TSUGA CANADENSIS (EASTERN HEMLOCK) IN THE SOUTHERN APPALACHIAN MOUNTAINS: FOREST-ENVIRONMENT RELATIONSHIPS, REGENERATION DYNAMICS, AND DISTURBANCE REGIMES

by

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(Under the Direction of Albert J. Parker)

ABSTRACT

The goal of this research is to provide baseline data on the compositional characteristics, regeneration dynamics, and disturbance regimes of *Tsuga canadensis* forests in the southern Appalachian Mountains prior to large-scale forest alterations induced by climatic changes and hemlock woolly adelgid (*Adelges tsugae* Annand.) infestation. To achieve this goal, I established 50 plots within mature *Tsuga canadensis* forests of Great Smoky Mountains National Park (GSMNP), a landscape of biogeographical importance because it is situated near the southern range terminus of *Tsuga canadensis*. Cluster analysis identified four *Tsuga canadensis* forest types, which differed compositionally and environmentally in terms of slope aspect, litter depth, tree species richness and diversity. Detrended correspondence analysis (DCA) identified landscape-scale gradients in *Tsuga canadensis* forest composition and regeneration, reflecting differences in soil nutrient availability and sand content, and geographical location. Models relating *Tsuga canadensis* regeneration to site factors emphasize understory *Rhododendron maximum* cover, litter depth, soil nutrient availability and sand content as important controls on seedling and sapling abundance. Local indices of dispersion indicate significant within-plot spatial aggregation of regeneration. Models relating the local indices of dispersion to site factors show that the spatial aggregation of regeneration is controlled by soil nutrient availability, canopy disturbance, and geographical location. These results elucidate the contrasting suites of forest-environmental factors controlling the abundance and spatial pattern of regeneration, and that these controls shift in importance as seedlings and saplings grow larger. Forest-environmental characteristics from a subset of four forest stands in the Cataloochee Watershed of GSMNP show that sites with successful *Tsuga canadensis* regeneration are located above 1000 m in elevation on well-drained, moderately steep slopes and have the greatest canopy openness. Structural characteristics and disturbance regimes at these four forest stands elucidate a history of more or less continuous regeneration at sites where *Tsuga canadensis* seedling and sapling establishment is currently successful. Moreover, disturbance chronologies show that forest stands with successful *Tsuga canadensis* regeneration are disturbed more frequently by canopy disturbance events, especially those of moderate intensity.

INDEX WORDS: *Tsuga canadensis*, Eastern hemlock, Hemlock-hardwood forest, Forest-environment relationships, Tree regeneration, Old-growth forest, Spatial pattern, Canopy dynamics, Disturbance regimes, Appalachian Mountains

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DEDICATION

This dissertation is dedicated to Mother Earth for providing me with wonderful places to live, work, and play.

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CHAPTER 1

INTRODUCTION

At its roots, ecosystem management depends on empirical research. Two of the main foci of ecosystem management involve data collection/research and the maintenance of ecological integrity (Grumbine 1994). There exists a critical need to provide baseline data and research that will allow land managers to maintain biodiversity and the ecological patterns and processes supporting this diversity. The overall purpose of this dissertation is to provide the necessary data and research so that land managers may better manage eastern hemlock (*Tsuga canadensis* (L.) Carr.) forests and, in turn, maintain biological diversity in the southern Appalachian Mountains. Specifically, this research seeks to characterize the overstory composition, regeneration and disturbance dynamics of *Tsuga canadensis* forests in the southern Appalachian Mountains. This baseline information will be valuable for effectively managing *Tsuga canadensis* forests now, and can aid forest restoration programs in the future as the species recovers from the much anticipated decline forecasted to occur with the spread of hemlock woolly adelgid (*Adelges tsugae* Annand) across its range. The present study is also biogeographically interesting because it examines *Tsuga canadensis* near its southern range boundary, which to date has been understudied when compared to more northern areas such as the Great Lakes region and New England. As Yost et al. (1994) commented, results from more northern locations may not pertain to the southern Appalachian Mountains.

