Radial growth responses of host and non-host trees to hemlock woolly adelgid infestation in Connecticut

by

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Abstract

Hemlock woolly adelgid (HWA), *Adelges tsugae*, is an invasive insect from Japan that has slowly spread across the eastern United States since entering Virginia in 1950. HWA is a little understood pest causing a gradual decline in native tree species on the East Coast, such as eastern hemlock, *Tsuga canadensis*, and Carolina hemlock, *T. caroliniana*. To increase our understanding of forest dynamics following long-term HWA infestation, seven *T. canadensis* stands in south-central Connecticut were visited. At each site increment cores of both *T. canadensis* and hardwood trees were collected to analyze for radial growth trends in response to continued HWA infestations. In the lab, increment cores were sanded and annual ring-widths measured. For each core, the observed growth trend prior to infestation was fitted to a mathematical model and extended into the post-infestation period using the EXTRAP software program. Ring-width indices (RWI), based on the ratio of observed to expected growth, were calculated for the post-infestation period, with a RWI = 1 representing expected growth. A one-sample t-test was used to determine whether post infestation growth was significantly different from expected growth. Between 75-100% of the hardwood trees at each site showed a statistical significant increase in RWI, while 56-100% of the *T. canadensis* trees at each site showed a significant decrease in ring widths due to HWA. Results showed that *T. canadensis* had diminished growth during and following the HWA infestation, while the hardwood species present in the understory before HWA infestation took advantage of a canopy gaps and showed a positive growth response.

Table of Contents

List of Figures

List of Tables

Preface

The design and collection of data for my honors thesis took place before I knew of the honors program. In the summer of 2005, I was participating in the research experience for undergraduates (REU) program at Harvard Forest, Harvard University's ecology field station. The National Science Foundation funds REU programs at colleges throughout the country giving students a positive experience performing scientific research, hoping to lead to the student's continued commitment to studying science in graduate school and a career. In order to reach the REU's goals, the program is designed around students being placed with a scientist mentor for the summer. My mentor was Dr. David Orwig, a forest ecologist at the Harvard Forest. I basically followed him around all summer, collecting data for his research projects, entering the data in the computer, and gaining an understanding of the various tasks performed while conducting field and lab research. In addition to helping him, as part of the REU program, I was given the opportunity to conduct my own research project under his guidance. The experimental protocol that I designed and the data that I collected and analyzed as part of this research became my honors thesis project.

Throughout my honors thesis I have experienced both a personal and intellectual journey leading me to this final product, and this is how it went. Upon acceptance to the REU at Harvard Forest I began to immerse myself in my pre-summer readings to gain a better understanding of the effect hemlock woolly adelgid was having on the New England forests. This reading was the beginning of becoming an "expert" in my field of study for the summer. Once at Harvard Forest, I continued reading journal articles and learning the methods of data collection that my mentor used. This project was the first time I had done a research project that I felt was really mine and lasted more than a week.

I learned about the copious quantities of background research necessary before a project is even designed or fully developed. After several weeks of helping my mentor collect data, I began to develop my own questions and looked for aspects of his project that could be expanded upon in the summer time frame. My project began to develop when the deadline approached for giving a five minute presentation about my summer project. The past summer I had cored stripped maples as part of my final project for the ecological monitoring and biological assessment class at Cranberry Lake Biological Station, which sparked my interest in dendrochronology. My project at Harvard Forest developed into examining the radial growth patterns of both *T. canadensis* and the surrounding hardwoods to better understand the effects HWA was having on Connecticut forests. My mentor and I collected most of my tree cores (data) together in the field as he taught me how to collect sound, scientific data of appropriate sample size. As the summer progressed, another student and I visited my sites and collected the rest of my tree cores on our own. Back in the lab, I analyzed my data, learning about how difficult dendrochronology can be when trees are barely growing. The REU summer program ended with a symposium on student research, where I presented my research to fellow students and faculty at Harvard Forest. At the end of the summer I was given the opportunity to join the honors program, with the idea that my summer project was of appropriate magnitude to become my honors thesis project.

When I returned to ESF in the fall, I sought an advisor at ESF to assist me in further analysis and writing the paper. Finding an advisor was difficult because no one at ESF works with both hemlock woolly adelgid and dendrochronology, leaving me slightly discouraged; however, I found an advisor, Dr. Eddie Bevilacqua, who agreed to help.

When the spring semester started I tackled my data analysis in full force, only to become completely frustrated and bewildered from being in the honors program. As I became more overwhelmed with the slow progress of my data analysis and the approaching deadline of creating a scientific poster for the Spring Spotlight on Student Research, I tried to bail out of the program, which Dr. Bevilacqua was not about to let me do. At the perfect time, my writing professor, Don Wagner, was talking about the difficulties that arise when writing a large paper. He invited a small group of students to share their frustrations, making me feel better. As I got back on track and worked on my poster in my writing class, relatively painlessly I finished my data analysis, completing a major mental hurdle of my project, making a poster and paper suddenly possible in my mind. As the Student Spotlight Symposium approached I was fully prepared, due to the excellent preparation Don Wagner provided in my writing for science professionals class, and I was proud of my poster and was involved in many conversations with interested people at the student spotlight. At the end of the spring semester, I left with the hopes of writing the body of my thesis during the summer.

I participated in another REU program, this time at Flathead Lake Biological Station in northwestern Montana. Montana was my dream location, and I could not have been more excited to go there, except that after several weeks of working on a the Nyack floodplain, bordering Glacier National Park, I began to miss the northeastern forest, a feeling I thought I would never feel, considering I have always dreamed of being in the west. I did not know all the trees and plants in Montana, like I did in New England. Typing my honors thesis brought me back to a topic I understood better than what species was growing in my plot on the floodplain. Nights of beautiful sunsets and breezy, warm afternoons when I needed a break from my work, I resorted back to writing, having more inspiration and motivation after clearing my mind of this paper for a while and experiencing the world from a different view.

As I complete this honors thesis, I am glad I continued with it. Even though, at times, the frustration seemed overwhelming, the final product is worth the effect. Writing this paper has helped me develop as a writer and given me more confidence in my writing skills. I have also learned about the effort that goes into writing a larger paper, and the processes and time management skills associated with research.

Advice to Future Honors Students

Try to make writing an honors thesis the best experience possible. Choose an advisor carefully; pick someone who has time to provide you with the assistance you need. My advisor found time to help me, and I knew when I could find him, which was very helpful when I had questions. Make sure you actually want to do an honors thesis because you are interested in doing your own research project. Writing an honors thesis just because it will look good on your resume may not end up being very enjoyable. If you think you need to refresh your writing skills or may need a little extra support writing your honors thesis, then take a writing class; it helped me tremendously.

You are going to experience frustration at some point, either collecting or analyzing your data or when writing your paper. In the end, you will be proud of your accomplishments if you persevere and struggle through them. Talk to your advisor or second reader if you are having problems because they are experienced doing research and it is their job to help you.

Doing more work early on is better than waiting. My data analyses took an entire semester, so start early and you will not seemed rushed even when parts take longer than expected. While writing your paper you may need to set it aside for a while and come back to it later to make the experience more enjoyable.

Acknowledgements

Collecting all the data for this project was part of the research experience for undergraduates (REU) program at Harvard Forest in the summer of 2005, funded by the National Science Foundation. I was fortunate to have Dr. David Orwig as a mentor at Harvard Forest. I can not thank him enough for all the time, patience, and heart he put into making that summer a life-changing experience I will never forget. I am especially thankful for the knowledge he shared with me and for treating me as his colleague, not just another summer student. I am grateful for the field assistance and motivation Sasha Lodge provided on tiring, hot days in the field. I also thank all my fellow REU students and the Harvard Forest faculty for the supportive environment they provided. I thank Dr. Eddie Bevilacqua for being my advisor at ESF, for being patient and spending time to help me analyze my data, not letting me give up on this task, and answering a lot of questions. I thank Donald Wagner for assistance making a scientific poster to display my project, editing my drafts, and for your approachable, supportive personality that provided mental support when this task started to daunt me. Writing this honors thesis would have been much more challenging without the endless mental support, knowledge, editing, and inspiration provided by James Willacker, who eased my fears and celebrated every accomplishment with me throughout the journey.

