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IMPACTS OF HEMLOCK WOOLLY ADELGID ON TSUGA CANADENSIS FOREST COMMUNITIES IN GREAT SMOKY MOUNTAINS NATIONAL PARK, USA

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by

Kurt J. Krapfl

B.S., Southern Illinois University, 2008

A Thesis
Submitted in Partial Fulfillment of the Requirements for the
Masters of Science Degree

Department of Forestry
In the Graduate School
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Approved by:

Eric Holzmueller, Chair

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AN ABSTRACT OF THE THESIS OF

Kurt J. Krapfl, for the Masters of Science degree in Forestry, presented on April 8, 2010, at Southern Illinois University Carbondale.

TITLE: IMPACTS OF HEMLOCK WOOLLY ADELGID ON *TSUGA CANADENSIS* FOREST COMMUNITIES IN GREAT SMOKY MOUNTAINS NATIONAL PARK, USA

MAJOR PROFESSOR: Dr. Eric Holzmueller

Tsuga canadensis (L.) Carr. (eastern hemlock), a long lived and shade tolerant coniferous tree species native to eastern North America, is currently threatened by the hemlock woolly adelgid (*Adelges tsugae* Annand, HWA). This exotic, invasive insect poses a serious threat to *T. canadensis* stands throughout their native range. The loss of this unique tree species is often coupled with numerous ecological consequences. HWA-induced mortality has exceeded 95% in some forest types, and will likely continue to decimate *T. canadensis* populations in the coming years. Shortly after HWA was found in Great Smoky Mountains National Park (GSMNP), long-term monitoring plots were established across a gradient of *T. canadensis* associated forest communities to monitor HWA impacts and stand decline. Our objectives were to (1) determine how *T. canadensis* populations have changed in conjunction with HWA infestation, and (2) document how HWA has affected vegetative community dynamics following five to six years of infestation in GSMNP.

We assessed *T. canadensis* associated overstory communities and determined that crown density, top dieback, and *T. canadensis* stem density has significantly declined over the observational period. Furthermore, we found that midstory *T. canadensis* trees were experiencing greater rates of decline than those of the overstory. Even with these losses, overstory and midstory community composition did not significantly change from 2003 to 2008/09.

Many studies have documented rapid pulses of understory vegetative productivity in conjunction with *T. canadensis* defoliation, which often allows increased amounts of solar radiation to reach the forest floor. Although we observed significant *T. canadensis* mortality at most plots sampled, understory species composition did not significantly change following HWA infestation. We attribute this lack of species response to the overwhelming abundance of *Rhododendron maximum* in the mid/understory, which restricts increased light from reaching the forest floor despite the formation of small overstory gaps. However, we found that understory composition significantly varied among ecological groupings, and differences were largely associated with soil properties and elevation.

Overall, results of this project suggest that *T. canadensis* may largely disappear from southern Appalachian forests resulting from infestations of HWA. Although community composition of *T. canadensis* associated stands has not yet been altered, changes are likely to occur as duration of infestation progresses.

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CHAPTER 1

INTRODUCTION

Tsuga canadensis (L.) Carr. populations face the threat of elimination from forested areas throughout eastern North America by hemlock woolly adelgid (*Adelges tsugae* Annand, HWA), an invasive insect introduced from Japan. *Tsuga canadensis* has little resistance to the effects of this exotic insect and populations of *T. canadensis* have been greatly reduced by HWA in the northern United States (Orwig & Foster, 1998; Jenkins, Aber, & Canham, 1999; Small, Small, & Dreyer, 2005; Eschtruth, Cleavitt, Battles, Evans, & Fahey, 2006). An examination of forested stands throughout south-central Connecticut determined HWA infests *T. canadensis* of all size and age classes, with over 90% of infested trees exhibiting greater than 50% defoliation (Orwig & Foster, 1998). Following nine years of infestation at Delaware Water Gap National Recreation Area, Eschtruth et al. (2006) observed mortality or severe decline in 25% of monitored overstory *T. canadensis*, coupled with significant declines in tree vigor and crown densities. Fifteen years of infestation in the Connecticut College Arboretum resulted in a 70% decrease in overstory *T. canadensis* basal area, and a greater than 80% decrease in *T. canadensis* stem density (Small et al., 2005). While much is known about the impacts of HWA in the northern range of *T. canadensis,* little is known about the impacts the exotic insect will have on *T. canadensis* in the southern portion of its range. Further research is needed to determine the influence of site factors and biological control measures upon mortality.

Literature Review

Tsuga canadensis

Tsuga canadensis is an extremely shade tolerant tree species native to forests throughout eastern North America, dominating about 931,000 ha of forest from the southern Appalachians to southern Canada and west to the central Lake States (McWilliams & Schmidt, 2000). *Tsuga canadensis* is commonly found at elevations ranging from 610 to 1520 m in its southern range, while northern stands typically occur between sea level to about 730 m (Fowells,1965). Stands often consist of trees approaching 400 years of age and heights of approximately 30 meters, although individuals exceeding 800 years old with heights approaching 50 meters have been reported (Godman & Lancaster, 1990).

Tsuga canadensis is a dominant component of forested stands throughout its northern range, while southern stands are often limited to drainages characterized by dense thickets of *Rhododendron maximum* (L.) (rosebay rhododendron) in the midstory (Ellison et al., 2005). It can be found as a component of multiple forest types as both an understory and/or overstory species, however, *T. canadensis* does best on steep, undisturbed, northerly facing sites (Godman & Lancaster, 1990; White, Patterson, Weakley, Ulrey, & Drake, 2003).

Undisturbed *T. canadensis* forests develop unique microclimates and cast deep shade upon the forest floor, and their deep, highly acidic litter layer aids in retaining high levels of soil moisture (Godman & Lancaster, 1990). *Tsuga canadensis* rarely germinates in forest gaps or open areas (Godman & Lancaster, 1990). Seedlings are tolerant of low light levels, and are characterized by slow growth and shallow rooting systems (Godman & Lancaster, 1990). Herbaceous layers, when present, often consist of false lily-of-the-valley (*Mianthemum canadense),* starflower (*Trientalis borealis),* woodfern (*Dryopteris* spp*.)*, common woodsorrel (*Oxalis Montana),* clubmoss (*Lycopodium* spp.), and sedges (*Carex* spp.) (Godman & Lancaster, 1990).

Because of its longevity and distribution on a wide variety of site conditions, *T. canadensis* is regarded as a keystone species for a variety of wildlife and plays vital roles in nutrient cycling and hydrological processes. Commercially, it is an important species to paper and pulp manufacturers (Godman & Lancaster, 1990). Furthermore, *T. canadensis* is a popular ornamental tree and is highly valued for its aesthetic qualities.

Hemlock Woolly Adelgid

Hemlock woolly adelgid was accidentally introduced to Virginia in the early 1950s from southern Japan, and began significantly reducing *T. canadensis* populations throughout the Mid-Atlantic states and southern New England in the 1980s (Stoetzel, 2002; Havil, Montgomery, Yu, Shiyake, & Caccone, 2006; Lovett et al., 2006). HWA now occupies the eastern portion of *T. canadensis* native range and extends northward from Georgia to southern Maine, with significantly higher mortality rates reported in northern latitudes (Paradis, Elkinton, Hayhoe, & Buonaccorsi, 2008; Orwig, Foster, & Mausel, 2002; Figure 1.1.). This trend of preferential infestation levels at southern versus northern latitudes suggests that impacts of HWA may be more pronounced in southern stands, and may reflect an inability of HWA to overwinter in cooler northern climates.

Although HWA infests *T. canadensis* of all sizes, crown classes, and stand densities, there is some evidence that site conditions may play a role in infestation levels (Orwig et al., 2002; Royle & Lathrop, 1999). A long-term study conducted by Small et al. (2005) determined HWA caused higher rates of basal area decline in ledge sites versus ravines, suggesting elevation, temperature, soil moisture, and light availability may influence *T. canadensis* mortality and post-adelgid species composition. Although *T. canadensis* exhibits mortality across all topographical aspects, the xeric conditions associated with south-western and western facing slopes may predispose *T. canadensis* trees outside of optimal growing conditions to infestation (Orwig et al., 2002; Mayer, Scudder, & Chianese, 1996; Bonneau, Shields, & Civco, 1999). A study performed in Connecticut by Orwig et al. (2002) observed a positive correlation between stand size and overstory mortality, suggesting that HWA may reproduce and distribute itself more efficiently in large contiguous stands.

HWA is quite mobile prior to its selection of an acceptable feeding site. Wind, animals, and humans aid in the dispersal of HWA and distribute it throughout all heights of the crown (McClure, 1990; Evans & Gregoire, 2006). Highly travelled areas such as roads, trails, and riparian zones contribute to the transport of HWA by birds and humans (Koch, Cheshire, & Devine, 2006).

Adelgid colonization in densities greater than 4 individuals/20 mm² of branch has been shown to significantly deter new growth on *T. canadensis* trees in the following year, forcing nymphs to feed upon less preferred older growth and significantly reducing densities in subsequent years (McClure, 1991). After settling on the needlebases of young *T. canadensis* growth, the adelgid inserts its stylet into xylem ray parenchyma cells and feeds upon cell fluids (Young, Shields, & Berlyn, 1995; McClure & Cheah, 1999).

The life cycle of HWA is parthenogenetic, polymorphic and produces two generations per year. Adults of the wingless (sistens) generation deposit eggs which hatch into mobile nymphs (crawlers) and settle on young twigs near the base of the needles. These nymphs mature into second generation progrediens, which can be winged (sexuparae) or wingless. Wingless progrediens continue to feed and reproduce on *T. canadensis* while winged sexuparae fly from *T. canadensis* in search of a spruce (*Picea)* species on which to deposit eggs and fulfill their lifecycle (Cheah et al., 2004). No suitable *Picea* species is present in North America, therefore the production of sexuparae constitutes a significant mortality factor for HWA on *T. canadensis* (McClure, 1991).

Ecological Consequences of HWA

Significant ecological and structural changes occur over the course of infestation and stand decline. Short-term impacts associated with the actions of HWA upon *T. canadensis* include foliar defoliation, loss of vitality, and death of infested individuals; consequentially triggering long-term changes in species composition and a loss of the unique structure and microclimatic conditions associated with *T. canadensis* forest types (Lovett, Canham, Arthur, Weathers, & Fitzhugh, 2006). Large reductions in forest productivity and substantial defoliation rates create openings in previously closed canopy forests, allowing increased amounts of direct sunlight to reach the forest floor. Utilizing hemispherical photography to estimate Gap Light Index, an estimate of understory light availability, Jenkins et al. (1999) found a significant trend of increased light availabilities in conjunction with HWA infestation in southern New England. The increased soil temperatures and biological activities associated with high levels of solar radiation work to accelerate nitrogen mineralization, nitrification, and N turnover rates in the forest floor, creating high potential for nitrate leaching following *T. canadensis* decline (Jenkins et al., 1999).

Stand microclimate and ecosystem processes are highly dependent upon species such as *T. canadensis*, further amplifying the importance of identifying exotic pest outbreaks as a serious threat to eastern forests (Eschtruth et al., 2006). Infested *T. canadensis* support lower needle densities and biomass than uninfested trees, and typically exhibit much poorer than average crown health and greater percentages of open sky in the canopy (Stadler, Muller, Orwig, &

Cobb, 2005; Cobb, Orwig, & Currie, 2006). Increased light availabilities and soil temperatures as a result of *T. canadensis* decline have been shown to result in increased species richness, introduction of exotic species, and conversion of *T. canadensis* forest types to deciduous forest cover (Eschtruth et al., 2006). Rapid growth and abundance of hardwood species, particularly *Betula lenta* (L.) (black birch) and *B. alleghaniensis* (Britton) (yellow birch)*, as well as Fagus grandifolia* (Ehrh.) (American beech)*, Acer rubrum* (L.) (red maple)*, Sassafras albidum* (Nutt.) Nees. (sassafras)*, Prunus serotina* (Ehrh.) (black cherry), and *Quercus spp.* (L.) (oak), has been reported following *T. canadensis* decline at its northern range (Small et al., 2005)*.* The short and long-term impacts in structure and functionality attributable to the loss of *T. canadensis* are unlikely to be mitigated by recruitment of invading hardwood species, which will not provide the unique soil conditions created by *T. canadensis* dominated forests (Lovett et al., 2006).

The dense canopy provided by *T. canadensis* in moist sites and drainages is a key component in hydrologic processes throughout the southern Appalachian Mountains. The loss of this riparian evergreen which maintains year-round transpiration rates is estimated to result in a reduction in annual stand-level transpiration by roughly 10% and reduction of winter and spring transpiration by 30% (Ford & Vose, 2007). In addition to increased annual base flows, increased soil temperatures caused by *T. canadensis* defoliation may result in dramatic shifts in stream chemistry. Increased available nitrogen pools in the form of leachable nitrates, as well as increased calcium and magnesium concentrations following *T. canadensis* decline are typical in *T. canadensis* dominated watersheds following mortality (Jenkins et al., 1999; Lewis & Likens, 2007).

Tsuga canadensis provides cover, tree cavities, coarse woody debris, and/or mast for nearly 100 avian and 50 mammalian species (DeGraaf & Rudis, 1986; Yamasaki, DeGraff, & Lanier, 2000). Avian communities associated with *T. canadensis*, such as the black-throated green warbler (*Dendroica virens)*, blackburnian warbler (*Dendroica fusca)*, and acadian flycatcher (*Empidonax virescens),* are highly dependent upon its unique, multi-layered canopy structure and will likely experience habitat loss following *T. canadensis* mortality (Tingley, Orwig, Field, & Motzkin, 2002). Fish, salamanders, and other animals in streams and riparian zones will be affected by the loss of *T. canadensis* canopy, which is likely to result in increased stream temperatures and algal growth (Brooks, 2001; Ellison et al., 2005; Lovett et al., 2006). In a study conducted at Delaware Water Gap National Recreation Area, brook trout (*Salvelinus fontinalis)* and brown trout *(Salmotrutta Linnaeus)* had higher populations in *T. canadensis* dominated drainages compared to hardwood dominated drainages (Ross et al., 2003). Streams draining *T. canadensis* encourage greater diversity and species richness of aquatic invertebrates, and provide more consistent temperature and hydrologic regimes than hardwood forests (Snyder, Young, Lemarie, & Smith, 2002). Furthermore, in regions dominated by deciduous forests, *T. canadensis* provides thermal cover for moose, white-tailed deer, ruffed grouse, turkey, songbirds, and other wildlife species during the winter months (McWilliams & Schmidt, 2000).

