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Impacts of Hemlock Decline and Ecological Considerations for Hemlock Stand Restoration Following Hemlock Woolly Adelgid Outbreaks

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ABSTRACT

We present a synthesis of current knowledge and information of hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) impact on hemlock forests and a conceptual framework of restoring damaged hemlock stands by HWA infestation. Native to Asia, HWA has been thriving in the eastern United States since the early 1950s and has become a serious pathological agent of both eastern hemlock (*Tsuga canadensis* (L.) Carrière) and Carolina hemlock (*Tsuga caroliniana* Engelm.) even since. By 2007, it was established in portions of 16 States from Maine to Georgia, where infestations covered about half of the range of hemlock and continuously spreading. The impacts of HWA induced hemlock mortality and decline on key ecosystem resource and processes are still not fully understood. Successful and effective restoration of the declined hemlock population is challenging and involves a complex process that commonly spans many years. Development of a management and restoration strategy that will establish priorities, standards, and practices could facilitate objective decisions and allocation of limited resources. In addition to encourage natural regeneration of hemlock in the damaged forest stands and both chemical and biological control, three strategies seem to stand out as possibilities: growing off-site stocks of hemlock seedlings for replant, creating hybrid hemlocks that are resistant to HWA, and replanting with the already resistant western hemlock or Chinese hemlock. Other ecological considerations in the context of restoring hemlock forests following HWA are also discussed.

Keywords: Adelges tsugae, hemlock decline, natural regeneration, restoration planning

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INTRODUCTION

One of the greatest pressures threatening forest ecosystem health in the United States is the introduction of non-native forest insects (Tingley *et al.* 2002). How and why insect outbreaks are initiated is not well-understood (Maron *et al.* 2001). However, it is known that outbreaks are more catastrophic when a species in the infested habitat exerts a strong control over ecosystem structure and function (Eschtruth *et al.* 2006). Because insects form unique assemblages associated with specific trees (Dilling *et al.* 2007), the introduction of a non-native insect pest will likely cause alterations to its invaded forest ecosystem (Stadler *et al.* 2005). Additionally, the introduction of one non-native species can promote subsequent introductions of other non-native species (Evans and Gregoire 2007).

Because understanding the ecology of an invasive species is difficult, restoring the ecology of its invaded habitat poses a serious challenge (McClure and Cheah 1999). This paper discusses hemlock woolly adelgid (*Adelges tsugae*, HWA), a non-native invasive insect of eastern North America, in terms of its impact on forest structure and function as well as conceptual framework and management techniques best suited to restoring forests which it has impacted.

HEMLOCK WOOLLY ADELGID

HWA has been thriving in the eastern United States since 1951 (Gouger 1971). It is a destructive, tiny aphid-like insect pest and causes damage by depleting starch reserves in eastern hemlock (*Tsuga canadensis*) and Carolina hemlock (*Tsuga caroliniana*), which in return reduces the tree's ability to grow and produce new roots (Ward *et al.* 2004). Displacing both cultivated hemlock trees and hemlock forests in the mid-Atlantic, HWA first became problematic during the 1980s (Del Tredici and Kitajima 2004). It then moved into regions of the southern Appalachian Mountains, where it continues today to threaten the dynamics and structure of eastern forests of North America (Koch *et al.* 2006). HWA also exists in western North America and whether it is native or introduced there is unknown (Havill *et al.* 2006). Eastern North American populations of HWA, on the con-

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trary, likely derived from southern Japan, and there is a clear distinction between North American and Japanese adelgids in retrospect to Chinese and Taiwanese adelgids (Havill *et al.* 2006).

The threats that HWA pose to the sustainability of its invaded territories are evident and detrimental to both the ecosystem and its individual components. Hemlock woolly adelgid damages hemlock foliage directly by feeding at the base of individual needles and therefore causing individual needle mortality followed by branch and crown mortality (Cobb *et al.* 2006), the growth and survival of eastern hemlock is reduced significantly (McClure 1991). Ecological impacts are difficult to define, because estimations of populations must be precise (Gray *et al.* 1998). The ecological threats that HWA pose are indirect; however, they are dramatic and may even be lasting to the structure and function of hemlock stands (Cobb *et al.* 2006; Nuckolls *et al.* 2009).