Introduction

Presently, human travel between land masses is a frequent occurrence, and with that mobility comes both the intentional and unintentional transfer of organisms over large geographical areas. As global trade increases, so do the number of opportunities for the introduction of new species to an area. Even though only about 1% of newly introduced species survive in their new surroundings, those few that do can become established and adversely affect the new environment. This number may seem insignificant, but the results can be enormous. For example, an invasive species can outcompete, hybridize, displace, predate, and lead to the extinction of native species (Mooney and Cleland 2001). Understanding the impact of invasive species is a complex task due to all the ecological processes that take place in any given community and because the impacts of invasion may not be seen for decades (Mooney and Cleland 2001).

The hemlock woolly adelgid (HWA), *Adelges tsugae*, is an example of an introduced invasive species (Fig. 1). HWA was accidentally introduced into Virginia from Japan in the 1950s and has been spreading throughout the native range of its food source (Fig. 2), *Tsuga canadensis* and *T. caroliniana* (USDA 2005). There are no natural predators of HWA in the eastern United States, and neither *Tsuga* species appear to have a resistance or tolerance to prevent infestation. HWA reached New England in 1985 and has raised much attention because of many ecological changes in the affected *T. canadensis* forests (Orwig and Foster 1998).

T. canadensis, an ecologically important foundation tree species, is a long-lived, late successional, and shade tolerant species that is distinct in the niche it occupies

(Ellison et al. 2005; Fig. 3). It grows on moist soil and develops a dense canopy blocking light to the understory, creating a dark, cool, humid, and acidic microclimate with little competing vegetation (Hardin et al. 2001). Because of their evergreen foliage, the unique microclimate underneath a *T. canadensis* stand has relatively stable temperatures, important for organisms living in the local habitat and nearby streams (Ellison et al. 2005). In Connecticut, nearly ninety bird species depend on *T. canadensis* for food or shelter; expectant plants, such as *Mitchella repens* (partridgeberry) and *Chimaphila macaulata* (striped wintergreen), thrive under its shade; and brook trout depend on water temperatures cooled beneath *T. canadensis* stands (McClure et al. 2001). When HWA infests a tree, it may take ten years or more for death to occur (Orwig 2001). This gradual process makes HWA more difficult to study than many other pests, for example, the gypsy moth (*Lymantria dispar*) and spruce budworm (*Choristoneura fumiferana*), which almost immediately display detrimental effects on a tree.

A study by Orwig (2001) showed how the plant community changed underneath *T. canadensis* after HWA infestation by monitoring the changes in herbaceous vegetation since 1995. In 2001, the density of the understory vegetation had increased significantly relative to six years earlier, changing from sparse numbers due to the cool, dark microclimate maintained by *T. canadensis,* to dense coverage, with a high proportion of aggressive pioneer vegetation. Species such as *Betula lenta*, *Dennstaedita punctilobula* (hay-scented fern), *Carex* spp. (sedge), *Mianthemum canadense* (Canada mayflower) primarily increased in cover (Orwig 2001).

In a study by Ellison et al. (2005), explained the consequences to forest structure and dynamics when a foundation species, specifically *T. canadensis*, was lost. As stands were replaced by hardwood trees, increased similarity of flora, fauna, and soils between forest types occurred. Similar homogenization consequences have occurred from loss of the *Castanea dentata* (American chestnut) and *Pinus albicaulis* (whitebark pine); however, methods for controlling invasive species and reducing their effects have not been developed yet.

A lack of understanding exists about the short and long term effects HWA has on an ecosystem (Orwig and Foster 1998). It is thought that HWA inserts its stylet mouthpiece, which is three times the length of the body, into the base of a *T. canadensis* needle. The stylet then travels through the epidermal cells into the vascular tissue, specifically the parenchyma cells of the xylem rays. These cells transfer and store nutrients, so HWA is tapping into the food reserves of the tree, resulting in foliage loss and lack of bud formation due to stress, and eventually leading to tree mortality, often without regeneration (McClure et al. 2001). The HWA lifecycle consists of two generations each year, increasing in numbers quickly without any known natural predators (Stadler et al. 2005). Since there are no known native predators of HWA, management experiments include releasing an exotic predator beetle, either *Pseudoscymnus tsuga* or *Laricobuius nigrinus*, that would help control HWA populations. Experiments in Virginia and Connecticut have shown that both these beetles actively hunt and feed on many life stages of HWA, and that the *P. tsuga* beetle can successfully reduce HWA populations by up to 87% in five months (Save our hemlocks action team 2004). However, non-native biological introductions are risky due to unpredictable affects on other species that may not be discovered for years. Other forms of HWA control are by injection of pesticides and insecticidal soaps and oils, but these controls are too labor-intensive and expensive for large forest expanses and are more promising for individual trees on private property (Save our hemlocks action team 2004).

This thesis focuses on the effects that HWA has on stand dynamics, including both the overstory *T. canadensis* trees and presently co-dominate hardwood trees (*B. lenta*, *Acer* spp., *Carya glabra*, and *Quercus* spp.) already growing in the stands before the HWA infestation. As *T. canadensis* trees die, the forest stand goes through successional processes because of gaps formed in the canopy. Gaps change light levels, nutrient content, water levels, and soil in the gap microenvironment, which can increase plant diversity compared to the surrounding forest (Anderson and Leopold 2002). These changes make gaps important for the succession of a forest because the species filling a gap are good predictors of the future stand composition. There are many examples of conifer dominated forests changing over time into hardwood stands because of the shade-intolerant species that pioneer in the gaps (Kneeshaw and Bergeron 1998).

I examined the radial growth of *T. canadensis*, infested with HWA for over ten years, to determine if there was a change in growth rate between pre- to post-infestation. Also, I examined the radial growth response of presently co-dominate trees following defoliation of *T. canadensis*. My hypothesis was the radial growth of *T. canadensis* will decrease, while the radial growth rates of the surrounding hardwoods will increase. The objective of the study is to understand the effects of HWA on stand dynamics, especially the overstory trees and possibly how future forest composition may change if *T. canadensis*, a dominant species, is eliminated. Understanding the ecology of this ecosystem is important because it could be applied to future invasive forest pests to predict what may happen and recommend management alternatives that might minimize the negative affects to native trees.

Methods

The methods included the selection of study sites, collection of increment cores and mortality data, preparation, counting and measurement of tree-rings, and data analysis.

Study Sites

The seven study sites used in this research (Fig. 4, Table 1) were located in central to southern Connecticut in the lower Connecticut River Valley, characterized by short warm summers and long cold winters. This region had been used for previous research by Orwig (1998, 2001), who chose the location based on recent HWA infestation, long-term access, protection of the area, and based on recommendations from Connecticut State Foresters, The Nature Conservancy, and the U.S. Forest Service (Orwig and Foster 1998). The sites were identified as Tri-mountain (TM), Ruth Hill (RH), Chapman Pond (CP), Burnham Brook (BB), Selden Creek (SC), Foster's Pond (FP), and Guilford (G) (Orwig 1998). The sites, containing predominantly sandy loam soils, range in elevation from 0 to 180 meters above sea level and 8 to 175 ha in size. Before HWA infestation, *T. canadensis* dominated at each of the seven, long-term study sites, having importance values ranging from 49 to 88 of all tree stems (Orwig 2001). A more detailed description of each study site follows.

Tri-Mountain

The TM site, located on state land in central Connecticut in public forest, was within a five minute walking distance of a road. This site had the highest elevation of

123-168 meters and the greatest slope of 25% (Fig. 5). The aspect was northwest and *T. canadensis* had a relative importance value (relative basal area + relative density/2) of 49 in 1995. The next important tree was *B. lenta* (importance value equaled 16) and *Q. velutina* (importance value equaled 12; Orwig and Foster 1998). My observation of TM included talus fields on the slopes.

