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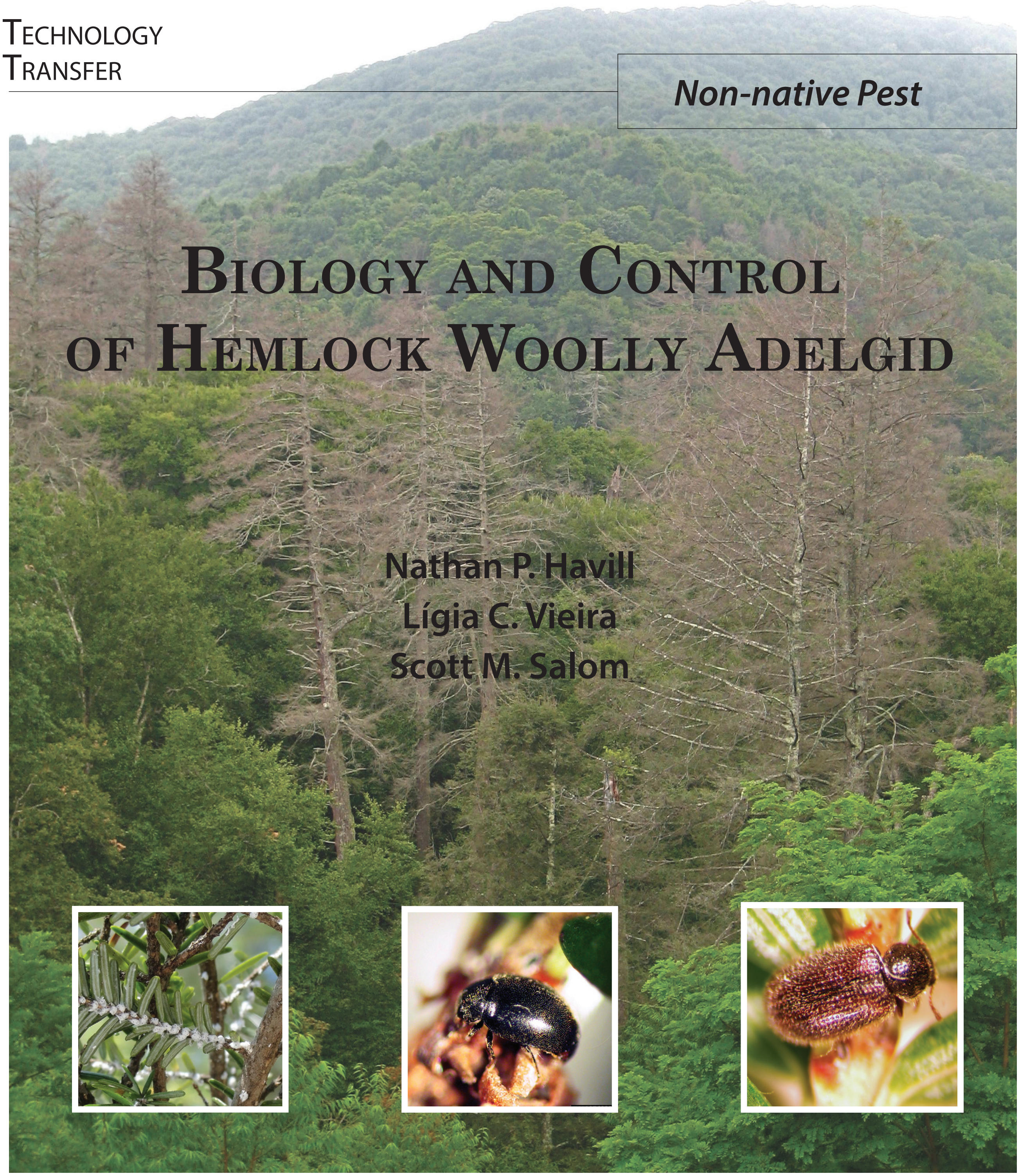

BIOLOGY AND CONTROL OF HEMLOCK WOOLLY ADELGID

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Forest Health Technology
Enterprise Team

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The Forest Health Technology Enterprise Team (FHTET) was created in 1995 by the Deputy Chief for State and Private Forestry, USDA Forest Service, to develop and deliver technologies to protect and improve the health of American forests. This book was published by FHTET as part of the technology transfer series.

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On the cover:

Background image: Hemlock mortality, Jason Van Driesche, Bugwood.org

Bottom left to right: HWA white ovisacs on eastern hemlock branch , Scott M. Salom, Virginia Tech; Sajiscymus tsugae, Carol Cheah, Bugwood.org; Laricobius osakensis, Ligia C. Vieira, Virginia Tech.

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Preface

This publication is a substantial revision of FHTET 2001-03, *Hemlock Woolly Adelgid*, which was published in 2001. This publication contains information on the native range of hemlock and range of hemlock woolly adelgid, the importance of hemlocks in eastern forest ecosystems, and on hosts, life cycle, control, and population trends of the hemlock woolly adelgid.

For copies of this publication or information concerning hemlock woolly adelgid, contact Dr. Scott Salom in Blacksburg, VA at 540-231-2794, Dr. Richard Reardon in Morgantown, WV at 304-285-1566 or the local Cooperative Extension Service Office. The entire publication is available online at http://www.fs.fed.us/foresthealth/technology/pub_programareas.shtml

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Biology and Control of Hemlock Woolly Adelgid

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Table of Contents

Introduction

The hemlock woolly adelgid (HWA) (*Adelges tsugae* Annand) (Figure 1) is a destructive, non-native pest of forest and ornamental hemlock trees in eastern North America. As a member of the Adelgidae, it shares many characteristics with its relatives, the true aphids (Aphididae) and phylloxerans (Phylloxeridae), such as a complex life cycle with sexual and asexual generations. Adelgids are different from true aphids in that they are oviparous (lay eggs) in all generations and use only certain conifer genera as hosts. The Adelgidae also includes other invasive pests such as the balsam woolly adelgid, *A. piceae* (Ratzeburg), on true firs in North America, and the pine adelgids, *Pineus pini* (Macquart) and P. *boerneri* Annand, in pine plantations around the World.

