Important Mortality Factors in the Life Cycle of Hemlock Woolly Adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae) in the Northeastern United States

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Abstract

Populations of hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae), in the northeastern United States are injurious and unregulated, and fluctuate greatly in response to various abiotic and biotic factors. Because the life stages of *A. tsugae* are sedentary and firmly attached to hemlock twigs throughout most of the year, they are unable to escape the deleterious effects of weather, competitors, and natural enemies. Unusually cold winter temperatures in northern Connecticut in January 2000 following a period of relatively mild temperatures caused major mortality to overwintering sistens nymphs of *A. tsugae*. Unfrozen and flowing bodies of water near sites and snow cover on lower branches buffered sistens nymphs from cold-temperature-related mortality. Intraspecific competition through negative density-dependent feedback is another important mortality factor on *A. tsugae*. However, the importance of interspecific competition between *A. tsugae* and other hemlock pests, such as *Fiorinia externa* Ferris (Homoptera: Diaspididae) is unknown. Mortality of *A. tsugae* from native predators is generally inconsistent and low. However, exotic predators, in particular *Pseudoscymnus tsugae* Sasaji and McClure (Coleoptera: Coccinellidae), are important mortality factors of all life stages of *A. tsugae* and have good potential for biological control.

Keywords:

Adelges tsugae, mortality factors, *Fiorinia externa*, cold temperature, competition.

Introduction

Adelges tsugae has a complex, polymorphic life cycle that involves both hemlock (*Tsuga*) and spruce (*Picea*) (McClure 1989). There are three parthenogenetic generations of *A. tsugae* that mature on hemlock. The sistens are wingless individuals that begin development in late spring, aestivate (remain inactive) during summer, resume development in autumn, and mature by late winter. The progrediens are wingless progeny of the sistens that develop during spring and produce the next sistens generation by late spring. The sexuparae are other progeny of the sistens that develop on hemlock in spring. However, adult sexuparae are winged and must leave hemlock to find a *Picea* species on which to lay their eggs to begin the sexuales generation (McClure 1989). None of 15 native and exotic *Picea* species that grow in the eastern United States are suitable hosts for sexuparae (McClure 1987, 1992). *Picea jezoensis hondoensis* Siebold and Zuccarini and/or *P. polita* Carriere may be the alternate host(s) for *A. tsugae* in Japan (Inouye 1953; McClure 1996). The ramifications of *A. tsugae* not having a suitable alternate host in the eastern United States are discussed in the “Intraspecific Competition” section.

A detailed description of the life stages and seasonal development of *A. tsugae* in the northeastern United States has been provided by McClure (1987, 1989, 1996). Stages of development are identical in Asia and North America, but adelgid phenology varies greatly among sites and is related to elevation, hemlock phenology, temperature, and photoperiod (McClure 1996; Salom et al. 2001). All three generations of *A. tsugae* on hemlock have six stages of development: the egg, four nymphal instars, and the adult. Eggs and first instar nymphs of the three generations are indistinguishable; the presence and sclerotization of thoracic sutures and wing bud notches, and the size and shape of the body, the thorax, and the antennae distinguished the later instars and adults (McClure 1989).

Populations of *A. tsugae* on hemlock in Asia and western North America are maintained at low innocuous densities by a combination of host resistance and natural enemies (McClure 1992, 1995a, 1995b, 1996). However, in the eastern United States where *A. tsugae* was introduced, adelgid populations are injurious and unregulated, and fluctuate greatly in response to various abiotic and biotic factors. Once a nymph inserts its feeding stylet into the young hemlock twig, it is committed to that feeding site throughout the remainder of its development. Thus it is unable to escape the deleterious effects of weather, competitors, and natural enemies. As we shall see, these are important mortality factors for *A. tsugae* in the eastern United States.

Weather

Eggs and mobile first instar nymphs, called crawlers, are the stages of *A. tsugae* that are most readily dispersed by wind, birds, deer, and humans (McClure 1990; also see these proceedings). They also are the stages that are most vulnerable to dislodgement from hemlock branches by weather events such as strong winds and heavy rain. Eggs and crawlers dislodged from branches have very little chance of finding their way back onto the tree (McClure 1995b). The potential influences of wind and rain and other weather factors such as drought and high summer temperature on the mortality of *A. tsugae* in the eastern United States are unknown and warrant investigation.

