IMPACT OF HEMLOCK WOOLLY ADELGID ON EASTERN HEMLOCK STANDS IN THE BLACK ROCK FOREST, CORNWALL, NEW YORK

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PREAMBLE

This thesis, presented to fulfill the requirements for a Master of Science degree from the Graduate School of Environmental Studies at Bard College, is written in an alternative format approved by the thesis committee. This thesis includes an introductory chapter, two chapters written as individual papers prepared for submission to scholarly journals for publication, and a chapter that discusses the utility of the findings from a managerial perspective. Research presented in the papers is new and all data were gathered by the author. Some of the results of the research conducted for this thesis have already been published (Kimple and Schuster 2002).

CHAPTER I: Introduction and Literature Review

Abstract:

An aphid-like insect from Japan, the hemlock woolly adelgid (HWA) was accidentally introduced into the eastern United States in the 1950's. HWA has been found to cause mortality in eastern hemlock and threatens its continued existence in northeastern forests. Research to date on this invasive insect has focused largely on methods of population control. However, we do not know whether spatial patterns of progressing infestations can yield information useful for impact predictions and control strategies. We also lack basic information about HWA's physiological impact on trees and, by extension, stand level gas exchange and water use. This study was designed to determine 1) if there are spatial patterns associated with damage induced by HWA infestations, and 2) how HWA activity affects physiology and water use by individual trees with implications for forest hydrology. This study was conducted in three stands of eastern hemlock located at the Black Rock Forest, a 1530 ha private forest preserve located 81 km north of New York City in Cornwall, New York. The results of this study will allow forest managers to better evaluate options for management and possible control of HWA, and understand the consequences of the loss of eastern hemlock on whole-stand water use and productivity.

Introduction:

Pests and pathogens are natural forest managers that regulate, and in turn are regulated by, the patterns and processes in forest ecosystems, although the effects may not be compatible with human management objectives (Castello et al. 1995). The

periodic introduction of new elements into forest ecosystems has shaped species composition throughout ecological history. Recently however, the rate at which exotic pests and pathogens are being introduced into forest ecosystems has increased. Modern technology has allowed rapid exchange of goods between countries, establishing global markets and economies, which in turn have helped shape a global ecology. Exotic pests and pathogens are being distributed across boundaries once maintained by distance and natural barriers. Forest ecosystems are being inundated with non-native species to which the native species have not adapted.

The introduction of non-native pathogens and pests has caused dramatic changes in many forests, including those of the eastern United States, over the past century (Orwig 2002a). These imported species have selectively eliminated several dominant tree species from their natural ranges and greatly limited others (Orwig and Foster 1998a). Chestnut blight (*Cryphonectria parasitica*) removed overstory American chestnut (*Castanea dentata* [Marsh.] Borkh.) from the ecosystem; the American elm (*Ulmus americana* L.) has succumbed to "Dutch" elm disease (*Ophiostoma* [*Ceratocystis*] *ulmi)*; gypsy moth (*Lymantria dispar* L.) defoliated hundreds of thousands of acres of oak forests over the last several decades; and now the eastern hemlock (*Tsuga canadensis* [L.] Carr.) is threatened by an aphid-like insect (*Adelges tsugae* Annand.) inadvertently imported from Japan (McClure 1991b). Dominant tree species are being affected by foreign pest species to which they have no evolved defenses. In many cases these imported pests and pathogens do not have any effective natural enemies that can help keep their populations under control. In such cases only the elimination of the food source or environmental barriers (i.e. extreme temperatures) limits the ability of the

population to survive. As a result, the movement of exotic organisms is rapidly changing native landscapes (Foster 2000).

Eastern hemlock is a dominant component of the forests of the eastern United States. It is a late successional species that provides unique habitat for forest biota and tends to create microclimatic and edaphic conditions that are more stable than surrounding forest areas (Benzinger 1994, Finzi et al. 1998). The range of eastern hemlock extends from Nova Scotia west to Lake Superior, and south to Georgia (Kessel 1979). Eastern hemlock has been a component of these forests since the early Holocene (Fuller 1998). The dense evergreen canopy of eastern hemlock creates a unique habitat within otherwise deciduous-hardwood forests that is critical for many species (Ward and Smith 1999). Little sunlight penetrates the canopy of a hemlock grove (Rogers 1978, 1980, Orwig and Foster 1998a), little understory is found in hemlock stands, and summer air temperatures can be as much as 5 ° C cooler in hemlock groves than in the surrounding forest (Mitchell 1999). Streams that run through hemlock stands are generally cooler and, as a result, may maintain higher dissolved oxygen content compared to streams in hardwood forests. Brook trout (*Salvelinus fontinalis*), whose optimal temperature range is between 2 and 20 ° C, are more commonly found in streams bordered by eastern hemlock. Water temperature is the most important factor determining the distribution of brook trout (McClure et al. 1996, Karas 1997) and the loss of eastern hemlock from riparian areas could negatively affect this important species (Snyder et al. 2002). It has been estimated that at least 96 avian and 47 mammalian species utilize hemlock habitat (DeGraaf and Rudis 1986, DeGraaf et al. 1992). Mitchell (1999) noted that eastern hemlock stands are the preferred habitat of five species of birds: the black-

throated green warbler (*Dendroica virens*), the Canada warbler (*Wilsonia canadensis*), the hermit thrush (*Catharus guttatus*), the magnolia warbler (*Dendroica magnolia*), and the solitary vireo (*Vireo solitarius*). Hemlock stands also provide critical winter habitat for white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), ruffed grouse (*Bonasa umbellus*), and wild turkey (*Meleagris gallopavo*; McWilliams and Schmidt 1999). Clearly a disruption of the patterns of hemlock cover could have significant impacts on future species occurrence and distribution, as well as ecosystem function (Yamasaki et al. 1999, Tingley et al. 2002).

Eastern hemlock has been shown to alter the nature of the soil underneath its canopy (Finzi et al. 1998). The high tannin levels and low pH of hemlock needles result in a slow rate of organic decomposition. The result is the formation of a thick, highly acidic litter layer underneath hemlock stands. The nature of the soil affects other aspects of stand chemistry, including the availability of cations such as calcium and magnesium. Metals such as aluminum and iron become increasingly soluble as pH decreases, out-competing other exchangeable cations for binding sites. Calcium and magnesium can be bound by organic or mineral acids and transported to lower soil horizons or lost from the ecosystem (Finzi et al. 1998). These chemical changes may widely affect stream chemistry and biotic communities.

R.T. Paine defined a keystone species as one that controls both the species composition and the physical appearance of entire communities (Paine 1966). Paine was referring to predatory species, but eastern hemlock meets most points of the definition. Power et al. (1996) expanded Paine's definition because they believed that a keystone species is better defined as one whose effect on the community or ecosystem is

disproportionately large relative to its abundance. Eastern hemlock arguably meets these criteria as well, because it can influence the biotic and abiotic aspects of entire watersheds and forests in which it occurs.

The continued presence of eastern hemlock in northeastern forests is threatened by hemlock woolly adelgid (HWA). The first documented report of HWA in the United States was in the Pacific Northwest in 1924. HWA was found in Virginia in 1951, began to migrate northward, and has continued to spread at an estimated rate of 30 km a year (Gouger 1971, Souto et al. 1996). It was reported in southeast Pennsylvania in the 1960s, and was first found on hemlocks in Connecticut in 1985 (McClure 1987). HWA was first recorded in New York State in the 1990's (Onken et al. 1995, Souto et al. 1996). Since its introduction HWA has spread to 15 states and currently covers approximately one third of the range of eastern hemlock (Orwig and Foster 1998b, Parker et al. 1998). Unlike some pests and pathogens that have attacked dominant tree species in the past, inducing a gradual shift from one hardwood species to another, HWA is initiating a rapid transition from conifer-dominated to hardwood-dominated ecosystems (Orwig et al. 2002).

In its native country of Japan, HWA has a life cycle that lasts two years and includes five developmental stages that alternate between two species of tree, a primary host (a Japanese species of *Tsuga*) and an alternate host (generally a species of *Picea*). There are no known species of spruce suitable for HWA in North America, and, as a result, in the northeastern United States HWA feeds exclusively on eastern hemlock. In the southeastern U.S., HWA feeds on Carolina hemlock (*Tsuga caroliniana* Engelm). The lack of an obligatory migratory morphology has fostered the build-up of exceptionally large colonies (Montgomery 1996). In the U.S., HWA populations consist

entirely of parthenogenetic females that reproduce twice per year, with up to three hundred eggs per generation (McClure 1996). These factors allow HWA populations to expand rapidly.

Both abiotic and biotic factors aid the spread of HWA. McClure (1990) determined that biotic vectors of HWA dispersion include deer, birds, mammals, and humans. The tendency of eastern hemlock to occur in large homogeneous stands may accentuate the impact of HWA. In Asia, hemlocks are restricted to narrow bioclimatic zones on steep slopes in mountainous terrain where other species are dominant (Montgomery 1996). Larger stands more easily intercept wind-borne HWA and, once established, HWA has an ample food source that allows for a population explosion. As with many imported pests and pathogens, the spread of HWA may be assisted by human disturbances within natural areas. Forest fragmentation and corridors resulting from human development may increase the rate at which HWA is able to spread.

The HWA feeding strategy makes it severely damaging to eastern hemlock. HWA has several life stages. The first instar is termed the crawler stage, which is confined primarily to the tree upon which it hatched unless it is borne by wind or animal to another tree. The crawler then develops through four more instars and becomes an adult. HWA has two adult forms, the wingless progrediens and the winged sexuparae. In its native Japan, the winged adult flies to spruce trees, which serve as a temporary platform for further development. This stage is ineffective in the eastern United States because the spruce trees in this region cannot support HWA.

The HWA has piercing and sucking mouthparts that penetrate hemlock twigs at the base of the needles (Young et al. 1995, McClure et al. 1996). The stylet of HWA

penetrates deep into the vascular tissue, to the parenchyma cells of the xylem rays, and takes up the nutrients that are stored there. Xylem rays function to connect the phloem and the xylem, but this function is interrupted by HWA feeding. This method of feeding results in needle desiccation, and eventually twig and branch mortality. As the crawler feeds it may also inject a toxic substance into the tree via its saliva (McClure 1991a). The saliva may restrict water uptake, cause rapid desiccation, and prevent new growth by killing buds (McClure et al. 1996).

The HWA feeding pattern is not limited to mature hemlocks. It feeds on hemlocks at all canopy levels, including saplings and seedlings, and eastern hemlock has no known resistance to HWA (Orwig and Foster 1998a). Hemlock seedlings may suffer higher mortality and adult trees produce less new foliage in areas with a large HWA population. Parker et al. (1998) presented evidence that cold winter temperatures may limit the extent of damage that HWA will cause to a hemlock stand. However, mortality within HWA populations occurs only during extended periods of sub-freezing temperatures, and even extreme cold spells (e.g. –30° C) may not cause complete mortality of populations (Parker et al. 1998). Even in regions typically subject to harsh winter conditions, a mild winter can release populations of HWA previously constrained by cold temperatures (Parker et al. 1998, 1999).

Currently, thorough dousing of trees with pesticide sprays is one of the most effective methods of controlling HWA. Horticultural oil and insecticidal soap, which are relatively safe for the environment, are effective at controlling HWA but need to be applied annually (McClure 1991b). Their use is restricted to individual ornamental trees, however, because the application methods required are not practical in forest

environments (McClure 1991b). Microinjection and implantation of concentrated chemical pesticides into the stem or roots of individual trees have also been shown to control HWA infestations, but these methods suffer several of the same limitations as spraying (McClure 1991b). Much of the recent research pertaining to HWA has focused on possible biological methods for controlling the species. Native North American insect species, such as midges (Cecidomyiidae), flower flies (Syrphidae), and lacewings (Chrysopidae) have been shown to attack HWA, but the frequency of these attacks is insufficient to reduce HWA densities (McClure 1987). A ladybird beetle (*Pseudoscymnus tsugae* [Coccinellidae]) and an oribatid mite (*Diapterobates humeralis*), two species found in association with HWA in its native Japan, show the most promise for controlling the insect (McClure 1995a, 1995b). The ladybird beetle eats the eggs and nymphs of HWA. The mite eats the woolly secretion that covers the egg masses, releasing them from the tree and thus killing them (McClure 1991a). In laboratory and field studies *P. tsugae* demonstrated potential for suppressing HWA populations (McClure et al. 1999). The beetles reproduced, dispersed, overwintered, and showed significant short-term predation on HWA populations. Importing the native predators of HWA from Asia may not, however, control populations established in the United States. In Asia, HWA is associated with a complex of predators with different feeding strategies, and together they control the adelgid population. Montgomery (1996) found nine species of ladybird beetle that feed on HWA in China. The extent to which any single imported predator will help control U.S. populations of HWA has not been ascertained.

Orwig and Foster (1998b) suggested that understanding the spatial and temporal patterns of infestations at stand and landscape levels, and the factors that control them, is

fundamental to understanding the history, dynamics and function of forests. A central purpose of my study was to explore these spatial and temporal patterns. The ecological and environmental response of forest ecosystems to the loss of hemlocks has not been fully analyzed. There has been little study of patterns of HWA infestations within hemlock stands, although understanding these patterns may provide insights for more efficient management strategies. Moreover, while studies have documented how HWA leads to hemlock mortality, the ecological implications of the loss of whole stands of hemlocks are not well understood (Orwig et al. 2000, Yorks et al. 2000, Orwig 2002, Yorks 2002). The loss of these stands may profoundly affect biogeochemical cycles, watershed hydrology, and the carbon balance of ecosystems. In this study I examine the impacts of HWA on eastern hemlock in the Black Rock Forest, southeastern New York State, to address two fundamental questions: 1) What are the current patterns of HWA infestation, impact, and stand decline with respect to topography, stand composition and tree size? 2) How is HWA affecting tree physiology, as indicated by tree sap flow, and thus whole tree and stand-level carbon balance and water use?