HWA Control

Several control measures are available for landowners interested in preserving the health of *T. canadensis* on their property, with the most common form being the application of insecticide. Management of HWA with the application of the neonicotinoid insecticide known as imidicloprid has been shown to be effective in decreasing adelgid densities over multiple years (Cowles, Montgomery, & Cheah, 2006; Frank, Ahern, & Raupp, 2007; Webb, Frank, & Raupp, 2003), and can be applied in the form of foliar or systemic treatments. Long-term control is highly reliant upon releases of biological predators of the adelgid, the most common being *Sasajiscymnus tsugae* (Coleoptera: Coccinellidae)*.*

The foliar application of horticultural oils and insecticidal soaps by spraying is an effective treatment measure which rapidly reduces adelgid densities and has demonstrated great success, especially for small trees and hedges (Royalty, 2008). Horticultural oils and soaps have minimal impacts upon the environment, coexisting organisms, and the applicator because instead of killing by means of ingestion, they act to effectively suffocate adelgids (McClure, 1998). However, its usage is limited to easily accessible *T. canadensis* trees in which complete foliar coverage can be achieved. This type of coverage is important because only needles receiving direct coverage of imidicloprid will display resistance, which is often unattainable in undisturbed forests with large *T. canadensis* or at high stand densities. The ruggedness and remoteness of terrain associated with *T. canadensis* stands limits the accessibility and mobility of spraying equipment. There is further concern that spraying in riparian zones and moist drainages may contaminate waterways by means of aerial drifting. Therefore, foliar spraying may be an effective control measure for HWA in urban and highly travelled environments, but has definite limitations for landscape-scale usage.

Systemic usage of imidacloprid is performed through stem injections or soil applications. This type of application allows for the upward and downward movement of imidacloprid and enables transport of these xylem-mobile materials throughout all parts of the tree (Tattar & Tattar, 1999). Imidicloprid, applied as a soil drench of Merit® 75 WP in a residential landscape in Maryland, proved to be effective in controlling the activities and spread of adelgids throughout all states of decline following a single application (Webb et al., 2003). Cowles and colleagues (2006) observed an average reduction in adelgid populations of 80% in as little as one year following soil application and 95% adelgid mortality two years after initial application. Stem injection methods have shown limited success (Cowles et al., 2006) and are generally avoided, as there is possibility to wound the tree during injection and provide further access of pests or diseases via entrance holes. However, injections may be performed upon *T. canadensis* in close proximity to water sources in an effort to prevent stream contamination.

Biological control agents may prove to be a long-term solution to the HWA problem, although further research is needed to confirm their effectiveness outside of laboratory studies. Several types of beetles have been tested for introduction into eastern North America, with determining factors being rates of dispersal, as well as ability to overwinter and reproduce in cold climates. One of the most promising biological control agents is the coccinellid S*. tsugae,* which shares a life cycle similar to the adelgid, and feeds upon all developmental stages of its prey (McClure & Cheah, 1999). *Sasajiscymnus tsugae* has a relatively long life span over which it sustains reproductive activities and exerts facultative diapause (Cheah & McClure, 1998). Release sites in Connecticut, New Jersey, and Virginia observed a 47-88% reduction in adelgid densities following five months of activity by *S. tsugae* (McClure & Cheah, 1999). Further releases of *S. tsugae* will determine its effectiveness on the landscape level, which is likely to vary based upon site conditions, elevation, and level of infestation.

Specific Objectives

HWA has proven itself to be highly effective predator of *T. canadensis* in the eastern United States. It has demonstrated its ability to disperse, infest, overwinter, and reproduce on *T. canadensis* trees throughout the northern part of their distribution. Several treatment measures successfully mitigate HWA impacts, unfortunately the immense scale of infestation and rapid stand decline has made HWA control a daunting task.

Early literature has focused upon HWA interactions in the northern portion of its range, where *T. canadensis* is a large component of forested stands. High infestation rates throughout the southern Appalachian Mountains have been reported, but little is known about how HWA is impacting this region. The goal of this study is to assess the impacts of the HWA on *T. canadensis* populations and forest communities containing *T. canadensis* in the southern Appalachians. Specific objectives of this research project were to:

1. Determine how *T. canadensis* populations have changed in conjunction with HWA infestation in Great Smoky Mountains National Park (GSMNP).
2. Document how HWA has affected vegetative communities in GSMNP.

The following three chapters describe the results of the field surveys conducted in Great Smoky Mountains National Park to address these objectives.

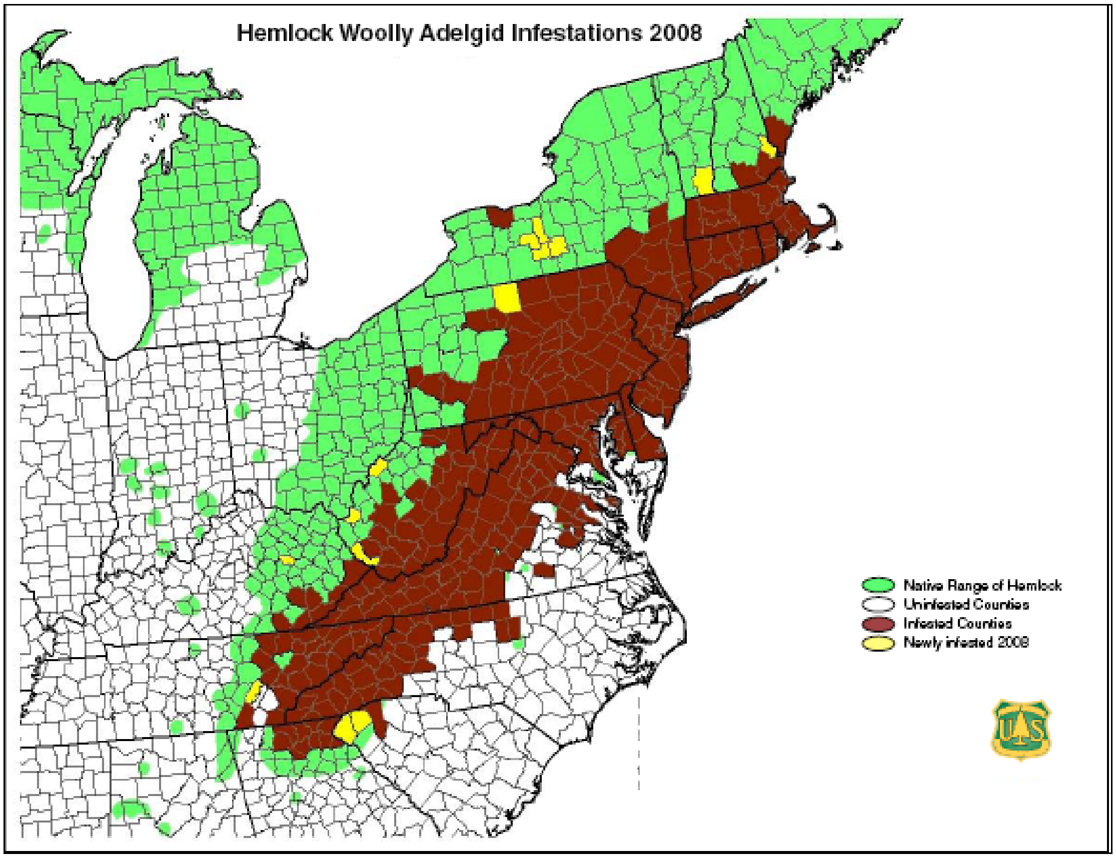

Figure 1.1.

Distribution of *Tsuga canadensis* and Hemlock Woolly Adelgid in the United States (USDA Forest Service, 2008)

CHAPTER 2

EARLY IMPACTS OF HEMLOCK WOOLLY ADELGID IN *TSUGA CANADENSIS* FOREST COMMUNITIES OF THE SOUTHERN APPALACHIAN MOUNTAINS

Introduction

Tsuga canadensis (L.) Carr. (eastern hemlock), is a long lived, extremely shade tolerant tree species native to forests throughout eastern North America, dominating approximately 931,000 ha of forest from the southern Appalachians to southern Canada and west to the central Lake States (Godman & Lancaster, 1990; McWilliams & Schmidt, 2000). *Tsuga canadensis* is commonly found across a wide range of aspects, elevations, and in multiple forest types as both an understory and/or overstory species, however, the species does best on steep, undisturbed, northerly facing sites (Fowells, 1965; Godman & Lancaster, 1990; White et al., 2003). Because of its longevity and distribution on a wide variety of site conditions, *T. canadensis* is regarded as a keystone species for a variety of wildlife species (DeGraaf & Rudis, 1986; Yamasaki et al., 2000), influences nutrient cycling and stream water chemistry (Jenkins et al., 1999; Lewis & Likens, 2007), and plays a vital role in hydrological processes of forests (Ford & Vose, 2007).

Hemlock woolly adelgid (*Adelges tsugae* Annand, HWA) is currently the single greatest threat to the long-term survival of *T. canadensis* trees throughout eastern North America. This small, aphid-like insect settles at the needlebase of healthy *T. canadensis* foliage and inserts its stylet into xylem ray parenchyma cells, feeding upon nutritious cellular fluids (McClure & Cheah, 1999; McClure, Salom, & Shields, 2001; Young, Shields, & Berlyn, 1995)*.* The continual depletion of vital nutrient reserves by HWA, in combination with the injection of toxic saliva, creates heavy foliar losses in otherwise healthy trees, and severely inhibits further growth and development (Cheah et al., 2004; Young et al., 1995). Although HWA was first reported in North America in the 1920s on *Tsuga. heterophylla* (Raf.) Sarg. (western hemlock) and *Tsuga mertensiana* (Bong.) Carr. (mountain hemlock), established populations of natural predators and host resistance has kept these species generally unaffected by the presence of HWA (Cheah et al., 2004; McClure et al., 2001). However, *T. canadensis* is highly susceptible to HWA infestation, and has displayed little resistance to the effects of this exotic insect.

HWA was accidentally introduced to Virginia in the early 1950s from southern Japan, and has decimated *T. canadensis* populations throughout the Mid-Atlantic states and southern New England since the 1980s (Cheah et al., 2004; Havill et al., 2006; Lovett et al., 2006; Stoetzel, 2002). Its combination of high mobility, rapid reproduction, and lack of natural predators has facilitated its further spread throughout eastern North America (McClure, 1987; McClure, 1990; McClure, 2001). HWA now occupies about half of the *T. canadensis* native range, and extends northward from Georgia to southern Maine (USDA Forest Service, 2008). Although HWA has the potential to invade the majority of *T. canadensis* native range (McClure, 1996), low winter temperatures (≤ -20°C) can cause significant reductions in adelgid densities (Cheah & McClure, 2002; Parker, Skinner, Gouli, Ashikaga, & Teillon, 1999; Skinner, Parker, Gouli, & Ashikaga, 2003), and may limit its spread into northernmost latitudes.

Population densities of *T. canadensis* have been greatly reduced wherever HWA invades (Eschtruth et al., 2006; Jenkins et al., 1999; Kizlinski, Orwig, Cobb, & Foster, 2002; Orwig & Foster, 1998; Small et al., 2005). For example, an examination of forested stands throughout south-central Connecticut determined that HWA infests *T. canadensis* trees of all size and age classes, with over 90% of infested trees exhibiting greater than 50% defoliation (Orwig & Foster, 1998). Following nine years of infestation at Delaware Water Gap National Recreation Area, Eschtruth et al. (2006) observed mortality or severe decline in 25% of monitored overstory *T. canadensis* trees, coupled with significant declines in *T. canadensis* tree vigor and crown densities. Fifteen years of infestation in the Connecticut College Arboretum resulted in a 70% decrease in overstory *T. canadensis* basal area, and a greater than 80% decrease in *T. canadensis* stem density (Small et al., 2005).

The impacts of HWA infestation upon *T. canadensis* have been studied since the late 1980s in northeastern forests, however, the impacts of the insect have received less study in the more temperate conditions of the southern Appalachians, where HWA has invaded more recently. By resampling a series of long-term vegetation plots established in 2003, we will address four hypotheses related to the effects of HWA on forest ecosystems: (1) short-term mortality rates will be greater in the southern Appalachians than in the northern range of

T. canadensis due to lower winter temperature extremes, (2) mortality will be greater in the midstory compared to the overstory because of the reduced energy reserves of suppressed individuals, (3) decline and mortality will vary with site conditions, and (4) mortality of *T. canadensis* will result in variable changes in community composition across the wide range of forest types in which the species occurs.

Materials and Methods

Study Area

Located on the Tennessee/North Carolina border, Great Smoky Mountains National Park (GSMNP) contains one of the oldest and most ecologically diverse mountain chains in the world. Over 70 unique community associations comprised of over 1,300 native plant species have been identified throughout the Park (Jenkins, 2007). Elevations range from 267 to 2025 m, and the landscape is generally rugged. Regional climate is warm and humid in the summer months, and winters are mild, providing excellent, nearly year-round growing conditions for some associated flora. Annual precipitation rates vary from 140 to 200 cm per year, and are largely influenced by elevation (Jenkins, 2007).

