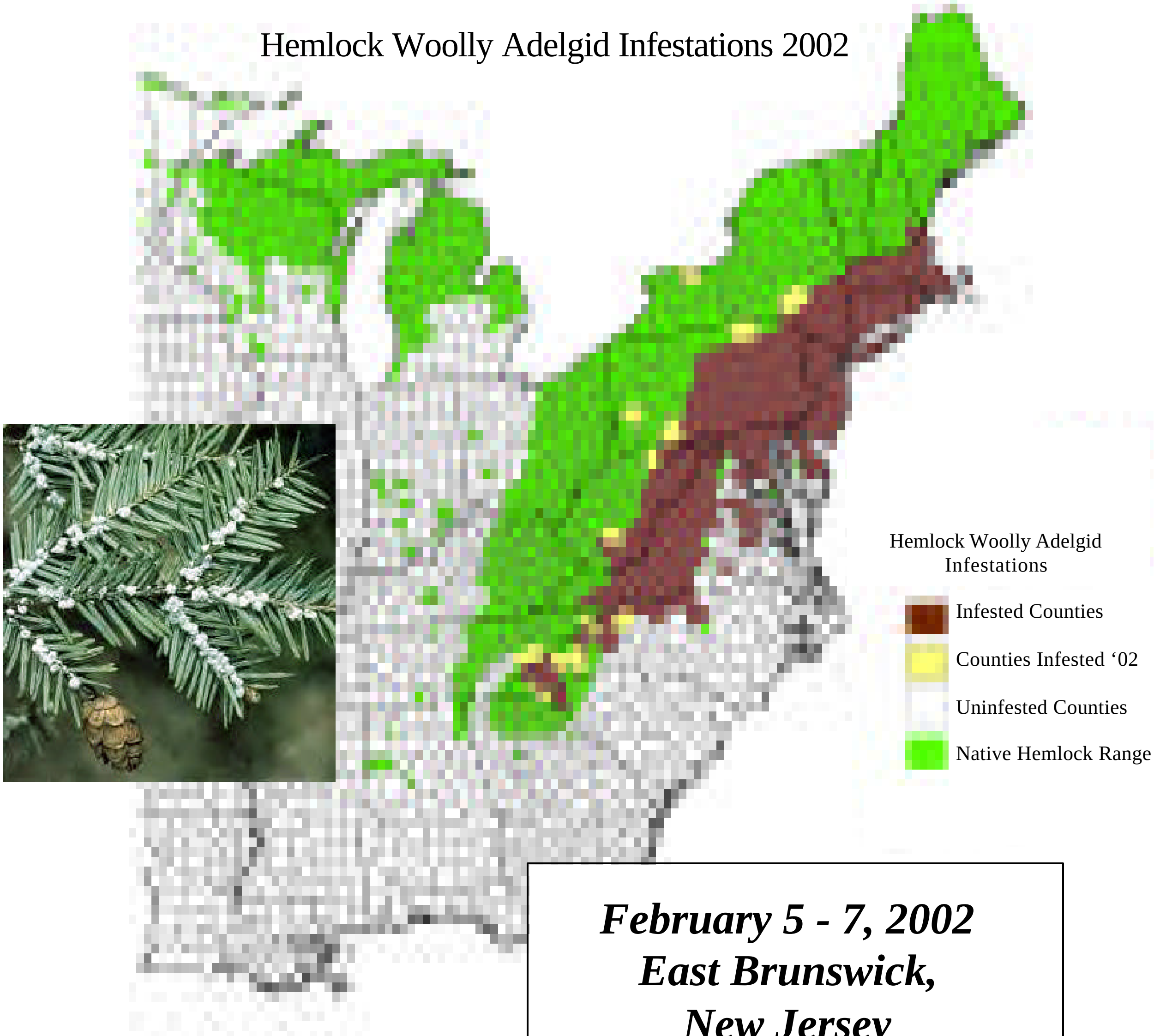
Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium



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Impacts of Hemlock Woolly Adelgid Infestation on Decomposition: An Overview

