



Biology and Management of the Hemlock Woolly Adelgid in the Eastern U.S.

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Figure 1. Hemlock needles with striped underside (a) and a hemlock cone (b).

Introduction

Hemlock trees in eastern forests are late successional tree species that provide shade for the forest understory. Globally, there are ten species of hemlock, with populations located in Asia and eastern and western North America¹². Eastern hemlock (*Tsuga canadensis*) and Carolina hemlock (*Tsuga caroliniana*)

grow in the eastern U.S. These trees have great ecological and cultural value in forests. However, the invasive hemlock woolly adelgid (*Adelges tsugae* or HWA) is decimating hemlock populations throughout much of the trees' native range, altering landscapes, and threatening these iconic tree species in both rural and urban areas.

Identification and Biology

HEMLOCK DESCRIPTION AND DISTRIBUTION

Eastern hemlock is a slow growing, long-lived, and shade tolerant conifer. Hemlocks may live up to

800 years and grow as high as 175 feet tall. Hemlock needles are ½ - 1 inch long with two whitish stripes running longitudinally along the underside of the needles (Fig. 1a). They attach singly along thin, flexible twigs. Hemlock bark appears grayish in color, and the tree has a cone-like silhouette. Small brown cones are about an inch long (Fig. 1b). In eastern North America, hemlocks grow from northern Georgia and Alabama north into Canada. In the southeastern U.S., eastern hemlock is often found growing in damp valleys or on the eastern and northern slopes of hills and mountains⁵.

Unlike other hemlock species, eastern and Carolina hemlock are susceptible to severe impact from HWA²¹.

Carolina hemlock has a more limited range than eastern hemlock, growing in small, isolated populations on drier mountain sites¹⁶. Thus, most of the focus on HWA damage has centered on eastern hemlock, which is more widely distributed and sometimes used in the landscape industry.

HEMLOCK WOOLLY ADELGID DISTRIBUTION AND BIOLOGY

Hemlock woolly adelgid is native to China, Japan, and western North America¹¹. The population in the eastern U.S. was likely accidentally introduced to Virginia on ornamental plants from Japan as early as the 1920's. HWA has now expanded from Virginia to 20 eastern states (Fig. 2, next page).

Adelgids are soft-bodied, aphid-like insects. HWA adults are purplish-blackish in appearance and produce a white protective woolly material that covers their bodies²⁰. A hemlock branch infested with HWA will appear to have small cotton balls on the branches where the needles meet the twig (Fig. 3).



Figure 3. HWA appear as white woolly masses on hemlock twigs.

Hemlock woolly adelgid has a complicated life cycle, with two generations per year (called sistens and progrediens, Fig. 4). Females do not need to mate to reproduce, and each female lays up to 175 eggs that stay within her woolly mass (ovisac). In the southeastern U.S. the sistens generation lives for about 10 months, from early summer to the following spring. This generation aestivates, or becomes inactive, during the summer and begins feeding in late fall. The progrediens generation lives about three months, from early spring to early summer. The first instar, or life phase, is called a crawler (Fig. 5), and this is the only HWA instar that can move, other than a winged female – all other life stages are sessile (i.e., fixed in one place). Crawlers cannot move far on their own, but they can be carried longer distances by wind, wildlife, or humans. Generally, crawlers move along a branch and find a spot at a needle base. They insert their long, straw-like mouthpart into the hemlock and begin feeding. Once HWA is feeding, they will grow and begin producing the protective wool. When mature, adults lay eggs under the protective wool (Fig. 6). The progrediens generation also includes production of winged females, which cannot reproduce in North America.