GSMNP was established in 1934 to protect remaining tracts of pristine southern Appalachian forest from anthropogenic disturbances such as extensive logging and catastrophic fire. Spanning approximately 212,000 ha, this is the largest as well as, the most heavily visited National Park in the eastern United

States (Johnson et al., 2005). Approximately 80% of the Park has been subject to past logging practices, but the remaining 20% is old growth forest with tree ages exceeding 400 years (Johnson et al., 1999; Pyle, 1988).

For decades, the effects of fire suppression have contributed to the increased presence of *T. canadensis* in GSMNP (Harrod, White, & Harmon, 1998; Jenkins & White, 2002). Today, *T. canadensis* is a dominant species throughout GSMNP, and plays an important ecological role in a variety of ecosystems. Although Madden et al., (2004) identified only 2% (2,023 ha) of the park as *T. canadensis* forest, the species is a common component of a wide variety of forest associations (Jenkins, 2007) that cover 35,399 ha of the Park (Welch et al., 2002).

Ecogroups

We assessed the influence of HWA across six ecological groups (hereafter ecogroups). Ecogroups are aggregates of forest associations developed as midscale units to represent similar ecological conditions and environmental gradients (White et al., 2003). These associations provide a broad description of general site characteristics which can be identified in the field. Ecogroups in this study range from low elevation, topographically protected coves and drainages, to high elevation northern hardwood forests. Specific ecogroups we sampled were acid hardwood, northern hardwood, floodplain, hemlock, montane cove, and montane oak-hickory forests (Table 2.1.).

Data Collection

Thirty-two 100 m^2 plots were established in the summer of 2003 and resampled in the summer of 2008/2009 in accordance with GSMNP vegetation monitoring protocol (Jenkins, 2008). Within each plot we tagged, recorded the diameter at breast height (dbh), and assessed the tree condition (percentage of crown dieback; 1 = No dieback, 2 = 0-25% dieback, 3 = 25-50% dieback, 4 = 50-75% dieback, 5 = > 75% dieback, 6 = dead, 7 = down, 8 = missing) of all trees ≥ 10 cm dbh (overstory). Woody stems ≥ 1.4 m in height, but < 10 cm (midstory) were tallied in the following categories: 0-0.9 cm, 1.0-2.4 cm, 2.5-4.9 cm, and 5.0-9.9 cm. In addition to tree condition, *T. canadensis* health was further evaluated for randomly selected overstory *T. canadensis* trees utilizing “visual crown rating” methods developed by the USDA Forest Service (USDA Forest Service, 2007). These measurements examined changes in *T. canadensis* health occurring from 2003 to 2008/09 based upon crown density (relative density or “fullness” of existing foliage) and top dieback (dieback occurring from top of tree down).

Statistical Analyses

We utilized two-way repeated measures analysis of variance (ANOVA) to compare changes in total, overstory, and midstory *T. canadensis* densities and basal areas between the sampling interval and among forest types (SAS, 2004). When ANOVA revealed significant main effects or a significant interaction, we used the Tukey multiple comparison test for post-hoc comparisons. Regression analysis was used to define relationships between aspect, slope, elevation, initial *T. canadensis* density and *T. canadensis* mortality (SAS, 2004). Aspect values were transformed (aspect = cosine (45 – azimuth degrees) + 1) prior to analysis (Beers, Dress, & Wensel, 1966). To determine species dominance, importance values [IV = ((relative density + relative basal area)/2) x 100], were calculated for select species among the six ecogroups. We calculated relative densities of dominant overstory and midstory species, and utilized paired t-tests to examine changes in species composition from 2003 to 2008/9 (SAS, 2004).

Results

Tsuga canadensis

In 2003, *T. canadensis* density varied across plots, ranging from 10 to 2,940 stems ha^{-1}, and averaged 494 stems ha^{-1}. Across all plots, 24% of all overstory stems and 24% of the overstory basal area was comprised of *T. canadensis*, with stem density and basal area averaging 101 stems ha^{-1} and 9 m² ha^{-1}, respectively. In the midstory, 9% of all stems and 18% of basal area was comprised of *T. canadensis*, and average stem density was 393 stems ha^{-1} and basal area was 0.55 m² ha^{-1}. Relative importance values of *T. canadensis* ranged from 4 to 35% across all ecogroups, and was highest in the *T. canadensis* ecogroup and lowest in the acid hardwood ecogroup (Table 2.1.).

We observed a highly significant decrease in total *T. canadensis* density from 2003 to 2008/09 (P = 0.004; Table 2.2.). *Tsuga canadensis* density did not significantly differ across all forest associations (P = 0.206), and lack of an interaction effect between forest type and sampling interval (P = 0.421) indicated changes in density did not significantly differ among ecogroups. We observed no significant changes in total *T. canadensis* basal area between 2003 and 2008/08 (9 to 9 m^2 ha^{-1}, P = 0.182). Individual site characteristics, including aspect (P = 0.37), elevation (P = 0.15), slope (P = 0.96), LAI (P = 0.22), and initial *T. canadensis* density (P = 0.45), were not significantly correlated with mortality across all sampled plots.

In the overstory, *T. canadensis* density was significantly lower in 2008/09 than in 2003 (101 to 90 stems ha^{-1}, P = 0.017; Table 2.2.), and an interaction effect between forest type and sampling interval indicated decline differed among forest types (P = 0.016). Overstory *T. canadensis* basal area did not significantly change between 2003 and 2008/08 (9 to 8 m^2 ha^{-1}, P = 0.270). Within ecogroups, the floodplain association experienced a 59% reduction in *T. canadensis* density (230 to 95 stems ha^{-1}, P < 0.001; Figure 2.1.). Measurements of overstory *T. canadensis* health determined mean crown density (35 to 21%, *P* < 0.0001) was significantly reduced from 2003 to 2008/09 (Figure 2.2.). Meanwhile, mean overstory top dieback doubled over the study period (12 to 25%, P = 0.01; Figure 2.2.). Although we observed a relatively modest rate of overstory mortality (11%), the majority of sampled trees were in moderate to poor condition (69%), and only 20% of overstory *T. canadensis* were considered to be in good condition by 2008/09 (Figure 3.3.).

Midstory *T. canadensis* density significantly decreased from 2003 to 2008/09 (395 to 260 stems ha^{-1}, P = 0.008; Table 2.2.). Density did not differ across forest types (P = 0.222), and changes in density did not differ among forest types (P = 0.421). Midstory *T. canadensis* basal area did not significantly change between 2003 and 2008/08 (0.6 to 0.4 m^2 ha^{-1}, P = 0.092). According to Tukey pairwise multiple comparisons tests, midstory *T. canadensis* density within the montane cove and hemlock associations decreased between the two sampling intervals. Decline was greatest in the montane cove ecogroup, where mean *T. canadensis* density decreased by 42% (357 to 207 stems ha^{-1}, P = 0.05). In hemlock forests, *T. canadensis* density decreased by 33% (894 to 598 stems ha^{-1}, P = 0.012).

Forest Composition

Species composition was highly diverse, with 44 overstory and 79 midstory species found across all sampled plots. Ten species made up 75% and 76% of overstory relative density in 2003 and 2008/09, respectively: *Acer rubrum* (L.) (red maple), *Betula alleghaniensis* (Britton) (yellow birch), *Betula lenta* (L.) (black birch), *Fagus grandifolia* (Ehrh.) (American beech), *Halesia tetraptera* (Ellis) (mountain silverbell), *Liriodendron tulipifera* (L.) (tuliptree), *Oxydendrum arboretum* (L.) DC. (sourwood), *R. maximum, Tilia americana* (L.) (American basswood), and *T. canadensis* (Table 2.3.). Five species: *Acer pensylvanicum* (L.) (striped maple), *F. grandifolia, Kalmia latifolia* (L.) (mountain laurel), *R. maximum,* and *T. canadensis* made up 79% and 72% of midstory relative density in 2003 and 2009 (Table 2.4.). All other species comprised less than 3% of overstory and midstory relative density. No significant changes in the relative density of overstory species were observed across all sampled plots ($P \geq 0.07$). Additionally, relative density of overstory species did not significantly change within ecogroups ($P \geq 0.06$). In the midstory, no significant changes in relative density were observed across all sampled plots ($P = 0.06$), or within ecogroups ($P \geq 0.07$).

Discussion

***Tsuga canadensis* Mortality**

In its northern range, HWA can effectively infest and kill *T. canadensis* in as few as 4 to 10 years following initial infestation (Eschtruth et al., 2006; Mayer et al., 1996; McClure, 1991; Small et al., 2005). We hypothesized greater short-term mortality rates in the southern Appalachians compared to the northern range of *T. canadensis* because of warmer winter temperatures that create favorable conditions for HWA survival and spread (Evans & Gregoire, 2006; Ward, Montgomery, Cheah, Onken, & Cowles, 2004). We observed considerable needle loss and dieback in *T. canadensis* trees in our study (Figure 2.2.), and 11% of overstory trees experienced mortality over the 5-6 year study period. While climatic conditions in the southern Appalachians (mild winters, hot summers, abundant rainfall, etc.) may favor HWA survival and spread, these conditions may be outweighed by conditions even more favorable to *T. canadensis* trees, allowing them to grow with greater vigor than trees in the northern range of the species. This increased vigor may have provided trees in the southern Appalachians with greater resistance to short-term mortality.

Nevertheless, considering the decline rates we observed, the trees we sampled are likely to die in a timeframe similar to those of the north.

As we hypothesized, midstory *T. canadensis* trees suffered higher mortality rates than overstory trees (34% versus 11%, respectively). These findings are in agreement with previous studies (Eschtruth et al., 2006; Orwig & Foster, 1998) which suggest *T. canadensis* mortality initially occurs in individuals of intermediate size classes occupying sub-dominant positions in the canopy. Orwig & Foster (1998) attributed these losses to the associated stressors of overstory competition and incomplete development of rooting systems. This type of dieback has important implications for the long-term sustainability of *T. canadensis* in GSMNP. Most importantly, a significant loss of midstory *T. canadensis* demonstrates a bottom up approach to the elimination of the species. Even if *T. canadensis* persists in the overstory in the short-term, untreated trees are most likely to eventually suffer mortality from HWA-related symptoms. With rapid mortality of midstory *T. canadensis* stems, future recruitment of *T. canadensis* into overstory positions will severely limited, regardless of overstory treatment. Therefore, we may see a near-complete loss of *T. canadensis* once overstory individuals perish.

While most *T. canadensis* trees were still living in the 2008/09 sample, the poor condition of many of the overstory trees (Figures 2.2. and 2.3.) suggests that their functional influence may already be diminished. Litter layers beneath dense *T. canadensis* canopies are typically deep and highly-acidic which aids in the retention of greater levels of soil moisture compared to hardwood dominated stands (Godman & Lancaster, 1990), and the loss of *T. canadensis* canopy coverage in riparian settings may reduce stand-level transpiration rates and severely impact hydrologic regimes (Ford & Vose, 2007). This type of decline is not unprecedented. For example, *Castanea dentata* (Marsh.) Borkh. (American chestnut) once exerted strong microclimate control and often defined forest communities until its eventual demise in the 1930s as a result of the actions of the invasive chestnut blight (*Cryphonectria parasitica*). Although *C. dentata* still occurs on the landscape in small size classes, its most defining characteristics such as high mast production (Diamond, Giles, Kirkpatrick, & Griffin, 2000), tremendous biomass, and allelopathic properties (Vandermast, Van Lear, & Clinton, 2002) have been lost. Ellison et al. (2005) described these types of losses as functional extinctions. While we do not have sufficient evidence of the functional extinction of *T. canadensis* throughout GSMNP, the impact of the loss of this species may rival the impact of the loss of *C. dentata* in many areas.

Influence of Site

Although HWA infests *T. canadensis* of all sizes, crown classes, and stand densities (Orwig et al., 2002), previous research has shown the positioning of *T. canadensis* stands on the landscape may be a determining factor of *T. canadensis* mortality rates. In southern New England, a long-term study observed higher rates of mortality on exposed, ledge sites versus mesic, protected ravines (Small et al., 2005). Other findings throughout New England, Connecticut, and New Jersey determined the xeric conditions associated with south-western and western facing slopes may predispose *T. canadensis* outside of optimal growing conditions to infestation (Bonneau et al., 1999; Mayer et al., 1996; Orwig et al., 2002). While it seems likely that similar patterns of decline would emerge in southern Appalachian *T. canadensis* forests, we did not observe any factors (e.g., aspect, slope, elevation, or initial *T. canadensis* density) that were strongly correlated with *T. canadensis* decline or mortality in GSMNP. However, among changes within the ecogroups, we found that *T. canadensis* density was reduced at low-elevation, mesic sites: the floodplain, hemlock, and montane cove forest associations. This was unexpected, as previous authors have hypothesized topographically protected coves and drainages may provide *T. canadensis* trees with more favorable site conditions allowing them to grow with increased vigor and greater short-term resistance to HWA (Orwig et al., 2002; Weckel, Tirpak, Nagy, & Christie, 2006).

Species Composition

Previous studies examining the associated impacts of HWA have noted dramatic changes in species composition following HWA infestation. For example, rapid growth and increased abundance of hardwood species, particularly *B. lenta* and *B. alleghaniensis,* as well as, *F. grandifolia, A. rubrum, Sassafras albidum* (Nutt.) (sassafras)*, Prunus serotina* (Ehrh.) (black cherry), and *Quercus spp.* (L.) (oak) were noted following *T. canadensis* decline in New England (Small et al., 2005). Following nine years of infestation at Delaware Water Gap National Recreation Area, greater levels of solar radiation in response to *T. canadensis* decline contributed to increased species richness, and particularly favored early successional species such as *L. tulipifera*, *Nyssa sylvatica* (Marsh.) (blackgum), *S. albidum,* and *Betula* spp. (Birch) (Eschtruth et al., 2006). Similarly, *B. lenta* was a leading competitor following canopy dieback in central Connecticut (Orwig & Foster, 1998).

