Stand Dynamics Associated with Chronic Hemlock Woolly Adelgid Infestations in Southern New England

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Abstract

Vegetation dynamics were monitored for 6 years in eight hemlock (*Tsuga canadensis* (L.) Carriere) stands with varying levels of hemlock woolly adelgid (HWA) *(Adelges tsugae* Annand) damage in southcentral Connecticut to examine the patterns of overstory hemlock mortality and subsequent community reorganization associated with chronic HWA infestations. Since 1995, overstory and understory mortality has risen 5 to 15% per year to overall values of 50 to 99%. There has been no sign of tree recovery and the health and vigor of remaining trees deteriorated in all infested stands. Results suggest that trees on some sites can remain alive for more than 10 years following initial infestation and remain standing for 6 to 8 years following mortality. Rapid recolonization of black birch (*Betula lenta* L.) occurred at most sites along with low densities of red maple (*Acer rubrum* L.), and oak (*Quercus* L.) species. Seedling densities increased in moderately damaged stands and thinned but increased rapidly in height, reaching 3 to 7 m tall in heavily damaged stands. The few hemlock seedlings found contained HWA infestation. Shrub cover remained low following infestation while herbaceous cover, consisting primarily of hay-scented fern (*Dennstaedtia punctilobula* (Michx.) Moore), has gradually increased over time. Cover of the invasive Japanese stilt grass (*Microstegium vimineum* (Trin.) A. Camus.) increased in one of the stands. Tree-ring analysis of hardwood and declining hemlock trees, coupled with age-structure analysis of newly established birch saplings, was effective in determining the timing of initial HWA impact in stands of unknown infestation date. Over the last 10 years, radial growth of hemlock declined precipitously in most stands, while oak and maple growth exhibited concomitant, large annual increases. Results suggest dramatic stand structure and composition changes accompany heavy HWA infestations that continue long after hemlock mortality.

Keywords:

Stand dynamics, hemlock woolly adelgid, tree-ring analysis, hemlock.

Introduction

Introduced pests and pathogens are major agents of human-driven global change, displacing native species, altering habitat, and controlling the rate and direction of vegetation and ecosystem processes (Castello et al. 1995; Everett 2000; Mack et al. 2000). Pest invasions can substantially alter tree growth, mortality, and reproduction, leading to severe ecological and economic impacts (Liebhold et al. 1995). Exotic pests and pathogens have resulted in dramatic overstory losses and structural changes in eastern U.S. forests following the selective removal of chestnut (*Castanea dentata* (Marshall) Borkh.) (Illick 1921; Korstian and Stickel 1927), elm (*Ulmus americana* L.) (Huenneke 1983), beech (*Fagus grandifolia* L.) (Twery and Patterson 1984), and fraser fir (*Abies fraseri* (Pursh) Poiret.) (Witter and Ragenovich 1986).

Eastern U.S. forests are now under attack from the hemlock woolly adelgid (HWA) *(Adelges tsugae* Annand), an introduced aphid-like insect from Japan that attacks and kills all sizes and age classes of eastern hemlock (*Tsuga canadensis* (L.) Carr.). HWA is spreading unimpeded across the eastern United States (Souto and Shields 2000) where it is generating extensive mortality and stimulating widespread logging of hemlock (Orwig and Foster 1998; Orwig and Kizlinski this volume). HWA reached southern New England in 1985, produced widespread mortality by 1988, and is currently distributed throughout Connecticut, Rhode Island, and more than 33% of Massachusetts (McClure 1990; C. Burham personal communication). Tragically, HWA has the potential to cause a regional decline or elimination of this ecologically and aesthetically important late successional species. Due to the unique ecological characteristics of hemlock (extraordinary shade tolerance; longevity; importance in old-growth, riparian, and wetland forests), the potential exists for substantial changes to forest structure, microenvironment, ecosystem process, and habitat quality that warrants comprehensive study.