The study area, the Black Rock Forest, is a 1530 ha forest preserve located in Cornwall, New York, approximately 80 km north of New York City. The forest typifies the mixed hardwood forests of the Highlands Physiographic Province, which ranges from eastern Pennsylvania to western Connecticut (Raup 1938). Currently the dominant canopy species is northern red oak (*Quercus rubra* L.). Chestnut oak (*Quercus prinus* L.) and white oak (*Quercus alba* L.) are also prominent throughout the forest and red maple (*Acer rubrum* L.) is the most common understory tree. Other common species found in the forest include yellow, gray and black birches (*Betula alleghaniensis* Britton, *B.*

populifolia Marsh., and *B. lenta* L.), sugar maple (*Acer saccharum* Marsh.), pignut hickory (*Carya glabra* [Mill.] Sweet), and black and scarlet oaks (*Quercus velutina* Lam. and *Q. coccinea* Muenchh.).

Eastern hemlock has been a component of the Black Rock Forest flora for the last 10,000 years (Maenza-Gmelch 1997), typically growing in nearly monospecific stands in steep ravines with good drainage, a typical growth pattern for eastern hemlock in the northeastern U.S. (Godman and Lancaster 1990, D'Arrigo et al. 2001). Three large stands of hemlock currently exist within the forest: the Black Rock Brook stand (38 ha), the Canterbury Brook stand (16 ha), and the Mineral Springs stand (12 ha). HWA was first documented in the Black Rock Brook stand in 1992 and in the Canterbury Brook stand in 1994 (W. Schuster, pers. comm.). It is believed that the Mineral Springs Stand became infested more recently. In this study I document the spatial pattern of hemlock infestation and stand damage to ascertain whether the impact follows a predictable course with respect to time, topography, environmental gradients or stand composition, as well as whether parts of the stand are more susceptible or resistant to HWA infestations. Young et al. (1999) found that slope, elevation, light conditions, and distance from the stream exhibited relatively strong correlations with hemlock decline, and suggested that these same conditions are either controlling HWA or making hemlock more susceptible to infestation. Sap flow data gathered in my study document diurnal and seasonal patterns of tree water use. Relating these data to HWA induced damage will allow me to quantify physiological impacts of HWA on the hemlocks of the Black Rock Forest. These findings may assist ecosystem impact assessments and facilitate management recommendations.

There are other factors that may affect eastern hemlock health. In the Black Rock Forest the presence of another imported pest may be compounding the impact of HWA. A scale insect (*Fiorinia externa* Ferris) native to Asia that was also inadvertently imported to the United States may be contributing to the decline of eastern hemlock in the Black Rock Forest (Danoff-Burg and Bird 2002). This species of scale feeds on the mesophyll of young needles causing discoloration and premature drop of the needles. Unlike HWA, the scale feeds on numerous species of conifer, not exclusively on eastern hemlock (McClure 1986). The two insect pest species may compete for fresh needles on eastern hemlock. McClure (1977, 1985a, b) found that the fitness of scale in Japan is enhanced on hosts that occur in cultivation or on the edge of their natural range. He surmised that this was due to stress on the host from unfavorable growing conditions. It may be that this pattern is repeated on eastern hemlock here in the United States when the trees become stressed by the presence of HWA. HWA may enable scale populations to rapidly expand. Danoff-Burg and Bird (2002) suggested that HWA and scale in combination may cause mortality in eastern hemlock in the Black Rock Forest, although the interaction of these two species needs to be explored further (Evans et al. 1996, McClure et al. 2000).

CHAPTER II: Spatial Analysis of Hemlock Woolly Adelgid Induced Damage Within Stands of Eastern Hemlock in the Black Rock Forest

Abstract:

This study was designed to determine whether consistent patterns of HWA impact could be detected in infested stands of eastern hemlock. Determination of patterns of population damage expansion could potentially allow land managers to develop strategies for protecting eastern hemlock within forests and/or mitigate the impacts of hemlock loss. Three distinct stands were examined in the Black Rock Forest, Cornwall, New York. A modified version of the point quarter method was utilized to study stand composition, stand density, and tree damage in order to assess the spatial patterns of damage. After approximately 6 to 8 years of infestation the average level of defoliation was greater than 50% for each of the stands, and hemlock mortality was between 13 and 14%. The findings of this study suggest that HWA populations may progress from areas of initial contact into forest interiors via natural corridors. In the case of the Black Rock Forest, these corridors were streams that traverse the length of the stands. In two of the three stands surveyed the degree of HWA damage was significantly correlated with distance from the edge of the stand and distance from a natural stream corridor. HWA induced mortality ($r_s = -0.75$) and damage ($r_s = -0.15$) were significantly negatively correlated with distance from the stream corridor across all three stands ($p < 0.01$). These patterns existed despite differences in hemlock basal area and density trends between stands. There was evidence, however, that these patterns become less distinct with time.

Introduction:

Hemlock woolly adelgid (HWA; *Adelges tsugae* Annand), an introduced aphid-like insect, is having a devastating impact on eastern hemlock (*Tsuga canadensis* [L.]

Carr.) in many northeastern forests by weakening and killing trees and entire stands of hemlock. Eastern hemlock, and land managers who wish to maintain its presence, are disadvantaged by the lack of effective native predators and the lack of hemlock resistance to the detrimental impacts of HWA (McClure 1987, Orwig and Foster 1998b). HWA continues to expand through the range of eastern hemlock, carried between stands by wind and animals. Since it was first detected in Virginia in the 1950's, HWA has been advancing northward at about 30 km per year (Gouger 1971, Souto et al. 1996). Although the geographical pattern of HWA movement northward and across certain landscapes has been well documented (Orwig et al 2002), HWA migration and damage patterns within stands are not well understood. This study was designed to help determine whether or not stand characteristics and/or topography affect HWA migration and patterns of damage within stands.

I studied three distinct stands of hemlock within the Black Rock Forest, a private forest preserve in Cornwall, New York. The stands are all found along stream corridors that often have steep sided ravines. All three stands extend from upper headwater areas in the forest interior to developed areas outside of the forest (Figure 1). It has been hypothesized that roads and highways have acted as dispersal corridors into these stands for HWA, which then progressed inwards through the stand via the stream corridors. This study was designed to determine if spatial patterns exist that might suggest whether: 1) HWA infestations move sequentially from developed areas at the perimeter of stands into the interior, 2) streams act as corridors for HWA population expansion within stands, and 3) topographic position, stem density, or other tree characteristics appear to influence HWA damage patterns.

Often land managers faced with the loss of hemlock from their ecosystem are overwhelmed by infestations since HWA reproduces rapidly and affects trees of all ages. Many control methods in forest settings are expensive and/or impractical and it has not yet been determined whether biological control methods can successfully regulate HWA populations. Information about spatial patterns of infestations and damage may help focus control and mitigation efforts, potentially saving time and money.

Methods:

Three stands of eastern hemlock located in the Black Rock Forest, Cornwall, New York were surveyed in the summer of 2000 for this study. The stands ranged from 12 to 38 ha in size and encompassed three of the forest's major stream courses. In all three stands HWA was first noticed in trees found along forest boundaries exposed to human development. These areas also happened to be the point at which the streams that flow through each stand exit the forest. HWA was first noticed in the Black Rock Brook stand at the boundary exposed to Route 9W, a four lane highway, in 1992. HWA was found near the boundary exposed to a housing development immediately south of route 9W in the Canterbury Brook stand in 1994 (W. Schuster, pers. comm.). Approximately four years later HWA was noticed in the Mineral Springs Brook stand along the forest boundary exposed to a small residential area and a two lane road. Transects were established every 100 meters along each of the streams starting from where the stand contacted the forest boundary at the point where it was exposed to development, and progressing inwards towards the forest interior and stream headwaters. The main stream channels in the Black Rock Brook and Canterbury Brook stands fork into two branches

while still in the hemlock stand. Distance measures up stream were continued sequentially up each tributary from the point closest to the fork in both stands. In the Black Rock Brook stand (BRB) and Mineral Springs Brook stand (MS), the Black Rock Forest boundary represents the exposed edge of the stand. The stand at Canterbury Brook (CB) extends beyond the Black Rock Forest boundary onto private property for approximately 200 m. Each of the transects was oriented perpendicular to the steam course on each side, beginning at the stream bed and terminating at the point where hemlocks were no longer present.

The point quarter method (Cottam and Curtis 1956, Brower et al. 1990) was used to gather stand composition data at survey points every 30 linear meters along these transects. The 100 m distance between transects was enough to ensure adequate space between forks for deciduous vegetation to interrupt the hemlock grove and prevent duplication of sampling (e.g. Danoff-Burg and Bird 2002). At each point data were gathered on the closest tree to the plot center in each of four quadrants designated using cardinal compass bearings. Data collection included the tree species, tree diameter at breast height (DBH), distance of the tree from the point, and canopy class (in three categories: Dominant/Co-dominant, Intermediate, and Suppressed). Trees with a DBH less than 2.54 cm were not surveyed. Hemlocks were assigned a damage class depending on the degree of HWA induced damage by using the following scale: (0) trees with all their needles; (1) trees that had lost between 1 and 5 percent of their needles; (2) trees that had lost between 6 and 25 percent of their needles; (3) trees that had lost between 26 and 50 percent of their needles; (4) trees that had lost between 51 and 75 percent of their needles; (5) trees that had lost between 76 and 99 percent of their needles; and (6) dead

trees that had lost all of their needles. For category 6 trees, visual cues (fine twig retention, bark retention, and overall state of rot) were used to determine whether or not the trees had been killed prior to the HWA infestation. If so, they were assumed to have been killed by other causes not related to this study, and were not surveyed. All hemlocks determined to have died after the known date of infestation were included in the survey.

Total basal area, density, and frequency were calculated for each tree species surveyed. An overall estimate of the influence of a plant species, an importance value, was calculated for each species (Curtis and McIntosh 1951, Brower et al. 1990, Smith 1990) as the sum of the relative density, relative frequency, and relative basal area for that species. Relative importance values ranging from 0 to 100 percent were calculated for all species to enable inter-species comparisons. Data analyses showed that data for key variables such as damage class and density measures were not normally distributed. In response to these findings I chose to calculate non-parametric Spearman rank order correlations (r_s), which have been shown to be robust to departures of data from normality (Sokal and Rohlf 1981). Statistica, a statistical software package developed by Statsoft (www.statsoft.com), was used to conduct all statistical analyses.

Results:

The three stands of hemlock surveyed in the Black Rock Forest varied in size, species composition, and hemlock density (Table 1). At 38 hectares, the Black Rock Brook stand is the largest of the three stands. The survey of this stand encompassed a total of 156 plots and 624 trees. Stand density was a low 388 trees ha^{-1} and the basal area was also low, 16 m^2 ha^{-1}. The survey of the Canterbury Brook stand (16 ha) included 58

points and 232 trees. The stand density was 874 trees ha^{-1} and the basal area was 40 m^2 ha^{-1}. In the Mineral Springs Brook stand (12 ha) 43 points and 172 trees, were surveyed. Stand density was high at 1435 trees ha^{-1}, but basal area was low at 24 m^2 ha^{-1}.

The Black Rock Brook stand showed the greatest overstory species richness of the three stands (n = 23, Table 2), due at least in part, to higher sample size (624 trees in Black Rock Brook, 232 in Canterbury Brook, versus 172 in Mineral Springs). Fifteen tree species were found at points in the Canterbury Brook stand and thirteen species were found in the Mineral Springs Brook stand. Hemlock was the dominant species in each of the three stands. Hemlock importance was 40% in the Black Rock Brook stand, 45% in the Canterbury Brook stand, and 47% in the Mineral Springs Brook stand. Sugar maple had an importance value of 10% in the Black Rock Brook stand, and 13% in the Canterbury Brook stand, making it the second most important species for both of these stands (Table 2). In the Mineral Springs Brook stand, red maple was the second most dominant species, with an importance value of 9%.

Characteristics of each stand were compared to distance measures away from the stream and up the stream from the forest edge (Table 3). Stand density (all species) did not correlate with either distance from the stream or up the stream into the forest for any of the stands except for the Black Rock Brook stand where it was positively correlated with the distance from the stream ($p < 0.01$). Stand basal area was also significantly positively correlated with distance from the stream in the Black Rock Brook stand. Stand basal area was not correlated with either of the distance measures in the Black Rock Brook stand or Canterbury Brook stand. The density of hemlock was significantly positively correlated with distance up the stream and distance away from the stream in

the Black Rock Brook stand but not in either of the other stands. Hemlock basal area was significantly negatively correlated with distance from the stream in the Mineral Springs Brook stand.

Mean HWA induced damage was lowest in the Mineral Springs Brook stand at 4.2 (average indicates loss of over half of needles). Average amount of damage per point ranged from 1.0 to 6.0 in this stand. The average was 4.6 for both the Black Rock Brook and Canterbury Brook stands. The average damage per plot in these stands ranged from 2.0 to 6.0 and 3.0 to 6.0, respectively. Stand characteristics were compared with HWA damage class (Table 4). Stand density and stand basal area were significantly negatively correlated with damage class in the Black Rock Brook stand and significantly positively correlated with damage in the Canterbury Brook stand. No significant relationships were found between stand density and basal area in the Mineral Springs Brook stand. Significant positive correlations were found between hemlock density and damage class the Canterbury Brook stand and a significant negative relationship was found between these two factors in the Black Rock Brook stand. Hemlock basal area was significantly positively correlated with HWA damage class in the Mineral Springs Brook stand and Canterbury Brook stand.

In the Black Rock Brook and Mineral Springs Brook stands, the average damage per plot was negatively correlated with both distance from the stream and distance up the stream into the forest (Table 5). Average damage per plot showed a highly significant ($p<0.01$) negative relationship with distance from the stream when data were combined for all three streams but no significant relationship was revealed between damage per plot and distance up the stream.

HWA induced mortality estimates were 13% for Mineral Springs and 14% for both the Black Rock Brook stand and the Canterbury Brook stand. Mortality was not significantly correlated with distance up the stream from the forest edge for any of the three stands (Table 6). Hemlock mortality was significantly negatively correlated with distance away from the stream in all three stands.

