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Hemlock Woolly Adelgid in the Eastern United States: What Have We Learned?

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TITLE: Hemlock Woolly Adelgid in the eastern United States: What have we learned?

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Abstract

Adelges tsugae Annand (Hemlock Woolly Adelgid) is a small piercing-sucking insect that feeds on hemlock trees (*Tsuga* spp.). Native to Asia and the Pacific Northwest, the Hemlock Woolly Adelgid is invasive in the eastern United States where it attacks *Tsuga canadensis* (Eastern Hemlock) and *T. caroliniana* (Carolina Hemlock). It is currently found in 19 eastern states and has caused extensive mortality to hemlock forests. The ecological and economic impacts of this pest are significant, widespread, and often difficult to quantify. As the Hemlock Woolly Adelgid continues to disperse throughout the range of Eastern and Carolina Hemlocks, management techniques aimed at controlling it are being researched, implemented, and assessed. This introductory paper provides an overview of the biology, life cycle, ecology, and history of this pest in the eastern US as a foundation for this special issue.

Introduction

Adelges tsugae Annand (Hemlock Woolly Adelgid) is a small (~3 mm adult) piercing-sucking insect that feeds on conifers in the genus *Tsuga* and *Picea* (Havill and Foottit 2007). The population invasive to the eastern US is native to Japan (Havill et al. 2006). Although it has minimal impact on its native host plants (McClure 1997), it has become a major pest in the eastern US. In the eastern US, the adelgid feeds on *T. canadensis* Carrière (Eastern Hemlock) and *T. caroliniana* Engelmann (Carolina Hemlock), two hemlock species that have little or no defense against this insect (Montgomery et al. 2009). The resulting loss of hundreds of thousands of trees from forests ranging from Georgia to Massachusetts has profoundly affected both local communities and the associated ecosystems (Ellison et al. 2005).

This special issue of Northeastern/Southeastern Naturalist explores the adelgid's impacts and the challenges posed by its invasion. It contains articles surveying the wide range of adelgid-related questions researchers are addressing throughout the invaded range. In the following pages, we provide an overview of adelgid biology, its interactions with and impacts on other species at the community and ecosystem level, and the current status of control efforts.

Biogeography and history of the invasion

Hemlock Woolly Adelgid was first described as a species in the early 1920's from infestations on *T. heterophylla* Sargent (Western Hemlock) in the northwestern US (Annand 1924). The adelgid is genetically diverse throughout its native range, with different lineages associated with particular regions and host plant species. Hemlock Woolly Adelgid in the northwestern US is genetically different from the population native to Asia and the invasive population in the eastern US, which originated from low-elevation populations infesting *Tsuga sieboldii* Carrière (Southern Japanese Hemlock) in central Japan (Havill et al. 2006). Hemlock Woolly Adelgid in the eastern US was first reported in the early 1950s near Richmond, Virginia (Souto et al.1996). Although it was initially thought to be mainly a pest of ornamentals, by the 1980s the adelgid had also begun to harm forest hemlock. It is currently found in 19 eastern states, ranging from northern Georgia to southern Maine (USFS 2012).

Life cycle

The Hemlock Woolly Adelgid has two generations per year in the invaded range (Figure 1). In the early spring, first-instar nymphs of the spring generation (progrediens, plural progredientes) emerge and seek out suitable feeding sites in the leaf cushion at the base of hemlock needles (McClure 1989, Oten et al. 2012). These first-instar nymphs are known as crawlers and can either move actively upon their natal host or be dispersed passively by wind, birds, deer, or humans (McClure 1990, Turner et al. 2011). Once the crawlers find an appropriate feeding site, they settle permanently and use their feeding stylet bundle to probe and feed from xylem ray parenchyma cells (Young et al. 1995). Adelgids go through four larval instars before maturing into adults; because Hemlock Woolly Adelgid in the invaded range reproduces asexually, each mature individual is theoretically capable of producing 20-30 summer-generation (sistens, plural sistentes) offspring in early summer (McClure 1989, Paradis 2011). After the summer-generation crawlers settle at the base of new-growth hemlock needles, they aestivate until late fall, when they begin to feed. They feed throughout the winter, and each adult is theoretically capable of producing 50-100 offspring the following spring (Paradis 2011).