Ruth Hill

The RH site was located on state land in the Connecticut River Valley in central Connecticut within a five minute walk of roads. The relative importance value of *T. canadensis* in 1995 was 74 and for *B. lenta* was 12. The elevation was 30-98 meter with a northwest aspect and a 15% slope (Orwig and Foster 1998). In 2005, the canopy was relatively closed compared to other sites and dense mats of *Dennstaedtia punctilobula* (hay-scented fern) carpeted the ground (Fig. 6).

Chapman Pond

The CP site, located on The Nature Conservancy land in the Connecticut River Valley, was in central Connecticut. This landscape had many rock ledges and the site was in a flat upland region. The elevation was 0-80 meters and a 6% slope with west-southwest aspects. In 1995, the *T. canadensis* relative importance value was 58, followed by *B. lenta* (relative importance equaled 17), and *Q. veluntina* (relative importance equaled 15). In 2005, dense mats of invasive *Microstegium vimineum* (Japanese stilt grass) had increased in coverage since 1995 (Orwig and Foster 1998).

Burnham Brook

The BB site was located in central Connecticut slightly east of the other six sites on The Nature Conservancy land. The study area consisted of many rock ledges and small ravines on a hilly landscape; however, the study sites were located on an upland portion. The elevation ranged from 91-123 meters, a slope of 15%, and a northwest aspect. In 1995, *T. canadensis* had a relative importance value of 66, followed by a relative importance value of 11 for *A. rubrum* (Orwig and Foster 1998). My observation of the site in 2005 included many dense patches of *B. lenta* saplings, patches of *Kalmia latifolia* (mountain laurel), and other areas with dry, bare ground (Fig. 7 and 8).

Selden Creek

The SC site was also located in the Connecticut River Valley on The Nature Conservancy land characterized by rock ledges and patches of fern. The relative importance values in 1995 for *T. canadensis* and *B. lenta* were 69 and 18 respectively. The elevation was 0-46 meters with west-northwest aspects and a 9% slope (Orwig and Foster 1998).

Foster's Pond

The FP site was located in south-central Connecticut upslope of a Foster's Pond on state owned land. The elevation was 30-60 meters, with a northeast aspect, and a 12% slope. In 1995, *T. canadensis* had a high relative importance value of 88. *A. rubrum* had the next highest relative importance value of 6 (Orwig and Foster 1998). In 2005, this site had a relatively dense, closed canopy compared to the other sites, with sections heavily infested and damaged by gypsy moth (Fig. 9).

Guilford

The G study site was located on state land near the town of Guilford on the coast of the Long Island Sound in south-central Connecticut. In the past, the site was used for walking and mountain biking, being conveniently located next to neighboring homes.

The elevation ranged from 0-40 meters with a 7% slope and northwest-southeast aspects. In 1995, *T. canadensis* had a high relative importance value of 75, followed by *Q. prunus* with a value of 9 (Orwig and Foster 1998). In 2005, when the site was sampled, the area was closed to public recreation due to a high danger of falling *T. canadensis* trees (Fig. 10).

Collection of increment cores and mortality

At each site, up to twenty increment cores were taken at the lowest possible height (around 20 cm), one core per sampled tree. Ten cores were from presently dominant and co-dominant hardwood trees (*B. lenta*, *Acer* spp., *C. glabra*, and *Quercus* spp.) and ten from living *T. canadensis* trees. A few cores were discarded because of rotting or indistinguishable rings. At some sites, fewer than twenty cores were obtained because of high *T. canadensis* mortality and limited gathering time. The diameter at breast height (DBH; Table 2) and current canopy dominance status for each cored tree was also recorded. Increment cores were transported in plastic drinking straws until mounting. In continuation of a previous study by Orwig and Foster (1998), mortality of overstory *T. canadensis* was calculated by counting the number of live *T. canadensis* trees in designated long-term study plots and compared to the number of those alive in 1995.

Preparation and counting

In the lab, each core was mounted to ensure that the xylem cells (tracheids in *T. canadensis* and mainly vessels in hardwoods) were vertically oriented to provide precise identification and measurements of annual growth rings. Each core was sanded with progressively finer sandpaper (200-800 grit) to better distinguish each annual ring. Using a dissecting microscope (10x to 50x magnification), individual growth rings were identified, and starting with the most recent one, i.e. 2000, each decade was penciled on the core. Then with a Velmex microscope system (East Bloomfield, NY), which consisted of a Velmex dissecting microscope, moveable stage, and the ability to record precise distances, was used to measure the width of each ring to the nearest 0.01 mm. These measurements were then digitally sent to the computer and saved in a data file.

Analysis of increment cores

Cross-dating was attempted, but limited time, short chronologies (less than 30 years), and low correlation values (due to large variations in localized microsites beneath *T. canadensis* trees) prevented any substantive improvement in cross-dating accuracy relative to ocular identification of rings (example of cross-dating results shown in Table 3). I determined that the visual identification and count of annual rings were sufficiently accurate for the subsequent analysis. Only ring width measurements recorded from samples taken between 1970 and 2004 were used for subsequent analyses.

Since the year of initial HWA infestation could be estimated relatively well for each site (Table 1), each sampled core chronology could be separated into two parts: a pre- and post-infestation period. Using the EXTRAP software, available online from the dendrochronology library (Holmes and Cook 2006), pre-infestation ring widths (from 1970 to the infestation year) were used to extrapolate the expected growth curve into the post-infestation period (from infestation year to 2004). EXTRAP standardized the ring widths to produce ring width indices (RWI) by taking the ratio of actual to expected ring width, which removed the age-related growth trends from each core. An RWI equal to one signified a tree was growing at the expected rate, while RWI less than one represented lower than expected growth. To assess the changes in growth rate due to HWA infestation, the mean post-infestation RWIs for each tree were compared to an RWI of one using a one-sample t-test ($\alpha = 0.05$).

Results

Each tree has a slightly different growth response due to localized stresses and environmental differences; however, among the seven sites, between 56% and 100% of the *T. canadensis* trees and 75% to 100% of the hardwood trees showed statistical ($\alpha = 0.05$) differences in ring width indices during the post-infestation period compared to expected growth (Fig. 11). In 1995, the overstory mortality of *T. canadensis* ranged from 14% to 96%. In 2005, the mortality ranged from 79% to 99%, showing a large increase in overall mortality at all sites (Fig. 12).

Selden Creek

At SC, the infestation year was 1989, at which *T. canadensis* slowly decreased in RWI, while the hardwood trees increased in average RWI (Fig. 13). Seven of the ten *T. canadensis* trees had a statistically significant ($\alpha = 0.05$) decline in growth, while all ten hardwood trees had a statistically significant increase in growth. In 2002, the average hardwood RWI was the highest at 4.58, while the *T. canadensis* RWI hovered between 0.60-0.66 during 1995-2004. The overstory mortality of *T. canadensis* increased from 62% in 1995 to 93% in 2005.

Guilford and Foster's Pond

At both the G and FP sites, a similar growth pattern as SC was statistically evident, with 56% and 60% of the *T. canadensis* trees decreasing in growth respectively, and with 100% of the hardwood trees increasing in growth. However, the degree of growth reduction at these sites was not as great as observed at some of the other sites. At the G site, the decrease in *T. canadensis* growth was gradual, in contrast to the sudden increase in hardwood growth, which peaked at an RWI equal to 6.405 (Fig. 14). At the G site, the overstory mortality of *T. canadensis* was 99% in 2005, with nearly every *T. canadensis* tree laying dead on the forest floor, compared to 69% morality in 1995. The FP site was similar except there was a spike in *T. canadensis* growth in 2004, reaching an RWI equal to 4.58 (Fig. 15). The overstory *T. canadensis* morality was 82% in 2005 compared to a low 32% morality in 1995.