Early attempts of estimating HWA spread have been exaggerated (Evans and Gregoire 2007). HWA spreads at a rate of approximately 12.5 km/yr; however, under the most optimal conditions, HWA can spread at a rate of 20.8 km/yr (Evans and Gregoire 2007). Orwig *et al.* (2002) suggest that HWA infestations coincide with the northward colonization trend; thus, concentrations of HWA infestations decline from south to north. Although HWA has invaded at least half the range of eastern hemlock (Bentz *et al.* 2002), some hemlock stands have survived HWA infestations over a decade later (Pontius *et al.* 2006). A trend in one experiment in eastern hemlock stands of Connecticut found that a) HWA abundances increase rapidly during the first year of infestation and then rapidly decline throughout the second year, b) populations rebound at a lower abundance during the third year and then rapidly decline to very low abundances, and c) HWA populations then disappear when all hemlock trees die (McClure 1991).

Air temperature is a primary constraint on the spread of HWA (Gouli *et al.* 2000; Pontius *et al.* 2006; Evans and Gregoire 2007). Because brief exposure to subfreezing temperatures is destructive to some of its cell types, HWA establishment may be reduced (Parker *et al.* 1999; Gouli *et al.* 2000). However, as air temperature rises, the spread of HWA into new territories is likely (Paradis *et al.* 2008). Birds, deer, humans, and wind may play significant roles in the spread of HWA (McClure 1990). Long distance dispersal of HWA is enabled by connectivities (e.g., roads) (Koch *et al.* 2006). As a result of the rapid mortality rate of the hemlocks, logging operations in the northeast United States began; and these logging operations may also spread HWA long distances (McClure 1990).

Fig. 1 Hemlock woolly adelgid (*Adelges tsugae* Annand). Connecticut Agricultural Experiment Station Archive, Connecticut Agricultural Experiment Station, Bugwood.org.

Fig. 2 A hemlock woolly adelgid infested stand in the Coweeta watershed along a riparian corridor in western North Carolina, USA. (Photo by Weimin Xi, April, 2010).

IMPACTS OF HWA

In the eastern United States, eastern hemlock is one of the oldest and most prolific species (Orwig *et al.* 2002); it grows on almost 7.69 million ha of forest and is the predominant species on 1.17 million ha (Ward *et al*. 2004). The range of eastern hemlock extends from Nova Scotia in Canada to Georgia and westward to Minnesota, while Carolina hemlock, occurs in small areas in the southern Appalachians (Lagalante 2006).

Hemlocks are important species because their multi-layered canopies are unique and because of their extreme tolerance to shade (Orwig and Foster 1998; Zilahi-Balogh *et al.* 2002; Bentz *et al.* 2002; Rentch *et al.* 2009; **Fig. 1**). The dense, evergreen canopy associated with mature hemlock forest creates a unique environment that is critical habitat for many animal and plant species. More than 120 vertebrate species utilize mature hemlock stands, and hemlock forests also provide thermal cover and forage for a variety of mammals, including porcupines (*Erethizon dorsatum*) and white-tailed deer (*Odocoileus virginianus*). Nearly 90 bird species can be found in hemlock forests (Ward *et al*. 2004).

Eastern and Carolina hemlocks of all ages are attacked by HWA (Koch *et al.* 2006). Infested hemlocks display poor average crown health (McClure 1991; Cobb *et al.* 2006), and they exhibit chlorosis and abscission of needles, reduced growth of terminal branches, and twig dieback (McClure 1991; Cowles 2009). Consequently, as a result of weaker health, hemlocks eventually die (Cowles 2009). Death of hemlocks can occur in as little as four years (McClure 1991). The modification of stands from evergreen coniferous forests to broad-leaved deciduous forests has contributed to the loss and replacement of eastern hemlocks without any indication that hemlocks will again flourish in forthcoming years (Kizlinksi *et al.* 2002; Daley *et al.* 2007).

Increased hemlock mortality associated with HWA infestations inhibits the abundance of some avian species due to their low adaptability in either the new surrounding matrix or in the replacement habitat with less canopy cover

(Tingley *et al.* 2002). As hemlock mortalities increase, species such as black-throated green warbler (*Dendroica virens*), blackburnian warbler (*Dendroica fusca*), blue-headed vireo (*Vireo solitarius*), hermit thrush (*Catharus guttatus*), Acadian flycatcher (*Empidonax virescens*), and ovenbird (*Seiurus aurocapillus*) are disadvantaged from the changes of forest composition (Tingley *et al.* 2002).