Although several studies have described overstory mortality patterns associated with HWA infestation (Mayer et al. 1996; Royle and Lathrop 1997; Bonneau et al. 1999; Young et al. 2000; Orwig et al. 2002), few have examined detailed vegetation dynamics following HWA-induced decline and mortality of hemlock (Orwig and Foster 1998; Orwig and Kizlinski, this volume). In this paper, vegetation and tree-ring data from permanent plots established in Connecticut (Orwig and Foster 1998) is presented to examine the timing and magnitude of changes in vegetation structure and composition associated with chronic HWA infestations.

Methods

Study Site. The study area in southcentral Connecticut encompasses the lower Connecticut River Valley and portions of the eastern uplands and coastal slopes, and is characterized by a humid, continental climate with long, cool winters and short, mild summers (Hill et al. 1980). Elevations range from 0 to 180 meters above sea level and soils are predominantly sandy loams formed from weathered gneiss, schist, and granite (Reynolds 1979). Prior to HWA infestations, the importance of overstory hemlock in the forests investigated ranged from 49 to 88% and stands were classified as being nearly pure hemlock or hemlock-hardwood mixtures with trees such as black birch (*Betula lenta*) and oak (*Quercus*) species sharing overstory importance. A total of eight study sites were used in the evaluation and identifed as BB, CHAP, G, SC, RH, FP, TM, and SR. More detailed site descriptions can be found in Orwig and Foster (1998).

Vegetation and Tree-ring Sampling. Vegetation was measured in 46 (0.04 ha) plots established in eight stands varying in size from 8 to 175 ha. All trees (≥ 8 cm diameter breast height (dbh)) were tallied by species and dbh, and assigned a canopy position based on the amount of intercepted light received by the tree crown (Smith 1986). Crown vigor was estimated for each hemlock tree based on the amount of retained foliage. Saplings (< 8 cm dbh and > 1.4 m tall) were also tallied by species within the 0.04 ha plots. Ten (1 m^2) subplots were randomly established in each overstory plot to assess cover of seedling, herb, and shrub species using a modified Braun-Blanquet scale. Seedling heights were determined for a subsample of the tallest stems in each subplot. Plots and subplots were resurveyed every other year from 1995 to 2001 for analysis of temporal stand dynamics.

During the initial sampling, eight randomly selected live trees were cored at 1.37 m in each plot for age determinations. Cores were air dried, mounted, sanded, and aged with a dissecting microscope. Ring widths were measured to the nearest 0.01 mm with a Velmex (East Bloomfield, New York) measuring system. Overstory tree-ring patterns were combined with data on black birch sapling age-structure to estimate the timing of HWA impact in two heavily damaged stands with unknown infestation dates (cf. Veblen et al. 1991). Several hardwood trees were cored in 2001 to examine growth following hemlock mortality at the BB site. Sapling ages were determined from ring counts of stems cut at ground level in the same plots used for overstory age determinations.

Results

Hemlock Damage. Hemlock damage varied widely among stands at the beginning of the study, ranging from near zero to greater than 95% mortality (Figure 1). Over time, moderately damaged stands experienced 5 to 15% additional mortality per year, reaching more than 50% in most stands by 2001. Stands deteriorated at different rates, as some stands experienced steadily increasing mortality (e.g., SC and FP), and others exhibited large pulses of mortality in certain years (e.g., G and TM). All surviving hemlock trees sampled at seven of the sites continued to be infested with HWA, contained varying amounts of gray foliage, and suffered 25 to 95% foliage loss. The one stand that initially served as a control stand (SR) was recently infested and contains low densities of HWA. Although not quantified in this study, coarse woody material continued to accumulate as stands deteriorated. In addition, many trees are still standing in heavily damaged stands, even 6 to 8 years after they died. Hemlock saplings experienced similarly high mortality rates over time, and by 2001, only 20 to 30% were alive at any of the sites (data not shown).

