Is Pseudoscymnus tsugae the Solution to the Hemlock Woolly Adelgid Problem?: An Early Perspective

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Abstract

Hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae) is native to Japan where it is an innocuous inhabitant of *Tsuga diversifolia* Masters and *T. sieboldii* Carriere. Native populations of this insect are regulated by host resistance and natural enemies. However, introduced populations in eastern North America attain damaging levels on *T. canadensis* (L.) Carriere and *T. caroliniana* Engelmann and are regulated mainly by weather and negative density-dependent feedback mechanisms related to host deterioration. The current hope for suppressing introduced populations of hemlock woolly adelgid in eastern North America lies with the exotic predator, *Pseudoscymnus tsugae* Sasaji and McClure (Coleoptera: Coccinellidae). Extensive laboratory and field studies of the biology and predatory ability of *P. tsugae* revealed that it has great potential for biological control. Nearly 120,000 adults of *P. tsugae* were released in hemlock forests in Connecticut, New Jersey and Virginia from 1995 through mid-June 1999. *P. tsugae* reproduced, dispersed, overwintered, and showed remarkable short-term impact on *A. tsugae* by reducing adelgid densities 47 to 88% in only five months on release branches at the early sites. Spiders, the most important natural enemies of *P. tsugae*, reduced efficacy at some sites. In addition, the recent string of relatively mild winters has been conducive to the survival of *A. tsugae* and of the elongate hemlock scale, *Fiorinia externa* Ferris (Homoptera: Diaspididae) another introduced pest from Japan. Consequently, adelgid and scale populations at some sites have grown and trees have continued to decline despite the presence of *P. tsugae*. Larvae and adults of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), a polyphagous predator from Japan, were observed in high numbers from April through September at several study sites, especially those where trees were heavily infested with *A. tsugae*. Considering how rapidly hemlock trees are injured following adelgid attack, *P. tsugae* must establish, reproduce and disperse quickly following a release of relatively few beetles. To become a permanent solution to the hemlock woolly adelgid problem in North America, *P. tsugae* must also be able to consistently maintain adelgid populations below injurious levels. Studies to evaluate the long-term efficacy of releasing 10,000 adults of *P. tsugae* in 5-10 acre infested hemlock forests were initiated in spring 1998 in Connecticut, Virginia and New Jersey and were expanded in 1999 to include additional sites there and others in Maryland, Massachusetts, New York, North Carolina, Pennsylvania, Rhode Island, and West Virginia.

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Introduction

Hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae) is native to Japan where it is an innocuous inhabitant of *Tsuga diversifolia* Masters and *T. sieboldii* Carriere throughout their natural growing areas. Native populations of *A. tsugae* in Japan are maintained at low densities on hemlock by a combination of host resistance and natural enemies (McClure 1992, 1995a, 1995b). The previously unknown beetle, *Pseudoscymnus tsugae* (Coleoptera: Coccinellidae)(Sasaji and McClure 1997), was the most common and effective insect predator of *A. tsugae* in Japan. It occurred at 24 of 66 infested sites where it killed 86-99% of adelgid eggs (McClure 1995a).

A. tsugae is a destructive introduced pest of *T. canadensis* (L.) Carriere and *T. caroliniana* Engelmann in 11 eastern states from North Carolina to southern New England. Although populations of *A. tsugae* on ornamental hemlocks can be managed successfully using a program that relies heavily on chemical pesticide applications (McClure 1987a, 1995c), adelgid populations in the forest are presently unmanaged and threaten to eliminate *T. canadensis* and *T. caroliniana* throughout much of their natural ranges. Introduced populations of *A. tsugae* are host-destroying and self-annihilating (McClure 1991a). None of the native natural enemies which inhabit hemlock forests in eastern North America are effective biological control agents. Therefore, the dynamics of adelgid populations is driven mainly by weather (McClure 1989, 1996) and the negative density-dependent consequences of host deterioration on adelgid performance (McClure 1991a).