Hemlock canopy damage induced by HWA allows for an increased amount of light to penetrate to the forest floor (Orwig and Foster 1998; Stadler *et al.* 2005; Cobb *et al.* 2006; Eschtruth *et al.* 2006; **Fig. 2**). Thus, the establishments of invasive plant species such as Asiatic bittersweet (*Celastrus orbiculatus*), tree of heaven (*Ailanthus altissima*), Japanese barberry (*Berberis thunbergii*), and Japanese stilt grass (*Microstegium vimineum*) are promoted (Orwig and Foster 1998). Despite the increased temperature flux that occurs as sunlight reaches the forest floors, litter decomposition does not increase (Cobb *et al.* 2006).

Ecological impacts are difficult to define because estimations of populations must be precise (Gray *et al.* 1998). The ecological threats that HWA pose are indirect; however, they are dramatic and may even be lasting to the structure and function of hemlock stands (Cobb *et al.* 2006; Nuckolls *et al.* 2009). The occupation of exotic invasive plants in permanent vegetation plots increased from 0% in 1994 to 35% in 2003 (Eschtruth *et al.* 2006). Over a period of 9 years, the total cover of vascular plants increased from 3.1 to 11.3% in an infested habitat (Eschtruth *et al.* 2006). While some argue that species richness may decline as hemlocks continue to disappear (Tingley *et al.* 2002), others have argued that species richness will increase (Eschtrutch *et al.* 2006).

Without disturbance of HWA infestation, eastern hemlock maintains a strong control of the environment's microclimate because of its shade; additionally, it maintains a strong control of the soil conditions because of its acid litter deposition (Eschtruth *et al.* 2006). Due to the chemistry of decomposing litter, during the later stages of infestation, the C: N ratios of the forest floors are reduced (Kizlinski *et al.* 2002; Cobb *et al.* 2006; Orwig *et al.* 2008). Enhanced decomposition additionally increases the level of Nitrogen in infested hemlock stands (Orwig *et al.* 2008). In addition to increased levels of foliar nitrogen, dissolved organic carbon and cations in throughfall beneath infested trees also increase in levels (Stadler *et al.* 2005). In a study in central Connecticut and Massachusetts, organic soil moisture decreases with infested hemlock stands and organic soil moisture levels are controlling decomposition in HWA-infested forests (Cobb *et al.* 2006).

Additionally, as increased light penetrates to the forest floor as a result of breaks in hemlock canopy, oak species (*Quercus* spp.), red maple (*Acer rubrum*), black birch (*Betula lenta*), and black cherry (*Prunus serotina*) increase in average heights and densities compared to uninvaded stands (Orwig and Foster 1998).

CONTROL

The livelihood of infested trees may be improved by imidacloprid treatments (Doccola *et al.* 2003; Webb *et al.* 2003). While pesticides could effectively control HWA, these chemical means are neither economically nor environmentally feasible (Hoover *et al.* 2009). Chemical control cannot be implemented in sensitive habitats, and it is impossible to implement it in inaccessible hemlock tree stands (Flowers *et al.* 2006).

Non-native biological control agents offer a viable solution for controlling HWA infestations, since native predators present no control over adelgid populations (Wallace and Hain 2000). While some argue that management of HWA by biological control agents is the most effective means both economically and environmentally (Conway *et al.* 2005), biological control agents have not been effective as immediate remedies (Reardon and Onken 2004). Tens of millions of US dollars have been spent on biocontrols for HWA, but very few, if any, examples exist where it has prevented or minimized the effects of an outbreak. Because fungi occur naturally in HWA populations, they are potential biological candidates for control of hemlock woolly aldegid (Gouli *et al.* 1997). McClure (1995) suggests that an oribatid mite native to Japan (*Diapterobates humeralis*) may control HWA within North America. This is because of its ability to acclimate in a wide range of environmental parameters, its ability to remove HWA eggs from trees, and its compatibility to live with other organisms that it is introduced to (McClure 1995).