Discussion:

HWA exhibits clear spatial patterns of damage and mortality in the Black Rock Forest. In all three stands average defoliation was greater than 50% after approximately six to eight years of HWA presence. Patterns related to HWA damage and distance measures were similar for the Black Rock Brook and Mineral Springs Brook stands, and all three stands exhibited strong negative correlations between mortality and distance from the stream course. The patterns of damage and mortality are consistent with a hypothesis that developed areas and stream courses represent corridors that provide access to, and pathways within, forest stands.

Tree species richness for the three stands varied, with the Black Rock Brook stand showing the greatest number of species. The lowest species richness occurred in the survey of the Mineral Springs Brook stand. Hemlock density and basal area were greatest in the Mineral Springs Brook stand. These same parameters had their lowest values in the Black Rock Brook stand. These data indicate that the hemlock community in Black Rock Brook was composed primarily of large trees, with more openings allowing for the establishment of other species. The findings in Mineral Springs indicate a dense stand of hemlock trees, smaller in size than the trees of the Black Rock Brook.

Hemlock distribution patterns within a stand may influence HWA dispersal throughout a stand over time, as a consequence of host availability. The relative density of hemlock was positively correlated with the distance up the stream into the forest in the Black Rock Brook stand. Hemlock basal area was also positively correlated with distance up the stream for the Black Rock Brook stand. In contrast hemlock basal area was significantly negatively correlated with distance up the stream in the Mineral Springs Brook stand. Because hemlock basal area and density were correlated with amount of damage in two of the three stands it might be expected that patterns of damage would mirror patterns of hemlock composition within stands.

In the Black Rock Brook stand the degree of damage decreased as distance up the stream into the forest increased, opposing the pattern of hemlock basal area and density. While the correlation between damage and distance in the Canterbury Brook stand was not significant, damage was positively correlated with hemlock density and basal area. Hemlock relative density and basal area in the Mineral Springs Brook stand, however, were the inverse of the spatial patterns in the Black Rock Brook and Canterbury Brook stands, but the patterns of damage showed the same relationship of decline as distance up the stream into the stand increases. The fact that the Black Rock Forest Stand and Mineral Spring Brook Stand revealed the same trends in HWA patterns of movement in relation to distance up the stream from the exposed forest boundary despite the opposing trends in hemlock basal area and density supports the hypothesis of HWA movement up stream corridors from exposed forest boundaries into the forest interior.

Although only one of the stands showed any significant relationship between distance away from the stream and density of hemlock, a significant negative correlation

was found between distance away from the stream and damage in the Black Rock Brook and Mineral Springs Brook stands. In all three stands, hemlock mortality was negatively correlated with distance away from the stream. These findings further suggest that patterns of damage may be more related to how and where HWA comes into contact with a stand than the nature of hemlock distribution within a stand. If hemlock damage were strictly a function of hemlock basal area or density, then stands would consistently show the highest degree of damage in the areas with the greatest amount of hemlock basal area.

Young et al. (1999) also found that HWA damage was correlated with distance to streams during a five-year survey in Virginia forests. They suggested that this correlation was the result of environmental conditions rather than streams functioning as a dispersal corridor. The fact that two of the three stands surveyed in Black Rock displayed similar patterns of HWA damage, despite differences in patterns related to hemlock density and basal area, suggests that, in this instance, the pattern may be more closely associated with the dispersal of HWA along stream corridors. Since the pattern was less pronounced in the longer-infested Black Rock Brook stand, it appears that streamside trees have the most concentrated damage at first, but that similar damage eventually occurs to trees away from streams. This pattern may be related to McClure's (1990) findings, which suggested that HWA prefers to feed on healthy trees rather than stressed trees. Trees located in close proximity to stream courses may be less prone to water stress than peripheral trees. The patterns revealed in my study may also be associated with soil conditions. Bonneau et al. (1999a) found that hemlocks growing in deep, medium textured entisols with a high infiltration rate were healthier than hemlock trees growing in

areas characterized by shallow, course-textured inceptisols with a very slow infiltration rate.

In two of the three stands the highest levels of defoliation were found closer to the forest boundary near roads and developed areas. The degree of damage decreased as the survey progressed away from the exterior of the forest towards the interior of the forest, with the healthiest trees growing in the upper reaches of the stand. The Black Rock Forest is bordered by roads and residential areas (Figure 1). Route 9W, a four-lane highway, directly contacts the forest's eastern and northern boundaries. Both the Canterbury Brook and Black Rock Brook hemlock stands extend from the northern border of the Black Rock Forest near Route 9W into the interior of the forest. Within 300 m downstream of the Mineral Springs Brook stand there is a two-lane road and a few residences. It may be, at least in this region, that an anthropogenic landscape has created corridors through which HWA is dispersed and establishes initial contact with hemlock stands.

In situations like that of the Black Rock Forest, once contact is made with a stand's edge, natural stream corridors may provide access to trees in the interior portion of the stand. In the Black Rock Forest, trees exhibited greater damage closer to stream channels, with damage decreasing as the survey progressed away from the streambed. It is not known, however, whether this signifies that adelgids spread up stream drainages before they move laterally up slopes or if damage is directly related to topoedaphic conditions. These findings differ from those presented by Bonneau et al. (1999a). Bonneau et al. used LANDSAT data to determine if HWA damage was associated with topographical features of hemlock stands in Connecticut. They found that trees in valleys were significantly healthier than trees on ridges.

Orwig and Foster (1998b) found that HWA-induced damage and mortality was patchy within stands and did not present any discernible patterns, however, their study was conducted on a larger spatial scale than this study. They suggested that initial patterns of infestations could gradually blend to a complete loss of eastern hemlock from the stand. In later publications they suggested that any patterns related to the infestation may have already been eliminated by the spread of HWA throughout the stands (Orwig 2002b, Orwig et al. 2002). Age of the infestation and the size of the stand may be partially responsible for the fact that the infestation in the Canterbury Brook stand did not reveal any significant patterns between the degree of damage and distance measures. The Black Rock Brook stand is a little over twice the size of the Canterbury Brook stand and the infestation is only approximately two years older. The large size of this stand may have resulted in a longer time period needed for HWA to spread through the stand, prolonging the existence of distinguishable patterns. The Mineral Springs Brook stand, on the other hand, is 4 hectares smaller than the Canterbury Brook stand, but the infestation is much younger and the patterns related to it are more distinct. HWA may not have had time to spread to a point where the patterns have been obliterated by the overall damage of the infestation. This suggests that stands may initially exhibit strong spatial patterns of HWA infestation and damage, but these correlations become less significant as infestation duration increases. It may be that after HWA's initial contact with the stand, it disperses throughout the stand at a rate related to stand size, eventually affecting the entire stand, and making related patterns more difficult to interpret. However, strong correlations between mortality and distance from the stream were found in Canterbury

Brook suggesting that HWA may have moved through the stand in a similar pattern in all three stands.

The data gathered in my study suggest a pattern of HWA spread through a stand. Managers may be able to use the results in attempts to prevent HWA from infesting healthy stands or to control the effects of ongoing infestations. The data from the Black Rock Forest suggest that, in forests bounded by an anthropogenic landscape, HWA may contact stands along boundaries exposed to human development. In the case of the Black Rock Forest, patterns of heavier damage are more closely associated with proximity to the forest boundary than other stand or site characteristics examined in this study. Managers responsible for small stands in developed areas that have not yet been affected can establish monitoring programs on stand exteriors exposed to human development. Monitoring regimes should involve biannual surveys, once in the spring and once in early fall, with inspection of the underside of hemlock needles in potentially sensitive areas, such as roads and residential areas. A program of this nature would involve a minimum amount of time and would allow for an early detection of HWA. Managers faced with already established infestations should try to assess the age of the infestation and the extent to which it has affected the stand. Monitoring along corridors within the stand may provide useful information for tracking the movement of HWA within a stand. If time and money allow, or if managing hemlock is determined to be a primary goal of land management, managers addressing stands already infested with HWA can focus resources on areas of the stand that are most likely to respond to their efforts. My data suggest that monitoring should focus on the edges of stands and along existing corridors within stands.

The patterns found in my study support research suggesting (Orwig and Foster 1998b, Orwig 2002b) that once HWA is present in a stand, the entire stand is threatened. Managers need to be prepared for the changes that will result from the loss of hemlock and must determine strategies for re-vegetating areas once dominated by hemlock. Managers have the choice of letting natural succession proceed or planting to direct succession. Replanting a site affected by HWA with eastern hemlock seems futile until an effective control has been found, since HWA attacks hemlock at all stages of its growth.

Allowing the forest to recover naturally is an obvious management option, but managers should be prepared for a dramatic transition. Initially, areas may be subject to increased fire danger, as well as periods of erosion and nutrient loss (Jenkins et al. 1999, Yorks 2002). Streams will receive more sunlight and water temperatures will rise. Soil chemistry will fluctuate until plant growth recovers, perhaps extending into the new plant regime. Research in Connecticut showed that succession for that region, following the loss of hemlock, involved tree species like birch (*Betula lenta* L.), red maple (*Acer rubrum* L.), and red oak (*Quercus rubra* L., Orwig and Foster 1998a, Orwig 2002b). It is unclear how these species will interact with the site characteristics, such as steep slopes, frequently associated with eastern hemlock. It may be that their roots will fail to establish in areas with shallow, steep soils. It seems unlikely that any tree species will fill the ecological niche of eastern hemlock in northeastern forests.

Managers hoping to address hemlock loss by planting tree species to replace hemlock will be faced with the question of whether or not they are going to try to replicate the environment created by eastern hemlock. Few species grow in stands as dense, with canopies that are as impenetrable to light as eastern hemlock. Species of pine,

if planted densely, will generate shade, but seldom to the degree that hemlock does. Managers will also be confronted with the question of whether or not the species they select for planting will be able to handle the steep gradients and rocky soils that are often a part of the landscape in which hemlocks grow.

The results of my study offer some indication of how HWA moves through stands and the rate at which it can spread. In less than ten years HWA damage and mortality were widespread in all three of Black Rock's hemlock stands. Each of the stands revealed strong spatial patterns related to stand characteristics. Damage was worst at the exterior edge of two of the three stands and along stream corridors in all of the three stands, and mortality was greatest along the stream corridor for all of the stands. These patterns may be related to edaphic conditions but are likely to be most strongly associated with the pattern of the spread of infestation. The hypothesis that the observed patterns are related to how HWA enters and is spread through a stand is supported by the fact that the same patterns of damage were observed in both the Black Rock Brook stand and the Mineral Springs Brook stand, despite the opposite patterns of hemlock basal area and density observed within these stands.

My study indicated that damage patterns related to HWA infestations are lost over time as the adelgid population grows and expands. While further study is needed to understand the commonness and consequences of the observed patterns, knowledge of their existence may help focus the limited resources of managers in their attempts to maintain stands of eastern hemlock. In-depth studies of uninfested stands and monitoring the establishment and progress of new infestations over time would assist in further clarifying the long-term spatial patterns of HWA in these stands. Monitoring prevailing

wind patterns in conjunction with observational data related to HWA infestation results over time would allow researchers to determine the role of wind and corridors in dispersing HWA. Traps designed to catch wind-borne insects hung in the various regions of threatened forests could be examined weekly to see if HWA is found on any of the traps in a pattern related to the prevailing winds (McClure 1990). Other factors, outside of the HWA-eastern hemlock relationship, may play a role in the rate and pattern of an infestation. Chronic HWA infestations may allow other parasites to take advantage of weakened trees (Danoff-Burg and Bird 2002). Hemlock stands in Black Rock are also heavily infested by scale, another species of insect imported from Asia that is also detrimental to hemlock health. However, Danoff-Burg and Bird (2002) did not find any significant correlations between scale density and measures of distance in the Black Rock Forest, suggesting that hemlock mortality and damage are associated primarily with HWA. The extensive presence of scale in hemlock stands in the Black Rock Forest does suggest that the relationship could involve a more complicated sequence of events that is initiated by adelgid feeding. Bonneau et al. (1999b) found that hemlock stands in Connecticut revealed the most dramatic and persistent declines in health in areas where multi-species infestations occur. The nature of these relationships is not fully understood. What is certain is that, even without the interaction of other infestations, HWA is causing dramatic changes to the hemlock-dominated portions of many northeastern forests, with associated landscape-level patterns of impact even beyond affected stands.

Table 1: Tree data for each of the three stands surveyed in the Black Rock Forest.

	Black Rock Brook	Canterbury Brook	Mineral Springs Brook
Stand Density (trees ha^{-1})	388	874	1435
Stand Basal Area (m^2 ha^{-1})	16	40	24
Hemlock Density (% of total)	47	57	60
Hemlock Basal Area (% of total)	39	38	40
Hemlock Frequency (% of plots)	84	90	95
Hemlock Relative Importance (%)	40	45	47
# Trees Surveyed	624	232	172
# Hemlocks Surveyed	232	132	102

Table 2: Relative importance values (in percent) for each of the tree species found in the three stands surveyed. NF indicates species that were not found within the stand.

Species	**Black Rock Brook**	**Canterbury Brook**	**Mineral Springs Brook**
Tsuga canadensis	40	45	47
Acer saccharum	10	13	5
Quercus rubra	9	11	7
Acer rubrum	9	5	12
Quercus prinus	9	4	11
Betula lenta	7	5	5
Quercus alba	4	NF	NF
Fagus grandifolia	2	3	NF
Quercus velutina	2	NF	NF
Juglans nigra	2	NF	NF
Nyssa sylvatica	1	2	NF
Fraxinus americana	1	3	5
Betula alleghaniensis	1	NF	NF
Liriodendron tulipifera	NF	4	NF
Miscellaneous	2	6	9
Total Number of Tree Species	**23**	**15**	**13**

Table 3: Spearman rank order correlations between stand characteristics and distance.

