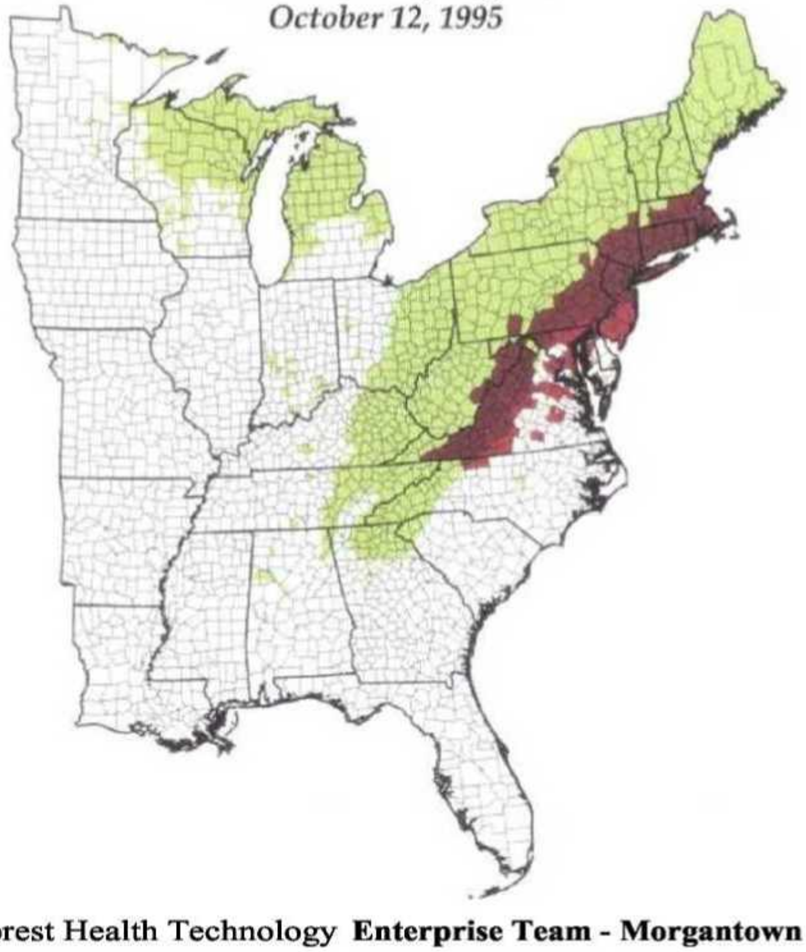
Forest Health Technology Enterprise Team

TECHNOLOGY
TRANSFER

Hemlock Woolly
Adelgid

Proceedings of the First Hemlock Woolly Adelgid Review

Charlottesville, Virginia
October 12, 1995



Forest Health Technology **Enterprise Team - Morgantown**

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PREFACE

The hemlock woolly adelgid (HWA) has become a very important pest of eastern and Carolina hemlocks in the eastern United States. It is significant because this pest has killed and continues to kill trees, ranging from landscape shrubs to treasured giants. This pest knows no boundaries and has impacted National Parks, Recreation Areas, and Forests; State Forests; commercial and private landowners; and urban and suburban communities. Not surprisingly, the people involved in solving or minimizing this problem are as equally varied: university, federal, and state forest entomologists, ecologists, forest managers, urban foresters, and extension agents.

Because adelgid outbreaks surfaced in the 1980s and grew steadily in acreage and impact, four individuals initiated a Hemlock Woolly Adelgid Working Group Committee in 1993. They are: Brad Onken, Dennis Suoto, Rusty Rhea, all with USDA Forest Service, Forest Health units, and Keith Watson from the Shenandoah National Park. The committee organized an initial working group meeting at Hoover Camp, Shenandoah N.P., in July of 1994. The participants included many of the individuals who at the time were working or planning to work on hemlock woolly adelgid. One of the goals of the meeting was to learn about what research was going on. The informal setting encouraged lively discussions. A meeting outcome was a "Strategic Plan" for prioritizing research areas for future funding. Another outcome was a plan to hold a larger-scale meeting the following year to update everyone on current research activities and future research needs.

The follow-up meeting was held at the Virginia Department of Forestry Meeting Hall in Charlottesville, Va., on October 12, 1995. It was attended by 80 individuals. Fifteen formal presentations were made, of which 14 are included as manuscripts in these proceedings. We feel the coverage given in these presentations is both a good introduction into the current problem resulting from HWA and a good departure point for continued and future research efforts. It is obvious that while there are many interested and talented people working on the HWA problem, a great deal more work needs to be done if we are to reduce the impact of HWA on our treasured hemlocks. Funding for research continues to be a struggle and lacks a coordinated effort among state and federal agencies and private organizations. It is hoped that this publication can play a part in building a coordinated and decently funded effort for this very serious problem.

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PROCEEDINGS OF THE FIRST HEMLOCK WOOLLY ADELGID REVIEW

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VALUE AND IMPORTANCE OF HEMLOCK ECOSYSTEMS

IN THE EASTERN UNITED STATES

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ABSTRACT

Little information in the literature quantifies the value of a hemlock (Tsuga *canadensis)* ecosystem. There was a time when hemlocks were large, plentiful, and a considerable economic resource. The old-growth hemlock was exploited for both bark and wood. That era ended approximately a century ago when the last old-growth trees were harvested. However, there can be no doubt that hemlock is still an extremely important component of the forest. The combination of longevity, shade tolerance, and crown density make hemlock unique and invaluable in our forest ecosystems.

HISTORY OF HEMLOCK

Upon arrival in North America, the early European colonists found forests that contained vast numbers of large hemlocks (Frothingham 1915). It was not uncommon for hemlocks to be 100 to 160 feet tall and five to six feet in diameter (Frothingham 1915), and be more than 500 years old (Godman and Lancaster 1990). Examples of these trees, albeit not quite as large or as old, can still be seen in park and natural areas that are under protection (Swartley 1984). Because hemlock survives well in the shade of an overstory, and is very adaptable to a variety of soil types, it successfully encroached into stands that had remained undisturbed for centuries (Brisbin 1970). Although there are no good records of hemlocks' ancient distribution, there is reason to believe that it was once considerably more common than it is today. Whitney (1990) estimated, through the records of one Samuel Dale's 1814-15 land survey of the Allegheny Plateau, that hemlock comprised 19.9 percent of the trees in the forest at that time. A survey conducted in 1973 indicated that the proportion of hemlock (based on trees >5 inches dbh) had fallen to 5.8 percent, roughly 30 percent of what it once was.

ECONOMIC VALUE OF HEMLOCK

From a purely economic perspective, hemlock has probably the most variable record of any tree species. Initially, the most highly prized tree species in the old-growth forests was white pine. Even though hemlock trees were comparable in size, the white pine had superior strength for ships' masts and was the preferred wood for construction and furniture. Hemlock wood is coarse-grained, brash, and difficult to fashion into cabinetry. It is also subject to splitting, a consequence of a defect known as wind shake. However, once the old-growth white pine was gone or inaccessible, the lumber barons looked to hemlock for economic opportunities. Actually, hemlock turned out to be valuable for both its wood and its bark. The bark has high concentrations of tannin and was heavily used by the hide tanneries, and the wood was quite suitable for framing, sheathing, subflooring, and crating. Because of these attributes, the old-growth hemlocks were exploited until that resource was mostly depleted.

During the years subsequent to the old-growth removal, hemlock trees were too small and poorly distributed to be much of an economic consideration. As other sources of tannin were developed, the economic utility of hemlock to the tanneries dropped precipitously. However, the economic status of hemlock is now changing. The second-growth hemlocks have matured sufficiently such that there is now a market for both the lumber and pulpwood (Godman and Lancaster 1990). The consumption of hemlock sawlogs in Pennsylvania in 1988 was 27,000,000 board feet, which was 2.4 percent of the total, and more than twice that of white pine.

One misconception in many of the historic references on hemlock, including Frothingham (1915), is that the hemlock logs were left in the woods to rot after the bark was removed. This perception was challenged by Bennett (1986), who stated that the logs were left in the woods only until after the peeling season was over, whereupon *the crews* would *return to remove* them. Bennett based his conclusion on the observation that there were no remnant logs to be found in the forests of 1986. This finding is consistent with the work of Tyrrell and Crow (1994), who estimated that it takes nearly 200 years for hemlock logs to lose structural *integrity* and *become* partially incorporated into the soil.

Another common misperception about hemlock is that it is toxic. The tea made from hemlock needles is not only tasty, it's rich in vitamin C. The aborigines of North America made a palatable food from the inner bark of hemlock (Swartley 1984). Oil of hemlock, distilled from the leaves of hemlock, was used medicinally for many years (Draemel 1950). Various poultices derived from the inner bark and sap of hemlock have been used effectively to heal wounds. In fact, according to Swartley, no part of the hemlock tree is poisonous.

HEMLOCK ECOSYSTEM

Tsuga canadensis (L.) ranges from Nova Scotia across southern Ontario and northern Michigan to northeastern Minnesota. Also, isolated stands of hemlock occur in Indiana, Kentucky, and Ohio. The species is found throughout New England, New York, Pennsylvania, and the Middle Atlantic States, extending westward from central New Jersey to the Appalachian Mountains, then southward into northern Georgia and Alabama (Godman and Lancaster 1990). Extant hemlock ecosystems are patchy in distribution. Hemlock, because it grows slowly in the understory, usually does not dominate a stand for centuries. Thus, it will be some time before hemlock can regain its presettlement status in the second-growth forests. Hemlock is a long-lived, late-successional/climax species, so if a site remains undisturbed by human development, or other forces, it will eventually dominate a stand.

Hemlock has a very shallow root system. Consequently, it does best in situations where the soil remains moist throughout the year. The best hemlock stands are found on north- and east-facing slopes, and in gorges where there is high humidity and it stays relatively cool (Benzinger 1994a, b, c). Deep, fertile loams of alluvial or colluvial origin seem to be the ideal for hemlock. Hemlock is adaptable, though, to a variety of soils. It can be found on rocky, acid soils, loams, and silt loans, as well as moist benches, flats, and swamp borders that are less well drained and heavier in texture (Hough 1960). Because the roots of hemlock are situated so near the soil surface, any extremes in soil moisture, either too dry or too wet, will quickly and adversely affect hemlocks. Drought or flooding will often lead to mortality of hemlock trees (Graham 1943, McIntyre and Schnur 1936, Secrest et al. 1941, Stickel 1933).

In time, a hemlock stand tends to create an environment that is suitable for perpetuating itself. First, it modifies the environment where it grows. There are no darker, cooler places in the forest than under a hemlock canopy; thus, the soil surface of the stand is kept from drying out. Second, because hemlock is extremely shade tolerant, its regeneration survives well in the understory. The seedlings of other tree species simply cannot tolerate heavy shading and do not survive. In instances cited by Hough (1960), some hemlocks persisted in a suppressed state for more than 350 years and were still quite healthy. Some of the trees mentioned by Hough were more than 100 years old and were only one inch in diameter. According to Lancaster (1985), old, suppressed hemlock trees respond quite well when the overstory is removed either by cutting or natural disturbance. Hemlock's extreme shade tolerance and longevity allows it to outlast other species, so that, given adequate moisture, it is strongly represented in the climax forest (Simpson et al. 1990, Swartley 1984).

Hemlock is susceptible to wind throw because of its shallow root system. It is not uncommon for stands of hemlock to fall domino-fashion during wind storms, particularly if the ground is wet. The forest floor in most eastern hemlock types is marked by hollows and mounds resulting from such blowdowns (Willis and Coffman 1975). Because these windfalls open up hemlock stands to sunlight, and expose mineral soil, other species are allowed to encroach. Yellow birch and sugar maple, especially, benefit from this type of disturbance.

Hemlock possesses genetic attributes that may offer species resistance to hemlock woolly adelgid, the elongate hemlock scale, and other pests. According to Swartley (1984), hemlock appears to be the most genetically complicated of tree species and exhibits a range of variants wider, perhaps, than can be found in any other tree species. While these characteristics do not guarantee hemlock resistance to any particular pest, it is reason for continued study.

ECOLOGICAL VALUE OF HEMLOCK

A number of wildlife species benefit from the environment that exists in hemlock stands. Hemlock is an important cover species for ruffed grouse, turkey, snowshoe hare, and rabbit (Jordan and Sharp 1967). The foliage of hemlock makes a suitable forage and habitat for deer, particularly in the winter (Lapin 1994). Lapin (1994) discusses the importance of hemlock ecosystems to birds, fish, invertebrates, amphibians, reptiles, mammals, threatened and endangered species and communities, and water quality and soils. Among these, she notes a number of species that are obligate of eastern and Carolina hemlock (T. caroliniana Engelm.). She lists almost 90 species of birds in Connecticut that use hemlock as a food source, a nesting site, a roost site, or a winter shelter. Benzinger (1994a, b, c) identified three bird species that appear to be hemlock obligates, including the black-throated green warbler, the solitary vireo, and the northern goshawk. Two other classifications, the primary and secondary " facultatives," included 12 other species of birds.

Other species that flourish on the kind of habitat provided by hemlock stands include leatherwood, rattlesnake plantains, bunchberry, goldthread, *Lycopodium* spp., bluebead, Canada mayflower, wood sorrels, and many other herbs and shrubs (Willis and Coffman 1975, Alverson et al. 1988). The ground cover of hemlock-northern hardwood forests is strongly influenced by the amount of hemlock in the overstory. Low light levels, acidic, nutrient-poor litter, and reduced precipitation reaching the forest floor may all be responsible for a marked reduction in ground cover and species diversity (Simpson et al. 1990). Brook trout are found more commonly in streams in hemlock ecosystems because of the cooling effect of the hemlock canopy. Studies show that the removal of the riparian vegetation, especially that within 80 feet of the stream, can cause a temperature elevation of 6 to 9 degrees Celsius (Lapin 1994). In short, while species diversity tends to be limited within dense hemlock stands, the species that are there are dependent on those conditions, and many would be negatively affected in the absence of the hemlock ecosystem (Black and Mack 1976). Studies on a hemlock ecosystem conducted at the Delaware Water Gap National Recreational Area during the past three years have shown a considerable number of associations among both plants and animals in hemlock stands there. I will defer to Richard Evans to tell you about those observations later in these proceedings.

Devlin and Crownover (1983) estimated the value of coniferous forest cover, of which hemlock is a significant component in Pennsylvania, to be worth at least $40 per acre per year in its contribution to wildlife welfare. They considered the economic value based on sport hunting as well as the social values related to nonconsumptive *activities*. However, ecological values proved to be too intangible to quantify. They did state that "many wildlife species depend on coniferous cover in some form for either food, cover, or nesting sites," and that a minimum of five percent coniferous cover in the forest is essential to support adequate numbers and diversity of wildlife species.

AESTHETIC VALUE OF HEMLOCK

Aesthetically, the hemlock has no equal in the east. Frothingham (1915) stated, "During youth, hemlock is the most graceful and beautiful of eastern conifers." Even as a mature tree, hemlock is broadly appealing. These attributes no doubt helped prompt Gifford Pinchot to nominate eastern hemlock to be the official "state tree" of Pennsylvania.

Hemlock's habit of growing along mountain streams and lakes, plus the shade afforded by its dense foliage, makes it ideal for recreational habitats (Burnham et al. 1947). One would need to visit only a sampling of state or national parks in the northeastern United States to validate that hemlock stands are attractive to humans. This should come as no surprise. Hemlock stands are cooler than hardwood stands in the summer because of the dense shade they provide. Paradoxically, hemlock stands may seem warmer than the hardwoods in the winter by *virtue of the* protection from winds afforded by the trees' crowns. These parks provide recreational opportunities for millions of people annually and, doubtless, the popularity of woodland parks would be considerably lower if hemlocks were not present.

There is also no disputing the appeal of hemlock in the landscapes of our homes, cities, parks, cemeteries, and other public areas. According to Swartley (1984), there are 274 cultivars of eastern hemlock, making it one of the most cultured and cultivated landscape tree species. Hemlock is popular as a hedge, for shrubbery, as Christmas trees, and as trees for the yard or border (Hough 1960). The dark green boughs of hemlock make it a splendid backdrop for many flowering trees and shrubs. Hemlock makes the ideal landscape plant; it provides habitat for birds and other wildlife, moderates the heat in the summer, blocks the wind in the winter, is an excellent noise absorber, and is aesthetically pleasing. Two drawbacks of hemlock in the landscape are that it can get too large for the site in which it is planted (although probably not in your lifetime), and it is susceptible to a number of insect and disease pests, including: the hemlock woolly adelgid *(Adelges tsugae)*, the elongate hemlock scale (*Fiorinia externa)*, the hemlock looper *(Larnbdina fisceIlaria)*, and, when it .is under drought stress or any other stress, it can be easy prey to the hemlock borer *(Melanophila fulvoguttata)* and the shoestring root rot (Armillaria mellea). The latter two pests are usually fatal to the tree when they successfully invade it.

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PAST AND CURRENT STATUS OF HWA IN EASTERN AND CAROLINA HEMLOCK STANDS

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ABSTRACT

Although hemlock woolly adelgid (*Adelges tsugae*) has existed in eastern (*Tsuga canadensis*) and Carolina (*T. caroliniana*) hemlock stands for the past 40 years, concern and interest have been concentrated in the last ten years. The interactions between hemlock woolly adelgid (HWA) and other stressors (abiotic and biotic) have been an important part of HWA's history in the eastern USA.

HWA now occurs in parts of eleven states along the eastern seaboard from North Carolina to Massachusetts. HWA impacts on eastern and Carolina hemlock vary greatly and are difficult to predict because they are strongly influenced by site conditions and other stressors. In 1995, all states report poor crown condition and reduced terminal growth on infested trees and stands. Four states report noticeable tree mortality this year. In fact, this mortality has increased sharply since 1994. The drought of 1995 raises additional concern about increasing tree mortality in 1996 and beyond.

HISTORY

The hemlock woolly adelgid, *Adelges tsugae*, was first reported on eastern hemlocks in Richmond, Virginia, in 1953 or 1954. The trees were located in a large municipal park (Maymont Park) that originally had been the estate of an avid plant collector. Hemlock woolly adelgid (HWA) may have actually arrived in Richmond earlier in this century. Thus, HWA's story in the east begins with ornamental trees and lack of clarity -- themes that will be repeated.

In the next 30 years (1955-1985), HWA slowly spread through the mid-Atlantic states. However, it was considered no more than an annoying ornamental pest that could be controlled with insecticides. For example, Pennsylvania first reported it in the 1960s and New York in the early 1980s-yet concern surfaced in both states only in the late 1980s.

Even in Virginia, FIWA was considered only an ornamental pest despite its spread from ornamental hemlocks in Richmond to Ashland, Danville, and Rocky Mount (Figure 1). Native hemlocks were first reported infested in the early 1960s at the foot of the Blue Ridge about 10 miles west of Rocky Mount. Once HWA reached native hemlocks in Virginia, the outbreak's behavior changed; the rate of spread and intensity of damage increased sharply. In the mountains, infested hemlocks (both eastern and Carolina) quickly began to show severe stress, with scattered mortality, as was reported at the Peaks of Otter area in the Blue Ridge Parkway National Park (elevation about 2400 feet).

Two abiotic events occurred in 1985 that significantly affected the F I W A outbreak in the east. (We will see future abiotic events that influence H W A as well.). In January a severe cold wave moved across southwestern Virginia. At elevations above 2000 feet, temperatures of --20 to -28 degrees F were common. Subsequent surveys revealed that HWA was absent above 2000 feet and that population abundance was greatly reduced at lower elevations. The HWA outbreak in Virginia had been (temporarily) broken.

Hurricane Gloria hammered the east coast in September 1985. In 1986, Mark McClure (Connecticut Agricultural Experiment Station) found HWA in southern Connecticut. This new infestation may have been carried from infested areas on Long Island by the hurricane. The discovery of HWA in Connecticut coincided with the beginning of increased visibility and concern about HWA. No longer would HWA be viewed as simply an ornamental pest that could be controlled with some effort.

Between 1985 and 1995 the HWA infestation spread north and south along the eastern seaboard. Concerns grew as hemlock tree condition deteriorated in the oldest infested areas. HWA recovered slowly but steadily from the severe cold wave of January 1985 in Virginia. By 1995, tree mortality was again reported in the Blue Ridge Parkway area. Uninfested states in northern New England (Vermont, New Hampshire, and Maine) instituted quarantines to prevent HWA from reaching their considerable hemlock resources. A very cold winter in 1993-1994 markedly decreased HWA abundance throughout its range -- the 2nd time that winter weather had affected HWA. However, just as with the cold wave in Virginia 8 years before, H W A recovered steadily.

Only New York reports HWA's northward spread to have stopped. Within the Hudson River corridor, no new HWA infestations have been reported since 1992. It is intriguing that this location also marks the northernmost limit of red pine scale and red pine adelgid spread.

CURRENT STATUS

HWA infests all or parts of North Carolina, Virginia, West Virginia, Maryland, Delaware, Pennsylvania, New Jersey, New York, Connecticut, Rhode Island, and Massachusetts (Figure 2). The rate of spread into uninfested areas is about 10-15 miles a year but is very unpredictable (Figure 3). In infested towns and counties, HWA is becoming more commonly distributed between known infested sites.

HWA impacts on eastern and Carolina hemlocks vary widely. One extreme example is the complete mortality of dominant hemlocks at Sparta Glen in northwestern New Jersey. At the opposite end of the spectrum are hemlock stands in Pennsylvania that appear vigorous despite HWA presence -- in some cases for as long as 20 years. Most states report impacts between *these* two extremes, with infested trees exhibiting poor crown condition and sharply reduced terminal branch growth. Many states report that trees stressed by other factors often show the greatest impacts from HWA attack. These predisposing stressors range from poor site conditions, drought, and elongate hemlock scale to defoliators such as hemlock looper moth and gypsy moth.