HWA inserts its long, piercing-sucking mouth parts (Figure 2) into the base of hemlock needles and feeds on nutrients stored in the xylem ray cells. In addition to removing the tree's nutrients, the adelgid is thought to cause a hypersensitive response that restricts water transport in the tree. Other stress factors can intensify these effects, causing decline and death of trees of all age classes.

The first record of HWA in the eastern United States is from museum specimens collected in 1951 in Richmond, Virginia. It arrived there some time prior to this date, directly from southern Japan, probably on live plant material. The HWA genotype that was introduced to the United States is one of several, very different lineages found on hemlocks in Asia. In addition to the four known Asian lineages (mainland China, Taiwan, and two in Japan), there is a distinct lineage in western North America,

Figure 1. HWA on eastern hemlock (Image: Scott M. Salom, Virginia Tech).

which is now known to be native to that region. The first records of HWA in the West date from as early as 1916 in British Columbia, but these records have no relevance to the introduction in the East because it is a different lineage. Introduction of additional genotypes which are native to different places could worsen the pest problem in the eastern United States.

The HWA genotype that was introduced to the eastern United States from southern Japan can alternate between southern Japanese hemlock, *T. sieboldii* Carrière, and tiger-tail spruce, *Picea torano* (K. Koch) Koehne. On spruce, there is a sexual generation and gall formation. When this spruce species is not present, HWA can have continuous cycles of asexual generations on hemlock. This is the type of life cycle that the Japanese adelgids exhibit in eastern North America because they were separated from their primary host when they were introduced. The western North American adelgids also have an asexual life cycle, but their separation from a suitable spruce host may have happened millions of years ago when they dispersed naturally from Asia.

Figure 2. Slide-mounted HWA adult (left) and first instar (right) (Photos: Nathan Havill, USDA Forest Service).

In Japan, HWA can occasionally reach high densities on individual trees, but it is very rare that it causes damage. This is probably due to a combination of host resistance, host tolerance, and a diverse complex of arthropod predators that seems to regulate HWA populations.

Hosts and Spread in Eastern North America

In eastern North America, HWA is a destructive pest of eastern hemlock, *Tsuga canadensis* (L.) Carrière, and Carolina hemlock, *T. caroliniana* Engelman. Both species have shown very limited resistance to HWA feeding, and many trees growing under a wide variety of natural and ornamental conditions have died.

The geographic range of eastern hemlock extends from the Canadian Maritime Provinces, west to the Great Lakes region, and as far south as northern Georgia and Alabama, with many separated populations to the south and west of its main range (Figure 3). Carolina hemlock has a much smaller range with isolated pockets in Virginia, North Carolina, South Carolina, Tennessee, and Georgia.

Currently, HWA occupies approximately half of eastern hemlock's natural range (Figure 4). The initial spread was predominantly to the North, but this has slowed as HWA reaches colder areas. To the South, spread is very rapid and HWA has almost filled the entire southern range of hemlock. New, isolated range expansions associated with movement of ornamental hemlock trees in places such as Michigan and southern Ontario are met with vigorous eradication efforts.

Since the HWA lineage that arrived in eastern North America from Japan is adapted to *T. sieboldii*, a species limited to southern Japan at low elevations, it is expected that HWA would not survive as well in colder areas. This appears to be the case, as tree mortality is occurring at a slower pace in northern New England, while in the South the decline has been more rapid.