		Stand Density	Stand Basal Area	Hemlock Density	Hemlock Basal Area
Black Rock Brook	Away From Stream	0.53***	0.57***	0.51***	0.003
	Up Stream	0.13	0.12	0.21**	0.16*
Canterbury Brook	Away From Stream	-0.02	0.02	-0.08	0.03
	Up Stream	0.09	0.18	0.20	0.20
Mineral Springs Brook	Away From Stream	-0.05	-0.15	-0.08	-0.22
	Up Stream	0.18	0.08	-0.08	-0.30*

* $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$

Table 4: Spearman rank order correlations between hemlock woolly adelgid damage and stand characteristics.

	Black Rock Brook	**Canterbury Brook**	**Mineral Springs Brook**
Stand Density	-0.23***	0.25*	0.06
Stand Basal Area	-0.17**	0.35**	0.12
Hemlock Density	-0.16*	0.26*	0.23
Hemlock Basal Area	0.14	0.34**	0.31**

* $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$

Table 5: Spearman rank order correlations between hemlock woolly adelgid damage class and spatial distance measures.

	Black Rock Brook	**Canterbury Brook**	**Mineral Springs Brook**	**All Stands**
Distance Away From Stream Corridor	-0.20***	+0.01	-0.53***	-0.15***
Distance Up Stream Corridor	-0.16***	-0.08	-0.28***	-0.06

* $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$

Table 6: Spearman rank order correlations between mortality and spatial distance measures.

	Black Rock Brook	**Canterbury Brook**	**Mineral Springs Brook**	**All Stands**
Distance Away From Stream Corridor	-0.76**	-0.71**	-0.80**	-0.75***
Distance Up Stream Corridor	-0.11	-0.20	-0.48	-0.25

* $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$

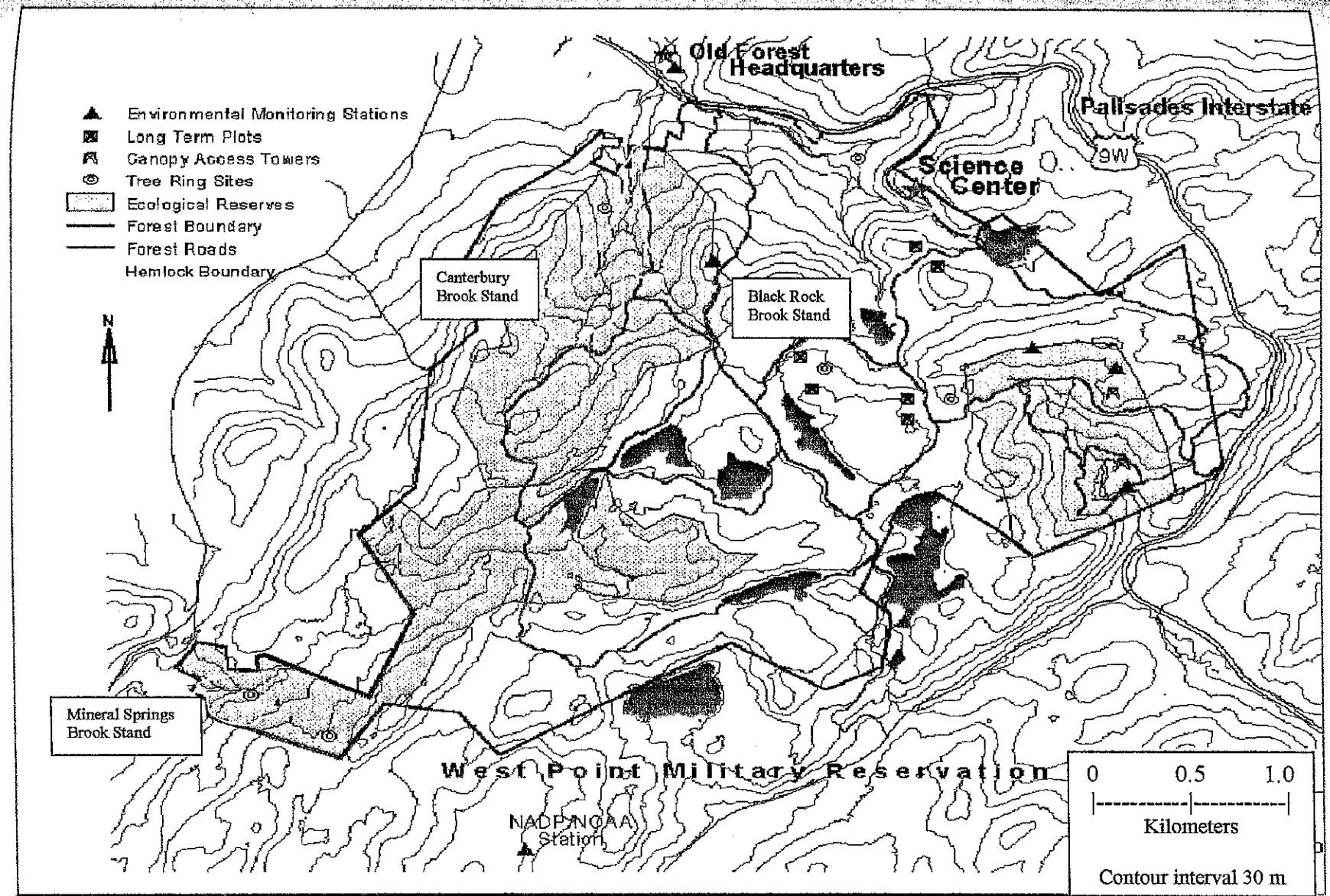


Figure 1: Map of the Black Rock Forest field station showing the limits of three eastern hemlock stands included in the study.

CHAPTER III: Analysis of the Impacts of Hemlock Woolly Adelgid Damage on Sap Flow in Eastern Hemlock

Abstract:

Granier developed an accurate method of measuring sap flow using thermal dissipation techniques to estimate whole tree transpiration, how tree transpiration responds to environmental factors, and how this in turn is reflected in forest hydrology. I utilized the heat dissipation technique to address questions related to how a non-native predatory insect, the hemlock woolly adelgid (HWA), influences a native dominant conifer species, eastern hemlock. Eastern hemlock trees are dying in northeastern forests as a result of HWA and its loss will have a dramatic impact on these ecosystems. The specific question I addressed in this study is whether or not hemlock woolly adelgid has an impact on the transpiration rate of eastern hemlock in the Black Rock Forest, southeastern New York. Sap flow rates were measured on twelve trees with varying amounts of HWA damage. The results demonstrated that when needles are removed from trees the rate of transpiration declines. However, the decline was not gradual. Instead, a sudden decline in transpiration rates occurred only after significant defoliation (approximately 50%) had occurred. Trees with low or moderately low levels of damage showed significantly higher sap flux densities than heavily damaged trees ($p < 0.05$). The data also revealed seasonal differences in transpiration rates of trees in different damage categories. During the fall, as physiological operations decreased in all trees, sapflow rates decreased more rapidly in trees with moderately high and high levels of damage. The results indicated that a threshold level of defoliation of about 50% may lead to substantial damage to the operating physiology of trees with potentially significant hydrologic implications.

Introduction:

An invasive, aphid-like insect, the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand.), is threatening the future of eastern hemlock (*Tsuga canadensis* [L.] Carr.), a dominant coniferous species of northeastern forests. Our understanding of the impact that these insects are having on hemlocks is incomplete. Young et al. (1995) thoroughly described the mechanism by which HWA feeds on eastern hemlock and the nature of the damage that it causes. However, the answers to questions such as how HWA damage leads to mortality and how the loss of these trees will impact the forest ecosystems in which they are found are not fully understood. The outlook appears bleak for eastern hemlock. HWA has only been present for a short time in eastern North America relative to an evolutionary time scale and hemlock trees have not developed any apparent resistance to HWA. This lack of resistance is compounded by the fact that no native species are known to prey on HWA intensely enough to control its populations (McClure 1995, Montgomery 1996). A better understanding of how HWA influences the operating physiology of hemlock trees might help quantify the impacts of HWA infestations on ecosystem processes and facilitate the development of management solutions.

One way to measure the physiological impact of HWA on eastern hemlock is to determine whether they have a measurable influence on the transpiration rates of infested trees. The analysis of transpiration rates provides a means to study the response of stomata, which control both carbon uptake and water loss, to environmental factors (Granier and Loustau 1994). One of the most accurate methods for estimating the transpiration rates of individual trees is to monitor the upward movement of sap within

the xylem (Steinberg et al. 1990, Grime 1992, Grime et al. 1995, Zhang et al. 1997). Most methods of monitoring sap flow were developed to provide estimates of total tree or stand water use for hydrological studies (Nadezhdina 1999). Forest hydrologists utilize these estimates to evaluate the role of transpiration in forest hydrology, to quantify the water requirements of forested areas, and to analyze issues of water resource management. Tree physiologists have utilized estimates of water use from sap flow studies to partition the control of canopy transpiration and to assess patterns of xylem water flux in different tree species (Wullschleger et al. 1998).

Granier (1987) developed one of the simplest, most accurate methods for measuring sap flow in individual trees by measuring the movement of heat between probes inserted into the xylem. He utilized his method of monitoring sap flow to estimate individual tree and stand transpiration rates in beech trees (*Fagus sylvatica* L.), Douglas-firs (*Pseudotsuga menziesii* [Mirb.] Franco), and maritime pine (*Pinus pinaster* Ait., Granier 1987, Granier et al. 1990, 2000). Granier's widely used methods have been incorporated into studies that measure whole-plant water storage and usage in order to evaluate transpiration in a number of different species. These data have been extrapolated to determine the impacts of thinnings and cuttings on site water balance, to investigate the hydrologic impact of monocultures, and to draw comparisons between different stands in terms of water usage (Wullschleger et al. 1998).

In this study I investigated how HWA influences the physiology of eastern hemlock as measured by sap flow, an indicator of transpiration rate. Specifically, my objective was to determine if HWA damage induces a change in tree water use and transpiration or if these parameters are only impacted upon mortality. It may be that trees

that are infested can recover if HWA is removed before they have sustained a certain degree of damage. The determination of threshold damage to operative physiology (point at which there is little or no chance of recovery) for eastern hemlock trees subject to HWA infestation could help managers and researchers alike identify areas that might respond best to HWA management projects such as the release of imported predators, insecticide applications, or salvage cutting.

Prior research suggests that a negative correlation between HWA damage and sap flow within a tree might be expected. Granier (2000) found that among-tree variability in sap flow was linked to crown status. Hatton and Wu (1995) also found that water use of individual trees was directly related to leaf area during periods of abundant soil water. Simpson (2000) found that trees with larger crowns have greater sapwood areas and use more water. In his study of maritime pine, Granier (1990) noted that new needles exhibited higher rates of conductance than 2-year-old needles. These findings may be relevant to damage induced by HWA. HWA preferentially feed on newer succulent needles (Young et al. 1995), potentially translating into a major impact on the transpiration rate of trees suffering from HWA damage. Tree transpiration, scaled up to the stand or forest level, has a major influence on forest hydrology (Engel et al. 2002). Eastern hemlock typically grows in dense stands, along the banks of streams (Montgomery 1996). Hemlock trees directly impact forest hydrology, stream quality, and the fauna in forest ecosystems (Snyder et al. 2002). Jenkins et al. (1999) found that net N mineralization and nitrification rates were higher at sites experiencing an HWA infestation. It has been documented that sites infested with HWA experience increased

light levels (Orwig and Foster 1998). Increased soil and air temperatures may also result, though further study in this area is needed.

Previous sap flow studies have focused primarily on the hydrological aspects of transpiration, often ignoring nighttime sap flow. Most of the water supplied for transpiration comes from the soil, but a portion is drawn from the tree's internal storage (Nadezhdina 1999). The internal store that is partially utilized during the day is replenished at night. The rate of nighttime sap flow is low compared to day time rates and is not important from a quantitatively hydrological point of view, however, it is extremely important for plant survival and is of particular interest in studies concerned with drought stress in plants. It may also prove vital to hemlocks that are impacted by HWA.

It is important to note that HWA feeding alone may not result in the death of eastern hemlock. It may be that HWA reduces hemlock resistance to other species that actually induce mortality, or it may be that the ability of hemlock trees to resist an HWA infestation may have already been reduced by other factors. Eastern hemlock is especially sensitive to drought. Parshall (1995) noted that the warmer, drier climate of the 20th century hindered eastern hemlock's ability to regenerate and that drought stressed trees with mechanically weakened wood and roots are more susceptible to physical forces, insects, and pathogens. The elongate hemlock scale (*Fiorinia externa* Ferris), also imported from Asia, has been found on hemlock trees in the Black Rock Forest (Danoff-Burg and Bird 2002). Scale densities in the Black Rock Forest are high, and it may be that the trees are not able to withstand the compounding effects of these invasive species (e.g. Evans et al. 1996, McClure et al. 2000). McClure (1995) has noted that HWA has

caused mortality of eastern hemlock trees within four years, suggesting that it can do so without assistance from any other species. However, studies at Black Rock Forest suggest that the role of scale in hemlock damage and mortality may be substantial (Danoff-Burg and Bird 2002).

The main purpose of this study was to assess the short-term effects of HWA infestation on tree transpiration, and potentially on forest hydrology, as indicated by sap flow. Sap flow rates of twelve hemlock trees with varying degrees of HWA-induced damage were monitored continuously throughout the summer and fall of 2000 using heat sensing probes (Granier 1985) to determine if HWA was having an impact on transpiration rates.

Methods:

Twelve trees within the upper reaches of the Black Rock Brook hemlock stand were selected for sap flow monitoring using Granier heat probes connected to Campbell Scientific data loggers. The degree of damage for each of the trees was visually assessed by estimating needle loss, using the following scale: 0 = 0% defoliation, 1 = 1-5% defoliation, 2 = 6-25% defoliation, 3 = 26-50% defoliation, 4 = 51-75% defoliation, 5 = 76-99% defoliation, and 6 = 100% defoliation (dead). Two cylindrical probes, 1.5 mm in diameter, were encased in aluminum tubes (2 mm outside diameter) and inserted radially into the stem of the twelve trees to the depth of 20 mm, one located 100 mm below (upstream) of the other. Care was taken to ensure that the probes were inserted beneath the level of nonconducting cambium and bark. The thermally conductive aluminum sleeve is designed to minimize temperature gradients along the probe (Granier 1987).