Hemlock borer is a typical secondary agent that attacks and kills trees weakened by other stressors such as HWA and drought. For example, Virginia reports increased hemlock borer activity in 1995 in hemlock stands that have the oldest HWA infestations. A drought in Pennsylvania in 1930-1931 resulted in significant hemlock mortality caused by hemlock borer (Knull and Perry 1931). Because hemlock is a shallow-rooted species, drought kills many fine roots near the surface. The 1995 drought could increase tree mortality in the next few years, particularly among trees/stands already weakened by HWA; hemlock borer may become important in this equation.

Because of predisposing factors and the presence of secondary agents, many stressors may be involved in killing hemlock trees. That is why it is so difficult to predict where, or how much, hemlock mortality will occur. At the same time, it explains how two hemlock stands can respond so differently to HWA attack.

Tree mortality is reported in 1995 from Virginia, New Jersey, New York, and Connecticut. In fact, the trend is accelerating tree mortality. For example, the New jersey Department of Agriculture established permanent plots in 1988 in 11 hemlock stands to monitor impacts. Since 1992 they have monitored tree mortality in the stands as well as in their permanent plots. Tree mortality increased sharply in some stands between the 1994 and 1995 observations. Again, the hemlock stands with the oldest HWA infestations have the greatest mortality.

CONCLUSIONS

Based on the past and current status of HVVA in eastern and Carolina hemlock stands, we believe 3 questions are critically important to answer if we are to effectively manage hemlock and HWA in the future. They are:

1) How far will HWA spread?

2) How many hemlocks will die and most importantly WHERE?

3) How best to protect hemlock in vulnerable forests and ornamental landscapes?

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Native Range of Eastern Hemlock in Virginia

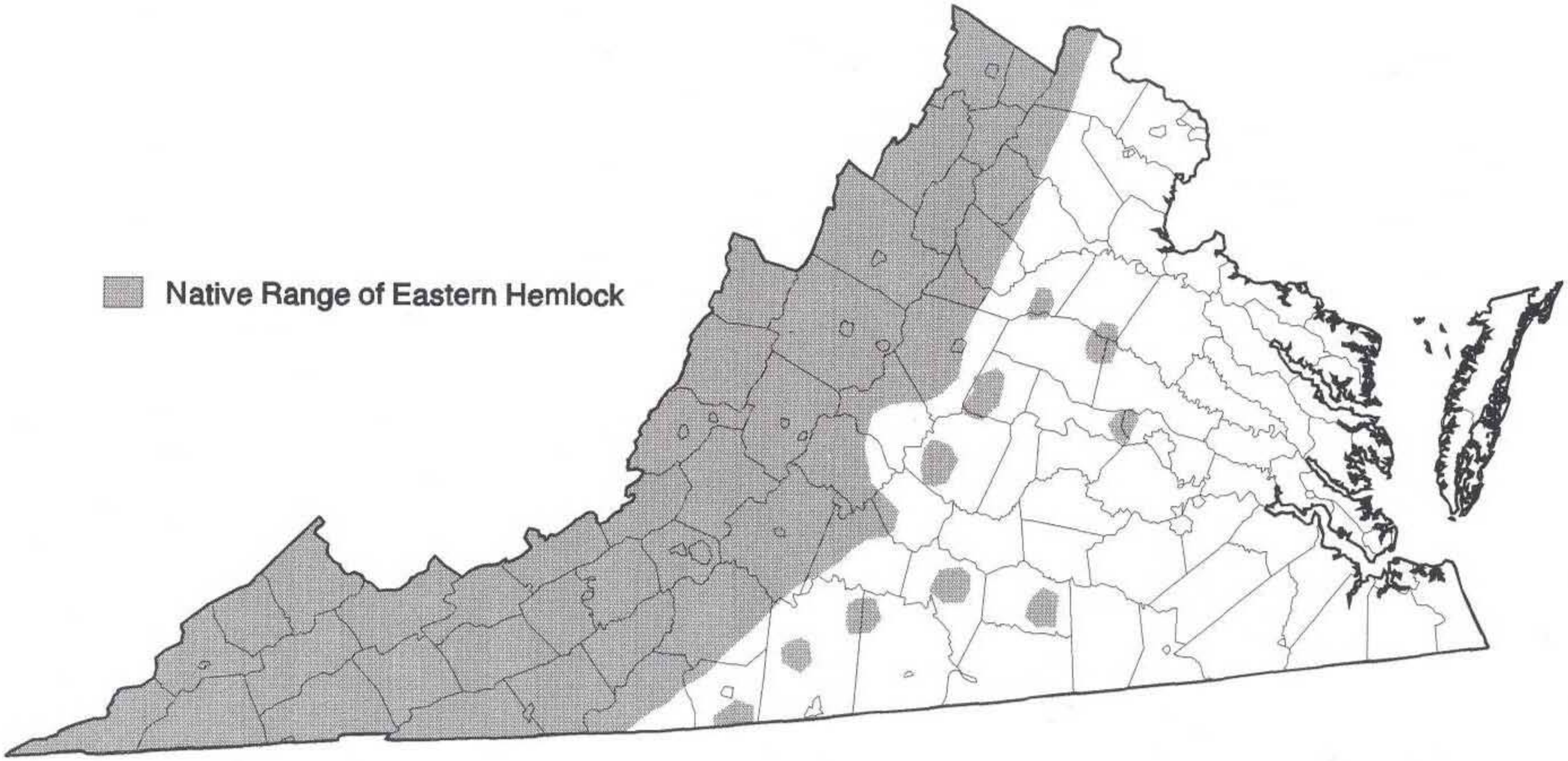

Figure 1. Native Range of Eastern Hemlock in Virginia

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10/95

Hemlock Woolly Adelgid Distribution - 1995

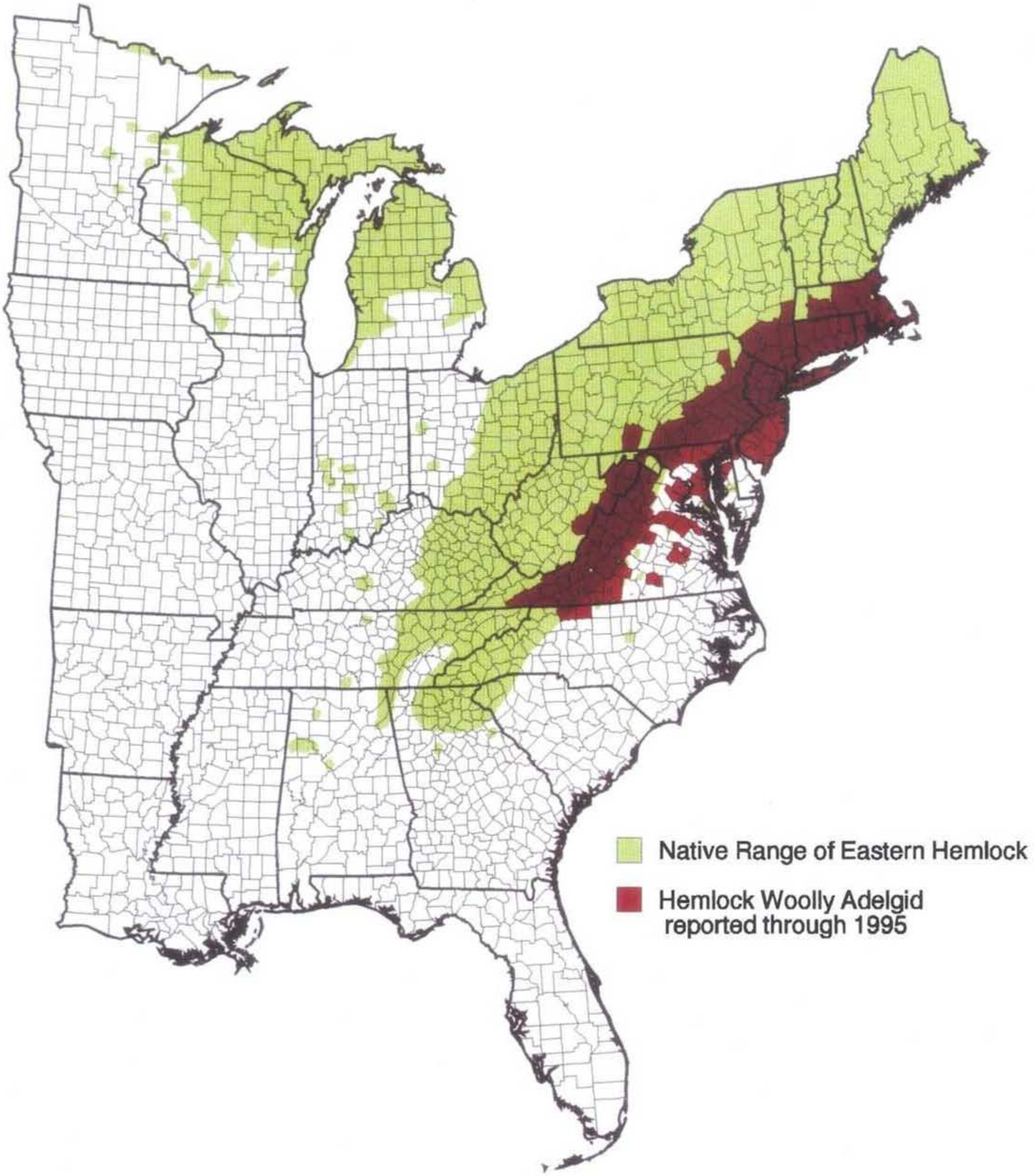

Figure 2. Hemlock Woolly Adelgid Distribution - 1995

Produced by: USDA Forest Service, Northeastern Area - Forest Health Protection GIS Group

9/95

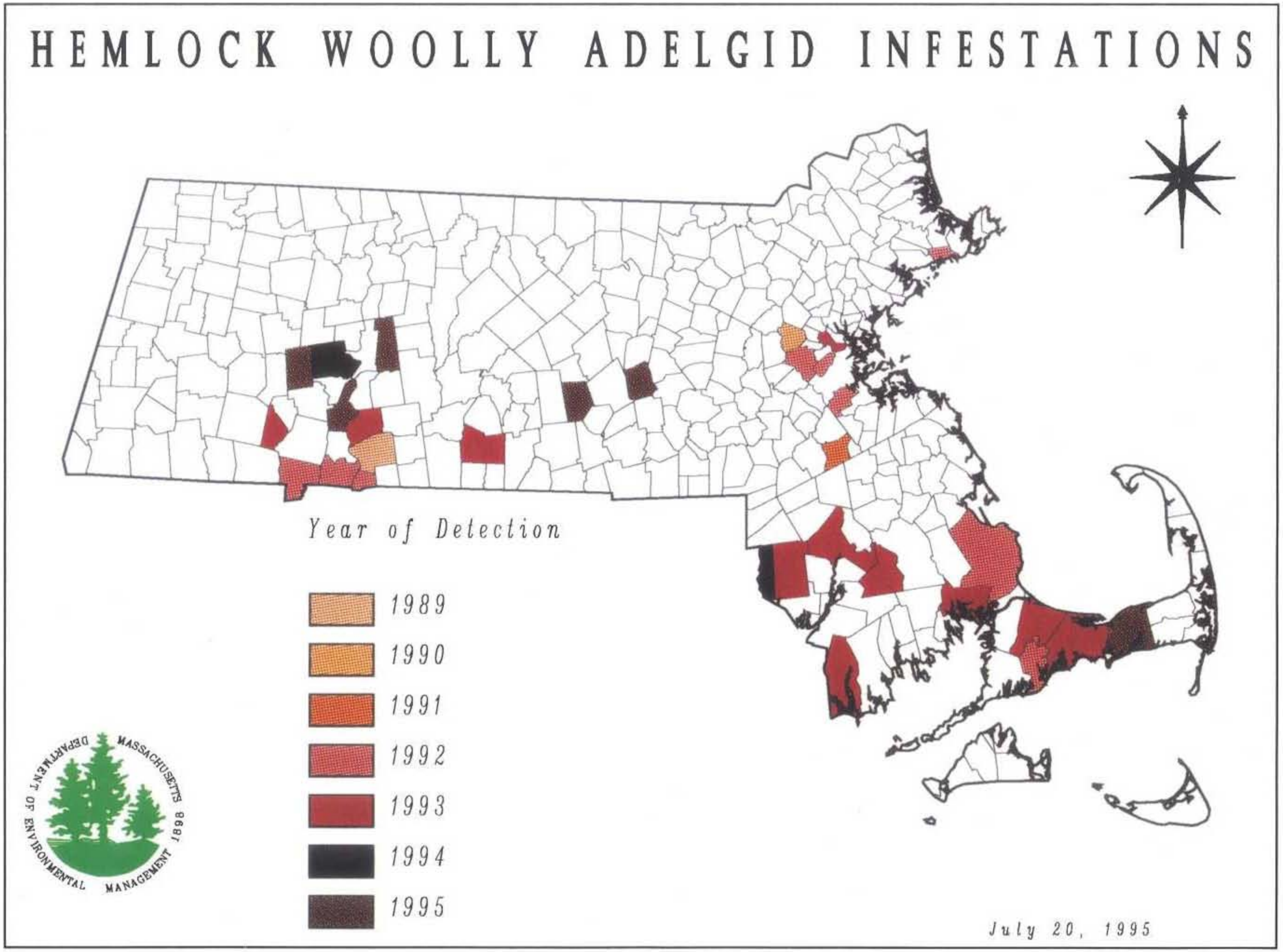

Figure 3. Hemlock Woolly Adelgid Infestations in Massachusetts

BIOLOGY OF ADELGES TSUGAE AND ITS POTENTIAL FOR SPREAD IN THE NORTHEASTERN UNITED STATES

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ABSTRACT

In Japan and the northeastern United States, hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae), is parthenogenetic and has a polymorphic life cycle that involves both hemlock *(Tsuga)* and spruce *(Picea).* Stages of development are identical in both countries, but in Japan adelgid phenology varies greatly among sites and is related to elevation and hemlock phenology. All three generations of *A. tsugae* on hemlock have six stages of development: the egg, four nymphal instars, and the adult. Eggs and first instar nymphs of the three generations are indistinguishable; the presence and sclerotization of thoracic sutures and wing bud notches, and the size and shape of the body, the thorax, and the antennae distinguish the later instars and adults. Native populations of *A. tsugae* on *Tsuga diversifolia* and *T. sieboldii* in Japan are maintained at low innocuous densities by host resistance and natural enemies. Introduced populations on *T. canadensis* in Connecticut are injurious and unregulated, and are adversely affected by density-dependent effects on survival, fecundity, and sexuparae production.

Some of the offspring produced by the sistens in June become winged adult sexuparae and migrate to spruce where they produce eggs of the sexuales. However, because no sexuales nymphs survive on any of the spruce species available in the northeastern United States, there is substantial mortality to the population on hemlock there each year. Nevertheless, *A. tsugae* still thrives because of its two annual generations, its high reproductive potential, and the lack of any other significant mortality factors. The presence of adelgid galls on *P. jezoensis hondoensis* and *P. polita* in Japan implicates these species as primary native hosts.

In Japan *A. tsugae* incurs less than 25% mortality during winter at high elevations (1500 - 1650 m) where minimum daily temperatures often reach -35° C. The high mortality (> 90%) observed in Connecticut during the severe winter of 1993-94 suggests that the adelgids originally introduced into eastern North America from Japan were from a less cold-hardy stock. Although low winter temperatures may retard the spread of *A. tsugae* in eastern North America, the adelgid will probably develop sufficient cold-hardiness to expand its distribution northward.

INTRODUCTION

Hemlock woolly adelgid, *Adelges tsugae* Annand, is a destructive introduced pest of forest and ornamental eastern hemlock, *Tsuga canadensis (L.)* Carriere, in at least 10 of the eastern United States. This same adelgid is widely distributed throughout central Japan, the probable homeland, where it is an innocuous inhabitant of *Tsuga diversifolia* Masters and *Tsuga sieboldii* Carriere (McClure 1995a). Although this insect has been known to occur in Asia (Formosa and Japan) since 1936 (Takahashi 1937), in western North America (Vancouver, British Columbia; California; Oregon) since the early 1920's (Annand 1924), and in eastern North America (Virginia) since 1951 (Gouger 1971), its biology remained unstudied anywhere until it invaded Connecticut in 1985 (McClure 1987a). Before then *A. tsugae* was thought to have a simple monomorphic life cycle represented only by the parthenogenetic sistens that are restricted to hemlock. Host plants other than hemlock and winged and sexual stages of this adelgid were unknown (Annand 1928). However, studies in Connecticut and in Japan discovered new developmental stages and revealed a complex polymorphic life cycle of *A. tsugae* that implicates spruce (*Picea* spp.) as an alternate host for this adelgid (McClure 1987b, 1989, 1996).

Here I review the biology of *A. tsugae* in Connecticut and in Japan and, on the basis of that review, evaluate the potential of this destructive pest to expand its distribution in the eastern United States.

BIOLOGY IN THE NORTHEASTERN UNITED STATES

Stages of development:

There are three generations of *A. tsugae* each year on *T. canadensis:* the sistens (overwintering generation); the progrediens (spring generation that remains on hemlock); and the sexuparae (spring generation that migrates to spruce). All three of these generations have six stages of development: the egg; four nymphal instars; and the adult. Detailed descriptions and drawings of these life stages, and of the procedures used in collecting, preserving, mounting and measuring *A. tsugae* are given elsewhere (see McClure 1989, 1991).

Eggs are oblong and amber colored; they measure 0.36 ± 0.04 mm long by 0.23 ± 0.03 mm wide for sistens, and 0.35 ± 0.04 mm long by 0.21 ± 0.03 mm wide for progrediens and sexuparae. Eggs of the latter two generations are produced simultaneously by the adult female sistens in what appears to be a homogeneous cluster. Therefore, eggs of these two types can not be distinguished from one another. Eggs of sexuales produced by the sexuparae on spruce measure 0.37 ± 0.05 mm long by 0.25 ± 0.04 mm wide.

Nymphs of sistens and progrediens are very similar in size and appearance throughout development and can not be distinguished from one another reliably by morphological features. Upon hatching, the crawlers (mobile first instar nymphs) are 0.44 ± 0.05 mm long by 0.27 ± 0.03mm wide. Once they settle, insert their stylets, and begin to feed, these nymphs become much more heavily sclerotized and convex. The lengths and widths of these settled nymphs are as follows: first instar (0.43 ± 0.04mm long by 0.27 ± 0.03mm wide); second instar (0.57 ± 0.05mm long by 0.34 ± 0.04mm wide); third instar (0.67 ± 0.06mm long by 0.43 ± 0.04mm wide); fourth instar (0.74 ± 0.06mm long by 0.47 ± 0.05mm wide).

The first instar nymphs of sexuparae and progrediens hatch simultaneously from eggs produced by the same adult female sistens. Because hatching nymphs appear to be a homogeneous lot, progrediens and sexuparae can not be separated. However, the remaining instars of sexuparae differ from those of sistens and progrediens in size, shape, and morphology, especially with regard to thoracic and antennal structures. Sexupara nymphs are somewhat larger than those of sistens and progrediens and measure as follows: second instar (0.60 + 0.07mm long by 0.35 ± 0.04mm wide); third instar (0.77 ± 0.07mm long by 0.47 ± 0.05mm wide); fourth instar (0.89 ± 0.09mm long by 0.49 ± 0.05mm wide). Enlargement of the thoracic areas in the third and fourth instars of sexuparae, related to the development of wings, provides an obvious means for distinguishing this generation of A. *tsugae.* In addition to their larger size, second, third and fourth instar sexuparae also differ from sistens and progrediens by having a distinguishing suture between the prothoracic and mesothoracic dorsal plate and a distinct wing bud notch along the posterior margin of the mesothoracic dorsal plate. The antennae of sexuparae after the first instar also differ greatly from those of sistens and progrediens both in shape and in size.

Adults of sistens and progrediens are readily distinguished from one another by their body size and by the relative lengths of their antennal segments. Sistens adults measure 1.41 ± 0.17mm long by 1.05 ± 0.12mm wide, nearly twice as large as progrediens adults, which measure 0.87 ± 0.09mm long by 0.63 ± 0.07mm wide. Adult sistens are also more heavily sclerotized than adult progrediens and have many more wax-producing glands distributed throughout the dorsum. The length of the terminal antennal segment of an adult sistens is subequal the length of the two basal segments combined, while the length of the terminal segment of an adult progrediens is nearly twice the length of the combined basal segments.

The winged adult sexuparae measure 1.09 ± 0.10mm long by 0.51 ± 0.06mm wide and are dark brown and heavily sclerotized. Their long five-segmented antennae together with the presence of compound eyes and four textured wings readily distinguish them from adult sistens and progrediens.

<u>Life cycle:</u>

The life cycle reported below for *A. tsugae* in Connecticut (McClure 1987a, 1989)(Fig. 1) was determined from weekly or biweekly (March - November) or monthly (December - February) samples collected from hemlock forests in Essex and in Haddam from March 1986 through February 1988, a period that was characterized by relatively normal weather conditions. However, observations during the past eight years indicate that development of the sistens generation can be accelerated or delayed by as much as two weeks in response to weather conditions between October and March (McClure unpubl.).