P. tsugae has clearly evolved as a specialized predator-prey system in Japan and appears to be the most promising biological control candidate. Extensive studies in Connecticut on the biology and predatory ability of *P. tsugae* revealed that it possesses many attributes of a successful biological control agent (Cheah and McClure 1996, 1998). In addition, P. *tsugae* is amenable to mass culturing on live *A. tsugae* collected from the field and three or more generations can be reared each year in the laboratory under controlled temperature conditions (McClure and Cheah 1998). This paper evaluates the performance of *P. tsugae* during its first three years in the field and provides an early perspective on whether or not this predator will be a solution to the hemlock woolly adelgid problem in eastern North America

Materials and Methods:

Field releases of *P. tsugae*

During the past five years we have released more than 120,000 adults of *P. tsugae* at 14 sites in Connecticut, one in New Jersey and two in Virginia (Table 1). The 14 release

Table 1.—Location and description of hemlock forests where we released *Pseudoscymnus tsugae* between 1995 and 1999 in Connecticut (CT), New Jersey (NJ), and Virginia (VA). Infestation levels for hemlock woolly adelgid (HWA) and elongate hemlock scale (EHS) when *P. tsugae* was first released are: None (N) present; Low (L) = most trees and branches not infested and without injury; Moderate (M) = about half the trees and branches infested and some injured; High (H) = most trees and branches infested and injured, Very High (V) = all trees and branches infested and greatly injured. See also Fig. 1.

							P. tsugae	
					Infestation		Year first	Total released
Site	State	County	Town	Elevation (ft)	HWA	EHS	released	to date
1.	CT	Fairfield	New Fairfield	700	V	V	1997	2,100
2.	CT	Litchfield	New Hartford	600	L	M	1996	10,505
3.	CT	"	Washington	776	L	H	1998	10,500
4.	CT	"	"	580	L	L	1999	5,000
5.	CT	Hartford	Bloomfield	500	M	M	1996	10,760
6.	CT	"	Granby	780	L	N	1999	10,000
7.	CT	"	Suffield	570	M	N	1999	10,000
8.	CT	"	Windsor	150	M	M	1995	3,125
9.	CT	Middlesex	East Haddam	210	M	L	1999	6,086
10.	CT	New Haven	Cheshire	260	H	M	1995	100
11.	CT	"	Hamden	250	H	H	1997	3,600
12.	CT	New London	Voluntown	390	M	N	1999	3,000
13.	CT	Tolland	Union	920	L	N	1999	10,000
14.	CT	Windham	Pomfret	270	M	N	1998	5,084
15.	NJ	Sussex	Vernon	1,235	H	H	1998	10,000
16.	VA	Albemarle	Charlottesville	400	M	N	1998	10,500
17.	VA	Rockbridge	Montebello	3,200	M	N	1997	10,100

sites in Connecticut represent all eight counties and include sites in the southern part of the state where *A. tsugae* has been present for more than 10 years and where many hemlocks have been killed or severely weakened, sites in the central and north-central parts where adelgid infestations are 5-10 years old and where trees are in varying levels of decline, and sites in the northeast and northwest towns where adelgid infestations are patchy and light and where trees are mostly unaffected (Fig. 1).

Between 100 and 10,760 adults of *P. tsugae* (~1:1 sex ratio) were released at study sites in the spring by placing beetles directly on trees. The number of beetles released initially and in subsequent years and the pattern of their release within the site were determined by the nature of the study. In early studies 2,000-3,000 beetles were released onto relatively few trees to investigate local impacts of *P. tsugae*. To enhance the establishment of *P. tsugae*, some of these sites were later augmented to achieve release densities of at least 10,000 beetles. A minimum of 5,000 beetles were released at other new sites in an effort to establish *P. tsugae* throughout Connecticut. Later studies to evaluate dispersal and long-term impacts involved the release of at least 10,000 adult beetles over a larger area. Observations were made at sites prior to and periodically following release of *P. tsugae* to monitor hemlock health, abundance of nymphs and adults of *A. tsugae*, overwintering ability of *P. tsugae*, and the presence of any other arthropod pests of hemlock or their natural enemies.