Tsuga canadensis, commonly known as eastern hemlock, is a slow growing and shade-tolerant coniferous tree species of eastern North America. Individuals have survived in a suppressed state for over 200 years, and it is common for tree ages to approach 400 years in many forest stands (Godman and Lancaster 1990). The northern limit of *Tsuga canadensis* ranges from Ontario to Novia Scotia, Canada. In the United States, the species can be found from Minnesota to Maine and throughout the Appalachian Mountains to northern Georgia and Alabama. Disjunct populations of *Tsuga canadensis* exist to the east and west of this range (Figure 1.1). *Tsuga canadensis* can be found from approximately 600 to 1500 m in elevation on cool and moist, north-facing slopes. The species also tends to occur within valleys, ravines, and on rock outcroppings (Little 1998; Kemp 1998). In Great Smoky Mountains National Park (GSMNP), location of the current research, Johnson et al. (2000) estimated that *Tsuga canadensis* forests occupy 1528 ha of the park, with many of these areas harboring trees exceeding 400 years of age. *Tsuga canadensis* throughout its range is currently facing an imminent threat from a non-native insect pest from Asia, the hemlock woolly adelgid, which can cause tree death within four years (McClure 1991), and 50-100% *Tsuga canadensis* mortality in invaded stands (Orwig and Foster 1998; Orwig et al. 2002). While no widespread mortality has been observed in GSMNP, many areas are experiencing stress and decline as a result of hemlock woolly adelgid infestation. Clearly, baseline data on *Tsuga canadensis* forest composition, regeneration and dynamics is necessary to effectively manage, and if possible restore, these forest systems now and in the future.

The Society of American Foresters recognizes *Tsuga canadensis* as a major component of four forest cover types in the northern and central forest regions: *Tsuga canadensis*, *Tsuga canadensis-Betula alleghaniensis* Britt., *Pinus strobus* L.-*Tsuga canadensis*, and *Liriodendron tulipifera* L.-*Tsuga canadensis*. The species is also a common associate in seven other forest types and a minor component of 18 more types (Godman and Lancaster 1990). In the southern Appalachian Mountains, researchers have documented the occurrence of the *Tsuga canadensis*, *Tsuga canadensis-Betula alleghaniensis*, and *Liriodendron tulipifera-Tsuga canadensis* forest types (Callaway et al. 1987; MacKenzie and White 1998; Elliott et al. 1999). The *Pinus strobus-Tsuga canadensis* forest type has not been reported. The present study supports these findings, but further distinguishes the *Tsuga canadensis*-mesic and *Tsuga canadensis*-submesic forest types.

Many researchers have mentioned that *Tsuga canadensis* is failing to regenerate in certain areas, and have attributed this to a variety of causes, including lack of an adequate seed source, climate, substrate availability, mammal browsing pressure, and disturbance (e.g. Frelich and Lorimer 1985; Parshall 1995; Waller et al. 1996; Rooney and Waller 1998; Rooney et al. 2000). *Tsuga canadensis* regenerates most successfully when a good seed crop coincides with a series of moist years. The rate of germination is reduced under dry conditions, and because the species is slow growing and shallow rooted, it is highly susceptible to desiccation (Olsen et al. 1959; Coffman 1978). This is especially true of seedlings that established on leaf litter, which prevents root penetration to moist mineral soil (Barnes 1991). Decaying wood is often mentioned as an important regeneration substrate which retains moisture and promotes the growth of mycchorizae (Stearns 1951; Rooney and Waller 1998). It is also claimed that this elevated substrate type relieves seedlings of ground competition from other forest species

