VEGETATION DYNAMICS OF A CAROLINA HEMLOCK COMMUNITY AT BLUFF MOUNTAIN, NORTH CAROLINA, USA

A Thesis
by
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ABSTRACT

VEGETATION DYNAMICS OF A CAROLINA HEMLOCK COMMUNITY AT BLUFF MOUNTAIN, NORTH CAROLINA, USA

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The goal of this thesis was to examine the Carolina hemlock (*Tsuga caroliniana* Engelm.) forest at the early onset of hemlock woolly adelgid (*Adelges tsugae* Annand) infestation to establish baseline data used to measure anticipated changes in Carolina hemlock forest dynamics. I quantified the composition and structure of the Carolina hemlock forest overstory and understory, as well as collected increment cores from all trees within five 0.05 ha plots located in Carolina hemlock dominated stands. Based on basal area and canopy class, Carolina hemlock was the most dominant species in the understory and overstory. The diameter distribution and density of seedlings and saplings indicated that Carolina hemlock is successfully and continuously regenerating. The stand had several characteristics indicative of old-growth status with gap-phase dynamics.

I used dendroecological techniques to quantify the frequency and spatial distribution of canopy disturbances during the period of AD 1870-2000, examined climate-growth relationships, and determined if there was an age-related difference

in the climate-growth relationship. There were no stand-wide disturbance events, only gap-phase dynamics. Analysis of the climate-growth relationships indicated that older Carolina hemlocks prefer cool, moist summers. There were age-related differences in climate response as younger Carolina hemlock were less responsive to precipitation and PDSI than older Carolina hemlock. However, both older and younger had a negative relationship between radial growth and temperature during the month of May and July, respectively. I also used tree age data to conduct a preliminary study investigating the influence of age on foliar nitrogen and carbon content and found an increase in nitrogen content with tree age.

Future research on Carolina hemlock at Bluff Mountain will include resampling plots and using the results of this thesis to quantify changes in stand structure and composition of the Carolina hemlock forest. Understanding the dynamics of the Carolina hemlock forest at the site level will provide insight about the anticpated changes across the species' range. This information will serve land managers attempting to preserve Carolina hemlock and the wildlife that relies upon this species.

DEDICATION

This thesis is dedicated to my parents for their support and motivation to pursue an education in the field of my choice. I would also like to dedicate this to my partner, Emily Thompson, and daughter, Lily, for their patience throughout my graduate school experience.

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CHAPTER 1

INTRODUCTION

1.1 Biogeography of Carolina hemlock

Carolina hemlock (*Tsuga caroliniana* Engelm.) is a long-lived tree species endemic to small isolated populations in Virginia, Georgia, Tennessee, and the Carolinas (James, 1943; Rentch *et al*., 2000) (Figure 1). The typical habitat of Carolina hemlock is along exposed ridges in the southern Appalachian Mountains (James, 1943). It can occur in pure or mixed stands at elevations between 600 and 1500 meters. However, Carolina hemlock also occurs streamside along moist, cool ravines (Humphrey, 1989). The Carolina hemlock range is limited to the south by high summer temperatures, historically frequent fires, and the limited areas of cliffs and rock outcroppings (Jetton *et al*., 2008). Conversely, its range to the north is likely restricted by lower summer precipitation and less frequent fires that lead to increased hardwood competition (Jetton *et al*., 2008).

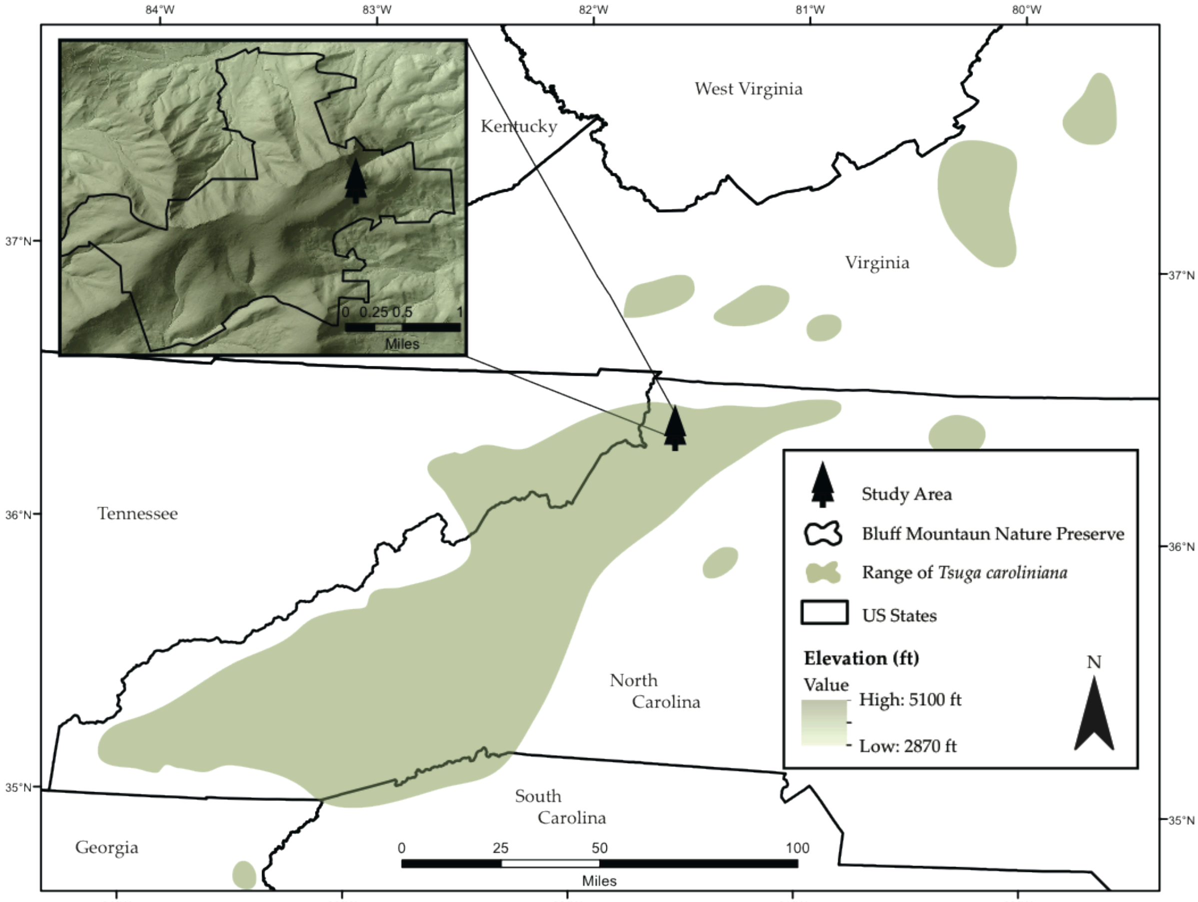

Figure 1. Map of natural range of *Tsuga caroliniana* and digital elevation model of study site at Bluff Mountain Nature Preserve, Ashe County, North Carolina.

Carolina hemlock cones, pollen, and leaves first appeared during the Pliocene Epoch, approximately 5.3 to 2.5 million years before present (LePage, 2003). Fossil records indicate that Carolina hemlock had a much wider distribution in the northern hemisphere during the geologic past. The current range is likely from Pleistocene glaciations that isolated hemlocks in their current refugia in North America and Asia.

An assessment of genetic diversity of Carolina hemlock populations supports the evidence of a larger historic distribution (Jetton *et al*., 2008). Carolina hemlock has greatest genetic diversity towards the southern portion of its range, suggesting a potential Pleistocene glacial refuge in northwestern South Carolina and possibly the North Carolina Piedmont Province (Jetton *et al.,* 2008). Several small remnant populations exist today outside of the species' normal distribution in northwest South Carolina and the Piedmont of North Carolina and Virginia at elevations between 100 m and 600 m (Stevens, 1976; Jetton *et al*., 2008).

Carolina hemlock and eastern hemlock (*Tsuga canadensis* L.) have been thought to be closely related species because Carolina hemlock's range overlaps eastern hemlock's range (Szafer, 1949). This may account for the disproportional amount of Carolina hemlock specific literature. However, LePage (2003) and Orwig and Foster (1998) have noted that based on cone shape, cone-scale, and seed morphologies, the two species are very distinct and only distantly related. Carolina hemlock is more closely related to Asian hemlocks (*Tsuga dumosa* [D. Don] Eichler, *Tsuga sieboldii* Carrière, *Tsuga chinensis* [Franch.] Pritz., *Tsuga diversifolia* [Maxim.] Mast.) than eastern hemlock (LePage, 2003). The community dynamics of Carolina hemlock should be thoroughly studied to understand the differences between the two species and possible differences in response to hemlock woolly adelgid (*Adelges tsugae* Annand) (HWA) infestation.

1.2 Hemlock woolly adelgid

Carolina hemlock is facing multiple stressors including elevated white tailed deer (*Odocoileus virginianus* Zimmerman) populations, elongate hemlock scale (*Fiorinia externa* Ferris), and the HWA. The HWA threatens to eliminate Carolina hemlock throughout its native range. It has spread unimpeded since its initial infestation in Richmond, Virginia during the early 1950s (Morin *et al*., 2009). HWA causes needle loss, bud mortality, and tree mortality within a decade by feeding on xylem ray parenchyma at the base of needles (McClure, 1991; Orwig *et al*., 2002). Ray parenchyma cells function in storage, photosynthesis, and as the bulk of ground and vascular tissues (Eschtruth *et al.,* 2006). HWA populations increase rapidly because they are parthenogenetic (all individuals are female and capable of reproduction), complete two generations each year, and have no known natural enemies in eastern North America (Orwig and Foster, 1998). They are also capable of rapid dispersal by wind, birds, deer, and human activity such as logging (McClure, 1990).

Carolina hemlock and eastern hemlock both appear to be susceptible to the HWA. Orwig and Foster (1998) found the rate and intensity of infestation are not attributable to a specific site factor or stand characteristic. Therefore, there is no impediment to the widespread expansion of HWA and devastation of eastern hemlocks across its range. It is likely that both species may become functionally extinct during the next 50 years (Beane *et al*., 2010). However, phylogenetic and morphological studies indicate that Carolina hemlock is more closely related to hemlock species in western America than eastern hemlock. Western hemlock species are highly resistant to HWA (LePage, 2003).

Winter temperatures likely limit the abundance of HWA in the eastern United States. The longer HWA are exposed to winter temperatures, the less cold tolerant they become (Skinner *et al.,* 2003). A mean winter temperature of -5° C is required to prevent HWA populations from expanding and spreading in the eastern United States (Dukes, 2009). There is great concern that as temperatures increase with global warming, HWA will continue to expand its range and HWA populations will increase during less severe winters (Dukes, 2009). Increased HWA populations would likely result in a more rapid decline of Carolina hemlock and eastern hemlock.

Carolina hemlock plays an important ecological role in the southern Appalachians as a foundation species (Ellison *et al.,* 2005). The Carolina hemlock overstory creates microclimates in the understory that have uniformly low seasonal light level variability and relatively small daily temperature fluctuations (James, 1943; Eschtruth *et al.,* 2006). The ability of Carolina hemlock to modify stand soil conditions and microclimate by depositing acidic litter and maintaining low light levels in the understory influences fundamental community and ecosystem characteristics (Jenkins *et al*., 1999). Carolina hemlock forests should be studied while the research opportunity exists. Currently, research is lacking in Carolina hemlock community ecology (James, 1943; Humphrey, 1989; Rentch *et al*., 2000; Jetton *et al*., 2008).

