fairhurst, 1983), but such birds are generalist predators and not suitable for use in classical biological control. Marković and Stojanović (2012) conducted a faunal survey of phloem-xylophagous insects and their parasitoids and predators on *Ulmus minor* Miller in Serbia and found few predators, perhaps because of the sampling methods used.

Entomopathogens The endoparasitic nematode *Parasitaphelenchus oldhami* Rühm (Aphelenchida: Parasitaphelenchidae) (reported as the larval form of *Parasitylenchus scolyti* Oldham) was found infesting 60% of the adults in a population of *S. multistriatus* in England, in which about 39% of the beetles were rendered sterile (Oldham, 1930). Hunt and Hague (1974) found the same species, also in England, infecting 44–55% of *S. multistriatus* with a mean of 10–12 nematodes per beetle. However, despite this high level of incidence, no pathological effects were observed on the beetled. Saunders and Norris (1961) found the same species in Wisconsin, noting that the levels of infection appeared to be density dependent, but no pathological effects on the host were apparent. Lipa (1968) found the microsporidians *Stempellia scolytii* (Weiser) and *Nosema scolytii* Lipa infecting nearly one-third of the larvae, pupae, and adults of *S. multistriatus* sampled in Poland.

Because relatively few entomopathogens have been found infesting *S. multistriatus* in field studies, most of the studies on pathogens associated with this host have involved laboratory tests with isolates previously recovered from other insects and conducted in much the same manner as insecticide screenings, as for example, the work of Finney and Walker (1977) and Poinar and Dechamps (1981) with nematodes; Doberski (1981a, b), Houle et al. (1987), and Jassim et al. (1990a) with fungi; and Doane (1960) and Jassim et al. (1990b) with bacteria. Although several pathogens in these studies were reported as killing or having other adverse effects on *S. multistriatus* and other *Scolytus* species, Mazzone and Peacock (1985) noted that development of delivery systems to provide the pathogens access to beetle stages developing within the logs seemed impractical. Tomalak and Welch (1982) noted that the main problem with the use of nematodes was their lack of resistance to desiccation. Jassim et al. (1990a) demonstrated pathogenicity to *S. multistriatus* larvae for certain fungi in an artificial rearing system, but thought it unlikely that treating elm trees with these pathogens would reduce larval populations substantially. An overview of European pathogens of bark beetles is provided by Wegensteiner (2007).

Antagonists of the plant pathogen Lines of research involving acquired immunity, such as proposed by Chester (1933) and conducted by Scheffer et al. (1980), are beyond the scope of this review. However, several antibiotics have been found to be detrimental to *C. ulmi* in laboratory studies, including clavacin and actinomycin

(Waksman and Bugie, 1943), candicidin (Lechevalier et al., 1953), and cerulenin (Nickerson et al., 1982). All of these compounds inhibit the growth of the fungus, but introduction into the tree appears to be a problem (Mazzone and Peacock, 1985).

A number of fungi have been found to have antagonistic activity on the DED pathogen. Gemma et al. (1984) found that *B. bassiana*, *Nomuraea rileyi* (Farlow) Samson, and *Metarhizium anisopliae* (Metchnikoff) Sorokin were antagonistic to *C. ulmi* and *C. novo-ulmi* under four combinations of light and temperature, and that *M. anisopliae* produced the highest level of inhibition. In a follow up study (Gemma et al., 1985), culture filtrates of *N. rileyi* and *M. anisopliae*, as well as the commercial toxin beauvericin, were shown to have antagonistic effects on *C. ulmi*. *Trichothecium roseum* Link has also been reported to be an antagonist of *C. ulmi* (Gibbs and Smith, 1978; Richards, 1988). Probably the most promising antagonist found to date has been from the *Verticillium* isolate WCS850, a form of *V. albo-atrum* (Cornelissen et al., 2003). The developmental research that went into making this isolate into a commercial product (Dutch Trig) that can be used effectively for protection of valuable elms in landscape settings has been reviewed by Scheffer et al. (2008). The product has been registered in both Europe and the United States; however, it has to be injected into trees for inoculation to occur, so it does not appear to be practical for use in forests.

Host Range Test Results

The host range of *D. protuberans* was not assessed at the time of the project (1960s). It was deemed sufficient that this wasp was confirmed as a primary parasitoid (no braconids are hyperparasitoids) of bark beetles, all of which are considered to be forest pests. In addition, the potential risk presented by the extinction of the American elm by DED was considered to outweigh any harm that might occur to indigenous bark beetles, many of which are extremely destructive. In the late 1960s, *D. protuberans* was sent to Hawaii for trials against the black twig borer, *Xylosandrus compactus* Eichhoff (Coleoptera: Curculionidae: Scolytinae), an ambrosia beetle; however, it did not parasitize black twig borer in the insectary (Davis and Chong, 1970). Nevertheless, releases in the field in Hawaii were made, but without recoveries

Releases Made

Introductions of natural enemies of the smaller European bark beetle into the United States began in 1965 and ended in 1973. Candidate natural enemies discovered by scientists working for USDA, Commonwealth Agricultural Bureaux International (CABI), or the Institute of Plant Protection in Zemun (in the former Yugoslaviw, now Serbia), were shipped to the Agriculture Research Service (ARS) quarantine facility at Moorestown, New Jersey, for preliminary clearance, elimination of unwanted organisms (hyperparasitoids and inquilines), and biological evaluation, after which they were sent either to the USDA Forest Service's Central States Experiment Station Laboratory at Delaware, Ohio or to Michigan State University for further biological evaluation and development (Dix, 2000).

Three parasitoids—*D. protuberans, Coeloides* spp. (mostly *scolyticida*), and *E. ergias*—were collected by USDA-ARS personnel in France and ultimately shipped to the USFS laboratory at Delaware, Ohio. Following biological studies, emphasis was placed on *D. protuberans* because it was easily reared in the laboratory, able to overwinter in the midwestern United States, and established readily in the field (Kennedy, 1970). To enrich the gene pool of the laboratory colony, additional shipments of *D. protuberans* from the former Yugoslavia, where parasitism levels up to 73%, were recorded in 1972 and 1973 (Maksimović, 1986). After development of an artificial diet for the host, it was possible to rear the parasitoid and host in large numbers (Kennedy and Galford, 1972), and millions of individuals were reared for release in infested areas (Dix, 2000).

Consignments of *D. protuberans*, *E. silesiacus*, and *C. scolyticida* were collected by CABI scientists in Germany and Austria, screened in quarantine at Moorestown, New Jersey, and then shipped to Michigan State University; work done there is summarized by Truchan (1970). Material destined for use in Canada (Ontario) was apparently sent there directly.

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

Dendrosoter protuberans Initial releases of *D. protuberans* were made in Ohio and Missouri, where it readily became established (Kennedy, 1970). It was the dominant species recovered in post-release studies in

Ohio, but not in Missouri, where the native *S. laflammei* was dominant. Overwintering parasitism levels by *D. protuberans* in these states were 18% and 6.7%, respectively (Kennedy, 1970). Because most of the founders were collected in southern France (near Avignon), there were concerns that it might not become established in colder regions; however, Truchan and Butcher (1970) conducted studies on the supercooling points of *D. protuberans* prepupae and concluded that the species could survive in the southern parts of Michigan. However, additional research and surveys led Truchan (1970) to conclude that its establishment was questionable and that elm bark thickness was a limiting factor. If bark thickness was >12 mm, *D. protuberans* could not oviposit and reach the cambium where *S. multistriatus* larvae feed. Likewise, Hostetler and Brewer (1976) studied overwintering survival of *D. protuberans* near Fort Collins and Denver, Colorado. They found this braconid could successfully overwinter in Colorado east of the Rocky Mountains, and permanent establishment seemed likely. Gardiner (1976) conducted laboratory and field tests on the parasitism of *H. rufipes* and *S. multistriatus* by *D. protuberans* in Ontario. Thed found high mortality of the parasitoid in elm logs, if kept uncovered by snow in winter, and concluded that, because only a very small proportion of elm bark beetles overwintered below the snow cover, *D. protuberans* could not contribute effectively to the control of either vector of DED in central Ontario.

However, by 1979, *D. protuberans* had been recovered not only in Ohio, Missouri, Michigan, and Colorado, but also in Virginia and Wisconsin (Marsh, 1979). Hajek and Dahlsten (1981) recovered this species in California. Brood mortality of *S. multistriatus* at their study sites averaged from 46% to 86%, but overall levels of parasitism were low (Hajek and Dahlsten, 1985b). Hanula and Beresford (1984) employed sticky traps and trap logs of *Ulmus alata* Michx. and *U. americana* to study the seasonal flight activity and adult emergence patterns of *S. multistriatus* and its associates in Georgia, and concluded the dominant parasitoids of the beetle there were *S. laflammei* and *E. ergias*. They did not recover *D. protuberans*. Cook et al. (2010) made observations on bolts infested by *S. multistriatus* taken from "Frontier" elm, *Ulmus* (*carpinifolia* Geldtish X *parvifolia* Nikolaus von Jacquin) in the Snake River Valley of northern Idaho, and found *D. protuberans* to be the second most abundant parasitoid recovered. Because some insects had emerged before sampling, exact rates of parasitism by species could not be determined; however, based on beetle and parasitoid exit-hole counts /number of beetle egg niches, beetle brood survival and parasitism (by all species combined) were calculated as 10.6% and 46.1%, respectively.)

Entedon ergias This is an exotic species that merits some discussion. It was accidentally introduced into North America. Galford (1967) recovered this egg-larval parasitoid from field-collected larvae of *S. multistriatus* reared to maturity in the laboratory. Kennedy (1970) also recovered *E. ergias,* as well as two larval braconid parasitoids, *C. quadrum* and *S. laflammei*. Based on emergence data from trap logs, Hanula and Beresford (1984) concluded that *E. ergias* was better synchronized with *S. multistriatus* than was *S. laflammei*. Hajek and Dahlsten (1985a) also recovered *E. ergias* in California.

Entedon ergias is the only exotic parasitoid of *S. multistriatus* that enters the oviposition gallery to lay its eggs in host eggs (Beaver, 1966; Kennedy, 1970), and because of this behavior, it is not limited by bark thickness as are the other species in the parasitoid complex, all of which must drill through the bark to reach the host (Kennedy, 1970; Hajek and Dahlsten, 1981). Being an egg-larval endoparasitoid, unless the *E. ergias* larva is nearly mature it is killed by larval ectoparasitoids such as *D. protuberans,* and in cases of multiple parasitism possibly *S. laflammei* and *C. quadrum*, (Kennedy, 1981). This is precisely the type of intrinsically inferior parasitoid that Zwölfer (1971) suggested should be introduced first in importation programs to give such species an opportunity to demonstrate their full control potential, before superior competitors are introduced. Although *E. ergias* was established before the introduction of *D. protuberans*, other parasitoids such as *S. laflammei* and possibly *C. quadrum* were already present. Generally, *E. ergias* has been found to be a subdominant member of the *S. multistriatus* parasitoid complex in North America, except in Georgia where it appeared to be a co-dominant with *S. laflammei* (Hanula and Beresford, 1984) (although *D. protuberans* was not present in Georgia at the time of this study.)

Cheiropachus quadrum This was the dominant parasitoid recovered by Hajek and Dahlsten (1985b) in California, but its maximum parasitism was only 2%. It was also the dominant parasitoid recovered from *S. multistriatus* by Cook et al. (2010) in Idaho. It did not appear to be very important in the eastern United States in early studies (Kennedy, 1970). Nevertheless, its accidental introduction into North America might have been harmful, because Mills (1991) found that females of this species frequently displaced females of the braconid *Coeloides filiformis* Ratzeburg ovipositing on the ash bark beetle, *Leperisinus varius* (Fabricius), and stole the host located by the braconid *C. filiformis*. It is conceivable that *C. quadrum* could be adversely affecting the efficacy of *D. protuberans* or *S. laflammei*, but this has not yet been demonstrated.

Native parasitoids In the eastern United States, *S. laflammei* was found in studies to be either the dominant parasitoid of the smaller European elm bark beetle, or co-dominant with *D. protuberans* (Kennedy, 1970) or *E. ergias* (Hanula and Beresford, 1984). It was not even reported in the studies in California (Hajek and Dahlsten 1985a) or Idaho (Cook et al. 2010). This braconid has a rather wide host range (Marsh and Strazanac, 2009) and has even been recovered from the recently introduced emerald ash borer, *Agrilus planipennis* Fairmaire (Duan et al., 2009), so the relative ease with which it has exploited *S. multistriatus* in the eastern United States is not surprising. However, the lack of reports of this parasitoid from this host in the western United States is surprising, because the parasitoid is known to occur throughout North America (Marsh and Strazanac, 2009).

Another relevant native species that attacks this bark beetle is the pteromalid *R. maculatus*, a Holarctic species with a wide distribution in North America and Europe. It appears to be more important in Europe than North America, and was one of the species selected for mass rearing to control elm bark beetles in Spain by González-Ruiz et al. (2006). No other native parasitoids appeared to exert significant levels of mortality on *S. multistriatus*.

Nontarget Effects

Although the host ranges vary among the introduced or invasive parasitoids of the smaller European elm bark beetly, no cases of attacks on threatened or endangered species have been reported, and all records are from major or minor pests.

Dendrosoter protuberans Cook et al. (2010) compiled a partial host list of this species from the literature, which included 18 bark beetles and three cerambycids, mostly Palearctic species. The only host records of attacks on species in North America were of *S. multistriatus* and the shothole borer, *Scolytus rugulosus* Müller, a polyphagous species attacking many hardwoods. Like *S. multistriatus,* this beetle also was introduced from Europe. However, Hajek and Dahlsten (1981) also reported rearing this parasitoid from the western ash bark beetle, *Hylesinus californicus* Swaine.

Entedon ergias Burks (1979) listed *S. multistriatus* and *S. rugulosus* as hosts for *E. ergias*. Apparently, the host range of *E. ergias* is restricted to the genus *Scolytus* (Kenis et al., 2004).

Cheiropachus quadrum This species differs from *E. ergias* in being more polyphagous, attacking hosts in several genera. In addition to *S. multistriatus* and *S. rugulosus*, Burks (1979) listed the bronze apple tree borer (*Magdalis aenescens* Leconte), the northern cedar bark beetle (*Phloeosinus canadensis* Swaine), and the western cedar bark beetle (*Phloeosinus punctatus* Leconte) as hosts of *C. quadrum* in North America. It has also been recovered from the recently introduced banded elm bark beetle, *S. schevyrewi*, by Negrón et al. (2005).

Broad Assessment of Factors Affecting Success or Failure of Project

Because North American elms are highly susceptible to the Dutch elm disease pathogen, it would be unrealistic to expect introduction of natural enemies of the vector, *S. multistriatus*, to eliminate the problem, especially since biological control does not result in 100% control of the target pest. Thus, some beetles survive to emerge and infest new trees and sustain the disease cycle, each year. Moreover, the fungus also can be spread by root grafts among neighboring elms, which can occur in urban plantings along streets (Fig. 2), walkways, or canals (Neely and Himelick, 1963), allowing the pathogen to spread among trees without a vectoring insect.

Van Driesche et al. (1996) point out that, in the hope that introductions would lower vector populations in North America, the importation of natural enemies was predicated on the assumption that populations of *S. multistriatus* were lower in Europe than in North America. However, there have been no experimental or comparative quantitative studies undertaken to support this rationale. Finally, no long-term monitoring was done following the release and establishment of *D. protuberans*, which is needed to document the dispersal and build-up of a natural enemy's population and corresponding decline in the pest's population (Pschorn-Walcher, 1977).

The recent introduction of banded elm bark beetle, *S. schevyrewi*, complicates the picture for making recommendations concerning *S. multistriatus*. The two species occur allopatrically in the Palearctic Region, but are sympatric in North America. Three factors suggest that *S. schevyrewi* represents a greater threat to elms in North America than *S. multistriatus*: (1) *S. schevyrewi* may vector *Ophiostoma novo-ulmi* Brasier (Jacobi et al., 2007), the aggressive strain of DED; (2) being from Asia, this insect could exploit some of its habitual hosts, such as Siberian elm (*Ulmus pumila* L.), which has been widely planted in parts of North America as a replacement for American elm; and (3) population surveys and other comparative studies (host plant finding ability, larval competition) of these two bark beetles in seven western states suggest that *S. schevyrewi* might be displacing *S. multistriatus* (Lee et al., 2010, 2011). Literature reports suggest it has a much broader host range than *S. multistriatus*, including weeping willow (*Salix babylonica* L.), several species of *Prunus* (cherries and plums), and Russian olive (*Elaeaganus angustifolia* L.) (Shi and Chen, 1990; Wang, 1992). However, in North America it has only been recovered from elms, so some records from Asia might be in error.

It is suggested that research emphasis be shifted from *S. multistriatus* to *S. schevyrewi*. With reference to biological control research, densities of *S. schevyrewi* should be compared between Asia and North Americr and an inventory of parasitoids, predators and pathogens of *S. schevyrewi* should be compiled. A few natural enemies are known to occur in Asia, including an ectoparasitic mite on adults and three species of hymenopterous larval parasitoids: *Cheiropachus* sp., *Elachistocontrum* sp. (Hymenoptera: Pteromalidae), and an unidentified braconid, which might be a factor in maintaining stable populations of *S. schevyrewi* (Yang et al., 1988; Wang, 1992). If such studies suggest that populations of the beetle are substantially lower in Asia and that there is a mature, well balanced natural enemy complex, quantitative evaluations or experiments should be undertaken to gauge the importance of the natural enemies present. Also, monitoring studies at several North American sites, where both introduced elm bark beetles occur, should be conducted to see to what extent the *S. multistriatus* natural enemy complex expands its host/prey range to include *S. schevyrewi*. If there is little or no expansion, differential rates of parasitism promote displacement of *S. multistriatus* by *S. schevyrewi*. If there appear to be missing ecological homologues in the complex attacking *S. schevyrewi*, this could indicate what kind of natural enemy might be the most promising to use.

It is quite possible, of course, that *S. schevyrewi* will not displace *S. multistriatus*, or only do so in certain regions. In this case, the recommendations made by Van Driesche et al. (1996) would still apply, i.e.: to continue importations of European natural enemies that failed to become established or were not even tried. For example, the larval parasitoids *E. silesiacus* and *C. scolyticida*, the microsporidia found by Lipa (1968) in Poland, and the sterilizing nematode Oldham (1930) found in England might be suitable for importation. In their review of parasitoids and predators of bark beetles, Kenis et al. (2004) pointed out that cleptoparasitism is probably common behavior among bark beetle parasitoids, so pre-introduction studies on candidate species for classical biological control should screen for this undesirable characteristic, too. In addition, augmentation and conservation approaches should be combined with classical biological work done to date or anticipated in the future. Because of the huge areas involved, augmentative releases of natural enemies might not be practical in forest,; however, mass releases of *C. quadrum, R. maculatus,* and *D. protuberans* were used successfully, in conjunction with sanitation, pheromone traps, and insecticide applications, to protect high-value elm trees in Granada, Spain (González-Ruiz et al., 2006). Conservation approaches such as planting preferred nectar sources for parasitoids (see below), determining and using favorable wood removal dates, and baiting trap logs with kairomones could enhance parasitoid or predator effectiveness. Finally, Kenis et al. (2004) pointed out that a full evaluation of the classical biological control program in North America has never been made and remains something worth doing.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Details of the biology of the major European primary parasitoids of the smaller European elm bark beetle have been presented by Beaver (1966) for *E. ergias*; by Kennedy (1970) and Manojlović et al. (2003) for *D. protuberans*; by Manojlović et al. (2000a) for *E. silesiacus*; by Fransen (1931, 1939) for *C. scolyticida*, and by González-Ruiz and Campos (1990) and Campos and Lozano (1994), using *L. varius* and *Phloeotribus scarabaeoides* (Bernard) as hosts for *C. quadrum*. Most of the research on parasitoids of *S. multistriatus* done since the review by Van Driesche et al. (1996) has been in Europe, especially the Balkans, but the approach has largely been ecological, because the target pests were indigenous and no importations of natural enemies were involved. Building on earlier work by Maksimović (1986), Manojlović et al. (2000b) studied the nectar sources used by different elm bark beetle parasitoids and found that some enhanced their longevity significantly. Manojlović (2003) concluded that the egg number deposited by *D. protuberans* depends on female longevity, which was directly dependent on additional nutrition. Maksimović (1979) found that, when feeding on nectar of flowers growing on forest meadows under natural environmental conditions, *D. protuberans*, often parasitised over 80% of elm bark beetles in the adjacent elm: enhancing the nutrition of this parasitoid in the field would seem to be a useful conservation approach.

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V Gypsy Moth

(*Lymantria dispar* L.) (Lepidoptera: Erebidae: Lymantriinae)

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DESCRIPTION OF PEST

Taxonomy

The invasive population of the gypsy moth (*Lymantria dispar* [L.]) in North America (NAGM) is a subpopulation of the European gypsy moth (EGM) that was accidentally introduced into eastern Massachusetts in 1869 (Forbush and Fernald, 1896a; Liebhold et al., 1989). These two populations are biologically identical and are characterized by having females that are normally incapable of sustained flight (level flight over any appreciable distance). Taxonomically, these two geographically different populations constitute the nominate subspecies, *Lymantria dispar dispar* (L.) (Lepidoptera: Erebidae: Lymantriinae), following the subgeneric and subspecies designations proposed by Schintlmeister (2004). The species was formerly placed in the genus *Porthetria*. Higher-level taxonomy is based on current understanding of morphological (Fibiger and Lafontaine, 2005; Lafontaine and Fibiger, 2006) and molecular characteristics (Mitchell et al., 2005). For a discussion of the extensive synonymy found in the literature on these populations, see Pogue and Schaefer, (2007).

Distribution

Gypsy moth is native to most of Europe and the Mediterranean region (including North Africa), the Caucasus Mountains, and temperate Asia, including Central Asia, much of China, Mongolia, Siberia, Japan, and the southern part of the Russian Far East (A.M. Liebhold, pers. com.) (Fig. 1). Gypsy moth was first introduced to

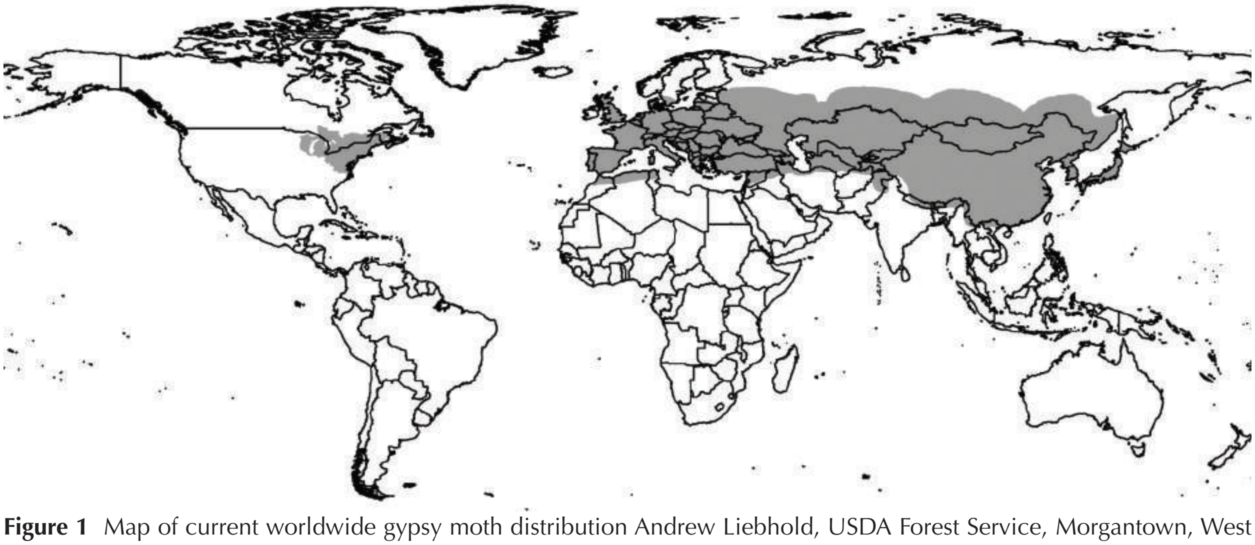

Figure 1 Map of current worldwide gypsy moth distribution Andrew Liebhold, USDA Forest Service, Morgantown, West Virginia, USA).

northeastern North America in the Boston area. Populations in North America are continuing to spread to the west and south at various speeds and are currently found in Wisconsin, Illinois, Indiana, Ohio, West Virginia, Virginia, and North Carolina (Fig. 2) In addition to natural dispersal, artificial dispersal can occur when people transport gypsy moth egg masses long distances on cars, recreational vehicles, firewood, nursery stock, household goods, or other items (Schneeburger, 2008). Such human-assisted movement can move insects thousands of miles, with disjunct populations having occurred in the western United States (Oregon or Washington); however, once detected, such isolated infestations can be eradicated with existing technologies.

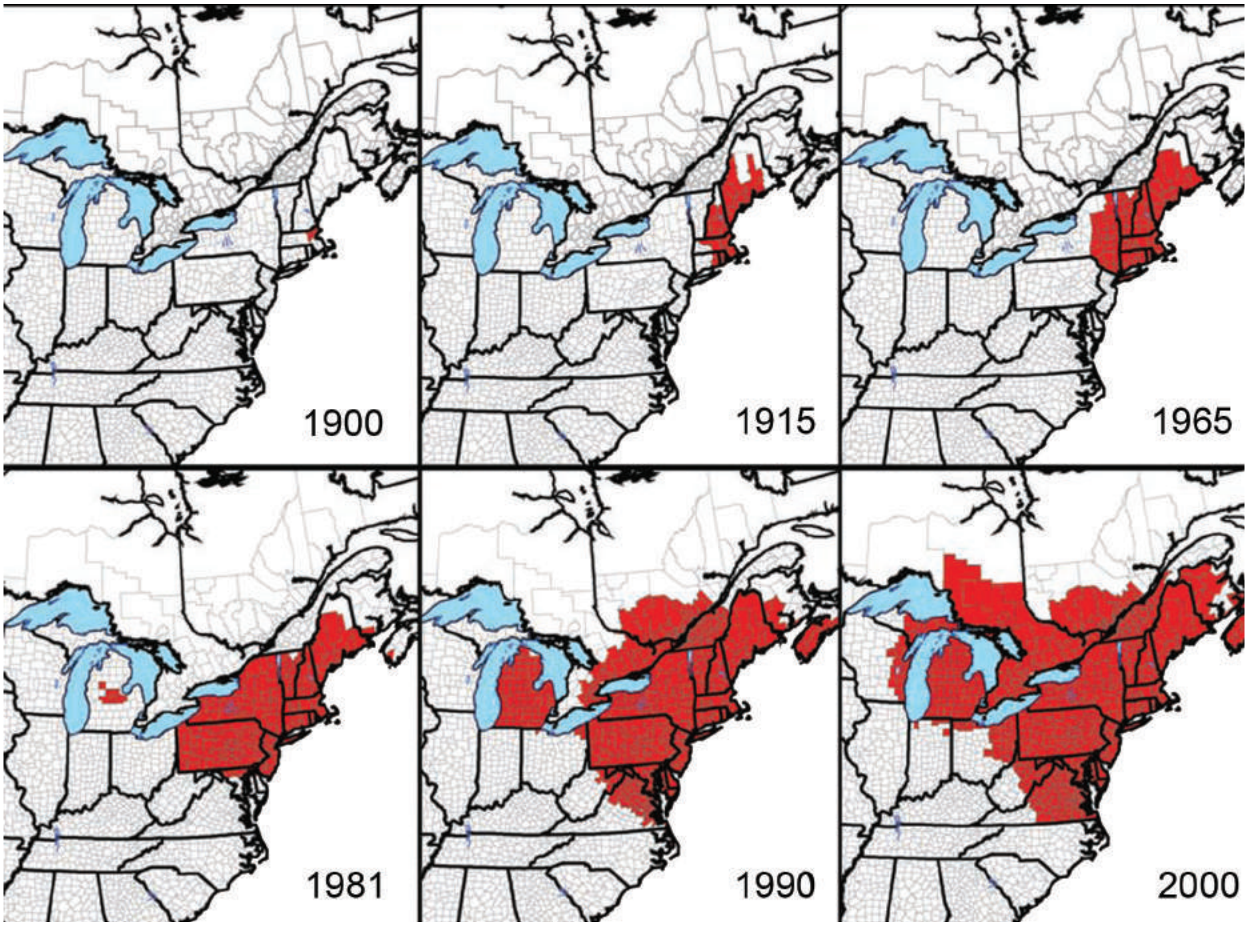

Figure 2 Map of historical spread by gypsy moth over time in North America (from Liebhold et al., 2007).

Damage

Type The gypsy moth is a defoliator that affects many deciduous tree species, in both forests (Fig. 3) and urban areas. Oaks (*Quercus*) are the preferred host (Kegg, 1973; Houston, 1981), but apple (*Malus*), sweetgum (*Liquidambar styraciflua* L.), linden (*Tilia*), gray birch (*Betula populifolia* Marshall), white birch (*Betula papyrifera* Marshall), poplar (*Populus*), willow (*Salix*) and many others can serve as hosts

Figure 3 Gypsy moth defoliation Timothy Tigner, Virginia Department of Forestry, Bugwood.org.

(Liebhold et al., 1995). Gypsy moths avoid ash (*Fraxinus*), yellow-poplar (*Liriodendron tulipifera* L.), sycamore (*Platanus occidentalis* L.), black walnut (*Juglans nigra* L.), catalpa (*Catalpa*) black locust (*Robinia pseudoacacia* L.), American holly (*Ilex opaca* Aiton), and most evergreen shrubs such as mountain laurel (*Kalmia latifolia* L.), rhododendron (*Rhododendron*), and arborvitae (*Thuja occidentalis* L.) (McManus et al., 1979). Larvae also feed on deciduous conifers such as larch (*Larix*) (Miller and Hanson, 1989) and bald cypress (*Taxodium distichum* [L.] Rich.) (Wanner et al., 1995). Older larvae will feed on evergreen conifers such as hemlock (*Tsuga*), pine (*Pinus*), spruce (*Picea*), and Atlantic white cedar (*Chamaecyparis thyoides* [L.]) (McManus et al., 1979).

Gypsy moth outbreaks can kill trees outright or contribute to subsequent mortality. Two or more successive defoliations are required to kill deciduous trees, but evergreen conifers may be killed by a single defoliation (Campbell and Sloan, 1977a; Davidson et al., 1999). Defoliation also predisposes oaks to attack by other pests such as the buprestid twolined chestnut borer (*Agrilus bilineatus* Weber) (Muzika et al., 2000) and shoestring fungi (*Armillaria* spp.) (Wargo, 1977).

Because of its ability to kill susceptible trees, the European gypsy moth can produce significant changes in forest stand composition (Davidson et al., 1999), shifting stand dominance toward less-favored species such as red maple (*Acer rubrum* L.), yellow-poplar (*L. tulipifera*), black cherry (*Prunus serotina* Ehrhart), and yellow (*Betula alleghaniensis* Britton) or black birch (*Betula lenta* L.). A single year of defoliation causes temporary declines in wood growth (Naidoo and Lechowicz, 2001) and mast (acorns or other nuts) production (Gottschalk, 1989), as well as increased light on the forest floor, which enhances growth of non-host plants (McEwan et al., 2009).

Indirect ecological damage can also be significant. Populations of small mammals, such as the gray squirrel (*Sciurus carolinensis* Gmelin) are affected by decreased mast volume (Gorman and Roth, 1989). Some bird species decline temporarily (DeGraaf, 1987), frequently because of increased nest predation due to more open conditions (Thurber et al., 1994). Woodpecker populations may increase because of increases in the abundance of wood-boring insects that breed in weakened trees. Because of their relatively large size and voracious feeding, gypsy moth caterpillars can out-compete larvae of other forest Lepidoptera, especially oak-feeding species (Schultz and Baldwin, 1982). Loss of a healthy tree canopy also may reduce shade needed to maintain stream temperatures and lower dissolved oxygen, affecting trout and cold-water aquatic macroinvertebrates (Downey et al., 1994).

During widespread defoliation events, on a temporary basis decomposition of leaf fragments and caterpillar frass can reduce oxygen levels in water and increase nitrogen levels, giving rise to algal blooms in some cases (Eshleman et al., 1998). Acidification of water courses can be increased (Webb et al., 1995). Defoliation also tends to increase temperatures and reduce the moisture content of soil and litter content (Hunter, 2001), factors that result in transitory upsurges in the rates of soil decomposition, mineralization, and plant productivity.

People living in or near areas with defoliated trees can be affected directly by exposure to the gypsy moth or insecticidal treatments to control it. Some people develop skin rashes to the caterpillars' urticating hairs (Aldrich et al., 1997). Finally, in forested neighborhoods and urban parks, dead trees may pose a safety hazard.

Extent Economic loss due to reduced attendance at recreational areas or resorts may occur during outbreaks. During gypsy moth outbreaks in the 1970s, U.S. homeowners' control costs ranged from $76 to $292 per home, while public campgrounds and recreation areas sustained average losses of $152 and $607 per site, respectively (Moeller et al., 1977). Wallner (1996) estimated that from 1980 to 1996, gypsy moth caused losses that exceeded $30 million annually.

Economic losses in forests have been reported from many countries within gypy moth's native range in Eurasia west of the Ural Mountains or North Africa (Fraval, 1984; Roy et al., 1995; Pogue and Schaefer, 2007; Orozumbekov et al., 2009). In North America, outbreaks first occurred in Massachusetts in the 1880s (Burgess and Baker, 1938). By 1912, the pest had spread to Rhode Island, Connecticut, New Hampshire, and Vermont, and by 1922, it had reached New York (McManus and McIntire, 1981). Extensive outbreaks occurred during the early 1950s, with 0.6 million ha defoliated in 1953: a plan to prevent the moth from spreading further was developed (Perry, 1955), but failed for lack of funding (McManus, 2007). In 1956, an eradication effort using DDT was carried out over Pennsylvania, New Jersey, and New York. The program reduced defoliation to <0.5 km^2, but the program was soon discontinued due to concerns for bioaccumulation of DDT in food and detrimental effects on nontarget organisms (Gypsy Moth Digest, 2005). Attempts to restrain spread of the insect were abandoned for several decades, during which time basic and applied research on the gypsy moth control was conducted (McManus, 2007). Massive outbreaks throughout the northeastern United States in the 1980s showed that the gypsy moth would continue to spread to the south and west and that forest resources in states lying outside the northeastern United States would be highly susceptible to gypsy moth (McFadden and McManus, 1991). A cost-benefit analysis for a program to retard the spread of gypsy moth indicated that such an effort would be worthwhile and a program ("Slow the Spread") was initiated in 1992 in West Virginia, Virginia, North Carolina, and Michigan (McManus, 2007) and continues to the present. The USDA Forest Service has compiled annual surveys of gypsy moth defoliation since 1924 (Fig. 4).

Biology

The flightless gypsy moth female in North America has little ability to actively disperse. Instead, populations disperse by larval "ballooning," in which newly hatched first instars climb to branch tips and spin silk threads. When the thread breaks, the larva is carried passively to a new location, ideally a suitable host tree. This process may be repeated several times if a suitable food source is not immediately found. This dispersal process functions because gypsy moth is highly polyphagous and can develop on hundreds of different tree species (Mosher, 1915; Liebhold et al., 1995). Liebhold et al. (1995) list some 478 tree species in the two most acceptable food-plant categories. Preferred genera (in alphabetical order) include *Alnus, Betula, Crataegus, Populus, Pyrus, Quercus, Salix,* and *Tilia* (Liebhold et al., 1995) but especially oaks. Females lay a single egg mass (Fig. 5), often on the tree bole, limbs, or other protected niches, on stones, or man-made objects. Eggs overwinter and hatch the following spring. There is one generation per year.

There are 5–6 larval instars in males and usually 5–7 in females, with full-grown larvae being 35–70 mm long (Fig. 6). Pupae are reddish brown with scattered reddish hairs, and male pupae tend to be much smaller than those of females (Fig. 7). Adult male moths usually emerge several

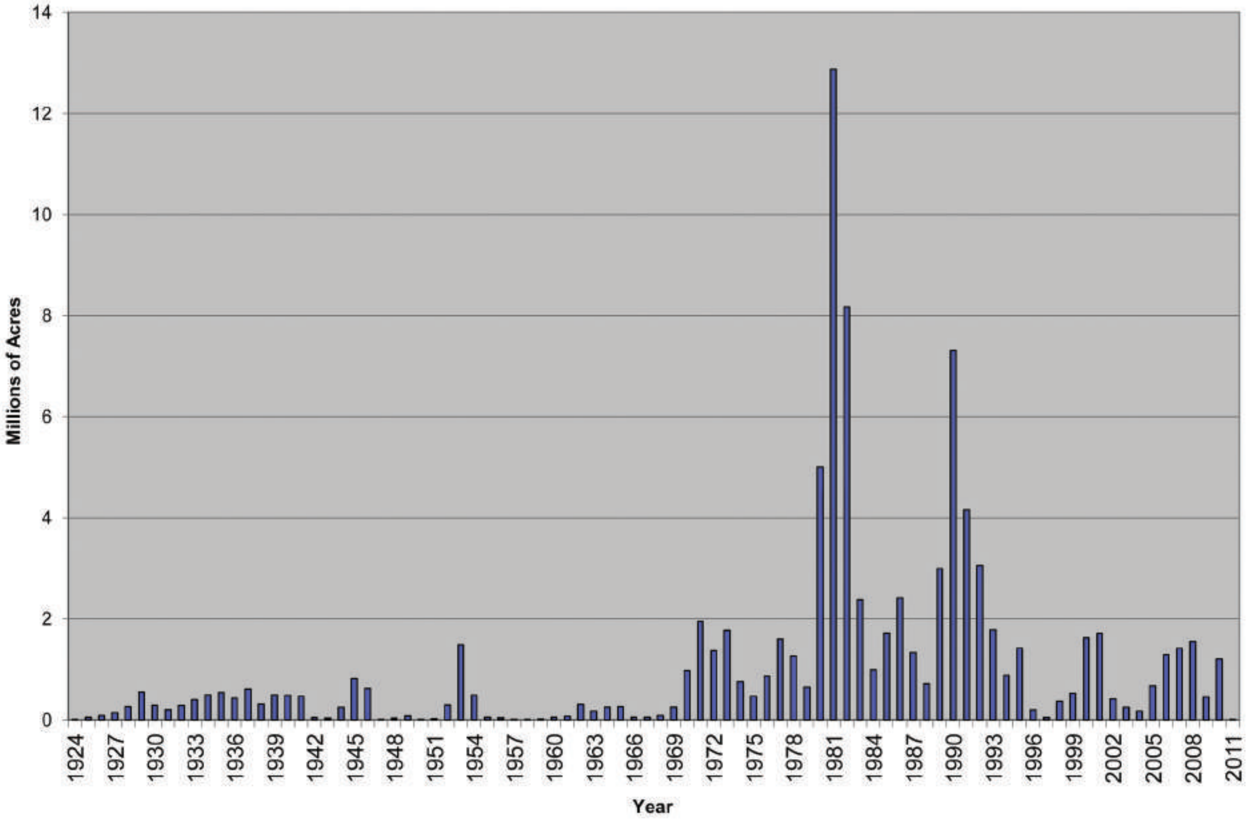

Figure 4 Historical defoliation levels by gypsy moth in U.S., 1924-2011 (from Man, 2012)

Figure 5 Gypsy moth egg mass. Milan Zubrik, Forest Research Institute - Slovakia, Bugwood.org.

Figure 6 Gypsy moth larva. John H. Ghent, USDA Forest Service, Bugwood.org.

days before females. Males are dark brown in appearance (Fig. 8), diurnally active, and rapid fliers that are attracted to pheromones of calling females. Females are white with faint black markings (Fig. 8) and use a sex pheromone identified as (7R,8S)-*cis*-7,8-epoxy-2-methyloctadecane or (+)-Disparlure (Bierl et al., 1970; Cardé et al., 1977; Plimmer et al., 1977) to attract the males. The pheromone (+)-Disparlure is a standard tool used in surveys to detect gypsy moth populations.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

North American gypsy moth is the only member of the genus *Lymantria* in the Nearctic region. Based on Ferguson's (1978) revision of the former family Lymantriidae, the most closely related native North American species are in the genera *Orgyia* and *Dasychira*. There are 10 species of *Orgyia* in the United States (Ferguson, 1978), and all females of this genus have wings reduced to vestigial pad-like structures. Best known of these species is the white-marked tussock moth, *Orgyia leucostigma* (J. E. Smith). There are 16 species of *Dasychira* in the United States and Canada (Ferguson, 1978). However, all these *Dasychira* species overwinter as larvae, not as eggs, as in the North American gypsy moth and all *Orgyia* species.

Figure 7 Gypsy moth pupae. Milan Zubrik, Forest Research Institute - Slovakia, Bugwood.org.

Figure 8 Gypsy moth male and female adults. USDA APHIS PPQ Archive, USDA APHIS PPQ, Bugwood.org.

Native Natural Enemies Affecting the Pest

Most of the early work on native natural enemies attacking gypsy moth was done by Forbush and Fernald (1896a), who cited a number of birds, including yellow-billed (*Coccyzus americanus* L.) and black-billed cuckoos (*Coccyzus erythropthalmus* Wilson), Baltimore oriole (*Icterus galbula* L.), chipping sparrow (*Spizella passerine* Bechstein), crows (*Corvus brachyrhynchos* Brehm), red-eyed (*Vireo olivaceus* L.) and yellow-throated (*Vireo flavifrons* Vieillot) vireos, as being noteworthy predators. They noted the introduction of the English sparrow (*Passer domesticus* L.) seemed to adversely affect populations of several species of birds, and the gypsy-moth populations increased where the English sparrow became abundant (Forbush and Fernald, 1896a). Other vertebrate predators cited included the skunk (*Mephitus mephitica* Shaw) and several amphibians (Forbush and Fernald, 1896b). Later work by Campbell (1975) and others measured the impact of mammalian predators, especially the white-footed mouse, *Peromyscus leucopus* (Rafinesque), and found it to be quite substantial in low density gypsy-moth populations. Other mammalian predators of gypsy moth include shrews (*Blarina* and *Sorex* spp.), raccoons (*Procyon lotor* L.), and opossums (*Didelphis viginiana* Kerr). A number of invertebrate predators, including ants (Formicidae, especially species in genus *Camponotus*), several species of vespid wasps, predaceous stinkbugs (Pentatomidae), and ground beetles (Carabidae, including native species of *Calosoma*), harvestmen (Phalangiidae), and spiders (Araneida) have been reported as feeding on gypsy moth (Forbush and Fernald, 1896b, Smith and Lautenschlager 1978, and Schaefer, 1991).

Only two hymenopterous pupal parasitoids, *Theronia hilaris* (Say) and *Pimpla pedalis* Cresson, both ichneumonids, were noted by Forbush and Ferrnald 1886b) as attacking gypsy moth in the United States. In addition, they provided a list of known hymenopterous parasitoids of gypsy moth reported from Europe, noting that neither those nor any closely related species had been found attacking gypsy moth in North America. Although it was hoped that native parasitoids would adapt to the new invader, levels of parasitization exerted by native parasitoids never exceeded 10% and averaged only about 2%, suggesting that native parasitoids could not suppress the pest (Howard and Fiske, 1911). Though native parasitoids do not successfully parasitize many gypsy moth immature stages, it was later found that the ichneumonids *T. hilaris*, *C. pedalis, Theronia atalantae* (Poda) and *Itoplectis conquistador* (Say) killed many more gypsy moth pupae by ovipositor insertion than were successfully parasitized (Campbell, 1963).

Five species of native hypocrealean entomopathogenic fungi have been reported as infecting gypsy moth larvae in the eastern United States (Majchrowicz and Yendol, 1973; Podgwaite, 1981; Hajek et al., 1997). Infections due to *Isaria farinosa* (Holmsk.) Fr. (= *Paecilomyces farinosus* (Holmsk.) A. H. S. Br. & G. Sm.) occurred at the majority of sites in one study, averaging 4.9-12.2% infection across two years (Hajek et al., 1997). Infections due to *Beauveria bassiana* (Bals.) Vuillemin were next most common, ranging from 0-6.0% infection (Majchrowicz and Yendol, 1973; Hajek et al., 1997).

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Previous reviews of biological control of gypsy moth in North America include Howard and Fiske (1911), Burgess and Crossman (1929), Dowden (1962), Hoy (1976), Clausen (1978), Doane and McManus (1981), and Kenis and Vaamonde (1998). Here we discuss the major efforts to find biological control agents useful against the gypsy moth in North America.

Area of Origin of Insect

The North American gypsy moth is endemic to western and eastern Europe and to northern portions of Africa. The exact point of Old World origin is unknown, but it is believed that the founders of the gypsy moth population that became established in North America were collected during the 1860s by Leopold Trouvelot on a trip to France (Liebhold et al., 1989). Another account suggests that eggs of *L. dispar* were obtained from Germany (Spear, 2005). Keena et al. (2008) evaluated 46 geographic strains of *L. dispar* for flight capability and related traits and found that females of *L. dispar* capable of strong directed flight occur in northeastern parts of Europe, but no flight-capable females were found in strains from the United States or southern and western Europe. Thus, it appears likely that the North American gypsy moth population originated in southern or western Europe.

Areas Surveyed for Natural Enemies

Europe Intermittent exploration for natural enemies of the gypsy mothewas undertaken from 1900 to 1995 by U.S. government entomologists or their cooperators. Results of the first era of work (1900–1910) are summarized by Howard and Fiske (1911); the second phase (1911–1923), by Burgess and Crossman (1929), and the third (1970–1995) by various authors (Drea and Fuester, 1979; Hedlund and Mihalache, 1980; Fuester et al., 1983, 1988; Cameron and Hérard, 1995). Additional surveys were conducted by CABI Bioscience (formerly Commonwealth Institute of Biological Control) in cooperation with the Canadian Forest Service (Kenis and Vaamonde, 1998; Nealis et al., 2002). Finally, studies of the resident natural enemy complexes of gypsy moth were carried out by many European entomologists. Virtually all regions of Europe were explored except for the United Kingdom, where gypsy moth became extinct as a breeding species about 1900, and Scandinavia, where it is generally a migrant (Giese and Schneider, 1979).

North Africa Additional explorations were conducted in Morocco (Lépiney, 1930, 1932; Hérard, 1979; Hérard and Fraval, 1980; Villemant, 1995; Villemant and Fraval, 1995), north of the High Atlas Mountains, where gypsy moth feeds primarily on oaks (*Quercus*) and fruit trees.

Asia In 1905–1908, a Japanese egg parasitoid, *Ooencyrtus kuvanae* (Howard) (Hymen: Encyrtidae) was obtained (Howard, 1910), shipped to Massachusetts in 1909, and established. In 1909, G. P. Clinton of the Connecticut Agricultural Experiment Station traveled to Japan to collect an undetermined fungus known to be infecting gypsy moth larvae. He returned with two cadavers infected with a fungus (Speare and Colley, 1912) that later was described as *Entomophaga maimaiga* Soper et al. (Soper et al., 1988).

In India, 1960–1972, sporadic exploration on dog the Indian gypsy moth (IGM), *Lymantria obfuscata* Walker, as the survey host took place. Two tachinids (E*xorista rossica Mesnil* and *Palexorista disparis Sabrosky*) and several hymenopterous larval parasitoids were collected and studied (Marsh, 1979). In 1972, *Brachymeria lasus* (Walker) (Hymenoptera; Chalcididae), a solitary pupal parasitoid, was obtained and shipped to the United States.

In Sapporo, Japan, In 1975, the Asian Parasite Laboratory was established to study natural enemies of the Asian gypsy moth (AGM) *sensu latu*. A variety of species were found and studied but none were imported to the United States (Schaefer, 1981; Schaefer and Ikebe, 1982; Schaefer et al., 1979, 1988, 1989).

At the same time, other work occurred in northeastern China (Schaefer et al., 1984) and Japan (Schaefer and Shima, 1981). General surveys of natural enemies of gypsy moth were done in South Korea from 1982 to 1993 (Pemberton et al.; 1993; Lee, J. and Pemberton, 2009a), with intensive investigations on some natural enemies (Lee, H., et al., 1989; Lee, J. and H. Lee, 1989). Surveys were conducted in several provinces in China, in 1991–1993 (Yan et al. 1992, 1993, 1994) and in the Prymorye Territory of the Russian Far East in 1994 (Lee, J. and Pemberton, 2009b).

From 1985 to 1990, investigations in India were resumed and surveys examined natural enemies of *L. obfuscata* to identify species potentially suitable for biological control in North America (Dharmadhikari et al., 1985; Fuester and Ramaseshiah, 1989; Chacko and Singh, 1990; Ramaseshiah, 1997).

In summary, field surveys or studies on individual natural enemies were carried out in Japan (on all major islands), South Korea (including the island of Cheju [Lee, J. et al., 2002]), China (southwestern, central and northeastern parts), Russian Far East, Mongolia (Schaefer, unpubl. 2004-5), Iran (Hérard et al., 1979), and India. Exploration for additional natural enemies of the gypsy moth ceased after the mid-1990s, as populations of gypsy moth in much of eastern North America have come under biological control, in part from the accidental introduction of the fungal pathogen *E. maimaiga*.

Natural Enemies Found

Parasitoids/Parasites Several hundred species of parasitoids have been discovered attacking gypsy moth and/or Indian gypsy moth in the Old World. Gupta (1983) reports 24 ichneumonids confirmed as parasitoids of the gypsy moth. Marsh (1979) provides a similar review for the Braconidae, and Sabrosky and Reardon (1976) for the Tachinidae. Not all of these species were imported for further investigation, and even fewer were released. In the first phase of work, some 40 species were imported (Howard and Fiske, 1911). From 1963 to 1985, 75 species of natural enemies were imported to quarantine laboratories in the United States for study (Coulson et al., 1986), but fewer than half were received in large enough numbers to establish laboratory colonies, and even fewer were released into the environment. Here we cover only the species that were most consistently recovered by investigators in one or more regions.

(1) Europe Hoy (1976) summarized the parasitoids recovered, imported and released from Europe up to 1976. To update that report, we note that several additional species were later discovered, including: (1) *Aphantorhaphopsis* (= *Ceranthia*) *samarensis* (Fallén), an oligophagous larval parasitoid found in Austria (Fuester et al., 1983). Studies by Mills and Nealis (1992) of low density gypsy moth populations in Alsace, France, showed it was the dominant tachinid at that location, causing up to 45% parasitism. (2) Two porizontine ichneumonids, *Hyposoter* (= *Limneria*) *tricoloripes* (Viereck) and *Casinaria tenuiventris* (Gravenhorst), reported as rare by Pschorn-Walcher (1974), were found to be locally abundant in Austria and France (Fuester et al., 1983, 1988). However, both species are multivoltine, requiring alternate hosts and thus making them unacceptable for modern biological control. (3) The mermithid nematode *Hexamermis albicans* Siebold was recovered from gypsy moth by Drea et al. (1977) in Austria and Germany.

(2) North Africa From Morocco, 17 species of parasitoids were discovered, most of which were known from Europe (Hérard, 1979; Hérard and Fraval, 1980), including the egg parasitoids *O. kuvanae* (introduced from the Far East)*; Gryon* sp., and *Telenomus* spp.; the larval parasitoids *Dolichogenidea lacteicolor* (Viereck), *Cotesia melanoscela* (Ratzeburg)*, Glyptapanteles porthetriae,* (Muesebeck) *Meteorus pulchricornis* (Wesmael), *Senometopia* (= *Carcelia*) *separata* (Rondani), *Compsilura concinnata* (Meigen)*, Palexorista inconspicua,*(Meige); the pupal parasitoids *Brachymeria intermedia* (Nees), *Pimpla instigator* (Fabricius), *Pimpla turionellae moraguesi* (Schmiedeknecht), *Pimpla* sp., *Vulgichneumon* (= *Melanichneumon*); a few undetermined ichneumonid; and several undetermined tachinids.

For the most part, the parasitoid complex in North Africa is considered relatively depauperate compared to Europe, and inefficient (Hérard and Fraval, 1980, Villemant and Fraval, 1995), except when climatic conditions in the autumn and winter induce a prolonged hatching period of gypsy moth eggs the following spring. This pattern allows some hymenopteran parasitoids (notably the braconids *C. melanoscela*, *G. porthetriae,* and *M. pulchricornis* that prefer young larvae and the chalcidid pupal parasitoid *Brachymeria intermedia* (Nees) to undergo several generations, resulting in elevated parasitism. This parasitism then reduces both gypsy moth population levels and defoliation. Parasitism usually remains high through the following year (Villemant and Fraval, 1995).

(3) Far East Asia *Pimpla disparis* Viereck and *Pimpla luctuosus* Smith (Hymenoptera: Ichneumonidae), two very similar species, were found routinely in host pupae in Asia and could readily be reared in the laboratory. Also, a mermithid nematode (*Hexamermis* sp.) was recovered from Asian gypsy moths in Japan.

(4) India The more significant parasitoid species discovered in India on Indian gypsy moth include the egg parasitoid *Anastatus kashmirensis* Mathur (Hymenoptera: Eupelmidae); two ichneumonid larval parasitoids, *Casinaria arjuna* Maheshwary and Gupta and *Hyposoter lymantriae* Cushma; four braconid larval parasitoids, *Aleiodes* (= *Rogas*) *indiscretus* Reardon (Reardon, 1970), *Glyptapanteles indiensis* Marsh, *Glyptapanteles flavicoxis* Marsh, and *C. melanoscela*; three tachinids, *Exorista rossica* (Mesnil), *Palexorista disparis* Sabrosky, *Palexorista inconspicua* Meige; the mermithid nematode *Hexamermis* sp.; two chalcidid pupal parasitoids, *B. intermedia* and a uniparental strain of *B. lasus*; and two ichneumonid pupal parasitoids, *Pimpla disparis* and *Theronia atalantae himalayensis* Gupta (Ramaseshiah, 1990, 1997). Although several of these species were eventually released, only *Pimpla disparis* became established in North America.

Predators A variety of predatory species, mostly beetles, attack gypsy moth eggs, larvae, or pupae in various regions, as indicated below.

(1) Europe Several ground beetles (Carabidae) were found preying on gypsy moth in Europe, including *Calosoma inquisitor* (L.), *Calosoma reticulatum* (Fabricius), and *Calosoma sycophanta* (L.). Only *C. sycophanta* (L.) was reported as having a preference for gypsy moth (Dowden, 1962). In addition, several species of *Carabus*, including *C. arvensis* Herbst, *C. auratus* L., *C. glabratus* Paykull, *C. luczoti* (Dejean), *C. nemoralis* Mueller, and *C. violaceus* L. were noted feeding on gypsy moth in Europe (Smith, 1959; Dowden, 1962; Thompson and Simmonds, 1964), but all were broadly polyphagous. The carabid *Habrocarabus latus* var. *gougeleti* Reiche was found attacking gypsy moth stages in Spain: studies indicated it was unlikely to be important in gypsy moth controd, so it was not released (Burgess and Crossman, 1929). The silphid beetle *Xylodrepa quadripunctata*

Schreber was observed feeding on larvae of gypsy moth in Spain, Hungary, and the former Czechoslovakia (Burgess and Crossman, 1929) and Yugoslavia (Drea, 1981).

(2) North Africa Predators and dismantlers of gypsy moth egg masses are significant mortality factors in Morocco (Hérard, 1979; Hérard and Fraval, 1980; Villemant and Andreï-Ruiz, 1999). These include larvae of two moths, *Niditinea fuscipunctella* (Hawarth) (Tineaidae) and *Aglossa caprealis* (Hübner) (Pyralidae), and of several beetles, namely *Trogoderma versicolor meridionalis* (Kraatz), *Dermestes lardarius* (L.), *Anthrenus versicolor meridionalis* Menier & Villemant, *Anthrenus vladimiri* Menier & Villemant (all Dermestidae), and *Tenebroides maroccanus* (Reiter) (Trogossitidae). Combined with the egg parasitoid *O. kuvanae*, the above mentioned species sometimes destroy 50% of the eggs.

(3) Asian Far East At least one carabid, *Calosoma chinense* Kirby, was found attacking gypsy moth in China. Field work in the northern regions of Japan, particularly in Hokkaido, revealed the presence of a predatory pentatomid bug, *Dinorhynchus dybowskyi* Jakovlev, attacking gypsy moth larvae (Schaefer et al., 1979)

Earlier foreign exploration in Asia was summarized by Hoy (1976), but since then, a wealth of new information on natural enemies has come to light. More recent faunal surveys discovered some new species (e.g., *Cotesia schaeferi* [Marsh] and *Protapanteles lymantriae* [Marsh], both Hymenoptera: Braconidae). Further information was recorded on other braconids (Marsh, 1979), ichneumonids (Gupta, 1983), tachinids (Sabrosky and Reardon, 1976; Schaefer and Shima, 1981), and other taxa. Among the most frequently recovered species were *O. kuvanae*, an egg parasitoid; *Glyptapanteles liparidis* (Bouché) (Hymen: Braconidae) and *Exorista japonica* (Townsend) (Dipt.: Tachinidae) as larval parasitoids, and *Pimpla disparis* and *P. luctuosus* (both Hymen: Ichneumonidae) as pupal parasitoids. In localized forest settings, the parasitic nematode *Hexamermis* sp. (Mermithidae) had a significant effect on low density gypsy moth populations in Hokkaido (Schaefer and Ikebe, 1982).

Pathogens The entomophthoralean fungus *E. maimaiga* was collected in Japan near Tokyo in 1910 and again, from Ishikawa Prefecture, in 1984 (Hajek et al., 1995a). As for viral pathogens, a baculovirus "*Lymantria dispar* multiple nucleopolyhedrovirus" (LdMNPV) is widely distributed in the Palearctic Region, but it apparently does not occur in Morocco (Hérard and Fraval, 1980; Villemant and Fraval, 1995). Field exploration for microsporidia in gypsy moth larvae was conducted from 1985 to 2005 in nine countries, predominantly in central and eastern Europe. Five species of microsporidia, (*Nosema lymantriae* Weiser, *Nosema serbica* Weiser, *Nosema portugal* Maddox and Vavra [Maddox et al., 1999], *Vairimorpha disparis* (Timofejeva) and *Endoreticulatus schubergi* Zwolfer), have been reported from European gypsy moth. No microsporidia were found in Siberian gypsy moth populations (Solter and Hajek, 2009). Other pathogens known to infect gypsy moth (i.e., a cypovirus, several bacteria and several hypocrealean fungi) have not been investigated extensively (Podgwaite, 1981).

Host Range Test Results

Parasitoids Most of the releases of imported parasitoids took place before 1980, and none of the released species underwent host-range testing. In fact, some species released before 1940 (e.g., *C. concinnata*) were released despite being known to be broadly polyphagous. In most cases, agents were released after screening for hyperparasitoids without any laboratory rearing (Hoy, 1976). *Monodontomerus aereus* Walker, a torymid wasp recovered from pupae of both gypsy and brown-tail moths (*Euproctis chrysorrhoea* [L.]), was one of the first parasitoids to be released (1906).However, it was later found to be a hyperparasitoid of tachinids, so no further releases were made after 1910 (Burgess and Crossman, 1929). This species is now rather rare (Hoy, 1976).

Nevertheless, host range tests of a sort were conducted on some species to identify important alternate hosts. Such studies were done for the braconids *Glyptapanteles porthetriae* (Muesebeck) and *G. liparidis* (Raffa, 1977), because they are important natural enemies of the gypsy moth in their native range (Burgess and Crossman, 1929; Hoy, 1976; Fuester et al., 1983). In addition, several species were tested to see if they presented threats to nontarget organisms. In studies on *A. kashmirensis*, an egg parasitoid of *L. obfuscata* from India, Weseloh et al. (1979) found it preferred to attack cocooned larvae of the primary parasitoid *C. melanoscela* than to attack *A. japonicus*, the Eurasian species established earlier. Because *A. kashmirensis* was not superior to *A. japonicus* in laboratory tests, it was not released.

Hedlund and Schroder (1981) reviewed host range studies on gypsy moth parasitoids done up to 1981. Although host range tests on *Pimpla disparis* resulted in four lepidopteran species being added to its known host range, the tests with bagworm, *Thyridopteryx ephemeraeformis* (Haworth), were negative (Hedlund and Schroder, 1981). However, this species was later reared from field collections of bagworm (Schaefer et al., 1989). Compilation of host range trials and host records showed this species would attack a variety of lepidopteran pupae (Schaefer et al., 1989). *Pimpla disparis* seems to prefer to attack species that pupate in concealed places such as bagworms (Ellis et al., 2005). During quarantine evaluations, *Pimpla luctuosus*, a pupal parasitoid from Japan, was found to attack an iconic species (monarch butterfly, *Danaus plexippus* L.; subsequently, no releases were made (Schaefer, unpublished data). Based on studies on the host range of *A. samarensis* in Europe and in quarantine in North Americd, concluded that *A. samarensis* had a narrow host rangg limited to the lymantriid genera *Lymantria* and *Orgyia*. No host-range studies were conducted on the nematode *Hexamermis* sp. due to the inability to rear the species in the laboratory at the time of the release.

Predators The stinkbug *D. dybowskyi* was found to complete its development on gypsy moth caterpillars. When offered, it also accepted the larvae of several plant pests (forest tent caterpillar, *Malacosoma disstria* Hübner, and alfalfa weevil, *Hypera postica* Gyllenhal (Fuester, unpublished data); however, plant tissue alone did not support survival (Schaefer et al. 1979). Despite this lack of specificity, *D. dybowskyi* was released, but appears not to have become established (see below).

Pathogens The host range of *E. maimaiga* was first evaluated with insects from laboratory colonies and from field collections by dipping into a conidial suspension, showering with conidia, or injecting insects with fungal protoplasts. Insects tested included adults of the coccinellid *Epilachna varivestis* Mulsant, the chrysomelid *Diabrotica undecimpunctata howardi* Barber, and the acridid grasshopper *Camnula pellucida* (Scudder), as well as larvae of sixteen lepidopteran species (in seven families) (Soper et al., 1988). Infection of >50% was found only in one lymantriine species (*Orgyia pseudotsugata* [McDunnough]) and lower levels (<35% infection) occurred in two noctuids (*Helicoverpa zea* [Boddie] and *Trichoplusia ni* [Hübner]) and two lymantriines (*Dasychira dorsipennata* [Barnes & McDunnough] and an unidentified field-collected species). All other insects tested were uninfected (Soper et al., 1988).

Further studies were conducted with 78 lepidopteran species, predominantly native to Appalachian forest: larvae were either dipped into a conidial suspension or injected with protoplasts. At least one larvafof 23 species inoculated externally with conidi, died and produced spores. Infection levels >50% occurred only in the sphingid *Manduca* sexta (L.), the lasiocampid *Malacosoma disstri*r, and all four of lymantriines tested (*Dasychira basiflava* [Packard], *Dasychira obliquata* [Grote & Robinson], *Orgyia definita* Packard, and *Orgyia leucostigma* [J. E. Smith]) (Hajek et al., 1995b).

For the next stage of testing, native lepidopteran larvae were collected during spring either in forests in Virginia, where moderate density gypsy moth populations occurred, or in low density gypsy moth sites in Virginia, Michigan, or New York. At sites with moderate gypsy moth density, *E. maimaiga* caused 41–98% infection in resident gypsy moths, while only two of 1,511 nontarget larvae belonging to 52 species were infected, and both were common species, *M. disstria* and *Catocala ilia* Cramer) (Hajek et al., 1996a). No nontarget species were infected in the sites with low gypsy moth density. Because gypsy moth larvae become infected when caged on the soil surface, studies of nontarget lepidopteran larvae taken from the leaf litter were conducted. Of such larvae, only two individuals (the noctuid *Agrochola bicolorago* Guenée and the larva of an unidentified gelechiid) became infected of 358 nontarget individuals collected, in contrast to 37% infection of gypsy moth larvae at the site (Hajek et al., 2000).

Further field studiesnspecific to lymantriine were conducted, because these appeared to be at highest risk based on laboratory bioassays anr field studies. During five years of field collections, and only three of seven species of native lymantriines from mountain forests of Virginia and West Virginia were found sometimes to be infected by *E. maimaiga*, but never at high rates (> 50%), despite 8-21% infection of gypsy moth larvae at collection sites (Hajek et al., 2004).

Another pathogen of gypsy moth, the *Lymantria dispar* multiple nucleopolyhedrovirus, was accidentally introduced to North America, but subsequent host range tests have demonstrated it infects only gypsy moth larvae (Barber et al., 1993).

Among microsporidia, species in three genera infect gypsy moths in Europe, including *V. disparis* and *N. lymantriae*. These two species have been tested against approximately 50 species of Lepidoptera native to eastern North America (Solter et al., 1997) to determine their host ranges. Some infections in selected nontarget host were found, but infections did not lead to disease transmission to conspecific hosts (Solter and Maddox, 1998), suggesting that these infections were laboratory artifacts. In field surveys in Bulgaria, three species of microsporidia (*V. disparis, Nosema* sp., and *Endoreticulatus* sp., (the latter two now known to be *N. lymantriae* and *E. schuberg*]), were isolated from native gypsy moth larvae (1.3% overall infection among 2,103 gypsy moth larvae collected in 1997–1998 alone). The microsporidian species that occur naturally in gypsy moths were not recovered from any of 1,495 nontarget individuals of sympatric forest Lepidoptera from ten families (Solter et al., 2000) In Europe (Slovakia), when *V. disparis* and *N. lymantriae* were applied at high concentrations, several nontarget individuals became infected with *V. disparis* at low rates but no further nontarget infections were found over a 2-year study period (Solter and Hajek, 2009).

Releases Made

Parasitoids For a list of releases of parasitoids and predators made from 1906 to 1959 see Clausen (1978). For a similar listing for 1963 to 1977, see Reardon (1981). The names of some of these species have changed because of taxonomic revision: for an updated list of the 34 parasitoids released, see Table 1. Numbers released for most species can no longer be determined because of the many agencies involved. Here, we discuss releases since about 1960, for which better records exist.

No new introductions to the United States of gypsy moth egg parasitoids were made after 1977, although *O. kuvanae* and *A. japonicus* were introduced to new states during this period. Several new species of larval parasitoids were released after 1960. (1) Some 30,847 adults of the braconid *A. indiscretus* from India were released from 1968 to 1977 in New Jersey, Massachusetts, Connecticut, or Pennsylvania (Metterhouse,1981), but establishment was not detected until Schroder and Sidor (1997) discovered *A. indiscretus* attacking larvae of *Dasychira basiflava* (Packard). The current status of *A. indiscretus* as a parasitoid of *L. dispar* is uncertain). (2) Four additional larval parastioids from India (*G. indiensis, G. flavicoxis, C. arjuna*, and *H. lymantria*)— were released in substantial numbers (> 8,000 each), mostly in Delaware, New Jersey, Pennsylvania, and Virginia, but none became permanently established). (3) The tachinid larval parasitoid *Aphantorhaphopsis* (= *Ceranthia*) *samarensis* (Fallén), was released in both the United States and Ontario, Canada, between 1992 and 1996, and there was evidence of successful parasitism by the fly in the experimental host populations in the year of release (Nealis and Quednau, 1996); however, follow-up studies using laboratory-reared gypsy moth sentinel larvae failed to recover *A. samarensis* (Nealis et al., 2002). In addition, *Blondelia* (= *Lydella*) *nigripes* (Fallén), a species released between 1906 and 1932 (Sabrosky and Reardon, 1976), was again released in New Jersey, 197–78, but did not become established. Among pupal parasitoids, only one species, *Pimpla disparis*, was released since 1960, mostly in the Mid-Atlantic States, where it did become established.

Predators Between 1979 and 1981, 1704 nymphs of the stinkbug *D. dybowskyi* were released over four sites in Pennsylvania, Maryland, and Connecticut, but establishment was not confirmed (Schaefer, 1996).

Pathogens *Entomophaga maimaiga* was transported from Japan in 1909 as two fungus-filled cadavers, which were used as to produce infected insects that were subsequently released in the Boston area in 1910 and 1911. This release is thought to have failed (Speare and Colley, 1912). In 1984, the pathogen was isolated from the Ishikawa Prefecture in Japan and released in southwestern New York in 1985 and in Shenandoah National Park, Virginia, in 1986, but there was no evidence that either of these releases resulted in establishment. In 1989, however, *E. maimaiga* was detected in seven northeastern U.S. states, and it subsequently spread throughout the contiguous gypsy moth distribution (Andreadis and Weseloh, 1990; Hajek et al., 1995a). The source location for the strain of *E. maimaiga* that successfully became established is Japan, although it is doubtful that the 1909 releases became established (Hajek et al., 1995a; Nielsen et al., 2005). To speed the spread of *E. maimaiga*, it was subsequently released in Maryland, Pennsylvania, Virginia, and West Virginin, 1991–1992 (Hajek et al., 1996b), and Michigan in 1991–1993 (Smitley et al., 1995). In 1996 and 2000, *E. maimaiga* resting spores taken from areas where it had been recovered in Connecticut were released in Levishte, Bulgaria, and infections were found there in 2002, 2003, and 2004 (Hajek et al., 2005). In 1999, *E. maimaiga* resting spores from Massachusetts were released in Karlovo, Bulgaria, resulting in establishment but only low levels of

Table 1 Eurasian and North African parasitoids of the gypsy moth released against gypsy moth in North America categorized by success or failure to become established.

Parasitoids established in North America	Host stage attacked [a]	Host range [b]	Life cycle [c]	Alternate host required	Original host[d]
1. *Anastatus japonicus* Ashmead (=*disparis* Rushka) (Eupelmidae)	E	P	U	No	EGM
2. *Ooencyrtus kuvanae* (Howard) (Encyrtidae)	E	P	M	?	AGM
3. *Cotesia melanoscela* (Ratzeburg) (Braconidae)	L	O	M	No	EGM
4. *Aleodes* (= *Rogas*) *indiscretus* (Reardon) (Braconidae)	L	O	M	Yes	IGM
5. *Phobocampe unicincta* (Gravenhorst) (=*disparis* Viereck) (Ichneumonidae)	L	M	U	E	EGM
6. *Blepharipa pratensis* (Meigen) (Tachinidae)	L	O	U	No	EGM
7. *Compsilura concinnata* (Meigen) (Tachinidae)	L	P	M	Yes	EGM
8. *Exorista larvarum* (L.) (Tachinidae)	L	P	M-U	Yes	EGM
9. *Parasetigena silvestris* (Robineau-Desvoidy) (Tachinidae)	L	O	U	No	EGM
10. *Monodontomerus aereus* Walker (Torymidae)	P	P	M		EGM
11. *Brachymeria intermedia* (Nees) (Chalcididae)	P	P	U-M	?	EGM
12. *Pimpla disparis* Viereck (Ichneumonidae)	P	P	U	No	AGM
Parasitoids released but not establish					
13. *Cotesia schaeferi* (Marsh) (Braconidae)	L	O	M	Yes	AGM
14. *Glyptapanteles flavicoxis* (Marsh) Braconidae	L	O	M	Yes	IGM
15. *Glyptapanteles indiensis* (Marsh) Braconidae	L	O	M	Yes	IGM
16. *Glyptapanteles liparidis* (Bouché) (Braconidae)	L	O	M	Yes	EGM
17. *Glyptapanteles porthetriae* (Muesebeck.) (Braconidae)	L	O	M	Yes	EGM
18. *Meteorus pulchricornis* Wesmael (Braconidae)	L	O	M	Yes	EGM
19. *Aleodes lymantriae* (Watanabe) (Braconidae)	L	O	M	Yes	AGM
20. *Casinaria arjuna* Cushman (Ichneumonidae)	L	O	M	Yes	IGM
21. *Hyposoter lymantriae* Gupta and Maheshwary (Ichneumonidae)	L	O	M	Yes	IGM
22. *Aphantorhaphopsis* (=*Ceranthia*) *samarensis* (Villeneuve) (Tachinidae)	L	O	M	No	EGM
23. *Blondelia nigripes* (Fallén) (Tachinidae)	L	P	M	Yes	EGM
24. *Senometopia* (=*Carcelia*) *separata* (Rondani) (Tachinidae)	L	P	M	Yes	EGM
25. *Exorista japonica* (Townsend) (Tachinidae)	L	P	M	Yes	AGM
26. *Exorista rossica* (Mesnil) (Tachinidae)	L	P	M	Yes	IGM
27. *Exorista segregata* (Rondani) (Tachinidae)	L	P	M	Yes	EGM
28. *Palexorista disparis* (Sabrosky) (Tachinidae)	L	?	M	Yes	IGM
29. *Palexorista inconspicua* (Meigen) (Tachinidae)	L	P	M	Yes	EGM
30. *Zenillia libatrix* (Panzer) (Tachinidae)	L	O	M	Yes	EGM
31. *Brachymeria lasus* (Walker) (Chalcididae)	P	P	M	Yes	AGM
32. *Pimpla hypochondriaca* (Retzius) (=*instigator* F.) (Ichneumonidae)	P	P	M	Yes	EGM
33. *Pimpla moraguesi* (Schmiedeknecht) (Ichneumonidae)	P	P	M	Yes	EGM
34. *Pimpla turionellae* (L.) (Ichneumonidae)	P	P	M	Yes	EGM*

[a]E = egg, L = larva, P = pupa. [b]P = polyphagous, O = oligophagous, M = monophagous
[c]M = multivoltine, U = univoltine. [d]AGM = Asian gypsy moth, EGM = European gypsy moth, IGM = Indian gypsy moth

infection (Hajek et al., 2005). In 2002, *E. maimaiga* resting spores from Virginia were released in the Novosibirsk region, but establishment was not confirmed (Hajek et al., 2005).

The gypsy moth nucleopolyhedrovirus was first found in the United States in the early 1900s (Glaser and Chapman, 1913), but its introduction was not deliberate, and most likely occurred through the introduction of virus-contaminated parasitoids.

The microsporidia *N. portugal* and *Endoreticulatus* sp. were released in Maryland in 1986 using contaminated host egg masses. No infected larvae were found the following year at the *Endoreticulatus* sp. release site, but low levels of infection by *N. portugal* were detected in 1987, with some persistence for three years following release (Hajek et al., 2005). *Nosema portugal* was released in Michigan in 1992 and 1993, resulting in low levels of infection but little persistence. In 2008 and 2010, *V. disparis* and *N. lymantriae*, both from Bulgaria, were released in Illinois. In 2009, no infection was found in hosts collected at the 2008 release site. Soon after the 2010 release, *V. disparis* infections were found in larvae that died of *E. maimaiga* infections, but host populations densities were subsequently low, and long-term persistence was not demonstrated (L. F. Solter, personal communication).

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

The classical biological control effort against gypsy moth in North America is very likely the most intensive effort of its kind, directed against any species, worldwide. It spanned most of the 20th century and resulted in the establishment of thirteen parasitoid species (Table 1), three predator species, and two pathogens. Despite this effort, defoliation by gypsy moth has continued in many parts of the eastern United States, and the range of gypsy moth has continued to expand in midwestern and southern states. Most of the natural enemies that established in North America did so before 1920 (Howard and Fiske, 1911; Burgess and Crossman, 1929). A major worldwide effort supported by the USDA to seek and establish additional species in the 1960s and 1970s (see Reardon et al., 1981) led to the establishment of just two additional specie, the pupal parasitoid *Pimpla disparis* and the larval parasitoid *A. indiscretu*, whose impacts on gypsy moth population densities thus far appear minimal (Schaefer et al., 1989; Shaw, 2006). Additional efforts to establish parasitoids, primarily species from the Asian Far East and India, continued into the 1990s, but no species became established.

The spread of the various species of natural enemies from their initial points of colonization was very uneven. Some, such as the pathogen *E. maimaiga* (Elkinton et al., 1991) and the tachinid fly *C. concinnata*, spread quite rapidly. Indeed, the latter species spread up to 40 km/year (Hoy, 1976) and, being polyphagous, expanded its range beyond that of the gypsy moth. Others, such as the egg parasitoid *A. japonicus* (Burgess and Crossman, 1929), spread quite slowly.

Suppression of Target Insect Pest

Despite many decades of research, our understanding of the effect of parasitoids on the population dynamics of gypsy moth in North America remains poor. A long-term study conducted by Williams et al. (1992, 1993) on the effects of larval and pupal parasitoids on low-density gypsy moth populations in New Jersey showed that several species caused density dependent mortality, but levels of mortality for individual species were never higher than about 30%. Other analyses, in higher density populations indicated that parasitoids caused inversely density dependent mortality (Ticehurst et al., 1978). Studies on experimentally created populations of gypsy moth in hectare-sized plots demonstrated that parasitoids, especially *C. concinnata,* can regularly cause larval parasitism exceeding 90%, a level associated with dramatic declines in gypsy moth density (Liebhold and Elkinton, 1989; Gould et al., 1990; Ferguson et al., 1994). However, such high levels of parasitism have not been noted in naturally occurring populations of gypsy moth in North America. The difference is presumably the small spatial scale (typically one ha) of these experimental populations, which allows an aggregation response from outside the artificially infested plots by polyphagous species such as *C. concinnata,* which are likely maintained at elevated densities by alternate hosts. Natural populations of gypsy moths rise and fall on a scale of many km^2 and aggregation effects from surrounding low density areas to high density infestations of gypsy moth, typically>>1 ha in size, would be diluted.

Several more recent studies have recorded parasitism of natural gypsy moth populations along the advancing front of the invasion in North America. Hoffman et al. (2008) recorded 32% parasitism by *C. concinnata* of gypsy moth larvae in a recently invaded area of Wisconsin during one study year. In another Wisconsin study, Hajek and Tobin (2011) recorded total larval parasitism that varied between 2 and 12%, while in Ontario Timms and Smith (2011) showed that parasitism was 3 to 6% in successive years. In all three of these studies, *C. concinnata* caused more larval mortality than any of the other five larval parasitoids. This is in stark contrast with studies on parasitism in natural gypsy moth populations conducted before the great *E. maimaiga* fungal epizootics that began in 1989, when the the oligophagous tachinids *Parasetigena silvestris* (Robineau-Desvoidy) and *Blepharipa pratensis* (Meigen) frequently predominated, especially in outbreak and declining host populations (Tigner, 1974; Reardon, 1976; Ticehurst et al., 1978; Hedlund and Angalet, 1979; Williams et al., 1992). Larvae of *C. concinnata* tend to exit from hosts sooner than the aforementioned oligophagous species (Ticehurst, 1984) and perhaps may be less harmed by *E. maimaiga*. In any case, it seems likely that the ability of *C. concinnata* to attack many other species of Lepidoptera may enable it to cause higher levels of parasitism among low density or newly established gypsy moth populations than parasitoid species with narrower host ranges. These studies support the conclusions of earlier studies, that parasitism of gypsy moth causes only a relatively small proportion of total mortality and is unlikely to regulate the density of gypsy moth.

As noted above, the level of parasitism recorded in European studies has often been much higher than that observed for the same parasitoid species on gypsy moth in North America (Reardon, 1976; Elkinton and Liebhold, 1990). A study by Sisojević (1975) in the former Yugoslavia appeared to show a classic host-parasitoid oscillation between gypsy moth and two oligophagous tachinid species, *P. silvestris* and *B. pratensis*, with parasitism as high as 90% and coinciding with gypsy moth population declines. For unknown reasons, These same tachinids cause much lower levels of parasitism in North America (Elkinton and Liebhold, 1990). One possible explanation is that the nun moth, *Lymantria monacha* (L.), which serves as an alternative host of *P. silvestris* in Europe (Prell, 1915), is missing in North America. (This might account for the higher abundance of *P. silvestris* in Europe, as well.) Though known primarily as a defoliator of conifers, *L. monacha* also attacks a number of hardwoods, including genera favored by gypsy moth, such as *Quercus, Fagus, Betula*, and *Carpinus* (Grijpma, 1988). Nun moth might serve as a reservoir host for *P. silvestris* and other gypsy moth parasitoids, conferring stability on the natural-enemy complex. Nearly all of the other imported larval parasitoids of gypsy moth in Europe that became established in North Americ, *C. melanoscela, B. pratensis, C. concinnata,* and *Exorista larvarum* (L.) have been reported from *L. monacha* as well (Thompson, 1946).

The most dramatic change affecting the degree of biological control of the gypsy moth in North America since 1980 has been the establishment and spread of *E. maimaiga,* beginning in New England in 1989 (Hajek et al., 1990). Various reports indicated that high levels of mortality (>50%) from this pathogen frequently occurred in low density populations, indicating that this agent served to prevent outbreaks (Hajek, 1999), instead of merely terminating outbreaks as the gypsy moth virus formerly often did (Doane, 1970). In the New England states, there have been no widespread outbreaks of gypsy moth since 1989. However, in the Mid-Atlantic States and midwestern United States, outbreaks and population spread of gypsy moths have continued. Recent analyses of gypsy moth-defoliation data indicate that the presence of *E. maimaiga* may have altered the amplitude but not the frequency of outbreaks (Tobin et al., 2012).

Nontarget Effects

Boettner et al. (2000) demonstrated that the tachinid *C. concinnata* caused high levels of mortality to experimentally deployed larvae of several species of giant silk moths (Saturniidae), and proposed that *C. concinnata* may be responsible for the observed declines of various saturniid species in North America that seem to have occurred in the 20th Century. Similar high rates of parasitism were also reported in Virginia in luna moth (*Actias luna* [L.]) caterpillars (Kellogg et al., 2003). Conversely, much lower parasitism rates were observed for *C. concinnata* in New York (Parry, 2008) and for the barrens buck moth (*Hemileuca maia* Drury) on Cape Cod, Massachusetts (Selfridge et al., 2007). *Compsilura concinnata* has been recovered from over 200 species of moth and sawfly larvae in North America (Arnaud, 1978; Boettner et al., 2000; Strazanac et al., 2001). However, its importance in the population dynamics of these hosts has rarely been studied. The deleterious effects of *C. concinnata* on nontarget species are somewhat offset by its effectiveness as a natural enemy of the brown-tail moth, another lymantriine defoliator introduced from Europe (Elkinton and Boettner, 2012).

Pimpla disparis, a polyphagous pupal parasitoid introduced from Asia, is known to have a broad host range that includes pierid and papilionid butterflies and saturniid, lasiocampid, and yponomeutid moths (Townes et al., 1965). Schaefer et al. (1989) reported that *Pimpla disparis* caused approximately 31% mortality in eastern tent caterpillar, *Malacosoma americanum* (F.), populations, but only a mean of 1.3 % parasitism of gypsy moth pupae.

Little is known about the potential impacts of the other polyphagous parasitoids introduced to control gypsy moth, apart from their recovery from nontarget species (Schaffner, 1934; Schaffner and Griswold, 1934; Prokopy, 1968; Hedlund and Schroder, 1981; Shaw, 2006).

Such nontarget effects led to a call for stronger standards for host-range testing and ending the introduction of polyphagous parasitoids (e.g., Simberloff and Stiling, 1996; Strong and Pemberton, 2000). The USDA responded with a more rigorous permitting process to govern the importation and release of non-native, carnivorous biological control agents (Hoddle, 2004).

Broad Assessment of Factors Affecting Success or Failure of Project

Researchers interested in overall gypsy moth population dynamics have long focused on the idea that predation by small mammals was important in maintaining gypsy moth populations at low density in the intervals between outbreaks (Bess, 1961; Campbell and Sloan, 1977b). Elkinton et al. (1996) and Jones et al. (1998) provided data linking changes in gypsy moth density to that of white-footed mice (*P. leucopus*), whose density is in turn determined by acorn mast abundance, the principal food of overwintering white-footed mice. Campbell and Sloan (1977c) promoted the idea that predation by small mammals maintained a low density equilibrium in gypsy moth populations, from which they occasionally escaped into outbreak phase. There exist no studies indicating that predation by mice increases with density at very low gypsy moth densities, as predicted by such a model. However. there are some data supporting the idea that predation rates by mice decline as gypsy moth density increases at intermediate densities, allowing rapid expansion of populations to outbreak levels (Elkinton et al., 1989). Elkinton et al. (2004) found that the functional response of deer mice to the abundance of gypsy moth pupae was Type II, not Type III, as previously believed (Campbell, 1975); therefore, one would not expect white-footed mice to regulate gypsy moth densities.

Other studies showed that outbreak populations of gypsy moth formerly declined due to epizootics of a nuclear polyhedrosis virus (Doane, 1970). The virus occurs naturally and has been associated with gypsy moth probably since it was first introduced to North America. Dwyer et al. (2004) proposed a model that combined predation by generalist predators such as white-footed mice with a host-pathogen model. That model had no low density equilibrium and oscillated with a period of approximately every ten years. Recent analyses by Bjornstad et al. (2008, 2010) confirm the existence of a periodicity of approximately ten years in gypsy moth defoliation and suggested a modified version of the Dwyer et al. (2004) model. None of these analyses have assumed that parasitoids play a critical role. In fact we do not know what the gypsy moth population dynamics or the frequency of outbreaks would be in the absence of parasitoids. In the northeastern states, levels of parasitism exerted by tachinid parasitoids on gypsy moth populations before 1989 appeared to have been greatly diminished by competition with *E. maimaiga* since the latter's introduction (Blumenthal and Wilt, 1998), and a similar pattern seems to be emerging in Wisconsin along the gypsy moth invasion front (Hajek and Tobin, 2011) as well as in Europe at sites where the fungus recently has become established (Georgiev et al., 2012).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

The biologies of 12 species of natural enemies (parasitoids, predators, and pathogens) of gypsy moth are discussed below, listed alphabetically.

Aphantorhaphopsis (= Ceranthia) *samarensis* (Fallén)

The biology of *A. samarensis* was described by Quednau (1993) as follows. Newly emerged females mate with older (5–6 day old) males, and a 1–12 day gestation period follows mating. Hatch occurs as soon as the egg is deposited on the host. The neonate maggot rapidly bores into the host, a sequence called ovolarviposition. The mean number of progeny produced by a female over its lifetime is 55, and females live an average of 41 days. Most tachinids attack late instars, but *A. samarensis* attacks 2nd and 3rd instars. Maggots develop internally, forming a respiratory funnel with a marked circular scar on the host cuticle. Development in the host takes 6–14 days, and the full grown maggot emerges from 3rd or 4th instars, stages that usually exhibit low rates of parasitism in North America (Ticehurst, 1984). Diapause is facultative; in Europe, 83-90% of field-collected parasitoids entered diapause (Mills and Nealis, 1992), suggesting that an alternate host is not required. The fly hibernates as an adult inside the puparium. The only other reported host is the tussock moth *Orgyia recens* (Hübner) (Mihalyi, 1986).

Blepharipa pratensis

Blepharipa pratensis (Dipt.: Tachinidae) is a univoltine, oligophagous tachinid whose biology was summarized by Burgess and Crossman (1929). The fly overwinters within the puparium in the soil and adults (Fig. 9) emerge slightly before gypsy moth eggs hatch. Gravid females oviposit on leaves browsed by gypsy moth larvae (Odell and Godwin, 1979; Godwin and Odell, 1984). Each female can lay up to 5,000 eggs, which hatch after being ingested by gypsy moth larvae. Fully grown maggots emerge from host larvae or pupae and then drop to the ground where they form their puparia. Parasitism is higher in female hosts and is usually highest in gypsy moth populations of intermediate density (Ticehurst et al., 1978; Williams et al., 1992). As for habitat preferences, Skinner et al. (1993) found that *B. pratensis* was more important than *P. silvestris* on xeric ridge tops in Vermont, but Bess (1961) and Fuester and Taylor (1996) found it to be scarce in xeric habitats on the Atlantic coastal plain. Studies in the 1980s and 1990s, in Delaware (Fuester et al., 1997b), New Jersey (Fuester and Taylor, 1996), and Pennsylvania (Blumenthal and Wilt, 1998) indicated that parasitism by *B. pratensis* (and *P. silvestris* as well) declined in importance, perhaps due to the inability of these flies to complete their development in hosts infected by *E. maimaiga*.

Figure 9 *Blepharipa pratensis* adult. Sanja565658, http://en.wikipedia.org/wiki/File:Blepharipa_pratensis_01.JPG.

Brachymeria intermedia

Brachymeria intermedia (Hymenop.: Chalcididae) is a solitary endoparasitoid that often causes high mortality in gypsy moth populations during outbreaks (Ticehurst et al., 1978; Elkinton et al., 1989), but it is rarely found in low density gypsy moth populations (Williams et al., 1993). Egg hatch, larval feeding, and pupation occur within the host pupa. In the field, parasitism is biased towards male gypsy moth pupae (Fuester and Taylor, 1996). Mated females overwinter in aggregations in the litter, under loose bark, or around man-made objects (Dowden, 1935; Schaefer, 1993). While this species is generally considered to be polyphagous (Howard and Fiske, 1911; Dowden, 1935), it is seldom recovered from hosts other than gypsy moth in the United States (Kerguelen and Cardé, 1996a). However, it is occasionally recovered from other Lepidoptera (e.g., Prokopy, 1968; Leonard, 1975). Dowden (1935) recorded the survival of 113 hibernated females that had emerged from gypsy moth hosts from July 22 to August 5 of the previous year and found that females died between June 18 and August 9, with only moderate rates of mortality before late July. This long adult life suggests that this chalcid does not require other hosts in order to survive, at least when gypsy moth populations are high. But its ability to occasionally attack other species (Kerguelen and Cardé, 1996b,c) provides it with hosts when gypsy moths are scarce.

Calosoma sycophanta

Calosoma sycophanta (Fig. 10) is a large, metallic green, arboreal carabid beetls. Both larvae and adults search for prey on the upper boles and branches of trees, feeding

Figure 10 *Calosoma sycophanta* adult. Gyorgy Csoka, Hungary Forest Research Institute, Bugwood.org

extensively on gypsy moth larvae and pupae when densities are high (Howard and Fiske, 1911; Dowden, 1962; Romanyk, 1965). The population dynamics of this predator are closely linked to those of the gypsy moth, and it enters a reproductive diapause when the gypsy moth population densities become low (Vasić, 1971). Thus, beetle larvae are abundant only when gypsy moth is abundant. Adult beetles overwinter in the soil and can live up to four years. Development of the immature stages requires only about a month, from egg hatch to adult emergence (Clausen, 1978). There are three larval instars, and the full grown larvae form pupation chambers in the soil, where new adults overwinter. Adults of *C. sycophanta* feed primarily on gypsy moth larvae, while the larvae consume pupae. About 100–150 eggs are laid per female beetle per year, over its multiyear lifespan (Burgess and Crossman, 1929). Levels of predation by this beetle on gypsy moth pupae can be as high as 40% (Weseloh, 1985; Fuester and Taylor, 1996). Weseloh (1985) found that adult beetles can consume 70% of the gypsy moth larvae resting on tree boles, in Connecticut in an increasing gypsy moth population. This beetle's range currently includes at least southern Maine and the remaining New England states, south and west into Pennsylvania, Delaware, Maryland, and West Virginia (Schaefer et al., 1999).

Compsilura concinnata

Compsilura concinnata (Dipt.: Tachinidae) is a highly polyphagous, multivoltine, larval parasitoid (Culver, 1919). Burgess and Crossman (1929) indicate that the fly overwinters as larvae in living caterpillars of various hosts. Hibernating larvae complete their feeding in early spring and form puparia in the litter. Adults (Fig. 11) emerge in May, when gypsy moth larvae are present. Females are viviparous, each producing 100 or more larvae that are injected into the host midgut or body cavity (Culliney et al., 1992). In summer, development from larviposition to adult emergence takes about 20 days. Because of its broad host range, this fly can survive even when gypsy moth populations are quite low, and it is frequently the dominant tachinid found associated with low density gypsy moth populations (e.g., Barbosa et al., 1975; Skinner et al., 1993).

Figure 11 *Compsilura concinnata* adult. Joyce Gross, UCB, Bugwood.org.

Cotesia melanoscela

Cotesia melanoscela (Hymenop.: Braconidae) is a solitary, oligophagous, bivoltine endoparasitoid of small gypsy moth larvae. The biology of this species was summarized by Crossman (1922) and Burgess and Crossman (1929). Adults (Fig. 12) of the overwintered generation emerge in April or May, at peak hatch of gypsy moth eggs. Females deposit 50–1,000 eggs singly in 1st and 2nd instars. After completion of feeding, the larvae emerge from the hosts and spin their cocoons on the substrate where the host dies. The life cycle of the 1st generation takes 13–21 days, depending on temperature (Gould and Elkinton, 1990). However, the emergence of first generation adults is poorly synchronized with their host requirements, most host larvae being 3rd or 4th instars, which are not easily attacked (Weseloh, 1976). Parasitoids overwinter in cocoons. The second generation of this parasitoid is heavily attacked by hyperparasitoids (Muesebeck and Dohanian, 1927; Wieber et al., 1996). Parasitism of 1st and 2nd instars by this species can reach 40% (Tigner, 1974), but parasitism of 3rd or 4th instars rarely exceeds 10-15%. Factors that slow the

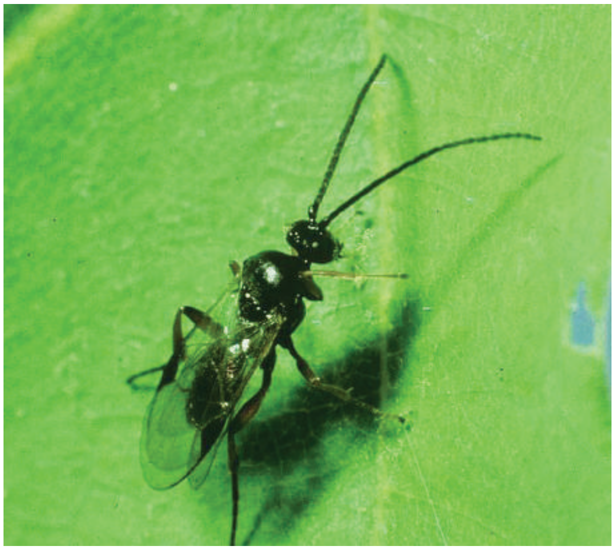

Figure 12 *Cotesia melanoscela* adult. Roger Fuester, USDA Agricultural Research Service, Newark, Delaware, USA.

development of young gypsy moth larvae, such as ingestion of sublethal doses of *Bacillus thuringiensis* (Berliner), can increase parasitism of the second host generation by *C. melanoscela* (Weseloh and Andreadis, 1982). Host larvae stung by this braconid suffer additional mortality from causes other than wasp development and emergence, so actual levels of mortality from this parasitoid may be underestimated in many field studies (Werren et al., 1992). This species does well in xeric forests, such as those on ridge tops (Skinner et al., 1993) or areas of sandy soil, such as Cape Cod (Liebhold and Elkinton, 1989). This parasitoid is easily reared (Ticehurst and Fusco, 1976; Chenot and Raffa, 1996), but sex ratios in laboratory colonies are often male-biased (Kruse and Raffa, 1997).

Entomophaga maimaiga

Entomophaga maimaiga is an obligate fungal pathogen in the Order Entomophthorales that causes acute disease. After a spore lands on a larva, the fungus penetrates through the larval cuticle to infect the host (Hajek, 1999). This pathogen produces two types of spores: relatively short-lived conidia that are actively ejected from cadavers, and long-lived resting spores that are produced within cadavers. Early instar larvae killed by *E. maimaiga* generally die within the tree canopy, while older larvae often die attached to tree trunks (Fig. 13) from where the resting spores eventually wash or fall into the soil. Resting spores germinate only in spring when moisture is available and only some resting spores germinate each year, creating a spore reservoir in the soil. Titers of soil-borne resting spores can be very high, especially after epizootics. Simulation models of the *E. maimaiga*/gypsy moth system suggest that 4–9 cycles of infection (from infection of one larva to the next) may occur in one year (Hajek et al., 1993) and the majority of infections occur in older larvae. Epizootics of this pathogen can control gypsy moth populations (e.g., Hajek, 1997; Webb et al., 1999), checking incipient outbreaks (Elkinton, 2003). During individual years or at individual sites, high levels of infection have been recorded from both low (Hajek et al., 1990) and high density gypsy moth populations (Hajeigk, 1997). Infection rates may (Webb et al., 2004) or may not (Elkinton et al., 1991; Webb et al., 1999) be correlated to larval density, but larval density is more important to modeling infection levels than resting-spore load in the forest (Weseloh, 2004). Many studies have demonstrated that moisture is critically important for infection to occur (Hajek, 1999). Field sampling showed that high abundances of airborne conidia occur during epizootics (Hajek et al., 1999), and some conidia persist

Figure 13 Gypsy moth larva killed by *Entomophaga maimaiga*. Steven Katovich, USDA Forest Service, Bugwood.org.

in local areas (e.g., Hajek et al. 1996b). Between its first detection in North America in 1989 (Hajek et al., 1990) and 1992, *E. maimaiga* spread rapidly across the part of the northern United States that is widely infested with gypsy moth, at >100 km/year, likely due to long distance dispersal by conidia during favorable periods. When *E. maimaiga* and *Ld*NPV co-infect gypsy moth larvae, under spring-time temperatures, in most larvae only *E. maimaiga* successfully reproduces, because it kills its host more quickly than does *Ld*NPV (Malakar et al., 1999).

Microsporidia

Microsporidia are obligate intracellular pathogens now known to be related to fungi. Microsporidia infect hosts when ingested. Inside the gut, spores evert a filament that punctures a cell of the gut wall and the microsporidian moves into the cell and multiplies. Many species of microsporidia develop within specific host tissues. The three *Nosema* species *N. lymantriae*, *N. serbica,* and *N. portuga*, associated with gyspy moth develop within the silk glands, gonads, Malpighian tubules, and fat body, and these microsporidian species are vertically transmitted from adult female moths to eggs. *Endoreticulatus schubergi,* in contrast, develops within the gut and *V. disparis* primarily develops in the fat body, but late in its infection process it attacks the midgut, Malpighian tubles, and gonads (L. F. Solter, pers. comm.). Most gypsy moth microsporidia cause chronic disease rather than death, although mortality can occur in early host instars that have been infected in the egg stage (Solter and Hajek, 2009). Of the five microsporidian species infecting gypsy moths, *V. disparis* is the most virulent (Solter et al., 1997) and is the only species to make packets of eight spores (octospores) within hosts.

Although there have been small inoculative introductions of microsporidia into isolated gypsy moth populations (see above), none of these have been monitored for extended periods to detect pathogen persistence. Thus, there are no data to suggest that microsporidia are naturally occurring or are cycling post-release in North American gypsy moth populations. Prevalence of microsporidia in gypsy moth populations in Europe is highly variable among years and sites, although generally infections occur at low, enzootic levels. Pilarska et al. (1998) reported finding *E. schubergi*, *N. lymantriae,* and *V. disparis* alone, in each of three relatively isolated host populations in Bulgaria. *Vairimorpha disparis* persisted at low levels at one of these study sites for over 15 years.

Ooencyrtus kuvanae

Ooencyrtus kuvanae (Hymenop.: Encyrtidae) is an egg parasitoid that is generally considered to have poor dispersal ability (Crossman, 1925; Brown, 1984), but nevertheless it has spread well (Dowden, 1961) and is now found nearly everywhere gypsy moth occurs, except for the northernmost part of the gypsy moth's range in North America (Griffiths and Sullivan, 1978). Females of this multivoltine species overwinter in the leaf litter, resuming activity around mid-April. There are one or two generations in the spring on gypsy moth eggs of the previous year, and three or four generations in summer on newly laid eggs, depending upon the climate (Crossman, 1925). Females lay an average of 100–150 eggs (Brown and Cameron, 1982). Males typically remain on the host egg mass as long as there are mating opportunities, whereas mated females disperse within 24 h, seeking new egg masses (Crossman, 1925; Brown, 1984). Foraging females (Fig. 14) are attracted by airborne volatiles from gypsy moth egg masses, as well as from the accessory glands of adult moths. Field rates of parasitism by *O. kuvanae* are usually in the 10–40% range (Brown, 1984). Attack rates of *O. kuvanae* are limited by ovipositor length, which restricts parasitism to the outermost layers of the gypsy egg mass. Thus, levels of parasitism are inversely related to egg mass size (Brown and Cameron, 1979). Parasitism

Figure 14 Foraging adults of *Ooencyrtus kuvanae* on gypsy moth egg mass. Gyorgy Csoka, Hungary Forest Research Institute, Bugwood.org.

rates are higher on small, thin egg masses that are laid on flat surfaces, such as smooth-barked trees, and lower on dome-shaped egg masses laid on twigs (Bellinger et al., 1988). Consequently, the impact of *O. kuvanae* tends to be greatest in declining gypsy moth populations when egg masses are smaller (Williams et al. 1990).

Parasetigena silvestris

Parasetigena silvestris (Dipt.: Tachinidae), a univoltine, oligophagous tachinid (Fig. 15), is probably the most consistent larval parasitoid associated with 5th and 6th instars of gypsy moth (Reardon, 1976; Ticehurst et al., 1978; Elkinton et al., 1989; Williams et al., 1992) and is often the dominant parasitoid recovered in Europe (Bogenschutz and Kammerer, 1995; Hoch et al., 2001; Zolubas et al., 2001) and the Asian Far East (Pemberton et al., 1993). Its biology is summarized below from Burgess and Crossman (1929). The fly overwinters in the puparia and adults emerge in May. After mating and a 5–7 day gestation period, the females, which live up to 50 days, lay large white eggs on the integument of large larvae. Hatched maggots bore into the host haemocoele, construct a respiratory funnel, and pass through three instars during larval development (requiring 16-35 days). When fully grown, maggots exit from the host, drop to the soil, and form puparia. Superparasitism occurs frequently, but the distribution of eggs is aggregated, not random (Gould et al., 1992). In the United States, peak rates of parasitization (>50%) usually occur in declining host populations or those that have recently stabilized at low levels (Reardon, 1976; Ticehurst et al., 1978; Elkinton et al., 1989). Even higher rates of parasitization (>95%) have been reported in declining host populations in Germany (Maier, 1990, 1995). Positive density-dependent responses by this species have been reported in artificially elevated host populations in Massachusetts (Liebhold et al., 1989; Gould et al., 1990; Ferguson et al., 1994) and natural populations in New Jersey (Williams et al., 1992), but negative responses have been reported in Pennsylvania (Ticehurst et al., 1978).

Figure 15 *Parasetigena silvestris* adult. Patrick Derennes, patrick.derennes@9online.fr.

Pimpla disparis

Pimpla disparis (Hymenop.: Ichneumonidae) overwinters as mature larvae in pupae of the fall webworm, *Hyphantria cunea* (Drury), in the Far East where this species is introduced, and it probably utilizes the same host in the United States (where fall webworm is native). Weseloh and Anderson (1982), using field cage studies, demonstrated that immature stages of *P. disparis* can successfully overwinter within hosts in Connecticut. Laboratory studies by Fuester et al. (1989) indicated that *P. disparis* can parasitize gypsy moth prepupae and pupae (up to 9-days-old), but that female prepupae are suboptimal hosts. Sex ratios are female biased (72-87% female). Developmental time varies according to host stage, age, and gender, and females develop more slowly than males (Fuester and Taylor, 1993). Field studies (Fuester et al. 1997a) indicate that pupae of *L. dispar* stung by *P. disparis* (Fig. 16) sustain higher mortality from causes other than wasp development than do unstung hosts, so mortality that should be credited to this biotic agent tends

Figure 16 *Pimpla disparis* female probing gypsy moth pupae. Paul Schaefer, USDA Agricultural Research Service, Newark, Delaware, USA.

to be overlooked in field studies. Fuester et al. (1997b) found that parasitism of gypsy moth by *P. disparis* on the Delmarva Peninsula was generally low (<5%).

Virus (LdMNPV)

The nucleopolyhedrovirus (*Ld*MNPV) causes lethal infections of gypsy moth larvae. From the early 1900s until the 1990s, this pathogen was generally considered the primary factor causing dense gypsy moth populations to collapse (Podgwaite, 1981). Larvae are usually infected when they eat virus-contaminated foliage but may also become infected mechanically through ovipositor insertion by parasitoids (Raimo et al., 1977). *Ld*MNPV replicates within the nuclei of cells throughout the body of gypsy moth larvae, eventually forming occlusion bodies, which are many-sided structures, from 1–10 μm in diameter, that consist of a crystalline protein matrix containing groups of virions packaged within envelopes. The protein matrix of inclusion bodies protects virions from ultraviolet light and other harmful environmental factors and enhances virion persistence in the environment. Infected larvae often climb upward before death (Murray and Elkinton, 1992; Hoover et al., 2011). After death, dark shiny cadavers, often attached to substrates only by a few anterior prolegs, hang limply in an inverted V (Fig. 17) and the thin, fragile cuticle ruptures, releasing occlusion bodies, which are washed by rain downward within the forest canopy. Gypsy moth larvae that feed on virus-contaminated foliage cause new infections (D'Amico and Elkinton, 1995). Mechanisms for persistence of *Ld*MNPV in nature have been studied extensively. *Ld*MNPV overwinters as occlusion bodies in the soil and on tree trunks (Podgwaite et al., 1979). Gypsy moth egg masses may become contaminated with virus if they are laid on contaminated substrates (Murray and Elkinton, 1990). Vertical transmission of *Ld*MNPV from moth to eggs has also been demonstrated in the laboratory (Myers et al., 2000). Gypsy moth larvae in dense populations are more susceptible to virus infection (Reilly and Hajek, 2008), but healthy larvae can detect and avoid cadavers of virus-killed larvae on leaves (Parker et al., 2010). A bimodal temporal pattern of mortality due to *Ld*MNPV has been recorded during epizootics, with peak rates occurring during the second wave of mortality (Woods and Elkinton, 1987). Infection by this pathogen is density dependent (Solter and Hajek, 2009), so highest levels of mortality occur in dense gypsy moth populations.