Chapman Pond

At the CP site, overstory *T. canadensis* mortality was 99% in 2005, leaving only two *T. canadensis* trees available for sampling. In 1995, the overstory *T. canadensis* mortality was similar at 96%. Both sampled, alive *T. canadensis* trees initially decreased in growth during post-infestation, then increased in 1999, and reached peak growth in 2003 at a RWI equal to 1.51. The hardwood trees increased in growth post-infestation, peaking in 2000 at a RWI equal to 1.73, with about the same growth rate as *T. canadensis* for the last four years (Fig. 16). Both of the *T. canadensis* trees sampled had growth rates statistically different than expected, and seven of the nine hardwoods significantly increased in growth rates.

Tri-Mountain

The infestation year for the TM site started in 1988 and by 2005, 82% of the *T. canadensis* trees had died; however, the same trend as CP was followed, which was a decrease in *T. canadensis* growth and an increase in hardwood growth post-HWA infestation. In 1995, TM had the lowest overstory *T. canadensis* mortality of only 14%.

Eighty-two percent of the *T. canadensis* and 75% of the hardwood trees had statistically significant differences in growth compared to the expected growth curve (Fig. 17). In 2000, the *T. canadensis* RWI was 0.25, considerably below the expected growth of one, and in 1998, the hardwood growth reached a high of 1.94, above the expected growth of one.

Ruth Hill

At the RH site, the responses of both *T. canadensis* and hardwoods were more subtle (Figure 18), but still 80% of *T. canadensis* trees and 88% of hardwoods responded statistically to HWA infestation. The hardwoods slowly increased in growth rate, which peaked in 2004 at 2.29, while the *T. canadensis* growth rate consistently stayed just below one. The overstory *T. canadensis* mortality was 79% in 2005, the lowest mortality of all the sites, and in 1995 the morality was 40%.

Burnham Brook

Observations at the BB site showed a slightly different response occurring, the hardwoods still increased in radial growth, but the *T. canadensis* growth fluctuates yet did not decrease in post-infestation years (Fig. 19). Still, 67% of *T. canadensis* trees and 87% of hardwoods differed statistically significantly from the expected growth. The hardwood growth rate peaked in 1996, at 4.2 and the *T. canadensis* growth rate peaked in 1997 at 1.31, which was above the expected growth rate. The *T. canadensis* overstory mortality was 97% in 1995 and 98% in 2005, with most of the growth rates measured from trees sampled in the understory.

Discussion

Though many of the sites had similar trends, each had slightly different responses due to microsite differences and staggered HWA infestation dates. The overall trend for *T. canadensis* was a statistically significant decrease in growth following HWA infestation, with over 56% of the sampled trees having slower growth than expected. This result supports my hypothesis that HWA infestation is reducing *T. canadensis* growth. Similarly, over 75% of hardwood trees have an increase in growth. These growth responses are most likely connected to HWA because an abrupt, sustained growth change is a good sign of a disturbance, and HWA disturbance occurs at the time of growth change (Lorimer and Frelich 1989). As HWA infests a stand, some trees die immediately, while others become stressed and live several more years with little radial growth. Many of the dead *T. canadensis* trees at the study sites were snapped or completely down, creating a large gap and many alternations in the gap environment that caused a response from the hardwood trees. These changes included increased light levels (Orwig and Foster 1998), warmer temperatures near the ground, changes in water levels, and increased substrate heterogeneity (Anderson and Leopold 2002). At many of the sites, *T. canadensis* growth demonstrated a gradual decline, while a more noticeable increase in growth occurred in hardwoods. This response was likely the result of conditions becoming favorable to a shade intolerant understory hardwood, increasing steadily in growth when the opportunity arose, while *T. canadensis* was barely alive. *B. lenta*, an aggressive pioneer on moist, well-drained gaps (Hardin et al. 2001), increased in growth at many sites, as did *A. rubrum* and *Quercus* spp., while other hardwoods showed less response.

At SC, the HWA infestation which continued from 1989 to 2005 caused *A. rubrum* and *B. lenta* to increase in growth, most likely a result of increased light levels. With 93% *T. canadensis* overstory mortality, the radial growth on the remaining trees was less than one millimeter per year. The TM site showed a similar trend with a dramatic decrease in *T. canadensis* growth, which allowed the hardwoods to show a positive response.

The G, FP, and RH sites showed a similar pattern as SC. G, located in southern Connecticut where HWA infestation started in 1987, experienced a longer time for changes to occur, and reflected high *T. canadensis* mortality. The figures for these sites showed little changes in the *T. canadensis* radial growth relative to the large increase in hardwood growth when presented on the same graph; however, when separated, a gradual decrease in *T. canadensis* growth was observed.

At the CP site, the overstory *T. canadensis* mortality was high, so only two *T. canadensis* trees were available for coring, giving a small sample size. The curve in Fig. 8 may not be an accurate display of *T. canadensis* growth and should not be considered statistically significant because only two trees could be standardized. The hardwood trees showed a positive growth response, possibly because of increased light levels resulting from high *T. canadensis* mortality.

A slightly different response occurred at BB. The hardwoods showed positive responses, but *T. canadensis* did not have the same pattern of decline as shown in the previous sites. The sample cores from this site came from predominantly younger *T. canadensis* trees, (as evidenced by small diameters of the cored trees, Table 2), due to the fact that there was 98% mortality of the older trees (Fig. 4). *A. rubrum* and *Quercus* spp.

still increased in growth rate because almost all the large trees died, creating a gap in the canopy; younger *T. canadensis* trees also grew in the understory. *T. canadensis* regeneration did not seem to occur at any of the sites, except at BB. The reason for this regeneration at BB was not understood because HWA was present on these young trees even though they were growing relatively fast compared to other sites. Lack of regeneration was common in *T. canadensis* in stressed situation as observed by Ellison et al. (2005). Future monitoring at this site is important to see if these *T. canadensis* trees were possibly tolerant of, or resistant to, HWA, or if their accelerated growth rate was due to their young age.

Overall, HWA is having a significant impact on New England forests, as *T. canadensis* stands are slowly being replaced by hardwood stands. Continued research is necessary to better understand HWA and prevent HWA from spreading. The outlook for *T. canadensis* is currently negative, with continued decline and loss of valuable *T. canadensis* stands.

Conclusion

The overall trends in decline of *T. canadensis* and increase in hardwood radial growth rates show that the invasive HWA is having an effect on stand dynamics. This invasive insect, without native predators, has found a niche in the forest, and is feeding on and killing *T. canadensis*. The effects are low radial growth rates and high mortality of *T. canadensis*, putting it at risk for declines in population and changes in forest composition.

The future forest composition may be reflected by the species found in these gaps created by *T. canadensis* mortality and become a mixed hardwood forest. Future research and management plans are necessary to continue to understand the habits of HWA and *T. canadensis* populations. Monitoring *T. canadensis*-dominated stands over the next decade will be important to see if these forests change in species composition and if HWA continues to spread throughout the eastern United States. Also, continued research and monitoring for the possible detection and identification of tolerant and/or resistant *T. canadensis* trees could give this species a better chance of survival in HWA infested forests.

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Appendix I

Fig. 1: A *T. canadensis* branch infested with HWA. The small white, woolly balls are created by HWA and contain individual adelgids inside (USDA Forest Service 2006).