1.3 Forest impacts of removal of a dominant species

As Carolina hemlock mortality increases from HWA, some observed effects include changes in ecosystem diversity, forest composition and structure, and microenvironments. HWA infestations can lead to increased forest floor pH, significantly lower carbon: nitrogen ratios (C:N), and decreased organic matter content than uninfested sites (Orwig *et al.,* 2008). Other changes in ecosystem function from hemlock defoliation include an increase in light reaching the understory. Increased light causes an increase in forest floor temperature and decrease in forest floor moisture content. Orwig *et al*. (2008) found forest floor N cycling, total soil N pools, and nitrate (NO_3) capture were significantly and positively correlated with forest floor temperature. As hemlock canopies succumb to the HWA, forest floor temperatures should continue to increase and lead to accelerated N cycling and greater N availability (Jenkins *et al.,* 1999). HWA also affects seedlings as well as larger trees. Reduced seedling density will result in ammonium (NH_4-N) production and subsequent nitrification that will exceed inorganic N seedling demand (Orwig *et al.,* 2008). Unbalanced inorganic N will lead to nutrient leaching because nitrate production is not balanced by vegetative uptake if hemlocks continue to decline. Nutrient leaching may have long-lasting effects as hemlock forests transition to deciduous forests that commonly have greater decomposition and N-cycling rates.

In the absence of disturbance, hemlock stands are characterized by low light levels, low density understories, and relatively stable forest composition (Eschtruth *et al.,* 2006). Hemlock mortality leads to substantial pulses of woody debris, changes in forest age, forest structure and composition, altered wildlife habitat, and an increase in the amount of light reaching the previously shaded forest floor (Orwig and Foster, 1998; Jenkins *et al.,* 1999; Yamasaki *et al*., 2002). Significant changes in species composition were not observed in eastern hemlock stands in the Great Smoky Mountains National Park (Krapfl *et al.,* 2011). However, HWA has only recently invaded the southern Appalachian Mountains. Studies have speculated that the presence of great laurel (*Rhododendron maximum* L.*),* that is lacking in northeastern hemlock forests, may result in the development of great laurel heath balds following hemlock decline in the southern Appalachian Mountains (Krapfl *et al.,* 2011). Healthy hemlock stands appear to be fairly resistant to plant species' invasion and hardwood succession (Orwig and Foster, 1998).

1.3.1 Wildlife species response to species-selective processes

Hemlock has a dense multilayered evergreen canopy that makes it structurally unique and critically important to wildlife species (Yamasaki, 2002; Tingley *et al*., 2002). Hemlock supports moderate levels of avian diversity, including several species that are largely restricted to hemlock stands as well as several species of mammals and amphibians (Brooks, 2001; Tingley *et al.,* 2002). For example, the black-throated green warbler (*Dendroica virens* Gmelin*)*, blackburian warbler (*Dendroica fusca* Müller*)*, and acadian flycatcher (*Empidonax virescens* Vieillot) are strongly associated with hemlock forests in southern New England and appear to be sensitive to hemlock removal (Tingley *et al.,* 2002). Hemlocks provide food from seeds and bark for birds and mammals. Some animals that use hemlock bark as a food source include beaver (*Castor Canadensis* Kuhl), porcupine (*Erethizon dorsatum* Linneaus), and eastern cottontail (*Sylvilagus floridanus* J.A. Allen) (Yamasaki *et al.,* 2002). The dense canopy also provides thermal cover essential for shelter and bedding of white-tailed deer (*Odocoileus virginianus* Zimmermann) during winters in New England (Yamasaki *et al.,* 2002).

Increasing hemlock mortality and the creation of canopy openings provides an influx of early successional bird species into interior forest habitat (Tingley *et al*., 2002). Increased bird species diversity will result in a short-term increase in species richness. However, greater species richness will not remain without further disturbances. Species richness of gap-dependent bird species and bird diversity will decrease as regenerating stands mature. A possible consequence of the influx of early successional bird species into interior forest habitat is changes in forest composition from the seeds that birds deposit (Tingley *et al.,* 2002).

1.4 Conservation and management efforts

Scientists have investigated methods to mitigate HWA infestations in hemlock stands (Butin *et al.,* 2004; Lamb *et al.,* 2005; Lamb *et al.,* 2006; Cowles, 2009;

Joseph *et al.*, 2011). The literature includes possible solutions as well as attempts to measure the ecological effects of treatments to protect hemlock from HWA (Butin *et al.*, 2004; Hain, 2006; Jetton *et al.*, 2008; Cowles, 2009; Joseph *et al*., 2011). One area of particular importance is research pertaining to the prevention of HWA infestion (Hain, 2006). The focus of prevention research is learning from past infestation and applying that knowledge to prevent future invasions through the development of comprehensive research programs designed to prevent the spread of invasive insects, pathogens or plants, and rehabilitate and restore native ecosystems (Hain, 2006). Prevention programs would require an interdisciplinary approach and communication between land management agencies and the public. Other possible solutions that have been explored include biological controls, insecticides, and ex-situ conservation (removing the population from a threatened habitat and placing it in a new location) (Butin *et al*., 2004; Jetton *et al*., 2008; Cowles, 2009).

The use of the insecticide Imidacloprid is commonly used to mitigate HWA infestations. Joseph *et al*. (2011) found that the pesticide has proven effective at reducing HWA density and increasing eastern hemlock growth in Helena, Georgia. However, Carolina hemlock commonly occurs on steep slopes in remote areas with sensitive ecosystems. Insecticides may have adverse effects on the forest ecology and the water quality (Cowles, 2009). Research has been conducted by Cowles (2009) to determine proper dosage and techniques that may minimize the risk of exposing ecosystems to Imidacloprid. Imidacloprid, applied based on basal area, can provide an effective HWA treatment while minimizing ecological impacts (Cowles, 2009). While this research is useful for individual trees, it is somewhat inefficient to derive a dosage for every tree in a large hemlock forest. Cowles (2009) also suggests that insecticides should be viewed as a temporary solution until effective biological controls have been developed.

Other attempts to control HWA infestations have focused on the development of biological controls to reduce HWA populations (Butin *et al.,* 2004; Lamb *et al.,* 2005; Lamb *et al.,* 2006). However, this may cause unpredicted negative impacts on ecosystems (Strong and Pemberton, 2000). Butin *et al.* (2004) examined feeding preferences and potential effects of the ladybird beetle (*Sasajiscymnus tsugae,* Sasaji and McClure) from Japan, the lady beetle (*Scymnus ningshanensis* Yu and Yao) from China, and the harlequin ladybird beetle (*Harmonia axyridis* Pallas) from Japan. Lamb *et al.* (2005) speculated a suite of predators would be necessary to reduce HWA populations across the large geographic and variable environments where hemlock species live.

A last resort approach also exists to preserving hemlock species if insecticides and biological controls are unsuccessful. Scientists are taking sample populations of

Carolina hemlock and distributing seedlings in areas where HWA does not occur (Jetton *et al.,* 2008). A program called FloraMap was used to predict places that Carolina hemlock could successfully maintain populations (Jetton *et al.,* 2008). These possible planting locations include Central Chile, the Ozark region in Arkansas, and South Brazil (Jetton *et a*l., 2008). The replanting approach is thought to maintain Carolina hemlock in the event that efforts to stop HWA fail in the southeastern United States. However, this approach could also have ecological implications because humans would be introducing an exotic species to new locations.

1.5 Age-related shifts in foliar chemistry

Tree aging has been studied by dendrochronologists and biologists (Larson, 2001; Knapp and Soulé, 2010; Copenheaver *et al.,* 2011). However, some dendrochronology-based studies rely solely on radial growth as a proxy for physiological processes (Copenheaver *et al.,* 2011). Other studies have incorporated radial growth and isotopic analysis to examine water-use efficiency during the life of living trees (Knapp and Soulé, 2010). More studies with similar mixed-methods approaches tracking both radial growth and quantification of physiological processes during the lives of trees will provide insight about the relationship between aging and tree physiology.

One possible explanation for age-related shifts in foliar C and N content is the direct result of the aging process. According to Erwin et al. (2001), foliar glycosides and tannins vary between mature and juvenile trees and can result from age-related shifts. Richardson *et al*. (2001) quantified morphological traits of western hemlock needles and found differences in plant plasticity that were attributed to differences in tree age. However, Richardson *et al*. (2001) also speculate that changes in plasticity with age may be species specific. Further comparisons between multiple species is needed to determine if the age-related shifts are a function of aging or represent changes in trees' competitive strategies. Pontius *et al*. (2006) have linked HWA susceptibility with foliar N content. Understanding changes in foliar chemistry with aging may provide insight into the relationship between HWA susceptibility and tree age. The relative longevity of Carolina hemlock makes it well suited for studies investigating the relationship between age and tree physiology.

1.6 Goals of Thesis

As part of this thesis, I investigated a Carolina hemlock community at Bluff Mountain Nature Preserve, Ashe County, North Carolina. Carolina hemlock, an endemic species to the southern Appalachian Mountains, is facing the threat of extinction from the HWA. The arrival of HWA in Ashe County was documented in 2001 (USDA Forest Service, 2012). Despite the remote location of Carolina hemlocks on Bluff Mountain and limited public access, they have not escaped the spread of HWA throughout the southern Appalachian Mountains. HWA monitoring plots at Bluff Mountain recorded the presence of HWA egg masts in 2006 (D. Munro, Resident Steward of Bluff Mountain, personal communication, 7 April 2012). It is crucial that Carolina hemlock communities get thoroughly inventoried and monitored while the opportunity still exists.

1.6.1 Research questions

1. What is the current composition and structure of the Carolina hemlock forest at Bluff Mountain, North Carolina?
2. Is Carolina hemlock successfully regenerating in a Carolina hemlock dominated forest? If so, is regeneration intermittent or continuous over the last century?
3. What is the pre-HWA disturbance regime of the Carolina hemlock forest at Bluff Mountain?

4. Is there a relationship between climate and radial growth of Carolina hemlock? If so, is the climate-growth relationships age dependent?
5. Is Carolina hemlock foliar N and C content influenced by tree age?

CHAPTER 2

STUDY AREA

2.1 Geography

I conducted this study at Bluff Mountain Nature Preserve in Ashe County, North Carolina. The preserve has been owned and managed by The Nature Conservancy since 1978 (Skeate, 2004). The mountain is located at approximately 36° 23′ 52.044″ North, 81° 32′ 55.716″ West. The study area is within the North Fork of the New River watershed. Bluff Mountain is part of the Blue Ridge Physiographic Province. The Blue Ridge Mountains range in elevation from approximately 300 m to 1800 m above sea level and support some of the highest biodiversity in North America (NCNHP, 1999). Bluff Mountain is a high-elevation area of ecological significance in the Blue Ridge Mountains of North Carolina (Skeate, 2004).

Bluff Mountain rises from approximately 1067 m elevation to a central peak of 1546 m (Tucker, 1972). The mountain is part of a small collection of old-growth forest preserves in the Blue Ridge Mountains (Nash, 1999). Many of the vegetation assemblages characteristic of the Blue Ridge Physiographic Province inhabit Bluff Mountain, including: rock outcrop communities, a Carolina hemlock forest, dwarf oak (*Quercus* spp.) forests, and a southern Appalachian fen (Tucker, 1972; Lynch and

Fields, 2002). More than 48 endangered, threatened, or rare vascular plant species have been identified on Bluff Mountain (Tucker, 1972; NCNHP, 1999; Skeate, 2004).