Figure 17 Cadaver of gypsy moth larva killed by nucleopolyhedrovirus. Steven Katovich, USDA Forest Service, Bugwood.org.

RECOMMENDATIONS FOR FURTHER WORK

It is difficult to make recommendations that are likely to result in significantly improved biological control of the gypsy moth in North America. Kenis and Vaamonde (1998) proposed several strategies for biological control of gypsy moth using three approaches: (1) re-introduction of natural enemies that failed to become established (e.g., doing so along the leading edge of the gypsy moth expansion), (2) introduction of new species (e.g., the tachinid larval parasitoid *Blepharipa schineri* Mesnil [Fuester et al., 1997c] and dermestid egg predators [Villemant and Andreï-Ruiz, 1999]), or (3) introduction of new biotypes of natural enemies already present in North America (e.g., *P. silvestris* from the Rhine Valley of France and Germany, where parasitism is consistently high). We believe these ideas are worth considering.

Perhaps the biggest disappointment in the parasitoid colonization effort was the failure of either *G. porthetriae* or *G. liparidis* to become established, despite being released in many states in large numbers—a failure that might presumably be due to stringent alternate host requirements (Hoy, 1976; Fuester et al., 1988). Both species are considered important regulating agents of the gypsy moth in their native areas of distribution (Muesebeck, 1928;

Burgess and Crossman, 1929; Vasić, 1971; Higashiura and Kamijo, 1978; Schopf et al., 1997, Schopf and Hoch, 1998). Yet host range tests in North America showed that both species could develop on at least one resident species of Lepidoptera (Raffa, 1977; Hedlund and Schroder, 1981).

The fungal pathogen *E. maimaiga* recently has become established in Serbia and Bulgaria, where it has caused the collapse of gypsy moth outbreaks at several locations (Tabaković-Tošić et al., 2012). Monitoring the populations of *L. dispar* at such locations to see which parasitoid species rebound most quickly following such fungal epizootics might suggest possible introductions likely to be useful in the United States.

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VI BROWNTAIL MOTH

(*Euproctis chrysorrhoea* [L.]) (Lepidoptera: Erebidae; Lymantriinae, formerly Lymantriidae)

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DESCRIPTION OF PEST

Taxonomy

The browntail moth, *Euproctis chrysorrhoea* (L.) (Lepidoptera: Erebidae; Lymantriinae), was originally described as *Bombyx chrysorrhoea* by Linnaeus (1758). Synonyms include: *Nygmia phaeorrhoea* Donovan (Swinhoe, 1922) in North America and *Orgyia chrysorrhoea* in Russia. All lymantriines have recently been assigned to the subfamily Lymantriinae within the Eribidae, based on new findings in molecular systematics (Zahiri et al., 2011, 2012). Browntail moth is one of several lymantriines introduced from Europe to North America, along with gypsy moth, (*Lymantria dispar* [L.]) and satin moth (*Leucoma salicis* L.). See Pogue and Schaefer (2007) for a review of *Lymantria*. Other species in the genus *Euproctis* occur mainly in the Russian Far East. The only other introduced *Euproctis* species recorded in North America is *Euproctis similis* Fuessley, which has been recovered several times in North America but is not known to have established.

Distribution

The browntail moth is widely distributed throughout Europe and Russia, where it undergoes occasional outbreaks in many localities. Sterling and Speight (1989) studied populations in England, where persistent populations were largely confined to coastal areas. Frago et al. (2011) studied populations in Spain.

Browntail moth was accidentally introduced to North America and the first outbreak was noted in 1897 in Somerville, Massachusetts (Fernald and Kirkland, 1903). Subsequently, browntail moth spread rapidly, reaching high population densities across a large area in northeastern North America (Fig. 1) (Burgess and Crossman, 1923). Early researchers considered it a threat equal to or greater than that posed by the invasive gypsy moth; an ambitious, but apparently unsuccessful, control effort was undertaken based primarily on mechanical removal of overwintering larval colonies (Fernald and Kirkland, 1903). However, after 1915 browntail moth began an unexpected decline (Burgess and Crossman, 1923) (Fig. 1), and it eventually disappeared from most of its former invasive range in North America (Schaefer, 1974; Elkinton et al., 2006, 2008). Browntail moth is currently restricted to coastal enclaves at the tip of Cape Cod, Massachusetts, and on the islands and peninsulas of Casco Bay in Maine, where high densities have persisted for decades (Fig. 1) (Schaefer, 1974; Elkinton et al., 2006, 2008).

Damage

Type Browntail moth once caused widespread defoliation of many tree species. The host range of browntail moth is extremely broad, comprised of nearly all genera of deciduous trees in North America, including poplar (*Populus*), birch (*Betula*), cherry (*Prunus*), elm (*Ulmus*), oak (*Quercus*), and maple (*Acer*) (Fernald and Kirkland, 1903; Tietz, 1972; Schaefer, 1974; Robinson et al., 2002). Browntail moth caused severe defoliation of various fruit trees, including apple (*Malus*) and pear (*Pyrus*). On Cape Cod, the favorite host is beach plum (*Prunus maritima* Marshal) and it is also common on other shrubs such as *Rosa rugosa* Thunber and *Myrica pennsylvanica* Mirbel. In Casco Bay, browntail moth frequently defoliates apple, black cherry (*Prunus serotina* Ehrhart), and red oak (*Quercus rubra* L.) (Schaefer, 1974).

In addition to causing defoliation, browntail moth larvae pose a public health hazard because their urticating hairs cause a severe skin rash when larvae are handled

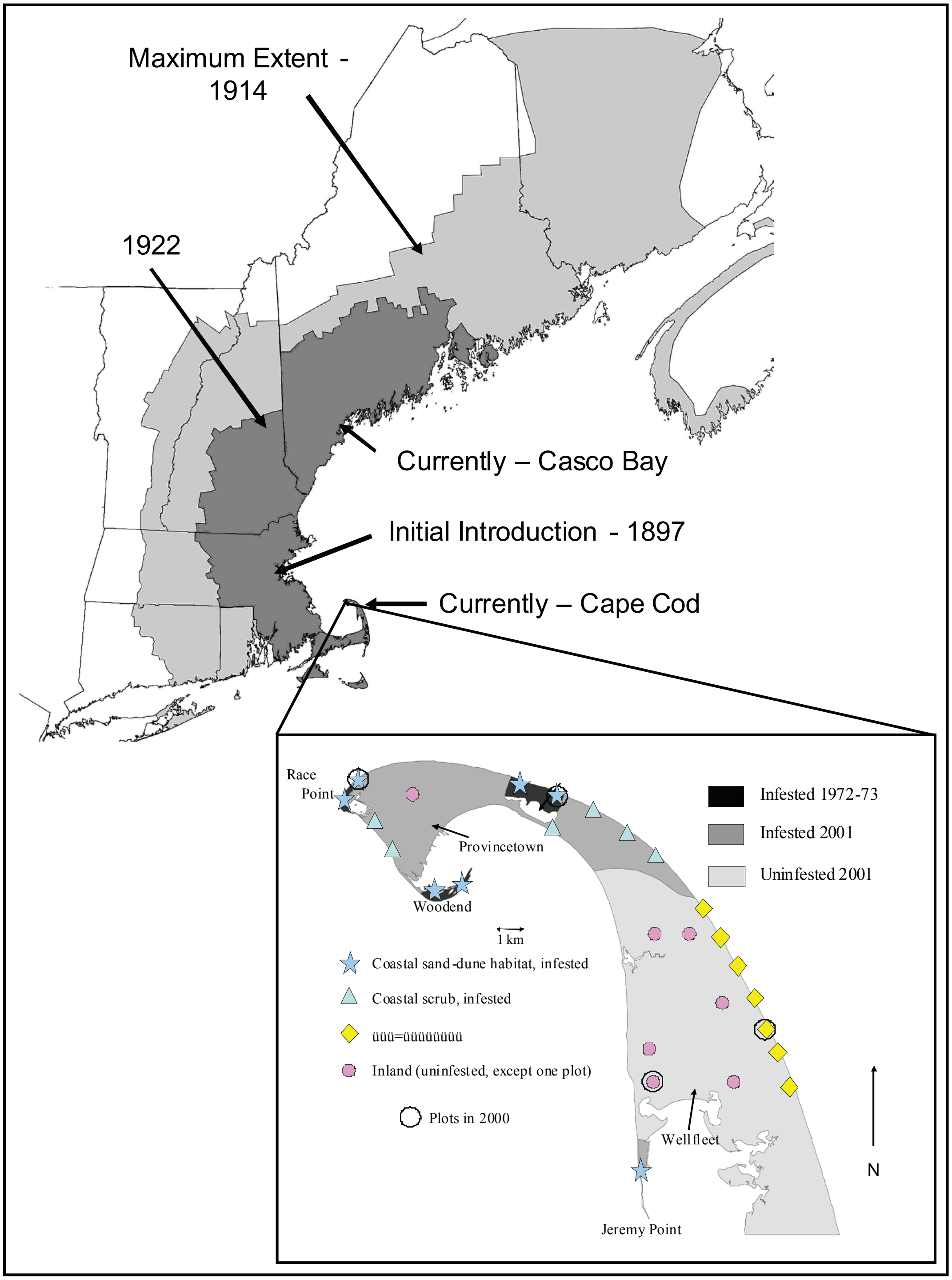

Figure 1 Distribution of browntail moth in New England, showing the maximum reached in 1915 (light shading), its status in 1922, and its subsequent retreat to coastal enclaves. Dark shading indicates browntail moth distribution in 1922 (redrawn from Burgess and Crossman [1923]). Inset: Outer Cape Cod showing plot locations of experimentally created browntail moth populations in the region generally infested (intermediate gray) or uninfested (light gray) with browntail moth in 2000 and 2001. Areas marked with the darkest shading show browntail moth distribution recorded in 1972–1973 by Schaefer (1974). These areas are sand-dune habitats, which still contain the highest densities of browntail moth. Symbols indicate locations of experimental browntail moth populations in different habitat types as described in Elkinton et al. (2006). Reprinted with permission from the Ecological Society of America from Elkinton et al. (2006).

(Blair, 1979). These hairs are most abundant on late instars and the cast larval integuments associated with the pupae. Inhalation of these hairs can cause death.

Extent Browntail moth currently has only a tiny North American distribution and apart from some beach-goers, few people have contact with this species. However, at the height of its maximal distribution in 1914 (Fig. 1) over half of New England and part of New Brunswick were infested.

Biology of Pest

First instar larvae of browntail moth emerge in August and feed communally, skeletonizing leaves (Fig. 2, A). They spin silk and eventually envelop whole leaf clusters, where they feed. Such structures become the winter webs (Fig. 2, B) where second and third instar larvae overwinter. Overwintered larvae leave webs in April of the following year and resume feeding as solitary larvae (Fig. 2, C). Larvae mature in late June, spin cocoons that web together several leaves, and pupate inside the cocoons. The pupal stage lasts approximately two weeks. Adult females emerge in midsummer (Fig. 2, D), mate, and lay egg masses containing 20–300 eggs on the foliage of host plants. Larvae from several egg masses may merge together to overwinter in supercolonies of a thousand or more larvae (Schaefer, 1974).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

There are no native *Euproctis* species in North America. The Lymantriinae include over 2900 species in 360 genera; however, these are primarily from the Old World tropics (Kitching and Rawlings, 1998). The most closely related moths native to North America are tussock moths in the genera *Dasychira* (16 species) and *Orgyia* (10 species).

Native Natural Enemies Affecting the Pest

At least twelve native North American parasitoids have been found attacking life stages of browntail moth. Most of these are polyphagous species and some are facultative

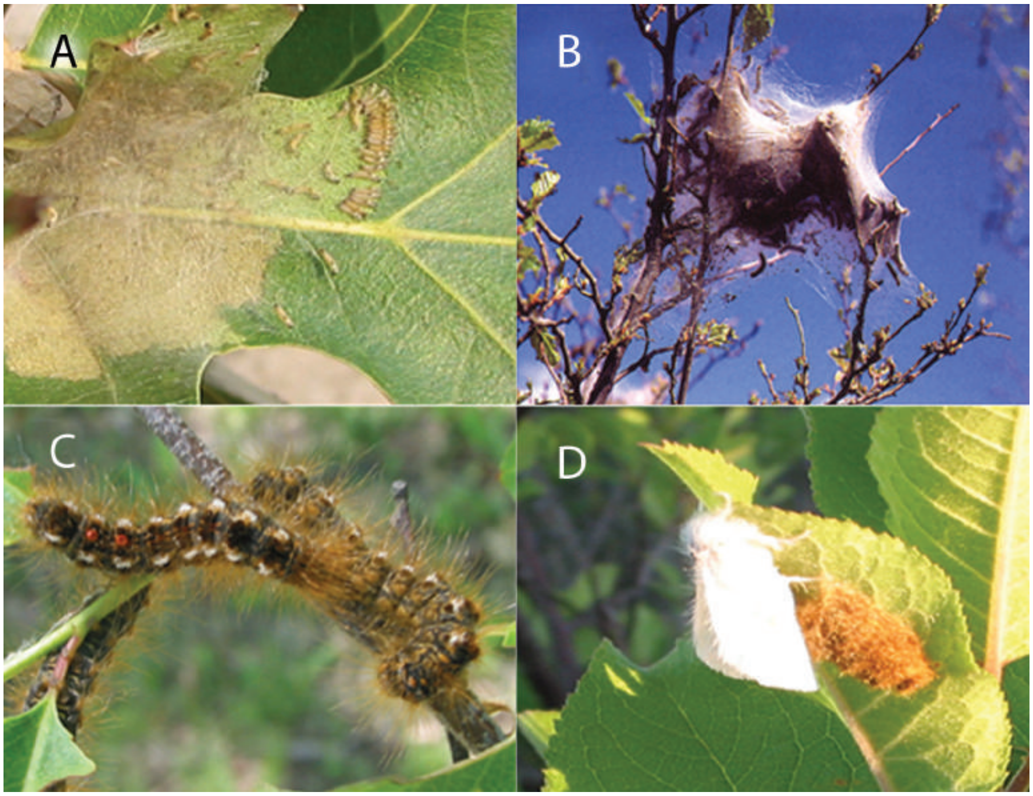

Figure 2 Life stages of browntail moth: A) early instars feeding communally on leaf surface (in August); B) winter web (in October–April); c) late instars (in May–June) and D) adult female with egg mass. (in July).

hyperparasitoids. These include: (1) *Coccygomimus pedalis* Cresson (Hymenoptera: Ichneumonidae), which has been recovered from 28 species of Lepidoptera and may be locally abundant (Carlson, 1979); (2) *Theronia atalantae fulvescens* Cresson: (Hymenoptera: Ichnuemonidae), an occasional primary or hyperparasitoid associated with browntail moth (Carlson, 1979); (3) *Dibrachys cavus* (Walker). (Hymenoptera: Pteromalidae), a highly polyphagous species able to function as a primary, secondary or tertiary parasitoid that attacks many orders of insects and even spiders (Carlson, 1979); (4) *Aprostocetus esurus* (Riley) (Hymenopter.: Eulophidae), recorded from 14 species of Lepidoptera (Carlson, 1979); (5) *Exorista mella* Walker (Diptera: Tachinidae), a generalist parasitoid that attacks many species of Lepidoptera (Arnaud, 1978); (6) *Chetogena claripennis* Macquart (Diptera: Tachinidae), an extremely generalist parasitoid reported from browntail moth (Fernald and Kirkland, 1897; Howard and Fiske, 1911) known from 90 hosts native to North America (Schaffner and Griswold, 1934; Arnaud, 1978); (7) *Leschenaultia reinhardi* Toma and Guimaraes (Diptera: Tachinidae), recorded from browntail moth by Howard and Fiske (1911), and recorded from six native species (Schaffner and Griswold, 1934; Arnaud, 1978); (8) *Madremyia saundersii* Williston (Diptera: Tachinidae), recorded from browntail moth by Aldrich and Webber (1924), and recorded from 30 native species in North America (Schaffner and Griswold, 1934; Arnaud, 1978); (9) *Patelloa leucaniae* Coquillet (Diptera: Tachinidae), recorded from browntail moth by Aldrich and Webber (1924) and Tothill (1913), and recorded from seven other native hosts (Arnaud, 1978); (10) *Patelloa pachypyga* Aldrich and Webber (Diptera: Tachinidae), recorded from browntail moth by Aldrich and Webber (1924) and Tothill (1913), and recorded from two native hosts (Arnaud, 1978); (11) *Lixophaga discalis* Coquillett (Diptera: Tachinidae), recorded from browntail moth by Howard and Fiske (1911) but no native hosts are known (Arnaud, 1978); and (12) *Carcelia amplexa* Coquillett (Diptera: Tachinidae), recovered from browntail moth (Howard and Fiske, 1911) and gypsy moth (Sellers, 1943), and recovered from ten native species in North America (Schaffner and Griswold, 1934; Arnaud, 1978).

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Browntail moth was accidentally introduced to North America from Europe, which is part of its native range. Fernald and Kirkland (1903) concluded that the introduction into Somerville, Massachusetts, in the early 1980s was via a shipment of roses from Holland.

Areas Surveyed for Natural Enemies

In one of the first and largest insect biological control efforts ever attempted in the United States, efforts to find natural enemies of browntail moth were combined with efforts to locate agents for use against gypsy moths, as described by Howard and Fiske (1911). From 1905 to 1910, several hundred thousand browntail moth winter webs were shipped from Russia and several countries within western Europe to government parasitoid-rearing facilities established in Saugus and Melrose Highlands, Massachusetts (Howard and Fiske, 1911). The search for parasitoids was halted during World War I but resumed in 1922 (Burgess and Crossman, 1929).

Host Range Test Results

In the early 20th century, there was little concern about possible effects of biological control agents on nontarget hosts. It was well known that many of the introduced parasitoids directed at browntail moth or gypsy moth were polyphagous (Howard and Fiske, 1911). In fact, this trait was viewed as advantageous because it implied that the parasitoid could maintain high densities when the target host was at low density. Howard and Fiske (1911) (see page 91) provide an extensive list of alternate hosts utilized by the many species of parasitoids released to control browntail moth.

Releases Made

Six species of parasitoids were released specifically to control browntail moth: (1) *Apanteles lacteicolor* Viereck (Hymen: Braconidae), introduced and established in New England by 1908 (Burgess and Crossman, 1929); (2) *Meteorus versicolor* (Wesmael) (Hymen: Braconidae), introduced for control of browntail larvae; overwinters in host larvae in winter webs.

(Burgess and Crossman, 1929); (3) *Townsendiellomyia nidicola* Townsend (Diptera: Tachinidae), specific to browntail moth, its only known host; (4) *Compsilura concinnata* Miegen (Diptera: Tachinidae) (Fig. 3), introduced repeatedly from 1906–1986 for control of 13 pest species, including browntail moth; an extreme generalist with several hundred known lepidopteran hosts (Arnaud, 1978; Boettner et al., 2000; Strazanac et al., 2001); (5) *Carcelia laxifrons* Villeneuve (Diptera: Tachinidae), a browntail moth specialist); (6) *Monodontomerus aereus* Walker (Hymenop.: Torymidae) introduced against both browntail moth and gypsy moth, and firmly established by 1909 (Howard and Fiske, 1911); adults overwinter in browntail webs and attack pupae of browntail moth, where they function as a primary, secondary, or tertiary parasitoid depending on previous parasitism conditions (Howard and Fiske, 1911).

Figure 3 *Compsilura concinnata* (photograph by Michael Thomas).

In addition to the above species, three other parasitoids were targeted at gypsy moth but were later recovered from browntail moth: (1) *Exorista larvarum* L. (Diptera: Tachinidae), recovered from browntail moth on Cape Cod, Massachusetts (2000–2001) (Elkinton unpublished); a generalist known from 54 Lepidoptera in nine families in Europe (Herting, 1960); (2) *Pimpla disparis* Vierick (Hymenop.: Ichnuemonidae), released from the 1970s through 1990s; recovered from browntail moth pupae on Cape Cod, Massachusetts (Elkinton unpublished); an extreme generalist with many hosts in Europe; and (3) *Blepharipa pratensis* Miegen (Diptera.: Tachinidae) recovered from browntail moth (Burgess, 1924); known from ten other Lepidoptera in North America (Arnaud, 1978).

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

The release of many thousands of individuals of six browntail parasitoids resulted in the establishment and rapid spread of all six (see above). Howard and Fiske (1911) reported the firm establishment of *M. aereus* by 1909. Burgess and Crossman (1929, see Fig. 3 of reference) provide a map showing that by 1927 four browntail moth parasitoids (*C. concinnata*, *T. nidicola, A. lacteicolor,* and *M. versicolor*) were widely established from central Maine to Rhode Island, with significant levels of parasitism by *C. concinnata*, *T. nidicola*, and *A. lacteicolor* in many locations. Burgess and Crossman (1929) also report evidence of the establishment in Maine, New Hampshire and Massachusetts of the sixth browntail moth parasitoid, *C. laxifrons*. These observations were coincident with the general retreat of browntail moth from interior portions of New England (Burgess and Crossman, 1923).

Interest in this invasive species waned as the threat posed by browntail moth receded. Schaefer (1974) provides virtually the only study of browntail moth in North America in the 50 years that followed the report of Burgess and Crossman (1929). Schaefer (1974) found relatively low parasitism of browntail moth (8–23%) in the sand-dune habitats of Cape Cod (Massachusetts) and in Casco Bay (Maine). As a result, he concluded that natural enemies were not responsible for the decline of browntail moth in North America. In contrast, the data collected in the 1920s by Burgess and Crossman (1929) showed that one wasp, *A. lacteicolor,* and three tachinids (*T. nidicola*, *C. laxifrons,* and especially *C. concinnata*) caused substantial mortality of browntail moth, although with high between-site variability. Elkinton et al. (2006) re-examined the parasitism data presented by Burgess and Crossman (1929) and discovered a previously unrecognized pattern. Parasitism by all three tachinid species in inland habitats was twice as high as in the coastal sites, and parasitism by *C. concinnata* alone was five times higher, inland. Elkinton et al. (2006) hypothesized that *C. concinnata* was the primary cause of the decline of browntail moth in North America. They tested this hypothesis by creating experimental populations of browntail moth by collecting and deploying winter webs at various sites, many of which were just outside the generally infested areas at the northern tip of Cape Cod. They showed that *C. concinnata* caused very high mortality among browntail moth larvae in inland or coastal locations with rich vegetation, but was essentially absent from the sand dune habitat where browntail moth populations persist at high density, today. They speculated that the sparser vegetation in these habitats lacked the alternate hosts that were required by the third and fourth generations of *C. concinnata* in late summer. In further work, Elkinton et al. (2008) tested the alternate hypothesis advanced by Schaefer (1974) that browntail moth's retreat from the interior toward the coast was due to higher overwinter mortality due to colder temperatures of larvae in webs at inland locations. Whereas they found confirming evidence that winter mortality was indeed higher in interior locations, they found no evidence for historical changes in winter temperature that could account for the rapid expansion of the range of browntail moth between 1897 and 1915 and its subsequent retreat after that. These results provide strong support for the hypothesis that *C. concinnata* was the primary factor responsible for the extirpation of browntail moth from most of its former range in North America.

Nontarget Effects

Boettner et al. (2000) demonstrated that *C. concinnata* (Fig. 3) caused high levels of mortality to several species of giant silk moths (Saturniidae) in central Massachusetts and proposed that *C. concinnata* may be responsible for the observed decline of some saturniid species in North America during the 20th century. Similar high rates of parasitism were also reported in Virginia in luna moth (*Actias luna* [L.]) caterpillars (Kellog et al., 2003). Conversely, much lower parasitism rates were observed for *C. concinnata* in New York (Parry, 2008) and by the barrens buck moth (*Hemileuca maia* Drury) on Cape Cod, Massachusetts (Selfridge et al., 2007). *Compsilura concinnata* has been recovered from over 200 species of moth and sawfly larvae in North America (Arnaud, 1978; Boettner et al., 2000; Strazanac et al., 2001); however, its importance in the population dynamics of these hosts has rarely been studied.

Pimpla disparis, discovered attacking browntail moth pupae in North America (Parry, 2008), is known to have a broad host range in Europe that includes pierid and papilionid butterfly and saturniid moth pupae. These facts suggest this species may be affecting various rare moths and butterflies, which merits further investigation.

Recovery of Affected Tree Species or Ecosystems

Since this pest has been extirpated over most of its former North American range, it can logically be assumed that any effects the species had on eastern deciduous trees have disappeared.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Apanteles lacteicolor

Apanteles lacteicolor (Hymenoptera: Braconidae) is a solitary European parasitoid of browntail moth that attacks young larvae soon after eggs hatch. Larvae of this parasitoid overwinter inside browntail moth larvae in their webs but emerge from the larvae soon after they leave their webs in the spring. Parasitoid larvae then spin white cocoons and pupate. There is a second generation and possibly a third generation on other hosts (Burgess and Crossman, 1929).

Meteorus versicolor

The biology of *M. versicolor* (Hymenoptera: Braconidae) is similar to that of *A. lacteicolor*. This species attacks early instar browntail moth in late summer and overwinters inside larvae in the winter web. Its cocoons are brown. The first generation attacks other lepidopteran hosts in June. This species is uncommon (Burgess and Crossman, 1929).

Monodontomerus aereus

Monodontomerus aereus: (Hymenoptera: Torymidae) overwinters as adults in browntail moth webs (Howard and Fiske, 1911). However, it is primarily a secondary parasitoid of *Apanteles* cocoons or, more often, of tachinid puparia associated with gypsy moth or browntail moth (Howard and Fiske, 1911). The female oviposits in the cocoons of braconids and in tachinid puparia. Development from egg to adult takes about three weeks (Burgess and Crossman, 1929). Generally, there are two generations per year but first-generation females have been taken through the winter (Burgess and Crossman, 1929).

Townsendiellomyia nidicola

Townsendiellomyia nidicola (Diptera: Tachinidae) adults attack early instar larvae but overwinter inside caterpillars in winter webs. Adult flies delay emerging from browntail pupae to coincide with browntail egg hatch. There is one generation per year.

Compsilura concinnata

Compsilura concinnata (Diptera: Tachinidae) has 3–4 generations per year, the first of which often attacks browntail moth or gypsy moth. Eggs hatch in fly oviducts and maggots are inserted into host larvae. The maggot feeds and develops rapidly, often killing its host within 5–10 days, depending on host size, temperature, and the number of competing fly maggots. Generally, late-instar caterpillar hosts are preferred, but Boettner et al. (2000) recovered *C. concinnata* even from first-instar, silk-moth caterpillars. Gypsy moth and browntail moth produce 1–5 flies per host; however, in bigger hosts, such as giant silk-moth larvae, up to 15 flies may occur. Flies emerge as maggots from the host and pupate in soil.

Carcelia laxifrons

Carcelia laxifrons (Diptera: Tachinidae) has one generation per year and is species-specific on browntail moth. Females lay a single egg on third instars of browntail moth as they emerge from their winter webs in spring; *C. laxifrons* can walk on the silk of overwintering webs to attack larvae. Fly maggots emerge from late-instar larvae. Pupation occurs in the soil, where overwintering occurs.

Entomophaga aulicae

The *Entomophaga aulicae* (species complex) (Zygomycetes: Entomophthorales) is presumed to be a native North American pathogen that was first recovered from *Pyrrharctia isabella* Smith (Lepidoptera: Arctiidae), and inoculum from that source was used successfully to infect browntail moth populations (Hitchings, 1906). This fungus was later noted as an important source of mortality to browntail moth larvae in Maine (Speare and Colley, 1912) and may have been the cause of population declines in browntail moth seen in Casco Bay in the early 2000s (Elkinton et al., 2003). In contrast, this agent was absent or rare in samples from Cape Cod, Massachusetts (Schaefer, 1974; Elkinton et al., 2006). Its biology is similar to that of other *Entomophaga* species. It spreads by means of conidiophores that are released into the air from host larval cadavers. These land on or near uninfected host larvae, germinate under moist conditions, and penetrate the larval integument. Several cycles of conidiophore production and host death occur in each host generation. Near the end of the host larval stage, *E. aulicae* produces resting spores or zygomycetes that overwinter inside larval cadavers at the base of the tree and germinate the following spring.

RECOMMENDATIONS FOR FURTHER WORK

Future work should focus on explaining the population fluctuations of browntail moth in both Casco Bay, Maine, and on Cape Cod, Massachusetts. To prevent the accidental movement of browntail moth life stages to other parts of the United States, particularly where *C. concinnata* might be absent, the very small population that exists on Cape Cod should be considered for eradication in the years when very few winter webs can be found. Eradication would be much more difficult in Casco Bay, where trees are much taller and moth populations are larger and occur on scattered islands. However, the location in Maine might provide good experimental areas for future work on the effects of the browntail moth virus.

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VII Larch Casebearer

(*Coleophora laricella* [Hübner]) (Lepidoptera: Coleophoridae)

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DESCRIPTION OF PEST

Taxonomy

The larch casebearer, *Coleophora laricella* [Hübner]), was originally described as *Tinea laricella* Hübner, 1817. Synonyms include *Coleophora nigricornis* Heinemann & Wocke. There are about 1409 named species in the genus *Coleophora* (from Encyclopedia of Life: http://www.eol.org/pages/33964). See also Baldizzone et al. (2008) for an overview of species in the genus.

Distribution

Larch casebearer (Fig. 1) is an invasive species that was first recorded in 1886 in North America in Massachusetts and is believed to have been introduced on nursery stock (Otvos and Quednau, 1984). *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 of Washington, Oregon, Idaho, and western Montana (Drooz, 1985). This distribution follows that of its principal two North American hosts, eastern (*Larix laricina* [Du Roi] K. Koch) and western larch (*Larix occidentalis* Nuttl.). An on-line map of larch casebearer's distribution in North America is available at http://www.fs.fed.us/nrs/tools/afpe/maps/LC.pdf. See also Otvos and Quednau (1984).

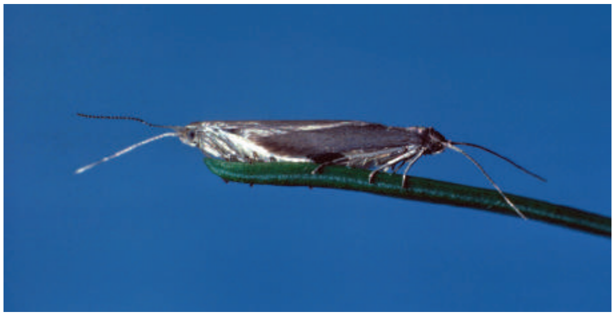

Figure 1 Mating adults of larch casebearer (*Coleophora laricella* [Hübner]). Roger Ryan, USDA PNW Station, Bugwood.org.

Damage

Type Larvae of larch casebearer begin as needle miners and then become external needle feeders, with case-bearing larvae moving between feeding sites. Feeding reduces tree growth, but does not kill trees. Reduction in growth of up to 80% was recorded in stands of western larch in northern Idaho after repeated defoliation by larch casebearer (Long, 1988).

Extent Damage has been recorded in some parts of Europe (the native range) (Kadocsa, 1917; Malenotti, 1924; Schönwiese, 1937; Eidmann, 1965) and in China (Li et al., 1989). Outbreaks first occurred in eastern North America, in the early 1900s (e.g., Felt and Bromley, 1932). In the 1940s and 1950s in eastern Canada, outbreaks were widespread and prolonged (Webb and Quednau, 1971). In the 1950s, outbreaks still occurred in central Ontario in areas that had not yet been colonized by introduced European parasitoids. After the introduced parasitoids were present, outbreaks in most parts of eastern North America became local and brief. After larch casebearer's 1957 invasion of the western United States, it was considered one of the top two pests of larch in Oregon and Idaho (Schmidt et al., 1976) until it was also successfully suppressed there by introduced parasitoids (Ryan et al., 1987; Ryan 1990, 1997).

Biology of Pest

Larch casebearer has one generation per year. Adults emerge in late spring and deposit eggs singly on needles in early summer. Each neonate larva bores into a needle, where it feeds as a needle miner (Fig. 2). Eventually a portion of the mined-out needle is cut off and functions as the larva's case. Larvae overwinter in cases fixed to branches (Fig. 3). In the spring, larvae resume feeding on new foliage. They move about (Figs. 4, 5) and consume many needles, enlarging their cases as they grow. Hollowed-out needles turn brown but remain attached to branches (Figs. 6, 7), making feeding damage readily visible. However, two needle diseases also cause brown foliage and their symptoms could be confused from a distance, as in aerial surveys, with larch casebearer damage. Upon reaching maturity, larvae pupate in their cases from which moths later emerge (Drooz, 1985).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

No analysis was made of North American *Coleophora* species to see if any native species might be within the host ranges of the European parasitoids introduced for control of this pest.

Native Natural Enemies Affecting the Pest

In North America, before importation of exotic species, the native parasitoids or predators attacking larch casebearer. were recorded in several locations. In New Brunswick, birds were one of the more important groups of natural enemies affecting larch casebearer, while 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) recorded 20 species of parasitoids attacking larch casebearer. Miller and Finlayson (1974) recovered 32 species of parasitoids from larch casebearer in British Columbia. However, there were not able to suppress the density of larch casebearer.

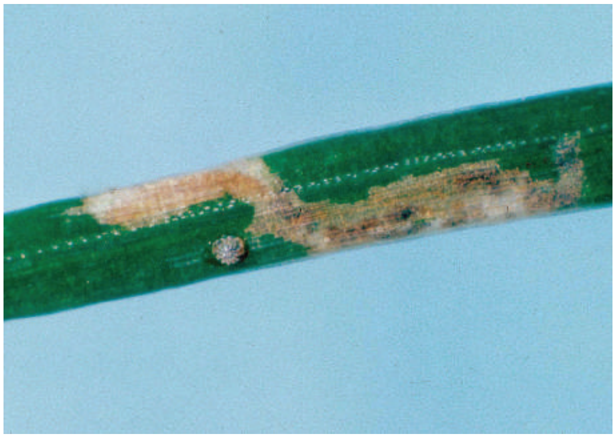

Figure 2 Young larva of larch casebearer in needle-mining phase. Roger Ryan, USDA PNW Station, Bugwood.org.

Figure 3 Cluster of overwintering larch casebearers in cases at tip of twig. Roger Ryan, USDA PNW Station, Bugwood.org.

Figure 4 Older larva of larch casebearer in case. Roger Ryan, USDA PNW Station, Bugwood.org.

Figure 5 View of larch casebearer larva with case partially removed. Victor Ryabincov, Russian Federation, Bugwood.org.

Figure 6 Close view of damage to needles caused by larch casebearer larva feeding. Ferenc Lakatos, University of West-Hungary, Bugwood.org.

Figure 7 Damage at branch level due to feeding of larch casebearer; all yellow foliage has been partly consumed. Roger Ryan, USFS PNW Station, Bugwood.org.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Europe is the area of origin of larch casebearer (Clausen, 1978).

Areas Surveyed for Natural Enemies

Areas in Europe where natural enemies of larch casebearer were studied included Austria, Poland, Sweden, the UK (see the following section), Italy, the former Yugoslavia, Switzerland, and Japan. Work in Japan was done in relation to the outbreak in the western United States following the pest's 1957 invasion there.

Natural Enemies Found

In Europe, the resident natural enemy complexes were investigated by local entomologists concerned with damage from the pest and by North American biological control scientists seeking natural enemies for importation. Thorpe (1933) studied parasitoids of larch casebearer in the United Kingdom. Both parasitoid species that ultimately controlled the pest in North America, *Agathis pumila* (Ratzburg) (Fig. 8) and *Chrysocharis laricinellae* Ratzburg (Fig. 9), were present in the United Kingdom, but were rare. *Agathis pumila*, however, was noted as being abundant in southern France. The most common parasitoid found in Thorpe's (1933) study was *Diadegma laricinellum* (Strobl.) (listed in the publication as *Angitia nana* Gravenhorst). Collections made by Dowden (1934) in Austria included both *C. laricinellae* and *A. 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 *C. 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*) were both present; note, Jagsch (1973) reported *C. laricinellae* under the synonym *C. novellus* (Wlk.). Similarly in Poland, parasitism rates were very low (1–3%) (Skrzypczynska, 1978).

Figure 8 The braconid *Agathis pumila* (Ratzburg), one of two key species giving successful biological control of larch casebearer in North America. Roger Ryan, USDA PNW Station, Bugwood.org.

Figure 9 The eulophid *Chrysocharis laricinellae* Ratzburg, one of two key species giving successful biological control of larch casebearer in North America. Roger Ryan, USDA PNW Station, Bugwood.org.

Host Range Test Results

Host ranges of the parasitoids introduced as biological control agents of larch casebearer were not estimated at the time of the project. Rather, it was felt sufficient that the parasitoids were confirmed as primary parasitoids of the target pest and derived from the pest in its native range.

With regard to the two parasitoids that eventually established and controlled the pest (*A. pumila* and *C. laricinellae*), no other host records were found in the abstracting service of the Commonwealth Agricultural Bureau (CAB) or the catalogue of Krombein et al. (1979) for the braconid *A. pumila*. For the eulophid *C. laricinellae*, no host records were found in CAB, but Krombein et al. (1979) lists *Fenusa pusilla* (Lep.), *Fenusa ulmi* (Sund.) and *Heterarthrus nemoratus* (Fall.) as additional hosts of this parasitoid in North America. Parasitism in North America of the tenthredinid *Scolioneura betuleti* Klug by *C. laricinellae* has also been recorded (Nystrom and Evans, 1989). These four species are all invasive European tenthredinid sawflies that mine birch or elm leaves. However, it is likely that rearing of related native leafminers might detect parasitism by *C. laricinellae*.

Releases Made

Two separate projects, in different time periods, were conducted for biological control of larch casebearer in North America, with the first being in eastern Canada in the 1930s and the second in the western United States in the 1960s, 1970s, and 1980s.

Eastern North America As early as 1922, interest existed in importing parasitoids of larch casebearer from Europe for release in eastern Canada and the United States (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 eastern Canada is given by Webb and Quednau (1971). Ultimately, four parasitoids were released, but only *A. pumila* and *C. laricinellae*, proved significant.

Western North America A second project against larch casebearer followed the pest's 1957 invasion of the larch forests of Idaho and Oregon, which are isolated from the larch forests of eastern North America. Consequently, the pest arrived without its parasitoids and quickly reached damaging levels (Fig. 10), causing sustained defoliation. Importations of *A. 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 (1972–1985) by importation, rearing and release of four additional parasitoids from Europe and one from Japan (Ryan, 1980, and unpublished release reports on file at the USDA ARS Beneficial Insects Research Laboratory, Newark, Delaware).

Figure 10 Damage at stand level due to feeding of larch casebearer; all reddish-brown foliage has been partly consumed. William M. Ciesla, Forest Health Management International, Bugwood.org.

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pests

Eastern North America Following releases in the 1930s and 1940s in eastern North America, *A. pumila* spread more rapidly than *C. laricinellae* (Graham, 1958). This in turn led to evaluations of the interaction of these two species in the field to account for successful control of the pest (Quednau, 1970a). While results of the project in eastern North America were not as extensively documented as those obtained later in the western United States, this first biological control project against larch casebearer is rated as a complete success (Webb and Quednau, 1971). Before the 1930s, outbreaks of larch casebearer in eastern Canada were long and widespread, but by the1940s, once the introduced parasitoids had become well distributed, outbreaks of the pest were reduced in both extent and duration.

Western North America Ultimately, the same species that controlled larch casebearer in eastern North America, *A. pumila* and *C. laricinellae,* became established in areas of western larch as well. In a long-term study in the Blue Mountains of Oregon, Ryan (1997) found that casebearer moth density was reduced from an average of 50 moths per 100 buds during the first ten years of his study to 1.6 per 100 buds in the last ten years (Fig. 11). Ryan concluded that *A. pumila* alone was largely responsible for successful biological control of the pest, while *C. laricinellae* played only a minor, supporting role. That was because of the generally higher rates of parasitism achieved by *A. pumila* that necessarily reduced casebearer densities more, and because the reduction invariably occurred concurrently with *A. pumila* buildup. Conversely, parasitism by *C. laricinellae* was low to moderate at best and in many consecutive years was not recorded at all.

To illustrate the role of *A. pumila,* we present data from one of the research plots (Tollgate plot) for Ryan's work in Oregon (Fig. 12, A), which shows that before *A. pumila* became established and exerted its influence, casebearer densities cycled at quite a high level**.** After *A. pumila* reached a certain density, both the casebearer's rate of population increase and its density declined markedly. Thereafter, the pest's rate of increase resumed its cyclical pattern, but at a much lower mean density. The role of *A. pumila* in maintaining its host's density at that low level is shown in Fig. 12B. Following the buildup of *A. pumila* to

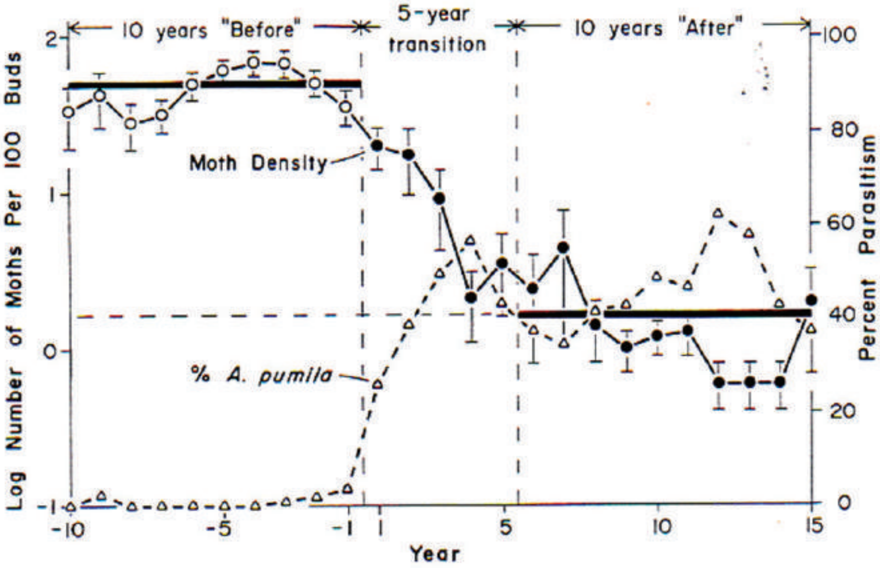

Figure 11 Changes in density of larch casebearer in Oregon (USA) over a 25 year period, in relation to the introduction of the parasitoid *Agathis pumila,* showing a drop in density of approximately 97% in the "after" period as compared to the "before" interval, demonstrating effective and sustained biological control of this pest. R. Ryan [1997] *Environmental Entomology* 26: 703–715; reproduced with permission.

a level sufficient to reduce the host's density, the wasp's own population necessarily declined because of low casebearer numbers. This relationship was statistically linear at the Tollgate plot and some other sites as well. More importantly, *A. pumila* was responding to casebearer density in the previous generation, therefore serving to regulate casebearer density over the long term.

Recently, there have been reports of an apparent increase in the amount of defoliation of western larch by larch casebearer in northeastern Oregon (affecting 80,000 acres in 2007 and 40,000 in 2008) (http://www.fs.fed.us/wwetac/projects/shaw2.html). However, since some needle diseases exist in the region whose visual appearance in aerial photographs is similar to feeding damage from larch casebearer, further investigation is needed to ascertain the current extent of casebearer damage and the status of the introduced parasitoids in any local outbreaks.

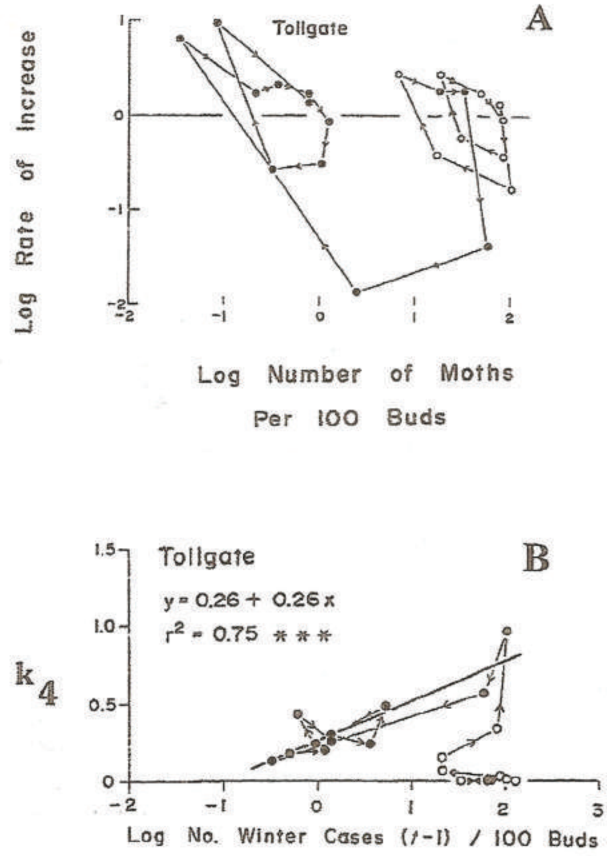

Figure 12 Causality of *A. pumila* parasitism as the factor suppressing larch casebearer density: (A) Log10 rate of population increase (vertical axis) of moths as a function of log10 density of moths (horizontal axis) in one of 13 plots, showing shift from high to low density with the establishment of *A. pumila*. (B) Casebearer mortality (as k-value) caused by *A. pumila* (vertical axis) in one of 13 plots as a function of log10 density of winter cases in the previous generation. Hollow circles are samples taken before *A. pumila* exceeded a threshold of 10% parasitism and solid circles are samples taken after this threshold was reached. R. Ryan [1997], *Environmental Entomology* 26: 703-715; reproduced with permission.

Nontarget Effects

No effects on native nontarget species were recorded in association with this project, but no formal efforts to observe them were made either.

Recovery of Affected Tree Species or Ecosystems

A return to normal growth rates by western larch, the species defoliated by the introduced larch casebearer in western North America, was observed after the biological control project reduced defoliating outbreaks (Long, 1988).

Broad Assessment of Factors Affecting Success or Failure of Project

No unusual conditions were encountered in this project. Once events in eastern North America showed which of the various introduced parasitoids were most effective, their reuse in other areas simplified the process. Despite shifts in exact host tree species (from Europe to eastern North America and then again to western North America), variation in tree resistance did not prove important enough to prevent the introduced parasitoids from suppressing the pest on new members of the genus *Larix*.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

The life histories of the two key parasitoids used in this project, *A. pumila* and *C. laricinellae,* were investigated in depth by Quednau (1966, 1967, 1970b).

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VIII Birch Casebearer

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

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DESCRIPTION OF PEST

Taxonomy

The synonymy of *Coleophora serratella* (L.) is discussed by Coshan (1974). The species was originally described as *C. serratella* L. in 1761, but until the 1970s this casebearer was referred to most often under the synonym of *C. fuscedinella* Zeller. The original name (*C. serratella*) was then misapplied in the 1930s to another species, now known as *C. cerasivorella* Packard (Benander, 1939; Toll, 1962). In the early 1970s, the name *C. serratella* was re-associated by Kloet and Hincks (1972) with the species it originally described. As a consequence of this history, citations using the term *C. serratella* between 1938 and 1972 are likely to refer to another species (the one now known as *C. cerasivorella*). In general, any citation to *C. serratella* feeding on plants other than birch (*Betula*), alder (*Alnus*), or hazel (*Corylus*) should be suspected of being a misapplication of the name.

Distribution

Birch casebearer is native to Europe, where it occurs widely (Coshan, 1974) (Fig. 1). In North America, *C. serratella* is invasive and was first recorded in Maine in 1927 (Salman, 1929). The species subsequently spread northward throughout the Canadian Maritimes and westward, reaching Manitoba by 1969. An infestation (likely from a separate introduction) was found in Victoria, British Columbia, in 1962 (Raske, 1984). It is likely that this species now occurs from Newfoundland to British Columbia and adjacent parts of the United States wherever suitable species of birch, alder, or hazel occur. Its distribution in western Canada has not been well delimited by surveys.

Figure 1 Adult of birch casebearer, *Coleophora serratella*. © Ian Kimber, http://ukmoths.org.uk/useofimages.php

Damage

Type Larvae of *C. serratella* feed on birch, alder, and hazel. Damage consists of browning and reduction of foliar area from larval feeding in early summer (Bryant and Raske, 1975) (Figs 2–5). The larva feeds as a leafminer, attaching its case to a spot and then mining all the foliage it can reach without leaving the case, producing a blotch-shaped injury (Raske, 1984). After one spot is consumed, the larva moves to a new area and repeats the process. Mined areas turn brown, giving leaves a scorched appearance. A more severe kind of damage also can occur in spring when large numbers of early instar larvae may consume the flushing buds, killing branches or even whole trees (Raske, 1984) (Fig. 6). In Europe, species of alder (*Alnus*), birch (*Betula*), and hazel (*Corylus*) serve as hosts. In North America, outbreaks have been limited to paper (*Betula papyrifera* Marsh.) and gray (*Betula populifolia* Marsh.) birches (Guèvremont and Juillet, 1974; Bryant and Raske, 1975).

Extent Birch casebearer was considered the most important defoliator of white birch (*B. papyrifera*) in

Figure 2 Young larva of birch casebearer in case. © Ian Kimber, http://ukmoths.org.uk/useofimages.php

Figure 3 Mature case of birch casebearer. © Ian Kimber, http://ukmoths.org.uk/useofimages.php

Figure 4 Larva of birch casebearer, with the case removed. © Thérèse Arcand, Natural Resources Canada, Canadian Forest Service.

Figure 5 Larva of birch casebearer. © Ian Smith, http://ukmoths.org.uk/useofimages.php.

Figure 6 Several larvae of birch casebearer in cases on young white birch leaf. © Thérèse Arcand, Natural Resources Canada, Canadian Forest Service.

southeastern Canada and the northeastern United States up to the 1980s (Raske, 1984). Large outbreaks have been reported from Quebec to Newfoundland and in Victoria, British Columbia (Raske, 1984). In Europe, despite a large number of associated parasitoids, this casebearer is at times an economic pest, especially in areas with significant air pollution, e.g., in the Czech Republic (Kula, 1995) and Poland (Chodny, 1983). In Poland densities of birch casebearer increased with increases in sulfur dioxide and dust (Chodny, 1983).

Biology of Pest

There is one generation of birch casebearer per year. Raske (1984) summarizes the life cycle as follows. In Canada, eggs of birch casebearer are laid in July on the undersides of leaves. Larvae hatch in August and mine leaves until early September. After their first molt, larvae cut leaf pieces to form cases and then continue to feed through the fall (Fig. 7). Just before leaf drop, larvae crawl to the crotches of branches or the bases of buds where they overwinter. Larvae reach full growth by early summer of their second year, after which they pupate and new adults are in flight by July.

Figure 7 White birch defoliated by birch casebearer. Claude Monnier, Natural Resources Canada, Canadian Forest Service.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

There are about 1400 named species in the genus *Coleophora* (Encyclopedia of Life; http://www.eol.org/pages/33964; Baldizzone et al., 2008). Because of the timing of this project, no analysis was made of the relatedness of these species to the target pest.

Native Natural Enemies Affecting the Pest

Factors affecting population density of birch casebearer were examined in both Newfoundland (Raske, 1974a, 1978) and Quebec (Guèvremont and Juillet, 1974) in the period between the pest's invasion and the introduction of the parasitoids from its native range for its biological control.

Raske carried out investigations in Newfoundland in the 1970s. Several sources of mortality affecting the population were assessed. Egg mortality reached 99% at sites where egg density was 40–80 per leaf, and this was likely due to the mite *Triophtydeus triophthalmus* (Oudm.) (Raske, 1974a). Thirty one species of parasitoids and hyperparasitoids were reared from birch casebearer pupae collected in western Newfoundland, 1967–1968 (Raske, 1978), but only three were common: *Itoplectis quadricingulata* (Provancher), *Cirrospilus cinctithorax* (Girault), and *Habrocytus semotus* (Walker). In western Newfoundland, parasitism by these native or self-introduced species ranged from 5.4% in 1973 to 16.3% in 1975.

In Sherbrooke, Quebec, from 1971 to 1973, Guèvremont and Juillet (1974) constructed life tables for three generations of *C. serratella* on grey birch. During the study, casebearer density was low and fairly constant and 17 species of parasitoids were reared. Guèvremont and Juillet (1975) discuss 19 species of Hymenopterous parasites reared from 1971 to 1973 from mature larvae or pupae of *C. serratella* on grey or white birch in Quebec, and they provide a key for their identification.

The life systems of the birch casebearer differed in many respects between Quebec and Newfoundland (Raske, 1984). In Quebec, undetermined deaths of first and second instars and parasitism of pupae were the most important mortality factors. In contrast, in Newfoundland the pest's density seemed to be regulated at chronically high pest levels by variable egg mortality. Parasitism in Newfoundland was low, around 10% when summed over all stages (Raske, 1984). Many of the parasitoids attacking birch casebearer in North America were generalists associated with other forest insects.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

In 1968, the Commonwealth Institute of Biological Control (CIBC) of Canada started a biological control program against birch casebearer, with parasitoids being sought in its native Europe. Releases were made in 1971 and the project ended in 1975 after parasitoid releases had been made, but before evaluation of their effects on densities of the pest.

Areas Surveyed for Natural Enemies

Surveys were conducted in Europe from 1969 to 1975 (Pschorn-Walcher, 1969–1975) to collect and identify natural enemies of birch casebearer. Collections were made in Germany, Austria, and Switzerland (Raske, 1984).

Natural Enemies Found

In Europe, parasitoids appeared to play an important role in regulating the density of birch casebearer (Pschorn-Walcher, 1969–1975). Also, the genera of the dominant parasitoids attacking birch casebearer in Europe differed from the genera of the parasitoids attacking the pest in North America. In Europe, most parasitoids were in the genera *Apanteles* (Braconidae) and *Campoplex* (Ichneumonidae).

In England, parasitoids reared from birch casebearer included the braconids *Apanteles dilectus* (Hal.) and *Bracon osculator* Nees, the ichneumonids *Campoplex* (*Omorga*) *borealis* (Zett.) and *Gelis* (*Hemiteles*) *areator* (Panz.), and the eulophids *Miotropis unipuncta* (Nees), *Closterocerus trifasciatus* Westw., *Cirrospilus pictus* (Nees), and *Chrysocharis laricinellae* (Ratz.) (Coshan, 1974).

In the Rhone Valley in Switzerland, population fluctuations and parasitoids of birch casebearer on alder were investigated at three sites over nine generations from 1970–79 (Pschorn-Walcher, 1980). The abundance and constancy of 25 larval or pupal parasites, their synchronization with the host, and their host specificity are discussed. Young larvae were attacked by well synchronized, specific parasitoids and the parasitoid diversity was greater in the floodplain forest habitat than in field windbreak strips of forest. Birch casebearer density was lowest in floodplain forest. In forest habitats, parasitoids had lowered mean host density but did not regulate year-to-year population density.

Host Range Test Results

Host ranges of the parasitoids introduced as biological control agents were not formally estimated but the collector, Pschorn-Walcher, surmised host ranges in Europe under field conditions (Pschorn-Walcher, 1980).

Releases Made

Between 1971 and 1975, five species of European parasitoids were released against birch casebearer in Newfoundland (Raske, 1977): *Campoplex borealis* (Zett.), *Campoplex* sp., *Apanteles coleophorae* Wilk., *Apanteles mesoxanthus* Ruschka, and *Apanteles corvinus* Reinh.). The latter two species were released in very small numbers. Limited evidence of recovery for some species was obtained in 1973–75, but further work was seen as needed at the time (Raske, 1977).

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

After parasitoid releases were made in Newfoundland, surveys determined that *Campoplex* sp. nov. had become established on the island, but *C. borealis* had not. *Campoplex* sp. nov. adults were found to emerge in August in Newfoundland and to be well synchronized for attack on the susceptible life stage of the host. Identification of living specimens to species was not possible and so exact numbers of each species released are unknown. Also, only a small proportion of the parasitoids collected in Europe successfully emerged in Canada. Therefore, very low numbers were released. The project was halted prematurely and further work is needed to determine the final outcome of these releases.

Nontarget Effects

No studies were done in Canada to assess potential attack of the released parasitoids on other species. New studies are needed to determine if any of the released parasitoids have had any harmful impacts on native nontarget insects.

Recovery of Affected Tree Species or Ecosystems

Work on this project was halted before the impact of the released parasitoid was determined.

Broad Assessment of Factors Affecting Success or Failure of Project

This project's effects still need to be assessed. Which parasitoids permanently established, what level of control of the pest was achieved, and whether any impact occurred on nontarget species are all unknown. If further work were done, species of parasitoids recovered would need to be identified using modern methods.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

The life histories and habits of eight European parasitoids of birch casebearer were studied in their native range (Europe) by Raske (1974b).

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IX European Pine Tip Moth

(*Rhyacionia buoliana* [Denis and Schiffermüller]) (Lepidoptera: Tortricidae)

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DESCRIPTION OF PEST

Taxonomy

Rhyacionia buoliana (Denis and Schiffermüller) (Lepidoptera: Tortricidae) was formerly placed in the genus *Evetria*. Within the family Tortricidae, at the world level, there are about 9700 species, and within the genus *Rhyacionia* (worldwide) there are about 72 species.

Distribution

European pine tip moth, also known as the European pine shoot moth, *R. buoliana,* is known from Europe (the presumed native range), the eastern end of the Mediterranean basin (Israel and the surrounding area), and Japan. It also occurs in North and South America (United States, Canada, Chile), where its invasion was recorded within the last 100 years (CAB, 1978). The most recently invaded of these areas is Chile (Espiñoza Zuñiga et al., 1986). The species was first recorded in the United States in 1914 on Long Island, New York, where it was believed to have entered via nursery stock (Busck, 1914). 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 west to Illinois. A separate infestation exists from British Columbia south through Oregon (CAB, 1978).

Damage

Type Young larvae feed on needles, and older larvae enter and feed on the buds, especially the leaders of hard pines, such a red pine (*Pinus resinosa* Sol. ex Aiton). Buds of branches are also attacked. Damage results in the death of leaders, which leads to deformed, bushy trees (Drooz, 1985). Hosts in North America of particular interest that are affected by this species include several pines: Scots (*Pinus sylvestris* L.), Austrian (= European black pine) (*Pinus nigra* J.F. Arnold), red (*P. resinosa*), ponderosa (*Pinus ponderosa* Douglas ex C. Lawson), eastern white (*Pinus strobus* L.), jack

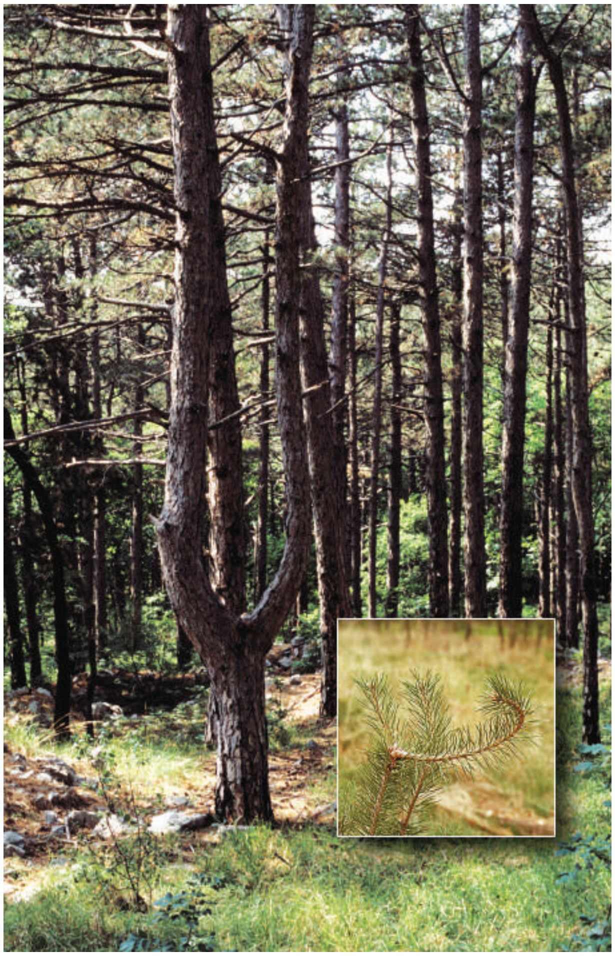

Figure 1 Eventual tree shape (here, "Y") due to leader death from feeding European pine shoot moth. Fabio Stergulc, Università di Udine, Bugwood.org. (Inset) Deformation of shape of pine leader in young tree. Jan Liska, Forestry and Game Management Research Institute, Bugwood.org.

(*Pinus banksiana* Lamb.), pitch (*Pinus rigida* Miller), longleaf (*Pinus palustris* Miller), and Virginia (*Pinus virginiana* Miller).

Extent In some areas in the eastern United States, infestation rates were high enough that red pine was not recommended for planting (Kulman, 1966). In Chile, infestation of Monterrey pine (*Pinus radiata* D. Don) in plantations reached 23–32%, causing growth reduction of 9–15% (Araya and de Ramirez, 1989).

Biology of Pest

Drooz (1985) summarizes the life cycle as follows. Adults fly in late spring (Fig.2) and lay eggs singly or in small groups at the base of buds, on needles or twig tips, or on the bark of shoots (Fig. 3). Newly hatched larvae form webs (coated with resin) between needle sheaths and stems of current-year growth, where they bore in and feed on the bases of the needles. In mid-summer, larvae move to new buds, where they form new webs (Fig. 4). Larvae stop feeding in August and overwinter as larvae in feeding tunnels in or near a bud. In April of the following year, feeding resumes and larvae move onto new buds and shoots. Larvae mature in May and pupate in their feeding tunnels in May or June (Fig. 5). There is one generation per year, which is divided over two calendar years (Fig 6).

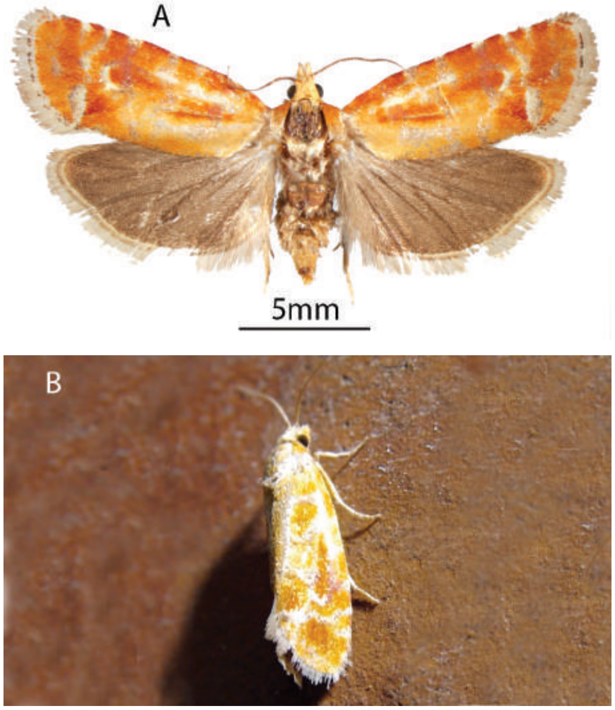

Figure 2 Adults of European pine shoot moth, *Rhyacionia buoliana*. (A) Pest and Diseases Image Library, Australia, Bugwood.org. (B) Cheryl Moorehead, Bugwood.org.

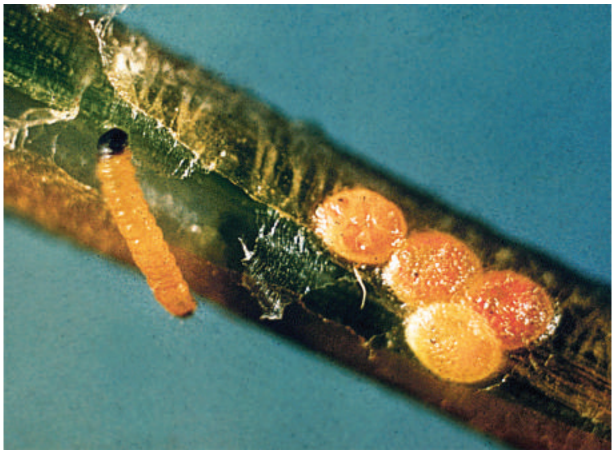

Figure 3 Eggs (right) and first instar larva (left) of European pine shoot moth. USDA Forest Service - Ogden Archive, Bugwood.org.

Figure 4 Larva of European pine shoot moth feeding in shoot. Fabio Stergulc, Università di Udine, Bugwood.org.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

In the genus *Rhyacionia,* 22 species are native to the United States or Canada (Baixeras et al., 2010). A list of all species worldwide, with notes on the type location for each, is given by Baixeras et al., 2010) at http://www.tortricidae.com/catalogueSpeciesList.asp?gcode=820.

Native Natural Enemies Affecting the Pest

Many species of parasitoids have been reared from *R. buoliana* in both Europe (see below) and North America.

Figure 5 (A) Live pupa of European pine shoot moth in damaged shoot; (B) pupa dissected from shoot (middle). USDA Forest Service, Ogden Archive, Bugwood.org.

Figure 6 Cast pupal skin (right) from damaged leader. USDA Forest Service, Ogden Archive, Bugwood.org.

At the world level these were summarized by Harman and Kulman (1973). A key to Nearactic species is provided by Yates (1967). Surveys in North America have recorded the parasitoids (native or introduced) that attack this species in various parts of the United States or Canada. In Connecticut, Friend and West (1933) recorded seven native parasitoids, while Coppel and Arthur (1953) in Ontario found eight native and three introduced species. Kulman (1966) found 20 species of parasitoids or associated organisms in West Virginia and Maryland. Rates of attack on larvae by native parasitoids were usually about 10% (Watson and Arthur, 1959; Torgersen and Coppel, 1969), although higher rates have been reported in some studies (e.g., 14–39% in West Virginia and Maryland [Kulman, 1966]). In North America, the most common parasitoid found associated with the European pine tip moth before introductions of species from Europe was, in many areas, *Elachertus* (*Hyssopus*) *thymus* Girault (Friend et al., 1938; Syme 1971a), followed by others, such as *Exeristes* (*Ephialtes*) *comstockii* (Cresson) and *Eurytoma pini* Bugbee (Watson and Arthur, 1959). Interestingly, *E. thymus* was exported to Germany from North America to increase biological control of *R. buoliana* in its native range in Scots pine plantations (Gelmroth, 1972).

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

The native range of this species is assumed to be Europe.

Areas Surveyed for Natural Enemies

Surveys or studies of natural enemies of *R. buoliana* in Europe were carried out in Germany (Tempel, 1925; Schindler, 1960, 1965; Fankhänel, 1963), the United Kingdom (Thorpe, 1930; Brooks and Brown, 1936), Serbia (Vasic, 1967), and Poland (Kolk, 1984).

Natural Enemies Outside of North America

In Europe, natural enemies of *R. buoliana* have been recorded, because the species was of interest as a pest in Scots pine plantations, and because surveys were done to support introductions of parasitoids to North America for biological control of the pest there. A series of European parasitoid species were released in North America to attempt to suppress the species, whose densities in North America at the time were believed to be about 8–fold higher than in Europe (Miller, 1962). Early parasitoid surveys from this host in Europe include those of Smits van Burgst (1919) (18 spp. recorded), Feytaud (1921) (16 spp.), Tempel (1925) (six 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 in Europe were the ichneumonid *Temelucha* (formerly *Cremastus*) *confluens* (Gravenhorst) 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* (Gravenhorst) and *O. 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 (Bogenschutz, 1969). Studies in Poland (Kolk, 1984) also record high levels (55%) of larval parasitism, particularly in pine plantations near areas of natural woody vegetation. The most common parasitoid species in Poland was *O. obscurator*. In the United Kingdom, in contrast to many other sites, *Eulimneria rufifemur* Thomson 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 JuilIet (1961).

Host Range Test Results

In Canada, 13 species of parasitoids attacking *R. buoliana* were released in two periods, 1928–1938 and 1954–1958. In the United States 15 species were introduced from 1931 to 1937 (Clausen, 1978). However, in this period, host range testing of introduced parasitoids was not considered necessary, and so the host ranges of these parasitoids were not estimated. Similarly, no efforts were made to predict any potential harm to nontarget species, such as native *Rhyacionia,* before exotic parasitoids were introduced into North America.

Releases Made

Natural enemies released in Canada and the United States are listed by Clausen (1978), who summarizes the history of the releases, providing tables of the parasitoid species released, by year and number released. Efforts in Canada are summarized by Syme (1971b, 1984). Arthur and Juillet (1961) provide an analysis of work in Canada, pointing out which introduced parasitoids were thought most likely to be successful and which, such as *Ephialtes ruficollis* (Gravenhorst) and *Exeristes roborator* (Fabricius), might merit further investigation.

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

Of the many species released, very few seem to have become established. Of those that have, in the United States, the most frequent and widespread seems to be *O. obscurator* and the tachinid *Lypha dubia* Fallén (Drooz, 1985). Broadly, releases in North America of European parasitoids have had only limited effect in most areas, although in some specific locations greater suppression appears to have resulted from the establishment of *O. obscurator* (Beiqué, 1960; Syme 1971b, 1984).

Nontarget Effects

No efforts were made to determine if, after their release, the European species of parasitoids introduced against European pine tip moth eventually attacked other tortricids in North America. From the literature since the time of the project, we see that *O. obscurator* has been reported as a minor parasitoid of the poplar twig borer, *Gypsonoma aceriana* (Dup.) (Lepidoptera: Tortricidae) (Georgiev and Samuelian, 1999) in Bulgaria. The same parasitoid has been reported to attack the beet webworm, *Loxostege sticticalis* L. (Lepidoptera: Pyralidae) (Lebedyanskaya, 1931) in Ukraine. The tachinid *L. dubia* has been reported attacking winter moth (*Operophtera brumata* L. [Geometridae]) (Galli and Krüger, 1997) in Germany.

Recovery of Affected Tree Species or Ecosystems

It is unclear from the literature whether or not damage from European pine moth in North America was reduced by importations of European parasitoids.

In Chile, where biological control of this species was a more recent effort and the goal was simpler (protection of exotic pines grown in plantations), the results are suspected of being positive, but complicated. *Orgilus obscurator* established and reached high (50–96%) levels of parasitism (Ide et al., 2007). However, as the system matured, native parasitoids and hyperparasitoids made the life system affecting the pest in pine plantations more complex, and therefore made it more difficult to determine the level of control produce by the introduced species (Ramos Sanz and Lanfranco Leverton, 2010).

Broad Assessment of Factors Affecting Success or Failure of Project

Assessment of the effects of the attempted biological control of European pine tip moth in North America is hindered by several factors: (1) The species is also sometimes a pest in its native range, although not to the same degree (e.g., Zethner and Bejer-Petersen, 1972; Bejer-Petersen, 1972); (2) most of the large number of parasitoid species released in North America failed to establish; (3) the most effective parasitoid, *O. obscurator*, appears to be effective mainly at sites with suitable nectar sources (such as *Daucas carota* L. or similar species) growing nearby, and (4) in North America, damage on red pine, one of the hosts of interest, decreases spontaneously as trees grow, because they become less attractive for moth oviposition, confounding long term studies of population dynamics. Research interest in this species' control in the United States ended by the 1980s and so our understanding of the system is incomplete and out of date

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

The biology of *Tetrastichus turionum* Htg. (Hymenop.: Eulophidae), a parasitoid of *R. buoliana* in Spain, was studied (for possible introduction to Chile) (Huerta et al., 2002). Syme and Green (1972) discuss the developmental biology of *O. obscurator* when reared on European pine tip moth. Syme (1977) describes the oviposition habits of the adult of *O. obscurator* and its use of nectar sources.

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X Introduced Pine Sawfly

(*Diprion similis* [Hartig]) (Hymenoptera: Diprionidae)

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DESCRIPTION OF PEST

Taxonomy

The introduced pine sawfly*, Diprion similis* (Hartig), is a member of the conifer-sawfly family Diprionidae (Hymenoptera). The family contains two recognized subfamilies, Monocteninae and Diprioninae; *Diprion, Zadiprion*, *Neodiprion* and *Gilpinia* are placed in the latter subfamily. The Palearctic genus *Diprion* contains five or six species, of which is the only species that has been introduced into North America. *Gilpinia* is also a Palearctic genus, while *Zadiprion* and *Neodiprion*, with the exception of *Neodiprion sertifer* (Geoffroy), are Nearctic genera (Smith, 1979).

Distribution

Diprion similis is native to Eurasia (where it is known as the white pine sawfly) and occurs from western Siberia to the United Kingdom, and from the Russian Federation in the north to Italy in the south (Liston, 1995). It also has been reported from China (Xiao et al., 1983). The sawfly was first discovered in 1914 in North America in a nursery at New Haven, Connecticut, (Britton, 1915), where it was probably accidentally introduced on imported nursery or ornamental stock (McGugan and Coppel, 1962). By 1977, it had reached North Carolina (Drooz et al., 1979). As of October 2010, the distribution of the sawfly across the United States included 23 northeastern states, ranging from Maine to North Dakota in the north, south to North Carolina, and west to Tennessee (USDA-FS, 2010). The species was first encountered in Canada at Oakville, Ontario, in 1931 and in a nursery in Montreal, Quebec, in 1933 (Monro, 1935). The sawfly was recorded for the first time in Manitoba in 1982, where it caused light to moderate defoliation of Scots pine (*Pinus sylvestris* L.) (Wong, 1983). The species now also occurs throughout the three Canadian Maritime Provinces and into Newfoundland (NRCan, 2010).

Damage

Type The favored host of *D. similis* is the eastern white pine, *Pinus strobus* L. (Fig. 1), but other species of *Pinus* are also suitable hosts (Coppel et al., 1974). Other North American pines reported as hosts for this sawfly include *P. banksiana Lamb.*, *P. flexilis* James, *P. ponderosa* Lawson, *P. resinosa* Ait., *P. rigida* Mill., *P. taeda* L., and *P. virginiana* Mill. Eurasian hosts include *P. cembra* L., *P. densiflora* Sieb. & Zucc., *P. koraiensis* Sieb. & Zucc., *P. mugo* Turra (as *montana*), *P. nigra* Arnold, *P. sibirica* Du Tour, *P. sylvestris* L., and *P. walachiana* Jacks (as *griffithi*). The damage to pines is caused by larvae feeding on needles of the host plant. The sawfly is bivoltine in much of its range and consequently there are two periods of feeding damage, one in the early summer and a second in late summer and fall. Tree mortality can result when a large second generation damages buds the following year (Mertins and Coppel, 1971). The larvae feed preferentially on the old foliage and only consume the new foliage as it ages or after older foliage has been consumed (Coppel et al., 1974). Although trees of all ages are attacked, feeding is particularly severe in exposed locations and in the overstory, where defoliation may cause branch mortality (Mertins and Coppel, 1971). The sawfly is primarily a pest of plantations, nurseries, and ornamentals, but it is also a serious threat to eastern white pine forests (Mertins and Coppel, 1971).

Figure 1 Eastern white pines defoliated by larvae of *Diprion similis*. John H. Ghent, USDA Forest Service, Bugwood.org.

Extent The sawfly is a common pest of pines in Europe, where it is frequently found in close association with the congeneric species *Diprion pini* (L.) (McGugan and Coppel, 1962). A review of the Forest Insect and Disease Conditions in the United States, 1973–2005 (USDA-FS 1973-2005) revealed several infestations of the insect. Localized outbreaks were reported in Minnesota in 1976 and in Michigan, Wisconsin, and Vermont in 1979. The sawfly was detected for the first time in 1985 in eastern North Dakota. White pine in North Carolina was heavily defoliated beginning in 1978, causing some tree mortality. Lack of biological control agents and the occurrence of three complete generations per year by the pest were blamed for the damage. This outbreak was the impetus for a pilot project to collect parasitoids of *D. similis* in Wisconsin and release them in North Carolina. By 1981, this southern infestation had expanded from 15,540 to 25,900 km^2, and also included areas in Tennessee and Virginia. In 1983 and 1984, populations in Tennessee and Virginia remained low but increases took place in North Carolina. By 1986, populations in North Carolina, Virginia and Tennessee were at low levels. Significant localized defoliation occurred again in North Carolina in 1989 and severe defoliation was reported over a large area in one county in 1990. This outbreak again prompted more parasitoid releases.

A similar review of the *Annual Report of the Forest Insect Disease Survey* in Canada (FIDS, 1932–1995) revealed a slowly expanding range, characterized by localized outbreaks of short duration. Although the sawfly was first detected in Canada in 1931 in south central Ontario, there were no reports of its activity from 1932 to 1939. The pest was also detected in Montreal, Quebec, in 1940 and in Ottawa in eastern Ontario in 1941. Slight expansion in range in Ontario had occurred by 1948, but in 1949 there was a dramatic increase in numbers and noticeable defoliation in Scots pines. Slight population fluctuations and expanded distribution records occurred annually, and by 1962 the species had reached the southern shores of Georgian Bay. In 1970 the distribution of the insect in Ontario took two dramatic jumps with its detection in Sault Ste. Marie in north central Ontario and in northwestern Ontario near

Fort Frances. The area of defoliation of white pines in the latter locale was approximately 388 km^2 and was believed to be an extension of the Minnesota infestation. The sawfly was detected for the first time in the Maritime province of Nova Scotia on eastern white pine in 1975. In 1983, 1200 ha of severe defoliation occurred on small scattered islands in Lake-of-the-Woods in westernmost Ontario near the Manitoba border. Moderate to severe defoliation was detected in 1993 and 1994 along the shoreline and on islands of Georgian Bay where mature shoreline trees were killed, significantly affecting the values of vacation properties. In 1994 and 1995, seed orchards in Quebec were being lightly defoliated by this pest.

Biology of Pest

The biology of *D. similis* was described by Coppel et al. (1974) and is summarized here. Although the insect normally is bivoltine (two generations per year), the species varies from univoltine in some parts of Asia to possibly trivoltine in some parts of North America. There is considerable overlap of the generations within a growing season. In most locations, the first adults of the spring generation emerge in April, with emergence continuing through May and June. The long term sex ratio of adults in Wisconsin was 49% males (Fig. 2), but this varied by season, location, and year. A potent female-produced sex pheromone was postulated for *D. similis* (Coppel et al., 1960) and was later characterized by Jewett et al. (1976). Females (Fig. 3) are mated soon after their emergence from the cocoon and usually begin oviposition on the same day. Eggs (Fig. 4) are deposited sequentially in slits cut into the edge of the host needles by the female's saw-like ovipositor and the exposed portion is sealed with a glandular secretion produced by the female. The number of eggs per needle ranged from 1 to 19, with a mean of 5.3 in Wisconsin populations. Although some females oviposit for up to a week, most females lay the majority of their eggs within three days. Eggs take 11 to 15 days to hatch at ambient temperatures in the spring. In Wisconsin, eggs appear in mid-May and larvae of the first generation are evident from late May until early August. Most first-

Figure 2 Adult male of *Diprion similis*. John H. Ghent, USDA Forest Service, Bugwood.org.

Figure 3 Adult female of *Diprion similis*. John H. Ghent, USDA Forest Service, Bugwood.org.

Figure 4 Eggs of *Diprion similis* bulging out of a needle of the host plant. John H. Ghent, USDA Forest Service, Bugwood.org.

generation larvae spin their cocoons by late July, with a few stragglers completing larval development in August. Second generation eggs in Wisconsin are present from mid-July to the end of August, with larvae occurring from late July to early October with a peak in early August. At higher ambient temperatures, second generation eggs take seven to nine days to hatch. Females and males have six and five actively feeding instars, respectively, and both sexes have an additional ultimate non-feeding instar. Most larvae (Fig. 5) have spun cocoons (Fig. 6) by mid-September. The larval development takes an average of 30 days in the first generation and 38 days in the second generation. Larvae feed gregariously in the first to third instars moving from the tip of the needle towards the base. Towards the end of the third instar, larvae become solitary feeders and disperse in search of available foliage, even moving to other trees. The non-feeding final instar of *D. similis* is characterized by reduced pigmentation and sclerotization. The free-living period of this stage is less than 24 hours and ends with it spinning the cocoon. Cocoons are generally spun on a solid object above ground level (Fig. 6). Within the cocoon, the last instar contracts in length and the duration of this eonymphal stage is about two days in the first generation and about eight months in the overwintering generation. Thus, winter is spent as a diapausing eonymph in the silken cocoon. The eonymph state is followed by the pronymphal state, which lasts about two days, wherein the pupal eyes become visible and the terminal abdominal segments straighten out. The pronymphal larva molts, forming the pupa. The pupal stage lasts about seven days in Wisconsin and is terminated by the emergence of the adult from the pupal exuvia within the cocoon. Adults may remain quiescent for three or four days before chewing their way out of the cocoons.

Figure 5 Late-instar larva of *Diprion similis*. USDA Forest Service, Region 8, Southern Archive, USDA Forest Service, Bugwood.org.

Figure 6 Cocoons of *Diprion similis*. John H. Ghent, USDA Forest Service, Bugwood.org.

ANALYSIS OF RELATED NATIVE INSECTS IN NORTH AMERICA

Native Insects Related to the Pest (Nontarget Species)

In North America, there are two subfamilies within the family Diprionidae, and within each subfamily there are two native genera: in the Monocteninae, *Monoctenus* (three species) and *Augomonoctenus* (two species) and in the Diprioninae, *Zadiprion* (two species) and *Neodiprion* (33 species) (Smith, 1979). There are no native North American species in the genera *Diprion* or *Gilpinia*.

Native Natural Enemies Affecting the Pest

Coppel et al. (1974) listed 35 species of parasitoids reared from cocoons of *D. similis* based on work in Wisconsin and literature records (Table 1). Of these species, 28 are native to North America and have shifted to this host from other species. Thompson et al. (1977) added a native species to the list when they reared a single specimen of *Perilampus hyalinus* Say (Hymenoptera: Perilampidae) from

Table 1 Species of parasitoids reared from *Diprion similis* in North America, with distributions based on major collections.

Species	Distribution by State/Province						Ecological Traits as Parasitoids of *D. similis*			
	CT[2]	MA[3]	ON[4]	WI[5]	MN[6]	NC[7]	Primary/ Hyperparasitoid	Solitary/ Gregarious	Endoparasitoid/ Ectoparasitoid	Abundance
Order: Hymenoptera										
Family: Ichneumonidae										
Scambus hispae (Harris)				X	X		P & H	S	En	uncommon
Pimpla pedalis (Cresson)				X			P			
Itoplectis conquistador (Say)		X	X	X	X		P & H	S		common
Delomerista japonica (Cushman)	X		X	X	X	X	P	S	En	common
Delomerista novita (Cresson)				X	X		P	S		rare
Exenterus amictorius (Panzer)[1]			X	X	X	X	P	S		common
Exenterus canadensis Provancher				X	X		P	S		rare
Exenterus nigrifrons Rohwer						X				uncommon
Gelis tenellus (Say)	X			X	X	X	P & H	S	Ec	common
Pleolophus basizonus (Gravenhorst)[1]			X			X				
Gambrus ultimus (Cresson)				X			P			
Agrothereutes lophyri (Norton)			X	X	X	X	P	S	Ec	uncommon
Family: Eulophidae										
Dahlbominus fuscipennis (Zetterstedt)[1]				X	X	X	P & H	G	Ec	uncommon
Tetrastichus coerulescens Ashmead				X	X		H	S	En	rare
Cirrospilus flavicinctus Riley				X			P & H			
Pediobius tarsalis (Ashmead)				X	X		H			
Elasmus apenteli Gahan				X			H	G		rare
Eupelmus cyaniceps Ashmead			X							
Eupelmus spongipartus Foerster[1]	?		X	X	X		H	S		rare
Eupelmella vesicularis (Retzius)[1]			X	X	X	X	P & H	S	Ec	uncommon
Family: Perilampidae					X					
Perilampus hyalinus Say					X		H			rare

[1] Species introduced into North America
[2] CT, from Connecticut in Britton and Zappe, 1918
[3] MA, from Massachusetts in Webber, 1932
[4] ON, from Ontario, in Raizene, 1957; Finlayson, 1962
[5] WI, from Wisconsin in Coppel et al., 1974
[6] MN, from Minnesota in Weber, 1977, Thompson et al., 1977
[7] NC, from North Carolina in Drooz et al., 1985
[8] Introduced as *Sturma inconspicua* Meigen

Table 1 Species of parasitoids reared from *Diprion similis* in North America, with distributions based on major collections, *continued*.

Species	Distribution by State/Province						Ecological Traits as Parasitoids of *D. similis*			
	CT[2]	MA[3]	ON[4]	WI[5]	MN[6]	NC[7]	Primary/ Hyperparasitoid	Solitary/ Gregarious	Endoparasitoid/ Ectoparasitoid	Abundance
Order: Hymenoptera										
Family: Pteromalidae										
Amblymerus verditer (Norton)	X			X	X	X	P & H	G	Ec	uncommon
Tritneptis diprionis Gahan			X							
Trineptis scutellata (Muesebeck)				X	X		P & H	G		uncommon
Dibrachys cavus (Walker)	X		X	X	X	X	P & H	G	Ec	uncommon
Eupteromalus viridescens (Walsh)				X			H			
Catolaccus cyanoideus Burks				X			H	S		uncommon
Habrocytus thyridopterigis Howard				X			P & H	G	Ec	uncommon
Family: Eurytomidae										
Eurytoma pini Bugbee	?			X	?	X	P	S		rare
Family: Chalcidae										
Spilochalcis albifrons (Walsh)				X			P & H	S		rare
Order: Diptera										
Family: Tachinidae										
Spathimeigenia spinigera Townsend				X			P	S		rare
Bessa harveyi (Townsend)				X	X		P	S		uncommon
Diplostichus lophyri (Townsend)	X			X	X		P	S		common
Euphorocera sp. (prob. *edwardsii* Williston)				X			P			rare
Drino bohemica Mesnil[1, 8]		?								?
Winthemia quadripustulata Fabricius		X								
Family: Torymidae										
Monodontomerus dentipes (Dalman)	X	X	X	X	X	X	P & H	G	Ec	common

[1] Species introduced into North America

[2] CT, from Connecticut in Britton and Zappe, 1918

[3] MA, from Massachusetts in Webber, 1932

[4] ON, from Ontario, in Raizene, 1957; Finlayson, 1962

[5] WI, from Wisconsin in Coppel et al., 1974

[6] MN, from Minnesota in Weber, 1977, Thompson et al., 1977

[7] NC, from North Carolina in Drooz et al., 1985

[8] Introduced as *Sturma inconspicua* Meigen

a cocoon of *D. similis* in Minnesota. The parasitoid was hyperparasitizing the exotic parasitoid *Exenterus amictorius* (Panzer) (Hymenoptera: Ichneumonidae) (Fig. 7). Another native species, *Exenterus nigrifrons* Rower was reported from North Carolina (Drooz et al., 1985). No parasitoids have emerged from egg collections in Wisconsin (Mertins and Coppel, 1971) and none were known from the North American literature (Coppel et al., 1974).

Figure 7 Adult of the ichneumonid parasitoid *Exenterus amictorius*. John H. Ghent, USDA Forest Service, Bugwood.org.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Introduced pine sawfly is of European origin.

Areas Surveyed for Natural Enemies

During the years 1933 to 1940, almost 32 million cocoons from eleven species of spruce or pine-feeding sawflies were collected from Europe and Japan and sent to the Entomology Laboratory, Belleville, Ontario, to rear parasitoids for release against *Gilpinia* (formerly, *Diprion*) *hercyniae* (Hartig) in Canada (Finlayson and Finlayson, 1958). European sawfly cocoons were collected from the former Czechoslovakia, and Estonia, Hungary, Sweden, Germany, Netherlands, Romania, and Poland. Egg parasitoids collected from *D. pini* in Europe were released in North Carolina in 1981 and 1982. These egg parasitoids were provided by the Commonwealth Institute of Biological Control, Delémont, Switzerland, but the origin of the insects was not reported (Drooz et al., 1985).

Natural Enemies Found

Of the 37 species of parasitoids listed in Table 1, the following seven species were accidentally or intentionally introduced into North America: *Monodontomerus dentipes* (Dalman) (Hymenoptera: Torymidae) (Fig. 8), *E. amictorius*, *Pleolophus basizonus* (Gravenhorst) (Hymenoptera: Ichneumonidae), *D. fuscipennis* (Fig. 9), *Eupelmus spongipartus* Foerster, *Eupelmella vesicularis* (Retzius) (Hymenoptera: Eupelmidae), and *Drino bohemica* Mesnil (Diptera: Tachinidae). The identification of the latter species was questionable (Coppel et al., 1974).

Figure 8 Adult of the torymid parasitoid *Monodontomerus dentipes*. John H. Ghent, USDA Forest Service, Bugwood.org..

Figure 9 Adults of the eulophid parasitoid *Dahlbominus fuscipennis*. John H. Ghent, USDA Forest Service, Bugwood.org.

Of the 32 million sawfly cocoons mentioned above over 4 million *D. similis* cocoons were collected in Poland in 1937. Among the more than 15 species of parasitoids reared from these cocoons were *M. dentipes*, *E. amictorius* and *P. basizonus*

(Finlayson and Finlayson, 1958). *Monodontomerus dentipes* was reported as numerous, and *E. amictorius* and *P. basizonus* (as *Aptesis basizonia*) were present in substantial numbers. All three of these species, plus *D. fuscipennis*, were among the parasitoid species reared from the other European sawfly species (Finlayson and Finlayson, 1958). The tachinid *D. bohemica* was also reared from these collections, but there is some confusion about the taxonomy of the species reared, and the record of *D. bohemica* reported from *D. similis* may be erroneous (Coppel et al., 1974). Over 30,000 specimens of *E. amictorius* were reared (McLeod, 1972). The two exotic parasitoids, *M. dentipes* and *D. fuscipennis*, which had been previously introduced into North America, were reared from host cocoons collected near Amery, Wisconsin, for release in North Carolina (Drooz et al., 1985). The parasitoids were mass reared using the procedures developed by Fedde (1975).

Host Range Test Results

No host specificity tests were carried out and in this period such work was not considered necessary.

Releases Made

Few releases of exotic parasitoids were made specifically against *D. similis*, but biological control of the species was achieved by the release of oligophagous parasitoids against related introduced sawfly species (Coppel et al., 1974). Of the exotic species of parasitoids that later were recovered from *D. similis* in North America, the following were originally released in eastern Canada (against *G. hercyniae* between 1933 and 1949): 288,036 *P. basizonus*, 882,360,000 *D. fuscipennis*, and 30,960 *E. amictorius* (McGugan and Coppel, 1962).

Exenterus amictorius The first releases of *E. amictorius* were made against *Gilpinia frutetorum* (Fabricius) at Niagara in 1935 (McGugan and Coppel, 1962). *Extenerus amictorius* was released in various localities from Nova Scotia to Ontario and became one of the most successful of the introduced species becoming established on *Neodiprion swainei* Middleton in Quebec, *N. sertifer* in Ontario, and *D. similis* in Wisconsin (McLeod, 1972).

Pleolophus basizonus In total, nearly a half million individuals of *P. basizonus*, were released as biological control agents against *G. hercyniae*, *N. sertifer,* and other diprionid sawflies in New Brunswick, Quebec, Ontario, and Manitoba from 1933 to 1949. This parasitoid was recovered near the release points in all provinces except Manitoba from 1934 to 1958 (McGugan and Coppel, 1962).

Monodontomerus dentipes Some 2,397 *M. dentipes* (reared from insects collected from populations of *D. similis* in Oakville, Ontario) were released in Montreal, Quebec, in 1935 (Finlayson and Reeks, 1936). The establishment of *M. dentipes* was confirmed in 1936, when an additional 12,000 parasitoids were also released (McGugan and Coppel, 1962). Releases of 13,900 mated females of *M. dentipes* that were mass reared for the biological control of *D. similis* in North Carolina were made in 1979–1981 (Drooz et al., 1985).

Egg parasites Low numbers of three egg parasitoids, *Chrysonotomyia ruforum* (Krausse), *Chrysonotomyia ormosa* (Westwood) (both Hymenoptera: Eulophidae), and *Dipriocampe diprioni* (Ferriere) (Hymenoptera: Tetracampidae), were released along the Blue Ridge Parkway in North Carolina in 1981 (Drooz et al., 1985). The parasitoids, which had been reared from the European sawfly *Diprion pini*, were obtained from the Commonwealth Institute of Biological Control, Delémont, Switzerland. A second release of 71 *C. ruforum* and four *C. ormosa* was made in the Linville Falls area of North Carolina the following year.

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

The only two exotic parasitoids in North America that consistently occur in numbers high enough to influence the population suppression of *D. similis* are *M. dentipes* and *E. amictorius* (e.g., in Wisconsin, see Coppel et al., 1974). Neither of these species, nor *D. fuscipennis*, was introduced into North America specifically for control of *D. similis*; rather, they established serendipitously in populations of *D. similis* either by accidental introduction or intentional introduction from releases against other sawfly species. The only purposeful biological control attempts against *D. similis* were the translocation of established parasitoid populations to areas where the parasitoids were absent or in low density (i.e., augmentative biological control), and a failed introduction of egg parasitoids into North Carolina from Europe. Consequently, few attempts have been made to quantify the impact of these parasitoids on *D. similis* populations.

Monodontomerus dentipes This parasitoid probably arrived accidentally in North America with its host *D. similis* because it was recovered soon after the sawfly was first detected in North America in 1914 (Britton and Zappe, 1918). According to Finlayson and Reeks (1936), *M. dentipes* was already established in 1931 in Oakville, Ontario, Canada on *D. similis*. The parasitoid is considered a key factor in the control of the introduced pine sawfly (Fedde, 1974). Surveys in North Carolina populations of *D. similis* in 1978 failed to detect any *M. dentipes,* which was the impetus for a mass rearing project for that species. However, in 1979, before the first parasitoid releases were made, two individuals of *M. dentipes* were reared from local populations showing the species was already present in the area. After the first release, *M. dentipes* populations parasitized 45% of host cocoons collected in 1980, but declined significantly in subsequent years (Drooz et al., 1985). The population density of *D. similis* declined in 1982 in North Carolina, which was attributed to the release of the parasitoid *M. dentipes*, which had been introduced from insects reared from collections in Wisconsin (USDA-FS, 1973–2005).

Exenterus amictorius This parasitoid was first collected in Wisconsin in 1961 from *D. similis*, having probably spread from releases in Canada, and subsequently replaced *M. dentipes* as the most abundant parasitoid of *D. similis* (Mertins and Coppel, 1973). In Minnesota, *E. amictorius* was the most abundant of the 16 parasitoids encountered, with parasitism rates over 44% in both sawfly generations (Thompson et al., 1977)

Dahlbominus fuscipens This parasitoid established following its release in North Carolina (Drooz et al., 1985), from material collected in Wisconsin, but populations of the parasitoid did not increase dramatically as did those of *M. dentipes*.

Egg parasitoids None of the egg parasitoids released in North Carolina in 1981–1982 became established, likely because of the small numbers released, poor timing, and logging in the release area (Drooz et al., 1985).

Nontarget Effects

No nontarget effects of the biological control of *D. similis* have been reported.

Recovery of AffectedTree Species or Ecosystems

Based on the review of occurrence records (USDA-FS, 1973-2005; NRCan, 1932–1995) for *D. similis* in North America, outbreaks are usually of short duration with limited tree mortality.

Broad Assessment of Factors Affecting Success or Failure of Project

Many parasitoids were released into North America for control of various exotic and native conifer-feeding sawflies. Only two of those species, *M. dentipes* and *E. amictorius*, now seem to regulate populations of *D. similis* (Coppel et al., 1974). McGugan and Coppel (1962) listed *M. dentipes* as widely distributed in the range of *D. similis* and "exerting a measurable degree of control." It is worth noting that *M. dentipes* arrived accidently into North America with its host and became established before its deliberate introduction, so the only new impact of the biological control program was the establishment of *E. amictorius*.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Three species of exotic hymenopterous parasitoids, *M. dentipes, E. amictorius*, and *D. fuscipennis,* have become established in *D. similis* populations in North America and seem to regulate the sawfly's density.

Monodontomerus dentipes (Hymenoptera: Torymidae)

This species was one of the two most common parasitoids of *D. similis* in Wisconsin (Mertins and Coppel, 1971) and Minnesota (Weber, 1977) in the 1960s and early 1970s. *Monodontomerus dentipes* usually attacks sawflies in the genera *Diprion* and *Neodiprion*. Other hosts reported in the literature that are attacked less frequently include other Hymenoptera, Diptera and Lepidoptera (Fedde, 1974). *Monodontomerus dentipes* is a gregarious ectoparasitoid that attacks and emerges from the host's cocoon (Mertins and Coppel, 1971). The female immobilizes the host within the cocoon with her ovipositor and inserts a banana-shaped egg into the host cocoon (Fedde, 1974). The female usually deposits five or six eggs within a cocoon, but up to 15 have been observed. Within the cocoon, the parasitoid passes through four larval instars, all of which feed externally on the host. The parasitoid pupates within the cocoon but does not form its own cocoon (Fedde, 1974). Adult parasitoids emerge about 40 days after eggs are laid, but some emerge much later, suggesting that they have entered diapause (Fedde, 1975). The parasitoids mate immediately after emergence (Fedde, 1975). The size of the adult of *M. dentipes* depends on the size of the host and the number of adults emerging from the cocoon (Fedde, 1974). The wasp occasionally acts as a hyperparasitoid, and multiparasitism or superparasitism can occur (Fedde, 1974).

Exenterus amictorius (Hymenoptera: Ichneumonidae)

This species is a primary parasitoid of larvae and it emerges from the cocoon (Mertins and Coppel, 1971). It lays its eggs in the last instar before cocoon formation (Coppel et al., 1974). According to McLeod (1972), based on observations on *N. swainei*, the eggs of *E. amictorius* are usually laid externally on the dorsum of the thoracic segments of the host. The first instar larva hatches after the host has spun its cocoon and feeds externally on the host. The parasitoid larva overwinters as a first or second instar, and resumes development in May. Pupation occurs in late May or early June and the adults emerge about five days later, first males and then females after about one week. This oliphagous parasitoid is multivoltine and in its alternate generations it attacks related diprionid species that are present as pre-spinning eonymphs, including *Neodiprion pratti banksianae* Rohwer, *Neodiprion nanulus* Schedl, and *D. hercyniae* in June and July (McLeod, 1972). Adult *E. amictorius* emerge from these hosts during August, before pre-spinning eonymphs of its host *N. swainei* are available.

Dahlbominus fuscipennis (Hymenoptera: Eulophidae)

Dahlbominus fuscipennis is the third European species that became established on *D. similis* in Wisconsin. Athough it is regularly reared from the sawfly, it is seldom numerous (Mertins and Coppel, 1971). *Dahlbominus fuscipennis* is a multivoltine pupal parasitoid of diprionid sawflies. It is a primary gregarious ectoparasitoid that attacks and emerges from the host cocoon (Mertins and Coppel, 1971). The parasitoid oviposits 10 to 50 eggs onto the surface of the host. Eggs hatch in about two days and the neonate larvae bore into the host (Rostás et al., 1998). The parasitoid larvae complete the fifth instar in 7 to 12 days, at which time they pupate inside the host cadaver. Adults emerge one to two weeks later (Rostás et al., 1998). The parasitoid overwinters within the host cocoon as a larva, prepupa or pupa (McGugan and Coppel 1962).

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XI European Pine Sawfly (Geoffrey)

(*Neodiprion sertifer* [Geoffroy]) (Hymenoptera: Diprionidae)

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DESCRIPTION OF PEST

Taxonomy

The European pine sawfly, *Neodiprion sertifer* (Geoffroy), is a member of the Diprionidae, a small family of about 91 species and 11 genera of pine feeding sawflies, worldwide (Discover life, 2012). Originally described as *Tenthredo sertifera* Geoffroy, 1785, synonyms for *N. sertifer* (Geoffroy) are *Tenthredo pectinata rufa* Retzius, *Tenthredo pini rufa* Villers, *Tenthredo juniperi* L., *Tenthredo rufa* Latreille, *Lophyrus piceae* Lepeletier, and *Lophyrus basalis* Matsumura (Discover life, 2012).

Distribution

This sawfly is an invasive Palearctic sawfly that is native from western Europe eastward to Korea and Japan. It was first recorded in North America in New Jersey (USA) in 1925 (Schaffner, 1939) and in Canada in 1939 (Griffiths et al., 1971). In Canada, it was first found in Ontario, where it remained for a long time, spreading gradually into other provinces, including Newfoundland, Nova Scotia, New Brunswick, Quebec, and British Columbia. In the United States, *N. sertifer* is found from New England west to North Dakota, and south to Missouri. A common method of invasion of new areas is movement of nursery stock.

Damage

Type Larvae feed only on old foliage. Consequently, affected trees are not often killed because new foliage is not eaten. Damage consists of reduced tree growth in forests or decline in the quality of Christmas trees.

Extent Defoliation by this species in Ontario in the early 1960s was variable geographically, and also among years, with localized outbreaks (Fig 1.). Later in the decade, outbreaks increased and the pest became more widespread (Griffiths et al., 1971). Damage was of greatest concern in young pine plantations and in Christmas tree plantings of Scots pine (*Pinus sylvestris* L.). Currently, this

Figure 1 Damage to red pine by European pine sawfly larvae; note that only old needles are eaten. Steven Katovich, USDA Forest Service, Bugwood.org.

species is considered only a minor pest in Canada (van Frankenhuyzen, 2002), but local outbreaks are occasionally reported.

Biology of Pest

European pine sawfly feeds on many species of pines, but especially Scots (*P. sylvestris*), red (*Pinus resinosa* Sol. ex Aiton), jack (*Pinus banksiana* Lambert), Japanese red (*Pinus densiflora* Siebold & Zucc.), and Table Mountain (*Pinus pungens* Lamb.) pines (Fig. 2). Other species of pines may also be defoliated if they grow near an outbreak of this sawfly.

Figure 2 Adults of European pine sawfly, *Neodiprion sertifer*; top, female; bottom, male (note enlarged antennae). Louis-Michel Nageleisen, Département de la Santé des Forêts, Bugwood.org.

The biology of this species in North America is discussed by Lyons (1964). The following is summarized from Drooz (1985). Winter is passed as eggs, which hatch in early spring. Larvae feed gregariously, eating old needles only (Fig. 3). Larvae move from tree to tree as necessary for food. Mature larvae drop from the foliage to the ground, where they spin cocoons in the duff and pupate (Fig.4). In some cases, cocoons may be formed in protected sites on the host trees (Fig.5). Adults emerge in late summer or fall and lay six to eight eggs per needle in current year foliage, in slits cut into needles, where eggs remain until the following year. There is one generation per year.

Figure 3 Egg scars of European pine sawfly in needles of Scots pine. Andrea Battisti, Universita di Padova, Bugwood.org.

Figure 4 Larvae of European pine sawfly. Top, Steven Katovich, USDA Forest Service; bottom, Gyorgy Csoka, Hungary Forest Research Institute. Both Bugwood.org.

Figure 5 Pupal cocoons of European pine sawfly. Jim Occi, BugPics, Bugwood.org.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

Neodiprion is a genus with about 33 native North American members. *Neodiprion sertifer* is placed within the *sertifer* group, which contains 13 North American species (Discover life, 2012).

Native Natural Enemies Affecting the Pest

Over time, this invasive species was exploited as a host by many native North American parasitoids, which were later detected in surveys and studies. By 1968, 28 species of native primary parasitoids had been reared from *N. sertifer* in Canada (Griffiths et al., 1984). The effects of both native and introduced natural enemies on the population dynamics of *N. sertifer* were studied in the 1960s and 1970s in Ontario (Lyons et al., 1971; Lyons, 1977).

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Neodiprion sertifer is native to the Palearctic, from western Europe to Japan.

Areas Surveyed for Natural Enemies

Parasitoids released against this species were collected in Europe, from this or related species of sawflies, and released in Canada. Some of the parasitoids introduced into Canada were later moved to the United States. Some species released in Canada had already been released for control of the spruce sawfly (*Gilpinia hercyniae* [Hartig]) and originally had been collected in Europe from *N. sertifer*.

Natural Enemies Found

In Europe, work of Eichhorn et al. (1965) showed that the parasitoid complex is quite different between years of high and low host density, with *Exenterus abruptorius* (Thunberg) and *Lophyroplectus oblongopunctatus* (= *luteator*) (Hartig) being dominant at high host densities, accounting for 80–90% of all parasitism. Between 1940 and 1949, twelve species were collected and released in Canada (Clausen, 1978), including three eulophids, *Achrysocharella ruforum* (Krausse), *Closterocerus ovulorum* (Ratz.), *Dahlbominus fuscipennis* (Zett.); six ichneumonids, *Agrothereutes abbreviator* (F.), *E. abruptorius, Exenterus amictorius* (Panz.), *Lamachus eques* (Htg.), *Lophyroplectus luteator* (now *oblongopunctatus*) (Hartig), and *Pleolophus basizonus* (Gravenhorst); one tetracampid, *Dipriocampe* (*Tetracampe*) *diprioni* (Ferr.), and two tachinid flies, *Sturmia* sp. and *Drino bohemica* Mesnil.

Subsequent to work in North America, the nucleopolyhedrosis virus of this sawfly was also exploited effectively as a biopesticide in European countries (e.g., Poland [Skrzecz et al., 1998]), as well as in other parts of the world (Fig.6). Life table studies in Sweden, suggest

Figure 6 European pine sawfly larvae killed by a virus (note the characteristic position, hanging head down). John D. Kegg, New Jersey Department of Agriculture, Bugwood.org.

that populations appear to be regulated by egg parasitism and cocoon predation by small mammals (Olofsson, 1987). Studies in Finland (Hanski and Parviainen, 1985) also found that small mammals (shrews and moles) were important predators of cocoons on the ground, but that small mammal numbers were higher on fertile sites. On sandy, nutrient-poor sites, small mammals were less abundant and predation was lower. In Estonia, Mihkelson (1980) found that the egg parasitoid *A. ruforum* was an important source of mortality, with parasitism rising from 10 to 70% during the course of an outbreak. Levels of egg parasitism were higher in mixed stands.