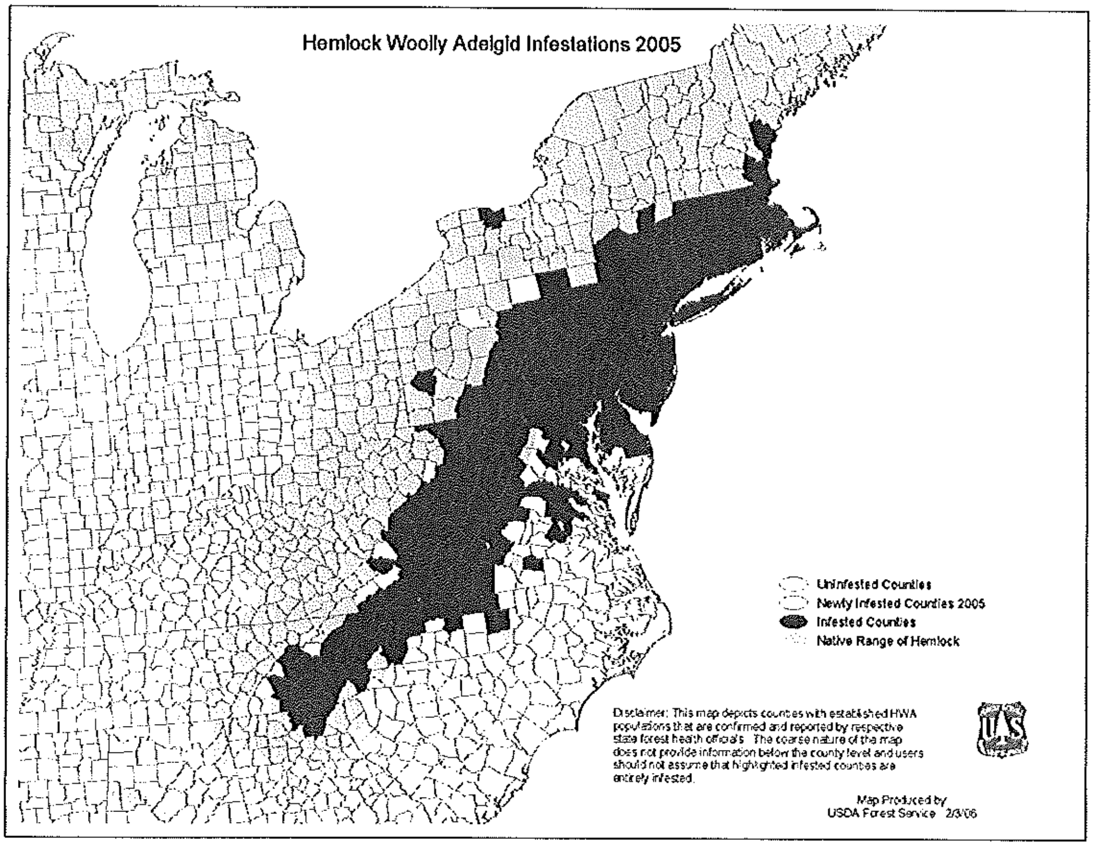

Fig. 2: Range map of HWA infestation as of 2005 (USDA Forest Service 2005).

Fig. 3: *T. canadensis* tree at BB site, showing the dense evergreen foliage, which creates a cool, moist microclimate underneath the tree.

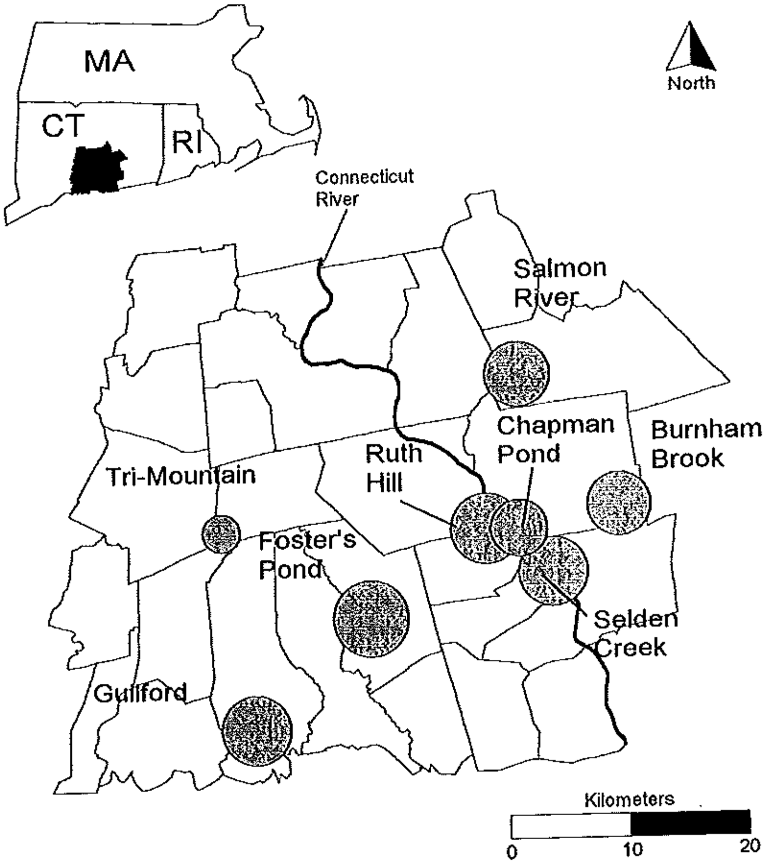

Fig. 4: Map of the study sites in south-central Connecticut, increment cores were taken from all sites except Salmon River (Orwig 1998).

Fig. 5: The TM site in the summer of 2005. The steep slope and rocky landscape is evident in this photograph, which is a unique characteristic of this study site.

Fig. 6: This photograph of the RH site shows the dense mat of hay-scented fern that covers the ground (summer 2005). Also, the photograph shows the lack of shrubs and few understory trees.

Fig. 7: Dense thickets of *B. lenta* saplings at the BB site (summer 2005). *T. canadensis* trees are seen on both sides in the foreground and hardwood trees in the center of the background.

Fig. 8: Three dead and snapped *T. canadensis* trees are the BB site (summer 2005). The canopy is opened when *T. canadensis* trees snap allowing hardwood species to take advantage of the increased light.

Fig. 9: Recently killed *T. canadensis* trees, which still have small twigs on the branches at the FP site (summer 2005). Several snapped *T. canadensis* trees and hardwood trees are also present in the photograph.

Fig: 10: A warning sign alerting users of the G site to enter at their own risk because of falling *T. canadensis* trees and limbs (summer 2005).

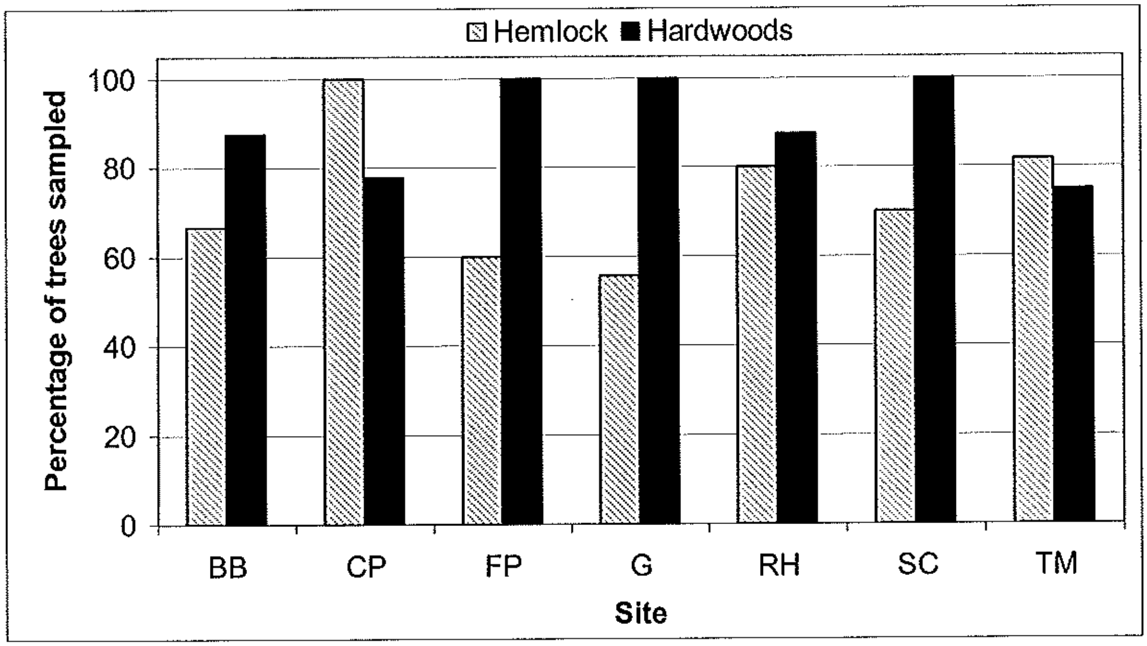

Fig. 11: Percentage of *T. canadensis* and hardwood trees at each of seven sites whose growth is statistically different than expected