The lady beetle (*Sasajiscymnus tsugae* formerly *Pseudoscymnus tsugae*) could be a promising control agent for HWA (Sasaji and McClure 1997; McClure *et al.* 2000). In 1995, *S. tsugae* was first released into Connecticut, and now over 1 million *S. tsugae* beetles have been released throughout 15 states (Cheah 2004). Conway *et al.* (2005) suggest that because *S. tsugae* and HWA have synchronized life cycles, it would be a promising biological control agent. Throughout all its life stages, *S. tsugae* feeds on all life stages of HWA (McClure and Cheah 1999). Additionally, they can be reared in the laboratory (McClure and Cheah 1999). Releases have been noted to reduce HWA concentrations by 47-83% (McClure and Cheah 1999). However, according to Salom *et al.* (2001) *S. tsugae* may not be the best suitable candidate for biological control, because it will not begin to produce eggs until at least four months after HWA sistens break diapause.

In 2003, the tooth-necked fungus beetle (*Laricobius nigrinus*) was released as a biological control agent (Zilahi-Balogh *et al.* 2006). Because of the inverse relationship between total eggs laid by HWA and population density of *L. nigrinus*, *L. nigrinus* is a promising biological control agent (Lamb *et al.* 2006). Feeding tests indicate that *L. nigrinus* consumes more eggs of HWA than eggs of balsam woolly adelgid (*Adelges piceae*), pine bark adelgid (*Pineus strobi*), and eastern spruce gall adelgid (*Adelges abietis*) (Zilahi-Balogh *et al.* 2002). Additionally, when in the presence of HWA, basalm woolly adelgid, eastern spruce gall adelgid, pine bark adelgid, spruce shoot aphid (*Cinara pilicornis*), and white pine needle scale (*Chionaspis pinifoliae*), *L. nigrinus* completes its larval development on only HWA, where it prefers to oviposit in its ovisacs (Zilahi-Balogh *et al.* 2002).

Flowers *et al.* (2006) suggests a combination of multiple HWA predators because HWA is most greatly impacted by the Asian lady beetle (*Harmonia axyridis*) in the summer and by the *L. nigrinus* in the spring (Flowers *et al.* 2006).

RESTORATION

Successful restoration of damaged hemlock forests by HWA is challenging and involves a complex process that commonly spans many years. While experimental restoration projects have been conducted at the stand-level in United States, very little research has been documented on restoring hemlocks in a natural setting. Below we provide a brief synthesis of current knowledge in the context of the management and restoration of damaged hemlock forests.

Restoration of hemlock forests is a process of regaining some basic ecological and esthetic attributes associated with hemlock forests before they were damaged by HWA. The goal of the restoration efforts is to speed recovery at least some of these attributes of the hemlock forests. Following HWA outbreaks, active management (such as stand thinning, cut of the infested trees, removal of competing trees, re-planting) and restoration planning and subsequent monitoring are essential of a successful operation (Goerlich and Nyland 2000). Development of a restoration plan that will establish priorities, standards, and practices will facilitate objective decisions and allocation of limited resources. Because of the cost associated with management and restoration activities, it is necessary to have a protocol established for prioritizing hemlock stands as part of the planning process. Unique stand characteristics and relative importance of factors such as wildlife habitat esthetic and recreational values should be considered. Accessibility and the presence (or lack) of hemlock regeneration might also serve as a criteria for prioritizing hemlock stands. In the planning stage, engaging public input also is critical for educating concerned citizens about the potential negative consequences of HWA and the financial considerations of alternative methods (Ward *et al*. 2004).

Regeneration of hemlock in the damaged forest stands should be encouraged after removal of the infested hemlock trees and site preparation, despite natural regeneration of the species is generally limited in hemlock-dominated communities. While hemlock is one of the most frequent and abundant cone producers among eastern conifers, seedling regeneration may fail due to its low light requirement and intra-species competition. Silvicultural practices may be needed to promote hemlock regeneration. Hemlock generally succeeds in small openings, and in some states of eastern U.S. (e.g., Wisconsin), light selecting cutting, shelterwood methods, group selecting cutting, and cutting large canopy gaps have been recommended as reproduction methods. The chances for successfully regenerating hemlock seem best at those sites less favorable to hardwoods. To enhance the establishment of hemlock seedlings, site preparation includes scarifying the surface, mixing the humus with mineral soil, and removing competing hardwoods.