Each of the probes was wrapped in a coil of insulated constantan wire, and the downstream probe (the probe highest on the trunk) was heated by applying a known voltage across the heating element. The temperature of the two probes was measured with T-type thermocouple junctions inserted halfway along the inside of each probe connected to a Campbell Scientific CR10X datalogger. Probe temperatures were recorded every 5 seconds and a mean of the measurements was stored in the datalogger every 20 minutes. Clearwater et al. (1999) suggest that averaging intervals of 30 minutes or less be used to avoid errors induced by temporal variations. The temperature difference between the two probes (dT) at times of positive sap flow was used to calculate the sap flux density (U, kg m^{-2} sapwood area s^{-1}) for each of the trees by inserting the product into the equation: $U=0.116*((dTm - dT)/dT)^{1.2}$ (Granier et al. 1990), where dTm represents the maximum temperature difference between the heated and reference probes, occurring at times of no flow (pre-dawn).

Monitored trees were classified into four major categories: high damage (trees with a damage index of 5), moderately high (damage index of 4), moderately low (damage index of 3), and low (damage index of 1 or 2). Three four-day periods approximately 35 days apart were selected to represent sap activity in the latter part of the growing season: one in August (day of year 215 to 218), one in September (day of year 252 to 255), and one in October (day of year 290 to 293). Average maximum sap flux densities (SFD) were compared for the four categories using one-way ANOVA. Average hourly sap flux densities for the same three four-day periods were compared to environmental data gathered hourly at Black Rock's Lowland meteorologic station, established in an open field. Comparisons were made among the average sap flux density

(SFD), photosynthetically active solar radiation (PAR), vapor pressure (VP), temperature, and precipitation. Data were collected and stored in a Campbell datalogger, model CR10X. Precipitation data on a per event basis were obtained from the Black Rock Forest database, collected using a U.S. Forest Service collector situated in the same field as the Lowland Station since 1960.

Sapwood depth was determined for each of the monitored trees by obtaining increment cores from the trees and dissecting these into 0.5 cm segments for water content testing (Granier et al. 2000). The cores were taken from the trees immediately following a rain event in order to be certain that the xylem of the tree was filled to capacity. The cores were wrapped in aluminum foil to prevent water loss, segmented, and weighed within an hour of extraction. The segments were then dried in an oven at 70° C for two days and weighed again. The difference in weights was used to determine the depth of the sapwood. A second core was taken from each of the trees at the same time and growth rings were counted to estimate tree age. The weights of segmented core samples were plotted against the diameter at breast height (DBH) of sampled trees. A second order polynomial trendline was fit to the data and the equation for the line was used to recalculate the sapwood depths for all the trees in order to obtain estimates for those trees that had not produced sound cores.

Data analyses revealed that some of the SFD data exhibited significantly positive skewness and kurtosis. In order to compensate for these deviations from normality I chose to use non-parametric Spearman rank order correlation statistics, which have been shown to be robust in analyzing data that are not normally distributed (Sokal and Rohlf

1981). All statistical tests were conducted using the statistical program Statistica developed by Statsoft (www.statsoft.com).

Results:

Records from the Black Rock Forest show that the growing season precipitation (May through November) for 2000 exceeded the 40-year average by 200 mm (Table 1). Spring precipitation was average, but June through September precipitation amounts were 165% of the 40-year average. The monthly total for August (244.1 mm) exceeded the 40-year average by 134 mm. The month of October was much drier, with total precipitation levels 86 mm below the monthly mean.

All the trees selected were subcanopy trees, meaning that their canopies did not receive direct sunlight, because intermittent, large, deciduous trees covered much of the canopy in the upper reaches of the Black Rock Brook stand. The DBH of trees selected for monitoring ranged from 16.6 cm to 32.8 cm (Tables 2 and 3). Plots did not differ significantly for any of the measured variables and were thus not used as factors in any subsequent tests. When trees were grouped by damage categories, the average DBH for trees with a high degree of damage was 23.1 cm, compared to 20.3 cm for trees with moderate to high damage, 23.9 cm for trees with moderate to low damage, and 27.5 cm for trees with low damage. Minimum tree age ranged from 53 to 145 years. The average minimum age for trees with high damage was 92 years, compared to 63 years for trees with moderate to high, 67 years for trees with moderate to low damage, and 96 years for trees with low damage (Table 3). One-way ANOVA analyses revealed significant statistical relationships between damage categories and age and DBH ($p < 0.05$). The

weights of segmented core samples were plotted against the DBH of sampled trees and a second order polynomial trendline was produced with an r^2 value of 0.92 (Figure 1). The resulting equation was used to calculate the sapwood depths for those trees that had generated outliers. Adjusted sapwood depths ranged from 0.88 cm to 5.64 cm.

Across all trees, no correlations were found between tree age and the degrees of HWA damage, or between average maximum SFD and the average age or DBH of the trees monitored (Table 4). A significant negative correlation was found between mean damage and mean maximum SFD. When trees were grouped by damage category, group means for all factors were compared with the average maximum SFD for all twelve days. This comparison revealed a positive linear relationship between DBH and SFD with a correlation of 0.84. A linear relationship was also found between the average age of the trees and the average DBH for trees in each of the four categories ($r_s = 0.88$).

When viewed over time, average maximum SFD for the three four-day periods indicate a seasonal decline in transpiration rates across all the categories of damage. The results demonstrate, however, that heavily damaged hemlocks had a much lower transpiration rate throughout the year compared to trees that were only lightly damaged or moderately damaged (Figure 2). Summer sap flow in a relatively wet year was reduced by approximately fifty percent in heavily damaged trees, compared to all others. Trees with a moderately high degree of damage showed an initial sap flux density that was comparable to trees with lower damage. However, sap flux density for these trees decreased to levels comparable to heavily damaged trees earlier in the season than trees with low and moderately low levels of damage. Trees with low or moderately low

damage consistently showed higher sap flux density levels over all measurement periods ($p < 0.05$, ANOVA).

Hourly SFD demonstrated a diurnal cycle significantly positively correlated with PAR and air temperature, although trees in all the categories displayed an average 3-hour time lag for the initiation of sap flow (Figure 3). Transpiration continued after PAR had declined to zero, resulting in measurable nighttime sap activity. Time lags did not significantly differ among damage categories. Trees that showed high amounts of damage and trees that showed low amounts of damage initiated transpiration at the same time and ended sap activity at the same time. During the day trees with low amounts of damage transpired significantly more than trees with high damage.

Hourly SFD means were compared with hourly means for air temperature, vapor pressure photosynthetically active solar radiation (PAR) and precipitation (Table 5). Air temperature, vapor pressure and PAR demonstrated significant positive relationships with SFD. No significant relationships were found between precipitation and SFD.

Discussion:

In this study SFD was closely correlated with PAR, temperature, and vapor pressure with a diurnal pattern that nearly mirrored that of PAR. The observed lag time in SFD behind PAR may be, in part, the result of the placement of the probes at the base of the trees. Water initially used in transpiration is stored near the top of the tree and there can be a time lag until water stored at the base of the tree begins to flow. Storage of water in the trunk of the tree may also explain continued sap flow after the decline of PAR. Water is still drawn into the trunk of the tree by capillary action even though it is no

longer being lost through the stomata, and then is held until the next morning when the stomata open and transpiration resumes. Since the summer of 2000 was relatively wet, water was not a limiting factor for transpiration as it would have been under drought conditions. Precipitation most directly affected SFD by limiting photosynthetically active solar radiation due to cloud cover that accompanied the rain. Trees demonstrated normal diurnal transpiration cycles and appeared to refill completely each evening. No differences were found in the amount of lag time experienced by trees in different damage categories.

In a study of pacific silver fir (*Abies amabilis* Dougl. ex Loud.) Martin et al. (1997) observed positive correlations of leaf area and canopy size with transpiration rates and SFD. In general my results show similar correlations. The significance of these findings was not diminished by the correlations between damage categories and mean age and DBH of trees within the categories. Trees in the moderately-high and moderately low categories did not out perform trees in the low or high damage categories despite being significantly younger. In addition, trees in the low category did not have significantly higher sap flow rates than trees in the moderately low category though they did have a significantly higher mean DBH. Heavily damaged trees showed significantly reduced SFD throughout the measurement period compared to low and moderately low damage trees. HWA has a direct impact on the leaf area of eastern hemlock, killing needles and reducing the ability of trees to generate new needles. Heavily damaged trees have less than 25 percent of the needles that are found on healthy, uninfested trees. The loss of needles directly decreases the ability of trees to photosynthesize and transpire. This effect is further compounded by the tendency of HWA to feed on new growth, preventing its

proper development. Phillips et al. (1996) noted that new growth is more effective at transpiring than old.

Under certain conditions, however, eastern hemlock may compensate for HWA induced reduction of transpiration. Oren et al. 1999 state that tree transpiration rates are linearly related to leaf area in trees that have a low leaf area index (LAI). They found that trees increase stomatal conductance to compensate for sudden reductions in LAI (loss of leaf area as result of hurricane). They found that the low LAI trees allowed their stomata to remain more open than they could at full leaf area, the result of a reduction in stomatal sensitivity to vapor pressure deficit. Pataki et al. (1998) also found that transpiration rates per unit leaf area and water vapor generally increased with decreasing leaf area. This may explain the findings here that only trees with more than 75% needle loss had consistently reduced SFD and that trees with between 50 and 75% needle loss only had reductions in SFD compared to less defoliated trees at the end of the season. At these higher damage levels, apparently needle loss eventually becomes so great that it limits transpiration, despite increased stomatal conductance. It may be that this represents the threshold level of damage to tree physiology at which trees are not likely to be able to recover. However, we did not have the ability to simultaneously measure the function of healthy, completely uninfested trees, so we cannot be certain whether they would have significantly higher transpiration compared to the light and moderately light damage trees.

The results of this study may prove of interest to managers faced with the loss of large stands of hemlock from their watersheds. It is clear from the data that HWA damage reduces tree sap flow and transpiration. This is not, however, a simple linear function of damage, at least as estimated by defoliation damage class. During the

relatively wet summer of 2000 heavily damaged trees exhibited only 50% of the sap flow of trees with lighter degrees of damage. Trees with lighter levels of damage showed no significant reduction. During the fall, however, as physiological operations decreased in all trees, sapflow dropped more rapidly in trees with moderately high and high levels of damage. These results demonstrate that the age of an infestation will influence the amount of water that will be used in tree transpiration. Managers can expect that both productivity and water use may be little impacted until a threshold level of damage has occurred. In young infestations enhanced soil moisture and stream flow may first be noticed only toward the end of the growing season as transpiration in moderately damaged trees drops rapidly. As the infestation ages and more trees reach heavily damaged status, water uptake and transpiration should be severely reduced throughout the growing season, leading to more substantial water loss via evaporation, runoff, and/or use by other plant species.

Microclimate changes in the system may initially act to counter any potential increases in stream outflow resulting from a decrease in hemlock transpiration. Needle loss should result in increased sunlight reaching the forest floor, affecting system response in several ways. For example, additional sunlight will increase soil temperatures and evaporation from soil and litter should increase. In addition, hemlock mortality will enable other species to establish. Studies of fossil pollen show that a range-wide decline of eastern hemlock that occurred in North America around 4800 years ago resulted in an increase in birch, followed by oak, maple, and beech (Foster and Zebryk 1993, Fuller 1998). Maenza-Gmelch (1997) confirmed that Black Rock showed a similar pattern of hemlock loss and an increase in birch around this same time. Yellow birch has been

shown to rapidly establish itself when gaps form in some hemlock stands (Woods 2000). Recent surveys of Black Rock and other forests in the region suggest that many of these same species are establishing themselves under waning hemlock trees (Orwig and Foster 1998a, Orwig et al. 2002).

The extent to which the changes in the microclimate and species composition will impact the water not subsequently used in hemlock transpiration is not known. If increases in evaporation and uptake by other plants are less than the water normally used during hemlock transpiration, there may be observable increases in runoff. Evaporation and uptake by other species may be limited due to the habitat in which eastern hemlock is typically found. Steep slopes, especially those with north exposures, will typically receive limited direct sunlight on any given day. Compensatory factors may also impact only soil layers close to the surface. Establishment of other plants may also be reduced in portions of hemlock stands with steep slopes and higher erosion potential.

This preliminary study suggests many areas for further research. The study could be repeated in canopy trees to extend the applicability of the findings. This particular study also got a late start, with all stations operating by mid-July. Further studies should be initiated earlier in the year, before the start of the growing season, so that the full annual pattern can be studied. Extension of this study into multiple years would provide even better results, allowing for data collection under a variety of environmental conditions (such as years with average or lower available moisture) and enabling study of the impacts of multiple generations of HWA.

In this study only a single pair of probes were installed into the base of the north, shaded side of each tree. Transpiration can vary within a tree, in part because of the

amount of sunlight varies around the canopy. The sunnier side of the tree will often transpire more. To compensate for this, probes should be installed in at least two sides of the tree, and the data from the probes averaged, but this was beyond the scope of the money and time available in this study. The equipment used to gather sap flow data is expensive and requires substantial maintenance. In addition, the probes that were used to measure SFD were constructed by hand, a process that is very labor intensive. Spare probes should be kept on hand to maintain continuous data streams. Installing additional probes higher up on the trunk of the tree would also be recommended to reduce the effects of the time lags that result from water being stored in the trunk of the tree.

Vertessey et al. (1997) argue that heat dissipation probes should be calibrated for any species monitored. Each species has its own wood characteristics and growth patterns, which will affect transpiration rates. Very little, if any, data related to eastern hemlock sap flow and transpiration have been previously documented. A baseline should be established for this species, clearly establishing maximum expected SFD values, and clarifying diurnal patterns. The findings of this study suggest that, with established base line SFD values, sap flux could be used as a diagnostic tool, providing quantification of the degree of HWA damage. However, this possibility is currently limited by the complex systems required to monitor sap flow.