Host Range Test Results

Host ranges of the introduced parasitoids were not estimated in this project and indeed many were known to attack other species of *Neodiprion* (see section "Nontarget effects," below). Of the species released, one of the more specialized is believed to be *L. luteator* (now *oblongopunctatus*) (Griffiths et al., 1971).

Releases Made

From 1940 to 1949, twelve species of parasitoids were released in Canada against *N. sertifer* (three egg, six larval, and three pupal parasitoids) (Clausen, 1978), but many of these failed to establish because they were poorly synchronized with field occurrences of necessary host life stages. Better-timed releases were made later in Canada for five of the original twelve species released (Clausen, 1978), including *A. ruforum*, *D. diprioni*, *L. eques*, *L. luteator* (now *oblongopunctatus*), and *E. abruptorius*. Introductions from Europe and relocations within Canada of *N. sertifer* parasitoids continued until 1980 (Griffiths et al., 1984).

Six of the twelve European parasitoids imported to Canada also were released in the United States, 1939–1941, being *D. fuscipennis*, *E. abruptorius*, *E. amictorius*, *L. eques*, *L. luteator* (now *oblongopunctatus*), and *P. basizonus* (Dowden, 1962). More releases of *L. oblongopunctatus* (formerly *luteator*) were made later, because the first releases had been poorly timed. These later releases better synchronized with the required host life stage, were carried out in both Canada (1962) and Wisconsin (1979), and the parasitoid established in both areas (Drooz, 1985).

A nucleopolyhedrosis virus infecting *N. sertifer* in Europe also was imported to Canada, and later to the United States, and was developed for use as a biopesticide (Bird, 1953).

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

Field collections and observations in Ontario made shortly after parasitoid releases (1941–1949) found that the introduced species of parasitoids, at that time, contributed little to *N. sertifer*'s control. Six of the introduced species may have established (Griffiths et al., 1971; Drooz, 1985): (1) *D. fuscipennis,* (2) *D. bohemica* (but only on other sawflies, not *N. sertifer*), (3) *E. abruptorius* (but data are weak and so establishment is not certain), (4) *E. amictorius* (but data are weak), and (5) *L. oblongopunctatus* (formerly *luteator*); and (6) *P. basizonus*). But in this historical period, these parasitoids caused only low (<10%) levels of parasitism (Finlayson and Finlayson, 1958). In the same general area, surveys done from 1952 to 1955 showed similar results (Griffiths, 1959). But by the 1960s, further work in the same region showed that *D. fuscipennis* and *P. basizonus* had attained a wide distribution and had become common parasitoids of *N. sertifer* (Rose and Sippell, 1966). Species that seem clearly to have failed to establish in Canada include *A. ruforum*, *A. abbreviator*, *C. ovulorum*, *D. diprioni*, and *Sturmia* sp. For details of the releases and recoveries of these parasitoids in Canada see Griffiths et al. (1971).

In the United States, four of the six species released appear to have become established: (1) *D. fuscipennis*, (2) *E. abruptorius* (but data are weak), (3) *L. luteator*, and(4) *P. basizonus*. In New Jersey, *D. fuscipennis* became locally abundant after its release (Girth and McCoy, 1946), *P. basizonus* became well established, and limited recoveries were made of *E. abruptorius* (Clausen, 1978). However, none of these species provided adequate control in the decade of release (Drooz, 1985). *Lophyroplectus oblongopunctatus* was released in the 1970s in Wisconsin and also became established (Drooz, 1985).

The introduced European nucleopolyhedrosis virus of *N. sertifer* provided effective control when applied as a biopesticide (Bird, 1953). In addition, multi-year effects occurred post application, due to virus recycling and persistence at treated sites (Bird, 1961), enhancing the efficacy of this virus. This virus was widely applied to control outbreaks of *N. sertifer* in plantations in Ontario. In Europe, while applications of virus were found to persist for several years within treated areas, experiments in Sweden showed that epidemics did not spread well enough to control the pest in adjacent, non-treated areas (Olofsson, 1988).

Nontarget Effects

During efforts to establish European parasitoids of *N. sertifer* in Canada in the 1940s, it was known that many of them attacked other North American *Neodiprion* sawflies, and populations of these species were often used as release locations to help establish the parasitoids. All species of defoliating *Neodiprion* sawflies were regarded as pests and their use as alternative hosts for parasitoids of *N. sertifer* was seen as beneficial. Species against which *N. sertifer* parasitoids were released included the following parasitoid/host combinations: (1) for *D. fuscipennis* nontarget hosts included *Neodiprion pratti paradoxicus* Ross in New Jersey; *Neodiprion lecontei* (Fitch) in Alabama, Tennessee and Michigan; *Neodiprion fulviceps* (Cresson) in South Dakota; *Neodiprion abietis* (Harris) in Maine; and *Neodiprion swainei* Middleton in Wisconsin (Clausen 1978). Dowden (1962) reported that *Diprion frutetorum* (F.) in Connecticut was heavily parasitized by *D. fuscipennis*; (2) *E. abruptorius* was released against *N. pratti paradoxicus* in Massachusetts but did not establish, and (3) *P. basizonus* was released against several species in a number of states and has been recovered from *N. pratti paradoxicus* (Dowden, 1962).

Recovery of Affected Tree Species or Ecosystems

By 1970, damage from European pine sawfly in pine plantations in Canada was reduced, compared to the 1940s and 1950s. Problems were limited to young plantations (4–6 years after planting), and damaging populations tended to be short lived, declining naturally as natural enemies built up against the pest. Sawfly populations tended to remain low and not return to outbreak levels after the collapse of an outbreak (Griffiths et al., 1984). Outbreaks in stands of larger trees tended to last longer (Lyons, 1977). Parasitoids (native and introduced) of both pre-spinning and of cocooned larvae were a factor for declines in population outbreaks. Also, contributing to decline was treatment in the 1950s and 1960s of many *N. sertifer* populations in southern Ontario with preparations containing the European nucleopolyhedrosis virus of *N. sertifer* (Cunningham and Kaupp, 1995).

Broad Assessment of Factors Affecting Success or Failure of Project

Most of the introductions made in this project occurred during the 1940s, an era during which the practice was to introduce all plausible agents with minimum study. As a consequence (1) some species never established either because they did not prefer to attack the target species or timing of releases did not match the availability of required host stages and (2) several introduced parasitoids attacked various native *Diprion* species.

Work in the 1960s and 1970s focused more on understanding the natural enemies and less on making new introductions. The problem in plantations seems to have declined by then, but data are local and patchy. Introduced parasitoids may have played a role in this decline, but so also did native parasitoids and the introduced virus. The status of the pest in natural forests was investigated less often, so less is known about the severity of the pest or if biological control efforts were beneficial in forests (as opposed to plantations).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Interactions among Species

The competitive interactions among parasitoids of *N. sertifer* in Europe were studied by Pschorn-Walcher (1987). Competitiveness of each species varied with host density. During outbreaks, when densities were high, the ectoparasitoid *E. abruptorius* was intrinsically superior to both of the endoparasitoids, *L. luteator* (now *oblongopunctatus*) and *L. eques*, and *L. luteator* was superior only to *L. eques*. The effect of the superior competitor *E. abruptorius* on *L. luteator* in one generation was largely compensated in the next by the fertility of *L. luteator*, which was about five times higher than that of *E. abruptorius*. At low host densities, *L. eques* became the dominant species because of its better searching ability.

Dahlbominus fuscipennis

The eulophid *D. fuscipennis* is native to Europe, where it is known to attack several species of diprionid sawflies, especially *N. sertifer*. Its biology and habits have been discussed by Morris and Cameron (1935), based on studies in Hungary on another host. It is a gregarious, external parasitoid of prepupae (inside cocoons). It also attacks the European spruce sawfly, *D. hercyniae*. There can be up to two and a partial third generations per year, and winter is passed as mature larvae, prepupae, or pupae. Each female deposits an average of 45 eggs. The sex ratio is variable and female-biased. These features give this parasitoid a higher rate of population increase than *N. sertifer* (summarized from Clausen, 1978).

Exenterus abruptorius

The ichneumonid *E. abruptorius* is the most important parasitoid of *N. sertifer* in central Europe. It also attacks *D. hercyniae*. The parasitoid partially inserts its egg into the host larvae, but hatching is delayed until the host prepupa has spun a cocoon. The parasitoid larva then feeds externally on the host prepupa. In northern Europe there is just one generation per year and winter is passed as a mature larva in the host cocoon (summarized from Clausen, 1978).

Pleolophus basizonus

The ichneumonid *P. basizonus* attacks several species of Diprionidae in Europe and was the second most common species reared from *N. sertifer* cocoons collected in eastern and northern Europe for introduction to Canada. It is a solitary external parasitoid of the eonymph in the sawfly cocoon and never attacks the more advanced pronymphs or pupae. Attacked hosts are paralyzed at the time of oviposition and the egg is usually deposited free in the cocoon. There are three or more generations per year and there is a distributed commitment to diapause, with some individuals of each generation entering diapause (summarized from Clausen, 1978).

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XII EUROPEAN SPRUCE SAWFLY

(*Gilpinia hercyniae* [Hartig]) (Hymenoptera: Diprionidae)

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DESCRIPTION OF PEST

Taxonomy

The European spruce sawfly, *Gilpinia hercyniae* (Hartig), is a member of the genus *Gilpinia,* whose 24 species are all native to either Europe or Asia. Two species have invaded North America: *G. hercyniae* and *Gilpinia frutetorum* F., the nursery pine sawfly (Smith, 1974). Taxonomic synonyms for *G. hercyniae*, or other names used in the literature, include *Diprion polytomum* (Htg.), *Diprion hercyniae* (Htg.), *Gilpinia polytoma* (Htg.), *Gilpinia polytomum* (Htg.), and *Lophyrus hercyniae* Htg. *Gilpinia* is the recognized genus for this species, but much of the literature from North America published before the 1950s on European spruce sawfly incorrectly assigned the species to *Diprion* (Smith, 1974). Two bibliographies summarize the literature on uropean spruce sawfly (Smith, 1979; Adams and Entwistle, 1981).

Distribution

European spruce sawfly was introduced to North America sometime before the 1880s (Balch et al., 1941; Reeks and Barter, 1951) and was first recorded in Canada near Ottawa, Ontario, in 1922 and in the United States from Mt. Washington, New Hampshire, in 1929 (Balch et al., 1941). The exact origin of the introduced population, where it was first introduced in North America, and the pathway of its introduction, are not known with certainty, although importation on nursery stock is a likely source. Dowden (1939, 1962) detailed surveys done to determine the pest's distribution across the United States; McGugan and Coppel (1962) describe spread in Canada, survey efforts to detect populations, and the biological control program in Canada against this species. Wong (1972) describes the spread into western Canada.

The European spruce sawfly in North America is recorded from the New England states, New York, New Jersey, and Minnesota (Schaffner, 1943; McGugan and Coppel, 1962), and the Canadian provinces of Newfoundland and Labrador, Nova Scotia, Prince Edward Island, Quebec, Ontario, and Manitoba (Natural Resources Canada Canadian Forest Service, 2012). In eastern North America, the range of European spruce sawfly approximates that of its main host, black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenburg). However, black spruce also occurs in western Canada and Alaska, where European spruce sawfly has not yet invaded, being confined to Manitoba and areas further east.

In eastern North America, the European spruce sawfly feeds primarily on black spruce, but also will attack red spruce (*Picea rubens* Sarg.), white spruce (*Picea glauca* [Moench] Voss), and other native spruce species planted within its range (McGugan and Coppel, 1962). In its native range, this sawfly feeds primarily on Norway spruce (*Picea abies* [L.] H. Karst.), but it will attack other species. The sawfly has been recorded attacking Sitka spruce (*Picea sitchensis* [Bong.] Carr.) (Billany and Brown, 1977) in plantations in the United Kingdom, but not from natural stands of Sitka spruce in North America. Blue spruce (*Picea pungens* Engelm.) may also be a host (CAB International and European and Mediterranean Plant Protection Organization, 2004) in Europe, but it is not recorded as a host in North America.

Damage

Type Larvae of the European spruce sawfly are defoliators, consuming needles on the host trees (Fig. 1).

Figure 1 European spruce sawfly, *Gilpinia hercyniae*, damage to spruce. Natural Resources Canada, Canadian Forest Service.

The larvae prefer 1–3 year old foliage, but will consume new foliage (i.e., < one year old foliage) if the tree is heavily defoliated (Balch, 1936). Defoliation by European spruce sawfly does not affect radial growth but does reduce growth in tree height (Reeks and Barter, 1951). This effect can persist even after defoliation has ceased (Reeks and Barter, 1951).

The European spruce sawfly can kill its host, albeit slowly. One estimate predicts that an infested black spruce can sustain up to 25% defoliation every year for six years before dying (Balch, 1936); however, depending on the density of the infestation, young, small trees may die sooner than older, large trees because young trees have fewer old needles. Infested trees usually die from the bottom up as larvae consume the old foliage. Secondary pests (e.g., bark beetles) can kill trees weakened by defoliators such as the European spruce sawfly (Balch and Simpson, 1932). White spruce may be slightly more resistant than black spruce to European spruce sawfly because white spruce can sustain up to a 90% loss of old foliage and up to a 50% of new foliage before dying (Reeks and Barter, 1951).

Extent The first outbreak of this sawfly in North America was detected in the Gaspé region of Quebec in 1930 (Balch and Simpson, 1932). During the 1930s, infestations were recorded in Nova Scotia, Prince Edward Island, New Brunswick, Quebec, and in the adjacent U.S. states (Dowden, 1939; McGugan and Coppel, 1962). The outbreaks in eastern Canada began to collapse in the late 1930s following the accidental introduction of a viral pathogen (Bird and Elgee, 1957). By 1945, most populations had been reduced to low levels. In the United Kingdom, an outbreak was reported on plantations of Sitka spruce and various native spruce in the 1970s in Wales (Billany et al., 1978).

Biology of Pest

European spruce sawfly has one to three generations per year (Balch, 1936), with the number of generations tending to decrease with increasing latitude. In Canada, most populations have two generations per year (McGugan and Coppel, 1962). The European spruce sawfly is thelytokous (obligatory parthenogenesis); however, males have been observed in the field (Balch et al., 1941) and have been reared from laboratory colonies (Balch, 1936). Copulation has been observed, leading to speculation that mating may occur in flight (Balch, 1936). Despite these observations Balch et al. (1941) calculated there to be about one male for every 1200 females, suggesting males are relatively rare in most populations. Females are 6.0–9.6 mm long and black with yellow markings, while males are 4.0–8.5 mm long, and black with yellow to white or yellow to reddish-yellow markings, and with plumose antennae (Reeks, 1937). Extensive descriptions of the adult morphologies are given by Reeks (1937).

Oviposition occurs in July and August, with females laying their eggs singly in needles. Eggs hatch approximately ten days after oviposition. Larvae feed on old needles, but they will consume new foliage if the tree is already severely defoliated (Balch and Simpson, 1932). The insect has five feeding instars, with larvae progressing in color from pale yellow to dark green as they age (Fig. 2). The fifth instar has five fine white longitudinal stripes. The sixth,

Figure 2. Late instar of European spruce sawfly, *Gilpinia hercyniae*. Natural Resources Canada, Canadian Forest Service.

non-feeding instar has one dorso-medial and two dorso-lateral light green stripes (Balch and Simpson, 1932). The development time of larvae may depend on the host, with larvae on white spruce developing more rapidly than those on black spruce and red spruce (Balch, 1936). The insect overwinters underground as a pupa and is able to withstand temperatures as low as -27 °C (Balch, 1936). Overwintering diapause is normally broken the following summer; however, in the 1930s, 75–98% of some populations failed to break diapause, staying underground through their second summer (Balch and Simpson, 1932). Where this occurred, there would have been significant overlap among the subsequent generations.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

There are no native species of *Gilpinia* in North America. At least 28 of the parasitoid species released in North America against this sawfly were obtained from European or Asian sawflies with close relatives in North America (e.g., species of *Neodiprion*), but none of these parasitoids were subjected to host-range testing before introduction. Ten species of introduced parasitoids—*Drino bohemica* Mesn., *Dahlbominus fuscipennis* (Zett.), *Dipriocampe diprioni* (Ferrière), *Pleolophus basizonus* (Grav.) (released as *Aptesis basizona* [Grav.]), *Oresbius subguttatus* (Grav.), *Exenterus abruptorius* (Thunb.), *Exenterus amictorius* (Panz.), *Exenterus confusus* Kerr, *Lamachus eques* (Htg.), and *Lophyroplectus oblongopunctatus* (Htg.)—originally targeted against the European spruce sawfly, were also deliberately released against one or more native North American species of *Neodiprion* or *Pikonema* (Table 1).

Native Natural Enemies Affecting the Pest

Some of the early work on the European spruce sawfly reported predation by birds and small mammals. Mice (*Mus* sp.), squirrels (*Sciurus* sp.), and shrews (e.g., *Sorex* sp.) were observed to prey on cocoons (Balch and Simpson, 1932; Balch, 1936). However, predators were never observed to consume more than 50% of the population and never caused significant population reduction (Balch, 1936). Birds were observed to take larvae from trees growing on cleared land but not from trees growing in forested areas (Balch, 1936). Balch (1936) also observed that occasionally larvae would spin cocoons on needles and birds would take these. *Podisus serieuextris* Uhl. (Hemiptera: Pentatomidae) was common among the predacious insects attacking this sawfly in New Brunswick in 1935, (Balch, 1936). *Bessa selecta* Mg., a tachinid parasitoid of *Pristiphora erichsonii* (Htg.), was recovered from three European spruce sawfly cocoons, although this parasitoid may itself have been introduced (Balch, 1936). Native parasitoids were rarely found attacking this sawfly. Balch (1936) recorded rearing only eight parasitoids from thousands of pupae that were sampled; other authors subsequently calculated a rate of only 0.02% parasitism for native parasitoids on this sawfly (Bird and Elgee, 1957). Wireworms (Elateridae) and small mammals also contributed to suppression of low-density populations of this sawfly in New Brunswick after outbreaks collapsed (Neilson and Morris, 1964). In Newfoundland, the masked shrew (*Sorex cinereus cinereus* Kerr) (locally introduced) also may have contributed to sawfly suppression and maintenance of low population densities (Magasi and Syme, 1984).

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Europe is the area of origin for the European spruce sawfly.

Areas Surveyed for Natural Enemies

Estonia, Finland, Germany, Hungary, Japan, Poland, Sweden, the former Czechoslovakia, and other unspecified areas in Europe were surveyed for natural enemies of this sawfly (Table 1). Nebraska and Oregon were also surveyed to support releases made in the eastern United States (Dowden, 1939).

Natural Enemies Found

Thirty-five parasitoids obtained from Asian, European, or western North American hosts were released in eastern North America (Table 1). Most were the subject of some study in their home range (e.g., Morris et al., 1937) and appear to have been selected as biological control agents

Table 1 Parasitoids released in North America for the control of European spruce sawfly, *Gilpinia hercyniae*, 1933–1951.

	Origin (as reported)	Native Host(s) (as reported)	Number released against *G. hercyniae* (Canada/USA)	Also released against (in Canada)	Recovered from (in Canada)
Diptera: Tachinidae					
Blondelia inclusa (Htg.)	Europe (Eur.)	Lepidoptera, but reared from sawfly cocoons	744 / 0		Not recovered
Drino bohemica Mesn.	Europe, Finland (FI), Germany (DE), Sweden (SE)	Various Lepidoptera and sawfly hosts including *G. hercyinae* (Htg.)	245,302 / 392	*Gilpinia frutetorum* (Fabr.), *Neodiprion abietis* (Harris), *Neodiprion lecontei* (Fitch), *Neodiprion pratti banksianae* Rohwr, *Neodiprion sertifer* (Geoffroy), *Neodiprion swainei* Middleton, *Neodiprion tsugae* Middleton, *Pikonema alaskensis* (Rohwer)	*Croesus latitarsus (Nort.), G. hercyinae, N. abietis* complex, *Neodiprion nanulus* Schedl., *N. p. banksianae, Neodiprion pratti paradoxicus* Ross., *Neodiprion virginianus* complex, *P. alaskensis, Pikonema dimmokii* (Cresson)
Drino spp.	Japan (JP)	*Diprion nipponicus* Roh.	5,170 / 0	*N. lecontei*	Not recovered
Lydella sp.	Eur.	Not reported	0 / 348		Not released in Canada
Chetogena lophyri (Towns.)	US: Nebraska	Not reported	0 / 394		Not released in Canada
Vibrissina spinigera (Towns.)	US: Nebraska	Not reported	0 / 611		Not released in Canada
Hymenoptera: Eulophidae					
Closterocerus ruforum (Krausse)	Eur.	*N. sertifer*	6,368 / 0	*N. lecontei*, *N. sertifer*	Not recovered
Dahlbominus fuscipennis (Zett.)	Eur.	*N. sertifer, Diprion pini* L., *Diprion similis* (Htg.), *G. frutetorum, G. hercyniae*	882,360,000 / 257,773,000	*G. frutetorum, N. lecontei, Neodiprion nanulus nanulus* Schedl., *N. p. banksianae, N. sertifer, N. tsugae*	*Coleophora laricella* (Hbn.), *G. frutetorum, G. hercyniae, Glypta fumiferanae* (Vierr.), *N. n. nanulus, Neodiprion pinetum* (Nort.), *N. p. banksianae, N. sertifer, N. swainei*
Dipriocampe diprioni (Ferrière)	former Czechoslovakia (CS), Hungary (HU), SE	*N. sertifer*	18,651 / 0	*N. lecontei, N. p. banksianae, N. sertifer*	Not recovered

Sources: Dowden (1939), McGugan and Coppel (1962), Neilson (1971)

Table 1 Parasitoids released in North America for the control of European spruce sawfly, *Gilpinia hercyniae*, 1933–1951, *continued.*

	Origin (as reported)	Native Host(s) (as reported)	Number released against *G. hercyniae* (Canada/USA)	Also released against (in Canada)	Recovered from (in Canada)
Hymenoptera: Ichneumonidae					
Pleolophus basizonus (Gravenhorst)	Europe	Diprionid sawflies, most from *N.sertifer* and *D. similis*	288,036 / 94,025	*G. frutetorum, N. lecontei, N. sertifer, N. swainei, N. virginianus complex*	*G. hercyniae, N. sertifer*
Oresbius subguttatus (Gravenhorst)	CS, HU, Poland (PL)	*D. similis, N. sertifer*	45,704 / 285	*N. lecontei*	*G. hercyniae*
Delomerista japonica Cush.	US: Oregon	Not reported	0 / 1,178		Not released in Canada
Exenterus abruptorius (Thunb.)	Europe, JP	*D. pini, N. sertifer*	1,207,885 / 92,136	*G. frutetorum, N. lecontei, N. n. nanulus, N. sertifer*	*G. hercyniae, N. lecontei, N. p. banksianae,* *N. sertifer, N. swainei*
Exenterus adsperus complex	Europe, JP	*G. hercyniae*	11,465 / 0		*G. hercyniae*
Exenterus amictorius (Panz.)		*G. hercyniae*	30,960 / 5,056	*G. frutetorum, N. n. nanulus, N. p. banksianae, N. sertifer*	*D. similis, G. hercyniae, N. lecontei, N. n. nan-ulus, N. sertifer, N. swainei, N. virginianus* complex
Exenterus confusus Kerr.		*G. hercyniae*	13,116 / 0	*G. frutetorum, N. p. banksianae*	*G. hercyniae, N. abietis, N. n. nanulus*
Exenterus pini Cush.	Europe	Not reported	0 / 64		Not released in Canada
Exenterus spp.	Europe	Not reported	0 / 147		Not released in Canada
Exenterus spp. (prob. *vellicatus* Cush.)			846 / 0		*G. hercyniae, N. abietis*
Exenterus tricolor Rom.	Northern and central Europe, CS, FI	*G. hercyniae, N. sertifer*	631 / 156		*G. hercyniae*
Olesicampe ratzeburgi (Tschek)	Europe	*G. hercyniae*	18,129 / 429		Not recovered
Ischnojoppa lueator (Fabr.)	Europe	Not reported	0 / 389		Not released in Canada
Itoplectis quadricingulata (Prov.)	US: Oregon	Not reported	0 / 1,282		Not released in Canada
Lamachus albopictus Cush.	**JP**	*D. nipponicus*	**22 / 0**		**Not recovered**
Lamachus eques (Htg.)	CS, Estonia (EE), HU, SE	*G. frutetorum, N. sertifer*	10,882 / 825	*N. sertifer*	Not recovered

Sources: Dowden (1939), McGugan and Coppel (1962), Neilson (1971)

Table 1 Parasitoids released in North America for the control of European spruce sawfly, *Gilpinia hercyniae*, 1933–1951, *continued.*

	Origin (as reported)	Native Host(s) (as reported)	Number released against *G. hercyniae* (Canada/USA)	Also released against (in Canada)	Recovered from (in Canada)
Lamachus coalitorius (Thunberg)	Eur, CS, DE	'several sawflies' including *Gilpinia abieticola* (Dalla Torre), *N. sertifer*, & *G. hercyniae*	13,140 / 484		Not recovered
Lamachus sp.	JP	*D. nipponicus*	830 / 0		Not recovered
Lamachus sp.	Eur.	Not reported	0 / 114		Not released in Canada
Lamachus sp. 1	Eur.	Not reported	732 / 0		Not recovered
Lamachus sp. 72	Eur.	Not reported	437 / 0		Not recovered
Lophyroplectus oblongopunctatus (Htg.)	CS, EE, HU, PL, SE	*N. sertifer, D. similis*	49,881 / 0	*N. lecontei*, *N. sertifer*	Not recovered
Lophyroplectus sp.	JP	*D. nipponicus, N. sertifer*	24 / 0		Not recovered
Hymenoptera: Pteromalidae					
Mesopolobus subfumatus (Ratz.)	Eur.	Several diprionid sawflies, including *G. hercyniae*	13,421/ 0		Not recovered
Hymenoptera: Torymidae					Not recovered
Monodontormerus dentipes (Dalm.)	Eur.	Not reported	0 / 368		Not released in Canada
Monodontomerus japonicus Ashm.	JP	*D. nipponicus*	1,037 / 0		Not recovered

Sources: Dowden (1939), McGugan and Coppel (1962), Neilson (1971)

based on their parasitism of *Diprion nipponicus* Roh., *G. hercyinae*, *Neodiprion sertifer* (Geoffroy), or another closely related species (Table 1). The tachinid fly *D. bohemica* (also released as *Sturmia inconspicua* Meig.) was recorded as a significant parasitoid of European spruce sawfly, although the parasitoid is actually polyphagous and attacks many Lepidoptera and tenthredinids (Morris et al., 1937). The first releases of *D. bohemica* were made in 1934, but later taxonomic study revealed that the introductions were likely a combination of five separate species (McGugan and Coppel, 1962). Of those five species of *Drino*, only *D. bohemica* was ever recovered from *G. hercyniae* in North America, and subsequent work at the biological control laboratory in Belleville, Ontario, focused on producing only that species. The eulophid wasp *D. fuscipennis* was observed by Morris et al. (1937) to be an important parasitoid of *N. sertifer,* but would also attack cocoons of the European spruce sawfly (McGugan and Coppel, 1962). *Exenterus adsperus* Htg. was found to be an important parasitoid of pine sawflies in general, but also was very common on *G. hercyniae* (Morris et al., 1937). Later taxonomic work demonstrated that *E. adsperus* was in fact a complex of three species: *E. amictorius*, *E. confusus*, and *Exenterus vellicatus* (Cush.). Of these three species, only *E. vellicatus* was found to be an important parasitoid of *G. hercyniae*. The bionomics of many of the remaining 31 species is discussed by Morris et al. (1937), and all the species released in Canada were reviewed by McGugan and Coppel (1962). Dowden (1962) reported the release of an additional eight species that were released only in the United States, including four species that were obtained from western states (Table 1). Bionomic information on these species is not available.

Host Range Test Results

There were no host-range tests done for any of the parasitoids released for the control of European spruce sawfly in North America. The primary concern was to identify species that had an association with *G. hercyniae* or an allied species of *Diprion* or *Neodiprion*. Observations made after releases indicate that some parasitoids did attack a number of native species and other introduced species (Table 1). There has been no investigation of fate of any of the released parasitoids in the United States or Canada since 1977 (Magasi and Syme, 1984).

Six parasitoid species released against European spruce sawfly–*D. bohemica*, *D. fuscipennis*, *E. abruptorius*, *E. amictorius*, *E. confusus*, and *Exenterus* sp. (probably *E. vellicatus*) were eventually recovered from one or more native hosts in Canada or the United States (Dowden, 1962; McGugan and Coppel, 1962; Neilson and Morris, 1964; Magasi and Syme, 1984) (Table 1).

Four parasitoid species released against European spruce sawfly (*D. bohemica*, *D. fuscipennis, E. vellicatus*, and *E. amictorius*) were eventually determined to have established and become common (Dowden, 1962; Neilson and Morris, 1964). I reviewed the host records for these four species in the catalogues of Arnaud (1978) and Krombein et al. (1979). The only native North American species recorded as being parasitized by these four species are those that were identified during the original biological control program in the 1930s and 1940s (Table 1). However, *D. bohemica* is recorded from three other introduced sawflies: *Hemichroa crocea* (Geof.), *P. erichsonii*, and *Pristiphora geniculata* (Htg.).

Releases Made

Releases against European spruce sawfly began in Canada in 1933 and in the United States in 1936; the last releases were made in the United States in 1943 and in Canada in 1951 (Dowden, 1962; McGugan and Coppel, 1962). Twenty species were released in the United States; 25 species were released in Canada (Table 1). Contemporary records (Dowden, 1962; McGugan and Coppel, 1962) list a total of 37 species, but taxonomic revisions since then have reduced that number to 35 (Table 1). Releases against *G. hercyniae* were made in Connecticut, Maine, Massachusetts, New Hampshire, New York, Vermont, New Brunswick, Newfoundland, Labrador, Nova Scotia, Ontario, Prince Edward Island, and Quebec (Dowden, 1962; McGugan and Coppel, 1962). Releases of *D. fuscipennis* and *D. bohemica* were also made in British Columbia, Manitoba, and Saskatchewan but were targeted against two native sawflies, *Neodiprion tsugae* Middleton and *Pikonema alaskensis* [Rohwer] (McGugan and Coppel, 1962).

Between 1933 and 1951, over 1.1 billion insects were released against the European spruce sawfly, 257 million of which were released in the United States (Table 1). The number of individuals released varied widely among species, from as low as a few tens of individuals to millions. The vast majority (> 99%) of releases were of four species, *D. bohemica, D. fuscipennis, E. amictorius*, and *P. basizonus* (Table 1). An extensive history of the biological control effort in Canada is given by McGugan and Coppel (1962) and later updated by Neilson et al. (1971). Dowden (1962) summarizes the releases made in the United States.

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

Four of the 35 species released were observed to provide some control of *G. hercyinae* populations. Control of Canadian populations of the sawfly was attributed to *D. bohemica* and *E. vellicatus*. In the United States, Dowden (1962) attributed control at high population densities to *D. fuscipennis* and *E. amictorius,* and at low densities to *D. bohemica* and *E. vellicatus*. The remaining species either failed to establish on *G. hercyniae*; established on *G. hercyniae* but did not have an impact; or established on a different species. Regardless of the fate of the individual parasitoid species, eventually the impact of all insect biological control agents was overshadowed in both countries by a nuclear polyhedrosis virus GhNPV (also called *Borrelinavirus hercyniae*). GhNPV was first detected in North America in the late 1930s in laboratory colonies and soon afterwards in wild populations (Bird and Elgee, 1957). The origin of the virus was unknown, but it is assumed GhNPV was inadvertently imported to Canada from Europe during the introduction of parasitoids. GhNPV increased rapidly in both its prevalence and range, such that by the mid-1940s the disease killed >90% of larvae in some plots (Bird and Elgee, 1957). Eventually, complete suppression of the pest by the virus was observed in most parts of Canada and the United States. In contrast, the disease showed a density-dependant relationship with weak control at low densities (Wong, 1972); regulation of low density populations was attributed to the action of parasitoids and predators.

No large outbreaks of the European spruce sawfly have been reported in North America since 1945, but small, localized outbreaks occasionally were reported until the 1970s (Magasi and Syme, 1984). A few of these outbreaks were associated with the use of insecticides to control *Choristoneura fumiferana* (Clements), which might have killed European spruce sawfly parasitoids (Magasi and Syme, 1984). When the insecticide applications ceased, populations of *G. hercyniae* initially increased, but were soon suppressed by the action of the virus and parasitoids (Magasi and Syme, 1984).

Nontarget Effects

A number of North American sawfly species are used as hosts by some of the introduced parasitoids (Table 1). The effects of these parasitoids on the densities of those native sawflies have not been investigated, and no other effects on nontarget species have been reported.

Recovery of Affected Tree Species or Ecosystems

The only serious tree mortality caused by this introduced sawfly occurred in the Gaspé region (Quebec) and was associated with the early outbreaks (Reeks and Barter, 1951). The recovery of these ecosystems was never documented. Trees that were defoliated suffered reduced growth that could persist for as much as six years after defoliation events ended (Reeks and Barter, 1951). Most of this reduction in growth occurred in height, with no observable impact on radial growth. Magasi and Syme (1984) speculated that, if a renewed outbreak of European spruce sawfly occurred in the 1980s, it would have had a greater impact, because spruce plantations had become more common than they were in the 1930s and 1940s.

Broad Assessment of Factors Affecting Success or Failure of Project

The successful control of the European spruce sawfly was due in large part to the accidental introduction of GhNPV. That this occurred as a "side effect" of the introduction of parasitoids was fortuitous, but also it means that the introduction of parasitoids by itself did not control the epidemic. Several species of introduced parasitoids were effective at maintaining sawfly populations at low densities in areas where the virus was not effective, and through this mechanism the introduced parasitoids have likely contributed to the long-term suppression of the European spruce sawfly in North America.

This project serves also to demonstrate many features of biological control projects that were commonplace at one time, but that would not be acceptable today. For example: (1) the release of generalist parasitoids; (2) the lack of host-range testing; (3) large scale release programs without follow-up assessment and tracking; and (4) lack of pre-introduction studies of the pest's impact.

It is possible that there have been consequences from this approach that have gone undetected, as yet. Future work might examine if there were any undesired ecological impacts of the suppression efforts against the sawfly.

There were positive aspects of this project, not the least of which was that the work against European spruce sawfly contributed in part to the development of expertise in Canada in the use of biological control, specifically with insects and viruses, that has continued well after the program ended. In retrospect, the project appears to have been typical of its time; outbreaks were taken as sufficient evidence of damage and massive amounts of funds and personnel were quickly applied to the suppression of the insect. Eventually, the project appeared to have been successful and the lack of outbreaks after that was taken as sufficient evidence of the positive outcome.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

The life histories of the key biological control agents were reviewed by Morris et al. (1937) and McGugan and Coppel (1962). Information on the biology and action of GhNPV was published by Balch and Bird (1944), Bird and Elgee (1957), Bird and Burk (1961), and Neilson and Morris (1964).

RECOMMENDATIONS FOR FURTHER WORK

Currently, the European spruce sawfly does not cause economic losses or pose a risk to forest health in eastern North America. That said, a need exists for investigations into the fate of the introduced parasitoids and their effects on the ecology and densities of both native sawflies and Lepidoptera, and other introduced sawflies.

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XIII Larch Sawfly

(*Pristiphora erichsonii* [Hartig]) (Hymenoptera: Tenthredinidae)

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DESCRIPTION OF PEST

Taxonomy

The larch casebearer, *Pristiphora erichsonii* (Hartig), was originally described as *Nematus erichsonii* Hartig (*erichsoni* is an alternative spelling) (Fig. 1). Synonyms include *Nematus leachei* Dahlbom and *Nematus notabilis* Cresson, while *Lygaeonematus erichsonii* (Hartig) is an alternative generic placement (Krombein et al., 1979).

Figure 1 Adult of larch sawfly, *Pristiphora erichsonii,* Natural Resources Canada, Canadian Forest Service. Roy Van Driesche, Bugwood.org.

Distribution

Larch sawfly occurs in Canada and the United States throughout the natural range of its three larch hosts, and in larch plantations planted outside the trees' native ranges. In Canada, the range extends from Newfoundland and Nova Scotia to eastern British Columbia (Turnock and Muldrew, 1971), northward into the Yukon and Northwest Territories; it is least common in Saskatchewan and Manitoba, because of the lack of larch forests (Fig. 2). In the United States, larch sawfly occurs in the Pacific northwestern states of Oregon, Washington, Idaho, Montana, and Alaska; in the Great Lakes and central states of Minnesota, Wisconsin, Michigan, Iowa, Illinois, and Indiana; and the northeastern states of Ohio, West Virginia, Pennsylvania, Maryland, Delaware and all remaining states to the northeast (Drooz, 1985; Eastern Forest Threat Center, 2012).

Damage

Type Larvae feed on and defoliate (Figs. 3, 4, 5, 6) all three North American species of larch, tamarack (*Larix laricina* [Du Roi] K. Koch), western larch (*Larix occidentalis* Nutt.), and alpine larch (*Larix lyallii* Park.), and introduced Asian and European species and hybrids (Drooz, 1960). Because of its deciduous growth habits, larch is more tolerant than most conifers (Krause and Raffa, 1996a), so defoliation rarely kills the trees (Krause and Raffa, 1996b). However, defoliation over several consecutive years can greatly reduce wood growth.

Extent Outbreaks of larch sawfly have occurred in many regions of Canada since at least 1882 (Turnock and Muldrew, 1971) and perhaps much earlier (Nishimura and Laroque, 2010). Possible outbreaks beginning in 1732, 1752, 1806, and 1812 have been inferred from tree growth ring studies (Nishimura and Laroque, 2010 and references therein). Such inferences are based on use of a non-host tree, such as black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenburg]), which has a similar growth response as larch to climate, as the control against which to identify missing

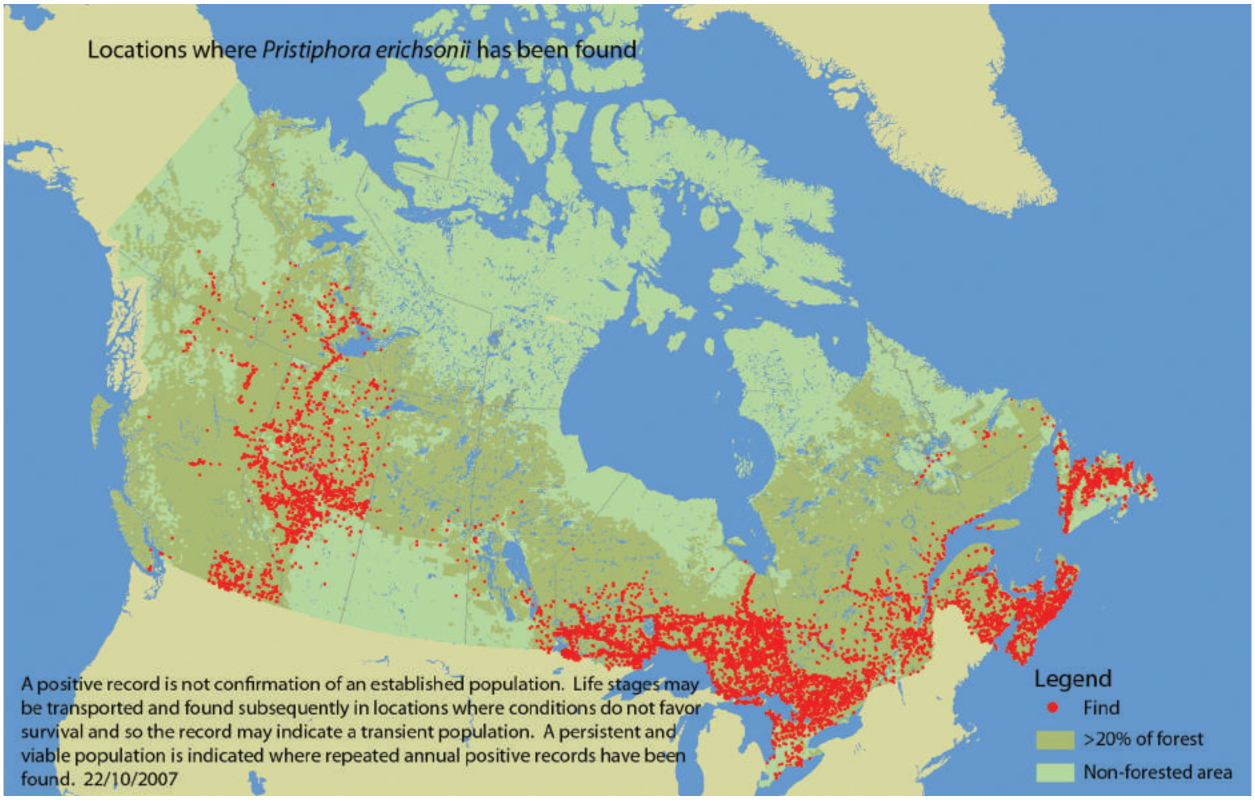

Figure 2 Distribution of larch sawfly in Canada. Natural Resources Canada, Canadian Forestry Service, http://www.exoticpests.gc.ca/static/images/maps/Pristiphora_erichsonii_eng.gif

Figure 3 Young larvae of larch sawfly feed in groups. Steven Katovich, USDA Forest Service, Forestryimages.org.

Figure 4 Mature larva of larch sawfly; older larvae feed individually. Steven Katovich, USDA Forest Service, Forestryimages.org.

Figure 5 Larch needles showing feeding by larch sawfly larvae. Dayle D. Bennett, Forestryimages.org.

growth in larch in some periods (Nishimura and Laroque, 2010). Sample information for the very earliest putative outbreaks is not robust, but it seems likely that the insect was present in North America before 1880.

The most severe and prolonged, known outbreak of larch sawfly in Canada began in Nova Scotia in 1938 and eventually extended to northeastern British Columbia. Between 1958 and 1969, moderate to severe outbreaks of larch sawfly (40% or more of foliage consumed) occurred over more than half of the Canadian range of this pest. In some of these outbreaks, stands were defoliated for 6 to 9 consecutive years. Stands on better sites were more heavily attacked, while sites on very wet organic soils were less attacked due to a lack of new growth (Turnock and Muldrew, 1971). The effects of these outbreaks was to reduce net growth to near zero (Nairn et al., 1962), with top-killing of some trees and in some cases loss of whole stands, due to the combination of sawfly defoliation and other stresses, such as flooding or bark beetle outbreaks (Drouin and Turnock, 1967). In the 1970s in eastern Canada, outbreaks continued in numerous but scattered and desynchronized patches (Ives and Muldrew, 1984). Between the 1950s and 1980s in Minnesota, defoliation by larch sawfly caused an estimated 40% reduction in the volume of larch sawtimber and pulp (Drooz, 1985) (Fig.6).

An estimate of the difference in density of larch sawfly in Canada and its native range in Europe can be made by comparing the work effort required to collect the insect (as number collected per man hour) in each area. In Europe, in the years immediately following 1958, at the best collection locations, work in Austria yielded 3–17

Figure 6 A larch stand in Minnesota showing partial (50%) defoliation caused by larch sawfly. Arnold T. Drooz, USDA Forest Service, Forestryimages.org.

larch sawfly cocoons per hour; in larch plantations in Bavaria (Germany), there were 22–180 collected (Pschorn-Walcher and Eichhorn, 1963). In contrast, from 1948 and 1969, workers in southern Manitoba collected 1000–2000 cocoons per hour (Turnock and Muldrew, 1971).

Biology of Pest

Larch sawfly overwinters as cocoons in the duff and adults emerge in spring or early summer. Eggs are inserted into new shoots in the summer causing them to curl. Young larvae feed gregariously and when mature, drop to the duff to spin cocoons (Fig. 7). There is one generation per year (Lejeune, 1955; Drooz, 1960; Turnock, 1960; Ives, 1976).

Figure 7 Cocoons of larch sawfly, showing adult emergence holes. Arnold T. Drooz, USDA Forest Service, Forestryimages.org.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

In North America, the genus *Pristiphora* includes 44 species, of which 34 are Nearctic, seven are Holarctic, and three are Palearctic introductions into the Nearctic (Krombein et al., 1979).

Native Natural Enemies Affecting the Pest

Important native species of parasitoids and predators that affect larch sawfly in North America include one tachinid parasitoid, *Bessa harveyi* (Townsend) (Diptera: Tachinidae), and small mammals, especially shrews. In some periods and locations this has been the most abundant parasitoid affecting larch sawfly. It attacks feeding larvae (Turnock and Melvin, 1936). Some evidence suggests that it has affected population trends in Manitoba (Ives, 1967).

Small mammals are believed to be important predators of larch sawfly cocoons, but are not believed to regulate population trends. For example, the masked shrew, *Sorex cinereus cinereus* Kerr, is native to eastern Canada, was introduced to the island of Newfoundland where it did not occur, and became established (Buckner, 1966).

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Populations of larch sawfly present in North America are believed to have more than one origin. Based on evidence in tree rings, it is likely that some larch sawfly populations existed in Canada before 1880 (Nishimura and Laroque, 2010). Wong (1974) suggested that larch sawfly is Holarctic, with populations native in both North America and Europe. He proposed that five races could be recognized based on morphology and that of the five, two (Aweme and Fernie) were likely present in North America well before 1900. Two other strains (Ambleside and Thirlmire) appear to have been introduced into North America starting in 1910 vis-à-vis the introduction of cocoons of larch sawfly collected in Europe that were subsequently released in forests in Canada to promote the establishment of European parasitoids of larch sawfly. (Batches of European field-collected cocoons were placed in the field in Canada for parasitoid emergence, but not all cocoons were parasitized). A fifth strain (Salzberg) is known only from Europe. This proposed population structure for North American larch sawfly has yet to be corroborated with modern molecular methods.

Areas Surveyed for Natural Enemies

Parasitoids of larch sawfly were collected in Europe (England, Germany, and Austria) and Japan. Pschorn-Walcher and Zinnert (1971) collected natural enemies of larch sawfly in central Europe and provide details on members of the parasitoid guild and relative abundance of various species.

Natural Enemies Found

Collections of life stages of larch sawfly in Europe led to the importation of four species of larch sawfly parasitoids: (1) *Mesoleius tenthredinis* Morley (Hymenop.: Ichneumonidae); (2) *Hyalurgus lucidus* (Meig.) (Diptera: Tachinidae); (3) *Olesicampe* sp. nr. *nematorum* (Tschek) (sometimes listed as *Olesicampe* sp. and later named *Olesicampe benefactor* Hinz) (Hymenop.: Ichneumonidae); and (4) *Hypamblys albopictus* (Gravenhorst) (Ichneumonidae).

Two species of parasitoids were imported from Japan: *Myxexoristops stolida* (Stein) (Tachinidae) and *Vibrissina turrita* (Meig.) (Diptera: Tachinidae).

Host Range Test Results

No efforts were made in this period to estimate the host ranges of introduced parasitoids, other than to assure that there were primary parasitoids of the pest. Both generalists and specialists were likely to have been introduced. Among the parasitoids collected, comments of workers from the period suggest that *M. tenthredinis* and *O. benefactor* were specific to the target pest, while *M. stolida*, *H. lucidus*, and *V. turrita* were known to be polyphagous, and the status of *H. albopictus* was considered uncertain (Turnock and Muldrew, 1971).

Releases Made

From the collections made in Europe and Japan, parasitoids were introduced in several distinct periods.

1910–1920 *Mesoleius tenthredinis* (a cocoon parasitoid) was imported in large numbers from England and released in Ontario (Hewitt, 1912). Collections made in 1916–1920 yielded more individuals of this same species, which were subsequently released in Manitoba (Criddle, 1928). Parasitoids collected from initial release sites in Canada were later released elsewhere in Canada, including in British Columbia, where the sawfly was found in the 1930s. By the 1950s, the originally released strain of *M. tenthredinis* was widely established in Canada (Graham, 1953), but its effectiveness was failing in some areas due to encapsulation. In this period, limited releases of *M. tenthredinis* parasitoids were made in the United States (Michigan, Massachusetts, New Hampshire, and Minnesota), but in very small numbers.

1930s In this decade, The eastern North American native tachinid, *B. harveyi*, was collected and released in British Columbia, where it established (McLeod, 1954). Other collections were made in Japan in 1934 that yielded the tachinid *M. stolida* (listed as *Zenillia rox* Hall) which was subsequently released in British Columbia and New Brunswick (Clausen, 1978).

1958–1967 During this period, 23 species of parasitoids were collected, 16 in Europe and seven in Japan (see full list of species collected in this period in Turnock and Muldrew [1964]). In Europe, Most collections were from Germany and Austria (including *M. stolida*, *H. lucidus,* and *Olesicampe* sp. (= *O. benefactor*), *H. albopictus*, and *M. tenthredinis*) and Japan (including *V. turrita*). Most releases in this period were made in Manitoba.

Of particular note was the introduction of a strain of *M. tenthredinis* from Bavaria, Germany. Unlike the form of this parasitiod introduced during the 1910–1920 period, it was not encapsulated by certain strains of larch sawfly (Turnock and Muldrew, 1964). Importantly, in the laboratory this strain's immunity from encapsulation was maintained in progeny when the Bavarian strain was crossed with the strain released in the 1910–1920 period, an event expected to occur in the field.

1969–1980 No new species of larch sawfly parasitoids were released, but work continued on the redistribution of *M. tenthredinis* (Bavarian strain) and *O. benefactor* to new parts of Canada. *Olesicampe benefactor* was released in Minnesota in the early 1970s (Kulman et al., 1974)

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

Mesoleius tenthredinis Release of this species in 1910–1920 resulted in its establishment in Canada. Initially, it suppressed larch sawfly in parts of Canada (McGugan and Coppel, 1962), but the appearance and spread of a strain of larch sawfly capable of encapsulating eggs of this species (Muldrew, 1953, 1964) rendered this parasitoid ineffective by the 1930s, except in British Columbia (Hopping et al., 1943) and the Maritimes. In British Columbia, parasitism rates remained high and pest densities became low and non-damaging (McLeod, 1952, 1954). Due to encapsulation, this parasitoid, in the form introduced in 1910, proved ineffective in the United States (Drooz, 1957, 1960, 1961).

As evidenced by rising rates of parasitism, the Bavarian strain of this species (resistant to encapsulation) released in 1963 and 1964 in Manitoba appears to have established (the two forms are morphologically identical) (Turnock and Muldrew, 1971); however, the degree to which this new race has replaced the older one and increased parasitism over larger areas is unknown. This strain was introduced into Minnesota in 1971 and 1972, where it established (Kulman et al., 1974). Richmond et al. (1995) found that this species was the dominant parasitoid of larch sawfly cocoons collected in Alaska in 1993 and 1994; however, the strain of the parasitoid was not identified. Should it prove possible to extract DNA from preserved specimens in collections, development of markers to distinguish the strains of *M. tenthredinis* would allow new research into the interaction (if any) of these strains in the field.

Bessa harveryi In the 1930s, this tachinid species, native to eastern North America and believed to be important in Manitoba (Ives, 1967), was introduced to British Columbia, where it established (McLeod, 1954).

Olesicampe benefactor From the releases made in the 1960s, *Olesicampe* sp. (later described as *O. benefactor*) readily established (Muldrew, 1967). Rates of parasitism from this parasitoid increased from <1% in the early-to-late 1960s to 80–98% in the late 1960s (Turnock and Muldrew, 1971). However, due to a rise in hyperparasitism by *Mesochorus dimidiatus* Hlmgr., a European parasitoid that was also naturally present in North America, parasitism fell to low levels. At some sites, hyperparasitism rose rapidly. For example, at Pine Falls, Manitoba, hyperparasitism was <1% in 1966 but reached 61% by 1968 (Turnock and Muldrew, 1971). However, rates of hyperparasitism in the 1960s, remained low in some locations, e.g., New Brunswick (Turnock and Muldrew, 1971). At other sites, rates of hyperparasitism continued to increase, reaching very high levels (>80%) in the 1970s (Ives and Muldrew, 1984).

In the United States*,* *O. benefactor* was introduced into Pennyslvania (Drooz et al., 1985) and Maine in 1967 (Embree and Underwood, 1972), and into Minnesota in 1971 and 1972 (Kulman et al., 1974). It established and spread slowly in Maine and Minnesota. However, its hyperparasitoidism was quickly noticed in Minnesota

Other species Other parasitoids released either failed to established or remained of limited importance.

Nontarget Effects

No studies were conducted to look for effects of the introduced parasitoids on native *Pristiphora* species. However, because it was thought at the time that some of the species being released in the 1960s were polyphagous, efforts were made to sample native sawflies found in the general area surrounding release locations to see if such native sawflies were serving as alternative hosts, i.e., were being attacked. Of the species released in the 1960s in Manitoba—*H. lucidus*, *Hypamblys* sp., *M. tenthredinis*, *M. stolida*, *O. benefactor*, and *V. turrita*—none were later reared from any of the following nontarget sawflies collected from the field (Turnock and Muldrew, 1971): *Anoplonyx luteipes* Cresson from larch (*Tamarix*); *Pikonema alaskensis* Rohwer from spruce (*Picea*); *Neodiprion pratti banksianae* Rohwer from jack pine (*Pinus banksiana* Lamb.); *Nematus* spp. from aspen (*Populus*); *Nematus limbatus* Cresson and *Pristiphora sycophanta* Walsh from willow (*Salix*); and *Cimbex americana Leach* and *Hemichroa crocea* (Fourcroy) from alder (*Alnus*).

These observations are not conclusive, but suggest that other sawflies were not heavily parasitized by the introduced parasitoids.

Recovery of Affected Tree Species or Ecosystems

Densities of the target pest seem to have been reduced in some times and places, but outcomes have varied with location and period of time. Assessment of the impact of the biological control program overall is at best sketchy. Also, because the original project was framed as an effort to protect larch as a source of wood and pulp, no information was collected on the impacts of this sawfly on native larch forest health or biodiversity. Consequently, the extent to which this biological control project contributed to the ecological health of larch forests is not clear. However, it is reasonable to surmise that it did so, by improving health of larch trees.

Broad Assessment of Factors Affecting Success or Failure of Project

This project was more complex than most classical biological control projects. First, it is not clear if the pest was native, introduced, or a combination of both. Second, early introductions of parasitoids appeared to have brought additional strains of the pest to North America, which possibly reduced the value of the introduced species *M. tenthredinis* (through encapsulation). Second, another strain of *M. tenthredinis* was later introduced, but means to separate it from the first strain were not available at the time, apart from rates of parasitism and encapsulation. It is not clear if this second strain has done more than just establish. Third, the parasitoid *O. benefactor*, which effectively suppressed the pest, was itself quickly suppressed by a pre-existing hyperparasitoid (*M. dimidiatus*). Before the introduction of *O. benefactor*, life tables for larch sawfly did not reveal any density-dependent factor capable of regulating the species (Ives, 1976). However, *O. benefactor*, with *M. dimidiatus*, did act in a density-dependent manner and for a time appeared to provide regulation (Ives, 1976). The status of parasitoids of larch sawfly in Minnesota in the 1970s was similar to that in Manitoba (Thompson and Kulman 1976). The current status of both the larch sawfly and its parasitoids in both Canada and the United States is unclear. Although no single natural enemy appears to provide complete control by itself, the combination of introduced parasitoids, native rodents, induced host defenses, and high host tolerance to defoliation that allows biological control agents time to build up during outbreaks, appears to substantially reduce the impacts of larch sawfly in the system (Krause and Raffa, 1992, 1996b).

Key questions that remain unanswered or were never asked are the following.

(1) Was the assessment by Wong (1974) concerning the population structure of this species correct? DNA work on this problem would be able to answer that question.

(2) Has the Bavarian strain of *M. tenthredinis* introduced in the 1960s become widespread and caused high levels of parasitism on strains of larch sawfly that can encapsulate the 1910–1920 strain of this parasitoid?

(3) Is larch sawfly currently suppressed by *O. benefactor,* despite high levels of hyperparasitism, either alone or in combination with the Bavarian strain of *M. tenthredinis*?

(4) Have the introduced parasitoids that established become important mortality agents for native, non-pest species of *Pristiphora* in North America?

(5) What were the benefits to natural larch forests of this biological control project?

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Mesoleius tenthredinis

This species is a solitary internal parasitoid of sawfly larvae. It overwinters as first or second instars inside host larvae in their cocoons in the duff. Pupation occurs in the spring and cocoons are spun inside the host cocoons. Adult parasitoids emerge from June on. There is one generation per year. This species can be encapsulated by some strains of the larch sawfly (summarized from Clausen, 1978).

Bessa harveyi

This species is a native North American tachinid. It occurs widely in eastern and central Canada and the eastern United States, where it parasitizes various sawflies. In the 1930s and thereafter, it became the dominant parasitoid of larch sawfly in some areas where the effect of *M. tenthredinis* had been reduced by encapsulation. Eggs are macrotype and are laid on mature sawfly larvae. The maggot penetrates a larva soon after oviposition but defers its development until the host has matured, dropped to the ground, and spun its cocoon. The maggot passes the winter as a first instar in the host in its cocoon and then in the spring feeds and completes its development. At maturity the maggot pupates in or near the host cocoon. There are two generations of this fly per year, but the second generation is poorly synchronized with larvae of larch sawfly (summarized from Clausen, 1978).

Olesicampe benefactor

This ichneumonid wasp is a solitary internal parasitoid of sawfly larvae. It attacks only first instar host larvae. Eggs hatch quickly and the parasitoids pass the winter as partly grown larvae inside host larvae in their cocoons in the duff. Parasitoid larvae complete their development and pupate in the spring, inside the hosts' cocoons. The emergence of adult parasitoids in late spring through summer coincides with the presence of new larch sawfly larvae. There is one generation per year (summarized from Clausen, 1978).

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XIV Mountain Ash Sawfly

(*Pristiphora geniculata* [Hartig]) (Hymenoptera: Tenthredinidae)

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DESCRIPTION OF PEST

Taxonomy

Pristiphora geniculata (Hartig) is the accepted name of mountain ash sawfly. A former generic placement was *Nematus geniculatus* Hartig. One synonym, *Nematus cheilon* Zaddach, is listed by Krombein et al. (1979)

Distribution

Mountain ash sawfly (Fig. 1) is a European species that invaded the United States in 1926 (Schaffner, 1936). It was first recorded in Canada in 1934 (Petch, 1935). In 1980, its range in Canada included Newfoundland and New Brunswick, and parts of Labrador Quebec, and Ontario (Quednau, 1984). In the United States, mountain ash sawfly is found from New England to Minnesota, and southeast to West Virginia in mountainous areas (Drooz, 1985), consistent with the range of its host plant (Fig. 2).

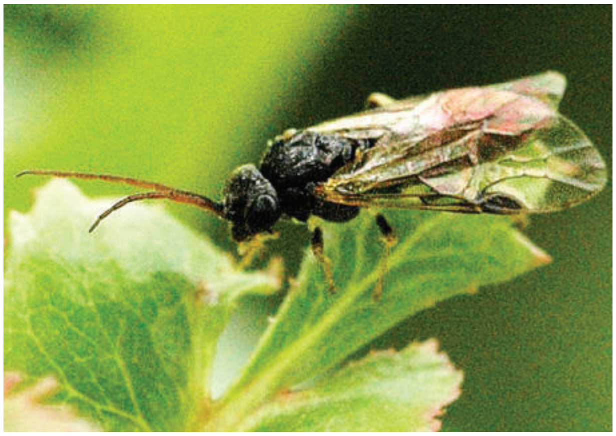

Figure 1 Adult of mountain ash sawfly, *Pristiphora geniculata*. James Lindsey, Bugwood.org.

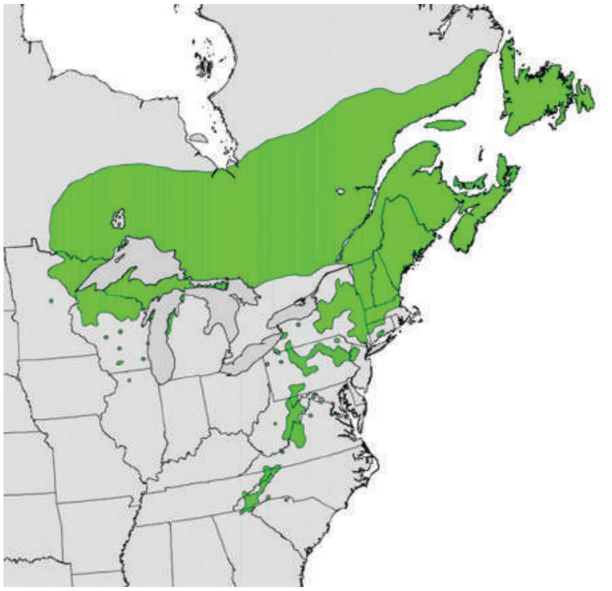

Figure 2 Distribution of *Sorbus americana* (mountain ash), a native shrub/tree in North America. Elbert L. Little , Jr., *Atlas of United States Trees,* 1999, Geological Survey, digital representation, Wikipedia.org.

Damage

Type Larvae of this sawfly defoliate species of *Sorbus*, especially mountain ash (*Sorbus americana* Marshall) (Fig. 3–5). The tree is seldom killed. Of direct concern to people, such as landscapers, is the loss of the plant's aesthetic qualities. The motivation for the biological control project was to reduce the use of pesticides in urban areas.

Ecological damage has not been measured, but this plant is present in high latitude and high altitude habitats as a native shrub/small tree. It produces significant quantities of fruit, which are eaten by many birds and small mammals, e.g., ruffed grouse (*Bonasa umbellus* [L.]), ptarmigans [*Lagopus* spp.], sharp-tailed grouse [*Tympanuchus phasianellus* [L.], blue grouse (*Dendragapus* spp.), American

Figure 3 Young larvae of mountain ash sawfly feed in groups. Steven Katovich, USDA Forest Service, Bugwood.org.

Figure 4 Older larvae of mountain ash sawfly feed individually. E. Bradford Walker, Vermont Department of Forests, Parks and Recreation, Bugwood.org.

Figure 5 Defoliation of mountain ash (*Sorbus americana*) by mountain ash sawfly larvae. Joseph O'Brien, USDA Forest Service, Bugwood.org.

robins (*Turdus migratorius* L.), other thrushes (*Turdus* spp. and other Turdidae), waxwings (*Bombycilla* spp.), jays (several genera of Corvidae), squirrels, and rodents. Mountain ash is a preferred browse for moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) and the plant may be heavily browsed by moose in the Great Lakes states. Other mammals, such as fishers (*Martes pennanti*), marten (*Martes* spp.), and snowshoe hare (*Lepus americanus*), also browse mountain-ash (USDA, FS, Management Considerations, 2012)

Extent The extent of damage from this pest seems not to have been systematically estimated, either in urban landscapes or natural areas.

Biology of Pest

The insect overwinters as prepupae in cocoons in the soil or duff and pupation occurs in the spring. Adults emerge in spring and lay eggs inserted in leaves. Larvae feed externally and mature in two to three weeks. Young larvae feed gregariously, but older larvae feed alone. There is a partial second generation consisting of about 20% of the first generation. Adults of the second generation are present in late July. There are males and females but reproduction is facultatively parthenogenic. Insects may remain in the soil as diapausing larvae for up to five years (Forbes and Daviault, 1964).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

The genus *Pristiphora* includes 44 species, of which 34 are Nearctic, seven are Holarctic, and three are Palearctic introductions into the Nearctic (Krombein et al., 1979).

Native Natural Enemies Affecting the Pest

Native North American species may attack mountain ash sawfly, but have not been reported.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Mountain ash sawfly is native to Europe.

Areas Surveyed for Natural Enemies

Parasitoids of mountain ash sawfly were collected in Austria, Germany, and Switzerland (Eichhorn and Pschorn-Walcher, 1978).

Natural Enemies Found

In Europe, through surveys or creation of artificial outbreaks on *Sorbus* species using adult sawflies from cocoons collected in Quebec (Quednau, 1984), nine species of larval parasites (including one hyperparasitoid) were found attacking *P. geniculata*. Of these, four—*Rhorus* sp., *Olesicampe* sp., *Eridolius hofferi* (Gregor) (all three, tichneumonids), and *Hyalurgus lucidus* (Mg.) (Tachinidae)—were found regularly and were common, at least in mountainous areas. Two species, *Rhorus* sp. and *Olesicampe* sp. (later described as *O. geniculatae* Quednau and Lim [Quednau and Lim, 1983]), were shipped to Canada.

Host Range Test Results

No efforts were made to test the host range of the introduced parasitoids against native *Pristiphora* species in North America. At the time of release, *O. geniculatae* was believed to be host-specific, but this was not demonstrated by testing against North American species of *Pristiphora*.

Releases Made

Releases of *Rhorus* sp. 3 were made in cages at a nursery in Quebec from 1973 to 1977 and one male was recovered in 1978. The release is presumed to have failed. Releases of *O. geniculatae* were made at the same location in 1977 by placing laboratory-mated females into field cages placed over *Sorbus* trees that were previously stocked with *P. geniculata* larvae. New larvae were placed into field cages daily and exposed larvae returned to the laboratory for rearing to the fourth instar, at which time larvae were returned to the field site and covered with wire screens that allowed mature larvae to drop through cages to the soil to form overwintering cocoons.

Subsequently (1981–1983), *O. geniculatae* from sites in Quebec were released in the St. John's area of Newfoundland (West et al., 2002).

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

While *Rhorus* sp. 3 did not establish, *O. geniculatae* readily did so in 1977 at the original release site (Beaumont Nurseries, in Beaumont, Quebec) following its release there in 1977. Sawfly densities fell from 500 colonies per ha in 1980 to 30 colonies per ha the following year. By 1981, the parasitoid was observed to have spread 30 km from the point of release, and rates of parasitism at seven sample locations averaged 48% (range 4–82%). High rates (ca 60%) of hyperparasitism by *Mesochorus globulator* Thnb. were observed (Quednau, 1984). Releases in Newfoundland also were successful (West et al., 1994). In 1988, the parasitoid was recovered from 91% of 78 survey plots where the host was present, and parasitism values ranged from 2 to 97%. A general pattern emerged as the parasitoid spread to new areas within Newfoundland in the1990s: parasitism was variable but substantial and the number of locations infested with colonies of mountain ash sawflies declined (West et al., 2002), indicating the project had successfully suppressed the pest.

Nontarget Effects

No studies were conducted to look for effects of the introduced *O. geniculatae* on native *Pristiphora*. There is still a need to do so.

Recovery of Affected Tree Species or Ecosystems

No information was collected on the effects of this sawfly on mountain ash in nature. The project was defined as an effort to protect landscape plants, and this objective was achieved.

Broad Assessment of Factors Affecting Success or Failure of Project

This project's success in terms of protecting landscape plants was clearly documented. However, the extent of reduction in any original, but unmeasured, level of ecological damage caused by the pest is unknown.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Rhorus sp. no. 3 (Hymenoptera: Ichneumonidae)

A solitary endoparasitoid, *Rhorus* sp. no. 3 is probably specific to *P. geniculata* and closely related to *Rhorus lapponicus* Roman, whose biology has been described by Pschorn–Walcher and Zinnert (1971). Little is known of the its biology of species no. 3, because it failed to establish in North America and was difficult to breed in the laboratory.

Olesicampe geniculatae (Hymenoptera: Ichneumonidae)

A solitary endoparasitoid believed to be specific to *P. geniculata*, this parasitoid attacks first and second instars. There is one generation and a partial second generation each year. The biology is essentially the same as *Olesicampe benefactor* Hizn (Pschorn-Walcher and Zinnert, 1971). Females can live up to three weeks at 22ºC and 75% RH and lay up to 400 eggs (Quednau, 1984). Rearing of this species is described by Quednau (1990).

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XV Birch Leafminer

(*Fenusa pumila* Leach) (Hymenoptera: Tenthredinidae)

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DESCRIPTION OF PEST

Taxonomy

The birch leafminer is currently designated as *Fenusa* (*Fenusa*) *pumila* Leach (Hymenoptera: Tenthredinidae) (Taeger and Blank, 2008). Synonyms include *Fenusa pumila* (Klug) and *Fenusa pusilla* (Lepeletier). The genus *Fenusa* is divided into two subgenera, *Fenusa* and *Kaliofenusa* (Taeger et al., 2010), and all of the species in these subgenera are from the Palearctic region. In the subgenus *Fenusa* there are two species, *F. pumila* and *Fenusa dohrnii* (Tishbein), both of which are invasive in North America (although some authors also list *F. dohrnii* as native to the Nearctic). In the subgenus *Kaliofenusa*, there are four species, *Kaliofenusa altenhoferi* (Liston), *Kaliofenusa laevinota* (Benson), *Kaliofenusa ulmi* (Sundevall), and *Kaliofenusa zinovjevi* (Liston). Of these only one, *K. ulmi*, is found in North America, where it is invasive. Also included in the genus *Fenusa*, but not assigned to a subgenus, are two species from the Oriental region, *Fenusa crassicornis* Malaise and *Fenusa sinobirmana* Malaise.

Distribution

Figure 1 Adult birch leafminer (*Fenusa pumila*). Cheryl Moorehead, Bugwood.org.

The birch leafminer has a Palearctic distribution that ranges from Ireland through Siberia, China, and Japan (Digweed et al., 2009). It was first reported in North America in 1924, and by 1931 it was present in all of the New England states, as well as New York, New Jersey, and the Canadian province of New Brunswick (Friend, 1931). *Fenusa pumila* (Fig. 1) was recorded in Ontario, Canada, in 1922 (Digweed et al., 2009). It now occurs from Newfoundland south to the U.S. state of Maryland, and west to the Canadian province of Alberta, the Great Lakes States, and the U.S. state of Iowa, with isolated populations in the U.S. states of Washington, Oregon, and Alaska (Casagrande et al. 2009a).

Damage

Type This leafminer lays its eggs in newly emerged birch leaves in spring, or on new growth or sucker leaves later in the season. Oviposition causes a grayish discoloration of the leaf tissue. Initial feeding on leaf tissue arrests leaf growth, resulting in wrinkling and asymmetrical growth. Numerous leafmines cause leaf death and abscission, leaving terminal twigs bare in midseason (Friend, 1931) (Figs. 2 and 3). In the mid-Atlantic part of the eastern United States, the preferred hosts are grey birch (*Betula populifolia* Marsh.), paper birch (*Betula papyrifera* Marsh.), and silver birch (*Betula pendula* Roth) (Fuester et al., 1984). In Europe, heaviest infestations of birch leafminer usually occur in open country, especially along highways and in parks and gardens, but seldom in forests (Eichhorn and Pschorn-Walcher, 1973). This is also the pattern in North America.

Figure 2 Birch leafminer damage to individual leaves. Whitney Cranshaw, Colorado State University, Bugwood.org.

Figure 3 Birch leafminer damage at the whole tree level. Ronald S. Kelley, Vermont Department of Forests, Parks and Recreation, Bugwood.org.

Extent *Fenusa pumila* is widely distributed over much of Europe, where it is a common but not serious pest (Eichhorn and Pschorn-Walcher, 1973). Heavy infestations were common in parts of the eastern United States, and these remained relatively constant from year to year (Fuester et al., 1984). In recent years, damage from this pest has declined dramatically in New England and surrounding states (Casagrande et al., 2009b), and a recent survey across Canada found that *F. pumila* was absent or rare at most of the locations surveyed (Digweed et al., 2009).

Biology of Pest

Fenusa pumila overwinters in the soil as prepupae. In spring prepupae complete their development and adults emerge coincident with the development of new birch foliage, where adults lay their eggs (Digweed et al., 2009). Eggs are inserted into the palisade parenchyma of the leaf tissue, mostly near the leaf midrib (Eichhorn and Pschorn-Walcher, 1973). Eggs hatch in about eight days, and larvae pass through four instars, each of 2–3 days duration, while mining the leaf. The fifth instar (Fig. 4) exits the leaf and drops to the ground where it forms a pupal cell at a depth of 2–5 cm in the soil (Eichhorn and Pschorn-Walcher, 1973). There are generally 3–4 generations in the United States (Friend, 1931; Van Driesche et al., 1997), and up to three in Canada (Digweed et al., 2009). An increasing percentage of each succeeding generation goes into diapause. For example, in Rhode Island 73% of the first generation larvae and 83% of second generation larvae enter diapause (Van Driesche et al., 1997).

Figure 4 Heavily mined leaf with mature larvae exiting the leaf. E. Bradford Walker, Vermont Department of Forests, Parks and Recreation, Bugwood.org.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

All the known species in the genus *Fenusa* in North America are invasive European species. This lack of native species in the genus provided adequate specificity, as each of the two European parasitoids released in North America against *F. pumila* had genus or lower level of specificity (as evidenced by surveys in Europe, before parasitoid introductions [Eichhorn and Pschorn-Walcher, 1973]).

The genus *Fenusa* is part of the tribe Fenusini (all of which are leafminers), in which Smith (1971), in describing the Neartctic fauna, included eight additional genera: (1) *Bidigitus* (two species, but only one of which is Nearctic: *Bidigitus platani* [Burks] on *Plantanus* in California); (2) *Fenella* (11 species, all Palearctic)*;* (3) *Messa* (see discussion of this group in next paragraph); (4) *Metallus* (21 species, of which only three are found in the Nearctic; *Mettalus lanceolatus* [Thomson] [but, which some authors considered invasive in North America], *Metallus ochreus* D. R. Smith, and *Mettalus rohweri* MacGillivray); (5) *Nefusa* (three species, but only one Nearctic species: *Nefusa ambigua* [Norton]); (6) *Profenusa* (14 species, of which four species—*Profenusa alumna* [MacGillivray], *Profenusa canadensis* [Marlatt], *Profenusa inspirata* [MacGillivray], and *Profenusa lucifex* [Ross]—are native to the Nearctic, and one—*Profenusa thomsoni* [Konow] —is a Palearctic species that is invasive in the Nearctic); (7) *Prolatus* (a monotypic genus with one Nearctic species, *Prolatus artus* D. R. Smith); and (8) *Setbara* (a monotypic genus with one Nearctic species, *Setbara histrionica* MacGillivray).

The four species placed by Smith (1971) in *Messa* are now placed in the genus *Fenusella* (also in the *Fenusini*). There are eleven species in the genus, of which three are native to North America, two are Eurasian species that have invaded the Nearctic, and the remaining six are Palearctic. North American species include *Fenusella alaskana (*Kincaid), *Fenusella leucostoma* (Rohwer), and *Fenusella populifoliella* (Townsend), and the species that have invaded North America are *Fenusella hortulana* (Klug) and *Fenusella nana* (Klug). The genus *Scolioneura* was added to the tribe Fenusini by Nyman et al. (2006). This genus is comprised of four Palearctic species, one of which, *Scolionuera betuleti* (Klug), has invaded North America.

Another group of birch mining sawflies occurs in the genus *Heterarthrus*, placed in the tribe Heterarthrini by Nyman et al. (2006). This is a large genus with 20 Palearctic and one Oriental species, of which two of the Palearctic species, *Heterarthrus nemoratus* (Fallén) and *Heterarthrus vagans* (Fallén), have invaded North America.

A recent phylogeny of leafmining tenthredinids in the subfamily Heterarthrinae (Leppäne et al., 2012) shows that the nearest relatives of the target pest, *F. pumila*, are *F. dohrnii* (one branching point), followed by *Fenella nigrita* (Westwood) (two branching points), *Fenusa ulmi* (three branching points), and then species of *Scolioneura* or *Fenusella* (four branching points) (see above discussion for notes on presence of species in these groups in North America). Of these, the only species native to North America are three *Fenusella* species, *F. alaskana, F. leucostoma*, and *F. populifoliella*.

Another means to estimate safety of introduced parasitoids is to see if the target's host plant acts as a filter. That this is the case for birch leafminer parasitoids is implied but not formally proven by the survey results of Eichhorn and Pschorn-Walcher (1973). If attraction to birch is a filter, then elements of the nontarget, native leafminer fauna in North America potentially at risk would be further reduced, given the following host affiliations: *Profenusa* (birch [but introduced species] and oak, *Fenusella* (birch, willow and poplar), *Metallus* (blackberry [*Rubus*]), *Bidigitus platani* (*Plantanus*), *Prolatus artus* (host unknown, from Oregon), and *Setbara histrionica* (no information). Focusing just on groups known to feed on birch trees, the most logical native species to investigate would be the birch feeding species of *Fenusella*.

Native Natural Enemies Affecting the Pest

Cheng and LeRoux (1969) reported 22 North American parasitoids known to attack *F. pumila*. The 15 of these parasitoids reared in Quebec by Cheng and LeRoux (1969), included one egg parasitoid (*Trichogramma minutum* Riley) causing 2.1–4.8% mortality, and 14 larval parasitoids collectively causing 1.8–7.1% larval mortality. The most notable of these larval parasitoids was *Chrysocharis laricinellae* Ratz., an introduced European parasitoid that accounted for about one-third of total parasitism. In contrast, in Europe *F. pumila* is attacked by a complex of 17 parasitoids, and larval parasitism ranges from 38 to 47% (Eichhorn and Pschorn-Walcher, 1973).

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Fenusa pumila has a native Palearctic distribution. The origin of the North American introduction is unknown, but may have been associated with the movement of European nursery stock to North America, which was unregulated until the early part of the 20th century.

Areas Surveyed for Natural Enemies

At the request of the Canadian Department of Environment in 1968, scientists from the Commonwealth Institute of Biological Control initiated surveys in Europe for parasitoids of *F. pumila* (Eichhorn and Pschorn-Walcher, 1973). Areas surveyed included Switzerland, Germany, Austria, France, and Denmark.

Natural Enemies Found

Seventeen parasitoids of *F. pumila* were located in Europe, including four in the family Ichneumonidae, one in the Braconidae, and 12 in the Eulophidae. Of these species, *Lathrolestes nigricollis* (Fig. 5) and *Grypocentrus albipes* Ruthe were identified as the most promising candidates for introduction to North America (Eichhorn and Pschorn-Walcher, 1973)

Figure 5 *Lathrolestes nigricollis* on a mined leaf. Richard A. Casagrande, Department of Plant Sciience & Entomology, University of Rhode Island.

Host Range Test Results

Host ranges of the parasitoids introduced to North America for biological control of the birch leafminer were surmised based on field observations in their native range. Host range was discussed by Eichhorn and Pschorn-Walcher (1973), who report that, based on European field observations, "*G. albipes* is a highly specific parasite, which has so far been obtained only from *F. pusilla* and from no other leaf-mining sawfly on birch or alder." Also, they reported that "*G. albipes* is highly host-specific (probably monophagous) and *L. nigricollis*, possibly also so." They described *Chrysocharis nitetis* (Walker) as polyphagous.

Releases Made

Lathrolestes nigricollis and *G. albipes* were released in Canada in Newfoundland and Labrador in 1973, in Quebec in 1974–78; in Edmonton, Alberta, in 1994–96 (Digweed et al., 2009); and in the eastern United States in 1976–1982 (Fuester et al., 1984). *Lathrolestes nigricollis* was also moved from Pennsylvania to Massachusetts and Rhode Island in 1989–90 (Van Driesche et al., 1997). Two other species were released against *F. pumila* in the eastern United States in 1979–81 (Fuester et al., 1984): *C. nitetis* (Eulophidae) was introduced in 1980–81 before it was known already to be present in North America (Hansson, 1985, 1987) and *Shawiana* nr. *cantenator* (Haliday) (Hymenoptera: Braconidae) which was introduced under the name *Phanomeris* sp. probably *catenator* Haliday.

EVALUATION OF PROJECT OUTCOME

Establishment of Agents and Effect on Pest

Forty seven individuals of the braconid *S.* nr. *cantenator* were collected in central France and released in Pennsylvania in September, 1979, but no recoveries were made. The failure of establishment for this species was attributed to the small number of parasitoids released and the late release date, when relatively few host larvae were present (Fuester et al., 1984.)

The eulophid *C. nitetis* was recovered at a Pennsylvania release site in 1982–1983, but it is now known to be Holarctic in distribution and has been found attacking several birch leafmining sawflies, including *F. pumila*, *H. nemoratus* (Fallén), and *Scolioneura vicina* Konow in North America and *F. nana* (Klug) and *P. thompsoni* (Konow) in Europe (Digweed et al., 2009). Its extensive host list also includes leafmining moths and beetles (Eichhorn and Pschon-Walcher, 1973). It was found to kill very few larvae of *F. pumila* or *P. thompsoni* in Alberta, Canada, but did kill 22% of the *H. nemoratus* sampled by Digweed (1998). There have been no further reports on the incidence of this parasitoid in the northeastern United States since Fuester et al. (1984).

Grypocentrus albipes was recovered in 1979 at one release site in Pennsylvania, but it has not been recovered in the United States since then (Fuester et al., 1984). In Canada, it became established near Quebec City (Quednau, 1984) and in Alberta, where it spread only a short distance and had minimal impact on *F. pumila* populations three years after its release (Langor et al., 2000). Establishment of this species proved difficult and Quednau (1984) lists many failed release attempts.

In contrast*, L. nigricollis,* established quickly and did so at all North American release sites (Digweed et al., 2009). This parasitoid appears to spread very quickly, but it may take many years to exert its full impact upon *F. pumila* populations (Casagrande et al., 2009). Digweed et al. (2009 reported that in Alberta this species spread 280 km west in seven years. At a rate of 40 km per year, the parasitoids released in Pennsylvania in 1979 or Quebec in 1974 may have managed to spread to central Massachusetts by 1989, and throughout southern New England a few years later. Thus, it is not clear whether the widespread distribution of this parasitoid found in 1990–92 surveys (Van Driesche et al., 1997) was due to the release made in Massachusetts in 1979 or to natural spread from more distant release locations.

Substantial reductions in leaf damage have been associated with establishment of *L. nigricollis*. Van Driesche et al. (1997) noted a decline in the percentage of leaves mined at release sites in Amherst, Massachusetts, from about 50% in 1979–80 to 1–3% in 1990–95 as parasitism rates increased from undetectable in 1979–80 to 30–80% in the 1990s. Similar observations were made at a site in Rhode Island, where the percentage of mined leaves declined from 87% in the 1990s to about 3% in 2004–2008, as parasitism by *L. nigricollis* rose from 6% in the 1990s to 38% in 2004. Thereafter, larvae could not be found at the site to measure parasitism rates (Casagrande et al., 2009b).

A survey conducted in 2007 at 183 sites in seven states in the northeastern United States revealed that in five of the seven states, *F. pumila* populations and resulting damage had declined to barely detectable levels (Casagrande et al., 2009b). Damaging populations were only found in the southernmost survey sites (southern New Jersey and Delaware), primarily south of 40° NL. Digweed et al. (2009) also reported that *F. pumila* was rare or absent at most sites surveyed for this pest in Canada. Recent conversations with entomologists in the midwestern United States revealed that, although *F. pumila* densities have not been measured, this pest has declined from regular outbreak status in the mid-1990s to low density populations that do not require control in Ohio, Michigan, Indiana, and Minnesota (D. Herms, C. Sadof, and S. Katovich, personal communication). In the absence of survey data, it is difficult to positively attribute this population decline to *L. nigricollis*; however, based on the 40-km per year estimate of spread to the west, this parasitoid should have moved throughout these midwestern states in 1985–1996. The decline of *F. pumila* in the midwestern United States resembles that observed in the northeastern region

Nontarget Effect

No effects on nontarget species have been attributed to *L. nigricollis* or *G. albipes*, the two introduced exotic parasitoids of *F. pumila* that successfully established in North America. Neither parasitoid species has been reported to attack other birch leafmining sawflies in either North America or Europe (Digweed et al., 2009).

Recovery of Affected Tree Species or Ecosystem

Fenusa pumila caused extensive defoliation of native birches, but did not directly kill host trees in North America. This defoliation no longer occurs where the pest is under biological control. Trees in ornamental settings have increased aesthetic value and there is less need to use insecticides to prevent damage

Broad Assessment of Factors Affecting Success or Failure of Project

This biological control program appears to be an unqualified success in the northeastern United States and Canada, with benefits apparently extending into the midwestern United States. It has been less successful south of 40° NL. Possible reasons for this failure in the more southern area could be that the parasitoids released in this area were collected in Austria at 47–48 ° NL (possibly affecting diapause timing), or that the host trees in this area are also well out of their natural range and growing under stressed conditions (Casagrande et al., 2009b).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

The life histories of the two key parasitoids used in this project, *L. nigricollis* and *G. albipes*, were investigated in depth by Eichhorn and Pschorn-Walcher (1973).

Lathrolestes nigricollis has proven to be the key species for biological control of the birch leafminer. It is a multivoltine endoparasitoid that primarily attacks semi-mature and mature larvae. Parasitoids overwinter in host cocoons in the soil. Females lay about 120 eggs. Eggs hatch in 3–7 days, and larval and pupal development requires about 31 days, so the total immature development is completed in about 5 weeks. From 23–28% of the parasitoids that attack the first generation of *F. pumila* emerge and attack the second and third host generations. Most parasitoids enter diapause and emerge the following spring. Parasitism rates generally increase with each succeeding generation of *F. pumila*. However, in southern New England each succeeding generation of the pest has fewer individuals than the previous generation, so most parasitoids are produced by the first and second generations (Van Driesche et al., 1997).

RECOMMENDATIONS FOR FURTHER WORK

A survey of birch leafminer densities and parasitism rates in the midwestern United States, similar to the survey of Casagrande et al. (2009b), would very likely show that *F. pumila* is under good biological control in that region, and that control recommendations and fact sheets could be revised, accordingly.

It is possible that a search of southern Europe or areas closer to the Atlantic coast might provide a source of parasitoids that are better suited for southern New Jersey and the mid-Atlantic portion of the eastern United States. However, another solution, at least in urban landscapes, might be to replace the species of birches used as ornamentals with species better suited to that climate, such as heat-tolerant cultivars of *Betula nigra* L. This species would be a reasonable replacement for the susceptible birches and offer resistance not only to *F. pumila*, but also to the bronze birch borer (*Agrilus anxius* Gory), a serious pest in that region.

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XVI HEMLOCK WOOLLY ADELGID

(*Adelges tsugae* Annand) (Hemiptera: Adelgidae)

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DESCRIPTION OF PEST

Taxonomy

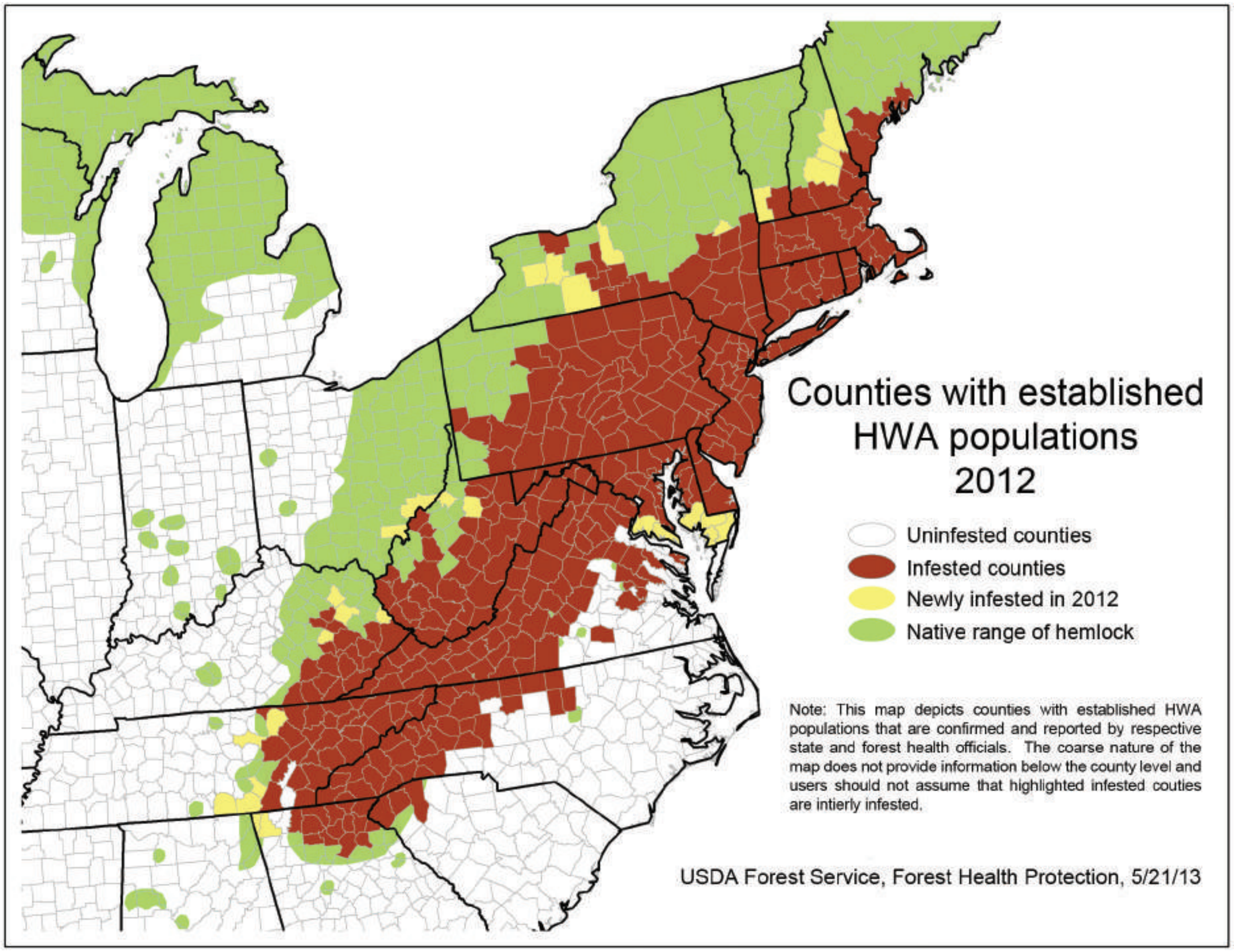
The hemlock woolly adelgid (HWA), *Adelges tsugae* Annand 1924 (Hemiptera: Adelgidae), was first described from specimens collected in Eugene, Oregon (Annand, 1924, 1928), on western hemlock (*Tsuga heterophylla* [Raf.] Sargent) trees. Synonyms for the species are *Chermes funitectus* Dreyfus, *Chermes tsugae* (Annand) and *Aphrastasia tsugae* Annand (Annand, 1928; Keen, 1952; Havill and Foottit, 2007). Worldwide, the family includes two genera (*Adelges* and *Pineus*) and about 65 species (Havill and Foottit, 2007).

Distribution

Hemlock woolly adelgid is native to Asia and western North America, and through DNA analysis the population invasive in eastern North America was determined to have originated in southern Japan (Havill et al., 2006). It has become the most important pest of eastern hemlock (*Tsuga canadensis* [L.] Carrière) and Carolina hemlock (*Tsuga caroliniana* Engelmann). Voucher specimens in the United States National Museum and a report from the Virginia Department of Agriculture and Consumer Services (Miller, 1988) indicate that HWA was first identified in eastern North America in Richmond, Virginia, in 1953 or 1954. A number of Japanese gardens were known to be present in the area during the early 20th century and it is likely that the adelgid was transported on nursery stock of Asian hemlocks.

Hemlock woolly adelgid spread among ornamental hemlocks to the north and west of Richmond, Virginia, and was reported in native hemlock forests in the Blue Ridge Mountains in the late 1960s or early 1970s (Miller, 1988), Pennsylvania in the 1960s, and New York in the early 1980s (Souto et al., 1996). In 1985, HWA was reported in Connecticut after the passage of a hurricane, which may have moved HWA northward from Long Island (McClure, 1987a). Today, HWA ranges from New England to the southern Appalachians and inland to Kentucky and western New York (USDA Forest Service, 2011) (Fig. 1). As of 2011, nineteen states were known to be infested, representing a major portion of the ranges of eastern and Carolina hemlocks in the United States (Morin et al., 2005). It continues to spread to the north and west. Winter temperatures in some areas slow HWA's spread northward or to higher elevations (Evans and Gregoire, 2007; Morin et al., 2009) and curtail the damage along the northern boundary. However, HWA is capable of adapting to cold climates (Butin et al., 2005), and the current warming trend in the world's climate suggests that this pest eventually might spread and damage eastern hemlock in areas that are currently too cold for the insect.

In spring and summer (April–July) first instar HWA ("crawlers") disperse by crawling or attaching themselves to birds and other forest animals (McClure, 1990). Wind also passively disperses crawlers over large distances. The spread of HWA into un-infested areas was calculated to have averaged 12.5 km/yr from 1990 to 2005 (Evans and Gregoire, 2007). HWA eggs also may be moved about if the sticky, flocculent ovisacs become attached to animals. Roads, hiking trails, and riparian areas are correlated to spread, perhaps because various animals use such corridors (Graham et al., 2005; Koch et al., 2006). Apart from crawlers, the insect is sedentary and does not move from where it feeds at the base of needles. Also, HWA has


Counties with established HWA populations 2012

Note: This map depicts counties with established HWA populations that are confirmed and reported by respective state and forest health officials. The coarse nature of the map does not provide information below the county level and users should not assume that highlighted infested couties are intierly infested.

USDA Forest Service, Forest Health Protection, 5/21/13

Figure 1 Distribution of hemlock woolly adelgid in the eastern United States in 2012.

been moved between states on infested nursery stock, as documented in Michigan (D. McCullough, pers. comm.) and Vermont (Burns et al., 2005).

Damage

Type HWA is specific to hemlock and the adelgid inserts its piercing-sucking mouthparts (i.e., the stylet bundle) just below the needle abscission layer, where it feeds on ray parenchyma cells (Young et al., 1995), inhibiting shoot growth, causing bud mortality, twig dieback, foliage discoloration, and premature needle loss (Fig. 2). Parenchyma cells in the sapwood store and distribute the carbohydrates that supply energy for the tree. By feeding on these cells, HWA damages the tree's energy reserves and water transport such that both growth and survival decline. The damage is analogous to the damage from balsam woolly adelgid, *Adelges piceae* (Ratzeburg) (Hemiptera: Adelgidae) (Hain, 1988). In the western United States, HWA also has been observed feeding on branches and stems with thin bark (Annand, 1924; Keen, 1952).

High HWA densities kill buds and reduce shoot growth the following growing season, which in turn may reduce HWA density because the insect has low survival on branches lacking new growth (McClure, 1991). Hemlocks and HWA populations typically resume growth the next growing season, but hemlocks never fully recover. As such, the trend in tree health is towards death with iterations of decline and recovery. Hemlock woolly adelgid slowly kills trees of all ages (including seedlings), sizes, and vigor levels in as little as four years (McClure, 1991), a scenario that is typical in hemlock's southern range (Fig. 3). However, some trees may survive for decades in a damaged or moribund state (Orwig and Foster, 1998). The time from initial infestation until tree death likely varies based on tree vigor (i.e., as determined by tree age, drought, other insects and diseases), site and soil conditions, the degree of HWA mortality due to low winter temperatures, and host tolerance (Pontius et al., 2006). In central Connecticut, few stand and landscape variables affect hemlock susceptibility and mortality, but trees succumb faster on xeric sites, and the duration of infestation is the primary factor that explains patterns of hemlock decline in this region (Orwig et al., 2002).

Extent In Asia, HWA is not considered a forest pest, as it appears to be under control by host resistance and natural enemies. Similarly, in western North America HWA populations are typically low, but populations occasionally increase to levels able to damage or kill trees (Annand, 1924; Furniss and Carolin, 1977; Keen, 1952; Collman, 1972). In Virginia, HWA caused significant damage and mortality to ornamental and native hemlocks in the late 1960s or early 1970s, but was not considered a major pest (Miller, 1988). Through the work of Mark McClure at the Connecticut Agricultural Experiment Station, HWA is recognized as a major invasive forest pest (see McClure and Cheah, 1999 and references therein).

Figure 2 Damage symptoms by high HWA densities include tip dieback, bud mortality, and premature needle loss. David Mausel, Virginia Polytechnic Institute and State University (Virginia Tech.), Bugwood.org

Figure 3 Hemlock decline and mortality in the Nantahala National Forest, North Carolina. William M. Ciesla, Forest Health Management International, Bugwood.org.

Hemlock mortality is extensive but variable throughout the southern Appalachians, mid-Atlantic states, and southern New England. Eastern hemlock mortality caused by HWA has confounded sustainable forest management plans (Orwig and Kittredge, 2005), because hemlock is one of the most common conifers in northern hardwood forests, can form unique stands and habitats, and often is located in sensitive riparian areas. Hemlock woolly adelgid has increased the costs of ornamental/park tree management by requiring pesticide treatments or hazard-tree removals. As well, HWA has damaged nutrient cycles, ecosystem structure and function, stream bank stability, and water quality (D'Amato et al., 2008).

Ecological effects of hemlock loss on other species have been studied in the Delaware Water Gap National Recreation Area in New Jersey and Pennsylvania (Evans, 2002). With loss of hemlock, stands shift toward deciduous trees (Orwig, 1998), which are less able to maintain cool habitats and low stream temperatures. This can lead to losses of some species found in such habitats (Buck et al., 2005), including a decline in native trout populations in affected streams. In contrast, Siderhurst et al. (2010) did not find evidence that long-term light levels and stream temperatures would be affected by the loss of *T. canadensis*. Nevertheless, HWA has the potential to reduce biodiversity in general and cause far-reaching and unanticipated environmental effects.

Biology of Pest

HWA has two wingless asexual generations per year on hemlock in the eastern United States (McClure, 1989). White cottony flocculence covers the apterous HWA life stages (Fig. 4) in the sistens (summer–early spring) and progrediens (spring) generations (except during summer diapause) (Fig. 5). There are six female developmental stages: egg (amber colored), four nymphal instars, and the adult. The adults and nymphs are reddish black to dark purple, and 0.4–1.4 mm long. Eggs are laid within the flocculence at the rear of the adult (this region is called the ovisac). Only first instar nymphs (crawlers) of each generation are capable of moving, and this stage lacks white flocculent material (Fig. 6). Sistens adults can lay up to 350 eggs and progrediens up to 75 eggs, but fecundity varies greatly with host condition (McClure, 1991). Sistens eggs hatch in late spring, and the nymphs settle on the needle's pulvinus (the woody "peg-like" part of the stem). Nymphs enter summer diapause, complete development in the fall/winter, and in the late winter or early spring adults lay the eggs, giving rise to the progrediens generation (McClure, 1987a; McClure, 1989; Gray and Salom, 1996; Zilahi-Balogh et al., 2003a). Specific timing of HWA phenological events depends on regional climate, elevation, and microclimate. Sistens survive for approximately nine months. Lagalante et al. (2006) proposed that sistens go into aestivation (summer diapause) to avoid chemical

Figure 4 High-density HWA infestation on eastern hemlock. Michael Montgomery, USDA Forest Service, Bugwood.org.

Figure 5 Aestivating sistens on eastern hemlock. Ashley Lamb, Virginia Polytechnic Institute and State University (Virginia Tech.), Bugwood.org.

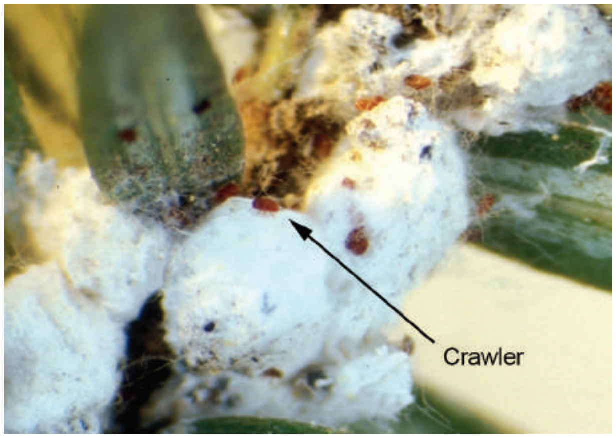


Figure 6 Crawlers, the only mobile stage of sistens and progrediens generations. Pennsylvania Department of Conservation and Natural Resources, Bugwood.org.

defenses of the host tree (Fig. 5). However, Salom et al. (2001), showed that aestivation is maternally regulated and can be prevented by exposing progrediens during the egg through 2^{nd} instar stages to temperatures below 14.5°C at a photoperiod of 12:12 L:D. The progrediens eggs hatch in the early spring, nymphs develop, and new adults lay sistens eggs by late spring. Progrediens stages are present for approximately three months. Sistens can produce a winged generation (termed the sexuparae) in response to poor hemlock health (McClure, 1991).

Holocyclic species of *Adelges* have spruce (*Picea*) species as a primary host and *Tsuga, Larix, Pseudotsuga,* or *Abies* as secondary hosts (Moran, 1992; Blackman and Eastop, 1994; Havill and Foottit, 2007). The primary host of HWA in Japan is the tiger-tail spruce, *Picea torano* (Siebold ex K. Koch) Koehne (Blackman and Eastop, 1994). Secondary hosts of HWA are restricted to the genus *Tsuga,* of which there are nine species worldwide (Farjon, 1990). The HWA life cycle in North America is anholocyclic on hemlock, because sexuparae offspring apparently do not survive past the first instar on the spruce or hemlock species available (McClure, 1987a, b). Thus, the ability to migrate and reproduce sexually is lost. Alate sexuparae have not been observed in western North America (Annand, 1924; Zilahi-Balogh *et al*., 2003a; Kohler et al., 2008), indicating that this HWA population has completely lost the sexual part of the life-cycle (Blackman and Eastop, 1994; Havill and Foottit, 2007).

ANALYSIS OF RELATED NATIVE INSECTS IN THE EASTERN USA

Native Insects Related to the Pest (Nontarget Species)

Nontarget species at risk of harm from introduced natural enemies are most likely to be closely related to HWA, such as other Sternorrhyncha (i.e., aphids, other adelgids, scales, etc.). For example, the woolly alder aphid, *Paraprociphilus tessellatus* (Fitch) (Hemiptera: Aphidiae), is a species of special concern because it is a prey item for larvae of the harvester butterfly, *Feniseca tarquinius* F. (Lepidoptera: Lycaenidae), the only predaceous butterfly in the United States (Baker, 1994). According to the latest review of the Adelgidae (Havill and Foottit, 2007), native species potentially at risk in the eastern United States include *Pineus strobi* (Hartig) *Adelges lariciatus* (Patch), *A. abietis* L., *P. coloradensis* (Gillette), *P. floccus* (Patch), *P. patchae* (Borner), *P. pinifoliae* (Fitch), *P. similis* Gillette, and *P. sylvestris* Annand. Adelgid species not native to the eastern United States, that are of no nontarget concern, include the balsam woolly adelgid (*A. piceae* [Ratzeburg]), Cooley spruce gall adelgid (*A. cooleyi* Gillette), and the larch adelgid (*A. laricis* Vallot).

Native Natural Enemies Affecting the Pest

To determine what natural enemies may be needed for biological control of HWA, surveys for native or previously established, exotic natural enemies of HWA have been conducted by McClure (1987a) and Montgomery and Lyon (1996) in Connecticut, and by Wallace and Hain (2000) in North Carolina and Virginia. These surveys found a small guild of natural enemies, consisting of mostly generalist predators, that consume some HWA life stages. A survey of entomopathogenic fungi of HWA in the eastern United States indicates that several generalist pathogens also attack this pest (Gouli et al., 1997; Reid et al., 2010).

McClure (1987a) found species of Cecidomyiidae, Syrphidae, and Chrysopidae associated with HWA, but densities were too low to reduce adelgid populations. Surveys by Montgomery and Lyon (1996) on HWA-infested eastern hemlock growing together with eastern white pine (*Pinus strobus* L.) and Scotch pine (*Pinus sylvestris* L.) recovered *Scymnus suturalis* Thunberg (Coleoptera: Coccinellidae), *Laricobius rubidus* Leconte (Coleoptera: Derodontidae), and a brown lacewing (Hemerobiidae).

Scymnus suturalis, *L. rubidus Leucopis* (*Neoleucopis*) sp. (Diptera: Chamaemyiidae), and a *Tetraphleps* sp. (Hemiptera: Anthocoridae) were recovered on *P. strobi*-infested eastern white pine. Both *S. suturalis* and *L. rubidus* were abundant on pine and hemlock. *Scymnus suturalis* is of European origin and was introduced into Michigan in the 1960s (Gordon, 1985). Surveys by Wallace and Hain (2000) on HWA-infested eastern hemlock in three forested sites over two years in northern North Carolina and southern Virginia recovered *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae); *Chrysoperla harrisii* (Fitch) (Neuroptera: Chrysopidae); *Hemerobius humulinus* L. and *Hemerobius* sp. (Neuroptera: Hemerobiidae); *Aphidoletes abietis* Kieffer, *Aphidoletes aphidimyza* Rondani, and other *Aphidoletes* species, *Lestodiplosis* sp., and *Trisopsis* sp. (Diptera: Cecidomyiidae); *Leucopis* sp. (Diptera: Chamaemyiidae); species of Syrphidae (Diptera: Syrphidae); and *L. rubidus*. Predators were collected in very low numbers in both years. Overall, *H. axyridis*, Neuroptera (collectively), and Cecidomyiidae (collectively) were most abundant. Cage-exclusion experiments indicated that these predators had no significant effects on the density of HWA populations.

One of the few specialized predators of HWA in eastern North America, *L. rubidus,* feeds exclusively on adelgids and is able to complete its development and survive well on an exclusive diet of HWA (Zilahi-Balogh et al., 2005). This predator is present in Connecticut (Montgomery and Lyon, 1996), North Carolina, Virginia (Wallace and Hain, 2000), Maine, New Hampshire, Massachusetts, District of Columbia, Pennsylvania, New York, Michigan, Quebec, Ontario, and New Brunswick (Lawrence, 1989). The primary host of *L. rubidus* is the pine bark adelgid, *P. strobi* on eastern white pine (Clark and Brown, 1960).