2.2 Climate

The climate at Bluff Mountain is classified as Cfb under the Köppen climate classification system (Christopherson, 2009). Marine west coast climates are characterized by mild winters and cool summers in contrast to the subtropical climate of the southeastern United States (Christopherson, 2009). The average January temperature is approximately 0.7°C with average July temperatures of 20°C (PRISM Climate Group, 2011). Yearly average temperatures are approximately 10°C and annual precipitation averages 125 cm (PRISM Climate Group, 2011). July and August have the highest average monthly precipitation (approximately 12 cm each month) and November has the lowest average precipitation, 8.7 cm (PRISM Climate Group, 2011). Annual snow accumulation averages 71 cm (SCONC, 2011). The average growing season length in Ashe County is 139 days (SCONC, 2011).

2.2 Geology and soils

Bluff Mountain, as part of the Blue Ridge Physiographic Province, is also part of the Amphibolite Mountains of northwestern North Carolina (Mowbray and Schlesinger, 1988). Soils formed from amphibolites (metamorphosed basalt) are high in calcium, magnessium, and iron (Mowbray and Schlesinger, 1988; NCNHP, 1999).

The Amphibolite Mountains are of national significance and home to many rare floral and fauna species (Poindexter and Murrell, 2008). The Bluff Mountain ridgeline is composed of a hornblende gneissic rock that provides calcium and potassium for vegetation in slightly acidic, Porters stony loam soils (Lynch and Fields, 2002). The soil type at Bluff Mountain is shallow Lichic dystrochrepts, coarse loamy, mixed, with a considerable percentage of cobbles and stones (24-35%) (Humphrey, 1989). Carolina hemlock is typically found in dry coarse sandy to sandy loam soil conditions. These sites tend to be nutrient poor, well-drained, and highly acidic (Harlow *et al.*, 1996).

CHAPTER 3

METHODS

3.1 Field methods

3.1.1 Stand structure, composition, and tree age

In August 2011, I established five 0.05 ha fixed radius (r=12.66 m) plots at Bluff Mountain, North Carolina. The plots were located in forest stands with >50% Carolina hemlock in the canopy. I divided each plot into four quadrants to examine the spatial distribution of the species in each plot. I recorded tree height, diameter at breast height (dbh; 1.37m), and crown class for each tree to quantify the vertical and basal area structure of the stand. I based crown class categories (overtopped, intermediate, codominant, and dominant) on the amount and direction of intercepted light (Oliver and Larson, 1996). I measured tree heights using a digital hypsometer. I tallied all tree stems ≥5 cm dbh by species in each plot. I collected two radial cores from every tree below 30 cm height, except from American chestnut (*Castanea dentata* Marsh.), to determine establishment dates, growth rates, and radial growth patterns. I also recorded Global Positioning System (GPS) points from the center of each plot.

I established a nested 0.01 ha fixed radius (r=5.66 m) subplot in the center of each overstory plot. I considered stems ≥1m in height and less than 5.0 cm dbh saplings and stems <1 m in height as seedlings. I tallied saplings and seedlings by species. I also visually estimated percentage cover of mountain laurel (*Kalmia latifoli* L.) and Catawba rhododendron (*Rhododendron catawbiense* Michx.) to the nearest 5% for each understory quadrant.

3.1.2 Foliar chemistry

In October 2011, I collected foliar samples from nine Carolina hemlocks using a forestry throw line. I selected trees that represented three age classes: 50–100, 100–150, and 150–200 years old. I collected needles from the upper canopy of nine trees (three from each age class). I located trees that met the age criteria using field notes from previous sampling. I determined the ages of the selected trees prior to revisiting the site for foliar collection.

3.2 Laboratory and quantitative methods

3.2.1 Tree-ring preparation

I followed standard dendroecological procedures to prepare tree cores for analysis (Stokes and Smiley, 1968; Fritts, 1976). I allowed the collected cores to air-dry before I glued them to wooden core mounts and sanded the cores with progressively finer sandpaper (100-400 grit) to reveal the cellular structure of the wood (Orvis and Grissino-Mayer, 2002). I hand-sanded cores with light rings with 600 grit sand paper. I visually examined each core with a stereozoom microscope under 10X magnification to establish patterns of narrow and wide rings and other tree ring characteristics to assist with crossdating. I recorded years with distinct rings (*e.g.*, unusually wide or narrow rings) and compared them with other cores (Yamaguchi, 1991). Once visually crossdated, I assigned a calendar year beginning at the last year of growth (2011) and dated backwards to the innermost ring or pith. I measured ring width to the nearest 0.001mm using WinDendro software. I scanned cores measured by WinDendro using an Epson® Expression 1000 XL flatbed scanner and saved the image as a TIF image file with resolution set at 1200 dpi. I visually inspected all ring widths identified by WinDendro against reference decadal markings assigned from visual crossdating.

I statistically crossdated Carolina hemlock cores (series) using the program COFECHA to ensure the proper growth ring was assigned to the correct year of formation (Holmes, 1983; Grissino-Mayer, 2001). COFECHA uses segmented time series correlation analyses to determine the strength of association between 50-year segments lagged 25 years from each individual series against a master chronology created from the remaining series (Grissino-Mayer, 2001). COFECHA removes all low-frequency trends using spline-fitting algorithms and autoregressive modeling to maximize the climate signal needed for accurate crossdating (Grissino-Mayer, 2001). Segments that fell below the predetermined significance threshold ($r = 0.32, p > 0.01$

were flagged by the program. I visually checked all flagged segments for possible dating errors.

3.2.2 Climate-growth analysis

After I was confident that all Carolina hemlock tree rings were successfully dated correctly, I developed two tree-ring chronologies from 25 young (44 – 61 years old) and 25 old (103 – 176 years old) trees. I detrended each series using the program ARSTAN to remove the influence of increasing circumference with age, microsite, and local stand dynamics (Cook, 1985; Cook and Holmes, 1996). I applied a Friedman super smoother to all cores (Cook and Holmes, 1996). I selected the Friedman super smoother to preserve long-term trends and minimize the effects of stand dynamics such as suppressed growth or abrupt growth increases.

I used the old and young ARSTAN master chronologies for statistical analysis. I selected the ARSTAN master chronologies because it combines standard and residual chronologies to enhance climatic signals from trees growing under a closed-canopy forest (Copenheaver *et al.*, 2011). I analyzed the climate radial growth relationship of each chronology using correlation analysis between the growth index and climate variables: mean monthly maximum temperature, monthly total precipitation, and monthly Palmer Drought Severity Index (PDSI) values. I analyzed the climate-growth relationships during the period of AD 1895–2010 for the old

Carolina hemlock chronology and AD 1951–2010 for the young chronology. PDSI is often used in dendroclimatic studies because it is a good measure of available soil moisture conditions during the growing season (Alley, 1984). I obtained data for monthly mean maximum temperature and monthly total precipitation from the PRISM Climate Group (2011). The PRISM data represents a grid cell at the longitude and latitude -81.548 and 36.397, respectively. The grid cell has a resolution of 2.5 minutes and elevation of 981 meters. I obtained PDSI data for the northern mountains region of North Carolina from the National Climate Data Center (NCDC, 2011).

3.2.3 Disturbance reconstruction

I used dendroecological techniques to identify release events of 38 Carolina hemlock canopy trees to examine the frequency and spatial distribution of canopy disturbances. I selected the core with the longest record per tree for analysis. Release calculations are a common practice in dendroecology for reconstructing canopy disturbance events (Nowacki and Abrams, 1997; Rubino and McCarthy, 2004; Hart *et al.,* 2012). Releases events are changes in radial growth relative to a predetermined threshold identified using a percent growth change equation (Nowacki and Abrams, 1997; Rubino and McCarthy, 2004). Releases typically are the result of an increase in light availability or water availability following a disturbance that damages a nearby tree (Rubino and McCarthy, 2004). I analyzed changes in raw-ring widths with respect to the running mean of the previous and subsequent ten years. I calculated percent growth change for a year using the following equation:

$$\%GC = (M_2 - M_1) / M_1 * 100$$

where %GC equals percentage growth change between preceding and subsequent ten year means, M_1 equals mean growth over the prior ten years, including the current year, and M_2 equals mean growth over the subsequent ten years. The criteria for a release was a period with raw-ring widths ≥25% of the ten year preceding and superseding mean that were sustained for a minimum of three years (Rubino and McCarthy, 2004). The criteria for a standwide disturbance were release episodes that were detected among ≥25% of the tree-ring series at least 10 years of age at the time of the release (Nowacki and Abrams, 1997; Rubino and McCarthy, 2004; Hart *et al.,* 2008; Hart and Grissino-Mayer, 2008).

3.2.4 Stand composition and biodiversity

I calculated density, dominance (basal area), and importance values to describe forest composition. Density is the number of individual plants per unit area. It is calculated by counting the number of trees of each species at a designated site. I standardized tree density at the hectare level by using a blow-up value. I sampled a total of 0.25 ha of the Carolina hemlock forest. Therefore, I used the following equation:

$$(0.25 \text{ ha} * 4 = 1 \text{ ha})$$

where 0.25 equals the area sampled and 4 is the blow-up value.

I also calculated relative density, which is the number of individuals of one species as a percent of the total, of each species. This is a dimensionless value that is scale independent. I divided the amount of each tree species per hectare by the total amount of trees per hectare to determine relative density. I converted the dbh measure of every tree sampled and multiplied it by the constant of 0.00007854 to determine basal area (m^2) (Husch *et al.*, 2003). I summed the basal area of all trees by species and multiplied the species basal area by the blow-up value of 4 to calculate basal area by species per hectare. Next, I calculated relative dominance of each species by dividing total basal area per species by the total basal area of all species per hectare. I averaged relative density and relative dominance of each species to determine relative importance (Hart *et al.,* 2008).

To quantify species biodiversity, I calculated species richness (*S),* evenness (*J),* and Shannon diversity (*H')* for trees and the understory species (Ludwig and Reynolds, 1988). Species richness is the total number of species observed in the study area. However, it is scale-dependent and does not indicate the relative abundance of each species. Evenness is a measure of the distribution of individuals across the species represented. Evenness values range from 0 to 1. A high *J* value indicates each species has a similar population size and a low *J* values indicates population sizes are variable. Shannon diversity is a commonly used measure of biodiversity (Ludwig and Reynolds, 1988). It is a scale-independent, dimensionless index that includes species richness and evenness (Ludwig and Reynolds, 1988). Shannon diversity is calculated:

$$H' = -\sum pi \ln \mathrm{pi}$$

where pi is the proportion of the *i*th species and ln is the natural logarithm. To calculate H' and J, I used the online program Chang BioScience Diversity Calculator (Chang, 2011).

3.2.5 Stand structure

I calculated crown class per species per hectare and average tree height of overstory and understory trees to determine the vertical structure of the stand. I analyzed size structure, based on dbh, to determine how the density and dominance of species are likely to change over time. I also used the percent cover of mountain laurel and Catawba rhododendron data to determine average cover for each species.

3.2.6 Foliar chemistry

I divided foliar samples by age and freeze-dried samples after collection. After samples dried, I ground them to a talcum powder consistency (250 um or less) using a wiley mill. I placed samples in a combustion capsule and weighed them at the microgram level (Hauck, 1982). After preparation was complete, I determined N and C content using Micro-Dumas combustion analysis using Thermo Finnegen Flash EA 1112 (Hauck, 1982). I analyzed the relationship between tree age and foliar chemistry using linear regression analysis with JMP 9 software. The foliar chemistry data consisted of N concentration, C concentration, and C:N ratio.