Based upon these findings, we hypothesized mortality of *T. canadensis* would result in variable changes in community composition across the wide range of ecogroups in which the species occurs. Although we observed considerable dieback and mortality of *T. canadensis*, community composition was not significantly impacted within the forest associations we sampled. However, HWA is a relatively recent invader of southern Appalachian forests, and our study only monitored species composition over a five to six year period. As infestation progresses, further studies conducted over longer time scales (10 to 20 year intervals) will be helpful in determining future successional pathways of declining *T. canadensis* forests of the southern Appalachian Mountains. In addition, perhaps the most obvious difference between *T. canadensis* forests of the northeastern United States and those of the southern Appalachian Mountains is the presence of *R. maximum*. This species often dominates midstory composition in southern Appalachian Mountain forests, allowing little direct sunlight to reach the forest floor and severely inhibiting hardwood regeneration (Van Lear et al., 2002). *Tsuga canadensis* seedlings are highly tolerant of shade and are well suited for this environment where they persist in the midstory for many decades before recruiting into the overstory (Phillips & Murdy, 1985; Webster & Lorimer, 2003). However, with HWA causing significant decreases in *T. canadensis* density, development of *R. maximum* heath balds is possible in ecogroups previously dominated by *T. canadensis*.

Management Implications

Our findings have important implications for those attempting to control or prevent the spread of HWA. In uninfested forests, efforts to establish long-term vegetative plots and continually monitor forest composition and *T. canadensis* health can provide valuable information regarding the spread and severity of HWA infestations. Furthermore, if *T. canadensis* trees in the southern Appalachian Mountains experience losses comparable to those of *C. dentata,* documentation of the pre-adelgid condition of these unique and ancient forest communities may prove historically valuable. In forests already infested by HWA, it is important for land managers to set realistic treatment objectives and use on-site information to focus conservation efforts. Because *T. canadensis* trees rapidly decline following HWA infestation (Eschtruth et al., 2006; Nuckolls et al., 2008; Orwig & Foster, 1998; Orwig et al., 2002; Small et al., 2005), and as vitality decreases so does *T. canadensis* response to insecticide treatments (Webb et al., 2003), land managers need to take calculated steps in HWA management as time is of the essence. In large forested tracts it may not be possible to mitigate the impacts of HWA across the entire landscape, so land managers must prioritize where conservation efforts should be devoted. As a world renowned center for biological diversity and the most visited national park in the United States, GSMNP requires a multi-faceted approach to HWA management. Special consideration should be given to high traffic areas such as major trails, campgrounds, and picnic areas, which often coincide with old growth *T. canadensis* forests and are highly valued for their aesthetic qualities. In addition, *T. canadensis* trees in riparian areas should also be treated when possible to preserve the unique ecosystem functions this species provides. Therefore, we promote a concentrated yet modest management approach which identifies high priority stands based upon accessibility, species associations, and presence of HWA, and focuses available resources towards these areas of highest management potential at rates which can be sustained as long as HWA persists on the landscape.

Conclusions

By monitoring HWA-induced decline and mortality of *T. canadensis* across a wide spectrum of site variables and ecogroups throughout GSMNP, we have gained valuable insight regarding how this exotic invader may impact forested communities throughout the southern Appalachian Mountains in coming years. Our results indicate that *T. canadensis* trees are experiencing mortality, however, these rates do not appear to be exceeding those found throughout the mid-Atlantic and New England regions. We observed no individual site or stand condition predisposes any given site to HWA infestation. While the majority of overstory *T. canadensis* trees on our plots were still living, they were in a state of severe decline induced by HWA-associated defoliation, and midstory *T. canadensis* trees are experiencing greater mortality rates than those in the overstory. This significant loss of *T. canadensis* advanced regeneration, in combination with the decline and mortality of overstory trees, suggests that the species may largely disappear from southern Appalachian forests. Despite considerable losses in *T. canadensis* density across a wide range of ecogroups, community composition was not significantly impacted over the observational period, and further studies are needed to determine species response to *T. canadensis* mortality throughout this region. However, the overwhelming presence of *R. maximum* in high densities suggests it may define future successional patterns throughout the southern Appalachian Mountains.

Table 2.1.

Initial (2003) Overstory Species Composition and Stand Characteristics of Tsuga canadensis associated Ecogroups throughout GSMNP. Ecogroups are Arranged in Order of Decreasing Importance Value of T. canadensis

	Hemlock (n=5)	Northern hardwood (n=7)	Floodplain (n=2)	Montane Oak-Hickory (n=4)	Montane cove (n=11)	Acid Hardwood (n=3)
Elevation (m)	942 ± 49	1278 ± 41	503 ± 15	960 ± 77	928 ± 31	1275 ± 138
Aspect (°)	60 - 280	260 - 360	145 - 325	45 - 145	50 - 340	70 - 280
Slope (%)	40 ± 10	50 ± 9	18 ± 8	58 ± 6	40 ± 7	58 ± 10
Soil pH	5.2 ± 0.3	4.4 ± 0.2	5.3 ± 0.5	4.9 ± 0.2	5 ± 0.2	5.1 ± 0.4
Basal area (m^2 ha^{-1})	34 ± 1	42 ± 7	27 ± 3	43 ± 5	31 ± 3	36 ± 5
T. canadensis basal area (m^2 ha^{-1})	13 ± 5	15 ± 5	6 ± 5	9 ± 7	6 ± 2	1 ± 1
Density (stems ha^{-1})	381 ± 86	331 ± 40	735 ± 115	511 ± 20	406 ± 48	372 ± 87
T. canadensis (stems ha^{-1})	128 ± 37	89 ± 34	230 ± 130	115 ± 60	91 ± 18	17 ± 12
Importance Values						
T. canadensis	35 ± 12	29 ± 10	27 ± 17	21 ± 14	21 ± 4	4 ± 2
Betula alleghaniensis	6 ± 4	20 ± 8	0 ± 0	1 ± 1	11 ± 4	14 ± 13
Acer rubrum	12 ± 4	2 ± 1	6 ± 1	14 ± 6	8 ± 3	12 ± 9
Tilia americana	7 ± 7	11 ± 7	2 ± 0	0 ± 0	8 ± 5	0 ± 0
Quercus prinus	2 ± 1	0 ± 0	0 ± 0	19 ± 12	5 ± 4	17 ± 14

Table 2.2.

Repeated Measures Two-Way Analysis of Variance for Forest Type differences in Tsuga canadensis Stem Densities between 2003 and 2008/09

		Total density		Overstory		Midstory	
Source of Variation	df	MS[1]	P > F	MS	P > F	MS	P > F
Forest type	5	731276.4	0.206	15025.5	0.34	563809.4	0.222
Error (forest type)	2	468238.1		12621.0		374432.7	
Interval	1	333095.3	0.004	6662.6	0.01	245539.4	0.008
Forest type × interval	5	40073.1	0.349	3575.4	0.01	30913.7	0.421
Error	2	34143.4		1031.4		30028.1	

[1] MS = Mean squares.

Table 2.3.

Relative Density (% ± 1SE) of Dominant Overstory Species in Tsuga canadensis associated Ecogroups throughout GSMNP. Species are Arranged in Order of Decreasing Importance Value

	Hemlock (n = 5)		Northern Hardwood (n = 7)		Floodplain (n = 2)		Montane Oak-Hickory (n = 4)	
Species	2003	2008/09	2003	2008/09	2003	2008/09	2003	2008/09
Tsuga canadensis	31.6 ± 8.6	34.6 ± 8.3	26.8 ± 9.3	26.8 ± 9.2	31.3 ±13.7	30.9 ±11.2	22.5 ±12.2	20.6 ±13.3
Betula alleghaniensis	6.9 ± 4.3	5.9 ± 4.0	16.8 ± 7.8	16.2 ± 7.4	0.0 ± 0.0	0.0 ± 0.0	1.5 ± 1.0	1.0 ± 1.0
Acer rubrum	12.1 ± 5.6	11.2 ± 5.7	1.4 ± 0.9	1.3 ± 0.9	6.6 ± 0.4	14.1 ± 7.0	19.0 ± 7.5	19.5 ± 7.9
Betula lenta	7.8 ± 3.3	7.1 ± 2.6	3.0 ± 1.6	2.9 ± 1.6	5.8 ± 0.5	1.8 ± 1.8	4.0 ± 2.8	3.9 ± 2.5
Tilia americana	6.9 ± 5.7	5.8 ± 4.6	12.8 ± 8.3	14.2 ± 8.3	1.5 ± 0.3	0.9 ± 0.9	0.0 ± 0.0	0.0 ± 0.0
Quercus prinus	1.3 ± 1.0	1.8 ± 1.5	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	10.4 ± 8.3	8.8 ± 7.3
Liriodendron tulipifera	5.5 ± 1.9	5.3 ± 1.9	0.0 ± 0.0	0.0 ± 0.0	17.2 ±10.9	11.6 ±11.6	1.5 ± 1.5	1.6 ± 1.6
Fagus grandifolia	0.3 ± 0.3	0.3 ± 0.3	10.7 ± 4.2	9.1 ± 3.4	0.0 ± 0.0	0.0 ± 0.0	4.8 ± 4.8	6.3 ± 6.3
Halesia tetraptera	4.2 ± 1.7	4.1 ± 1.7	7.5 ± 3.1	8.4 ± 3.4	0.0 ± 0.0	0.0 ± 0.0	3.3 ± 1.6	0.4 ± 0.4
Oxydendrum arboreum	4.3 ± 3.3	4.7 ± 3.7	0.0 ± 0.0	0.0 ± 0.0	1.9 ± 1.9	2.6 ± 2.6	7.8 ± 2.9	8.1 ± 2.8
Quercus rubra	2.2 ± 1.2	1.7 ± 0.8	0.8 ± 0.6	0.3 ± 0.3	0.6 ± 0.6	0.0 ± 0.0	0.0 ± 0.0	1.8 ± 1.8
Pinus strobus	4.6 ± 4.6	3.8 ± 3.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	5.3 ± 5.3	6.3 ± 6.3
Rhododendron maximum	2.2 ± 0.8	3.3 ± 1.3	2.9 ± 1.3	2.8 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	4.3 ± 3.7	4.3 ± 3.5
Magnolia fraseri	1.6 ± 1.0	1.5 ± 1.0	1.4 ± 0.7	1.4 ± 0.7	0.0 ± 0.0	0.0 ± 0.0	1.4 ± 1.4	1.3 ± 1.3
Aesculus flava	0.0 ± 0.0	0.0 ± 0.0	2.0 ± 1.3	1.8 ± 1.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Picea rubens	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Amelanchier laevis	0.0 ± 0.0	0.0 ± 0.0	1.0 ± 0.6	1.0 ± 0.7	0.0 ± 0.0	0.0 ± 0.0	1.4 ± 0.9	1.8 ± 1.3
Acer pensylvanicum	0.6 ± 0.6	0.6 ± 0.6	3.5 ± 2.0	4.4 ± 2.9	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.5	0.5 ± 0.5
Liquidambar styraciflua	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	8.1 ± 8.1	7.9 ± 7.9	0.0 ± 0.0	0.0 ± 0.0
Cornus florida	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	6.1 ± 2.6	1.8 ± 1.8	0.0 ± 0.0	0.0 ± 0.0

Table 2.3.

Relative Density (% ± 1SE) of Dominant Overstory Species in Tsuga canadensis associated Ecogroups throughout GSMNP (Cont.)

	Montane Cove (n = 11)		Acid Hardwood (n = 3)	
Species	2003	2008/09	2003	2008/09
Tsuga canadensis	22.4 ± 3.8	20.3 ± 4.1	4.5 ± 2.4	4.5 ± 2.4
Betula alleghaniensis	11.3 ± 4.2	11.2 ± 4.0	13.0 ±12.0	13.0 ±12.0
Acer rubrum	6.8 ± 2.3	6.6 ± 1.9	11.6 ± 7.9	10.8 ± 8.3
Betula lenta	11.4 ± 5.5	12.3 ± 6.2	4.2 ± 1.1	2.5 ± 1.6
Tilia americana	5.9 ± 3.5	5.6 ± 3.4	0.0 ± 0.0	0.0 ± 0.0
Quercus prinus	2.3 ± 1.6	2.0 ± 1.4	7.0 ± 6.0	5.2 ± 4.2
Liriodendron tulipifera	3.8 ± 2.3	3.9 ± 2.1	0.0 ± 0.0	0.0 ± 0.0
Fagus grandifolia	5.1 ± 2.5	4.0 ± 2.2	5.3 ± 5.3	7.0 ± 7.0
Halesia tetraptera	5.2 ± 1.5	5.1 ± 1.5	1.8 ± 1.8	0.9 ± 0.9
Oxydendrum arboreum	4.4 ± 2.1	5.4 ± 2.6	6.3 ± 6.3	7.2 ± 7.2
Quercus rubra	1.0 ± 0.5	0.7 ± 0.4	3.4 ± 3.4	3.5 ± 3.5
Pinus strobus	0.9 ± 0.9	0.9 ± 0.9	0.0 ± 0.0	0.0 ± 0.0
Rhododendron maximum	5.0 ± 2.8	6.4 ± 3.2	1.6 ± 0.8	1.6 ± 0.8
Magnolia fraseri	2.7 ± 1.3	3.4 ± 1.4	5.4 ± 5.4	7.2 ± 7.2
Aesculus flava	4.4 ± 3.3	5.2 ± 3.7	0.0 ± 0.0	1.8 ± 1.8
Picea rubens	0.0 ± 0.0	0.0 ± 0.0	6.4 ±10.8	14.7 ± 9.2
Amelanchier laevis	0.7 ± 0.5	0.4 ± 0.4	7.5 ± 7.5	6.9 ± 6.9
Acer pensylvanicum	1.0 ± 1.0	1.3 ± 1.0	2.5 ± 1.6	2.5 ± 1.6
Liquidambar styraciflua	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Cornus florida	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

Table 2.4.