Three replanting strategies seem are most promising: growing off-site stocks of hemlock seedlings for replanting, creating hybrid hemlocks that are resistant to HWA, and replanting with the already resistant western hemlock (*Tsuga heterophylla*) or hemlock that is native to the range of HWA, Chinese hemlock (*Tsuga chinensis*). Each of these strategies has its own unique advantages as well as ecological problems. Ornamental hemlocks exhibit higher densities of HWA than do forest hemlocks (McClure and Cheah 1999). Because of their tolerance to HWA infestations, it is argued that eastern hemlocks should be replaced by Chinese hemlocks in ornamental landscapes (Del Tredici and Kitajima 2004; Hoover *et al.* 2009; Weston and Harper 2009). Chinese hemlock is tolerant to HWA infestations: although hemlocks from Asia and the western United States (i.e., *Tsuga heterophylla*) are attacked by HWA, minimal damage is induced (Bentz *et al.* 2002; Zilahi-Balogh *et al.* 2002; Del Tredici and Kitajima 2004; Hoover *et al.* 2009; Weston and Harper 2009).

The hybridization of intolerant native hemlock species with adelgid-tolerant hemlock species may be able to produce HWA tolerant trees that are ornamentally desirable (Bentz *et al.* 2002). However, the replacement tree's ability to acclimate to new environmental conditions is important (Weston and Harper 2009). Fifty-nine hybrids of *Tsuga* spp. have been identified. Crosses between *T. caroliniana* and *T. chinensis* and crosses between Asiatic species also have successfully produced hybrids (Bentz *et al.* 2002). Most recently, the hybrids *T. chinensis*×*T. caroliniana* and *T. chinensis*×*T. sieboldii* have exhibited resistance to HWA in an experimental setting (Montgomery *et al*. 2009). However, it should be noted that these hybrids are only being investigated for replacement of ornamental hemlocks.

As natural regeneration of hemlock is often limited and no native conifer species has the combination of unique attributes of the hemlock, forest managers will have to select other species that best achieve management and restoration objectives for each particular site (Mladenoff 1995). Selection criteria should consider the importance of 1) using species native to Eastern North America, 2) growth rate, 3) response to competition, 4) resistance to browse damage, 5) site limitations, and 6) availability. Prescriptions for increasing regeneration could include thinning, prescribed burning, or under-planting with seedlings from a tree nursery. Fencing may be required where seedlings may be damaged by deer browsing.

In some cases, it may be possible to begin restoration before salvage operations by encouraging regeneration of desirable species, such as eastern white pine (*Pinus strobus*), Arizona cypress (*Cupressus arizonica*), Leyland cypress (*Cupressocyparis leylandii*) and eastern red cedar (*Juniperus virginiana*), which are similar ecologically, but are not affected by HWA.

Control of alien invasive species, such as burning bush (*Euonymus alatus*) and Japanese barberry (*Berberis thunbergii*), should be considered because they may compete with native shrubs and herbaceous species. Where alien invasive species are a potential problem, monitoring and eradication will be necessary in the rehabilitation process.

Once the restoration sites that need to implement restoration measures are identified, forest management practices to promote hemlock growth and development, tree planting activities, and adelgid control strategies should be implemented. Following implementation the site should be monitored to determine the success of restoration activities. This includes determining health, growth and survival of the hemlock, conducting adelgid predator surveys, and monitoring adelgid and other invasive plants and pests.

CONCLUSIONS

Developing effective and efficient landscape-level treatments to cease the spread of HWA and to minimize HWA damage, and restoring the damaged hemlock forest areas are challenging tasks that require further effort. Without proper silvicultural treatments and restoration practices, the hemlock forest damaged by HWA could be rapidly replaced by hardwood species such as birch and maple. In addition to the natural agents (e.g., birds, deer, and wind), human plays significant roles in the spread of HWA (McClure 1990). Long distance dispersal of HWA is enabled by the human-caused connectivity (e.g., roads, logging operations) (Koch *et al.* 2006). Because HWA is spread outside its natural biogeographic barriers anthropogenically, it is important for all people to make a conscious effort to eliminate transmission of HWA. While the recovery of hemlock forests may take hundreds of years, certain restoration practices are available to forest owners and managers to assist in the recovery of declined hemlock forests.

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