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

HWA is endemic to Asia and western North America, and these areas have been comprehensively surveyed for candidate biological control agents. Recent foreign exploration has focused on Japan, since the discovery that the origin of the infestation in eastern North America is from this location (Havill et al., 2006).

Areas Surveyed for Natural Enemies

All adelgid species lack parasitoids (Clausen, 1978), and the search for an effective HWA biological control agent has focused primarily on specialized predators in the Coccinellidae (*Scymnus* spp.), Derodontidae (*Laricobius* spp.), and Chamaemyiidae (*Leucopis* spp.) in Asia (Japan, China, and Taiwan) and western North America.

Natural Enemies Found

Surveys in Japan discovered the mite *Diapterobates humeralis* Hermann (Oribatida: Ceratozetidae), which eats the cottony flocculence covering HWA, leaving HWA eggs exposed to the environment and predation (McClure, 1995) by the coccinellids *Sasajiscymnus* (= *Pseudoscymnus*) *tsugae* (Sasaji and McClure), *Scymnus posticalus* Sicard, *Adalia conglomerata* (L.), and *Scymnus giganteus* Kamiya (Sasaji and McClure, 1997; Yu, 2001), and the derodontid predator *Laricobius osakensis* Montgomery and Shiyake (Montgomery et al., 2011).

Surveys in China discovered many HWA predators, especially Coccinellidae (Yu et al., 2000; Yu, 2001). *Tetraphleps galchanoides* Ghauri (Hemiptera: Anthocoridae) and three coccinellids–*Scymnus camptodromus* Yu and Liu, *Scymnus sinuanodulus* Yu and Yao, and *Scymnus ningshanensis* Yu and Yao–were collected. Additional surveys found two new species of *Laricobius*: *L. boaxingensis* Zilahi-Balogh and Jelínek and *L. kangdingensis* Zilahi-Balogh and Jelínek (Coleoptera: Derodontidae) (Zilahi-Balogh et al., 2007).

In Taiwan, many individuals of *Laricobius taiwanensis* Yu & Montgomery were collected in 1994 (Yu and Montgomery, 2007), but no further work has been done at this location.

A survey of HWA-infested western hemlock in the northwestern United States, 2005–06, recorded 55 species of predators (Kohler et al., 2008). *Laricobius nigrinus*, *Leucopis argenticollis* Zetterstedt, and *Leucopis atrifacies* (Aldrich) (last two, Diptera: Chamaemyiidae) comprised 59% of all the predators collected, with *L. nigrinus* being the most abundant.

Host Range Test Results

Host-range testing has been completed for *Sasajiscymnus tsugae*, *Scymnus ningshanensis* (Butin et al., 2004), *Scymnus sinuanodulus* (Montgomery and Keena, 2012), *L. nigrinus* (Zilahi-Balogh et al., 2002a), and *L. osakensis* (Vieira et al., 2011). All species appear to prefer HWA, but will feed on other adelgid species. *Leucopis argenticollis* and *Leucopis piniperda* Malloch (Diptera: Chamaemyiidae) also were tested: they preferred HWA but also developed on other adelgids, suggesting these species might not be specific to HWA (Grubin et al., 2011).

Testing of *T. galchanoides* (McAvoy et al., 2007 found that it feeds and develops on other adelgid and non-adelgid prey (unpublished data) and further work on this species was abandoned.

Tests with *L. kangdingensis* were begun, but due to our inability to rear this species successfully in the laboratory, and challenges associated with collecting it in its native habitat (Sichuan Province, China), host-range studies were not completed (Gatton et al., 2009).

Releases Made

Four predators of HWA have been released in the eastern United States either for experimental evaluation or to suppress HWA. According to the HWA Predator Release and Monitoring Database (2012), some 2.5 million *S. tsugae* were released at 731 sites, 1998–2011, and 164,381 *L. nigrinus* were released at 345 sites, 2003–2011. Between 2004 and 2011, nearly 19,000 adults of *S. sinuanodulus* were released at 27 sites throughout the eastern United States, as well as 43,000 eggs or larvae of that species that were released at 100 sites, all in Georgia (Montgomery and Keena, 2012). Additionally, 1,400 *S. ningshanensis* were released at four locations in Massachusetts, Connecticut, and North Carolina, between 2007 and 2009 (Montgomery and Keena, 2012).

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

Sasajiscymnus tsugae and *L. nigrinus* have established to varying degrees as localized populations at sites throughout a considerable portion of the current range of HWA. Establishment of *S. tsugae* has been inconsistent (McClure and Cheah, 2003; Hakeem et al. 2010); establishment of *L. nigrinus*, especially in plant hardiness zones 6a and 6b, has been more predictable (Mausel et al., 2010; Davis et al., in press). Thus far, evidence of HWA suppression has been limited to anecdotal observations (Cheah et al., 2005; McDonald et al*.,* 2008). Rigorous scientific efforts are underway to evaluate predator impact (Mech et al., 2010; Davis et al., 2011); long term studies are required in a variety of locations due to many uncontrollable variables that affect the interaction of HWA with its predators, host trees, and local climate.

The first *L. nigrinus* release liberated an estimated 10,344 eggs in early spring 2003 (Lamb et al., 2006). The eggs came from caged females, whose survival, predation, and oviposition were being studied. Also, in fall 2003, 258 adults were free-released in a planting of HWA-infested hemlocks to create a "field insectary" from which field-acclimated beetles could later be harvested to supplement mass rearing operations (Mausel et al., 2008).

From 2003–2005, a large-scale set of experimental releases (totaling 9,225 beetles) at 22 sites was used to investigate the effects of climate, release size, and release season on establishment rates (Mausel et al., 2010). With increased mass-rearing productivity (Lamb et al., 2005) and the successful mass-collection of adults in Seattle, Washington, releases of *L. nigrinus* continued at sites with adequate (i.e., increasing) populations of HWA prey. Several releases of *L. nigrinus* eggs were made in Georgia to further evaluate this release approach (M. Dalusky, pers. com.).

From 2007–2010, 2,686 beetles from the "inland strain" of *L. nigrinus* from Idaho and Montana, were released in the northeast and mid-Atlantic states to test the beetle's viability in New England and other areas with colder winter temperatures (Mausel et al., 2011).

Establishment of the coastal strain of *L. nigrinus* has been well documented and is extensive, especially in plant hardiness zones 6a and 6b (Mausel et. al., 2010). Both Mausel et al. (2010) and Davis et al. (2012) found that sampling for *L. nigrinus* larvae in the mid- to upper-canopy of trees most accurately reflects the presence of *L. nigrinus*. Though requiring less effort, beating branches for adults, more frequently failed to detect beetles at locations where the species had actually established.

A cage-exclusion experiment on branches (HWA colonies protected from attack by local predators) detected a significant effect of *L. nigrinus* on HWA mortality in the field two years after release of the predator at the study site (Mausel et al., 2008). At release sites in Virginia and Pennsylvania, *Laricobius* spp. densities reached levels comparable to those observed in its native range in western North America; however, the ratio of *Laricobius* spp. to HWA remains much lower at this time than that observed in their native range (Mausel, 2007; Davis, 2011).

Scymnus sinuanodulus adults and immature stages were released throughout the eastern United States, starting in 2004. Unfortunately, there is no evidence that this species has established: as a result, it may not merit further efforts in rearing and release (Montgomery and Keena, 2012). There were limited field releases of *S. ningshanensis* in 2007, but progeny of this species have yet to be recovered (Montgomery and Keena, 2012).

Nontarget Effects

Laricobius rubidus, native to eastern North America and a predator of the pine bark adelgid (PBA), *P. strobi*, was found on HWA-infested eastern hemlock (Montgomery and Lyon, 1996: Wallace and Hain, 2000). Zilahi-Balogh et al. (2005) found that *L. rubidus* can feed and develop on HWA, but strongly prefers its usual prey, *P. strobi.* At sites where *L. nigrinus* was released and white pine was present, both *Laricobius* species were found together on HWA-infested hemlock (Mausel et al., 2010, Davis et al., 2011). Larvae of these species are morphologically indistinguishable, yet sampling for the larval stage is the most reliable for determining presence of both species. To this end, molecular techniques were developed to accurately identify larvae to species (Havill et al., 2010; Davis et al., 2011). Story (2010) assessed performance and competition between *L. nigrinus* and *L. rubidus* and found no negative interactions between these species while they were engaged in their normal behaviors of predation on HWA and oviposition in HWA ovisacs.

Mausel et al. (2008) observed *L. nigrinus* and *L. rubidus* mating in a young HWA-infested hemlock plantation adjacent to a white pine plantation. Adults with physical characteristics intermediate to those of *L. nigrinus* and *L. rubidus* were collected at an increasing rate at field sites where *L. nigrinus* had previously been released (Davis et al., 2012). In 2008, interspecific mating between *L. nigrinus* and *L. rubidus* was studied in the laboratory. Inter-species pairings produced ten larvae, which were genetically analyzed and confirmed to be true hybrids (Nathan Havill, pers. com.). The occurrence and implications of hybridization between these two species in terms of biodiversity and biological control are being investigated (Fischer et al., 2010; Havill et al., 2012).

Recovery of Affected Tree Species or Ecosystems

Eastern hemlock and Carolina hemlock continue to decline throughout the invaded range of HWA, which continues to expand. The rate of tree decline appears quickest where the climate is most mild and slowest where the temperatures are coldest during the winter. Many other factors come into play, such as the age of the trees, soils, drought stress, other pests, and diseases. Until this system is sufficiently studied, we can only guess what role each factor plays alone and together in the decline and recovery of trees.

Broad Assessment of Factors Affecting Success or Failure of Project

It is too early to make this assessment. New predators, such as *L. osakensis* from Japan (Lamb et al., 2010) and *Scymnus coniferarum* Crotch from western North America (McDonald, 2010), continue to be studied and considered for release as biological control agents. While there are many successful aspects to the biological control program for HWA, the ultimate success of imported predators actually suppressing pest populations and returning hemlock trees to health still eludes us. Ultimately, an integrated program that involves the use of natural enemies as part of the solution, not necessarily the whole solution, may be required, as in the case of the invasive weed tree, *Melaleuca quinquenervia* (Cav.) S. F. Blake, in south Florida (Martin et al., 2011).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Sasajiscymnus tsugae

Sasajiscymnus tsugae is associated with HWA populations in Japan but also occurs with unknown associations in marshes (McClure, 1995; Sasaji and McClure, 1997) (Fig. 7). Its original genus name, *Pseudoscymnus*, was noted to be occupied, and consequently was changed to *Sasajiscymnus* (Vandenberg, 2004). Sasaji and McClure (1997) stated that this insect was the main predator of HWA in Honshu, Japan, between the months of May and June. Shiyake et al. (2008) collected *S. tsugae* between March and December, with peak numbers occurring in the summer, and suggested it was most likely responsible

Figure 7 *Sasajiscymnus tsugae*. Adult (above), late instar larva (below). Carole Cheah, Bugwood.org.

for the decline in number of diapausing HWA nymphs present during that period.

Sasajiscymnus tsugae has four larval instars, a pre-pupa, and pupa (Cheah and McClure, 1998). Adults overwinter on the trees and become active in April or May in Connecticut, feeding on nymphs of the progrediens generation (Cheah et al., 2004). *Sasajiscymnus tsugae* eggs are laid singly in concealed sites in curled bud-scales or, less frequently, in empty male cones or beneath the progrediens' ovisacs (Cheah and McClure, 1998). Larvae hatch and feed on progrediens nymphs and adults and sistens eggs. There are one or two generations per year (Cheah and McClure, 2000). This insect is easily mass-reared because it has a long life span in the laboratory, high fecundity (averaging 280 eggs per female), and no obligate diapause (e.g., Jubb, 2012).

Sasajiscymnus tsugae has been released in most HWA-infested states from Georgia to New Hampshire and is considered established in several states (McClure *et al.,* 2000; Palmer and Sheppard, 2002; Blumenthal, 2002). However, compared to *S. ningshanensis,* in sleeve cages it was found to have little impact on HWA population increase (Butin *et al*., 2003). Between-year effects on HWA densities in the field have not been demonstrated, despite some positive indications of impact during the year of release at some sites (Casagrande *et al*., 2002; Cheah and McClure, 2002). Some improvement in hemlock health has occurred at release sites, but high winter mortality of HWA may be the cause (Cheah *et al*., 2005). In whole tree enclosures containing *S. tsugae*, foliar transparency ratings did not increase, but average new growth on branch tips did increase (Wiggins et al., 2010).

Laricobius nigrinus

Laricobius nigrinus from western North America was identified early as a species for evaluation, because it was frequently collected from HWA-infested trees in British Columbia, Canada (Humble, 1994), and all *Laricobius* species studied feed exclusively on adelgids (Leschen, 2011). *Laricobius* is one of four genera in the family Derodontidae, which is in the Polyphaga supergroup of Coleoptera (Hunt et al., 2007). *Laricobius nigrinus* was first collected and described from Bear Springs, Oregon (Fender, 1945). Adults are small (2–3 mm), shiny black, covered with fine ashy hairs, have striate elytra (10 rows) 11-segmented antennae (scape, pedicel, and nine annuli), and 5-5-5 tarsal segmentation (Fig. 8). The life stages have been described by Zilahi-Balogh et al. (2006).

Laricobius nigrinus has one generation per year, which is synchronized with the phenology of HWA in both its native and introduced ranges (Mausel et al., 2008; Zilahi-Balogh *et al*., 2003a). Both the predator and HWA are active in the fall, winter, and spring, and dormant in the summer. Adult beetles emerge from the soil in the fall, disperse to hemlock branches, and feed in fall and early winter on nymphs of the sistens HWA generation. Beetles

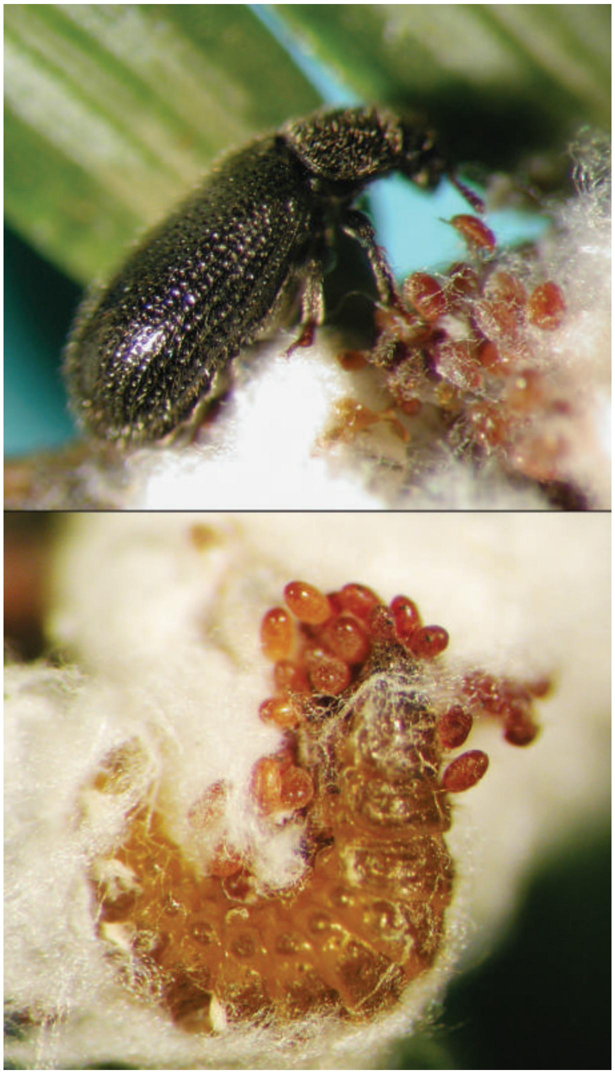


Figure 8 *Laricobius nigrinus*. Adult (above) and late instar larva (below). Rob Flowers, Virginia Polytechnic Institute and State University (Virginia Tech.).

reproduce in early spring and then die (Zilahi-Balogh et al., 2003b, c). The adults pierce HWA nymphs with pointed mandibles and consume their hemolymph and organs. In the laboratory, females oviposit up to 396 eggs (mean = 101), typically one egg per HWA sistens ovisac, but more than one is common if prey density is high. The larvae have four instars and feed on hundreds of progrediens eggs to complete larval development, which may require more than one ovisac. The most apparent signs of *L. nigrinus* feeding are disturbed ovisacs, which are useful for estimating the impact of this predator. By June, mature larvae drop to the soil where they form an earthen cell, in which they become pre-pupae and then pupae. Development from egg to adult takes 65 days at 15°C.

Laricobius osakensis Montgomery and Shiyake from Japan

Laricobius osakensis was first discovered in southern Japan in 2005 (Montgomery et al., 2011). It is a promising biological control agent for this pest, because it has co-evolved with the strain of HWA found in the eastern United States (Havill et al., 2006). It has been collected from both southern Japanese hemlock, *Tsuga seiboldii* (Carrière), and northern Japanese hemlock, *Tsuga diversifolia* (Maxim.), in fourteen prefectures, on the Japanese islands of Honshu, Kyushu, and Shikoku (Lamb et al., 2012).

Adults are 2–3 mm in length, elongate, dorsally convex, and ventrally flattened; the head has large pores or canals and 11-segmented antennae with a 3-segment club. The prothorax is narrow with esplanate sides, while the elytra are seriate or striate, and the abdomen has five visible sternites (Montgomery et al., 2011). There are two adult color morphs, one which has reddish elytra with darker maculation on the lateral edge, similar to *L. rubidus,* and a second that has nearly black (not piceous) elytra, similar to *L. nigrinus* (Fig. 9). When sorted by color, and dissected to confirm the sex by examination of the genitalia, about 90% of the reddish specimens are female, while about 80% of the dark-brown specimens are male. Following death, the reddish form turns various shades of brown. The eggs are light yellow and about 50% larger than an HWA egg. The larvae have a thin, white wax coating and usually feed inside the HWA woolly ovisac (Fig. 9).

The seasonal histories of *L. osakensis* and HWA were monitored in the Kansai area of Japan to predict the predator's ability to establish in the eastern United States. In Japan, phenology of *L. osakensis* was found to be synchronized with the winter generation of HWA on *T. sieboldii* (Lamb et al., 2012). *Laricobius osakensis* adults first appeared on trees in mid-November, approximately a week after HWA began its fall feeding activity. *Laricobius osakensis* adults remained on the trees throughout the winter and early spring. Adult *L. osakensis* began laying eggs in the woolly masses in late December, in synchrony with HWA oviposition, and continued to lay eggs throughout the winter and early spring. *Laricobius osakensis* eggs hatched from January to April and larvae fed on HWA eggs. In early spring and after developing through four instars, the larvae dropped

Figure 9 *Laricobius osakensis* adult female with typical reddish coloration (left), adult male with typical dark coloration (middle), and larva (right). Ashley Lamb, Virginia Polytechnic Institute and State University (Virginia Tech.)

from the branches and pupated in the soil. Aestivation of *L. osakensis* adults occurred from May through October. All of these life-history features show high specialization for predation on HWA.

Impacts of *L. osakensis* on HWA were assessed in the Kansai area of Japan using branch-sized exclusion cages. On 24 branches caged in January, about half the HWA were alive and produced ovisacs in May, whereas only 5% of the adelgids were alive on the 24 open branches sampled at the same time (Lamb et al., 2012). From a yearly survey of predators on *T. seiboldii* in the same region of Japan, the principal predator present in the winter was *L. osakensis*, with adult numbers peaking in March (Shiyake et al., 2008). In laboratory studies comparing *L. nigrinus* and *L. osakensis*, adults had similar functional responses to HWA as prey, but *L. osakensis* larvae had a greater functional response to HWA, and *L. osakensis* adults had a greater numerical response (Vieira et al., 2012), suggesting this species has strong potential as a biological control agent for HWA.

Host-range studies suggested that, because it can develop successfully and oviposit only on HWA, *L. osakensis* poses little risk to native nontarget insects (Vieira et al., 2011). These data led to the submission of a petition to release the insect from quarantine. In May 2010, this predator was removed from quarantine and given approval for release by the USDA APHIS. However, at about the same time (fall 2011), field collections of the beetle in Japan were found to be contaminated with a small number of another, similar species, the newly described *Laricobius naganoensis* Leschen (Leschen, 2011). Therefore, the colonies were returned to quarantine to be purified of this contaminant.

Laricobius spp. from China

Several apparently new, undescribed species of *Laricobius* have been discovered on HWA-infested hemlocks in Asia. In 1994, 62 specimens of a new species, *L. taiwanensis* Yu and Montgomery, were collected in Kaohsiung County, Taiwan, in late May (Yu and Montgomery, 2007). These insects were shipped to the USDA Forest Service Quarantine Laboratory in Connecticut, but died shortly after arrival. The high numbers collected in just a few hours suggest that this is a common and likely important predator. Two other new species*, L. baoxingensis, and L. kangdingensis*, were collected in Sichuan Province, China, in 2002 and 2004 (Zilahi-Balogh *et al*., 2007). Due to the difficulty in collecting additional insects from these very remote sites, the study of these species has not been a priority, with the exception of a laboratory study on the life cycle and development of *L. kangdingensis* (Gatton et al., 2009).

Scymnus spp. from China

Over 600 spp. of *Scymnus* have been described, this being the largest genus of lady beetles (Coccinellidae) (Montgomery and Keena, 2012). Most of these species feed on aphids or adelgids. Many species (>50) of coccinellids have been found on hemlock in China in association with HWA, including at least nine that are known to commonly feed on HWA (Montgomery *et al*., 2000; Yu *et al*., 2000). Three species (in the subgenus *Neopullus*) have been studied extensively: *Scymnus camptodromus, S. sinuanodulus*, and *S. ningshanensis* (Fig. 10). Based on abundance and observed adelgid specificity in their native habitat, these species were imported for further study, and two (*S. sinuanodulus*, and *S. ningshanensis*) have been released (Montgomery and Keena, 2012).

Figure 10. Adult *Scymnus camptodromus* (top), *S. ningshanensis* (middle), and *S. sinuanodulus* (bottom). Guangwu Li, Chinese Academy of Forestry.

Scymnus camptodromus This was the first *Scymnus* species studied and imported from Sichuan Province. It feeds voraciously on HWA in the laboratory (Zhao *et al*., 1998). Until 2009, laboratory rearing of this species was difficult because of an egg diapause lasting 4–8 months (Lu and Montgomery, 2000; Montgomery and Keena, 2012). This problem was resolved by chilling the eggs to 5°C, which shortened the time between oviposition and onset of development to about two months (Keena and Montgomery, 2010). This species has several characteristics that suggest it has potential to be a good biological control agent, including: (1) a life cycle that is well synchronized with HWA; (2) presence over a broad geographic range, including diverse habitats; and (3), presence at the greatest number of HWA sites in China (Montgomery and Keena, 2012).

Scymnus sinuanodulus This species was imported from Yunnan Province, into the USDA Forest Service Quarantine Laboratory in 1996, and aspects of its biology, including fecundity and development rate, have been quantified (Lu and Montgomery, 2000; Lu et al., 2002). Eggs are laid early in the spring, with a second peak later in the season by the next generation. This species was widely distributed in three counties in Lijiang Prefecture, Yunnan Province, with an average of 0.7 beetles per 0.5 m of HWA-infested hemlock branch in some areas. It was found most frequently on HWA-infested hemlock, but also was found in association with *Pineus armandicola Zhang, Zhong et Zhang* on *Pinus armandii* Franch (Montgomery and Keena, 2012). Field sleeve-cage studies suggested that the species significantly reduced HWA population increase (Montgomery *et al.,* 2003).

Scymnus ningshanensis This species was collected mostly in Shaanxi and Sichuan provinces, and to a much lesser extent in Yunnan Province (Montgomery *and Keena,* 2002). Its lifecycle is similar to that of *S. sinuanodulus*. Eggs are laid in the spring in bud scales, under sistens and progrediens ovisacs, and other partially concealed locations when and where HWA are present. HWA eggs must be present for *S. ningshanensis* to oviposit (Montgomery et al., 2002). Larvae prefer to feed on sistens and progrediens eggs. Adults feed on sistens eggs, and older progrediens nymphs and adults. In sleeve cage trials, this species suppressed HWA population growth under conditions where *S. tsugae* failed to do so (Butin *et al*., 2003).

Scymnus coniferarum from western North America

This species, with the common name of conifer lady beetle, was first described in 1874 from specimens collected on pine in California. They are small beetles, very similar looking to the Chinese *Scymnus* spp. discussed above (Fig. 11). Gordon (1976) provides a description of this species. The known geographic distribution of *S. coniferarum* is in western North America on both pine (Gordon 1976) and on hemlock in Washington (Montgomery et al., 2009). The larvae of *S. coniferarum* appear in May and probably continue to feed on progrediens and their sistens eggs in July in Seattle, Washington (D. McDonald, pers. com.). This predator feeds on the second (progrediens) generation of adelgids: therefore, it has the potential to complement the effect of *Laricobius* beetles, which principally affect sistens nymphs and adults and progrediens eggs.

Figure 11 *Scymnus coniferarum* adult (top) and larva (bottom). Nathan Havill.

Leucopis spp. from western North America

In Oregon, where HWA is native, the most abundant predator collected on western hemlock infested with HWA was *L. nigrinus*. Other common species were *L. argenticollis* and *L. piniperda* (Grubin et al., 2011). The latter species was initially reported as *Leucopis atrifacies* (Aldrich) (Kohler et al., 2008). Chamaemyiids, especially these species of *Leucopis*, have long been considered important predators of species of *Adelges* and *Pineus* (Zilahi-Balogh et al., 2002b). However, Grubin et al. (2011) have found that neither *Leucopis* spp. is specific to HWA. This may limit further consideration of these predators as biological control agents for HWA in the eastern United States

Tetraphleps galchanoides from China

Five of 12 described species of *Tetraphelps* worldwide have been found to feed on species of adelgids in the genera *Pineus* or *Adelges* (McAvoy et al., 2007). In a shipment of HWA-infested hemlock foliage sent from Niba Gou Forestry Farm near Quiaoji, Baoxing, Co., Sichuan to Virginia Polytechnic Institute and State University (Virginia Tech.) in fall of 2002, approximately 40 early instar nymphs of T. galchanoides were found feeding on HWA (McAvoy et al., 2007). Ten of these nymphs, nine males and one female, completed development on HWA under laboratory conditions. However, no progeny were produced. Recent host-range studies have shown that *T. galchanoides* is not specific to adelgids (McAvoy and Salom, unpublished data), and therefore is no longer under consideration as a potential biological control agent for HWA.

RECOMMENDATIONS FOR FURTHER WORK

Broaden Genetic Diversity of *S. tsugae* in Mass Rearing Colonies

Most of the *S. tsugae* previously reared for release in the United States came from a small number of beetles collected in Japan in the early 1990s (Sasaji and McClure, 1997). Lamb et al. (2008) reported collecting *S. tsugae,* which led to the recent shipment of wild beetles from Japan to the Beneficial Insects Laboratory of the North Carolina Department of Agriculture and Consumer Services. It is possible that lack of genetic diversity during mass rearing, without the infusion of wild beetles from Japan, is a detriment to the overall biological control effort with *S. tsugae*.

Develop an Odor-based Trap to Detect *L. nigrinus*

Broeckling and Salom (2001) demonstrated that *L. nigrinus* possess olfactory receptors on their antennae. Wallin et al. (2011) showed that in laboratory assays *L. nigrinus* is attracted to several western conifer species, and might use the volatiles of these plants to help find its adelgid hosts. Identifying cues used by the predator to find its prey could lead to the development of a trap. Finding adults using beat sheets is time consuming, limited to the lower canopy, and often fails to detect the species even when it is present (Mausel et al., 2010). The ability to attract and trap insects from all parts of a forest would be an important development for the program; it could help assess establishment and population levels at a particular location. Also, if a very powerful, attractant-based, live trapping system were developed, it could be used to collect large numbers of predators for redistribution to new areas.

Improve Methods to Measure Impacts of Predators on the Rate of Population Increase of HWA

Assessing the impact of released predators on HWA in all forest situations has been difficult (Davis, 2011). It is clear that intensive life-table analyses are warranted. Additionally, exclusion-cage studies need to be conducted over at least a 3-yr periods. Such studies are needed at both predator release and control sites. This is not easy to accomplish, because it is difficult to find study sites with similar levels of HWA and tree health. While observing trends in HWA densities is necessary, it is only meaningful in relation to changing tree health. There is a feedback cycle linking adelgid numbers and tree health, in which healthy trees can support higher populations of adelgids than unhealthy trees can (McClure 1991). As trees decline, they support fewer adelgids, allowing for partial recover of trees. When tree health has improved sufficiently, adelgids recolonize the trees. This cycle varies among sites at the local level because of variability in site conditions and climate.

Short-term Chemical Protection of Highest Value Hemlocks

Although some establishment and impact of introduced predators on HWA populations has occurred, eastern and Carolina hemlocks have little tolerance to HWA and tree death is rapid. Predators, released only in small numbers, often do not have an immediate protective effect. Therefore, it may be necessary to provide short-term insecticidal protection for the oldest or largest hemlocks in a stand, and simultaneously release predators in the understory to build future predator populations. Under this scenario, we imagine that as older trees lose their protection due to waning insecticide residues, an established population of predators would be present to provide control.

Optimizing Release Methods

The release of HWA predators, alone or in combinations of several species selected with regard to climate, is necessary and must be done in order to maximize chances for establishment. For example, the coastal strain of *L. nigrinus* is suitable for release in plant hardiness zones ≥ 6 (Mausel et al., 2010), and it has been hypothesized that a strain collected from inland areas (interior/continental strain) might be more suitable for release in plant hardiness zone 5 (Mausel et al., 2011). Also, it is important to attack the adelgid at all stages of its life cycle. Although the predator *S. tsugae* may contribute some level of mortality to the progrediens generation and to sistens eggs, more predators that attack the second generation of adelgids are needed. Finally, there is a need for a coordinated assessment of the impact of multi-species guilds.

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XVII Emerald Ash Borer

(*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae)

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DESCRIPTION OF PEST

Taxonomy

Agrilus planipennis Fairmaire, 1888 (type locality: China) is considered the senior synonym to *A. marcopoli* Obenberger, 1930 (type locality: China), *A. marcopoli ulmi* Kurosawa, 1956 (type locality: Japan), and *A. feretrius* Obenberger, 1936 (type locality: Taiwan) by Jendek (1994) in a revision of Eastern Palearctic *Agrilus* species.

Agrilus is the largest genus in the family Buprestidae with ~2,800 described species worldwide (Bellamy, 2008). Adults of this genus are flashy, metallic-colored beetles, frequently collected using nets or traps (Fig. 1). However, there is little interest in their immature stages, which must be collected from inside tree trunks, branches, or woody stems. Consequently, critical information on the biology, population dynamics, and host ranges of most *Agrilus* species is lacking.

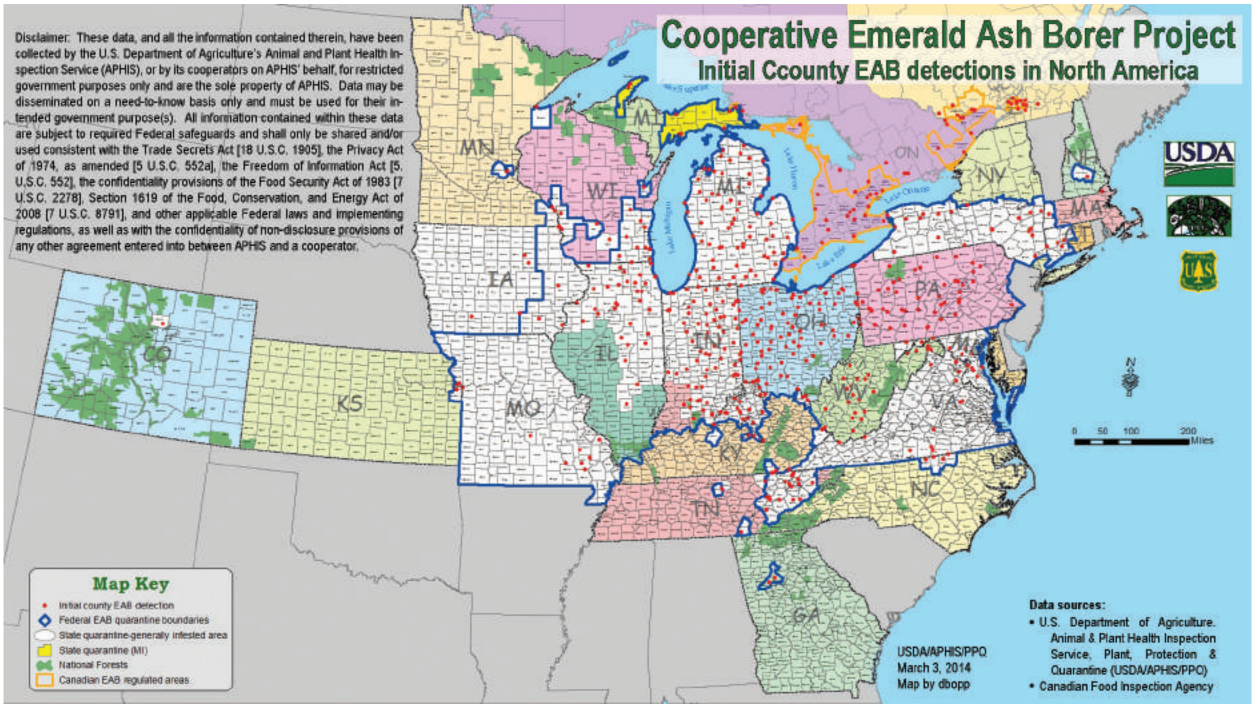
Figure 1 Adult of emerald ash borer (*Agrilus planipennis*) on ash leaf. Leah Bauer, USDA Forest Service, Northern Research Station, East Lansing, Michigan.

In the Palearctic region, species in this genus are grouped into 36 subgenera and 34 informal species-groups based on morphological characters of adults (Chamorro et al., 2012). On this basis, *A. planipennis* was placed in the subgenus *Uragrilus* Semenov (Alexeev, 1998). However, more recent analyses using adult and larval characters suggest *A. planipennis* be moved to the *Agrilus cyaneoniger* species-group (Jendek and Grebennikov, 2011; Volkovitsh and Hawkeswood, 1990).

Distribution

Countries in Asia where *A. planipennis* is reported include China, Korea, Russian Far East, Japan, Taiwan, Laos, and Mongolia (Ko, 1969; Kurosawa et al., 1956, 1985; Chinese Academy of Science, 1986; Yu, 1992; Akiyama and Ohmomo, 1997; Mühle, 2003; Wei et al., 2004; Fukutomi and Hori, 2004; Jendek and Grebennikov, 2011). In areas of northeast China, Korea, and the Russian Far East, the distribution of *A. planipennis* generally coincides with that of ash trees (*Fraxinus* spp.) including *F. chinensis* Roxb., *F. chinensis* var. *rhynchophylla, F. chinensis* var. *japonica, F. mandshurica* Rupr., *F. lanuginosa* Koidz., and the introduced Nearctic species *F. americana* L., *F. pennsylvanica* Marsh., and *F. velutina* Torr. (Liu, 1966; Hou, 1993; Chinese Academy of Science, 1986; Yu, 1992; Zhang et al., 1995; Liu et al., 1996; Liu et al., 2003; Duan et al., 2012a). However, in Japan, Taiwan, and Laos, confirmation that *A. planipennis* is native will require more information on species of *Agrilus* that feed exclusively on *Fraxinus* spp. (Mühle, 2003; Bray et al., 2011). In Mongolia, the genus *Fraxinus* is unknown (Grubov, 1982), thus an early, unconfirmed report of *A. planipennis* there is suspect (Alexeev, 1979).

In 2002, *A. planipennis* was discovered in North America after being reared from dead and dying ash trees from southeastern Michigan and nearby Ontario, Canada, (Haack et al., 2002). Due to the bright green coloration of *A. planipennis* adults, this species was given the common name of emerald ash borer (EAB) (Entsoc.org, 2012). In areas of North America currently infested with EAB, its host range and distribution (Fig. 2) coincides with that of *Fraxinus*).



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Data sources:
- U.S. Department of Agriculture. Animal & Plant Health Inspection Service, Plant, Protection & Quarantine (USDA/APHIS/PPQ)
- Canadian Food Inspection Agency

Figure 2 The known distribution and quarantines of emerald ash borer in North America as of June 1, 2012.

Genetic studies of EAB from North America and Asia, and tree-ring analyses of ash trees in southeast Michigan, indicate that this beetle was introduced from China during the 1990s (Siegert et al., 2009; Bray et al., 2011). The most likely route of entry was EAB-infested ash lumber used for the manufacture of crates, palettes, and dunnage used in international shipping. Within a few years of its detection, EAB was determined to be the cause of ash mortality in other nearby states and provinces (Fig. 2).

In 2006, EAB was found in Moscow, Russia, where it caused extensive mortality in urban plantings of *F. pennsylvanica* and *F. excelsior* L., ash species native to North America and Europe, respectively (Baranchikov, 2008; Izhevskii et al., 2010). The expansion of EAB's range to the Western Palearctic region threatens European ash species, including *F. angustifolia* Vahl., *F. excelsior*, and *F. ornus* L. (Wessels-Berk and Scholte, 2008). The invasive population of EAB in North America only attacks *Fraxinus* spp. (Anulewicz et al., 2008), and several studies report that species of Nearctic and European ash are more attractive and susceptible to EAB attack than are species of Asian ash, which coevolved with EAB (Liu et al., 2003; Rebek et al., 2008; Duan et al., 2012b).

Upon arrival in North America, EAB became established and spread throughout the Great Lakes Region, due in part to the abundance of ash trees in the urban and forested landscapes (MacFarlane and Meyer, 2005; Poland and McCullough, 2006; Pugh et al., 2011), limited EAB resistance to attack among native ash (Rebek et al., 2008), and release from its native natural enemies (Bauer et al., 2004, 2005; Duan et al., 2009). Although EAB adults are capable of long-distance flight (Taylor et al., 2010), much of the spread of EAB in North America is facilitated by human-assisted movement of infested ash firewood, nursery stock, and lumber (Cappaert et al., 2005; Poland and McCullough, 2006). In an effort to reduce the loss of North American ash trees, regulatory agencies in both the United States and Canada imposed quarantines on the movement of ash materials and attempted eradication of EAB by removal of the ash trees around known infestations. The eradication efforts ended when it was found that EAB was distributed across much of central and northeastern areas of North America. Infestations of EAB are now known in 22 states (Colorado, Connecticut, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Maryland, Massachusetts, Michigan, Minnesota, Missouri, New Hampshire, New York, North Carolina, Ohio, Pennsylvania, Tennessee, Virginia, West Virginia, and Wisconsin) and Ontario and Quebec, Canada (Fig. 2).

Damage

Type Emerald ash borer females lay their eggs (Fig. 3) singly or in small clusters between the layers of bark or in bark crevices of ash trees. Upon egg hatch, the neonates bore directly through the bark and into the tree until reaching the phloem and cambial region, where they feed (Cappaert et al., 2005). As larvae grow through four larval stages (Fig. 4), they leave behind increasingly large, frass-filled, serpentine galleries (Fig. 5). Larval feeding disrupts the transport of nutrients and water in the phloem and outer sapwood. At low EAB-larval densities, ash trees exhibit some immune response, notably the formation of callous around EAB galleries (Duan et al., 2012b). However, as larval densities increase over a period of two to five years, the phloem is consumed or sufficiently damaged to cause tree death (Figs. 6, 7) (Smith, 2006).

Figure 3 Emerald ash borer eggs are white (left) when freshly laid, but turn tan as they age (right). David Cappaert, Michigan State University, Bugwood.org.

Figure 4 Feeding stage larvae of emerald ash borer: above, second, third and 4th instars; below, full-grown 4th instar. David Cappaert, Michigan State University, Bugwood.org.

Extent The establishment and spread of EAB in North America has resulted in the death of tens of millions of ash trees in urban and forested ecosystems. In forested ecosystem of the eastern United States, there are an estimated 8 billion ash trees valued at $US 282.25 billion (Federal Register, 2003; Nowak et al., 2003). Until recently, ash trees were one of the most commonly planted landscape trees in the urban environment because they grow rapidly, tolerate adverse growing conditions, are easy to propagate, and were considered resistant to most pests. The costs for removal and replacement of ash trees killed by EAB to communities and smaller landholders are high; e.g., the expense for ash removal and replacement in six infested southeastern Michigan counties was estimated at $US 11.7 billion (Federal Register, 2003; Kovacs et al., 2010). The long-term ecological effects of EAB in forested and riparian ecosystems are more difficult to quantify (Federal Register, 2007). According to a recent study, EAB has killed virtually the entire ash canopy of southeast Michigan, and despite ash seedlings and saplings in gaps, recovery of an ash overstory is unlikely due to the continued EAB infestation across the landscape (Kashian and Witter, 2011). Models of EAB spread predict a rapid

Figure 5 Galleries caused by feeding emerald ash borer larvae. Left, Michigan Department of Agriculture, Bugwood.org. RIght, Edward Czerwinski, Ontario Ministry of Natural Resources, Bugwood.org.

Figure 6 Dead and dying ash in forest area due to emerald ash borer. Troy Kimoto, Canadian Food Inspection Agency, Bugwood.org.

Figure 7 Small trees with epicomic shoots due to the emerald ash borer. David Cappaert, Michigan State University, Bugwood.org.

expansion of the infestation throughout North America (BenDor et al., 2006; Muirhead et al., 2006; Prasad et al., 2010; Mercader et al., 2011), and researchers are concerned that EAB threatens all native ash tree species (Gandhi and Herms, 2010).

Biology of Pest

EAB requires one or two years to complete its development, depending on the climate and condition of the host tree (Cappaert et al., 2005; Wang et al., 2010; Tluczek et al., 2011). For EAB populations that complete development in a single year, adult emergence starts in the spring at 200 to 260 growing degree-days base 10°C (DD10), with peak emergence around 540 DD10 (Brown-Rytlewski, 2004, McCullough and Siegert, 2007a). EAB adults emerge from D-shaped exit holes and fly into the canopy where they feed on ash leaves. Mating begins about a week later, and females start laying eggs two to three weeks later, preferring to oviposit on ash trees under stress (McCullough et al., 2009a,b; Mercader et al., 2011). EAB females place eggs in concealed areas such as between layers of loose bark and in bark crevices. The eggs of EAB are ca. 1.0 mm in diameter and amber in color when mature. Neonate larvae hatch in about two weeks and bore through the bark until reaching the phloem, where they make galleries in the outer sapwood and inner bark as they feed. In late summer and fall, mature fourth-instar larvae excavate pupal chambers in the outer sapwood or outer bark, where they spend the winter folded into a J shape, also referred to as J-larvae (Duan et al., 2010). In early spring, the J-larvae shorten into prepupae before pupation. The pupae gradually darken as they mature and after about four weeks mature into pharate adults. For EAB with a two-year life cycle, larvae that are immature when cold weather arrives in the fall simply overwinter in their feeding gallery, complete development the following summer, spend their second winter as J-larvae, and emerge as adults in the following spring.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Nontarget Insect Species Related to the Pest

In North America, the family Buprestidae has 53 genera, of which *Agrilus* is the largest with 174 described species (Fisher, 1928; Poole, 1997; Bellamy, 2008). Species of *Agrilus* feed exclusively on woody angiosperms and are generally restricted to host species within a single genus or family. The only native species in the genus known to feed on ash trees in North America is *Agrilus subcinctus* Gory, a small beetle that feeds on the phloem of dead or dying ash twigs (Petrice et al., 2009). Other native wood-boring coleopterans that feed on ash include species of *Chrysobothris*, *Dicerca*, *Polycesta*, and *Spectralia* (Buprestidae), *Neoclytus* (Cerambycidae), and *Hylesinus* (Curculionidae) (Solomon, 1995).

Since the parasitoid guilds of *Agrilus* spp. are less specific to host tree than to host niche (e.g., host size, and location of feeding larvae) (Taylor et al., 2012), some native *Agrilus* are potentially susceptible to attack by parasitoids introduced for biological control of EAB. Although most *Agrilus* are considerably smaller than EAB (>8.5-mm long adults), some overlap in parasitoid-host ranges is possible between EAB and the larger species of *Agrilus*. *Agrilus* species that fall in this category in eastern North America are *A. acutipennis* Mannerheim, *A. anxius* Gory, *A. arcuatus* LeConte, *A. bilineatus* (Weber), *A. burkei* Fisher, *A. difficilis* Gory, *A. horni* Kerremans, *A. granulatus* (Say), *A. liragus* Barter & Brown, *A. macer* LeConte, *A. nigricans* Gory, *A. politus* (Say), and *A. vittaticollis* (Randall) (Solomon, 1995; Parsons, 2008). These species may be at some risk of attack by introduced parasitoids targeted at EAB.

Native Natural Enemies Affecting the Pest

From *Agrilus* species of similar size and habits as EAB, there are parasitoid species that also attack EAB, as has been demonstrated by field studies of EAB in North America (see references below). However, research on the population dynamics of native *Agrilus* is generally limited to pest species, which periodically experience outbreaks damaging to their host trees (Vansteenkiste et al., 2005). Consequently, the literature on natural enemies of *Agrilus* species is largely drawn from a few pests, of which a diverse group of hymenopteran parasitoids is known.

Perhaps the most studied species is *A. anxius* due to periodic and damaging outbreaks in birch stands (*Betula*) across much of North America (Nash et al., 1951; Barter, 1957; Loerch and Cameron, 1983). These authors report a variety of parasitoids from *A. anxius*, including five egg parasitoids from two families (*Ablerus* sp. [Aphelinidae]; *Avetienella* sp., *Ooencyrtus* sp., *Thysanus* sp., [Encyrtidae]), and over 15 species of larval parasitoids from four families (*Atanycolus* spp., *Doryctes* spp., *Spathius floridanus* Ashmead [= *S. simillimus* Ashmead], *Wroughtonia ligator* (Say) [all Braconidae]; *Phasgonophora sulcata* Westwood [Chalcididae]; *Tetrastichus* nr. *rugglesi* Rohwer [Eulophidae]; *Bephratoides agrili* (Ashmead), *Eurytoma* sp. [both Erytomidae]; and species of *Ephialtes*, *Dolichomitus, Glypta*, *Ichneumon*, *Olesicampe*, *Orthizema*, *Pimploterus* [all Ichneumonidae]). Egg parasitism averaged 55% in a New Brunswick study and 7% in a similar study in Pennsylvania, whereas larval parasitism averaged 20% in both studies (Barter, 1957; Loerch and Cameron, 1983).

Agrilus bilineatus, the two-lined chestnut borer, is another well-studied species prone to damaging outbreaks in drought-stressed oaks (*Quercus* spp.) and sometimes American beech (*Fagus grandifolia* Ehrh.). This species was originally a pest of the American chestnut (*Castanea dentata* (Marsh.) Borkh.). Several authors have documented a guild of larval parasitoids attacking *A. bilineatus* larvae that are similar to those attacking *A. anxius*, including *P. sulcata* (Chalcididae), *Atanycolus* spp., *Doryctes* spp., *S. floridanus*, and *W. ligator* (Braconidae) (Chittenden, 1897; Chapman, 1915; Dunbar and Stephens, 1976; Côté and Allen, 1980; Haack and Benjamin, 1982; Cappaert and McCullough, 2009). Of these, *P. sulcata* was the most abundant, averaging 10.5% parasitism in *A. bilineatus*. No egg parasitoids are known.

The population dynamics of *Agrilus liragus*, a periodic pest of poplars (*Populus* spp.), was studied in New Brunswick (Barter, 1965). Several parasitoids in the same genera were reported, including unknown species of egg parasitoids in the genera *Thysanus* and *Avetienella* (Encyrtidae) and the larval parasitoids *P. sulcata* (Chalcididae) and *S. floridanus*, *Atanycolus* spp., *W. ligator*, *Doryctes* spp., *T.* nr. *rugglesi*, and *Ephialtes* sp. (Braconidae). Of these, *P. sulcata* was the most prevalent, with parasitism ranging from 2 to 20%.

Interestingly, the guilds of egg and larval parasitoid from species of *Agrilus* are similar throughout the world (Taylor et al., 2012). In North America, *Agrilus* egg parasitoids are mainly from the family Encyrtidae (4 genera/5 species), and the larval parasitoids are from the Braconidae (7 genera/19 species), Ichneumonidae (10 genera/11 species), a few species from Eulophidae (2 genera), Eupelmidae (4 genera), Eurytomidae (2 genera), Pteromalidae (2 genera), and a single species of Chalcididae (Taylor et al., 2012). This indicates that the parasitoids of *Agrilus* are more specific to host niches than to host tree species.

From field studies since EAB's invasion in North America, a diverse guild of *Agrilus* parasitoids has been observed attacking EAB larvae. However, parasitoid prevalence is generally low and no native egg parasitoids are known (Taylor et al., 2012). In Michigan, the two most abundant native larval parasitoids are the solitary ectoparasitoids in the genus *Atanycolus* (Braconidae) (several species) and the solitary endoparasitoid *P. sulcata* (Chalcididae) (Cappaert and McCullough, 2009; Duan et al., 2012b). Other less less-common species reported from studies done in Michigan, Ohio, and Pennsylvania include *Atanycolus hicoriae* Shenefelt*, A. simplex* Cresson*, A. nigropopyga* Shenefelt*, A. disputabilis* (Cresson)*, S. floridanus*, *S. laflammei, Spathius n. sp.*, *Leluthia astigmata* (all Braconidae); species of *Dolichomitus, Orthizema, Cubocephalus* (Ichneumonidae); *Eulmus* sp.; and *Balcha indica* (Mani & Kaul) (Eupelmidae) (Bauer et al., 2005, 2008; Duan et al., 2009; Kula et al., 2010; Duan et al., 2012b). These parasitic hymenopterans are presumed to be native except *B. indica*, which is an exotic parasitoid of wood-boring beetle larvae in the eastern United States from Southeast Asia (Gibson, 2005).

Although several native or self-introduced hymenopteran species parasitize EAB larvae in Michigan, the overall level of parasitism is low (<4% combined parasitism) (Bauer et al., 2008; Duan et al., 2009). However, even though such parasitoids are generally scarce, *Atanycolus cappaerti* Marsh and Strazanac was recently discovered at several Michigan field sites with parasitism of EAB larvae ranging from 9% to 71% (Cappaert and McCullough, 2009). In another Michigan study, the prevalence of *Atanycolus* spp. increased from <1% to 19%, and that of *P. sulcata* from <1% to 13%, in one year (Duan et al., 2012b). The long-term impact that these native parasitoids will have on EAB population density and ash health is still unknown and must be determined by further monitoring.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Pest

The emerald ash borer is native to Asia, including northeast China (Jilin, Liaoning, Heilongjiang, Hebei, and Shandong provinces), Korea, the Russian Far East, Taiwan, and Japan (Chinese Academy of Science, 1986; Jendek, 1994; Jendek and Grebennikov, 2011).

Areas Surveyed for Natural Enemies

China In 2003, exploration for EAB natural enemies began in China with the sampling of Asian (*F. chinensis*, *F. mandshurica*) and North American (*F. pennsylvanica*, *F. velutina*) ash species for EAB in the cities of Beijing and Tianjin and the provinces of Hebei, Heilongjiang, Jilin, Liaoning, and Shandong (Liu et al., 2003; Liu et al., 2007). Evidence of past EAB infestations or active infestations was found in each city and province except Shandong. The authors also found that ash species native to North America and ash trees (of any species) planted in urban areas were more susceptible to EAB attack than ash species native to China and those growing in forested natural areas (Liu et al., 2003).

Russian Far East From 2007–2011, surveys for EAB were conducted in and around the cities of Vladivostok, Khabarovsk, and on Sakhalin Island (Yurchenko et al., 2007; Williams et al., 2010; Duan et al., 2012a). Researchers found that EAB in ash trees planted along city streets in Vladivostok, including green ash (*F. pennsylvanica*) from North America, *F. excelsior* from Europe, and the endemic ash species *F. mandshurica* and *F. chinensis* var. *rhynhophylla*. A report of EAB near the Korean border (Alexeev, 1979) was not confirmed during a survey for EAB in 2004, nor was EAB among the 36 species of *Agrilus* listed in collections at the Siberian Zoological Museum, Novosibirsk (Schaefer, 2005).

South Korea In north and central South Korea in 2004 and 2005, researchers searched for EAB in forested areas containing *F. chinensis* var. *rhynchophylla* and *F. mandshurica* (Williams et al., 2005, 2006). EAB is apparently rare in South Korea as these surveys failed to find EAB until a small EAB population was discovered attacking water-stressed *F. chinensis* planted along a road near the city of Daejeon in central South Korea in 2005. Another EAB population attacking *F. chinensis* trees damaged by construction was found in 2007 in the Yangsuri, which is about 50 km east of Seoul (Williams et al., 2010).

Japan EAB populations are extremely low and difficult to find in Japan, and EAB natural enemies were not found during foreign explorations in 2003 and 2004 (Schaefer, 2004, 2005).

Natural Enemies Found

Historically, emerald ash borer was considered only a minor, sporadic pest of native ash tree species in Asia. Thus, only limited literature was found in 2002, when it was discovered in North America. However, in areas of China and Russia, plantings of North American ash species, which are less resistant to EAB than are Asian ash species, have caused an increase in EAB density since the 1960s (Yu, 1992; Zhang et al., 1995; Liu et al., 1996, 2003, 2007; Zhao et al., 2005; Duan et al., 2012a). In rural parks, nurseries, and urban areas, where many of these non-native ash trees are planted, researchers have discovered several hymenopteran parasitoid species attacking EAB larvae and eggs. Three species from northeast China are being introduced in the United States for biological control of EAB. A fourth species from Russia is being evaluated for future release.

China The first report of a parasitoid attacking EAB came from the provincial port city of Tianjin, southeast of Beijing, whre EAB had become a major pest of *F. velutina*, a North American ash species that was planted extensively in the region. A gregarious ectoparasitoid, later described as *Spathius agrili* Yang (Braconidae) (Fig. 8), was found parasitizing EAB larvae in these ash plantings (Xu, 2003; Liu et al., 2003; Yang et al., 2005). It was also collected from EAB larvae infesting *F. pennsylvanica* and *F. mandshurica* trees in Jilin province (Liu et al., 2003) and in Beijing (LSB, unpublished). *Spathius agrili* is the dominant parasitoid of EAB in Tianjin (Wang et al. 2010); however, it is rare further north (JJD and JG, unpublished).

A second larval parasitoid, later described as *Tetrastichus planipennisi* Yang (Fig. 9) (Yang et al., 2006), was found attacking EAB larvae from *F. pennsylvanica* and *F. mandshurica* trees planted in Jilin province (Liu et al., 2006). This gregarious larval endoparasitoid is also found in Liaoning and Heilongjiang provinces (LSB and JJD, unpublished) and is the dominant parasitoid of EAB larvae in northeast China (Liu et al., 2007).

A third parasitoid of immature EAB, later described as *Sclerodermus pupariae* Yang and Yao (Wu et al., 2008; Wang et al., 2010; Yang et al., 2012), was discovered attacking EAB larvae and pupae in Tianjin. Due to its broad host range among woodborers (Tang et al., 2012), low prevalence in China, and propensity of some species in this genus to sting humans, *S. pupariae* was not considered further for use in biological control of EAB in the United States.

A solitary, parthenogenic egg parasitoid in the genus *Oobius* (Encyrtidae) was reared from EAB eggs collected from *F. mandshurica* and *F. pennsylvanica* trees in Jilin province in 2004. It was later described as *Oobius agrili* Zhang & Huang (Fig. 10) (Zhang et al., 2005). Another population of *O. agrili* was recently found in Liaoning province (JRG and JJD, unpublished). In 2010, an undescribed species of *Oenycyrtus* (Encyrtidae) was reared from EAB eggs

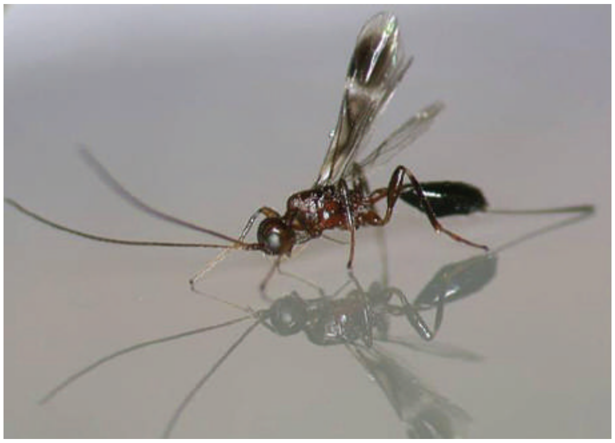

Figure 8 Adult *Spathius agrili*. Jennifer Ayer, Bugwood.org.

Figure 9 Adult *Tetrastichus planipennisi*. David Cappaert, Michigan State University, Bugwood.org.

Figure 10 Adult *Oobius agrili* ovipositing in an emerald ash borer egg. Debbie Miller, USDA Forest Service, Bugwood.org.

sampled the previous fall at the same site in Jilin province (LSB, unpublished).

Russian Far East From 2009–2011, surveys for EAB and its natural enemies in the Russian Far East led to the recovery of three larval parasitoids: *T. planipennisi, Atanycolus nigriventris* Vojnovskaja-Krieger, and the recently described *Spathius galinae* Belokobylskij (Williams et al., 2010; Belokobylskij et al., 2012*)*. Among these, *S. galinae* is the dominant parasitoid of EAB in this part of Russia, parasitizing up to 63% of larvae collected from *F. pennsylvanica* planted in and around Vladivostok (Duan et al., 2012a). In addition, an unidentified species of egg parasitoid (Hymenopteran: Encyrtidae) was collected from EAB-infested ash trees (*F. pennsylvanica*) trees in Vladivostok (Duan et al., 2012c).

South Korea *Spathius galinae*, a species of *Tetrastichus*, tentatively identified as *Tetrastichus telon* (Graham), and *Teneroides maculicollis* Lewis (Coleoptera: Cleridae) were found attacking EAB larvae in girdled ash trees in Daejeon in 2008 (Williams et al., 2010). Attempts to culture these species in quarantine in the United States were unsuccessful.

Host Range Test Results

Spathius agrili The host specificity of *S. agrili* was evaluated by comparing parasitism of EAB larvae to that in other insect species using no-choice-laboratory assays performed in both the United States and China (Gould et al., 2007; Yang et al., 2008). In these assays, groups of female and male *S. agrili* were exposed to either larvae of EAB or the following nontarget species (1) nine species of *Agrilus*, including three from the United States (*A. anxius*, *A. bilineatus*, and *A. ruficollis* [Fabricius]) and six from China (*A. auriventris* Saunders, *A. inamoenus* Kerremans, *A. lewisiellus* Kerremans*, A. mali* Matsumura*, A. sorocinus* Kurosawus, *A. zanthoxylumi* Li), (2) one other Chinese buprestid (*Sphenoptera*), (3) one cerambycid from China (*Thyestilla gebleri* Fann); (4) one curculionid from China (*Eucryptorrhynchus chinensis*); and (5) six lepidopterans from three families from China: Pyralidae (*Ostrinia orientalis* [Mutuura and Munroe], *Chilo luteellus* Motschulsky, *Sylepta derogate* F., unknown pyralid larvae), Cossidae (*Holcocerus insularis* Staudinger), and Carposinidae (*Carposina niponensis* Walsingham).

Larvae of each species were implanted into their respective natural host plants before exposure to *S. agrili* adults. The results of these no-choice assays showed that *S. agrili* parasitized and developed only in the larvae of the following *Agrilus* species: *A. anxius, A. bilineatus, A. inamoenus, A. mali,* and *A. zanthoxylumi.* Parasitism by *S. agrili* was significantly lower in these nontarget species than in EAB larvae (Yang et al., 2008).

Using a Y-tube olfactometer, the behavioral responses of adult *S. agrili* were assessed to leaf volatiles from 14 woody plant species growing in China from the following families: Oleaceae (2 spp.), Rutaceae (2 spp.), Rosaceae (3 spp.), Salicaceae (2 spp.), and one each in Celastraceae, Juglandaceae, Leguminosae, and Simaroubaceae. Only the leaves of *F. velutina*, *F. pennsylvanica* (Oleaceae), *Prunus persica* L., and *Ailanthus altissima* (Mill.) Swingle were attractive to *S. agrili* females, supporting the view that EAB is its primary host in China (Yang et al., 2008).

The above cited authors also sampled other insects from *F. velutina* and other tree species at field sites in China, recovering 17 species of wood-boring larvae, nine of which were buprestids and of those, six were *Agrilus* spp. (others were Cerambycidae and several were families of Lepidoptera). These wood-boring larvae were returned to the laboratory and reared for emergence of parasitoids, but neither *S. agrili* nor *T. planipennisi* emerged. However, other hymenopteran parasitoid species reared from the larvae of other species of *Agrilus* larvae included an unknown *Tetrastichus* sp. from *A. sorocinus* in Tianjin; *Tetrastichus* sp. and *Doryctes* sp. from *A. mali*, *Tetrastichus* sp. from *A. lewisiellus, Tetraichus* sp., and an unknown braconid from *A. zanthoxylumi* from Shaanxi; *Atanycolus* sp. and *Eupelmus* sp.

from *A. mali* in Xinjiang; and *Spathius* sp. from *A. auriventris* in Zhejiang (Yang et al., 2008). These findings support the host-specificity of *S. agrili* in China.

Tetrastichus planipennisi The host specificity of *T. planipennisi* was evaluated by comparing EAB-larval parasitism to that of other insect species in the United States using paired, no-choice laboratory assays with EAB larvae as positive controls (methods as per Badendreier, et al. [2005]). In these assays, groups of female and male *T. planipennisi* were exposed to larvae of EAB or other species that were similar in stage or size. Nontarget test species included eight buprestids (*A. anxius*, *A. bilineatus*, *A. ruficollis*, *A. subcinctus, Agrilus sulcicollis* Lacordaire, *Chrysobothris femorata (Olivier)*, *C. floricola* Gory, *C. sexsignata* Say), five cerambycids (*Neoclytus acuminatus* F.*, Megacyllene robiniae* Forster, *Astylopsis sexguttata* [Say], *Monochamus scutellatus* [Say], unknown sp. from apple), and one species of tenthredinid in the Hymenoptera (*Janus abbreviates* [Say]). The larvae of each species were implanted into their respective natural host plants. We also assayed the following non-wood-boring insect larvae by insertion into ash: Coleoptera: Tenebrionidae (*Tenebrio molitor* L.*)*, Lepidoptera: Pyralidae (*Galleria mellonella* L.), and Lepidoptera: Sphinghidae (*Manduca sexta* L.). The latter was tested as a surrogate for sphinx moths (Sphingidae) that pollinate the eastern prairie fringed orchid (*Platanthera leucophaea* [Nuttall] Lindley), a federally listed threatened orchid found in Michigan. Larvae of *M. sexta* were also exposed to *T. planipennisi* as they fed on tomato leaves (Federal Register, 2007). *Tetrastichus planipennisi* rejected the larvae of all species except EAB, indicating a narrow host range for this species (Liu and Bauer, 2007; Federal Register, 2007).

Oobius agrili The host specificity of *O. agrili* was evaluated by comparing *O. agrili* parasitism in EAB eggs laid on ash branches to those of other insect species in the United States using both no-choice and choice assays with EAB eggs as positive controls (Bauer and Liu, 2007; Federal Register, 2007). Female *O. agrili* females were exposed to eggs of EAB or those of six wood-boring buprestids (*A. anxius*, *A. bilineatus*, *A. egenus* Gory, *A. ruficollis, A. subcinctus, A. sulcicollis,*) and two cerambycids (*M. robiniae, N. acuminatus*) on their respective natural host trees. Also tested were eggs of several lepidopteran species (*Bombyx mori* L.*, Choristoneura rosaceana* (Harris)*, M. sexta, Pieris rapae* [L.]) laid on ash branches. In the no-choice assays, *O. agrili* did not parasitize eggs of the cerambycids, lepidopterans, or those of the smaller *Agrilus* spp. (*A. sucinctus, A. sulcicollis, A. egenus)*, although it did parasitize eggs of the larger *Agrilus* spp. (*A. anxius*, *A. bilineatus*, *A. ruficollis).* It was determined that *Agrilus* eggs laid by small *Agrilus* spp. were about half the size of those *Agrilus* eggs accepted by *O. agrili*, suggesting that egg size may limit acceptance. As a result, choice-laboratory assays were conducted by exposing *O. agrili* females to eggs of EAB and eggs from each of the three larger *Agrilus* species on their respective hosts: *A. anxius* on birch (*Betula*), *A. bilineatus* on oak (*Quercus*), and *A. ruficollis* on raspberry (*Rubus*). When given a choice, *O. agrili* preferred the EAB eggs on ash vs. eggs of the other three species on their respective host plants. These results show that *O. agrili* prefers eggs of EAB on *Fraxinus*, but will parasitize eggs of larger *Agrilus* spp. and can physiologically develop inside them.

Releases Made

After research on *O. agrili*, *T. planipennisi,* and *S. agrili* biology, laboratory rearing, and host specificity was completed in 2007, researchers submitted petitions to the North American Plant Protection Organization (NAPPO) and permit requests to USDA Animal, Plant Health Inspection Service (APHIS) for field release of these parasitoid species for the biological control of EAB in the United States (NAPPO, 2012; USDA APHIS, 2012a). From the NAPPO petitions, APHIS compiled an Environmental Assessment, which was posted on the *Federal Register* for public comment (Federal Register, 2007). Meanwhile, federal and state researchers and regulatory agencies, university faculty, tribal councils, and land managers evaluated the pros and cons of releasing these parasitoids in the United States for management of EAB. After the public comment period ended and a risk analysis was completed, APHIS posted a “finding of no significant impact” on the *Federal Register* (Federal Register, 2007). Following final approval by Michigan, APHIS issued release permits on July 23, 2007 to L. Bauer for release of *O. agrili* and *T. planipennisi* and to J. Gould for release of *S. agrili* (Bauer et al., 2008).

In the summer and fall of 2007, a combined total of ~2,900 *O. agrili*, *T. planipennisi,* and *S. agrili* females (count includes females only) were released at seven field sites in

Michigan (Bauer et al., 2008). The following year, similar numbers were released at 12 sites in Michigan, Ohio, and Indiana (Bauer et al., 2010). At this time, USDA APHIS determined there were no cost effective control methods to eradicate or prevent dispersal of EAB, and; therefore, they recommended that "authorities plan and prepare for an infestation of EAB" (USDA APHIS, 2012b). According to principal researchers, demand for EAB parasitoids far exceeded supply, based on rearing in research laboratories. To increase supply, Forest Service and APHIS scientists and managers initiated the EAB Biological Control Program (USDA APHIS, 2012c), which included the construction and staffing of the EAB Biocontrol Facility, an EAB parasitoid mass-rearing laboratory in Brighton, Michigan, which became operational in 2009 after researchers successfully transferred rearing technology and parasitoid colonies (Bauer et al., 2010; Emeraldashborer, 2012). More than 34,000 female parasitoids (all species combined) were produced in 2009, allowing for expanded releases in Michigan, Ohio, and Indiana, and the establishment of new research sites in Maryland and Illinois.

In 2010, USDA researchers wrote and posted the online manual, *Emerald Ash Borer Biological Control Release Guidelines*, which provides information on EAB and parasitoid biology, data collection, release-site selection, permits, and parasitoid-release methods. In 2012, the online manual was updated and expanded to include methods for determining parasitoid establishment or recovery from release sites and designated the "Emerald Ash Borer Biological Control Release and Recovery Guidelines" (USDA FS APHIS/ARS/FS, 2012).During this time, researchers continued to improve rearing methods and to transfer that technology to the EAB Biocontrol Facility, which led to improved parasitoid production (Ulyshen et al., 2010; Gould et al., 2011a; Duan et al., 2011a). In 2010, more than 100,000 female parasitoids (all species combined) were released in Michigan, Maryland, Illinois, Indiana West Virginia, Kentucky, and Minnesota. In 2011, more than 200,000 parasitoids were reared and released in states already involved in EAB biological control research and program releases, and new sites were started in New York, Pennsylvania, Virginia, and Wisconsin. To keep track of parasitoid releases and recoveries, APHIS and FS collaborated with Michigan State University to develop an online database (Mapbiocontrol, 2012).

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

EAB parasitoids are considered established in the field if they are detected by trapping or recovery from EAB eggs or larvae at least one year after a parasitoid species was last released (Bauer et al., 2011; USDA FS AUSDA/F/NRS, 2012). Depending on the species and the recovery method used, sampling for field recovery of EAB parasitoids is done in late summer or early fall when parasitoid densities are highest, or during late winter or early spring after parasitoids have broken diapause. The simplest parasitoid-recovery method involves felling EAB-infested ash trees, placing logs in large cardboard-rearing tubes in a brightly lit room, and collecting the parasitoid adults as they emerge and enter clear collection cups attached to the ends of rearing tubes. This method works for emergence of the EAB parasitoids and other insects living in and on ash logs. Alternatively, the logs can be debarked and EAB larvae and associated larval parasitoids collected from galleries. Parasitoids are then reared to the adult stage for identification (Bauer et al., 2011).

Less-destructive sampling methods for recovery of *O. agrili* developing or diapausing inside EAB eggs (laid on the outer bark of ash trees) include either collecting EAB eggs from the bark or placing egg-bearing bark samples in cardboard rearing tubes for emergence of *O. agrili* adults. After the bark samples are dry, eggs are recovered from sifted debris and evaluated for parasitism by *O. agrili*. Alternatively, a trap to detect parasitoids can be made by hanging logs, on which EAB eggs were laid in the laboratory, on ash trees in the field. These "egg sentinel logs" are then retrieved from the field after ten to 14 days of exposure, and each egg is then examined for an *O. agrili* exit hole, dissected, or reared in the laboratory to determine if the egg is parasitized (Bauer et al., 2013; USDA FS APHIS/ARS/FS, 2012).

A similar, non-destructive method for recovery of the larval parasitoids uses small ash logs, in which last-instar EAB larvae have been inserted under the bark. These "larval sentinel logs" are hung on ash trees in the field for a seven-day exposure period. The sentinel logs are then returned to the laboratory, and each larva is examined for parasitoids or reared for identification of adult parasitoids. Finally, yellow pan traps can also be used to recover EAB parasitoid species (Bauer et al., 2013; USDA FS APHIS/ARS/FS, 2012).

Since 2008, establishment of *O. agrili*, *T. planipennisi*, or *S. agrili* has been confirmed using a variety of methods at many study sites in Michigan. More recently, one or more of the parasitoid species were recovered at release sites in Ohio, Maryland, Indiana, Illinois, and Pennsylvania (Bauer et al., 2009, 2010, 2011, 2013; Gould et al. 2011b). More detailed studies are ongoing at six long-term study sites (each comprised of release and control plots) in southern Michigan, where *O. agrili*, *T. planipennisi*, and *S. agrili* were released between 2007 and 2010. Since the last release of *O. agrili* at these long-term study sites in 2009, EAB-egg parasitism has been monitored annually, and the establishment of *O. agrili* has been confirmed. From samples of EAB eggs and placement of egg sentinel logs at sites, parasitism of EAB eggs was approximately 5% in 2010 and 20% in 2011 (Duan et al., 2011b, 2012d; Abell et al., 2011). In 2011, EAB-egg parasitism was found from 73% of the sampled trees in parasitoid-release plots and 25% of trees in control plots, a dispersal of ~800 m (LSB, unpublished). These results confirm that established populations of *O. agrili* are expanding and gradually dispersing from the original release epicenters.

Changes in EAB larval parasitism are also being monitored each year at these study sites by destructively sampling EAB-infested ash trees (Duan et al., 2013). In 2012, three to four years after *T. planipennisi* releases, the proportion of sampled ash trees with at least one brood of *T. planipennisi* increased steadily from 33% to 92% in the parasitoid-release plots and from 4% to 83% in the control plots. Over the same period, EAB larval parasitism by *T. planipennisi* increased from 1.2% to 21.2% in the release plots and from 0.2% to 12.8% for the control plots. The results of this five-year study demonstrate that *T. planipennisi* is established and spreading throughout EAB populations of southern Michigan (Duan et al., 2013, 2014).

However, *S. agrili* has not been recovered from EAB larvae sampled in southern Michigan one or two years after release, although adults are occasionally recovered in yellow pan traps (Bauer et al., 2011; Gould et al., 2011b). Gould et al. (in press) suggested poor recovery of *S. agrili*, which was originally collected in Tianjin, China (39th parallel north), resulted from incompatible climate matching Tianjin and with northern regions of the United States. Although poor synchrony with required host life stages may be a factor, the establishment of *S. agrili* remains unknown in more southerly states, such as Maryland, West Virginia, and Kentucky because releases were done relatively recently. Until more information becomes available, APHIS plans to continue to release this parasitoid in areas below 40 NL north (USDA–APHIS/ARS/FS, 2013).

Nontarget Effects

Potential attack on nontarget *Agrilus* species. by the introduced larval ectoparasitoid *S. agrili* was examined at three sites in 2007, 2008, and 2009. Potted trees (large nursery stock) of European paper birch (*Betula pendula* Roth) and pin oak (*Quercus palustris* Münch) were planted at each site. To ensure these trees contained nontarget *Agrilus* larvae, adult bronze birch borers (*A. anxius*) were caged on the birch trees and adults of the two-lined chestnut borer (*A. bilineatus*) were caged on the oak trees. Ash, birch, and oak trees were felled at each site during the following winter after sufficient chill to break insect diapause. The logs were placed in cardboard-rearing tubes in a warm environment to stimulate insect emergence. All logs produced adult *Agrilus,* indicating that EAB and the nontarget hosts were available for attack by *S. agrili*. The native *S. floridanus* was found attacking all three *Agrilus* species at all sites. In 2009, five *S. agrili* emerged from a birch log, showing parasitism of *A. anxius*, but no parasitism by *S. agrili* from ash or oak logs was confirmed in 2008 or 2009. Although more *S.* a*grili* were released in 2010 and recovered from ash at all three sites, *S. agrili* was not reared from the test birch or oak logs that year. These results support the results of laboratory host-range testing that some parasitism of nontarget *Agrilus* species may occur in the field.

Recovery of Affected Tree Species or Ecosystems

The population density of EAB is difficult to determine in an absolute sense (number per unit area) and requires destructive sampling and considerable labor (McCullough and Siegert, 2007b). Therefore, trends in EAB population densities are based on indirect estimates using ash decline and mortality over time (Smith, 2006). Parasitoids were introduced at seven EAB biological control research sites in Michigan and two sites in Ohio in 2008 and 2009. At each research site, a release plot was paired with a non-release control plot, and 50 ash trees >4-cm DBH were selected and tagged in each plot. From 2008 to 2010, the following data were collected annually: GPS coordinates, crown class, epicormic shoots, EAB exit holes, DBH, and woodpecker feeding (Gould et al., 2011b). No significant differences were found between ash health at the release and control plots, with most of the larger trees dying from EAB attack before the exotic parasitoids were detectable at most sites. Future plans to assess the impact of EAB biological control at these and other sites include documenting growth and survival of young ash trees at the sites (the regrowth) and estimating the recruitment, growth, and survival of these new trees as they become large enough to be susceptible to EAB attack.

Broad Assessment of Factors Affecting Success or Failure of Project

At a limited number of study sites in Michigan, where the EAB parasitoids from China were first introduced, they are established and spreading, and their population densities are increasing. The long-term impact these parasitoids will have on ash health and recovery is not yet known; however, the longevity and condition of North American ash species planted in northeast China and the Russian Far East provide a basis for some optimism. Life-table studies in China and Russia indicate that the main mortality factors affecting EAB attacking North American ash in Asia are egg and/or larval parasitoids. To assess the effects of biological control in different ash species and genotypes across geographical regions, detailed data on ash density and health must be collected over time and analyzed.

Biological control is a long-term but sustainable management strategy, and EAB natural enemy complexes may eventually stabilize eventually and suppress host population densities below a tolerance threshold allowing the survival and reproduction of native ash species. As the EAB invasion spreads across North America, most ash trees die due the high EAB populations that develop in this abundant and susceptible resource. This tree mortality then results in collapse of EAB population, and provides an intense selection event that may favor the proliferation of EAB-resistant ash genotypes. In fact, several researchers are now screening the surviving ash trees in Michigan for EAB resistance. The parasitoids, both introduced and native species, are likely to be crucial in supporting the survival of ash seedlings and saplings that grow up in the aftermath of EAB. In the decades to come, researchers will need to continue to monitor the relative importance of the various interactions affecting ash survival and EAB population dynamics in North America.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Natural Enemies in the United States

***Antanyolus* spp.** In North America, eleven native species of *Atanycolus* are listed as parasitoids of *Agrilus* spp. (Marsh et al., 2009). These *Atanycolus* are solitary, ectoparasitic idiobionts of late-instar larvae, and several species parasitize EAB. Surveys of natural enemies in southeastern Michigan from 2003 to 2004 detected larval parasitism of EAB by *A. hicoriae* and *A. simplex*; however, total larval parasitism was <1% (Bauer et al., 2005). In 2007 and 2008, Cappaert and McCullough (2009) found that EAB larval parasitism ranged from 9 to 71% by a new species of *Atanycolus*, later described as *A. cappaerti* (Marsh et al., 2009). The following year, EAB populations collapsed in that area, and the prevalence of *A. cappaerti* fell to <1% (Tluczek et al., 2010). In a different Michigan study, at sites where EAB populations were building, EAB larval parasitism by *Atanycolus* spp. increased from <1% in 2009 to 19% in 2010 (Duan e al., 2012b). Of individuals reared to the adult stage and identified (n=383) in that study, 93% were *A. cappaerti,* 5% were *A. hicoriae*, ~1% were *A. tranquebaricae* Shenefelt, and <1% were *A. disputabilis*. *Atanycolus cappaerti* is known to parasitize other species of *Agrilus* in Michigan, indicating a broader host range for *A. cappaerti* than for other *Atanycolus* species (Cappaert and McCullough 2009). Long-term studies are needed to monitor successional changes occurring in parasitoid guilds associated with EAB populations, as EAB density declines due to ash mortality and as the introduced parasitoids increase in density.

Oobius agrili This species is a solitary and parthenogenic egg parasitoid discovered parasitizing EAB eggs sampled from ash trees in Jilin province, China, in 2004 (Zhang et al., 2005) and later in Liaoning province (JJD, unpublished) that has been released and established in the United States. Mature *O. agrili* larvae diapause during the winter inside EAB eggs and typically complete two generations each year (Bauer and Liu, 2007). Adult emergence is synchronized with the oviposition period of EAB, starting in late June and continuing into September in China (Liu et al., 2007). Similar emergence phenology for *O. agrili* was detected in Michigan, with adults starting to emerge in late June and peak parasitism in August (Abell et al., 2011). When reared in the laboratory at 24ºC, *O. agrili* completes one generation every three days with a realized fecundity of ~80 female progeny (LSB unpublished).

Phasgonophora sulcata *Phasgonophora sulcata* is a solitary endoparasitic koinobiont of larvae of native North American *Agrilus* species (Barter, 1957, 1965; Côté and Allen, 1980). In eastern North America, *P. sulcata* also parasitizes EAB larvae (Bauer et al., 2004, 2005; Duan et al., 2012b). Adults of this large chalcidid can be readily observed ovipositing through the bark of EAB-infested ash trees between June and August. Eggs and larvae of *P. sulcata* slowly develop in the hemocoel of EAB larvae, with maturation and pupation occurring the next year, often as their host larva enters the prepupal stage (LSB and JJD, unpublished). Laboratory studies are continuing on the biology of *P. sulcata* and to evaluate its impact on EAB populations in the field.

Spathius agrili A gregarious, ectoparasitic idiobiont of late-instar EAB larvae, this parasitoid was first reported in Tianjin province, China (Xu, 2003) and later in Jilin province (Liu et al., 2003; Yang et al., 2005) and has been released and recovered in the United States. *Spathius agrili* overwinter as mature larvae, and adults emerge in July and August (Wang et al., 2006). In Michigan, adults began to emerge in mid-July and continued into mid-September (LSB, unpublished). When reared in the laboratory at a day: night temperature cycle of 25: 20ºC, has a 4:1 female: male sex ratio and an estimated realized fecundity of ~40 female progeny during the female lifespan (average 61 days) (Wang et al., 2008; Gould et al. 2011a).

Spathius galinae A gregarious, ectoparasitic idiobiont parasitoid, this species was recently discovered in Primorskiy Krai of the Russian Far East, but was initially identified as a similar, closely related species (Yurchenko et al., 2007). This species is being held (as of 2014) in USDA quarantine facility for study. This parasitoid was repeatedly collected from EAB larvae in and around Vladivostok and in Daejeon, South Korea (Baranchikov, 2008; Williams et al., 2010; Duan al., 2012a). It was recently described as *S. galinae*, a new species (Belokobylskij et al., 2012). From EAB natural enemy surveys of infested green ash trees (*F. pennsylvanica*) planted up to 40 years ago in Vladivostok, parasitism by *S. galinae* ranged from 27.5 to 75.5% (Duan al. 2012a). *Spathius galinae* overwinters as mature larvae or prepupae, and adults emerge from EAB galleries in early spring. In the Vladivostok region, *S. galinae* completes two to three generations each year producing six to 15 larvae per EAB larva (Belokobylskij et al., 2012; Duan et al. 2012a). It is being evaluated for possible release in the United States for biological control of EAB, particularly in northern areas because of its greater cold-hardiness (Duan et al., 2012a).

Tetrastichus planipennisi This parasite, a gregarious endoparasitic koinobiont of EAB larvae, was discovered while surveying EAB-infested ash trees in Jilin and Liaoning provinces in 2003 (Liu et al., 2003) and later in Heilongjiang province (Yang et al., 2006), and has been released and established in the United States. *Tetrastichus planipennisi* parasitizes all larval stages of EAB, overwinters as a larva, and completes up four generations each year in Jilin province (Liu et al., 2007). Adult emergence begins in April or May, and females begin parasitizing overwintering *A. planipennis* larvae soon thereafter, with parasitism increasing up to 40% by August (Liu et al., 2007). Similar emergence phenology was found for *T. planipennisi* in Michigan, with adults starting to emerge in late April or early May (LSB, unpublished). The results of a recent study suggest that *T. planipennisi* may be more effective at parasitizing EAB larvae in thin-barked, small diameter ash trees (<12-cm DBH) due to its relatively short ovipositor (2.0 to 2.5 mm long) (Abell et al., 2012). When reared in the laboratory at 25ºC, *T. planipennisi* completes one generation every 27 days, has a 4:1 female:male sex ratio, and an average realized fecundity of ~45 female progeny during the female lifespan (average 42 days) (Liu and Bauer, 2007; Ulyshen et al., 2010; Duan et al., 2011a).

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XVIII Goldspotted Oak Borer

(*Agrilus auroguttatus* Schaeffer) (Coleoptera: Buprestidae)

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DESCRIPTION OF PEST

Taxonomy

The name, "goldspotted oak borer," is used to describe two species of phloem/wood-boring beetles, *Agrilus auroguttatus* Schaeffer and *Agrilus coxalis* Waterhouse, that attack oak trees. These two species are nearly identical in appearance, but have different historical distribution records.

Agrilus coxalis was originally described in 1889, and a female specimen collected in Juquila, Mexico was designated as the lectotype (Waterhouse, 1889). Since its description, specimens of *A. coxalis* have been collected throughout southern Mexico (i.e., in the states of Cordova, Chiapas, Veracruz, Jalisco, and Oaxaca), and also in northeastern Mexico and Guatemala (Coleman and Seybold, 2011).

Agrilus auroguttatus was first described by Schaeffer (1905), and representative specimens of this species have been collected primarily in Arizona, although one specimen was collected from Baja California Sur, Mexico in 1977 (Coleman and Seybold 2011).

Hespenheide (1979) synonymized with *A. coxalis*, because their morphological differences were minor. Hespenheide and Bellamy (2009) later described these differences as dissimilarities in the size of groups of setae on the elytra as well as small differences on the pronotum. However, in response to the elevated levels of oak mortality in San Diego County, California, Hespenheide and Bellamy (2009) re-evaluated the taxonomic status of the invasive population in California and gave subspecies distinction to the two original species. These subspecies designations were *Agrilus coxalis coxalis* (representing the Mexico and Guatemala populations) and *Agrilus coxalis auroguttatus* (representing the Arizona and California populations). These taxa were examined again recently, and based on the morphology of the male genitalia Hespenheide et al. (2011) concluded that the Arizona/California and Mexican/Guatemalan forms do indeed comprise separate species. Therefore, the populations in southern Mexico and Guatemala are recognized once again as *A. coxalis*, and the populations in Arizona and southern California are *A. auroguttatus*. Preliminary results from analyses of mitochondrial DNA sequences tentatively support this new morphology-based classification (Coleman et al., 2011a).

Distribution

The goldspotted oak borer (Fig. 1) is a buprestid beetle that is native to oak woodlands in southeastern Arizona and perhaps northern Mexico (based on the single *A. auroguttatus* specimen collected in Baja California Sur). This invasive insect was first detected in San Diego County, California, in 2004 by the California Department

Figure 1 Goldspotted oak borer, *Agrilus auroguttatus*, adult collected in San Diego County 2010. Mike Lewis, Center for Invasive Species Research, University of California, Riverside, Bugwood.org.

of Food and Agriculture (CDFA), during an exotic wood borer survey, but was not linked to oak mortality until 2008 (Coleman and Seybold, 2008a). Goldspotted oak borer was probably introduced into southern California via the movement of infested oak firewood. Unregulated movement of firewood has accidentally moved many exotic wood borers into new areas of the United States (e.g., the emerald ash borer, *Agrilus planipennis* Fairmaire [Haack et al., 2010]). However, due to the proximity between *A. auroguttatus*' native range in Arizona and the invaded range in southern California, Westcott (2005) hypothesized that the species may have expanded its distribution into California, naturally. However, geographical barriers such as the Mojave and Sonoran deserts make such natural range expansion into that part of California improbable, because deserts are host-free barriers in southern California. These desserts lack the oak hosts required for *A. auroguttatus* development. The separation of oaks by these two deserts has resulted in the geographical isolation of *A. auroguttatus* in Arizona. From its native range in Arizona, *A. auroguttatus* would have to fly unassisted for approximately 400 miles to reach suitable oak hosts in California. Additionally, the locations of initial infestation and the spread of oak mortality thereafter do not support range expansion (Fig. 2). The original populations of *A. auroguttatus* in southern California developed inland inside mature oak forests. The edges of the infested oak woodlands were not attacked first, so this observation is contrary to what would be expected from a natural range expansion from *A. auroguttatus* populations in Arizona or Mexico. The proximity of the initial California population to recreation areas, such as the Laguna Mountain Recreation Area in the Cleveland National Forest, Rancho Cuyamaca State Park, and William Heise County Park (all in San Diego County) further support the hypothesis that *A. auroguttatus* was introduced into southern California through firewood associated with outdoor recreational activities (e.g., camping). Additional support for this hypothesis is the satellite infestation that was found in 2009 at Marion Bear Memorial Park in urban San Diego, which is approximately 40 miles west of major infestation zones.

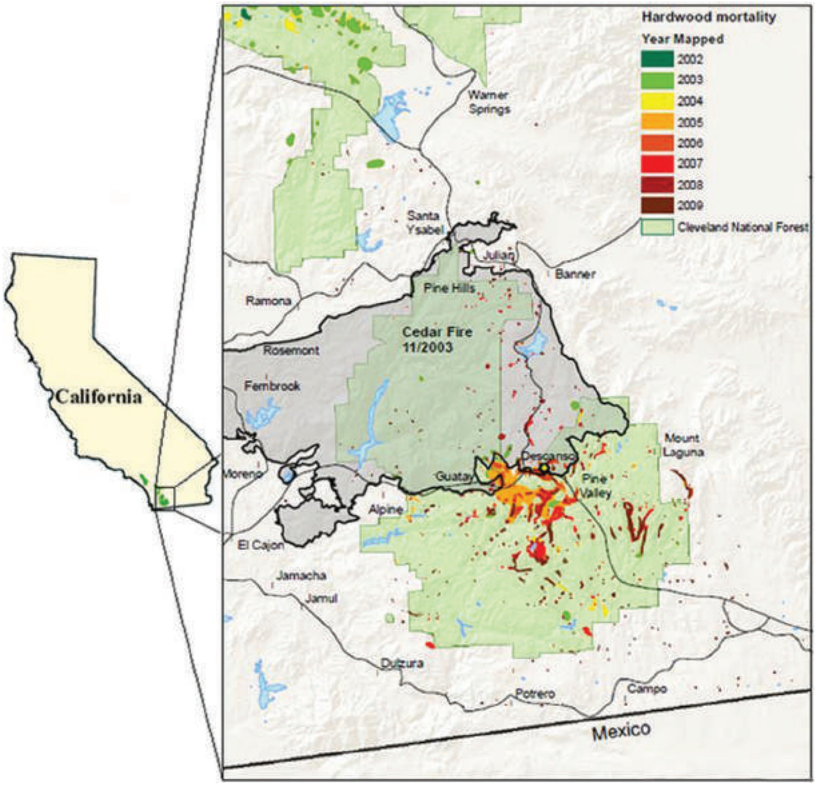

Figure 2 *Agrilus auroguttatus* range expansion map in San. Diego County from 2002–2009. Coleman and Seybold 2011, Bugwood.org.

The known distribution of *A. auroguttatus* (2013) is throughout southeastern Arizona (Cochise, Pima, and Santa Cruz Counties) and in San Diego County, California (Fig. 3). Historical data and recent collections indicate that *Agrilus auroguttatus* also occurs across the Chiricahua,

Figure 3 Map of the known distribution of *Agrilus auroguttatus* in Arizona and California. Tom W. Coleman, Bugwood.org.

Santa Catalina, Huachuca and Santa Rita mountains on the Coronado National Forest in Arizona (Coleman and Seybold, 2011). The distribution of *A. auroguttatus* in San Diego County is estimated to cover 212,460 ha in the Cleveland National Forest, Descanso Ranger District. The infestation crosses all land ownerships in San Diego County, including public, private, tribal, state, and county properties.

Damage

Type *Agrilus auroguttatus* larvae create extensive feeding galleries where the phloem and xylem interfaces with the bark (Fig. 4). Feeding damage to the xylem and phloem prevents nutrient flow, while simultaneously destroying the vascular cambium, the zone underneath the bark that gives rise to new xylem and phloem. The result is retardation of tree growth, and after several years of repeated feeding, tree mortality results. There are several external symptoms associated with *A. auroguttatus* infestation in oaks (Hishinuma et al., 2011), which include crown thinning and die back, bark staining, D-shaped exit holes produced by emerging adult beetles, and woodpecker damage caused by birds foraging for larvae. Typically, crown thinning and die back are the most readily observed symptoms, which begin with premature leaf drop and progress to twig and branch die back (Coleman and Seybold, 2008a). Bark staining (Fig. 5) is the result of extensive larval feeding beneath the bark, which causes necrosis of subcortical tissues and can lead to secondary infections by fungi. Bark staining appears as black and red stains or oozing sap, which may seep from under the bark or appear as blistering (Coleman and Seybold, 2008b). Bark staining is a common symptom of *Agrilus* injury in hardwoods (Solomon, 1995; Vansteenkiste et al., 2005). Typical of the genus, *A. auroguttatus* adults chew D-shaped exit holes through the bark after emerging from pupal cells located just beneath the bark surface. These exit holes (Fig. 6) are approximately 3 mm wide and indicate that larval activity has occurred within that particular region of the tree. Exit holes and bark staining are most common on the lower portion of the main stem

Figure 4 Feeding galleries of *Agrilus auroguttatus* larvae underneath the bark. Tom W. Coleman

Figure 5 Staining on the bark surface of coast live oak, *Quercus agricola*, resulting from *Agrilus auroguttatus* larval feeding. Tom W. Coleman, Bugwood.org.

Figure 6 *Agrilus auroguttatus* adult exit hole. Mark Hoddle, Bugwood.org.

(<3 m). Woodpeckers forage for late instar larvae or pupae during the dormant months (i.e., October through May), and removal by these birds reveals larval galleries and pupal cells in the outer phloem (Fig. 7). The presence of any life stage (larval, pupal, or adult) along with D-shaped exit holes or extensive wood pecker foraging on the main stem of oaks indicates infestation from *A. auroguttatus* in California (Coleman et al., 2011b). Similar injury symptoms associated with *A. auroguttatus* infestations are observed in oaks attacked by *A. coxalis* in southern Mexico (Coleman et al., 2011a).

Figure 7 Woodpecker foraging damage due to *Agrilus auroguttatus* infestation. Mark Hoddle, Bugwood.org

Extent Since its introduction into southern California, *A. auroguttatus* has caused widespread tree injury and mortality to three species of native California oaks: coast live oak (*Quercus agrifolia* Née), canyon live oak (*Quercus chrysolepis* Liebm.), and California black oak (*Quercus kelloggii* Newb.). *Agrilus auroguttatus* has also been observed to colonize Engelmann oak (*Quercus engelmannii* Greene) at a very low frequency. However, *A. auroguttatus*-

caused mortality of this species has not been observed, and infestation of *Q. engelmannii* is likely due to spill over from high populations of *A. auroguttatus* attacking more-favored oak species nearby. Tree mortality from *A. auroguttatus* has been estimated at >21,500 trees (Coleman and Seybold, 2011) (Fig. 8). *Agrilus auroguttatus* was first collected in southern California in 2004; however, aerial surveys of oak mortality by the USDA Forest Service in 2002 indicated that this beetle was probably introduced into the area several years before 2002, the first year in which increased oak mortality was noticed. Red oaks (section *Lobatae*), such as *Q. agrifolia* and *Q. kelloggii*, appear to be preferred hosts for *A. auroguttatus*, while intermediate oaks (section *Protobalanus*), such as *Q. chrysolepis*, are less preferred. White oaks (section *Quercus*), such as *Q. engelmannii,* are rarely attacked by *A. auroguttatus* in southern California, and injury to white oaks caused by *A. auroguttatus* has never been documented in Arizona. Coleman and Seybold (2011) hypothesized that phloem thickness, bark structure, and/or host chemistry within these different oak groups may influence host susceptibility to *A. auroguttatus*. Tree maturity also appears to affect the vulnerability to attack by these beetles because infestation and mortality are predominately observed in larger-diameter trees, typically >12 cm at breast height (Coleman et al., 2011b).

The low levels of oak mortality attributed to *A. auroguttatus* in southeastern Arizona, as compared to the elevated levels seen in San Diego, County, California, could be attributed to either decreased host resistance or the lack of co-evolved natural enemies in California (Coleman and Seybold, 2011). The varying levels of resistance by oak species native to Arizona and California may reflect evolutionary divergence and geographic isolation between these species and *A. auroguttatus*. Oak species in Arizona have experienced a much longer co-evolutionary period with *A. auroguttatus*, and therefore might be less susceptible to attack. On the other hand, California's oaks have not co-evolved with a species that causes similar damage; therefore, due to a lack of suitable defense mechanisms, the species could be more vulnerable to injury from *A. auroguttatus*.

The oak woodlands of southern California are largely composed of species from the red oak group, which are highly vulnerable to *A. auroguttatus* infestation. Coast live oak is a keystone species that forms monotypic stands in the coastal and foothill areas of California. These red oak-group species hold dominant and co-dominant positions in the canopy, so their widespread loss will likely harm forest ecosystems, especially in southern California. Loss of oaks as sources of habitat and food will likely affect many native animals, such as acorn woodpeckers (*Melanerpes formicivorus*), ground squirrels, mule deer (*Odocoileus hemionus*), specialist oak-exploiting insects, and the endangered arroyo toad (*Bufo*

Fig. 8. Tree mortality in San Diego County, California from *Agrilus auroguttatus* infestation. Mike Lewis, Center for Invasive Species Research, University of California Riverside, Bugwood.org.

californicus). Oaks also supply shade to riparian areas and the understory flora, which are critical components of these ecosystems. Also, the accumulation of dead oak litter from trees killed by borers will alter the fuel load in affected woodlands, increasing the risk and severity of wildfires (Coleman and Seybold, 2008b).

The loss of oaks also affects local residents. Oaks are culturally significant to the indigenous people in this region, who have traditionally used their acorns for food. Private landowners incur significant declines in property values when oaks die. To maintain property values, homeowners will have to replace dead oaks or protect healthy un-infested trees. Arboricultural consultants estimate the value of a 20-yr-old coast live oak tree to be approximately US$6,000, which equates to about US$300 per year of tree life. Since the oak trees that are being killed by *A. auroguttatus* are typically very old (some are more than 100 years old), the value added to residential properties by a one hundred year old tree is conservatively estimated by property appraisers and professional arborists at >$10,000. Given such economic values for individual trees, losses for whole towns in *A. auroguttatus*-infested oak woodlands may rise to millions or tens of millions of U.S. dollars.

Methods to kill adults or brood of goldspotted oak borer include systemic and topical insecticides, wood solarization, and grinding of infested wood. The effectiveness of insecticides is being tested. However, the use of insecticides to protect trees in forest stands is neither cost effective nor environmentally sensible. Pesticide use is best suited for private land owners or for saving heritage trees. Solarization (i.e., wrapping infested wood in plastic and heating in the sun to kill larvae or pupae in wood, or to trap and kill adults as they emerge) or grinding infested wood to kill larvae and pupae can provide localized control within an infested area, perhaps slowing expansion of the infestation. However, the most effective way to reduce spread is to stop the movement of infested firewood out of affected areas. Unfortunately, there are no mechanisms in place in California for controlling firewood movement out of infested areas at this time.

Biology of Pest

Before 2008, no information was available on the biology or life history of *A. auroguttatus* or *A. coxalis*. Since then, studies in southern California suggest that most *A. auroguttatus* larvae complete their development to adults in a single year (Coleman and Seybold, 2008b, 2011); however, some larvae and pupae are present under bark in October, which indicates some individuals require more than one year to complete development (Coleman and Seybold, 2008a). Adults emerge from May to October with peak flight activity in late June and early July (Coleman and Seybold, 2008a). *Agrilus auroguttatus* adults feed on oak foliage (Fig. 9) in the laboratory. However, leaf feeding is minor and has never been observed in the field. Mating has been observed on foliage in the laboratory, and it is likely that this may also occur in the field. In the laboratory, mated females lay eggs individually on oak bark or artificial substrates, but *A. auroguttatus* eggs (Fig. 10) have never been observed in the field due to their small

Figure 9 *Agrilus auroguttatus* adults feeding on oak foliage. Mike Lewis, Center for Invasive Species Research, University of California Riverside, Bugwood.org.

Figure 10 *Agrilus auroguttatus* eggs oviposited onto coffee filter paper. Mike Lewis, Center for Invasive Species Research, University of California Riverside, Bugwood.org.

Figure 11 Late instar larva of Agrilus auroguttatus in its feeding tunnel. Mark Hoddle, Bugwood.org.

size (approx. 1 mm in width). Based on information from other *Agrilus* species, it is likely that individual eggs are placed in bark crevices, which, coupled with small size, further compounds the difficulty of visual detection in the field. Once eggs hatch, larvae burrow through the bark to reach the vascular cambium, where they create feeding galleries. Early and late instar larvae have been observed to feed primarily in the cambial region (Fig. 11, above). When larval development is complete, larvae tunnel into the outer phloem and create pupal chambers underneath the outer bark. Larvae adopt a characteristic hair-pin configuration before pupation (Fig. 12).

In the laboratory (23°C, 14:10 L:D), females and males live an average of 52 and 24 days, respectively. Most females (72%) lay eggs, producing an average of 51 eggs per female per life time, of which approximately 90% hatched.

Figure 12 *Agrilus auroguttatus* larvae extracted from pupal chambers that are orientated into a hair-pin configuration. Mark Hoddle, Bugwood.org.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

Host range testing of potential biological control agents of this pest will require examination of susceptibility of native buprestids found in the same habitat. The location and identification of parasitoids with potential as biological control agents was initiated in 2009 (Coleman and Seybold, 2011). As of 2013, host-range analyses have not been conducted. Native and non-native insects related to *A. auroguttatus*, which may be part of future host-specificity tests, include the bronze birch borer (*Agrilus anxius* Gory), oak twig girdler (*Agrilus angelicus* Horn), twolined chestnut borer (*Agrilus bilineatus* Weber), emerald ash borer (*Agrilus planipennis*), and soapberry borer (*Agrilus prionurus*). Other non-congeneric species that occupy similar niches as *A. aurogutattus* that may be considered for testing include the nautical borer (*Xylotrechus nauticus* LeConte) and the flatheaded appletree borer (C*hrysobothris femorat*a Olivier). There are no known endangered or threatened species of Coleoptera in California that use oaks as hosts. Species selection will depend on the availability of field-collected insects and ease of rearing.

Native Natural Enemies Attacking the Pest

Four potential natural enemies of *A. auroguttatus* were detected by cage-rearing GSOP-infested logs from California forests: *Atanycolus simplex* Cresson (Hymenoptera: Braconidae), *Calosota elongata* Gibson (Hymenoptera: Eupelmidae), a bark gnawing beetle (Coleoptera: Trogossitidae), and a snakefly larva (*Agulla* sp., Neuroptera: Raphidioptera) (Coleman and Seybold,

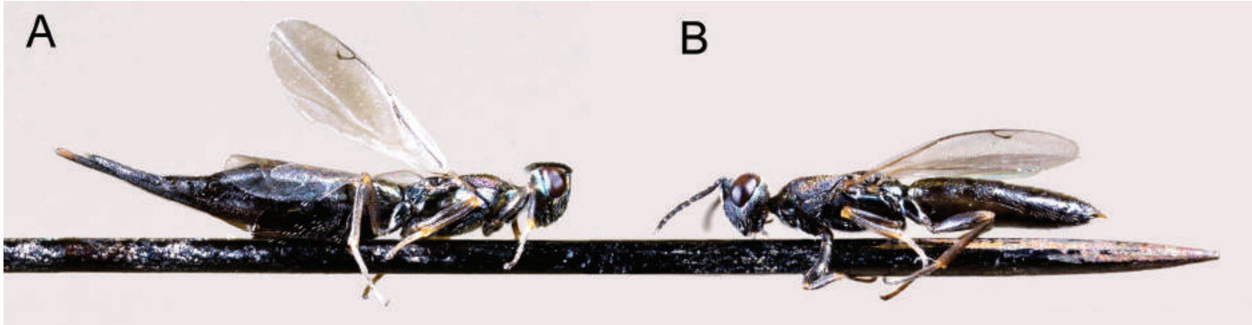

Figure 13 A) *Calosota elongata* (female), a potential larval ectoparasitoid of *Agrilus auroguttatus*. B) *Calosota elongata* (male). Mike Lewis, Center for Invasive Species Research, University of California Riverside, Bugwood.org.

2011). Bark gnawing beetles and *Agulla* sp. are generalist predators of bark beetles and wood borers that are found throughout the western United States (Furniss and Carolin, 1977).

Atanycolus simplex is a generalist larval parasitoid that has been associated with various buprestid and cerambycid beetles throughout the United States (Quicke and Sharkey, 1989; Krischik and Davidson, 2007; USDA Forest Service, 2010). This parasitoid was found associated with *A. auroguttatus* in southeastern Arizona in 2009 (Coleman and Seybold, 2011). It was reared from infested California oak logs in 2010.

The eupelmid parasitoid *C. elongata* (Fig. 13, above) was observed in southeastern Arizona, where it is a gregarious larval ectoparasitoid of *A. auroguttatus* (Coleman and Seybold, 2011) and was described by Gibson (2010) as a new species. In 2010, *C. elongata* was found in California near the center of the outbreak area (L. J. Haavik, pers. com.). Molecular analyses are currently underway to determine whether this parasitoid was introduced into southern California with *A. auroguttatus*. As of 2013, the effectiveness of *C. elongata* for the biological control of *A. auroguttatus* has not yet been assessed, but in San Diego County it appears its distribution is limited to the same area occupied by *A. auroguttatus*. This distribution may simply reflect intensive sampling and rearing efforts for *A. auroguttatus* in that area. *Calosota elongata* may be more widespread in California and its point of detection may be due to higher densities of suitable hosts.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

The area of origin of the California population of *A. auroguttatus* is possibly Arizona or northern Mexico (but not southern Mexico, that being a different species). Collecting of *A. auroguttatus* from various locations is ongoing and molecular analyses are currently in progress to identify the exact area of origin for the invasive California population within the known range of this buprestid.

Areas Surveyed for Natural Enemies

In 2009, natural enemy surveys were conducted in southeastern Arizona, where previous *A. auroguttatus* collections were made (e.g., Santa Rita, Huachuca, Chiricahua, and Santa Catalina Mountain ranges), and on the Descanso Ranger District of the Cleveland National Forest in San Diego County, California (Coleman and Seybold, 2011). Additional surveys were conducted in 2010 in the southern Mexican states of Chiapas and Oaxaca.

Field surveys (i.e., bark removal and extraction of larvae from infested trees) and rearing from cut logs in Arizona have identified *C. elongata* as a potential biological control agent for *A. auroguttatus* (Coleman and Seybold, 2011). This gregarious ectoparasitoid was initially found on *A. auroguttatus* larvae infesting Emory oak on the Coronado National Forest, and was an unknown species when first found, but it has subsequently been described (Gibson, 2010). The remaining natural enemies reared from *A. auroguttatus*-infested logs were generalist predatory and parasitoid species that are not suitable for introduction into California as classical biological control agents (Coleman and Seybold, 2011). Egg parasitoids of *A. auroguttatus* have not yet been identified and surveys for these parasitoids in Arizona are planned.

