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).

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.

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, 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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