CHAPTER 4

RESULTS

4.1 Forest composition

Carolina hemlock was the most abundant and dominant species in the forest canopy of Bluff Mountain. The overstory layer had the highest species richness (Table 1). Based on relative importance, the most important species was Carolina hemlock (Table 2). Northern red oak (*Quercus rubra* L.) and white oak (*Quercus alba* L.) were also important species. The most dominant overstory layer species (based on basal area) was Carolina hemlock. The next most dominant species were northern red oak and white oak. The mean dbh of Carolina hemlock was 13 cm, northern red oak was 22 cm, and white oak was 23 cm. These three species represent over 95% of tree biomass at the study site.

Carolina hemlock had the highest tree density (1048 trees ha^{-1}) and was nearly five times as abundant as any other species. The next most abundant species were northern red oak and white oak. Together these three species represented nearly 90% of all overstory tree species. There were several small American chestnut stump sprouts found at this site. Other than red maple (*Acer rubrum* L.) and hornbeam (*Carpinus caroliniana* Walt.), no other species represented more than 15 trees ha^{-1} or more than 1% of tree density.

Parameter	Layer		
	Tree	Sapling	Seedling
Density (stems/ha)	1608	2560	2600
Basal area (m/ha)	42.98	-	-
Species richness	9	4	6
Diversity (H’)	1.16	0.31	1.43
Evenness (J)	0.53	0.23	0.80

Table 1. Composition and structural measures for tree, sapling, and seedling layers at Bluff Mountain Nature Preserve, North Carolina.

Species	Density (stems/ha)	Relative Density	Dominance (m^2/ha)	Relative Dominance	Relative Importance
Tsuga caroliniana	1048	65.17	21.26	49.45	57.31
Quercus rubra	220	13.68	10.84	25.22	19.45
Quercus alba	176	10.95	8.86	20.61	15.78
Acer rubrum	92	5.72	1.37	3.19	4.45
Carpinus caroliniana	36	2.24	0.32	0.75	1.50
Betula lenta	12	0.75	0.04	0.10	0.42
Castanea dentata	12	0.75	0.06	0.15	0.45
Acer pensylvanicum	8	0.50	0.03	0.07	0.28
Prunus serotina	4	0.25	0.20	0.46	0.36
Total	1608	100	42.98	100	100

Table 2. Density, dominance, and importance values of trees (≤ 5 cm at DBH) at Bluff Mountain Nature Preserve, North Carolina. Values shown are per hectare.

Species	Seedlings/hectare	Relative Density (%)	Saplings/hectare	Relative Density (%)
Tsuga caroliniana	1060	41	2380	93
Acer rubrum	600	23	0	0
Quercus rubra	580	22	0	0
Hamamelis virginiana	240	9	120	5
Quercus alba	60	2	0	0
Fraxinus americana	60	2	40	2
Betula lenta	0	0	20	1
Total	2600	100	2560	100

Seedlings: < 1 m height; saplings: < 5 cm DBH, ≥ 1 m height

Table 3. Density and relative density for seedlings and saplings. Values shown are per hectare.

Shannon’s Diversity and evenness in the sapling layer was much lower than the forest overstory. The two most abundant species in the sapling stratum were Carolina hemlock and witch hazel (*Hamamelis virginiana* L.), representing 93% and 5%, respectively (Table 3). White ash (*Fraxinus Americana* L.) and witch hazel were present in the sapling stratum but absent from the overstory layer. Northern red oak, white oak, and red maple were absent from the sapling layer.

The seedling layer had the highest diversity and evenness value of the three stratums. The most abundant species in the understory stratum was Carolina hemlock, representing 41% of all seedlings and 93% of all saplings. Red maple and northern red oak were the next most abundant seedlings representing 23% and 22%, respectively. Sweet birch (*Betula lenta* L.) was absent from the seedling layer but present in the other stratums.

Catawba rhododendron and mountain laurel covered approximately 50% of the understory layer. Catawba rhododendron was the most abundant with a mean percent cover of 36% ±11.55. Percent cover of Catawba rhododendron ranged from 70% to 0% by plot (Figure 2). Mean percent cover of mountain laurel was 12.75 ± 3.2 and ranged from 3.75% to 22.5% by plot.

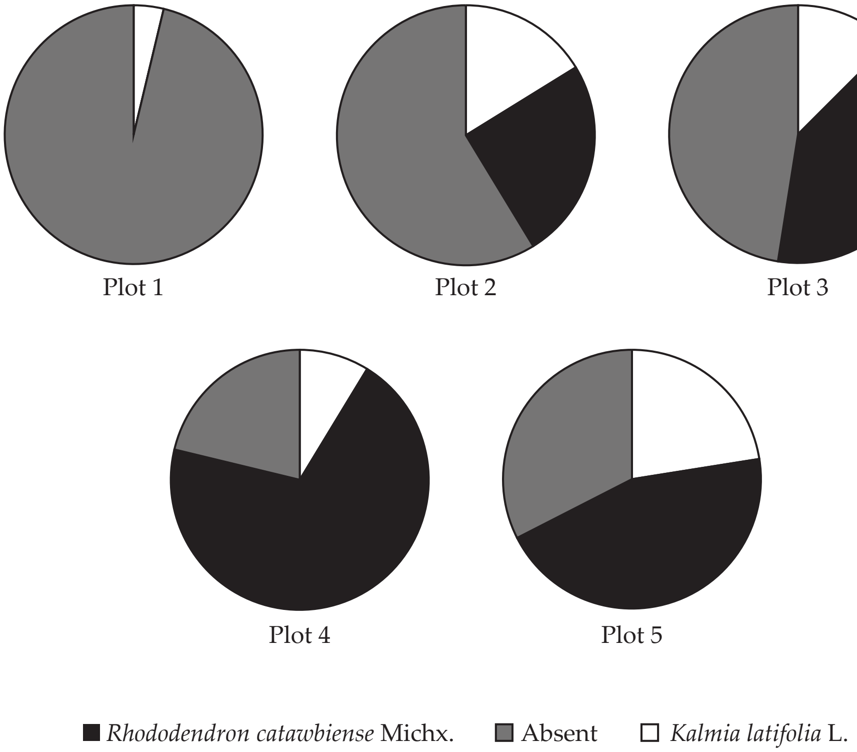

Figure 2. Percent cover of *Kalmia latifolia* L. and *Rhododendron catawbiense* Michx. visually estimated to the nearest 5%.

Carolina hemlock was the most abundant species in each canopy position (Figure 3). Northern red oak and white oak were the next most abundant species within the dominant and codominant canopy positions and the least abundant within the subcanopy positions (Figure 4). There were 276 individuals ha^{-1} with dominant canopy positions and 296 trees ha^{-1} with codominant positions. Dominant canopy species were Carolina hemlock (35%), northern red oak (33%), white oak (28%), and red maple (>1%). Carolina hemlock represented over 70% and 80% of all intermediate and overtopped trees, respectively. The average overstory and understory tree height was 10.5 m ± 0.2 m and 5.9 m ± 0.1 m, respectively.

Figure 3. Canopy class distributions per hectare, by group. Canopy class categories are based on the amount and direction of intercepted light. Dom: dominant, Codom: codominant, Int: intermediate, Otop: overtopped. Other species included *Acer rubrum*, *Carpinus caroliniana*, *Betula lenta*, *Castanea dentata*, *Acer pensylvancium*, and *Prunus serotina* and represented less than 10% of the forest canopy structure.

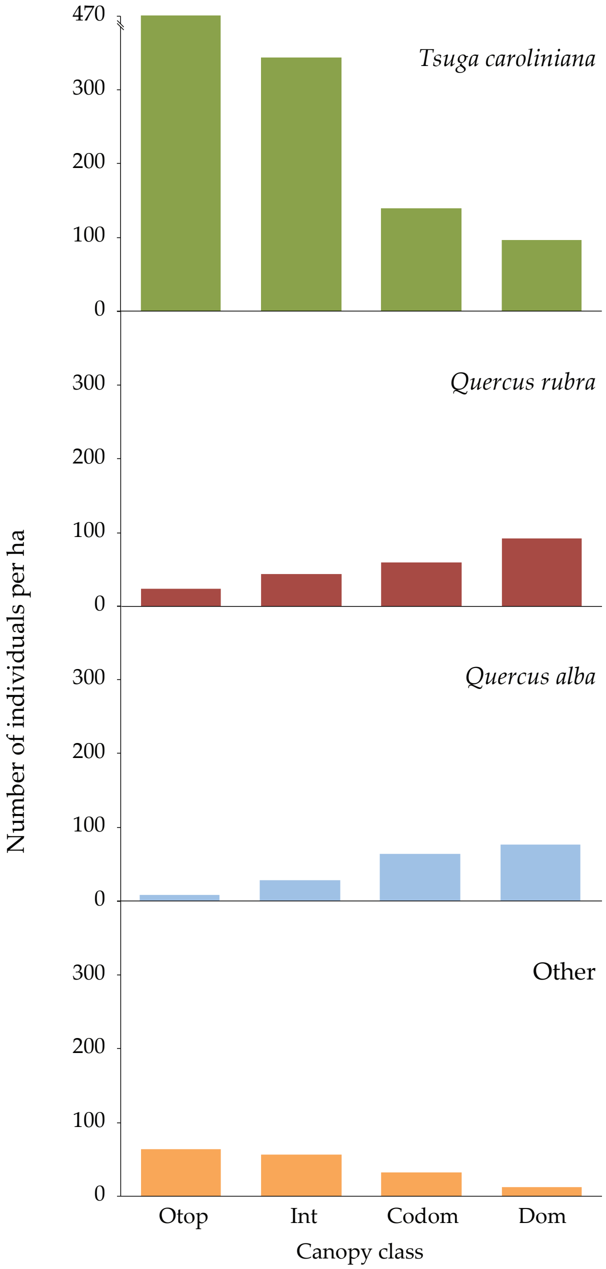

Figure 4. Canopy class distributions at Bluff Mountain Nature Preserve, North Carolina. Categories are based on amount and direction of intercepted light. Dom: dominant, Codom: codominant, Int: intermediate, Otop: overtopped. Other species included *Acer rubrum*, *Carpinus caroliniana*, *Betula lenta*, *Castanea dentata*, *Acer pensylvancium*, and *Prunus serotina* and represented less than 10% of the forest canopy.

4.2 Diameter and age structure

The diameter structure of all trees in the forest revealed an inverse J-shaped distribution with decreasing quantities from small size classes to large size classes (Figure 5). After grouping species into four categories (Carolina hemlock, northern red oak, white oak, and others), recruitment and regeneration patterns became clear. Carolina hemlock and the "others" groups exhibited a steady decline in stem density with increased tree size. The "others" group was sparse in the medium and large size classes and absent in the largest size classes. Northern red oak had a relatively uniform distribution from the smallest size class through the 30 – <35 cm size classes and then decreased in stem density. White oak was the only species with a unimodal distribution, with an apex in the 20 – <25 cm size class.

The age-diameter distributions revealed tree size generally increased with age (Figure 6). I documented a total of four trees > 40 cm dbh in the study plots. Two of the trees were Carolina hemlock and the other two trees were northern red oak and white oak. Despite the strong age-diameter relationship I documented a Carolina hemlock with a dbh of 6.9 cm that was 99 years old. The largest tree documented was a 176 year old Carolina hemlock with a dbh of 50.5 cm. There were 41 individuals ≥ 30 cm dbh.