The results of this study indicate that needle loss above a 50% threshold level due to HWA feeding directly reduces sap flow, undoubtedly impacting carbon uptake and growth, and thus may also substantially impact forest hydrology. HWA infestations in early stages may not lead to increases in surface runoff, or the increases may only be noticed if seasonal patterns are closely monitored, because transpiration rates of trees

with moderate levels of HWA damage decline earlier in the growing season than healthy trees. Once trees are heavily damaged, HWA infestations may lead to greater runoff throughout the growing season. Further studies could clarify the hydrologic implications of HWA infestations by determining whether microclimatic changes and the growth of new plant species will compensate for the decreased transpiration that results from HWA infestations.

Table 1: Monthly precipitation for the growing season of 2000 compared to previous years. Standard errors are enclosed in parentheses.

Month	Mean Monthly Precipitation (mm) 1960-2000	Monthly Precipitation in 2000 (mm)	Difference (mm)
May	116.4 (11.2)	102.6	-13.8
June	109.8 (9.7)	219.7	+109.9
July	104.7 (9.1)	131.6	+26.9
August	110.6 (10.4)	244.1	+133.5
September	114.9 (10.2)	130.0	+15.1
October	95.4 (8.6)	9.4	-86.0
November	118.0 (9.4)	125.7	+7.7
Seasonal Totals (May-Nov)	769.7 (26.4)	963.2	+193.5

Table 2: Physical characteristics of the twelve trees selected for sap flow monitoring. Adjusted depth of sapwood was calculated by plotting the measured sapwood depths on a graph and determining the equation for the resulting line of best fit.

Plot #	Tree #	Damage Class	Damage Description	Diameter at Breast Height (cm)	Measured Sapwood Depth (cm)	Adjusted Sapwood Depth (cm)	Minimum Calculated Age (years)
1	1	5	High	18.3	NA	1.75	60
1	2	5	High	18.1	1.5	1.65	72
1	3	3	Moderate	27.0	NA	4.83	52
2	1	4	Mod to High	18.5	1.5	1.85	62
2	2	3	Moderate	16.6	1.5	0.88	67
2	3	4	Mod to High	19.0	1.5	2.08	73
3	1	4	Mod to High	23.5	NA	3.86	53
3	2	3	Moderate	31.1	NA	5.51	74
3	3	5	High	32.8	NA	5.64	145
4	1	2	Low	29.4	5.0	5.29	87
4	2	3	Moderate	20.9	3.0	2.91	74
4	3	1	Low	25.5	5.0	4.46	104

Table 3: Average DBH and age for eastern hemlock trees in each of the damage categories. Standard errors are enclosed in parentheses.

Damage Category	Damage Class	Number of Trees	DBH (cm)	Age (years)
High	5	3	23.1 (4.9)	92.3 (26.6)
Mod-High	4	3	20.3 (1.6)	62.7 (5.8)
Mod-Low	3	4	23.9 (3.2)	66.8 (5.2)
Low	1-2	2	27.5 (2.0)	95.5 (8.5)

Table 4: Spearman rank order correlations for the mean tree characteristics for each damage category and the mean maximum SFD.

	Damage Category	Mean Age	Mean DBH	Mean Max SFD
Damage Category	----	-0.40	-0.80	-1.00 **
Mean Age	-0.40	----	0.80	0.40
Mean DBH	-0.80	0.80	----	0.80
Mean Max SFD	-1.00 **	0.40	0.80	----

* $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$

Table 5: Spearman rank order correlations between sap flow density of trees in the four damage categories and environmental variables.

	High	Moderately-High	Moderately-Low	Low
Air Temperature	0.66***	0.66***	0.70***	0.66***
Vapor Pressure	0.05	0.20***	0.08	0.04
PAR	0.55***	0.44***	0.54***	0.51***
Precipitation	-0.08	0.01	-0.06	-0.06

* $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$

Figure 1: Line of best fit relating tree diameter to sapwood depth. Adjusted sapwood depths were calculated using the equation shown.

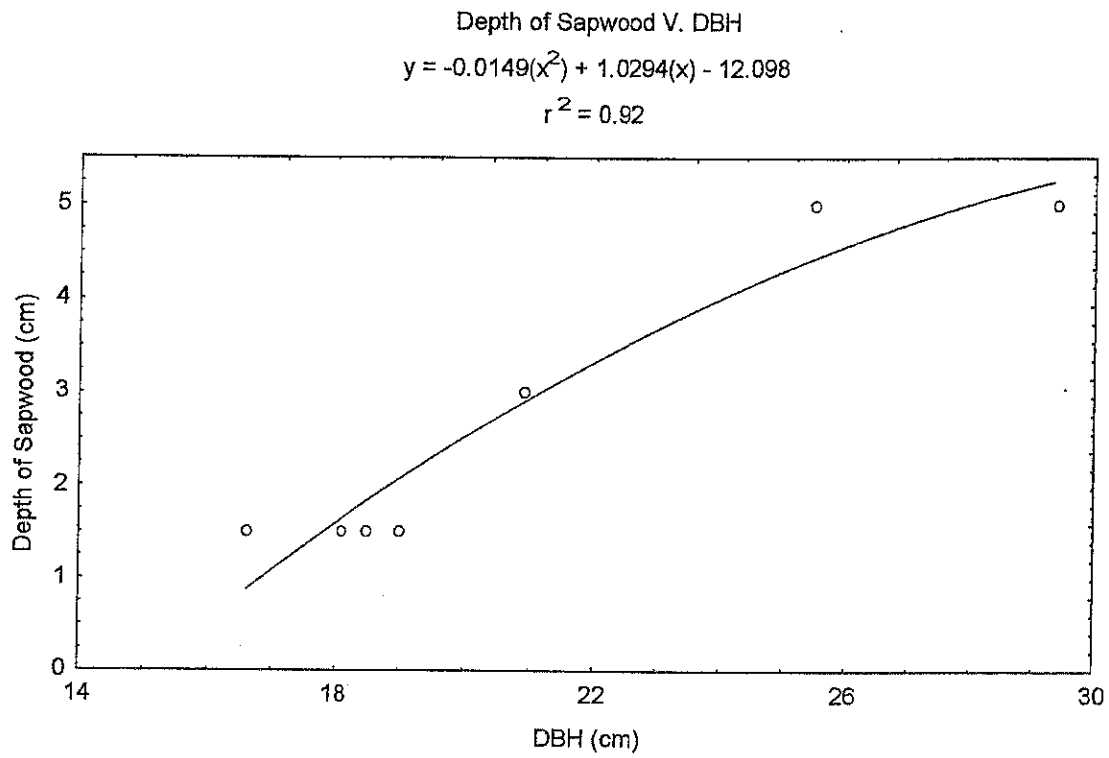


Figure 2: Maximum sap flux density for twelve hemlock woolly adelgid-affected hemlock trees in four damage categories for three four day periods during the latter part of the 2000 growing season; A: August, B: September, C: October.

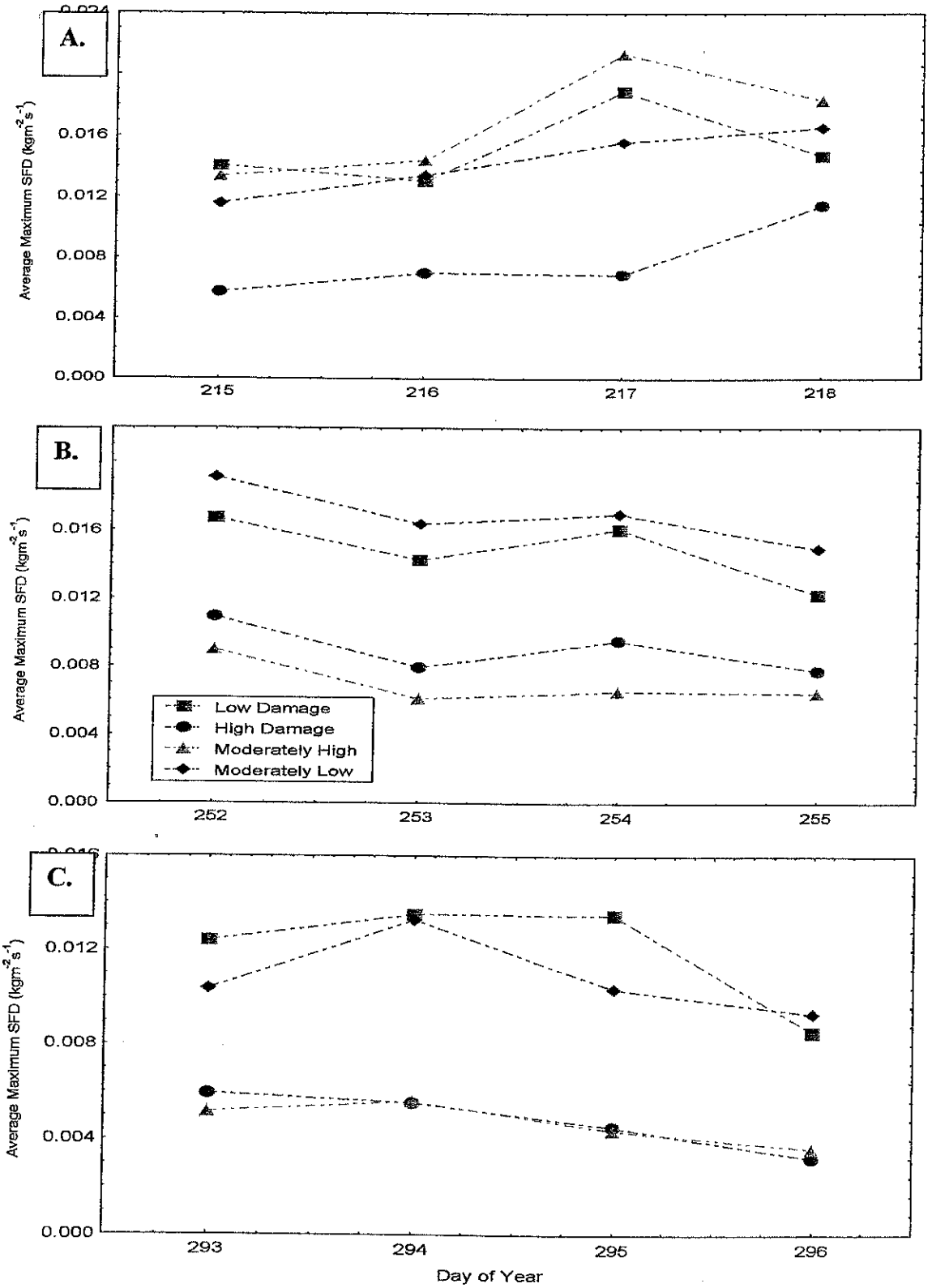
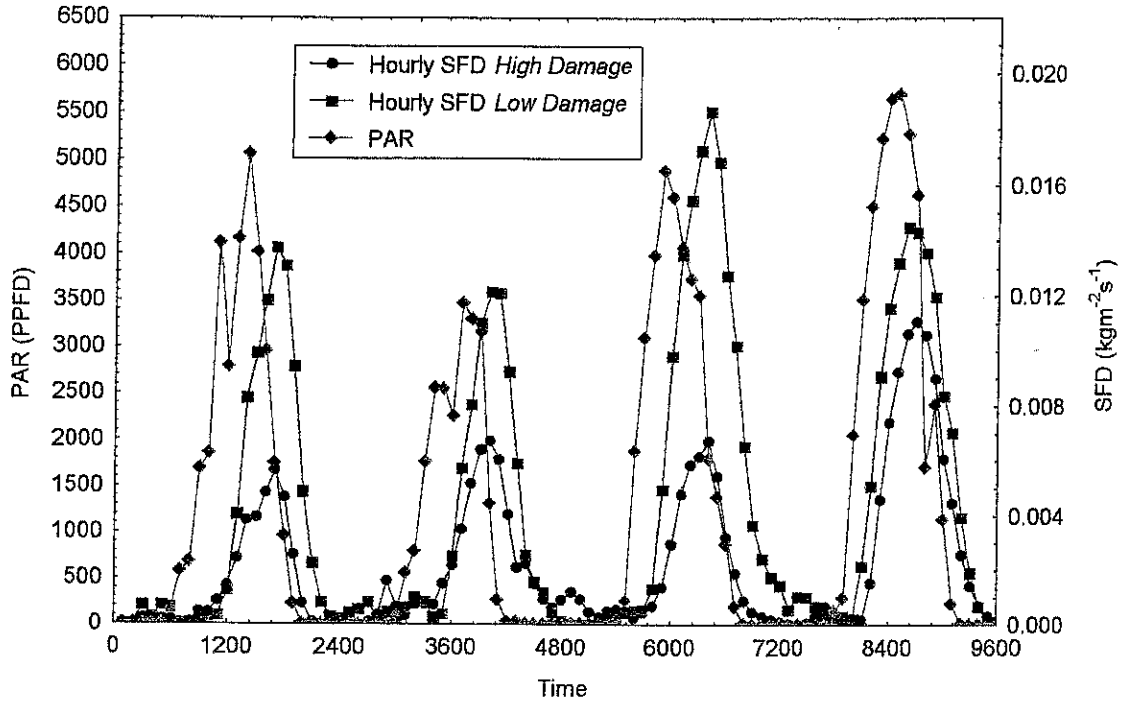


Figure 3: Photosynthetically active solar radiation (PAR) and sap flow density for hemlock trees with high and low degrees of hemlock woolly adelgid damage for the four day period from day 215 to day 218 of 2000.



CHAPTER IV: Applications for Land Managers

The findings of this study should be of value to land managers attempting to address hemlock woolly adelgid infestations or preparing for possible infestations in stands of eastern hemlock. It describes potential locations for initial HWA contact with stands. The study also describes patterns of damage and spread associated with infestations, and topographical features that may facilitate the spread and damage. Finally, the study describes the relationship between HWA damage and tree transpiration along with the potential affects of damage on forest hydrology and carbon storage.