Host Range Test Results

As of 2013, host-range tests have not been conducted on the known natural enemies of *A. auroguttatus*. However, once potential biological control agents are identified, host-range tests in quarantine will likely include native and non-native California insects which are evolutionarily and behaviorally related to *A. auroguttatus*. Potential nontarget test species may include the bronze birch borer (*A. anxius*), twolined chestnut borer (*A. bilineatus*), oak twig girdler (*A. angelicus*), nautical borer (*X. nauticus*), and flat-headed apple tree borer (*C. femorat*a).

Releases Made

As of 2013, no natural enemies of *A. auroguttatus* have been released.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

The life history for the potential biological control agent *C. elongata*, a gregarious larval ectoparasitoid, is unknown.

RECOMMENDATIONS FOR FURTHER WORK

Further research is needed on general biology and life history of *A. auroguttatus*. On-going molecular research will determine the geographic sources of the California populations of *A. auroguttatus* and *C. elongata*. Surveys for *C. elongata* in infested areas in California will be run using malaise traps. Parasitoids will be reared from caged, *A. auroguttatus*-infested logs, and trees will be deliberately girdled to promote beetle infestations for subsequent parasitoid attacks. All of this will provide information on parasitoid attack rates and the timing of development and emergence of natural enemies. The location and identification of suitable natural enemies is essential for the development of a successful classical biological control program, and this work will be facilitated by further surveys of *A. auroguttatus* populations in both its native and invaded ranges. Cut oak branches or cards infested with *A. auroguttatus* eggs will be deployed in southeastern Arizona and California to attract potential egg parasitoids of *A. auroguttatus*. Egg parasitoids show potential as biological control agents of *A. planipennis* (Liu et al., 2007), and if these natural enemies of *A. auroguttatus* exist, they would be of interest for use in the biological control of this pest

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XIX Winter Moth

(*Operophtera brumata* L.) (Lepidoptera: Geometridae)

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DESCRIPTION OF PEST

Taxonomy

Winter moth, *Operophtera brumata* L. (Lepidoptera: Geometridae), is in the subfamily Lateriinae and the Tribe Operophterini. The genera *Cheimatobia* Stevens 1829, *Thysanodes* Rambur 1870, *Cheimatophila* Plotz 1885, *Rachela* Hust 1896, and *Paraptera* Hust 1896 were found to be synonyms of *Operophtera* Hübner 1825 (Natural History Museum online: http://www.nhm.ac.uk). *Oporophtera* [sic] as spelled by McDunnough 1938, was incorrect. The following species names were found to be synonyms of *brumata* (L. 1758) (Natural History Museum online: http://www.nhm.ac.uk): *hyemata* Hufnagel 1767; *grisearia* de Villers 1789; *brumaria* Esper 1800; *vulgaris* Stephens 1829; *phryganea* Rambur 1871; *myricaria* Cooke 1882; *hyemata* Huene 1901; *brunata* L. sensu Paux 1901; *unicolor* Lamb 1912; *huenei* Prout 1914; *myrtillivora* Hoffman 1914; *harrisoni* Prout 1936; *brunnea* Lempke 1950; *fusca* Lempke 1950; and, *nigrescens* Lempke 1950. A revision of the North American species of *Operophtera* has been completed by Troubridge and Fizpatrick (1993). The genus contains two native species in North America: Bruce spanworm *Operophtera bruceata* Hulst 1886 and *Operophtera danbyi* Hulst 1896. The latter species occurs on the west coast of North America (Troubridge and Fitzpatrick, 1993). The Bruce spanworm subspecies (*O. b. bruceata)* occurs across North America, and the western subspecies of Bruce spanworm (*O. b. occidentalis* Hulst 1896) occurs along the west coast of North America, from Alaska to California (Troubridge and Fizpatrick, 1993). Some earlier authors treat these as separate species (Kimberling et al., 1986), a view supported by DNA analyses of these taxa by Gwiazdowski et al. (in press). There are two species in Europe: *O. brumata* and the northern winter moth, *Operophtera fagata* Scharfenberg 1805. A number of other species of *Operophtera* occur in Asia.

Distribution

The winter moth is widely distributed across Europe (Gwiazdowski et al., in press). It was introduced into Nova Scotia (Canada) some time before 1950 (Hawboldt and Cuming, 1950) and into Vancouver Island (British Columbia, Canada) in the 1970s (Gillespie et al., 1978). It subsequently spread to mainland British Columbia. Other populations of winter moth exist in Washington and Oregon (Kimberling et al., 1986), where it has been since the 1950s. In the late 1990s, a new outbreak of winter moth was observed in eastern Massachusetts, which was not correctly identified until 2003 (Elkinton et al., 2010). Populations of this insect now extend from southeastern Maine to Long Island, New York (Fig. 1) (Elkinton et al., 2010).

Damage

Type Typically, winter moth eggs hatch before bud burst of their host tree, and larvae then burrow into the expanding buds. Some of the damage they cause occurs before the leaves expand. Bud damage results in feeding

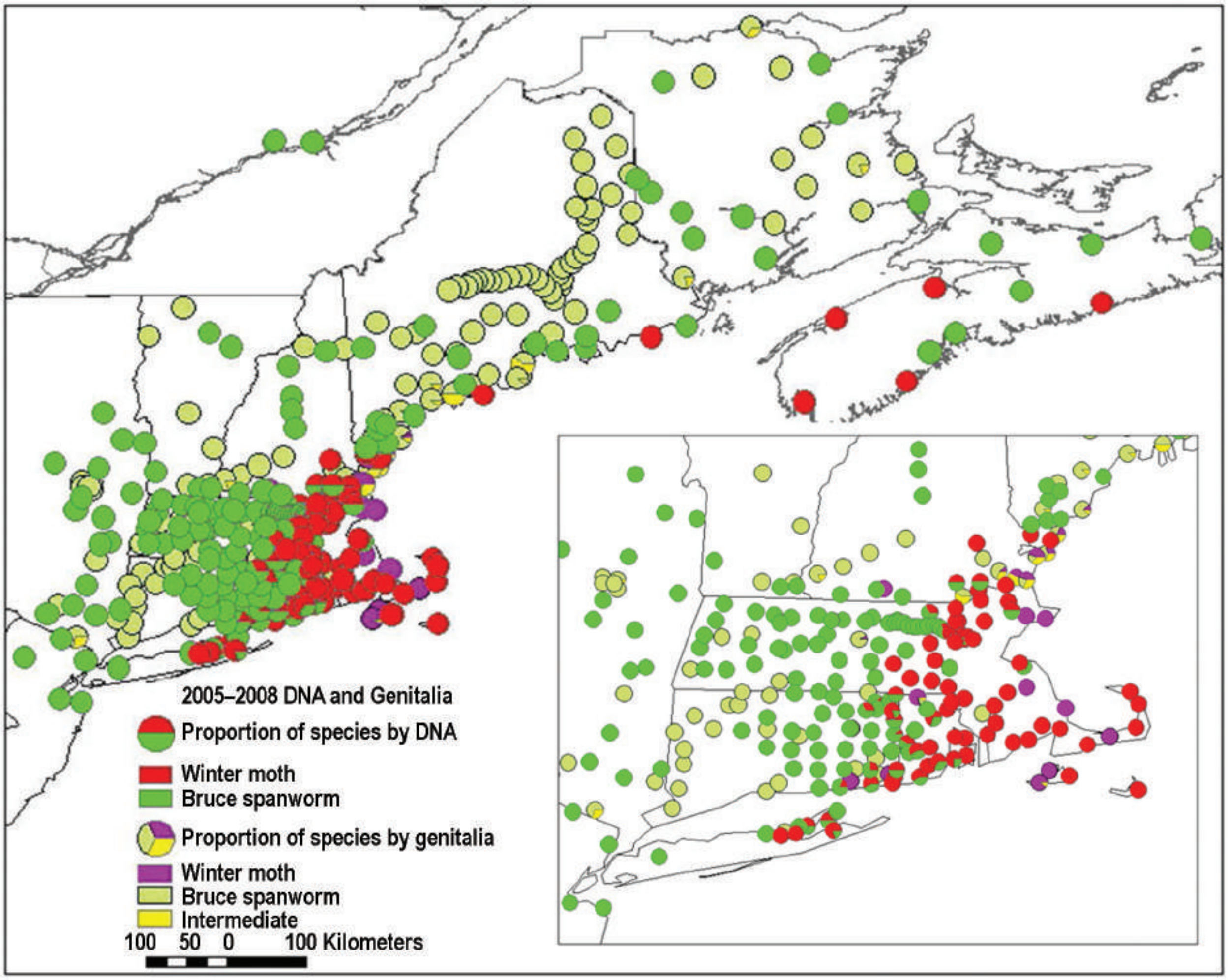

Figure 1 Distribution of winter moth, *Operophtera brumata*, and Bruce spanworm, *3*, in New England in 2007, based on pheromone trap captures (Elkinton et al., 2010). Reprinted with permission of the Entomological Society of America.

holes in the middle of leaves, rather than along leaf margins. This character is useful in surveys for detecting damage by winter moth and other bud feeders. Typical damage consists of a tattering of the leaves. Complete defoliation of host trees is rare even for high density populations.

Extent Winter moth larvae are extremely polyphagous, feeding mainly on a large number of deciduous trees. The most preferred hosts are oaks (*Quercus*) but winter moth also readily feeds on species of maple (*Acer*), willow (*Salix*), poplar (*Populus*), and apple (*Malus*) among others (Wint, 1983). Outbreaks of winter moth also have occurred on Sitka spruce (*Picea sitchensis* Bongard) (Watt and McFarlane, 1991) and heather (*Calluna vulgaris* L.) in Scotland (Kerslake et al., 1996). A large outbreak of winter moth occurred on mountain birch (*Betula pubescens* Ehrh.) in northern Scandinavia (Jepsen et al., 2008). In Massachusetts, winter moth is a major pest of blueberries (*Vaccinium*) and in Oregon is a pest of filberts (*Corylus*) (Kimberling et al., 1986).

Biology of Pest

The adult stage of winter moth emerges from pupae in the soil in late fall or early winter. In central Europe, the Pacific Northwest, and the northeastern United States, adults fly in late November through early January (hence the name winter moth). Male moths are light brown (Fig. 2A) and active whenever temperatures are above freezing. Females are gray with vestigial wings, unable to support flight (Fig. 2B). Females climb up the bases of trees and emit sex pheromone to attract males. After mating, females deposit 150–350 eggs, laid singly, typically under bark flaps or in crevices on the trunk of trees, where they overwinter. New eggs are green but turn red-orange within 3–4 weeks. In early spring, just before hatching, eggs turn dark blue. Depending on spring temperatures, eggs hatch from mid-March to mid-April in Massachusetts and in mid-May in Nova Scotia (Embree, 1970; Kimberling and Miller, 1988; Visser and Holleman, 2001). Hatch typically occurs before bud break of most host plants. Synchrony of egg hatch with bud burst is critical to larval survival, and variation in synchrony among years is a strong predictor of change in winter moth density (Varley and Gradwell, 1968; Embree, 1965). Visser and Hollerman (2001) present evidence that, in Holland, warmer spring temperatures in the 1990s disrupted the synchrony with oak bud burst and shifted winter moth larval feeding onto other tree species.

The main dispersal stage of winter moth is the first instar larva, which spins a silken thread and is then blown by wind between trees, a process known as ballooning. After settling on host plants, larvae burrow into the swelling buds and begin feeding. Most leaf damage from winter moth occurs before the leaves in buds expand.

Winter moth caterpillars are pale green and are typical inchworms (Fig. 2C). Older larvae feed in expanding leaf clusters and may defoliate their hosts. When their development is complete, larvae drop to the soil, where they pupate inside earthen cocoons in the soil or leaf litter (Fig. 2D). In most locations (northeastern and Pacific northwest United States and central Europe) pupation occurs in mid-to-late May and pupae remain in the soil or leaf litter until adult emergence in late autumn or early winter.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

The range of winter moth in eastern North America overlaps with its congener Bruce spanworm (*O. bruceata*

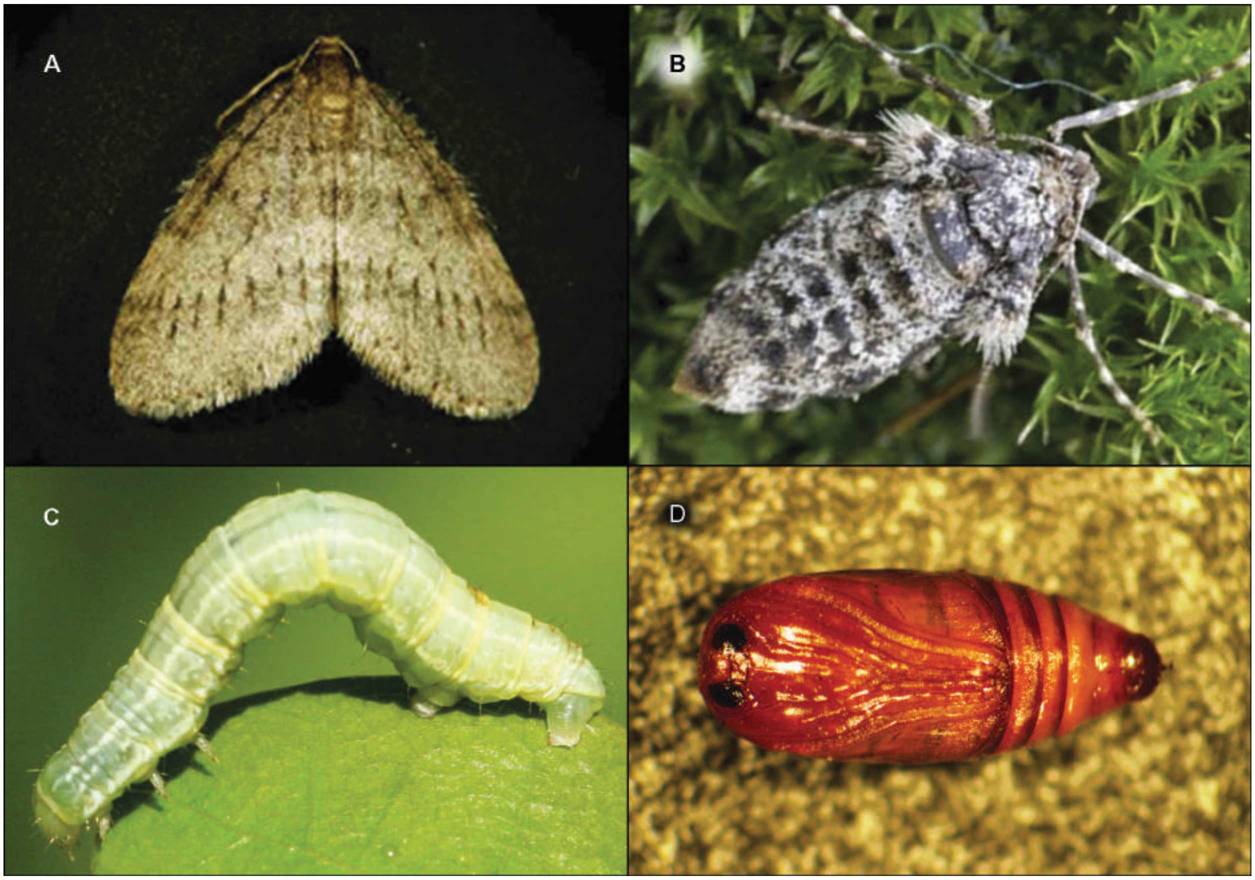

Figure 2 Life stages of winter moth. (A) Adult male. University of Massachusetts, http://www.massnrc.org/pests/pest-FAQsheets/popup_code/wintermothfig02.htm. (B) Adult female. Dave Wagner. (C) Larva. Milan Zubrik, Forest Research institute, Slovokia, Bugwood.org. (D) Pupa. Hannes Lemme, Bugwood.org. (Images are not to scale.)

bruceata). On the West Coast it overlaps with *O. bruceata occidentalis*. Bruce spanworm is as polyphagous as winter moth and has a very similar biology and ecology, although it only rarely erupts into outbreak phase. Outbreaks of Bruce spanworm are most common in aspen (*Populus tremuloides* Michx.) stands in western Canada and on aspen, sugar maple (*Acer saccharum* Marsh) and American beech (*Fagus grandifolia* Ehrh.) in northern New England or near the Great Lakes (Ives, 1984). Occasionally, it is a pest of apples. It uses the same pheromone as winter moth (Roelofs et al., 1982). Pheromone trap surveys (Elkinton et al., 2010) showed that winter moth populations in Maine, New Brunswick, and New Hampshire are confined to coastal areas, whereas Bruce spanworm occurs everywhere in this region, suggesting that it has higher tolerance of cold winter temperatures. Elkinton et al. (2010) confirmed reports that winter moth and Bruce spanworm do hybridize, although <5% of moths caught in pheromone traps in surveys in southern New England were hybrids.

Winter moth outbreaks in Nova Scotia and Massachusetts often co-occur with those of the native fall cankerworm (*Alsophila pometaria* Harris) and spring cankerworm (*Paleacrita vernata* Peck). These native geometrids are similar to winter moth in that they feed in early spring and produce flightless females that emerge, attract winged males, and lay eggs in November (fall cankerworm) or April and May (spring cankerworm).

Native Natural Enemies Affecting the Pest

Roland (1990, 1994) and Pearsall and Walde (1994) demonstrated the importance of native beetles in North America as predators of winter moth pupae in the soil. It appears that pupal predation plays a key role in keeping winter moth densities at low levels (Pearsall and Walde, 1994) in Nova Scotia and on Vancouver Island (Roland, 1990), much as it does in Europe (Varley and Gradwell, 1963; Frank, 1967; Varley et al., 1973; Raymond et al., 2002a). In contrast, parasitism by the tachinid *Cyzenis albicans* (Fallén) is less than 5% in these low-density populations (Roland, 1994; Pearsall and Walde, 1994). In Massachusetts, Whited (2007) observed that, even at high winter moth densities, pupal predation was quite high on deployed pupae. This suggests that, as population densities decline from parasitoids, pupal predators (such as shrews and carabid beetles) continue to play an important role in the dynamics of winter moths in the eastern United States.

Rearing of winter moth larvae collected each year in Massachusetts, between 2004 and 2012, and dissection of the subsequent pupal stage has revealed virtually no parasitism by native species (Elkinton and Boettner, unpublished). In contrast, in British Columbia a number of native parasitoids of winter moth have been recovered (Gillespie and Finlayson, 1981; Humble, 1985). Three native species—*Triclistus crassus* Townes & Townes (Hymenop.: Ichneumonidae), *Agrypon provancheri* Dalla Torre (Hymenop.: Ichneumonidae), and *Cyzenis pullula* Townsend (Dipt.: Tachinidae)—were recovered in 1976 and 1977 before releases of biological control agents (Humble, 1985). The recovery of the wasp *Phobocampe* sp. (Hymenop.: Ichneumonidae) by Gillespie and Finlayson (1981) also suggests host switching by a native parasitoid in British Columbia. Humble (1985) also recovered three native pupal ichneumonid parasitoids, *Coccygomimus hesperus* Townes & Townes, *Buathra dorsicarinata* Pratt, and an undescribed *Cratichneumon* sp. from both *O. bruceata* and *O. brumata*. Humble (1985) also recovered two *Cyzenis* hyperparasitoids, *Phygadeuon* sp. (Hymenop.: Ichneumonidae) and *Villa catulina* Coquille (Dipt.: Bombyliidae) and a third hyperparasitoid, *Mastrus* sp. (Hymenop.: Ichneumonidae), from *C. hesperus* and *B. dorsicarinata*.

A naturally occurring nuclear polyhedrosis virus disease (NPV) has been isolated from winter moth in Massachusetts (Burand et al., 2011). This virus causes up to 10% mortality among late instars. This same virus is known in European populations (Raymond et al., 2002a,b), where it causes significant mortality only occasionally. In contrast, the NPV of winter moth does not appear to cause the dramatic epizootics that terminate outbreaks, as do the baculoviruses of other forest Lepidoptera, such as those of gypsy moth or forest tent caterpillar, *Malacosoma disstria* Hübner. An NPV has been implicated in the decline of Bruce spanworm populations in North America (Ives, 1984).

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Winter moth in North America is from an unknown location in Europe. Recent DNA analyses by Gwiazdowski et al. (in press) did not resolve the question or determine whether there was one or several introductions to North America. Gillespie et al. (1978) argued that the introduction to Vancouver Island arrived on nursery stock from Nova Scotia. A separate introduction occurred in Oregon sometime before 1950 (Kimberling et al., 1986).

Areas Surveyed for Natural Enemies and Natural Enemies Found

Efforts to locate parasitoids of winter moth for its biological control in Nova Scotia began in 1952. Collections were made in France and Germany (Roland and Embree, 1995) with the help of the Commonwealth Institute of Biological Control. The most abundant species collected were the tachinids *C. albicans* and *Lypha dubia* Fallén, and the ichneumonid *Agrypon flaveolatum* Gravenhorst. A total of 63 parasitoid species of winter moth in Europe were considered for release in Nova Scotia (Wylie, 1960). The native range of *C. albicans* includes at least Europe and Japan (O' Hara and Cooper, 1992; O' Hara and Wood, 2004.)

Host Range Test Results

Because of the period of history in which the original releases of *C. albicans* in North America were made, formal host range testing was not done. Given that the species was already widely established in parts of the United States, this was not done during the recent introduction to Massachusetts. However, some insight into the degree of specialization of *C. albicans* is available from the literature. *Cyzenis albicans* has been reared primarily only from species of geometrids in the genus *Operophtera* (Arnaud, 1978). Nearly all host records for *C. albicans* are from the winter moth, *O. brumata,* but, Embree and Sisojevic (1965) also showed that in the laboratory, this parasitoid could be reared in Bruce spanworm. However, even after extensive field surveys in Canada, C. albicans has only been recovered from winter moth (Anon., 1956a,b, 1957, 1958; Embree, 1960, 1964, 1965, 1966; Cuming, 1964; Embree and Sisojevic, 1965; Graham, 1958; MacPhee, 1962; Williamson, 1963). Roland and Embree (1995) state that *C. albicans* rarely attacks Bruce spanworm and is unlikely to have a major impact on this species. O'Hara and Cooper (1992) report one recovery from spring cankerworm (*P. vernata*).

Embree and Sisojevic (1965) were unsuccessful in laboratory attempts to rear *C. albicans* on the geometrid *A. pometaria*, the lasiocampid *Malacosoma americanum* (Fabricius), or the olethreutid *Pseudexentera improbana* (Walker) (given as *Pseudexentera cressoniana* Clemens).

Releases Made

Nova Scotia In Nova Scotia (the first location in North America where biological control of winter moth was attempted), releases of *C. albicans* (Fig. 3A) were made at one location (Oak Hill), beginning with the release of 31 flies in 1954, followed by 1008 in 1955, 1005 in 1956, and 250 in 1957 (Graham, 1958). A total of 250 *A. flaveolatum* (Fig. 3B) were released in 1956. Releases of both parasitoids continued until 1965. Before 1963 they were collected in Europe; after that, collections were made at sites in Nova Scotia where the parasitoids had become abundant. Other species released were the tachinds *L. dubia* and *Phorocera obscura* (Fallén) and the ichneumonids *Phobocampe crassiuscula* (Gravenhorst) and *Pimpla turionellae* L. (Graham, 1958; Roland and Embree, 1995).

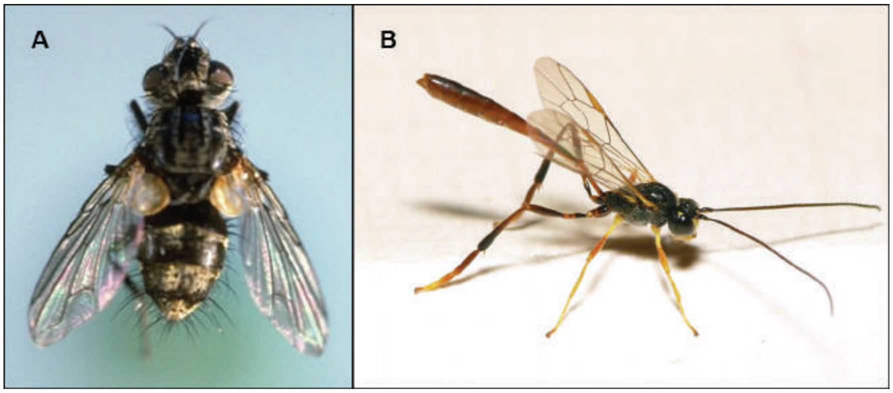

Figure 3 The introduced winter moth parasitoids. (A) The Tachinid fly *Cyzenis albicans*. Nicholas Conder, Canadian Forestry Service. (B) The Ichneumonid wasp *Agrypon flaveolatum*. Dick Belgers, waarneming.nl, wikimedia.org.

British Columbia In British Columbia (the second location where biological control of winter moth was attempted), 15,085 adults of *C. albicans* and 3,354 of *A. flaveolatum* were released from 1979 to 1980, spread evenly across 33 locations, over an area of 600 km^2 in and around the city of Victoria on Vancouver Island (Embree and Otvos, 1984; Roland and Embree, 1995). Releases were made primarily in stands of Garry oak (*Quercus garryana* Douglas ex Hook). Nearly all parasitoids came from Nova Scotia (a few came from Germany).

Oregon In Oregon, 3,745 *C. albicans* and 1,595 *A. flaveolatum* were released in 1982 in eleven commercial filbert orchards.

New England In Massachusetts and Rhode Island (the third area in North America where biological control of winter moth was attempted), the decision was made to release only *C. albicans* because, unlike *A. flaveolatum,* it is very host specific and because it caused higher levels of parasitism in Canada than did *A. flaveolatum*, especially in British Columbia (the area where parasitoids were collected for release in Massachusetts). Releases in New England began with the liberation of approximately 200 *C. albicans* females at one site in Massachusetts in 2005. Further releases were made annually through 2011 at one or two sites per year, each site receiving 700–2000 mated *C. albicans* adults (mostly females). In 2011, a total of 7000 *C. albicans* were released among 10 new sites, including one in Rhode Island. All *C. albicans* released were reared from winter moth larvae collected near Victoria, British Columbia.

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

Nova Scotia The first recovery of *C. albicans* at the release site in Nova Scotia was made in 1956. By 1959, parasitism was approximately 10%, and this increased to more than 70% by 1961. The winter-moth populations in Nova Scotia started to decline in 1962 as parasitism exceeded 78% (Fig. 4). *Agrypon flaveolatum* was recovered in 1957, one year after its release. No recoveries were made of any of the other four species released (Graham, 1958; Roland and Embree, 1995). In subsequent years, winter populations in Nova Scotia remained at low densities except for minor and short-lived eruptions (Roland and Embree, 1995).

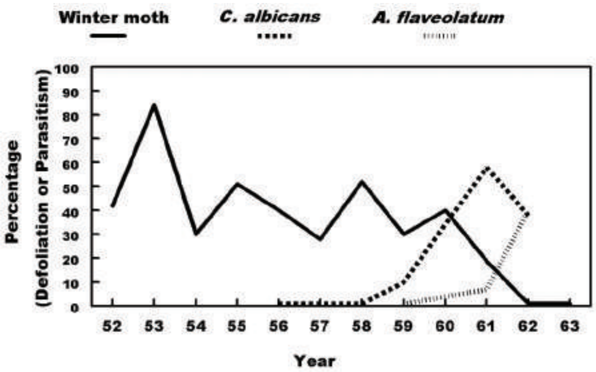

Figure 4 Decline in population density of the winter moth (heavy line) in Nova Scotia after release of *Cyzenis albicans* (heavy dots) and *Agrypon flaveolatum* (finer dots).

British Columbia Recovery of *C. albicans* occurred in British Columbia in 1982, and winter moth populations declined rapidly in 1983. *Cyzenis albicans* also was recovered on the mainland of British Columbia, but parasitism levels were low there (Horgan et al., 1999).

Oregon *Cyzenis albicans* was recovered at one site in Oregon in 1983 (Kimberling and Miller, 1986). No further studies were done in Oregon to record parasitism of winter moth by this species, but winter moth was not a local problem in subsequent years (Roland and Embree, 1995).

New England In Massachusetts, we expected there would be a longer delay between parasitoid release and subsequent detection or onset of significant parasitism than occurred in the earlier projects in Canada. This was because, in contrast to the scattered stands of high quality hosts in Nova Scotia or Vancouver Island, which may have helped to limit parasitoid dispersal following release, southeastern New England has extensive oak/maple forests, which provide a continuous supply of high quality hosts for winter moth. As of 2012, *C. albicans* was recovered at all six sites in Massachusetts where releases were made before 2010. At one of these sites, parasitism reached approximately 30% by 2012.

Nontarget Effects

Cyzenis albicans is extremely host specific. It will attack Bruce spanworm under laboratory conditions (Embree and Sisojevic, 1965) but has not been recovered from that species under field collections (Roland and Embree, 1995). Thus, as far as we know, winter moth is its only host. Six species of *Cyzenis* flies were reviewed by O'Hara and Cooper (1992). *Cyzenis pullula* (which attacks Bruce spanworm), and *C. albicans* are closely related sister species, and have potential to hybridize. Such hybridization could be an indirect effect of this biological control program; however, there is no evidence of hybridization at this time.

Host range testing for *A. flaveolatum* has been complicated by uncertainties in its taxonomy. Dasch (1984) reported that *A. flaveolatum* might be synonymous with *Agrypon alaskensis* (Ashmead) in the Pacific northwest and northern Canada. Schmid (1970) and Carlson (1979) believed it to be synonymous with *A. provancheri*. *Agrypon provancheri* is widespread across North America (Carleson, 1979) and has a wide host range among the Geometridae, including *O. bruceata* and *Melanolophia imitata* (Walker) (Barron, 1989). However, no *Agrypon* species have been recovered in eight years of rearing many thousand winter moth larvae in Massachusetts (Elkinton and Boettner, unpublished data), which suggests that *A. flaveolatum* and *A. provancheri* may be distinct species. Barron (1989) found morphological differences between *A. flaveolatum, A. provancheri,* and *A. alaskensis*.

Recovery of Affected Tree Species or Ecosystems

Except for minor outbreaks, winter moth has remained at low density in Nova Scotia since parasitism reached high levels in 1962 (Embree, 1966; Roland and Embree, 1995). Similarly, the winter moth population on Garry oak on Vancouver Island declined rapidly following the establishment of *C. albicans* and *A. flaveolatum,* but the winter moth densities on Vancouver Island remain higher than in Nova Scotia (pers. observation). Embree (1967) reported that red oaks in Nova Scotia suffered as much as 40% mortality due to winter moth outbreaks in the 1950s.

Broad Assessment of Factors Affecting Success or Failure of Project

The winter moth biological control project in Canada is viewed as a landmark of successful biological control (Caltagirone, 1981). There is little doubt that *C. albicans,* along with *A. flaveolatum,* caused a major and permanent reduction in winter moth density. Since the 1950s, when these parasitoids were established in Nova Scotia, there have been only minor and short-lived population expansions of winter moth about every ten years (Roland and Embree, 1995), often in association with similar eruptions of Bruce spanworm and fall cankerworm.

However, there is debate over the mechanism by which the suppression of winter moth density was achieved. Embree (1960) concluded that parasitism by *C. albicans* was the direct cause of the decline in winter moth density. Roland (1988, 1990, 1994) later suggested that the decline in winter moth density was caused not by *C. albicans*, but by an increase in the level of predation of pupae in the soil, which was influenced indirectly by parasitism. He hypothesized that the presence of parasitized winter moth pupae in the spring might serve to maintain higher densities of pupal predators, which would begin to attack winter moth soon after they pupated in June.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Cyzenis albicans

Cyzenis albicans (Diptera Tachinidae) lays microtype eggs on the foliage. Eggs are usually laid near actively feeding winter moth larvae, and the flies are attracted to the sap exuding from partially defoliated leaves, especially those of oak trees (Hassell, 1968; Roland, 1986). Roland et al. (1995) demonstrated that *C. albicans* is attracted to borneol, a plant volatile emitted from oak foliage. After winter moth larvae ingest the tachinid's eggs, the eggs hatch and immature parasitoids then burrow into the salivary glands of their hosts. They remain there until larvae pupate in the soil or leaf litter. The immature flies then complete development and form puparia inside winter moth pupae. The adult flies emerge in the spring at about the same time that winter moth eggs hatch. Adult flies mate soon after emergence and females have a pre-oviposition period of 10–14 days (Embree and Sisojevic, 1965). Each fly can lay up to 1300 eggs. Winter moth larvae must be at least in the third instar before they are big enough to consume a fly egg and become parasitized.

Agrypon flaveolatum

Agrypon flaveolatum (Hymenoptera: Ichneumonidae) has one generation per year and attacks the larvae of winter moth. Development is completed and adults overwinter inside the winter moth pupae. Adults emerge in the spring. Roland and Embree (1995) reported that the highest levels of parasitism from this species occur in low-density populations of winter moth.

RECOMMENDATIONS FOR FURTHER WORK

The outbreak of winter moths in Massachusetts and Rhode Island provides a new opportunity to study the population dynamics of this well known forest insect before *C. albicans* parasitism becomes a major source of mortality, and to understand the relative importance of parasitism and predation, as debated by Roland and Embree (1995). The release of *C. albicans,* but not *A. flaveolatum,* provides an opportunity to study the impact of the former species alone in the biological control of winter moth. If *C. albicans* provides insufficient control, then both host range testing and further taxonomic analyses would be required before *A. flaveolatum* could be released in New England.

The occurrence of hybridization between winter moth and Bruce spanworm implies that there may be gene flow between these two species. The genes exchanged could include those affecting host susceptibility to their respective species of *Cyzenis*: *C. albicans* on winter moth and *C. pullula* on Bruce spanworm. Moth hybridization also could affect genes for cold hardiness or whatever traits allow Bruce spanworm to occupy interior regions, where winter moth has not spread. The potential for competition or hybridization between the introduced *C. albicans* and the native *C. pullula* also should be investigated.

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XX AMBERMARKED BIRCH LEAFMINER

(*Profenusa thomsoni* [Konow]) (Hymenoptera: Tenthredinidae)

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DESCRIPTION OF PEST

Taxonomy

Ambermarked birch leafminer (*Profenusa thomsoni* [Konow]) is a member of the genus *Profenusa* MacGillivary, which has five named species in North America (Smith, 1971). In the tribe Fenusini there are nine genera with 21 species. Possible synonyms for this species include *Emphytus pumilio* [Hartig], *Fenusa pumilio* [Hartig], *Fenusa thomsoni* [Konow], and *Fenusella thomsoni* [Konow] (Taeger et al., 2010).

Distribution

The ambermarked birch leafminer (Fig. 1**)** is a European species that is invasive in North America. *Profenusa thomsoni* invaded North America at the beginning of the 20th century and was first reported in the eastern United States in 1923 (MacQuarrie, 2008), where it never became a high-density pest. In eastern North America, this sawfly occurs in the United States from New England to the Great Lakes States and in Canada from the Maritimes to Manitoba. In western North America, it was first reported in Alberta, which it invaded before 1970 (Digweed, 1995) and where it reached high densities in the early 1990s (Digweed, 1995). From Alberta, it spread north and west in Canada and reached Haines, Alaska in 1991 (Snyder et al., 2007) (Fig. 2). It was not recognized as invasive in Alaska until 1996 when it was discovered damaging birch (*Betula*) trees in Anchorage (Snyder et al., 2007). Possible routes of introduction to Alaska include movement of infested plants (MacQuarrie, 2008), movement of adults in vehicles (Digweed and Langor, 2004), general cargo introduced through the port of Anchorage (Snyder et al., 2007), or perhaps some combination of these routes. However, the actual source of introduction is unknown.

Figure 1 Adult ambermarked birch leafminer (*Profenusa thomsoni* [Konow]) on a leaf. Thérèse Arcand, Natural Resources Canada, Canadian Forest https://tidcf.nrcan.gc.ca/en/insects/factsheet/7926.

Damage

Type Larvae feed inside the leaf causing the leaves to turn brown and appear dead or dying (Fig. 3). The immediate damage to affected birch trees is aesthetic. Long-term effects on tree health are still unknown but it is hypothesized to slow tree growth (Hoch et al., 2000; Snyder et al., 2007). In Alaska, damage reached as high as 90% of leaves mined (Soper, 2012). Urban trees had a higher percentage of leaves mined than trees in forests due to an urban heat effect (Soper, 2012).

Extent The first surveys for damage from this pest in Alaska were conducted in 2004–2006 (Snyder et al., 2007), when *P. thomsoni* was found to be widespread throughout the south-central region of Alaska, as well as in the Fairbanks area. Aerial surveys conducted in 2003 estimated that the damage affected over 12,800 hectares in the Anchorage bowl and extended into the Matanuska-Susitna (Mat-Su) Valley (Whittwer, 2004; Snyder et al., 2007)

Figure 2 Birch trees (brown) in Alaska heavily mined by ambermarked birch leafminer. Chris MacQuarrie, University of Alberta, Edmonton, Alberta, Canada. Bugwood.org.

Figure 3 Branch with mines of ambermarked birch leafminer. Inset, mine of nearly mature larva of ambermarked birch leafminer. ThérèseArcand, Natural Resources Canada, Canadian Forest Service. https://tidcf.nrcan.gc.ca/en/insects/factsheet/7926.

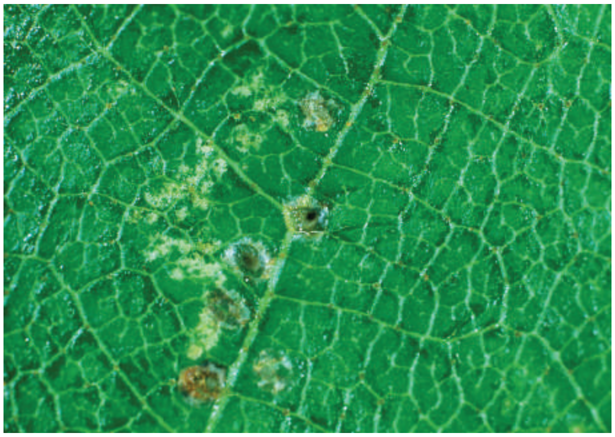

Figure 4 Eggs of ambermarked birch leafminer. Thérèse Arcand, Natural Resources Canada, Canadian Forest Service. http://imfc.cfl.scf.rncan.gc.ca/images_web/imfc/insectes/moyen/017578.jpg.

Biology of Pest

The ambermarked birch leafminer has one generation per year in Alaska but has two in Massachusetts (Soper, unpub.). Adult sawflies are parthenogenetic (consisting of all females) and in Alaska emerge from late June to August, and deposit their eggs singly on the midribs of birch leaves (Fig. 4). In late July and August, larvae feed on the inner layers of the leaf and convert the leaves into brown, crinkled mines as the larvae develop through five feeding instars (Fig. 5). In mid- to late August, mature larvae (sixth instars) drop to the soil, where they form earthen cells in which they overwinter as prepuae. In spring to early summer of

Figure 5 Older instar larva of ambermarked birch leafminer, with mine opened. Thérèse Arcand, Natural Resources Canada, Canadian Forest Service. https://tidcf.nrcan.gc.ca/en/insects/factsheet/7926.

Figure 6 Important parasitoids of ambermarked birch leafminer in Alaska: *Aptesis segnis*, (left), *Lathrolestes soperi* (center), and *Lathrolestes thomsoni* (right). Anna Soper, Bugwood.org.

the following year, pupation and adult emergence occur, completing the life cycle.

ANALYSIS OF RELATIVE NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

Worldwide, *Profenusa* contains 14 species, of which only four species are native to the Nearctic: *Profenusa alumna* (MacGillivray), *Profenusa canadensis* [Marlatt], *Profenusa inspirata* (MacGillivray), and *Profenusa lucifex* (Ross).

Native Natural Enemies Affecting the Pest

Other than the parasitoid *Lathrolestes thomsoni* Reshchikov (Hymenoptera: Ichneumonidae) found attacking the leafminer in Alberta, Canada, the only native natural enemies recorded from this leafminer were in Alaska. The larval endoparasitoid *Lathrolestes soperi* Reshchikov (Hymenop.: Ichneumonidae) and the ectoparasitoid *Aptesis segnis* [Gravenhost] (Hymenop.: Ichneumonidae) were both found to be important mortality factors affecting ambermarked birch leafminer densities (Soper, 2012) (Fig. 6, above).

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

The ambermarked birch leafminer is native to central Europe (Pschorn-Walcher and Altenhofer, 1989). Efforts to locate the pest there have been unsuccessful due to the extremely low population densities in its host range (Pschorn-Walcher and Altenhofer, 1989).

Areas Surveyed for Natural Enemies

Because a seemingly effective agent was already present in North America, no surveys for parasitoids of this species were done in Europe. In earlier work against *Fenusa pumila* Leach, Eichhorn and Pschorn-Walcher (1973) sampled the tenthredinid leafminer complex on birches in Europe and found that *P. thomsoni* had one generation per year and made up 0.2 to 1.6% of all tenthredinid leafminers on birch in central Europe in the year of the survey (1968). No parasitoids were reared from this species, likely due to the few specimens collected.

Natural Enemies Found

Three ichneumonid wasps, *L. thomsoni, L. soperi,* and *A. segnis,* were found attacking *P. thomsoni* in Alberta or Alaska. *Lathrolestes thomsoni* and *L. soperi* are internal parasitoids of larvae in leaf mines. *Lathrolestes thomsoni* was observed to provide control of ambermarked birch leafminer in Edmonton, Alberta and in Yellowknife, Northwest Territories (Canada) (under the name *Lathrolestes luteolator*) (Digweed et al., 2003). This species was later introduced to Anchorage, Alaska, where it successfully established (MacQuarrie, 2008; Soper, 2012).

Lathrolestes soperi was first observed attacking ambermarked birch leafminer during surveys conducted in Anchorage, Alaska, in 2006. Its origin is unknown and there are no records of it from other locations or attacking any other hosts. Both it and *L. thomsoni* attack early-instar larvae in leaf mines and then pupate the following spring in earthen cells made by the sixth instar host larvae after they drop to the ground in later summer.

The ichneumonid *A. segnis* attacks its hosts in their earthen cells in the soil, laying its egg external to the host. *Aptesis segnis* is also known to attack the hawthorn leafminer, *P. canadensis* (Pickering, 2012).

Host Range Test Results

No host range testing was done for *L. thomsoni* as it was moved from Canada to Alaska as part of the biological control project, because the species was already established in both Canada, where it was moving toward Alaska, and in the United States (in Massachusetts). As such, it was not considered a novel species by US Department of Agriculture, Animal and Plant Inspection Service (USDA APHIS) and, apart from interstate movement permits, a Federal permit was not required. Also, all birch leafminers in Alaska are considered invasive and so no additional risk was perceived to Alaskan insects.

Releases Made

No releases of any parasitoids were made in Edmonton, Alberta, against ambermarked birch leafminer, where the primary parasitoid (*L. thomsoni*) was found already to occur and to be attacking the leafminer (Digweed 1995). From 2006 to 2008, 3636 *L. thomsoni* adults were released in Alaska at seven release sites (Soper, 2012).

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

Through a combination of molecular and sweep sampling techniques, recovery of *L. thomsoni* has been confirmed at all release sites in Alaska, from Soldotna on the Kenai Peninsula, north to Fairbanks. In Anchorage, *A. segnis* caused an average of 26% parasitism, while parasitism by *L. soperi* ranged from 5 to 62% at certain release sites, and parasitism by *L. thomsoni* ranged from 1 to 25%. It is likely that relative importance of the introduced versus the pre-existing parasitoids is still changing.

Nontarget Effects

To determine if any parasitoid species had alternate hosts in Alaska, various other tree species were examined for other species of leafminers that *L. thomsoni, L. soperi,* or *A. segnis* might attack. However, no parasitoids were found attacking any other leafminer species sampled in Alaska (Soper, 2012).

Recovery of Affected Tree Species or Ecosystem

The percent mined leaves on birch trees in the Anchorage area has declined dramatically, but this is more likely due to the two pre-existing parasitoids, in particular *A. segnis*, than the introduced species *L. thomsoni* (Soper 2012).

Broad Assessment of Factors Affecting Success or Failure of Project

A few unusual circumstances occurred during this project, the first being that the biological control agent selected for release was initially incorrectly identified as *Lathrolestes luteolator*. As part of the project, a revision of the genus by Alexey Reschikov of the University of St. Petersburg, Russia, was commissioned. He determined that the wasp of interest was not *L. luteolator* but rather an unnamed species (Reshchikov et al., 2010). The wasp was described as *Lathrolestes thomsoni* to reflect its association with the host. The origin of the wasp is unknown. The second circumstance that occurred was that two additional wasps, *L. soperi* and *A. segnis,* were found in Alaska parasitizing the leafminer at the study location. The new species *L. soperi* (also described by Reshchikov), *Lathroleste soperi*, was found to have very similar biology to that of *L. thomsoni,* attacking early instar larvae of the pest in the leafmines. *Aptesis segnis* attacks leafminer pupae or pre-pupae in the soil. *Lathrolestes soperi* and *A. segnis* were found to cause significant mortality (estimated at 40%) in permanent study plots where *L. thomsoni* was not released (Soper, 2012).

In conclusion, of the three parasitoids found to be important in the suppression of the introduced pest, one was native (*A. segnis*), one was of unknown origin (*L. soperi*), and one (*L. thomsoni*) was, based on circumstantial evidence (presence in Massachusetts attacking the pest), believed to be an introduced species that co-invaded with its host during the original invasion of eastern North America. It is likely, based on trends in control sites, that density of ambermarked birch leafminer would have declined significantly in Alaska even without the introduction of this third species; however, the final status of this system is unresolved at this time and should be re-evaluated in 5–10 years.

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XXI Asian Chestnut Gall Wasp

(*Dryocosmus kuriphilus* Yasumatsu) (Hymenoptera: Cynipidae)

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DESCRIPTION OF PEST

Taxonomy

Dryocosmus kuriphilus Yasumatsu is a Palearctic species, invasive in North America, that feeds on chestnut (*Castanea*). No synonyms for *D. kuriphilus* are reported.

Distribution

The Asian chestnut gall wasp, *D. kuriphilus,* (Fig. 1) is native to China and is restricted to *Castanea* spp. It was first reported outside China as a pest in Japan in 1941, then in Korea in 1958 (Yasumatsu, 1951; Cho and Lee, 1963; Murakami et al., 1995; Moriya, 2010), and in the USA in 1974 (Payne et al., 1975). Later it invaded Nepal (1999) and Europe, including Italy (2002), France (2005), Slovenia (2005), Hungary (2009), Switzerland (2009), and Croatia (Graziosi and Santi, 2008; Zhang et al., 2009; Bosio et al., 2010; Matosevic et al., 2010).

Figure 1 Asian chestnut gall wasp, *Dryocosmus kuriphilus,* adult on chestnut bud. Jerry Payne.

In North America, the gall wasp was first discovered in Byron, Georgia, USA, infesting Chinese chestnut, *Castanea mollisima* Blume, growing in a chestnut plantation in 1974 (Payne et al., 1975; Rieske, 2007). By 1976 the gall wasp had spread to three adjacent counties and was reported infesting Japanese, *Castanea crenata* Siebold & Zuccarini, and European, *Castanea sativa* Miller, chestnut. In 1992, the gallmaker was reported on American chestnut, *Castanea dentata* (Marsh.) Borkhausen, in northern Georgia, 300 km north of the original infestation site (Rieske, 2007). Although the incidence of American chestnut in forests of eastern North America has been drastically reduced due to the exotic chestnut blight fungus, *Cryphonectria parastica* (Murrill) Barr (Griffin, 2000), suitable hosts for the gall wasp occur sporadically throughout eastern forests. These lingering American chestnut, coupled with chestnut breeding and restoration programs, reclamation projects, landscape plantings of Chinese chestnut, and chestnut plantations for nut production, provide adequate host material for proliferation of the gall wasp infestation. Gall wasp populations radiated through Georgia and Alabama, and later were likely dispersed longer distances by movement of infested plant material, establishing non-contiguous satellite populations (Cooper and Rieske, 2007ab; Rieske, 2007). The Asian chestnut gall wasp is now established in ten states in the eastern United States, including Georgia (1974), Alabama (1983), Tennessee (mid-1980s), North Carolina (1998), Virginia (2001), Kentucky (2003), Ohio (2002), Pennsylvania (2006), Maryland (2006), and West Virginia (2010) (Fig. 2). It has been reported infesting American and Chinese chestnuts and their hybrid crosses, European and Japanese chestnuts, as well as Allegheny chinquapin, *Castanea pumila* Miller (Rieske, 2007).

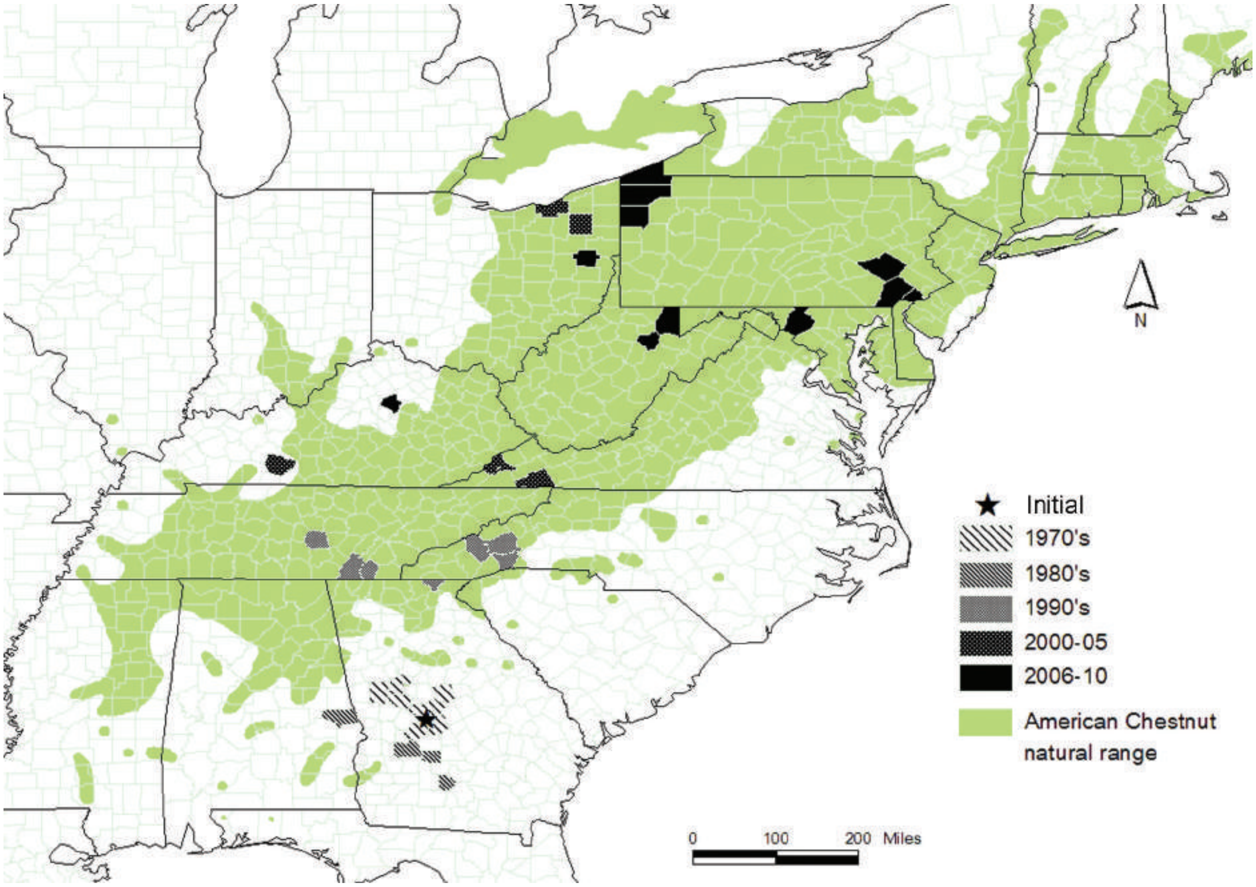

Figure 2 Distribution of chestnut gall wasp, *Dryocosmus kuriphilus,* in eastern North America (May 2011), showing the historic range of American chestnut, *Castanea dentata*. Ignazio Graziosi.

Damage

Type *Dryocosmus kuriphilus* induces 1–3 cm diameter, green to red galls on leaves, petioles, or shoots of infested chestnut (Fig. 3). Galling disrupts shoot and twig growth, impedes normal flowering, and weakens infested trees (Kato and Hijii, 1997). In its native China, the gall wasp causes yield losses as high as 30% (Zhang et al., 2009). No data on yield losses in North America or Europe exist, perhaps due to inherent variability in nut production attributable to physiological limitations and pre-existing stresses. However, in the absence of population suppression, yield losses attributable to *D. kuriphilus* are estimated to be 50–70% in North America (Payne et al., 1983) and in Europe (EPPO, 2005).

Figure 3 Galls of chestnut gall wasp, *Dryocosmus kuriphilus,* form rapidly in spring on leaves, petioles, and stems, and are reddish-green and 1–3 cm in diameter. Lynne Rieske.

Extent Initial infestations of *D. kuriphilus* in Korea and Japan decimated nut production (Yasumatsu, 1951; Murakami et al., 1995), but the impact was reduced by widespread planting of gall wasp-resistant varieties (Fukuda and Okudai, 1951). However, this resistance broke down with the emergence of virulent gall wasp biotypes, necessitating other means of managing infestations (Shimura, 1972).

In Europe, the gall wasp is highly invasive, due in part to the prevalence of European chestnut, *C. sativa*, in forests. Classical biological control programs focusing on *Torymus sinensis* Kamijo (Hymenoptera: Torymidae) have been implemented (Quacchia et al., 2009).

Following its introduction into the United States, the gall wasp devastated the fledging chestnut industry in Georgia (Payne et al., 1983). In response, Asian parasitoids, including *T. sinensis*, were released (Payne, 1978). However, because the industry was thought to be beyond rescue, the success of the parasitoid introductions was not evaluated. Today there is no chestnut industry in that region. In areas of North America newly invaded by the gall wasp, infestations are initially devastating, but as both introduced and native natural enemies increase, pest populations decline to lower densities, with some continued fluctuations (Murakami and Gyoutoku, 1995; Cooper and Rieske, 2011). In the northern part of its North American range, cold temperatures appear somewhat capable of regulating the population (LKR: pers. obs.).

Biology of Pest

The Asian chestnut gall wasp is univoltine and parthenogenetic. Adult females emerge from galls in late June to mid-July and lay 3–5 eggs per chestnut bud (Payne et al., 1975). Each female is capable of laying approximately 100 eggs (EPPO, 2005). Eggs hatch in mid- to late summer, and neonate larvae feed only slightly, develop slowly, and overwinter in dormant buds. Galls expand rapidly after bud expansion is initiated the following spring, (Fig. 3). Galls are single to many-chambered, and each chamber contains a developing gall wasp larva (Fig. 4). Larvae feed on nutritive tissue within the gall chamber throughout their development (~4 weeks) and pupate within the galls. Adult gall wasp emergence occurs in mid-summer. Adult wasps oviposit into chestnut buds to complete the cycle. Following adult emergence, galls turn brown and woody and may remain on the tree for more than two years (Fig. 5). Woody galls often retain their leaves through the winter, making them highly visible (Fig. 6). Population outbreaks are cyclical in China, with outbreaks of 2–3 years duration, approximately every ten years (Zhang et al., 2009). Similar oscillations appear evident in the USA, but long-term data are lacking (Cooper and Rieske, 2007a, 2011).

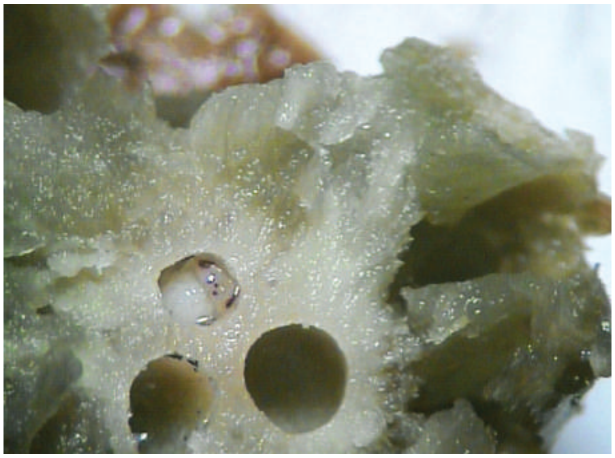

Figure 4 Galls are single to many-chambered; each chamber contains a developing gall wasp larva. Melanie Sprinkle.

Figure 5 Following adult emergence galls turn woody and brown, and may remain on the tree for two or more years. Lynne Rieske.

Figure 6 Galled shoots frequently retain their leaves through the winter, making them highly visible. Lynne Rieske.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

Dryocosmus is a genus in the Cynipidae and contains a Palearctic species on chestnut (*D. kuriphilus*) and 16 Nearctic species, most of which develop on oak (*Quercus*) (Burks, 1979; Nearctica, 1998). The phylogeny of the genus has recently been re-evaluated in light of molecular advances (Acs et al., 2007). *Dryocosmus* species endemic to North America were not evaluated for their suitability as hosts for the Asian parasitoids before parasitoid releases, but no instances of the Asian parasitoids attacking North American *Drycosmus* have been reported.

Native Natural Enemies Affecting the Pest

Two *Torymus* species, *T. tubicola* Osten-Sacken and *T. advenus* Osten-Sacken, were reportedly reared from dry woody galls collected in Georgia (USA) in 1976 (Payne, 1978). Five additional North American hymenopteran parasitoids have been found associated with the chestnut gall wasp (Cooper and Rieske, 2007ab), including *Ormyrus labotus* Walker (Hymenop.: Ormyridae), *Sycophila mellea* Walker (Hymenop.: Eurytomidae), *Pnigalio minio* Walker (Hymenop.: Eulophidae), *Eupelmus* sp. (Hymenop.: Eupelmidae), and *Pteromalus* sp. (Hymenop.: Pteromalidae). It is possible that additional parasitoids associated with native *Dryocosmus* species also parasitize *D. kuriphilus*.

In addition to hymenopteran parasitoids, an unidentified fungus causes lesions on the gall surface, and a second fungus fills the interior gall chambers and is associated with gall wasp mortality in the United States (Cooper and Rieske, 2006, 2007a, 2009, 2010) and Italy (Magro et al., 2010). The native chestnut weevil, *Curculio sayii* (Gyllenhal), also has been reported feeding on developing galls (Cooper and Rieske, 2007a, 2009). While direct interactions between the gall wasp and the weevil have not been observed, weevil feeding could create infection courts for potentially pathogenic microorganisms (Cooper and Rieske, 2010). Interestingly, inquilines have not been reported in association with *D. kuriphilus*.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

The native geographic range of *D. kuriphilus* is southeastern China (Zhang, 2009).

Areas Surveyed for Natural Enemies

Southern China, Japan, and Korea have been surveyed extensively for natural enemies of *D. kuriphilus* (Murakami et al., 1977; Murakami, 1981; Huang et al., 1988; Murakami et al., 1995; Guo et al., 1997), as have gall-infested chestnut trees in the eastern USA (Cooper and Rieske, 2006, 2007ab, 2010, 2011). Similar surveys have been conducted in Italy (Aebi et al., 2006; Quacchia et al., 2009) since the gall wasp became established in Europe.

Natural Enemies Found

The Chinese parasitoid *T. sinensis* has been the primary focus of classical biological control releases in Japan (Moriya, 1989a,b), the United States (Payne et al., 1983; Cooper and Rieske, 2007a, 2011), and Europe (Quacchia et al., 2009; Bosio et al., 2010). Attack by native parasitoids has been observed in areas invaded by *D. kuriphilus*, but any role in regulating the gall wasp population remains undocumented (Aebi et al., 2006; Cooper and Rieske, 2007a; Speranza et al., 2009).

In its native China, 28 parasitic hymenopterans from eleven families have been found associated with chestnut gall wasp (Huang et al., 1988; Zhang et al., 2009). In Japan, 26 parasitoids from eight families have been recorded (Otake et al., 1982; Aebi et al., 2006; Matsuo et al., 2011). Eight species of parasitoids (*T. sinensis*, *Torymus geranii* [Walker], *Ormyrus punctiger* Westwood, *Eurytoma setigera* Mayr, *Eurytoma brunniventris* Ratzeburg, *Sycophila variegata* [Curtis], *Eupelmus urozonus* Dalman, and *Eupelmus* sp.) from four families were associated with galls in Korea. In Italy, where the chestnut gall wasp first appeared in Europe, 16 parasitic hymenopteran species from five families have been associated with *D. kuriphilus* (Aebi et al., 2007). Also in Italy, a *Gnomoniopsis* fungus has been associated with leaf and gall necrosis and gall wasp mortality (Magro et al., 2010).

In the United States, seven native hymenopterous parasitoids from six families have been found in association with the gall wasp, including *Torymus tubicola* and *Torymus advenus* (Payne, 1978), *O. labotus*, *S. mellea*, *P. minio*, Eupelmus sp., and Pteromalus sp. (Cooper and Rieske, 2007a). The most abundant is *O. labotus*. Many of the native parasitoids species attacking chestnut gall wasp are multivoltine and polyphagous, with life cycles considerably shorter than those of their gall wasp hosts (Cooper and Rieske, 2010, 2011). Since *D. kuriphilus* galls are only inhabited by gall wasp larvae during the spring, these native parasitoids presumably use gall wasp hosts other than *D. kuriphilus* for subsequent generations. In addition to these native parasitoids, two unidentified fungi and a North American weevil exploit *D. kuriphilus* galls (Cooper and Rieske, 2007a, 2009, 2010).

Host Range Test Results

Host ranges of the introduced parasitoids were not evaluated when classical biological control for *D. kuriphilus* was first implemented in the USA in 1977 (Payne et al. 1983). The *T. sinensis* strain released in North America is apparently of Chinese origin (Cooper and Rieske, 2007a); it is phenologically synchronized with *D. kuriphilus* (Moriya et al., 1989a; Murakami et al., 1995), making it a particularly effective population regulator (Moriya et al., 2002; Cooper and Rieske, 2007ab, 2011). This synchrony of *T. sinensis* with *D. kuriphilus* may also limit its use of native gall wasps as hosts.

Releases Made

At the Fruit Tree Research Station in Ibaraki Prefecture, Japan, 260 mated *T. sinensis* females were released in 1982 (Otake et al., 1984), and within a decade the incidence of chestnut galling was reduced to tolerable levels (Moriya et al., 2002). In Japan a native parasitoid, *Torymus beneficus* Yasumatsu and Kamijo, hybridizes with *T. sinensis*; hybrids comprise about 22% of the *D. kuriphilus* parasitoids in Japan (Yara et al., 2010). *Torymus sinensis* is found in Korea though it was not released there (Murakami et al., 1995), apparently being misidentified as the con-specific *T. beneficus* in earlier work. *Torymus sinensis* was released in Italy in 2005, and parasitization rates of up to 25% have been reported (Quacchia et al., 2008).

Torymus sinensis, *T. beneficus, Torymus* sp., and *Megastigmus* sp., were released in Georgia, USA, in the mid- to late 1970s. These are the only confirmed releases of classical biological control agents of chestnut gall wasp in North America (Payne, 1978; Payne et al., 1983), but an archival reference suggests that *Torymus koreanus* Kamijo also may have been released (GPMN, 1997). Since the confirmation of establishment of *T. sinensis* in North America (Cooper and Rieske, 2006, 2007ab), chestnut growers have deliberately moved woody, brown winter galls (which only contain overwintering *T. sinensis*) to new locations (Cooper and Rieske, 2007b, 2010) in an effort to disperse *T. sinensis* to additional sites infested by gall wasps (LKR: pers. obs.).

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

Torymus sinensis populations in Japan and Korea are self-sustaining and usually maintain *D. kuriphilus* populations in chestnut orchards below economic injury levels (Otake et al., 1984; Moriya et al., 1989ab; Moriya et al., 1990; Murakami et al., 1995; Murakami and Gyoutoku, 1995; Moriya et al., 2002). In Italy *T. sinensis* has been established, but population regulation of *D. kuriphilus* by this parasitoid has not yet been documented (Quacchia et al., 2008, 2009).

Following parasitoid releases in the mid-1970s, chestnut production in the United States was thought to be beyond rescue (Payne et al., 1983), and therefore the outcome of parasitoid introductions was not evaluated. No record of parasitoid establishment in the United States was made until recoveries of *T. sinensis* were reported by Cooper and Rieske (2006). *Torymus sinensis* has since been identified from chestnut galls collected over a large geographic area, from Tennessee north to Pennsylvania, and from Maryland in the east to central Kentucky in the west. Two other introduced parasitoids, *T. beneficus* and *Megastigmus* spp., have not been recovered from chestnut galls in the USA.

Nontarget Effects

Torymus sinensis is not known to attack any other cynipids in North America. Potential indirect effects of *T. sinensis,* such as hybridization (as in Japan, see Yara [2010]), hyperparasitization, and competitive displacement are possible but not reported.

Recovery of Affected Tree Species or Ecosystems

Suppression of gall wasp populations following dispersal of *T. sinensis* to newly infested sites can be rapid (Moriya et al., 1989b; Cooper and Rieske, 2007), but see also Murakami and Gyoutok (1995). However, *T. sinensis* populations fluctuate, resulting in periodic resurgences of gall wasp populations and associated galling.

Broad Assessment of Factors Affecting Success or Failure of Project

All chestnut species are susceptible to *D. kuriphilus* galling. In North America as well as Europe, chestnut persists in a variety of habitats, including forests, orchards, and urban landscapes. American chestnut in North America has been reduced by the chestnut blight fungus to a sporadic, non-flowering, shrubby component of eastern deciduous forests. American chestnut restoration programs focus on planting blight-resistant American chestnut in highly disturbed habitats such as strip-mine reclamation sites (McCarthy et al., 2008). Chinese chestnut is an ornamental landscape tree and widely planted throughout the USA. Finally, European, Chinese, and Japanese species and their hybrids are grown in orchards for commercial nut production. Since all *Castanea* are susceptible to *D. kuriphilus* galling, the potential effects of various chestnut habitats are important considerations when implementing or assessing the effectiveness of biological control efforts against this gall wasp (Cooper and Rieske, 2011).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Torymus sinensis is frequently collected from chestnut galls in the United States (Cooper and Rieske, 2006, 2007ab, 2011), but the other parasitoids released for classical biological control have not been recovered. Of the seven native parasitoids associated with *D. kuriphilus* galls, only *O. labotus* appears abundant enough to provide population regulation of *D. kuriphilus*.

Torymus sinensis (Hymenoptera: Torymidae)

Torymus sinensis is univoltine and phenologically synchronized with *D. kuriphilus*. This synchrony allows *T. sinensis* to perform as a specialist against *D. kuriphilus* in habitats where chestnut and chestnut galls are abundant (Stone et al., 2002). As a consequence, *T. sinensis* is more abundant in chestnut orchards than is *O. labotus,* which is primarily a parasitoid of oak-gall wasps.

Ormyrus labotus (Hymenoptera: Ormyridae)

Ormyrus labotus is a multivoltine parasitoid of several oak-galling cynipids. Adults of the first seasonal generation opportunistically parasitize *D. kuriphilus*, and subsequent generations parasitize oak-galling hosts or hyperparasitize *T. sinensis* (Cooper and Rieske, 2007a, 2011). Because of this association with oak-galling wasps, *O. labotus* is more abundant than *T. sinensis* in forest habitats where oak and oak gallmakers are present (Cooper and Rieske, 2007a; Cooper and Rieske, 2011).

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XXII PINE FALSE WEBWORM

(*Acantholyda erythrocephala* [L.]) (Hymenoptera: Pamphiliidae)

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DESCRIPTION OF PEST

Taxonomy

The introduced pine false webworm, *Acantholyda erythrocephala* (L.) (Hymenoptera: Pamphiliidae), was originally placed in the genus *Tenthredo* by Linnaei (=Linnaeus) (1758). No synonyms are reported for this species (Smith, 1979). The genus is represented by about 60 species worldwide (Shinohara and Byun, 1996).

Distribution

Acantholyda erythrocephala is a Palearctic species, having been reported from Great Britain, central and northern Europe, north to Lapland, and east to the Caucasus, western Siberia, and Korea (Middlekauff, 1958). Similarly, Kenis and Kloosterman (2001) described the Eurasian range as Japan to Britain and Lapland to Italy. Shinohara and Byun (1996) reported *A. erythrocephala* along with two other species in the genus in Korea. This sawfly was first discovered in North America in a nursery in Chestnut Hill, Pennsylvania, in 1925 (Wells, 1926). The species was encountered next in New Jersey in 1937 (Soraci, 1938), in New York in 1938 (Middlekauff, 1938), and in Connecticut in 1942 (Plumb, 1945). The species also has been reported in Maine (USDA, 1970). Wilson (1977) listed the pine false webworm as occurring in the "Lake States," but Asaro and Allen (2001) were able to find collection records only for Wisconsin. In Canada, the species was first reported in Ontario in 1963 (Eidt and McPhee, 1963). The extent of the distribution and the damage caused by the sawfly in Ontario was not realized until the late 1970s because, previously, damage had been attributed to other sawflies (Howse et al., 1982). It was then reported throughout southern Ontario and in the Lake of the Woods region in northwest Ontario (Syme, 1981). In 1989, the sawfly was detected for the first time in western North America, in Edmonton, Alberta, where larvae were found defoliating Scots pine (*Pinus sylvestris* L.) (Emond and Cerezke, 1990). Another isolated population was discovered in easternmost Canada at St. Johns, Newfoundland (Hudak et al., 1996). According to the authors, the sawfly was unknown in Newfoundland before 1990. It was only causing light defoliation and seemed to prefer Austrian pine, *Pinus nigra* Arnold, followed in order of decreasing preference by mugo pine (*Pinus mugo* Turra), Scots pine, and jack pine, (*Pinus banksiana* Lamb.). The sawfly has been reported as only sparsely distributed in Quebec (Howse, 2000). The Canadian distribution and detection rate for the sawfly were mapped by Howse (2000).

Damage

Type Larvae of the pine false webworm, as the name implies, are defoliating pests of trees and shrubs of the genus *Pinus*. The sawfly has been recorded from red (*Pinus resinosa* Ait.), eastern white (*Pinus strobus* L.), mugo, mountain (*Pinus montana* Miller), Scots, Japanese red (*Pinus densiflora* Siebold & Zucc.), Table Mountain (*Pinus pungens* Lamb.), and Austrian pines (Middlekauff 1958), as well as jack pine (Howse, 2000). Eggs are laid on 1-yr-old needles and the larvae consume these needles and older needles before feeding on flushing current-year foliage (Lyons, 1995). Larvae are gregarious web spinners. As they develop they form a web of silk, frass, and uneaten needles that encloses uneaten foliage (Fig. 1) (Griswold, 1939). The larvae feed on the pine needles from within silken tubes inside this

Figure 1 Webs of pine false webworm, *Acantholyda erythrocephala*, on young plantation-grown red pine. Barry Lyons, Canadian Forest Service, Bugwood.org.

Figure 2 Larva of pine false webworm venturing out of web on silken threads. Barry Lyons, Canadian Forest Service, Bugwood.org.

web (Fig. 2, above). As the larvae grow, the webs expand over entire branches. Defoliation in several consecutive years can cause tree mortality (Fig. 3). Even minimal damage by *A. erythrocephala* in Christmas tree plantations can significantly reduce the market value of affected trees (Kessel, 2000).

Extent Outbreaks of *A. erythrocephala* occur periodically in Europe. Between 1828 and 1952, there were eight outbreaks in Europe (Rumphorst and Goosen, 1960). Jahn (1967) described an infestation of the sawfly in Austria in a plantation of *P. nigra* and some *P. sylvestris*. Outbreaks of *A. erythrocephala* in Europe are usually of lesser intensity

Figure 3 Aerial view of red pine plantation in Simcoe County, Ontario, showing tree defoliation and mortality caused by the pine false webworm. J. McFarlane.

and of shorter duration than those in North America, and this seems to be related to the greater abundance of natural enemies in Europe (Kenis and Kloosterman, 2001). The first record of damage by this species in North America seems to be the discovery in 1937 of several acres of defoliation in red and Austrian pines, 1.5 to 3.7 m tall, in a New Jersey nursery (Soraci, 1938). In Ontario, the species was described as "troublesome" on pines grown as ornamentals or Christmas trees (Syme, 1981), and later as a serious defoliator of several pine species and the most destructive insect encountered in surveys in young pine plantations (Syme, 1990). In 1993, the pest status of *A. erythrocephala* changed dramatically in Ontario, when expanding outbreaks were detected for the first time in stands of mature pines (Fig. 4) (Howse, 2000). A sustained infestation from 1981 to 1995 was reported in northern New York that ultimately affected 5,440 ha of eastern white pine, spread over 231,000 ha (Allen, 2000; Asaro and Allen, 2001). Annual volume increment was significantly reduced after the second year of moderate to severe defoliation, compared to non-defoliated trees, in a 67-year-old white pine stand in New York, and was reduced by 97% after five years of defoliation (Mayfield et al., 2005). Large plantations of mature eastern white pine on poor quality sandy sites are susceptible to defoliation (Mayfield et al., 2007). A relationship between tree mortality in the current year and defoliation by the pine false webworm in the previous year in Ontario red pine plantations suggested that defoliation levels in excess of 70% resulted in tree mortality (Lyons and Jones, 2000). However, this relationship did not take into consideration the cumulative effect of multiple years of defoliation.

Figure 4 Defoliation of pole size red pine caused by pine false webworm in Simcoe Co., Ontario (photograph D.B. Lyons).

Biology of Pest

Most pine false webworm populations are univoltine and most individuals overwinter as pronymphs (Fig. 5A) within soil cells constructed by larvae in the ground under host trees (Lyons, 1995; Lyons and Jones, 2000). Some individuals overwinter as eonymphs (Fig. 5B) and require more than one year to complete their life cycles. In New York State, 9–66% of the population remained in the soil for more than one year (Asaro and Allen, 1999). Soil cells containing the eonymphs, pronymphs, or pupae are found at depths of 5–11 cm below the humus layer in Europe (Schwerdtfeger, 1941; Jahn, 1967) and at depths 0–9 cm (average less than 5 cm) in the mineral soil in Canada (Lyons, 1995). The pupae are exarate and do not develop within silk

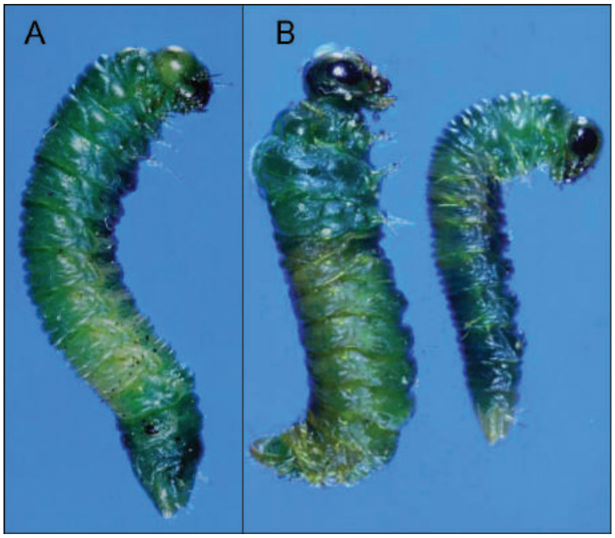

Figure 5 A) Eonymph of the pine false webworm removed from soil cell. B) Female (left) and male (right) pronymphs, based on head capsule size, of the pine false webworm collected from soil cells. E.R. Rayner.

cocoons. Pupation occurs in the spring, and adult eclosion occurs soon thereafter within these earthen cells. In late spring (late April to early June) (Lyons and Jones, 2000), males are the first to emerge from the ground, followed by the females (Lyons, 1995). Mating takes place shortly after emergence. The sexes of the pine false webworm are easy to distinguish (Fig. 6). The female has a red-orange head and distal portions of the prothoracic legs; the male has a blue-black head with yellow frons, mandibles and distal portions of the prothoracic legs (Lyons and Jones, 2000). Females crawl or fly up into the canopy of the host trees where they begin to oviposit, without any preoviposition period (Lyons, 1996). Most eggs dissected from females at emergence are mature and ready for oviposition, but some developing eggs are also present (Lyons, 1995). Females cut slits into the needles of the host plants, into which they insert a portion of the egg chorion during oviposition (Fig. 7) (Griswold, 1939). The large sausage-shaped eggs are positioned in rows end-to-end along the flat surface of the needles (Fig. 7). Realized fecundity is about 42.0 eggs per female at 26.6°C and female longevity ranges from 27 days at 14.9°C to 6.6 days at 26.6°C (Lyons, 1996). After the eggs hatch, the neonate larvae crawl down the needle to the twig where they begin to feed gregariously on the sides of the basal ends of the needles above the fascicle (Lyons, 1995). Later instar larvae attach silk guy lines to the needles, shear them off at the base, and feed on the needles as they draw them into their expanding web. The production of silk webbing, frass, and partially eaten needles form a web structure along the branch from within which the larvae feed. Larvae are seldom seen outside of the webs unless they have completely defoliated the branches or if they are preparing to drop from the tree (Lyons, 1995). The webs aid in thermoregulation (Lyons, 1994), facilitate mobility of the larvae, and secure the larvae to the host plant (Lyons, 1995). Male larvae develop through five instars, while females pass through six instars during their arboreal development (Schwerdtfeger, 1941; Lyons, 1995). After completion of feeding, the larvae drop from the branches to the ground (Lyons, 1994) in June to early July (Lyons and Jones, 2000). There, they burrow down into the mineral layer of the soil, where they spend the late summer, fall and winter, and form the pupal chambers by using their body movements to compact the sides around them and cementing a soil matrix around the chamber (Lyons, 1995). The larvae at this stage, known as eonymphs, retain the small larval eye. Most eonymphs emerge from diapause in the fall and become pronymphs, with the developing pupal eye visible through the integument (Lyons, 1995). The eonymphs that remain in diapause are the insects that will require at least another winter to complete development. Schwerdtfeger (1944) demonstrated conclusively that some individuals may take up to three years to complete development, and speculated that some individuals may take even longer. A female-produced sex pheromone attracts flying males in the field (Staples et al., 2009).

Figure 6 Adult male (blue head with yellow face) copulating with female (red head) of pine false webworm. D.B. Lyons, Bugwood.org.

Figure 7 Female of pine false webworm ovipositing on needles of red pine. D.B. Lyons, Bugwood.org.

ANALYSIS OF RELATED NATIVE INSECTS IN NORTH AMERICA

Native Insects Related to the Pest (Nontarget Species)

The genus *Acantholyda* is Holarctic in distribution, with 33 species reported in North America, including the introduced pine false webworm, *A. erythrocephala* (Middlekauff, 1958). Three other genera of pamphiliid sawflies are found in North America, including *Cephalcia* (10 species), *Neurotoma* (four species) (Middlekauff, 1958) and *Pamphilius* Latreille (24 species) (Smith, 1979). Species of *Acantholyda* and

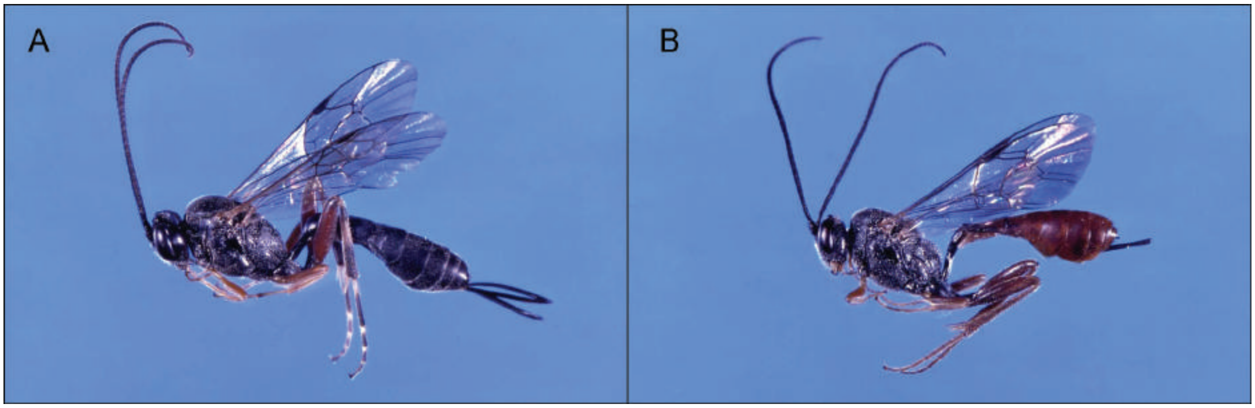

Figure 8 A) Adult female of *Sinophorus megalodontis,* a North American parasitoid of the pine false webworm. B) Adult female of an undescribed species of *Olesicampe* (Hymenoptera: Ichneumonidae), a North American parasitoid of the pine false webworm. E.R. Rayner.

Cephalcia feed on conifers, while those of *Neurotoma* and *Pamphilius* feed on deciduous trees and shrubs.

Native Natural Enemies Affecting the Pest

Barron (1981) described the new species, *Ctenopelma erythrocephalae* (Hymenoptera: Ichneumonidae), which had been observed ovipositing in eggs of the pine false webworm in Oakland, New Jersey. Two additional species of ichneumonids, *Sinophorus megalodontis* Sanborne (Fig. 8A, above) and an undescribed species (H. Townes, deceased, American Entomological Institute, Gainesville, Florida, pers. comm.) of the poorly known genus *Olesicampe* (Fig. 8B, above) were reared from eonymphs in Ontario, Canada (Lyons, 1999; Bourchier et al., 2000; Lyons et al., 2002). *Sinophorus megalodontis* is transcontinental in distribution and belongs to the *crassifemur* species group known to attack web-spinning pamphiliids on pines. (Sanborne, 1984). Another member of this species group, *Sinophorus crassifemur* (Thomson), attacks species of *Acantholyda* and *Cephalcia* in the Palearctic Region (Sanborne, 1984). Two species of *Olesicampe*, *O.* sp. nr. *nematorum* and *O. geniculatae* Quednau and Lim, have been introduced successfully into North America as biological control agents of other sawflies (Muldrew, 1967; Quednau and Lim, 1983), and another species, *Olesicampe monticola* (Hedwig), has caused significant mortality of *Cephalcia lariciphila* (Wachtl) in the United Kingdom (Billany et al., 1985). *Olesicampe* sp. and *S. megalodontis* are solitary endoparasitoids and like their host are univoltine (Lyons, 1995). *Olesicampe* sp. overwinters as late-instar larvae in the host eonymphs (Lyons, 1995). They emerge from the host cadaver in spring and spin cocoons in the host's earthen cell in which they pupate and subsequently emerge as adults. Emergence of *S. megalodontis* from the host cadaver occurs in the fall and the species overwinters in its own cocoon (Bourchier et al., 2000). Host larvae from which the parasitoids emerged were always eonymphs, indicating that the parasitoids prevented the transformation of the hosts to pronymphs. Both species of ichneumonids began to emerge protandrously from the ground in late May in Ontario. The emergence periods lasted about 16 days, while their flight periods lasted about 28 days (Bourchier et al., 2000). The sex ratio of emerging adults of *S. megalodontis* was approximately 1:1 (Lyons, 1999). The mean larval instar of the host at the peak of parasitoid emergence was 1.5, and emergence lasted until the mean host instar had reached 3.8. Eggs of *S. megalodontis* were dark brown and were readily observed through the integument of the host; the eggs of *Olesicampe* sp. were white and, unlike those of *S. megalodontis*, empty chorions were difficult to detect (Bourchier et al., 2000). Neonate larvae of the two parasitoids were of the ichneumonid mandibulate-caudate type. Unhatched eggs of both species were found in all larval instars of the host, indicating that all host instars are attacked (Bourchier et al., 2000). Parasitoid larvae were also found in all instars of the host, indicating that eggs hatch soon after oviposition. The two species are koinobionts, with larvae remaining as first instars until sometime after the host larvae leave the tree and enter the soil (Bourchier et al., 2000). Encapsulation of first-instar larvae of both parasitoids by host haemocytes was common. Encapsulation of eggs was rarely encountered (Bourchier et al., 2000). The effective parasitism rate by *S. megalodontis* was 9.0% and was limited by encapsulation, multiparasitism, and superparasitism

(Lyons, 1999). These two ichneumonid species also were captured flying in the vicinity of the webs of the pine false webworm in New York State (Asaro and Allen, 1999). Another ichneumonid, *Homaspis interruptus* (Provancher), a solitary endoparasitoid, emerged from 2.8 to 8.5% of the pronymphs in populations of the pine false webworm near Fort Jackson, New York (Asaro and Allen, 1999). The dark colored cocoons (12 mm long by 6 mm wide, with a light colored median band), of this wasp were recovered adjacent to pupal cells of the sawfly host. The species was observed attacking the pine false webworm from mid-May until mid-June in New York State (Asaro and Allen, 1999). The egg parasitoid *Trichogramma minutum* (Riley) complex (Hymenoptera: Trichogrammatidae) has been reared from eggs of *A. erythrocephala* in Ontario (Bourchier et al., 2000; Lyons et al., 2002). No egg parasitoids were observed by Asaro and Allen (1999) in New York, even though 3443 eggs were examined.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Pine false webworm is Palearctic in origin.

Areas Surveyed for Natural Enemies

Surveys for parasitoids of the pine false webworm were conducted in Poland, Switzerland, and Italy by staff of Commonwealth Agricultural Bureaux International (CABI) of Europe (Delémont, Switzerland).

Natural Enemies Found

Based on a review of the literature and field surveys in Poland, Switzerland, and Italy, Kenis and Kloosterman (2001) compiled a list of parasitoids of *A. erythrocephala* and two congeneric species in Europe. Egg parasitoids included five species of gregarious *Trichogramma* and three species of Eulophidae. Parasitoids of larvae included about ten species of Ichneumonidae and seven of Tachinidae (Diptera). Two egg parasitoids, *Trichogramma erythrocephalae* Pintureau and Kenis (Pintureau et al. 2000) and *Trichogramma semblidis* (Aurivillius), were reared from the same populations of *A. erythrocephala* and *Acantholyda posticalis* (Matsumura) in the Valle d'Aosta in northern Italy (Kenis and Kloosterman, 2001). The two species of Ichneumonidae most often associated with *A. erythrocephala* were *S. crassifemur* and *Xenoschesis fulvipes* (Gravenhorst). But specimens of *Xenoschesis* sp. collected from Italy and Poland and specimens of *Sinophorus* sp. collected from Poland were morphologically different from these species and were perhaps different species (Kenis and Kloosterman, 2001). The most commonly encountered tachinid species, *Myxexoristops hertingi* Mesnil (Fig. 9), the most abundant parasitoid of the pine false webworm, occurs throughout the European distribution of *A. erythrocephala* (Kenis and Kloosterman, 2001) and has been reported as the cause of a population collapse in an outbreak of *A. erythrocephala* in Germany (Rumphorst and Goosen, 1960). Of the parasitoid species listed by Kenis and Kloosterman (2001), two species, *M. hertingi* and *Trichogramma acantholydae*, were recommended as classical biological control agents of *A. erythrocephala* in North America.

Figure 9 Adult of *Myxexoristops hertingi,* a European parasitoid of the pine false webworm that was released in a pine plantation in Ontario. CABI Europe.

Host Range Test Results

Trichogramma acantholydae was screened against eggs of four lepidopteran species and failed to attack eggs of either *Anagastes kuehniella* (Zeller) (Pyralidae), *Actebia fennica* (Tauscher) (Noctuidae), or *Choristoneura fumiferana* (Clemens) (Tortricidae). Eggs of *Lambdina fiscellaria* (Guenée) (Geometridae) were attacked, but no development occurred (Bourchier et al., 2000). The eggs of two diprionid sawflies, *Diprion pini* L. and *Gilpinia frutetorum* F., also failed to elicit attacks (Kenis and Kloosterman, 2001). Thus, this univoltine species exhibited a higher degree of host specificity than most *Trichogramma* species (Bourchier et al., 2000).

The observations that the tachinid *Myxexoristops bonsdorffi* (Zetterstedt) attacks *A. posticalis*, and *Myxexoristops abietis* Herting attacks *Cephalcia* spp., attest to the host specificity of members of this genus (Kenis and Kloosterman, 2001). *Myxexoristops hertingi* was reared from *Acantholyda pumilionis* (Giraud) in the Swiss/Italian Alps, but based on the fly's biology and phenology, this record may have been from a tachnid sibling species (Kenis and Kloosterman, 2001).

Releases Made

Two strains of North American egg parasitoids, *T. minutum* and *Trichogramma platneri* Nagarkatti, were inundatively released against *A. erythrocephala* in Ontario (Bourchier et al., 2000; Lyons et al., 2002). Puparia of the tachinid *M. hertingi* were exported from Italy by staff of CABI Europe to the Great Lakes Forestry Centre, Canadian Forest Service, Natural Resources, for field release in Ontario, 2000–2004. In each year, adults were reared from puparia to eliminate the chance of releasing hyperparasitoids. In each year from 2000 to 2002, on a plantation near Apto, Ontario, flies were released into two 3.0 m-high by 1.8 m-square cages enclosing individual *A. erythrocephala*-infested red pine trees (44.53°N, 79.78°W). Twenty-five males and 95 females were released into cages in 2000, 64 males and 12 females were released in 2001, and 6 males and 36 females were released in 2002. In the fall following the releases, the soil under the trees in the cages was excavated and all sawfly larvae were recovered and held for parasitoid rearing. Open releases of *M. hertingi* also were made each year from 2002 to 2004 on a red pine plantation near Craighurst, Ontario (44.51°N, 79.71°W). Three hundred and thirty-four males and 187 females, 719 males and 210 females, and 405 males and 328 females were released into the wild in 2002, 2003 and 2004, respectively.

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

For the cage releases of *M. hertingi* undertaken in 2000 to 2002, *A. erythrocephala* larvae were excavated from the ground and reared, but no parasitism by the tachinid was encountered. Populations of *A. erythrocephala* collapsed shortly after the field releases. Consequently, the establishment of the parasitoid was difficult to assess.

Nontarget Effects

No nontarget effects are known from these releases.

Recovery of Effected Tree Species or Ecosystems

The degree of host suppression of affected tree species is unknown.

Broad Assessment of Factors Affecting Success or Failure of Project

Myxexoristops hertingi is difficult, but not impossible, to rear in the laboratory (Kenis and Kloosterman, 2001). Consequently, field collection of larvae and puparia from the source population was required. The parasitoids were shipped to Canada as puparia of known physiological age and programmed for synchronous emergence. Many puparia were moldy when received and were eliminated from rearing. Rearing of puparia was mandatory to eliminate hyperparasitoids (see below). Adults were reared from the puparia in Sault Ste. Marie, Ontario, and then transported to the release site ca. 600 km away. Many of the adults had deformed wings at emergence. In addition, *M. hertingi* adults were fragile and not amenable to handling. The combination of these factors resulted in small numbers of healthy flies being released into the field. Nonetheless, *M. hertingi* has the greatest potential as a classical biological control agent against the pine false webworm. The fly is the most abundant parasitoid in European populations of *A. erythrocephala*, is widely distributed climatically, is relatively host-specific, and fills an empty niche, as there are no tachinids reported from *A. erythrocephala* in North America (Lyons et al., 2002).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Trichogramma acantholydae

Unlike most other *Trichogramma* spp., the egg parasitoid *T. acantholydae*, appears to be univoltine and enters into an obligate diapause as a late instar larva within the egg of *A. erythrocephala* (Pintureau et al., 2000; Lyons et al., 2002). The parasitoid overwinters in the host egg and is apparently more host-specific than the majority of *Trichogramma* spp. (Kenis and Kloosterman, 2001). Three to 12 adults emerge per host egg in spring (Lyons et al., 2002).

Myxexoristops hertingi

The biology of the tachinid fly, *M. hertingi*, is described by Kenis and Kloosterman (2001). The tachinid is univoltine and well synchronized with the phenology of its host. The fly oviposits over 1000 microtype eggs (Fig. 10) on the needles of the pine tree host in the vicinity of actively feeding larvae of *Acantholyda* spp., which ingest the eggs. Bourchier et al. (2000) reported an average of 1,500 eggs per gravid female. Development of this endoparasitoid takes place within the host eonymph in the cell within the soil. The parasitoid overwinters in the host skin and in spring the maggot burrows to the soil surface where it forms a puparium. Emergence from puparia occurs in about a month and mating takes place soon thereafter. The preoviposition period in the laboratory is less than 10 days (Bourchier et al., 2000). Most of the parasitoid larval development occurred after the host left the host tree and entered the soil (Bourchier et al., 2000). The fly was difficult to rear in the laboratory due to low mating success and poor development after host ingestion. A hyperparasitoid, *Trichopria* sp. (Hymenoptera: Diapridae), has been reported to kill up to 20% of the puparia (Kenis and Kloosterman, 2001).

Figure 10 Microtype eggs of *Myxexoristops hertingi* on needle of *Pinus* sp. CABI Europe.

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XXIII Introduced Basswood Thrips

(*Thrips calcaratus* Uzel) (Thysanoptera: Thripidae)

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DESCRIPTION OF PEST

Taxonomy

The introduced basswood thrips, *Thrips calcaratus* Uzel, is a member of the family Thripidae. There are no synonyms for this name. *Thrips* is the largest genus in the family, with about 487 valid described species (Mound, 2012).

Distribution

Thrips calcaratus (Fig. 1) is believed to be a European species that has been introduced into North America, where it has been recorded from New England and Quebec, westward through Ontario, Pennsylvania, New York, the Great Lakes States, Illinois, and Iowa (Rieske and Raffe, 1995; Van Driesche et al., 1996). It has been in New York at least since the 1930s. It has a broad climatic tolerance range and is predicted to be spread throughout the North American range of its host, American basswood (*Tilia americana* L.) (Fig. 2) (Raffa, 1991). The new and abrupt appearance of this species in 1979 in northern Wisconsin, with persistent and expanding damage in that area ever since, argues strongly that this species is invasive in North America.

Figure 1 A.) Adult introduced basswood thrips, *Thrips calcaratus*. B.) Larva of introduced basswood thrips. Kenneth Raffa, University of Georgia, Bugwood.org.

Damage

Type Injury to the host tree begins with feeding by adult thrips, which emerge in early spring in time to feed on opening buds (inset, Fig. 2). Adult damage to immature leaf tissue is magnified as the leaf expands, such that damaged leaves show a shotgun pattern of tears and holes, which degrade the leaf over time. Damaged leaves become yellowed and may drop off if feeding is extensive, making defoliation (Fig. 3) this pest's principal effect on the plant. Larvae feed on mature leaves later in the season, but most impact on the tree is caused by early-season adult feeding on buds. Defoliation levels of 40% or greater reduced radial tree growth by half compared to growth of un-infested or lightly (<30% defoliation) infested basswood trees (Raffa, 1991).

Extent Damage has occurred principally in northern Wisconsin, where defoliation was first observed in 1979 (Raffa, 1991). Defoliation affected about 81,000 hectares yearly in Wisconsin from 1980 to 1988 (Raffa, 1991) and has continued intermittently since then.

Biology of Pest

Relatively little is known of the biology of this thrips, because it is not a pest of its native host in Europe. In

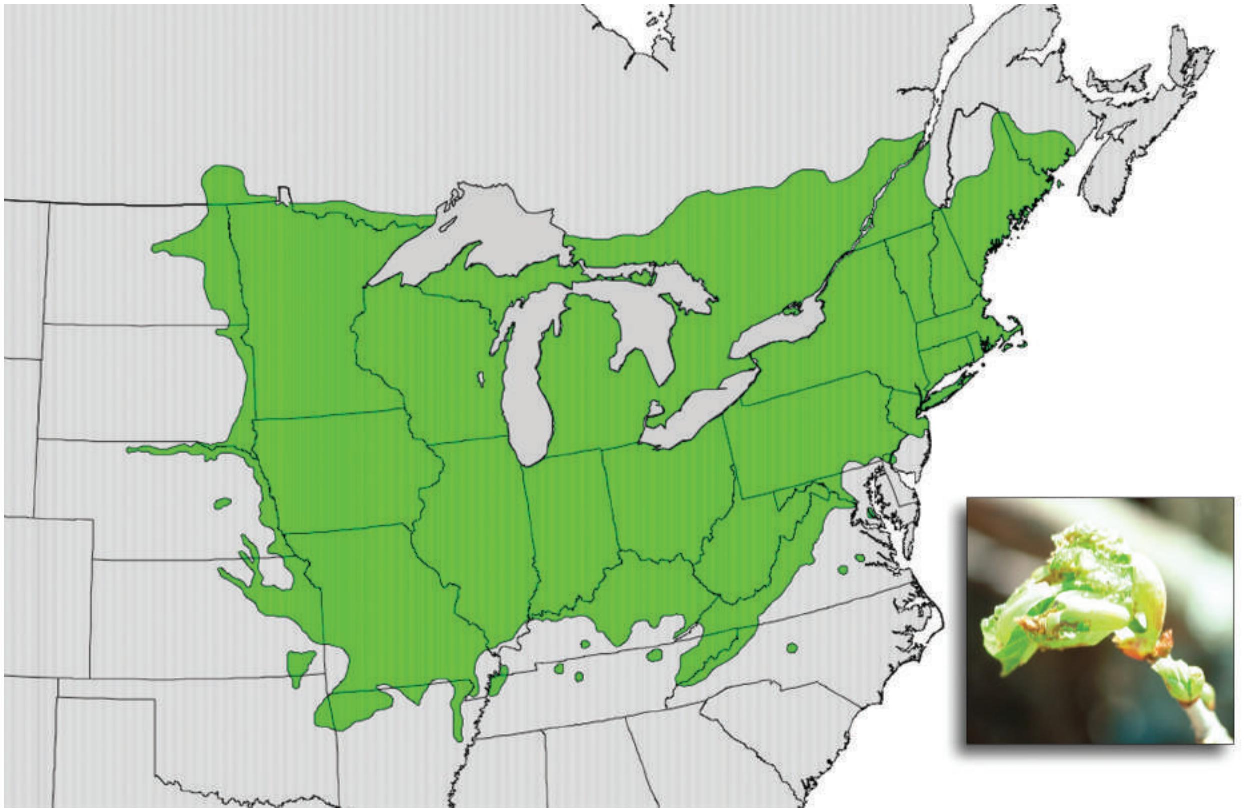

Figure 2 Range of American basswood, Tilia Americana. Records of introduced bass wood thrips include Iowa, Wisconsin, Illinois, Michigan, Pennsylvania, New York, the New England states, Quebec and Ontario). Minnesota, New Brunswick, while states in the southern part of American basswood's range remain uninvaded. Digital representation of *Atlas of United States Trees* Elbert L. Little, Jr., 1999. US Geological Survey. **Inset** Typical damage to basswood buds from thrips feeding (here by another thrips, *Neohydratothrips tiliae* [Hood]). Steven Katovich, USDA Forest Service, Bugwood.org.

Figure 5 Defoliation of American basswood by introduced basswood thrips. Steven Katovich, USDA Forest Service, Bugwood.org.

addition to *Tilia*, it has been recorded on species of maple (*Acer*), hickory (*Carya*), beech (*Fagus*), ash (*Fraxinus*), and oak (*Quercus*). However, it is unlikely that species in these other genera are suitable for reproduction, but rather more likely are just species on which the insect occasionally feeds. Data from Europe suggest that only *Tilia* species are suitable for breeding. The species appears to be all female, as males are unknown. In Europe this species occurs over many different climatic zones, from Denmark to Italy and from the UK to Ukraine. In the United States (Wisconsin), introduced basswood thrips overwinter as adults in the soil (Raffa, 1991). Adults emerge in Wisconsin in early May. Emergence is both highly synchronous and coincides with swelling of basswood buds. Adults feed in the opening buds as leaves begin to expand. Adults insert eggs into the main veins, from the lower surface. Larvae appear in June, by which time adults have died. Larvae feed on expanded leaves and when larvae mature in July they drop to the soil to overwinter, mostly in the soil beneath the litter. There is one generation per year in Wisconsin (all details above, from Raffa [1991]; see also Raffa et al. [1992]). Developmental times for life stages were determined by Rieske and Raffa (1996).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Thrips is a large genus in the family Thripidae that has been revised by Gentile and Bailey (1968) and Nakahara (1994). Nakahara's (1994) review of the genus in the Western Hemisphere lists 43 species of *Thrips* endemic to the United States and Canada, together with 18 introduced species and one species of uncertain origin.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

This species is believed to be Palearctic in origin and invasive in the North America, although evidence for that is circumstantial. No attempts have been made to survey for or import natural enemies of this species from Europe. However, Werner et al. (2006) have compared the preference of this thrips between the European host (*Tilia cordata* P. Mill.) and the North American host (*Tilia americana* L.) and found that imported basswood thrips shows no preference for the European species, and that timing of adult thrips emergence in Wisconsin, USA, coincides equally well with the bud break periods of both *Tilia* species. These findings seem to rule out host plant relationships (lower defenses, less favorable synchrony between plant and insect) as causes for the greater damage of this insect in North America versus Europe. This then supports the assumption that key natural enemies suppressing the pest exist in Europe, but are missing in North America. However, biological control of Thysanoptera has rarely been attempted and has never been definitively successful. That does not demonstrate that it cannot be done; rather, it shows it is likely to require considerable original research and investigation in Europe.

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XXIV Spruce Aphid

(*Elatobium abietinum* Walker) (Hemiptera: Aphididae)

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DESCRIPTION OF PEST

Taxonomy

Elatobium abietinum Walker is a spruce-feeding aphid that in Europe is referred to as the green spruce aphid (Day et al., 1998a) (Fig. 1). However, in North America *E. abietinum* is known simply as the spruce aphid, while the common name "green spruce aphid" refers to a different species, *Cinara fornacula* Hottes (Hemiptera: Aphididae) (http://www.entsoc.org/common-names). *Elatobium abietinum* is green-bodied with dull reddish eyes, 1–2 mm long (Johnson and Lyon, 1991; Koot, 1991), and it feeds on mature needles of dormant and nearly dormant spruce (*Picea*). Synonyms of *E. abietinum* include *Aphis abietina* Walker 1849, *Myzaphis abietina* Van der Goot 1913, *Neomyzaphis abietina* Theobald 1926, *E. abietinum* Börner 1930, and *Liosomaphis abietina* Börner & Schilder 1932 (Carter and Halldórsson, 1998).

Figure 1 Close up of one spruce aphid, *Elatobium abietinum*. Donald Owen, California Department of Forestry and Fire Protection, University of Georgia, Bugwood.org.

Distribution

Population behavior, life cycle, and genetic diversity indicate that *E. abietinum* originated in continental Europe on Norway spruce (*Picea abies* [L.] Karst) (Carter and Halldórsson, 1998; Nicol et al., 1998; Halldórsson et al., 2004). It is also found in central Asia on *Picea schrenkiana* (Fischer et C.A. Meyer) (Ismukhambetov, 1976; Lynch, personal observations). The distribution of this aphid expanded rapidly in the 1800s and 1900s in the British Isles, France, Iceland, and New Zealand after the widespread planting of Sitka spruce (*Picea sitchensis* [Bong.] Carr.). It was well established in Western Europe by 1930. In North America, it was first reported in 1915 from Vancouver, British Columbia, and in 1916 from San Francisco, California (Essig, 1917; Swain, 1919). By 1927, spruce aphid was well distributed along the western coasts of the United States and Canada and became an important pest of Sitka spruce (Koot, 1991; Holsten et al., 2001; Schultz et al., 2009). It was found in the southwestern United States in 1976, where it exhibits extensive, severe outbreaks on Engelmann spruce (*Picea engelmannii* Parry ex. Engelmann) and blue spruce (*P. pungens* Engelmann) in montane ecosystems (Lynch, 2003, 2004). There are occasional reports of *E. abietinum* in Utah and Nevada (Hagle et al., 2003) and in eastern North America (Fedde, 1971, 1972; Carter and Halldórson, 1998; Leaning, 2002). *Elatobium abietinum* now has an extensive global distribution, wherever spruce occur in areas with maritime climates (Carter and Halldórson, 1998). Until it was introduced to the southwestern United States, it caused significant economic damage only in areas with maritime climates, areas where the aphid, and often the tree, was exotic (Carter and Halldórson, 1998).

Damage

Type *Elatobium abietinum* aphids suck sap from needle phloem cells through needle stomata (von Scheller, 1963; Parry, 1971), causing stippling, chlorosis, and mortality of needles (Hussey, 1952; von Scheller, 1963; Fisher, 1987). Defoliation is the most noticeable symptom of attack (Fig. 2). A toxic substance may be injected into the needle with aphid saliva (Kloft and Ehrhardt, 1959; Parry, 1971; Fisher, 1987). If aphid population density is high for a prolonged period, extensive defoliaton may occur (Day and McClean, 1991; Day et al., 1998a; Straw et al., 1998; Lynch, 2004). Defoliation reduces tree shoot growth, radial and height growth, and root mass, and severe defoliation may kill trees (Carter, 1977; Koot, 1991; Straw, 2001; Straw et al., 2002; Lynch, 2004).

Extent The extent of damage varies by region.

(1) Forests maritime locations *Elatobium abietinum* is considered to be one of the most serious pests of spruce plantations, especially in Britain, Iceland, and other areas where Sitka spruce is grown commercially (Day and Leather, 1997; Nicol et al., 1998; Straw et al., 1998; Sigurdsson et al., 1999). Damage on the west coast of North America (from California to Alaska) is similar, with somewhat greater tree mortality, but commercial impact is less, because damage is mostly confined to coastal areas where Sitka spruce is not valued commercially (Koot, 1991; Holsten et al., 2001) (Fig. 3).