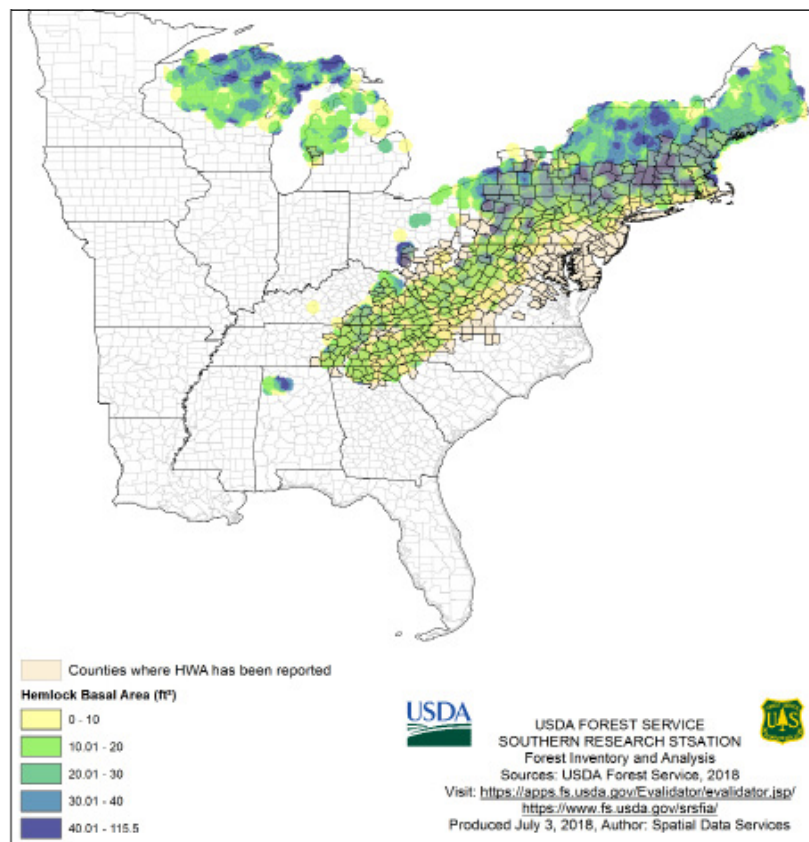


Figure 2. Hemlock woolly adelgid distribution map in the eastern U.S. Different colors represent different amounts of hemlock basal area, while counties where the adelgid has been reported are outlined in black

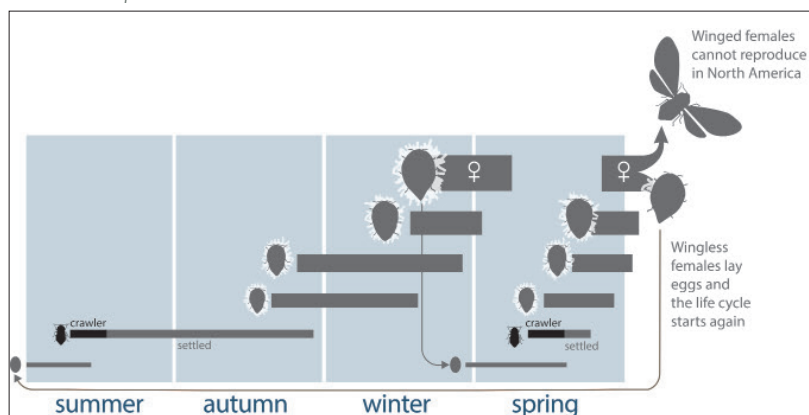


Figure 4. Hemlock woolly adelgid lifecycle.



Figure 5. Hemlock woolly adelgid crawler on a hemlock needle, as noted by the red arrow.



Figure 6. Hemlock woolly adelgid eggs and wool.



Figure 7. Hemlock woolly adelgid adult removed, shown with long mouthpart visible.

ECOSYSTEM FUNCTION

Eastern hemlock is a foundation, or keystone, species in eastern forests, creating an environment necessary for the survival of other organisms⁹. The loss of hemlock impacts many other plants and animals in eastern forests. Hemlocks produce deep shade and acidic leaf litter, which affect the temperature, moisture, and nutrients of the forest floor¹⁴, as well as stream flow rates and water quality⁸. Many animals live in hemlock canopies, and hemlock is an important source of food during the winter – for example, small mammals like squirrels and rabbits feed on the bark, and porcupines eat twigs. Hemlock occurs in several different forest types, with many different co-occurring plant species depending on the particular habitat and location.

Hemlock Woolly Adelgid Damage

PHYSICAL DAMAGE TO HEMLOCK

Hemlock woolly adelgid uses its straw-like mouthparts (Fig. 7) to retrieve carbohydrates from hemlock storage cells³¹. Once the tree's carbohydrate reserves are reduced, the hemlock will begin to decline. The visible symptoms of HWA feeding are greying needles, dead branches, and eventually canopy thinning (Fig. 8). Hemlocks can die from HWA feeding, leaving gray, needle-less hemlock tree "skeletons" scattered across the landscape (Fig. 9). In the Southeast hemlocks can die from HWA feed in as little as 2-4 years. Some trees, especially in more northern areas, can take up to a decade to die, while other trees may never die.