In Connecticut, *A. tsugae* completes two wingless parthenogenetic generations on *T. canadensis,* represented by the sistens, present from July through April, and by the progrediens, present from April through June. The sistens mature in February; from March through May each produces a single white cottony ovisac containing up to 300 eggs. Egg production is inversely density-dependent (McClure 1991). Some of these eggs become progrediens; the remainder become a migratory parthenogenetic generation, the sexuparae. Nymphs of both types begin hatching in April, quickly develop through four instars, and mature in June. Progrediens adults remain on hemlock, and during June and July they produce cottony ovisacs similar to, but smaller than, those produced by the sistens. These ovisacs contain up to 250 eggs each. The sistens crawlers, which hatch from these eggs within a few days, settle on young hemlock branches, begin to feed, and soon thereafter enter an aestivation period that lasts for several months. In October, aestivating nymphs resume development and mature by early February.

The winged sexuparae adults that mature on hemlock in June migrate to spruce, and in July each lays up to 15 eggs beneath its folded wings. Adult sexuparae produce eggs only on *Picea* species; those which do not migrate to spruce die on hemlock without producing eggs. The progeny of sexuparae produced on spruce represent the sexual generation of A. *tsugae* called the sexuales. The sexuales nymphs that hatch and begin to feed on spruce in July all die within a few days; none develop beyond the first instar on any of 15 different *Picea* species (McClure 1987, 1991). Varty (1956) and Eichhorn (1969) reported that for some adelgids the ratio of wingless to winged progeny produced by the sistens is determined preponderantly or completely by postnatal environmental influences and is density-dependent. McClure (1991) determined that the production of sexuparae by A. *tsugae is is* density-dependent and constitutes a major mortality factor for this adelgid in eastern North America.

Population trends:

Introduced populations of *A. tsugae* in hemlock forests in the northeastern United States are injurious and unmanageable (McClure 1995b) and are adversely affected by density-dependent mechanisms (McClure 1991). Studies in Connecticut reveal that hemlock woolly adelgid severely reduces the growth and survival of *T. canadensis,* and this adverse effect on the trees also has a major impact on the subsequent performance and population dynamics of this insect (McClure 1991). The presence of adelgids at all but relatively low densities (<4 individuals per 20 mm^2 of branch) totally inhibits the production of new growth by hemlocks the following year. Thus, adelgids are forced to feed on less preferred older growth where their survival and fecundity are significantly reduced and where a significantly greater percentage of developing nymphs become sexuparae, the generation which dies without reproducing, because no spruce host is available.

Adelgid performance is also strongly negatively correlated with adelgid density on 40 forest hemlocks that supported a wide range of initial adelgid densities (McClure 1991). Mortality ranges from 9 to 90% and sexuparae production from 0 to 100% on trees with densities of from two to 40 adelgids per 20 mm^2 of branch.

The population dynamics of *A. tsugae* in three hemlock forests in Connecticut during a 4-year period from the initial colonization of the stand to the death of all trees shows strikingly similar trends characterized by bimodal peaks of abundance (McClure 1991). Adelgid populations multiply rapidly and attain peak density during the first year of the infestation when trees are producing abundant new growth. Populations decline sharply during the second year when very little new growth is produced. During the third year, from 11% to 15% of the buds produce new growth, albeit severely stunted. Adelgids quickly colonize this young growth and resurge to a second, modest population peak, only to crash again during the fourth year when most trees die. Some trees survive longer than four years in a severely weakened condition, with only a sparse amount of foliage at the very top of the crown. These weakened trees have little chance for recovery, often fall victim to wood-boring insects and diseases, and are readily broken and thrown by wind.

Survival and fecundity of *A. tsugae* is significantly higher during the first and third years of the infestation, when new growth is being produced, than in the other two years when no new growth is produced. Percent production of sexuparae, however, shows a different pattern during the third year. Following the heavy damage to hemlock during the first year, more than 93% of the adelgids produced in each of the subsequent three years become sexuparae; in the fourth year only sexuparae are produced. Density-dependent production of the unsuccessful sexuparae plays a major role in the decline of *A. tsugae* populations on their deteriorating host (McClure 1991).

BIOLOGY IN JAPAN

Stages of development and life cycle:

Adelges tsugae has identical stages of development and the same polymorphic life cycle in Japan as it does in Connecticut (McClure unpubl.). This life cycle includes sexuparae, the generation that must complete its development on spruce. The discovery of adelgid galls on *P. jezoensis hondoensis* (Sieb. and Zucc.) and *P. polita* (Carriere) in three hemlock forests in Japan (McClure unpubl.) suggests that one or both of these native spruce species is a primary host of *A. tsugae* and substantiates an earlier report of *A. tsugae* on *P. polita* (Inouye 1953).

Although the developmental stages and generations of *A. tsugae* in Japan are the same as in Connecticut, adelgid phenology in Japan varies greatly among sites and is related to elevation and hemlock phenology. At each of three sites where hemlocks were sampled along an elevational gradient within a three-day period, the percentage of sistens eggs that had hatched is negatively correlated with elevation and positively correlated with the percentage of hemlock buds that had opened (Table 1). At the higher elevations most buds did not open, and most of the eggs produced by the overwintering sistens did not hatch until late June. This delay in development of the progrediens generation results in a proportional reduction in the length of the summer aestivation period (McClure unpubl.).

Population trends:

Studies in Japan reveal that native populations of A. *tsugae* are maintained at low innocuous densities in the hemlock forest by a combination of host resistance and natural enemies (McClure 1995a, 1995c, 1996). Significantly higher adelgid densities in most ornamental plantings of hemlock were attributed to lowered host resistance from less than optimal growing conditions. At a few ornamental sites where growing conditions were extremely poor (soil severely compacted, roots injured, irrigation insufficient or excessive, branches heavily sheared), A. *tsugae* abundance on Japanese hemlocks was as high as that observed on *T. canadensis* in North America (McClure 1995a, 1996). However, even at these sites where adelgid densities were at outbreak levels, no injury to the trees was observed. The high susceptibility of *T. canadensis* to attack by A. *tsugae* (McClure 1992) may hamper our biological control efforts, because exceptionally high mortality from natural enemies may be needed to maintain introduced pest populations at innocuous levels.

POTENTIAL FOR CONTINUED SPREAD

During the past 10 years A. *tsugae* has been expanding its distribution in the northeastern United States at the rate of about 30 km each year. This spread has undoubtedly been facilitated by wind, birds, forest-dwelling mammals, and humans (McClure 1990). Although mortality of *A. tsugae* sistens during a typical winter in Connecticut is between 60-70%, populations rebound quickly the following spring due to the high reproductive ability of this parthenogenetic insect. Significantly higher rates of mortality, between 90-96%, were recorded in Connecticut during the winter of 1993-94, a period that was characterized by record low temperatures and record high snowfall (McClure unpubl.). These facts suggest that winter mortality may limit the spread of *A. tsugae* northward. However, even though A. *tsugae* incurred high levels of mortality during that severe winter of 1993-94, its populations throughout Connecticut had recovered to high injurious levels by the following summer.

In Japan A. *tsugae* occurred in 14 prefectures at sites located between 34° and 40° N latitude and between sea level and 1,980 m elevation (McClure 1995a). At several sites located between 1500 - 1650 m elevation where minimum daily temperatures of -35°C are common during winter, sistens nymphs incurred less than 25% mortality (McClure unpubl.). These results indicate that A. *tsugae is* cold hardy in Japan and suggest that this adelgid has the potential to spread throughout the natural growing areas of T.

canadensis and *T. caroliniana* in eastern North America. However, the high mortality among sistens nymphs observed in Connecticut, especially during the severe winter of 1993-1994, suggests that the adelgids originally introduced into eastern North America were from a less cold-hardy stock in Japan. Although low winter temperatures may retard the spread of *A. tsugae* in eastern North America, the adelgid will probably develop sufficient cold hardiness to expand its distribution northward.

ACKNOWLEDGMENT

I am grateful to K. Ito, K. Kobayashi, E. Shibata, and F.Yamada for organizing the visit to Japan and to the Forestry and Forest Products Research Institute for providing research facilities, personnel, and equipment. B. Beebe provided valuable technical assistance. This research was supported in part from funds provided by the Horticultural Research Institute (Washington, D.C.), Steep Rock Association, Inc. (Washington, Conn.), and the U.S. Forest Service through the Northeastern Area State and Private Forestry, the National Center of Forest Health Management, and the Northeastern Forest Experiment Station.

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Table 1. Phenology of *Adelges tsugae* on *Tsuga diversifolia* and *T. sieboldi* along three latitudinal gradients in Honshu, Japan.

Prefecture	Latitude N°	Date	Elevation (m)	*Tsuga* sp.	% hemlock buds open	% adelgid eggs hatched
Nara	34°11′	5/25-27	700	*T.s.*	94	93
			1000	*T.s.*	56	75
			1200	*T.s.*	35	54
			1500	*T.d.*	10	13
			1660	*T.d.*	0	0
Nagano	35°47′	6/10-11	1260	*T.s.*	91	90
			1400	*T.d.*	84	62
			1500	*T.d.*	72	55
			1600	*T.d.*	45	15
			1660	*T.d.*	32	11
Tochigi	36°50′	6/22-23	1300	*T.d.*	100	100
			1400	*T.d.*	94	86
			1500	*T.d.*	87	73
			1600	*T.d.*	69	38
			1980	*T.d.*	44	3

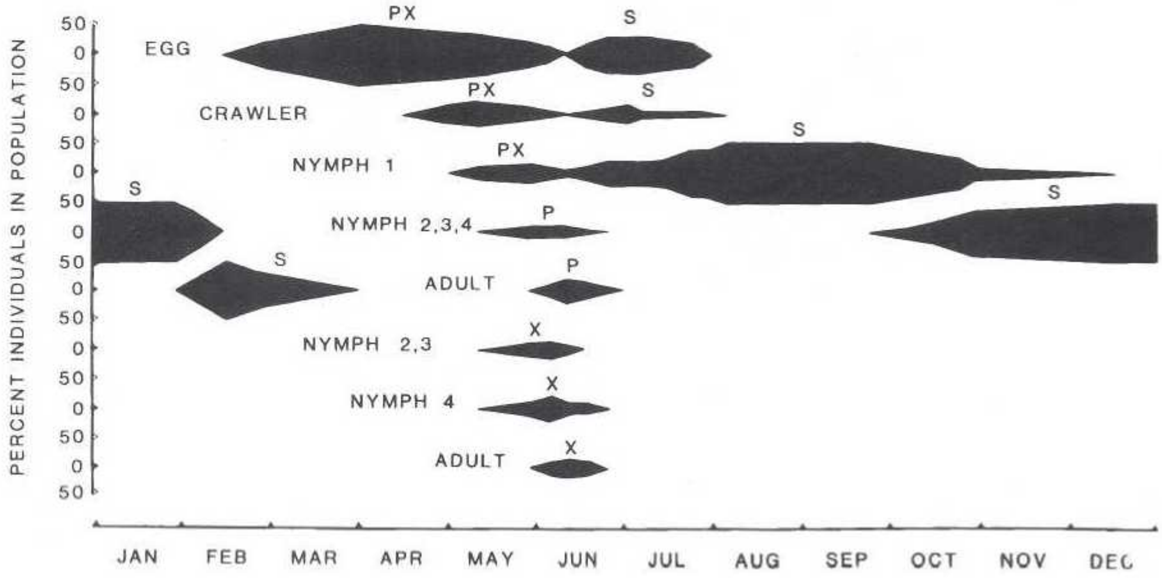

Fig. 1. Seasonal occurrence of *Adelges tsugae* on *Tsuga canadensis* in Connecticut (From McClure, 1987a). Generations are: sistens (S); progrediens (P); and sexuparae (X).

POTENTIAL IMPACTS OF HEMLOCK WOOLLY ADELGID

(Adelges tsugae) ON EASTERN HEMLOCK

(Tsuga canadensis) ECOSYSTEMS

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ABSTRACT

Eastern hemlock, an extremely shade tolerant, late successional ("climax") conifer with a dense, evergreen crown and an extensive, shallow, root network, strongly influences its environment and other species. Dense hemlock canopies create distinctive microclimates and an acidic "duff" layer. The characteristically dark, acidic conditions below dense hemlock canopies can alter fundamental community and ecosystem characteristics such as plant and animal species composition, succession dynamics, primary productivity, decomposition, and nutrient cycling. At a landscape scale, hemlock-dominated evergreen "patches" add diversity to the predominantly deciduous "matrix" of the eastern forest. Within mixed hardwood stands, scattered hemlock trees provide unique evergreen habitat structure. A number of bird species are strongly associated with hemlock throughout their ranges, or portions thereof. In New England, hemlock provides important winter wildlife shelter. Further south, hemlock probably helps provide summer habitat for cold water fish such as brook trout *(Salvelinus fontinalis)*, by shading and cooling streams.

The National Park Service sponsored studies of hemlock woolly adelgid (HWA) and hemlock health, understory vegetation, breeding song birds, small mammals, amphibians, terrestrial invertebrates, and environmental conditions such as light and temperature regimes, in two hemlock ravines at Delaware Water Gap National Recreation Area. Studies in these hemlock ravines have documented more than 300 plant species, including approximately 120 bryophyte species (moss and liverwort); 12 small mammal species (7 rodent, 5 soricid); 15 amphibian species (9 salamander, 4 frog, 2 toad); and 22 breeding song-bird species. Breeding populations of several bird species strongly associated with hemlock, including blackburnian warbler *(Dendroica fusca),* black-throated green warbler *(Dendroica virens)* and solitary vireo *(Vireo solitarius),* were estimated. Occurrences of several regionally rare species of plants and small mammals were documented. Stream temperature studies indicated that the cooling effect of the hemlock ravine was essential to maintain temperatures tolerable to brook trout.

The potential impacts of HWA infestations on ecosystems must be considered within a context of broader environmental and historical changes. The prevalence of hemlock throughout eastern forests has been dramatically reduced from what it was in presettlement times (prior to 1750). Currently, interactions among myriad potential forest stressors and disturbances -- including acidic deposition and ozone, elevated herbivore (deer) populations, and invasions of numerous exotic forest insects, diseases, plants, and animals -- may strongly influence not only the susceptibility and response of hemlock trees to H W A infestations, but also the ecosystem response to hemlock defoliation and mortality. Expected impacts include the following: reduced populations of birds associated strongly with hemlock; increased understory and stream light levels and temperatures; reduced populations of native brook trout, and possibly increased populations of non-native brown trout *(Salmo trutta)* and rainbow trout *(Oncorhynchus mykiss);* reduced biomass and species diversity of bryophytes; increased soil nitrate-nitrogen availability; increased primary productivity; increased deciduous leaf litter input to streams; increased biomass of understory plants (e.g. ferns) and stream algae; increased occurrences of invasive exotic plants, such as Japanese stilt-grass *(Microstegium vimineum);* and gap colonization and capture by "middle -successional" tree species, such as yellow birch *(Betula alleghaniensis)* and red maple *(Acer rubrum).*

INTRODUCTION

The effects of hemlock woolly adelgid (HWA) on eastern hemlock ecosystems should be considered not in isolation, but within a context of broader environmental and historical changes. Before eastern forests were cleared by European colonists (circa 1750-1850), hemlock dominated much more extensive areas than it does today (Foster and Zebryk 1993, Whitney 1990, McIntosh 1972). In Wisconsin and Michigan, only 0.5% of presettlement hemlock remains (Mladenoff 1995, White and Mladenoff 1994). In Pennsylvania, vast areas of hemlock were cut for use in the tanning industry during the late nineteenth and early twentieth centuries (Quimby 1996, Whitney 1990). Recent unsuccessful hemlock regeneration has been attributed, at least in part, to browsing by white-tail deer *(Odocoileus virginianus)* (Whitney 1990, Anderson and Loucks 1977, Hough 1965). As a late successional or "climax" species, hemlock forests require hundreds of years without major environmental disturbances to mature (Foster and Zebryk 1993, Tyrrell and Crow 1994). But it is clear that we are living in an era of increasing environmental stressors or "disturbances," such as air and water pollution (e.g. ozone, acidic deposition), habitat fragmentation, climate changes, elevated herbivore (deer) populations, and invasions of numerous other exotic forest insects, diseases, plants, and animals. Invasive exotic species can alter fundamental characteristics and processes of ecosystems, such as light and temperature regimes, primary productivity, and nutrient cycling, and thus change the "fundamental rules of existence" for all organisms within affected ecosystems (Vitousek 1990).

Gypsy moth *(Lymantria dispar),* Dutch elm disease *(Ophiostoma ulmi),* beech bark disease *(Nectria coccinea* and *N. galligena),* and white pine blister rust *(Cronartium ribicola)* are just a few examples of other exotic species that also affect the health and composition of eastern forests (Miller-Weeks et al. 1994). Hemlock defoliation and mortality provides opportunities for exotic plants such as tree of heaven *(Ailanthus altissima),* Japanese barberry *(Berberis thunbergii),* and Japanese stilt-grass *(Microstegium vimineum)* to invade and further disrupt forest ecosystems. Japanese stilt-grass has invaded at least one HWA-impacted hemlock stand in Connecticut (Lapin 1994). The numerous "agents of environmental change" affecting eastern forests diminish the likelihood that healthy, mature hemlock stands will persist long into the future. The interactions of all these "agents" also diminish the likelihood of successfully predicting the ecosystem effects of HWA infestations.

To identify the potential impacts of HWA on hemlock ecosystems, knowledge of two subjects is required: (1) the effects of HWA on hemlock trees, and (2) the ecosystem consequences of those effects. While it is clear that HWA represents a serious threat to eastern hemlocks (McClure 1991), research is needed to fill critical gaps in knowledge of both subjects. HWA has been closely associated with extensive, severe hemlock defoliation and mortality in Connecticut (McClure 1991), Virginia (Shenandoah National Park; Watson 1992), New Jersey (Ward et al. 1992), and other areas. The hemlock defoliation and mortality experienced in these areas have not occurred in hemlock stands free of HWA. However, these two lines of evidence do not force us to conclude that severe hemlock defoliation and mortality will occur within a specified number of years at all sites having HWA infestations. It is possible that the effects of HWA on hemlock trees vary geographically, depending on environmental site or stress factors and the genetics of particular HWA and hemlock populations. Environmental site or stress factors include: elevation, slope, aspect, soil moisture, and other characteristics; pollutants such as acidic deposition, ozone, and road salt; forest age and species composition; presence of "generalist" forest-defoliating insects such as gypsy moth (*L. dispar*) and fall cankerworm (*Alsophila pometaria*), as well as "specialist" hemlock feeding insects such as hemlock loopers (*Larnbdina fiscellaria* and *L. athasaria*), scales (*Fiorinia externa* and *Nuculaspis tsugae*), and borers (*Melanophilafulvoguttata*). Interactions among these factors may strongly influence the succeptibility and response of hemlock trees to HWA infestations.

Studies documenting the effects of HWA on hemlock ecosystems have not been completed. Such studies were initiated in 1993 by the National Park Service at Delaware Water Gap National Recreation Area, and are continuing. These studies are providing important "baseline" information about hemlock ecosystems, but have not yet documented ecosystem effects of HWA, since the hemlocks from the study area have not been significantly affected by HWA to date.

In the absence of completed ecological studies (and with assumptions about the rate and manner of hemlock defoliation and mortality caused by HWA), we can use two approaches to identify potential ecological impacts. First, we can use knowledge of the ecological roles of existing hemlocks, and the mechanisms of ecological interactions, to reach logical predictions about HWA impacts. Second, we can assume the ecological impacts of HWA will be "similar" to those of some other type of forest disturbance that has been studied, such as other forest insect defoliators, or tree gap dynamics. We use both approaches in this discussion, and present some results from the hemlock ecosystem studies conducted at Delaware Water Gap National Recreation Area. Lapin (1994) discussed potential impacts of HWA on resources in the lower Connecticut River valley.

OVERVIEW OF ECOLOGICAL RELATIONSHIPS INVOLVING HEMLOCK

Eastern hemlock is currently distributed from the maritime provinces of eastern Canada, west to Minnesota, south through Ohio, and along the Appalachian Mountains to the northern edge of Georgia and Alabama. On the existing, postsettlement landscape, hemlock is most typically dominant on cool, mesic sites with nutrient-poor soils (Rogers 1978). Hemlock requires a moist, temperate climate, and is susceptible to heat and drought stress (Quimby 1996, Secrest et al. 1941, Stickel 1933). Hemlock is generally more abundant and evenly distributed across the landscape in the northeastern part of its range than in the southern and western parts of its range, where it becomes increasingly restricted to isolated stands inhabiting moist cool valleys, steep ravines, coves, and north-facing bluffs (Eyre 1980, Keever 1973). Benzinger (1994a) provided an excellent review of hemlock ecology.

Eastern hemlock, an extremely shade tolerant, late successional ("climax") conifer with a dense, evergreen crown and an extensive, shallow root network, can strongly influence the surrounding environment and other species.

Research has documented a number of these influences, but additional research is needed to answer important questions and test hypotheses. At a landscape scale, "patches" of evergreen hemlock add diversity to the predominantly deciduous "matrix" of the eastern forest. Dense hemlock canopies intercept solar radiation, precipitation, and wind throughout the year, and can thus alter light, temperature, and moisture regimes, and create distinctive microclimates. During summer, many hemlock stands seem darker, cooler, and more humid than nearby hardwood stands. During winter, a hemlock canopy provides shelter from cold winds, and may retain radiant heat on exceptionally clear, cold nights. Research is needed to document such microclimates, and determine the extent to which hemlocks actually cause them, as opposed to merely responding to microclimates caused by other site conditions. Hemlock needles acidify the surrounding soil and create a distinctive "duff" layer.