(Waller et al. 1996; Rooney and Waller 1998). Similar findings have been reported for microtopographic mounds, which have been found to provide open, moist mineral soil and relief from deer browsing (Long et al. 1998). The present study did not find a significant link between *Tsuga canadensis* regeneration and decaying wood or microtopographic mounds, and instead found associations between regeneration and geographical, vegetation and soil factors. White-tailed deer (*Odocoileus virginianus* Zimmermann) browsing has often been reported to be reducing the recruitment of *Tsuga canadensis* seedlings into larger size-classes (Anderson and Loucks 1979; Frelich and Lorimer 1985; Alverson et al. 1988; Waller et al. 1996). Rooney et al. (2000) found that only medium to large-size saplings were significantly affected by deer browsing. However, Hart and Shankman (2005) reported no evidence of deer browsing in *Tsuga canadensis* populations of northern Alabama, nor was there evidence of it in the current study. Browsing pressure appears to be context dependent, and more chronic in northern areas where browsing by deer is primarily a winter activity (Mladenoff and Stearns 1993). The availability of many other preferred browse species and relatively mild winters may be why deer browsing of *Tsuga canadensis* is not a problem in the southern Appalachian Mountains. Furthermore, Mladenoff and Stearns (1993), using a LINKAGES model of forest dynamics, found that even without browsing, *Tsuga canadensis* will decline in importance over time in the Great Lakes region. They suggested that other factors, namely site, climate, and disturbance, are limiting *Tsuga canadensis* regeneration. In addition to the aforementioned need for research on *Tsuga canadensis* forest composition and environmental characteristics, more research on the regeneration dynamics of *Tsuga canadensis* is necessary as most of our knowledge concerning the regeneration of this species comes from the Great Lakes region.

Not only does it appear that successful *Tsuga canadensis* regeneration requires an adequate seed crop and subsequent moist years, but forest disturbances also seem to be important. *Tsuga canadensis* tends to regenerate via gap-phase processes where canopy gaps are created by local-scale, noncatastrophic disturbances involving single or multiple canopy tree mortality events such as blowdowns. Canopy gap creation increases light and nutrient availability at the forest floor. Indeed, local-scale, gap processes are seen as necessary for the regeneration of shade tolerant tree species such as *Tsuga canadensis* (Runkle and Yetter 1987). Research from both the Great Lakes region and southern Appalachian Mountains support this notion by showing that *Tsuga canadensis* regeneration is associated with gaps, especially young gaps, and that the species can increase in dominance across size-classes independent of major disturbances (Runkle 1998; Woods 2000a, 2000b). The current study, which examines the structure and canopy dynamics of *Tsuga canadensis* forests in the southern Appalachian Mountains, supports these findings by showing that sites with more continuously successful regeneration tend to be more frequently disturbed by canopy disturbance events.

The overall goal of this research is to provide baseline data on *Tsuga canadensis* forests of the southern Appalachian Mountains. In pursuit of this goal, this research explores three main aspects of *Tsuga canadensis* forests, namely their overstory composition, regeneration and disturbance dynamics. Chapter 2 describes the compositional and environmental characteristics of these forests. This chapter delineates four types of *Tsuga canadensis* forests and their environmental characteristics in the southern Appalachian Mountains. Chapter 3 examines the spatial structure and environmental controls of *Tsuga canadensis* regeneration, thus elucidating the forest-environmental factors that control regeneration abundance and spatial pattern.

Finally, Chapter 4 characterizes the structure and dynamics of *Tsuga canadensis* forests in the southern Appalachian Mountains. This chapter elucidates a link between canopy dynamics and *Tsuga canadensis* regeneration in the southern Appalachian Mountains. For figures illustrative of *Tsuga canadensis* forest conditions, see Appendix A.1-6.