Cold Winter Temperature. *Adelges tsugae* is widely distributed throughout the hemlock growing areas of Honshu, Japan. It was collected from 14 different prefectures at sites between 34˚ and 40˚N latitude and between sea level and 1,980 m elevation (McClure 1995b). The relatively low mortality (18% to 25%) to overwintering nymphs of the sistens generation at five sites in Japan located between 1,500 m and 1,925 m elevation suggested that *A. tsugae* is cold hardy and that this adelgid has the potential to invade much of the natural range of *T. canadensis* in the northeastern United States (McClure 1996). However, field observations in Connecticut (McClure 1995) and laboratory experiments by Parker et al. (1998, 1999) revealed that *A. tsugae* incurs much greater mortality during winter in the eastern United States than in Japan.

A two-week period of unusually cold temperatures in Connecticut during January 2000, which followed a relatively mild fall and early winter (Table 1), provided an excellent opportunity to examine the cold hardiness of *A. tsugae*. Between January 24 and April 7, 2000, hemlock trees were sampled at 39 sites in Connecticut. Between six and 17 branches infested with *A. tsugae* were examined microscopically in the laboratory and living and dead nymphs on new and old twigs were counted. The number of nymphs examined at each site ranged from 358 to 1,463 (mean = 1,039 $\pm$ 246). Temperature during the period was monitored using HOBO Data Loggers (Onset Computer Corp.), which had been deployed at or near eight sampling sites. Additional minimum temperature data was gathered from 12 weather stations in Connecticut using Climatological Data New England (2000).

Table 1. Mean Temperature (C°) Recorded at 20 Sites in the Three Climatic Divisions of Connecticut Defined by NOAA-NCDC, Asheville, North Carolina.

	Division 1 (three recording sites)			Division 2 (11 recording sites)			Division 3 (six recording sites)		
Period	Min.	Max.	Avg.	Min.	Max.	Avg.	Min.	Max.	Avg.
Dec. 1 to 31, 1999	-2.1	7.2	2.7	-4.0	5.4	0.7	-4.8	3.9	-0.4
Jan. 1 to 12, 2000	-0.1	9.8	4.4	-2.0	8.2	2.9	-2.5	7.5	2.1
Jan. 13 to 30, 2000	-12.0	-2.5	-7.1	-14.0	-4.4	-9.3	-15.0	-4.8	-10.0

The minimum temperature recorded at 20 sites in Connecticut from January 13 to 30, 2000, ranged from -17° to -23°C with warmest temperatures recorded in Climatic Division 1 along the coast and in the southern part of Climatic Division 2, and coldest temperatures recorded in Climatic Division 3 in northwestern Connecticut (Figure 1). Mortality of overwintering sistens of *A. tsugae* following the January 2000 cold period was relatively low among 10 coastal sites (range 11% to 28%; mean = 21.2%), but was remarkably high (range 83% to 100%; mean = 92.8%) at 23 of 29 sites in northern Connecticut (Figure 2). *A. tsugae* mortality was considerably lower than expected at six sites in the north (range 55% to 76%; mean = 65.7%) and in Ledyard in the south (mean = 11%) where sampled hemlocks were in close proximity to rivers, streams, or unfrozen lakes and ponds (Table 2). In Barkhamsted, Thomaston, and Washington, adelgid mortality was strikingly lower on trees along the river than on trees on the ridge nearby (Table 2). Likewise, in Ledyard, mortality of *A. tsugae* was 11% near a pond and 21% in a forest several hundred meters away. This effect was not observed at Burr Pond and Highland Lake in northern Connecticut where mortality of *A. tsugae* was 97% and 99%, respectively. These data suggest that at some sites, flowing and unfrozen bodies of water may have slightly moderated temperatures on hemlocks growing nearby, thus allowing greater survival of *A. tsugae* nymphs during the two-week cold period in January 2000.

Table 2. Mortality of Overwintering Sisten Nymphs of *Adelges tsugae* Following the January 2000 Cold Period at Eleven Sites in Seven Towns in Northern Connecticut[1].