While the spring generation is the same in the adelgid's native and invaded range, the summer generation differs substantially between the two areas. Summer-generation eggs hatch into either wingless asexual progrediens that feed on hemlock or winged sexually-reproducing sexuparae that feed on *Picea torano* Carriere (Tiger Tail Spruce) in the native range (Sato 1999). In the invaded range, however, there are no suitable spruce hosts and the sexuparae perish without reproducing. As a result, HWA in the eastern US is obligately asexual and genetic variability is limited. Despite this lack of genetic recombination, however, there is evidence for adaptive genetic variation in cold tolerance in the invaded population (Butin et al. 2005).

Population ecology

Although mature adelgids can produce a large number of offspring, both juvenile and adult adelgids also experience high mortality rates (McClure and Cheah 2002). The dispersing crawlers are wingless, passively dispersed, and stand a high probability of ending up in unsuitable habitat. Even under ideal conditions, early-instar mortality rates can approach 90% (Paradis 2011), and adults are susceptible to extreme heat in the summer and periods of intense cold in the winter (Trotter and Shields 2009). Because even low adelgid densities substantively affect tree health, its survival is highly density-dependent (McClure 1991), with the previous generation's density being the strongest predictor of survival (Paradis 2011). In the invaded range, this density-dependent mortality is compounded by the fact that sexuparae production increases in populations feeding on unhealthy or declining hosts. Both Eastern and Carolina Hemlocks are, however, higher-quality host plants for the invasive adelgid population than many hemlock species that have co-evolved with other lineages of the adelgid (Montgomery et al. 2009). This may provide one explanation for why the adelgid is so abundant in its novel range.

Community ecology

The Hemlock Woolly Adelgid has numerous predators in its native range (Cota Vieira et al. 2013, Hakeem et al. 2011, McClure and Cheah 1999), but no predators native to the invaded range appear capable of reducing adelgid densities sufficiently to consistently prevent hemlock decline and death (Havill et al., 2012). As a result, its most important intraspecific interactions likely involve those herbivores that co-occur on its host plant. Although *Lambdina fiscellaria* Guenee (Hemlock Looper) has historically been considered a major hemlock pest (Trial and Devine 1995), its densities appear to have declined in southern New England (E. Preisser, personal observation). In this region, the most commonly co-occurring hemlock herbivore is another invasive hemipteran, *Fiorinia externa* Ferris (Elongate Hemlock Scale) (Preisser et al., 2008). This sessile armored scale feeds on the underside of hemlock needles, reproduces sexually, and has one generation per year in the northeastern US and two generations in the South (Abell and Van Driesche 2012, McClure 1978). Its dispersing crawler stage settles on hemlock foliage in late spring, approximately one month after HWA crawlers have begun feeding; because of this, the adelgid was predicted to competitively exclude the scale from hemlock (McClure 1997). In reality, however, both the range and population density of the scale have increased sharply in adelgid-invaded areas of southern New England (Preisser et al. 2008).

Because the adelgid and elongate hemlock scale are both sessile and feed on different plant structures, they interact via their impact on the shared host plant. This fact is important because the two species have very different impacts on plant health; both experimental research (Miller-Pierce et al. 2010, Miller-Pierce and Preisser 2012, Preisser and Elkinton 2008) and landscape surveys (Preisser et al. 2008, 2011) have found that while the scale can reach higher densities than the adelgid, the adelgid has a greater impact on plant health. Experimental work assessing their interactions on hemlock branches found that each species decreased the other species' density by ~30% relative to when the species occur by themselves (Preisser and Elkinton 2008); at the whole-tree level, however, intraspecific competition is only measurable when one species arrives several years earlier than the other (Miller-Pierce and Preisser 2012). In such a scenario, HWA densities are 40% lower when settling on trees previously infested with the scale; by contrast, the prior presence of HWA does not significantly reduce scale densities (Miller-Pierce and Preisser 2012). Most recently, experimental work found that HWA crawlers avoided settling on EHS-infested branches, a finding supported by surveys showing that crawlers avoid settling at the base of EHS-infested needles (Gomez et al. 2013). These findings suggest that EHS, despite its apparent disadvantages, may actually be competitively dominant over HWA.