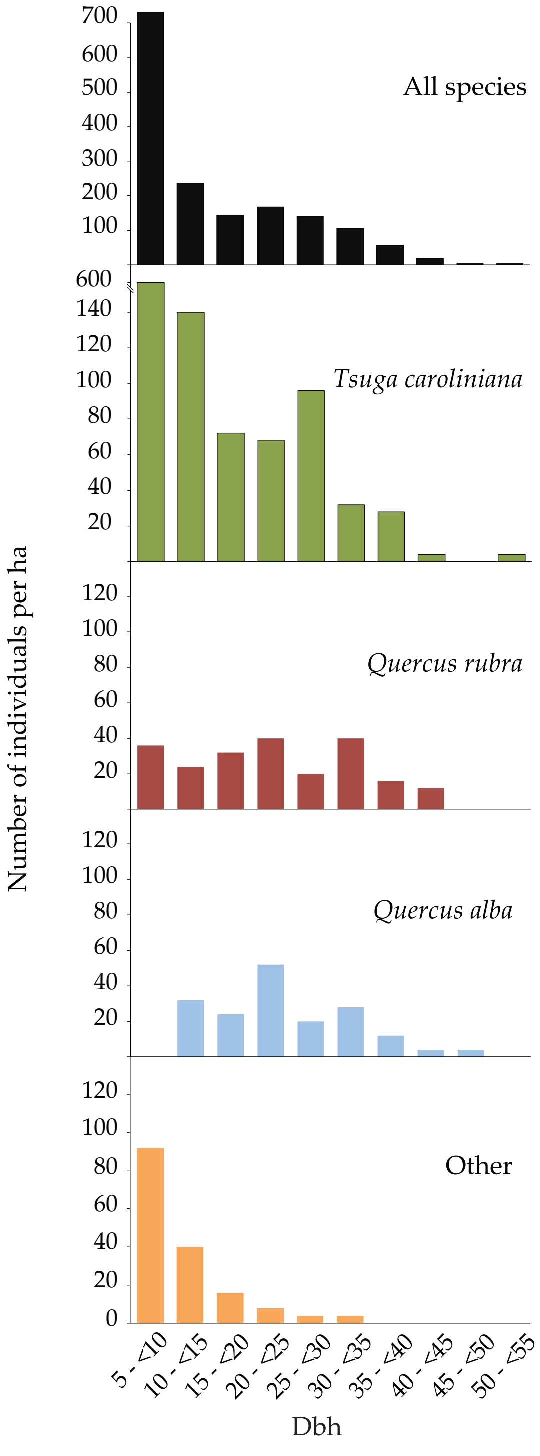

Figure 5. Number of trees (≥ 5 cm dbh) per hectare at Bluff Mountain Nature preserve, North Carolina. Other species included *Acer rubrum*, *Carpinus caroliniana*, *Betula lenta*, *Castanea dentata*, *Acer pensylvancium*, and *Prunus serotina* and represented less than 10% of the forest canopy structure.

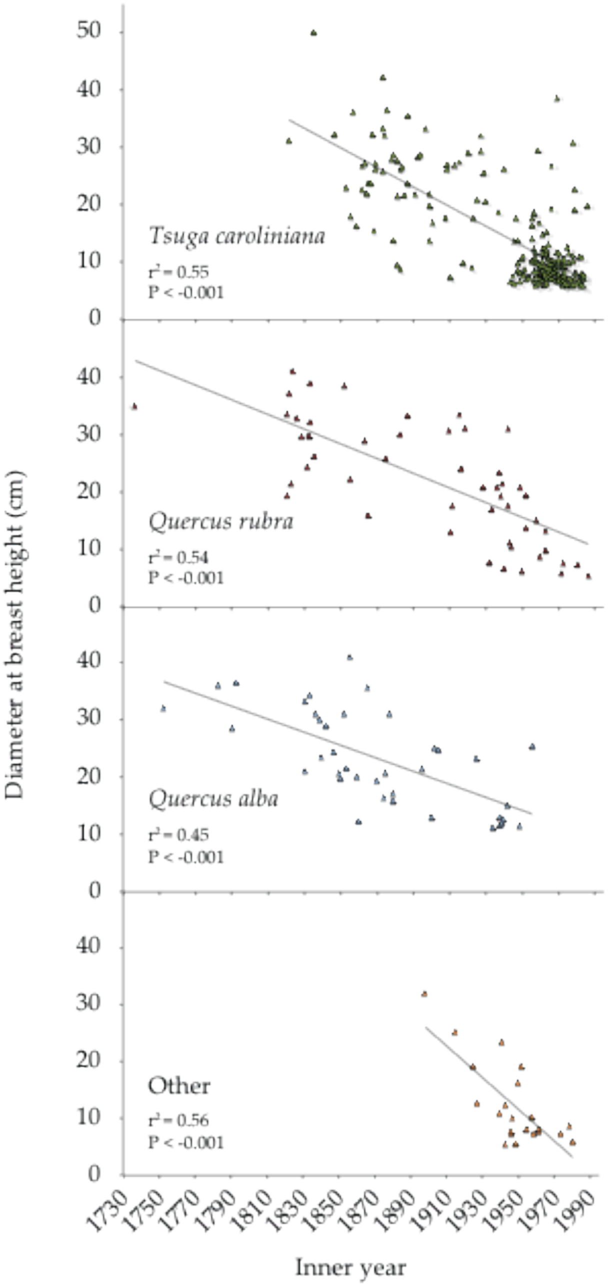

Figure 6. Diameter-age relationships for 357 trees in sample plots at Bluff Mountain Nature Preserve, North Carolina. Other species included *Acer rubrum, Carpinus caroliniana, Betula lenta, Castanea dentata, Acer pensylvancium,* and *Prunus serotina* and represented less than 10% of the forest canopy structure.

Of these trees, 14 were Carolina hemlock, 15 were northern red oak, 11 were white oak, and there was one red maple. The largest northern red oak and white oak was 41.5 cm dbh and 189 years old and 41 cm dbh and 156-years old, respectively. The largest red maple was 32.1 cm dbh and 112 years old. The largest trees were not necessarily the oldest despite the significant relationship between age and diameter.

Tree establishment was continuous for the three dominant species after 1820. The oldest Carolina hemlock established during 1821. The oldest trees within the study site were white oaks and northern red oaks. The oldest white oak was 258 years old and the oldest northern red oak was 276 years old. Thirty-nine Carolina hemlocks established prior to 1900. A second establishment period of Carolina hemlock occurred from 1950 to 1980. Within the “others” group, tree recruitment was mainly *Acer* species (68% of datable cores in the other category). However, approximately half of the cores collected from trees in the “others” category were unusable due to heart rot.

4.3 Snag characteristics

I recorded 88 snags ≥ 5 cm dbh ha^{-1} within the study site (Table 4). These snags represented 5 different species. I was able to identify 91% of all snags to the species level. I documented 72 snags ha^{-1} ≥ 10 cm dbh and 24 snags ≥ 30 cm dbh, over half of which were Carolina hemlock. Carolina hemlock also represented the most snag basal area, 2.71 m^2 ha^{-1}. The second most abundant snag species was northern red oak. It represented 18.1% of all snags and had a basal area of 0.85 m^2 ha^{-1}. Mean snag dbh was 21.6 ± 2.3(SE) with a maximum of 41.5 cm from a northern red oak individual. There was a unimodal distribution of snags by size class with the greatest amount in the 10 < 20 and 20 < 30 cm dbh of twenty-four snags (Figure 7).

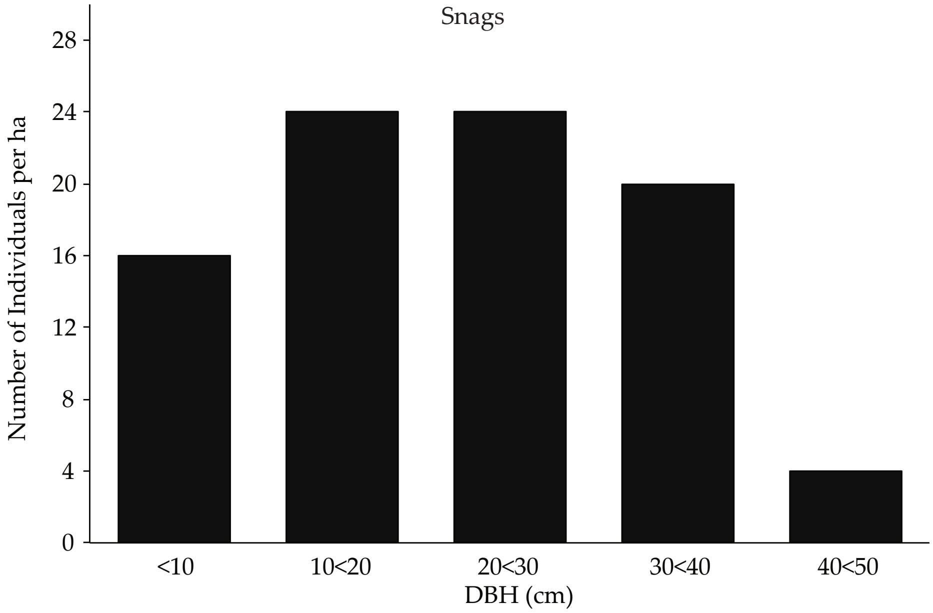

Figure 7. Number of snags (≥ 5cm dbh) per hectare by diameter class interval in a *Tsuga caroliniana* forest at Bluff Mountain Nature Preserve, North Carolina.

Species (Snags)	Density (stems/hectare)	Relative Density (%)	Dominance (m/ha)	Relative dominance (%)
Tsuga caroliniana	48	54.55	2.71	67.59
Quercus rubra	16	18.18	0.85	21.2
Quercus alba	4	4.55	0.12	2.98
Castanea dentata	8	9.09	0.25	6.24
Acer rubrum	4	4.55	0.03	0.65
Unidentified	8	9.09	0.05	1.24
Total	88	100	4.01	100

Table 4. Density and dominance values of snags (≥ 5 cm DBH). Values shown are per hectare.

4.4 Dendroclimatology

4.4.1 Age-related shifts in Carolina hemlock climate-growth relationships

Carolina hemlock at Bluff Mountain and eastern hemlock at other study sites both respond favorably to cool moist summer conditions (Cook and Jacoby, 1977; Abrams *et al*., 2000; D'Arrigo *et al*., 2001; Hart *et al.,* 2010). The two Carolina hemlock chronologies differed in mean sensitivity, series intercorrelation, and length because of the different ages of trees included (Table 5). The young chronology (44–61 year-old trees) had a lower mean sensitivity and series intercorrelation than the old chronology (103–176 year-old trees). Mean sensitivity is a measure of annual variability in tree-ring width and can indicate the climatic sensitivity of a chronology (Fritts, 1976). There was only one absent ring present in the old chronology. The narrowest rings in the old and young chronology occurred during 1881 (0.557) and 1988 (0.81), respectively (Figure 8). Both chronologies had above average growth in 1989. The young chronology was less responsive to precipitation and PDSI than the old chronology. However, both chronologies had a similar response to temperature.

4.4.2 Temperature

The older chronology was more sensitive to mean maximum summer temperature than the younger chronology. However, the younger chronology had a slightly higher correlation to temperature than the old chronology. The only significant relationship between the young chronology and temperature was a negative correlation with July temperature (r = -0.36, p < 0.01; Figure 9). The old chronology had a significant correlation with May temperature (r = -0.32, p < 0.01) and average summer temperature (r = -0.33, p < 0.01). It is noteworthy that the young chronology's response to temperature is two months later in the growing season than the old chronology.