The year-round shading and characteristically acidic conditions below dense hemlock canopies can alter fundamental community and ecosystem characteristics such as plant and animal species composition, succession dynamics, understory primary productivity, decomposition, and nutrient cycling. Mladenoff (1987) quantified the effects of hemlock stands on nitrogen mineralization (an example of nutrient cycling) and related processes by comparing these processes under intact hemlock canopies with those in treefall gaps and under sugar maple canopies. Increased hemlock canopy cover was correlated with increased soil acidity and decreased nitrification; as hemlock importance approached 50%, nitrification approached zero. Nitrification was more than double under gaps and under sugar maples than it was under hemlocks. Air, litter, and soil temperatures under the hemlock canopy were much lower than in gaps, and somewhat lower than under sugar maple canopies (particularly in spring, before leaf-out).

The ecological influences of a particular hemlock stand depend upon its size, shape, geographic location, species composition, and the size and age structure of its trees. Scattered hemlock trees within mixed hardwood forests typically retain their lower branches, and so provide unique evergreen habitat structure extending nearly from the forest floor to the upper canopy. Clearly, the ecosystem effects of a very small, sparse stand of young hemlocks will be very different from those of a very large, pure, "old growth" stand. Even among old growth stands, important differences exist. Tyrrell and Crow (1994) documented significant differences in structural characteristics (such as tree density, basal area of snags, volume of fallen logs, percent canopy area with open gaps, and sizes of individual canopy gaps) among hemlock stands in northern Wisconsin and the Upper Peninsula of Michigan ranging in age from about 175 to 375 years old. Structural characteristics of hemlock stands greater than 300 years old were distinctly different than those of stands less than 275 years old in their study. Thus, the structural and ecological characteristics of hemlock stands continue to change and develop for upwards of 300 years after original establishment.

The ecological roles of structurally similar hemlock stands can also be expected to vary over geographic regions. For example, hemlock does not seem to play as critical a role as winter shelter for wildlife (e.g. "deer yards") in the South as it does in New England. Conversely, hemlock probably plays a more critical role in the South than it does in New England for maintaining the cool summer stream temperatures required by native brook trout. Hemlock can play different ecological roles even within more restricted geographic areas. In northern Wisconsin, black-throated green warblers *(Dendroica virens),* blackburnian warblers *(Dendroica fusca),* and solitary vireos *(Vireo solitarius)* are strongly associated with mature hemlock stands, but in southern Wisconsin, magnolia warblers *(Dendroica magnolia)* and Canada warblers *(Wilsonia canadensis)* are hemlock associates (Howe and Mossman 1995). DeGraff et al. (1992) and DeGraff and Rudis (1986) provide much information about relationships of hemlock with wildlife species in New England.

HEMLOCK ECOSYSTEM AND BIODIVERSITY STUDIES AT DELAWARE WATER GAP NATIONAL RECREATION AREA

Delaware Water Gap National Recreation Area encompasses 70,000 acres along the northeastern edge of Pennsylvania and the northwestern edge of New Jersey, and surrounds the "Middle Delaware National Scenic and Recreational River" (a 40-mile-long segment of the Delaware River). The National Park Service initiated studies in two hemlock ravines within the recreation area during 1993 to provide basic information regarding (1) HWA infestations, (2) hemlock tree health, and (3) hemlock ravine biodiversity and ecosystem characteristics. We established a system of 60 permanent hemlock plots in the two hemlock ravines to monitor HWA infestation levels and hemlock tree health. We collected data from these plots during the past three years (1993-1995) using standardized USDA Forest Service protocols. Onken (1996) analyzed and summarized these data. We documented locations of the permanent hemlock plots with a global positioning system (GPS). HWA was first detected in one of the study ravines during 1994, and in the other ravine during 1995. Ecological studies in these two hemlock ravines have included small mammals, amphibians, terrestrial arthropods, understory vegetation, breeding birds, fish, and environmental conditions such as light and temperature regimes. These studies are summarized below. Results from other published studies are also presented for comparison.

Vegetation

The National Park Service contracted Cornell University to complete a quantitative survey of understory vegetation, including bryophytes, in the two hemlock ravines. A total of 92 understory vegetation plots were established; 60 of these were located in the center of the 60 permanent hemlock plots in the two study areas. Data were collected at each plot regarding the species composition and abundance of overstory trees, tree seedlings and saplings, ferns, flowering herbs, and bryophytes. At each plot, the percent of total available light reaching the understory vegetation throughout the growing season was calculated, and expressed as a "gap light index" (GLI). In addition, data were collected regarding slope, aspect, soil depth, temperature, and moisture at each plot. Multivariate statistical analyses (TWINSPAN and Canonical Correspondence Analysis) were used to detect patterns of species abundance in relation to each other and to the measured environmental variables. Statistical power analyses were completed to determine the minimum amount of change in plant populations that could be confidently detected. Finally, qualitative surveys of the vegetation in the two ravines were completed to identify species that did not occur within the permanent plots.

As is characteristic of understory vegetation in hemlock-dominated stands, vegetation in the study ravines was sparse, and concentrated in "patches." Yet, more than 300 plant species were identified, including 44 species of trees or shrubs, 26 species of ferns or fern-allies, 108 species of flowering herbs, and more than 120 species of bryophytes. Eastern hemlock comprised over 50% of the basal area of both study areas. Other prominent canopy trees included yellow birch *(Betula alleghaniensis),* sweet birch *(B. lenta),* sugar maple *(Acer saccharum),* red maple *(A. rubrum),* white oak *(Quercus alba),* and white pine *(Pinus strobus).*

Multivariate analyses indicated that vegetated areas within the ravines tended to be dominated by one of four groups: ferns, shade-tolerant herbs, tree seedlings, or bryophytes. Light availability (GLI) and soil moisture were the environmental variables exerting the most control over species distributions within the ravines. Dominant ferns were intermediate wood fern *(Dryopteris intermedia),* New York fern *(Thelypteris noveboracensis),* and hayscented fern *(Dennstaedtia punctilobula).* The most common tree seedlings were birches, sugar maple, and red maple. The most common flowering herbs were partridgeberry *(Mitchella repens),* Indian pipe *(Monotropa uniflora),* Northern white violet *(Viola pallens),* white wood aster *(Aster divaricatus),* Canada mayflower (or wild lily-of-the-valley *(Maianthemum canadensis),* and sessile bellwort (or wild oats, *Uvularia sessilifolia).* Several flowering herb species listed as threatened or endangered in Pennsylvania or New Jersey were present, such as white twisted stalk *(Streptopus amplexifolius),* checkered rattlesnake plantain *(Goodyera tesselata),* and long beech fern *(Thelypteris phagopteris).*

Amphibians, Small Mammals, and Terrestrial Arthropods

The National Park Service funded and assisted the New Jersey Division of Fish, Game, and Wildlife to complete a quantitative study of small mammals and amphibians using pit-fall and snap traps in both hemlock ravines. In each ravine, 36 trap arrays were established (locations documented with GPS technology) over an area of approximately 11 hectares. Numerous habitat characteristics in the vicinity of each trap were measured. Traps were "activated" for ten continuous days in August 1993 and August 1994, and terrestrial arthropods captured in the pit-fall traps were preserved for identification.

A total of 12 small mammal species (7 rodent, 5 soricid) and 15 amphibian species (9 salamander, 4 frog, 2 toad) were collected from the two hemlock ravines. The four most abundant small mammals captured were smokey shrews *(Sorex fumeus),* white-footed mice *(Peromyscus leuocopus),* masked shrews *(Sorex cinereus)* and red-backed voles *(Clethrionumys gapperi).* A Northern water shrew *(Sorex palustris),* which is rare in Pennsylvania, was captured for the first time in New Jersey, and pygmy shrews *(Sorex hoyi)* were captured for only the second time in New Jersey. The four most abundant amphibians collected were red-backed salamanders *(Plethodon cinereus),* red-spotted newts *(Notophthalmus viridescens),* American toads *(Bufo americanus),* and slimy salamanders *(Plethodon glutinosis).*

Both hemlock ravines apparently supported a relatively high number of small mammal species, and also a high total small mammal population density, in comparison to other forested habitats in Pennsylvania and New Jersey. In a two-year study methodologically comparable to ours (pit-fall and snap traps), but in two mixed deciduous forest sites (primarily maple and oak), Yahner and Smith (1991) captured only eight small mammal species. Dowler et al. (1985) captured only seven small mammal species, and Kirkland and Sheppard (1990) captured only nine small mammal species, even though both these studies included many different sites and habitats. Small mammal abundance, as indicated by the number of animals captured per 100 pit-fall "trap nights," was also high in our hemlock ravine study (20) compared to values found in other habitats in the studies cited above (maximum of 13) .

We have not yet compared the abundance and species richness of amphibians we found in the hemlock ravines to those found in studies of other habitats. The 15 species of amphibians we captured with pit-fall traps is a conservative, minimum estimate of the species present in the hemlock ravines, since many species (such as tree frogs) are not vulnerable to capture by this method. Amphibians seemed to be quite abundant in the hemlock ravines, as indicated by a capture rate of 36 individuals per 100 trap-nights. The generalization that hemlock ravines are "rather sterile as amphibian habitat" (Lapin 1994) may be more appropriately considered an hypothesis (or local condition) than confirmed truth.

Birds

Surveys of breeding song birds were conducted in the two hemlock ravines from late May to early July in 1994 and 1995. A modification of the point count method described by Ralph et al. (1993) was followed. Species were identified by song. The relative abundance (number of individuals per ten sample points) of each n species was estimated, and the probability of detecting a 50% or greater change i selected species populations was calculated.

Twenty-two breeding bird species were documented. Of these, three species that breed primarily within hemlock ravines were relatively abundant: blackburnian warbler *(Dendroica fusca),* 4/10 points; black-throated green warbler *(Dendroica virens),* 8/10 points; and solitary vireo *(Vireo solitarius), 4/10* points. The blackburnian warbler is associated with eastern hemlock throughout its range, and was once known as the "hemlock warbler." These are "northern" bird species which, in Pennsylvania, breed mainly within the Appalachian Plateau Province, and are associated with large, high-elevation, coniferous forests (Brauning 1992). Hemlock ravines provide the most suitable breeding habitat for these species within the Appalachian Valley and Ridge Province of the recreation area.

Benzinger (1994) provided an excellent review and discussion about the importance of eastern hemlock to breeding birds in New Jersey. He listed the black-throated green warbler, solitary vireo, and Northern Goshawk *(Accipiter gentilis)* as species that, within New Jersey, are found almost exclusively in hemlocks. He listed the Acadian flycatcher, winter wren, hermit thrush *(Catharus guttatus),* red-shouldered hawk *(Buteo lineatus),* and barred owl *(Strix varia)* as species that are usually found in hemlocks. He included the blackburnian warbler, magnolia warbler *(Dendroica magnolia),* red-breasted nuthatch *(Sitta canadensis),* and Cooper's hawk *(Accipiter cooperii)* as species often found in hemlocks, but that are also often found in some other habitat. Howe and Mossman (1995) found the blackburnian warbler, black-throated green warbler, and solitary vireo strongly tied to hemlock forests in Wisconsin and Upper Michigan. The highest population densities of black-throated green warbler, blackburnian warbler, and winter wren were found in mature hemlock forests in this study. Howe and Mossman (1995) also found higher bird diversity in uneven aged, mixed hemlock-hardwood stands than in even-aged, or pure hardwood, stands.

Stream Temperatures and Fish

In the region surrounding Delaware Water Gap National Recreation Area, naturally reproducing populations of native brook trout are closely associated with hemlock stands. Probably the single most important reason for this association is that brook trout need cold water (in summer), and most cold-water streams in this area are surrounded by hemlock stands. Brook trout are generally excluded from streams in which the mean July temperature exceeds 21deg. C (Flebbe 1994). Brook trout survive and grow best at water temperatures between 10°C and 20°C (about 50°F and *68°F),* and are severely stressed at water temperatures above

24°C (75°F) (Raleigh 1982). Water temperatures of many streams in the recreation area, even those surrounded by hemlock stands, can exceed 20°C for prolonged periods during summer, and thus can stress brook trout. Both brook trout and brown trout inhabit the two study streams (Ross and Bennett 1996).

We installed computerized electronic temperature recorders at the upper and lower ends of one of the hemlock ravine streams to determine if stream temperatures were consistently lower at the lower end of the ravine than at the upper end. Temperatures were recorded every one-half hour from June to November, 1995. Results revealed that maximum daily summer stream temperatures at the lower end of the ravine were consistently 3°C to 4°C (5.4°F to 7.2°F) cooler than at the upper end (Fig. 1). While stream temperatures at the lower end of the ravine reached levels somewhat stressful to brook trout (21°C), stream temperatures at the upper end reached extremely stressful, and perhaps lethal, levels (exceeding 25°C). The cooling effect of the ravine was essential to maintaining stream temperatures brook trout could tolerate. The cooler water at the lower end of the ravine could be caused by three factors: (1) shade produced by the dense tree (especially hemlock) canopy, (2) shade and "cold air basin" effects produced by the topography (steep slopes, etc.), and (3) cold water input (ground water, tributaries).

To find out if the cooler stream temperatures at the lower end of the hemlock ravine could have been caused by particular "point sources" of cold water input, we measured temperatures every 150 m along the length of the stream on 13 and 18 July, 1995. Two very small tributaries (one intermittent) contributed some cold (17°C) water to the stream, but the stream was not measurably cooler below the confluence of either tributary. Temperatures decreased gradually as the stream passed through the hemlock ravine, from 24°C at the upper end, to 18°C at the lower end.

ECOSYSTEM RESPONSES TO HWA

Disturbance Caused by HWA, and Vegetation Responses

HWA-induced defoliation and mortality of eastern hemlock is qualitatively and quantitatively different from catastrophic disturbances such as clear-cutting, fire, or large-scale wind-throws. It is also different from selectively cutting hemlock. Hemlock defoliation is expected to progress gradually over a period exceeding four years, and dead trees will remain standing for additional periods of time. Understory vegetation and soils will not be violently disturbed by immediate tree falls, and declining hemlock trees will continue to "buffer" the sub-canopy environment to some extent by intercepting light, precipitation, and wind. Forest floor resources previously monopolized and influenced by hemlock (e.g. light, soil moisture, nutrients) will gradually become available to other plants. In particular, more nitrate nitrogen and phosphorus will be available to plants

Mladenoff 1987). Sub-canopy growing season temperatures will be higher. In response, understory plants such as ferns and tree seedlings (e.g. yellow birch, black birch, red maple), and sub-canopy trees (yellow birch, red maple, white pine) will grow and expand to "fill the gap." Understory species composition will change more or less dramatically. In particular, many bryophyte species may be eliminated. Affected stands will appear to be a "mess," with many dead and dying hemlock trees, openings in the canopy, and apparent "weedy" growth. Primary productivity and decomposition rates will probably increase for a number of years.

Birds

Hemlock defoliation from HWA, even without hemlock mortality, represents the loss of important habitat, and is expected to significantly impact populations of several bird species. Because HWA-induced hemlock defoliation typically progresses from the lower to the upper crown, species dependent on the lower and middle hemlock crown will be affected first. Solitary vireos forage and nest in the lower levels of hemlock crowns, and black-throated green warblers forage and nest in the middle levels (Benzinger 1994b). Populations of both these species will probably be severely impacted in HWA-infested areas. Blackburnian warblers may be less immediately and directly impacted by HWA defoliation, because they nest in the highest levels of the hemlock canopy. However, their foraging and breeding success may be adversely affected by habitat changes lower in the canopy, and hemlock mortality is expected to severely impact local blackburnian populations. Extensive hemlock mortality, creating forest gaps, could provide invasion opportunities for avian nest predators and parasites, such as blue jays *(Cyanocitta cristata* and cowbirds *(Molothrus alter)* (Lapin 1994). Populations of woodpeckers, cavity nesters, and bird species associated with hardwoods and earlier successional stages can be expected to increase in affected areas.

Streams

Defoliation by HWA will probably result in pronounced changes in energy and nutrient inputs (solar radiation, leaf litter) to streams with substantial riparian hemlock. Defoliation will allow more solar radiation (light) into a stream, and probably result in higher summer stream temperatures. Since all biological processes (e.g. growth and development) are temperature sensitive (especially in aquatic environments), higher summer temperatures will have myriad effects. Increased light and temperature, especially in combination with possibly elevated nutrient (nitrogen, phosphorus) levels, will increase stream primary productivity, and probably result in algal (periphyton) "blooms." Gypsy moth *(Lymantria dispar)* defoliation of the riparian tree canopy of a Rhode Island stream increased solar radiation penetration from less than 18% to over 70% of incident values, and increased stream temperature 3.7°C (Sheath et al. 1986). In response, algal productivity increased, and the proportion of stream bottom covered by algae increased from below 35% to 80% (Sheath et al. 1986). Gypsy moth frass probably also increased nitrogen inputs and concentrations in this stream, but these were not measured. Defoliation by the fall cankerworm *(Alsophila pornetaria)* accompanied substantial increases in stream concentrations and export of nitrate nitrogen from three mixed hardwood watersheds in North Carolina (Swank et al. 1981).

Increased primary production and inputs of deciduous leaf litter would lead to increased detritus processing and secondary production (aquatic invertebrates and fish). Sites with steep slopes (e.g. ravines) could experience increased erosion, sedimentation, and runoff rates, and changes in physical habitat characteristics such as stream channel shape and substrate composition. Eventually, the number of fallen hemlock logs (which are very resistant to decomposition) in and around affected streams would increase. Changes in fish species composition are likely. Brook trout populations may be eliminated because of increased temperatures, light intensity, habitat changes, and competition with other species. In many areas, native brook trout must compete with introduced (European) brown trout *(Salmo trutta)* and rainbow trout *(Oncorhynchus mykiss),* and higher temperatures provide a competitive advantage to these introduced species (Flebbe 1994).

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BIOLOGY OF THE HEMLOCK WOOLLY ADELGID

IN THE SOUTHERN APPALACHIANS

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ABSTRACT

Construction of a time-specific life table is ongoing with data being collected from 4 sites in southwestern Virginia. Weekly, or twice monthly, estimates of frequency of each HWA life stage per cm of twig are being made from age-classified foliage collected from 3 trees per site. A multi-cohort model of insect development will simulate stage-specific frequencies at each sampling interval. Life table parameters will be estimated by maximizing the likelihood function of the observed and simulated stage frequencies. On-site dataloggers are recording hourly temperatures in order to estimate the effect of temperature on life-table parameters.

INTRODUCTION

The hemlock woolly adelgid (HWA), *Adelges tsugae* Annand, was introduced to Richmond, Virginia, in 1953 or 1954 probably from Japan (Souto 1996). In the most recent 10 - 12 years HWA has been identified in an increasing number of counties, and the range now extends from northern North Carolina to Massachusetts. The majority of published research directed at the HWA in eastern North America has been conducted in Connecticut since its discovery in that state in 1985 (McClure 1987). Investigations have addressed issues of life cycle (McClure 1989), population cycles (McClure 1991), dispersal (McClure 1991), and control (McClure 1987, 1995).

Native natural enemies of HWA have not demonstrated an ability to control HWA at levels below those that cause tree decline and ultimate death. Therefore, successful management of HWA in eastern North America, and preservation of eastern hemlock (*Tsuga canadensis* (L.) Carr.) as a forest and ornamental species, will likely depend on a balanced combination of introduction of exotic natural enemies and chemical control. These tactics would be part of a comprehensive integrated pest management (IPM) program. Such programs can be successful when reliable techniques exist to estimate sizes and trends of the pest and natural enemies populations, and where sufficient knowledge exists of the dynamics of the system comprised of the pest and its environment.

Population dynamics is that area of ecology concerned with the change in the distribution and abundance of a population in space and time (Berryman 1986). The study of population dynamics usually involves identification of the critical components of the system, identification of the major extrinsic forces affecting the components, a description of the manner in which the extrinsic forces affect the system, and a description of the manner in which the various components interact. At any point in time or in space the state of the component can be described by its abundance or its condition.

We illustrate the HWA system in Figure. 1. Within the ellipse on the right the HWA component of the system repeats its yearly life-cycle: adults of the overwintered sistens generation lay eggs that develop during the summer into either wingless progrediens adults or winged sexuparae adults; winged individuals disperse from the hemlock while wingless individuals lay eggs of the sistens generation (McClure 1989). Within the ellipse on the left, the hemlock host component of the system repeats its yearly cycle: in autumn new buds are set; in summer buds flush and new growth of twigs occurs.

The HWA and the hemlock host components may each be the most important biotic factor affecting the other. Greater numbers of HWA per twig will adversely impact the production of buds and new growth the following year leading to tree decline (McClure 1991). A reduction in new growth forces a greater proportion of HWA to feed on the less preferred older twigs, resulting in higher mortality and a higher proportion of migrating sexuparae (McClure 1991). A second important biotic factor affecting the HWA component of the system is the abundance of natural enemies; the abundance of HWA will in turn affect the abundance of natural enemies.

The most important abiotic factors driving the HWA cycle are probably temperature and photoperiod (Zaslavski 1988). During the year the abundance of the population is augmented by natality (twice), immigration (probably twice), mortality (continually, but not necessarily at a constant rate), and emigration (probably twice). Temperature and photoperiod will affect the timing and magnitude of these events. Temperature and photoperiod will also affect the HWA component indirectly by their influence on the life cycle of natural enemies.