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Abstract

Hemlock woolly adelgid (HWA), *Adelges tsugae* Annand, a small aphid-like pest, is initiating rapid and widespread changes in composition and structure in southern New England hemlock forests. Rapid HWA expansion and extensive eastern hemlock (*Tsuga canadensis*) salvage logging threaten a region-wide reduction of this ecologically unique, culturally and economically important forest type. The purpose of this paper is to describe the major results from a series of ongoing decomposition studies comparing the direct impacts of HWA feeding (damage to foliage, changes in soil microclimate) with indirect effects of forest harvest and community change. HWA canopy thinning rapidly alters soil temperature and moisture, retarding surface soil decomposition in stands suffering heavy damage and immediately following forest harvest. Fungal establishment and litter N retention at the most open sites were reduced. Regenerating stands had increased decomposition relative to noninfested hemlock forests, whether they where initiated after logging or by HWA-hemlock mortality. Initial results suggest that feeding by HWA did not alter foliar chemistry and only weakly influenced N retention in decomposing foliage. Replacement of hemlock by high foliar N black birch (*Betula lenta*) is likely to have persistent impacts on decomposition in these forests. These changes probably enhance N mobility in infested hemlock stands and potentially increase N export to forest streams.

Keywords:

Hemlock woolly adelgid, eastern hemlock, decomposition, microclimate, nitrogen, logging.

Introduction

Forests of eastern North America have a legacy of pest and pathogen outbreaks that have extensively altered forest composition (Castello et al. 1995; Liebhold et al. 1995). Forest decline resulting from the current hemlock woolly adelgid (HWA), *Adelges tsugae* Annand epidemic is one of the best modern examples of catastrophic forest change associated with an introduced pest. HWA is spreading rapidly and is likely to result in widespread decimation of the eastern hemlock vegetation type (McClure and Cheah 1999; Orwig et al. 2002). Community and structural change from forest decline (Orwig this volume) and logging (Orwig and Kizlinski this volume) are profound, creating an enormous challenge to forest managers throughout the eastern United States.

Insects alter forest nutrient cycling by multiple pathways that can differ dramatically from one insect-plant complex to another (Hunter 2001). We suggest that HWA is a novel case study of plant-insect interactions because HWA feeding causes little foliar damage and produces little frass (insect excretions) while it initiates dramatic changes in forest structure and composition (Orwig and Foster 1998). Forest structure has strong control on soil microclimate and plant community foliar chemistry (Orwig et al. unpublished data) which in turn interact strongly with decomposition (Meentemeyer 1978; Berg 2000). The purpose of this paper is to summarize results of past and current research by Harvard Forest scientists on the direct and indirect impacts of HWA infestation on decomposition. We believe this important ecosystem process will be altered by three mechanisms related to HWA forest structural change: altered soil microclimate, herbivory, and vegetation change.

Results From Field Studies

Macroclimate/Microclimate Decomposition Interactions. We studied the influence of HWA-induced microclimate change on hemlock litter decomposition in hemlock-dominated stands located throughout central Connecticut (cf. Cobb et al. 2002; Orwig et al. 2002). Stands with substantial HWA-related canopy damage were highly sensitive to inter-annual climate variability. Broadly, decomposition in heavily infested forests was retarded during dry years and enhanced during wet years. We determined the extent of decomposition changes within the soil profile using a common substrate (cellulose paper). Mass loss was greater below ground compared to the surface at all sites. Infested hemlock stands with largely intact crowns and tall, dense black birch forests in decimated stands had the greatest surface mass loss further indicating that desiccation is frequently in forests with open canopies. These desiccation events are restricted to very shallow surface soil layers (Cobb et al. 2002; R. Cobb and D. Orwig unpublished data).

Relative to other forest types, hemlock ecosystems tend to have a cool, dark understory that is buffered against seasonal microclimatological cycles (Daubenmire 1930; Hadley 2000), and N cycling in these forests generally reflects seasonal temperature patterns (Jenkins et al. 1999; D. Orwig et al. unpublished data). HWA canopy thinning increases the variability of forest floor light, temperature, and moisture (Orwig and Foster 1998). Our work suggests that decomposition is tightly linked to these factors and the process can be increased or retarded depending on seasonal extremes, particularly droughts and periods of high rainfall (Cobb et al. 2002; Orwig et al. unpublished data). Our work suggests that HWA-induced decomposition changes differ between stand types, vary within soil profiles, and are strongly influenced by climate.