Interaction with hemlock

While HWA is capable of quickly killing hemlock trees (McClure 1991, Orwig et al. 2002), the mechanism underlying such rapid HWA-mediated mortality has only recently begun to be addressed. Following initial infestation, the tree declines in health. This period is marked by needle drop, bud abortion, and inhibition of new growth (McClure 1991). A healthy hemlock can be killed in as little as four years, with many trees (especially in warmer climates) dying within ten years of infestation (McClure 1987, 1991; see the following 'larger-scale effects' section, below, for a more detailed description of adelgid-induced tree mortality). Some scientists hypothesized that hemlocks died from resource depletion; large numbers of adelgids essentially ‘starved’ the tree of nutrients (McClure 1991). This explanation was challenged by work that used scanning electron microscopy to identify the adelgid's precise feeding mode and cellular-level impact (Young et al. 1995). Because these researchers found that adelgid feeding caused relatively little cellular damage, they proposed that the adelgid’s impact on tree health was better explained by ‘toxicity’: fluids secreted by feeding adelgids, or the plant’s response to the feeding, had a disproportionately large impact on plant health. This explanation gained credence with the large increase in elongate hemlock scale densities in southern New England; similarly-sized to adelgids but more abundant (Preisser et al. 2008), these scales nonetheless had less impact on hemlock growth and survival (Miller-Pierce et al. 2010, Miller-Pierce and Preisser 2012, Preisser and Elkinton 2008, Preisser et al. 2008, 2011).

The large amount of damage induced by HWA feeding appears linked to a hypersensitive response in hemlock. The presence of HWA at the base of a needle causes extensive damage (measured by the presence of hydrogen peroxidase) to the needle itself as well as to nearby ‘new growth’ foliage that had not been colonized by HWA crawlers (Radville et al. 2011). The hypersensitive response acts to isolate sessile herbivores by killing nearby tissue and starving the feeding insect (Fernandes 1990, Fernandes and Negreiros 2001). In the case of HWA, the hypersensitive response causes the induction of ‘false growth rings’ in infested stems that interfere with solute transport and prevent the stems from obtaining the water necessary for photosynthesis (Domec et al. 2013, Gonda-King et al. 2012). As a result, the plant may experience chronic water stress and eventually be unable to carry out photosynthesis (Domec et al. 2013). Despite widespread cell death, induction of the hypersensitive response appears to cause relatively little harm to feeding adelgids. On the contrary, HWA may themselves biochemically manipulate the plant to induce this response. HWA possesses several enzymes similar to those used by related insects to feed upon and influence their host plants (Oten 2011). A detailed analysis of herbivore-mediated changes in hemlock amino acid concentrations found that adelgids actually induced substantial increases in local nutrient levels (Gómez et al. 2012). This manipulation may be similar to that occurring in galling insects, where sessile herbivores manipulate plant physiology to build protective structures (i.e., galls) that serve as both food and protection (Havill and Foottit 2007).

Larger-scale effects

The Hemlock Woolly Adelgid has killed so many hemlocks in the eastern US that the International Union for Conservation of Nature (IUCN) recently labeled Eastern Hemlock 'near threatened' and placed it on the Red List of Threatened Species (Farjon 2013). At the local level, adelgid-induced hemlock mortality has substantially impacted many natural areas; Virginia's Shenandoah National Park, for example, has lost ~90% of its mature hemlocks (Townsend and Rieske-Kinney 2006). While noticeable hemlock mortality and decline continues, however, the initial predictions of complete mortality of Eastern and Carolina Hemlock have not been realized (Preisser et al. 2008). Especially in the northeastern US, a substantial number of infested trees continue to persist: a long-term study in Delaware Water Gap National Park (located on the NJ-PA border) found that 73% of hemlocks survived for longer than ten years (Eschtruth et al., 2013). A recently-published analysis of Forest Inventory Analysis (FIA) data for 432 US counties made a similar point (Trotter et al., 2013). It found little evidence for large-scale decline and a slight increase in median live hemlock basal area between 1985 and 2005, a fact it attributed to the positive effects of reforestation and regeneration overwhelming the more recent negative impacts of the adelgid.