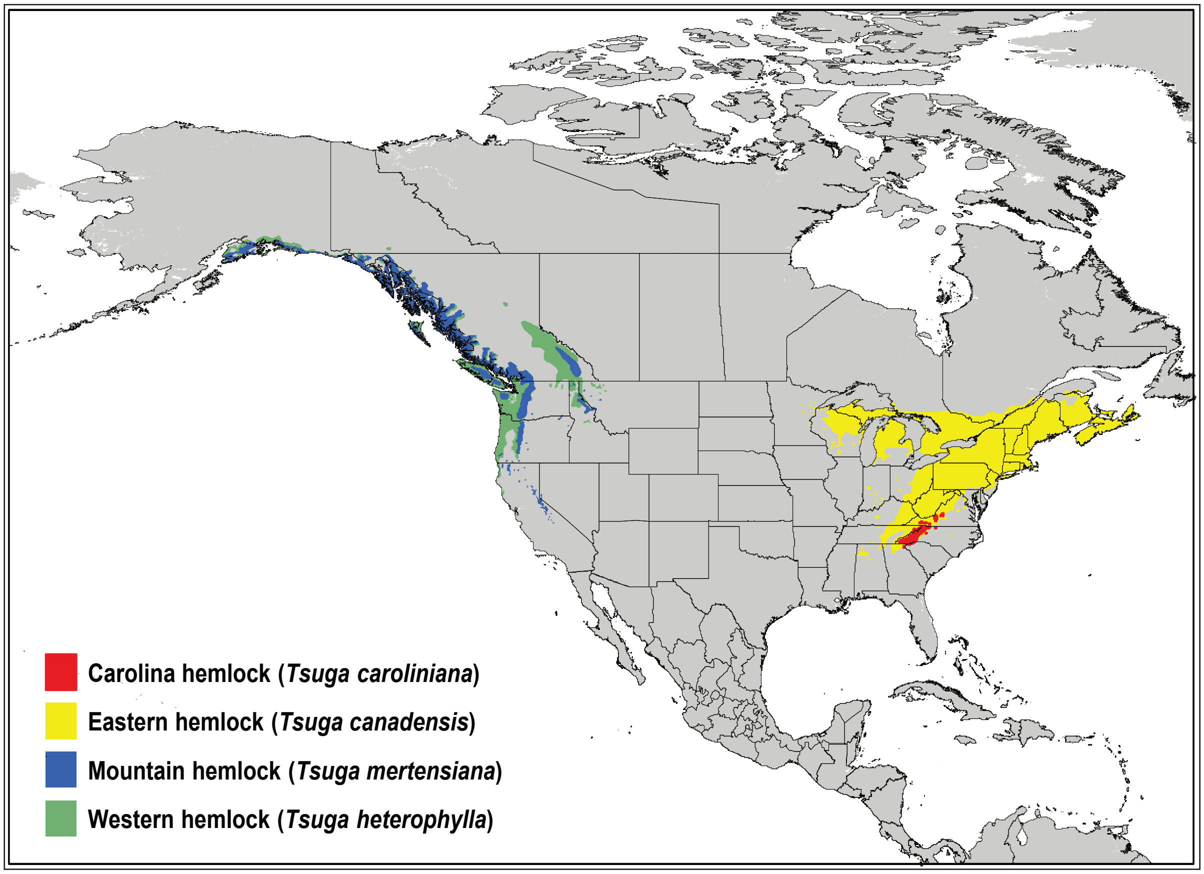

Figure 3. Geographic distribution of the four North American hemlock species — *Tsuga caroliniana* (red), *T. canadensis* (yellow), *T. mertensiana* (blue) and *T. heterophylla* (green). Redrawn from maps in USGS (1999).

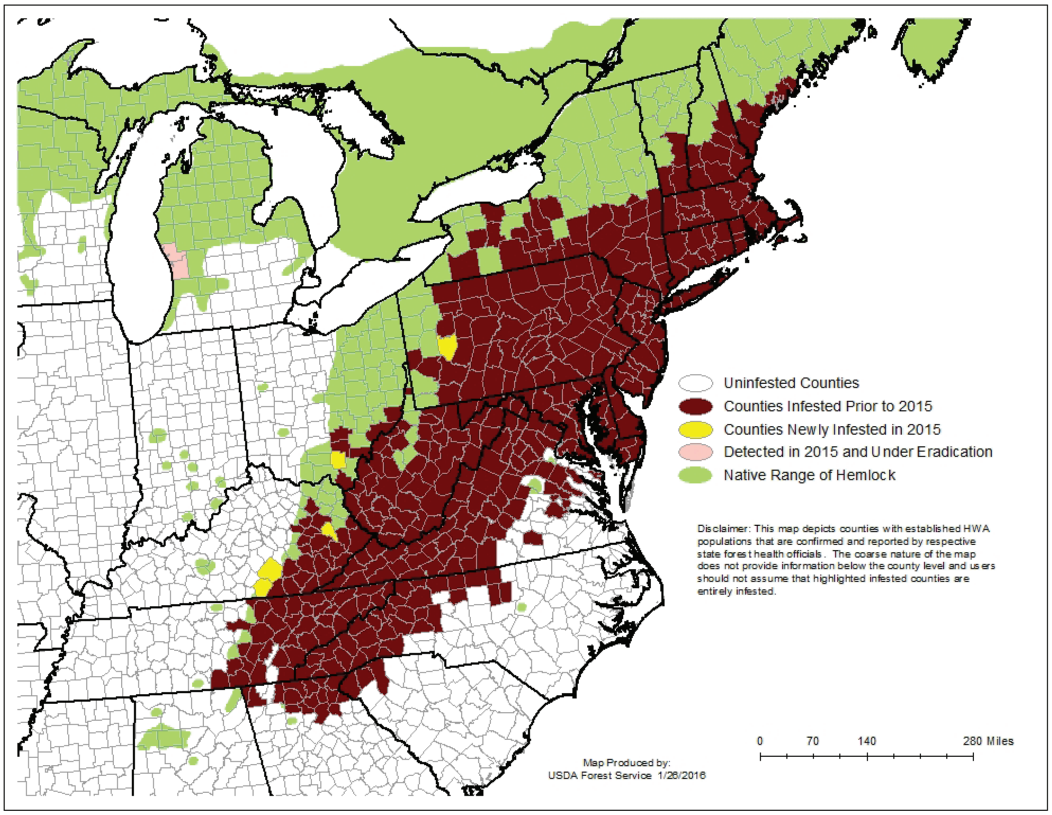

Figure 4. Map of eastern hemlock distribution and range of HWA. (2016)

Importance of Hemlock

Hemlocks are coniferous trees in the family Pinaceae, belonging to the genus Tsuga Carrière. The number of species described in this genus has changed over time, but contemporary authors generally accept ten species. The species native to eastern North America are eastern hemlock (*Tsuga canadensis* (L.) Carrière) and Carolina hemlock (*Tsuga caroliniana* Englem.).

There is a general recognition that hemlock forests have great ecological value, as they are frequently considered a foundation species in areas not recently disturbed. Foundation species are tree species that define the forest structure and control ecosystem dynamics. Hemlocks commonly grow along headwater streams, greatly influencing stream characteristics like temperature and nutrient cycling, as well as their biotic communities. Hemlocks have such a distinct influence on freshwater dynamics that streams flowing through hemlock forests support unique assemblages of salamanders, fish, and freshwater invertebrates that are intolerant of seasonal drying. Several wildlife species depend on the environment that exists in hemlock stands. Some, like the black-throated green warbler (*Dendroica virens*) and the blue-headed vireo (*Vireo solitarius*), are only present in forests with hemlocks (hemlock obligates).