4.4.3 Precipitation

The two chronologies responded differently to precipitation. The young chronology was not responsive to precipitation during any months of the current or previous year (Figure 10). The old chronology had a significant positive relationship with May precipitation (r = 0.32, p < 0.01). The old chronology also had a significant positive relationship with growing season precipitation (r = 0.31, p < 0.01). Growing season precipitation is defined as the sum of precipitation during April-September.

4.4.4 PDSI

The two chronologies also differed in their response to PDSI. The old chronology had the most significant correlations with PDSI out of the three climate parameters tested. However, the young chronology did not have any significant relationships with current or previous year PDSI. The old chronology had a significant correlation with eight of the thirty periods examined (Figure 11). The highest correlation between PDSI and the old chronology was average summer PDSI ($r = 0.38$, $p < 0.01$). Radial growth in the old chronology had positive significant relationships with PDSI in all of the months of the growing season except April. The month with the highest correlation between PDSI and the old chronology was August ($r = 0.36$, $p < 0.01$).

Chronology	Number of trees	Maximum age	Minimum age	Mean age	Series intercorrelation	Mean sensitivity
Old	25	176	103	135	0.581	0.247
Young	25	61	44	54	0.515	0.205

Table 5. Characteristics of the young (44–61 years old) and old (103–176 years old) *Tsuga caroliniana* chronologies from Bluff Mountain Nature Preserve, North Carolina.

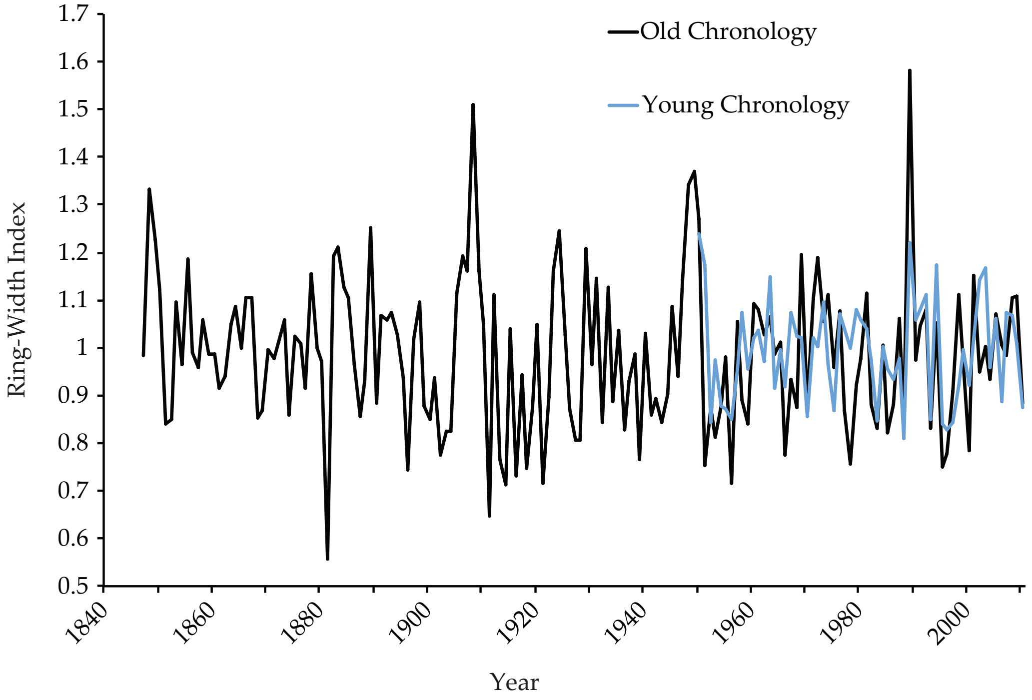

Figure 8. Comparison between the old (103–176 years old) and young (44–61 years old) *Tsuga caroliniana* chronologies.

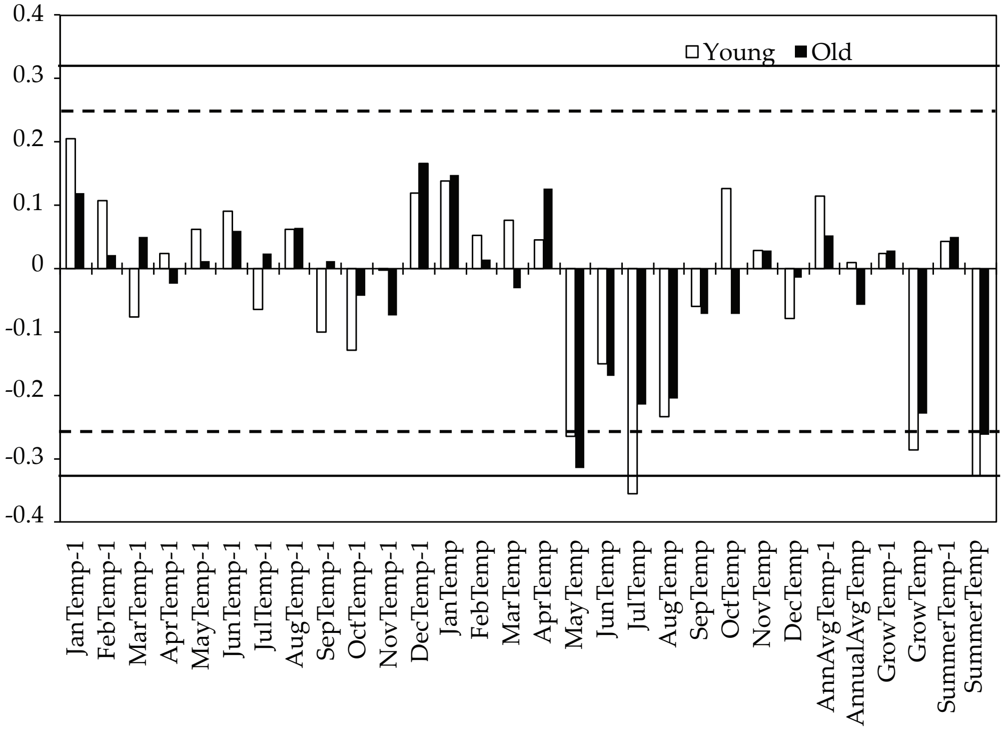

Figure 9. Correlation coefficients for ring-width index (RWI) and temperature for *Tsuga caroliniana* divided into two age classes from Bluff Mountain Nature Preserve, North Carolina. Dashed horizontal lines indicate significance at $p < 0.01$ for old chronology. Solid horizontal lines indicate significance at $p < 0.01$ for young chronology.

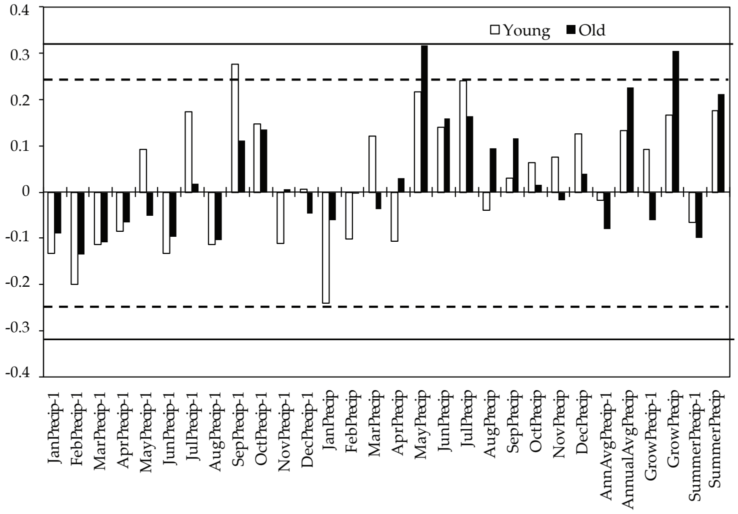

Figure 10. Correlation coefficients for ring-width index (RWI) and precipitation for *Tsuga caroliniana* divided into two age classes from Bluff Mountain Nature Preserve, North Carolina. Dashed horizontal lines indicate significance at $p < 0.01$ for old chronology. Solid horizontal lines indicate significance at $p < 0.01$ for young chronology.

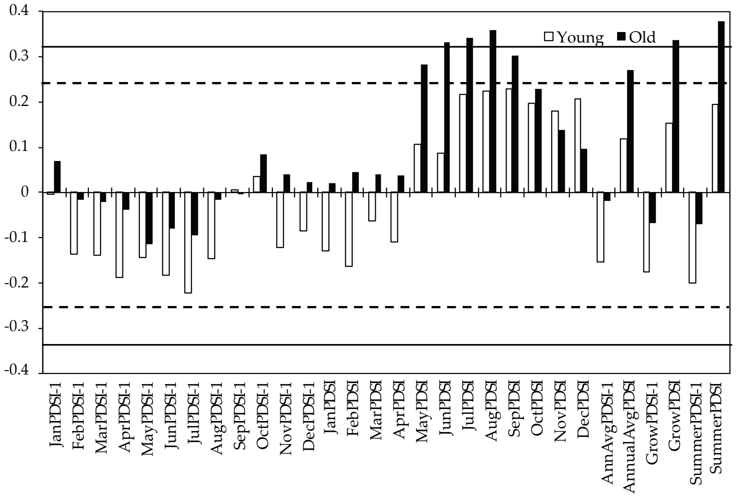

Figure 11. Correlation coefficients for ring-width index (RWI) and PDSI for *Tsuga caroliniana* divided into two age classes from Bluff Mountain Nature Preserve, North Carolina. Dashed horizontal lines indicate significance at $p < 0.01$ for old chronology. Solid horizontal lines indicate significance at $p < 0.01$ for young chronology.

4.4.5 Disturbance reconstruction of Carolina hemlock

Among the 38 Carolina hemlock tree-ring series analyzed using the running mean method, 35 (92%) revealed at least one release event. There were a total of 109 release events detected from the 38 series with 33 series (87%) experiencing multiple releases. The average number of releases per tree was 2.9 ± 0.17. The average release duration was 8.8 years ± 0.45. The longest sustained release in an individual tree was 29 years, from 1924–1952. However, it is likely that this resulted from multiple canopy disturbances between 1924 and 1952 rather than a single event. The longest period between release events in all trees was 6 years, from 1906–1911 (Figure 12). Many of the release events occurred in consecutive years. The longest common period of releases in all trees was seven years and occurred from 1899–1905 and 1953–1959. During these periods at least one tree exhibited a release each year. The decades with the most detected releases were 1950 and 1930 with 17 and 14 releases, respectively (Figure 13). The most annual releases were detected in 1937 (7). During 1937, 23% of Carolina hemlock analyzed experienced a release. There were no stand-wide disturbances detected. Gap-phase canopy disturbances occurred every decade between 1870 and 2000.