Seedling Dynamics. Sites exhibited different patterns in seedling densities over time. Black birch was the dominant seedling encountered throughout this study, representing over 75% of all tallied seedlings. Therefore, birch trends presented here broadly represent overall seedling dynamics (Figure 2). Some stands (e.g., BB, FP) experienced high initial seedling densities (11 to 13 m^{-2}) and then continuous declines over time to 2 m^{-2}, while others (e.g., CHAP, SC) contained low initial densities and then more recent increases to 5 to 12 m^{-2}. The two stands with the lowest initial overstory crown damage (TM and SR) exhibited very low seedling densities throughout the study. Average maximum

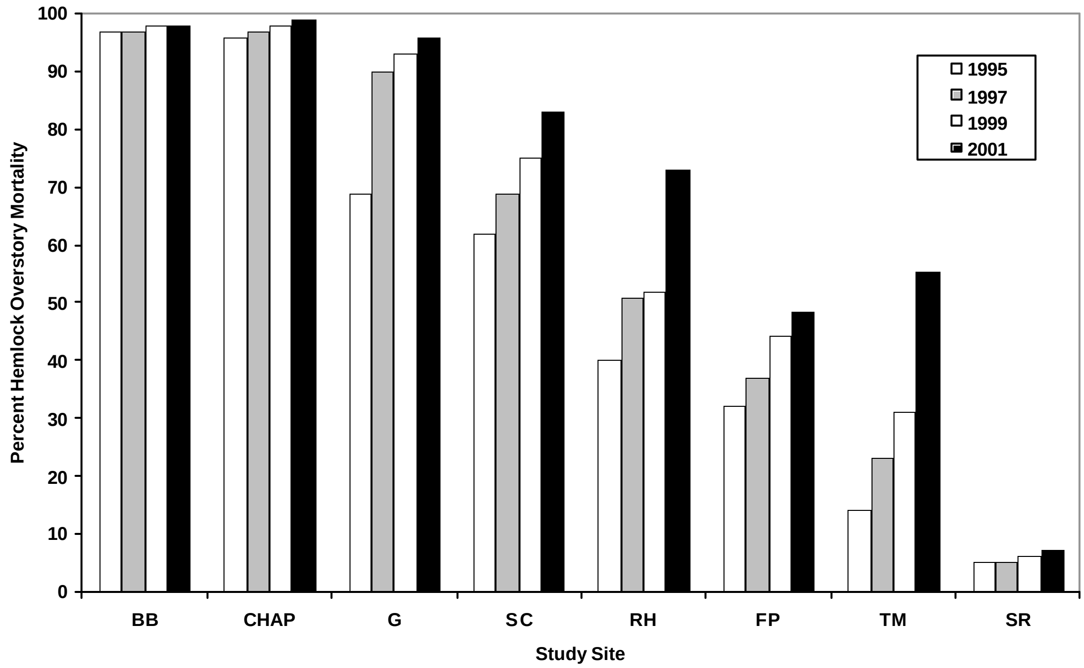

Figure 1. Overstory hemlock mortality patterns at eight sites in southern Connecticut resulting from chronic hemlock woolly adelgid infestation.