The most important abiotic factors affecting the hemlock component of the system may be precipitation, soil conditions, and perhaps acid rain. Trees that are stressed by lack of precipitation or poor soil conditions will produce less new growth each year. Genotype, inter-tree competition, and damage by other pests may be important biotic factors affecting the amount of new growth produced each year by the hemlock component. The amount of new growth will, in turn, affect the HWA component.

Thus the system is composed of several interacting components, as suggested by the arrows of Figure 1. Factors that affect one component will indirectly influence other components. An adequate understanding of the effects of the abiotic factors on system components, and of the interactions between the components, will increase the probability of a successful IPM program to manage HWA and preserve the hemlock resource.

Our objectives are two-fold. First, we wished to determine if any differences exist in the general life cycle of HWA as it has been described in Connecticut (close to the northern extent of its range) and Virginia (close to the southern extent of its range). Second, we wished to construct a life-table of HWA in southwest Virginia in order to estimate stage-specific development times and natality and mortality rates, and to estimate the effect of temperature and twig age on these characteristics. The "construction of a number of life-tables is an important component in the understanding of the population dynamics of a species." (Southwood 1978).

MATERIALS AND METHODS

In June 1994 we established four sampling sites in southwestern Virginia (Fig. 2). Sites were selected on the following basis: [1] stands that have a high proportion of eastern hemlock; [2] HWA populations were sufficiently high to result in a majority of non-zero samples; [3] sites varied in their elevation and/or aspect in order that temperatures differed among the sites. Sites 1 and 2 are along Stoney Creek in Bedford County at elevations of 600 and 475 m. Both sites have a weak southwestern aspect. Sites 3 and 4 are in Craig County. Site 3 is at 625 m with a strong eastern aspect. Site 4 is at 420 m with no aspect. At each site 3 trees were selected that had an HWA population and that were judged to be sufficiently healthy to survive the duration of the study. A Campbell CR10 datalogger (Campbell Scientific, Logan Utah) was placed at each site to record hourly temperatures.

At weekly, or twice monthly intervals, three equally spaced branch samples of at least 25 cm length are removed from the mid-crown of each tree. In our laboratory each sample is examined under a dissecting microscope, and the number of each HWA life-stage per cm is recorded on a minimum of 20 cm of twigs of each of current, 1-year old, and 2-year old foliage. Non-egg HWA life-stages are distinguished by the number of cast skins associated with each individual.

Life-tables where there is considerable overlap of life stages, as with HWA, and where the fate of a real cohort can not be measured, are termed time-specific (or vertical) life-tables (Southwood 1978). Simultaneous recruitment to, and loss from, a life-stage makes direct calculation of life table parameters such as stage durations, mortality, and fecundity impossible. Instead, their estimation requires age (or stage) determination at regular sampling intervals and adoption of a simulation model. The model provides expected values of the stage frequencies based on model parameter values. Model parameter values are then modified until the expected frequencies approximate the observed frequencies. The selection of parameter values that give the best approximation can be made by minimizing the sum of the squared deviation of the observed from the expected frequencies (least squares method), or by maximizing the probability of sampling the observed frequencies given the parameter values (maximum likelihood method).

We selected the model of Bellows and Birley (1981), as modified by Manly (1990a), to provide the expected values of the stage frequencies. This model was chosen because of what we considered to be its high level of realism. Model parameters to be estimated include stage-specific durations and survival rates. In addition, the rate of entry into the first stage does not need to be specifically known, but can be estimated. The model assumes that the duration of a stage is not uniform among all individuals. Rather, for each stage there is a distribution of developmental times, with some individuals being faster developers than others, and the distribution can be described by a probability density function h (or the cumulative density function H). There is a also a stage-specific probability of survival, s, in each time interval. Thus, the proportion of the population that moults from stage j to the succeeding stage, $j+1$, at time t is

$$P_{j+1}(t)=\sum_{i=0}^{t} P_j(i) s_j^{\,t-i} h_j(t-i) \quad [1]$$

That is, the proportion of the population that moulted to $j+1$ is made up of those individuals that moulted to j in each preceding time interval and survived to advance to $j+1$. Put another way, an individual will moult to $j+1$ if it has been in j long enough, and if it has survived.

The frequency of stage j at time t is then

$$f_j(t)=M\sum_{i=0}^{t} P_j(i) s_j^{\,t-i}\{1-H_j(t-i)\} \quad [2]$$

That is, the number of individuals in stage j at time t is the sum of the proportions of the population that have entered the stage during each preceding time interval, and that have survived to the present time, and haven't moulted to the next stage, multiplied by M, the total number of individuals that entered the first stage.

Entry to the first stage occurs over time, and the proportion of the population that does so at time t is estimated as

$$P_1(t)=H_0(t)-H_0(t-1) \quad [3]$$

We further modified the model to account for the parallel development of the progrediens and sexupara life stages. Specifically,

$$P_{4p}(t)=\sum_{i=0}^{t} P_3(i) s_3^{\,t-i} h_3(t-i)(1-\chi) \quad [4]$$

and,

$$P_{4X}(t)=\sum_{i=0}^{t} P_3(i) s_3^{\,t-i} h_3(t-i)(\chi) \quad [5]$$

That is, the proportion of the population that moulted to the 4th instar progrediens nymph at time t, $P_{4p}(t)$, is made up of the proportion of individuals that moulted to the third instar in each preceding time interval, and that survive to advance to the 4th instar, and that didn't moult to a 4th instar sexupara nymph, $(1-\chi)$. Our final modification provides fecundity estimation.

We have chosen a Weibull distribution to describe the stage-specific durations because it generates skewed distributions that have been observed experimentally (Sharpe et al. 1977), and the cumulative form is quite simple,

$$H_j = 1 - e^{-\left(\frac{t}{\beta}\right)^{\alpha}} \qquad [6]$$

where β is a location parameter (i.e. location of the distribution on the time scale), and α describes the degree of uniformity among individuals in their durations in the stage.

RESULTS

Frequencies of 12 life stages at each site are shown in Figures 3.1 - 3.4.

McClure (1989) reported that in Connecticut sistens adults mature in February and began ovipositing in March. In Virginia the first sistens adult appeared January 9 at site 1. Sistens adults were first observed at the remaining sites 9 to 28 days later. The earliest progrediens/sexuparae eggs appeared also at site 1 on February 6, and 13 to 44 days later at the remaining sites. McClure (1989) reported that progrediens adults mature in June and lay eggs of the sistens generation from June to July. In Virginia the first progrediens adults were observed from May 29 (sites 3 and 4) to June 5 (sites 1 and 2) and sistens eggs were observed from these same days to June 27 (sites 1 and 2) and June 29 (sites 3 and 4).

McClure (1989) reported that the sistens generation resumes post-aestival development in October. We first observed 2nd instar sistens nymphs (post-aestival) September 28 (sites 3 and 4), October 3 (site 2), and October 10 (site 1).

There was enormous temporal overlap of HWA life-stages in Virginia, similar to that reported by McClure (1987). The first appearance of sistens eggs was as little as one week after the last observation of progrediens/sexuparae eggs. As many as 12 life-stages were present at a single sampling date in late May (progrediens 1st instar nymphs through adult, sexuparae 1st instar nymphs through adult, sistens eggs, and sistens 1st instar nymphs).

Very heavy mortality occurred during both egg stages and both 1st instar nymphal stages. At site 1 maximum densities of progrediens/sexuparae eggs and 1st and 2nd instar nymphs were 23000, 4000, and 2000 per 25 cm twig respectively. Maximum densities of sistens eggs and 1st and 2nd instar nymphs were 11000, 5000 and 2000 per 25 cm twig respectively.

Although durations of some HWA life stages may have been reduced, and others increased, in Virginia compared to Connecticut, we detected no differences between the states in the basic life cycle.

We are in the process of estimating life table parameters via maximum likelihood estimation of model parameters, an exercise that has proven more problematic than anticipated. Initial trials using POPSYS-1f (Manly 1990b), software designed specifically for analysis of stage frequency data, were judged unsatisfactory when survival rates were estimated to exceed one in some non-reproductive stages. (A survival rate in a reproductive stage exceeding one is equivalent to reproduction.) Such estimates probably arise when relatively high sampling errors result in a lower frequency count in a sample than in a subsequent sample. Software flexibility does not extend to setting bounds on parameter values. Subsequent difficulties were encountered when we attempted to use commonly available searching algorithms, such as PROC NLIN (SAS 1990), on our own computer code. The search results were excessively influenced by the initial parameter values used to start the search and had a very high probability of converging on a local maximum rather than the global maximum of the likelihood function. We are currently investigating alternative searching algorithms that are less influenced by initial values. One promising option is simulated annealing (Kirkpatrick et al. 1983).

Once we have obtained reliable estimates of life-table parameters at each site, and on each tree within each site, we will begin to estimate the effect of temperature and foliage age on parameter values.

CONCLUSION

Development of the overwintering sistens generation may proceed at a faster rate in Virginia than in Connecticut. Sistens adults were observed in Virginia at an earlier date than reported by McClure (1989) in Connecticut. However, considerable caution must be exercised when comparing the reported observations. Temperature differences between years, rather than temperature differences between the States, may be responsible for observed differences in phenology. Results of our analysis hopefully will elucidate the effects of temperature on phenology, and make possible the estimation of time of phenological events at any location.

ACKNOWLEDGMENTS

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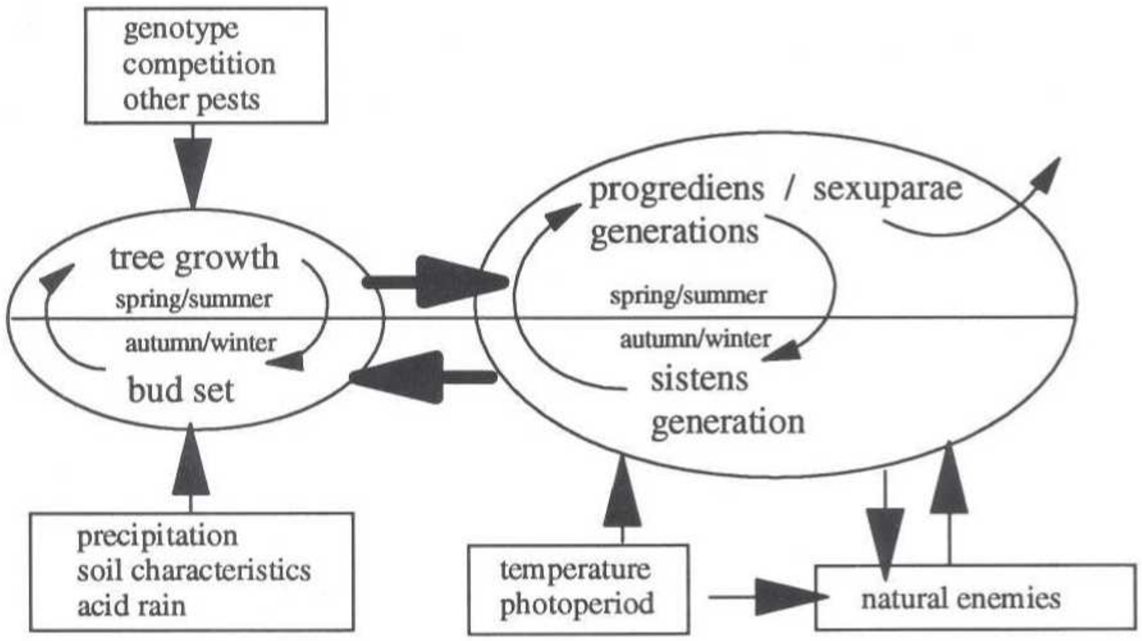


Fig. 1. Graphical representation of the important components of the HWA-hemlock population system and the interactions among the components (arrows).

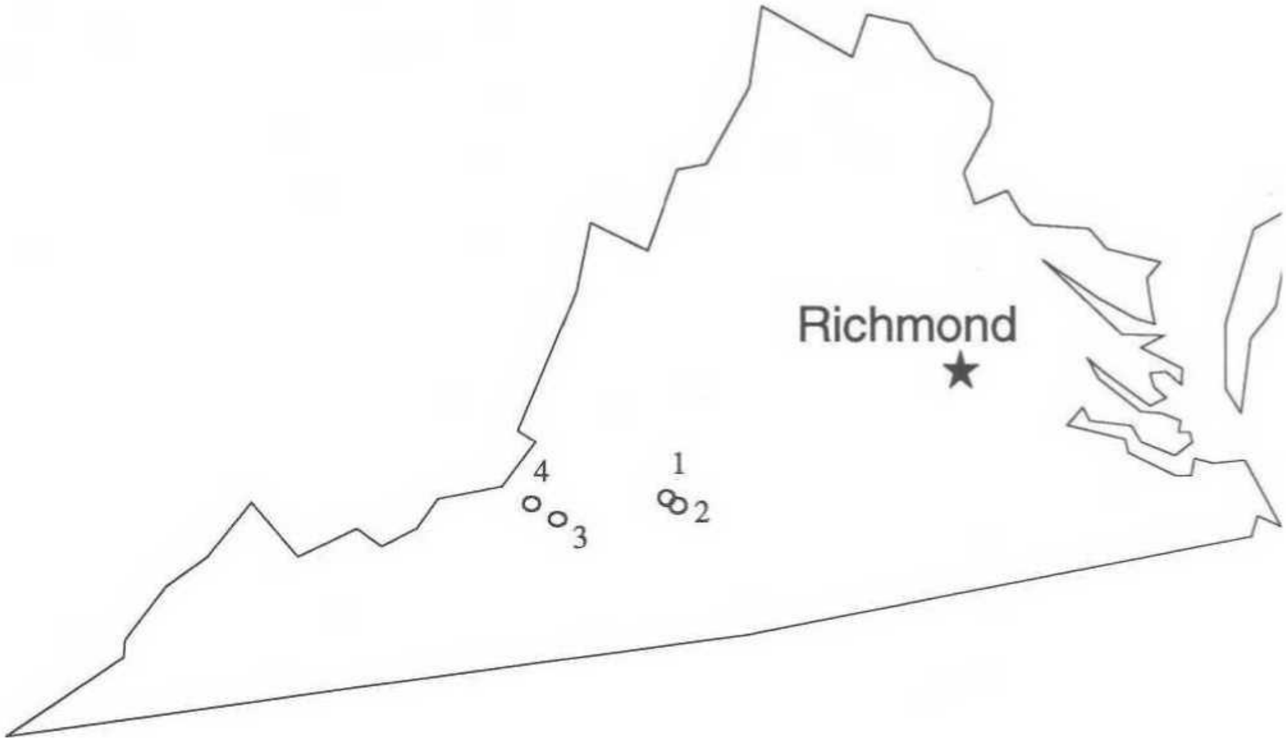
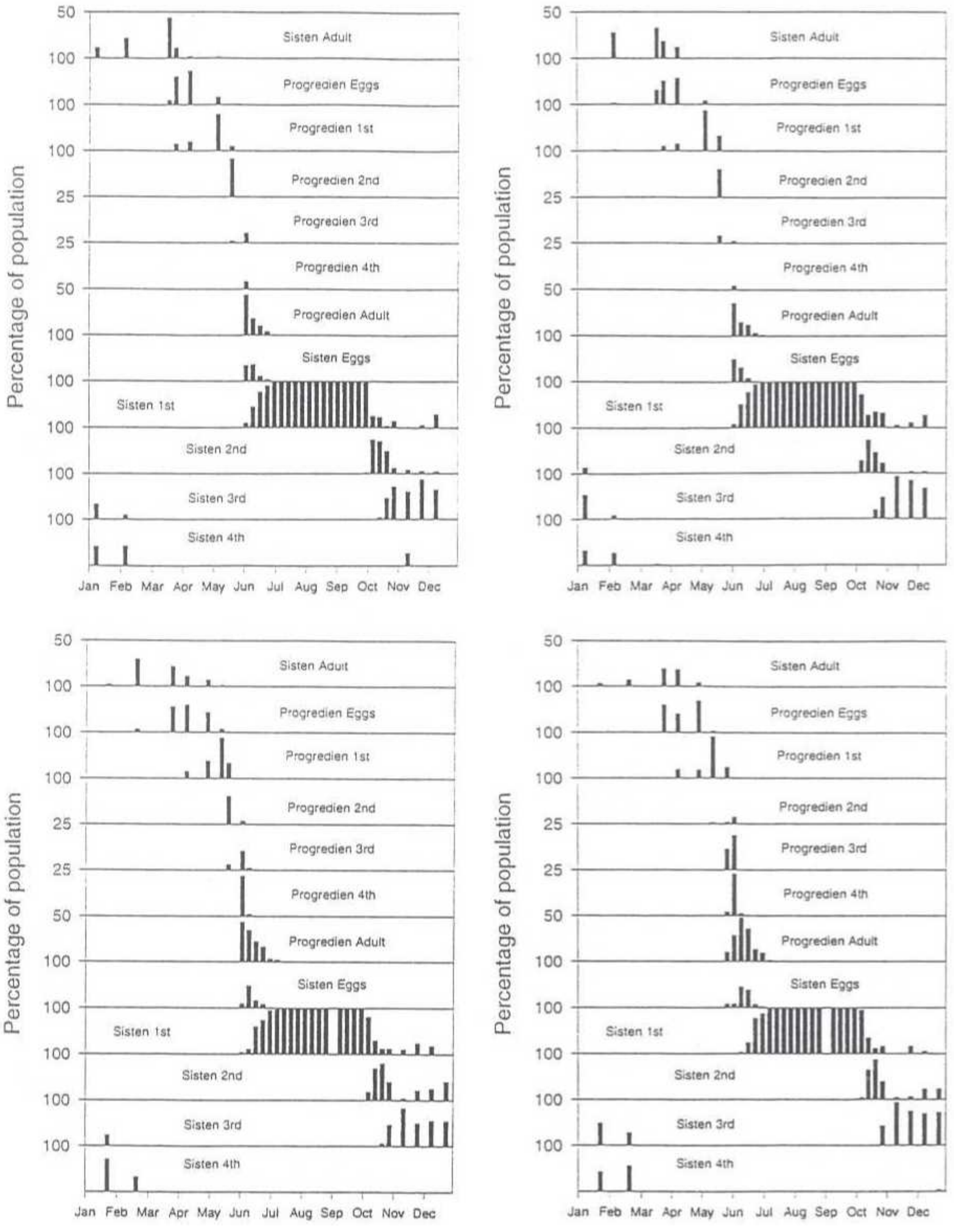


Fig. 2. Location of 4 sampling sites (a) in southwestern Virginia



Figs. 3.1 - 3.4. Estimated proportion of HWA population in each of 12 life-stages at each sampling interval at sites 1 through 4 (left to right, top to bottom). Note: for the purpose of graphical representation only, the number of eggs in each sample was reduced by a factor of 10 in order that their extremely high numbers did not overshadow the other life-stages.

HEMLOCK WOOLLY ADELGID FEEDING MECHANISMS

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ABSTRACT

The hemlock woolly adelgid, *Adelges tsugae* Annand (Hymenoptera: Adelgidae), has a stylet bundle comprised of two outer mandibular stylets and two inner maxillary stylets. The stylet bundle is inserted into the adaxial side of eastern hemlock, *Tsuga canadensis*, needles, proximal to the twig with respect to the needle abscission zone. Stylets are inserted primarily intracellularly through epidermal cells, but once inserted into the plant, the stylet bundle travels through the plant tissues both intracellularly and intercellularly, the latter predominating. The feeding site of this adelgid was found to be the parenchyma cells which comprise the xylem rays. *A. tsugae* produces abundant salivary secretions, salivary tracks, and salivary sheaths in the plant tissue.

INTRODUCTION

The hemlock woolly adelgid, *Adelges tsugae*, is an exotic pest threatening the health of eastern hemlock, *Tsuga canadensis*, and Carolina hemlock, *T. caroliniana*. This adelgid causes extensive damage to eastern hemlocks (McClure 1992), and infested trees have been reported to die in as little as four years (McClure 1991). Little is known about how *A. tsugae* kills its host plant, but this piercing-sucking insect is believed to injure hemlocks by sucking their sap and perhaps also by injecting a toxic saliva while feeding (McClure 1995). The objectives of the study reported here were to determine the site and method of stylet bundle insertion in the plant, to describe the pathway taken by the stylets through the plant tissues, to identify the feeding site, and to determine if saliva is secreted in the host plant tissues.

MATERIALS AND METHODS

At two-week intervals from May to late July, we removed twigs from adelgid-infested eastern hemlock trees. For light microscopy, samples were examined in a fresh state, or were fixed in formol-acetic-alcohol, dehydrated, and embedded in Paraplast-Plus. Specimens were serially sectioned and stained with Safranin O and Fast Green, or Auramine O and Methylene Blue, or napthol yellow-S. For scanning electron microscopy, specimens were fixed in buffered glutaraldehyde and osmium tetroxide, dehydrated with ethanol, and critical point dried.

RESULTS

The crawler stage of the hemlock woolly adelgid settled at the base of hemlock needles, and did not appear to stray far from its original attachment site. One or more exuviae, depending on the stage, were generally piled up in immediate proximity to each nymph. Although nymphs were generally situated distal to the abscission zone of the needle (Fig. 1), the actual site of stylet bundle penetration of the needle was proximal to the abscission zone, on the adaxial side of the needle (Fig. 2). The entire length of the stylet bundle was not inserted into the needle (about 15% of the length remained outside the plant). The stylet bundle is comprised of four stylets, two outer mandibular stylets and two inner maxillary stylets. The mandibular stylets have deep grooves in which the maxillary stylets lie, and the maxillary stylets can be extended from and retracted within the mandibular stylets.