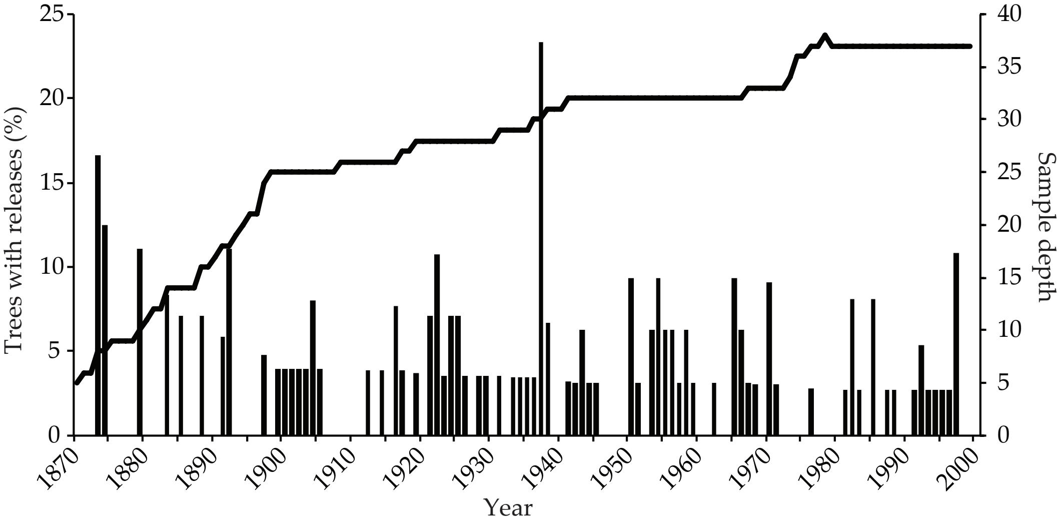

Figure 12. Annual release to sample depth ratio (%). *Tsuga caroliniana* releases were identified using the 10-year running mean method. Sample depth is the number of trees at least 10 years of age at the time.

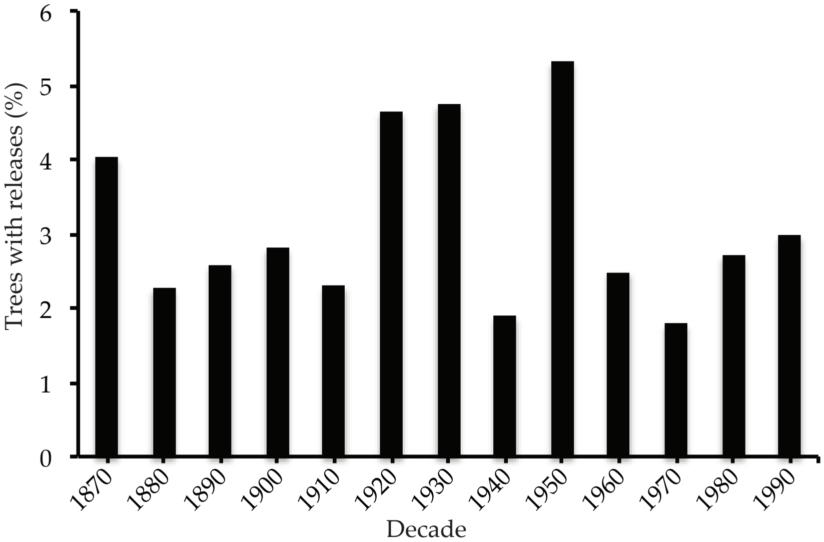

Figure 13. Release to sample depth ratio (%) by decade. Releases are identified using the 10-year running mean method. Sample depth is the number of trees at least 10 years of age at that time.

4.5 Foliar chemistry of Carolina hemlock

Pilot data from nine trees suggested that foliar chemistry is influenced by tree age. These results indicated that foliar N content increased with age ($R^2 = 0.56$) (Figure 14). The relationship between foliar C content and tree age was not significant (Figure 15). The foliar C:N ratio decreased with age (Figure 16). While the linear regression of the C:N ratio had a higher R^2 value than nitrogen, this is mainly a function of covariance between nitrogen and the C:N ratio.

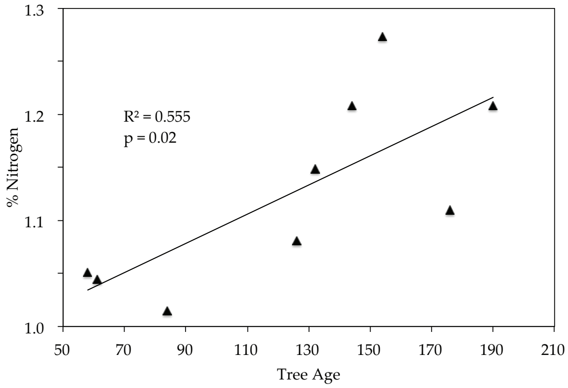

Figure 14. Scatterplot of *Tsuga caroliniana* tree age and foliar percent nitrogen.

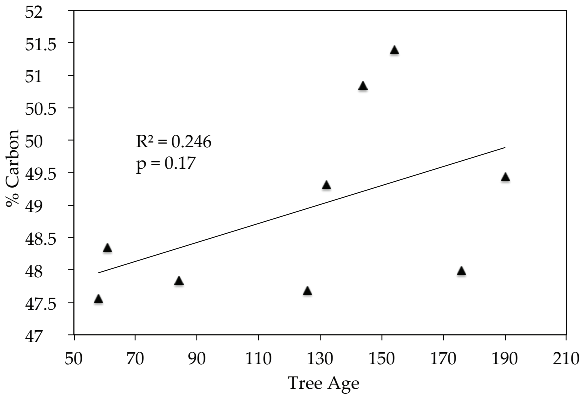

Figure 15. Scatterplot of *Tsuga caroliniana* tree age and foliar percent carbon.

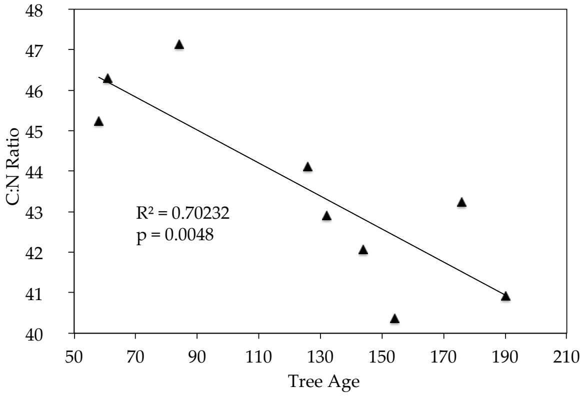

Figure 16. Scatterplot of *Tsuga caroliniana* tree age and foliar C:N ratio.

CHAPTER 5

DISCUSSION

5.1 Carolina hemlock forest development and succession

Although HWA has been present at Bluff Mountain since 2006, the forest composition and structure are still very similar to forest characteristics of a healthy Carolina hemlock forest at Bottom Creek Gorge, Montgomery County, Virginia reported by Rentch *et al.* (2000). Bluff Mountain and Bottom Creek Gorge had similar basal area, density, and importance values. The Carolina hemlock at Bluff Mountain have been impacted less than eastern hemlock forests that have been infested by HWA for five years (McClure, 1991; Orwig *et al.*, 2002). By collecting forest information at the beginning of an HWA infestation, this study provides critical information for establishing baseline data of Carolina hemlock forest stand structure and composition that will likely face drastic changes in the near future.

Carolina hemlock was the dominant species in both the overstory and understory, and is continuously regenerating successfully at the early onset of HWA. Carolina hemlock establishment at Bluff Mountain differs from the episodic recruitment reported by Rentch *et al.* (2000). Orwig and Foster (1998) reported an absence of hemlock in the understory. The Bluff Mountain Carolina hemlock forest is similar to Eschtruth *et al.* (2006), where a high density of hemlock was reported in the understory both before and after HWA infestation. Furthermore, deer herbivory does not appear to be limiting Carolina hemlock regeneration, despite being a preferred browse species (Rentch *et al.,* 2000). The lack of deer browse herbivory may be caused by the large predators that inhabit Bluff Mountain, such as black bear (*Ursa americanus* L.) and coyote (*Canis latrans* Say). The scat and tracks of both species were present within the study area.

The diameter distribution revealed a reverse J-shaped curve with the highest density of stems in the smaller size classes and a decline in density with increased tree size. The J-shaped curve is indicative of a regenerating forest (Abrams *et al.,* 2000; Hart *et al.,* 2008). I hypothesize that, if it were not for the HWA, hemlock would continue to shade out hardwood competition, become more dominant, and replace oak species as the stand continues to develop. The absence of oak species in the sapling stage indicates that oaks were not successfully regenerating. However, the forest composition is likely to change as Carolina hemlock continues to be affected by the HWA. The currently codominant oak species will likely claim the niche space created by HWA induced hemlock mortality and the Carolina hemlock forest will shift to an oak-dominated stand. A transition from a hemlock-dominated forest to a deciduous forest has been reported in New England by Orwig *et al.*

(2002), Eschtruth *et al.* (2006) and Orwig *et al*. (2008) and is likely to occur at Bluff Mountain with the removal of Carolina hemlock by HWA.

5.2 Diameter and age structure

The Carolina hemlock forest at Bluff Mountain has several characteristics of old-growth forest with gap-phase dynamics. The strong relationship between tree age and diameter at Bluff Mountain is indicative of an old-growth stand (Tyrell and Crow, 1994a; Hart *et al*., 2012). The Carolina hemlock forest is in a transition from mainly even-aged to an uneven-age stand (Tyrell and Crow, 1994a). The basal area at Bluff Mountain is also within the range reported for old-growth hemlock forests (Tyrell and Crow, 1994a; Hart *et al*, 2012). Furthermore, several trees are approximately 200 years old. While most of these trees are older oaks, there were older Carolina hemlocks reported by Humphrey (1989) at Bluff Mountain. I also observed several traits indicative of gap-phase dynamics. The stem density at Bluff Mountain is similar to those reported in younger stands (Tyrell and Crow, 1994a; Hart *et al*., 2012). Additionally, in old-growth hemlock forests, the distribution of stems is typically low across all sizes and has a unimodal distribution across all size classes (Tyrell and Crow, 1994a). The stem density and unimodal distribution are likely a result of frequent canopy disturbances. The exposed nature of Bluff Mountain makes trees prone to windthrow, which likely limits the frequency of trees reaching larger diameter classes. Therefore, the Carolina hemlock forest at Bluff Mountain resembles old-growth hemlock forests found in the southeastern United States.

5.3 Snag characteristics

One of the characteristics of old-growth forests is an abundance of coarse woody debris, including snags (Beane *et al*., 2010). I documented a high number of snags, 72 snags $ha^{-1} \geq 10$ cm dbh and 24 snags ≥ 30 cm dbh, over half of which were Carolina hemlock. Compared to old-growth eastern hemlock dominated forests, snag density and basal area at Bluff Mountain are more similar to mixed hemlock-hardwood old-growth stands (Tyrell and Crow, 1994a; Tyrell and Crow, 1994b; Beane *et al.,* 2010). The recent infestation of HWA and the lag between infestation and tree mortality, that usually represents five to ten years, suggests my results are representative of background mortality rather than HWA related mortality. I predict an increase in density and size of coarse woody debris caused by HWA.

5.4 Dendroclimatology

5.4.1 Age-related shifts in climate response

The climate-growth relationships of older Carolina hemlock at Bluff Mountain are similar to dendroclimatic studies on eastern hemlock (Abrams *et al.,* 2000; D'Arrigo *et al.,* 2001; Hart *et al.,* 2010). Carolina hemlock radial growth responds favorably to cool moist summers. Carolina and eastern hemlock respond similarly to cool moist summers despite differences in typical habitat and life histories. Bluff Mountain Carolina hemlock is located on the edge of a cliff and has a similar climate-growth relationship to low elevation cove forest typical of eastern hemlock (Cook and Jacoby, 1977; Abrams *et al.*, 2000; D'Arrigo *et al.*, 2001; Hart *et al.*, 2010).