ECOLOGICAL DAMAGE

Hemlock mortality changes forest ecosystems from the canopy all the way down to the forest floor and nearby streams. Arthropods living

nearby streams. Arthropods living in hemlock canopies no longer have habitats after hemlock trees die. Bird communities are altered when hemlock is not a part of the forest canopy²⁸. Hemlock is replaced by either hardwood tree species, such as birch, oak, maple, and/or tulip tree²⁶, or in the Southeast rhododendron can begin to dominate forests after hemlocks die. Unfortunately, rhododendron thickets tend to be very dense, restricting light to the forest floor and inhibiting the growth of other plant species³⁰. Declining hemlocks result in changes in soil nutrients and greater light availability on the forest floor when rhododendron is not present¹⁴. More light reaches streams when hemlocks have died and the canopy is opened, which leads to higher stream temperatures³⁰ and subsequent impacts on fish. Hemlock water use varies seasonally from that of hardwoods, resulting in different annual water balances⁸. In addition, stream insect communities can become less diverse as the overstory changes from hemlock-dominated to hardwood-dominated^{1,27}.

Unfortunately, hemlock seeds are only viable for about four years,

so hemlock renewal from seed germination many years later is unlikely²⁴. Currently, hemlock removal from a forest, along with the negative effects on the ecosystem, is permanent – especially since no other native evergreen tree species can fill hemlock's ecological role.

ECONOMIC DAMAGE

Tourism, hazard tree removal costs, property values, and the ornamental and nursery industries can all be negatively affected following hemlock loss due to HWA. Forests with a hemlock component are popular destinations for tourists. Dead hemlock "skeletons" littering views and hazard trees located near trails and campgrounds detract from a tourist's outdoor experience (Fig. 9).

Dead hemlocks in public areas such as parks, campgrounds, trails, roads, and yards are hazards to public safety. Federal and state parks, transportation departments, municipalities, and residents must pay for hazard tree removal. This expense is often a great financial burden to private entities, municipalities, and ultimately taxpayers.

Hemlocks add aesthetic and economic value to urban forests and other residential areas. The presence of yard trees accounts for approximately 1 – 5% of residential property value. Hemlock defoliation and subsequent mortality cause decreases in property value for



Figure 8. Declining hemlock tree.



Figure 9. Dead hemlocks on the landscape.

Table 1. Comparison of HWA management options.

Management tactic	Benefits	Limitations	Concerns	Use location
Horticultural Oil	- fast acting - generally considered less toxic	- entire hemlock canopy must be covered - short-term control - two applications each year - should not be applied adjacent to water	- harmful to other insects	- areas with easy access - landscapes - nurseries
Contact insecticides Organophosphates - Carbamates - Pyrethroids - Avermectins	- fast acting	- entire hemlock canopy must be covered - short-term control - two applications each year - should not be applied adjacent to water	- toxic to other insects	- areas with easy access - landscapes - nurseries
Neonicotinoid insecticides	- longer acting - systemic control - can be used in remote areas - ease of application	- persistence in the environment - should not be applied adjacent to water	- toxic to other insects - environmental persistence	- areas with easy access - landscapes - nurseries - forests
- Imidacloprid	- longer systemic control - approx. 5 - 7+ yrs	- effective slowly - three months for HWA mortality		- lightly to moderately infested hemlocks
- Dinotefuran	- effective quickly - one month for HWA mortality	- shorter systemic control - approx. 1.5 - 2 yrs.		- heavily infested hemlocks
Biocontrol	- no insecticides introduced in the environment - more sustainable control	- long time for effective control - robust effectiveness has not been demonstrated - not appropriate for all sites	- may not be effective before hemlocks die - possible interaction with native insects	- forests - applied by trained personnel with appropriate expectations
No control implemented	- no insecticides or non-native species introduced to the environment	- hemlocks will die - numerous ecological effects of hemlock mortality in forests	- hemlock mortality - permanent ecological effects	- locations where control measures are not used - usually a result of financial limitations or state regulations

Table 2. Most common predators assessed for biological control of HWA in the eastern U.S.