Stylet bundle insertion into the host plant was almost always intracellular through the epidermal cells, near the center of the adaxial side of the needle and proximal to the abscission zone, but distal to the juncture of needle and stem tissues (Fig. 3). Once the stylet bundle had penetrated to the vascular tissues of the plant, it followed a predominantly intercellular path along the vascular bundle in the xylem, only occasionally penetrating cells intracelluarly. At the end of its travel, the stylet bundle often penetrated one or several xylem ray parenchyma cells intracellularly. The final feeding site was almost always a parenchyma cell within the xylem rays (Fig. 4).

In all samples, we observed evidence of salivary secretions, tracks, and sheaths. Salivary tracks were most evident near the feeding site, where they appeared globular and stained intensely with protein stains (Fig. 5). Multiple tracks were sometimes present near the insertion site (Fig. 6), indicating probing behavior, and evidence of salivary tracks increased as the adelgid population developed.

DISCUSSION

Our results indicate that *A. tsugae* inserts its stylet bundle into the needle proximal to the plant with respect to the needle abscission zone. We can speculate that insertion occurs here because a more distal position might be too far away from the preferred tissues for feeding to occur, or perhaps the abscission zone is difficult for the stylets to traverse, or attempted penetration of the abscission zone might trigger needle abscission.

The salivary sheath secreted by *A. tsugae* may protect the stylets from plant chemical defenses and from wound responses of damaged plant cells. The salivary sheath may allow the insect to continue to feed throughout the season as the plant tissues mature; older plant tissues generally have lower nutrient levels and higher allelochemical content (Miles 1990). Salivary tracks may facilitate reinsertion of the stylet bundle after molting.

The predominantly intercellular pathway of the hemlock woolly adelgid stylets once within the plant tissue, coupled with the postive staining of the saliva for protein, suggests that the saliva contains enzymes, possibly pectinase. Toxic properties of the saliva are unknown.

Adelgids which infest spruce hosts feed on cortical parenchyma cells; they modify these cells to make them better conductors of solutes from the phloem and, in so doing, induce gall formation (Rohfritsch 1990). The hemlock woolly adelgid does not feed on cortical parenchyma. It feeds on the parenchyma cells of the xylem rays. These cells transfer and store nutrients in the plant. The hemlock woolly adelgid does not feed on plant sap; it feeds on storage cells. Therefore, it is quite possible that this insect's intense impact on eastern hemlock may not be due to a direct depletion of plant photosynthate. Perhaps its saliva contains a toxin, or has toxic properties when present in high concentration. It is also possible that the hemlock woolly adelgid depletes nutrients held in storage cells and, in so doing, renders the host plant more susceptible to other biotic or abiotic stressors.

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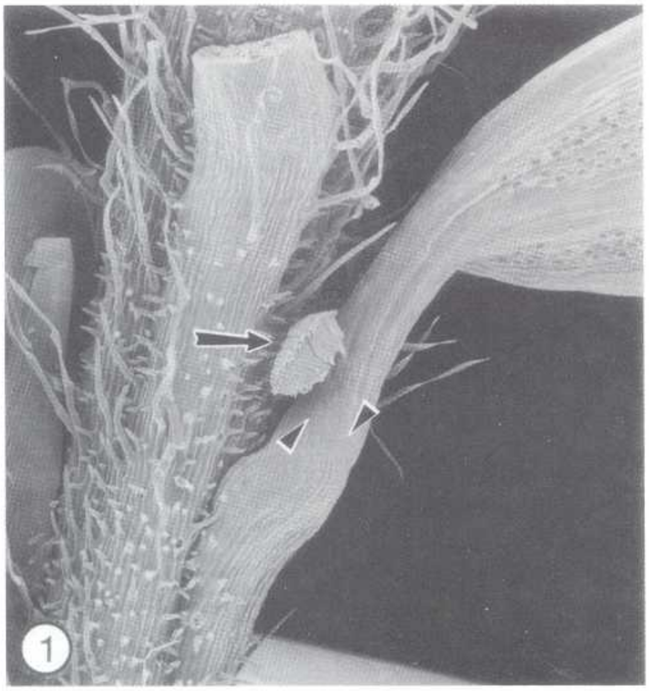

Fig. 1. *A. tsugae* (arrow) settled at base of needles on eastern hemlock. Arrowheads point to abscission zone. 40×

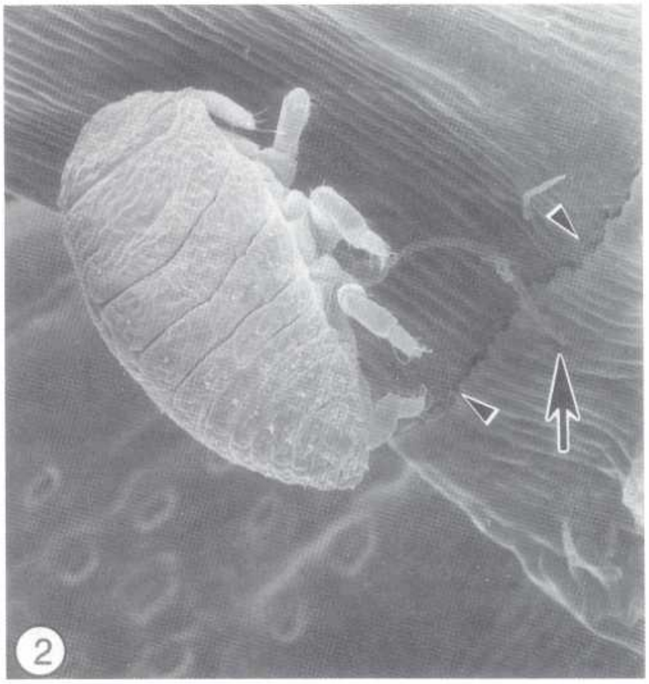

Fig. 2. A. tsugae nymph with stylet bundle inserted (arrow) proximal to the stem with respect to the needle abscission zone (arrowheads). 200×

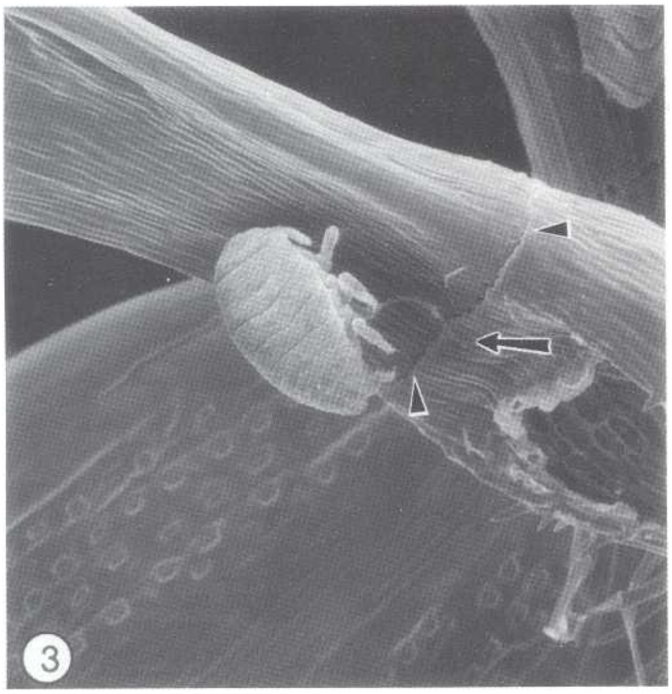

Fig. 3. Settled nymph showing stylet bundle insertion (arrow) near the center of the adaxial side of the needle, and proximal to the abscission zone (arrowheads), but distal to the juncture of needle and stem tissues. The jagged edge on the adaxial surface of the needle(s) indicates where the needle was intentionally torn away from the stem to reveal the insertion site. 100x

Fig. 4. Stylet bundle ending intracellularly in a xylem ray parenchyma cell (arrow). Saliva is present at the tip of the stylet bundle (arrowhead).

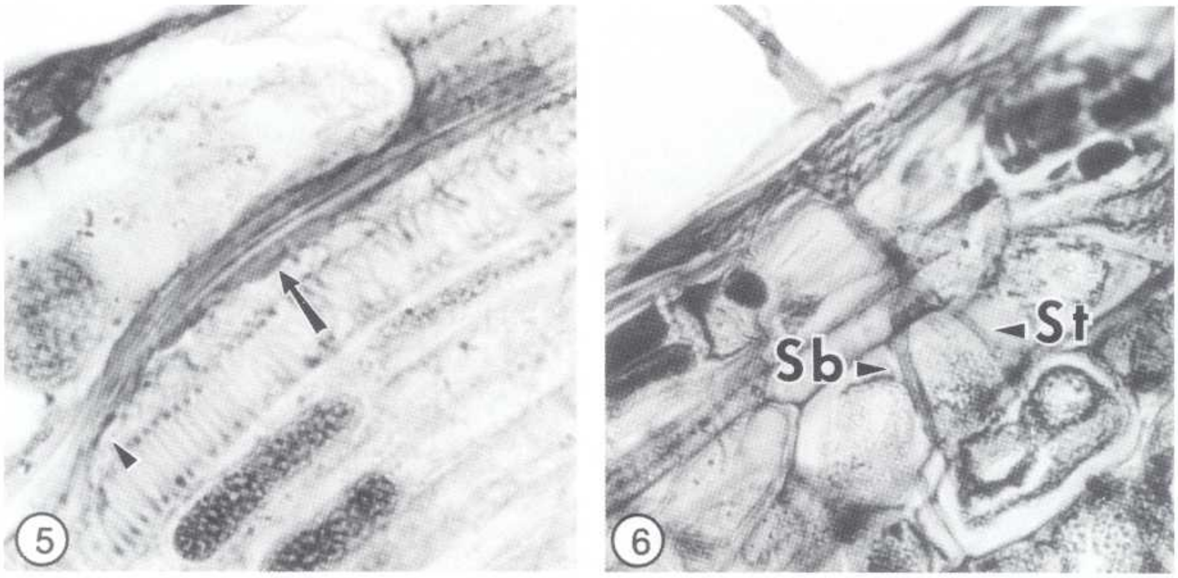

Fig. 5. Stylet bundle with salivary sheath (arrow). Salivary secretions are apparent at tip of the bundle (arrowhead).

Fig. 6. Stylet bundle (Sb) is inserted intracellularly. An additional salivary track (St) is visible near the insertion site.

LONG-TERM IMPACT ASSESSMENT OF EASTERN HEMLOCK FORESTS

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ABSTRACT

Permanent plots were established in Pennsylvania, New jersey, and West Virginia to monitor the long-term impacts of the hemlock woolly adelgid on eastern hemlock stands. Most plots were not predisposed to the adelgid but were anticipated to be so in the near future. Baseline data were collected in 1993 to measure changes in tree health using Visual Crown Rating methodology. Plot trees are re-examined annually and include estimates of new growth and adelgid population densities. Although few plots have been infested to date, preliminary results indicate that non infested hemlocks are showing a downward trend in crown health. Droughty conditions between 1991-93 are likely the cause of these observations.

INTRODUCTION

The hemlock woolly adelgid (HWA) was first reported in the Eastern United States in Virginia during the 1950s and southeastern Pennsylvania by the late 1960s (McClure 1987, 1990). Although the adelgid continued to spread, hemlock decline and tree mortality went virtually unreported until the mid 1980s when McClure described the adelgid-caused decline of hemlock in Connecticut (McClure 1990). In the following few years, reports of similar episodes began to appear in scattered hemlock stands in New Jersey, Pennsylvania, and Virginia while, at the same time, Quimby (personal communication) and others had observed infested hemlocks for a number of years in Pennsylvania with few noticeable impacts. These events elevated the concern over this exotic pest and raised many questions over the potential impacts on our eastern hemlock forests.

In 1993, a cooperative effort to monitor hemlock stands was initiated to address these issues. Permanent plots were established in West Virginia, Pennsylvania, and New Jersey in hemlock stands not previously infested but likely to be so in the near future (Onken et al. 1994). The purposes of this effort were to: 1) document the measured effects of HWA on the health of hemlock trees over time; 2) determine if hemlocks can survive and/or recover once infested; 3) identify other biotic or abiotic stress agents that may compound the observed impacts; and 4) evaluate both stand and site characteristics that may relate to a stand's susceptibility to an infestation or vulnerability to tree mortality.

METHODS

Each plot is a single strip transect and consists of a rectangle six meters wide and of variable length. The first 10 hemlock trees are selected based on a dbh greater than 2.54 cm (1 inch) with only 2 of the 10 trees less than 12.7 cm (5 inches). Plots are measured from the "outer" edge of tree number 1 to the "outer" edge of tree number 10.

Measuring changes in tree health. An annual assessment of each plot tree's crown is conducted to detect changes in tree health. Two methods are used -- the first of which involves using the Visual Crown Rating (VCR) standards established by the USDA Forest Service, Forest Health Monitoring Program (Millers et al. 1992). The VCR standards include an estimate of the crown ratio, crown dieback, crown density, foliage transparency, and measured crown diameter. All are estimated in 5 percent increments, except for crown diameter, which is measured to the nearest 10 cm. The second method involves an estimate of new growth. In each plot a 30.5 cm (12 inch) branch sample from 10 trees is measured in the field, and the numbers of lateral shoots with and without new growth are counted. The 10 plot trees are used if lower branches are within reach. McClure (1991) and Ward (1991) used similar methods to describe the relationship of HWA populations to impact on new growth.

Tree, stand and site characteristics. Within each plot, dbh and crown position of the 10 plot trees, stand density, species composition, slope, aspect, elevation, soil type (sand, loam, clay or rocky), and habitat conditions (xeric, mesic or hydric) were recorded. Tree and stand observations will be re-evaluated every 5 years.

HWA population monitoring. Annual field estimates of HWA populations are based on the same 30.5 cm branch samples used during the estimate for new growth. In this case, the presence or absence of at least one woolly mass is noted for each shoot of the previous year's growth.

Precipitation estimates. Rainfall data are collected from the nearest National Oceanic and Atmospheric Administration (NOAA) weather station for each plot. These data are summarized by month and year, and deficit patterns will be compared to changes in tree health.

RESULTS AND DISCUSSION

A total of 142 plots was established in hemlock stands in West Virginia (9), Pennsylvania (58), and the Delaware Water Gap National Recreation Area (75) during 1993-94. The general area around six plots (Mt. Minsi) in the Delaware Water Gap was known to have heavy populations of HWA in 1989, but no adelgids were observed in the plots in 1995. The remaining 69 plots in the Delaware Water Gap were also surveyed in 1995 and currently remain uninfested. In West Virginia, HWA-infested 3 plots by 1994, and 1995 surveys indicate populations are continuing to increase. The 58 plots surveyed in Pennsylvania were uninfested as of 1994; at the time of this report, 1995 surveys are incomplete.

Evaluating change in tree health. Using the 1993 Visual Crown Rating results of uninfested trees as a baseline, each tree was grouped by crown position (dominant/codominant, intermediate or suppressed) to determine the average or normal (mean std) range of the measured crown condition indicators (Table 1). The 60 trees on Mt. Minsi that may or may not have been infested prior to 1993 were separated from this analysis. Trees with average or better crown condition indicators are considered healthy and, regardless of crown position, were grouped to compare the relative changes from 1993 to 1995 (Table 2). Preliminary results indicate a downward trend for the relative number of trees in the average or better crown condition classes. For the uninfested trees, 4 out of 5 indicators show a decrease in the number of trees with an average or better crown condition. The most dramatic change occurred in foliage transparency, where the relative number of trees with healthy crowns decreased from 93 percent in 1993 to 7 percent in 1995. The only positive change occurred in crown density, where the number of trees increased from 83 percent in 1993 to 86 percent in 1995.

Excluding the 58 Pennsylvania plots that have not been surveyed in 1995, a total of 21 trees (<2 percent) has died between 1993 and 1995. Of the 21 trees, 14 were suppressed, 6 were intermediate, and 1 was in the codominant crown position. Even though natural mortality appears most often in suppressed and intermediate trees, the ability of a hemlock to produce new growth on at least the lower lateral branches does not appear to be influenced by crown position. In 1995, the majority of plot trees sampled had at least 50 percent new growth on lateral shoots.

Rainfall data. Eastern hemlock has long been recognized as a shallow-rooted species and, consequently, very intolerant of droughty conditions. A number of authors, including Stickel (1933) in Connecticut, McIntyre and Schnur (1936) in Pennsylvania, Secrest et al. (1939) in Wisconsin, and Graham (1943) in Michigan investigated various episodes of hemlock mortality and came to similar conclusions -- prolonged droughty conditions lead to a higher incidence of hemlock mortality.

Both Stickel (1933) and Graham (1943) recognized that hemlocks do not always succumb to droughty conditions in the driest year -- rather the greatest impact appears in the years following. This observation is further supported by several investigations of hemlock trees where entire root systems were dead but the crowns remained green (Secrest et al. 1939 and Graham 1943). It is important therefore to evaluate the impacts of drought over time.

Just how much or how prolonged droughty conditions must be before hemlock decline or mortality occurs is difficult to predict. Obviously, the health of the tree prior to drought as well as stand and site conditions are important variables to the tree's ability to survive. Also important would be additional stress agents such as the HWA.

As Stickel (1933) reported, the deficiency in precipitation that occurred between 1928 and 1931 caused considerable damage to the hemlock forests of southern New England, particularly in stands growing on trap rock ridges. During this period, below-normal rainfall was recorded in all four years, with the lowest precipitation recorded in 1929 and 1930 at 93.8 and 75.6 percent of the normal, respectively.

Likewise, in the fall of 1992 heavy hemlock mortality was observed near Stroudsburg on more than 1200 acres on Mt. Minsi, primarily along steep rocky ridges. Although ground observations attributed the cause to HWA, the recorded precipitation for the Stroudsburg area was 79 and 59.5 percent of the normal rainfall in 1991 and 1992 respectively. We can see a parallel to the previous event in Connecticut.

As of September 30, 1995, rainfall recorded for the year was only 68 percent of the normal in the Stroudsburg area, and similar conditions exist throughout much of the Northeast. Should these conditions continue, we could see significant hemlock mortality once again, particularly in trees already stressed by the hemlock woolly adelgid!

SUMMARY AND CONCLUSION

At present, the statistical analysis of most of the data remains incomplete. Expect to have a full report completed this winter. Although the level of significance has yet to be determined, hemlock health appears to be declining throughout most of our plots, based on 4 of the 5 crown condition indicators. To make matters worse, the drought of 1995 will likely compound the problem.

To date, only three plots are supporting any significant number of HWA. As additional plots become infested, we should have adequate baseline information to adequately evaluate the changes in tree health and the impacts caused by the HWA.

Table 1. Average crown condition of hemlock trees measured in 1993.

	Dom/Codominant (n=355)	Intermediate (n=284)	Suppressed (n=168)
Crown Ratio	45-65%	45-70%	45-70%
Crown Diameter	6.35-9.07 m	4.86-7.06 m	3.67-5.32 m
Crown Dieback	5-10%	5-10%	5-15%
Crown Density	45-65%	35-55%	30-50%
Foliage Transparency	10-15%	10-20%	15-20%

Table 2. Relative change in number of uninfested trees with average or better (healthy) crown conditions from 1993 to 1995.

	1993	1995	% Change
Crown Ratio	88%	84%	-4
Crown Diameter	83%	72%	-11
Crown Dieback	99%	95%	-4
Crown Density	83%	86%	+3
Foliage Transparency	93%	7%	-86

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THE USE OF REMOTE SENSING AND GIS TO DETECT AND EVALUATE HEMLOCK WOOLLY ADELGID IMPACTS AT THE LANDSCAPE LEVEL

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ABSTRACT

The role of satellite remote sensing for the identification of hemlock decline, due to woolly adelgid infestation, is illustrated in a southern reach of the Connecticut River valley. Landsat Thematic Mapper (TM) digital multispectral image data from May 1988 and April 1993 were processed to determine the extent of hemlock loss in the study area. Of the 5,141 hectares examined in this pilot project, 206 were classified as healthy hemlock cover in 1988, whereas this same cover type had declined to only 60 hectares in 1993. This loss of 146 hectares of healthy hemlock over the five-year period represents a decline of approximately 70 percent of that tree species, presumably to the woolly adelgid. During the course of investigation it was found that TM Bands 4 (near infrared) and 5 (middle infrared) provided the most revealing information about hemlock extent and conditions. This work is being continued with additional dates of Landsat data and will involve both an examination of a larger geographic area, and a wider array of analytical techniques, for detecting and characterizing hemlock decline.

INTRODUCTION

Eastern Hemlock. The Eastern Hemlock, *Tsuga canadensis*, grows from sea-level to 730 m in elevation across southeastern Canada to the Great Lakes, and its range extends south into the southern Appalachians at elevations from 610 to 1520 m (Goodman and Lancaster 1990). Hemlock is a shade-tolerant coniferous tree often found in rocky ravines in southern New England (Jorgensen 1978). It is the primary coniferous species in southern Connecticut and stands can be found in all counties of the state. Dickson and McAfee (1988) estimated that hemlock accounted for 53 percent of the softwood boardfeet and 10 percent of the total sawtimber boardfeet statewide.

These trees play a unique and important role in the region by providing habitat diversity that supports wildlife and maintains the quality of the ecosystem. Hemlocks are frequently found on steep, riparian slopes where they filter runoff, retain soil, and provide cooling shade for trout streams in the area. The hemlock has dense foliage and is the only conifer in the region that retains its lower branches (Jorgensen 1978;

Goodman and Lancaster 1990). Many neotropical birds favor the hemlock for its unique habitat and thermal cover, and their presence in the area would diminish with the decline of hemlock (Benzinger 1994).