Town	Site	% Mortality	Range	Total N
B	Ridge	92.1 $\pm$ 7.3	81.3 to 100	1017
	River	62.2 $\pm$ 17.0	38.6 to 87.7	1018
L	Forest	21.1 $\pm$ 7.3	11.6 to 31.6	1051
	Pond	11.1 $\pm$ 4.2	7.3 to 18.2	358
NH	Reservoir	75.9 $\pm$ 15.0	53.8 to 97.2	1041
S	Pond	70.2 $\pm$ 13.5	42.9 to 78.3	1182
T	Ridge	95.0 $\pm$ 3.6	87.5 to 100	1019
	River	73.1 $\pm$ 13.0	53.8 to 100	1138
TO	Pond	97.2 $\pm$ 4.5	84.2 to 100	1212
W	Ridge	100.0 $\pm$ 0.0	——	1331
	River	58.4 $\pm$ 12.0	33.8 to 74.0	1152
	River	55.4 $\pm$ 12.9	39.8 to 77.4	1463
WI	Lake	96.6 $\pm$ 0.6	98.4 – 100	1030

[1]Barkhamsted (B), New Hartford (NH), Simsbury (S), Thomaston (T), Torrington (TO), Washington (W), and Winchester (WI), and at two sites in southern Connecticut in the town of Ledyard (L).

There is evidence that snow cover also may protect *A. tsugae* from cold winter temperature. On May 11, 2000, two branches were sampled from the lower crowns (0 to 5 cm above ground) and upper crowns (~3 m) of three trees in Enders State Forest, Granby, Connecticut. The two branches taken from the lower crowns were nearly resting on the forest floor and had been covered with about 30 cm of snow during the January 2000 cold period. Branches in the upper crown were well above the snow cover. Mortality of sistens nymphs of *A. tsugae* was 92.7% (range = 90 to 95%) on snow less branches, but only 13.0% (range 8 to 18%) on branches where nymphs had presumably been protected from ambient cold temperature by snow. These preliminary data suggest that as *A. tsugae* spreads northward in the United States into areas with greater snowfall, snow-covered branches may provide refuge for overwintering sisten nymphs.

Cold winter temperature is an important mortality factor for the sistens generation and may retard the rate of spread of *A. tsugae* and ultimately limit its range in the northeastern United States. However, the greater degree of cold hardiness recorded in laboratory experiments for sisten nymphs of *A. tsugae* collected from colder instead of from warmer areas of the Northeast (Parker, these proceedings) suggests that *A. tsugae* is adapting rather quickly to increasingly cold winter temperatures as it spreads northward.

Competition

Intraspecific Competition. Field studies in Connecticut revealed that *A. tsugae* is greatly affected by intraspecific competition through negative density-dependent feedback (McClure 1991). The presence of *A. tsugae*, even in low densities, inhibited production of new growth in *T. canadensis*, which in turn caused high mortality of nymphs and low fecundity of adults in subsequent generations. Intraspecific competition also had a profound impact on the performance of the current generation of *A. tsugae*. Percent mortality of nymphs was strongly correlated with its own density on 40 forest hemlocks and ranged from about 10% on sparsely infested trees to nearly 90% on the most heavily infested trees (McClure 1991). Of even greater significance however, was the impact of density and host deterioration on the production of sexuparae, the winged stage that migrates to spruce. As adelgid densities on hemlock increased, an increasingly greater proportion of the progeny of the sistens became winged sexuparae, which then left hemlock and presumably died. Only about 14% of the progeny of the sistens that developed on sparsely infested trees became sexuparae, whereas nearly 90% of those that developed on heavily infested trees became sexuparae (McClure 1991). Clearly this density-dependent feedback mechanism is an important mortality factor for *A. tsugae* in the eastern United States.

Interspecific Competition. The elongate hemlock scale, *Fiorinia externa* Ferris, and a circular one, *Nuculaspis tsugae* (Marlatt) (Homoptera: Diaspididae) attack and injure *T. canadensis* in the northeastern United States. *Fiornia externa* outcompetes *N. tsugae* and quickly excludes it from mixed infestations (McClure 1980). Studies on the competitive interactions between *F. externa* and *A. tsugae* and on the role of natural enemies in the outcome of interspecific competition were initiated in Spring 2001. The initial findings of that ongoing investigation are reported elsewhere (see McClure, these proceedings).