Hemlocks are widely appreciated for their aesthetics. Their grandiosity and gracefulness captivated Pennsylvania into making it their State Tree in 1931. Hemlocks are commonly planted as a tree, shrub, or hedge in ornamental landscapes in the United States and Europe. There are at least 274 cultivars of eastern hemlock, making it one of the most cultured landscape tree species. The recreational appeal of hemlock forests is evident by the millions of people that visit hemlock stands in National and State Parks, recreation areas, and private lands in the eastern United States every year.

The economic value of hemlocks as timber and pulp is considerably low. However, there has been an effort to quantify the services provided by hemlock forests, as these resources are being threatened and forest managers need this information to evaluate the cost and benefits of treatment. Ecosystem services performed by hemlock forests have been valued at $969 per hectare per year. Several studies have also been conducted to determine how much people would be willing to pay to protect hemlock forests. Generally, these studies found that the value attributed to hemlock forests greatly exceeded the cost of controlling for exotic species. Additionally, it has been found that in an urban environment, good tree cover (between 40-60%) around a property has been associated with 0.5 to 6% higher property values.

Lifecycle of Hemlock Woolly Adelgid

Hemlock woolly adelgid has a complex life cycle that is typical of the Adelgidae (Figure 5). In Japan, HWA can alternate between *Tsuga sieboldii* and *Picea torano* in areas where these species coexist. *Picea* is considered the primary host because that is where sexual reproduction occurs. *Tsuga* is the secondary host because it supports only asexual generations. There are two asexual generations per year on hemlock with a proportion of the second generation developing into winged migrants, called sexuparae (Figure 6). When sexuparae land on a suitable spruce, they produce a very short generation of sexual females and males. Each mated female lays a single, relatively large egg, which develops into an asexual female (fundatrix) that settles near a bud to overwinter. In the spring, feeding by the fundatrix begins transforming the bud into a gall that will house her offspring. The fundatrix lays a large clutch of eggs. Upon egg hatch, crawlers walk into the developing gall. These individuals, called gallicolae, feed inside the multi-chambered gall causing the completion of gall formation. HWA galls have a characteristically round shape, unique among adelgid species (Figure 7). A single gall can house over 1,000 adelgids. When the winged gallicolae mature, they emerge from the gall as it dries, and fly back to hemlock.

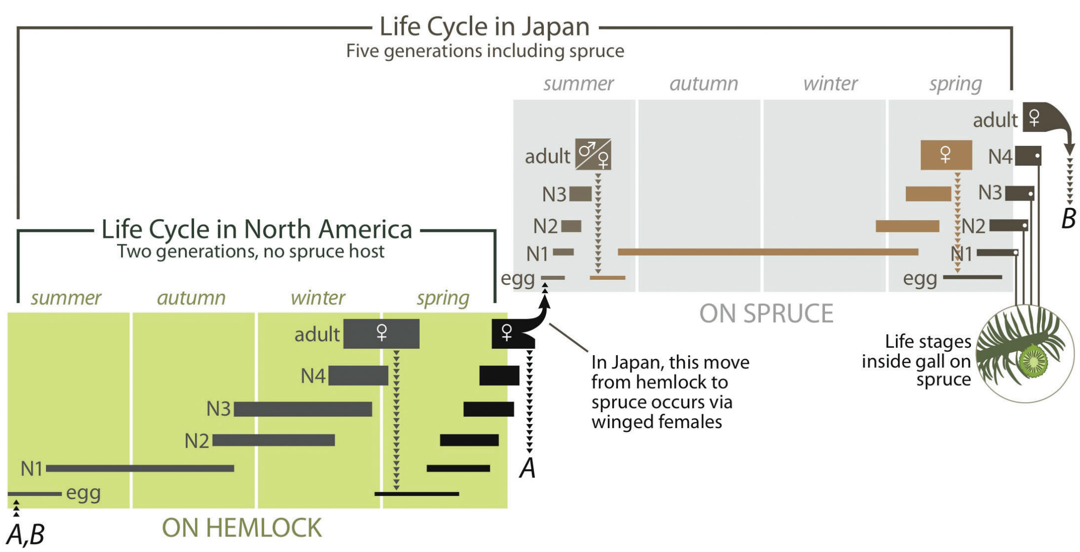

Figure 5. Multi-generation life cycle of HWA in its native range in Japan and its introduced range in eastern North America (Diagram: Vince D'Amico and Nathan Havill, USDA Forest Service.)

In North America and in areas of Japan where *P. torano* is not present, HWA completes a truncated life cycle. In this case, only the two asexual generations on hemlock are repeated each year because the offspring of migrant sexuparae do not survive. Sexupara production can therefore be viewed as a mortality factor in these areas. HWA is apparent on hemlock by the large, white, woolly ovisacs (Figure 1). The first generation is made up of sistentes (singular = sistens, from the Latin "to halt"), so-called because they have a long diapause in the first instar. The next generation is made up of individuals called progredientes (singular = progrediens, from the Latin "to proceed") that do not have a long diapause. As a consequence, the progredientes have a shorter generation time than the sistentes. Progrediens crawlers hatch in the spring and search for a suitable place to settle, mostly on the previous years' growth. They disperse within and between trees by crawling, being blown by the wind, or being transported by birds, deer, or other animals. They nearly always settle at the base of the needle, where they remain attached for the rest of their lives. The proportion of progredientes that become winged sexuparae increases with adelgid density. The wingless progredientes that remain on hemlock develop quickly to the adult stage and lay a smaller clutch of sistens eggs. The sistens crawlers settle, mostly on that year's new growth when available, and experience a long diapause in the first instar lasting through the summer. Development resumes in the autumn and progresses slowly through the winter until they reach the adult stage and lay eggs in late winter/early spring. Although the developmental stages and generations on hemlock in Japan and North America are the same, the phenology varies with elevation, latitude, and weather conditions. For example, the sistentes generally begin laying eggs in March in New England, compared to February in Virginia. In any case, there is enormous overlap of life stages during the spring and summer months, in part due to the long periods of egg laying and hatching.