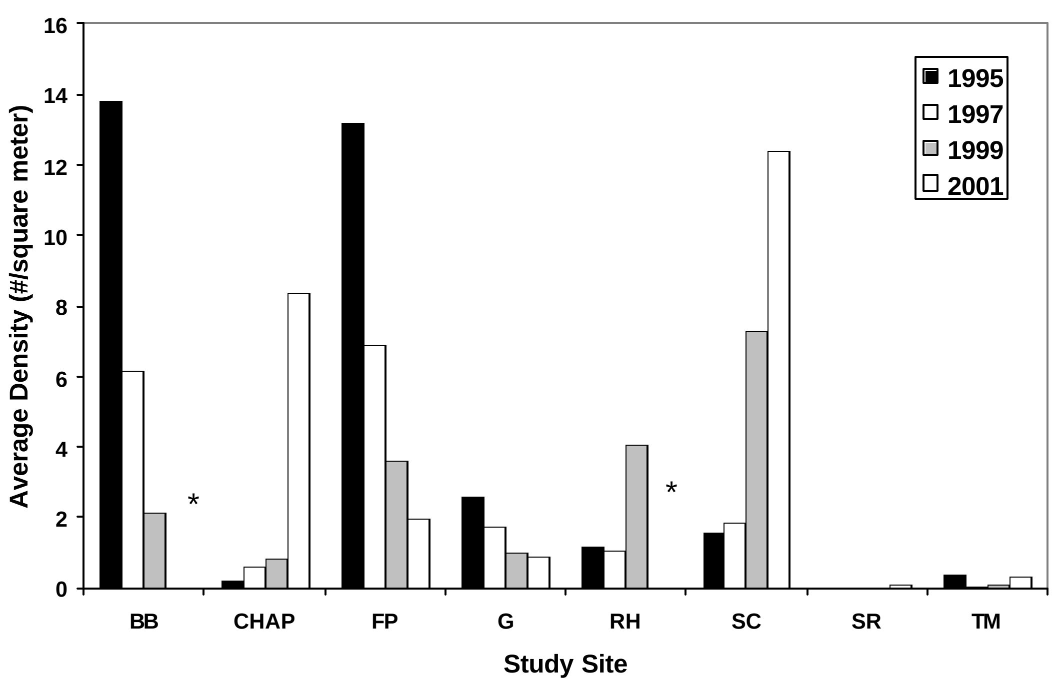

Figure 2. Black birch seedling density trends at eight sites in southern Connecticut during chronic hemlock woolly adelgid infestations. Sites with asterisks were not resurveyed in 2001.

birch height was less than 20 cm in five of the stands over time (data not shown). In contrast, three stands had initial birch heights greater than 50 cm, and two of the stands that have been measured through 2001 have average heights approaching 4 m, with several individuals greater than 7 m (data not shown). Red maple was the second most abundant seedling, averaged ~ 1 m^{-2} initially in damaged forests, and only increased to 3 m^{-2} by 2001. Compared to birch, height gain in red maple was modest, still more than 0.5 m in all stands (data not shown). Oak species were present in low densities (< 0.3 m^{-2}) during each sampling period. Hemlock seedlings were virtually absent from the seedling layer at seven of the sites, and the few that were tallied contained HWA.

Shrub and Herb Levels. Shrub cover was low (< 5%) and consistent as stands deteriorated, exhibiting only minor annual variations (Figure 3a). Species composition included mountain laurel (*Kalmia latifolia* L.), partridgeberry (*Mitchella repens* L.), and blackberry and raspberry (*Rubus* L.) species. In contrast, herbaceous cover increased gradually over time at most sites, comprising 5 to 20% average cover (Figure 3b). Hay-scented fern (*Dennstaedtia punctilobula* (Michx.) Moore) exhibited the largest increases, followed by sedge (*Carex* L. spp.) and Canada mayflower (*Maianthemum canadense* Desf.). An invasive species, Japanese stilt grass (*Microstegium vimineum* ((Trin.) A. Camus.) continued to spread and increase in cover at the Chapman's Pond (CHAP) site.

Tree-Ring Patterns. Hemlock radial growth exhibited large reductions beginning in the early 1990s at sites that experienced heavy infestation (Figure 4). Large radial growth increases in associated oak and maple species (data not shown) were synchronous with hemlock growth reductions (Figure 4). Hardwood trees commonly exhibited annual growth three to five times greater by the mid-1990s, and oak growth rates six years after substantial hemlock mortality at the BB site increased to almost 5 mm $yr.^{-1}$. Birch seedling establishment, determined from cut ages, occurred during the beginning of the hardwood growth increases and lasted for 4 years.

Discussion

Hemlock woolly adelgid continues to spread through forests and infest trees in southern Connecticut 10 to 15 years after it initially dispersed into these stands. Based on initial measurements of HWA infestation, mortality levels, and overall crown condition in 1995, longer-term results presented here suggest that trees can remain alive for extended periods of up to 12 years following initial infestation, albeit in a greatly deteriorated state. Tree health declined in all infested stands, leading to more open canopies and increased understory light levels (cf. Orwig and Foster 1998). Accumulation of treetops, branches, and in some cases tree boles has occurred in stands with heavy crown damage resulting from chronic infestation. Coarse woody debris will continue to accumulate over the next several years as trees continue to succumb to this pest.