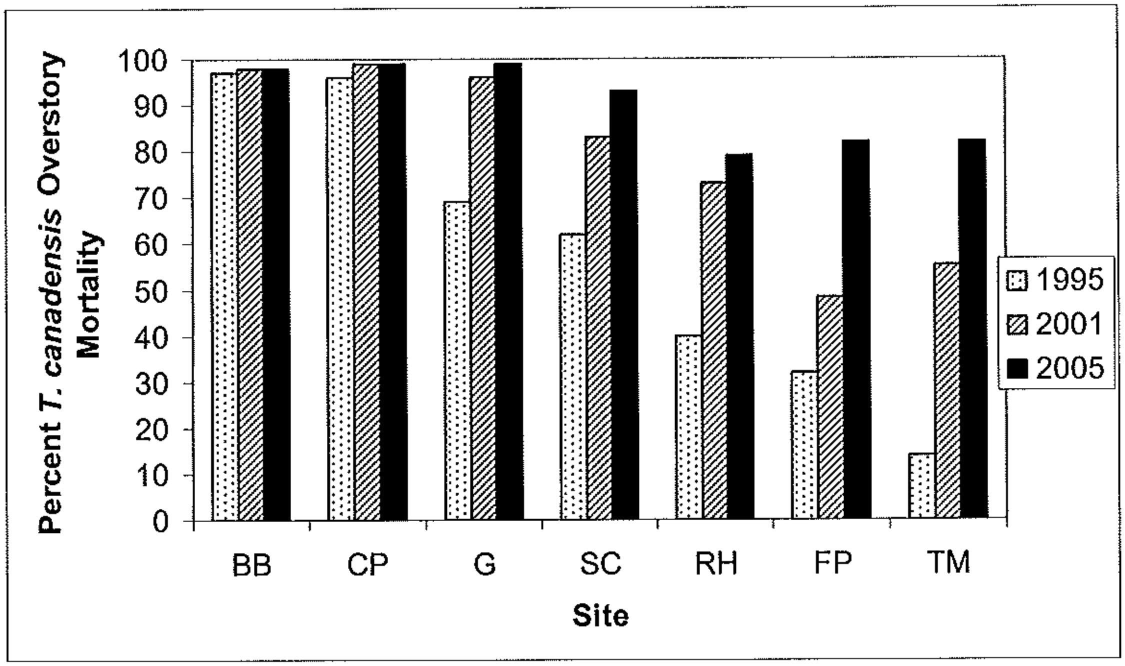

Fig. 12: Percent overstory *T. canadensis* mortality over ten years at the seven study sites in south-central Connecticut (Orwig unpublished).

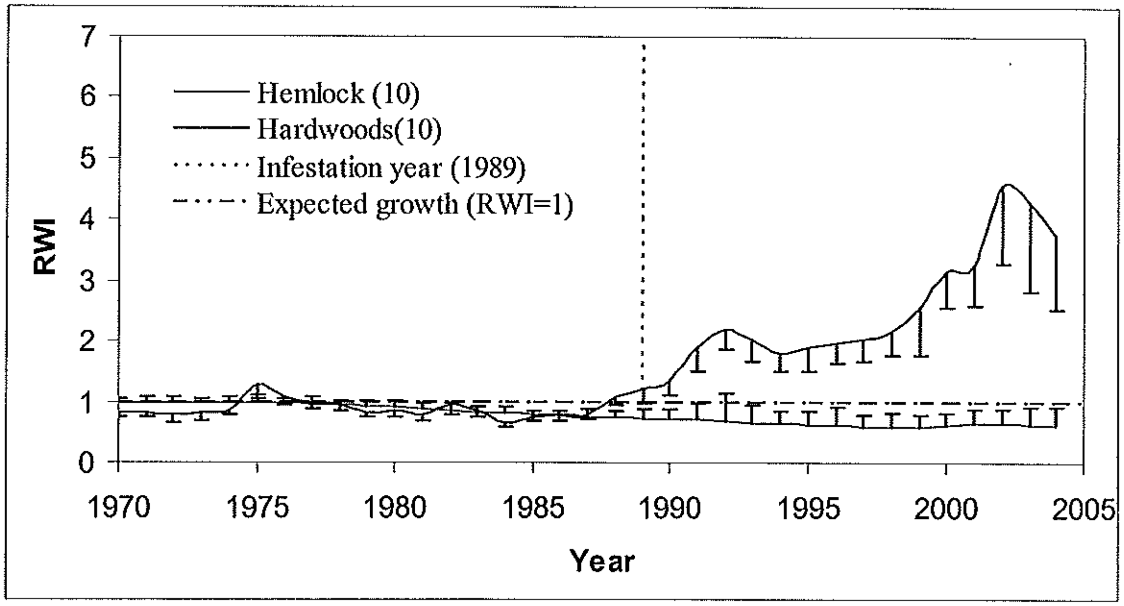

Fig. 13: The RWI for *T. canadensis* and hardwoods at Selden Creek, with HWA infestation around 1989. Post infestation, the RWIs for *T. canadensis* decrease and the hardwood RWIs increase.

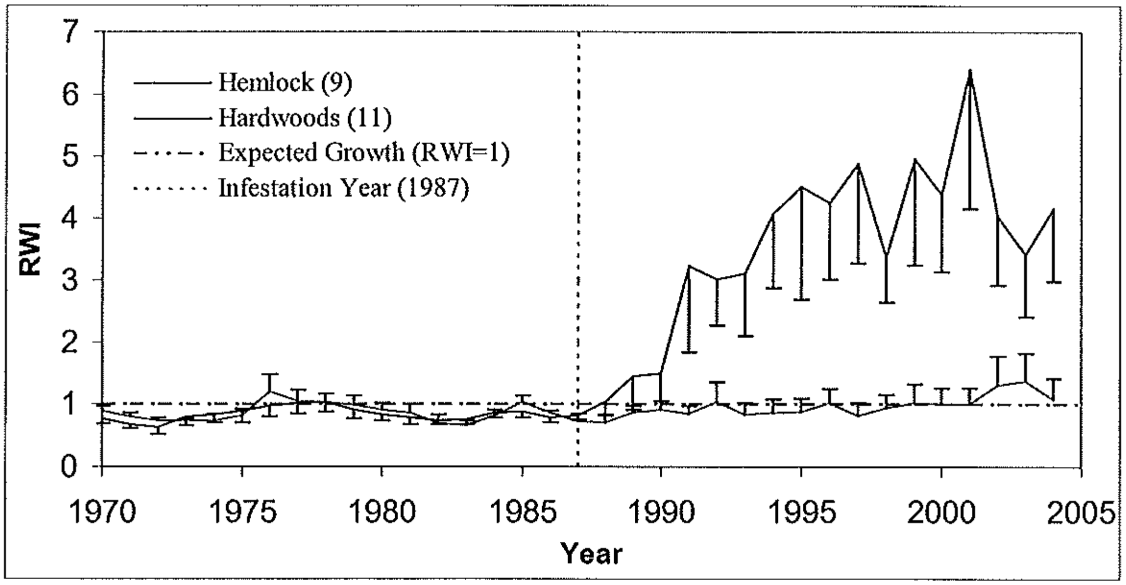

Fig. 14: The RWIs for both *T. canadensis* and hardwoods at Guilford, the southern most site in Connecticut (HWA infestation date was 1987). *T. canadensis* shows a gradual decline in RWI, while surrounding hardwoods trees increase dramatically.