Evaluating the efficacy of *P. tsugae*

1995 Experiment: The first field release of *P. tsugae* in North America was made in 1995 in a forest of eastern hemlock, white pine, and mixed hardwood species in Windsor (Table 1 & Fig. 1, Site #8). Hemlock woolly adelgid was prevalent in the forest, but hemlock trees had not yet suffered significant decline. Five hemlocks with full crowns and ranging in height from 10-20m and from 25-55cm dbh were selected for the study. On June 15, four infested branches located at the four cardinal directions of the lower crown of each tree were tapped three times to dislodge any native natural enemies and were then enclosed within 0.5x 0.25m nylon mesh sleeve cages to protect adelgids from *P. tsugae.* Four other infested branches located at the four cardinal directions of the lower crown of each tree were marked and were not caged. Between June 16-20, 50 adults of *P. tsugae* (1:1 sex ratio) were released onto each of the four marked branches giving a total of 200 adults released per tree. On May 1, 1996 the sleeve cages were removed and the four previously caged and the four marked, non-caged branches were removed from each tree and returned to the laboratory for examination. The number of adelgids present on 2cm lengths (measured from the base of the tip outwards and viewed from the underside only) of each of 20 youngest tips per branch were counted. This number included living and dead individuals of the overwintering generation and represents those that survived attack by predators during 1995.

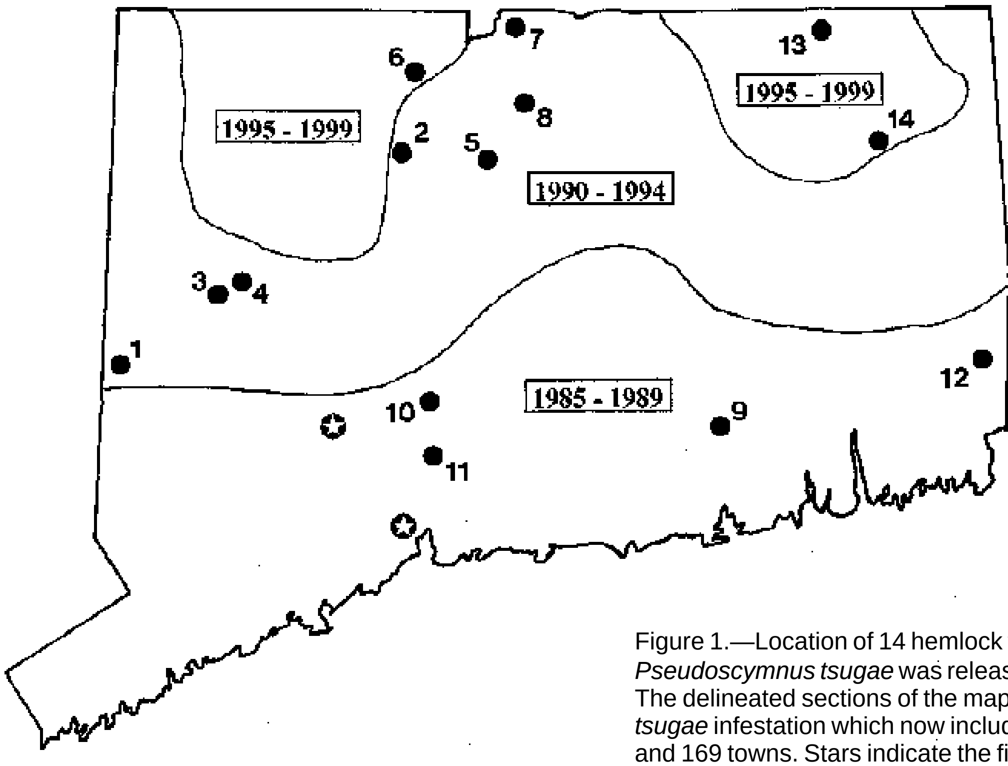

Figure 1.—Location of 14 hemlock forests in Connecticut where *Pseudoscymnus tsugae* was released between 1995 and 1999. The delineated sections of the map show the history of the *Adelges tsugae* infestation which now includes all of the state's 8 counties and 169 towns. Stars indicate the first and only known adelgid infestations recorded in 1985 in Middlebury and New Haven (both in New Haven County). See Table 1 for description of release sites.