Straw et al. (1998, 2002) summarize the results of studies of losses to Sitka spruce in Britain, Ireland, Norway, and Iceland, including manipulative studies of pot-grown seedlings and of outplanted young trees, as well as natural aphid outbreaks in spruce plantations. *Elatobium abietinum* rarely kills trees in Europe, and its main effect is to reduce annual tree growth increments, though significant mortality does occur on Sitka spruce in New Zealand (Bevan, 1966; Nicol et al., 1998; Straw et al., 1998). Winter/spring aphid feeding before or at the time of shoot extension has an immediate effect on height growth, potentially for several years. Following defoliation, radial growth may be reduced for up to 7–8 years in older trees. The economic losses from the effects of aphids on plantation forestry are negligible if episodes are infrequent or not severe, but frequent and severe outbreaks can reduce cumulative diameter and stem volume growth 20–40% over a 50 year period (Randle and Ludlow, 1998).

Figure 2 Close view of damage of spruce aphid (*Elatobium abietinum*). Elizabeth Willhite, USDA Forest Service, Bugwood.org.

Figure 3 Spruce aphid (*Elatobium abietinum*) damage (brown discoloration) to stand of Sitka spruce. Andris Eglitis, USDA Forest Service, Bugwood.org

(2) Forests in European montane areas Damage from *E. abietinum* is seldom noticeable (Bejer-Petersen, 1962; Bevan, 1966; Carter and Halldórsson, 1998; Nicol et al., 1998; Halldórsson et al., 2004).

(3) High-elevation spruce forests of the southwestern United States Spruce aphid has become a chronic source of damage in this region, including occasional, very severe outbreaks (Lynch, 2003, 2004, 2009) on Engelmann spruce and blue spruce. Impact studies show that the degree of defoliation is much higher on Engelmann spruce than on blue spruce and more severe in the lower canopy (Lynch, 2004). Average mortality from a single aphid outbreak was 10% (Lynch, 2004), but reached 24–40% in severely defoliated trees and 70% in trees with severe pre-existing infection by western spruce dwarf mistletoe (*Arceuthobium microcarpum* [Engelmann] Hawksworth & Wiens) (Lynch, 2004, 2009). Mortality may continue for up to three years after defoliation (Lynch, 2004). Retention of foliage in the upper-third of crowns is critical for tree survivorship. Differences in tree defoliation and mortality in these studies were not associated with stand stocking, host abundance, tree age, or tree size (except that damage was greater to sub-canopy trees in multi-storied stands), or with elevation, aspect, or slope steepness (Lynch, 2004, 2009). *Elatobium abietinum* is likely to significantly affect natural disturbance regimes and tree population dynamics in mixed-conifer and spruce-fir forests of the southwestern United States (Lynch, 2004, 2009). *Elatobium abietinum* has contributed to declines in habitat quality of the endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis* J. A. Allen) (Koprowski et al., 2005).

(4) In Christmas tree plantings and urban areas *Elatobium abietinum* is a significant pest of spruce trees in maritime and montane environments, and of Sitka spruce in urban parks, because of the unsightly nature of aphid-caused defoliation and the sooty mold that grows on aphid honeydew (Cain, 1989; Koot, 1991; DeAngelis, 1994; Carter and Winter, 1998; Holsten et al., 2001; Hagle et al., 2003). Infestations are not usually detected until foliage is discolored, by which time it is too late to prevent aesthetic damage. Trees may not recover a full complement of foliage for five years (DeAngelis, 1994). *Elatobium abietinum* is also a pest of seed orchards, and appears to reduce seed and cone production seriously (Ruth et al., 1982; Sawchuck, 1994; Partridge and Borden, 1997), but effects have not been quantified. Effects on wildlife habitat are not documented.

Biology of Pest

General biology Von Scheller (1963) provides descriptions and drawings of the different life stages of *E. abietinum.* Spruce aphid feeds and develops on all species of *Picea*, with North American species being the most susceptible (Theobald, 1926; Nichols, 1987; Carter and Halldórsson, 1998). This aphid has no alternate host (Bejer-Petersen, 1962). Occasional reports of *E. abietinum* on fir (*Abies*)*,* larch (*Larix*)*,* Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and pine (*Pinus*) probably either reflect accidental occurrences or non-persistent populations (Cunliffe, 1924; Dumbleton, 1932; Bejer-Petersen, 1962; Carter and Halldórson, 1998; Lynch, personal observation), or are actually the related species *Elatobium blackmani* Binazzi & Barbagallo (Blackman and Eastop, 1994).

Aphid biology and outbreak risk in coastal ecosystems of the North American Pacific Northwest are similar to what has been observed in Britain (Eglitis 1987, Koot 1991, Holsten et al. 2001). However, the life cycle, seasonal history, and damage are all quite different in inland montane ecosystems (Lynch, 2003, 2009).

The life cycle and biology of *E. abietinum* are described by von Scheller (1963) and Bevan (1966), including the holocyclic life history (which typically occurs in the aphid's native range), in which parthenogenetic reproduction is followed seasonally by sexual reproduction, which starts another annual cycle with the laying of winter eggs. In maritime areas, the species is anholocyclic (i.e., completely parthenogenetic), and it is on this form that most biology, impact, and control studies have been done. *Elatobium abietinum* has the capacity for rapid parthenogenetic population growth in spring or autumn, when foliage is dormant and temperature is favorable. In most maritime environments, this form of reproduction occurs in spring, but in Iceland and montane ecosystems of the southwestern United States, it occurs in autumn. In the colder areas of Europe and western Asia where *E. abietinum* is indigenous, the occasional outbreaks are minor and local (Bejer-Petersen, 1962; Bevan, 1966; Ismukhambetov, 1976; Carter and Halldórsson, 1998; Nicol et al., 1998; Halldórsson et al., 2004).

Elatobium abietinum sucks sap from needle phloem cells of the vascular bundles (Bevan, 1966). Old foliage is strongly preferred over new foliage, but new foliage becomes acceptable as it matures and trees enter dormancy. Population development and decline are influenced primarily by temperature and the effects on aphid fecundity of seasonal variation in the levels of soluble nitrogen in needle sap (Parry, 1974; Day, 1984; Fisher and Dixon, 1986; Crute and Day, 1990; Dixon, 1998; Day et al., 2004). The nutritional quality of the food resource increases in autumn and decreases in spring as trees enter and exit dormancy, respectively, and aphid fertility is strongly associated with seasonal changes in amino acid concentration in needle sap (Day, 1984; Fisher and Dixon, 1986; Day et al., 2004). This effect is independent of crowding (Day et al., 2004). New foliage is nutritionally inadequate (Day et al., 2004) and chemically protected by terpenes in the epicuticular wax (Jackson and Dixon, 1966), Consequently, new foliage is not infested until it matures and dormancy is initiated (Bevan, 1966; Carter, 1977; Straw et al., 1998). Day et al. (2004) discuss the relative importance of density-dependent and density-independent factors that contribute to summer survival and spring and autumn population density changes. Usually, population development in autumn is limited by seasonal cooling (Hussey, 1952; Bejer-Petersen, 1962; Parry, 1979), except in Iceland and the southwestern United States (Halldórsson et al., 2004; Lynch, 2003, 2004, 2009). Sap quality can also determine whether or not aphids survive freezing temperatures in winter (Powell, 1974; Powell and Parry, 1976).

There is no summer aestivation (Parry, 1979). Low density of *E. abietinum* in summer coincides with low soluble nitrogen (Bevan, 1966; Parry, 1974, 1979; Carter, 1989), and summer survival is dependent on the ability of a few aphids of all instars to survive on nutritionally inadequate foliage, possibly due to higher fat reserves or the ability to feed on marginally superior trees or shoots (Parry, 1979). Many aphids in the summer generations fail to reproduce in summer (Parry, 1974; Day, 1984; Day et al., 2004).

Biology in maritime locations In areas with mild winters, including the North American Pacific Northwest (northern California to southeastern Alaska), *E. abietinum* is predominantly anholocyclic, overwintering as apterous parthenogenetic viviparae (female aphids that give birth to nymphs) (Parry, 1974; Carter and Halldórson, 1998)**.** Alate viviparae sometimes are produced in spring and early summer (Hussey, 1952; Carter and Cole, 1977; Parry, 1973; Day, 1986) and occasionally in autumn (Hussey, 1952; Fisher and Dixon, 1986). When female alates are produced, they contribute significantly to rapid population spread (Dumbleton, 1932; Halldórsson et al., 2004). Ovipares (sexual females that mate and lay eggs) and male alates are rarely observed in autumn (Fisher and Dixon, 1986; Harding and Carter, 199; Carter and Halldórson, 1998). Population density peaks in late spring or early summer and then collapses, primarily due to reduced fecundity as trees break dormancy, but also due to starvation, needle scarcity, loss of aphids on falling needles, emigration by alates, and the effects of parasitoids and predators (Hussey, 1952; Bevan, 1966; Parry, 1969a; Leather and Owuor, 1996).

Springtime outbreaks follow mild winters and early initiation of tree dormancy in the previous fall (Ohnesorge, 1961; Bejer-Petersen, 1962; Carter, 1972; Powell and Parry, 1976; Carter and Nichols, 1988) and can be terminated by late-season frost (Carter, 1972). Outbreaks occur in late winter and spring if the mean monthly temperatures of the preceding year remained above freezing and the minimum ambient temperatures remained above -7 to -14°C (Bejer-Petersen, 1962; Carter, 1972; Powell and Parry, 1976). Aphids are inactive at or below 6°C and may starve during prolonged cold periods (Powell and Parry, 1976). Overwintering survival is facilitated through accumulation of cryoprotectant chemicals in the haemocoel, but these chemicals vary seasonally and are lost in the spring (Parry, 1969b; Carter, 1972; Day and Kidd, 1998). Aphid mortality occurs when ice nucleation progresses from host needle tissue to feeding aphids or possibly from rime ice (Carter, 1972; Powell, 1974; Carter and Halldórson, 1998). Outbreaks do not occur after every mild winter, due to the effects of predator and parasitoid populations (Crute and Day, 1990; Day and Kidd, 1998; Straw et al., 2009).

Sexual forms are rare in Great Britain (Hussey, 1952; Parry, 1973; Carter and Halldórsson, 1998). Though the life cycle is predominantly anholocyclic in maritime ecosystems, the occasional production of oviparae, male alates, and eggs in Britain, Denmark, and Norway (Fisher and Dixon, 1986; Carter and Austarå, 1994; Harding and Carter, 1997; Carter and Halldórsson, 1998) and evidence of gene flow among Great Britain, France, and Iceland (Halldórsson et al., 2004) indicate that parthenogenetic populations retain the capacity of a holocyclic life cycle.

The role of natural enemies in the dynamics of anholocyclic populations of *E. abietinum* has been the subject of controversy, particularly regarding the relative importance of host-plant nutrition (as discussed earlier) and natural enemy regulation (Austarå et al., 1998; Day and Kidd, 1998; Day et al., 2004, and papers cited therein). Current evidence suggests that thermal conditions and seasonal changes in spruce needle sap nutrients are the primary factors influencing aphid population development and decline. However, in some circumstances natural enemies have the capacity to determine the amplitude of seasonal population fluctuation (Crute and Day, 1990; Leather and Owuor, 1996; Day and Kidd, 1998, Day et al., 2006; Straw et al., 2009), 2009) and such density-dependent effects can lead to population declines (Leather and Owuor, 1996; Austarå et al., 1998; Day and Kidd, 1998; Day et al., 2004; Straw et al., 2009). Straw et al. (2009) found that the abundance of generalist predators was more closely associated with the abundance of alternate prey than with *E. abietinum*. Outbreaks sometimes fail to occur after a mild winter, presumably because of predator and parasitoid population response to aphid populations the previous year (Crute and Day, 1990; Day and Kidd, 1998; Straw et al., 2009).

Population biology in Iceland is similar to that in Great Britain, except that populations develop in the autumn, with a minor peak in springtime (Austarå et al., 1997). Gene flow indicates that some sexual reproduction occurs (Halldórsson et al., 2004).

Biology in montane locations The life cycle and temperature relationships in North American montane ecosystems are presumably similar to those in colder continental European habitats, where *E. abietinum* is holocyclic, with population development and production of female apterae in spring and autumn, oviparae and male alates in autumn, and a cold-hardy overwintering egg (Kloft et al., 1961; Bejer-Petersen, 1962; von Scheller, 1963; Bevan, 1966). In high-elevation spruce-fir forests of Arizona, the life cycle includes parthenogenetic reproduction throughout the entire year when winters are mild, damaging populations in autumn and early winter, occasional damaging populations in spring, occasional female alatae in spring, and oviparae and male alatae in autumn (Lynch, 2003, 2009). The egg stage has not been confirmed in this region (Lynch, 2003).

Autumn populations of *E. abietinum* in the montane forests of the southwestern United States are more cold-hardy than populations in maritime Europe and the North American Pacific Northwest. Day and Kidd (1998) observed that *E. abietinum* reared in cool conditions acquire greater cold hardiness. At 2400-3500 m elevation in Arizona, populations develop at temperatures below thresholds that prevent or diminish spring outbreaks in maritime ecosystems (Lynch, 2009). Aphids are typically active on warm, sunny autumn and early winter days, and aphids that survive nighttime temperatures and acute or prolonged cold events are able to reproduce (Lynch, 2009). Populations persisted in the Arizonan White Mountains after temperatures fell to -30°C in December 1990, with an extensive outbreak five years later (Lynch, 2009). Winter survival is probably ensured by the production of cold hardy eggs, though this stage has not been confirmed in Arizona. Likely explanations for greater cold hardiness in the montane ecosystem include acclimatization as a consequence of the cool and diurnally variable thermal conditions, genetic adaptation, and greater cold hardiness of Engelmann spruce, which would diminish the threshold at which ice nucleation begins in the needle.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

There are no other known species of *Elatobium* in the Western Hemisphere (Carter and Halldórsson, 1998). The biology and distribution of other *Elatobium* species are not well known, but they are native to China, Japan, Taiwan, eastern Siberia, Turkey, and Italy (Blackman and Eastop, 1994; Carter and Halldórsson, 1998).

Native Natural Enemies Affecting the Pest

No surveys or studies have been made of natural enemies of *E. abietinum* in North America. Generalist predators, such as green (*Chrysoperla*) and brown lacewings (*Hemerobius*) (both Neuroptera: Chrysopidae), coccinellid beetles, spiders, and syrphid flies are associated with *E. abietinum* infestations in Arizona (Lynch, personal observations). Some spiders are active predators all year on foliage in Arizona except in mid-winter during colder years. Infections by Entomophthorales fungi are also common in Alaska and Arizona. These predators and fungi do not appear to regulate *E. abietinum* populations in either spring or autumn, the main periods of aphid population increase.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

There are four known conifer-feeding species of *Elatobium: E. abietinum* on spruce (*Picea*), *E. blackmani* on true fir (*Abies*) in Italy and Turkey (and possibly more widespread), *Elatobium laricis* (Rupais) on *Larix sibirica* Ledebour in eastern Siberia, and *Elatobium momii* (Shinji) on *Abies firma* Siebold. & Zucc. in Japan (Blackman and Eastop, 1994; Carter and Halldórsson, 1998). Of these, only *E. abietinum* is known to exist in North America, where it is introduced. *Elatobium abietinum* is the only significant pest of the four. Population behavior, life cycle, and genetic diversity indicate that *E. abietinum* originated in continental Europe on Norway spruce (*P. abies*) (Carter and Halldórsson, 1998; Nicol et al., 1998; Halldórsson et al., 2004). It is found as a normally innocuous insect in Kazakhstan on *Picea schrenkiana* (Fisch. et May) (Ismukhambetov, 1976; Lynch, personal observations), and it might have a more extensive distribution in Asia than has been reported in the literature.

Areas Surveyed for Natural Enemies

Natural enemies of *E. abietinum* have been studied in Denmark, Great Britain, Iceland, Ireland, New Zealand, and Norway (Dumbleton, 1932; Austarå et al., 1997, 1998; Nielsen et al., 2000, 2001; Day et al., 2006; Straw et al., 2009), but surveys have not been conducted in North America. Von Scheller (1963) includes a brief report of natural enemies known from Germany.

Natural Enemies Found in the Native Range or other Invaded Areas outside USA

The influence of natural enemies in suppressing *E. abietinum* populations in maritime areas of Europe is not clear, but the overriding influences of climate and host nutrition (von Scheller, 1963; Parry, 1969b; Day and Kidd, 1998), and the aphid's seasonal avoidance of natural enemies suggests that the effectiveness of natural enemies is limited. Von Scheller (1963) indicates that parasitism rates are very low (1–2%) in Germany, the presumed native range of *E. abietinum*. Predators may be important in reducing aphid populations during the late summer and autumn in Europe, and in years following high populations (Crute and Day, 1990; Leather and Kidd, 1998).

Table 1 Known parasitoids and entomopathogenic fungal pathogens of *Elatobium abietinum*, compiled from von Scheller (1963), Austarå et al. (1997, 1998), Nielsen et al. (2001), and Nielsen and Wraight (2009).

Species	Collection Location
Hymenoptera: Aphidiidae	
Lysaphidus schimitscheki Starý	Germany, Great Britain, Norway
Praon sp.	Germany, Great Britain, Norway
Hymenoptera: Aphelinidae	
Aphelinus abdominalis (Dalman)	Norway
Aphelinus sp.	Germany
Hymenoptera: Pteromalidae	
Asaphes suspensus (Nees)	Norway
A. vulgaris Walker	Germany, Great Britain
Coruna clavata Walker	Norway
Entomophthorales: Ancylistaceae	
Conidiobolus obscures (Hall & Dunn)	Great Britain
C. coronatus (Costantin) Batko	Great Britain
Entomophthorales: Entomophthoraceae	
Entomophthora planchoniana Cornu	Denmark, Iceland
E. pyriformis (Thoizon) Bałazy	Iceland
Pandora neoaphidis Remaudikre & Hennebert	Denmark
Entomophthorales: Neozygitaceae	
Neozygites fresenii (Nowakowski)	Great Britain, Denmark, Iceland, Norway
Zoophthora phalloides Batko	Denmark

Elatobium abietinum is attacked by a wide range of invertebrate generalist predators, several species of parasitoids, and entopathogenic fungi (Bejer-Peterson, 1962; von Scheller, 1963; Austarå et al., 1997, 1998; Nielsen et al., 2001; Day et al., 2006). These authors provide lists of parasites, predators, and entomopathogens associated with *E. abietinum* in different regions (Table 1, above). The most important of the generalist predators include green lacewings, brown lacewings, coccinellid beetles, spiders, harvestmen, syrphid flies, cantharid beetles, and elaterids. The relative importance of the different predators varies considerably between locations and years, but generally the lacewings and coccinellids seem to be the most common, followed by cantharids and syrphids.

Records of parasitoids are much less frequent than records of predators and parasitoids appear to be less effective, with parasitism rates rarely exceeding 10% (von Scheller, 1963; Parry, 1969; Austarå et al., 1998; Leather and Kidd, 1998). There appear to be few specialized parasitoids of this aphid (Blackman and Eastop, 1994; Austarå et al., 1997, 1998). Halme (1992) indicates that *Ephedrus koponeni* Halme is specific to *E. abietinum* in Finland, but this parasitoid has not been found elsewhere (Austarå et al., 1997, 1998).

Entomophthorales fungi (Zygomycotina), particularly *Entomophthora planchoniana* Cornu, *Conidiobolus obscures* (Hall & Dunn), *Conidiobolus osmodes* Dreschler, *Pandora neoaphidis* Remaudikre & Hennebert, and *Neozygites fresenii* (Nowakowski), are prevalent but sporadic and infect *E. abietinum* throughout its current distribution (Austarå et al., 1997; Nielsen et al., 2000).

Releases Made

Classical biological control of this aphid has not been attempted in North America, so no releases of natural enemies have been made. *Aphidecta obliterata* (L.) (Coleoptera: Coccineldiae) was introduced to the North Sea island of Amrum, Germany, in 1966 for control of *E. abietinum* (Schneider, 1966), but effectiveness has not been reported (Leather and Kidd, 1998). *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae) and *Chrysopa* sp. (Neuroptera) were introduced to New Zealand in 1921 for biological control of various aphids, including *E. abietinum*, without success (Dumbleton, 1932).

RECOMMENDATIONS FOR FURTHER WORK

Sitka spruce in coastal environments and Engelmann spruce in montane ecosystems are being affected by both *E. abietinum* and climate change, which could reduce their presence in future forests (Lynch, 2004, 2009). Population growth by *E. abietinum* in late autumn and early winter and in early spring is an effective strategy to avoid parasitoids and predators (Bejer-Petersen, 1962; Parry, 1969b), and that phenology reduces the potential for successful biological control of this species. Also, the low commercial value of these spruce in North America makes substantial investment in management and biological control of *E. abietinum* or in the development of resistant host varieties uneconomical. Should these circumstances change, development of resistant varieties is likely to be a useful approach to management (Day et al., 1998b; Lewis et al., 1999; Harding et al., 2003) and would be facilitated by identification of, and seed collection from, resistant trees.

Surveys should be conducted to identify native North American natural enemies of *E. abietinum*. Further research is also needed to better understand the effects of predators and entomopathogens on population dynamics of *E. abietinum*, especially on the effects of summer- and autumn-active agents on moderating aphid population density the following year. Surveys and collections of natural enemies in continental Europe and western and central Asia should focus on autumn-active agents and should be conducted in warm, dry years, when *E. abietinum* is more likely to be at higher densities. Further research is also needed on the ecological requirements of potential biological control agents in maritime and cold ecosystems.

Because the seasonality of *E. abietinum* population growth (in autumn and early spring) limits the influence of parasitoids and predaceous insects on this aphid, and because the most effective known predators are generalists requiring alternate prey, it may be useful to study the entomophthoralean fungi associated with this aphid. Fungal pathogens known from *E. abietinum* include species of *Batkoa, Conidiobolus, Entomophaga, Entomophthora, Neozygites, Pandora* (= *Erynia*), and *Zoophthora* (Latgé and Papierok, 1988; Humber, 1989, 1992; Bałazy, 1993; Nielsen et al., 2000; Keller, 2006, Nielsen and Wraight, 2009). With few exceptions, host ranges of the species reported from spruce aphid are restricted to the Aphididae (Keller, 2006; Nielsen and Wraight, 2009). Despite taxonomic diversity, the differrent species exhibit similar life cycles and ecology with rapid sporulation and infection, traits that facilitate exploitation of short windows of favorable environmental conditions and rapid spread within host populations (Pell et al., 2001; Nielsen and Wraight, 2009). Transmission of entomophthoralean fungi is possible between different aphid host species, and other aphid species may serve as reservoirs for entomophthorales when *E. abietinum* is scarce (Nielsen et al., 2001). Additional studies are needed to determine the natural occurrence, diversity, environmental requirements, and pathogenicity of entomophthoralean fungi in different areas infested by *E. abietinum*. These studies might identify candidates for release in new areas. Entomophorales have had some success as biological control agents (Pell et al., 2001). Release of *Zoophthora radicans* (Brefeld) Batko contributed to the decline of the spotted alfalfa aphid (*Therioaphis trifolii* f. *maculata* [Buckton]) (Hemiptera: Aphididae) as a pest in Australia, although biological control is primarily attributed to the parasitoid *Trioxys complanatus* Quilis (Hymenoptera: Braconidae) (Hughes et al., 1987; Pell et al., 2001). Releases of *Neozygites fresenii* (Nowakowski) Batko against cotton aphid (*Aphis gossypii* Glover) (Hemiptera: Aphididae) in California and *Entomophaga grylli* (Fresenius) Batko against grasshoppers (Orthoptera: Acrididae) in Australia had some success (Pell et al., 2001; Steinkraus et al., 2002), but long-term effectiveness was not determined. The sporadic nature of entomophthorales epidemics in high density aphid populations suggests that they may require specific environmental conditions. Still, in North America the overriding objective of biological control is likely to be conservation of *Picea* spp., so biological control measures that moderate the most severe outbreaks would probably be sufficient.

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XXV Elongate Hemlock Scale

(*Fiorinia externa* [Ferris]) (Hemiptera: Diaspididae)

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DESCRIPTION OF PEST

Taxonomy

Elongate hemlock scale, *Fiorinia externa* (Ferris), has no synonyms. There are 66 described species in the genus *Fiorinia* (ScaleNet, 2012), all of Asian, Australasian, or Afrotropical origin.

Distribution

Fiorinia externa is indigenous to Japan (Takagi, 1963; Watanabe and Uchida, 1967) and was first reported in the United States in 1908 on Long Island, New York (Ferris, 1942). Since then, elongate hemlock scale has spread along the Appalachian Mountains, from Massachusetts to northern Georgia and South Carolina, and west to Ohio, Michigan, and Minnesota. Since 1998, elongate hemlock scale has spread further north in New England and increased in density (Preisser et al., 2008a). This spread, together with experimental evidence (Preisser et al., 2008b), demonstrates that elongate hemlock scale is evolving greater cold tolerance and will likely continue to move northward.

Damage

Type Elongate hemlock scales settle permanently on the undersides of hemlock needles and insert their mouthparts to feed on fluids within the needle. Several scales feeding on the same needle can cause needle death, and on trees with heavy infestations, this density of feeding can result in the loss of a large proportion of a tree's foliage. Sustained heavy infestations of elongate hemlock scale can cause tree mortality.

Extent In North America, elongate hemlock scale density varies widely, from 21 to 420 scales per 100 needles (McClure and Fergione, 1977; McClure, 1978). In its native Japan, density ranges from 0.0 to 0.15 scales per 100 needles (McClure, 1986; Abell, 2010).

Biology of Pest

A complete description of all stages of both male and female elongate hemlock scale can be found in Wallner (1965) and detailed description of the adult male can be found in Lambdin et al. (2007). In Kyoto Prefecture, Japan, elongate hemlock scale has two generations per year (McClure, 1986). In the United States, elongate hemlock scale has 1–1.5 generations at northern latitudes and two at southern latitudes (Garrett and Langford, 1969; McClure, 1978; Stimmel, 1980; Lambdin et al., 2007; Abell, 2010; Abell and Van Driesche, 2012). Unlike in Japan, where elongate hemlock scale appears to have discrete life stages and generations, both of these overlap in the United States (Garrett and Langford, 1969; McClure, 1978, 1986; Stimmel, 1980; Lambdin et al., 2007; Abell, 2010; Abell and Van Driesche, 2012). After emerging from an egg, the crawler searches for a suitable feeding location, typically on newly flushed foliage, inserts its stylets, and feeds in this spot for the duration of its development (Fig. 1). Females molt twice, with the adult remaining within the second instar test. The adult female contracts to the anterior portion of the second instar test and fills the remaining space with eggs (Fig. 2). Males molt four times, resulting in a winged adult that does not feed, but searches for females with which to mate.

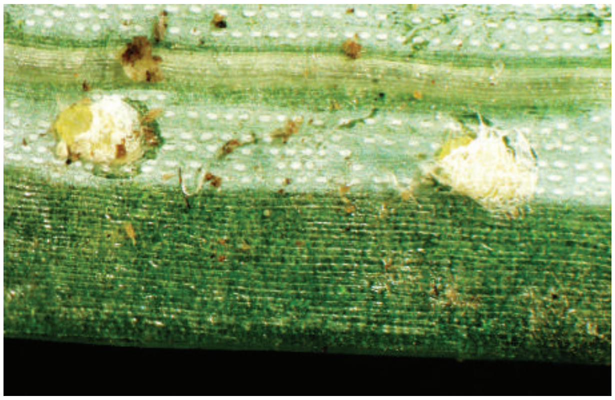

Figure 1 First instar elongate hemlock scale (*Fiorinia externa*) settled on the underside of eastern hemlock needle.

Figure 2 Adult female elongate hemlock scale with eggs.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

An analysis of North American scale insects that might be at risk from imported natural enemies of elongate hemlock scale has not yet been done. However, the genus is predominantly native to Asia, and the tribe Fiorinini has no known native species in North America. This group is most closely related to the genus *Pseudaulacaspis*, which also has no known native North American species (B. Normark, pers. comm.). Also, *Fiorinia* scales are "pupillarial" (adult is enclosed in exoskeleton of the second instar), which is unusual and may influence parasitoid host selection if any parasitoids are encountered that oviposit in adult females. The only North American scales with this habit are found in the deserts of the southwestern United States. Identification of "rare" insects in the Diaspididae is difficult because it is a group that attracts few collectors.

Native Natural Enemies Affecting the Pest

The cosmopolitan polyphagous aphelinid *Encarsia citrina* Crawford (Fig. 3) is the only parasitoid known to attack elongate hemlock scale in North America. Parasitism rates by *E. citrina* on elongate hemlock scale in Connecticut vary widely from near zero to greater than 90% (McClure, 1981). In Tennessee parasitism rates ranged from 20–22% in forested areas and 16–33% in urban areas (Lambdin et al., 2005).

Figure 3 Adult *Encarsia citrina*.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Elongate hemlock scale originates in Asia, specifically Japan and China.

Areas Surveyed for Natural Enemies

Surveys have been conducted in Japan for natural enemies of elongate hemlock scale.

Natural Enemies Found

The first natural enemies found in Japan were from the Kyoto area (McClure, 1986). Only two parasitoids were detected: *E. citrina* and *Arrhenophagus albitibiae* Girault. *Encarsia citrina* accounted for 88.4% of all parasitoids reared from elongate hemlock scales in that area. A subsequent survey conducted throughout Japan found seven relatively common, genetically distinct parasitoids associated with elongate hemlock scale (Abell, 2010). Two of the seven were in the family Encyrtidae–*Zaomma lambinus* Walker, a hyperparasitoid, and *A. albitibiae,* as mentioned in McClure (1986). The remaining five species were all aphelinids, including an unidentified *Aphytis* species and four *Encarsia* species, the most common of which was *E. citrina*. Comparative DNA analyses of *E. citrina* from Japan and the United States found no differences. The remaining three *Encarsia* represent new host associations with elongate hemlock and, together with the *Aphytis* species, may be potential candidates for biological control in the United States (Japoshvili et al., 2013).

Host Range Test Results

Host range testing has not been done for any of the newly discovered *Encarsia* or *Aphytis* species from Japan. However, some estimate of the likely host specificity of these species can was obtained from the same survey, which collected all seven diaspidid scales found on hemlock in Japan. *Encarsia citrina*, is known to be polyphagous. Excluding its main host, elongate hemlock scale, *E. citrina* attacked five of the six other scales found on hemlock in Japan. In contrast, the three newly discovered *Encarsia* species were found only on *F. externa*.

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XXVI ASPEN/WILLOW SCALE

(*Diaspidiotus gigas* [Thiem and Gerneck]) (Hemiptera: Diaspididae)

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DESCRIPTION OF PEST

Taxonomy

Diaspidiotus gigas (Thiem and Gerneck), known as the aspen scale, willow scale, or poplar scale, is also mentioned in older literature under other synonyms or combinations: *Aspidiotus (Euraspidotus) gigas* Thiem and Gerneck, *Aspidiotus multiglandulatus* Borchsenius, *Aspidiotus gigas* Thiem and Gerneck, and *Quadraspidiotus gigas* (Thiem and Gerneck). There are at least eight other species of *Diaspidiotus* found in the United States (see Table 1 below).

Distribution

Diaspidiotus gigas is native to Europe and has been found in Bohemia, Moravia, Slovakia, Germany, Holland, Switzerland, France, Italy, Yugoslavia, Bulgaria, Hungary, Russia, Turkey, and Algeria (Alleláková-Dusková, 1963). Miller and Davidson (2005) observed infested material from Canada, Germany, and Russia. *Diaspidiotus gigas* has been intercepted by U.S. quarantine officers on *Salix* and *Populus* from all regions of Europe and on *Tilia* from Bulgaria (Nakahara, 1982). Specimens have been identified from across the United States in Colorado, Idaho, Montana, New York, Ohio, Oregon, Pennsylvania, Rhode Island, Utah, Washington, Wisconsin, and Wyoming. Miller and Davidson (2005) indicate the scale has been introduced into many countries around the world.

Damage

Type *Diaspidiotus gigas* prefers areas of smooth bark on the host trunk and branches. The scales can form thick crusts (Fig. 1) on poplar (*Populus* spp.) bark and cause weakening, branch dieback, and death of part or all of the host tree, especially saplings (Lelláková-Dusková, 1963). Early symptoms of a heavy infestation include drooping or weeping of the entire crown (Fig. 2). All stem sizes (Fig. 3) may be attacked and damaged by this scale. Stem death (Fig. 4) is common following one year of severe infestation. In older infestations, the scale forms hollows or pits in the tree trunk or branches (Fig. 5), rendering the wood worthless to industry. *Diaspidiotus gigas* spreads rapidly within parts of weakened trees or over whole stands, especially on poor growing sites (insufficient moisture, heavy frosts, or other unsuitable conditions), or when trees are stressed by disease. Various beetles and lepidopteran

Figure 1 *Diaspidiotus gigas* can form a thick crust on the bark of aspen. Laura Lazarus.

Table 1 Other species of native or introduced (**bold**) *Diaspidiotus* scales in North America.

Scientific name	Common name	Region of origin	Hosts	Citations
1. *D. aesculi* (Johnson)	buckeye *Aspidiotus*	Nearctic	Polyphagous on various woody plants	ScaleNet, 2012
2. *D. ancylus* (Putman)	Putnam scale	Nearctic	Wide variety of deciduous trees and shrubs	Arnett, 2000
3. *D. bumeliae* Ferris	none	Nearctic	Moraceae: *Maclura*; Rosaceae: *Crataegus*; Sapotaceae: *Bumelia*	ScaleNet, 2012
4. D. braunschvigi **(Rungs)**	**braunschvigi scale**	**Introduced from Palearctic**	**Anacardiaceae: Pistacia atlantica; Moraceae: Ficus**	**ScaleNet, 2012**
5. *D. caryae* Kosztarab	hickory scale	Nearctic	Juglandaceae: *Carya*	ScaleNet, 2012
6. *D. coniferarum* (Cockerell)	conifer scale	Nearctic	Various species of Cupressaceae and Pinaceae:	ScaleNet, 2012
7. *D. crescentiae* Ferris	none	Nearctic (Mexico) and Neotropical (Panama)	Agavaceae: *Alibertia;* Bignoniaceae: *Crescentia*	ScaleNet, 2012
8. *D. crystallinus* Ferris	none	Nearctic	Fabaceae: *Acacia, Olneya*	ScaleNet, 2012
9. *D. ehrhorni* (Coleman)	Ehrhorn scale	Nearctic	Various species of Cupressaceae and Pinaceae:	ScaleNet, 2012
10. *D. hunteri* (Newell)	none	Nearctic	Fagaceae: *Quercus*; Grossulariaceae: *Grossularia*	ScaleNet, 2012
11. *D. forbesi* (Johnson)	Forbes scale	Nearctic–North America	Wide host range, 20 genera of trees in 11 families	Miller and Davidson, 2005
12. *D. juglansregiae* (Comstock)	walnut scale	Nearctic–North America	Wide variety of deciduous trees and shrubs	Miller and Davidson, 2005
13. *D. liquidambaris* (Kotinsky)	sweet gum scale	Nearctic	Aceraceae: *Acer*; Hamamelidaceae: *Liquidambar*	ScaleNet, 2012
14. *D. mccombi* McKenzie	McComb pine scale	Nearctic	Pinaceae: *Pinus*	ScaleNet, 2012
15. *D. osborni* (Newell & Cockerell, in Osborn)	Osborn scale	Nearctic	Wide variety of deciduous trees and shrubs	Arnett, 2000
16. D. ostreaformis **(Curtis)**	**European fruit scale**	**Introduced from Palearctic**	**Wide variety of deciduous trees and shrubs**	**Miller and Davidson, 2005**
17. D. perniciosus **(Comstock)**	**San Jose scale**	**Introduced from Palearctic-China?**	**Very wide host range, deciduous trees**	**Miller and Davidson, 2005**
18. *D. piceus* (Sanders)	none	Nearctic	Lauraceae: *Sassafras*; Magnoliaceae: *Liriodendron;* Oleaceae: *Fraxinus*	ScaleNet, 2012
19. *D. socialis* (Hoke)	none	Nearctic	Fagaceae: *Quercus*	ScaleNet, 2012
20. *D. taxodii* (Ferris)	none	Nearctic N. America	Bald cypress (*Taxodium distichum*)	ScaleNet, 2012
21. *D. tillandsiae* (Takagi & Tippins)	none	Nearctic	Bromeliaceae: *Tillandsia*	ScaleNet, 2012
22. *D. uvae* (Comstock)	grape scale	Nearctic	Wide variety of deciduous trees and shrubs	Arnett, 2000

Figure 2 Drooping or weeping branches are symptomatic of *Diaspidiotus gigas* stem and branch infestations on aspen. Laura Lazarus.

Figure 3 Recent *Diaspidiotus gigas* infestation on bole of aspen tree showing early signs of spotty feeding damage to phloem tissue. Laura Lazarus.

Figure 4 Aspen stem mortality and branch dieback caused by *Diaspidiotus gigas*. Laura Lazarus.

Figure 5 Sunken pit damage caused by older infestations of *Diaspidiotus gigas* feeding on aspen stems. Laura Lazarus.

defoliators have also been identified as damaging agents that may increase susceptibility of trees to aspen scale infestation. In combination with such factors, this scale can cause loss of vigor and tree death. Young trees (nursery stock) are especially vulnerable (Lelláková-Dusková, 1963).

Within portions of its introduced range in North America, *D. gigas* is viewed as a pest primarily in landscaped and planted areas. Large infestations can damage aspens, killing all or portions of infested trees. Honeydew produced by the insect may create a nuisance on walkways and parked vehicles. In some cases, infested trees are stressed, but usually survive if they have received ample water and fertilization.

Extent Lelláková-Dusková (1963) reported this scale had killed as much a hectare inside larger stands of *Populus* in some parts of the former Czechoslovakia. Miller and Davidson (1990) considered *D. gigas* a serious pest in only a few small areas of the world. In China, it has been noted as a serious pest on *Populus berolinensis* (K. Koch) Dippel and *Populus simonii* Carr. (Hu et al., 1982; Xie et al., 1995). Xie et al. (1995) suggested that outbreaks were caused by urban pollution. Lelláková-Dusková (1963) published a list of host species on which *D. gigas* has been found.

Interestingly, Lelláková-Dusková (1963) stated that *D. gigas* prefers warmer climates and protected places within the Palearctic region. It colonizes willows (*Salix*) and poplar (*Populus*) growing in areas with sandy soil along rivers and streams, where temperature and humidity are favorable to the scale (Lelláková-Dusková, 1963). However, in the United States this scale became a serious pest on planted quaking aspen trees (*Populus tremuloides* Michx.) in high-elevation (1700 to 2600 m) communities in Colorado and Idaho, and scales were found on native aspen growing in a riparian area in Ketchum, Idaho. Field observations suggest a correlation with colder winter/spring temperatures and reduced scale populations on planted aspen in Idaho (Lazarus and Progar, 2008).

Biology of Pest

The adult female scale averages 2–2.6 mm in diameter, roughly round, sometimes slightly oval, and flat. Color depends on what the scale is resting on and age of the scale. Typically they are light to dark gray; however, very light-colored scales can be found on some hybrid poplars. The males are elongate, with parallel lateral margins and are 1.8–2 mm in diameter. Lelláková-Dusková (1963) completed a detailed study of the lifecycle and biology of *D. gigas*. The scale has one generation each year, individual instars requires 2–3 weeks to complete, depending on local climate, host, and aspect of scale position. *Diaspidiotus gigas* overwinters as second-instar larvae. Adult males and females emerge and mate in May. Females lay an average of 145 eggs from late June through early September. However, the majority of eggs are deposited during July and August. The eggs hatch within 2–3 days. The first instar crawlers move around the tree seeking a suitable location to settle. They use their mouthparts to fasten themselves to the tree within two days, and immediately thereafter begin to form a protective, round scale cover. The scale cover is white at first, but darkens with time. The first larval instar requires about 50 days for completion. Near the end of October, most scales are second instars, and these overwinter in diapause.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

Many species in the genus *Diaspidiotus* are found in agricultural and/or wildland settings. ScaleNet (2012) lists 23 species of *Diaspidiotus* in the Nearctic Region (North America), of which three, in addition to aspen/willow scale, are introduced (Table 1, above). These scales vary from species that are highly polyphagous to species with relatively narrow host ranges.

Native Natural Enemies Affecting the Pest

Although *D. gigas* has been observed to be parasitized in the field (Fig. 6), none of the parasitoids has been identified.

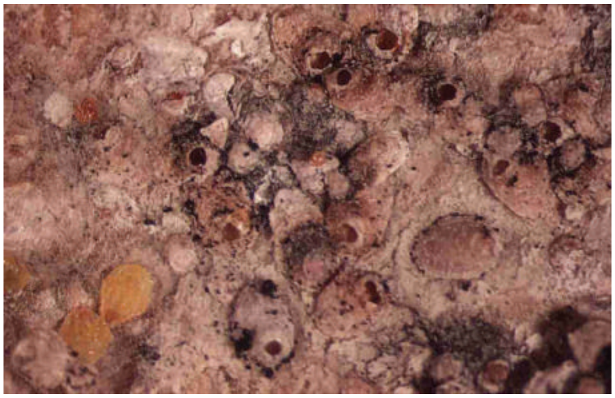

Figure 6 Exit holes from an unidentified parasitoid of *Diaspidiotus gigas* adult scales from aspen host in 2007, Ketchum, Idaho. Bob Hammon.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of the Insect

Diaspidiotus gigas is native to Europe.

Areas Surveyed for Natural Enemies

Although some surveys have been made in both the native ranges and parts of the invaded range of the scale, this species has not yet been chosen as a biological control target for natural enemy introduction into the United States. In Europe *D. gigas* was studied in Germany, Hungary, and the Czech Republic (native range). Studies also were conducted in northern China (part of the invaded range) that report natural enemies (see below for details).

Natural Enemies Found

In the former Czechoslovakia, Lelláková-Dusková (1963) documented 50–90% parasitism of *D. gigas*. *Aphytis mytilaspidis* (Le Baron) and *Pteroptrix dimidiatus* (Westw.) [det. A. Hoffer] (both Hymenop.: Aphelinidae) were common. These same two parasitoids have been found in Germany (Schmutterer, 1953) and Hungary (Kosztarab, 1956). *Aphytis mytilaspidis* is a widely distributed (Europe, Asia, N. America), polyphagous species that frequently parasitizes coccid scales. *Pteroptrix dimidiatus* is also widespread and found in Italy, France, Austria, Hungary, North Africa, Sri Lanka, and North America (Schmutterer, 1959). In Hungary, Kosztarab (1956) reared *P. dimidiatus* and *Azotus matritensis* Merc. (Hymenop.: Aphelinidae) from *D. gigas* on *Populus nigra L. "italica"*.

Larvae of the lady beetles (Coccinellidae) *Chilocorus bipustulatus* (L.) and *Coccinella bipunctata* (L.) feed voraciously on *D. gigas*, and sometimes occur in large numbers on scale-infested trees (Lelláková-Dusková, 1963). The twice-stabbed lady beetle, *Chilocorus stigma* Say, was found feeding on *D. gigas* collected from aspen trees in Colorado (Fig. 7). In northern Germany (Elbe region), the predatory bugs *Loricula pselaphiformis* Curt. and *Loricula elegantula* Baerensprung (Hemiptera: Microphysidae) as well as *Ectemnus nigriceps* E. Wagner and *Temnostethus longirostris* (Horv.) (Hemiptera: Anthocoridae) were found on poplar trees attacked by *D. gigas* (Lelláková-Dusková, 1963).

Figure 7 The twice-stabbed lady beetle, *Chilocorus stigma*, feeding on *Diaspidiotus gigas*, from aspen host in Aspen, Colorado. Vince Urbina.

Host Range Test Results

Because this scale has not yet been a target of natural enemy introductions, no efforts to determine the true host ranges of the parasitoids or predators associated with the scale in its native range have been made. However, for some species, other host records show that some are polyphagous (see section below). No clearly specialized natural enemy of this scale has been determined.

Releases Made

No releases in North America have been made for biological control of aspen/willow scale.

EVALUATION OF PROJECT OUTCOMES

No biological control project has yet been conducted against this species.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Aphytis mytilaspidis

A solitary ectoparasitoid that feeds on the exterior of the scale body (Graora et al., 2009). It is also a common parasitoid of oystershell scale (*Lepidosaphes ulmi* [L.] and San Jose scale (*Diaspidiotus perniciosus* [Comstock)](Hortnet, 2012). There are no known males (Rössler and DeBach, 1973). The female lays an egg under the scale cover on the exterior of the scale body (Karsemeijer, 1973). The wasp has three larval instars and a prepupal stage and then pupates and emerges as an adult wasp. This process leaves behind visible black particles of frass (meconia). There are several generations per year and the parasitoid overwinters in the larval stage. *Aphytis* wasps generally lay 30–60 eggs in their lifetime. The adult wasps also feed on scales by piercing the hosts with an ovipositor and drinking the hemolymph. This activity can cause significant scale mortality.

Chilocorus bipustulatus

The lady beetle *C. bipustulatus* is a polyphagous predator of scale insects (Avidov and Harpaz, 1969). It is a Palearctic species that has been spread widely as a biological control agent. Along with *Aphytis* spp., *Chilocorus* spp. were found to be among the more effective natural enemies for the biological control of diaspidid scales (DeBach, 1960; Bedford, 1968; Ben-Dov and Rosen, 1969; Soylu, 1978). Lady beetles may play a role in suppressing *D. gigas* (Fig. 2, above).

Loricula species (minute pirate bugs)

Loricula pselaphiformis is not often reported but is widely distributed. It occurs on trees such as hawthorn (*Crataegus*), beech (*Fagus*), and birch (*Betula*). Originally from Europe, this bug was first found in North America in 1976 on European beech (*Fagus sylvatica* var. *purourea* Ait.) in Halifax, Nova Scotia (Hoebeke and Wheeler, 1983). *Loricula elegantula* has been collected from Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco.) and Norway spruce (*Picea abies* L.) in Europe (Gobner et al., 2004).

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XXVII Pine Bast Scale

(*Matsucoccus matsumurae* [Kuwana]) (Hemiptera: Matsucoccidae)

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DESCRIPTION OF PEST

Taxonomy

Pine bast scale, *Matsucoccus matsumurae* (Kuwana), is the senior synonym of what was once called red pine scale, *Matsucoccus resinosae* Bean and Godwin, in the United States (Booth and Gullan, 2006). Evidence for the synonomy of *M. resinosae* with *M. matsumurae* includes attraction to the same pheromone (Young et al., 1984) and recent molecular data (Booth and Gullan, 2006). *Matsucoccus matsumurae* (Fig. 1) from Japan is the type species of its genus, which is now placed in the family Matsucoccidae. Worldwide, there are 39 species in the genus *Matsucoccus* and they have a Holarctic distribution (Foldi, 2001). All members of the Matsucoccidae feed exclusively on pines (Foldi, 2005 [2004]). A list of all species in the family, plus information on their distributions and host plants is given in Foldi (2005 [2004]).

Figure 1 Pine bast scale, *Matsucoccus matsumurae*. Alessandra Rung, California Department of Food and Agriculture, Bugwood.org.

Distribution

Pine bast scale is found in Japan (the presumed native range) and in various invaded areas: China (McClure, 1983a), South Korea, Sweden, and a limited part of eastern North America (Bean and Godwin, 1955, 1971). The largest invasive infestation appears to be in China (see Wei [2002] for a review).

The scale was first detected in the United States in Easton, Connecticut, in 1946 (Bean and Godwin, 1971) in red pine (*Pinus resinosa* Ait.) stands planted south of that pine's normal range. It is now in Connecticut, Long Island and southeastern New York, northern New Jersey, and northeastern Pennsylvania (Bean and Godwin, 1955; Stimmel, 1981; Drooz, 1985; USDA Forest Service, 2010). The U.S. infestation, while limited in area has continued to spread. Limited spread of the scale northward into the native range of red pine has been attributed to its inability to survive winter cold at high latitudes. McClure (1983a) suggested that in China and North America, the distribution of this scale is limited both northward and southward by climatic factors, with high winter mortality in areas north of the scale's typical distribution (more than 96%) and high summer mortality (70–90%) in the south. However, Stephens (1977) suggested that pine bast scale in the United States may be adapting to colder winters, allowing it to spread northward. Indeed, comparison of the species' range map in 1971 (Bean and Godwin, 1971) to that in 2010 (USDA Forest Service, 2010) shows considerable northward expansion in Connecticut, from a coastal distribution in 1971 to the border with Massachusetts in 2010. The range of the scale (USDA FS, 2010) now overlaps slightly with that of the native range of red pine in the lower Hudson River Valley of New York (Fig. 2). This may increase the rate of northward spread as cold-adapted individuals in the scale population may now have more direct contact with hosts more continuously in the northward direction.

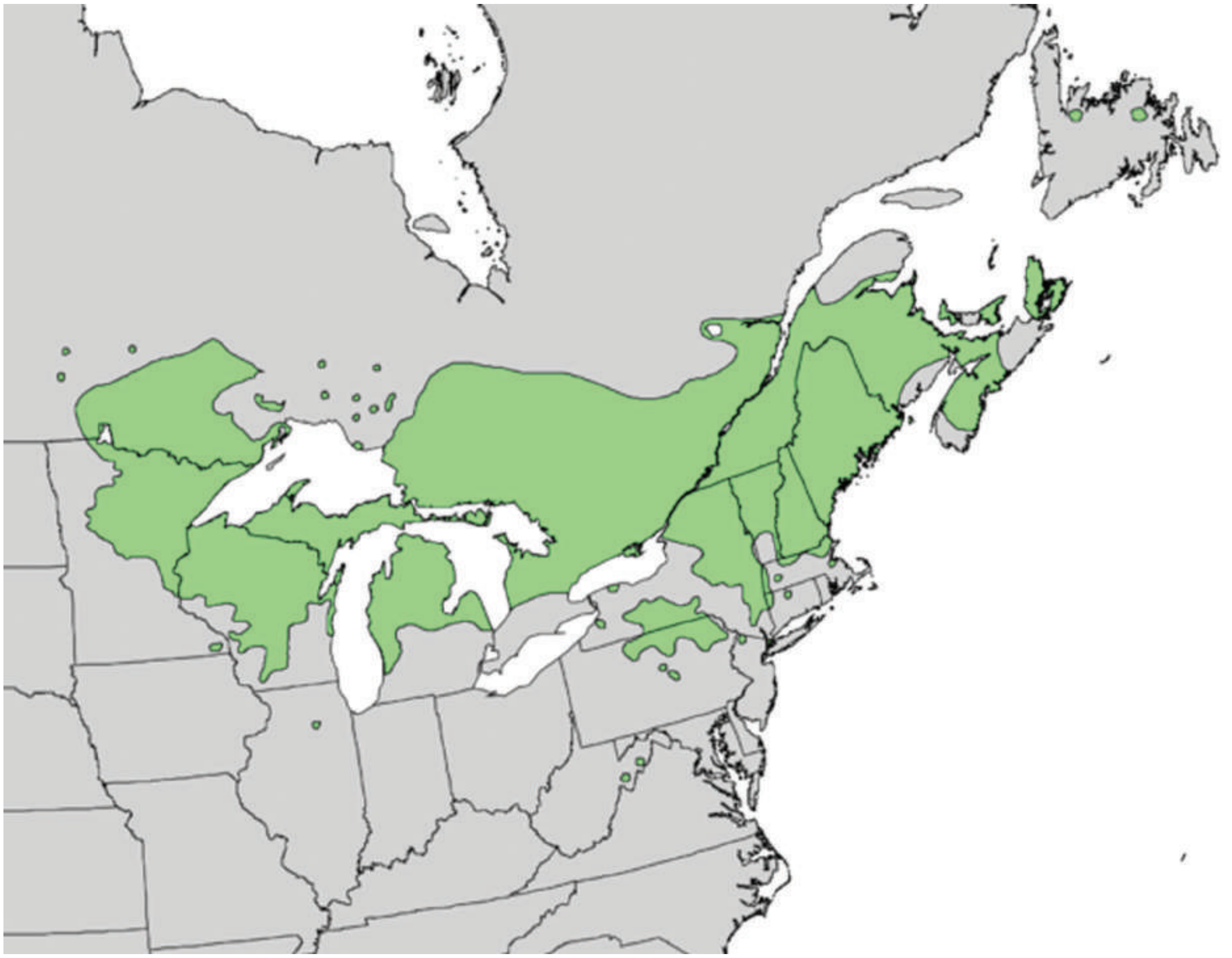

Figure 2 Natural distribution of red pine (*Pinus resinosa*) in North America. United States Geological Survey.

Damage

Type Pine bast scales attack at least six species of Asian pines (all in the *sylvestris* subsection of *Pinus*), including the Japanese red (*P. densiflora* Sieb.), Japanese black (*P. thunbergii* Parl.), Chinese red (*P. tabuliformis* Carr.), Okinawan (*P. luchuensis* Mayr), and Masson's (*P. massoniana* Lamb.) pines (Taketani, 1972); however, its only native North-American host is red pine (*P. resinosa*) (the only North American pine in the *sylvestris* subsection of *Pinus*) (McClure, 1983a). In North America, damage to red pine planted in plantations outside the native range of the tree can be severe. The foliage is discolored (first light olive green, then later, yellow to red) and new growth is shorter than normal (Bean and Godwin, 1971). Masses of male cocoons (appearing as white tufts) are found on the undersides of branches. The bark appears swollen or cracked. Areas of dead tissue appear beneath feeding scales (Drooz, 1985).

Extent In the 1970s pine bast scale was viewed as one of most series threats to red pine in the United States (Bean and Godwin, 1971) (Fig. 2). In red pine plantations in Connecticut (USA), damage was severe, with entire plantations being killed over a number of years (McClure, 1983b). In China, damage is greater in pine plantations of younger trees (10–25) grown on the "shady" side of mountains (Chen et al., 2005).

Biology of Pest

McClure et al. (1983) describes the damage, life cycle, hosts, distribution, and predators of this scale in China. In Connecticut, USA, there are two generations per year and the species overwinters as a first instar (the crawler) in bark cracks. In April, the cyst stage appears and by the end of the month, waxy sacks of the developing males are visible on branches. In May, eggs of the first generation are laid. In May and June, adults and eggs are present.

Eggs occur in masses of wool at the rear of females. Eggs hatch in about two weeks and crawlers of the summer generation become adults by August. Eggs of the second generation are laid in late August and September. Shortly thereafter, the overwintering crawlers appear and then overwinter (from Bean and Godwin, 1971; Drooz, 1985).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

The genus *Matsucoccus* is among the more primitive of scales and is specialized to feed only on pines. Of the 39 known species (Foldi, 2001), there are 15 recorded from the United States (Foldi, 2005 [2004]). Of these, eleven occur in the western United States. East of the Mississippi River, there are four species: *M. gallicolus* Morrison (found widely in the eastern United States on at least seven species of pines), *M. alabamae* Morrison (found on several species of southern pines), *M. macrocicatres* Richard (found Ontario to Massachusetts on white pine [*Pinus strobus* L.]), and *M. banksianae* Ray and Williams (found in Minnesota on jack pine [*Pinus banksiana* Lamb.]). While the eleven western species in the genus might be included in any host range testing of natural enemies of pine bast scale, the four eastern species would be the logical and most ecologically relevant species, especially the three species with northern ranges that overlap with that of red pine.

Natural Enemies Affecting the Pest in the United States

Natural enemies associated with pine bast scale in North America (Connecticut and surrounding areas (Fig. 3) are principally generalist predators. These include the cecidomyiid fly *Lestodiplosis* sp. nr. *grassator* (Fyles) (McClure, 1983b), as well as the predacious anthocorid bug *Elatophilus inimica* D. and H., the coccinellid *Mulsantina picta* (Rand.), and the hemerobiid, *Hemerobius stigmatus* Fitch (Bean and Godwin, 1971). However, none of these species causes sufficient mortality to prevent the buildup of the pest's density.

Figure 3 Distribution of the pine bast scale infestation in the United States ca 1971 (Bean and Godwin, 1971).

The coccinellid *Harmonia axyridis* Pallas (invasive in the United States but also promoted as a biological control agent, see Tedders and Schaefer [1994]) feeds on this scale and is now found throughout the pest's range in the northeastern United States. Effects of *H. axyridis* on the scale in Connecticut were studied (McClure, 1983c), including field releases of the predator in sleeve cages onto scale-infested branches (McClure, 1987). In field sleeve cages predation on scale eggs, cysts, and adults was high (>80%), but was significantly lower if scales were predominantly first instars concealed beneath pine bark. Freely released adults of this predator dispersed and no definitive results were obtained on its ability to suppress bast scale density over a whole generation under natural conditions.

In Tennessee, USA, traps baited with pheromones of *Matsucoccus* species attracted the predatory bug *Elatophilus inimica* Drake & Harris and the brown lacewings *Hemerobius stigma* Stephens and *Hemerobius stigmaterus* Fitch (Nelson et al., 2002 [2001]; Mendel et al., 2004), suggesting that these predators might be somewhat specialized as predators of *Matsucoccus* scales.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

The native range of this scale is believed to be Japan (McClure, 1983a).

Areas Surveyed for Natural Enemies

Natural enemies of pine bast scale have been studied in Japan (McClure, 1986ab) and China (Cheng and Ming, 1979; Ming et al., 1983; McClure, 1983c) (see below) but no attempts have been made to survey for natural enemies suitable for introduction to the United States.

Natural Enemies in the Native Range or Invaded Areas outside the United States

In China (an invaded area), predation on eggs and young nymphs by the anthocorid *Elatophilus nipponensis* Hiura was a key mortality factor in life tables of a population of the pest (Cheng and Ming, 1979). Introduction of *E. nipponensis* to a new location within China (Soochow) from Nanking in May 1977 controlled pine bast scale at the site of introduction (Cheng and Ming, 1979). The generalist predatory coccinellid *H. axyridis* is believed to suppress this scale's density in China (McClure, 1983c) and Japan (McClure, 1986b). On scale-infested pines in Japan, this coccinellid was the most abundant scale predator (84% of all individuals captured) and caused 97% mortality to the scale in one heavily infested stand (McClure, 1986b). Also, Chai (1998) mentions the following species as predators of *M. matsumurae* in China: *H. axyridis*, *Sticholotis punctata* Crotch (Coleop.: Biphyllidae), *Exochomus mongol* Barovsky (Coelop.: Coccinellidae), *Iridomyrmex anceps* (Roger) (Hymenop.: Formicidae), and *Polyrhachis dives* Smith (Hymenop.: Formicidae). In China, Gao (1984) reported the lacewing *Sympherobius weisong* (synonym for *Sympherobius tessellates* Nakahara) as a predator of *M. matsurmurae* and later Gao (1987) observed populations of the anthocorid *Dufouriellus ater* (Dufour) feeding intensively on *M. matsurmurae*. Hu et al. (1978) reports that the coccinellid *Ballia obscurosignata* Liu was an effective predator of pine bast scale in Chekiang and Liaoning Provinces, having 3–4 generations per year on the scale.

In Japan, the coccinellid *H. axyridis* accounted for 70% of the beetles associated with the black pine bast scale (*Matsucoccus thunbergianae* Miller and Park) and was considered to be an efficient predator of that scale (Choi et al., 1995).

ScaleNet (2012) provides a complete list of all recorded natural enemies, as well information on hosts, distribution records, and an index to all other information published on this insect. Mendel et al. (2004) and Branco et al. (2006) showed that several groups of predators were attracted to the pheromones of *Matsucoccus* scales, including that of *M. matsumurae*. Groups of predators responding to bast scale pheromones included flower bugs in the genus *Elatophilus,* neuropterans in the genera *Hemerobius* and *Sympherobius,* and some coccinellids. Species trapped varied by region (Israel, western Europe, the United States) and scale species. Some predators came to pheromones of all scales tested, others to just some.

Host Range Test Results

No species have been proposed for introduction to the United States; no host range testing has been done.

Releases Made

No natural enemies have been imported into the United States for control of pine bast scale; however, the generalist coccinellid *H. axyridis*, imported for biological control of aphids (Tedders and Schaeffer, 1994) also attacks this scale.

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

In China, the anthocorid *E. nipponensis* was successfully moved and established at a new site and provided control (Cheng and Ming, 1979). In the United States, the coccinellid *H. axyridis* was predicted by McClure (1986b) to control pine bast scale and this predator is now abundant in the region of the United States where pine bast scale is found. However, no definitive evaluations of the ladybird's impact on the scale have been carried out. Doing so would provide important information on the current status of the biological control and current pest status of this scale.

Nontarget Effects

No species of natural enemies have been introduced for the control of pine bast scale in the United States, but *H. axyridis*, introduced for aphid control, has caused important nontarget impacts on native ladybird beetles, and the impacts have been well documented (e.g., Koch, 2003).

Recovery of Affected Tree Species or Ecosystems

The current status of red pine in areas infested with pine bast scale should be re-evaluated to determine if the severity of this infestation has declined following the invasion of *H. axyridis*.

Broad Assessment of Factors Affecting Success or Failure of Project

No importations against this species were conducted. The generalist predator *H. axyridis* is now present in bast scale-infested areas and its ability to control this pest should be assessed. The literature on natural enemies of *M. matsumurae* cited only predators, and surveys in the native range for parasitoids attacking pine bast scale should be conducted, even though no parasitoids have been reported attacking any member of the genus.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Information on the biology of *H. arxyridis* is available (Koch, 2003).

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XXVIII Beech Scale

(*Cryptococcus fagisuga* Lindinger) (Hemiptera: Eriococcidae)

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DESCRIPTION OF PEST

Taxonomy

Synonyms of beech scale, *Cryptococcus fagisuga* Lindinger, include *Cryptococcus fagi* Douglas and *Cryptococcus fagi* (Baerensprung). This species is in the family Eriococcidae (Cook et al., 2002; Cook and Gullan, 2004). A molecular analysis by Gwiazdowski et al. (2006) suggested that this species forms a clade with at least two other species placed in the same genus (*C. nudatus* Brittin, *C. williamsi* Kosztarab and Hale) and two other taxa from different genera (*Pseudochermes fraxini* [Kaltenbach] and *Madarococcus totarae* [Maskell]). One species, presently in the genus *Cryptococcus, C. ulmi* Tang and Hao, did not group with this clade, and two other species, *C. aceris* Borchsenius and *C. integricornis* Danzig, were not included in this study.

Distribution

Beech scale invaded North America via Nova Scotia about 1890 (Hewitt, 1914). It is now widespread in Nova Scotia and New Brunswick, Canada, and New England, New York, and northern parts of Pennsylvania and New Jersey, USA, with isolated infestations in Michigan and in the southern Appalachian Mountains in parts of Tennessee and North Carolina, USA (Northeast Area Forest Service, 2005) (Fig. 1). See Wainhouse and Gate (1988) and Morin et al. (2007) for information on the historical spread of beech scale in the northeastern United States and adjacent parts of Canada. In Europe, beech scale is widely distributed, especially in northern and central parts of the continent (Hoy, 1963; ScaleNet, 2012), from the U.K. to Bulgaria. It is also present in the Caucasus Mountains of Georgia (personal observation). In Asia it is known from Turkey, Iran, and Azerbaijan (ScaleNet, 2012), but is not known from East Asia (see Gwiazdowski et al., 2006) or South Asia.

Damage

Type Beech bark disease in American beech is initiated by the arrival of the invasive beech scale. In what Houston (1994a) called “phase 1,” scale densities rise sharply shortly after a new stand in infested. By themselves, scales slow tree growth; however, because they do not damage the cambium, they do not kill the tree. The native fungus *Neonectria galligena* (Bresadola) (a generalist pathogen attacking a variety of hardwoods) soon infects scale-infested trees, using bark lesions caused by scale feeding to enter tree tissues. A second pathogen, formerly given as *Neonectria coccinea* var. *faginata* (Lohman, Watson and Ayers), but now considered a distinct species, *Neonectria faginata* Castlebury et al. (Castlebury et al., 2006) (known only from North America) eventually invades the stand and largely replaces *N. galligena*. The combined effect of the scale and these pathogens gradually kills most beech stems greater than 25 cm in diameter (Houston, 1994a) (Fig. 2). The growth rate of scale-infested trees is suppressed earlier than the external signs of infestation would suggest. The proportion of internally defective wood better predicts reduction in growth rates than do external cankers (Gavin and Peart, 1993).

Unlike other beech species, American beech re-sprouts from its roots (Houston, 1994a), at least in some areas, which remain alive as stems are killed by beech-bark disease.

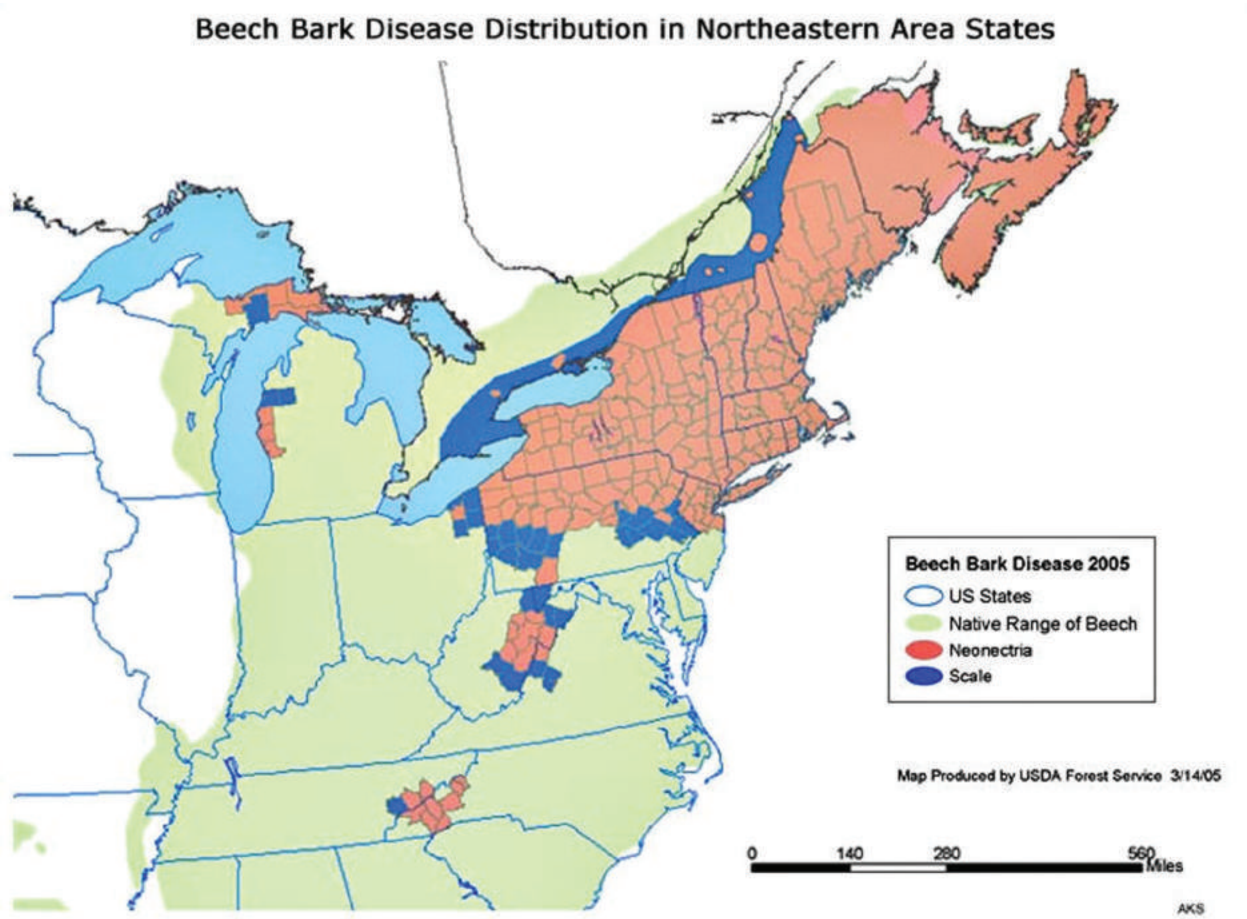

Figure 1 Distribution of beech scale, *Cryptococcus fagisuga*, and its associated invasive pathogen in North America in 2005, following its introduction in about 1890 in Halifax, Nova Scotia (Northeast Area, Forest Service 2005).

Figure 2 Beech trees in forest killed by beech bark disease. Joseph O'Brien, USDA Forest Service, Bugwood.org.

This leads to the formation of thickets of beech saplings, all of susceptible genotypes. Symptoms or signs of beech bark disease include the scale on the bark (Figs. 3, 4), bark cracking (Fig. 5A), bark exudates (Fig. 5B), discoloration of the sapwood (Fig. 5C), and as infections mature, the red fruiting bodies of the *Neonectria* fungus emerging from the bark (Fig. 5D). The increase in bark cankering, which is correlated to scale density, is negatively related to rainfall in the fall of the previous year and to extreme cold in the preceding winter (Houston and Valentine, 1988).

Extent Most American beech (99%) lack resistance to beech bark disease. Since the scale's introduction to Nova Scotia, an epidemic has moved south and west killing most beeches in infested stands (Hewitt, 1914; Hawboldt, 1944; Houston, 1994ab; O'Brien, 2001). In New Hampshire, in the 1950s, 80–90% of beech trees were infested with scale and in unmanaged stands today well over 60% of the total

Figure 3 Contrasting smooth grey bark of healthy American beech (left) to cracked bark of tree with beech bark disease (right). Joseph O'Brien, USDA Forest Service, Bugwood.org.

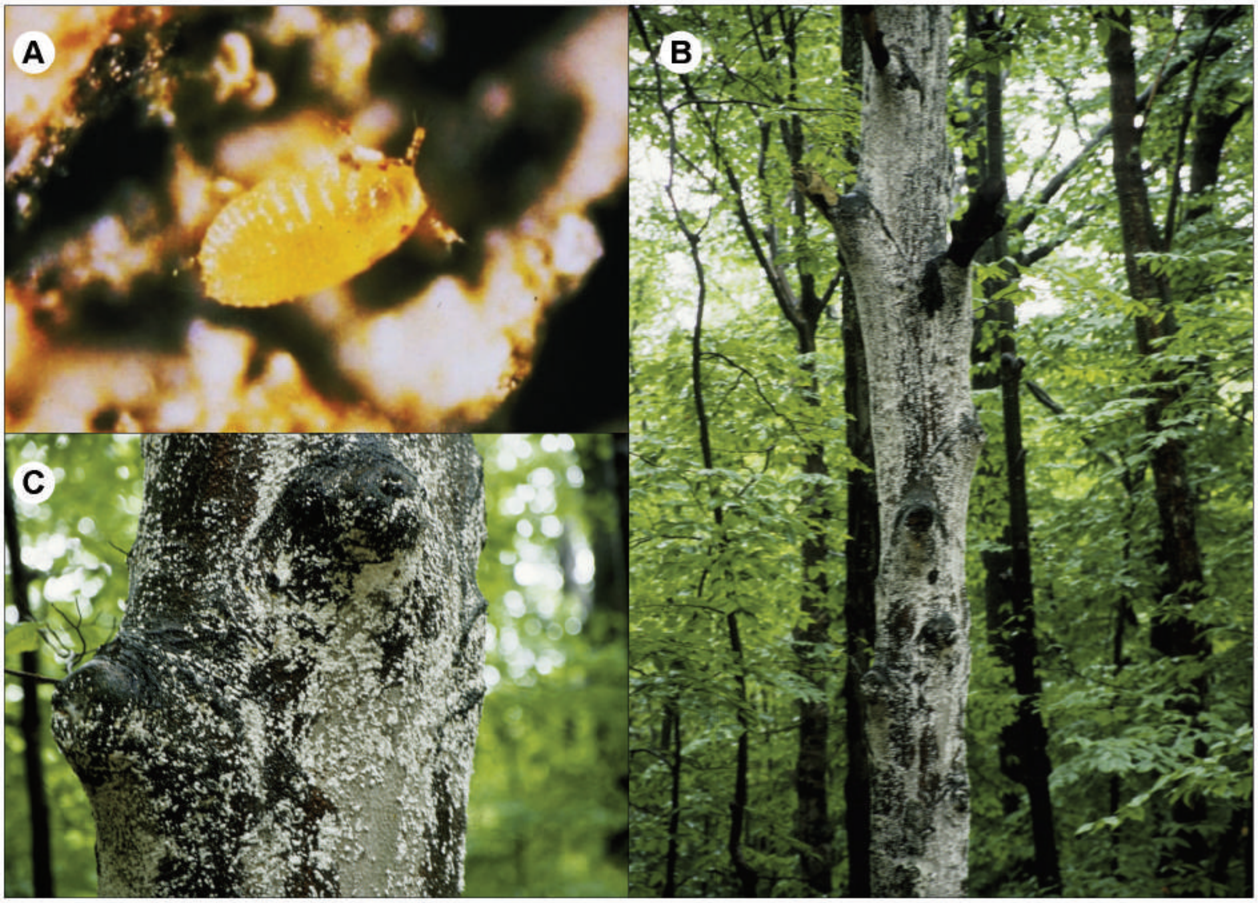

Figure 4 (A) First instar nymph (crawler) of beech scale, *Cryptococcus fagisuga*. (B) View of trunk of American beech infested with beech scale (light colored material). (C) Beech scale on bark of severely damaged American beech. Note lumpy cankers on trunk caused by beech bark disease. Joseph O'Brien, USDA Forest Service, Bugwood.org.

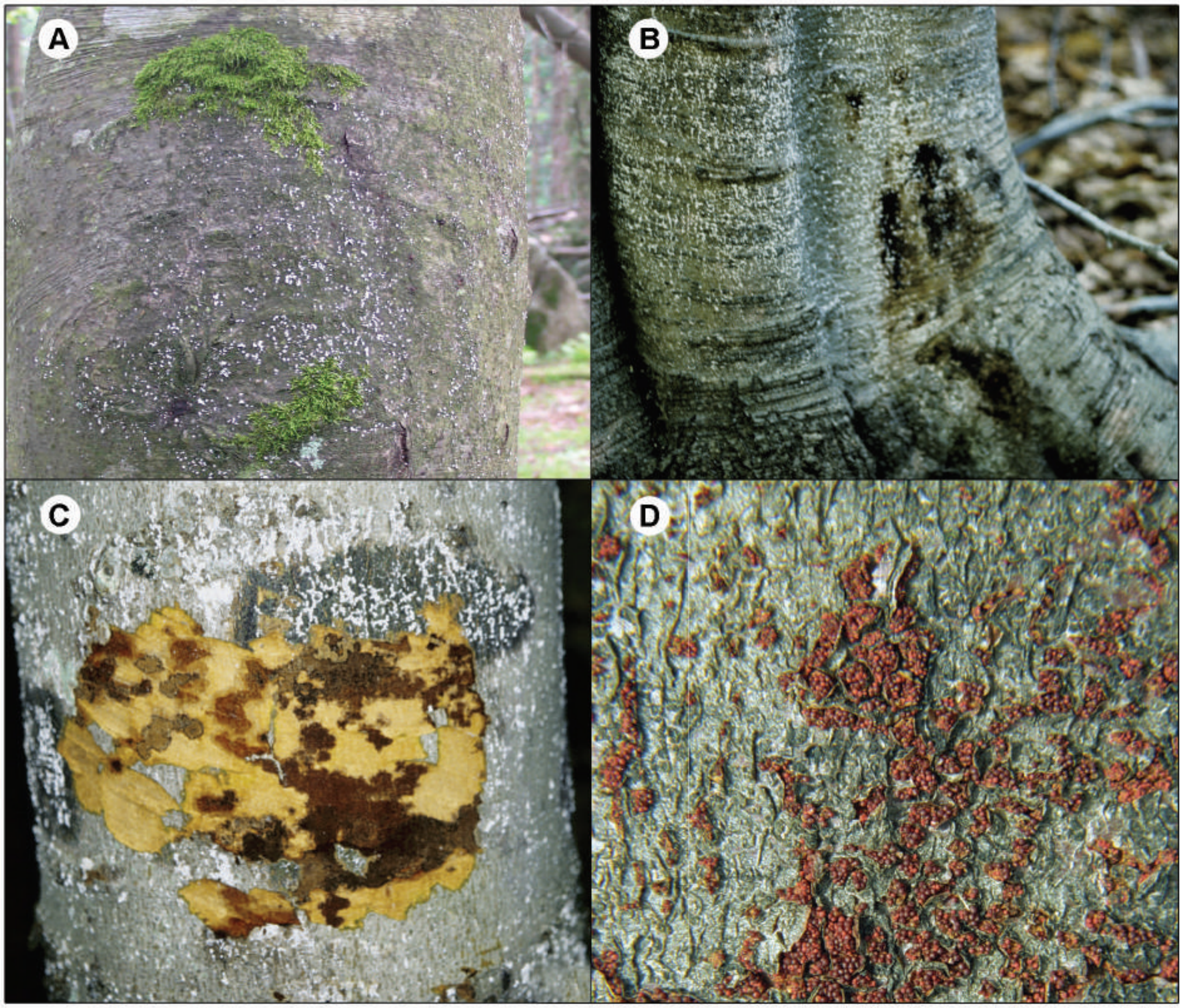

Figure 5 (A) Bark cracking and growth of epiphytes (here moss) on trunk are other signs of beech bark disease. Milan Zubrik, Forest Research Institute, Slovakia, Bugwood.org. (B) Dark, weeping spots are also a sign of beech bark disease. (C) Discoloration under bark due to *Nectria* cankers. (B,C) Joseph O'Brien, USDA Forest Service, Bugwood.org. (D) Orange fruiting bodies of *Nectria* on beech bark. Andrej Kunca, National Forest Centre-Slovakia, Bugwood.org.

basal area of beech consists of stems that are infested with beech scale (Leak, 2006). In the Great Smoky Mountains National Park (North Carolina, 1994–1997), 56–89% of the beech trees were infested with scale and 16–27% of trees died (Wiggins et al., 2004). Losses due to beech scale in Vermont alone, which is about 5% of the infested North American area, were estimated in 1977 as 300 million board feet (Miller-Weeks, 1983). Losses in the whole infested area in Canada and the United States are likely to be at least one order of magnitude (≈3 billion board feet) greater. Trees that are not killed produce wood of a lower grade due to the presence of cankers (Burns and Houston, 1987). Also, losses continue year after year as new growth of healthy beech fails to occur. In some stands, replacement of beech by maple or other species occurs (Lovett et al., 2010) and this change may offset most of this economic loss. However, when stands are dominated by smaller-diameter beech re-grown from the roots of dead trees, losses would continue to accrue. Additionally, scale infestation lowers seed production by beech, affecting both tree reproduction and the availability of this seed resource for small mammal populations (Rosemier and Storer, 2010).

Biology of Pest and Associated Pathogens

Beech scale is best known in western Europe and North America, where it is univoltine and feeds on the bark of several species of *Fagus*. In North America, the only native beech is *Fagus grandifolia* Ehrh. In the northeastern United States, beech scale overwinters as settled crawlers. Development to second instars occurs in the spring (April to June) followed by adults (May to September), although stages overlap widely (Wainhouse and Gate, 1988). However, in Europe, in the Caucasus Mountains of Georgia, the adult females are present and ready to oviposit in April, suggesting that the pest may be multivoltine there or if univoltine, has desynchronized and overlapping life stages.

The species consists of only females, both in North America and Europe. In North America, female scales lay about 50 eggs each over their lifetime (Wainhouse and Gate, 1988). Oviposition occurs from June to September in North America (Houston, 1994a). Scales show a preference to infest smaller trees (11–31 cm DBH) (Fernandez and Boyer, 1988), but damage, which is cumulative, is greatest on larger trees. Scale feeding induces bark cracking, which allows entry of *Neonectria* fungal pathogens, which infest and slowly kill the tree. Two *Neonectria* species occur in North America, *N. faginata* and *N. galligena*. The former is the more significant pathogen and was once believed to be invasive in North America, being more closely related to European than American populations of its closest relative, *Nectria coccinea* var. *coccinea* (Mahoney et al., 1999). Currently, this species is known only from North America (Castlebury et al., 2006) and thus may be native, although not necessarily.

Establishment of scale crawlers on individual American beech trees is affected by both the tree's level of resistance and by bark epiphytes (lichen and moss). About 1% of American beech trees are highly resistant to scale (Houston and Houston, 1987), but because of the clonal nature of American beech, resistant trees are usually clumped. Bark of resistant American beech has a lower concentration of some amino acids and lower total amino nitrogen than bark of susceptible trees (Wargo, 1988), and this is believed to constrain scale growth. Bark epiphytes may favor or deter settling of scale crawlers. Some mosses and crustose or foliose lichens provide favorable habitat for scales on American beech (Ehrlich, 1934; Houston, 1983a); however, other crustose lichens strongly inhibit scale establishment (Houston 1983a).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

The only North American congener of beech scale is *C. williamsi*, which occurs in New England, New York, Viriginia, Iowa, Ontario, and Quebec on sugar maple (*Acer saccharum* Marshall) and red maple (*Acer rubrum* L.) (ScaleNet, 2012).

Native Natural Enemies Affecting the Pest

In the United States, no parasitoids and no specialized predators of beech scale have been found (Houston, 1983b). The coccinellid *Chilocorus stigma* Say is commonly seen feeding on beech scale in the United States, but is not believed to have any effect on scale density (Mayer and Allen, 1983).

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

Historically, it was assumed that western Europe was the native home of beech scale, because it was widely distributed there and was known to have been introduced to North America from there. However, several factors suggest that western Europe itself may have been the subject of an earlier invasion by beech scale. As described below, one impediment to Europe as the scale's native range, is that in Europe the natural enemies of beech scale are all generalist predators, and parasitoids are unknown, which is unusual for members of the Hemiptera in their native ranges (Schwenke, 1972; Baylac, 1980, 1986). While it is true that beech scale has a small adult body size (0.5–1.0 mm body length [Kosztarab, 1996]), this is insufficient to explain the absence of parasitoids, because beech scale's congener *C. williamsi* (0.61–0.86 mm) is attacked by parasitoids (*Coccophagoides* sp., Eulophidae) (Kosztarab and Hale, 1968). Also, Gwiazdowski et al. (2006) states, there is actually considerable evidence from the literature of "first arrivals" and/or spreading beech scale in various European locations, which would not be the case for a native insect in, for example, (i.e., England [M'Intosh, 1849], France [Viennot-Bourgin, 1935], Holland [Anon., 1921], Ireland [Anon., 1926]). Indeed, the mechanism for such arrival (movement of plant material) is suggested by the fact that, in seven cases the first record of the scale in a region was at a botanical garden or park, that is, institutions likely to import foreign plant material in (i.e., Nova Scotia [Hewitt, 1914], Massachusetts [Ehrlich, 1932], Ohio [Houston, 1994a], Ireland [Carpenter, 1903], Scotland [Ehrlich, 1934], Germany [Baerensprung, 1849], and Spain [Soria et al., 1993]. Given that genetic evidence suggests the native range of beech scale is in southeastern Europe (Bulgaria), Turkey, or the Caucasus region, movement of oriental beech (*Fagus sylvatica orientalis* Lipsky), native to that region, was the likely mechanism of spread. Beech scale is recorded from that host in Iran, Turkey, and the Caucasus Mts. (Adeli and Soleimanì, 1976; Van Driesche and Japoshvili, 2012).

Hypotheses about how to identify a species' native range include (1) the location where the host plant group evolved, (2) the location where the closest relatives of the pest species occur, and (3) the location where the pest species shows the greatest genetic diversity. These are discussed in detail by Gwiazdowski et al. (2006), but briefly the first hypothesis would point to East Asia (China, Japan), which is the evolutionary area of origin of the genus *Fagus* (Peters, 1997). However, However, extensive surveys on two *Fagus* species in Japan and four species in China (Gwiazdowski et al., 2006) failed to detect beech scale at any surveyed location or on any host species.

The second area-of-origin hypothesis suggests that one should look to the region where the congener species of the pest is most abundant. Other members of *Cryptococus* (or the glade as studied by Gwiazdowski et al. [2006]) are found in several widely separate regions (Miller et al., 2011): *C. williamsi* (eastern North America), *M. totarae* and *C. nudatus* (New Zealand), *P. fraxini* and *C. aceris* (in Europe), and *C. integricornis* (in the Russian Far East). Based on genetic information, the Chinese member of the genus (*C. ulmi*) seems to be misplaced taxonomically and is not a *Cryptococcus* species. In terms of deep evolutionary time, the clade within which these species are nested appears to have had its origin in New Zealand; however, the target pest species is not known from there, so this is not an area of origin for the species.

The third hypothesis about native ranges is that they are where the species shows the greatest genetic diversity. This was explored for beech scale by Gwiazdowski et al. (2006) and the haplotype diversity of beech scale was greatest in Turkey and the Caucasus Mountains region.

Areas Surveyed for Natural Enemies and Natural Enemies Found

Western and central Europe Surveys for natural enemies in western and central Europe have produced results similar to surveys in North America. That is, no parasitoids have been detected and most predators observed have been generalist feeders. In France, beech-scale predators include the coccinellids *Exochomus quadripustulatus* (L.) and *Chilocorus renipustulatus* Scriba, the anthocorid *Temnostethus gracilis* Horváth, and several lacewing species (Baylac, 1980). A somewhat more specialized predacious fly, *Lestodiplosis* sp., also was observed in France, but its population increased too slowly to control the scale (Baylac, 1986). In Germany, the coccinellids *E. quadripustulatus, C. renipustulatus,* and *C. stigma* feed on beech scale (Schwenke, 1972).

Eastern Europe, Turkey, and the Caucasus Mountains region In 2002, Marc Kenis (CABI) conducted a survey in eastern Europe (Slovakia, Romania, Bulgaria) on behalf of the USDA Forest Service and found the scale throughout the survey region. Natural enemies encountered were limited to generalist predators with the exception of southeastern Bulgaria, where a few scale mummies from which parasitoids appeared to have emerged were found (Kenis et al., 2003). In 2003, Kenis conducted a second survey in Bulgaria and then moved east to Turkey and Georgia (country). No further evidence of parasitism was detected in Bulgaria (from 4000 scales). Scale density was much lower in Turkey and Georgia than in western and central Europe. No parasitism was detected at sites in Turkey, from which 600 scales were collected. In Georgia, only the coastal region near the city of Batumi was surveyed, and over one four-day period in June, about 1200 scales were collected. No parasitoids were detected.

A much more extensive survey was begun in Georgia in 2011. Sites were selected at higher attitudes, over a wider area, and in climatically better-matched locations with good beech forests. Also, those parts of southern Georgia that escaped the effects of glaciation, and thus are likely to have a richer native fauna, were included. Survey sites were selected in both the Greater Caucasus Mts. and in the lesser Caucasus Mts. in southern Georgia. In addition, the densities of beech scale (# per 100 cm^2) in Georgia were measured at six sites and compared to three sites in Massachusetts. Densities in Georgia were found to be only 2% of that in Massachusetts (63.6 vs. 1.4 scales per 100 cm^2) (Van Driesche and Japoshvili, 2012), strongly supporting the idea that either oriental beech is highly resistant, or natural enemies are effectively restricting scale density in Georgia. Future work in Georgia will include a cage exclusion study designed to compare host tree resistance against natural enemies as potential factors responsible for the low density of beech scale in the Caucasus Mts.

CONCLUSIONS

Beech scale has degraded American beech over a large part of its range and continues to spread and kill trees. Europe is not likely to be the native range of this pest, but rather this is likely in Bulgaria, the Caucasus Mountain Region (Georgia), Turkey, or Iran. Comparative surveys in Georgia (country) and Massachusetts (USA) have shown beech scale density in the invaded range to be 45 times greater than in its native range (Georgia).

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XXIX Redbay Ambrosia Beetle

(*Xyleborus glabratus* Eichoff) (Coleoptera: Curculionidae)

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DESCRIPTION OF PEST

Taxonomy

The redbay ambrosia beetle, *Xyleborus glabratus* Eichoff, (Fig. 1) and its associated fungus *Raffaelea lauricola* T.C. Harr., Fraedrich & Aghayeva are exotic species, recently invasive to the United States. Together, they cause a vascular wilt disease that is highly destructive to some species in the Lauraceae (Fraedrich et al., 2008). *Xyleborus glabratus* is a member of the subtribe Xyleborina, within the subfamily Scolytinae. No synonyms are reported (Rabaglia et al., 2006).

Distribution

Xyleborus glabratus is native to Asia, recorded from Bangladesh, India, Myanmar (Burma), and Taiwan (Rabaglia et al., 2006). Harrington et al. (2011) reported capturing it in Japan. The first record in the United States occurred at Port Wentworth near Savannah, Georgia, in 2002, followed by Hilton Head Island, South Carolina, in 2004. The current distribution of laurel wilt and the redbay ambrosia beetle is concentrated in parts of Florida, Georgia, and South Carolina (Fig. 2). Outlying sites in Mississippi, western Florida, and the northern part of South Carolina suggest that human movement of infested wood is also spreading the beetle.

Damage

Type This invasion has the potential to cause ecological and economic losses.

Ecological losses These can result through severe damage to native redbay (*Persea borbonia* [L.] Spreng.) and swampbay (*Persea palustris* [Raf.] Sarg.) trees. These aromatic, broadleaf evergreens are usually of small to medium size, although rare large individuals may reach diameters in excess of 100 cm. Some taxonomists do not consider redbay and swampbay to be distinct species;

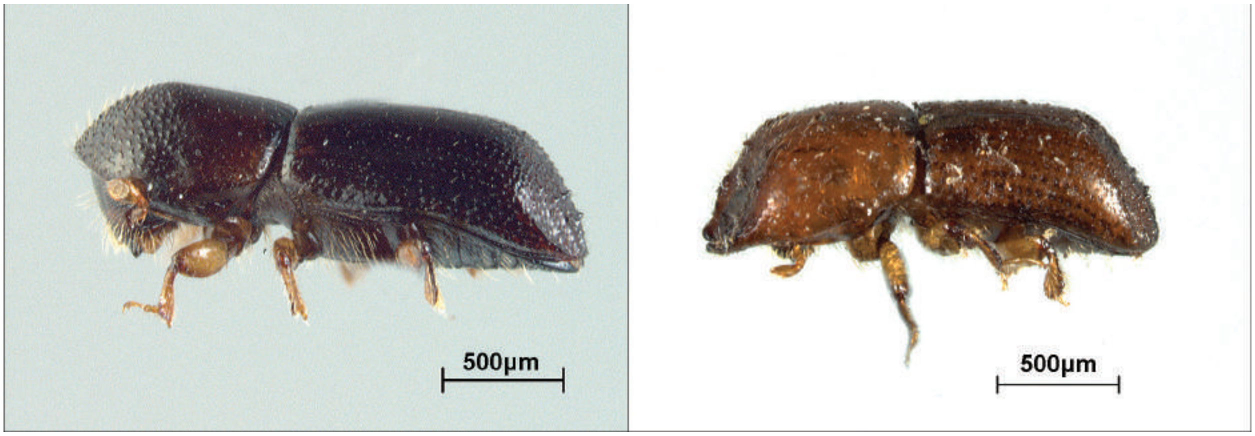

Figure 1 Female (left) and male redbay ambrosia beetle, *Xyleborus glabratus*. J. L. Hanula.

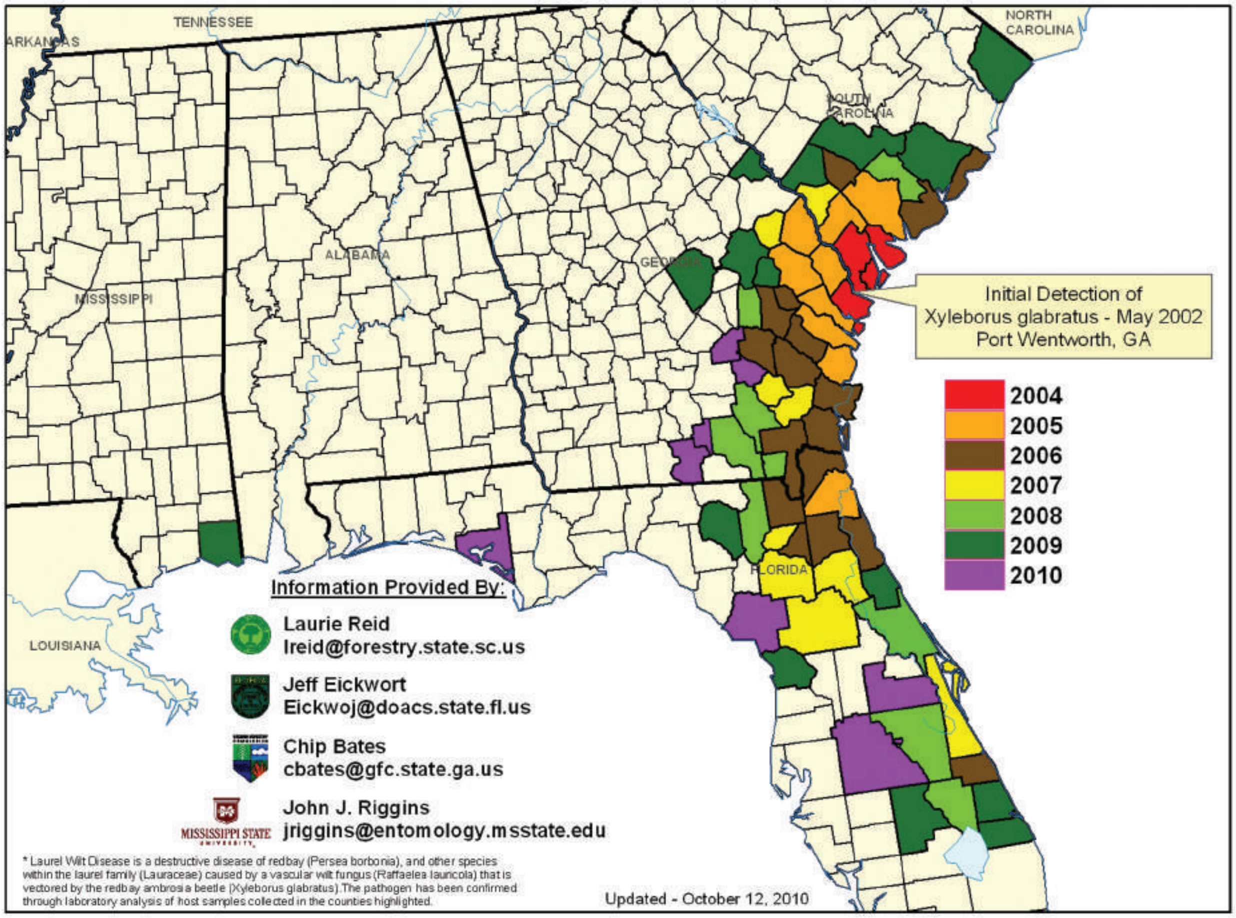

Figure 2 Distribution of redbay ambrosia beetle and laurel wilt by county over time. http://www.fs.fed.us/r8/foresthealth/laurelwilt/dist_map.shtml).

these species, in combination with silkbay (*Persea borbonia* [L.] Spreng. var. *humilis* [Nash] L.E. Kopp), are sometimes collectively referred to as "redbay." All appear to be equally susceptible to laurel wilt. Redbay (broadly defined) dies within a matter of weeks to a few months after attack by the redbay ambrosia beetle and infection with the laurel wilt fungus. The pathogen moves systemically in the xylem, causing dark vascular discoloration (Fig. 3) and eventual wilting. Within five years of initial infestation, almost all redbay and swampbay trees greater than 2.5 cm diameter die, although numerous seedlings and stump sprouts commonly survive in infested areas. Lower density populations of the beetle persist in areas where mature redbays have been eliminated (Hanula et al., 2008), so it is likely that as these seedlings and saplings mature they will also be attacked. However, redbay are abundant as small bushes or shrubs in pine forests that receive frequent prescribed burns. Due to the persistence of this class of smaller individuals, the extinction of redbay as a species seems unlikely, although it is uncertain if it ever will reach tree status again.

Very little is known about the ecological role of redbay trees, although they are or were one of the most common trees on barrier islands and in the transitional zone between xeric upland and bottomland swamps or wetlands. According to Brendemuehl (1990), redbay are often associated with the rich, moist, mucky soils along swamp borders, but they also can grow in xeric sites, such as sandy soils associated with old dunes. Redbay is a major component of the Sweetbay-Swamp Tupelo-Redbay cover type (Society of American Foresters Type 104). It is also common in the loblolly pine-hardwood (Type 82), pond pine (Type 98), baldcypress-tupelo (Type 102), and water tupelo-swamp tupelo (Type 103) cover types, and is a minor component of several others (Brendemuehl, 1990). Its overall role in these forests is unknown, but it does serve as the primary host for the palamedes swallowtail (*Papilio palamedes* [Drury]), a common swallowtail butterfly on the

Figure 3 Dark discoloration in the outer sapwood of a redbay *(Persea borbonia)* affected by laurel wilt. Albert Mayfield, USDA Forest Service, Bugwood.org.

coastal plain (Minno et al., 2005). Because small seedlings, saplings, and stump sprouts can serve as host material for the larvae, the butterfly is not likely to disappear, although in many forests the amount of foliage available has been drastically reduced. The effect this will have on numbers of the palamedes swallowtail has not been studied. Redbay (broadly defined) is also the only known host of the gall-forming redbay psyllid (*Trioza magnoliae* [Ashmead]) (Hall, 1999). Galls of these psyllids are so ubiquitous on both immature and mature trees that they can aid in recognition of redbay (Nelson, 1994). The effect of losing mature redbay trees on populations of the psyllid is unknown: They will likely persist but perhaps at lower population levels. Redbay flowers are primarily pollinated by bees, so losing all mature redbay trees in forest tracts is likely to affect bee species that use redbay pollen. Redbay fruits are eaten by songbirds and wild turkey. These fruits are ranked fifteenth out of 63 fruits in dietary importance for these birds, on a volumetric basis (Brendemuehl, 1990).

In addition to redbay and swampbay, redbay ambrosia beetle and laurel wilt also kill sassafras (*Sassafras albidium* [Nutt.] Nees). Reports of sassafras mortality are increasing (C. Bates, pers. comm.) as the beetle reaches the edge of the range of redbay in Georgia, USA. There are questions regarding the attractiveness of sassafras to the beetle (Hanula et al., 2008), and it is uncertain if sassafras will sustain beetle populations as large as those on redbay. One factor likely to influence the spread of *X. glabratus* in sassafras is this tree's more widely scattered distribution and smaller size in the Atlantic Coastal Plain and Piedmont, in contrast with higher densities and larger trees found in the southern Appalachian mountains and northward (Koch and Smith, 2008). A second factor that might influence the beetle's spread on sassafras is that sassafras wood appears to be relatively unattractive to *X. glabratus* (Hanula et al., 2008), and when beetles do attack it, brood production is lower than in redbay (Mayfield and Hanula, 2012). These attributes, combined with the lower densities of sassafras, could reduce the natural spread of *X. glabratus* into the Piedmont beyond the range of redbay. Very little is known about ecological role of sassafras, although it might be an important pioneer species aiding in restoration of depleted soils (Auten, 1945).

The laurel wilt fungus has been recovered from wilted pondspice (*Litsea aestivalis* [L.] Fern.) and southern spicebush (*Lindera mellisifolia* [Walt.] Blume), both of which are in the Lauraceae (Fraedrich et al., 2008). *Xyleborus glabratus* has been recovered from diseased pondspice (AEM unpublished data), but not from southern spicebush. Pondspice is a shrub that grows to 3 m in height. It is listed as endangered in Florida and Maryland and threatened in Georgia (USDA, Natural Resource Conservation Service, 2012). Southern spicebush is a low shrub rarely exceeding 2 m in height. It is on the federal list of endangered species. Although laurel wilt was recovered from wilted stems of both species in the field by Fraedrich et al. (2008), additional instances of infected pondberry occurring in areas of widespread redbay mortality have not been reported. Laurel wilt symptoms have subsequently been observed on pondspice stems at a number of locations in Florida, but pathogen confirmation was attempted at only one of these sites (Surdick and Jenkins, 2009, 2010).

Both the redbay ambrosia beetle and laurel wilt fungus have been recovered from avocado (*Persea americana* Mill.) trees in Florida (Mayfield et al., 2008ab), and avocado wood is as attractive to the beetles as redbay wood (Hanula et al., 2008). Avocado is native to Central America and Mexico (USDA GRIN, 2012) and is widely planted throughout tropical and subtropical regions of the world, including southern California and the Caribbean Islands. Although not native to Florida, avocado trees are widely planted as ornamental fruit trees throughout much of the state and it is an economically important fruit crop in the southern tip of Florida (see below), the Caribbean islands, California, and Mexico. This beetle, should it spread westward to Mexico and into Central America, could have catastrophic consequences for this industry and could strongly affect subtropical species dependent on avocado.

Laurel wilt also has been recovered from camphor trees (*Cinnamomum camphora* [L.] Sieb.), an invasive species native to Asia (Smith et al., 2009a). Although Smith et al. (2009a) did not recover redbay ambrosia beetle from the trees, it is most likely the vector, because the camphor trees were in areas with extensive redbay mortality and high beetle populations. In this case, redbay ambrosia beetle and laurel wilt could have a positive ecological impact since camphor trees are considered invasive in Florida (Florida Exotic Pest Plant Council, 2009) and other areas. However, unlike redbay, camphor trees do not exhibit rapid decline and death but only localized wilt symptoms on one or a few branches (Smith et al., 2009a). Thus, its ability to rid forests of this invasive is probably going to be limited. Recent field trials have demonstrated that cut camphor wood is attractive to *X. glabratus* (Mayfield and Hanula, 2012); however, it is a poor host for brood production.

Camphor trees' ability to survive attack suggests some form of resistance or tolerance to the fungus, possibly derived through co-evolution in their native range. The ability of laurel wilt to infect and kill a wide variety of trees in the southeastern United States suggests that trees lacking a similar co-evolutionary history are likely to be equally susceptible. Thus, the ability of redbay ambrosia beetle and laurel wilt to cause harm to Lauraceae throughout the world should not be underestimated.

Economic losses These vary with the species of tree affected. Redbay beetle and laurel wilt kill redbay, sassafras, and avocado trees. Redbay trees have minor economic value. Larger trees mixed in with more economically important tree species are often cut during harvest and sold for pulpwood or cut up for lumber (for pallets, etc). Redbay wood is also used for cabinetry, but only on a very limited basis (Brendemuehl, 1990). Like redbay, sassafras trees are not widely used for pulp or lumber. For both species, the greatest economic impact may be through reduced property values for homeowners who have either species as ornamental plantings near their homes and incur the cost of removing dead trees. The latter is an additional cost for parks, where redbay trees occur along trails or in campgrounds, or utility companies that may have trees fall across their lines.

The greatest potential economic impact of redbay ambrosia beetle and laurel wilt could be to the multimillion-dollar avocado industry in south Florida and, potentially, California. Homeowners with dooryard avocados could experience similar losses and costs as those with redbay trees. Evans et al. (2010) estimated that losses to the avocado industry due to redbay ambrosia beetle and laurel wilt could range from $356 million if nothing is done to $183 million if damage control is 50% effective. Even ignoring reduced property values and management costs associated with tree removal (a component of this estimate), the adverse impact on the regional economy from lost avocado production alone could range from $54 million if nothing is done to $27 million if treatments are 50% effective. However, these estimates are based on the assumption that all avocado varieties will prove to be completely susceptible to laurel wilt, which may not turn out to be the case. For example, Mayfield et al. (2008b) reported that only one of five cultivars in their test wilted and died after exposure to *X. glabratus* in a cage experiment, although *R. lauricola* was recovered from all five. In addition, avocado trees from Florida have been grown successfully in Taiwan since the early 1900s (Ling, 2003) in the presence of a local native population of *X. glabratus* carrying *R. lauricola* (Harrington, et al. 2011). There are no reports of a comparable wilt disease in avocados in Taiwan or elsewhere in Asia. Therefore, the situation may not be as dire as a total loss of the Florida crop. The discovery of dead and dying avocado trees in homeowner yards is cause for concern (Mayfield et al., 2008a) and, more recently, Ploetz et al. (2011) reported that avocado cultivars commonly used in Florida were moderately susceptible to laurel wilt. Thus, if the beetle can vector the fungus efficiently among avocado trees, avocado production in Florida may be harmed.

Extent of losses Three studies have examined the impact of redbay ambrosia beetle and laurel wilt on redbay trees in southeastern U. S. forests. Fraedrich et al. (2008) monitored 132 redbay trees ranging in size from 2.5 cm to >20 cm diameter at 1.4 m above ground (DBH) from July 2005 (when mortality was still relatively low) to January 2007. The largest trees died most rapidly, with 100% mortality of trees >20 cm by January 2006. Other size classes were infected and killed over a longer period of time. Over 90% of trees >5 cm were dead by the end of the study, while 20% of trees in the 2.5–5 cm size class were still living.

Goldberg and Heine (2009) compared forest composition on a barrier island in northeastern Florida in 2008 to a previous study on the same island conducted in 1983 (Stalter and Dial, 1984). By 2008, there was a 32% decrease in mature redbay trees.

In another study, Hanula et al. (2008) estimated beetle and tree densities at seven locations, ranging from areas outside the known infestation to the areas where the beetle was first discovered. Live redbay trees >2.5 cm diameter densities were 4–9 trees/ha in the Savannah, Georgia area, where the beetle had been present the longest, compared to >460 tree/ha at the site outside the infested area. Numerous dead or dying trees in the other study plots indicated that the high number of trees at the un-infested site was probably consistent for areas of the lower coastal plain and barrier island forests, where redbay thrives. Therefore, based on these data we estimate that 95–98% of the trees have been killed in the Savannah area study sites. Koch and Smith (2008) provided tree density maps for redbay and sassafras based on USDA Forest Service, Forest Inventory and Analysis data. Although their results take into account all forest types within redbay's range, based on the extensive forested area likely to be affected by redbay ambrosia beetle and laurel wilt it is safe to say that 100 million or more redbay trees will be killed if the infestation spreads throughout the tree's range.