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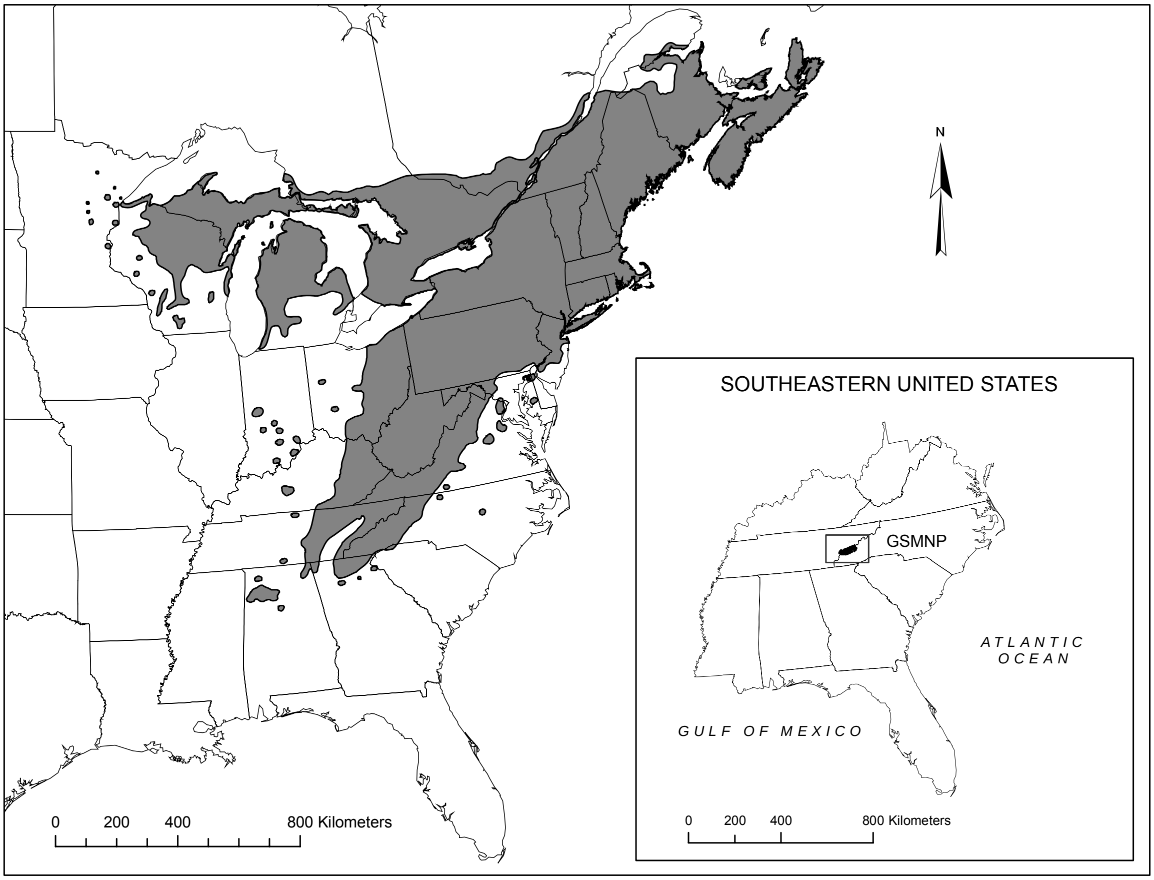

Figure 1.1. Map showing the range of *Tsuga canadensis* (L.) Carr., including southern Canada and the United States.

CHAPTER 2

COMPOSITIONAL AND ENVIRONMENTAL CHARACTERISTICS OF *TSUGA CANADENSIS* (L.) CARR. FORESTS IN THE SOUTHERN APPALACHIAN MOUNTAINS

Introduction

Although general forest patterns in the southern Appalachian Mountains have been well documented, there is a dearth of studies that specifically quantify and describe the compositional and environmental characteristics of eastern hemlock (*Tsuga canadensis*) forests in this region. Therefore, most of our knowledge concerning *Tsuga canadensis* forests comes from studies examining general forest patterns (e.g. Whittaker 1956; Golden 1981; Callaway et al. 1987; MacKenzie and White 1998; Elliott et al. 1999) or research in more northern locales (e.g. Brown et al. 1982; Foster 1988; Mahan et al. 2004). With the invasion of southern *Tsuga canadensis* forests by the hemlock woolly adelgid (*Adelges tsugae* Annand), an exotic insect pest that has caused 50-100% mortality in invaded stands of the northeastern United States (Orwig and Foster 1998; Orwig et al. 2002), it is imperative that we document the compositional and environmental characteristics of these forests to serve as a baseline for management and future vegetation change.

Historically, *Tsuga canadensis* was valued by the tanning industry for the tannins within its bark, and by the paper industry as a source of pulp. *Tsuga canadensis* is still used in the pulp and paper industry, but other values have now eclipsed these traditional extractive uses.