1996 Experiment: A second study was conducted in another area of the Windsor forest during 1996 to evaluate the impact of *P. tsugae* on *A. tsugae* without using cages to exclude predators. Four mature, well-infested hemlocks with full crowns were selected for the study. On June 5, six infested branches (~ 0.5m long) in the lower portion of the crown of each tree were marked and the number of adelgid egg masses on newest growth on each branch was counted. Then 40 adults of *P. tsugae* (1:1 sex ratio) were released onto each of four adjacent marked branches on each tree (160 beetles per tree); no beetles were released onto the remaining two branches per tree which were located together as far away from the other four branches as possible. On December 5, 1996 and again on May 15, 1997 marked branches were reexamined for the presence of living adelgids on newest growth. Adelgid densities on release and non-release branches were compared.

1997 Experiment: Field evaluations of the efficacy of *P. tsugae* against *A. tsugae* were expanded to three additional forests in Connecticut and one in Virginia in 1997. The three new Connecticut study sites were located in Bloomfield (Table 1 and Fig. 1, Site # 5), New Hartford (Site # 2), and Hamden (Site # 11); the Virginia site was located near Montebello (Table 1, Site # 17). Each of these sites was a mixed conifer-hardwood forest in which eastern hemlock was well represented in the overstory and understory. The adelgid infestation was light to moderate at Bloomfield, New Hartford and Montebello and heavier and more widely distributed at Hamden. Each area was sufficiently large to identify distinct release and control areas that were very similar in terms of habitat, hemlock size, age, condition, and level of adelgid infestation, and yet the areas were separated by a distance of at least 500m. A minimum of 40 and 13 infested hemlock branches were marked within the release and control areas, respectively, at each site. No more than four branches were selected from any single tree. The number of adelgid egg masses present on 30cm of newest growth (measured from the base of the tip outwards and viewed from the underside of the branch only) on each marked branch was counted. At the New Hartford and Montebello sites an additional 10 branches within the release area were marked, examined for number of adelgids present, and then enclosed within nylon mesh sleeve cages, described previously, to exclude *P. tsugae.* Between April 29 and June 19, 2,400 adult beetles (1:1 sex ratio) were released at each site by placing 60 adults on each of the 40 non-caged, marked branches in each release area. Hemlocks in the release and control areas were examined periodically during the spring and summer and the presence of *P. tsugae* larvae and adults was recorded. In October each of the previously marked branches in the release and control areas, including those within cages were reexamined and the density of adelgid on each branch was determined as before. Overwintering ability was evaluated in late winter 1998 as described below.

Overwintering ability

The ability of *P. tsugae* to survive the first winter (1995-96) at Windsor was determined by hanging yellow sticky traps, which are attractive to both male and female adults, in late winter in the hemlock forest. Subsequently it was deemed more suitable to sample for beetles in late winter using beating sheets or by visually inspecting branches and foliage for beetles. Minimum daily temperatures for the overwintering period were obtained from published data from the nearest official weather station. In later studies, temperature data recorders were deployed in the field at some sites in Connecticut, New Jersey and Virginia during the overwintering period.

Statistical methods

Data were analyzed using parametric and non-parametric, 2-sample or paired sample t-tests according to normality of data and equal variance assumptions with the Number Cruncher Statistical System (Hintze 1995). For normal data with equal variances, the equal variance t-test was used, while data with non-equal variances were analyzed using the Aspin-Welch Test. Data with different distributions were analysed using the Komolgorov-Smirnov test for non-normal data with unequal variances while non-normal data with equal variances were tested using the Wilcoxon Rank-Sum Test. For multiple comparisons of non-normal data, the Kruskal-Wallis procedure was used.

Results and Discussion

Field releases of *P. tsugae*

P. tsugae has established, reproduced, spread and has shown remarkable short-term impact on *A. tsugae* at several release sites. Unfortunately however, adelgid populations have increased dramatically in recent years not only at the release sites, but also throughout the eastern United States, probably due in part to a series of relatively mild winters that have been conducive to adelgid survival. Indeed, *A. tsugae* is spreading at an alarming rate and infested hemlocks are experiencing rapid decline. Coincident with this recent proliferation of *A. tsugae* has been the increased presence on adelgid-infested hemlocks of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) (McClure and Cheah 1998), a polyphagous predator that was introduced from Asia. Larvae and adults of *H. axyridis* were observed from April through September at several study sites, especially those where trees were heavily infested with *A. tsugae* (Table 2). Preliminary observations suggest that *H. axyridis* can complete its development on *A. tsugae* (McClure and Cheah 1998). The potential of this opportunistic predator as a biological control agent for hemlock woolly adelgid is currently being investigated.