Studies examining vegetation patterns following the selective removal of overstory trees by pests and pathogens often document subtle composition changes. For example, dynamics following overstory removal by beech bark disease, chestnut blight, Dutch elm disease, and balsam woolly adelgid largely reflected replacement by pre-existing species rather than dramatic establishment of new species (Illick 1921; Korstian and Stickel 1927; Barnes 1976; Huenneke 1983; Twery and Patterson 1984; Witter and Ragenovich 1986). In contrast, the microenvironmental conditions associated with the dramatic structural changes occurring in declining hemlock stands has lead to striking vegetation changes. In stands that initially contained depauperate understories, black birch seedlings established rapidly following moderate levels of hemlock crown damage and overstory mortality. In heavily damaged stands, dense carpets of black birch seedlings that were present in

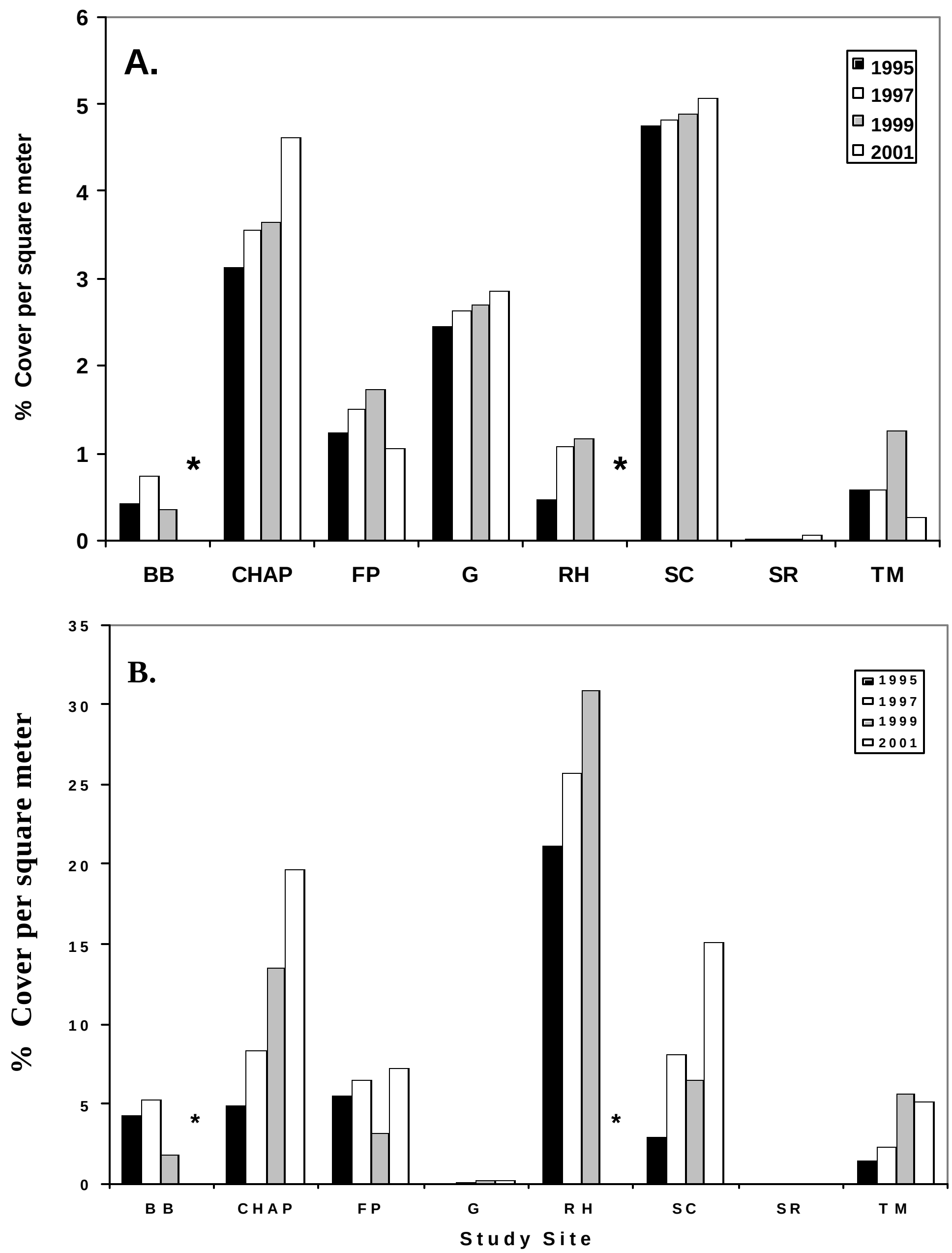

Figure 3. Average shrub (a) and herbaceous (a) cover at eight sites in southern Connecticut during chronic hemlock woolly adelgid infestations. Sites with asterisks were not resurveyed in 2001.

1995 developed into sapling thickets 3 to 5 m tall in only 6 years. The scarcity of hardwood saplings that existed prior to HWA and the continuous removal of hemlock saplings on these sites by HWA damage has made birch the dominant vegetation component in these forests. Based on these findings, similar understory observations elsewhere (Orwig et al. 2002), and the abundance and survival of overstory black birch in many CT forests (Kittredge and Ashton 1990; Smith and Ashton 1993; Ward and Stephens 1996), black birch should continue to be the dominant forest type replacing hemlock across the southern New England landscape for decades to come.

Hardwood species like maple and oak also are becoming established in many declining hemlock stands, although at much lower densities. Maple dynamics over time suggest that seedling germination occurred in most sampling periods, but survival was low. In addition, the seedlings that have survived for 6 years have experienced slow height growth, with no individuals exceeding 0.5 m in height. Oak seedlings experienced similar low survival, as few have survived for 6 years. The presence of oak and maple in the overstory of these stands certainly suggests that these species may slowly increase in importance over time (Oliver 1978).