Relative Density (% ± 1SE) of Dominant Midstory Species in Tsuga canadensis associated Ecogroups throughout GSMNP. Species are Arranged in Order of Decreasing Importance Value

	Hemlock (n = 5)		Northern Hardwood (n = 7)		Floodplain (n = 2)		Montane Oak-Hickory (n = 4)	
Species	2003	2008/09	2003	2008/09	2003	2008/09	2003	2008/09
Rhododendron maximum	44.0 ± 5.6	47.7 ± 4.9	55.8 ±14.4	55.5 ±15.0	13.2 ±12.8	3.6 ± 3.6	40.4 ±13.8	40.3 ±12.9
Tsuga canadensis	15.3 ± 4.7	14.5 ± 5.6	7.3 ± 4.5	4.6 ± 3.2	21.8 ±11.3	36.1 ±26.6	13.4 ±12.4	12.5 ±11.0
Kalmia latifolia	4.9 ± 2.7	2.2 ± 1.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	28.8 ±14.9	18.1 ±11.2
Fagus grandifolia	0.3 ± 0.3	0.3 ± 0.3	14.5 ± 8.4	9.2 ± 5.6	7.9 ± 5.6	8.9 ± 6.5	1.1 ± 1.0	0.4 ± 0.4
Acer pensylvanicum	1.5 ± 0.7	1.3 ± 0.7	6.2 ± 4.2	4.7 ± 3.6	1.7 ± 0.1	1.8 ± 0.0	0.4 ± 0.3	1.3 ± 0.9
Acer rubrum	2.6 ± 0.9	1.9 ± 0.7	0.6 ± 0.6	0.2 ± 0.1	1.3 ± 0.9	0.5 ± 0.5	1.9 ± 0.6	2.9 ± 0.9
Pyrularia pubera	12.2 ± 7.7	11.3 ± 7.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.5	2.2 ± 1.3	1.5 ± 0.9
Halesia tetraptera	3.3 ± 2.0	2.6 ± 1.3	2.6 ± 1.1	3.8 ± 2.2	3.2 ± 2.7	1.8 ± 1.8	2.3 ± 2.2	2.2 ± 2.0
Carpinus caroliniana	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	25.0 ±21.8	25.3 ±22.6	0.0 ± 0.0	0.0 ± 0.0
Leucothoe fontanesiana	0.0 ± 0.0	0.0 ± 0.0	2.2 ± 2.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	3.1 ± 3.1	2.9 ± 2.9
Tilia americana	0.9 ± 0.5	0.9 ± 0.7	1.9 ± 1.2	2.2 ± 2.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Betula alleghaniensis	1.0 ± 0.6	0.5 ± 0.3	0.4 ± 0.2	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.2 ± 0.2
Aesculus flava	0.5 ± 0.3	0.3 ± 0.2	0.2 ± 0.2	0.0 ± 0.0	1.6 ± 1.6	0.6 ± 0.6	0.0 ± 0.0	0.0 ± 0.0
Smilax sp.	0.6 ± 0.6	0.7 ± 0.5	1.6 ± 1.3	7.1 ± 5.1	5.2 ± 5.2	0.6 ± 0.6	1.4 ± 0.6	1.1 ± 0.6
Magnolia fraseri	0.6 ± 0.4	1.0 ± 0.5	0.5 ± 0.3	0.7 ± 0.4	0.7 ± 0.7	0.6 ± 0.6	0.3 ± 0.2	0.3 ± 0.2
Betula lenta	1.3 ± 0.9	1.5 ± 0.9	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 0.2	2.1 ± 0.3	0.1 ± 0.1	1.3 ± 0.9
Viburnum lantanoides	0.0 ± 0.0	0.1 ± 0.1	2.9 ± 2.3	3.1 ± 2.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Ilex montana	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.2 ± 0.2
Hydrangea arborescens	1.0 ± 0.7	2.0 ± 2.0	0.3 ± 0.3	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Quercus rubra	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1

Table 2.4.

Relative Density (% ± 1SE) of Dominant Midstory Species in Tsuga canadensis associated Ecogroups throughout GSMNP (Cont.)

	Montane Cove (n = 11)		Acid Hardwood (n = 3)	
Species	2003	2008/09	2003	2008/09
Rhododendron maximum	69.3 ± 6.7	58.3 ± 7.1	54.3 ±17.6	52.4 ±22.2
Tsuga canadensis	5.2 ± 2.5	4.6 ± 1.9	0.5 ± 0.3	0.7 ± 0.5
Kalmia latifolia	2.2 ± 0.9	1.7 ± 0.9	29.1 ±15.3	24.6 ±14.3
Fagus grandifolia	2.5 ± 1.8	3.4 ± 2.2	0.1 ± 0.1	0.2 ± 0.2
Acer pensylvanicum	3.3 ± 1.5	3.8 ± 2.1	0.9 ± 0.9	0.9 ± 0.8
Acer rubrum	0.6 ± 0.2	0.6 ± 0.2	0.1 ± 0.1	0.3 ± 0.2
Pyrularia pubera	0.7 ± 0.5	0.6 ± 0.4	0.6 ± 0.6	0.2 ± 0.2
Halesia tetraptera	0.7 ± 0.3	0.9 ± 0.5	0.1 ± 0.1	0.1 ± 0.1
Carpinus caroliniana	0.2 ± 0.2	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Leucothoe fontanesiana	4.7 ± 2.4	9.7 ± 5.4	0.1 ± 0.1	0.0 ± 0.0
Tilia americana	1.1 ± 0.6	1.4 ± 1.0	0.0 ± 0.0	0.0 ± 0.0
Betula alleghaniensis	1.0 ± 0.6	1.5 ± 1.2	0.3 ± 0.2	0.2 ± 0.2
Aesculus flava	1.5 ± 0.9	0.9 ± 0.5	0.1 ± 0.1	0.1 ± 0.1
Smilax sp.	1.6 ± 1.1	4.2 ± 2.2	3.1 ± 1.8	7.2 ± 3.8
Magnolia fraseri	0.4 ± 0.2	0.8 ± 0.4	1.3 ± 0.9	1.4 ± 0.8
Betula lenta	0.1 ± 0.0	0.3 ± 0.2	0.0 ± 0.0	0.2 ± 0.1
Viburnum lantanoides	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Ilex montana	0.2 ± 0.1	0.1 ± 0.0	2.1 ± 1.9	4.4 ± 4.4
Hydrangea arborescens	0.4 ± 0.4	0.2 ± 0.1	3.0 ± 3.0	0.6 ± 0.6
Quercus rubra	0.3 ± 0.2	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0

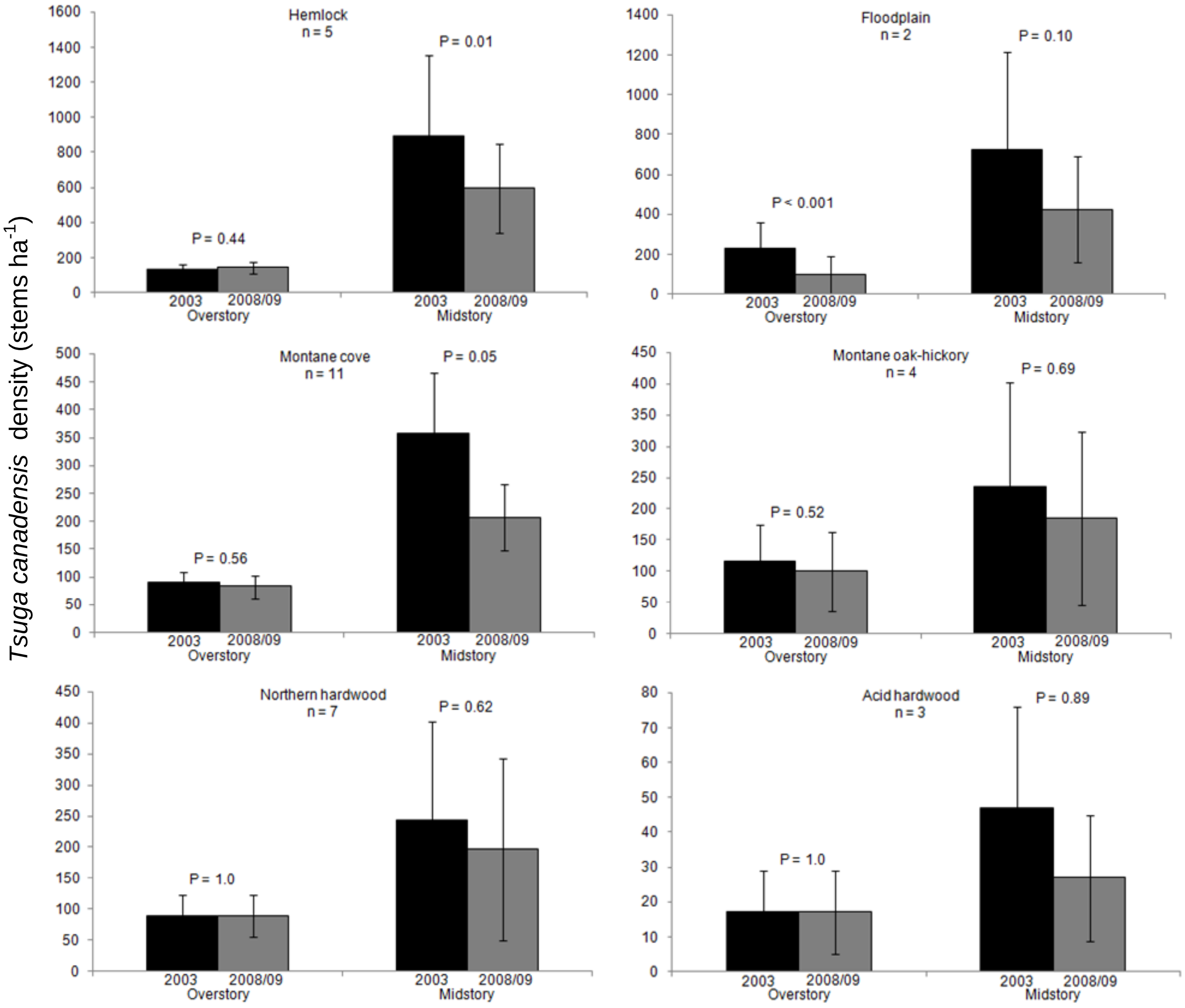

Figure 2.1.

Density (mean ± 1 SE) of Overstory and Midstory *Tsuga canadensis* in the Hemlock, Floodplain, Montane Cove, Montane Oak-Hickory, Northern Hardwood, and Acid Hardwood Ecological Groups for 2003 and 2008/09

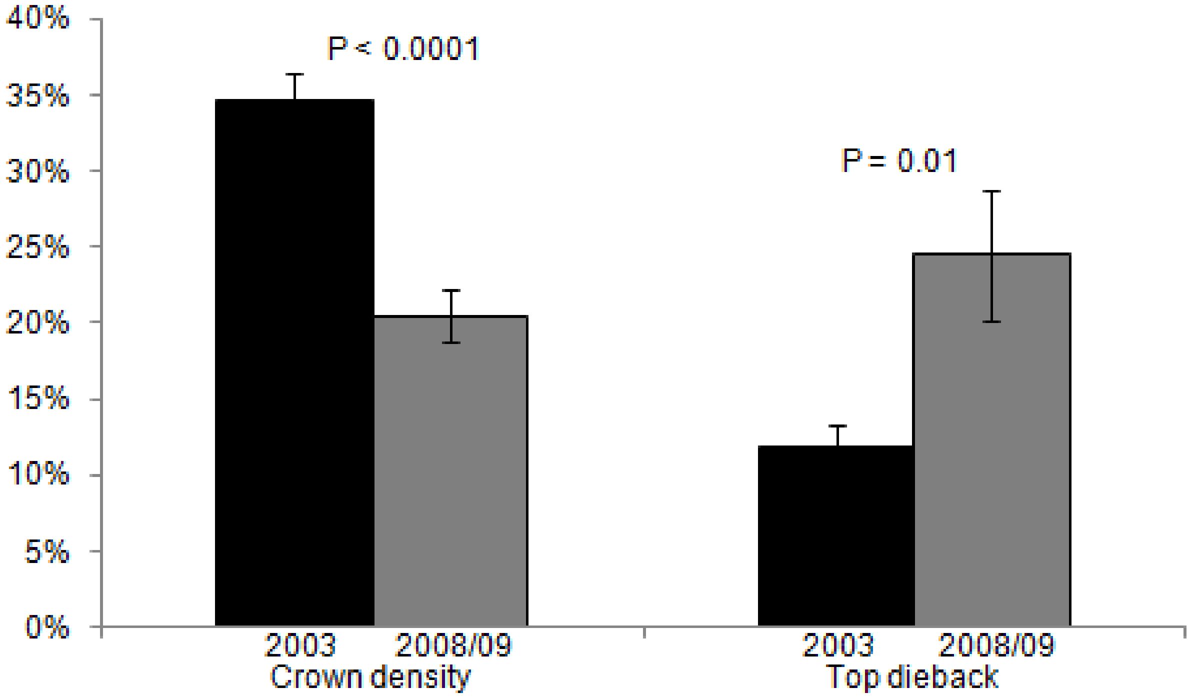

Figure 2.2.