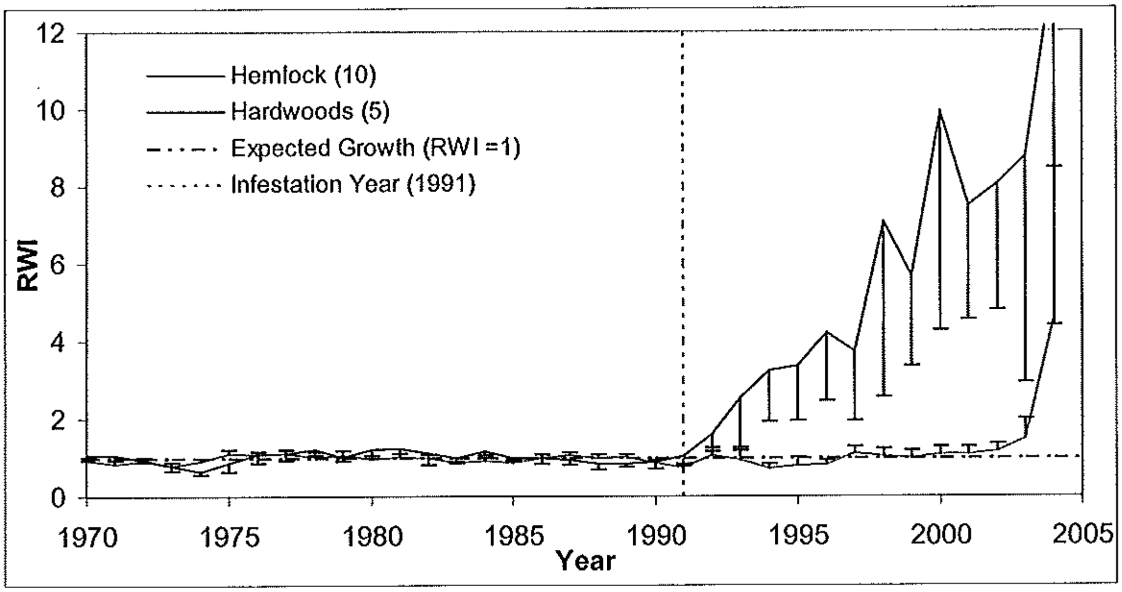

Fig. 15: Graph depicting the RWIs for *T. canadensis* and hardwoods at Foster's Pond, with an infestation date of 1991. This site shows a similar trend as seen in the preceding figures.

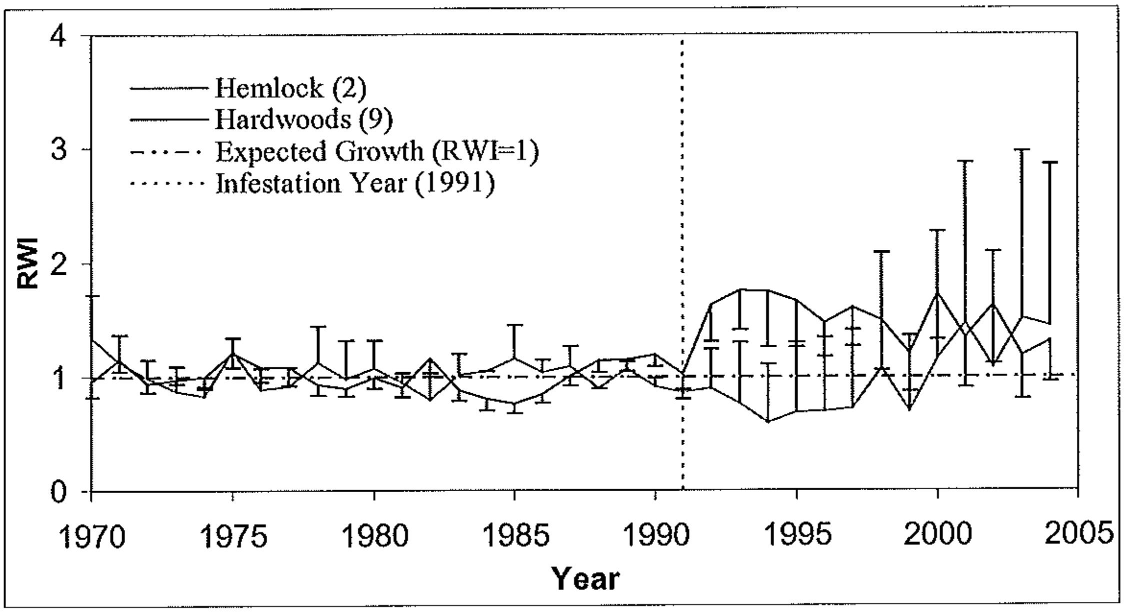

Fig. 16: At Chapman Pond the HWA infestation year is 1991. The RWIs fluctuate greatly; however, *T. canadensis* decreases in growth and the hardwoods increase in growth significantly.

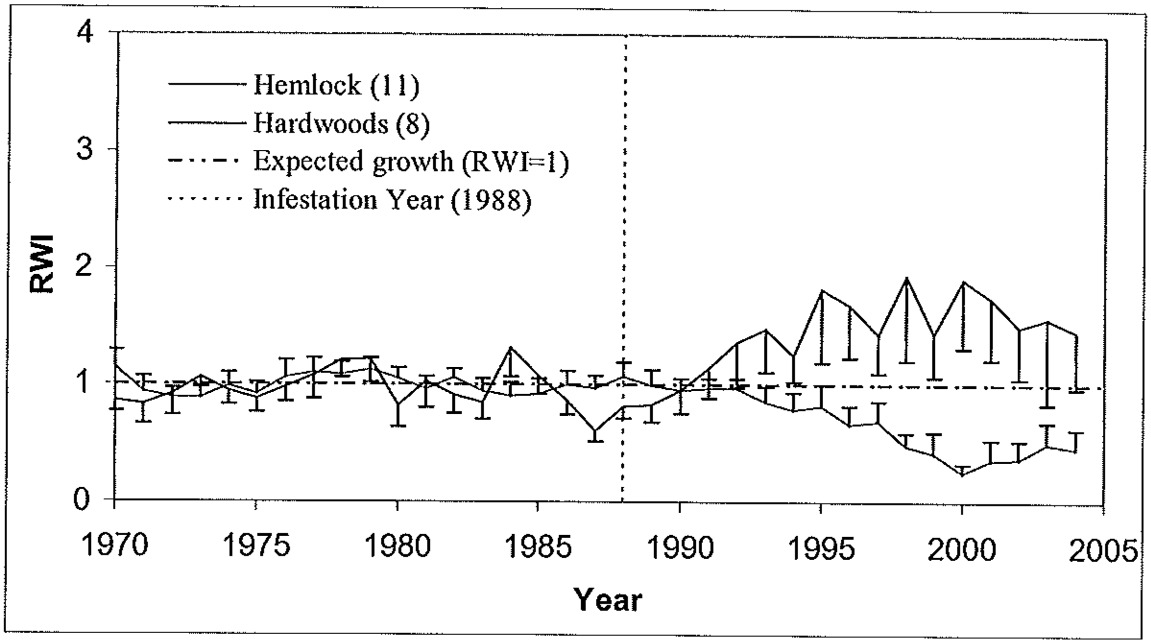

Fig. 17: At Tri-Mountain, the RWIs fluctuates around one until slightly after infestation in 1988, when the hardwoods show a large increase in RWI and *T. canadensis* declines greatly in growth.