The results of this study suggest that HWA will most likely make initial contact with hemlock stands in areas that are not bordered by contiguous tracks of forest. In the Black Rock Forest, stands of hemlock showed patterns of HWA damage closely associated with proximity to the forest boundary and areas of human development. Forests of the northeastern U.S., the region that is currently being affected by HWA, have been extensively altered by human development. Roads and development dissect what were, at one time, contiguous forests into a patchwork of contrasting land uses and vegetation types. Roads and development may act as corridors for HWA to be carried between stands and, if development occurs at the edge of stands, serve as a point of initial contact for HWA. Managers responsible for stands that have not yet been infested with HWA might focus surveys designed to detect HWA along stand perimeters in areas affected by human development. Monitoring regimes should involve biannual surveys, once in the spring and once in early fall. Focused surveys would save managers time and money and provide a greater chance of determining whether or not HWA has contacted the stand. If managers are provided with a budget allocated to the prevention or

containment of HWA, it may be helpful to focus their expenditures in areas where stands border development.

This study suggests that patterns exist for how HWA moves through stands once it is present. Managers may be able to use these findings in attempts to control the spread of infestations. Managers faced with already established infestations should try to assess the extent of damage and the rate of HWA spread. Hemlock mortality associated with HWA was greatest near natural streambeds in all hemlock stands of the Black Rock Forest. These areas may function as natural dispersal corridors for HWA. Tactics designed to prevent the spread of HWA or to maintain the health of existing hemlocks may benefit from an approach that focuses on natural corridors within stands. Or, if managers are concerned about stands that have well entrenched HWA infestations they can dedicate resources to preserving areas of the stand that are most likely to respond to their efforts. The data gathered in this study suggest that preservation programs may be most successful if they are focused on the healthy trees in forest interior locations.

The results of this study also indicate that a predictable temporal pattern occurs in the spread of HWA-related damage through hemlock stands. Damage to trees may be light at first, but within about six years HWA was found throughout all three hemlock stands, moderate to high levels of needle loss were widespread, and significant mortality had already occurred. Sap flow sensors could potentially be used as diagnostic tools to track the progress and impacts of infestations, although at this point the effort and expense involved to do this remain considerable.

The findings of my study suggest forest hydrology will be affected by reduced levels of sap flow in eastern hemlock as a result of needle loss and mortality, and

managers may be able to predict when these changes will have impacts on a watershed level. The relationship between damage and transpiration is not a simple, negative linear function. Managers can expect that both productivity and water use may be little impacted until a threshold level of damage has been reached. In the Black Rock Forest, during the relatively wet summer of 2000, heavily damaged trees exhibited only 50% of the sap flow of trees with lighter degrees of damage. Trees with lighter levels of damage showed no significant reduction. During the fall, however, as physiological operations decreased in all trees, sapflow decreased most rapidly in trees with moderately high and high levels of damage. Sapflow data from the Black Rock Forest suggest that HWA infestations in early stages may not lead to consistent increases in surface runoff because eastern hemlock may be able to compensate for needle loss and maintain transpiration rates. However, the data also suggest that late season increases in runoff may result because trees with moderate levels of HWA damage decline earlier in the growing season than healthy trees. Once trees are heavily damaged, HWA infestations should lead to greater runoff throughout the growing season. These results demonstrate that the age of an infestation will influence the amount of water that will be used in tree transpiration. Enhanced soil moisture and stream flow may initially be apparent in the fall and become more consistent throughout the growing season as infestations become more wide-spread and damage more extensive. The implications of increased runoff can include nutrient losses, erosion, and increased sediment in streams. Further studies could clarify the hydrologic implications of HWA infestations by determining to what extent microclimatic changes and the growth of new plant species will compensate for the decreased transpiration that results from HWA infestations.

Managers should benefit from a better understanding of the dispersal patterns of HWA infestations, stand level changes, and the implications for forest hydrology. They should be better prepared for the changes that will result from HWA infestations and will have a greater understanding of the timing of those changes.

LITERATURE CITED

Abrams, MD, and DA Orwig. 1996. A 300-year history of disturbance and canopy recruitment for co-occurring white pine and hemlock on the Allegheny Plateau, USA. Journal of Ecology 84: 353-363.

Becker, P. 1998. Limitations of a compensation heat pulse velocity system at low sap flow: implications for measurements at night and in shaded trees. Tree Physiology 18: 177-184.

Becker, P and WRN Edwards. 1999. Corrected heat capacity of wood for sap flow calculations. Tree Physiology 19: 767-768.

Benzinger, J. 1994. Hemlock decline and breeding birds. 1. Hemlock ecology. New Jersey Audubon 20: 2-12.

Bonneau, LR, KS Shields, and DL Civco. 1999a. Using satellite images to classify and analyze the health of hemlock forests infested by the hemlock woolly adelgid. Biological Invasions 1: 255-267.

Bonneau, LR, KS Shields, and DL Civco. 1999b. A technique to identify changes in hemlock forest health over space using satellite image data. Biological Invasions 1: 269-279.

Bowers, WW, SE Franklin, J Hudak, and GJ McDermid. 1994. Forest structural damage analysis using image semivariance. Canada Journal of Remote Sensing 20: 28-36.

Breda, N, H Cochard, E Drier, and A Granier. 1993. Water transfer in a mature oak stand (*Quercus petrea*): seasonal evolution and effects of a severe drought. Canadian Journal of Forest Research 23: 1136-1143.

Brower, JE and JH Zar. 1990. Field and laboratory methods for general ecology. Wm.C. Brown Company Publishers, Dubuque, Iowa.

Castello, JD, DJ Leopold, and PJ Smallidge. 1995. Pathogens, patterns, and processes in forest ecosystems: pathogens influence and are influenced by forest development and landscape characteristics. Bioscience 45: 16-24.

Cermák, J, E Cienciala, J Kucera, A Lindroth, and E Bednářová. 1995. Individual variation of sap-flow rate in large pine and spruce trees and stand transpiration: a pilot study at the central NOPEX site. Journal of Hydrology 168: 17-27.

Cienciala, E, A Lindroth, J Cermak, JE Hallgren, and Jiri Kucera. 1994. The effects of water availability on transpiration, water potential and growth of *Picea abies* during a growing season. Journal of Hydrology 155: 57-71.

Clearwater, MJ, FC Meinzer, JL Andrade, G Goldstein, and NM Holbrook. 1999. Potential errors in measurement of nonuniform sap flow using heat dissipation probes. Tree Physiology 19: 681-687.

Curtis, JT and RP McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32:476-496.

Danoff-Burg, J and S Bird. 2002. Hemlock woolly adelgid and elongate hemlock scale: partners in crime?. Pp 254-268 in Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium, East Brunswick, NJ. United States Department of Agriculture, Forest Service.

D'Arrigo, RD, DM Lawrence, ER Cook, W Schuster, M Wiljanen, and RD Thetford. 2001. Climate-growth relationships of eastern hemlock and chestnut oak from Black Rock Forest in the Highlands of southeastern New York. Tree-Ring Research 57: 183-190.

DeGraaf, RM and DD Rudis. 1986. New England wildlife habitat: habitat, natural history, and distribution. General Technical Report NE-108. Broomall, PA: US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 491 p.

DeGraaf, RM, M Yamasaki, WB Leak, and JW Lanier. 1992. New England wildlife: management of forested habitats. General Technical Report NE-144. Radnor, PA: US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 271 p.

Dugas, WA, ML Heuer, and HS Mayeux. 1992. Diurnal measurements of honey mesquite transpiration using stem flow gauges. Journal of Range Management 45: 99-102.

Dye, PJ, and BW Olbrich. 1993. Estimating transpiration from 6-year-old *Eucalyptus grandis* trees: development of a canopy conductance model and comparison with independent sap flux measurements. Plant, Cell and Environment 16: 45-53.

Edwards, WRN, P Becker, and J Cermak. 1996. A unified nomenclature for sap flow measurements. Tree Physiology 17: 65-67.

Engel, VC, M Stieglitz, M Williams, and KL Griffin. 2002. Forest canopy hydraulic properties and catchment water balance: observations and modeling. Ecological Monitoring 154: 263-288.

Evans, RA, E Johnson, J Shreiner, A Ambler, J Battles, N Cleavitt, T Fahey, J Sciascia, and E Pehek. 1996. Potential impacts of hemlock woolly adelgid on eastern hemlock ecosystems. Pp. 42-57. in Salom, SM, TC Tigner, and RC Reardon (eds.). First Hemlock Woolly Adelgid Review, 12 October 1995, Charlottesville, Virginia. United States Department of Agriculture, Forest Service, Morgantown, West Virginia.

Finzi, AC, CD Canham, and N Van Breemen. 1998. Canopy tree-soil interactions within temperate forests: species effects on pH and cations. Ecological Applications 8: 447-454.

Foster, DR, TM Zebryk, P Schoonmaker, and A Lezberg. 1992. Post-settlement history of human land-use and vegetation dynamics of a *Tsuga canadensis* (hemlock) woodlot in central New England. Journal of Ecology 80: 773-786.

Foster, DR. 2000. Hemlock's future in the context of its history: an ecological perspective. Pp. 1-4 in McManus, KA, KS Shields, and DR Souto (eds.) Proceedings, Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America, 22-24 June 1999, Durham, New Hampshire. United States Department of Agriculture, Forest Service, Newtown Square, Pennsylvania. General Technical Report NE-267.

Foster, DR and TM Zebryk. 1993. Long-term vegetation dynamics and disturbance history of a *Tsuga*-dominated forest in New England. Ecology 74: 982-998.

Friday, KS and JB Friday. 1985. Black Rock Forest Inventory 1985. Internal Report, Black Rock Forest Publications, Black Rock Forest, Cornwall, NY.

Fuller, JL. 1998. Ecological impact of the mid-Holocene hemlock decline in southern Ontario, Canada. Ecology 79: 2337-2351.

Godman, RM and K Lancaster. 1990. *Tsuga canadensis* (L.) Carr. Pp. 604-612 in Burns, RM and BH Honkala (eds.) Silvics of North America Volume 1 Conifers: Agriculture Handbook 654. United States Department of Agriculture, Forest Service, Washington, DC.

Gouger, RJ. 1971. Control of *Adelges tsugae* on hemlock in Pennsylvania. Science Tree Topics 3: 1-9.

Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiology 3: 309-320.

Granier, A and D Loustau. 1994. Measuring and modeling the transpiration of maritime pine canopy from sap flow data. Agricultural and Forest Meteorology 71: 61-81.

Granier, A, P Biron, and D Lemoine. 2000. Water balance, transpiration and canopy conductance in two beech stands. Agricultural and Forest Meteorology 100: 291-308.

Granier, A, V Bobay, JHC Gash, J Gelpe, B Saugier, and WJ Shuttleworth. 1990. Vapour flux density and transpiration rate comparisons in a stand of maritime pine (*Pinus pinaster* Ait.) in Les Landes forest. Agricultural and Forest Meteorology 51: 309-319.

Gray, DR and SM Salom. 1995. Precision and relative efficiency of a binomial sampling protocol for the hemlock woolly adelgid. Entomological Society of America, Conference Papers Index, u 1000 Animal and Plant Science, 3224274.

Grime, VL. 1992. Thermal methods for measuring sap flow through intact plant stems. PhD Thesis, University of Reading, UK.

Grime, VL, JIL Morison, LP Simmonds. 1995. Including the heat storage term in sap flow measurements with the stem heat balance method. Agricultural and Forestry Meteorology 74: 1-25.

Hain, FP. 1988. The balsam woolly adelgid in North America. Pp. 87-109 in Baerryman, A.A. (ed.), Dynamics of Forest Insect Populations: Patterns, Causes, Implications. Plenum, NY.

Hatton, TJ and HI Wu. 1995. Scaling theory to extrapolate individual tree water use to stand water use. Hydrological Processes 9: 527-540.

Hurlbert, SH. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

Jenkins, JC and JD Aber. 1998. Effects of hemlock woolly adelgid (*Adelges tsugae*) infestation on ecosystem processes in eastern hemlock (*Tsuga canadensis*) forests. Ecological Society of America, Conference Papers Index, u 1000 Animal and Plant Science, 3382971.

Jenkins, JC, JD Aber, and CD Canham. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Canadian Journal of Forest Research 29: 630-645.

Kalma, SJ, PJ Thorburn, and GM Dunn. 1998. A comparison of heat pulse and deuterium tracing techniques for estimating sap flow in *Eucalyptus grandis* trees. Tree Physiology 18: 697-705.

Karas, N. 1997. Brook trout: a thorough look at North America's great native trout – its history, biology, and angling possibilities. Lyons and Burford, NY, NY. 371 p.

Kessel, SR. 1979. Adaptation and dimorphism in eastern hemlock, *Tsuga canadensis* (L.) Carr.. American Naturalist 113: 333-350.

Kimple, A and W Schuster. 2002. Spatial patterns of HWA damage and impacts on tree physiology and water use in the Black Rock Forest, southern New York. Pp. 344-350 in Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium, East Brunswick, NJ. United States Department of Agriculture, Forest Service.

Loustau, D and A Granier. 1993. Environmental control of water flux through maritime pine (*Pinus pinaster* Ait.). In Water Transport in Plants under Climatic Stress, Cambridge University Press, New York, NY. 325 p.

Lu, W and ME Montgomery. 1997. Chinese Coccinellidae for biological control of *Adelges tsugae* Annand. Entomological Society of America, Conference Papers Index, u 1000 Animal and Plant Science, 3347988.

Maenza-Gmelch, TE. 1997. Holocene vegetation, climate, and fire history of the Hudson Highlands, southeastern, New York, USA. The Holocene 7: 25-37.

Maher, N. 2000. Black Rock Forest. Hudson Valley Regional Review 16: 21-40.

Martin, TA, KJ Brown, J Cermák, R Ceulemans, J Kucera, FC Meinzer, JS Rombold, DG Sprugel, and TM Hinckley. 1997. Crown conductance and tree and stand transpiration in a second-growth *Abies amablis* forest. Canadian Journal of Forest Research 27: 797-808.