Figure 6. HWA sexupara, the stage that migrates from hemlock to spruce in Japan (Image: Nathan Havill, USDA Forest Service.)

Figure 7. HWA gall on tiger-tail spruce in Japan (Image: Shigehiko Shiyake, Osaka Museum of Natural History.

Feeding

Figure 8. HWA nymphs settled and feeding at the base of needles.

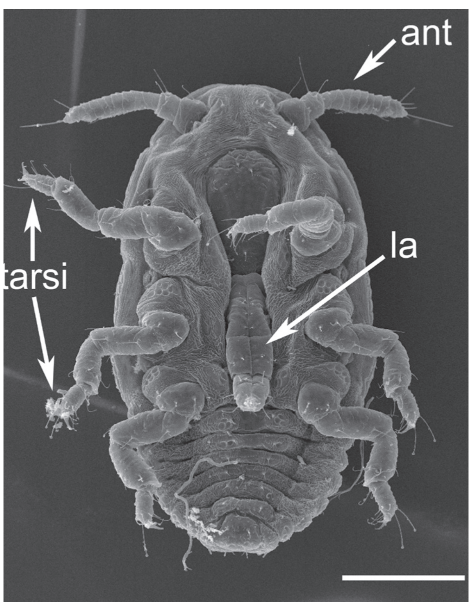

Figure 9. Ventral view of an HWA crawler. Scale bar = 100µm. ant, antenna; la, labium (Photo: Kelly Oten, NC State University).

After hatching from the eggs, the crawlers search for a suitable site to insert their feeding stylets into the plant tissue (Figure 8). The crawler has prominent bristles on its antennae, legs, and mouth parts that are probably sensory organs that help locate a suitable settling site (Figure 9). HWA has a stylet bundle, which is located on the underside of the insect and composed of four individual stylets (Figure 10, arrow). The stylets fit together to form two canals: one injects saliva into the tree, and the other transports nutrients from the tree to the insect (Figure 11). The stylets are typically inserted into the stem near the base of the needle, at the point where the waxy cuticle of the needle cushion is thinnest. Occasionally, when populations are very high, a few HWA individuals can settle on the woody part of the stem and survive to reproduce.

HWA inserts its stylets through the epidermal cells at the plant surface to reach the vascular tissue. The stylet bundle is more than three times the length of the first instar adelgid (Figure 2), and penetrates deep within the plant tissue (Figure 12). Once the stylets have reached the vascular tissue, they travel along the vascular bundle in the xylem, passing between cells until they terminate in the parenchyma cells of the xylem rays. These cells have the function of transferring and storing plant nutrients in the tree and contain large amounts of carbohydrates.

The adelgid probes the tree tissue with its stylet bundle, sometimes pulling back and then inserting along a different path. While doing so, it secretes saliva within the plant tissue. Some components of the saliva harden around the stylets and form a salivary sheath, made up mostly of proteins. At each molt, the stylet bundle is retracted from the tree and the cuticle is shed. After the new cuticle has hardened, the stylet bundle is reinserted. The xylem ray parenchyma cells are the feeding site for all life stages of the insect. Thus, HWA does not deplete nutrients directly from the sap, but removes food reserves from the tree's storage cells.

HWA has up to five different types of endosymbiotic bacteria living inside its body, one of which is found in the salivary glands of first instars. Some of these bacteria are necessary for adelgid survival and probably serve a purpose related to nutrition.

Figure 10. HWA nymph with stylet bundle (arrow) inserted into base of needle. Arrowhead indicates point of stylet insertion.

Figure 12. Hemlock needle torn away from stem shows position of nymph (arrow) and its stylet bundle (arrowheads) within the plant.

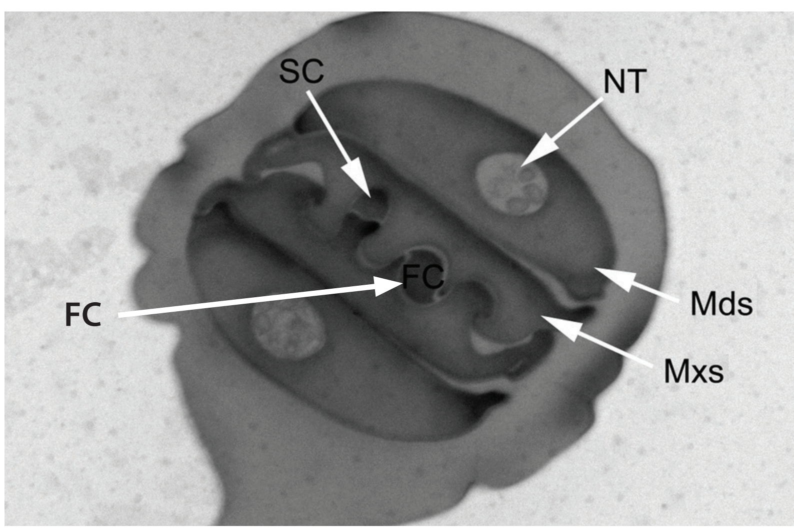

Figure 11. Cross-section of hemlock woolly adelgid stylets. FC, food canal; Mds, mandibular stylet; Mxs, maxillary stylet; NT, neurotubules of mandibles; SC, salivary canal. Scale bar= 1μm (Photo: Kelly Oten, NC State University).

Impact on Hemlock

Figure 13. A mature eastern hemlock in decline following its infestation from HWA (Photo: Bugwood.com)

Eastern and Carolina hemlocks are highly susceptible to damage from HWA feeding. Symptoms consist of discoloration, desiccation, loss of the needles, and dieback of branches. The feeding impact of HWA results in a depletion of the stored nutrients which compromises the tree's ability to produce new growth. Recent evidence also suggests that HWA feeding causes a hypersensitive response around colonized tissue causing the induction of 'false growth rings' in infested stems that interfere with solute transport and prevent the stems from obtaining the necessary water for photosynthesis.