Even if Eastern and Carolina Hemlock persist in eastern US ecosystems, the large losses caused by adelgid infestation will substantially alter eastern forest ecosystems. Hemlocks are a shade-tolerant 'foundation' species that shade and cool headwater streams that are home to trout and a wide variety of aquatic invertebrates (reviewed in Ellison et al. 2005, Orwig and Foster 2000). They also assist in soil stabilization and controlling hydrologic regimes (Ford and Vose 2007). Over a nine-year period, adelgid-induced hemlock decline in the Delaware Water Gap National Recreational Area (NJ) more than doubled understory light levels, increased vascular plant cover nearly fourfold, and led to invasive plants colonizing 35% of the surveyed plots (Eschtruth et al. 2006). Hemlock stands are also critical habitat for a number of bird species (Rabenold et al. 1998), and the loss of hemlocks can substantially affect invertebrate community composition (Adkins and Rieske 2013, Dilling et al. 2007, Ingwell et al. 2012).

There are 274 cultivars of eastern hemlock, “making it one of the most cultured and cultivated landscape tree species” (Quimby 1996, Swartley 1984) that is often used as a hedge because of its response to shearing (Swartley 1984). It is also desired for its color, graceful habit, and, until recently, its freedom from disease and insects. According to 1995 nursery inventories in Tennessee and North Carolina, the value of eastern hemlock was approximately $34 million (J.R. Rhea, personal communication, cited in Bentz et al. 2002). The invasion of the adelgid has reduced the importance of native hemlocks for ornamental use and will likely also affect the more than 4 million cubic feet of timber produced in the region annually (Rhea 1995, Woodsen 2001). Land values also deteriorate as a result of adelgid infestations. A study in residential New

Jersey found that 25-50% hemlock defoliation by the Hemlock Woolly Adelgid led nearby property values to decline by an average of more than $7,000.00 (Holmes et al. 2005). The future use of hemlocks as ornamentals relies in part on the ability to effectively manage the adelgid.

Management methods

Chemical control. Management of the Hemlock Woolly Adelgid is largely focused on biological control and chemical control (McClure 2001, McClure and Cheah 1999, Montgomery 1999, also see Onken and Reardon 2011). Chemical control is currently the most effective method and is widely used in ornamental and landscape settings, but it is generally impractical in forest settings due to prohibitive costs and the potential environmental impacts of wide-scale use (Cowles 2009, McClure 1992). The biggest limiting factor is cost. Trees must be treated individually, often leading managers to target a series of 'high value' trees for treatment. Because chemicals degrade over time, they must be periodically re-applied to ensure continued control; in addition, there is the potential for non-target environmental impacts. The water-solubility of systemic insecticides allows for rapid uptake and internal transportation of the chemical throughout the tree, but also allows them to impact aquatic organisms in nearby water bodies. Imidacloprid, for example, has been detected in water at sites with low soil organic matter (U.S. EPA 2003). The mode of chemical application may also affect hemlock forest-associated fauna. Soil injections of imidacloprid, for example, can cause significant declines in the abundance and richness of soil-dwelling springtails and other non-target organisms (Reynolds 2008). Forest applications may be limited due to geographical and logistical constraints such as difficulties in bringing equipment into a forest (Cowles et al. 2006). Lastly, pesticides are not a fail-proof method. In Joyce Kilmer Memorial Forest (NC), for example, pesticide applications appear relatively ineffective in reducing adelgid populations (Bompey

11/08/2010). Despite these concerns, research into chemical treatment options has decreased their environmental impacts while increasing their efficacy (e.g., Cowles 2009). While chemicals are often the best option in ornamental settings, they are generally impractical in forests as a stand-alone management tool. Sustainable long-term adelgid management in forest settings will likely require an integrated pest management program incorporating multiple management techniques (Bentz et al. 2002, Del Tredici and Kitajima 2004, McClure and Cheah 1999).