The elongate hemlock scale, *F. externa* Ferris (Homoptera: Diaspididae) occurred at more than half of the *P. tsugae* release sites in Connecticut and at the New Jersey release site (Table 1). This scale, which is also native to Japan, attains damaging levels on *T. canadensis* and *T. caroliniana* throughout the eastern United States, despite the presence of its principal natural enemy from Japan, *Aspidiotiphagus citrinus* Craw (Hymenoptera: Aphelinidae)(McClure 1986) and several predators, mainly Chilocorus spp. (Coleoptera: Coccinellidae)(McClure 1977). Like *A. tsugae*, populations of *F. externa* are affected mainly by weather and negative density-dependent feedback mechanisms related to host deterioration (McClure 1980, 1986) and have probably been encouraged in recent years by mild winter weather. Although *F. externa* is less destructive than *A. tsugae*, probably because it feeds on needles rather than on twigs (McClure 1991b), it is also capable of severely weakening and killing trees (McClure 1980). Simultaneous feeding by both insects hastens the decline of hemlock, but *A. tsugae* suppresses populations of *F. externa* in mixed infestations through competition (McClure 1991b). Hundreds of hours of laboratory and field observations revealed that *P. tsugae* does not attack *F. externa*. Consequently, the selective predation of the adelgid by *P. tsugae* would stimulate scale population growth and thereby continue the decline of hemlock even if biological control of *A. tsugae* were effective. The continued presence and high abundance of various developmental stages of *Chilocorus* spp. at several of the *P. tsugae* release sites (Table 2) suggests scale population growth. Therefore the presence of *F. externa* should be considered when selecting beetle release sites and when evaluating the efficacy of *P. tsugae* on the basis of hemlock health.

Evaluating the efficacy of *P. tsugae*

1995 Experiment: Adelgids were 79% less abundant on branches that had been exposed to *P. tsugae* than on ones which had been caged to protect adelgids from beetles which suggests that *P. tsugae* had significantly reduced adelgid numbers in a single growing season. Mean density of adelgids was 0.78 ± 0.32 (n=18) individuals per cm of newest growth on exposed branches and 3.79 ± 2.25 (n=20) on caged branches. These differences were significant ($p < 0.05$, Komolgorov-Smirnov test, Dmn = 0.85). Unfortunately, the 1995 experiment could not rule out the possibility that the cages themselves had somehow enhanced adelgid survival, for example by excluding incidental native predators or by favorably moderating the microclimate of the branch. The 1996 and 1997 experiments addressed this issue.

1996 Experiment: Fall adelgid densities on release and non-release branches were compared using Komolgorov-Smirnov test and found not to be significantly different ($p > 0.05$), particularly, as the available data for non-release branches were highly variable (Table 3). A paired comparison made between initial spring pre-release egg mass counts and December nymph counts using the Wilcoxon Rank-Sum test, was however, highly significant ($Z = 3.4651$; $p < 0.001$) for release branches but not for non-release branches ($p > 0.05$). This suggests that the impact of a small initial release of *P. tsugae* in one season, though marked, is rather localized on the same release tree.

A further comparison between counts in 1996 and 1997 indicated the importance of overwintering mortality and

Table 2.—Occurrence of larvae (L), pupae (P), and adults (A) of the two coccinellid beetles, *Harmonia axyridis* and *Chilocorus* spp. at *Pseudoscymnus tsugae* release sites in Connecticut.