Hemlocks provide an important thermal cover for second- and third-order streams in the region. Gregory et al. (1991) found that canopy density in riparian areas was the most critical factor in determining heat input of a stream reach. This heat input contributes to the oxygen levels and nutrient dynamics of these streams (Karr and Schlosser 1977). Clearly, if hemlock trees are defoliated, more energy will reach the surface of these streams, impacting the biota of the watersheds.

Hemlock Woolly Adelgid. The hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae) is an introduced insect of Asian origin that feeds on eastern hemlock. These 2 mm long, dark, oval insects have piercing-sucking mouthparts that are used to draw sap from hemlock and may introduce toxins (Lighari and Adams 1988; McClure 1991a).

A. tsugae was first discovered in the Pacific Northwest in 1922, where it had little impact on the western hemlock *T. heterophylla*. The adelgid was first observed in the East in Virginia in the 1950s and was first reported in Connecticut in 1985 (McClure 1987, 1991b). It is believed that Hurricane Gloria blew the adelgid from Long Island to the Connecticut coast in 1985. It subsequently spread along the coast and up the reaches of major rivers (McClure 1990).

Remote Sensing of Forests. Vegetation differentially reflects, absorbs, and transmits solar radiation across the electromagnetic spectrum. Satellites have been designed to capture reflected radiation and convert the data to a series of digital brightness values. This is the basis of remote sensing technology at the landscape level (Avery and Berlin 1992).

Several characteristics of vegetation control the quantity and wavelength of reflected energy. Chlorophyll absorbs energy in the visible portions of the spectrum. Foliage is a strong reflector of near infrared energy, and leaf moisture content controls the brightness of energy in the middle infrared portion of the spectrum. It is possible to identify different vegetation types and conditions by analyzing relative brightness values across these portions of the electromagnetic spectrum (Avery and Berlin 1992; Howard 1991).

Numerous studies have identified and mapped forests using satellite-based, remotely-sensed data. Most recently, Schriever and Congalton (1995) used images from several seasons to improve differentiation between forest types in New Hampshire. Bauer et al. (1994) used multi-stage sampling techniques, combined with multi-temporal images, to classify forest types in northeastern Minnesota. Congalton et al. (1993) combined remotely-sensed data and a Geographic Information System (GIS) to map old-growth forests in the Pacific Northwest and to identify preferred habitat of the northern spotted owl. Ferrarotti (1991) used satellite images to discriminate between hemlock and white pine stands in the northwestern part of Connecticut, with a reported accuracy in excess of 90 percent.

Remote Sensing of Pests. Formerly, monitoring and mapping forest and agricultural field pest infestation was a time-consuming, costly, error-prone process (Muchoney and Haack 1994; Joria and Ahearn 1991). Remote sensing of wide areas, coupled with automated analysis, can significantly increase the level of accuracy and consistency in classification of infested areas while lowering cost and time (Joria and Ahearn, 1991; Sharp et al., 1985).

Computer-assisted analysis of remotely sensed images offers photo interpreters new ways to view data. Several techniques have been investigated to improve early detection of pest infestation in vegetation. Sharp et al. (1985) developed a series of vegetation indexes that were effective in discriminating between diseased and healthy wheat cultivars. Muchoney and Haack (1994) developed a false-color composite image, based on principal component analysis of brightness values, that was found to be a quick and accurate way to identify areas of gypsy moth defoliation. Joria and Ahearn (1991) used a multi-stage process to determine gypsy moth defoliation in their study of Michigan forests. They eliminated all non-forest areas from their images and performed a cluster analysis of only the forested areas.

Once data have been captured and analyzed, they are suitable for use in a Geographic Information System (GIS). MacDonald and Comeau (1981) used a GIS to track defoliation caused by the spruce budworm. They developed information layers for tree species and volumes, land ownership, infestation distributions in different years, and other ancillary data that allowed them to assess quickly the spread of the pest and its impact on the forest and its owners.

Because of the unique role that hemlocks play in our ecosystem, and the devastation caused by the adelgid, it is critical that the extent of this infestation be measured and its change monitored over time. Remote sensing and GIS technologies provide a means of analyzing changes in forest health at the landscape level.

METHODS

Classifying the May 4, 1988 image. This study covers 5,141 hectares of forested hills and ravines in central Connecticut. It was necessary to develop a baseline landcover map of this area from satellite data. The ERDAS software package was used to analyze and classify a Landsat Thematic Mapper (TM) image dated May 4, 1988 (Fig. 1).

The first step in classifying the image was the creation of spectral signatures to represent various landcover categories. For each signature, the ERDAS SEED module was used to select an initial point within a spectrally unique polygon. The program combined neighboring pixels with similar values to the initial "seed" pixel, to create a spectrally homogenous training site. Training sites varied in size from a minimum of 18 to more than 60 pixels. Because each pixel represents a 30-meter square, the smallest minimum training site covers an area of 1.6 hectares. The program next averages the digital values of all pixels in the training site to create a statistical model of the six reflectance bands for the class. In addition to field trips, a variety of supplemental information, such as topographic maps and aerial photographs, was used to identify and provide ground truth for each selected training site. This process was repeated until 32 distinct signatures were developed for this image.

The minimum-distance algorithm of the MAXCLASS module was used to classify the TM image. This algorithm calculates the Euclidean distance, in 6 dimensions, between a pixel's reflectance value and that of each training class. It then assigns the pixel to the closest category. Several landcover categories are based on more than one signature, in order to handle variations in brightness values caused by topographic differences and other environmental factors. For example, the brightness values of an oak forest on a southern slope are different from the values of the same forest on a western slope. The RECODE module was used to combine similar categories and produce a consolidated 14-category landcover map of the study area (Fig. 2).

The study area is primarily forested. Mixed hardwoods cover 84% of the area, hemlock another 4%, and wetlands an additional 3.5%. Human impact on the landscape, as viewed from space, is apparent only in agricultural areas and impervious surfaces such as roads, buildings, and parking lots, covering approximately 7.5% of the area. Water and barren or sandy areas comprise the remainder of the study site.

Classifying the April 25, 1993 image. The Landsat TM image dated April 25, 1993, was obtained for analysis and comparison (Fig. 3). This image required pre-processing before it could be used for this study. In order to georeference the 1993 image to the 1988 image, common ground-control points were selected in both images. The NRECTIFY module was used to update the new image with the proper Universal Transverse Mercator (UTM) coordinates. Because the images were taken at different times, and under different atmospheric conditions, there were variations in the brightness values of similar locations. The spectral properties of the second image were adjusted to those of the first image by aligning the histograms of each band using the HSTMATCH module.

Areas that had previously been identified as hemlock now showed changes in their spectral reflectance patterns. Signatures were created for these areas and classified as dead or dying hemlock. These new signatures were added to the file of signatures used with the 1988 image. The 1993 image was classified and consolidated using the techniques applied to the May 4, 1988, image. Because this study focused only on the change in hemlock forests over time, the "non-hemlock" areas of the May 4, 1988, image were overlaid onto the classified April 25, 1993, image. This procedure provided a final classification of the April 25, 1993, image containing updated information only in areas that were formerly hemlock forest. The RECODE module was used as above to combine similar categories and produce a 15-category landcover map of the study area (Fig. 4).

RESULTS

In 1988 four percent of this area (206 hectares) was covered by healthy hemlock forests. Five years later 146 hectares of hemlock forest were dead or dying and only 60 hectares of hemlock forest remained healthy (Table 1). The analysis and classification of these images indicate that 70 percent of the hemlocks in this area were severely stressed or died during this 5-year period.

This analysis was based on the validity of separating spectral reflectance signatures of hemlock stands into healthy or dead/dying categories. To verify this classification, the statistical means for each of the signatures in the hemlock portions of the study area were extracted and compared. Two signatures were used to identify hemlock in 1988. For the 1993 image one healthy hemlock signature and two dead/dying hemlock signatures were created. Figure 5 compares the mean brightness values of these signatures for TM sensor bands 2 through 5. The profiles for the two dead/dying hemlock (DH) signatures are substantially different from the profiles of the three healthy hemlock (HH) signatures. The mean brightness values for the DH increase continuously across the electromagnetic spectrum, while the magnitude of the mean brightness values for the HH vary by wavelength. The brightness values for all three HH signatures are lower than the DH values at the red and middle infrared portion of the spectrum and are higher than DH at the near-infrared wavelength.

DISCUSSION

Remote sensors capture brightness values for each pixel in an image at several locations along the electromagnetic spectrum. When the brightness values for adjacent pixels of similar values are combined into classes, the mean brightness values across a portion of the electromagnetic spectrum produce unique patterns. An analyst can use these remotely sensed patterns, or spectral signatures, to discriminate between landcover categories. The patterns exhibited by the healthy hemlock signatures in figure 5 follow the general pattern of spectral signatures for healthy vegetation (Avery and Berlin 1992).

While chlorophyll absorbs most of the visible light, it absorbs a relatively greater percentage of light in the blue and red wavelengths. The healthy hemlocks show a decrease in reflectance in the red portion of the spectrum, but these values increase for the dead/dying hemlock signatures. This result implies that the chlorophyll content of the trees at these sites was lower in 1993 than in 1988. Leafy matter reflects energy in the near infrared portion of the spectrum. The healthy hemlocks for both years have greater brightness values, and presumably more needles, than do the dead/dying hemlocks. Moisture in vegetation absorbs energy at the middle infrared wavelength.

The dead/dying hemlock reflect more energy here than the healthy hemlock, indicating that they have a lower moisture content.

The signatures identified as healthy hemlock follow a pattern typical of healthy vegetation, so the evidence indicates that these sites do represent healthy vegetation in their respective years. An on-site inspection confirmed that these signatures were generated in a forest dominated by eastern hemlock. The signatures for dead/dying hemlock are dramatically different from the above signatures, or from those found in other healthy vegetation. Brightness values in areas of the spectrum affected by chlorophyll absorption, leaf reflectance, and leaf moisture content are all different. This evidence indicates that these trees may be considered not healthy. Again, this conclusion has been confirmed by an on-site inspection of the trees in the area. The few hemlocks that remain healthy are found along stream banks and the south side of a hill, as depicted in the landcover map in figure 4.

The healthy hemlock signature for the 1993 image deviated from the "classic" vegetation signature in the infrared portions of the spectrum. The brightness values in the middle infrared band were greater than the values of the near infrared band, perhaps because of a reduction in brightness values in band 4, an increase in values in band 5, or a combination of these factors. One explanation may be that band 5 brightness values were elevated because of reduced moisture in the trees, caused by a very dry year. Another possible explanation is that these trees were undergoing early stages of stress, from attacks by the hemlock woolly adelgid, which reduced foliar reflectance recorded by band 4. More work should be done to determine the cause of this discrepancy. Because remote sensing provides a broad view of the landscape, with information beyond the visible spectrum, it can provide early indications of forest problems.

It has been demonstrated that variations in brightness values in the near and middle infrared bands of the spectrum can be used to determine hemlock health status. These values can be used to calculate ratios that can then be used to classify TM images for several years, and would thus provide a map of changes in hemlock health over space and time. It may be possible to correlate these changes in forest health to landscape features using various spatial analysis techniques, leading to a predictive model of HWA distribution and/or impact. This is the basis of current research being performed by the University of Connecticut and the USDA Forest Service in the hemlock forests of central Connecticut.

CONCLUSION

This study has demonstrated that remote sensing can be used to identify changes in landcover over time. By analyzing the mean brightness values of the signatures by band, it is possible to correlate these signatures to the health of vegetation. Once confirmed by observation on the ground, these signatures can be used to map forests over extensive areas rapidly. Remote sensing and GIS technologies have proved to be important tools for the management of forests and the detection of vegetation changes at the landscape level.

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Table 1 - Results of the landcover classifications of the area in and around Devil's Hopyard State Park based on satellite images from 1988 and 1993. Data are for those portions of the study area that were classified as healthy hemlock in 1988. Percent of area is based on the total study area of 5141 hectares.

Year	Class	Hectares	Percent of Area
1988	Healthy hemlock	206	4.0%
1993	Healthy hemlock	60	1.2%
1993	Dead/dying hemlock	146	2.8%

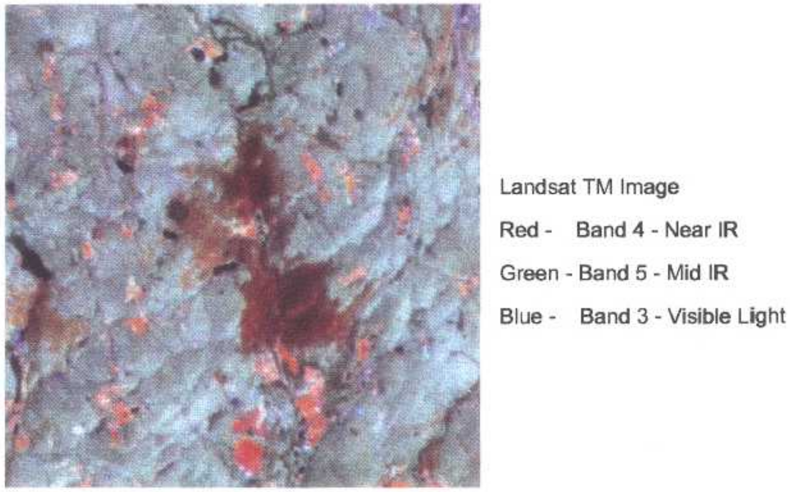

Figure 1. Landsat TM image dated May 4, 1988. The dark red area in the center of the image indicates a healthy hemlock forest.

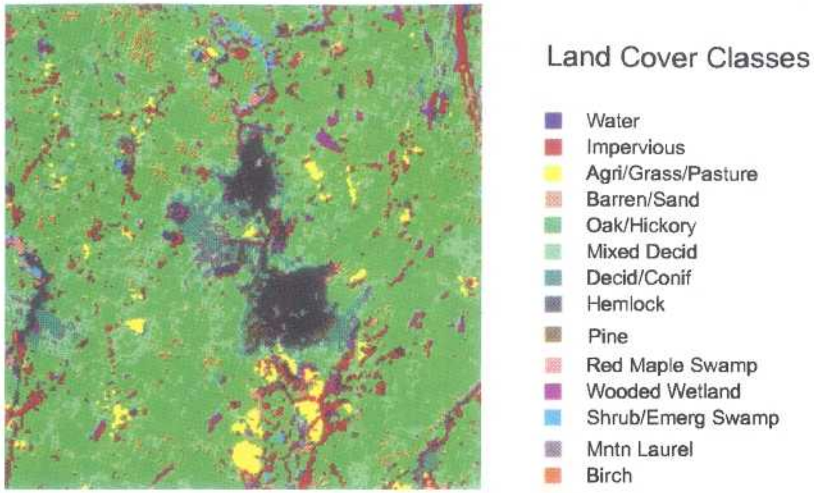

Figure 2. Landcover classification of the May 4, 1988 image.

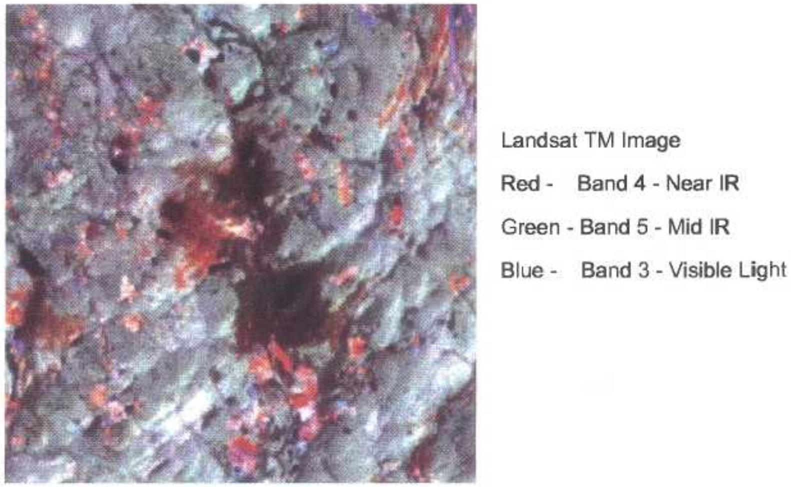

Figure 3. Landsat TM image dated April 25, 1993. The dark green and black areas in the center of the image indicate a stressed hemlock forest.

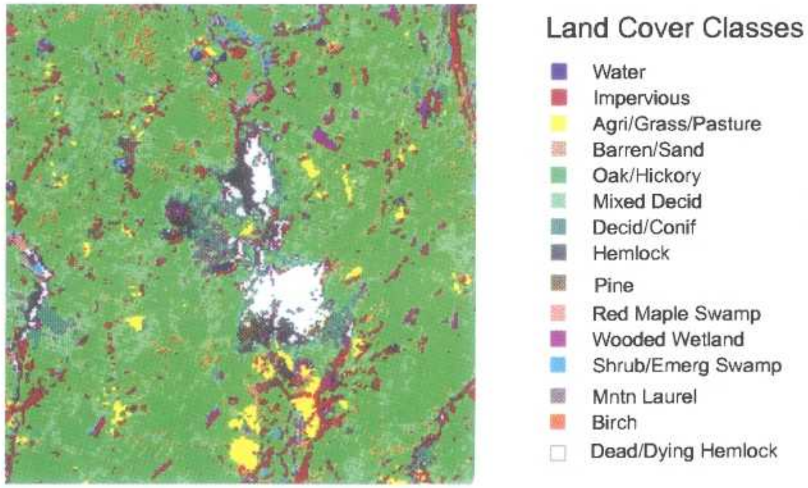

Figure 4. Landcover classification of the April 25, 1993 image. The white area in the center represents dead and dying hemlock forests.

ECOSYSTEM MANAGEMENT IN THE CONNECTICUT RIVER BASIN: IDENTIFICATION OF DESIRED FUTURE CONDITIONS AND EXPERIENCE-BASED BEST MANAGEMENT PRACTICES FOR ECOSYSTEMS IMPACTED BY THE HEMLOCK WOOLLY ADELGID

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Landowners, natural resource managers, and stakeholders in the Connecticut River Basin are very concerned about on-going and potential loss of hemlock due to the hemlock woolly adelgid (HWA). Loss of hemlock from eastern forest ecosystems would result in significant disturbance of riparian lands and loss of unique social, educational, and environmental assets. These losses, in turn, could cause significant impacts to the stability of forested riparian ecosystems, threaten water quality, destroy fish and wildlife habitat, and reduce valued aesthetic diversity.

No management guidelines specifically address the complex resource issues associated with loss of healthy hemlock ecosystems. Responding to requests from landowners and stakeholders in the lower Connecticut River Basin, scientists at the Northeastern Center for Forest Health Research organized a workshop to develop Management Practices (MPs) for protecting and restoring forested ecosystems impacted by HWA infestation and associated hemlock decline and mortality. Workshop attendees received an HWA "white paper" (Lapin 1994) describing the current knowledge of the pest and its impacts on natural resources in the lower Connecticut River Valley. Forty people participated, including natural resource experts, stakeholders, and private landowners, representing federal and state agencies, universities, utility companies, and non-profit organizations.

At the workshop, participants first described characteristics of the hemlock forest and defined Desired Future Conditions (DFCs) that would replicate these qualities. Identification of DFCs was the most important result of the workshop because these DFCs are the conditions around which resource management objectives will be formulated. Participants then developed a matrix that related the effect of certain management practices on the desired conditions, based on the current state of knowledge. The information in the matrix is being transformed into user-appropriate brochures, videos, and presentations.

A cooperative project to develop alternative management strategies has been initiated. The research will complement on-going projects in the lower Connecticut River Basin. These include the Silvio Conte U.S. Fish and Wildlife Refuge Planning Project, the Nature Conservancy's Tidelands Project, the Connecticut Department of Environmental Protection's Connecticut River Planning Project, the University of Connecticut Cooperative Extension Service's Forest Ecosystem Management Education Program for Landowners, and Harvard Forest's investigation of impact and response of forests impacted by HWA. Research and management partners include the USDI Fish and Wildlife Service, USDA Forest Service Research and Forest Health Protection, Natural Resources Conservation Service, state foresters, The Nature Conservancy, Northeast Utilities, regional water authorities, Harvard Forest, and watershed associations.

LITERATURE CITED

Lapin, Beth. 1994. The impact of hemlock woolly adelgid on resources in the lower Connecticut River Valley. 45 p. In review for publication.

MAPPING HEMLOCK DECLINE IN NORTHERN NEW JERSEY USING LANDSAT TM IMAGERY

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ABSTRACT

Throughout much of the northeastern USA, the Eastern Hemlock (*Tsuga canadensis*) is undergoing a decline due mainly to Hemlock Woolly Adelgid (*Adelges tsugae*) infestation. The utility of Landsat Thematic Mapper data and change detection techniques in mapping hemlock decline were analyzed for a 650-square-mile study area in northern New Jersey. The change in NIR/red reflectance between Landsat TM images from November 1984 to November 1994 was evaluated. Field measurements were collected from 217 circular plots, 90 meters in diameter, selected from 25 stands that represented a gradient from low to high change. 127 plots were used in determining the regression equation; 61 plots were reserved for accuracy assessment. Change in NIR/red reflectance from 1984 to 1994 was highly correlated to hemlock damage as measured on the ground ($R = 0.85$). It was not possible to adequately distinguish light defoliation from healthy hemlock; thus these two classes were lumped (e.g. healthy/light). Accuracy assessment showed that hemlock decline can be predicted within $\pm$ one damage class, with an overall accuracy of 62%. Of the 13,937 acres of hemlock forest in the study area in 1984, 40% had experienced moderate to severe defoliation, and 5% were dead by 1994. This study has proven that Landsat TM-based change detection can be used to map hemlock decline at the landscape scale.