Crown Density (Relative Density or "Fullness" of Existing Foliage) and Top Dieback (Dieback Occurring from Top of Tree Down) for Randomly Selected Overstory *Tsuga canadensis* trees in 2003 and 2008/09 across all Plots. Assessment of Stems was made according to Visual Crown Rating Protocol Developed by the USDA Forest Service (USDA Forest Service, 2007)

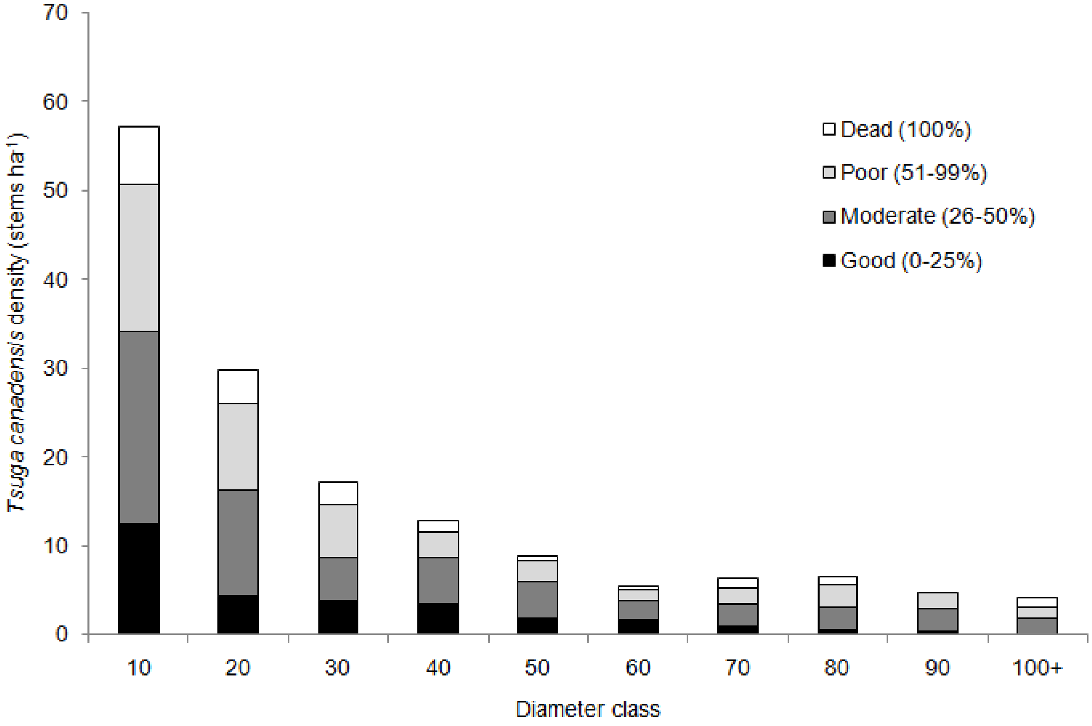

Figure 2.3.

Diameter Distribution of Overstory *Tsuga canadensis* Density in 2008/09 across all Plots by 10 cm Diameter Classes (10 cm Diameter Class included Trees from 10 -19 cm DBH, the 20 cm Diameter Class included Trees from 20 -29 cm, etc.). Within each Diameter Class, density was separated into Four Classes based on Tree Condition (Percentage of Crown Dieback): 1. Good (0-25% Dieback), 2. Moderate (26-50% Dieback), 3. Poor (51-99% Dieback), and 4. Dead

CHAPTER 3

UNDERSTORY COMPOSITION OF FIVE HEMLOCK ASSOCIATED COMMUNITIES IN GREAT SMOKY MOUNTAINS NATIONAL PARK

Introduction

Tsuga canadensis (L.) Carriere (eastern hemlock) is a shade tolerant, coniferous tree species indigenous to forests of eastern North America. This species ranges from the southern Appalachians to southern Canada and west to the central Lake States, and can be found across a wide variety of site conditions and species associations as both an overstory and/or understory species (McWilliams & Schmidt, 2000). Southern stands often occur in drainages ranging from 610 to 1520 m in elevation (Fowells, 1965), and are characterized by dense understory thickets of *Rhododendron maximum* (L.) (rosebay rhododendron) (Ellison et al., 2005). In this environment, *T. canadensis* often shares overstory dominance with a variety of broadleaf deciduous trees (MacKenzie & White, 1998; McWilliams & Schmidt, 2000), and is a common component across wide spectrum of forested communities (Jenkins, 2007). Meanwhile, *T. canadensis* stands at their northerly distribution typically occur between sea level to 730 m (Fowells, 1965), and generally support lower species richness (Ellison et al., 2005). Here, *T. canadensis* typically plays a much more dominant overstory role, and nearly pure stands are common (McWilliams & Schmidt, 2000). Regardless of distribution, *T.*

canadensis dominated stands often form dense, multi-layered canopies which cast deep shade upon the forest floor (Hadley, 2000; Rankin & Tramer, 2002), retain high levels of soil moisture (Caspersen & Kobe, 2001; Godman & Lancaster, 1990), and strongly influence soil chemistry (Elliott, Elliot, & Wyman, 1993; Rogers, 1978; Finzi, Van Breemen, & Canham, 1998). Over time, these conditions promote the development of unique localized microclimates favoring *T. canadensis* regeneration (Rogers, 1978; Hadley, 2000) and encouraging its long-term dominance in the absence of exogenous disturbance (Foster, Orwig, & McLachlan, 1996).

Tsuga canadensis populations currently face the threat of near-complete elimination from forested areas throughout eastern North America resulting from infestations of hemlock woolly adelgid (*Adelges tsugae* Annand, HWA). This exotic, invasive insect causes significant ecological and structural changes as it invades *T. canadensis* forests, and mortality often occurs within a decade of initial infestation (Eschtruth et al., 2006, Mayer et al., 1996; McClure, 1991; Small et al., 2005). Short-term impacts associated with the actions of HWA include foliar defoliation, loss of vitality, and death of infested individuals (Stadler et al., 2005); consequentially triggering long-term changes in species composition and a loss of the unique structure and microclimatic conditions associated with *T. canadensis* forest types (Lovett et al., 2006). Large reductions in forest productivity and substantial defoliation creates gaps in previously closed canopy forests which allow increased amounts of direct sunlight to reach the forest floor, often impacting species composition (Jenkins et al., 1999; Eschtruth et al., 2006; Orwig & Foster, 1998).

While the overstory community composition of hemlock associated forest types has been well documented (Eschtruth et al., 2006; Jenkins, 1999; Jenkins, 2007; McWilliams & Schmidt, 2000; Orwig & Foster, 1998; Orwig et al., 2002; Small et al., 2005; Weckel et al., 2006; White et al., 2003), understory community composition of these forest types are not as well understood. Furthermore, it is unclear how the recent invasions of HWA will influence understory community composition in the southern Appalachian Mountains. By resampling a series of permanent vegetative plots across a gradient of *T. canadensis* associated communities in southern Appalachia, we attempt to fill this gap in knowledge. Specific objectives of this paper are to (1) determine the understory community composition of *T. canadensis* associated forests in the southern Appalachians, (2) explore how site characteristics influence understory community composition in the southern Appalachian Mountains, and (3) determine if understory community composition has changed in *T. canadensis* forests following five to six years of HWA infestation.

Methods

Study Area

Great Smoky Mountains National Park, a world renowned center for biodiversity and the most heavily visited national park in the United States, supports some of the richest and most diverse assemblages of plants and animals in North America (Cain, 1930; Jenkins, 2007; Whittaker, 1956). Much of the Park's diversity can be attributed to its mountainous terrain, which forms the state line between east Tennessee and North Carolina. The landscape is characterized by a long, nearly-continuous ridge, from which varying secondary ridges branch (Whittaker, 1956) to form twenty-seven distinct watersheds throughout the park. Parent material consists primarily of metamorphic sandstone, quartzites, and slates, although small pockets of exposed limestone do occur (Jenkins, 2007; Southworth, Shultz, & Denenny, 2005; Whittaker, 1956). Vegetative plots in this study had a wide range of site conditions (Table 1). Elevation ranged from 940 to 1278 m, and plots were located across several slope aspects. Slopes were often steep, and averages ranged from approximately 40 to 60%. Soil pH was somewhat variable, ranging between 4.4 to 5.2. Cation exchange capacity ranged from 1.6 to 5.9 meq/100g, and was lowest in the montane oak-hickory ecogroup.

Vegetation Sampling

In the summer of 2003, twenty-nine permanent vegetative plots were established across a variety of ecological groupings (hereafter ecogroups) within Great Smoky Mountains National Park (GSMNP). Plots were sampled in accordance with GSMNP Vegetation Monitoring Protocol (Jenkins, 2008). At the time of initial sampling, total *T. canadensis* relative density ranged from 32 to 5% across ecogroups (Table 1). Each site consisted of a 0.1 ha (20 X 50 m) plot, divided into ten 10 m^2 modules. In four adjacent modules (intensive sampling modules), we identified presence and estimated vegetative ground cover for all species < 0.5 m in height (herbs, shrubs, trees, ferns, bryophytes, and lichens) using a modified Daubenmire scale (1 = Few; 2 = Few-1%; 3 = 1-2%; 4 = 2-5%; 5 = 5-10%; 6 = 10-25%; 7 = 25-50%; 8 = 50-75%; 9 = 75-95%; 10 = 95-100%) (Daubenmire, 1959; Peet, Wentworth, & White, 1998). To determine seedling density, all woody stems <1.4 m in height were tallied by species in 3.2 X 3.2 m subplots nested inside the four intensive sampling modules. Species occurring on the 0.1 ha plot, but not within intensive sampling modules, were assigned a cover value of 0.06% (one-half of the lowest coverage possible from averaged intensive sampling quadrants), to allow their inclusion in quantitative data analysis (Jenkins & Parker, 2000). Soil samples were collected along the center transect of each plot, and analyzed for chemical properties (cation exchange capacity (CEC), pH, and cation saturation of potassium (K), calcium (Ca), and magnesium (Mg)) by A & L Analytical Laboratories, Inc., located in Memphis, TN. Plots were resampled in the summers of 2008 and 2009 to determine changes in species composition over time and across ecogroupings. Leaf area index (one sided green leaf area per unit ground area, LAI) was measured in the 2008/2009 field season using hemispherical photography, and WinSCANOPY® was utilized to edit and analyze photographs.

Statistical Analyses

Coverage was averaged among the four intensive sampling modules at each plot to provide mean values per plot. To test for differences in *T. canadensis* seedling densities across groups and between sampling intervals, we used two-way repeated measures ANOVA (SAS, 2004). Associations between strata (coverages versus seedling densities) and across sampling intervals (2003 to 2008/09) were assessed utilizing Mantel tests in PC-ORD 5.1. This procedure evaluates associations between two independent dissimilarity matrices describing the same entities, and tests if associations are greater than would be expected by chance using 1000 Monte Carlo randomizations (Sokal & Rohlf, 1995). Species richness, evenness, and Shannon's diversity index were calculated utilizing PC-ORD 5.1, and were also analyzed with ANOVA (SAS, 2004).

We utilized non-metric multidimensional scaling (NMS) analysis in PC-ORD 5.1 to illustrate differences in species composition within and among ecogroups. For this analysis, a matrix of site variables (aspect, elevation, LAI, slope, CEC, pH, K, Ca, and Mg; Table 1) was created to evaluate the impacts of these variables upon understory community composition, and differences were explored with the bi-plot function. Pearson's correlation coefficient test (SAS, 2004) determined cation saturations of Ca and Mg were significantly correlated with CEC, therefore, these variables were not used in the NMS analysis. Multi-response permutation procedures (MRPP) were utilized to test for differences in species composition between ecogroups, and validated illustrated differences between groups shown in the NMS ordination. MRPP tests for variations using a null hypothesis of no difference between groups, without requiring assumptions of a normally distributed dataset (McCune & Grace, 2002). Indicator species analysis was utilized to describe the explanatory power of each species in predicting environmental conditions indicative to particular ecogroups. This analysis measures the degree to which each species separates among groups using information on species concentration and faithfulness of occurrence (McCune & Grace, 2002).

To reduce variation in the dataset, we deleted species with fewer than three occurrences, and quantitative variables were relativized by maximum prior to analysis (D' Amato, Orwig, & Foster, 2009; McCune & Grace, 2002). Sørensen distances were used when conducting NMS, MRPP, and Mantel tests (McCune & Grace, 2002), and aspect values were transformed (aspect = cosine (45-azimuth degrees) + 1) prior to analysis (Beers et al., 1966). We used the "slow and thorough" setting with autopilot mode when contemplating optimum dimensionality of NMS ordinations. Autopilot mode assists the user in selecting appropriate dimensionality of a dataset by gradually stepping down from the greatest number of axes to one, assessing solutions based upon lowest stress levels, and testing these solutions with subsequent Monte Carlo tests (McCune & Grace, 2002). The ordination was rigidly rotated to place CEC (the variable explaining the greatest amount of variation), on Axis 1. Significance for the bi-plot analysis was set at the default $r = 0.20$, all other analyses used a significance level of $P = 0.05$.

Results

Vegetative community composition did not significantly change from 2003 to 2008/09 (Mantel test, $r = 0.82$, $P < 0.001$). Similarly, vegetative ground cover and seedling density were positively correlated (Mantel test, $r = 0.31$, $P = 0.001$), indicating that established seedlings likely emerged from understory communities similar to those currently on site. For this reason, we present species composition of ecogroups in the 2008/09 measurement only.

Understory Composition and Diversity

In 2008/09, we observed a total of 77 herbs, 32 shrubs, 43 trees, and 12 species of ferns across all sampled plots, and average coverage ranged from 4 to over 13% (Table 2). MRPP analysis across forest types determined that the composition of plots we sampled significantly differed between ecogroups ($P = 0.05$). However, the small effect size ($A = 0.01$) calculated from the MRPP suggests vegetative composition was variable within ecogroups. These differences were noticeable in the ordination, which explained 62.4% of the variation in understory composition (final stress = 15.23, final instability < 0.00001; Figure 1). The majority of observed variation was explained in Axis 1 (46.5%). This axis was primarily representative of soil conditions, and progressed from soils with high K to those of increasing CEC and pH. Axis 2 explained 15.9% of the variation in our dataset, and was primarily representative of elevation. Despite subtle differences, understory coverage ($P = 0.28$), richness ($P = 0.09$), evenness ($P = 0.58$), and diversity ($P = 0.22$) was similar across ecogroups (Table 2).