Biology of Pest

The redbay ambrosia beetle attacks and bores into living trees and inoculates the sapwood with *R. lauricola*, which causes a vascular wilt disease known as laurel wilt (Fraedrich et al., 2008). Laurel wilt is lethal to redbay and swampbay: it has killed thousands of these trees in Florida, Georgia, South Carolina, and Mississippi, and landscape avocado trees in Florida (Mayfield, et al. 2008a) and sassafras trees in Florida, Georgia, and South Carolina (Fraedrich et al., 2008; Smith et al., 2009b).

Xyleborus glabratus is a typical ambrosia beetle but has some unique characteristics. Like other ambrosia beetles, it bores into the xylem or wood of dead and dying trees and lays its eggs in the tunnels it creates. During excavation, the tunnels are inoculated with an ambrosia fungus from mycangia situated at the base of each mandible (Fraedrich et al., 2008). The mycangia can contain up to four species of *Raffaelea* fungi at one time, and a total of six different species have been isolated from redbay ambrosia beetle mycangia (Harrington and Fraedrich, 2010). However, Harrington and Fraedrich (2010) note that it is unusual for ambrosia beetles to have so many fungi associated with them. *Raffaelea lauricola* was isolated from all but one of the beetles studied (Harrington and Fraedrich, 2010), which suggests it is the ambrosia fungus on which larvae feed. This is also the only known case where a mycangial fungus of an ambrosia beetle causes a lethal wilt disease (Fraedrich et al., 2008; Harrington et al., 2008; Harrington and Fraedrich, 2010).

Little information is available on the natural history of redbay ambrosia beetle from its native range. Rabaglia et al. (2006) (and references therein) list *Litsea elongata* (Nees) Benth. et Hook. f., *Lindera latifolia* Hook. f., *Shorea robusta* C. F. Gaertn., *Phoebe lanceolata* Wall. ex Nees) Nees, *Lithocarpus edulis* (Makino) Nakai, and *Leucaena glauca* (L.) Benth as hosts in Asia; however, it is unknown whether the beetle attacks these species while they are living or only after they die. There is no information to indicate that the fungus is lethal to these Asian hosts. The fact that so little is recorded about *X. glabratus* in Asia suggests that its mycangial fungi do not kill trees in its native range. The only life-history information available is based on studies in the southeastern United States, where adult beetles are active throughout the year, although peak flight occurs in late August and early September (Hanula et al., 2008, 2011). Very few beetles were caught from December through

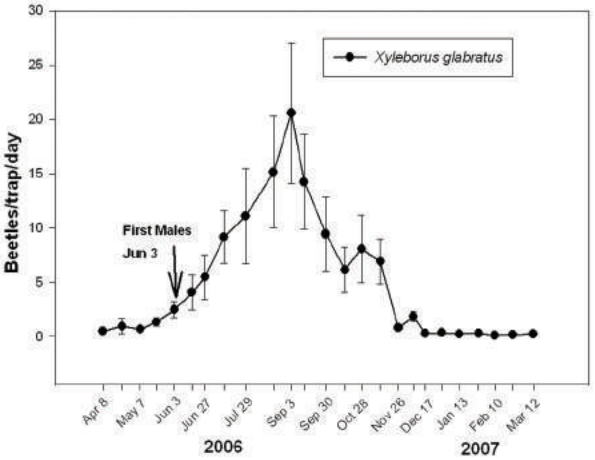

Figure 4 Seasonal arrival of redbay ambrosia beetles to trees infected with the laurel wilt fungus. (Hanula et al., 2008).

March, after which the adult abundance increased until it peaked in early September (Fig. 4, above).

Although adults are active all year, the low numbers in winter suggest that the adult stage may not be the primary overwintering form. Larvae are present in galleries in the winter (JLH, personal observation), but an infested tree cut in late October produced adult beetles in December and January in the laboratory so it is likely that development occurs as long as warm temperatures prevail. Thus, beetles flying in the winter may be newly emerged adults and not overwintering ones. Regardless, healthy trees wounded in late March were attacked and infested within one week (Hanula et al., 2008). Traps hung on trees to capture arriving beetles also caught males, and since males are flightless they most likely came from the trees on which the traps were hung. Based on these first males (Fig. 4), Hanula et al. (2008) suggested that brood development took approximately 56 days. More recently a preliminary effort to rear beetles from the galleries of individual females in logs resulted in initial adult brood emergence 56–63 days after the logs were exposed to attack (JLH, unpublished data), confirming the results from the previous study. This is consistent with other *Xyleborus* spp. (Hanula et al., 2008). Forty-five beetles were produced from one gallery (JLH, unpublished data). Most beetles fly within two meters of the ground, but a few were caught as high 15 meters (Hanula et al., 2011).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

The genus *Xyleborus* contains 20 species found in North America, twelve of which are native (Rabaglia et al., 2006); however, because native ambrosia beetles are rarely pests in North America north of Mexico, little is known about the majority of species. Bright (1968), Furniss and Carolin (1977), Drooz (1985) and Solomon (1995) provide generalized descriptions of the biology of Xyleborini ambrosia beetles, but little information about individual species. Of the species occurring in North America, the most detailed information is available on *Xyleborus dispar* (F.) (invasive) and *Xyleborus celsus* Eichhoff (native). *Xyleborus celsus* attacks dead or dying hickory trees (*Carya* spp.), but is not considered a pest.

Native Natural Enemies Affecting the Pest

No natural enemies of this species have been reported.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

There have been some attempts at controlling insect vectors of plant pathogens, although most targeted species have biological and life-history traits very different from those of redbay ambrosia beetle. One of the earliest reports of a parasitoid apparently suppressing a vector population and subsequently the disease is that of the carrot-willow aphid, *Cavariella aegopodii* (Scopoll), from Europe, which was found vectoring carrot mottle virus in Australia (Stubbs, 1948). The braconid *Aphidius salicis* (Halliday) was introduced in 1962 and reportedly caused dramatic declines in aphid populations, based on aphid trapping data (Hughes et al., 1965). A corresponding decline in disease prevalence also was reported (Clausen, 1978). Waterhouse (1985) cited Stubbs et al. (1983) as stating that carrot mottle virus could no longer be found in Australia. However, Waterhouse's (1985) discovery of carrot red leaf virus in Australia, another virus vectored by *C. aegopodii*, brought into question previous claims of vector suppression by the parasitoid. The discovery of red leaf virus showed that the vector, *C. aegopodii*, was still present and an effective disease vector in Australia. The decline in dwarf mottle virus could not definitely be attributed to the parasitoid introduction, and indeed Büchen-Osmond (2010) suggest that the parasitoid's introduction in 1962 coincided with the use of more aphid resistant/repellent carrot cultivars, which may have caused the declines in aphids and disease prevalence.

In a second case, biological control of the beet leafhopper (*Circulifer tenellus* [Baker]), which vectors a curly top virus of a wide variety of crops (Bennett, 1971; Bayoun et al., 2008), was attempted. Nine egg parasitoids from Iran were imported to California where they were released from 1996 on (Bayoun et al., 2000). Bayoun et al. (2008) sampled beet leafhopper eggs at eight locations and determined that the most commonly recovered parasitoid was a native species. They found no evidence that it or the released species had any significant effect on beet leafhopper populations.

A recent, more successful example is that of glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), that was first discovered in California in 1989 (Sorensen and

Gill, 1996), where it vectored the bacterium *Xylella fastidiosa* (Wells) to many plant species, including many important crops (Purcell, 2010). Releases of the egg parasitoid *Gonatocerus triguttatus* Girault began in 2000 (Pilkington et al., 2005), followed by releases of *Gonatocerus ashmeadi* Girault, *Gonatocerus morilli* Howard, and *Anagrus epos* Girault. It was later determined that *G. ashmeadi* and *G. morilli* had already naturally invaded the area before these releases (Pilkington et al., 2005). Glassy-winged sharpshooter populations in the area were tracked in an organic lemon grove from 2002 to 2006 and found to decline 68% over this period (Hoddle, 2006), in the presence of ~20% egg parasitism each year (Hoddle, 2006). Grandgirard et al. (2009) reported that the parasitoid *G. ashmeadi* caused more than 95% reduction in the density of glassy-winged sharpshooter populations in the Society, Marquesas, and Austral archipelagos of French Polynesia, and that sharpshooter populations remained low in the year following population collapse.

Another important ongoing example of biological control of a vector concerns the Asian citrus psyllid, *Diaphorina citri* Kuwayama and citrus greening. Early biological control efforts against this pest are reviewed by Halbert and Manjunath (2004). On Réunion Island in the Indian Ocean, parasitism by the introduced parasitoid *Tamarixia radiata* (Waterston) was as high as 70% (Aubert, 1987), and was associated with improved citrus production (Aubert et al., 1996). In Florida, suppression of this vector has been less successful (Supriyanto and Whittle, 1991; Toorawa, 1998; McFarland and Hoy, 2001; Michaud, 2004), perhaps because of intraguild predation of mummies by coccinellids (Michaud, 2004). New parasitoid species have recently been imported to California from Pakistan, the native range of the vector. They have been established in the field and evaluations are underway.

Thus far, biological control programs aimed at controlling vectors of disease organisms have had mixed results. In all cases mentioned above, the targets were sucking insects, in which at least some life stages were relatively exposed. In two of those examples, parasitoids contributed to substantial reductions in vector populations, but both cases were on small islands (Aubert, 1987; Grandgirard et al., 2009).

The only biological control effort against an insect vector of a tree pathogen comparable to redbay ambrosia beetle is the case of the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham), a vector of Dutch elm disease, which is caused by the fungi *Ophiostoma ulmi* (Buism.) Nannf. (formerly called *Ceratocystis ulmi*) and *Ophiostoma novo-ulmi* Brasier. The elm bark beetle and Dutch elm disease are similar to redbay ambrosia beetle and laurel wilt, in that inoculation of a tree by a single beetle can result in tree death and the dead tree can then serve as host material for beetle brood development. *Scolytus multistriatus* was first reported in the United States in 1904 near Boston, and subsequently spread across the country. Because of its devastating effect on many city landscapes, a major effort was launched to develop control strategies, including biological control. The biological control of elm bark beetles has been reviewed elsewhere (Van Driesche et al*.,* 1996; Bellows et al., 1998). One braconid parasitoid, *Dendrosoter protuberans* (Nees), was introduced from France (Kennedy, 1970) and became widely distributed throughout much of the United States (Hajek and Dahlsten, 1985). In addition to *D. protuberans*, *S. multistriatus* had a wide variety of other natural enemies (Van Driesche et al., 1996; Bellows et al., 1998), but their impacts on host populations are unknown. For example, Hajek and Dahlsten (1985) reported 67% mortality of elm bark beetle larvae, but attributed only 2% to parasitoids. Hanula (1981) reported 5–8% cumulative parasitism for two parasitoids, depending on height in the tree. Bellows et al. (1998) report that, despite extensive study, relatively little comparative information is available about the population dynamics of *S. multistriatus* in the United States and its native range.

Unlike phloem-feeding bark beetles, whose natural enemies include parasitoids that can oviposit into host larvae through the bark, ambrosia-beetle natural enemies must either eat their prey while they are on the bark surface or crawl into the galleries. Female ambrosia beetles excavate their galleries over extended periods of time so they are constantly pushing boring dust and frass through and out of them. It is unknown whether this behavior limits a parasitoid's or predator's ability to move into the galleries and find eggs or larvae, but it seems likely that it would. A third factor limiting biological control in the case of redbay ambrosia beetle is the limited information available about *X. glabratus* in its native range. Finally, any biological control project would need to consider the potential effects of exotic natural enemies on native ambrosia beetles (Hoddle, 2004), which are relatively rare compared to invasive species in the genus (Miller and Rabaglia, 2009).

Redbay ambrosia beetle and laurel wilt were first identified as damaging agents in 2004. Because of their recent discovery, rapid spread, the ability of a single beetle to inoculate and kill a tree, and the lack of successful biological control for similar pest complexes (e.g., the smaller European elm bark beetle and Dutch elm disease), there has been little interest or hope for biological control of this insect. We are unaware of any attempted biological control programs for ambrosia beetle species.

One factor limiting interest in biological control of the ambrosia beetle may be the lack of information on its natural enemies in general. Our search for literature on insect natural enemies of ambrosia beetles (Table 1) found only a few studies that document or describe natural enemies from a small number of ambrosia beetle species, but even fewer (e.g., Novák, 1960; Darling and Roberts, 1999) that provide detailed biological information or comment on potential for these organisms to influence population dynamics of their hosts. About half of these reports are from ambrosia beetles in the Platypodinae, a different subfamily from that of *X. glabratus* (Scolytinae). As for insect enemies of other *Xyleborus* species, perhaps the most interesting reference is to that of the parasitoid wasp *Phymastichus xylebori* Lasalle (Hymenoptera: Eulophidae), which was recovered from *Xyleborus perforans* (Wollaston), a pest of macadamia trees in Hawaii (Chang, 1993; LaSalle, 1995). This parasitoid has apparently not been studied since the mid-1990s. It is uncertain whether the lack of study of natural enemies is due to an actual lack of natural enemy species, and/or lack of interest.

RECOMMENDATIONS FOR FURTHER WORK

Clearly, more work is needed on natural enemies of ambrosia beetles in general and on the natural enemies of *X. glabratus* in particular. Thus far, there is no evidence that any native parasitoids in North America have begun using *X. glabratus*, despite the pest's high numbers. In Asia, *X. glabratus* is poorly known and unstudied. Since there are no reports of it associated with tree mortality in Asia, it most likely acts like other ambrosia beetles, attacking dead or dying trees or branches. The lack of information from Asia on *X. glabratus* suggests it is not an abundant species, but the role of natural enemies in regulating populations there is unknown. Thus, more detailed studies of the biology of *X. glabratus* and exploration for natural enemies in its native range is warranted.

Table 1 Insect natural enemies of ambrosia beetles (Coleoptera: Curculionidae)

Enemy Species	Enemy Group	Host Species	Host Subfamily	Plant Species	Region	Reference
Parasitoids						
Phymastichus xylebori LaSalle	Hymenoptera: Eulophidae	*Xyleborus perforans* (Wollaston)	Scolytinae	*Macadamia integrifolia* Maiden & Betche	Hawai'i, USA	
Perniphora robusta Ruschka	Hymenoptera: Pteromalidae	*Trypodendron lineatum* (Olivier), *T. domesticum* (L.), *Xyleborus dispar* (F.)	Scolytinae	various	various	Chang, 1993; LaSalle, 1995
Perniphora americana Miller	Hymenoptera: Pteromalidae	Assoc. with *Trypodendron betulae* Swaine	Scolytinae	*Betula papyrifera* Marsh., *B. alleghaniensis* Britton	Maine, USA; New Brunswick, Canada	Novák, 1960; Kenis et al., 2004
Cryptoxilos beaveri Shaw and Berry	Hymenoptera: Braconidae	*Hypothenemus curtipennis* (Schedl), *H. dorsosignatus* (Schedl).	Scolytinae	*Commersonia bartramia* (L.) Merr.	Fiji	Miller, 1965

Table 1 Insect natural enemies of ambrosia beetles (Coleoptera: Curculionidae), *continued.*

Enemy Species	Enemy Group	Host Species	Host Subfamily	Plant Species	Region	Reference
Cryptoxilos lymantori Deyrup	Hymenoptera: Braconidae	*H. dorsosignatus* (Schedl), *Lymantor decipens* Wood & Bright	Scolytinae	*Acer saccharum* Marsh.	Indiana, USA	Shaw and Berry, 2005
Eurytoma polygraphi Ashmead	Hymenoptera: Eurytomidae	*T. lineatum, T. domesticum*	Scolytinae	Not specified	Not specified	Deyrup, 1981
Monacon robertsi Bouček	Hymenoptera: Perilampidae	*Crossotarsus barbatus* Chapuis	Platypodinae	*Xanthophyllum papuanum* Whitmore ex Meijden, *Ficus* sp.	Papua New Guinea; Indonesia	Darling and Roberts, 1999
Monacon tricorne Bouček	Hymenoptera: Perilampidae	*Crossotarsus kuntzeni* Schedl	Platypodinae	Not specified	Not specified	Darling and Roberts, 1999, citing Bouček, 1980
Predators						
Sosylus spp.	Coleoptera: Colydiidae	Various, Platypodinae	Platypodinae	various	Nigeria; Papua New Guinea	Roberts, 1969, 1980
Ommadius spp.	Coleoptera: Cleridae	Unspecified Platypodinae	Platypodinae	Not specified	Not specified	Darling and Roberts, 1999
Cyphagogus splendens Kleine	Coleoptera: Brentidae	*Crossotarsus biconcavus* Schedl; *C. barbatus* Chapuis; *Platypus selysi* Chapuis	Platypodinae	Not specified	Papua New Guinea	Thompson, 1996
Cyphagogus modiglianii Senna	Coleoptera: Brentidae	Unspecified Platypodinae	Platypodinae	Not specified	Papua New Guinea	Thompson, 1996
Thanasimus dubius (F.)	Coleoptera: Cleridae)	*Platypus flavicornus* (F.)	Platypodinae	*Pinus* sp.	Texas, USA	Clarke and Menard, 2006
Rhizophagus depressus (F.) and *R. dispar* (Payk.)	Coleoptera: Rhizophagidae	*T. lineatum*	Scolytinae			Kenis et al., 2004, and references therein

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XXX Soapberry Borer

(*Agrilus prionurus* Chevrolat) (Coleoptera: Buprestidae)

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DESCRIPTION OF PEST

Taxonomy

The soapberry borer, *Agrilus prionurus* Chevrolat, is a native North American beetle in the subfamily Agrilinae, genus *Agrilus,* subgenus *Agrilus*. French entomologist Louis Alexandre Auguste Chevrolat first described *A. prionurus* in 1838 from a specimen presumably collected in Mexico (Chevrolat, 1838, labeled the holotype only as "Mexique"). The genus *Agrilus* (family Buprestidae - commonly called jewel beetles or metallic wood boring beetles) is a cosmopolitan genus that contains 2,783 described species (Bellamy, 2008), including numerous species in North America. It is believed to be the largest genus in the entire animal kingdom (Bellamy, 2003). *Agrilus* species are primarily twig and branch borers, using recently dead wood for larval development. A few species are recognized as tree-infesting pests, e.g., A*grilus anxius* Gory (bronze birch borer) and *Agrilus bilineatus* (Weber) (two lined chestnut borer). Others, like *A. prionurus*, are not considered major pests in their native ranges, but have become highly damaging in new areas. The latter include *Agrilus planipennis* Fairmaire (emerald ash borer) (Cappeart et al., 2005; Poland and McCullough, 2006) and *Agrilus auroguttatus* Schaeffer (goldspotted oak borer) (Coleman and Seybold, 2008).

Distribution

The soapberry borer is believed to be native to northern Mexico (Wellso and Jackman, 2006; Westcott and Hespenheide, 2006). It was first reported in Texas (USA) in 2003, infesting and killing western soapberry, *Sapindus saponaria* var. *drummondii* (Hook. & Arn.) L. Benson in Travis Co. (Wellso and Jackman, 2006) (Fig. 1). This tree is the borer's only known host. Western soapberry is a small- to medium-sized deciduous tree (7.7–15.4 m tall) found in Texas and surrounding states as well as in northern Mexico.

Figure 1 Western soapberry (*Sapindus saponaria* var. *drummondii*) trees can be distinguished from Chinaberry trees (*Melia azerdarach* L.) by the single sets of compound leaves and the off-set midveins and lack of serration on the individual leaflets. Ronald F. Billings, Texas Forest Service, Bugwood.org.

In the United States, it is valued for its fruits, colorful fall foliage, and utility as a landscape tree (Fig. 2) (Little, 1950; Phillips and Gibbs, 1953; Dirr, 1990). *Sapindus saponaria*, used for medicinal purposes in Mexico, is found in various states, including Sonora, Guerrero, Oaxaca, Quintana Roo (Argueta et al., 2012), San Luis Potosi (Rzedowski, 1978), Tamaulipas, and Veracruz (Westcott and Hespenheide, 2006).

The native range of the insect is unknown, but is presumed to be Mexico because of the origin of the type specimen. A specimen in the Texas A&M University insect collection in College Station was labeled as collected in 1978 in Rio Sabinas, El Encino, in the State of Tamaulipas, Mexico (Westcott and Hespenheide, 2006). Another specimen was collected in 1984 from 80 km south of Ciudad Victoria, also in the State of Tamaulipas (Wellso and Jackman, 2006). How this insect arrived in Texas, assuming it is not native, remains unknown. Texas and Mexico are separated by semiarid grasslands with scattered non-host shrubs and cactus along the southern border and by arid desert along the western border. This hostile environment creates an environmental barrier that has historically prevented tree-infesting insects from invading Texas from the south. But increased planting of western soapberry as an ornamental in Texas and possibly northern Mexico and a series of mild, frost-free winters may have favored the natural spread of the insect to the north. Conceivably, the insect could have arrived in infested firewood, a common means of long-distance transport for wood-boring insects.

Reports by landowners and arborists indicate that the insect had probably been infesting soapberry trees in Texas since the 1990s. Infested trees were observed in Travis and McLennan counties as early as 1998 (J. Pulley, personal communication). In 2009 and 2010, the Texas Forest Service received many reports from residents near

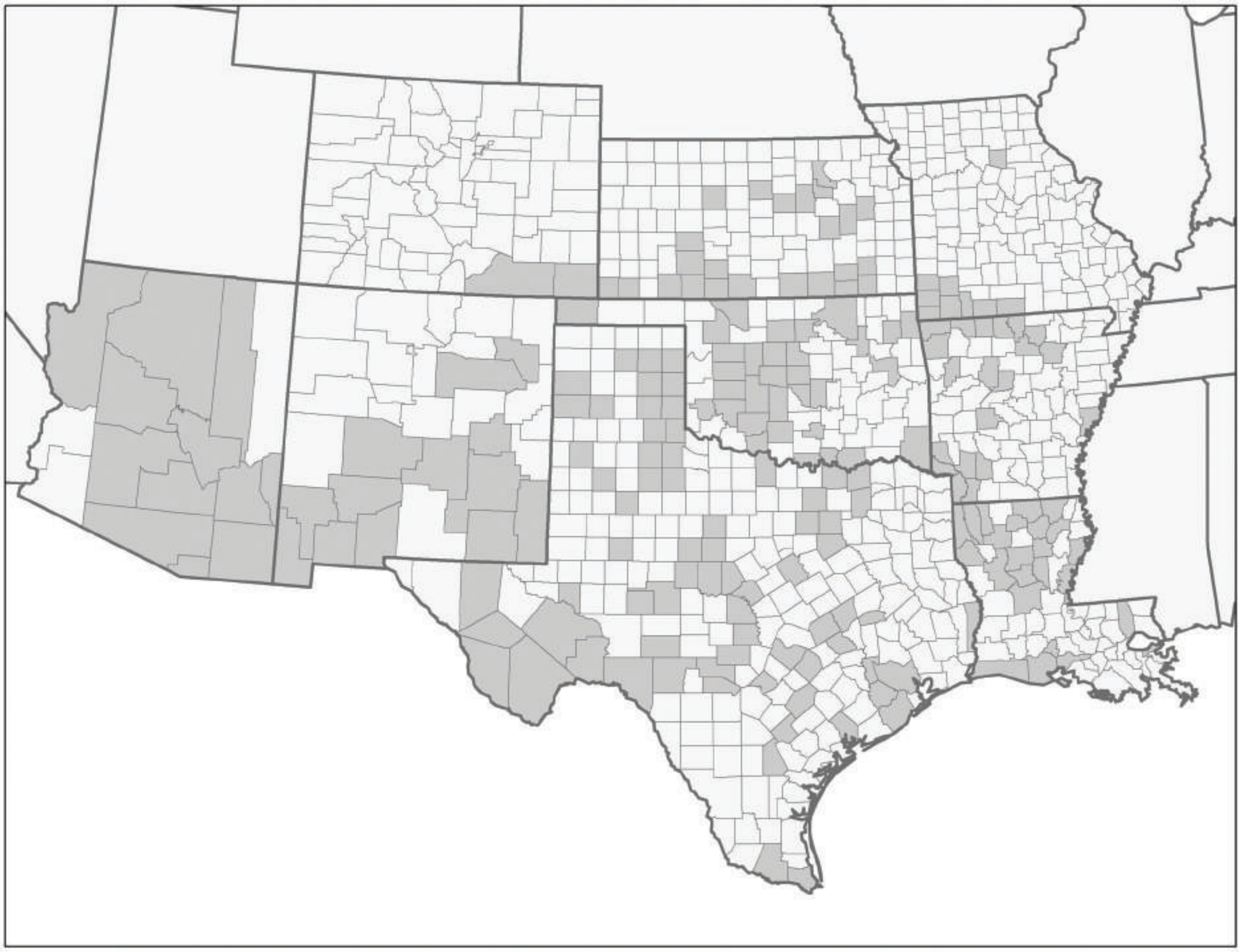

Figure 2 Counties (shaded) with western soapberry in the United States, based on USDA Natural Resource Conservation Service records.

Houston and Dallas of soapberry borers killing soapberry trees in urban and rural settings. In addition, Texas Forest Service entomologists observed multiple-tree infestations in Fort Bend, Brazos, and Dallas counties during this period (Billings et al., 2012).

Damage

Type Damage from this borer is similar to that of other wood borers in the genus *Agrilus*. Larvae feed under the bark in the phloem, and if numerous, can girdle and kill trees in a manner similar to that of the more familiar emerald ash borer.

Extent As of January 2012, infestations of this insect had been reported in 50 counties in Texas, including areas near or within the cities of Fort Worth, Dallas, Waco, College Station, Austin, Houston and Corpus Christi (Fig. 3). No infestations have been observed or reported from adjacent states.

In 2009–2011, it was common for *A. prionurus* to kill essentially every western soapberry tree larger than 6 cm in diameter at breast height (dbh) upon invading an area (Billings et al., 2012). However, in the past year, new infestations have been few and reports from concerned landowners have subsided, presumably due to the freezing temperatures experienced in February 2011. Infested areas are being monitored to determine if this invasive insect will recover and continue its spread in Texas and beyond. It is too early to know the full impact of *A. prionurus* on soapberry trees in the United States, as is the case with a related wood borer, the European oak borer, *Agrilus sulcicollis* Lacordaire. This latter insect was first collected from oaks in Michigan in 2003 (Jendek and Grebennikov, 2009) and subsequently in New York, and Ontario, Canada (J. Zablotny, personal communication), but its economic impact on North American oaks remains to be determined.

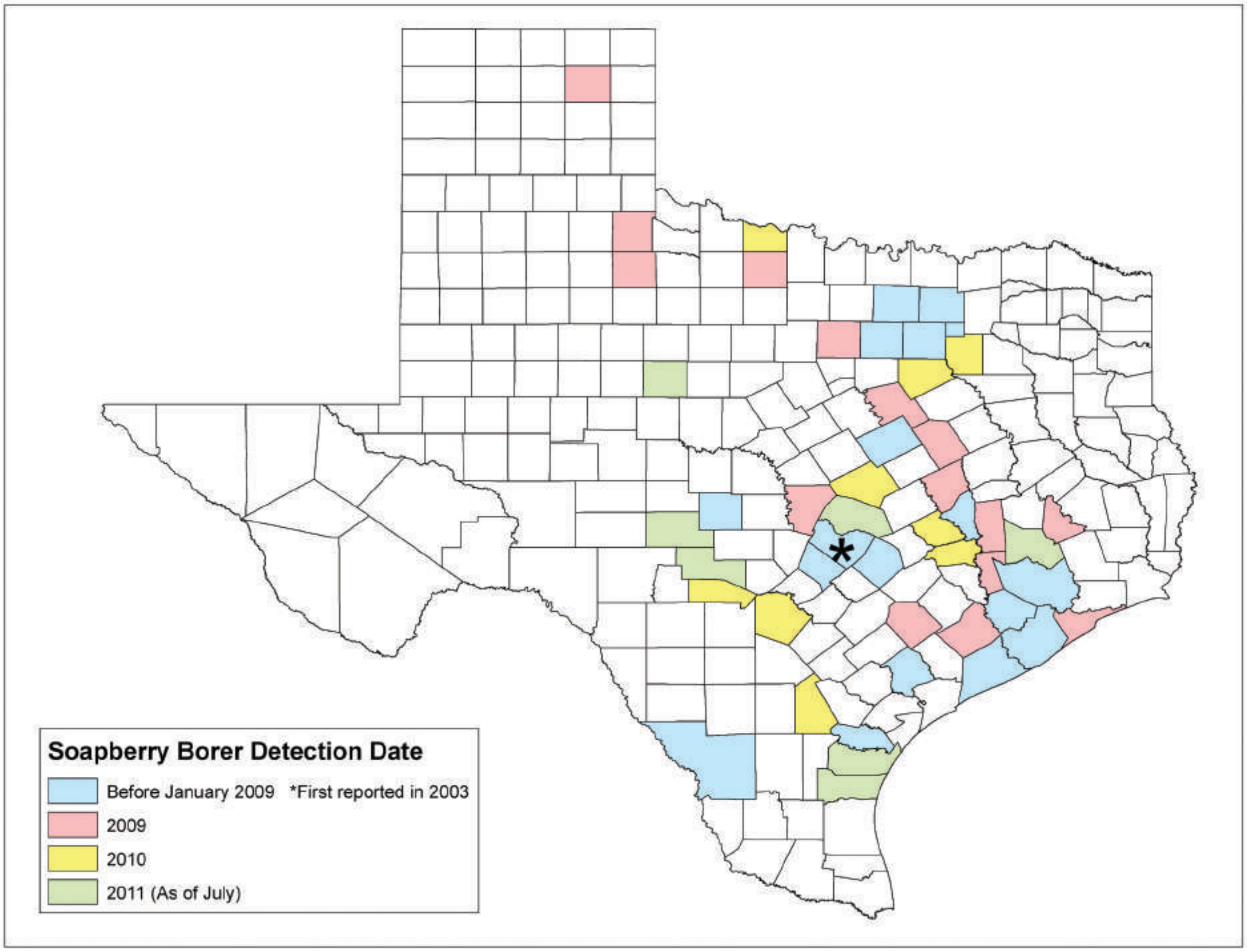

Figure 3 Counties in Texas known to be infested by *Agrilus prionurus* (soapberry borer) in Texas by year of detection as of April 2012 showing spread since the insect was first detected in Travis County (*) in 2003.

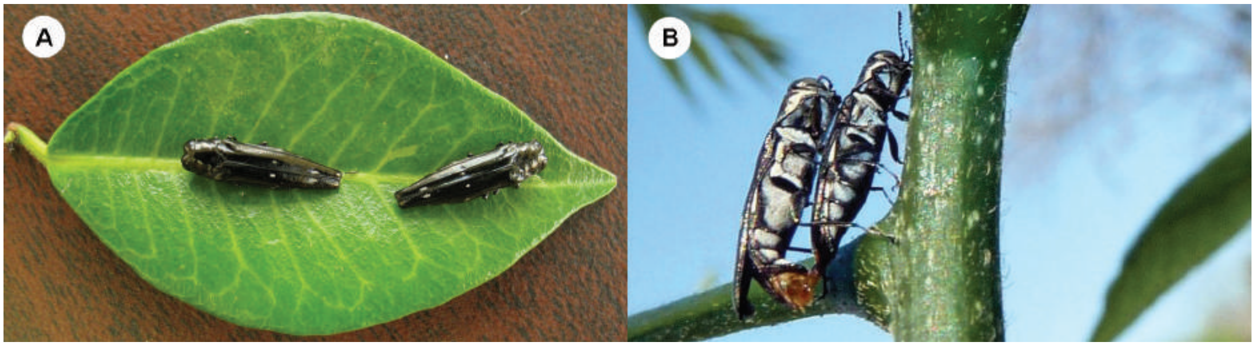

Figure 4 (A) Adults of *Agrilus prionurus* are about 10 mm long and have shiny black bodies with four white dots on the elytra. Ronald F. Billings, Texas Forest Service, Bugwood.org. (B) Adults of the native *Agrilus limpiae* Knull are common on soapberry, but are smaller (about 5 mm long) and have white markings on the underside of the abdomen.

Biology of Pest

The adult of *A. prionurus*, 8–12 mm long, has a shiny, black to slightly green body that is distinctively marked with four white dots on the elytra (Fig. 4A). The adult female lays eggs on the bark of live western soapberry trees, and the larvae develop beneath the bark in winding galleries (Fig. 5). The larvae are up to 3 cm long when mature. After feeding beneath the bark, the larvae bore into the wood to complete development and pupate. New adults emerge through the bark, leaving "D"-shaped exit holes, characteristic of all species of *Agrilus*.

Figure 5 Galleries and larvae of *Agrilus prionurus* under bark of infested western soapberry. Ronald F. Billings, Texas Forest Service, Bugwood.org.

Signs of soapberry borer infestations are similar to those of the destructive emerald ash borer, a close relative not yet found in Texas (Wilson and Rebek, 2005). The first sign of soapberry borer infestation usually noticed by landowners is large chips of bark that flake off the bole (Fig. 6) and accumulate at the base of the infested tree, a result of woodpeckers feeding on the larvae. Infested trees eventually die back from the top, often producing abundant epicormic shoots on the lower trunk (Fig. 7). Infested trees typically die within two or three years after the initial attack.

Figure 6 The first signs of soapberry borer infestation are trees with bark missing from the tree bole and bark chips at the tree base. Ronald F. Billings, Texas Forest Service, Bugwood.org.

Figure 7 The winding larval galleries are visible on the bark chips and sapwood. Infested trees characteristically die from the top downward and exhibit numerous epicormic shoots along the lower trunk. Ronald F. Billings, Texas Forest Service, Bugwood.org.

The authors have conducted several rearing studies to determine when *A. prionurus* adults emerge in Texas. Peak emergence occurred in May from infested log sections collected near Houston and Austin and as late as August from infested material collected near Dallas. In 2004, some beetles were observed to emerge as early as February 29 (from infested logs collected near Austin in September, 2003). No emergence occurred after August in any of the rearing studies.

Purple and green sticky traps developed for the emerald ash borer have proven largely ineffective in catching soapberry borer adults, even in established infestations (Billings et al., 2012). In one survey, 16 traps were deployed within four known soapberry borer infestations in mid-June (six traps near Richmond, and two near College Station, Texas in 2009; six in Allen and two in Mesquite, Texas in 2010) and monitored until mid-August, only two adult soapberry borers were collected from these traps, both from Brazos County and both from the single unbaited trap. One adult was collected on June 23 and the second on July 2, 2009. The presence of manuka oil on nine of the traps did not increase trap catches. The fact that peak emergence of *A. prionurus* was determined from rearing studies to occur in May in Texas suggests that the traps may have been placed in the field at sub-optimal times. Data from rearing and trapping studies suggest that the soapberry borer has one generation per year in Texas, with adult emergence occurring primarily from May through mid-August.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

Large numbers of a related native borer, *Agrilus limpiae* Knull, were collected from both the survey traps and rearings of infested soapberry logs (Billings et al., 2012). Adults of *A. limpiae* were observed mating on foliage of western soapberry in Dallas County on April 1, 2011 (Fig. 4B, above). *Agrilus limpiae* is one of seven native buprestids known to occur on western soapberry in the United States. Unlike *A. prionurus*, all the native species are believed to be secondary woodborers, infesting only dying or dead trees, including *Agrilus egeniformis* Champlain & Knull, *Agrilus exsapindi* Vogt, *A. limpiae* Knull, *Agrilus ornatulus* Horn, *Agrilus sapindi* Knull, *Agrilus scitulus* Horn, and *Agrilus taeniatus* Chevrolat. Stan Wellso collected adults of *A. exsapindi* and *A. taeniatus* from western soapberry on the Santa Ana Wildlife Refuge in Hidalgo County near the Texas-Mexico border. Interestingly, one specimen of *A. exsapindi* was collected in Mexico at the same site that John Jackman collected *A. prionurus*. Several of these native species might be at risk if nonnative biological control agents were imported to control *A. prionurus*. The potential for this side effect to occur should be evaluated before release of new species of natural enemies against soapberry borer.

Native Natural Enemies Affecting the Pest

To date, no natural enemies have been reared from *A. prionurus* or host material infested with its immature stages in Texas. Natural enemies of this wood borer within its native range of northern Mexico are unknown.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

The authors know of no collections of *A. prionurus* between 1838, when Chevrolat described the species, and 1978, when a specimen was collected in Rio Sabinas, El Encino, State of Tamaulipas, Mexico (Westcott and Hespenheide, 2006). In 1984, entomologist John Jackman (Texas A&M University) collected this insect using a sweep net along a primitive road 80 km south of Ciudad Victoria, Mexico (Wellso and Jackman, 2006). Based on a specimen in the Museum National d'Histoire Naturelle (Paris, France), the insect also has been collected from Córdoba in the State of Veracruz, Mexico (Westcott and Hespenheide, 2006). The location where Jackman collected the insect in Mexico is ~450 km from the Texas border. The host at the time was unknown. Interestingly, Wellso and Jackman also collected another species of *Agrilus* from a *Sapindus* species in the same area of Mexico. This beetle, subsequently described as *A. lautuelliformis* Hespenheide*,* is considered a secondary wood borer and has not been found in Texas.

RECOMMENDATIONS FOR FURTHER WORK

To date, no attempts have been made to conduct a biological control program against *A. prionurus*. If this insect continues to be a pest on western soapberry in Texas or other states in the southwest United States, a biological control project, modeled after the ones being developed for *A. planipennis* (emerald ash borer) in Michigan (Bauer et al., 2008) or *A. auroguttatus* (goldspotted oak borer) in California (Seybold and Coleman, 2010), would be warranted. Studies to identify parasites or predators of various life stages of *A. prionurus* in Mexico and to explore the possibility of introducing these into Texas for biological control have yet to be conducted.

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XXXI Walnut Twig Beetle

(*Pityophthorus juglandis* Blackman) (Coleoptera: Curculionidae: Scolytinae)

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DESCRIPTION OF PEST

Taxonomy

The walnut twig beetle, *Pityophthorus juglandis* Blackman (Scolytini: Pityophthorina), was initially described by Blackman (1928) from specimens collected on black walnut (*Juglans nigra* L.) in Lone Mountain, New Mexico, and Paradise, Arizona (Blackman, 1928; Cranshaw, 2011; LaBonte and Rabaglia, 2012). There are no synonyms in the literature.

In Blackman's revision of the genus *Pityophthorus* Eichhoff, he included species that (1) possessed numerous setae on body surfaces or were glabrous, (2) had several asperities (short cuticular protuberances) on the pronotum, (3) had elytra that partially covered the metepisternum, and (4) had clubbed antennae with five segments. This genus includes more than 100 species found throughout the United States (Arnett et al., 2002). Most species in this genus infest conifers, while only a few attack hardwoods. Because of the many species present in North America and their small size, LaBonte and Rabaglia (2012) provided a pictorial key to aid in identifying the key characteristics of *P. juglandis*.

Adults of walnut twig beetle are 1.5–1.9 mm long and may be distinguished from other species by the possession of 4 to 6 usually medially broken, concentric rows of asperities on the pronotum, and the acute declivity at the posterior of the elytra, with minute granules (Blackman, 1928; Bright, 1981) (Fig. 1). While specimens of *Pityophthorus lautus* Eichhoff are occasionally found on black walnut in eastern Tennessee, this species may be distinguished from *P. juglandis* by its possession of fused asperities on all but the first two lines on the pronotum (Blackman, 1928) and the more convex declivity on the posterior of the elytra. Because *P. juglandis* is known to infest only species of *Juglans*, the common name designated for this species is the walnut twig beetle (WTB).

Distribution

The WTB was collected in New Mexico as early as 1896 (Blackman, 1928) and by 1992 its distribution was known to include New Mexico, Arizona, southern California, and Chihuahua, Mexico (Wood and Bright, 1992). Excluding records from California, the earliest reported range of WTB appears to overlap the northern range of Arizona walnut (*Juglans major* Torr. [A. Heller]) (Cranshaw, 2011) (Fig. 2). The earliest records of WTB in California are from 1959 in Los Angeles County and were associated with eastern black walnut (*Juglans nigra* L.) and southern California walnut (*Juglans californica* S. Watson). Records from the Central Valley region date from the 1970s (Bright and Stark, 1973; Cranshaw, 2011).

The reported range of WTB has increased substantially since 1992, with the addition of new records from Colorado, Utah, Nevada, Idaho, Oregon, and Washington (Cranshaw, 2011; Seybold et al., 2011), which were associated primarily with unusual mortality of *J. nigra* and other *Juglans* species.

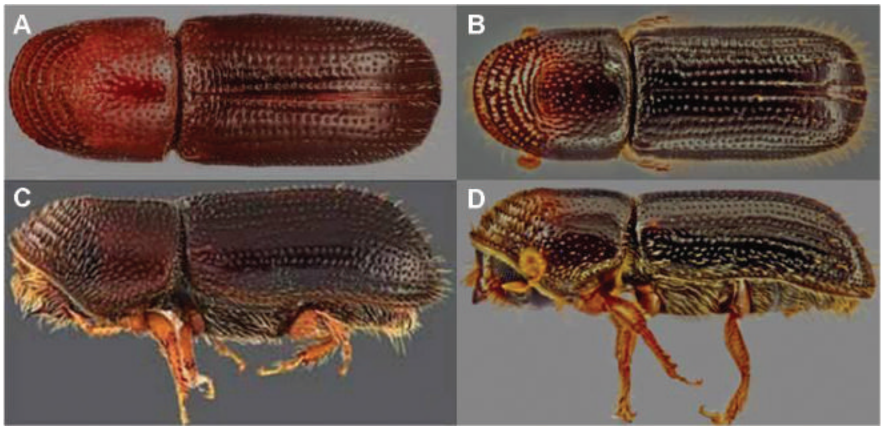

Figure 1 Adults of walnut twig beetle (*Pityophthorus juglandis*): A) female, dorsal view, B) male, dorsal view, C) female, lateral view, D) male, lateral view. Steve Valley, Oregon Department of Agriculture, Agriculture Plant Division, Salem, Oregon, USA.

Figure 2 Native range of Arizona walnut, *Juglans major*, in North America. US Geological Survey. http://www.thousandcankers.com/media/images/juglmajo.pdf

Juglans nigra is native to the eastern United States, but has been planted widely in western states for ornamental and commercial use. Unusual *J. nigra* mortality in Colorado and other western U.S. states was eventually determined to be caused by aggressive attacks of the WTB and associated cankers caused by a fungal symbiont, *Geosmithia morbida* Kolařík, Freland, Utley, and Tisserat (Tisserat et al., 2009; Kolařík et al., 2011). This insect-pathogen complex causes a disease known as "thousand cankers disease" due to the large number of cankers formed in association with WTB attacks and tunnels in the bark (Tisserat et al., 2009). The origin of *G. morbida* and the reason for WTB's presumed recent invasion of new geographic areas and hosts are uncertain. Recently, thousand cankers disease and the WTB were detected within the native range of *J. nigra* in the eastern United States (Grant et al., 2011), and as of 2012 there were known infestations in eastern Tennessee, Virginia, and eastern Pennsylvania (Seybold et al., 2011). Eastern black walnut is widely distributed in the eastern half of the coterminous United States, and continued expansion of the distribution of WTB is anticipated and would be very damaging.

Damage

Type Before the early 2000s, WTB was not reported in association with any *Juglans* decline or mortality, and the fungal symbiont *G. morbida,* which causes thousand cankers disease, was unknown (Tisserat et al., 2009). In *J. nigra*, thousand cankers disease is characterized by progressive decline and mortality that takes 2 to 4 years after the onset of symptoms, although some diseased trees may live several years longer. Early symptoms include yellowing and thinning of leaves in the upper crown and eventual twig and branch dieback. Early attacks by WTB may be detected by the extremely small circular entrance holes in the bark of small diameter branches. Careful removal of thin layers of bark reveal shallow beetle galleries surrounded by diffuse brown to black cankers in the phloem (Fig. 3). Although infection with *G. morbida* is not systemic and cankers remain localized (within 4 cm) around beetle galleries or other attack points, if beetle density is high, attacks are so abundant that cankers coalesce. Eventually, the cankers extend into the cambium, girdling and killing branches. As the disease progresses, attacks by the WTB and associated cankers occur in larger branches, limbs, and trunks, causing crown dieback and death (Tisserat et al., 2009; Tisserat and Cranshaw, 2011) (Fig 4).

Figure 3 Walnut twig beetle galleries and associated cankers caused by *Geosmithia morbida* in a small-diameter black walnut (*Juglans nigra*) branch. Photo by Albert Mayfield, USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA.

Figure 4 Black walnut with branch and crown dieback caused by thousand cankers disease. Photo by Albert Mayfield, USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA.

Extent Thousand cankers disease has been found in twelve states in the United States, nine in the West (Arizona, California, Colorado, Idaho, Nevada, New Mexico, Oregon, Utah, and Washington) and three in the East (Pennsylvania, Tennessee, and Virginia) (Seybold et al., 2011). Extensive mortality of black walnut (*J. nigra*) has been observed wherever WTB and thousand cankers disease occur (Tisserat and Cranshaw, 2011). *Geosmithia morbida* has been isolated from WTB galleries in Arizona walnut (*J. major*) in Arizona and New Mexico, but branch dieback and mortality characteristic of thousand cankers disease has not been observed in this species (Tisserat and Cranshaw, 2011). Walnut twig beetle has been widely recovered from dying/declining southern California walnut (*Juglans californica* S. Wats.) and northern California walnut (*Juglans hindsii* [Jeps.] Jeps. Ex R. E. Sm.) growing along roads and in natural habitats. Commercial orchards of English walnut (*Juglans regia* L.) have experienced infestationd of WTB but without significant damage or mortality. *Juglans regia* appears to have some level of resistance to development of thousand cankers disease, but WTB attacks and disease symptoms have been observed on some Paradox rootstocks (a hybrid between English and black walnut) in *J. regia* orchards (Tisserat and Cranshaw, 2011).

Concern is high over the potential impact of WTB and thousand cankers disease on eastern black walnut (*J. nigra*) in its native range. The beetle and associated disease are well established and causing substantial black walnut mortality in at least three eastern U.S. states. The WTB and associated pathogen can be moved to new areas via transportation of infested logs, firewood, or ornamental plants, and as of 2012, quarantines on the movement of walnut material have been enacted in many counties in Tennessee and Virginia and one county (Bucks) in Pennsylvania (Tennessee DAC, 2012; Virginia DACS, 2012; Pennsylvania DAC, 2012). Eastern black walnut is highly valued for lumber and veneer, and growing stock in the United States is estimated to be worth over half a trillion dollars (Newton et al., 2009). It is planted by landowners for timber and nut production and thus is an important agroforestry crop, especially in mid-western states such as Missouri. Although it comprises a small component of eastern hardwood forests, black walnut carries high economic, cultural, and ecological value due to its beautiful wood, mast production, medicinal qualities, and use as an ornamental (Newton et al., 2009).

Biology of Pest

Pityophthorus juglandis is a bisexual species with at least two overlapping generations per year. Attacks occur only on *Juglans* species. In east Tennessee, adults of the overwintering generation emerged and were collected from containerized bolts beginning in late April. Adult activity continued until early December (K. Nix, Univ. Tenn., unpublished data). Emergence of the adults appears to be temperature-dependent, and in the western United States adults may fly on warm days even during winter months (S. Seybold, USDA Forest Service, pers. comm. 2012). Both sexes produce an aggregation pheromone that attracts both sexes in flight (Seybold et al., 2010). Upon discovery of a suitable walnut tree, beetles attack the twigs, limbs, and trunk, where they bore holes through the bark to the outer cambial layer (Fig. 5A). The entrance tunnels are often located near cracks or in rough areas of the bark and extend from the surface to the cambial layer just underneath the bark (Cranshaw and Tisserat, 2008). Males initiate colonization and development of the brood chambers on walnut branches (Graves et al., 2010). This

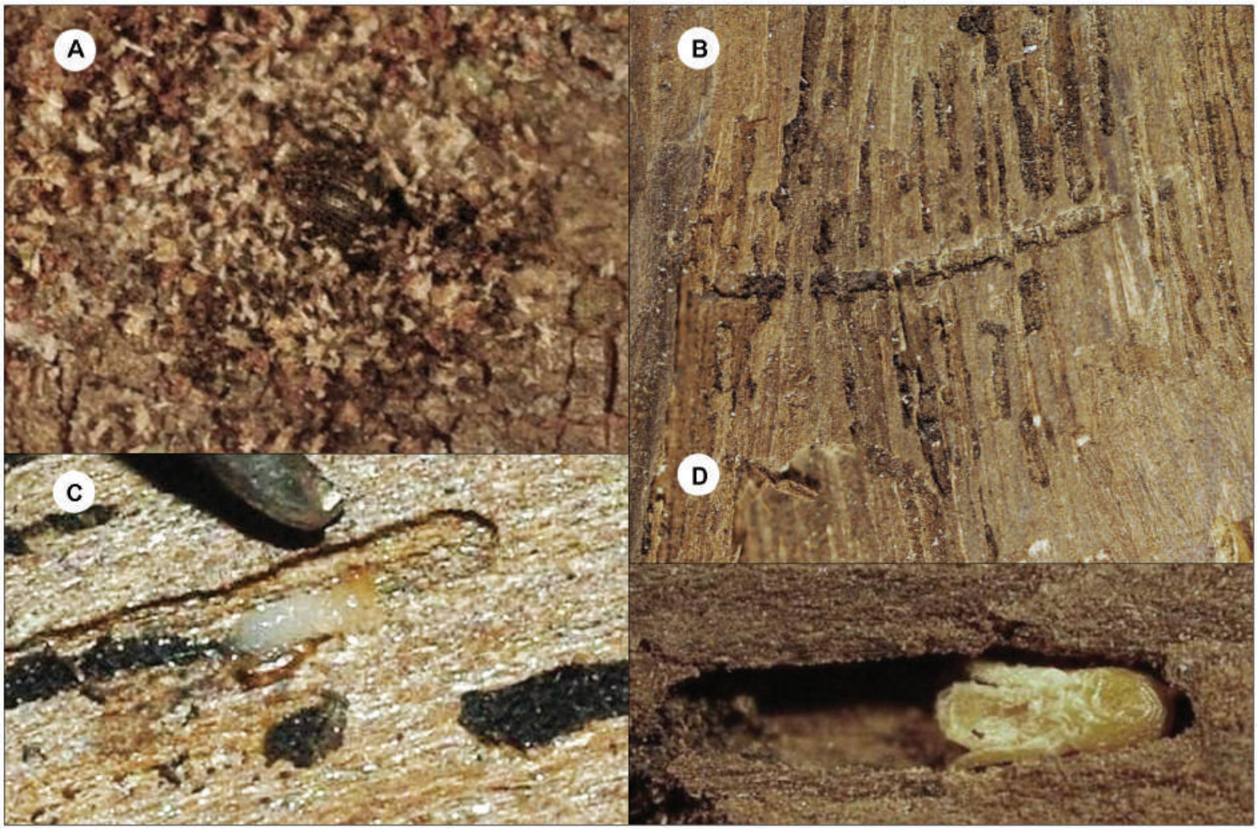

Figure 5 Development of walnut twig beetle: A) adult boring into twig, B) gallery formation, C) larva in gallery, D) pupa in gallery. Katheryne Nix, University of Tennessee, Knoxville, Tennessee, USA.

species appears to be polygynous, with one or two females observed within the same tunnel as the male.

Females lay minute, individual, cream-colored eggs. After egg hatch, the larvae begin to form single unbranched tunnels ~1.1– 1.3 cm long. The brood galleries are constructed against the grain within the area of the phloem and xylem surfaces (Graves et al., 2010), leaving an imprint on the upper cambial tissue and the underside of the bark (Fig. 5B). However, it appears the developing larvae construct their tunnels with the grain in infested black walnuts in eastern Tennessee. The larvae are white with reddish-brown heads and are found within the tunnels underneath the bark (Fig. 5C). The mature larvae create cells in which to pupate at the ends of their larval tunnels (Fig. 5D). By late July, most pupae have developed into adults. All stages of development, except the eggs, were documented to occur within the larval tunnels. By the end of larval development, the tunnels are packed with dark brown boring dust. The emerging adults either re-infest the host tree or fly to other host trees to mate and reproduce (Graves et al., 2010). This invasive species has the ability to increase rapidly in population size and spread over large areas in a relatively short period of time.

As they disperse and bore into new host trees, beetles carry the fungal conidia of *G. morbida* on their exoskeleton, often attached to the setae. The WTB is the only known vector of the thousand cankers pathogen. *Geosmithia morbida* was originally isolated and identified from branch and twig cankers surrounding the tunnels (Tisserat et al., 2009). The fungal growth occurs outside the tunnels in the region of the phloem and cambium, resulting in the development of many small cankers. As the cankers coalesce, the trunks and limbs become girdled by "thousands of cankers"—hence the common name of the disease (Cranshaw and Tisserat, 2008; Tisserat et al., 2009).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

Pityophthorus Eichhoff is a large, diversified, and widespread genus of bark beetles with over 200 species in North and Central America (Bright, 1981). Many of these species breed in the inner bark or pith of twigs and small branches, although some attack larger stems. Because most *Pityophthorus* colonize twigs of dead, dying, or injured hosts, they are of little economic importance, although some species are suspected vectors of the pitch canker fungus, *Fusarium circinatum* Nirenberg and O'Donnell, in pines (Storer et al., 2004, Sakamoto et al., 2007). There is a notable lack of published information on natural enemies of *Pityophthorus* species, perhaps historically due to their lack of importance as pests.

Of the 220 North and Central American *Pityophthorus* species treated by Bright (1981), 141 attack coniferous hosts and 101 of these utilize only pines (*Pinus* spp.). Other coniferous host genera include *Abies*, *Picea*, *Pseudotsuga*, and *Larix*. Of the remaining 79 species, 26 attack deciduous trees, 3l use vines or shrubs, and 22 have unknown or unrecorded hosts (Bright, 1981). There are three subgenera, *Hypopityophthorus*, *Gnatholeptus*, and *Pityophthorus*. The subgenus *Pityophthorus* contains most of the species and is further subdivided into various taxonomic groups. *Pityophthorus juglandis* is one of 13 species in Juglandis group, for which there is very limited information on biology and host associations, although most appear to be associated with non-coniferous shrubs and vines (Bright, 1981) (Table 1). *Pityophthorus lautus* Eichhoff, classified as part of the Lautus group, has been collected from a number of deciduous tree species in the eastern United States and is the only member of the genus besides *P. juglandis* reported to attack *Juglans* species (Bright, 1981) (Table 1). If potential biological control agents were identified for *P. juglandis*, *P. lautus* should be considered as a potential nontargethost species. Other potential nontarget *Pityophthora* might include additional species in the Juglandis and Lautus groups and others reported to attack non-coniferous hosts (Table 1). Presumably, compared to those that use conifers, natural enemies of *P. juglandis* would be more likely to affect nontargetinsects of deciduous species. Seybold et al. (2012) listed 30 species of bark beetles (Coleoptera: Curculionidae: Scolytinae) that were collected in pheromone-baited survey traps for WTB in California, Idaho, Tennessee, Utah, and Virginia, including two species of *Pityophthorus* (*P. crinalis* Blackman and *P. pulicarius* [Zimmermann]) and numerous other bark and ambrosia beetles. These and additional bark beetles that may be recovered from *Juglans* spp. or in pheromone traps for the WTB should also be considered as possible nontargetspecies in a biological control program.

Native Natural Enemies Affecting the Pest

Little has been recorded of the natural enemies of the WTB. Seybold (2010) listed three potential generalist predators, *Temnochila chlorodia* (Mannerheim) (Coleoptera:

Table 1 *Pityophthorus* species of North and Central America in the Juglandis and Lautus groups, and other species with non-coniferous host records in Bright (1981).

Pityophthorus species	Recorded Distribution	Recorded host plant species
Juglandis group		
P. burserae Wood	central Mexico	*Bursera* sp.
P. costabilis Wood	central Mexico	*Thevetia* sp.
P. costatulus Wood	southern Mexico	*Thevetia* sp.
P. detentus Wood	central Mexico	shrubs (*Rhus* sp.) and unknown vines
P. diligens Wood	central Mexico	unknown shrub
P. franseriae Wood	New Mexico; host occurs southwestern U.S.	probably *Ambrosia deltoidea* (Torr.) W.W.Payne
P. galeritus Wood	Costa Rica; host occurs Oaxaca to Panama	*Garcinia intermedia* (Pittier) Hammel
P. indigens Wood	Mexico	*Bursera* sp.
P. juglandis Blackman	southern California to New Mexico, south into northern Mexico	*Juglans* spp.
P. nanus Wood	southern Mexico	*Bursera* sp., *Pinus* sp.
P. pudicus Blackman	Jalisco, Mexico	*Sambucus* sp.; unknown shrubs
P. strictus Wood	Costa Rica; host occurs Oaxaca to Panama	*Garcinia intermedia* (Pittier) Hammel
P. tenax Wood	Guatemala	unknown
Lautus group		
P. *borrichiae* Wood	Florida	*Borrichia* spp.
P. *concentralis* Eichhoff	Cuba and Florida	*Metopium toxiferum* (L.) Krug & Urb.
P. *corruptus* Wood	central Mexico	*Rhus* spp. (*Toxicodendron*)
P. *crinalis* Blackman	eastern U.S.	*Rhus* spp. (*Toxicodendron*), *Quercus alba* L.
P. *lautus* Eichhoff	eastern North America	*Acer* spp., *Cercis* sp., *Hammamelis* spp., *Juglans* spp., *Quercus* spp., *Rhus* spp.
P. *liquidambaris* Blackman	southeastern U.S.	*Liquidambar styraciflua* L.
P. *molestus* Wood	Mexican distribution of sweetgum	*Liquidambar styraciflua* L.
P. *morosus* Wood	Chiapas and Veracruz, Mexico to Honduras	*Critonia daleoides* DC; unknown woody plants
P. *nemorolis* Wood	Honduras, Costa Rica, throughout Central America	*Aristolochia anguicida* Jacq.; unspecified vines
P. *paulus* Wood	central Mexico	*Baccharis* sp., unknown plants
P. *perexiguus* Wood	Costa Rica, Panama	unknown
P. *sambuci* Blackman	Jalisco, Mexico	*Sambucus* sp.
Other species with non-coniferous hosts		
P. alni Blackman	Veracruz and prob. elsewhere in southern Mexico	*Alnus* spp.
P. alnicolens Wood	southern Mexico	*Alnus* sp.
P. arceuthobii Wood	Durango, Mexico	*Arceuthobium globosum* Hawksw. & Wiens
P. attenuatus Blackman	Southern Mexico to El Salvador, prob. throughout Central America	*Quercus* sp., *Alnus* sp., unidentified shrubs
P. conspectus Wood	Costa Rica	prob. *Quercus* sp.
P. *coronarius* Blackman	Mexico	*Sambucus* sp. and prob. other shrubs

Table 1 *Pityophthorus* species of North and Central America in the Juglandis and Lautus groups, and other species with non-coniferous host records in Bright (1981), *continued.*

Pityophthorus species	Recorded Distribution	Recorded host plant species
P. debilis Wood	Probably throughout central Mexico	*Rhus* sp. amd *Mauria heterophylla* Kunth
P. exquisitus (Blackman)	Central Mexico; probably a larger area	*Sambucus* sp. and other unknown shrubs
P. guatemalensis Blanford	Durango, Mexico to Guatemala, possibly TX	*Quercus* spp.
P. hermosus Wood	Honduras, prob. throughout southern Mexico to Costa Rica	*Perymanium grande*[1] and *Critonia daleoides* DC.
P. hylocuroides Wood	Hidalgo, Mexico	*Rhus* sp.
P. medialis Wood	Costa Rica	*Quercus* spp.
P. melanurus Wood	Chiapas, Mexico	Quercus sp.
P. mendosus Wood	Costa Rica; probably throughout Central America	*Phosphoro* sp.[1]
P. *mexicanus* Blackman	Northern and central Mexico	*Parthenium argentatum* A.Gray
P. nebulosus Wood	Veracruz, Mexico	*Bursera* sp.
P. parilis Wood	Honduras	*Quercus* spp.
P. scitulus Wood	Costa Rica, Panama	*Quercus* spp.
P. *scriptor* Blackman	Southeastern U.S., west to Texas and Oklahoma	*Rhus spp.*
P. torridus Wood	New Mexico	probably *Ambrosia deltoidea* (Torr.) W. W. Payne
P. *virilis* Blackman	Southern Idaho and Wyoming to northern Mexico and western Texas	*Rhus spp.*

Note: With the exception of the Juglandis and Lautus groups (which are listed in full), species with hosts recorded only as "unknown", "unknown vine", "unknown shrub", or other ambiguous host records in Bright (1981) are not included in this table. [1]The identity of the species associated with the names *Perymanium grande* and *Phosphoro* sp. is uncertain.

Trogositidae), an unknown beetle in the family Laemophloeidae, and an unknown beetle in the family Monotomidae, as well as two parasitoids, *Neocalosoter* sp. (Hymenoptera: Pteromalidae) and *Plastanoxus westwoodi* (Hymenoptera: Bethylidae), as natural enemies of WTB on *J. hindsii* in California. Additional information on natural enemy complexes found in association with WTB in its native and invaded ranges is being compiled (S.J. Seybold, USDA Forest Service, pers. comm. 2012). Due to the discovery of the WTB in 2010 in Knox County, Tennessee, and the associated severe damage to black walnut, surveys were initiated to find potential biological control agents. A variety of natural enemies were observed to be associated with the WTB on *J. nigra* in Tennessee, including the predators *Enoclerus nigripes* (Say), *Madoniella dislocatus* (Say), and *Pyticeroides laticornis* (Say) (all Coleoptera: Cleridae) (Fig. 6) and an unknown parasitoid. Specimens of the predaceous clerids were observed on the bark and in the tunnels of walnut twig beetle in walnut bolts maintained in the laboratory. These predators are widely distributed within the eastern United States and Canada (Leavengood, 2008). Both adults and larvae are predators of bark beetles. A study was initiated to determine if these clerids would feed on walnut twig beetle life stages, which they did in laboratory choice and no-choice consumption tests (K. Nix, Univ. Tennessee, pers. comm. 2012). One primary endoparasitoid was discovered emerging from adult, female, walnut twig beetles.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Enoclerus nigripes

Synomyns for *E. nigripes* include; *Clerus nigripes* Say, *Clerus incertus* Lec., *Clerus quadriguttatus* Auctt., Oliv., *Clerus quadriguttatus* Say var. *nigripes* Say, *Enoclerus quadriguttatus*

Oliv., and *Enoclerus quadriguttatus* var. *nigripes* Say. *Enoclerus nigripes* is widely distributed throughout the eastern and midwestern United States and Canada, where it is associated with bark beetles in both conifers and hardwoods. Adults are active during the spring and early summer. The distinguishing characteristics of the adults are that the beetle is 5.0–7.0 mm long and has reddish brown elytra with two transverse yellow bands, outlined with traces of white pubescent setae (Downie and Arnett, 1996) (Fig. 6a).

Madoniella dislocatus

Synomyns for *M. dislocatus* include; *Enoplium dislocatum* Say, *Phlogistosternus dislocates* (Say), and *Phyllobaenus dislocatus* Say. *Madoniella dislocatus* is widely distributed throughout the eastern United States and Canada. It has been found in Florida, Georgia, Indiana, Illinois, Iowa, Kansas, Maine, Massachusetts, Michigan, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, South Carolina, Tennessee, Texas, West Virginia, and Wisconsin, as well asOntario, Canada (Leavengood, 2008). It is a generalist predator associated with bark beetles in several species of conifers and hardwoods, including *P. juglandis.* Adults are diurnal and active from March into May. The key characteristics that distinguish this species are a slender and elongate appearance (3.5–6.0 mm long), an entirely brown pronotum, three yellowish markings on the elytra, emarginate eyes, and a three-segmented antennal club that is shorter than the remaining antennal segments (Leavengood, 2008) (Fig. 6b).

Pyticeroides laticornis

Synomyns for this clerid include *Ellipotoma laticornis* Say, *Enoplium laticorne* Say, *Ichnea laticornis* Say, and *Neichnea laticornis* Say. *Pyticeroides laticornis* is found in the eastern and central United States and has been recorded in Alabama, Arkansas, Colorado, Connecticut, District of Columbia, Florida, Georgia, Illinois, Indiana, Kansas, Kentucky, Maine, Maryland, Massachusetts, Michigan, Missouri, Mississippi, New Jersey, New York, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, and West Virginia, as well as Ontario, Canada (Leavengood, 2008). This species is a generalist, diurnal predator of bark beetles that feeds on prey in several hardwood species, attacking all stages of bark beetles in their galleries. The females lay an egg at the entrance hole of the prey, and upon hatching, the larva enters the tunnel and feeds on all the soft tissue of the adult prey, leaving only the exuviae. Mature larvae are believed to overwinter within the tunnel. The key characteristics that distinguish this species are nine antennomeres and a three-segmented antennal club that is longer than funicular, an orange pronotum, and elytra that are entirely black and patternless (Leavengood, 2008) (Fig 6c).

There is very little published information on natural enemies of the walnut twig beetle, especially in its native range in the southwestern United States and northern Mexico. However, with the recent discovery of natural enemies feeding on *P. juglandis* in the invaded range in eastern North America, species of natural enemies from the pest's native range must be evaluated to assess their potential for use as biological control agents in the beetles invaded range. With the rapid spread of this damaging insect-pathogen complex, further consideration and work is needed to develop and implement an integrated pest management program at state and regional levels. Given that 1) the thousand cankers disease pathogen is not systemic, 2) large numbers of beetles are required to kill the tree, and 3) mortality is a gradual process, biological control may be a promising option, compared with other insect/disease complexes such as redbay ambrosia beetle (*Xyleborus glabratus* Eichoff)/laurel wilt, which can kill

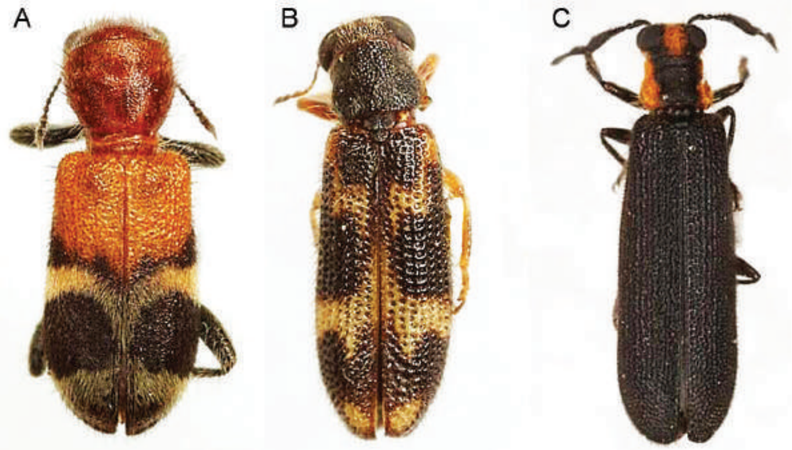

Figure 6 Predators of walnut twig beetle in Tennessee: A) *Enoclerus nigripes* B) *Madoniella dislocatus,* and C) *Pyticeroides laticornis*. Photos by Mike Quinn, TexasEnto.net.

hosts rapidly with a single, beetle-vectored inoculation with a systemic pathogen. The combined use of biological control, chemical control, sanitation, and regulatory limits on the movement of walnut material may have potential to maintain this invasive pest below ecologically damaging levels.

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XXXII Sirex Woodwasp

(*Sirex noctilio* Fabricius) (Hymenoptera: Siricidae)

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DESCRIPTION OF PEST

Taxonomy

Sirex noctilio (Fig. 1) from "Germania" was first described in 1793 by Fabricius. Synonyms were published in 1871 (*Sirex melanocerus* Thomson) and 1909 (*Paururus atlantidis* Ghiji) (Schiff et al., 2012). The genus *Sirex* has been revised for the Western Hemisphere where 14 species are known (one invasive and 13 native) from North America, Mesoamerica (an area from central Mexico to Guatemala), and the Greater Antilles, and more species are expected to exist. A total of 28 species are known from the Northern Hemisphere (Schiff et al., 2012).

Figure 1 Adult *Sirex noctilio* female ovipositing into the side of the cardboard barrel containing the pine bolt from which it emerged. E. Erin Morris.

Distribution

Sirex noctilio is native to Eurasia and northern Africa and has been known from New Zealand since 1900 (Miller and Clark, 1935). It is assumed to have been introduced into New Zealand in timber from Europe (Talbot, 1977). From New Zealand, *S. noctilio* continued to spread in the Southern Hemisphere, being first discovered in Tasmania in 1952, mainland Australia in 1961, Uruguay in 1980, Argentina in 1985, Brazil in 1988, South Africa in 1994, and Chile in 2001 (Hurley et al., 2007; Beèche et al., 2012). In 2004, *S. noctilio* was collected for the first time as an invasive species in the North Hemisphere, in New York State (Hoebeke et al., 2005), and in 2005 it was found in Ontario, Canada (de Groot et al., 2006). By 2012, the distribution of *S. noctilio* in North America included New York, Pennsylvania, Vermont, Michigan, Ohio, Connecticut, and New Jersey (NAPIS, 2012). The introduction of *S. noctilio* to North America likely occurred before 2004, based on the extent of the infestation when first detected. The North American invasion is the first instance of a *S. noctilio* introduction into a region with native pines, supporting native species of siricids (including species of *Sirex*) and their parasitoids.

Damage

Type *Sirex* species are generally considered pests of secondary importance in their native areas (Furniss and Carolin, 1977; Madden, 1988; Spradbery and Kirk, 1978), where they attack trees that are already stressed. *Sirex noctilio* differs because it is aggressive when invasive, attacking and killing seemingly healthy trees. *Sirex noctilio* females lay eggs within trees, at the same time depositing cells of a white rot fungus, *Amylostereum areolatum* (Chaillet ex Fr.) Boidin, and phytotoxic mucous. When mucous is injected, it initially causes tissue desiccation, collapse of phloem cells, and changes in plant respiration. Collectively these symptoms reduce the tree's resistance to the fungus (Coutts, 1969a; Fong and Crowden, 1973). The fungus subsequently dries out the sapwood by restricting sap flow to the crown (Coutts, 1969b; Kile and Turnbull, 1974). Together, the fungus and mucous kill the tree. *Sirex noctilio* prefers pines

(*Pinus* spp.), although other conifers, including *Auricaria* spp., are sometimes attacked (Madden, 1988; Ryan and Hurley, 2012).

Extent Although *S. noctilio* was first reported in New Zealand in 1904, it was not documented as a serious pest in New Zealand until approximately 1926 (Cameron, 2012). By 1946–51, up to one third of the 120,000 hectares of Monterey pine trees (*Pinus radiata* D. Don) on the North Island in New Zealand had been killed by the pest (Gilmour, 1965). Today, throughout much the Southern Hemisphere where *S. noctilio* has been introduced, this species is a major pest of pines, causing extensive damage and monetary loss in pine plantations. In the 1980s, a total of 1.8 million Monterey pine trees in southeastern Australia were killed due to a particularly dramatic outbreak population of *S. noctilio* (Haugen and Underdown, 1990). Outbreaks of *S. noctilio* are particularly associated with stands of pines that are stressed by overstocking and/or drought (Talbot, 1977; Cameron, 2012).

Biology of the Pest

The white rot fungus that *Sirex* females inject into coniferous trees during oviposition is required for development of their larvae. Therefore, the life cycle of *S. noctilio* must be explained in conjunction with that of its mutualistic fungus. Larvae benefit because the fungus rots and dries the wood and thus provides the environmental conditions, enzymes, and nutrients needed for larval growth (Madden and Coutts, 1979). Larvae of *S. noctilio* carry the fungus with them in their hypopleural organs, while adult females of *S. noctilio* carry fungal cells in a pair of intersegmental organs called mycangia, at the base of the ovipositor. In addition, females also have a reservoir containing phytotoxic mucous in their abdomens, and they inject this mucous into trees when they deposit eggs or fungus.

Sirex noctilio usually has one generation per year, but in colder climates one generation may require two to three years (Ryan and Hurley, 2012). Adult *S. noctilio* are highly variable in size, ranging from 9–35 mm in length (Hoebeke et al., 2005). Adults emerge from early summer to early autumn and then mate. Adult females are pro-ovigenic and each contains from 30–450 eggs upon adult eclosion, with the number of eggs depending on the size of the female (Madden, 1974). Females use their sawtooth ovipositors to drill into trees. Often, initial single drills by females are exploratory while females search for trees with acceptable osmotic pressure levels in the phloem sap. Once a female has accepted a tree, she creates an external hole in the bark and drills 1–4 holes, at different angles, up to 12 mm into the sapwood (Coutts and Dolezal, 1969). If there is only a single drilling event, fungal arthrospores and mucous are deposited, but when there are multiple drilling events in a tree, eggs and mucous are deposited in each insertion, except the last drill when fungus plus mucous are inserted. In an attacked tree, the fungus quickly begins to grow in the wood, and once eggs hatch, early instar larvae feed on the fungus (Madden and Coutts, 1979). There is some uncertainty if later instars of *S. noctilio* feed directly on the fungus or on the fungal-invaded wood, but later instars of the related *Sirex cyaneus* F. are reported as eating their symbiotic fungus (*Amylostereum chailletii* [Pers.] Boidin) to acquire the enzymes for digestion of wood (Martin, 1987), and *S. noctilio* may be similar in this regard. *Sirex noctilio* is considered to be more aggressive towards trees in comparison with other species of *Sirex* from Europe and North Africa, as it is the only European siricid tested that causes phytotoxicity in trees (Spradbery, 1973). Also, the mucous gland and reservoir of *S. noctilio* are larger than those of other siricids from Europe (Spradbery, 1977). A comparable evaluation of the mucous glands of native North American *Sirex* species has not been conducted, although North American *Sirex* generally do not kill vigorous trees (Morgan, 1968).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

Thirteen species of *Sirex* are native to North America, Mesoamerica (an area from central Mexico to Guatemala), or the Greater Antilles, and among these, three *Sirex* species are native to the northeastern and north central United States, where *S. noctilio* now occurs. These eastern North American *Sirex* species show preferences for different tree genera: *Sirex nigricornis* F. (now including *S. edwardsii* Brullé [Goulet, 2012]) is predominantly reared from pine (*Pinus*). *Sirex nitidus* (T. W. Harris) is predominantly reared from spruce (*Picea*), and *S. cyaneus* is predominantly reared from fir (*Abies*). Although there is some flexibility in host use by each of these *Sirex* species, there is a greater chance that *S. noctilio* will develop in the same trees as the native *S. nigricornis*, as both of these species prefer pines. In addition, five siricid species in the genus *Urocerus* are also native to North America and there is one invasive *Urocerus*. Because most species of *Urocerus* have broad host ranges that include some pines, there is also the chance that these insects could bore in the same trees as *S. noctilio*.

Native Natural Enemies Affecting the Pest

In 1951, the native New Zealand parasitoid *Guiglia schauinslandi* (Ashmead) (Hymenop.: Orussidae) was found attacking *S. noctilio* larvae (Rawlings, 1957). In 1967, the native Tasmanian ichneumonid *Certonotus tasmaniensis* Turner was found parasitizing about 12% of *S. noctilio* larvae (Hocking, 1967). However, as would be predicted by the enemy release hypothesis, after introduction, populations of *S. noctilio* in the Southern Hemisphere reached outbreak levels without adequate levels of attack by these local natural enemies before classical biological control programs were carried out.

The situation is different in North America, because *S. noctilio* was introduced to a region with native siricids that prefer pine. Therefore, a natural enemy community already exists that may attack this invasive sawfly. Thus far, there is circumstantial evidence that native North American parasitoids are parasitizing *S. noctilio*. Long et al. (2009) studied parasitoids emerging from Scots pines (*Pinus sylvestris* L.) in New York State co-infested by *S. noctilio* and the native *S. nigricornis* (*S. edwardsii* is mentioned, but this species has now been synonymized with *S. nigricornis* [Goulet, 2012]). In this study, the ibaliid *Ibalia leucospoides ensiger* Norton caused 20.5% parasitism of the mixed species of siricids, while the ichneumonids *Megarhyssa nortoni* (Cresson) and *Rhyssa lineolata* (Kirby) each caused <1.0% parasitism. Because *S. noctilio* was much more abundant than *S. nigricornis* (94.3% of siricids emerging from wood were *S. noctilio*), the authors speculated that the majority of parasitoids from this study most probably had attacked *S. noctilio*. Ryan et al. (2012) reported similar levels of parasitism by *Ibalia leucospoides* (Hochenwarth) in pines infested by *S. noctilio* and *S. nigricornis* in Ontario, Canada. In New York State, Standley et al. (2012) reported that, in pines predominantly infested by *S. noctilio,* the cleptoparasite *Pseudorhyssa nigricornis* (Ratzeburg) attacked 26% of rhyssine parasitoids found.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

It is thought that *S. noctilio* was initially introduced to the Southern Hemisphere from Europe, although the exact origin of the introduction is not known. *Sirex noctilio* was subsequently moved among pine-growing countries in the Southern Hemisphere, country to country. The exact origin of *S. noctilio* introduced to North America is still uncertain, although one study suggests that the introduction came from Europe and not from the infestations in the Southern Hemisphere (Nielsen et al., 2009).

Areas Surveyed for Natural Enemies

Beginning in 1928, parasitoids of *S. noctilio* were collected in Europe with the goal of releasing them in New Zealand for permanent establishment. However, after *S. noctilio* was detected in Tasmania and mainland Australia, a much larger program of foreign exploration (1963–1970) was undertaken, funded by the Australian National Sirex Fund (Spradbery and Kirk, 1978). Approximately 400, 1 m long pieces of *Sirex*-infested wood were collected during fall and winter from 19 European countries, Turkey, and parts of North Africa. Wood was debarked and shipped to the United Kingdom, where it was placed in cages to rear out Hymenopteran parasitoids and parasitic nematodes from various *Sirex* species (Fig. 2). In addition, collections

Figure 2 Cages containing *Sirex*-infested logs collected during foreign exploration and used for rearing natural enemies at Silwood Park, Ascot, United Kingdom between 1963-1970. P. Spradbery.

were made by collaborating organizations and scientists in Canada (Vancouver and New Brunswick), the United States (California, Nevada, Arizona, New Mexico and the southeast), and Asia (India, Pakistan, and Japan) (Taylor, 1976; Bedding and Akhurst, 1978; Cameron, 2012). During foreign exploration, areas with Mediterranean climates were emphasized, when possible. Host collections were not restricted to *S. noctilio*, but included other conifer-feeding woodwasps (Murphy, 1998; Cameron, 2012), perhaps under the assumption that parasitoids of concealed hosts are frequently idiobionts, which often are not limited to single species (Quicke, 1997).

Natural Enemies Found during Foreign Exploration

Parasitoids Between 1928 and 1968, one species of stephanid, four species or subspecies of ibaliids and 13 species or subspecies of ichneumonids (all Hymenoptera) were found in the United States, Canada, Europe, or Asia and were sent to New Zealand or Australia (Table 1). One species, *R. lineolata*, a North American ichneumonid, was found in New Zealand without having been purposefully introduced there (Nuttall, 1974). Among these collections, Spradbery and Kirk (1978) reported that during their foreign exploration of Europe, Turkey, and North America, seven species of hymenopteran parasitoids were found (Table 2). It was discovered that one of these parasitoids, *P. nigricornis* (Ratzeburg) (previously reported as *P. maculocoxis* and *P. sternata*), was a cleptoparasite (Spradbery, 1969), and therefore work with this species was not continued. The six remaining parasitoid species reported by Spradbery and Kirk (1978) were collected in association with many species of siricids (Table 2).

Initially, right after *S. noctilio* was found in Australia in 1960, parasitoid shipments resulting from foreign exploration were compromised by low survival of parasitoids, but survival during transit later improved as the program continued (Cameron, 2012). Parasitoids released later in Southern Hemisphere countries other than New Zealand and Australia (including Tasmania) were redistributions from Southern Hemisphere areas infested earlier.

Table 1 Parasitoids found during foreign exploration and sent to New Zealand or Australia (Taylor, 1976; Nuttall, 1989; Hurley, 2007).

Species	Locations found
Family Stephanidae	
Schlettererius cinctipes (Cresson)	USA
Family Ibaliidae	
Ibalia leucospoides leucospoides (Hochenwarth)	Europe
Ibalia leucospoides ensiger Norton	USA
Ibalia rufipes rufipes Cresson	USA
Ibalia drewseni Borries	Europe
Family Ichneumonidae	
Megarhyssa nortoni nortoni (Cresson)	USA
Megarhyssa nortoni quebecensis (Provancher)	Canada
Megarhyssa praecellens (Tosquinet)	Japan
Megarhyssa emarginatoria (Thunberg)	Europe
Rhyssa persuasoria persuasoria (L.)	Europe
Rhyssa persuasoria himalayensis Wilkinson	India, Pakistan
Rhyssa amoena Gravenhorst	Europe
Rhyssa alaskensis Ashmead	USA
Rhyssa crevieri (Provancher)	Canada
Rhyssa hoferi Rohwer	USA
Rhyssa lineolata (Kirby)*	Canada
Odontocolon geniculatus (Kreichbaumer)	Europe

*This species was discovered in New Zealand without being purposefully introduced (Nuttall, 1974).

Table 2 Records of siricid hosts and their hymenopteran parasitoids reared from infested wood collected during foreign exploration of Eurasia and North Africa, 1963–1970 (from Spradbery and Kirk, 1978).

Host	Parasitoid Species					
	Rhyssa persuasoria (L.)	*Rhyssa amoena* (Gravenhorst)	*Megarhyssa emarginatoria* (Thunberg)	*Ibalia leucospoides leucospoides* (Hochenwarth)	*Ibalia rufipes drewseni* Borries	*Odontocolon geniculatum* (Kriechbaumer)
Sirex noctilio F.	+	-	-	+	+	+
Sirex torvus M. Harris[*]	+	+	+	+	+	+
Sirex juvencus (L.)	+	+	+	+	+	+
Urocerus gigas (L.)	+	+	+	+	+	+
Urocerus augur (Klug)	+	+	+	+	+	+
Urocerus sah (Mocsáry)	+	-	-	+	+	-
Urocerus fantoma (F.)	+	-	-	-	-	-
Xeris spectrum (L.)	+	+	+	+	+	

[*] Presented as *S. cyaneus* by Spradbery and Kirk (1978) but this European species has recently been designated as *S. torvus* (Schiff et al., 2012).

Predators During foreign exploration conducted by Spradbery and Kirk in Europe from 1963–1971, wood was collected in which woodpecker predation of *S. noctilio* larvae was evident (Spradbery, 1990). It was hypothesized that the great spotted woodpecker (*Dendrocopos major* [L.]) and black woodpecker (*Dryocopus martius* [L.]) were responsible for the majority of this predation.

Nematodes The nematode *Deladenus siricidicola* Bedding (= *Beddingia siricidicola* [Bedding]) was first found parasitizing *S. noctilio* in New Zealand in 1962 (Zondag, 1962), where it was thought to have been transported when *S. noctilio* itself invaded New Zealand. After *S. noctilio* was found in Australia in 1960, a worldwide search for parasitoids of siricid woodwasps in their native ranges in the Northern Hemisphere occurred (1963–1970), and in addition to parasitoids, this effort detected several hundred strains of seven species of *Deladenus* nematodes parasitizing various siricids (Bedding and Akhurst, 1978) (Table 3). Only two species of fungal symbionts were found to be associated with the collected siricids: the basidiomycete white rot fungi *A. areolatum* and *A. chailletii*. These nematode species had both mycophagous and parasitic phases and, consequently, cultures of the mycophagous phases were established in the laboratory. Strains of the nematodes were grown using potato dextrose agar cultures of the species of *Amylostereum* with which the siricid hosts were associated.

Several factors were used to evaluate the nematode species and strains collected by Spradbery and Kirk (1978) as potential biological control agents of *S. noctilio* in Australia. First, the candidate nematode had to be able to parasitize *S. noctilio*. Second, the nematode should not parasitize the hymenopteran parasitoids of *S. noctilio*. Third, the nematode had to be able to survive when feeding on *A. areolatum,* the symbiotic fungus carried by *S. noctilio*. Of all the nematode species found, most were able to survive only on one species of fungi, either *A. areolatum* or *A. chailletii*. Only one nematode, *Deladenus wilsoni* Bedding, was able to survive on both species of fungi (Bedding and Akhurst, 1978). The only nematodes that were able to feed on *A. areolatum* were *D. siricidicola* and *D. wilsoni*, but the latter species was rejected as a biological control agent because it also parasitized some of the parasitoids of *S. noctilio* (Bedding and Akhurst, 1978).

Once *D. siricidicola* was selected for use in biological control, different strains of this species were evaluated further for their suitability for use in a control program. Some strains of *D. siricidicola* that were eliminated from consideration were able to parasitize *S. noctilio* but failed to enter the eggs of the host and therefore were non-sterilizing (Bedding, 1972). Of the remaining strains of

Table 3 Records of insect and tree hosts of *Deladenus* nematodes collected during worldwide foreign exploration (from Bedding and Akhurst, 1978).[*,**]

Deladenus species	*Amylostereum* species	Insect hosts[**]	Tree hosts	Collection locations
Deladenus canii Bedding	*Amylostereum chailletii* (Pers.) Boidin	*Sirex cyaneus* F.	*Abies* *Picea*	Europe North America
Deladenus imperialis Bedding	*A. chailletii*	*Sirex imperialis* Kirby	*Abies*	Pakistan
Deladenus nevexii Bedding	*A. chailletii*	*S. cyaneus* *Sirex longicauda* Middlekauff *Urocerus californicus* Norton *Urocerus albicornis* (F.) *Xeris spectrum* (L.) *Xeris morrisoni* (Cresson)	*Abies*	Europe North America Japan
Deladenus proximus Bedding	*A. chailletii*	*Sirex nigricornis* F.	*Pinus*	North America
Deladenus rudyii Bedding	*A. chailletii*	*Sirex juvencus* (L.) *S. cyaneus* *Urocerus gigas* L. *Urocerus augur* (Klug) *Urocerus japonicas* (Smith) *Urocerus antennatus* Marlatt *X. spectrum*	*Abies* *Chamaecyparis* *Cryptomeria* *Picea*	Europe North America Japan
Deladenus siricidicola Bedding	*Amylostereum areolatum* (Chaillet ex Fr.) Boidin	*Sirex noctilio* F. *S. juvencus* *Sirex nitobei* Matsumura *S. cyaneus* *X. spectrum*	*Larix* *Picea* *Pinus*	Europe North America Australia New Zealand Japan
Deladenus wilsoni Bedding	*A. chailletii*, *A. areolatum*	*S. juvencus* *S. cyaneus* *U. gigas* Multiple Rhyssines[***]	*Abies* *Cedrus* *Larix* *Picea* *Pinus*	Europe Turkey North America Japan India Morocco

[*] For each nematode species, entries for fungal associates (*Amylostereum*), insect hosts, tree hosts and collection locations demonstrate the diversity seen in foreign exploration collections; some more detailed data on associations at different locations can be found in Bedding and Akhurst (1978).

[**] Names for insect hosts in some cases are being revised or have recently been revised (Schiff et al., 2012; H. Goulet personal communication). Names presented in this table are those used by Bedding and Akhurst (1978).

[***] A list of 12 species of rhyssine ichneumonids is presented in Bedding and Akhurst (1978; Table 3).

D. siricidicola, the one ultimately chosen was from Sopron, Hungary, originating from a single specimen of *Sirex juvencus* (L.). In addition to its ability to parasitize and sterilize *S. noctilio* and grow on *A. areolatum*, the Sopron strain caused nearly 100% parasitism of emerging *S. noctilio*. Also, emerging adults of *S. noctilio* infected by this strain of the nematode were larger than adults parasitized by other strains of *D. siricidicola*. The large size of parasitized *S. noctilio* was important because larger individuals were able to fly farther and lay more eggs, thus helping to disseminate the nematode (Bedding, 2009).

Host Range Test Results

Southern Hemisphere Pines are not native to the Southern Hemisphere; therefore, there was no native community of pine-associated insects to use for host-range testing. However, tests were conducted to make sure that natural enemies to be released did not harm each other. Different species and strains of *Deladenus* were tested to evaluate their effect on parasitic Hymenoptera that also were being introduced. *Deladenus siricidicola*, the nematode that was chosen for release, did not parasitize any of these siricid-attacking parasitoids, but *D. wilsoni*, another candidate nematode, was rejected because it did (Bedding and Akhurst, 1978). In Europe, the wood-boring melandryid beetle *Serropalpus barbatus* (Schaller) is known to be parasitized by *D. siricidicola* (as well as by *D. wilsoni*), but this beetle does not occur in the Southern Hemisphere.

Northern Hemisphere In North America, the Kamona strain of *D. siricidicola* (Fig. 3) (so named because it was collected in the Kamona forest in Tasmania, the site where the original Sopron strain from Europe was released) was injected into pines naturally infested with *S. noctilio* and related insects in the field. Injected pines were subsequently taken to a rearing facility and insects reared out, preventing field release of *D. siricidicola*. Nontarget species in the nematode-injected trees were evaluated to see whether any had been parasitized by the Kamona strain of the nematode. These studies are ongoing and results have yet to be published.

Figure 3 Adult mycophagous *Deladenus siricidicola* Kamona strain female with eggs. E. Erin Morris.

Releases Made

Southern Hemisphere: Parasitoids Hurley et al. (2007) provide an excellent summary of the extensive literature on *Sirex* parasitoids released in the Southern Hemisphere. A total of 10 species or subspecies of parasitic Hymenoptera were variously released in Tasmania, mainland Australia, or New Zealand from 1962 to 1973. However, the large rearing program employed resulted in some mixing of parasitoid strains such that it is possible that some of the *I. leucospoides* released in New Zealand were actually hybrids between *I. l. ensiger* and *Ibalia leucospoides leucospoides* (Hochenwarth), and the *Rhyssa persuasoria* (L.) released were hybrids between *Rhyssa persuasoria persuasoria* (L.) and *Rhyssa persuasoria himalayensis* Wilkinson (Nuttall, 1989).

Subsequently, parasitoids, including putative hybrids, were accidentally or purposefully introduced into South America and South Africa (Hurley et al., 2007; Cameron, 2012). In South America, *I. leucospoides* was found in Uruguay in 1984, and it is thought to have been introduced when *S. noctilio* or the siricid *Urocerus gigas* L. were introduced. This parasitoid spread, either on its own or with human assistance, throughout the various parts of America infested with *S. noctilio*. *Ibalia l. leucospoides* arrived in Chile along with *U. gigas* and readily switched to *S. noctilio* (Cameron, 2012). *Rhyssa persuasoria* and *M. nortoni* were also released in various South American countries, including Brazil (1996 and 1997, respectively), where *S. noctilio* was established (Hurley et al., 2007). In South Africa, *I. l. leucospoides* and *M. nortoni* were released in the Western Cape region, while only *I. l. leucospoides* was released in the KwaZulu-Natal and the Eastern Cape region (Hurley et al., 2007).

Southern Hemisphere: Nematodes After Zondag's discovery that *S. noctilio* populations on the North Island of New Zealand were parasitized with *D. siricidicola,* these nematodes were introduced on the South Island of New Zealand in 1969 (Zondag, 1979). By 1971, a strain of *D. siricidicola* called the Sopron strain (after its collection origin in Sopron, Hungary) had been selected for biological control and the Sopron strain was released throughout the Australian *Sirex* infestations. Also, the Sopron strain was released in Brazil in 1989 (Hurley et al., 2007). However, during an outbreak of *S. noctilio* in the Green Triangle in southeastern Australia in 1987–1990, it was discovered that the Sopron strain had declined in virulence (Bedding, 1993). Due to continuous rearing (over 20 years) of the nematode as the mycophagous form in laboratory cultures, this strain could no longer be induced to produce the infective form (Haugen and Underdown, 1993). To remedy this problem, in 1991 virulent nematodes were collected at one of the sites, Kamona forest, Tasmania, where the Sopron strain had originally been released. These nematodes were used to re-establish laboratory colonies capable of parasitic as well as mycophagous growth. This re-isolated strain was named the Kamona strain (Fig. 3), and it continues to be used in biological control programs across the Southern Hemisphere (Bedding, 2009). Precautions are now taken in laboratory rearing procedures to ensure that the Kamona strain does not lose the ability to readily switch to the parasitic form. The Kamona strain was introduced into Uruguay (1987), Argentina (1989), Brazil and South Africa (1995), and Chile (2006) (Hajek et al., 2005; Beèche et al., 2011).

Northern Hemisphere No natural enemies of *S. noctilio* have been released to date in North America (see Recommendations section below).

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

Southern Hemisphere parasitoid impact In New Zealand, the first country where parasitoids were introduced, *R. p. persuasoria*, *I. l. leucospoides*, *I. l. ensiger,* and *Megarhyssa nortoni nortoni* (Cresson) were recovered after release. Subsequently, parasitism by *I. l. leucospoides* and *Rhyssa* spp. was reported at 70% or more in some areas (Nuttall, 1989).

In Tasmania, where parasitoids were introduced next, the same species became established, as well as the stephanid *Schlettererius cinctipes* (Cresson) (Taylor, 1978). *Megarhyssa nortoni* and *R. persuasoria* were reported as the most abundant parasitoids and were considered responsible for reducing *S. noctilio* populations significantly from 1965 to 1974. In Tasmania, parasitism of *S. noctilio* by *I. l. leucospoides* was found to be density-independent, while parasitism by *R. p. persuasoria* and *M. n. nortoni* showed delayed-density dependency (Taylor, 1978).

In Australia, where parasitoids were next released, three species of *Rhyssa* (*R. p. persuasoria*, *Rhyssa hoferi* Rohwer, and *R. lineolata*), two species of *Ibalia* (*I. l. leucospoides* and *I. l. ensiger*), *S. cinctipes,* and *M. n. nortoni* were recovered after release. In Victoria and New South Wales, *Ibalia* species were the most abundant parasitoids, causing up to 40% parasitism (Hurley et al., 2007).

In South America*, I. leucospoides* now occurs throughout areas infested by *S. noctilio* (Hurley et al., 2007). Percent parasitism in Brazil reached 39% but averaged 25%, and in the Patagonian region of Argentina, parasitism by *I. leucospoides* was 20–40%. *Rhyssa persuasoria* and *M. n. nortoni* have been mass-reared and released in Brazil but have not become established.

In South Africa, *I. l. leucospoides* was introduced but established only in some areas. *Megarhyssa n. nortoni* was released but has not yet been recovered following its release.

In summary, both establishment and degree of impact of different parasitoid species released in the Southern Hemisphere have varied widely among regions and parasitoid species. In some instances the numbers of parasitoids released or the numbers of individuals used to establish colonies were very small; this could have caused genetic bottlenecks that may explain lack of establishment in some cases and variable impacts in others (Hurley et al., 2007; Cameron, 2012).

Southern Hemisphere nematode impact The strain of *D. siricidicola* discovered on the North Island of New Zealand was the first strain of this nematode to be released (on the South Island). By 1975, >75% of the *S. noctilio* recovered from un-inoculated trees at some places in the South Island were found to be parasitized by *D. siricidicola*.

Subsequent to the releases from the North to South Island of New Zealand, efforts shifted to releasing the Sopron strain of *D. siricidicola* from Hungary. Releases of the Sopron strain in Australia resulted in almost 100% parasitism (Bedding and Akhurst, 1974). Releases in Tasmania in 1970 resulted in the presence of Sopron strain in 92% of *S. noctilio*-infested trees.

A third nematode isolate (the Kamona strain) was used for releases after it was discovered in 1987–1990 that the Sopron strain had lost virulence. The Kamona strain was released in Australia, South America, and South Africa. High levels of parasitism (>70%) by this strain of *D. siricidicola* were subsequently reported in Brazil (Iede et al., 2012), while in Argentina, parasitism by *D. siricidicola* was 58% in 2002, but increased to nearly 100% by 2007 (Klasmer and Botto, 2012). In the Cape Region of South Africa, 23% parasitism by the Kamona strain was reported after introduction, but two years later parasitism had increased to 96.1% (Tribe and Cilié, 2004). In the summer-rainfall region of South Africa, the Kamona strain of *D. siricidicola* initially parasitized <10% of *S. noctilio* (Hurley et al., 2007) although five years later, parasitism by the Kamona strain had risen to 50% in the bottom sections of trees at some sites (Hurley et al., 2012). Studies investigating why *D. siricidicola* success in South Africa has been low in some areas demonstrated that low moisture levels in the drier tops of trees are associated with poor nematode establishment (Hurley et al., 2008). In addition, competition between *A. areolatum* and sap staining fungi within trees may have limited the growth of *A. areolatum* and therefore the growth of the nematode, especially under conditions of lower water potential (Hurley et al., 2012).

Nontarget Effects

No nontarget effects from releases of natural enemies have been reported for the Southern Hemisphere.

Recovery of Affected Tree Species or Ecosystems

In the Southern Hemisphere, no native plant communities were affected by the *S. noctilio* invasion and it is too soon to discern the effect of this species on the native pine forests of North America. In pine plantations in the Southern Hemisphere, the introduction of the parasitic nematode and species of parasitic Hymenoptera have proven to be important components of an integrated control program against *S. noctilio*, when used in concert with silvicultural practices that promote forest health. It does not seem possible to identify whether nematodes or parasitoids or silviculture are the most important agent/practice. In these Southern Hemisphere areas, land managers must maintain diligence. Classical biological control introductions do not remain established at high enough levels forever. At sites with low densities of *S. noctilio*, the introduced nematode does not persist for more than a decade (Carnegie and Bashford, 2012); therefore, if increasing *S. noctilio* populations are detected in such areas, the nematode must be reintroduced, using an inoculative strategy. For this purpose, Ecogrow Environment (Queanbeyan, NSW, Australia) mass produces and sells the Kamona strain of *D. siricidicola*.

Broad Assessment of Factors Affecting Success or Failure

The factors affecting the success of biological control of *S. noctilio* in the Southern Hemisphere are discussed by Slippers et al. (2012). As in many classical biological control programs, differences in phenology between areas can make movement of natural enemies difficult, an extreme case being the inversion of seasons that must be overcome when biological control agents are moved between the northern and southern hemispheres. For example, when parasitoids are emerging in the Southern Hemisphere, *S. noctilio* in the field in Europe and North America is in the larval stage in the middle of the winter.

In addition, agents used in the Southern Hemisphere may not be climatically adapted to colder continental climates of the invaded area in North America because the original foreign exploration from 1963–1970 emphasized the collection of parasitoids from areas with milder climates similar to the invaded areas of Australia (Cameron, 2012).

One factor that strongly affected the success of this project in Australia was the loss of infectivity of the nematode *D. siricidicola* in mass rearing, when growing only the mycophagous phase for many generations. Currently, methods have been developed to maintain the virulence of nematode strains under mass rearing conditions (see Recommendations below).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

The Nematode *Deladenus siricidicola*

Deladenus siricidicola has two very different life stages, including a free-living form and a parasitic form. The free-living form of feeds on the symbiotic fungus used by *S. noctilio*, while the parasitic form invades larvae of both female and male *S. noctilio*, leading to sterilization of adult females (Bedding, 2009). Individual nematodes from the two life cycles of *D. siricidicola* differ in morphology as well as biology. Mycophagous and parasitic nematodes differ so much in morphology that initially, it was thought that *D. siricidicola* from the different life cycles belonged to two different nematode families. The fungal-feeding forms are larger in size, with spermatozoa 10–12 um in diameter, and are usually oviparous. The parasitic forms are smaller, with spermatozoa 1–2 um in diameter, and ovoviviparous (Bedding, 1972). The fungal-feeding form of *D. siricidicola* lives in pine trees and undergoes 20–30 generations per year, during which the nematodes eat the growing hyphal tips of *A. areolatum* (Bedding, 2009). Mycophagous nematodes spread through the tracheids of the wood as they follow the growth of the fungus. However, the presence of *S. noctilio* larvae in the vicinity of the nematode, induces transformation to the parasitic stage via environmental cues. Mycophagous male and female nematode larvae respond to elevated CO_2 levels and lower pH and develop into parasitic adults. Parasitic adults mate and then from 1–100 adult females invade a single *S. noctilio* larva. Once inside the host, the female nematodes shed their outer cuticles so they can absorb food directly from the host blood via microvilli that cover their bodies. Females grow rapidly, increasing up to a 1000 fold in volume within a few weeks, although their reproductive system is not triggered to develop eggs until the pupation of the host. Nematode eggs hatch into juveniles that then migrate to the reproductive organs of the host. In female hosts, juvenile nematodes travel into the ovaries, where virulent forms (including the biological control strain) penetrate the developing host eggs before the chorions harden. When adult females of *S. noctilio* emerge from trees as adults, they mate and lay eggs filled with juvenile nematodes in new trees. The nematodes within infected host eggs are injected into the tree by the woodwasp, along with the fungus *A. areolatum*. At this point in their life cycle, the juvenile nematodes develop into the mycophagous form (Bedding, 2009). Male *S. noctilio* hosts are a dead end for *D. siricidicola*, as the nematodes invade the testes after sperm has already been transferred to the vesiculae seminales, and the nematodes are not transferred to females during copulation. One generation of the mycophagous form of *D. siricidicola* is thought take about two weeks, while one generation of the parasitic form requires 1–3 years (Bedding, 1972).

Parasitoids (*Ibalia*, *Rhyssa,* and *Megarhyssa*)

There are two main groups of parasitic Hymenoptera that attack *S. noctilio*: Ibaliidae and Ichneumonidae. Species of *Ibalia* (Family Ibaliidae) oviposit in first or second instar larvae, close to the bark. Oviposition occurs either during summer, after *S. noctilio* eggs hatch, or in spring if hatching of host eggs has been delayed (i.e., in cases where *S. noctilio* oviposited into trees late in the season).

Species of *Rhyssa* (Fig. 4) and *Megarhyssa* (Ichneumonidae) parasitize *S. noctillio* by using their very long ovipositors to lay eggs on older instar host larvae deep within the wood. These ichneumonids are idiobionts: adults paralyze larval hosts with venom and then larvae feed as ectoparasitoids outside of the host.

Figure 4 Adult *Rhyssa lineolata* female ovipositing in a pine tree. Jessica Nix Greenberg.

Several *S. noctilio* parasitoids (e.g., the *Ibalia* species, *R. persuasoria,* and *M. nortoni*) are attracted to the symbiotic fungus carried by *S. noctilio* (Madden, 1968; Spradbery, 1970, 1974), which helps them find trees and areas on trees where *S. noctilio* larvae are located within the sapwood.

EVALUATION OF THE POTENTIAL FOR CLASSICAL BIOLOGICAL CONTROL OF *SIREX* IN NORTH AMERICA

After *S. noctilio* was found in North America, a pest risk analysis was conducted, both to estimate the potential damage that *S. noctilio* could cause in the United States and to make control recommendations. *Sirex noctilio* was rated as "high risk" with regard to numerous factors. Control strategies recommended by the risk analysis included restricted movement of infested trees and logs, population monitoring, good silvicultural practices in managed stands or plantations to raise tree resistance, and the release of biological control agents, primarily *D. siricidicola* (Borchert et al., 2007).

Parasitic Hymenoptera

During exploration for natural enemies to release in the Southern Hemisphere, collections were made in California, the southwestern and southeastern United States, British Columbia, and New Brunswick, but collections were not made from the areas of eastern North America where the *S. noctilio* invasion was located in 2012. Regardless, most widespread hymenopteran parasitoids of native siricids attacking conifers in North America (Coyle and Gandhi, 2012) were released or accidentally introduced in the Southern Hemisphere (Taylor, 1976; Hurley et al., 2007; Krombein and Hurd, 1978). Unfortunately, the full ranges of specific host associations for most of the *Sirex*-associated parasitoids in North America are unknown, in large part because the larval stages that are attacked live within wood and the host larvae often have not been determined. While many of the parasitoid species introduced against *S. noctilio* in the Southern Hemisphere already occur in North America and attack native siricids, some of the siricid parasitoids that were found in Europe and released in the Southern Hemisphere do not occur in North America. However, since most siricid parasitoids have broad host ranges, European siricid parasitoids are probably unsuitable for introduction to North America, because they likely would parasitize other siricid species. At this time, release of parasitic Hymenoptera against *S. noctilio* in North America is not being considered and extensive host range testing would be necessary before this would be possible.

Parasitic Nematodes

In contrast to parasitoids, the nematode *D. siricidicola* has been considered for introduction to North American against *S. noctilio* populations, although there are numerous aspects that must be considered before proceeding. However, there are several key differences between applicability of *D. siricidicola* in the Southern Hemisphere (where this nematode has been released in many countries) and North America:

(1) Exotic plantations vs. complex natural forest communities Pines are not native to the Southern Hemisphere, but have been introduced and are grown on plantations. In North America, there are many native *Pinus* species both in natural forests and plantations, as well as native species of *Sirex* woodwasps that carry their own species and strains of *Amylostereum* as well as of *Deladenus*. Consequently, the rich diversity that exists within the North American *Pinus-Sirex-Amylostereum* complex plus associates may complicate a biological control program involving *D. siricidicola*.

(2) Climatic tolerances and fungal requirements of nematodes We do not know if the Kamona strain of *D. siricidicola* would survive the winters of northeastern North America (see Williams et al., 2012). However, the Kamona strain of *D. siricidicola* will grow on a diversity of *A. areolatum* strains (Hurley et al., 2012; Morris et al., 2012); and as long as this fungal species is present in a tree, the nematodes should survive in the mycophagous forms until *S. noctilio* larvae are present.