HWA Herbivory. HWA attack differs from other plant-insect complexes in ways that may interact with decomposition in infested forests. HWA produces little frass except for the woolly material that covers the insect's egg sacks. Woolly material is C and N rich (65.7 % and 2.68 %, respectively) compared to hemlock and black birch foliage. Mass of this material in infested stands has not been quantified and it is unclear if it is a significant part of total forest N. The solubility of N contained in this material has not been determined, though high concentrations of soluble N would presumably increase through-fall N and influence soil N mobility (Stadler et al. 2001).

Insect infestations may increase decomposition and N cycling (Belovsky and Slade 2000; Hunter 2001), but these increases may be mediated by altered foliar chemistry in response to tissue wounding (Findlay et al. 1996). Our preliminarily work suggests that HWA has a negligible influence on foliar chemistry (Cobb et al. 2002; S. Meyer unpublished data) because feeding results in little physical needle damage (Young et al. 1995). Feeding may directly influence decomposition and N cycling by altering the quality of hemlock litter. To address this question we studied foliar chemistry and decomposition of infested and noninfested foliage. HWA feeding had little impact on foliar chemistry and did not significantly affect foliar lignin, N, and C. Foliage from infested stands lost mass, and retained N at similar rates compared to noninfested foliage. HWA is distinguished from other forest herbivores in that it does not directly alter foliar chemistry and decomposition.

Black Birch vs. Hemlock: Community and Chemistry. Forest structural and community change associated with HWA infestation are dramatic (Orwig and Foster 1998; Orwig this volume). Concomitant with vegetation change is the shift from relatively low N concentration litter (hemlock) to relatively high N litter (black birch and red maple). Hemlock and black birch foliage have substantially different morphology and chemistry, which will have a long lasting impact on N cycling. Jenkins et al. (1999) found that stands with black birch regeneration had increased N cycling rates compared to noninfested forests. Community change and its associated inputs of N rich litter may create a positive feedback for N cycling, potentially favoring different soil microbial communities and functional groups (Prescott and McDonald 1994; Othoen et al. 1992).

Logging vs. HWA: Interactions with Forest Management. Harvest is one of the primary management options for forest landowners and is occurring extensively in the range of HWA (Orwig et al. 2002). Forest harvest results in abrupt changes in forest floor light and microclimate but initiates communities that are similar to HWA-degraded stands (Orwig and Kizlinski this volume). Kizlinski (2002) quantified decomposition, N cycling, and vegetation change in a chronosequence of harvest age from one to 13 years and contrasted these stands with adjacent noninfested and infested forests. Surface soil desiccation and retarded decomposition occurred immediately following harvest but these impacts were short lived. Decomposition accelerated to levels similar to HWA-infested stands between three and seven years following logging. Post-harvest forests often show increased decomposition and N cycling associated with favorable microclimate (Trettin et al. 1996; Prescott 1997). Increased N cycling and decomposition was observed by Kizlinski (2002) in the oldest harvests (13 years) suggesting that microclimate and high N litter in regenerating hardwood stands are creating a positive feedback for both processes. Many of these dynamics are similar to HWA-declining stands.

Continuing Studies. To develop an understanding of decomposition and N cycling associated with HWA community and structural change, we are currently studying black birch, hemlock, and mixed black birch-hemlock litter decomposition at sites located throughout central Connecticut and Massachusetts. We are studying sites that range from noninfested hemlock-dominated stands to HWA-degraded forests dominated by greater than 10-year-old black birch. With this study we will be able to address important questions regarding degrading forests: Does black birch litter retain more N compared to hemlock? How do inputs of high N black birch litter influence the N cycle in these forests? Do decomposer communities exhibit substrate preference when two chemically different foliage types are incubated together?

Conclusions

HWA infestation initiates major structural and community changes, transforming mature, deeply shaded, cool forests to a high light environment dominated by young trees with nutrient-rich litter. These changes occur rapidly, and alter the dynamics of decomposition over time and spatially within the soil profile. Our studies suggest that decomposition is greater overall in infested forests with the greatest potential decomposition in regenerating stands. Structural change probably has a cascading effect, impacting plant and probably soil microbial communities. These in turn strongly influence ecosystem processes like decomposition. Although forest understory composition is similar between managed and unmanaged forests, subtle structural differences and site factors may have a persistent impact on ecosystem dynamics. Through our current and future efforts, we will determine the controls and magnitude of these changes across a spectrum of site, community, and management factors. These results can be applied to proactive management of the estimated nine billion cubic feet of hemlock in New England (Smith and Sheffield 2000).

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