Biological control. There appear to be no predators native to the invaded range capable of consistently lowering adelgid densities sufficiently to prevent tree decline and death (Montgomery and Lyon 1996, Wallace and Hain 2000, Havill et al. 2012). Researchers searching for effective adelgid predators began to explore Asia and northwestern North America, the native range of the Hemlock Woolly Adelgid, for organisms useful in a classical biological control program. Since the 1990s, biological control has been a major focus of adelgid research and management (McClure and Cheah 2002, Onken and Reardon 2011), an effort that expanded considerably with the development of the Hemlock Woolly Adelgid Initiative in 2003. The current program includes 28 federal and state agencies, 24 universities, seven institutions in China and Japan, and numerous private industries (Onken and Reardon 2011).

Several beetle species have been released in hopes of controlling the Hemlock Woolly Adelgid. The first was a coccinellid beetle, *Sasajiscymnus tsugae* Sasaji and McClure, that is native to Japan and was first released in 1995 (Cheah 2008, 2011; Cheah and McClure 1998). Since then, there have been more than two million *S. tsugae* released on more than 400 sites in 16 states (Cheah 2011, Grant et al. 2010, Salom et al. 2008). It successfully reproduces and disperses following release, and is capable of surviving extreme climatic events (Cheah 2011).

Between 2004 and 2011, more than 61,000 individuals of *Scymnus sinuanodulus* Yu and Yao, another coccinellid beetle native to China, have been released (Montgomery and Keena 2011). Because research suggests that this species is most climatically suited to the southern portion of the hemlock range in the eastern US (Salom et al. 2008), most of these releases have occurred in Georgia, North Carolina, and Tennessee. When released in these areas, the species does not seem to require additional efforts to assist in its establishment (Montgomery and Keena 2011). Other beetles in the same genus have also been (*S. ningshanensis* Yu and Yao) or are currently being pursued (*S. coniferarum* Crotch and *S. camptodromus* Yu and Liu) as biological control agents. Native to western North America, the beetle *S. coniferarum* seems especially promising since its feeding habits temporally complement that of *Laricobius nigrinus* Fender (discussed in the next paragraph). Releases of *S. coniferarum* have begun, and research and efficacy trials continue (Montgomery et al. 2011). Initial problems in rearing *S. camptodromus* slowed this species' evaluation, but it is still being pursued because it diapauses at the same time as the adelgid, has a broad geographic distribution, and is active during a critical period in the adelgid life cycle (Montgomery and Keena 2011).

Laricobius nigrinus (Coleoptera: Derodontidae), a specialist adelgid predator native to Oregon and Washington (Kohler et al. 2008), shows particular promise as a biological control agent. Since its initial release in 2003, more than 380,000 beetles have been released throughout the eastern US (Mausel et al. 2011, Salom et al. 2008). While its role as a biological control agent seems promising given its field recovery success and ability to reduce adelgid populations, it is hybridizing with a native beetle, *L. rubidus* LeConte (Klein et al. 2010), with unknown consequences (Havill et al. 2012). This native beetle, which feeds primarily on *Pineus strobi* Hartig (Pine Bark Adelgid), can be found feeding on Hemlock Woolly Adelgid in areas where white pine and hemlock co-occur (Montgomery and Lyon 1996, Wallace and Hain 2000). The fact that *L. nigrinus* feeds exclusively on spring-generation eggs and nymphs (Kohler et al. 2008, Zilahi-Balogh et al. 2002) suggests that it will be most effective as part of a suite of predators. Another beetle in the same genus that is native to Japan, *L. osakensis* Montgomery and Shuyake, is also being researched and released. This beetle is especially important since is native to the region where the invasive lineage of the adelgid also occurs (Havill et al. 2006, Lamb et al. 2011). In 2012, 2000 *L. osakensis* were released (K. Mooneyham, pers. comm.) and research and releases continue.