Herb and shrub dynamics resulted from a combination of pre-existing and newly established species. For example, shrub composition was stable and largely reflected the few pre-existing laurel that were present. In contrast, several opportunistic herbaceous species, particularly, hay-scented fern, became established and/or increased tremendously in cover in declining stands. Post-disturbance fern increases have been reported (Peterson and Pickett 1995; Cooper-Ellis et al. 1999) or predicted (Yorks et al. 2000) elsewhere and may play an important role in revegetation dynamics of hemlock stands by precluding additional seedling establishment (Horsley and Marquis 1983).

In addition to rapid understory composition changes, overstory hemlock decline and mortality led to substantial changes in growth patterns of remaining trees. Hemlock radial growth declined for 4 to 6 years in sites with heavy infestations while hardwoods, mainly oak and maple species, exhibited dramatic growth increases. Several hardwoods that shared the overstory with hemlock for decades and previously grew at very low annual rates are continuing to experience growth increases 6 years after hemlock mortality. Similar patterns have been observed in non-host trees in many forests impacted by tree pests and pathogens (Veblen et al. 1991; Swetnam and Lynch 1993; Fajvan and Wood 1996). Additional work examining long-term patterns in radial growth of non-host species would be useful in estimating stand productivity changes following the loss of hemlock (cf. Sprugel 1984).

Conclusions

The outlook for hemlock survival in southern New England remains grim. Chronic HWA infestations in southern Connecticut will likely lead to complete hemlock mortality on many sites. Falling tree boles and accumulations of coarse woody material are important management problems that should be considered well in advance of heavy infestations in parks and public access areas. The loss of hemlock is resulting in rapid and dramatic changes in forest structure and composition, transforming stands into distinct, new assemblages of hardwood species.

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