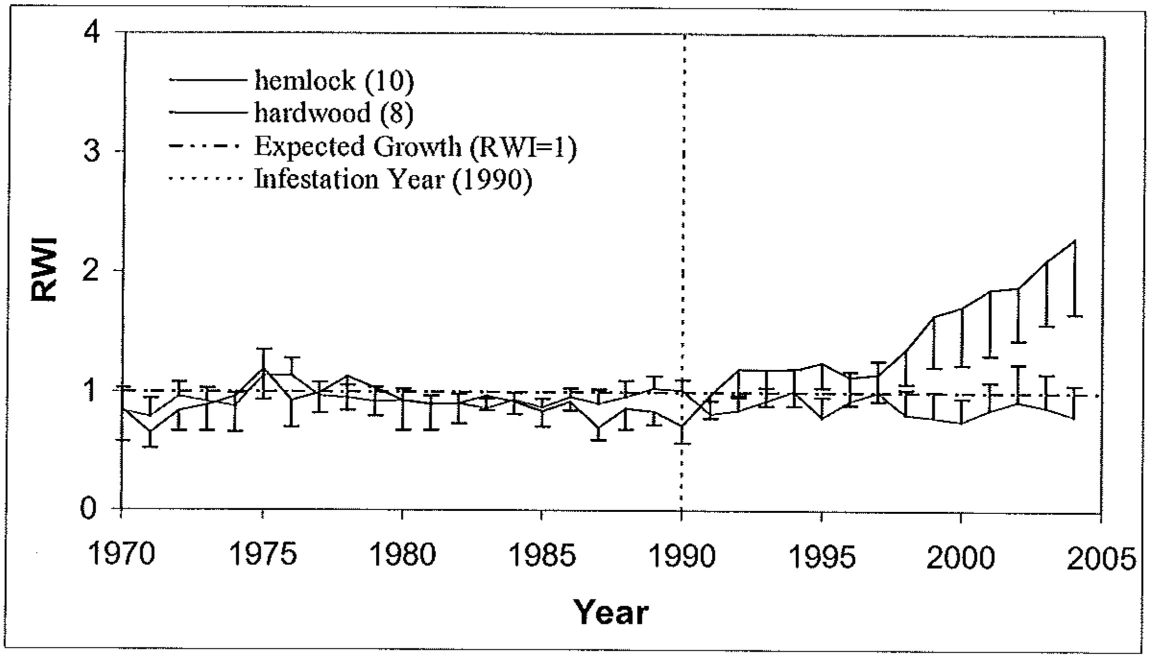

Fig. 18: The RWIs for *T. canadensis* and hardwoods at Ruth Hill with an infestation occurring in 1990. Post-infestation hardwood trees increased in growth as *T. canadensis* slowly declined in growth.

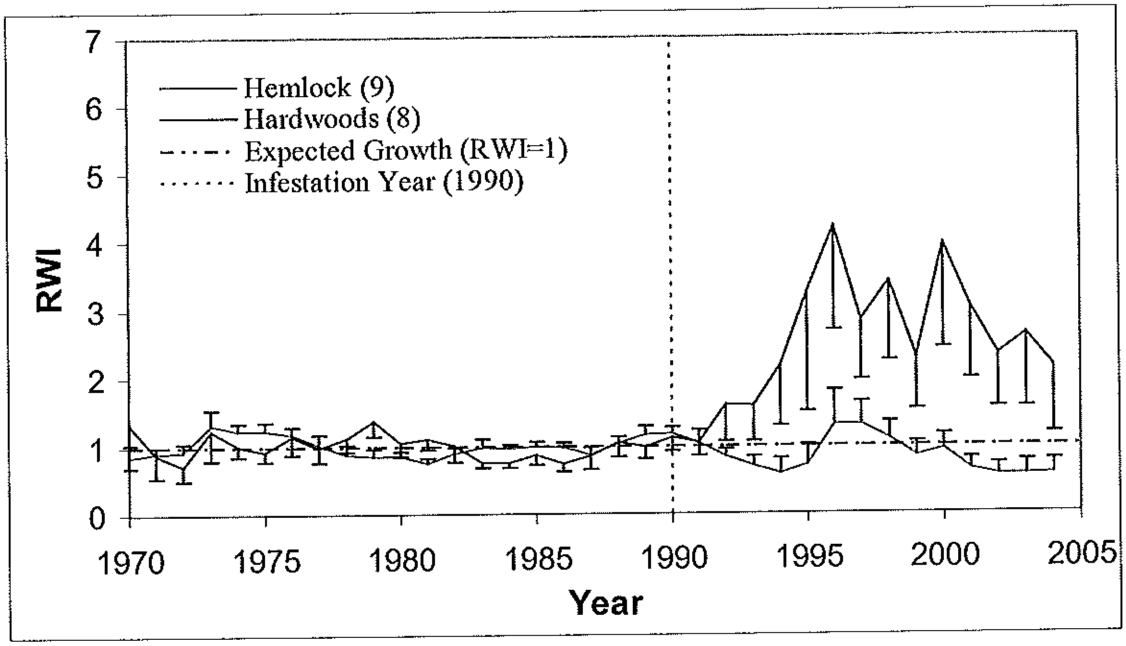

Fig. 19: Burnham Brook was infested with HWA around 1990. The *T. canadensis* trees display a fluctuating line, increasing in RWI at times, and decreasing at other times. The hardwoods trees increase in RWI after HWA infestation.

Appendix II

Table 1: Summary information of study sites.

Site Name	Size (ha)	Elevation (m)	Estimated year of initial HWA infestation	*T. canadensis* importance value[1] in 1995
Burnham Brook	175	91-123	1990	66
Chapman Pond	60	0-80	1991	58
Guilford	54	0-40	1987	75
Selden Creek	85	0-46	1989	69
Ruth Hill	31	30-98	1990	74
Foster's Pond	8	30-60	1991	88
Tri-Mountain	15	123-168	1988	49

[1] Importance = (relative basal area + relative density) / 2

Table 2: Summary statistics of sampled trees.

Site	*T. canadensis*		Hardwood	
	Number of trees sampled	Range in DBH (cm)	Number of trees sampled	Range in DBH (cm)
Burnham Brook	9	9.2 - 24.7	8	14.5 - 26.7
Chapman Pond	2	38.3 - 44.8	9	12.9 - 39.0
Guilford	9	14.5 - 35.9	11	15.3 - 24.3
Selden Creek	10	12.5 - 59.0	10	12.2 - 30.3
Ruth Hill	10	19.5 - 53.4	8	10.2 - 34.8
Foster's Pond	10	10.1 - 56.8	5	14.3 - 33.0
Tri-Mountain	11	12.0 - 49.1	8	10.8 - 27.6

Table 3: Cross-dating results from ten trees at Selden Creek. Each core (abbreviated under series by species and core number) was divided into segments by COFECHA. Then the number of rings to be added or subtracted to get a high correlation value was given. Several correlation values for each segment are outputted.

Series	Segment	Add/ Subtract	Correlation	Add/ Subtract	Correlation	Add/ Subtract	Correlation
hem11	1970 1994	2	0.5	7	0.25	4	0.15
	1975 1999	-4	0.44	2	0.39	4	0.27
	1980 2004	-4	0.27	-1	0.1	-7	0.09
hem15	1970 1994	0	0.26	1	0.14	10	0.12
	1975 1999	-4	0.73	1	0.2	-1	0.19
	1980 2004	-4	0.67	-1	0.35	-10	0.18
hem19	1970 1994	4	0.25	1	0.14	0	0.13
	1975 1999	-4	0.71	1	0.26	-5	0.24
	1980 2004	-4	0.65	-5	0.35	0	0.23
hem2	1970 1994	1	0.22	8	0.06	0	0.05
	1975 1999	-4	0.41	-5	0.16	1	0.12
	1980 2004	-4	0.51	-5	0.3	-8	0.24
hem4	1970 1994	9	0.34	6	0.3	8	0.22
	1975 1999	-3	0.18	5	0.06	3	0.04
	1980 2004	-8	0.28	-6	0.09	-9	0.05
bb14	1970 1994	0	0.4	9	0.34	10	0.07
	1975 1999	-5	0.56	0	0.33	-3	0.25
	1980 2004	-5	0.44	-3	0.4	0	0.36
bb16	1970 1994	1	0.27	0	0.24	3	0.06
	1975 1999	1	0.38	-1	0.34	2	0.29
	1980 2004	-1	0.42	-4	0.22	-10	0.15
bb17	1970 1994	2	0.16	8	0.15	5	0.05
	1975 1999	-1	0.3	-3	0.2	-2	0.2
	1980 2004	-9	0.3	-3	0.29	0	0.25
bb3	1970 1994	0	0.63	10	0.25	1	0.19
	1975 1999	0	0.55	-4	0.18	-2	0.17
	1980 2004	-1	0.41	0	0.37	-4	0.22
bb6	1970 1994	0	0.56	8	0.16	9	0.04
	1975 1999	-5	0.47	0	0.41	-1	0.15
	1980 2004	-5	0.4	-4	0.32	-1	0.22