As the infestation progresses, crown vigor decreases (Figure 13), eventually leading to branch dieback and death of the tree. HWA can be fatal to hemlocks of all ages in 4-15 years, depending on moisture availability and other stress factors. In some areas, mortality due to HWA infestation has been as high as 95% (Figure 14). In other areas, especially in the North, where winter temperatures help regulate adelgid survival, hemlock trees can continue to survive in a weakened state for more than 15 years following the initial infestation.

Figure 14. A stand of dead eastern hemlock trees in the Great Smoky Mountains National Park (Photo: Scott M. Salom, Virginia Tech.)

Initially, adelgid populations will be found in the canopy in aggregated distributions. As HWA populations increase on a tree and in a stand, their distribution becomes more uniform to the point where virtually all of the new or current year's shoots become infested. This level of infestation leads to a reduction in shoot growth, which in turn leads to a crash in the HWA population. Since the sistentes prefer new growth, the density of adelgids will tend to follow tree vigor. The reduced abundance of new growth and acceptable feeding sites consequently leads to a decline in HWA populations. Often, trees are eventually impacted to the point where they cannot recover.

The loss of eastern hemlock due to HWA has led to immediate, short- and long-term changes in ecosystem structure and function. Initially, hemlock death results in increased light penetration to the forest floor and carbon and nutrient inputs in soil and streams, which in turn impacts the flora and fauna taking advantage of the increased resources. In many locations, eastern hemlock does not naturally re-establish following mortality due to HWA. It is often replaced by a different ecosystem type altogether, dominated by species such as birches (*Betula* spp.), oaks (*Quercus* spp.), and maples (*Acer* spp.), and by Rhododendron in riparian areas or yellow poplar (*Liriodendron tulipifera* L.) when Rhododendron is absent. This change in ecosystem type impacts ecosystem processes, and leads to the loss of terrestrial arthropods, amphibians, plants, fish, and aquatic invertebrate species associated uniquely with hemlock forests.

Factors Regulating HWA Populations

Low winter temperature is the most prominent mortality factor controlling HWA populations and limiting its spread in the eastern United States. However, recent studies have called attention to: 1) the effects of climate change, which would make previously unsuitable habitats, suitable, and may lead to the expansion of this pest's distribution; and 2) the possibility that HWA is adapting to conditions in the introduced range, exhibiting a greater tolerance to colder temperatures.

Tree health also has an impact on HWA populations. The amount of time a hemlock tree can withstand HWA feeding can be affected by several environmental variables. Water stress has been consistently associated with a faster decline in tree health. Latitude and longitude are also correlated with HWA infestation as it relates to the infestation front; that is, the risk of a hemlock stand becoming infested is correlated with the proximity of infested stands nearby. Other landscape characteristics such as elevation, slope, aspect, and terrain shape index have also been found to be relevant, but less consistently. HWA also seems to be regulated in part in a density-dependent manner, where a high density of progrediens crawlers negatively impacts the fecundity and survival of subsequent generations. This effect could be mediated by HWA impacts on tree health.

Host Plant Resistance and Tolerance

While the eastern and Carolina hemlocks were found to be highly susceptible to HWA, the Chinese hemlock (*T. chinensis* (Franch.) E. Pritz.) was found to be highly resistant to the pest. Attempts have been made to create resistant hybrids between eastern North American and Asian hemlock species that retain as much as possible the characteristics of the native species. Crosses between Carolina and

Chinese hemlocks have resulted in hybrids with intermediate resistance to HWA. However, crossing Chinese and eastern hemlock has not been successful.

Reports of individual hemlock trees and stands surviving in areas otherwise devastated by HWA have raised doubts about the complete absence of innate resistance in eastern and Carolina hemlocks. In order to guide the search for resistant trees, characteristics that might confer resistance have been studied. Terpenoid volatiles, foliar chemistry, and physical and chemical characteristics of the needle cushion have been associated with resistance. All of these characteristics vary within eastern and Carolina hemlock populations, and the foliar chemistry has been associated with some level of resistance in these species.

Foliar concentrations of calcium, potassium, nitrogen, and phosphorous were found to be strongly correlated with HWA densities. Higher nitrogen and potassium concentrations were associated with higher HWA densities, while higher calcium and phosphorous concentrations were associated with lower densities. Nitrogen is a limiting nutrient for most plants and animals. Nitrogen fertilization increases tree health, which can make it more capable of withstanding attacks, but also increases the nutritional quality of the tree for the pest.

Genetic Resource Conservation

In the event of the worst-case scenario where the management of HWA fails and eastern and Carolina are eliminated from most of their range, there is a program of gene conservation with seed collections and ex situ conservation. The first efforts focused on Carolina hemlock due to its smaller population size and the fact that HWA has rapidly impacted all of its geographic range. Seed collections throughout its range were completed in 2006, and the genetic variability in the seed samples was found to adequately reflect the genetic variability in natural stands of Carolina hemlock. Seed collections for eastern hemlock have been ongoing since 2005, and efforts were initially focused on the southern part of the species' geographic range due to higher levels of genetic diversity and the greater threat the species faced from HWA in this region. Seed collections have subsequently expanded across the entire geographic range of eastern hemlock in the United States, and now include interior populations in the Southern Appalachian, Mid-Atlantic, Northeastern, and Upper Midwest regions, and disjunct populations that occur to the east and west of main species distribution. At this time more than 2.5 million hemlock seeds have been placed into conservation, either stored in seed banks at the USDA National Center for Genetic Resources Preservation in Fort Collins, CO, the USDA Forest Service Ashe Seed Facility in Brooklyn, MS, and at North Carolina State University in Raleigh, NC, or planted into conservation seed orchards in Brazil, Chile, and the United States.