Stages of *Harmonia axyridis*	Date of observation	Location (CT)	Stages of *Chilocorus* spp.	Date of observation	Location (CT)
L	6/8/95	Ashford	A	5/28/96	Windsor
L	4/9/96	Hadlyme	A	9/15/96	"
L	5/7/96	"	A, P, L	7/15/97	Hamden
A	5/5/96	Windsor	A	9/9/97	Bloomfield
L	7/15/97	Hamden	A	9/10/97	New Hartford
A	5/7/98	New Fairfield	A	9/16/97	Hamden
A, L	5/19/98	Hamden	A, L	6/2/98	New Hartford
L	6/2/98	New Hartford	A	"	Bloomfield
L	"	Bloomfield	A, L	6/17/98	Washington
A, L	6/9/98	New Hartford	A, P, L	7/13/98	"
L	6/10/98	Windsor	A , L	9/1/98	Bloomfield
L	6/18/98	Hadlyme	A, L	9/1/98	New Hartford
A, L	6/24/98	Windsor	A, L	9/2/98	Washington
L	7/13/98	Washington	A	9/14/98	Hamden
L	9/1/98	Bloomfield	A	10/22/98	New Hartford
L	9/8/98	Pomfret	A	11/25/98	"
L	6/10/99	Washington	A	"	Washington
A, L	6/16/99	Pomfret	A	4/3/99	"
			A, L	6/10/99	"

Table 3.—Density and mortality of *Adelges tsugae* on release and non-release branches in the Windsor hemlock forest in spring 1996, prior to the release of *Pseudoscymnus tsugae* and in fall 1996 and spring 1997 following release.

Windsor	1996 spring No. of egg masses/branch	1996 fall No. of nymphs /branch	Overwintering + negative feedback mortality	1997 spring No. of egg masses/branch
Release	136.7 ± 9.8 *a* (n=15)	36.9 ± 44.5 *b* (n=16)	69.2 ± 18.8 *e* (n=12)	10.7 ± 13.2 (n=15)
Non-Release	114.1 ± 22.2 *c* (n=7)	170.4 ± 176.2 *c* (n=7)	59.4 ± 24.5 *e* (n=7)	49.1 ± 47.9 (n=7)

Means followed by different letter significantly different at $p < 0.01$; means followed by the same letter not significantly different ($p > 0.05$).

reduced survival due to density-dependent negative feedback. Differences between fall nymph counts in 1996 and spring egg mass counts in 1997 were calculated for % mortality per branch. Percentage mortality on non-release and release branches were not significantly different (equal variance t-test; $p > 0.05$) and the overall mean overwintering mortality was 66.1 ± 19.5 % for 1996-1997. Again the data were highly variable due to small sample size and although reductions of 93.5 ± 8.1% on release branches and 61.0 ± 30.5% on non-release branches were recorded, this was clearly a combined result of predation, negative feedback and overwintering mortality.

1997 Experiment: Table 4 summarizes the fall density counts of nymphs for release, caged controls and control area tips. Data were analyzed separately for new growth tips and older tips to account for density-dependent negative feedback effects. As much of the data were not normal, appropriate non-parametric t-tests were used in analysis (Hintze 1995). Overall, in all four sites, adelgid densities on release tips were significantly lower than densities on either caged branches or in the control area ($p< 0.05$ - $p < 0.001$). Concurrently, comparison of densities in caged controls with densities in control areas for Montebello and New Hartford showed no significant differences ($p > 0.05$), indicating the minor role of native predators and cage effects in adelgid survival.

Table 4.—Density of *Adelges tsugae* on new and older hemlock tips on caged and uncaged branches in the release and control areas five months after the release 2,400 adults of *Pseudoscymnus tsugae* in spring 1997 at each of four sites in Connecticut and Virginia.

1997 Sites	Release area New tips Caged	Release area New tips Uncaged	Release area Older tips Caged	Release area Older tips Uncaged	Control area New tips	Control area Older tips
Montebello VA	5.8 ± 2.3 *a* (n=5)	2.6 ± 2.1 *b* (n=38) *e*	2.8 ± 1.7 *c* (n=6)	1.3 ± 0.6 *d* (n=5)	5.3 ± 3.0 (n=11) *f*	5.1 ± 3.1 (n=3)
New Hartford CT	9.6 ± 1.6 *a* (n=10)	2.8 ± 2.8 *b* (n=36) *e*	6.3 ± 3.5 *c* (n=6)	0.9 ± 1.1 *d* (n=22) *h*	8.9 ± 4.7 (n=21) *f*	6.7 ± 5.2 (n=8) *g*
Bloomfield CT	-	5.0 ± 4.2 (n=33) *a*	-	1.3 ± 1.4 *c* (n=28)	9.4 ± 3.7 (n=24) *b*	4.5 ±3.2 *d* (n=16)
Hamden, CT	-	2.1 ± 1.5 (n=37) *a*	-	0.7 ± 0.9 *c* (n=19)	12.5 ± 4.6 (n=24) *b*	2.0 ±2.0 *d* (n=16)