Averaging over fifty species per plot, the hemlock ecogroup supported some of the richest and most diverse understory communities sampled (Table 3). These plots were often located in northerly facing ravines ranging from approximately 780 to 1080 m in elevation. Here, dominance was shared by *R. maximum* and *Pyrularia pubera* (Michx.) (buffalo nut). However, several shrub and tree species including *Acer rubrum* (L.) (red maple) and *A. pensylvanicum* (L.) (striped maple), *Betula lenta* (L.) (black birch), *Halesia tetraptera* (Ellis) (mountain silverbell), *Rubus spp.* (L.) (blackberry), and *Smilax rotundifolia* (L.) (roundleaf greenbrier) were also common. Two species of ferns: *Dryopteris intermedia* (Muhl. ex Willd.) (intermediate woodfern) and *Polystichum acrostichoides* (Michx.) Schott (Christmas fern) often regenerated in high densities, although their distribution was patchy. A wide variety of herbs were associated with this ecogroup, the most common being *Viola spp.* (L.) (violet), *Mitchella repens* (L.) (partridgeberry), *Medeola virginiana* (L.) (Indian cucumber), and *M. canadense*. *Tsuga canadensis* was not especially common in understory conditions associated with the hemlock forest type.

In the montane cove ecogroup, which occurred on northerly facing sites between 716 to 1052 m, herbaceous layers were often characterized by high abundances of *M. canadense* and *Viola rotundifolia* (Michx.) (roundleaf yellow violet). *Dryopteris intermedia* was the dominant fern in these environments, although *P. acrostichoides* was also common. Despite high coverages of *R. maximum, Gaylussacia ursina* (M.A. Curtis) Torr. and A. Gray ex A. Gray (bear huckleberry) and *S. rotundifolia* were locally abundant. *Acer rubrum* and *B. lenta* were often common tree species in these understory communities.

Plots of the montane oak-hickory ecogroup were generally located on eastern facing slopes between 760 to 1100 m in elevation. In this ecogroup, no one herbaceous species was especially prevalent, but dominance was shared by multiple species including *M. repens, M. virginiana, Galax spp.* (Sims) (galax)*, M. canadense,* and *Gaultheria procumbens* (L.) (eastern teaberry)*.* Common shrubs consisted of *R. maximum, Leucothoe fontanesiana* (Steud.) Sleumer (doghobble)*,* and *P. pubera,* although *S. rotundifolia* and *Kalmia latifolia* (L.) (mountain laurel) were also present. As was the case with many of the other ecogroups, *A. rubrum* and *B. lenta* were dominant understory components, however, *A. pensylvanicum, H. tetraptera,* and *T. canadensis* also regenerated well in these communities.

With the exception of *Galax spp.* and to a lesser extent *Goodyera pubescens* (Willd.) R. Br. (downy rattlesnake plantain)*,* herbaceous species were somewhat sparse in acid hardwood communities. This could have been due to the high bryophyte coverage and rocky soils observed in these plots. Instead, shrubs such as *K. latifolia, S. rotundifolia,* and *R. maximum* were especially prevalent. *Acer rubrum* and *A. pensylvanicum* were some of the most common tree species found in these understories, and *D. intermedia* was the dominant fern. These plots were located on southern facing slopes between approximately 1000 to 1500 m in elevation.

The final grouping was northern hardwood communities, which were generally found on northwesterly facing aspects between 1140 to 1430 m. *Mitchella repens, M. virginiana,* and *Viola spp.* were the dominant herbs of this group. A club moss, *Huperzia lucidula* (Michx.) Trevis. (shining club moss), was also present at high densities in these environments. The fern *D. intermedia* regenerated well below dense *R. maximum* subcanopies of these associations. *Halesia tetraptera* and *Fagus grandifolia* (Ehrh.) (American beech) were by far the most common tree species, and *T. canadensis* did not regenerate in northern hardwood understories.

Tree Seedlings

Average seedling densities ranged from 21250 to 42350 seedlings ha^{-1} across all sampled plots (Table 4). *Tsuga canadensis* advanced regeneration was most pronounced in the montane oak-hickory ecogroup, followed by the hemlock and montane cove groups. However, *T. canadensis* was not a dominant seedling in any of the ecogroups sampled, and its regeneration was not present in the acid hardwood or northern hardwood ecogroups. Two-way ANOVA determined the density of *T. canadensis* seedlings did not significantly differ over the sampling interval ($P = 0.46$), or across ecogroups ($P = 0.21$; Table 5). Furthermore, a lack of an interaction effect between ecogroup and sampling interval ($P = 0.06$) indicated *T. canadensis* density did not vary among forest types. *R. maximum* had the greatest seedling densities in all ecogroups except hemlock, where *B. lenta* was the dominant species (Table 4).

Indicator Species Analysis

Indicator value analysis identified a total of fifteen indicator species across four of the five ecogroups (Table 6). Significant indicators consisted of three herbaceous, three shrub, one vine, and eight tree species. Of these, five were identified as indicators of the hemlock ecogroup, and included: *Dioscorea villosa* (L.) (wild yam)*, Euonymus americanus* (L.) (bursting heart)*, Toxicodendron radicans* (L.) Kuntze (eastern poison ivy)*, Carya glabra* (Mill.) Sweet (pignut hickory)*,* and *Quercus alba* (L.) (white oak). Eight species were indicative of the montane oak-hickory ecogroup: *Epigaea repens* (L.) (trailing arbutus)*, Monotropa uniflora* (L.) (Indian pipe)*, G. procumbens, Vaccinium pallidum* (Aiton) (blue ridge blueberry)*, Oxydendrum arboreum* (L.) DC. (sourwood)*, Pinus strobus* (L.) (eastern white pine)*, Sassafras albidum* (Nutt.) Nees (sassafras), and *T. canadensis.* Furthermore, *Acer spicatum* (Lam.) (mountain maple) was an indicator of northern hardwood forests, and *Picea rubens* (Sarg.) (red spruce) was indicative of acid hardwood forests.

Discussion

Changes Over Time

Despite increasing evidence that overstory composition in *T. canadensis* forests is changing following HWA infestation in the southern Appalachian Mountains (Krapfl, Holzmueller, & Jenkins, 2010; Nuckolls et al., 2008), few studies have specifically investigated how herbaceous and regenerative layers in this region are impacted by this exotic invader. Our results suggest that understory composition has not been significantly altered following five to six years of HWA infestation within GSMNP. These findings were unexpected, considering previous studies throughout the northeast have noted increased abundances of understory *A.rubrum, B. lenta* and *B. alleghaniensis* (Britton) (yellow birch)*, F. grandifolia, Lirodendron tulipifera* (L.) tuliptree*, Magnolia fraseri* (Walter) (mountain magnolia)*, Nyssa sylvatica* (Marsh.) (blackgum)*, Prunus serotina* (Ehrh.) (black cherry)*, Quercus spp.* (L.) (oak)*,* and *S. albidum* in conjunction with *T. canadensis* mortality (Eschtruth et al., 2006; Orwig & Foster, 1998; Small et al., 2005; Stadler et al., 2005). However, these studies monitored *T. canadensis* decline over longer timescales than our study. Thus, a relatively brief observational period (five to six years) may partially explain the lack of species response in this study.

However, *T. canadensis* forests in this region are vastly different from those found at northern latitudes, and therefore, regeneration patterns could differ. For example, many of the plots we sampled had understories dominated by *R. maximum,* an ericaceous shrub uniquely characteristic of Appalachian *T. canadensis* forests (Krapfl et al., 2010). This species tends to form dense thickets and its spreading foliage intercepts the majority of direct sunlight passing through the overstory strata, often influencing regenerative patterns (Nilsen et al., 1999; Phillips & Murdy, 1985; Van Lear et al., 2002). In the northeastern United States, the development of overstory gaps caused by HWA induced defoliation typically results in increased levels of solar radiation, which trigger pulses in understory vegetative productivity (Eschtruth et al., 2006; Jenkins et al., 1999). Based upon the overstory *T. canadensis* decline documented in a companion study (Krapfl et al., 2010), it was surprising that understory coverage and seedling densities didn't change over time. Direct comparisons between understory light availabilities following infestation could not be made, as LAI was not sampled in 2003, however, we were able to test for differences in light availabilities between ecogroups, and found that LAI did not differ by type. While our data do not entirely support the hypothesis that the presence of *R. maximum* inhibits tree regeneration, seedling densities of *R. maximum,* which varied from 4400 to over 10000 stems ha, were likely dense enough to have an impact on understory light availabilities. We suggest *R. maximum* may be creating a unique situation in which overstory gaps are forming, yet dense understory vegetation restricts increased light levels from reaching the forest floor. For this reason, understory vegetation in the southern Appalachians may not be as highly responsive to overstory gap formation as forests of the northeastern United States.

Composition of Ecogroups

The majority of the observed compositional variation in this study was attributed to physical and chemical properties of underlying soils, as well as elevation (Figure 1). This was expected, as past efforts to categorize plant communities throughout GSMNP have recognized the importance of such variables (Cain, 1930; Calloway, Clebsch, & White, 1987; Harmon, Bratton, & White, 2004; Kincaid, 2007; Kincaid, 2008; MacKenzie & White, 1998; Whittaker, 1956). Interestingly, the original NatureServe classifications utilized to define the groups were based almost entirely upon surveys of terrestrial vegetation, rather than soil conditions or landscape features (White et al., 2003). The direct link between existing vegetation and site variables observed in this study provides evidence that community composition is at least partially driven by edaphic variables in GSMNP.

Cation Exchange Capacity is a measure of the total amount of negatively charged exchange sites available to attract positively charged ions in the soil solution (Tisdale, Nelson, Beaton, & Havlin, 1993). This variable explained the largest amount of variation between ecogroups. CEC, which is primarily driven by clay content and type, % organic matter, underlying parent material, and soil pH (Brady & Well, 2002), gives an indication of the soils capacity to hold nutrients. High CEC generally provides greater nutrition for vegetation than sites with low CEC, and therefore, species with greater nutrient demands are typically found on these soils. The similar trajectories of soil pH and CEC in the ordination, and their nearly inverse relationship with K saturation, provided further evidence of how these soil properties impact vegetative composition. Our findings are in agreement with those of Golden (1981), which cited soil pH and clay content as primary factors influencing the composition of forests in GSMNP. In this study, montane oak-hickory forests were exclusively found on soils with low CEC, low pH, and high K saturations. Hemlock, montane cove, and acid hardwood ecogroups demonstrated considerably greater variation across soil conditions. Northern hardwood forests were consistently found on sites with high CEC and soil pH, although they were found across varying K saturations.

Previous research has demonstrated the strong influence elevation can have upon community composition (Callaway et al., 1986; Golden, 1981; Whittaker, 1956). For this reason, we expected community composition to vary with elevation. Indeed, results of the bi-plot analysis identified this variable as a leading contributor to the occurrence of ecogroups in this study. This was not entirely surprising, as this variable in itself can manipulate a suite of environmental conditions including temperature, precipitation, topographic exposure, and soil moisture content (Harmon et al., 2004). In our study, hemlock and montane oak-hickory forests were typically found at the lowest elevations. Midslopes were dominated by montane cove forests with northern hardwood, acid hardwood, and hemlock forests interspersed throughout. Northern hardwood and acid hardwood plots had considerably wider distribution compared other ecogroups, suggesting that site conditions for these groups are less exacting than those of hemlock and montane oak-hickory forests. Although montane cove forests were widely distributed, this ecogroup appears to be driven more by soil properties than elevation.

Conclusions

We found that five to six years of HWA infestation has not significantly altered understory composition in *T. canadensis* associated communities of GSMNP. These results were unanticipated, since preceding findings utilizing data collected on the same plots indicated that the majority of overstory *T. canadensis* trees have experienced decline. Despite the formation of small overstory gaps caused by defoliation, our results indicate that understory species composition has not yet changed. This is probably due to the overwhelming presence of *R. maximum,* an ericaceous shrub which often forms dense understory thickets and intercepts light otherwise reaching the forest floor.

However, this lack of understory response has provided us with an excellent opportunity to examine understory communities prior to predicted alterations caused by *T. canadensis* mortality. Community composition significantly varied between ecogroups, and differences were greatly attributed to soil properties, as well as elevation. Understory composition in montane oak-hickory forests was the least variable, and species such as *E. repens, M. uniflora, G. procumbens, V. pallidum, O. arborescens, P. strobus, S. albidum*, and *T. canadensis* were indicators of these communities. Hemlock communities were found at low to mid elevations, and were characterized by the presence of *Dioscorea spp., E. americana, T. radicans, C. glabra,* and *Q. alba.* Soil properties were not exacting in montane cove forests, and species composition was highly variable. Northern hardwood and acid hardwood plots were found at mid to high elevations. *Acer spicatum* was consistently found in northern hardwood forests, and acid hardwood forests often contained *P. rubens.*

Table 3.1.

Site Conditions of Tsuga canadensis associated Ecogroups Sampled throughout GSMNP

Variable	Description	Hemlock	Montane cove	Montane oak-hickory	Acid hardwood	Northern hardwood
T. canadensis	Overstory relative density	32 (9)	22 (4)	23 (12)	5 (2)	27 (9)
Aspect	Range of aspects	60 - 280°	50 - 325°	45 - 145°	70 - 280°	260 - 360°
Elevation	Plot elevation (m)	942 (49)	940 (32)	960 (77)	1275 (138)	1278 (41)
LAI	Leaf area index (0 to 6)	2.8 (0.3)	2.9 (0.2)	2.2 (0.3)	2.8 (0.4)	2.6 (0.2)
Slope	Local slope angle (%)	40.3 (10.1)	43.6 (6.5)	57.5 (6.3)	57.5 (10.2)	50.0 (8.8)
pH	pH of topsoil	5.2 (0.3)	4.9 (0.2)	4.9 (0.2)	5.1 (0.4)	4.4 (0.2)
K	Cation saturation (%) K	7.2 (0.9)	6.3 (0.8)	8.8 (1.3)	3.7 (1.3)	2.8 (0.4)
Ca	Cation saturation (%) Ca	38.4 (6.1)	36.1 (5.6)	31.6 (5.9)	42.8 (12.5)	25.3 (5.1)
Mg	Cation saturation (%) Mg	15.0 (2.3)	12.4 (1.4)	13.8 (1.2)	10.1 (0.5)	7.5 (1.8)
CEC	Cation exchange capacity (meq/100g)	4.2 (1.8)	3.3 (1.0)	1.6 (0.2)	5.9 (2.0)	4.9 (0.7)

Table 3.2.