A number of other organisms also have potential as biological control agents. *Leucopis* spp. flies (Diptera: Chamaemyiidae) prey on Hemlock Woolly Adelgid in northwestern North America, but a lack of rearing methods and difficulty in species identification have slowed their development as control agents (Ross et al. 2010). A fungal agent, *Lecanicillium muscarium* Zare and Gams, is also under investigation (Salom et al. 2008). It is commercially available as Mycotal, a biopesticide. Some formulations of this fungal agent, which has been approved for use in the US and can already be found in eastern US hemlock forests, can reduce adelgid populations by up to 75%; research into the challenges posed by harsh abiotic conditions and the need for mass deployment is ongoing (Costa 2010, 2011).

While biological control agents may help manage Hemlock Woolly Adelgid populations, the high susceptibility of Eastern and Carolina Hemlock to the adelgid means that these agents must cause extremely high adelgid mortality in order to be successful (McClure 1996). This level of adelgid suppression will likely require a suite of predators (Cheah et al. 2004, Montgomery and Lyon 1996); biological control agents may ultimately be most successful when incorporated into a well-rounded integrated pest management program.

Host-plant resistance. When grown in the eastern US and experimentally infested with the Hemlock Woolly Adelgid, hemlock species native to Asia and the Pacific Northwest are tolerant of and/or resistant to this pest (Bentz et al. 2002, 2007; Del Tredici and Kitajima 2004; Jetton et al. 2008; Oten 2011). This suggests that host-plant factors may play a role, perhaps in concert with natural enemies and the scattered distribution of hemlocks, in keeping adelgid densities low in the native range (Montgomery and Lyon 1996).

Interspecific variation in hemlock resistance to the Hemlock Woolly Adelgid is well-documented and continues to be pursued as a key component in a long-term, integrated approach to adelgid management. Hybrid crosses between adelgid-resistant *T. chinensis* (Franch.) Pritzel ex Diels and the adelgid-susceptible Carolina Hemlock produce progeny that are more adelgid-resistant than Carolina Hemlocks (Montgomery et al. 2009). Similar hybridization attempts with Eastern Hemlock have been unsuccessful (Bentz et al. 2002, Pooler et al. 2002), but advances in hybridization methodology may assist in overcoming this obstacle.

There have also been reports of a few Eastern Hemlocks growing in heavily adelgid-damaged regions that appear to have remained healthy and vigorous. Their existence and continued vigor, despite coexisting with the Hemlock Woolly Adelgid for more than 20 years, suggests the potential for some degree of adelgid resistance/tolerance in Eastern and Carolina Hemlocks (Caswell et al. 2008). When cuttings from these putatively-resistant trees were grown and evaluated in conjunction with cuttings from known adelgid-susceptible trees, the putatively-resistant cuttings had lower adelgid settlement and higher adelgid mortality than did control cuttings (Ingwell and Preisser 2011).

While the development of resistant hemlocks suitable for forest restoration in the eastern US is a long process, initial investigations look somewhat promising. A long-term and sustainable approach to adelgid management will likely incorporate chemical control, biological control, and host-plant resistance into an integrated management program.

Conclusion

The past decades have seen substantial progress towards a better understanding of adelgid ecology and management. These accomplishments notwithstanding, we have yet to develop a long-term and cost-effective management strategy for the Hemlock Woolly Adelgid. It is our hope that the articles contained in this special feature move us closer to this goal, and to the preservation of our native hemlock trees.

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Figure 1: Hemlock Woolly Adelgid life cycle. In Japan, the adelgid alternates between Hemlock and Tigertail Spruce. Tigertail Spruce supports a sexual generation and gall formation. In the eastern United States there are only two generations on Hemlock, because winged migrants do not find suitable spruce species on which to complete the entire life cycle. The letters ‘A’ and ‘B’ refer to where the cycle begins again. Vince D’Amico and Nathan Havill created the artwork for this figure.