(3) Compatibility of Kamona* D. siricidicola *with North America S. noctilio population Another factor that could affect the use of *D. siricidicola* for biological control in North America is the possibility that the Kamona strain of *D. siricidicola* is incompatible with the strain of *S. noctilio* present in North America. Bedding (1972) found that parasitism by *D. siricidicola* differed in strains of *S. noctilio* from different geographic regions; the timing of host and nematode development must be well matched in order for the juvenile nematodes to migrate into the host eggs before the egg chorions have formed. This was demonstrated when *D. siricidicola* juveniles were unable to enter eggs of a Belgian strain of *S. noctilio*, but were able to enter eggs of Australian *S. noctilio* (recall that no one knows the exact Northern Hemisphere origin of *S. noctilio* in the Southern Hemisphere) (Bedding, 1972). Only when eggs are sterilized is the nematode an effective biological control agent. At least some of the *S. noctilio* populations present in North America are thought to differ from *S. noctilio* in the Southern Hemisphere (Nielsen et al., 2009; Bergeron et al., 2011). Studies are being conducted to investigate the relationship between the strain of *S. noctilio* present in North America and the Kamona strain of *D. siricidicola*.

***(4) Interactions with native North America species of* Deladenus** The presence of other nematodes parasitizing native *Sirex* species further complicates decisions regarding use of the Kamona strain of *D. siricidicola* for biological control of *S. noctilio* in North America. Bedding and Akhurst (1974) found several nematodes, i.e., *D. wilsoni*, *Deladenus nevexii* Bedding, *Deladenus proximus* Bedding, and *Deladenus canii* Bedding, parasitizing native *Sirex* species in North America. *Deladenus siricidicola*, *D. wilsoni*, and *D. proximus* all occur in pines, leading to potential co-infestation of trees with both the invasive *S. noctilio* and the native *S. nigricornis* or potentially other *Sirex* species. Studies are investigating the extent to which native nematodes might parasitize *S. noctilio* and the extent that the Kamona strain of *D. siricidicola* might parasitize native *Sirex*.

(5) Potential nontarget effects of Kamona nematode on native siricid Perhaps of greatest importance, it is presently not known whether the Kamona strain of *D. siricidicola* will parasitize and sterilize the native *Sirex* species, when they co-occur in the same trees as *S. noctilio*, or to what extent this might happen.

(6) ***Potential for hybridization of sterilizing and non-sterilizing strains of* D. siricidol** To complicate matters further, in 2007 and 200, a strain of *D. siricidicola* was found parasitizing *S. noctilio* in Ontario, Canada, pine forests. This was the first record of *D. siricidicola* in North America (Yu et al., 2009). Upon examination of the parasitized Canadian *S. noctilio* females, it was found that the juvenile nematodes were inside of the host egg sheath, but not inside host eggs and therefore were not sterilizing the hosts. It is considered most likely that this nematode arrived with *S. noctilio* when *S. noctilio* invaded. A recent study has documented the occurrence of the non-sterilizing strain of *D. siricidicola* within one individual of *S. nigricornis* (E. E. Morris unpublished data). However, parasitism of *S. nigricornis* by non-sterilizing *D. siricidicola* was only found in one out of fourteen parasitized *S. nigricornis* individuals, and all the others were parasitized by a native species of *Deladenus*. Conversely, two *S. noctilio* out of 19 included in this study were found to be parasitized by a native *Deladenus* usually found in *S. nigricornis*. The 'non-sterilizing' North American strain of *D. siricidicola* could pose a threat to a biological control program involving nematodes. Akhurst (1975) conducted a study in which different species and strains of *Deladenus* were crossed; it was found that while crosses between different *Deladenus* species only rarely produced viable eggs, crosses between strains of the same species of *Deladenus* always resulted in normal numbers of viable offspring. Based on this study, it seems possible that the non-sterilizing strain of *D. siricidicola* could hybridize with the Kamona strain, which might reduce parasitic sterilization of *S. noctilio* (Williams et al., 2012).

***(7) Effects of native species and strains of the fungus* Amylosterem** The presence of native species and strains of *Amylostereum* (Williams et al., 2012) is another factor that could influence the success of the *D. siricidicola* as a biological control agent against *S. noctilio* in North America. While native *Amylostereum* taxa might negatively affect activity and persistence of the Kamona strain of *D. siricidicola* (i.e., if the Kamona strain nematode will not feed or reproduce well on native *Amylostereum*), the opposite situation also could occur. Morris et al. (2012) found that the Kamona strain of the nematode *D. siricidicola* produced significantly different numbers of offspring when feeding on different strains of *A. areolatum*, with the highest number of nematodes being produced on a strain of *A. areolatum* native to North America. In the past, most North American *Sirex* species were believed to carry *A. chailletii* as their symbiotic fungus (Gilbertson, 1984), a fungus that *D. siricidicola* will not consume (Bedding and Akhurst, 1978). However, recent data demonstrate that at least some of the native *Sirex* in the eastern United States at times carry *A. areolatum* and not *A. chailletii* (Nielsen et al., 2009; R. Kepler and A. E. H., unpublished data). The native *S. nigricornis* is one of the species that carries both *A. areolatum* and *A. chailletii* and that species frequently develops in the same pines as *S. noctilio* (Long et al., 2009; Nielsen et al., 2009; Ryan et al., 2012; A.E.H. unpublished data). While there is potential for both *A. areolatum* and *A. chailletii* to co-occur within the same tree, these fungal species are vegetatively incompatible and will not grow in the same exact locations in a tree. Over time, *D. siricidicola* could spread throughout parts of a tree colonized by *A. areolatum*, but areas colonized by *A. chailletii* would not support the nematode. This could prevent the spread of nematodes throughout the tree and thus limit the ability of the nematode to locate and parasitize *S. noctilio* within trees.

(8) Effects of other native fungi Additionally, if they are able to out-compete *A. areolatum*, other fungi commonly found in pine wood might negatively influence *D. siricidicola* reproduction, . Ryan et al. (2011) found that *A. areolatum* strains that occur in Canada were poor competitors in the presence of two "blue-stain" fungi vectored by bark beetles, and Hurley et al. (2012) showed that *A. areolatum* strains present in the Southern Hemisphere were sometimes outcompeted by sap-staining fungi.

To begin answering some of the questions about release of the Kamona strain of *D. siricidicola* in North America, these nematodes were injected into *S. noctilio*-infested trees during four field seasons, and subsequently, the inhabitants of these trees were reared in cages (Williams and Mastro, 2011). In particular, these studies have been conducted to determine (1) if inoculation methods developed in Australia would work well in the United States, (2) if the Kamona strain of the nematode could establish in American pine species, and (3) if the nematode could survive the winter temperatures of the northeastern United States. Also, these studies hoped to measure the effects of parasitization by the non-sterilizing strain versus the Kamona strain of *D. siricidicola* in different pine species and the effects that different strains of *A. areolatum* might have on these nematodes.

CONCLUSIONS

Pines are economically important forest trees around the world. In the Southern Hemisphere where pines have been introduced, invasive *S. noctilio* populations have jeopardized this resource. As is true of projects using classical biological control, this invasive woodwasp is not considered a pest where it is native. In the Southern Hemisphere, introduction of a parasitic nematode and several species of parasitic Hymenoptera have been extremely important agents of biological control of *S. noctilio*, especially when combined with sound silvicultural practices (Slippers et al., 2012). It does not seem possible to identify whether nematodes, parasitoids, or silviculture practices were the most important factor, as is often typical of integrated pest-management programs. The recent introduction of *S. noctilio* to North America is the first time that this aggressive pine-killing woodwasp has been introduced to an area where pines, woodwasps, and their associates are native. At of 2012, *S. noctilio* only occurs in parts of northeastern North America, where pines are not the most abundant trees, and biological control has only been investigated in the laboratory. It is thought that the importance of *S. noctilio* as a pest in North America and the extent to which nematodes might be used for control will be determined within the next few decades, as this invasive spreads further south, where pines are major tree species and are extensively grown in plantations.

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XXXIII Japanese Pine Sawyer

(*Monochamus alternatus* Hope) (Coleoptera: Cerambycidae)

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DESCRIPTION OF PEST

Taxonomy

There are an estimated 35,000 species of Cerambycidae worldwide, with perhaps one-third more to be described from tropical areas (Allison et al., 2004). The North American fauna (north of Mexico) is estimated to include 956–1,400 species in 300 genera (Allison et al., 2004). In 1843, Hope first described *Monohammus* [original spelling] *alternatus* (Coleoptera: Cerambycidae) (Fig.1) as a new species, based on a specimen from China. There is one synonym, *Monochamus tesserula* White, with several alternative spellings: *Monochammus tesserula*, *Monohammus alternatus*, and *Monohammus tesserula* White (Davis et al., 2008; CABI, 2012). The genus, *Monochamus* Megerle, 1982 (Coleoptera: Cerambycidae), is comprised of about 163 species, with a worldwide distribution and different trophic specializations (Cesari et al., 2005).

Figure1 Japanese pine sawyer (*Monohammus alternatus*).

The most characteristic feature of adult cerambycids (longhorned or longicorn beetles) is their long antennae; in males they can be more than twice the length of the body (Allison et al., 2004). *Monochamus* taxonomy is so far based on several morphological features, such as body length and color, elytral shape, distribution of microsculpture, extent and color of the pubescence on the pronotum, elytra, and antennae (Cesari et al., 2005). Cesari et al. (2005) provided karyological and molecular characterization of the European species of *Monochamus* by analyzing the complete mitochondrial cytochrome oxidase I gene and a fragment of the small subunit RNA gene sequences (1,536 base pairs).

Distribution

Monochamus alternatus (Japanese pine sawyer, JPS) is native to China, Japan, Korea, Laos, and Taiwan (Kobayashi et al., 1984; ESK and KSAE, 1994; Kishi, 1995; CABI, 2012). Based on that distribution, Davis et al. (2008) stated its potential distribution within the United States would be east of the Mississippi River, an area with similar biomes as the countries listed above, that is to say temperate broadleaf and mixed forests, and tropical and subtropical moist broadleaf forests.

Damage

Type JPS attacks mainly species in the family Pinaceae, especially 25 species of *Pinus,* including Japanese red pine (*Pinus densiflora* Siebold and Zucc.) and Japanese black pine (*Pinus thunbergii* Parl.) in Japan and Masson's pine (*Pinus massoniana* Lamb.) in China. It also has been recorded from five species of *Picea*, three *Abies*, three *Larix*, and two *Cedrus* species (Kobayashi et al., 1984; Davis et al., 2008; CABI, 2012). In addition, JPS has been found in *Acer* spp., *Cryptomeria* spp., *Cunninghamia sinensis* R. Br. ex Rich. & A. Rich., *Fagus* spp., *Ginkgo biloba* L., *Juniperus* spp., *Larix gmelinii* Rupr., *Larix kaempferi* (Lamb.), *Liquidambar* spp., *Malus* spp., and *Metasequoia* spp. (Davis et al., 2008; CABI, 2012).

Monochamus beetles themselves do little damage to healthy trees in the absence of pine wilt nematodes (*Bursaphelenchus xylophilus* [Steiner and Buhrer] [Nematoda: Aphelenchoididae]) (PWN) (Fig.2). Pine wilt disease (PWD), being the effects of nematode infection, is transmitted by *Monochamus* beetles and has devastated forests in Asian countries such as Japan, China, and Korea. However PWN causes no damage in pine forests of North America where the nematode is in its native range (Rutherford and Webster, 1987). Pine wilt disease also invaded Europe (Portugal) in 1999 (Mota et al., 1999). The quick death of infected trees is characteristic of pine wilt disease. Affected pine trees will appear healthy in early summer but show reddish-brown foliage (Fig. 3) and die by late autumn (Mamiya, 1988). Japanese pine sawyer is known to be the most effective vector of the pine wood nematode in Japan. In Portugal, the PWN was found to be associated with the native beetle *Monochamus galloprovincialis* Olivier (de Sousa et al., 2001; Naves et al., 2006, 2007). The primary vector of the PWN in North America is *Monochamus carolinensis* Olivier (Akbulut and Stamps, 2012). Recently, the Sakhalin pine sawyer, *Monochamus saltuarius* Gebler, has been identified as another important vector of PWN in both Japan and Korea (Takizawa and Shoji, 1982; Kwon et al., 2006).

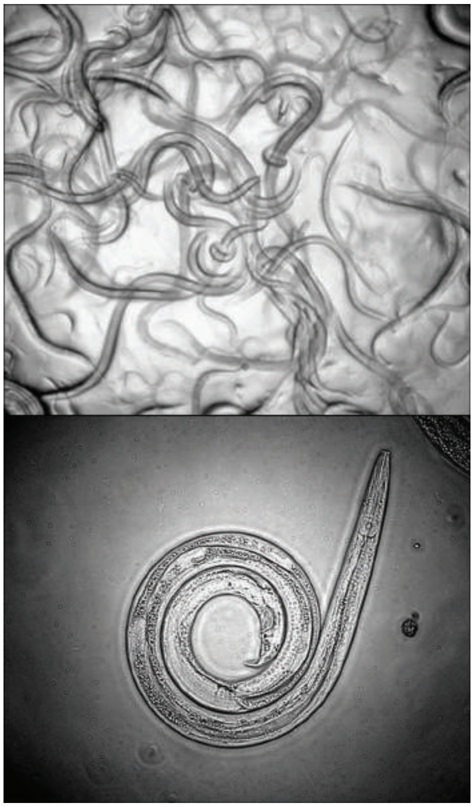

Figure 2 Pine wood nematode (*Bursaphelenchus xylophilus*).

Figure 3 Damage of PWD (*Bursaphelenchus xylophilus*) on pine tree (*Pinus thunbergii*) in Jeju, Korea in 2004.

Extent In Japan, an outbreak of pine mortality was reported in Kyushu in the early 1900s (Mamiya, 1988), but PWN was not described as the causal agent of pine wilt disease of native Japanese pines until 1971(Kiyohara and Tokushige, 1971). The annual loss of timber caused by pine wilt reached a peak of 2.4 million m^3 (25% of the production of the total pine forest area in Japan) in 1979 (Mamiya, 1988), but decreased to 663,500–835,200 m^3 annually in the period from 2000–2005 (Togashi and Shigesada, 2006). In China, the nematode was first discovered in Nanjing in 1982, from where it rapidly expanded its range into Jiangsu, Anhui, Zhejiang, Guangdong, and Shandong Provinces by 2002 (Wang et al., 2009). More than 40 million pines over an area of 87,000 hectares have been killed in China alone. The direct economic losses caused by the nematode in China are estimated at US $300 million, with indirect economic losses exceeding US $3 billion (Yang et al., 2003). In Korea, PWN was first found in Busan city in 1988 (Yi et al., 1989). In 2005, damage occurred on 7,811 ha and the number of diseased trees removed was 138,441 in 2003, 200,637 in 2004, and 862,542 in 2005. Yearly disease management costs were $6.9 million in 2003, $7.8 million in 2004, and $9.5 million in 2005 (Shin, 2008). In 2006, the damaged area in Korea covered 7,871 ha of *P. densiflora*, *P. thunbergii,* and *Pinus koraiensis* Sieb. et Zucc. forests (Han et al., 2008; Korea Forest Service, 2011). However, spread of the PWD epidemic has been significantly reduced since 2006 through successful control by log fumigation (Lee et al., 2003a), preventative trunk injections of nematicides (Shin, 2008), aerial application of insecticides (Lee et al., 2003b), and silvicultural methods (Kwon et al., 2011).

Biology of Pest

Monochamus beetles are usually associated with dead and declining conifers; therefore, they play an important role in the trophic network and energy flux of forest ecosystems (Cesari et al., 2005). The eggs are deposited in slits excavated by the females in the bark of recently killed (or PWN infected) pine trees. The larvae of *Monochamus* beetles initially feed in the phloem and later tunnel into the xylem, where they pupate. PWNs then migrate to the beetle pupae and invade the tracheal system through the spiracles. The aggregation of many nematodes in the beetle pupal chamber facilitates the transmission of PWNs to the JPS adult. Up to 19,000 nematodes can aggregate around a pupal chamber, and a similar number of nematodes can be carried by a single beetle (Sone et al., 2011). The adult beetles, which harbor PWNs in their tracheal systems, emerge from host trees the following spring and feed on the tender bark of healthy pine trees. PWNs invade these healthy trees through the beetles' feeding wounds (Linit, 1990), enter wood tissues and move throughout the tree via the resin canals of the xylem and cortex, feeding on the living epithelial cells and multiplying. Vascular dysfunction occurs rapidly in summer under hot, dry conditions, eventually resulting in the wilting and death of infected trees (Ichihara et al., 2000). In addition, Zhao et al. (2003) proposed that some phytotoxin-producing bacteria (*Pseudomonas* spp.) have a symbiotic relationship with PWN and play a role in pine wilt disease. After the death of a pine tree, PWNs feed on blue-stain fungi (*Ceratocystis* spp.) and other fungi that typically invade and infest dead and dying trees, maintaining nematode populations until the following year (Maehara and Futai, 2002). At the same time, mature JPS females lay eggs in recently killed trees, and the larvae hatch from the eggs, grow, and pupate. In addition to this method of nematode transmission, the transmission of PWN from JPS to *P. densiflora* trees via beetle oviposition also has been reported. Female beetles use their mandibles to cut the bark and then insert their ovipositors under the bark. Nematodes are transmitted into the tree through these oviposition wounds (Edwards and Linit, 1992). Transmission of PWN via oviposition wounds into dying or freshly killed trees that are incapable of mounting a resistance response is necessary for the persistence of this nematode in pine forest ecosystems in North America, where it does not cause pine wilt disease (Arakawa and Togashi, 2002). In this case, only the nematodes carried by female beetles contribute to the population's persistence.

Chemical communication between the sexes of this pine sawyer is mediated by a sex-specific pheromone, 2-(undecyloxy)-ethanol, which is produced only by males (Teale et al., 2011). Because males of JPS also show a significant response to pinene, a combination of 2-(undecyloxy)-ethanol with pine volatiles, ethanol and/or α-pinene is a valuable monitoring tool used for quarantine and management of JPS (Fan et al., 2007; Teale et al., 2011).

ANALYSIS OF RELATED NATIVE AND ESTABLISHED EXOTIC INSECTS IN NORTH AMERICA

Native Insects Related to the Pest (Nontarget Species)

Although exotic *Monochamus* species have not been recorded in the United States, there are five species of native *Monochamus* in North America (*M. carolinensis*, *M. mutator* LeConte, *M. scutellatus* [Say], *M. titillator* [Fabricius], and *M. marmorator* Kby.) and these serve as PWN vectors (Linit, 1988; Kishi, 1995; Akbulut and Stamps, 2012). Pine wilt disease caused by PWN is not symptomatic in pines native to North America but is symptomatic in exotic, often stressed plantings of exotic pines such as Scots (*Pinus sylvestris* L.), Austrian (*Pinus nigra* Arnold), Japanese red, and Japanese black pines (Akbulut and Stamps, 2012). Common pine species in Asia and Europe have not co-evolved with the nematode and consequently have little or no resistance to PWD (Akbulut and Stamps, 2012). Jikumaru and

Togashi (2000, 2008) suggest that low temperatures may inhibit nematode transmission, and this inhibition could be partially responsible for preventing pine wilt disease from devastating pine forests in cooler regions. Zhang and Linit (1998) conducted comparative studies on the life histories and oviposition behavior of *M. carolinensis*, the principal vector of the PWN in the United States, and *M. alternatus*, an important vector in Asia, under controlled conditions. They found that *M. alternatus* females lived longer than *M. carolinensis* females but had a lower oviposition rate. These differences offset each other, so that the fecundities of the species were similar. But, they found that, compared to *M. alternatus* females, *M. carolinensis* females had a shorter preoviposition period, resulting in less time to disperse before initiation of oviposition.

Natural enemies that may make a host shift to the pest

No predators or parasites have been observed in any of *Monochamus* spp. native to North America (Akbulut and Stamps, 2012). High mortality of *M. carolinensis* (85–94%) has been reported to occur due to either intraspecific larval competition among *M. carolinensis* or interspecific larval competition among *M. carolinensis* and other beetle species within logs (Akbulut and Stamps, 2012).

BROAD ASSESSMENT OF NATURAL ENEMIES AS POPULATION REGULATING FACTORS IN THE PEST'S NATIVE RANGE

Fungi (*Beauveria bassiana* [Balsamo] Vuill., *Verticillium* spp.) bacteria (*Serratia marcescens* Bizio), parasitic nematodes, predaceous and parasitic arthropods (predaceous beetles, ants, spiders, and parasitoids), and birds (woodpeckers) are all natural enemies of JPS (Kobayashi et al., 1984). In Japan, two predaceous beetles, *Temnochila japonica* Reitter (Trogossitidae) and *Thanasimus lewisi* Jacobson (Cleridae), are the most common and widely distributed natural enemies of JPS (Shimazu, 2008). In China, Zhang and Yang (2006) reported a total of 97 species of natural enemies: 17 microbes, 47 insects, and 33 birds. The authors suggested that four parasitoids, *Scleroderma guani* Xiao et Wu, *Scleroderma sichuanensis* Xiao [both Hymenoptera: Bethylidae], *Ontsira palliates* [Cameron] [Hymenoptera: Braconidae], and *Dastarcus helophoroides* [Fairmaire] [Coleoptera: Bothrideridae], and one insect predator, *Cryptalaus berus* [Candèze] [Coleoptera: Elateridae], have potential as biological control agents. Lim et al. (2006) found that *Sclerodermus harmandi* (Buysson) (a synonym: of *S. guani*) (Fig. 4) is widely distributed in Korea and is an ectoparasite of the larvae of various wood-boring insects, including *Monochamus* spp. The ectoparasitic beetle *D. helophoroides* also was observed in Korea. Kim et al. (2010) reported two parasitoids, *Dolichomitus nakamurai* (Uchida) and *Echthrus reluctator* L. (both Hymenoptera: Ichneumonidae), and two predators, *T. japonica* and *T. lewisi*, were frequently observed attacking *M. saltuarius*, another vector of PWN in Korea.

Figure 4 *Sclerodermus harmandi*, a potential biological control agent of Japanese pine sawyer.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Sclerodermus harmandi

Sclerodermus harmandi (Fig. 4) is an external parasitoid of wood-boring or stem-boring insect larvae and pupae. *Sclerodermus harmandi* overwinters as adults in the tunnels of host insects from late November or early December to the middle of March (Zhang et al., 1989). In Korea in 2005, *S.*

harmandi were collected nationwide from June to October (Lim et al., 2006). Developmental times of eggs, larvae, pupae, and the total immature stage of *S. harmandi* females reared at 25 ± 1 °C on fully grown larvae of JPS were 5.2, 7.4, 16.7, and 29.2 days, respectively. Developmental times of males were one day shorter than those of females. The success rate of oviposition by mated females of *S. harmandi* on *M. alternatus* larvae was 55%, and on pupae it was 96%. The emergence rate of *S. harmandi* reared on larvae of *M. alternatus* was 47% and the sex ratio of emerged *S. harmandi* adults was approximately 10: 1 (female: male) (Hong et al., 2008). The adult female lives about one month, whereas the male lives only 8 to 11 days. In general, a female lays 50–70 eggs, with a maximum of 120, during her lifetime (Zhang et al., 1989). Eggs and larvae are guarded by adult females until the full-grown larvae construct cocoons within the tunnel. Sixteen species of longhorn beetles have been recorded as hosts of *S. harmandi* in eastern Asia. JPS and *Corymbia rubra* L. were confirmed as hosts in Korea (Lim et al., 2006). In China, after the release of 5,000 *S. harmandi* wasps per hectare in a test forest in mid-July, the rate of parasitism of *M. alternatus* larvae was 67–84% (Xu et al., 2008).

Dastarcus helophoroides

Dastarcus helophoroides (synonym: *Dastarcus longulus* Sharp) (Fig. 5) is an important parasitoid of longhorned beetles in its native range in China (Qin and Gao, 1988). The larvae of this beetle are ectoparasitoids of late-instar larvae, pupae, and young adults of several longhorned beetles, including the Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky) (Wang et al., 1996), *Massicus raddei* (Blessig), *Apriona germari* (Hope), *Apriona swainsoni* (Hope), and *Batocera horsfieldi* (Hope) (Qin and Gao, 1988). *Dastarcus helophoroides* adults lay eggs twice a year, either on the outer surface of the bark near the host entrance hole or around the host larvae tunnel walls (Qin and Gao, 1988). After hatching, first-instar larvae, which have legs, actively move about to locate hosts; their legs degenerate once parasitism has occurred. One late-instar larva of Asian longhorned beetle or *M. raddei* can support the complete development of 10-35 *D. helophoroides* larvae (Qin and Gao, 1988). Among various volatile chemicals emitted from wood with longhorn beetle larval tunnels and frass, *D. helophoroides* adults were attracted only to (*R*)-(+)-limonene (Wei et al., 2008). The experimental release of adults of *D. helophoroides* in a pine stand damaged by pine wilt disease lowered *M. alternatus* survival in Japan; *M. alternatus* mortality in treated trees was higher (76.3% in 2002, 84.6% in 2003, and 57.2% in 2004) than in untreated control trees (18.8 in 2002, 5.3 in 2003, and 26.7% in 2004) (Urano, 2006).

Figure 5 *Dastarcus helophoroides,* a potential biological control agent of Japanese pine sawyer.

Contortylenchus genitalicola

Contortylenchus genitalicola Kosaka and Ogura (Kosaka and Ogura, 1993) is a tylenchid nematode that has both an insect-parasitic and a fungal feeding phase. It is known to be parasitic and to reduce the reproductive potential of JPS (Kosaka, 2003). Kosaka (2003) reported that JPS females infected with *C. genitalicola* have fewer offspring than uninfected females The inseminated infective (immature) females penetrate the larval stages and mature in synchronization with the gonad development of JPS. Mature females lay eggs in the reproductive organs of the adult host, where the hatched juvenile nematodes grow into fourth stage (J4) nematodes. The J4 nemas are deposited outside the host through beetle defecation or oviposition. Contact of the free-living J4 with JPS larvae produces an infective female; otherwise it assumes the fungal-feeding form (Kosaka, 2003).

In addition to natural enemies in its native range, microbial control of Japanese pine sawyer adults by *B. bassiana* should be considered to prevent transmission of pine wilt disease to healthy pine trees. *Beauveria bassiana* has been found to be a promising control agent (Kobayashi et al., 1984; Shimazu, 1994; Shimazu et al., 1995; Kishi, 1995; Maehara et al., 2007). When inoculated with the fungus,

Table 1 Key natural enemies of Japanese pine sawyer (JPS) beetle in its native range.

Scientific Name	Type	JPS Life Stage Attacked[1]	Host/Prey Specificity	Location	References
Coleoptera					
Cleridae					
Thanasimus lewisi Jacobson	Predator	*L*	–	Japan	Shimazu, 2008
Bothrideridae					
Dastarcus helophoroides (Fairmaire)	Parasitoid (ecto-)	*L, P, A*	Polyphagous	China, Japan, Korea	Wang et al., 1996; Naves et al., 2005; Shimazu, 2008; Lim et al., 2012
Trogossitidae					
Temnochila japonica Reitter	Predator	*L*	Polyphagous	Japan	Kishi, 1995
Hymenoptera					
Braconidae					
Bracomorpha ninghais sp. n.	Parasitoid (ecto-)	*L*	–	China	Wang et al., 2009
Atanycolus genalis (Thomson) (=*initiator* F.)	Parasitoid (ecto-)	*L*	Polyphagous	Japan	Urano and Hijii, 1991; Kishi, 1995; Naves et al., 2005; Shimazu, 2008
Bethylidae					
Scleroderma harmandi buysson (= *guani* Xiao et Wu)	Parasitoid (ecto-)	*L, P*	Polyphagous	China, Korea	Zhang et al., 1989; Lim et al., 2006; Xu et al., 2008; Li et al., 2009; Hong et al., 2008
Ichneumonidae					
Dolichomitus nakamurai (Uchida)	Parasitoid	*L, P*	–	Japan	Kishi, 1995; Naves et al., 2005
Dolichomitus sp.	Parasitoid	*L, P*	–	Japan	Kishi, 1995; Naves et al., 2005; Shimazu, 2008
Megarhyssa sp.	Parasitoid	*L, P*	–	Japan	Naves et al., 2005; Shimazu, 2008
Tylenchida					
Allantonematidae					
Contortylenchus genitalicola Kosaka and Ogura	Parasite	*L*	Monophagous	Japan	Kosaka and Ogura, 1993; Kosaka, 2003; Shimazu, 2008

[1] L Larvae, P Pupae, A Adult

Japanese pine sawyer adults feed less or stop feeding, thereby preventing the nematodes from entering pine twigs. More research regarding competitive interactions between the two closely related nematodes *B. xylophilus* and *Bursaphelenchus mucronatus* Mamiya et Enda is needed to better understand the vector biology of JPS. *Bursaphelenchus mucronatus* is native to Japan and Europe and is considered avirulent in *Pinus* species from those regions (Jikumaru and Togashi, 1995; Vincent et al. 2008). Jikumaru and Togashi (2004) reported that *B. mucronatus* inhibits molting of third-stage dispersal juveniles of *B. xylophilus* to fourth-stage dispersal juveniles, which in turn inhibits movement on nematodes onto beetle hosts. Interestingly, pre-inoculation of young pine trees in a nursery with avirulent PWN induced systemic resistance of trees against subsequent inoculation with the virulent PWN (Kosaka et al., 2001). The induced resistance of pine trees by use of the avirulent species *B. xylophilus* has high potential as a natural control method against PWD.

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XXXIV ASIAN PINK MOTH[1]

(*Lymantria mathura* [Moore]) (Lepidoptera: Noctuidae: Lymantriinae)

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DESCRIPTION OF PEST

Taxonomy

The Asian pink moth, *Lymantria mathura* (Moore), was thought to be a widespread species, with two subspecies (Schintlmeister, 2004). Earlier, Okano (1960) had named the Taiwan population as a third subspecies, but Schintlmeister (2004) synonymized that population with *L. mathura aurora*. However, recent molecular evidence has shown that the Taiwan population is a separate species and the name *L. subpallida* Okano was resurrected and applied to it (deWaard et al., 2010). Similarly, a population known only from Okinawa has been described as *Lymantria flavida* Pogue and Schaefer (Pogue and Schaefer, 2007). Whether *L. mathura* sensu stricto occurs on Taiwan or Okinawa in now in doubt. In India, populations of *L. mathura* vary in some aspects of color and oviposition behavior and their status is uncertain. In Sri Lanka, *L. mathura* is considered to have been replaced by *Lymantria grandis* Walker, but Schintlmeister (2004) found many morphological features of these two putative species to be virtually identical, the status of the species in this area remains uncertain. Other populations of *L. mathura* vary in aspects, such as responses to sex pheromones (Gries and Schaefer, unpubl. data) and ovipositional behavior, and it may be that not all these are conspecific.

Distribution

Lymantria mathura is known from many parts of Asia. It is not found in North America, but does pose an invasion risk. In Japan, it is recorded from all major islands (Inoue, 1957; Sugi, 1987), except Okinawa, where it is replaced by *L. flavida* (Pogue and Schaefer, 2007). Also, it is present in Korea (Nam and Kim, 1981; Kim et al., 1982) and the Russian Far East, in (1) Primorskii (= Pryorsky) Krai), (2) Siberia (Kozhanchikov, 1950; Gninenko, 2000), and (3) the south central part of the Chabarovsk region (Chelysheva and Orlov, 1986).

Lymantria mathura is widely distributed in China (Zhao, 2003), south to Hong Kong (Kendrick, 2000). Also, *L. mathura* is found in Vietnam (Schintlmeister, 1987), Thailand (Hutacharern et al. 1988), Bangladesh (Rosovsky, 2001), Nepal (Kishida, 1993), in much of India (Gupta, 1992), and as far west as eastern Pakistan (Chaudhry, 1966).

Damage

Type Larvae of this species defoliate deciduous hardwood forest, orchard, and ornamental trees. In Honshu, Japan, this includes an evergreen oak, *Quercus glauca* Thunb. (Fagaceae) (Funakoshi, 2004). Arai et al. (2010) recorded defoliation of apple trees and damage to fruits. In tropical India, Singh (1954) records damage to tropical fruit trees, e.g., mango (*Mangifera indica* L. [Anacardiaceae]) and lychee (*Litchi chinensis* Sonn. [Sapindaceae]), affecting leaves, bark of twigs, and flower panicles, leading to losses in fruit crops.

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[1] This common name, Asian pink moth, in English is used here for the first time, replacing previously used names (i.e., pink gypsy moth, rosy gypsy moth, rosy Russian moth). The new name is intended to emphasize the moth's origin, the female's color, and to remove any reference to gypsy moth, *L. dispar sensu lato*, a congener to which this species is not closely related.

Extent *Lymantria mathura* population densities are almost always low, with only a few isolated outbreaks. Nishigaya (1918) and Arai et al. (2010) recorded a severe outbreak in Japan that defoliated apple trees in northern Honshu. Outbreaks also have been noted in Korea (Hai-Poong Lee, pers. comm. 1996), Jilin Province, in China (You-Dekang, pers. comm. 1997), and forests in the southern parts of the Russian Far East (Chelysheva and Orlov, 1986). In India, defoliation occurs sporadically on *Shorea robusta* Roth (Dipterocarpaceae) (Roonwal, 1979). The most destructive outbreak appears to have been in India (Roonwal, 1953, 1979), where many tree species were severely defoliated.

Lymantria mathura can be found in low numbers in deciduous forests, often intermixed with *Lymantria dispar* (L.) *sensu lato* (Chelysheva and Orlov, 1986; Funakoshi, 2004). Similarly, the author observed *L. mathura, L. dispar japonica,* and *Lymantria lucescens* (Butler) on the oak *Q. glauca* in Japan (Schaefer, in press). It appears that *L. mathura* has many features and food preferences in common with its related, sympatric congeners and no doubt shares natural enemies with them.

Biology of Pest

Lymantria mathura is a sexually dimorphic species, with the male hind wings and abdomen washed with yellow, while in females the yellow is replaced with a pink or rosy color (Figs. 1, 2). Apart from this pink coloration, adult females have forewings that are gray with a charcoal mottled pattern and hind wings with a grayish banding near the outer margin. Males have two color morphs (Figs. 3, 4, 5). In a light color morph, the forewing is basically white with the gray mottled pattern in a much lighter gray (Figs. 3, 5). In the melanic form, males are darkened to nearly pencil-lead black, but with mottling in the forewings still evident and with hind wings mostly pale orange, with a charcoal gray discal spot and an interrupted charcoal band near the outer margin (Fig. 4). In India, in some male specimens the hind wings have apparently lost the yellow coloration and this has been replaced with a uniform brown (see images available on Wikipedia).

Lymantria mathura pupae are uniformly golden-brown, with two distinctive white tuffs of setae on the dorsal thorax either side of the midline (Fig. 6). The caterpillar is gray with patterns of black and white broken up by a regular pattern of steel gray veruccae (cuticular warts bearing tuffs of setae) (Fig. 7). The first pair of abdominal veruccae are greatly enlarged and the second pair is somewhat enlarged, as compared to all others. The dorsal abdominal glands have the same color as the overall integument. Larvae possess anterior-lateral hair pencils and posteriorly possess a fan-like pattern of prominent individual setae but no distinct hair pencil. Freshly laid eggs are yellowish, but darken as embryos develop.

Figure 1 Spread female (above) and two males of *Lymantria mathura*. In collection, Taiwan Forestry Research Station, Taipei. Paul W. Schaefer.

Lymantria mathura is a polyphagous hardwood-tree defoliator that overwinters in the egg stage. It is univoltine in temperate regions but bivoltine in southern areas (e.g., Hong Kong and India) (Roonwal, 1979). There may be a third generation in tropical areas (Kendrick, 2000). In China, Korea, and Japan, females lay eggs in masses within cracks or under bark scales on tree boles. In India, females lay eggs on various exposed surfaces and then cover them with whitish setae from their abdomens (Roonwal, 1954, 1979), as does gypsy moth, *L. dispar dispar,* in North

Figure 2 Female of *Lymantria mathura*, natural setting, Toyota, Aichi Prefecture, Japan, 14 July 2000. Paul W. Schaefer.

Figure 3 Light-phase male of *Lymantria mathura*, natural setting, Morioka, Iwate Prefecture, Japan, 18 Aug. 1996. Paul W. Schaefer.

Figure 4 Melanic or dark-phase male of *Lymantria mathura*, natural setting, reared ex larva collected Taiwan in USDA, BIRL, Quarantine Facility, Newark, Delaware. Emerged 19 June 1994. Paul W. Schaefer.

Figure 5 Male of *Lymantria mathura*, spread, in collection Cheju-do Museum, Cheju Island, Korea, collected on that island 9 Aug. 1996 by S. H. Jung. Photo taken 23 June 1999. Paul W. Schaefer.

Figure 6 Pupae of male (left) and female of *Lymantria mathura*, showing tuffs of white setae. Origin, Morioka, Iwate Prefecture, Japan, but reared ex ova at BIRL- Photo on 25 May 2007. Paul W. Schaefer.

Figure 7 Late larva of *Lymantria mathura*, natural setting, Mengjiagang, Heilongjiang Province, China, 1983. Paul W. Schaefer.

America. Eggs hatch in spring, and neonate larvae disperse on silk strands carried on the wind, perhaps to even greater distances than gypsy moth (Zlotina, 1999; Zlotina et al., 1999). Larvae eventually settle on vegetation and select suitable tree species as food.

In Japan, the polyphagous larvae feed on deciduous trees in many groups, including the Anacardaceae, Betulaceae, Combretaceae, Dipterocarpaceae, Fagaceae, Myrtaceae, Rosaceae, Sapidaceae, Theaceae, and Ulmaceae. In India, larvae are equally polyphagous, feeding on species in the Anacardiaceae, Apocynaceae, Celastraceae, Combretaceae, Fagaceae, Dipterocarpaceae, Euphorbiaceae, Caesalpinaceae, Papilionaceae, Leguminosae, Lythraceae, Meliaceae, Myrtaceae, and Rosaceae (see Pogue and Schaefer [2007] for listing of acceptable genera). Preferred host genera appear to include *Quercus, Malus,* and *Castanea* in the temperate areas of its range. Zlotina et al. (1998) found the most suitable trees are in the Fagaceae (*Fagus* and *Quercus*. In tropical areas, preferred host genera are *Acrocarpus, Mangifera*, *Quercus, Shorea, Syzygium, Terminalia* (Roonwal, 1979), and flowers of *Mangifera* (Mohn, 2001). Young larvae rest on leaves when not feeding, while mature larvae, rest on tree trunks, requiring mature larvae to move up and down the plant, daily.

Pupae are formed in loose silk webbing on tree leaves or bark, crevices, or man-made structures, or inside leaves that have been webbed together. Adult flight is nocturnal. Wallner et al. (1995) collected adults at lights in Mineralni, Russia, most frequently between 01:00–03:00 AM. Nocturnal flight occurs earlier (before 11:00 PM.) in the Tohoku region of Japan (Schaefer and Strothkamp, 2014). Mating occurs at night (Zlotina, 1999) when females emit pheromone (Gries et al., 1999; Oliver et al., 1999).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

There are no native species of *Lymantria* in the Western Hemisphere. However, *L. d. dispar* is an invasive species found in the northeastern United States and parts of southeastern Canada. Whereas *L. d. dispar* is diurnally active and has females that are unable to fly, both sexes of *L. mathura* are nocturnal and strong flyers. Two other Lymantriinae introduced into North America from Europe are *Euproctis chrysorrhoea* (L.) and *Leucoma salicis* (L.) (Barbosa and Schaefer, 1997). Native Lymantriinae in North America include *Orgyia* spp. (ten species) and *Dasychira* spp. (15 species) (Ferguson, 1978).

Native Natural Enemies that May Effect the Pest

There is a guild of natural enemies introduced in North America for biological control of gypsy moth, *L. d. dispar*, and many of these species undoubtedly would attack *L. mathura* if it were introduced into North America. This prediction is based on the similarity and overlap of the natural enemy complexes of these species in eastern Asia. Among the egg parasitoids, *Ooencyrtus kuvanae* (Howard) (Hymenoptera: Encyrtidae), a long established exotic Japanese parasitoid of gypsy moth in North America, will likely attack the eggs of *L. mathura*, but its impact on *L. mathura* will be limited because eggs of *L. mathura* are often inserted deep into cracks and under bark scales, reducing access for parasitoids. *Cotesia melanoscela* (Ratzeburg) and *Meteorus versicolor* (Wesmael) (both Hymenoptera: Braconidae) will likely attack larvae, and *Brachymeria intermedia* (Nees) (Hymenoptera: Chacididae) and *Pimpla disparis* Viereck (Hymenoptera: Ichneumonidae) are likely to attack pupae. Given the opportunity, the predaceous carabid beetle, *Calosoma sycophanta* L. (Coleoptera: Carabidae), likely would prey on larvae and pupae of *L. mathura*.

Among natural enemies native to North America, a few generalists, including *Trichogramma* spp. (Hymenoptera: Trichogrammatidae), several larval parasitoids, and the pupal parasitoid *Itoplectis conquistador* (Say) (Hymenoptera: Ichneumonidae), might attack *L. mathura.* Native predators that might attack *L. mathura* life stages include the Asopine pentatomids, such as *Podisus maculiventris* (Say), and related generalist predators.

KNOWLEDGE OF NATURAL ENEMIES OF PEST IN NATIVE RANGE

Lymantria mathura occurs in much of east and south Asia. With such a widespread range, extending from northern temperate areas in Russia, through sub-tropical parts of China, Thailand, India, and Pakistan, it is reasonable to ask if this might be a species complex. Barring that, collection locations would be selected based on access to collecting areas, DNA matching of the invasive population to a source population, and climate matching of the invaded region with parts of the native range. Various natural enemies of *L. mathura* are known from many climatic zones and various forest types, but information is very incomplete. A few of these might prove useful as biological control agents.

No foreign exploration has focused exclusively on *L. mathura*. In Korea, Lee and Lee (1996) studied the natural enemies attacking *L. mathura* in Kyonggi Province. They found a complex of species very similar to those known in Japan, Korea, and China to attack Asian gypsy moth, *L. d. asiatica* (Schaefer et al., 1988).

Incidental to work on gypsy moth, some insights have emerged relative to *L. mathura*. Working on the mermithid nematode *Hexamermis* sp., we found incidental emergence of immature nemas from the caterpillars of *L. mathura* (Schaefer and Ikebe, 1982). Likewise, working on the asopine pentatomid *Dinorhynchus dybowskyi* Jakovlev under laboratory conditions, we found that this asopine fed on *L. mathura* larvae. Other incidental studies contribute further insights on the potential natural enemies in India (Chacko and Singh, 1990). Still, much needs to be done to understand adequately the natural enemy complexes associated with *L. mathura* throughout its range. Based on studies cited above, we developed a preliminary list of natural enemies of *L. Mathura* (Table 1).

BROAD ASSESSMENT OF FACTORS AFFECTING REGULATION BY NATURAL ENEMIES

Classical biological control of *L. mathura* has never been attempted and consequently our knowledge of the biology and importance of the natural enemies observed attacking it is limited. However, biological control of gypsy moth does provide some lessons that might be applicable. First, many of this pest's natural enemies are multivoltine in their native ranges; therefore, they would require one or more alternate or overwintering hosts other than *L. mathura*. However, such species may be unacceptable today for introduction as classical biological control agents, either because required alternative hosts may not exist in North America, or they may be non-pest native species. In the latter case, it would be highly unlikely that such a polyphagous natural enemy would be permitted for introduction. Second, since overwintering *L. mathura* eggs are inserted into well protected niches, most eggs may be inaccessible to egg parasitoids, limiting their effectiveness. Third, many of the tachinid and hymenopteran parasitoids of larvae or pupae may be too polyphagous for use, limiting attack on these exposed stages. However, in some cases the species already introduced for gypsy moth are known or suspected to be able to attack *L. mathura.* To the extent that this occurs, population growth of an invasive *L. mathura* population might be checked by such species, naturally.

Table 1 Natural enemies attacking *Lymantria mathura* in Asia.

Species	Order/family	Biology	References	Location
Hexamermis spp.	Nematoda: Mermithidae	internal larval parasite	Schaefer and Ikebe, 1982; Chelysheva and Orlov, 1986	Japan, Russia
Aleiodes lymantriae (Watanabe)	Hymenoptera: Braconidae	solitary, parasitoid of intermediate instars	Chen and He, 1990	China
Apanteles sp.	Hymenoptera: Braconidae		Roonwal, 1979	India
Cotesia melanoscela (Ratzeburg)	Hymenoptera: Braconidae	solitary, early larval parasitoid; dominant parasitoid in study	Lee and Lee, 1996	Korea
Cotesia schaeferi (Marsh)	Hymenoptera: Braconidae	gregarious, early larval parasitoid	Lee and Lee, 1996	Korea
Pimpla disparis Viereck	Hymenoptera: Ichneumonidae	solitary pupal parasitoid		
Casinaria arjuna Maheshwary and Gupta	Hymenoptera: Ichneumonidae	larval endoparasitoid	Lee and Lee, 1996	Korea
Casinaria nigripes (Gravenhorst)	Hymenoptera: Ichneumonidae	larval endoparasitoid	Gupta, 1983	India
Casinaria tenuiventris (Gravenhorst)	Hymenoptera: Ichneumonidae	larval endoparasitoid	Gupta, 1983	India
Phobocampe lymantriae Gupta	Hymenoptera: Ichneumonidae	larval endoparasitoid	Gupta, 1983	India
Theronia atalantae (Poda)	Hymenoptera: Ichneumonidae	pupal parasitoid or likely hyperparasitoid	Lee and Lee, 1996	Korea
Brachymeria lasus (Walker)	Hymenoptera: Chalcididae	gregarious, pupal parasitoid	Lee and Lee, 1996	Korea
Carcelia amphion R.-D.	Diptera: Tachinidae	larval endoparasitoid	Schaefer and Shima, 1981	Japan
Carcelia gnava (Meigen)	Diptera: Tachinidae	larval endoparasitoid	Schaefer and Shima, 1981 (Togashi, 1977, recorded as *C. excavata* (Zett.)	Japan

Table 1 Natural enemies attacking *Lymantria mathura* in Asia, *continued*.

Species	Order/family	Biology	References	Location
Compsilura concinnata	Diptera: Tachinidae	endoparasite, emerging from host late larvae or pupae	Schaefer and Shima, 1981; Lee and Lee, 1996	Japan, Korea
Exorista japonica (Townsend)	Diptera: Tachinidae	larval or larval-pupal endoparasitoid	Lee and Lee, 1996	Korea
Turanogonia chinensis (Wiedemann)	Diptera: Tachinidae	endoparasitoid, host stage unclear	Schaefer & Shima, 1981	Japan
Winthemia sp. nr. *neowinthemoioides* Townsend	Diptera: Tachinidae	endoparasitoid, host stage unclear	Schaefer & Shima, 1981	Japan
Winthemia sp. nr. *neowinthemoioides* Townsend	Diptera: Tachinidae	endoparasitoid, host stage unclear	Schaefer & Shima, 1981	Japan
unidentified species	Diptera: Tachinidae?	endoparasitoid causing 80% mortality of larvae and pupae	Singh, 1954	India
unidentified species	Diptera: Sarcophagidae	pupal parasitoid	Lee and Lee, 1996	Korea
Beauveria sp.	fungus, Moniliaceae		Lee and Lee, 1996	Korea
unidentified species	nuclear polyhedrosis virus		Lee and Lee, 1996	Korea
unidentified species	nuclear polyhedrosis virus	from larva	Tsia and Ding, 1982; Lewis et al., 1984	China
unidentified species	cytoplasmic polyhedrosis virus	isolated from *L. dispar* but infective to *L. mathura*	Aratake and Kayamura, 1972	Japan
unidentified species	virus, polyhedral disease	decimated Indian outbreak population	Roonwal, 1979	India

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Glyptapanteles liparidis

Glyptapanteles liparidis (Bouché) (Hymenoptera: Braconidae) has been studied as a parasitoid of *L. dispar sensu lato* and *Dendrolimus* spp. (Lepidoptera: Lasiocampidae). It is not known to attack *L. mathura,* but is strongly suspected of doing so. It requires an overwintering host caterpillar, so it cannot sustain itself only on *L. mathura*, which passes the winter in the egg stage. The overwintering host in Asia is normally either a species of *Dasychira* or *Calliteara* (Noctuidae: Lymantriinae) or *Dendrolimus*. As such, this species is likely to be too polyphagous to be lawfully permitted for introduction to the United States. Larvae of *G. liparidis* emerge from their hosts gregariously and spin silken cocoons from which adults emerge in 2–3 weeks. Parasitoids mate and females then oviposit in other hosts, especially *Lymantria* spp., including *L. mathura*, and another generation begins. In total, 3 or 4 generations occur seasonally, with the final overwintering generation requiring 8–9 months to mature.

Cotesia melanoscela

Cotesia melanoscela (Hymenoptera: Braconidae) is of Eurasian origin and has long been established on *L. dispar* in North America. It is similar in its biology to *G. liparidi,* except that it is a solitary species that produces just one offspring per host. Lee and Lee (1996) record this species in their Korean study, but at less than 2% parasitism.

RECOMMENDATIONS FOR FURTHER WORK

Some issues remain concerning the species definition of *L. mathura* and the status of some local populations. Variability exists in the responses of different populations of this moth to pheromones, and in female ovipositional behavior. No comprehensive or widespread analysis of the natural enemies of *L. mathura* has been conducted, but such a study is needed to gain a better understanding of the importance of existing natural enemies and their potential for use in the biological control of *L. mathura*. Some of the natural enemies known to attack *L. dispar sensu lato* are also known to cross-over and attack *L. mathura*. We suspect that any comprehensive listing or study of key natural enemies of *L. mathura* would likely show many more commonalities than differences. Such studies have yet to be conducted and are central to any analysis of the potential for biological control of *L. mathura* regardless of the location involved, either within its native range or in any newly invaded territory.

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XXXV Nun Moth

(*Lymantria monacha* [L.]) (Lepidoptera: Noctuidae: Lymantriinae)

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DESCRIPTION OF PEST

Taxonomy

Nun moth*, Lymantria monacha* (L.) (Lepidoptera: Noctuidae: Lymantriinae) (Fig. 1), is among 2,500 known species of lymantriines, worldwide. Since early attempts to revise the Lymantriine group (Walker, 1855; Hampson, 1892; Dyar, 1897), no satisfactory classification has been proposed on a world basis. A few regional revisions have been written (e.g., Kozhanchikov, 1950; Inoue, 1957; Ferguson, 1978) and some synonymic lists (Kirby, 1892; Bryk, 1934; Chao, 1978; Nam and Kim, 1981; Zhao, 1982; Kim et al., 1982) published. This species was placed in various genera (*Phalaena*, *Noctua*, *Bombxy*, *Liparis*, and *Psilura*) before being assigned to *Lymantria* by Krulikovsky (1908). Pogue and Schaefer (2007) provide a list of synonyms and re-descriptions of this species.

Figure 1 Color variation in adult *Lymantria monacha* (females top and males bottom). Melody Keena, USDA Forest Service, Bugwood.org.

Distribution

Lymantria monacha is found in most parts of Europe and Russia (see Baranchikov [1997] for a map of its Russian distribution), and parts of East Asia (China, Korea, Japan). In Europe it is found from southern England, Denmark, Sweden and Finland, south to Spain, Portugal and Italy, in the latter countries at elevations of 1000–2000 m (Lipa and Glowacka, 1995; Commonwealth Institute of Entomology distribution map #60). The zone in which periodic outbreaks occur is generally bounded by the July isotherm of 16°C and September isotherm of 10.5°C (Bejer, 1988). These areas are semiarid and several studies have indicated that outbreaks are more frequent in drought-sensitive sites where the hosts are stressed (Bejer, 1988; Lipa and Glowacka, 1995).

Nun moth has not yet invaded North America, but is listed as an invasive species of concern by the U.S. Department of Agriculture. Port inspectors monitor for it and, as part of the Rapid Detection Pilot Project, pheromone traps are being placed near ports of entry to detect any breeding populations. To date, no *L. monacha* have been trapped. United States and Russian agencies are collaborating to monitor population levels near ports in the Russian Far East (Munson et al., 1995).

Damage

Type The economic damage caused by nun moth consists of widespread defoliation of a variety of important conifer species (Fig. 2). Nun moth is considered the most important forest pest in Poland, damaging 6.3 million ha of pine, spruce, and other conifers between 1978 and 1984 (Sliwa and Sierpinski, 1986). It is considered to be a major pest in many other areas, where periodic outbreaks cause widespread defoliation and death of spruce and pine (Bejer, 1988). Weather, site conditions, and stand composition are the most important factors involved in inducing nun moth outbreaks (Bejer, 1988; Grijpma, 1989). The epicenters of outbreaks are usually mature, even-aged spruce stands (Bejer, 1988) and outbreaks in such stands last longer (seven years) than those in pine stands (four years) (Schönherr, 1989). The interval between outbreaks is reported to be 10–11 years in central Europe, 12–14 years in Russia, and >70 years in Denmark (Wellenstein, 1942a; Marushina, 1978; Jensen, 1991).


Figure 2 Damage caused by *Lymantria monacha*. Landesforstpräsidium Sachsen Archive, Bugwood.org.

Nun moth poses an important risk of invasion via commerce into other areas, where susceptible hosts are present, because adults are readily attracted to artificial lights (Baranchikov et al., 2004) and will deposit eggs in crevices on containers, pallets, or other objects. Moths have been detected at sea ports in the Russian Far East (Munson et al., 1995). In a pest risk assessment for importation of larch from Siberia into the United States, *L. monacha* was identified as a pest posing a serious risk of invasion into the United States, because logs with intact bark could transport or hold eggs (Anon., 1991). Establishment of nun moth in the United States would likely be highly damaging, because of its wide host range, ability to colonize new habitats, and capacity for rapid spread through adult flight.

In Europe, nun moth feeds preferentially on Norway spruce (*Picea abies* [L.]) and Scots pine (*Pinus sylvestris* L.) (Lipa and Glowacka, 1995). Sliwa (1987) lists intensity of feeding of *L. monacha* larvae on trees and shrubs in Poland during the large outbreak of 1978–1984. In Russia, *L. monacha* prefers *P. abies* forests in the western part of European Russia and *P. sylvestris* from there east through the Urals up to the Yenisey River in central Siberia. In the upper Amur region, outbreaks in 1965–1967 occurred in *Larix cajanderi* Mayr forests (Nakonechnyi, 1973); in the Primoriye region, *L. monacha* outbreaks occurred in 1978–1983 in mixed broad-leaf coniferous forests, defoliating *Pinus koraiensis* Siebold & Zucc., *Abies nephrolepis* (Trautv. ex Max.) Max., and *Picea ajanensis* Fisch. ex Trautv. & C. A. Mey (Turova and Yurchenko, 1986). On Sakhalin Island, *P. ajanensis* was the primary host, and stands of *Betula ermanii* Cham. and *L. cajanderi* were partially defoliated during the outbreak of 1952–1955 (Turova and Yurchenko, 1986).

Laboratory investigations of adult nun moth preference and larval performance on Eurasian host plants showed that the preferred groups–spruce, pine and larch–are intermediate-to-low in food value for larvae (Bejer, 1988). Many studies have examined the relationship between bud burst of the key hosts (*P. abies* and *P. sylvestris*) and hatching of *L. monacha* larvae. This work has shown that host phenology is an important factor in determining survival and successful development of *L. monacha* larvae.

When larvae hatch before foliage buds burst, male flowers or buds of *Pinus* species are critical to larval survival and growth (Bejer, 1988). Keena (2003) tested 26 North American tree species and Withers and Keena (2001) tested *Pinus radiata* D. Don to predict the potential hosts at risk if nun moth were accidentally introduced into North America or New Zealand. Several species were found to be suitable hosts for *L. monacha,* including *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.*, Picea glauca* (Moench) Voss*, Picea pungens* Engelm.*, P. radiata, Tsuga canadensis* (L.) Carrière*, Betula populifolia* Marshall*, Prunus serotina* Ehrh.*, Quercus lobata* Né, and *Quercus velutina* Lambert.

The ecological damage caused by this species results from widespread mortality of selected conifer species, which has the potential to change the species composition of forests after outbreaks occur. Wildlife dependent on the affected tree species for food or nesting sites would be harmed. Nutrient and water cycling in the ecosystem might also be affected. During an *L. monacha* outbreak in Poland, massive frass and needle fall increased nitrogen and phosphorus in pine litter 2–3 fold and significantly increased potassium and manganese levels (Dziadowiec and Plichta, 1986)

Extent The first recorded outbreak of *L. monacha* (1853–1863) occurred in European Russia and damaged 403,000 km^2 of forest (Bejer, 1988). Since then, periodic outbreaks have occurred in Europe (Wellenstein, 1942b; Bejer, 1988; Schönherr, 1989; Lipa and Glowacka, 1995). During one outbreak (1978–1983), over 2 million ha of coniferous forests (one quarter of Poland's forests) were infested and partly defoliated (Schönherr, 1985). Defoliation by *L. monacha* reduced annual growth of pines in Poland (Beker, 1996). Over a five-year period in the Czech Republic, defoliation reduced spruce growth by 30–60% (Vins and Svestka, 1973). Establishment of *L. monacha* in North America has the potential to threaten approximately 70,000 ha of western forests west of the Cascade Range, high-elevation spruce/fir/pine in the upper Midwest, and northeastern North America (Anon., 1991; Wallner, 1996). This could result in annual losses of up to $60 million to timber producers and increased costs to consumers (Prestemon et al., 2006), not to mention the huge environmental impacts and as yet unestimated costs of control/eradication.

Biology of Pest

Moths fly at night from the middle of July to the beginning of September (exact dates depend on the climate of the region). Nun moths are variable in appearance, with the fore wing ranging from chalk-white, decorated with numerous dark wavy lines and patches, to almost black with flecks of white (Fig. 1 above). The genus *Lymantria* can be distinguished from other lymantriine genera by wing venation (Fig. 3), and *L. monacha* can be distinguished from *L. dispar* by its compound eyes, which are larger because they fly at night rather than at dusk (Ferguson, 1978). Keena et al. (1998) provides a method for distinguishing each stage of *L. monacha* from that of *L. dispar*, the only other *Lymantria* species found in North America. Males are nocturnal and females release pheromone to attract males (Fig. 4). Adults are most active near midnight. Although females can fly, they usually remain on stems and wait for males. Once mated, the females lay 70–300

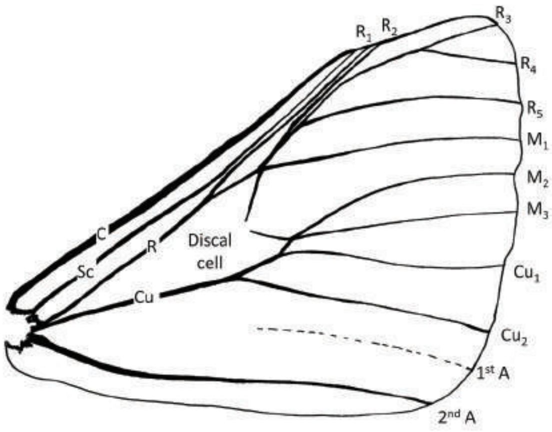

Figure 3 Forewing of *Lymantria monacha* showing the pattern of venation. Melody Keena.

Figure 4 Female *Lymantria monacha* (left) releasing pheromone and male (right) approaching to mate. Melody Keena, USDA Forest Service, Bugwood.org

eggs in clusters of approximately 40 eggs in bark crevices or under lichens on bark (Fig. 5). Females fly more actively after depositing eggs. The nun moth embryo in the egg completes development in 2–6 weeks, but remains in diapause for another 10 weeks. Eggs hatch in early May (Fig. 6). First- and second-instar larvae are capable of wind dispersal over considerable distances (Fig. 7). There are 5–7 larval instars (Figs. 8 and 9), and pupation occurs in July. The pupa is naked and reddish brown, with clumps of light-colored hairs (Fig. 10). Males emerge a few days before the females. For more information on the biology see the summaries by Bejer (1988), Grijpma (1989), and Lipa and Glowacka (1995).

Figure 5 Eggs of *Lymantria monacha* under a bark scale. Melody Keena, USDA Forest Service, Bugwood.org.

Figure 6 *Lymantria monacha* larvae soon after egg hatch. Stanislaw Kinelski, Bugwood.org

Figure 7 Second instar *Lymantria monacha* larva. Melody Keena, USDA Forest Service, Bugwood.org.

Figure 8 Fifth instar *Lymantria monacha* larva on spruce. Melody Keena, USDA Forest Service, Bugwood.org.

Figure 9 *Lymantria monacha larva* feeding, showing head capsule. Melody Keena, USDA Forest Service, Bugwood.org.

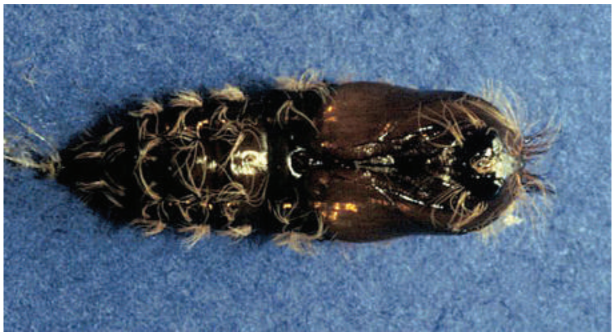

Figure 10 *Lymantria monacha* pupa. Melody Keena, USDA Forest Service, Bugwood.org.

ANALYSIS OF RELATED NATIVE AND ESTABLISHED EXOTIC INSECTS IN NORTH AMERICA

Native Insects Related to the Pest (Nontarget Species)

There are 33 species of Lymantriine native to North America, in four genera: *Gynaephora*, *Orgia*, *Acsala* and *Dasychira* (Ferguson, 1978). Species of *Acsala* and *Dasychira* are found only in North America. Species from all the native North American genera should be considered in host range testing if nun moth natural enemies, not already established in the United States, were to be considered for importation.

Natural Enemies that May Host Shift to the Pest

The only species of *Lymantria* known to be established in the Western Hemisphere is *Lymantria dispar* (L.). Several species of parasitoids that might parasitize *L. monacha* have been introduced and established for classical biological control of *L. dispar* in North America (see section on natural enemy biology below).

BROAD ASSESSMENT OF NATURAL ENEMIES AS POPULATION REGULATING FACTORS IN THE PEST'S NATIVE RANGE

Nearly 100 species of parasitoids have been reported from *L. monacha* in its native range (Tables 1–3). Several studies have evaluated the effectiveness and abundance of parasitoids as sources of mortality in nun moth populations, but there have been no attempts to rear or augmentatively release them to increase their abundance and improve control.

Pathogens of this insect have received more attention, and some are used as microbial pesticides in countries where outbreaks have occurred. As of 2012, only products containing *Bacillus thuringiensis* Berliner are available for operational use. There is some variation in efficacy among formulations (Glowacka, 1989, 1995). *Bacillus thuringiensis* has been used successfully in Germany (Altenkirch et al., 1986; Langenbruch, 1993), Russia (Bakhvalov et al., 1984; Marchenko, 1995), Belarus (Krushev and Marchenko, 1981), and the Czech Republic (Svestka, 1995). For more than a century, natural epizootics of the nuclear polyhedrosis virus have been observed to be a main factor that causes the collapse of *L. monacha* outbreaks (Grijpma, 1989). Several attempts to produce this virus have been made, but no large-scale production has yet been achieved.

The parasitoids of *L. monacha* in Europe have been catalogued by Thompson (1946) and Herting (1976) and studied in detail by Fahringer (1941) and Schedl (1949) in Austria, by Niklas (1942abc) in Germany, by Komarek (1937) and Kolubajiv (1962) in the Czech Republic, and by Romanyk and Riperez (1960) in Spain. The tachinid *Pales pavida* (Meigen) and the braconid *Cotesia melanoscela* (Ratzberg) are considered the most important parasitoids of nun moth in Europe (Grijpma, 1989). Lipa and Glowacka (1995) provide a list of all the parasitoids and pathogens reported for *L. monacha* in Poland. Mills and Schoenberg (1985) provide a listing of the more important parasitoids found in Europe. Publications on natural enemies of *L. monacha* in Russia are reviewed by Kolomiyets (1990); *Parasetigena takaoi* (Mesnil) and *Blepharipa schineri* Mesnil were shown to be the most effective parasitoids in the Russian Far East. No egg parasitoids were found in Russia, but some have been found in low abundance in Europe. Chao (1978) provides a list of *L. monacha* parasitoids in China.

Several species of birds, arthropods, and small mammals are reported to prey on eggs, larvae, pupae, and adults of *L. monacha* (Steinfatt, 1942). Birds are considered to be the main predators of both eggs and larvae, but may not have much influence during outbreaks (Wellenstein and Schwenke, 1978).

Table 1 Pathogens and predators of nun moth, *Lymantria monarcha*, in its native range in Europe and Asia.

Natural Enemy (Scientific Name)	Stage Attacked	Location	References [a]
Viruses			
Baculovirus efficiens	Larvae	Poland	2
Cytoplasmic polyhedrosis virus (CPV)	Larvae	Germany	3
Nucleopolyhedrosis virus (LmNPV)	Larvae	Throughout range	First described 7
Bacteria			
Enterobacter cloacae (Jordan)	Larvae	Poland	5, 10
Enterobacter aerogenes Hormacche and Edwards	Larvae	Poland	5, 10
Proteus vulgaris Hauser	Larvae	Poland	5, 10
Pseudomonas fluorescens Migula	Larvae	Poland	5, 10
Fungi			
Beauveria bassiana Balsamo (Vuillemin)		Poland	2, 8, 9, 10
Cephalosporium sp.		Poland	5, 10
Entomophthora sp.		Poland	9
Paecilomyces farinosus Brown et Smith		Poland	2, 8, 10
Invertebrate predators			
Calosoma sycophanta L. (Coleop.: Carabidae)	Larvae and Pupae	Germany, Poland, European Russia	6, 11, 12
Calosoma denticolle Gebl. (Coleop.: Carabidae)	Larvae and Pupae	European Russia	6
Formica rufa L. (Hymenop.: Formicidae)		Poland	1
Formica cinerea Wheeler (Hymenop.: Formicidae)		Russia	6
Neriene montana (Clerck) (Araneae: Linyphiidae)	Adults?	Poland	11
Piciromerus bidens F. (Hemiptera: Pentatomidae)	Larvae	Poland	4
Raphidia ophiopsis L. (Neuroptera: Raphidiidae)	Eggs, Larvae and Adults	Poland, European Russia	4, 6
Rhinocorus annulatus (Hemiptera: Reduviidae)	Larvae and Pupae	European Russia	6
Thomisus viaticus O. P. Cambridge (Araneae: Oxyopidae)	Adults?	Poland	11
Troilus luridus F. (Hemip.: Pentatomidae)	Larvae	Poland	4
Arma custos F. (Hemip.: Pentatomidae)	Larvae	Poland	4
Xylodrepa quadripunctata L. (Coleop.: Silphidae)		European Russia	6
Vertebrate predators			
Cuculidae spp. (bird)	Larvae	Germany	12
Corvidae spp. (bird)	Pupae	Germany	12
Paridae spp. (bird)	Eggs	Germany	12
Rana temporaria L. (frog)	Larvae	Poland	11

[a] References: [1] Ambros, 1954; [2] Glowacka, 1989; [3] Huger and Krieg, 1958; [4] Ilyinykh, 2010; [5] Karczewski, 1968; [6] Kolomiyets, 1990; [7] Komarek and Brendl, 1924; [8] Lipa, 1962; [9] Siemaszko, 1924; [10] Sliwa, 1987; [11] Steinfatt, 1942; [12] Wellenstein and Schwenke, 1978.

Table 2 Hymenopteran parasitoids of nun moth, *Lymantria monarcha*, in Eurasia.

Natural Enemy (Scientific Name)	Stage Attacked	Location	References [a]
Family Ichneumonidae			
Aoplus nubeculosus (Holmgren)	Pupae	Russia (Western Siberia)	6
Apechthis capulifera (Kriechbaumer)	Pupae	Poland, China	2, 3, 8
Apechthis compunctor (L.)	Pupae	Poland, Austria, Germany, Russia (European part, Western Siberia), China	2, 4, 6, 8, 10, 11
Apechthis quadridentata (Thomson)	Pupae	China	2
Apechthis rufata (Gmelin)	Pupae	China, Europe, Germany, Czech Republic	2,5, 7, 8, 12
Aphanistes ruficornis (Gravenhorst)	Larvae	China	2
Barichneumon nigritarius Gravenhorst		China	2
Callajoppa cirrogaster (Schrank)	Pupae	Russia (European part)	6
Campoletis rapax (Gravenhorst)		China	2
Casinaria nigripes Gravenhorst	Larvae	Austria, Germany, Czech Republic, Russia (European part ,Western Siberia), China	2, 4, 6, 7, 8, 10
Casinaria petiolaris (Gravenhorst)	Larvae	Russia (western Siberia), China	2, 6
Coelichneumon sugillatorius L.	Larvae	Poland, China	2, 11
Cotiheresiarches dirus (Wesmael)	Larvae	Poland, China	2, 11
Diphyus raptorius (L)	Larvae	China	2
Ephialtes (Apechthis) capulifera (Kreichbaumer)	Larvae, pupae	Austria, Germany, Czech Republic, Russia (European part)	1, 6, 7, 8, 10
Ephialtes tuberculatus Forster	Larvae	China	2
Goedartia alboguttatus (Gravenhorst)	Larvae	Poland, China	2, 11
Gregopimpla inquisitor (Scopoli)	Larvae	Europe, Germany, Czech Republic, Poland, China	2, 5, 7, 8, 11, 12
Ichneumon insidiosus Wesmael	Larvae	China	2
Ichneumon primatorius Forster	Pupae	Russia (European part), China	2, 6
Itoplectis alternans (Gravenhorst)	Pupae	Europe, Czech Republic, Russia (European part)	5, 6, 7, 12
Itoplectis viduata (Gravenhorst)	Pupae	Europe, Poland, Germany	5, 8, 11, 12
Lymantrichneumon disparis Poda	Pupae	Europe, Austria, Germany, Czech Republic, Russia (European part, Western Siberia, Far East), Poland, China	2, 3, 4, 5, 6, 7, 8, 10, 11, 12
Pimpla alternans Gravenhorst	Pupae	Poland, China	2, 11
Pimpla arctica Zetterstedt	Pupae	China	2

Table 2 Hymenopteran parasitoids of nun moth, *Lymantria monarcha*, in Eurasia, *continued*.

Natural Enemy (Scientific Name)	Stage Attacked	Location	References [a]
Pimpla examinator (F.)	Pupae	Poland, China	2, 3, 8, 11
Pimpla rufipes (Miller)	Pupae	Europe, Poland, Germany, Czech Republic, Russia (European part, Western Siberia), China	2, 3, 5, 6, 7, 8, 11, 12
Pimpla spuria Gravenhorst	Pupae	Russia (European part)	6
Pimpla turionellae (L.)	Pupae	Europe, Spain, Austria, Germany, Poland, Czech Republic, Russia (European part, Western Siberia), China	1, 2, 4, 5, 6, 7, 8, 9, 10, 11, 12
Spilothyrateles nuptatorius (F)	Larvae	China	2
Theronia atalantae (Poda)	Pupae	Europe, Austria, Germany, Poland, Czech Republic, China	2, 4, 5, 7, 8, 10, 11, 12
Xorides irrigator (F.)	Larvae	China	2
Family Braconidae			
Cotesia cajae (Bouché)	Larvae	China	2
Cotesia glomerata (L.)	Larvae	China	2
Cotesia melanoscela (Ratzberg)	Larvae	Europe, Germany, Poland, Czech Republic, Russia (European part, Western Siberia, Far East), China	2, 5, 6, 7, 8, 11, 12
Glyptapanteles inclusus (Ratzberg)	Larvae	Europe, Poland, Czech Republic, Russia (European part), China	2, 5, 6, 7, 11, 12
Glyptapanteles liparidis Bouché	Larvae	Russia (Western Siberia)	6
Glyptapanteles vitripennis (Curtis)	Larvae	Russia (Caucuses)	6
Macrocentrus collaris (Spinola)	Larvae	China	2
Meteorus monachae Tobias	Larvae	Russia (European part)	6
Meteorus pendulus (Müller)	Larvae	China, Russia (European part), Poland	2, 6, 11
Meteorus pulchricornis Wesmael.	Larvae	Russia (Far East)	6
Meteorus versicolor (Wesmael)	Larvae	Europe, Germany, Czech Republic, Russia (European part, Western Siberia), China	2, 5, 6, 7, 8, 12
Family Eulophidae			
Elachertus charondas (Wa1ker)	Larvae	Europe, Germany, Czech Republic	5, 7, 8, 12
Eulophus abdominalis Nees	Larvae	Russia (Western Siberia)	6
Eulophus larvarum (L.)	Eggs	China	2

Table 2 Hymenopteran parasitoids of nun moth, *Lymantria monarcha*, in Eurasia, *continued.*

Natural Enemy (Scientific Name)	Stage Attacked	Location	References [a]
Family Torymidae			
Monodontomerus minor (Ratzberg)	Pupae	Europe, Austria, Germany	1, 5, 8, 10, 12
Family Trichogrammidae			
Trichogramma evanescens Westwood	Eggs	Europe, Czech Republic, China	2, 5, 7, 12
Trichogramma fasciatum (Perkins)	Eggs	China	2
Trichogramma pretiosum Riley	Eggs	China	2
Family Heloridae			
Teleas laeviusculus (Ratzeburg)		China	2
Family Scelionidae			
Telenomus bombycis Mayr	Pupae	China	2
Telenomus phalaenarum (Nees)	Pupae	Europe, Germany, Czech Republic	5, 7, 8, 12

[a]References: [1]Burzynski, 1968; [2]Chao, 1978; [3]Finck, 1942; [4]Fahringer, 1941; [5]Herting, 1976; [6]Kolomiyets, 1990; 7Komarek and Brendl, 1924; [8]Niklas, 1942b; [9]Romanyk and Ruperez, 1960; [10]Schedl, 1949; [11]Sliwa, 1987; [12]Thompson, 1946.

Table 3 Dipteran parasitoids of nun moth, *Lymantria monarcha*, in Eurasia.

Natural Enemy (Scientific Name)	Stage Attacked	Location	References [a]
Family Tachinidae			
Bessa parallela (Meigen)	Larvae	Europe	4, 11
Blepharipa pratensis (Meigen)	Larvae	Russia (European part, Far East), China	2, 6
Blepharipa schineri (Mesnil)	Larvae	Russia (Far East)	6
Carcelia excisa Fallén	Larvae	Poland, China	2, 10
Carcelia lucorum (Meigen)	Larvae	Poland, China	2, 10
Carcelia puberula Mesnil	Larvae	Poland	10
Carcelia rasa (Macquart).	Pupae	China, Russia (Far East)	2, 6
Ceromasia rubrifrons (Macquart)	Larvae	China	2
Compsilura concinnata (Meigen)	Larvae, Pupae	Europe, Austria, Poland, Czech Republic, Russia (Western Siberia), China	1, 2, 3, 4, 6, 7, 9, 11
Drino inconspicua (Meigen)	Larvae	Poland, Russia (European part), China	1, 2, 6, 10
Ernestia rudis (Fallén)	Larvae	Germany, Czech Republic, Russia (Far East), China	2, 6, 7, 8
Erycia festinans (Meigen)		China	2
Erycilla ferruginea Meigen	Larvae	China	2

Table 3 Dipteran parasitoids of nun moth, *Lymantria monarcha*, in Eurasia, *continued.*

Natural Enemy (Scientific Name)	Stage Attacked	Location	References [a]
Exorista fasciata (Fallén)	Larvae	Russia (Western Siberia, Far East)	6
Exorista larvarum (L.)		Poland, Russia (European part, Western Siberia, Far East), China	2, 6, 10
	Larvae, Pupae		
Exorista nympharum (Rondani)	Larvae	China	2
Exorista rustica (Fallén)	Larvae	Russia (European part), China	2, 6
Exorista sorbillans (Wiedemann	Larvae	China	2
Lydella grisescens Robineau-Desvoidy	Larvae	Russia (Far East)	6
Masicera silvatica (Fallén)	Larvae, Pupae	Russia (European part), China	2, 6
Masicera sphingivora (Robineau-Desvoidy)	Larvae,	Russia (Far East)	6
Muscina assimilis Fallén	Larvae	Russia (European part, Far East)	6
Muscina stabulans Fallén	Larvae	Russia (Far East)	6
Pales pavida (Meigen)	Larvae	Europe, Austria, Germany, Poland, Czech Republic, Russia (European part, Far East), China	1, 2, 3, 4, 6, 7, 8, 9, 10, 11
Pales pumicata (Meigen)	Larvae	Poland, China	2, 10
Parasetigena takaoi (Mesnil)	Larvae	Poland, Russia (Far East)	5, 6, 10
Peleteria rubescens Robineau-Desvoidy	Larvae	China, Russia (Far East)	2, 6
Phorocera assimilis (Fallén)	Larvae	China	2
Phorocera obscura Fallen	Larvae	China	2
Phryno vetula (Meigen)	Larvae	China	2
Ravinia pernix (Haris)	Larvae	Russia (Far East)	6
Redtenbacheria spectabilis Schiner	Larvae	Poland, China	2, 5, 10
Tachina (Echinomyia) fera (L.)	Larvae	Europe, Poland, China	2, 4, 10, 11
Thelaira nigripes (F.)	Larvae	China	2
Thelymorpha marmorta (Fallén)	Larvae	China	2
Winthemia quadripustulata (F.)	Larvae	Poland	6
Zenillia libatrix F.	Larvae	Poland	10
Family Sarcophagidae			
Agria affinis (Fallen)	Larvae and Pupae	Europe, Germany, Czech Republic, Russia, (European part, Western Siberia, Far East), Poland, China	2, 4 6, 7, 8, 11
Agria monachae (Kramer)	Larvae	Poland, Russia (Western Siberia), China	1, 2, 6, 10
Angiometopa fallen Pape	Larvae	China	2

Table 3 Dipteran parasitoids of nun moth, *Lymantria monarcha*, in Eurasia, *continued.*

Natural Enemy (Scientific Name)	Stage Attacked	Location	References[a]
Parasarcophaga albiceps Meigen	Pupae	Russia (Far East)	6
Parasarcophaga harpax Pandellé	Pupae	Russia (Western Siberia)	6
Parasarcophaga tuberosa Pandellé	Larvae	Poland, China	2, 6
Sarcophaga carnaria L.	Larvae	Poland	10
Sarcophaga falculata Rondani	Larvae	China	2
Sarcophaga (Kramerea) schuetzei Kramer	Larvae and Pupae	Europe, Austria, Germany, Czech Republic, Russia (Western Siberia, Far East), China	2, 3, 4 6, 7, 8, 9, 11
Sarcophaga (Liosarcophaga) aratrix Pandellé	Larvae	China	2
Sarcophaga (Liosarcophaga) uliginosa Kramer	Larvae and Pupae	Europe, Germany, Czech Republic, Russia (European part, Western Siberia, Far East), China	2, 4 6, 7, 8, 11
Sarcophaga (Parasarcophaga) albiceps Meigen	Larvae	Poland, China	2, 10
Sarcophaga (Robineauella) caerulescens Zetterstedt	Pupae	Russia (European part, Western Siberia, Far East)	6
Sarcophaga (Sarcophaga)variegata Meigen	Larvae	China	2

[a]References: [1]Burzynski, 1968; [2]Chao,1978; [3]Fahringer, 1941; [4]Herting, 1976; [5]Karczewski, 1968; [6]Kolomiyets, 1990; [7]Komarek and Brendl, 1924; [8]Niklas, 1942b; [9]Schedl, 1949; [10]Sliwa, 1987; [11]Thompson, 1946.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

The key natural enemies of *L. monacha* also are primary parasitoids of *L. dispar,* and some species have been imported to North America, mass reared, and released. Two of the parasitoids considered the most important for *L. monacha* biological control in Europe (Grijpma, 1989) are described and their status in North America discussed.

Pales pavida

Pales pavida (Diptera: Tachinidae) is univoltine, oligophagus, and endoparasitic, and it overwinters as a pupa in the forest litter. Adult host-seeking activities are well synchronized with the timing of late-stage larvae and appear to be primarily visual, with the frequency of attack on larvae being directly related to how exposed the larvae are (ODell and Godwin, 1979). Once a host is located, the female parasitoid lays one or more microtype eggs on the exoskeleton of the larva posterior to the head capsule. The fly larvae enter the caterpillar when they hatch and kill the host as they consume it. This parasitoid may be limited in its ability to respond rapidly to increasing host numbers, because it has only one generation a year.

This tachinid has been collected from *L. monacha* in Austria, Germany, the Czech Republic, and other parts of Europe (Mills and Schoenberg, 1985). This and other tachinids are considered the most important parasitoids of *L. monacha* in northern Europe (Bejer, 1988; Lipa and Glowacka, 1995). Collections of this European parasitoid were made from *L. dispar* from 1924–1933 and 1941–1942 and then released in New England (Sabrosky and Reardon, 1976). This fly is widely established now in North America and, with parasitism rates up to 72%, is considered the most effective of the introduced *L. dispar* parasitoids (Ticehurst et al., 1978; Williams et al., 1992).

Cotesia melanoscela

Cotesia melanoscela (Hymen: Braconidae) is solitary, oligophagus, endoparasitic, and bivoltine. The second generation overwinters as larvae or pupae in cocoons attached to the undersides of branches or other objects. In general, first-generation adults attack first- and second-stage instars and, second-generation adults attack third- and fourth-stage larvae. Females of the first generation emerge about the same time host eggs hatch ad wasps lay a single egg per host, usually in the posterior half of the larva. The eggs take 4 to 6 days to hatch (Burgess and Crossman, 1929). The cocoons of the first generation are loosely woven and white to a light-yellow; cocoons of the second generation (the overwintering stage) are tightly woven and sulfur-yellow (Burgess and Crossman, 1929).

From 1911 to 1927, approximately 23,000 field-collected individuals from Sicily, and more than 132,000 laboratory-reared individuals, were released (Burgess and Crossman, 1929). The effectiveness of this parasitoid is reduced by a large number of hyperparasitoids that attack it, and because its second generation is not well synchronized with the appropriate host larval stages (Weseloh, 1976).

RECOMMENDATIONS FOR FURTHER WORK

It would be beneficial to determine if the parasitoids of nun moth already established on *L. dispar* in North America will attack *L. monacha*. This could be done using the quarantine laboratory colony of nun moth maintained by the USDA Forest Service in Ansonia, Connecticut. If it is found that these parasitoids will parasitize *L. monacha*, then they could serve as biological control agents ready to attack nun moth if it were to invade eastern North America. In addition, the nuclear polyhedrosis virus of *L. monacha* should be investigated for its potential as a biorational pesticide for the pest's control or use in tactical eradication efforts.

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XXXVI Siberian Moth

(*Dendrolimus sibiricus* [Chetverikov]) (Lepidoptera: Lasiocampidae)

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DESCRIPTION OF PEST

Taxonomy

The Siberian moth, *Dendrolimus sibiricus* Tschetvericov [Chetverikov] 1908, and the related taxon *Dendrolimus superans* (Butler) 1877 (Fig. 1) are closely related, allopatric entities that may be subspecies or separate species. The taxonomic revisions of the genus *Dendrolimus* by Rozkov (1963) and Lajonquière (1973) considered the Siberian population to be a subspecies, *D. superans sibiricus*. Recently, Mikkola and Ståhls (2008), using molecular as well as morphological information, concluded that *D. sibiricus* is a species distinct from *D. superans,* with the former being widespread across northern Asia and the latter being restricted to Honshu and Hokkoido Islands, Japan. This chapter follows this latest revision and treats references to *D. superans sibiricus* and *D. superans*, in areas other than on Hokkoido and Honshu, as belonging to the taxon *D. sibiricus*. A subspecies, *D. sibiricus albolineatus* (Matsumura), occurs on the Sakhalin and Kuril Islands.

Figure 1 *Dendrolimus sibiricus,* top = female, bottom = male.

Several common names have been applied to *D. sibiricus,* including the larch caterpillar, the Siberian spinner moth, the Siberian silk moth, and the silk moth. Russians usually refer to it as “sibirskiy shelkopryad,” which means Siberian silk moth and this common name has been used in pest risk assessments in North American (Davis et al., 2005). However, since it is not a silk moth (Saturniidae), Siberian moth is the preferred, common name.

The genus *Dendrolimus* is Palaearctic and contains 15 species (Mikkola and Ståhls, 2008). All species of *Dendrolimus* are considered serious pests of conifers. In addition to *D. sibiricus*, the most noteworthy include the European pine moth, *Dendrolimus pini* (L.), which occurs in Europe and in a long band through southern Siberia from the Urals to Transbaikalia; *Dendrolimus spectablilis* Butler, found in Japan, Korea, and northern China; *D. superans* (known as the hemlock caterpillar); the pine caterpillar, *Dendrolimus tabulaeformis* Tsai and Liu, found in eastern China; and the Mason pine caterpillar, *Dendrolimus punctatus* Walker, found in southern China and Taiwan.

Distribution

The Siberian moth does not occur in North America, but its introduction is considered a very high risk (EXFOR Database; Davis et al., 2005). Boreal and subalpine forests in North America would be at risk. Its current distribution is northern Eurasia.

Damage

Type Larvae of *D. sibiricus* feed on the foliage of more than 20 species of conifers in northern Asia. The most suitable host plant genera are, from most to least favorable, *Larix, Abies,* five-needle *Pinus* spp., *Picea,* and two-needle *Pinus* spp. (Kirichenko and Baranchikov, 2007). It is most destructive to fir (*Abies*) and the pines *Pinus koraiensis* Sieb. et Zucc. and *Pinus sibirica* Du Tour. Although it is the most important defoliator of the larches, *Larix gmelinii* Rupr. and *L. sibirica* Ledeb. larch can refoliate and are seldom killed. Because the insect has overlapping generations and life cycles extending over more than one growing season, it can defoliate stands in the spring, summer and fall; however, most defoliation occurs in spring, when older larvae feed. Forests with dead trees are susceptible to fire.

Dendrolimus sibiricus is oligophagous and can develop on a wide range of introduced European conifers, including (in descending order of suitability) *Larix decidua* Miller, *Abies alba* Miller, *Abies nordmanniana* (Steven) London, *Picea abies* (L.) Karst, *Pinus nigra* Arnold, and *Pinus sylvestris* L. The last two species are poor hosts (Kirichenko et al., 2009). Of North American conifers, mortality of first instar larvae was <20% on Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), *Pinus strobus* L., and *Picea sitchensis* (Bong.) Carr.*,* while up to 40% died on *Abies grandis* (Dougl. ex D. Don) Lindl. and *Tsuga canadensis* (L.) Carr. (Kirichenko et al., 2008a). Conifers from the families Taxaceae and Cupressaceae are not eaten (Kirichenko et al., 2008a). *Pseudotsuga menziesii* is an excellent host (Kirichenko et al., 2008b).

Extent *Dendrolimus sibiricus* is by far the most destructive species of needle-eating insects in northern Asia, and its outbreaks cause extensive defoliation (Fig. 2). In dark, coniferous forests (fir, spruce, five-needle pines), outbreaks occur at about ten-year intervals and last 2 to 3 years. An outbreak can defoliate thousands of hectares and affect entire forests. For example, in 1932–1957, *D. sibiricus* damaged 7 million ha of forests in western Siberia, with half of the damaged forest stands being killed (Kolomiyets, 1963). Periodic outbreaks of Siberian moth are a common feature of Mongolian larch forests. During 2002–2004, more than 480,000 ha of valuable larch forest were damaged by this species (Ghent and Onken, 2004). Because of Mongolia's extremely dry climate, outbreaks of Siberian moth cause larch dieback in mountainous areas (Baranchikov et al., 2008). During the 20th Century, there were nine large outbreaks in Krasnoyarsk Kray (south-central Siberia, Russia) and 10 million ha were defoliated (Baranchikov et al., 2001). The last outbreak (1989–1996) affected 1 million ha of forest, killing whole stands immediately on 120,000 ha, and an equal-sized area of weakened and stressed trees was killed by secondary pests. The value of the lost timber in this outbreak was $50 million (Farber et al., 2003). In 1999–2002 in the Republic of Yakutia (eastern Siberia), more than 8 million ha of larch stands were damaged (Vinokurov and Isaev, 2002).

Figure 2 Dark coniferous forest defoliated by *Dendrolimus sibiricus*.

Outbreaks of Siberian moth have caused not only enormous economic damage, but have been a powerful ecological factor changing the composition of conifer forests in the region. Both natural and man-made fires frequently occur after an outbreak; vegetative succession requires 180–200 years to regenerate mature conifer stands following a fire (Kuzmichev et al., 2001). See Baranchikov (2005) for a review of studies on ecological consequences of Siberian moth defoliation in Russia.

Pheromone traps with a 1:1 mixture of (Z, E)-5,7-dodecadien-1-ol and (Z, E)-5,7-dodecadienal are used to monitor Siberian moth populations in the Asian regions of Russia (Klun et al., 2000). Formulations of *Bacillus thuringiensis var. kurstaki* are widely used for control (Gninenko+ 2003). Laboratory investigations on the potential of the nuclear polyhedrosis virus of Siberian moth as a biopesticide were made (Orlovskaya et al., 2003) but no field application has been achieved.

Biology of Pest

Typically, *D. sibiricus* has a two-year (parts of three calendar years) life cycle. Most adults fly and lay eggs from late June to mid-July. During outbreaks, some individuals develop faster and only pass one winter as larvae. This accelerates population density growth (Baranchikov and Kirichenko, 2002).

Females lay eggs in chains or clusters on needles or branches (Fig. 3). Average fecundity is 300 eggs per female, with a maximum of 800 eggs. The egg stage lasts 17 to 19 days. Typically, the larvae reach the second or third instar and then overwinter in the forest litter. The next summer, larvae grow slowly and then overwinter a second time as fifth to seventh instars. In the third calendar year, mature larvae (Fig. 3) feed voraciously during the spring and pupate inside cocoons (Fig. 3) in tree crowns by early June. Adult moths appear in late June and July and the sexes are similar in coloration (Fig. 3); after mating, females may fly several kilometers to lay eggs.

Figure 3 Life stages of *Dendrolimus sibiricus*; clockwise from upper left: egg cluster, larva, pupal cocoons, and adults mating.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

There are no species in the genus *Dendrolimus* in North America. The family Lasiocampidae has 34 species in eleven genera in North America. The most important native forest species are the tent caterpillars in the genus *Malacosoma*. Other similar native species include the lappet moths, which like the tent caterpillars feed on hardwoods, although one, *Tolype laricis* (Fitch), feeds on larch. *Malacosoma* and *Tolype* are genera that are distant from *Dendrolimus*, while the genus in North America most closely related to *Dendrolimus* is *Gloveria,* which is restricted to the southwestern United States and Mexico (Reigier et al., 2000). Although in a different family, *Lymantria dispar* (L.), a non-native species widespread in eastern North America, has had many parasitoids introduced for its biological control that also attack *D. sibiricus* (see Table 1).

Native Natural Enemies that May Affect the Pest

Egg parasitoids, tachinid flies, sarcophagid flies, and a nucleopolyhedrosis virus are the important groups of natural enemies associated with the late stages of outbreaks of *Malacosoma disstria* Hübner (Witter and Kulman, 1979; Drooz, 1985). Species in the genera *Telenomus* and *Carcelia*, that attack *M. disstria* or other native forest pests in North America, and that also might attack *D. sibiricus* (see below), may be required.

KNOWLEDGE BASE FOR BIOLOGICAL CONTROL

Area of Origin of Insect

All species of *Dendrolimus* are restricted to Eurasia. *Dendrolimus sibiricus* has the largest geographic range, extending across Russia, from west of the Urals to the Russian Far East and Sakhalin Island, and south into northern Kazakhstan, northern Mongolia, northeastern China, and North Korea (Fig. 4). The species inhabits middle-taiga, south-taiga, and forest-steppe forests; it is a common species in mountain taiga.

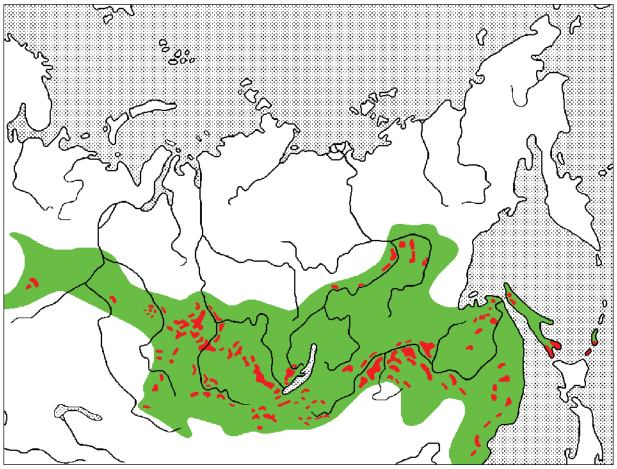

Figure 4 Map of *Dendrolimus sibiricus* distribution (green) and outbreak areas (red).

Area Surveyed for Natural Enemies

Extensive surveys of natural enemies of this pest have been done in Russia in Siberia and the Far East. Information also is available from northern China.

Natural Enemies Found

More than 40 species of parasitoids are known to attack *D. sibiricus* in Asia (Table 1). The most important are the egg parasitoids *Telenomus tetratomus* (Thomson) and *Ooencyrtus pinicola* Matsumura, the larval parasite *Rogas dendrolimi* Matsumura, and the larval-pupal parasitoids *Blepharipa schineri* (Mesnil.), *B. pratensis* Meigen, and *Lespesia frenchii* (Williston).

Diseases are common only in declining populations of *D. sibiricus,* when food for the larvae is inadequate. Pathogens observed include *Bergoldiavirus, Bacillus thuringiensis* Berliner, *Beauveria bassiana* (Bals.) Vuill., and *Isaria (Paecilomyces) farinosus* (Holmsk.) A.H.S. Br. & G. Sm.

Broad Assessment of Factors Affecting Regulation by Natural Enemies

Dry weather during 2 or 3 successive years promotes *D. sibiricus* outbreaks. The durations of outbreaks are very different in fir-dominated forests of southern taiga zone and the larch-dominated forests in the forest-steppe regions of southern Siberia. During a normal outbreak in the fir taiga, the eruptive phase lasts 2 to 3 years and the gradation cycle averages 10 years. In larch forests outbreaks develop slowly and the gradation cycle averages

Table 1 Natural enemies associated with Siberian moth, *Dendrolimus sibiricus,* in its native range.

Order or Family	Stage	Reported Parasitism in Region[2, 3, 4]						
Species	**Attacked[1]**	**WS**	**CS**	**ES**	**AM**	**PR**	**SA**	**CH**
Diptera								
Tachinidae								
Blepharipa pratensis Meigen	L	C	C	C	C	R	-	-
Blepharipa schineri (Mesnil)	L	R	R	R	A	A	-	+
Blepharipa zebina (Walker)	L	-	-	-	-	-	-	+
Carcelia matsukarehae Shima	P	-	-	-	A	-	-	+
Compsilura concinnata (Meigen)	L, P	R	R	R	R	R	-	+
Exorista fasciata (Fallén).	L	?	R	R	R	R	-	+
Exoista larvarum (L.)	L, P	C	A	C	R	R	R	+
Lespesia frenchii (Williston)	L, P	-	A	A	C	-	A	-
Mikia tepens (Walker)	P	R	R	-	C	C	-	+
Pales pavida (Meigen)	L	-	R	?	R	-	-	+
Tachina nupta (Rondani)	L	R	R	-	-	R	-	+
Tachina grossa (L.)	L	R	R	R	-	R	-	+
Winthemia venusta (Meigen)	L	-	-	-	-	-	-	+
Muscidae								
Muscina stabulans (Fallén)	L	C	C	C	C	C	?	?
Muscina levida (Harris)	L, P	C	C	C	C	C	?	?
Sarcophagidae								
Agria punctata Robineau-Desvoidy	P	C	C	C	C	?	A	?
Agria monachae (Kramer)	L, P	C	C	C	C	C	-	+
Kramerea schutzei (Kramer)	L, P	C	C	C	M	M	-	+
Parasarcophaga harpax Pandelle	P	C	C	C	C	-	-	?
Parasarcophaga uliginosa Kramer	L, P	C	C	C	M	-	M	?
Parasarcophaga albiceps (Meigen)	P	R	R	R	R	-	R	+
Parasarcophaga similis (Meade)	-	-	-	-	?	R	-	?
Robineauella pseudoscoparia (Kramer)	L, P	C	C	C	M	M	-	+
Sarcophaga carnaria L.	L	C	C	R	-	-	R	?
Hymenoptera **Braconidae**								
Rogas dendrolimi Matsumura = *Aleiodes esenbeckii* (Hartig)	L	C	C	C	C,A	C,A	A	+++
Apanteles ordinarius (Ratzeburg).	L	C	C	C	C,A	C,A	+	+
Apanteles liparidis (Bouché)	L	R	R	R	C,A	C,A	+	+
Ichneumonidae								
Apechthis capulifera Kriechbaumer	P?	-	-	-	C	-	-	?
Anilastus validus Pfankuch	L	R	R	R	C	C	R	?
Acropimpla didyma (Gravenhorst)	L	-	-	-	R	-	-	?
Acropimpla pictipes (Gravenhorst)	L	-	-	-	R	-	-	?
Casinaria nigripes (Gravenhorst)	L	R	R		C	C	-	++
Coccygomimus disparis (Viereck)	L	-	-	-	?	?	-	++
Pimpla instigator (F.)	L, P	C	C	C	-	-	-	-
Hyposoter takagii (Matsumura)	L	-	-	-	-	-	-	++
Therion giganteum (Gravenhorst)	L, P	R	R	R	C,A	C,A	A	?
Iseropus himalayensis (Cameron)	L	-	-	-	-	-	-	+
Iseropus stercorator Fabricius	L, P	R	R	R	C	C	R	?

Table 1 Natural enemies associated with Siberian moth, *Dendrolimus sibiricus*, in its native range, *continued*.

Order or Family	Stage	Reported Parasitism in Region[2, 3, 4]						
Species	**Attacked[1]**	**WS**	**CS**	**ES**	**AM**	**PR**	**SA**	**CH**
Lymantrichneumon disparis (Poda)	L, P	R	R	-	C	C	-	+
Habronyx gigas (Kriebl)	L, P	R	-	-	R	?	-	?
Encyrtidae								
Ooencyrtus pinicolus (Matsumura)	E	R	R	R	A	C	+	++
Trichogrammatidae								
Trichogramma dendrolimi (Matsumura)	E	C	C	C	C	C	C	+
Trichogramma lingulatum Pang et Chen	E	-	-	-	-	P	-	+
Eupelmidae								
Anastatus japonicus Ashmead	E	-	-	-	C	?	-	?
Scelionidae								
Telenomus dendrolimi (Matsumura)	E	-	-	-	-	?	-	+
Telenomus tetratomus (Tompson)	E	A	A	A	C	A	A	++

[1] Pest stages attacked**:** E = eggs, L = larvae, P = pupae.

[2] Regions**:** WS = Western Siberia (from The Urals to Krasnoyarsk Kray), CS = Central Siberia (Krasnoyark Kray, Republics of Khakasiya and Tyva), ES= Eastern Siberia (Irkutsk Oblast' and Transbaikalia), AM = lower Amur region (southern Khabarovsk Kray), PR=Primorskiy Kray, SA = Sakhalin Island, CH = northeastern China.

[3] Parasitism: quantitative data (R = rare, 0.1–5%, C = common, 6-50%; A = abundant, > 50%); qualitative data (- = not recorded, ? = no information but parasitism likely, + = minor parasitism, ++ = parasitism important).

[4] References (with regions in parenthesis): Boldaruyev, 1969 (ES); Chen and He, 2006 (CH); Kolomiyets, 1963; Kolomiyets and Artamonov, 1994 (WS, CS, ES, PR); O'Hara et al., 2009 (PR, CH); Yurchenko and Turova, 2002 (AM, PR, SA).

15 years (Kondakov, 2002). The adults often fly from the damaged stands and form secondary outbreaks. In fir forests of Krasnoyarsk Kray, the survival rate of the insects can be as low as 0.6% during the depression phase (just after an outbreak) and as high as 70% in the third year of the gradation before an outbreak culmination. The role of the parasitoids is most pronounced between outbreaks when overall survival is around 1.3% (Kondakov, 2002). Mortality declines with each developmental stage: eggs (80%), larvae (70%, being instar I-30%, II-23%, III-10% and IV-VI-4%). Pupal mortality varies considerably from place to place. Parasitoids (mainly *Telenomus* spp.) are the cause of egg mortality, while parasitoids (mainly *Rogas* and *Apanteles*) and pathogens are responsible up to half of larval mortality (Kondakov, 2002).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Telenomus tetratomus

Synonyms of *Telenomus tetratomus* (Thomson) (Hymenoptera: Scelionidae) include *Telenomus tetratomus* Kieffer, *Telenomus gracilis* Mayr, and *Telenomus dendrolimi* Matsumura. This egg parasitoid, referred to as *T. dendrolimi* in Japan and southern China, is widely distributed in Europe, Russia, Mongolia, Japan, and China. In addition to attacking several *Dendrolimus* species, this parasitoid parastizess eggs of *Dasychira abietis* Schiff. et Den., *Orgyia antiqua* L., *Gastropacha quercifolia* (L.), and *Macrothylacia rubi* (L.), although it is not clear if parasitism of species in these genera is merely incidental or if it represents misidentifications (Kolomiyets, 1963; Chen and He, 2006). A single specimen of this species, from Nevada, USA, (Johnson, 1992), might be a misidentification, although the host genus, *Gloveria*, is phylogenetically the group most closely related to *Dendrolimus* in North America.

Adult wasps overwinter in forest litter or in bark crevices near the base of tree trunks. They are very sensitive to frost, and temperatures below –4°C are lethal. After snow cover disappears (middle of May in Asian part of Russia), adult parasitoids move to forest borders, meadows, and gardens where they feed on flowers and aphid honeydew. In June, parasitoids search for the female pupae of their hosts, wait for the female moth to emerge and immediately attach themselves onto the dense hair of the moth's thorax (Fig. 5). The female moth may carry the wasps with them for several kilometers (Kolomiyets, 1963).

Telenomus tetratomus inserts its eggs in host eggs that are <3 days old. A female usually lays all of her available eggs each day, laying an average of ten eggs per host egg. The maximum fecundity of this parasitoid is about 230 eggs over 16 days. The wasp matures in 17–27 days (depending on temperature) with adults emerging a few days after unparasitized eggs would hatch (Fig. 5). Wasps quickly mate, and males die within a week. Females can immediately lay eggs, but usually wait for several months for a new generation of *Dendrolimus* eggs (Kolomiyets, 1963).

Figure 5 *Telenomus tetratomus* adults; top, on underside of female moth wing and bottom, emerging from host eggs.

Rates of parasitism of Siberian moth eggs by *Telenomus* are high and fairly constant–about 50% at the beginning of an outbreak, increasing to 99% by the end, when hosts become sparse (Yurchenko and Turova, 2002). The wasp is attacked frequently by the secondary parasite *Pachineuron solitaruis* Ratzburg. Overwintering wasps may be killed by ground fires in early spring after snow melt.

Species of *Telenomus* have been used for augmentative biological control of Siberian moth. The level of parasitism of Siberian moth eggs in the Baikal region was increased to 60% by moving infested eggs from a collapsing outbreak to areas where moth densities were increasing. *Telenomus tetratomus* has been reared in the laboratory (Boldaruyev, 1969).

Carcelia matsukarehae Shima

The tachinid *Carcelia matsukarehae* Shima, attacks only *Dendrolimus* species and is a widespread effective parasitoid. It is an important parasitoid of *D. sibiricus* in the broad-leaved forest of Primorye in Far East Russia (Yurchenko and Turova, 2002), *D. spectabilis* in Japan (Shima, 1969), and several species of *Dendrolimus* in China (Chen and He, 2006).

Carcelia matsukarehae has two generations per year in the southern Primorye region. The first generation overwinters as larvae in early instar Siberian moth larvae. The parasitoid larvae emerge from their hosts May to mid-June and pupate. Usually only one tachinid larva of this species develops per host. The adult flies emerge in June or July and deposit eggs on 5th- or 6th-instar larvae, and rarely pupa, of the Siberian moth to begin the second generation. Fly larvae pupate in mid-August and adults emerge a week later and infest young larvae of Siberian moth from August to September (Yurchenko and Turova, 1998). During Siberian moth outbreaks at Primorsky Kray in 1977, 1988, and 1997, *C. matsukarehae* parasitized up to 60% of the larvae and 20% of the pupae (Yurchenko and Turova, 2002).

RECOMMENDATIONS FOR FURTHER WORK

There is a diverse parasitoid fauna associated with Siberian moth in its native habitat, and the role parasitoids play in population regulation of the pest is very important. The vast majority of these parasitoids are polyphagous, but *C. matsukarehae* attacks only species of *Dendrolimus*. The egg parasitoid *T. tetratomus* tracks variation in the density of its host and parasitism rates are >50% at all host densities. This parasitoid can be reared in the laboratory and has been used for augmentative release. More information is needed on the role of these parasitoids in maintaining low densities of *D. sibiricus*. Because *D. sibiricus* has no close relatives in the United States, there probably are few native parasitoids that will adapt to it if it ever invades. However, several of the parasitoids that attack *D. sibiricus* in Asia already have been introduced to the United States for biological control of the gypsy moth, and it is assumed they would attack *D. sibiricus* in North America.

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