McClure, MS. 1977. Dispersal of the scale *Fiorinia externa* (Homoptera: Diaspididae) and effects of edaphic factors on its establishment on hemlock. Environmental Entomology 6:539-544.

----------. 1985a. Patterns of abundance, survivorship, and fecundity of *Nuculaspis tsugae* (Homoptera: Diaspididae) on *Tsuga* species in Japan in relation to elevation. Environmental Entomology 14: 413-415.

----------. 1985b. Susceptibility of pure and hybrid strands of *Pinus* to attack by *Matsucoccus matsumurae* in Japan (Homoptera: Coccoidea: Margarodidae). Environmental Entomology 14: 535-538.

----------. 1986. Population dynamics of Japanese hemlock scales: a comparison of endemic and exotic communities. Ecology 67: 1411-1421.

----------. 1987. Biology and control of hemlock woolly adelgid. Connecticut Agricultural Experiment Station, New Haven, Bulletin 851.

----------. 1989. Evidence of a polymorphic life cycle in the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae). Annals of the Entomological Society of America 82: 50-54.

----------. 1990. Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera: Adelgidae). Environmental Entomologist 19: 36-43.

----------. 1991a. Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. Environmental Entomologist 20: 258-264.

----------. 1991b. Pesticides will protect ornamentals from hemlock woolly adelgid. Frontiers of Plant Science 44: 2-3.

----------. 1995a. *Diapterobates humeralis* (Oribatida: Ceratozetidae): an effective control agent of hemlock woolly adelgid (Homoptera: Adelgidae) in Japan. Environmental Entomology 24: 1207-1215.

----------. 1995b. Using natural enemies from Japan to control hemlock woolly adelgid. Frontiers of Plant Science 47: 5-7.

----------, SM Salmon, and KS Shields. 1996. Introduced pest: hemlock woolly adelgid. United States Department of Agriculture Forestry Service FHTET 96-35. 14 p.

---------- and CA Cheah. 1998. Released Japanese ladybugs are multiplying and killing hemlock woolly adelgids. Frontiers of Plant Science 50: 6-8.

McClure, M and CA Cheah. 1999. Reshaping the ecology of invading populations of hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae), in eastern North America. Biological Invasions 1: 241-254.

McClure, M, CA Cheah, and TC Tigner. 1999. Is *Pseudoscymnus tsugae* the solution to the hemlock woolly adelgid problem? an early perspective. General Technical. Report NE-267. Durham, NH: US Department of Agriculture, Forest Service, Northeastern Research Station. 237 p.

McWilliams, WH and TL Schmidt. 1999. Composition, structure, and sustainability of hemlock ecosystems in eastern North America. General Technical Report NE-267. Durham, NH: US Department of Agriculture, Forest Service, Northeastern Research Station. 237 p.

Miller, BJ, PW Clinton, GD Buchan, and AB Robson. 1998. Transpiration rates and canopy conductance of *Pinus radiata* growing with different pasture understories and agroforestry systems. Tree Physiology 18: 575-582.

Mitchell, JM. 1999. Habitat relationships of five northern bird species breeding in hemlock ravines in Ohio, USA. Natural Areas Journal 19: 3-11.

Mladenoff, DJ. 1987. Dynamics of nitrogen mineralization and nitrification in hemlock and hardwood treefall gaps. Ecology 68: 1171-1180.

Montgomery, ME. 1996. Woolly adelgids in the southern Appalachians: why they are harmful and prospects for control. United States Department of Agriculture, Forest Service. Southern Appalachian Biological Control Initiative Workshop Proceedings.

Mueller-Dombois, D and H Ellenburg. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York, NY.

Nadezhdina, N. 1999. Sap flow index as an indicator of plant water status. Tree Physiology 19: 885-891.

Niering, WA. 1998. Forces that shaped the forests of the northeastern United States. Northeastern Naturalist 5: 99-110.

Onken, B, D Souto, R Rhea, and K Watsun. 1995. Hemlock woolly adelgid strategic plan. Unpublished report, United States Department of Agriculture, Forest Service, Northeastern Area Forest Experimentation Station.

Oren, R, N Phillips, BE Ewers, DE Pataki, and JP Megonigal. 1999. Sap-flux-scaled transpiration responses to light, vapor pressure deficit, and leaf area reduction in a flooded *Taxodium distichum* forest. Tree Physiology 19: 337-347.

Orwig, DA. 2002a. Ecosystem to regional impacts of introduced pests and pathogens: historical context, questions and issues. Journal of Biogeography 29: 1471-1474.

Orwig, DA. 2002b. Stand dynamics associated with chronic hemlock woolly adelgid infestations in southern New England. Pp. 36-46 in Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium, East Brunswick, NJ. United States Department of Agriculture, Forest Service.

Orwig, DA and MD Abrams. 1999. Impacts of early selective logging on the dendroecology of an old-growth, bottomland hemlock-white pine-northern hardwood forest on the Allegheny Plateau. Journal of the Torrey Botanical Society 126: 234-244.

Orwig, DA and DR Foster. 1996. Forest ecosystem response to hemlock woolly adelgid outbreak in southern New England. Bulletin of the Ecological Society of America 77: 335.

Orwig, DA, and DR Foster. 1998a. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. Journal of the Torrey Botanical Society 125: 60-73.

----------. 1998b. Hemlock woolly adelgid damage in relation to hemlock distribution across southern New England landscapes. Ecological Society of America, Conference Papers Index, u 1000 Animal and Plant Science, 3383703.

----------. 2000. Stand, landscape, and ecosystem analyses of hemlock woolly adelgid outbreaks in southern New England: an overview. General Technical Report NE-267. Durham, NH: US Department of Agriculture, Forest Service, Northeastern Research Station. 237 p.

Orwig, DA, DR Foster, and DL Mausel. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. Journal of Biogeography 29: 1475-1488.

Orwig, DA and ML Kizlinski. 2002. Vegetation response following hemlock woolly adelgid infestation, hemlock decline, and hemlock salvage logging. Pp. 106-117 in Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium, East Brunswick, NJ. United States Department of Agriculture, Forest Service.

Pacala, SW, CD Canham, J Saponara, JA Silander Jr, RK Kobe, and E Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecological Monographs 66: 1-43.

Paine, RT. 1966. Food web complexity and species diversity. American Naturalist 100: 65-75.

Pallardy, SG, J Cermak, FW Ewers, MR Kaufman, WC Parker, and JS Sperry. 1995. Water transport dynamics in trees and stands. In Resource Physiology of Conifers, Academic Press, Inc., San Diego, CA. 425 p.

Parker, BL, M Skinner, S Gouli, T Ashikaga, and HB Teillon. 1998. Survival of hemlock woolly adelgid (Homoptera: Adelgidae) at low temperatures. Forest Science 44: 414-420.

Parker, BL, M Skinner, S Gouli, T Ashikaga, and HB Teillon. 1999. Low lethal temperature for hemlock woolly adelgid (Homoptera: Adelgidae). Environmental Entomology 28: 1085-1091.

Parshall, T. 1995. Canopy mortality and stand-scale change in northern hemlock-hardwood forest. Canadian Journal of Forest Research 25: 1466-1478.

Pataki, DE, R Oren, G Katul, and J Sigmon. 1998a. Canopy conductance of *Pinus taeda*, *Liquidambar styraciflua* and *Quercus phellos* under varying atmospheric and soil water conditions. Tree Physiology 18: 307-315.

Pataki, DE, R Oren and N Phillips. 1998b. Responses of sap flux and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area. Journal of Experimental Botany 49: 871-878.

Petrides, GA. 1986. Peterson field guide: trees and shrubs. Houghton Mifflin Company, MA. 428p.

Phillips, N, R Oren and R Zimmermann. 1996. Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. Plant, Cell and Environment 19: 983-990.

Power, ME, D Tilman, JA Estes, B A Menge, WJ Bond, LS Mills, G Daily, JC Castilla, J Lubchenco, and RT Paine. 1996. Challenges in the quest for keystones: identifying keystone species is difficult – but essential to understanding how loss of species will affect ecosystems. Bioscience 46: 609-620.

Putrich, GS and JA Petty. 1971. Effect of balsam woolly adelgid, *Adelges picea* (Ratz.) infestation on xylem of *Abies grandis* (Doug.)(Lindl.). Journal of Experimental Botany 22: 946-952.

Raup, HM. 1938. Botanical studies in the Black Rock Forest. Black Rock Forest Bulletin No.7. Cornwall Press, Cornwall, NY. 161 p.

Rhea, JR. 1995. Economic and environmental impacts of the hemlock woolly adelgid, *Adelges tsugae* on the hemlock resources of Eastern North America. International Union of Forestry Research Organizations, Conference Papers Index, u 1000 Animal and Plant Science, 3182927.

Rogers, RS. 1978. Forests dominated by hemlock (*Tsuga canadensis*): distribution as related to site and postsettlement history. Canadian Journal of Botany 56: 843-854.

Rogers, RS. 1980. Hemlock stands from Wisconsin to Nova Scotia: transitions in understory composition along a floristic gradient. Ecology 61: 178-193.

Royle, DD and RG Lathrop. 1997. Monitoring hemlock forest health in New Jersey using Landsat TM data and change detection techniques. Forest Science 43: 327-335.

Ryan, MG, BJ Bond, BE Law, RM Hubbard, D Woodruff, E Cienciala, and J Kucera. 2000. Transpiration and whole-tree conductance in ponderosa pine trees of different heights. Oecologia 124: 553-560.

Salom, SM, WT Mays, and JW Neal. 1997. Duration of hemlock woolly adelgid life stages and aestival diapause under different constant temperatures and photoperiods. Entomological Society of America, Conference Papers Index, u 1000 Animal and Plant Science, 3347455.

Saugier, B, A Granier, JY Pontrailler, E Dufrene, and DD Baldocchi. 1997. Transpiration of a boreal pine forest measured by branch bag, sap flow, and micrometeorological methods. Tree Physiology 17: 511-519.

Simpson, DG. 2000. Water use of interior Douglas-fir. Canadian Journal of Forest Research 30: 534-547.

Smith, GF and NS Nicholas. 1998. Patterns of overstory composition in the fir and fir-spruce forests of the Great Smoky Mountains after balsam woolly adelgid infestation. American Midland Naturalist 139: 340-352.

Smith, RE. 1992. The heat pulse technique for determining water uptake of *Populus deltoides*. South African Journal of Botany 58: 100-104.

Smith, RL. 1990. Student resource manual to accompany ecology and field biology. HarperCollins Publishers, New York, NY.

Snyder. 2002. Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. Canadian Journal of Fisheries and Aquatic Sciences 59: 262-275.

Sokal, RR and FJ Rohlf 1981. Biometry, second edition. WH Freeman, New York.

Souto, D, T Luther, and B Chianese. 1996. Past and current status of hemlock woolly adelgid in eastern and carolina hemlock stands. Pp. 9-15 in: Proceedings of the First Hemlock Woolly Adelgid Review, United States Department of Agriculture, Forest Service, FHTET 96-10.

Steinberg, SL, MJ McFarland, JW Worthington. 1990. Comparison of trunk and branch sap flow with canopy transpiration in pecan. Journal of Experimental Botany 41: 653-659.

Stephenson, SL. 1986. Changes in a former chestnut-dominated forest after a half century of succession. American Midland Naturalist 116: 173-179.

Tingley, MW, DA Orwig, RC Cobb, and DR Foster. 2002. Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations. Journal of Biogeography 29: 1505-1516.

Tyrrel, LE and TR Crow. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology 75: 370-386.

Vertessey, RA, TJ Hatton, P Reece, SK O'Sullivan, and RG Benyon. 1997. Estimating stand water use of large mountain ash trees and validation of the sap flow measurement technique. Tree Physiology 17: 747-756.

Wakamiya-Noborio, I, JL Heilman, RJ Newton, and MG Messina. 1999. Diurnal changes in water conduction in loblolly pine (*Pinus taeda*) and Virginia pine (*P. virginiana*) during soil dehydration. Tree Physiology 19: 575-581.

Ward, JS and DM Smith. 1999. Dynamics of Connecticut hemlock stands. General Technical Report NE-267. Durham, NH: US Department of Agriculture, Forest Service, Northeastern Research Station. 237 p.

Whitehead, D, WRN Edwards, and PG Jarvis. 1984. Conducting sapwood area, and permeability in mature trees of *Picea stichensis* and *Pinus contorta*. Canadian Journal of Forest Research 14: 940-947.

Woods, KD. 2000. Dynamics in late-succesional hemlock-hardwood forests over three decades. Ecology 81: 110-126.

Wullschleger, SD, FC Meinzer, and RA Vertessey. 1998. A review of whole-plant water use studies in trees. Tree Physiology 18: 499-512.

Yamasaki, M, RM DeGraaf, and JW Lanier. 1999. Wildlife habitat associations in eastern hemlock – birds, smaller mammals, and forest carnivores. General Technical Report NE-267. Durham, NH: US Department of Agriculture, Forest Service, Northeastern Research Station. 237 p.

Yorks, TE. 2002. Influence of hemlock mortality on soil water chemistry and ground flora. Pp. 47-49 in Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium, East Brunswick, NJ. United States Department of Agriculture, Forest Service.

Yorks, TE, DJ Leopold, and DJ Raynal. 2000. Vascular plant propagule banks of six eastern hemlock stands in the Catskill Mountains of New York. Journal of the Torrey Botanical Society 127: 87-93.

Young RF, KS Shields, and GP Berlyn. 1995. Hemlock woolly adelgid (Homoptera: Adelgidae): stylet bundle insertion and feeding sites. Annuals of the Entomological Society of America 88: 827-835.

Young, JA, CD Snyder, J Akerson, and G Hunt. 1999. Assessment of landscape correlates of eastern hemlock decline due to hemlock woolly adelgid. General Technical Report NE-267. Durham, NH: US Department of Agriculture, Forest Service, Northeastern Research Station. 237 p.

Zhang, H, LP Simmonds, JIL Morison, and D Payne. 1997. Estimation of transpiration by single trees: comparison of sap flow measurements with a combination equation. Agricultural and Forest Meteorology 87: 155-169.