Understory Coverage, Richness, Evenness, and Diversity of Understory Vegetation in 2008/09 by Ecogroup

	Hemlock	Montane cove	Montane oak-hickory	Acid hardwood	Northern hardwood
Understory cover (%)	13.20 (0.65)	8.09 (1.87)	9.85 (1.60)	6.60 (1.70)	8.00 (2.09)
Richness (S)	50.80 (2.82)	32.60 (5.36)	40.00 (4.38)	27.67 (3.93)	30.14 (5.74)
Evenness (E)	0.92 (0.02)	0.87 (0.02)	0.90 (0.01)	0.89 (0.02)	0.89 (0.02)
Diversity (H’)	3.59 (0.04)	2.93 (0.22)	3.31 (0.10)	2.93 (0.20)	2.91 (0.27)

Table 3.3.

Coverage of Understory Herbs, Ferns, Shrubs, Trees, Bryophytes and Lichens in 2008/09. All Species shown have ≥ 1% Coverage across all Plots, and represent 70% of Total Coverage

Species	Hemlock	Montane cove	Montane oak-hickory	Acid hardwood	Northern hardwood
Herbs					
Galax spp.	1.0 (0.6)	1.1 (0.8)	1.4 (1.2)	4.1 (2.3)	0.1 (0.1)
Gaultheria procumbens	0.0 (0.0)	0.0 (0.0)	1.2 (7.1)	0.0 (0.0)	0.0 (0.0)
Maianthemum canadense	0.6 (0.3)	3.5 (2.9)	1.3 (0.0)	0.0 (0.0)	0.1 (0.1)
Medeola virginiana	1.6 (0.7)	1.2 (0.4)	1.5 (0.8)	0.6 (0.3)	1.8 (1.1)
Mitchella repens	1.8 (0.5)	1.8 (0.7)	2.0 (1.9)	0.0 (0.0)	3.2 (1.5)
Viola rotundifolia	0.0 (0.0)	3.9 (3.0)	1.6 (0.0)	0.7 (0.7)	0.6 (0.6)
Viola spp.	2.1 (0.8)	0.7 (0.3)	1.0 (0.6)	0.1 (0.1)	1.3 (0.8)
Ferns					
Dryopteris intermedia	2.4 (0.5)	2.1 (0.8)	2.4 (0.2)	1.7 (0.9)	4.1 (2.1)
Polystichum acrostichoides	2.4 (0.5)	1.6 (0.6)	1.4 (0.5)	1.0 (1.0)	0.8 (0.6)
Shrubs					
Gaylussacia ursina	0.5 (0.5)	2.6 (2.0)	1.4 (3.0)	0.0 (0.0)	0.0 (0.0)
Kalmia latifolia	0.9 (0.6)	1.2 (0.6)	1.2 (1.0)	2.9 (1.5)	0.0 (0.0)
Leucothoe fontanesiana	0.0 (0.0)	1.2 (5.5)	3.1 (5.1)	0.4 (0.4)	0.0 (0.0)
Pyrularia pubera	7.0 (4.7)	1.1 (0.4)	2.1 (2.3)	1.4 (1.4)	0.2 (0.2)
Rhododendron maximum	11.9 (8.5)	25.3 (7.1)	23.2 (4.3)	28.9 (22.5)	40.0 (17.0)
Rubus spp.	2.7 (2.1)	1.6 (0.3)	1.2 (0.2)	0.8 (0.4)	1.9 (1.0)
Smilax rotundifolia	1.9 (0.8)	2.3 (1.0)	1.9 (0.6)	1.9 (1.2)	1.1 (0.7)
Trees					
Acer pensylvanicum	1.8 (0.6)	1.1 (0.6)	1.4 (0.8)	1.9 (1.0)	0.9 (0.5)
Acer rubrum	2.2 (0.6)	2.6 (0.8)	2.4 (1.0)	2.0 (1.0)	1.2 (0.6)
Betula lenta	2.1 (0.4)	2.1 (0.9)	1.5 (0.3)	0.5 (0.5)	1.1 (0.6)
Fagus grandifolia	0.4 (0.3)	0.8 (0.4)	1.0 (0.2)	0.0 (0.0)	2.4 (1.1)
Halesia tetraptera	1.5 (0.6)	0.6 (0.4)	1.3 (0.7)	0.0 (0.0)	2.9 (1.4)
Tsuga canadensis	0.4 (0.2)	1.0 (0.5)	1.0 (0.8)	0.5 (0.4)	0.0 (0.0)
Other					
Bryophytes	7.1 (3.8)	12.0 (3.4)	10.0 (1.2)	25.7 (9.8)	4.3 (1.1)
Lichens	2.8 (0.4)	4.0 (0.7)	3.5 (1.0)	2.7 (1.1)	3.3 (1.2)

Table 3.4.

Seedling Densities of Select Species by Ecogroup in 2008/09

	Hemlock	Montane cove	Montane oak-hickory	Acid hardwood	Northern hardwood
Average seedlings ha^{-1}	42350 (15567)	33200 (5250)	39188 (1126)	21250 (2155)	29179 (5477)
Acer rubrum	6250 (3649)	3125 (1492)	3000 (1882)	1417 (741)	2107 (1244)
Betula lenta	11150 (7227)	1475 (675)	1188 (688)	500 (289)	2750 (1244)
Liriodendron tulipifera	750 (418)	125 (85)	1750 (1750)	0 (0)	0 (0)
Quercus rubra	500 (387)	200 (148)	63 (63)	0 (0)	36 (36)
Rhododendron maximum	4400 (1470)	8650 (2022)	5813 (2684)	6417 (3809)	10286 (3316)
Tsuga canadensis	450 (215)	300 (153)	1000 (677)	0 (0)	0 (0)

Table 3.5.

Two-Way Repeated Measures Analysis of Variance for Forest Type Differences in Tsuga canadensis Seedling Density in 2003 and 2008/09

		Seedling density	
Source of Variation	df	MS	P > F
Forest type	4	62783828.51	0.21
Error (Forest type)	24	39122953.87	
Interval	1	14453254.48	0.46
Forest type X interval	4	67029518.17	0.06
Error	24	25268787.20	

MS = Mean squares.

Table 3.6.

Significant Indicator Values (Percentage of Perfect Indication) for Understory Vegetation (Herbaceous, Shrub, Vine, and Tree Species) by Ecogroup in 2008/09. P –Value Represents the Proportion of Randomized Trials with an Indicator Value Equal to or Exceeding the Observed Indicator Value

Species	Species Type	Indicator group	Indicator value	P-value
Dioscorea spp.	Herbaceous	Hemlock	64	0.004
Epigaea repens	Herbaceous	Montane oak-hickory	43	0.03
Montropa uniflora	Herbaceous	Montane oak-hickory	50	0.02
Euonymus americana	Shrub	Hemlock	53	0.02
Gaultheria procumbens	Shrub	Montane oak-hickory	50	0.02
Vaccinium pallidum	Shrub	Montane oak-hickory	50	0.03
Toxicodendron radicans	Vine	Hemlock	47	0.03
Acer spicatum	Tree	Northern hardwood	49	0.02
Carya glabra	Tree	Hemlock	48	0.03
Oxydendrum arboreum	Tree	Montane oak-hickory	80	0.001
Picea rubens	Tree	Acid hardwood	58	0.01
Pinus strobus	Tree	Montane oak-hickory	47	0.03
Quercus alba	Tree	Hemlock	40	0.05
Sassafras albidum	Tree	Montane oak-hickory	67	0.005
Tsuga canadensis	Tree	Montane oak-hickory	64	0.001

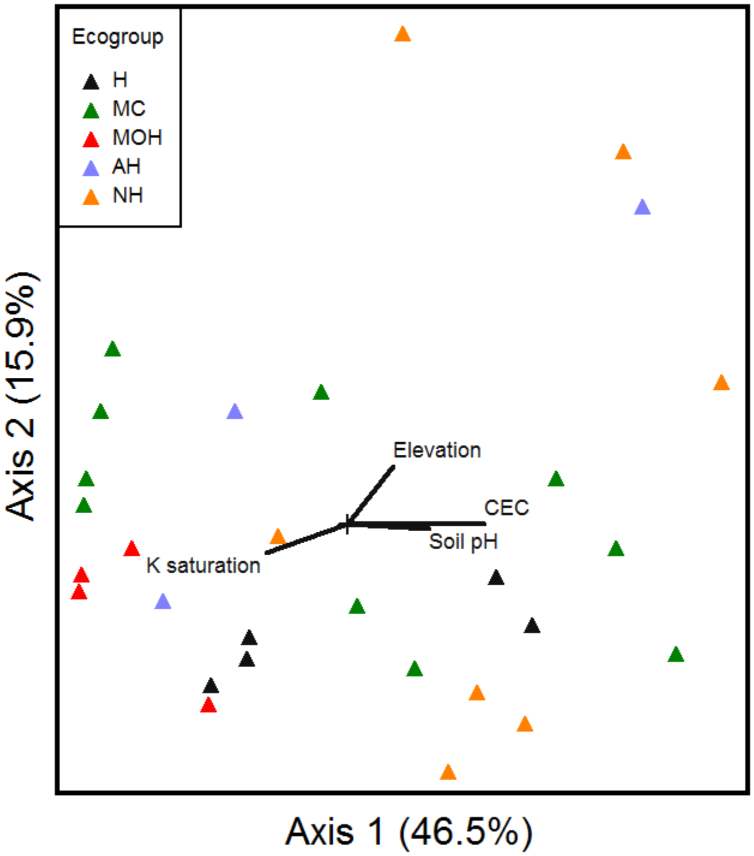

Figure 3.1.

Non-Metric Multidimensional Scaling Ordination of Understory Vegetation occurring in 2008/09 Census. Points are Color-Coded and Abbreviated by Ecogroup (H = Hemlock, MC = Montane Cove, MOH = Montane Oak-Hickory, AH = Acid Hardwood, NH = Northern Hardwood). Vector Length represents Explanatory Power of each Variable, and Presence Indicates Significance (r = 0.20). Ordination was Rigidly Rotated to place Cation Exchange Capacity (CEC, the Variable explaining greatest amount of Variation) Parallel to Axis 1

CHAPTER 4

SUMMARY AND CONCLUSION

This research project examined how *Tsuga canadensis* populations in Great Smoky Mountains National Park have been affected by recent invasions of an exotic, invasive insect known as hemlock woolly adelgid. Our study, which monitored the forest composition and health of *T. canadensis* stands over a five to six year interval, offers a rare glimpse into how *T. canadensis* associated communities are responding to HWA infestation in the southern Appalachian Mountains. Specific objectives of this project were to (1) determine how *T. canadensis* populations have changed in conjunction with HWA infestation in GSMNP, and to (2) document how HWA has affected vegetative community dynamics in GSMNP. Below, we briefly discuss the findings of two interrelated studies designed to form a better understanding of how HWA is influencing *T. canadensis* associated communities in GSMNP.

In Chapter 2, we examined the effects of HWA upon overstory and midstory forest ecosystems with *T. canadensis* associated affinities. We hypothesized that (1) short-term mortality rates will be greater in the southern Appalachians than in the northern range of *T. canadensis* due to lower winter temperature extremes, (2) mortality will be greater in the midstory compared to the overstory because of the reduced energy reserves of suppressed individuals, (3) decline and mortality will vary with site conditions, and (4) mortality of *T. canadensis* will result in variable changes in community composition across the wide range of forest types in which the species occurs. Our results indicate that *T. canadensis* trees are experiencing mortality, however, these rates do not appear to be exceeding those found throughout the mid-Atlantic and New England regions. We observed no individual site or stand condition predisposes any given site to HWA infestation. While the majority of overstory *T. canadensis* trees on our plots were still living, they were in a state of severe decline induced by HWA-associated defoliation, and midstory *T. canadensis* trees are experiencing greater mortality rates than those in the overstory.

In Chapter 3, we investigated how understory composition has responded to HWA infestation. Specifically, this study was developed to (1) determine the understory community composition of *T. canadensis* associated forests in the southern Appalachians, (2) determine if understory community composition has changed in *T. canadensis* forests following five to six years of HWA infestation, and (3) explore how site characteristics influence understory community composition in the southern Appalachian Mountains. We found that five to six years of HWA infestation has not significantly altered understory composition in *T. canadensis* associated communities of GSMNP. These results were unanticipated, since the majority of overstory *T. canadensis* trees had experienced decline. Despite the formation of small overstory gaps caused by defoliation, our results indicate that understory species composition has not yet changed. However, this lack of understory response provided us with an excellent opportunity to examine understory communities prior to predicted alterations caused by *T. canadensis* mortality. Community composition significantly varied between ecogroups, and differences were attributed to soil properties, as well as elevation. Results of this study suggest that presently, understory composition is still largely characteristic of pre-adelgid conditions.

Our results demonstrate that infestations of HWA have had an impact upon *T. canadensis* populations in GSMNP. We observed significant decreases in overstory *T. canadensis* densities and health from 2003 to 2008/09, coupled with significant losses of *T. canadensis* advanced regeneration. Despite losses in *T. canadensis* density across a wide range of ecogroups, community composition was not significantly impacted over the observational period, and further studies are needed to determine species response to *T. canadensis* mortality throughout this region. However, the overwhelming presence of *R. maximum* in high densities suggests this species may define future successional patterns throughout the southern Appalachian Mountains. Overall, our findings suggest that without the implementation of effective control measures of HWA, *T. canadensis* may largely disappear from southern Appalachian forests.

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