Chemical Control

Foliar insecticides were initially used with good efficacy, but the need for frequent re-application and to completely drench the foliage has diminished their use. In the early 1990's a new class of systemic insecticides, the neonicotinoids, became available. Several active ingredients (imidacloprid, dinotefuran, acetamiprid, and thiamethoxam) can successfully control HWA. Due to their systemic activity, neonicotinoids can be applied by soil drench, soil injection, and several methods of trunk injection. Since xylem sap flow is essential for transporting and distributing the insecticide from the soil to the canopy of the tree, treatment should be applied prior to severe damage to the trees. In healthy trees, it can take weeks to several months for the insecticide to be transported to where the adelgid feeds. In damaged trees, it can take longer because they have more difficulty transporting the insecticide. Treatment should be timed for spring or fall when water uptake by the trees is greatest. Soil and trunk application of imidacloprid were found to take 1-3 months to control HWA, while both dinotefuran and thiamethoxam were found to be faster. Residual activity of up to three years was observed for soil applications of imidacloprid, thiamethoxam, dinotefuran, and acetamiprid. Foliar applications of the neonicotinoids provide faster control, but soil applications provide longer residual activity.

In a large scale forest setting, chemical control as a ‘stand-alone' treatment is not viable, due to the costs involved and the potential environmental consequences. Imidacloprid was found to affect other canopy feeding arthropods and arthropods inhabiting the soil around the base of the tree. In addition, secondary pest outbreaks of spruce spider mites and hemlock rust mites have also been associated with imidacloprid treatments for the control of HWA. Considering the close association of eastern hemlock with bodies of water, the possibility of insecticide leaching has to be considered as well. Special care should be used when applying imidacloprid in areas with soil types that may not bind imidacloprid as tightly (e.g., low organic matter content). An optimization of the dosage for each tree and adoption of newer tablet formulations should also minimize the risk of contaminating aquatic resources.

Biological Control

With no specialist natural enemies present in eastern North America, HWA is able to flourish and spread unchecked. Searching for and studying natural enemies in western North America and parts of Asia with native lineages of HWA is considered critical. The primary objective of biological control is to introduce a group of natural enemies considered important in the native habitat and deemed safe for introduction into the eastern United States. Since no known parasitoids are associated with Adelgidae, the classical biological control program for HWA has focused on prey-specific predator species and entomopathogens.

Fungal Pathogens

Twenty fungal genera and 79 entomopathogenic fungus isolates were found in association with HWA in the eastern United States and southern China. Of all the isolates, no putative specialists were found. A combination of generalist fungi that included two strains of *Beauveria bassiana* Balasamo, one of *Lecanicillium lecanii* Zimmermann, and one of *Metarhizium anisopliae* Metchnikoff, demonstrated high efficacy against HWA. A commercially available *Lecanicillium lecanii* formulated with a whey carrier has been tested in small-scale forest trials and has been shown to be effective, especially against early instar HWA before they produce wool. This augmentative approach is still in the early developmental stages.

Predators

The first efforts toward the application of biological control of HWA in eastern North America started in 1992. Of the predators first collected from Japan, the most promising at the time, *Sasajiscymnus tsugae* (Sasaji and McClure) (Coleoptera: Cocinellidae) was imported, evaluated, mass reared, and cleared for release (Figure 15). Field releases started in 1995 in Connecticut and more than two million *S. tsugae* have been released throughout the introduced range of HWA. Post-release evaluations indicated successful overwintering, reproduction, and dispersal of *S. tsugae*, but establishment of the predator and impact on HWA populations has been inconsistent. In the South where establishment has been closely monitored, the predator population takes 5 to 7 years to reach a detectable level at

Fig 15. Sasajiscymnus tsugae adult (left) and late instar larva (right) (Photos: Carole Cheah, Bugwood.com.)

only some of the locations where releases were made. Large-scale rearing of this insect for release is being phased out, yet monitoring its presence and impacts will continue.

Additional foreign explorations for natural enemies were carried out from 1995 until 1997 in Yunnan, Sichuan, and Shannxi provinces in China. Three previously unknown lady beetles (Coleoptera: Coccinellidae), *Scymnus camptodromus* Yu et Liu, *Scymnus sinuanodulus* Yu et Yao, and *Scymnus ningshanensis* Yu et Yao, were found to be the most abundant predators in different locations. The predators were imported, evaluated in quarantine, and cleared for release. However, due to difficulties in mass rearing, releases of *S. ningshanensis* and *S. sinuanodulus* were delayed until 2004, and *S. camptodromus* was not released. There were no recoveries of the first two species following their limited releases, and work continues on rearing of *S. camptodromus*.

Laricobius beetles in the family Derodontidae are specialist predators of adelgids. In 1997, a predator native to western North America, *Laricobius nigrinus* Fender, was found to consistently feed only on HWA in the lab, and its life cycle was shown to be synchronous with HWA (Figure 16). Oviposition and subsequent larval development coincides with oviposition by the HWA sistens adults. Females oviposit within HWA ovisacs from January to March. After hatching, larvae go through four instars