Insect	Insect type	Scientific name	Region of Origin	Release Status
Lady beetle	(Coleoptera: Coccinellidae)	<i>Sasajiscymnus tsugae</i>	Japan	Widespread
Lady beetle*	(Coleoptera: Coccinellidae)	<i>Scymnus camptodromus</i>	China	Localized
Lady beetle*	(Coleoptera: Coccinellidae)	<i>Scymnus coniferarum</i>	Western North America	Localized
Lady beetle*	(Coleoptera: Coccinellidae)	<i>Scymnus sinuanodulus</i>	China	Localized
Predaceous Fungus Beetle	(Coleoptera: Derodontidae)	<i>Laricobius nigrinus</i>	Western North America	Widespread
Predaceous Fungus Beetle	(Coleoptera: Derodontidae)	<i>Laricobius osakensis</i>	Japan	Localized
Silver fly	(Diptera: Chamaemyiidae)	<i>Leucopis argenticollis</i>	Western North America	Assessment ongoing
Silver fly	(Diptera: Chamaemyiidae)	<i>Leucopis piniperda</i>	Western North America	Assessment ongoing

*While these three *Scymnus* spp. lady beetles do feed on HWA, establishment of beetle populations after a release has not yet been demonstrated.

the parcel on which the hemlocks are located as well as adjacent property¹³.

Hemlocks are important and valuable ornamental plantings. Hemlock management or replacement in yards is costly for residents. In addition, nurseries must control HWA in nursery plants and navigate quarantines for shipping hemlock between infested and uninfested areas. Hemlock in the nursery

industry, which boasts over 200 cultivars of eastern hemlock, has significantly declined in the eastern U.S.

Management Strategies

Options for hemlock management currently include contact insecticides, systemic insecticides, biological control, and doing nothing (Table 1), though silvicultural management strategies are being developed^{15,17}.

Site objectives and management goals will determine which management options are best for each location. Treating forest-grown hemlocks two miles from a road entails a different set of challenges than treating a single hemlock in an ornamental setting. Thus, different management options must be considered for each situation. When using an integrated pest management (IPM) approach in non-hemlock scenarios, insecticide use is generally a last resort choice. However, for most sites, insecticides may be the only option for hemlock preservation. **Always read and follow the pesticide label for specific information concerning applications near water and in sensitive areas, non-target injury, application rates, and application guidance. Keep in mind that it is illegal to use pesticides in a manner that is inconsistent with the label. It is highly recommended to contact a professional when working with pesticides.**

CONTACT INSECTICIDES

Many broad-spectrum contact insecticides, such as horticultural oil, organophosphates, carbamates, pyrethroids, and avermectins, can be used to suppress HWA. Contact insecticides provide fast HWA mortality. Applying a contact insecticide involves coating the entire canopy with a foliar spray. They should be applied twice a year and must be timed appropriately to target the mobile crawler stage. Applicators often use high-pressure sprayers to coat larger trees. Some practical limitations of contact insecticides include difficulty with uniform foliar coverage, lack of residual effectiveness, and tree accessibility. Contact insecticides are a management option for smaller landscape trees, hedgerows, and nursery settings. Although many of these products are labeled for forest settings, contact insecticides are not often used in forests due to site accessibility issues.

SYSTEMIC INSECTICIDES

Imidacloprid and dinotefuran are systemic neonicotinoid insecticides that are most commonly used for HWA suppression. Systemic insecticides are applied to either the soil or the hemlock trunk. The tree's vascular tissue moves the insecticide to the canopy, where HWA feeds. The systemic activity of these products allows greater flexibility with application methods, such as soil drench, soil injection, trunk injection, and trunk spray⁷. In addition, imidacloprid can be applied in a slow-release tablet formulation. Both products can be used in either landscape or forest settings. Treatment time recommendations may vary depending on geographical location. For example, in the South treatments are generally not applied during the summer, while in some northern areas treatments are not applied when soil temperatures

are near freezing. Check with state forestry agencies to receive guidance on treatment timing in specific areas.