At times, various other herbivores, such as spruce spider mite, *Oligonychus ununguis* (Jacobi); hemlock eriophyid mite, *Nalepella tsugifoliae* Keifer; hemlock looper, *Lambdina fiscellaria fiscellaria* (Guenee); gypsy moth, *Lymantria dispar* (L); and hemlock borer, *Melanophila fulvoguttata* (Harris) can become abundant and destructive pests of *T. canadensis*. The competitive interactions of these pests with *A. tsugae* are unknown and warrant further investigation.

Predators

Native Species. There are no known parasitoids of *A. tsugae* or of any adelgid species. However, there are a number of predators that attack *A. tsugae*. Species of flies (Diptera: Cecidomyiidae and Syrphidae) and lacewings (Neuroptera: Chrysopidae and Hemerobiidae) are the most common native predators observed feeding on *A. tsugae* in the eastern United States. Although these predators may cause significant mortality of *A. tsugae* from time to time, they appear to have very little potential for biological control (Montgomery and Lyon 1996; Wallace and Hain 2000).

Exotic Species. Several species of predators native to Asia and western North America are currently being evaluated as potential biological control agents of *A. tsugae* (these proceedings). Studies in Japan identified several predators that attack *A. tsugae*, the most important of which were a mite, *Diapterobates humeralis* (Hermann) (Oribatida: Ceratozetidae) which kills adelgid eggs by dislodging them from trees (McClure 1995b), and a previously unknown ladybird beetle, *Pseudoscymnus tsugae* (Sasaji and McClure) (Coleoptera: Coccinellidae) (McClure 1995a, b). *Diapterobates humeralis* has not shown good potential for biological control in the eastern United States because its long generation time and low reproductive output make it non-amenable to mass rearing (Cheah and McClure 1996). Furthermore, mites generally have not shown the same affinity for the woolly material enveloping adelgid eggs on *T. canadensis* that was observed on native hemlocks in Japan (McClure and Cheah 1999). On the other hand, *P. tsugae* has shown great potential for biological control (McClure and Cheah 1999; McClure et al. 1999; Cheah and McClure 1996, 1998, 2000). The life cycles of *A. tsugae* and *P. tsugae* are highly synchronous and larvae and adults of *P. tsugae* attack all life stages of *A. tsugae* (Cheah and McClure 2000). Approximately 600,000 adults of *P. tsugae* have now been reared and released at 100 sites in 11 eastern states.

Harmonia axyridis Pallas (Coleoptera: Coccinellidae), a polyphagous predator that was introduced from Asia to control aphids and scales, has shown an increased presence on *A. tsugae* –infested hemlocks in the eastern United States in recent years (McClure et al. 1999). *Harmonia axyridis* can complete its development and reproduce on *A. tsugae* and larvae and adults have been observed on infested trees from early spring through fall (McClure et al. 1999). We are currently investigating the potential of this opportunistic predator as a biological control agent.

Three other coccinellid beetles, *Scymnus* (*Neopullus*) spp., imported from China, are being studied under quarantine to determine their potential for biological control of *A. tsugae* (Montgomery et al. 1998; Lu and Montgomery 2001). All three species feed on all progrediens life stages of *A. tsugae*, but prefer the eggs. *Laricobius nigrinus* Fender (Coleoptera: Derodontidae), a predator commonly associated with *A. tsugae* in western North America, has been imported to Virginia where it also is being studied (Zilahi-Balogh et al. 1999).

Summary

Weather, competition, and predation are important mortality factors in the life cycle of *A. tsugae* in the eastern United States. Populations of *A. tsugae* on *T. canadensis* in the eastern United States fluctuate greatly in response to these and other factors. As other predators join *P. tsugae* and *H. axyridis* in the hemlock forest, mortality to *A. tsugae* may eventually be sufficiently high to sustain biological control. However, the complex interaction of these various mortality factors obscure cause and effect relationships and make evaluation of released biological control agents difficult. Rigorous life table studies and key factor analysis are needed to elucidate the mortality factors responsible for trends in the population dynamics of *A. tsugae* on eastern hemlock.

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