INTRODUCTION

Concern over the spread of Hemlock Woolly Adelgid (*Adelges tsugae*) and other insect pests (e.g. elongate hemlock scale, *Fiorinia externa*) prompted the Rutgers University Center for Remote Sensing and Spatial Analysis and the New Jersey Bureau of Forest Management to undertake a pilot project using remote sensing to map hemlock decline in the state. Hemlock Woolly Adelgid (HWA) infestations were noticed in native stands of Eastern Hemlock (*Tsuga canadensis*) by the mid-1980s. Sparta Glen, a popular hemlock ravine and municipal park in Sussex County, was once graced by impressive groves of majestic hemlocks, interspersed within a matrix of hemlock-mixed hardwoods forest. By 1994, most of the hemlock trees at the western end of the ravine were either dead or severely defoliated, and several acres had been cleared because falling trees presented a safety hazard to park visitors. In this small, industrialized state, hemlock ravines such as Sparta Glen are highly valued as significant natural and aesthetic features in the landscape, and their demise would be a serious loss for New Jersey.

Current HWA monitoring methods used by the New Jersey Bureau of Forest Management focus on crown evaluations of individual trees within 11 permanent study plots, with occasional aerial surveys of prominent stands from small aircraft. Although aerial surveys have been helpful in observing the general health of hemlock stands, it is difficult to detect all stages of decline at any one time of year from the air. These methods alone are not adequate for detecting, quantifying, and mapping hemlock decline over a large area.

As an alternative to aerial surveys and photography, Landsat Thematic Mapper TM satellite imagery provides an efficient, cost-effective tool for collecting forest data over large areas (Lachowski et al. 1992). Remote sensing has been successfully used to map damage and decline of forest canopy species. Vogelmann and Rock (1986, 1988) measured and mapped red spruce decline in Vermont using TM Simulator data and Landsat-TM data. Several studies have used remote sensing to detect and map forest damage caused by insects (Franklin and Raske 1994; Joria et al.1991; Moulton et al. 1990; Vogelmann and Rock 1989; Leckie and Ostaff 1988; Mukai et al. 1987; Nelson 1983).

The primary objective of this study was to assess the utility of Landsat TM change detection to map hemlock decline over a large geographic area in northern New Jersey.

METHODS

Study area. New Jersey's estimated 26,000 acres (10,522 hectares) of hemlock forest are concentrated in the northern half of the state (NJDEP 1989), where this graceful conifer occurs both as pure stands and as individuals in a hemlock-pine mixed hardwood forest (Airola and Buchholz 1982). Located in the Highlands physiographic province of northern New Jersey, the 650 mi^2 area selected for study encompasses the greatest concentration of the state's hemlock stands (Fig. 1). This area comprises an estimated 13,937 acres of hemlocks, representing approximately half of the state's hemlock forest, and about 6% of the forested landcover within the study area.

The Highlands province is characterized by broad mountain ridges oriented NE to SW, with steep slopes leading into broad valleys and narrow ravines. The landscape is dotted with numerous glacial lakes and wetlands, and remains largely forested, protected somewhat from development as watershed lands, state forests and parks. One of New Jersey's few native conifers, hemlock provides a unique habitat for a number of plant and animal species and is a source of food and winter cover for numerous species of birds and mammals (Benzinger and Angus 1992; Radis 1992).

Landsat TM Data and Image Processing. Landsat TM scenes (Path/Row 14/31 and 14/32) were obtained for November 8, 1984, and November 4, 1994. A cloud-free subset common to both scenes, and incorporating the greatest concentration of hemlocks, defined the study area. Landsat TM data have a ground resolution of 30 meters. Winter, or "leaf-off" image dates, are best for detecting coniferous forest.

Image processing was conducted on a SUN SparcStation using ERDAS software. The 1994 image was normalized to the 1984 image using 5 light and 5 dark ground targets, such as deep water reservoirs and bedrock ridges, presuming these ground areas would have similar reflectance in both 1984 and 1994 (Eckhardt et al. 1990). The normalized 1994 image was then registered to the 1984 image using 10 ground control points, with a registration error (RMS) of less than one quarter pixel (picture element). Nearest-neighbor resampling was used to preserve the original digital numbers for change detection purposes. A ratio of near infrared (NIR) to visible red wavebands (TM4/TM3) was employed to serve as a vegetation index to highlight the coniferous canopy cover, as well as to reduce slope shadows in this area of rugged terrain.

Healthy, green vegetation reflects NIR energy and absorbs red energy. The ratio of NIR/red is positively correlated with green vegetation amount and serves as a useful vegetation index (Spanner et al. 1990). As defoliation occurs in a forest, the biomass of green foliage is reduced, resulting in decreased NIR/red ratio. Because satellite imagery is digital in format, this change in reflectance can be measured by subtracting one image from the other, pixel for pixel (Lillesand and Kiefer 1994). Commonly known as "image differencing," this procedure has been shown useful in detecting and quantifying changes in forest cover over time (Bauer et al.1994; Sader 1995; Wolter et al. 1995; Nelson 1983).

Image differencing was performed by subtracting the 1994 data from the 1984 data, and adding a constant to eliminate negative values. The resulting change image, representing a difference in NIR/red reflectance from 1984 to 1994, was displayed as shades of a gray scale ranging from black to white. Medium shades of gray represented little or no change from 1984 to 1994. Darker shades represented a decrease in vegetation (defoliation), while lighter shades represented an increase in vegetation. The change image was then rectified to the Universal Transverse Mercator (UTM) coordinate system using 14 ground control points. Nearest neighbor resampling was used, with a registration error of less than one quarter pixel. The 1984 and 1994 coregistered images were also rectified to UTM for visual comparison with the change image.

Data from the 1984 image served as the baseline condition for change detection. Any changes in hemlock canopy as of 1994 were assumed to result from the various stressors leading to hemlock decline. Analysis was restricted to areas mapped as hemlock forest by NJDEP personnel from 1986 orthophotoquads (NJDEP 1989). This GIS vector map was converted to a raster image and used as a "mask" to retain only those portions of the Landsat image that were known to be hemlock stands, while blocking out the rest of the image.

Evaluating the extent of hemlock damage from the ground (reference data). In order to interpret the change image in terms of hemlock decline, field reference data concerning the condition of hemlock forest were collected. This study reflects an initial attempt at developing a simple ground survey method for evaluating the condition of hemlock canopy that would be quick, practical and comprehensive, yet relate to the spatial resolution of satellite imagery. Based on previous studies (Curran and Hay 1986), a window of 3 x 3 pixels in size (approximately a circular plot of 90 meters in diameter) was used to correlate ground variables with image data to account for satellite errors of location. The coordinates for the center point of the plot were determined with a differentially corrected Global Positioning System (GPS).

Twenty-five stands representing a gradient of low-to-high change across the study area were selected for closer examination. Plots were selected to represent a fairly uniform species composition. Sketches of irregular hemlock densities within the plot were made for future reference. A total of 217 plots was evaluated on 26 field days from April 25 to July 7, 1995. At each plot, percent canopy cover was determined for three tree classes: hemlock, deciduous hardwoods, and other conifers. An estimate was made of the percent cover of the hemlock component within each of the 5 damage classes (healthy, light, moderate, severe, dead), using percentage ranges of 0-5%, 5-25%, 25-50%, 50-75%, and 75-100%. Table 1 defines the conditions of each damage class. Due to the typical patchiness of HWA infestation and damage, even for adjacent trees, a plot could contain trees that represented 2 or more damage classes, making an overall visual assessment of damage more difficult. Thus a weighted damage class was assigned to each plot based on the percent cover within each damage class (i.e., Damage = E [class number x % hemlock canopy]). In order to prevent the underestimation of damage, the endpoints of each percentage range, rather than the midpoints, were used for weighting the damage.

Correlating damage with change in reflectance. Based on the GPS coordinates and field notes, the reflectance plots were located in the rectified TM difference and original imagery. Pixels representing water, roads, rock outcrops, deciduous forest, and other non-hemlock landcover were deleted from the change image for each 9-pixel window. Plots were removed from the dataset if fewer than 3 pixels remained in the window. The mean of the remaining pixels in the window became the difference image value (change) for that plot. The data for 188 remaining usable plots were stratified into 5 damage classes. Two thirds of the plots in each class were randomly selected for calibrating the regression model. A reduced major axis approach (Curran and Hay 1986) was used to relate the NIR/red image change value to the hemlock damage value. Once developed, the regression model was then used to assign each pixel in the change image to a damage class, resulting in an overall "damage map" for the study area.

RESULTS AND DISCUSSION

Graphical analysis showed a positive linear relationship (R = 0.85) between the image change (NIR/red 1984 - NIR/red 1994) and weighted damage values. There appeared to be little difference between the healthy and light classes. Linear regression analysis for those two classes alone indicated no significant statistical difference between them (R^2 = .002). Thus, healthy and light data were joined together as one class, resulting in four damage classes: healthy/light, moderate, severe, and dead. Linear regression analysis indicated that the TM NIR/red band ratio was highly correlated with the weighted hemlock damage (defoliation) value (Damage = -23.522 + 0.042 (Change), R^2 = 0.73, F = 342, p < 00001).

Based on the above regression model, the weighted hemlock damage value was predicted for the independent validation data set, based on the observed TM change values. The predicted weighted damage value was rounded to the nearest damage class and compared to the observed damage class, using a contingency matrix approach (Table 2). The major diagonal indicates agreement between the two data sets, and the overall accuracy is determined by dividing the total number of correctly classified test plots by the total number of plots in the test data set. Overall accuracy was 62%. However, it is important to consider the accuracy for individual damage classes in the matrix, and examine patterns of error.

Two commonly used methods of assessing classified maps are "producer's and user's accuracy" (Jensen 1996). Producer's accuracy is a measure of omission error, and is calculated by dividing the number of correctly classified plots for a damage class by the total number of reference plots for that damage class (column total). Producer's accuracy was highest for healthy/light, moderate, and dead sites (67, 64, 67%), and lowest for severe sites (45%). User's accuracy is a measure of commission error, and is calculated by dividing the total number of correctly classified plots in a damage class by the total number of plots classified in that damage class (row total). User's accuracy was highest for healthy/light (90%) and dead (86%) damage classes, followed by severe (45%) and moderate (39%) damage classes.

Though these numbers appear low, closer examination of the contingency matrix reveals that misclassification occurred between adjacent classes only. Accuracy was generally highest for the endpoints of healthy/light and dead classes. For example, a hemlock stand classified as severe by ground observations may be classified by the image change detection model as either dead (adjacent class above) or moderate (adjacent class below), but never as healthy/light. Misclassification with adjacent classes may be a function of canopy damage heterogeneity within a plot. Ground plots evaluated as "dead" or "healthy" generally contained fewer trees from other damage classes, which reduced error in damage estimation, and led to greater map accuracy. Conversely, plots evaluated as "moderate" or "severe" often contained a mixture of trees from adjacent damage classes. These mixtures, along with other complicating stand factors such as tree size and position in the canopy, could have biased the damage class weight toward an adjacent class. This bias would result in greater misclassification in the moderate and severe damage classes.

In the Sparta Glen example (Plate 1), healthy hemlock appears red in the 1984 Landsat TM image (Plate la). Hemlock forest defoliation and mortality can be seen as a reduction in the number and redness of the corresponding pixels in the 1994 image (Plate 1b). The prevalence of darker pixels in the difference image (Plate lc) indicates that hemlock foliage decreased dramatically from 1984 to 1994. In the damage map (Plate 1d), these areas of change were classified as severe (yellow) or dead (brown), as determined by the regression model.

The damage classification map for the entire study area showed that the New Jersey Highlands has been seriously impacted by HWA (Table 3). In 1984 there were 13,937 acres of healthy hemlock forest in the study area. By 1994, 45% of the hemlock forest, or 6,280 acres, had experienced defoliation to some degree. 5% of the hemlocks in the study area were dead, representing 737 acres._

Areas for Improvement. Although the band ratio was useful in reducing the shadows on steep slopes, it did not eliminate the problem of poor illumination on the steepest slopes. Additional image processing techniques, such as topographic normalization, should be investigated. Estimating percent cover of hemlock canopy for each damage class to the nearest 10% may reduce the variability in the data, and increase overall classification accuracy. The base map of hemlock forest cover could be further refined with the use of pertinent GIS raster files as masks, and by selectively removing non-hemlock coniferous forest from the study area. This procedure would provide a more accurate base map of hemlock forest for the entire state, which could then be used as a hemlock mask for future change detections and mapping.

CONCLUSIONS

Change detection techniques employing Landsat TM imagery present a reliable means of mapping hemlock decline at the landscape scale. Results of this pilot project show that the change in Landsat TM NIR/red reflectance ratio data from 1984 to 1994 was significantly related to hemlock damage ($R^2 = 0.73$). Based on the regression model approach used in this study, hemlock decline can be predicted within ± one damage class. Healthy/light and dead hemlock stands are more accurately detected and mapped than are hemlocks experiencing severe and moderate defoliation. These techniques can be easily employed to map and monitor hemlock decline elsewhere in New Jersey and the northeastern USA. The feasibility of applying the specific regression model developed in this study to other regions and Landsat TM image data sets, with appropriate modification (e.g. atmospheric correction), needs further investigation.

This study shows that hemlock decline is a serious problem in the northern Highlands region of New Jersey; 45% of the hemlock forest has experienced some degree of decline. Ongoing research is presently focused on analyzing the spatial distribution of hemlock decline in the New Jersey Highlands to determine if there are any significant relationships between patterns of decline and underlying environmental or anthropogenic factors.

ACKNOWLEDGMENTS

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Table 1: Damage class definitions.

Class	% Defoliation	Appearance From The Ground
Healthy	0 %	No visible damage. Canopy dense, dark green in color. Lower branches may be absent naturally.
Light	< 25 %	Dieback may be present at ends of branches. Canopy shows overall light loss of foliage.
Moderate	25 - 50 %	Lower half of tree crown sparse or dead. Upper crown still appears somewhat dense when viewed against the sky.
Severe	50 - 75 %	Most of crown dead, except for a small tuft of sparse foliage at the top.
Dead	75 - 100 %	Tree dead or almost dead. Bark may have been stripped by woodpeckers. Bole may be riddled with holes from bird and insect activity .

Table 2: Contingency matrix based on 61 test plots. Diagonal values (in bold) represent agreement between ground reference (observed - columns) and Landsat TM classified (predicted - rows) damage classes.

Ground Reference

Landsat TM

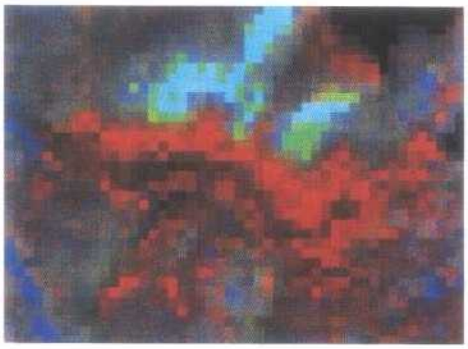
	H/L	M	**S**	**D**	**Total**
H/L	**18**	2	0	0	20
M	9	**9**	5	0	23
S	0	3	**5**	3	11
D	0	0	1	**6**	7
Total	27	14	11	9	**61**

Table 3: Acreage of hemlock forest in the study area.

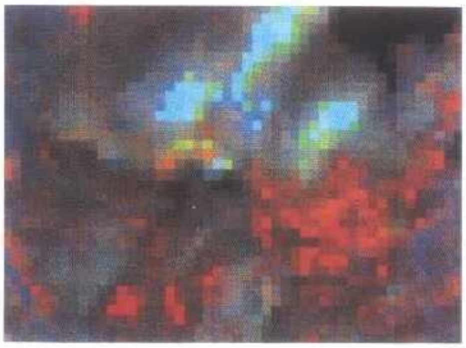
Year	Class	Acres	Percent
1984	Healthy	13,937	100%
1994	Healthy/Light	7,657	55%
	Moderate	3,902	28%
	Severe	1,641	12%
	Dead	737	5%

Figure 1: Map of Eastern Hemlock stands in New Jersey (NJDEP 1989) with study area outlined.

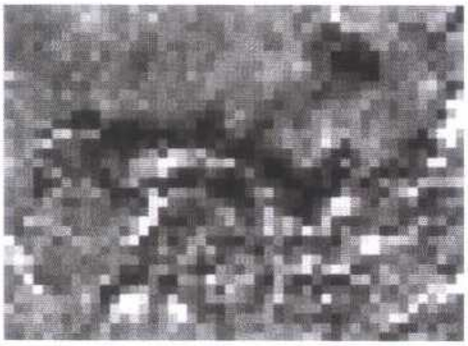
Hemlock Decline in Sparta Glen, NJ



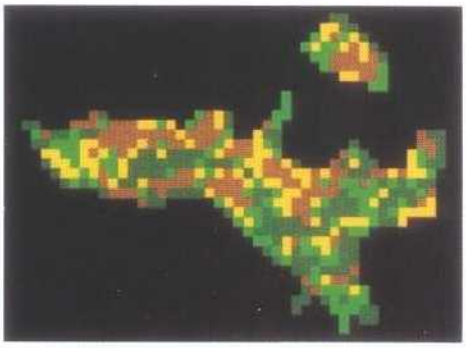
a. 1984



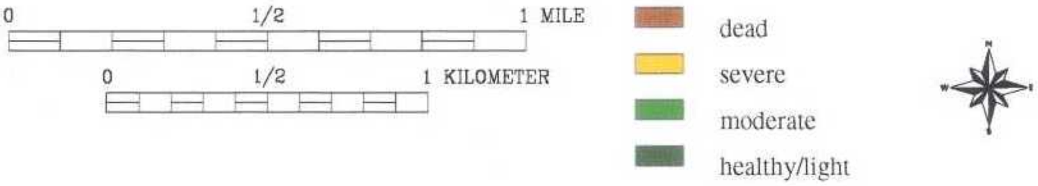
b. 1994



c. Difference Image



d. Damage Map



Color Plate

a. 1984 Landsat image. TM bands 4/3, 5, 3 (RGB). Hemlock forest appears red in color.

b. 1994 Landsat image. TM bands 4/3, 5, 3 (RGB).

c. Difference image showing change in NIR/red canopy reflectance from 1984 to 1994. Darker pixels depict hemlock defoliation.

d. Thematic map of hemlock damage classes for Sparta Glen, NJ.

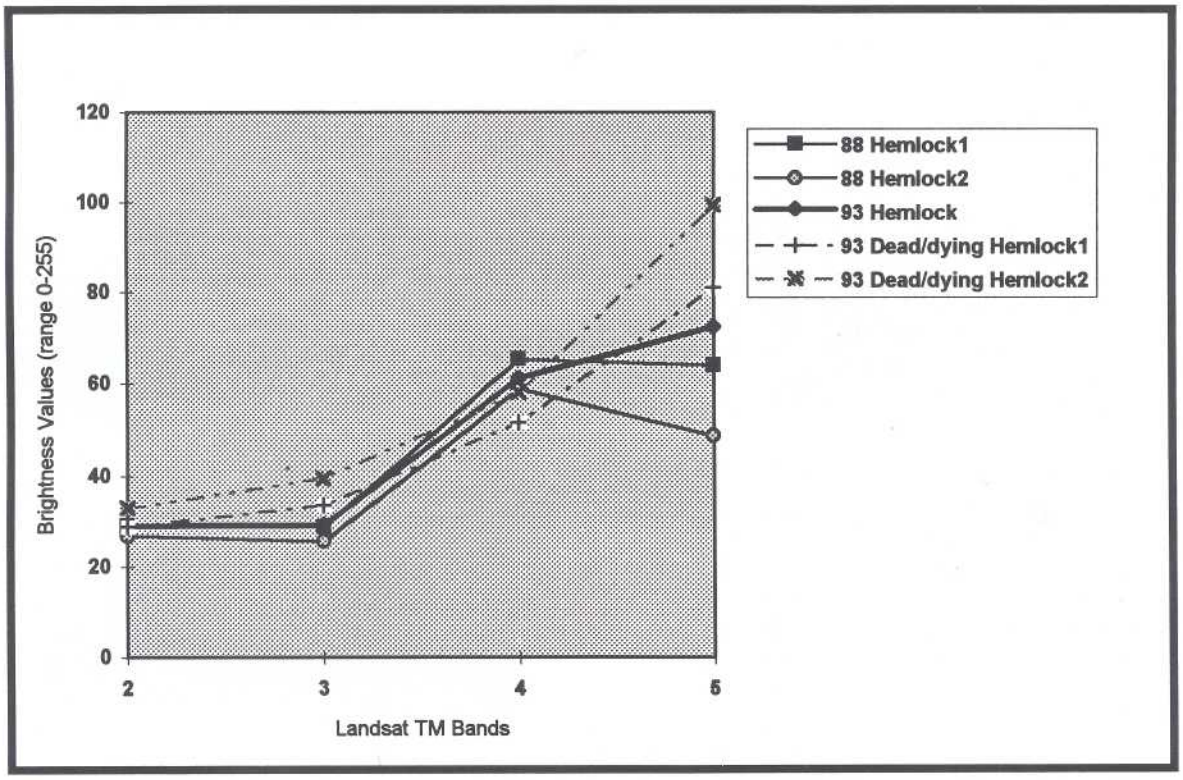


Figure 5. Four bands of the spectral signatures of hemlock taken from the classification of the May 4, 1988 TM image and the April 25, 1993 TM image.