One factor that contributes to age-related shifts in climate response is the Carolina hemlock trees' ability to respond to early summer conditions. Older trees respond to warmer conditions earlier in the growing season than younger trees (McMillan *et al.*, 2008; Rossi *et al.*, 2008; Copenheaver *et al.*, 2011). The longer growing season length of older trees may contribute to differences in growth response between varying age classes. The old chronology had significant relationships with May temperature, precipitation, and PDSI. The young chronology was only responsive to July temperature. The difference in summer temperature response between the young and old trees may be a function of differences in canopy structure. Canopy dominant trees intercept more incoming solar radiation than younger subcanopy trees that may create a lag between canopy and subcanopy temperatures.

Another factor that may cause age-related differences in climate response is differences in root biomass. Older Carolina hemlocks with larger root systems are more sensitive to soil moisture availability as measured by PDSI (Copenheaver *et al.*, 2011). Older trees have more established root systems at deeper soil levels. PDSI incorporates a modeled measure of moisture availability in the low soil levels that is similar to the conditions experienced by old trees with extensive root networks (Alley, 1984; Copenheaver *et al*., 2011). Younger trees typically have less biomass and less developed root systems (Copenheaver *et al*., 2011). Further investigation of soil depth variability at Bluff Mountain and age-related differences in root biomass would prove useful to understanding age-related radial growth differences in response to PDSI.

5.4.2 Disturbance reconstruction of Carolina hemlock

The lack of stand-wide disturbance events between 1870-2000 indicates that all release events were the result of single gap-scale canopy disturbances. Gap-scale disturbances result from damage or removal of a single or small group of canopy trees that only influences microenvironmental conditions (Nowacki and Abrams, 1997; Rubino and McCarthy, 2004; Hart *et al*, 2012). The 14 releases detected during the 1930s coincides with American chestnut [*Castanea dentata* (Marsh.) Borkh.] mortality from the chestnut blight (*Cryphonectria parasitica* Murr.) disease. The chestnut blight was reported in western North Carolina in 1926 (Elliott and Swank, 2008). The 1930s pulse in releases indicates that the chestnut blight may have reached Bluff Mountain during the late 1920s or early 1930s. Rentch *et al*. (2000) also speculate that chestnut blight occurred in a Carolina hemlock stand at Bottom Creek

Gorge, Virginia, based on an increased density of stems establishing in the 1930s. The diameter-age relationship at Bluff Mountain exhibits an increase in Carolina hemlock establishment during the 1950s, possibly from an increase in resources caused by the American chestnut mortality. The increase in establishment in the 1950s coincides with the decade with the most detected radial growth releases.

5.5 Foliar chemistry

The foliar analysis of tree ages (50–100, 100–150, and 150–200 years old) and nitrogen content shows a clear trend of increasing percent nitrogen and older tree age. The results of this study have implications for nutrient cycling in hemlock forests. A strong correlation exists between leaf chemistry and soil chemistry (Wardle *et al*., 2004). Understanding the influence of tree age on leaf chemistry will allow for improved understanding of nutrient cycling in maturing hemlock forests. Leaf litter with a low C:N value indicates that litter will decompose at a higher rate than litter with a high C:N value (Gholz *et al*., 2000). Furthermore, HWA infestation has been linked to increases in foliar N content (Pontius *et al.,* 2006). Hemlock mortality from HWA causes an increase in litter input, soil temperature, and light availability that produces elevated N mineralization rates (Jenkins *et al.,* 1999; Orwig and Foster, 2008). Raised N mineralization rates may lead to nutrient leaching, causing freshwater pollution, decreasing soil organic material quality and reduced future forest productivity (Jenkins *et al.,* 1999). The nine samples collected had HWA masses present and HWA was present on lower branches in all five plots. Future research examining the susceptibility of different aged trees to HWA would contribute to our understanding of nutrient cycling in endangered hemlock forests.

CHAPTER 6

CONCLUSION

I investigated the stand dynamics, disturbance history, climate-growth relationships, age-related differences in climate response, and foliar chemistry of Carolina hemlock at Bluff Mountain Nature Preserve, Ashe County, North Carolina. I found that, despite the arrival of HWA in 2006, the Carolina hemlock forest currently appears to be relatively unaffected. Carolina hemlock was still the dominant species in all stratums. Prior to HWA, the Carolina hemlock frequently experienced small-scale disturbance events and a large disturbance event that may have resulted from the removal of American chestnut by the chestnut blight fungus. Carolina hemlock mortality will increase with HWA pressure. As a result of HWA, disturbance frequency and magnitude will change and more resources will be available to hardwood species. Analysis of the climate-growth relationships indicates that Carolina hemlock prefers cool moist summer conditions and will likely be sensitive to increasing drought and temperature from climate change. The information gained from this study should be used by land managers to preserve this rare species.

6.1 Major Conclusions

1. The Carolina hemlock community will face changes in stand structure and composition as the HWA persists at Bluff Mountain, North Carolina.

Prior to the arrival of HWA, it appears that the Carolina hemlock was healthy and densely populated in the overstory and understory. Carolina hemlock was regenerating successfully and continuously between 1850-2010. The development of this old-growth Carolina hemlock forest will likely be halted by the HWA and result in an increase in northern red oak and white oak that resembles the forest community in other areas of Bluff Mountain. However, the removal of Carolina hemlock may also result in the increase of Catawba rhododendron and mountain laurel, preventing oak species from reestablishing in dense shade. The Carolina hemlock community at Bluff Mountain Nature Preserve should be continuously monitored to record changes in the forest's health and successional patterns.

2. Frequent small-scale canopy disturbances characterized the disturbance regime of Carolina hemlock at Bluff Mountain prior to the HWA.

Small-scale canopy disturbances appear to be a common occurrence among Carolina hemlock at Bluff Mountain. Small-scale canopy disturbances are likely a result of the exposed nature of the site, high wind, and icings that knock over snags and weakened trees in the Carolina hemlock forest. Based on the frequency of releases detected, canopy composition, and the abundance of seedlings and saplings, Carolina hemlock appears to be responsive to disturbance events and is capable of filling the canopy gaps with more Carolina hemlock. The frequency of releases detected in the 1930s indicate that Carolina hemlock may have claimed some of the niche space made available from the removal of American chestnut by the chestnut blight. Rentch *et al.* (2000) also speculated that removal of American chestnut by the Chestnut blight occurred in a Carolina hemlock forest at Bottom Creek Gorge, Montogomery County, Virginia. An increase in Carolina hemlock establishment and release events following the arrival of chestnut blight in western North Carolina and an increase in Carolina hemlock establishment in the 1950s suggest that American chestnut was removed from the Carolina hemlock forest at Bluff Mountain as well. However, it seems that Carolina hemlock may share the same fate as American chestnut and will be removed by the introduction of an exotic species. Information about the current disturbance regime will also be beneficial for establishing baseline information to monitor changes that may result from the large-scale removal of Carolina hemlock by the HWA.

3. Carolina hemlock radial growth at Bluff Mountain had a positive relationship with summer precipitation and PDSI and a negative relationship with summer temperature.

The strongest relationship between climate and radial growth observed was a positive relationship with summer PDSI and May precipitation. Carolina hemlock at Bluff Mountain benefited from moist summer conditions during the current year. The Carolina hemlock had an inverse relationship with summer temperature and preferred cool summer conditions. Further dendroclimatic studies of Carolina hemlock at different study sites will enable a regional understanding of the climate-growth relationship of the species throughout its range.

It is still unclear how precipitation regimes will change with a warming climate (Seagar *et al.,* 2009). The majority of global circulation models call for increases in drought while approximately one-third call for decreases or no change in the drought in the southeastern United States (Seagar *et al.,* 2009). Given the relationship between Carolina hemlock radial growth, summer PDSI, and precipitation, it is likely that an increase in drought would lead to reductions in growth and increase Carolina hemlock mortality. The small range and endemic distribution of Carolina hemlock make the species particularly vulnerable to climate shifts.

4. Tree age influences Carolina hemlock's climate response

Both the younger and older chronologies responded to average montly temperature. However, the older chronology responded to temperature two months earlier in the growing season than the younger chronology. Furthermore, the older chronology had significant relationships with precipitation and PDSI while the younger chronology did not. The older chronology was more responsive to PDSI than precipitation. Further research investigating age-related differences in root biomass and canopy structure would prove useful to determining a possible cause for the differences in response to precipitation and PDSI.

By understanding how Carolina hemlock responds to climate throughout its life, scientists can better differentiate the influence of climate during forest development. Incorporating dendroecological techniques into plant physiology studies enables scientists to examine processes using precise tree ages rather than relying on diameter as a proxy for tree age. By examining plant processes across a range of ages, scientists can determine when these processes may change and if the change is the result of endogenous or exogenous disturbance events.

5. Preliminary data suggests that foliar N content increases with tree age.

The results of my study indicate that foliar N content increases with tree age. It is possible that differences in HWA density may also influence foliar chemistry. Measuring HWA density and foliar chemistry may provide insight into the relationship between HWA feeding preference and foliar chemistry in a variety of age classes.

6.2 Future research and improvements

There are many areas of study that could build upon my research. Similar studies should be performed in other Carolina hemlock forests to allow for comparisons and expand the Carolina hemlock literature. Also, I did not investigate any of the Carolina hemlocks occurring on the cliff faces at Bluff Mountain. Cliff faces may provide older trees to extend the chronology (Larson, 2001). Incorporating cliff face ecology with my study would provide a more comprehensive understanding of the Bluff Mountain Carolina hemlock community.

My study investigating age-related shifts in foliar chemistry and climate would especially benefit from a greater sampling depth and investigating multiple species. Similar studies conducted with different species could determine if the shift in foliar chemistry and tree age is species-specific. Furthermore, analysis of foliar chemistry throughout the year would determine if Carolina hemlock foliar chemistry is stable throughout the year. Analyzing the climate-growth relationship of the northern red oak and white oak at Bluff Mountain would determine if there are species-specific differences in climate response. This would allow insight into the species' growth strategies. Future research at the Bluff Mountain should also include a disturbance reconstruction using oak species. This would prove useful to monitor the disturbance regime as Carolina hemlock is removed by the HWA and to compare species-specific differences in disturbance reconstructions.

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BIOGRAPHICAL SKETCH

David Austin was born on 2 August 1985 in Florence, Alabama. His parents, Rick and Linda Austin, raised him and his two older siblings, Jeff and Sharon. He has a life partner, Emily Thompson, and an inquisitive daughter named Lily. He began college to pursue a degree in finance, later to realize he was more intrigued by the natural world than financial statements. He began pursuing a Bachelor of Science degree with a major in Geography and graduated from the University of North Alabama in 2010. While studying Geography, he developed an interest in forest ecology and dendrochronology, and worked for Dr. Justin Hart as a research assistant. He continued to pursue his interests as a master's degree student at Appalachian State University and worked in the Appalachian Tree Ring Lab. He was awarded an out-of-state tuition waiver, the *Julian Yoder Fellowship in Geography,* the *Stephen Vacendak Fellowship in Geography*, and a National Science Foundation funded research assistantship by the Department of Geography and Planning, as well the Graduate Research Associate Mentoring (GRAM) award by the Cratis D. Williams Graduate School and Office of Research and Sponsored Programs to support his graduate education research interests. David earned the degree Master of Arts in Geography from Appalachian State University in August 2012.