Significance levels of comparisons of fall adelgid densities:
Montebello *a,b *; c,d *; e,f ***
New Hartford *a,b ***; c,d ***; e,f ***; h,g ***
Bloomfield *a,b ***; c,d **
Hamden *a,b ***; c,d **

Table 5.—Mean percent reduction in the density of *Adelges tsugae* from spring to fall 1997 on new and older tips using comparisons between release tips and (1) control tips and (2) tips enclosed in sleeve cages in the release area for four sites in Connecticut and Virginia where 2,400 adults of *Pseudoscymnus tsugae* were released in spring 1997.

1997 Sites	No. of nymphs/cm (new tips)	No. of nymphs/cm (older tips)
Bloomfield, CT	47.0 % ↓	70.0% ↓
New Hartford, CT	69.2 % ↓	86.6 % ↓
New Hartford (caged)	70.8 % ↓	85.6 % ↓
Hamden, CT	82.8 % ↓	62.8 % ↓
Montebello, VA	52.9 % ↓	78.1 % ↓
Montebello, VA (caged)	57.5 % ↓	48.1 % ↓

Results from the 1997 studies in Bloomfield, Hamden, and New Hartford, Connecticut and near Montibello, Virginia reveal remarkable short term impact by *P. tsugae* on *A. tsugae* (Table 5). Comparison between caged and uncaged branches within release areas and between uncaged branches in the release areas and those in the control areas at least 500m away revealed that adelgid densities had been reduced 47.0-82.8% on new tips and 48.1-86.6% on old tips in only 5 months by a starting population of only 2,400 to 3,600 adult beetles (Table 5).

Overwintering ability

Several adults of *P. tsugae* were captured at the Windsor release site on sticky traps during April, 1996 which documented its overwintering ability in North America for the first time. That winter was one of the coldest and snowiest on record in Connecticut with minimum temperatures in January and February, 1996 reaching -20°C or lower (Table 6). Each of the following three winters were relatively mild and dry (Table 6). In the later part of each of these three winters, adults of *P. tsugae* were easily observed on hemlock branches at six of the eight release sites in Connecticut. Only at the New Fairfield and Cheshire sites where relatively few beetles were released (Table 1) has overwintering ability not been documented. *P. tsugae* also survived each of the past two winters in Virginia and the past one in New Jersey.

Natural threats to the establishment of *P. tsugae*

Several adults of *Homalotylus* sp. (Hymenoptera: Encyrtidae), an Asian parasitoid with no close relatives in North America, emerged during the quarantine period from larvae of *P. tsugae* that were shipped from Japan in 1994.

However, since then there have been no parasitoids observed among the thousands of beetles either reared in the laboratory or examined in the field. As was noted earlier, *H. axyridis* sometimes occurs in high numbers on hemlocks that are heavily infested with *A. tsugae.* Although this beetle is often aggressive and cannibalistic in laboratory colonies and when food is in short supply (McClure 1987b), direct contact between it and *P. tsugae* in the field has not been observed. The direct interaction between these two predators, as competitors or mutual enemies, is currently being investigated. Spiders, which frequent hemlock trees throughout the growing season, represent the greatest threat to the establishment of *P. tsugae*. Spiders were especially evident at the Windsor site where fewer beetles than expected were recovered following each year of release. Webs were present on many branch tips at this site and beetles were sometimes seen entangled in webs and in the grasp of spiders. In an effort to explain the slow population increase of *P. tsugae* in Windsor compared to three other areas, we surveyed the population density of spiders at each of the four sites in July, 1997. Fifteen trees at each site were sampled by tapping a branch and collecting spiders on a 1m square sheet held beneath.