Systemic insecticides do not provide immediate HWA mortality because the insecticide takes time to move from the roots to the canopy. Imidacloprid takes three months to reach efficacy, but control lasts for up to seven years^{4,6}. Imidacloprid application can be optimized for the size of the hemlock, resulting in precise insecticide dosages, which reduces overall insecticide use (application guidance available online³).

Dinotefuran has quicker uptake, becoming effective in less than a month, but control only lasts for two years at most¹⁸. Imidacloprid is a good choice for light to moderate infestations. Treated hemlocks can survive HWA feeding until imidacloprid begins killing HWA. Dinotefuran is a better choice for hemlocks with heavy HWA infestations, because it will quickly reduce HWA populations. Sometimes both products will be used for heavily infested hemlocks in remote sites, because it is much more difficult to go back and treat trees with imidacloprid the next year due to site accessibility.

BIOLOGICAL CONTROL

Biological control is the use of natural enemies to reduce pest populations and keep them at low levels. It is generally employed for long-term management of a pest, as populations of the natural enemy require time to grow large enough to impact pest populations. Typically, biological control is applicable over a large area (landscape scale), because ideally natural enemies will reproduce and disperse in search of their target pest or prey².

Classical biological control employs natural enemies from the native range

of an introduced pest². Because they are from the same native range as the pest, some natural enemies will have very close or exclusive associations with the pest species, perhaps only feeding on the pest or requiring the pest to complete their life cycle. Although many natural enemies in the native range of a pest may be identified, only those that are determined as host-specific to the target pest, through controlled testing in laboratory and field studies, are selected for release against the pest. Classical biological control programs require much effort to identify natural enemies and considerable time to evaluate their suitability for release.

A classical biological control program against HWA began in the 1990s²⁵. This effort is centered on establishing a complex (multiple species) of biological control agents to reduce HWA populations to non-injurious levels. The native ranges of HWA have been explored, and several predators of HWA have been identified and evaluated for use as biological control agents (Table 2). Several laboratories in the eastern U.S. are responsible for raising and coordinating releases of predators of HWA²⁵. The most widely released natural enemies of HWA have been *Laricobius nigrinus* and *Sasajiscymnus tsugae*, and both species have established in some areas of release^{10,19}. However, other species, such as *L. osakensis*²³ and *Leucopis* spp.²², currently are being assessed for wide-scale releases to increase the diversity of introduced predators that feed on HWA.

Several factors must be considered before the use of biological control against HWA. Due to the developmental nature of this effort, biological control of HWA has typically been conducted on public lands by trained personnel, and some natural enemy species may not be available for use on private lands.

Because HWA can cause tree mortality quickly, especially in the southern U.S., predator populations often cannot grow large enough to decrease HWA populations if the infestation is too great. Also, the use of natural enemies to manage HWA is not suitable for individual trees or if immediate reduction in pest populations is required.

NO HWA MANAGEMENT

Treating individual trees with systemic insecticides can be expensive, and it is not possible to save every hemlock in the forest²⁹. In addition, many land management programs cannot treat hemlocks, either due to the cost, or because state regulations prohibit the use of insecticides in forests. However, doing nothing results in loss of hemlock, a foundation species from the forest. Hemlock loss will have many negative ecological consequences. In residential and park settings, hazard tree removal is costly and is a consideration when determining whether to treat. Every management tactic, including doing nothing, has both positive

and negative consequences. Any decision regarding invasive species management will involve making trade-offs between the benefits and limitations of management options.

Management Perspective

The approach to managing HWA on hemlock is dependent on the location and site goals. The use of appropriate tools depends on whether the goal is preserving one tree in a landscape setting or the integrity of an entire forest system. Single-tree management is generally a landscape/ornamental issue. Proper tools include horticultural oil, contact insecticides, and systemic insecticides (Table 1). The cost of treating a tree is far less than the cost of removing a dead tree that has become a safety hazard. However, the purpose of preserving hemlocks in forested areas is not just preservation of a single tree, but rather the preservation of an entire forest ecosystem. Unfortunately, many methods used in ornamental landscapes are either not allowable or not practical in forests. Systemic

insecticides and biological control are currently the management tactics best suited for hemlocks growing in forests or other natural areas.