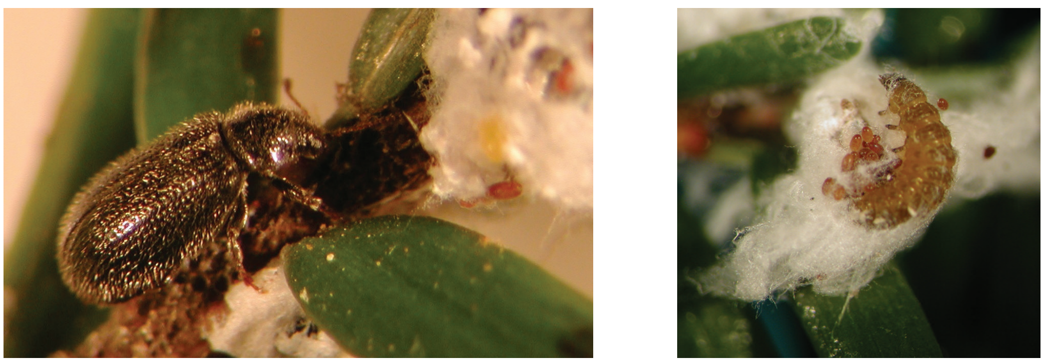

Fig 16. *Laricobius nigrinus* adult and its yellow egg (left) and late instar larva with HWA eggs (right) (Photos: Rob Flowers, Virginia Tech).

and mature larvae drop to the soil to pupate within two weeks. Eclosed adults remain in the soil in a state of aestival diapause that coincides with diapausing first instar sistentes. Adults resume activity in the fall coinciding with resumption of development by HWA.

Following host-range testing studies in quarantine, the predator was cleared for release in 2000. Rearing procedures were developed and releases began in 2003. To date, more than 200,000 beetles have been released at over 200 sites. Evaluations after release showed that establishment is positively correlated with minimum winter temperature and with the number of beetles released. Beetles initially disperse slowly up the release tree and then away from the release tree at a rate of close to 40 m/yr. Some anecdotal evidence suggests this could be greater at times.

Due to the difficulty in rearing *L. nigrinus*, only 500 beetles were available for each release in forested settings. As rearing has improved and beetles can now be collected and redistributed from already established sites, the numbers being released have increased to range from 750 – 2,000 beetles per site.

Laricobius nigrinus collected from coastal sites in the West (coastal strain) appear to establish better in warmer climates (plant hardiness zones 6a and higher). *Laricobius nigrinus* from Idaho and Montana (interior strain) that are better adapted to colder temperatures are being reared and are beginning to be released in the more northern range of introduced HWA.

A native eastern North American *Laricobius* species (*Laricobius rubidus* Le Conte) has also been found on HWA infested hemlock. This predator feeds mainly on native pine bark adelgid, *Pineus strobi* Hartig. It prefers this prey when given a choice, but is able to feed and develop on HWA. It is also active from fall through mid-spring and there is a considerable overlap of feeding by both beetle species. *Laricobius nigrinus* and *L. rubidus* have been found to interbreed at sites where *L. nigrinus* was released in the eastern United States. Research indicates that at these sites, *L. nigrinus* and *L. rubidus* are hybridizing at a steady rate (ca. 10 - 15%) and *L. nigrinus* over time may reduce the proportion of *L. rubidus* on hemlock, but not on white pine at sites where both tree species are present.

Because the strain of HWA that was introduced to eastern North America is from southern Japan, an additional effort was made to look for natural enemies in this location. A new species, *Laricobius osakensis* Montgomery and Shiyake, was discovered in 2005 and imported to quarantine to study its biology and host-range (Figure 17). The insect was also studied in its native habitat. *Laricobius osakensis* has host preferences similar to *L. nigrinus*, greater fecundity, and a higher predation rate then *L. nigrinus*. Lab studies showed that it cannot hybridize with the North American *Laricobius* species. In its native habitat, it is shown to be the key natural enemy on sistentes, being consistently present in association with HWA, and having a synchronous life cycle with HWA. Its population fluctuations were correlated with those of the HWA sistens population, and it was shown to reduce populations of HWA on *T. seiboldii*. Permission to remove *L. osakensis* from quarantine was received in 2010 and the first open releases began in 2012. Continued efforts toward large-scale operational releases and monitoring of this predator are underway.

Fig 17. *Laricobius osakensis* adult female with typical reddish brown coloration (upper left), adult male with typical dark coloration (upper right), and larva (bottom center) (Photos: Ligia C. Viera, Virginia Tech).

Additional predators from western North America that could target the progrediens generation include *Scymnus coniferarum* (Crotch) (Coleoptera: Coccinelidae), found in association with HWA in Washington, and silver flies (*Leucopis* spp.: Diptera: Chamaemyiidae) whose larvae and adults were found to be positively correlated to HWA densities in Oregon and Washington. Work is ongoing to determine their viability as biological control agents.

Toward Integrated Pest Management of HWA

Researchers working in open-grown hemlock plantations have noticed that trees growing under full sunlight do not appear to support dense populations of HWA. Trees in the shade and under forest canopies, or a tree's lower branches shaded by upper branches, tend to be colonized more readily by HWA. At this time we do not know if HWA survival is impacted by direct radiation and increased temperature or by physical differences in trees growing in direct sun versus those growing in shade. It has also been found that infested trees survive longer if they have higher live crown ratios, even those in the understory. The most vulnerable trees seem to be those that have small crowns relative to their stem and are therefore not producing enough carbohydrates to support growth under stress from HWA. It is therefore useful to consider that under certain conditions, trees may be less susceptible to HWA colonization and impact. For example, further investigations can test whether thinning stands to expose hemlock trees to more sunlight can be used to reduce HWA infestations and subsequent impacts on hemlock health. Note, that in dense hemlock stands, abrupt thinning could cause damage to shade needles, so it may be necessary to thin incrementally over several treatments.

It has recently been proposed that the integration of chemical and biological control on an area-wide scale may help save some hemlocks that otherwise would not survive in the long-term by any one control method used alone. The concept currently being tested involves the chemical treatment of a subset of mature infested hemlock while releasing predators on understory trees. The chemical treatment could provide short-term protection for the larger trees and allow the predator populations to build up in the understory. Once the larger trees lose their chemical protection, an established predator population might be more capable of controlling a building HWA population than a predator population still on the process of becoming established. These kinds of integrated approaches should continue to be evaluated while new management tools are developed for HWA control.

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