Table 6.—Minimum daily temperature recorded in Windsor between December and March from 1995 through 1999, a period during which nearly 40,000 adults of *P. tsugae* were released in Connecticut.

	Minimum temperature per month (°C)			
Year	December	January	February	March
1995-1996	-13.0	-20.0	-21.7	-15.0
1996-1997	- 9.4	-18.3	- 9.4	- 7.8
1997-1998	-10.6	-14.4	-11.1	-11.1
1998-1999	-12.2	-16.7	-13.3	-10.6

The densities of spiders at Windsor were significantly higher than at any of the other sites ($p < 0.05$; Kruskal-Wallis 1-Way ANOVA). There were 9.7 ($\pm$ 2.9) spiders per m^2 of branch in Windsor which was nearly three times more than in Hamden (3.7 $\pm$ 1.6) and nearly five times more than in Bloomfield (2.1 $\pm$ 2.1), New Hartford (1.9 $\pm$ 1.2), and Montebello (1.8 $\pm$ 1.6). Fortunately the high population density of spiders at Windsor was more the exception than the rule, and was probably due to the proximity of the site (within 50m) to a vast old field with abandoned barns that provided exceptional food and breeding and overwintering sites for spiders.

Summary

Laboratory studies have revealed that *P. tsugae,* possesses many important qualities of a successful biological control agent (Cheah and McClure 1998). It is relatively host specific, is multivoltine, and has a biology that is highly compatible with its prey. Furthermore, results of the initial release experiments reveal remarkable short-term impact on adelgid densities on release branches by *P. tsugae*. However, even though *P. tsugae* has established and increased its numbers in these release areas, trees have generally continued to decline. The recent string of relatively mild winters, which has been conducive to the survival and growth of adelgid and scale populations, as well as the explosive population increase of *F. externa* at some release sites have compounded the problem. Considering the lag time following the release of a successful biological control agent that is often required before control is achieved and the rapid rate of decline of hemlock trees that often occurs following adelgid attack (McClure 1991a), we are clearly in a race against time that we may not win. Indeed we are expecting more from *P. tsugae* in North America than in Japan where *A. tsugae* and *F. externa* do not injure their host.

Whether or not *P. tsugae* will become a permanent solution to the hemlock woolly adelgid problem in North America will depend upon its ability to establish, quickly increase its numbers, disperse, and consistently maintain adelgid populations below injurious levels following the initial release of relatively few adult beetles. Studies to evaluate the long-term efficacy of *P. tsugae* were initiated in spring 1998 in three relatively isolated, 10-15 acre stands of recently infested hemlock in Connecticut, Virginia and New Jersey. At each site, adelgid egg masses were counted on the release tree and on trees at 50m intervals along 200m transects prior to releasing 10,000 adult beetles. Establishment, reproduction and distribution of *P. tsugae*, tree health, and changes in adelgid population density along the transects were monitored in 1998 and will continue to be monitored in subsequent seasons. Studies in 1999 were expanded to include releases of 10,000 beetles in 10 eastern states (Connecticut, Maryland, Massachusetts, New Jersey, New York, North Carolina, Pennsylvania, Rhode Island, Virginia, and West Virginia) using a slightly revised protocol.

Should *P. tsugae* prove to be a successful long-term biological control agent for hemlock woolly adelgid, natural resource managers could then utilize this predator and the knowledge gained through these studies as a forest management tool. For example, early results indicate that *P. tsugae* may be more successful in recently infested forests at the fringe of the infestation where adelgid populations are low and trees are uninjured. Therefore, resource managers could play a prominent role by identifying new infestations of *A. tsugae*, releasing beetles in strategic locations throughout the forest, subsequently monitoring the changes in forest health, and implementing appropriate resource management strategies as needed. Our preliminary studies have also revealed that *P. tsugae* attacks and develops from egg to adult on other important adelgid pests as well including the balsam woolly adelgid and the Cooley spruce gall adelgid. These and other alternate adelgid hosts could serve to enhance the establishment and survival of *P. tsugae* in the conifer forests of eastern North America and increase its efficacy against *A. tsugae* and these other adelgid pests as well.

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