Conclusion

Hemlock woolly adelgid is a small insect that kills a mighty tree. The landscapes of eastern forests will be forever changed as a result of the introduction of this invasive species. While every hemlock cannot be saved, there are several management tactics to suppress HWA and preserve hemlock resources. Hemlocks can be protected for numerous years using one systemic insecticide treatment. Biological control predators are being assessed for their ability to reduce HWA populations. Landowners have the option of using insecticides to protect hemlock resources now while biological control tactics are being studied. Conserving hemlock trees is beneficial for overall forest health and is less costly than the expense of removing trees in landscape settings.

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Resources

For the location and phone numbers of state agencies in the southeastern U.S. providing forestry assistance and information, see the following websites:

Alabama Forestry Commission: <http://www.forestry.alabama.gov/>

Arkansas Forestry Commission:
<http://forestry.arkansas.gov/Pages/default.aspx>

Florida Forest Service: <http://www.floridaforestservice.com/>

Georgia Forestry Commission: <http://www.gatrees.org/>

Kentucky Division of Forestry:
<http://forestry.ky.gov/Pages/default.aspx>

Louisiana Department of Agriculture and Forestry:
<http://www.ldaf.state.la.us/>

Mississippi Forestry Commission: <http://www.mfc.ms.gov/>

North Carolina Forest Service: <http://www.ncforestservice.gov/>

Oklahoma Forestry Services: <http://www.forestry.ok.gov/>

South Carolina Forestry Commission:
<http://www.state.sc.us/forest/>

Tennessee Division of Forestry:
<https://www.tn.gov/agriculture/section/forests>

Texas A&M Forest Service: <http://texasforestservice.tamu.edu/>

Virginia Department of Forestry: <http://www.dof.virginia.gov/>

For the location and phone numbers of University Extension personnel in the southeastern U.S. providing forestry assistance and information, see the following websites:

Alabama Cooperative Extension System:
<http://www.aces.edu/main/>

University of Arkansas Cooperative Extension Service:
<http://www.uaex.edu/>

University of Florida's Institute of Food and Agricultural Sciences (UF/IFAS):
<http://solutionsforyourlife.ufl.edu/>

University of Georgia Extension: <http://extension.uga.edu/>

Kentucky Cooperative Extension Service:
<https://extension.ca.uky.edu/>

Louisiana Cooperative Extension Service:
<http://www.lsuagcenter.com/>

Mississippi State University Extension Service:
<http://extension.msstate.edu/>

North Carolina Cooperative Extension:
<https://www.ces.ncsu.edu/>

Oklahoma Cooperative Extension Service:
<http://www.oces.okstate.edu/>

Clemson Cooperative Extension (South Carolina):
<http://www.clemson.edu/extension/>

University of Tennessee Extension:
<https://extension.tennessee.edu/>

Texas A&M AgriLife Extension: <http://agrilifeextension.tamu.edu/>

Virginia Cooperative Extension: <http://www.ext.vt.edu/>

To locate a consulting forester:

Association of Consulting Foresters:
<http://www.acf-foresters.org/acfweb>.

Click on "Find a Forester", then select your state in the "People Search – Public" search page.

For more information on how to select a consulting forester, go to:

<http://msucare.com/pubs/publications/p2718.pdf>

<http://texashelp.tamu.edu/011-disaster-by-stage/pdfs/recovery/ER-038-Selecting-a-Consulting-Forester.pdf>

<http://www.uaex.edu/environment-nature/forestry/FSA-5019.pdf>

Additional information on the hemlock woolly adelgid is available at:

<http://southernforesthealth.net/>

http://protectnforests.org/hemlock_wooly_adelgid.html

<https://www.nature.org/ourinitiatives/regions/northamerica/unitedstates/tennessee/explore/hemlock.xml>

<https://www.fs.usda.gov/detail/r8/forest-grasslandhealth/insects-diseases/?cid=stelprd3842820>

https://www.nrs.fs.fed.us/disturbance/invasive_species/hwa/

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Figure 2: Samuel Lambert, USDA Forest Service.

Figure 5: Vincent D'Amico and Nathan Havill, USDA Forest Service.

Figure 8: James Johnson, Georgia Forestry Commission, bugwood.org.

Figure 9: Camcore, North Carolina State University.

References

- ¹Adkins, J. and L.K. Rieske. 2015. Benthic collector and grazer communities are threatened by hemlock woolly adelgid-induced eastern hemlock loss. *Forests* 6(8): 2719–2738.
- ²Bellows, T.S. and T.W. Fisher. 1999. *Handbook of Biological Control: Principles and Applications of Biological Control*. Academic Press, San Diego, CA.
- ³Benton, E. and R.S. Cowles. 2017. Optimized insecticide dosage for hemlock woolly adelgid control in hemlock trees. WSFNR-17-01. Warnell School of Forestry and Natural Resources. https://www.warnell.uga.edu/sites/default/files/publications/WSFNR-17-01%20Benton_0.pdf
- ⁴Benton, E.P., J.F. Grant, R.J. Webster, R.J. Nichols, R.S. Cowles, A.F. Lagalante, and C.I. Coots. 2015. Assessment of imidacloprid and its metabolites in foliage of eastern hemlock multiple years following treatment for hemlock woolly adelgid, *Adelges tsugae* (Hemiptera: Adelgidae), in forested conditions. *J. Econ. Entomol.* 108: 2672–2682.
- ⁵Burns, R.M. and B.H. Honkala, tech. coords. 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC., 877 p.
- ⁶Coots, C., P.L. Lambdin, J. Grant, and R. Rhea. 2013. Spatial and temporal distribution of residues of imidacloprid and its insecticidal 5-hydroxy and olefin and metabolites in eastern hemlock (Pinales: Pinaceae) in the southern Appalachians. *J. Econ. Entomol.* 106: 2399–2406.
- ⁷Cowles, R.S., M.E. Montgomery, and C.A.S.-J. Cheah. 2006. Activity and residues of imidacloprid applied to soil and tree trunks to control hemlock woolly adelgid (Hemiptera: Adelgidae) in forests. *J. Econ. Entomol.* 99: 1258–1267.
- ⁸Cowles, R.S., M.E. Montgomery, and C.A.S.-J. Cheah. 2006. Activity and residues of imidacloprid applied to soil and tree trunks to control hemlock woolly adelgid (Hemiptera: Adelgidae) in forests. *J. Econ. Entomol.* 99: 1258–1267.
- ⁹Ellison, A.M., M.S. Bank, B.D. Clinton, E.A. Colburn, K. Elliott, C.R. Ford, D.R. Foster, B.D. Kloeppel, J.D. Knoepp, G.M. Lovett, J. Mohan, D.A. Orwig, N.L. Rodenhouse, W.V. Sobczak, K.A. Stinson, J.K. Stone, C.M. Swan, J. Thompson, B. Von Holle, and J.R. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3:479–486.
- ¹⁰Hakeem, A., J.F. Grant, G.J. Wiggins, P.L. Lambdin, F.A. Hale, D.S. Buckley, J.R. Rhea, J.P. Parkman, and G. Taylor. 2013. Factors affecting establishment and recovery of *Sasajiscymnus tsugae* (Coleoptera: Coccinellidae), an introduced predator of hemlock woolly adelgid (Hemiptera: Adelgidae) on eastern hemlock (Pinales: Pinaceae). *Environ. Entomol.* 42: 1272–1280.
- ¹¹Havill, N.P., S. Shiyake, A.L. Galloway, R.G. Footitt, G. Yu, A. Paradis, J. Elkinton, M.E. Montgomery, M. Sano, and A. Caccone. 2016. Ancient and modern colonization of North America by hemlock woolly adelgid (Hemiptera: Adelgidae), an invasive insect from East Asia. *Mol. Ecol.* 25: 2065–2080.
- ¹²Holman, G., P. Del Tredici, N. Havill, N. S. Lee, R. Cronn, K. Cushman, S. Matthews, L. Raubeson, and C.S. Campbell. 2017. A new species and introgression in eastern Asian hemlocks (Pinaceae: Tsuga). *Syst. Bot.* 42: 1–14.
- ¹³Holmes, T.P., A.M. Liebhold, K.F. Kovacs, and B. Von Holle. 2010. A spatial-dynamic value transfer model of economic losses from a biological invasion. *Ecol. Econ.* 70: 86–95.
- ¹⁴Jenkins, J.C., J.D. Aber, and C.D. Canham. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. *Can. J. For. Res.* 29: 630–645.
- ¹⁵Jetton, R.M. and A.E. Mayfield III. 2018. Towards silvicultural management of the hemlock woolly adelgid. 2018. Proceedings of the 59th Southern Forest Insect Work Conference. p. 33.
- ¹⁶Jetton, R.M., W.S. Dvorack, and W.A. Wittier. 2008. Ecological and genetic factors that define the natural distribution of Carolina hemlock in the southeastern United States and their role in ex situ conservation. *For. Ecol. Manage.* 255: 3212–3221.
- ¹⁷Jetton, R.M., A.E. Mayfield III, W.A. Whittier, B. Mudder, R. Rhea, and G.R. Hodge. 2017. Silvicultural and genetic resource conservation strategies for management of the hemlock woolly adelgid. Proceedings of the 58th Southern Forest Insect Work Conference. p. 27.
- ¹⁸Joseph, S.V., J.L. Hanula, and S.K. Braman. 2011. Distribution and abundance of *Adelges tsugae* (Hemiptera: Adelgidae) within hemlock trees. *J. Econ. Entomol.* 104: 1918–1927.
- ¹⁹Mausel, D.L., S.M. Salom, L.T. Kok, and G.A. Davis. 2010. Establishment of the hemlock woolly adelgid predator, *Laricobius nigrinus* (Coleoptera: Derodontidae), in the eastern United States. *Environ. Entomol.* 39: 440–448.
- ²⁰McClure, M.S. 1989. Evidence of a polymorphic life cycle in the hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae). *Ann. Entomol. Soc. Am.* 82: 52–54.
- ²¹McClure, M.S., S.M. Salom, and K.S. Shields. 2001. Hemlock woolly adelgid. USDA Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV. FHTET-2001-03.
- ²²Motely, K., N.P. Havill, A.L. Arsenault-Benoit, A.E. Mayfield, D.S. Ott, D. Ross, M.C. Whitmore, and K.F. Wallin. 2017. Feeding by *Leucopis argenticollis* and *Leucopis piniperda* (Diptera: Chamaemyiidae) from the western USA on *Adelges tsugae* (Hemiptera: Adelgidae) in the eastern USA. *Bull. Entomol. Res.* 107: 699–704.
- ²³Mooneyham, K.L., S.M. Salom, and L.T. Kok. 2016. Release and colonization of *Laricobius osakensis* (Coleoptera: Derodontidae), a predator of the hemlock woolly adelgid, *Adelges tsugae*. *Northeastern Nat.* 23: 141–150.
- ²⁴Olson, J.S., F.W. Stearns, and H. Nienstaedt. 1959. Eastern hemlock seeds and seedlings: Response to photoperiod and temperature. *Bull. Conn. Agric. Expt. Sta.* 620: 1–70.
- ²⁵Onken, B., and R. Reardon. 2011. Implementation and status of biological control of hemlock woolly adelgid, USDA Forest Service, Morgantown, WV. https://www.fs.usda.gov/naspf/sites/default/files/naspf/pdf/bio_control-2012.pdf.
- ²⁶Orwig, D. A., D. R. Foster, and D. L. Mausel. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *J. Biogeogr.* 29: 1475 – 1487.
- ²⁷Snyder, C.D., J.A. Young, D.P. Lemarie, and D.R. Smith. 2002. Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. *Can. J. Fish. Aquat. Sci.* 59: 262–275.
- ²⁸Tingley, M.W., D.A. Orwig, R. Field, and G. Motzkin. 2002. Avian response to removal of a forest dominant: Consequences of hemlock woolly adelgid infestations. *J. Biogeogr.* 29: 1505–1516.
- ²⁹Vose, J.M., D.N. Wear, A.E. Mayfield III, and D. Nelson. 2013. Hemlock woolly adelgid in the southern Appalachians: Control strategies, ecological impacts, and potential management responses. *For. Ecol. Manage.* 291: 209–219.
- ³⁰Webster, J.R., K. Morkeski, C.A. Wojculewski, B.R. Niederlehner, E.F. Benfield, and K.J. Elliott. 2012. Effects of hemlock mortality on streams in the southern Appalachian Mountains. *Am. Midl. Nat.* 168: 112–131.
- ³¹Young, R.F., K.S. Shields, and G.P. Berlyn. 1995. Hemlock woolly adelgid (Homoptera: Adelgidae): stylet bundle insertion and feeding sites. *Ann. Entomol. Soc. Am.* 88: 827–835.