Contemporary *Tsuga canadensis* forests are now more valued as wildlife habitats, and for their aesthetic and recreational qualities (Godman and Lancaster 1990; Mahan et al. 2004). This is especially true of *Tsuga canadensis* forests with old-growth characteristics, or those located in protected areas such as Great Smoky Mountains National Park (GSMNP). To date, the responses of forest ecosystems to the selective removal of a dominant species such as *Tsuga canadensis* are poorly understood (Castle et al. 1995; Orwig and Foster 1998; Orwig et al. 2002). In the northern United States and adjacent parts of Canada, opportunistic native hardwood and invasive or exotic species have become established in the resulting canopy gaps caused by stand-wide *Tsuga canadensis* dieback (Hannah 1999; Orwig and Foster 1998; Parshall 1995). By documenting the characteristics of *Tsuga canadensis* forests in the southern Appalachian Mountains, this study will provide valuable baseline data on these forests for future monitoring and management efforts. Indeed, climatic changes or hemlock woolly adelgid induced mortality may have significant impacts on these forest communities and the species they support (Godman and Lancaster 1990; Mitchell 1999; Snyder 2000). In the southern Appalachian Mountains, some *Tsuga canadensis* forests have been treated for the hemlock woolly adelgid via local applications of pesticides or the introduction of predator beetles (*Pseudoscymnus tsugae* Sasaji and McClure) as a biological control; in addition to the baseline data on forest conditions, this study may prove useful as a standard for evaluating the effectiveness of various hemlock woolly adelgid control programs.

The overall objective of this research was to describe the compositional and environmental characteristics of *Tsuga canadensis* forests in the southern Appalachian Mountains. Two specific research questions were posed: 1) What is the nature of overstory compositional variability within *Tsuga canadensis* forests of the southern Appalachian

Mountains?; and 2) What vegetation-environment factors are controlling the distribution of *Tsuga canadensis* forest types in the southern Appalachian Mountains?

Study Area

I conducted this study within GSMNP, USA, which encompasses 212, 460 ha of land in the southern Appalachian Mountains of eastern Tennessee and western North Carolina (between Abram's Creek at 35° 36', 83° 51', and Mt. Cammerer at 35° 45', 83° 9') (Figure 2.1). The Great Smoky Mountains are a part of the Blue Ridge physiographic province, and are characterized by rugged, highly variable terrain. Elevations within GSMNP range from 256 m at Abrams Creek to 2025 m at the summit of Clingman's Dome. Annual precipitation varies from 1651 mm in the lowlands to 2235 mm at the highest elevations.

GSMNP was established in 1934 and was later designated an International Biosphere Reserve (1976) and a World Heritage Site (1983). World renowned for its biodiversity, GSMNP contains as many as 130 tree species. At the highest elevations (above 1300 m) *Picea-Abies* forest is dominant. As elevation decreases, the *Picea-Abies* forest type blends into northern hardwoods. Northern hardwoods dominate the middle elevations (1000-1500 m) with *Tsuga canadensis* being locally important, especially in proximity to streams. On drier mid-to-low elevation slopes a *Pinus-Quercus* forest persists. Despite abundant precipitation, areas supporting the *Pinus-Quercus* type are typically well-drained with fires being a common occurrence. At the lowest elevations, cove hardwoods come to dominate on moist sites. Cove hardwood forests are the most diverse type within GSMNP and can have a well developed *Tsuga canadensis* component. It is estimated that there are approximately 1,528 ha of *Tsuga canadensis* forests within GSMNP (Johnson et al. 2000).

Methods

Sampling was restricted to mature *Tsuga canadensis* stands with homogenous site conditions. I located stands using GSMNP maps (Madden et al. 2004), communication with park personnel, and observational field evidence. Sites were accessed by trail or road.

Vegetation Data

I used 14x21 m plots, comprised of a 2x3 arrangement of 7x7 m quadrats to sample vegetation at each site (after Rooney and Waller 1998; Rooney et al. 2000). A total of 50 plots were established throughout the park. Within the quadrats of each plot, all tree species ≥ 5 cm diameter at breast height (dbh = 1.4 m) were inventoried. The presence/absence of decaying wood and litter depth were recorded within the quadrats of each plot; these values were then used to calculate the occurrence of decaying wood, expressed as a percent of quadrats within a plot, and average plot litter depth. The percent cover of *Rhododendron maximum* and *Kalmia latifolia* was estimated using the line-intercept method along the central and perimeter long axes of the plots, providing 63 m of line measurement at each site. To obtain an estimate of canopy openness, a hemispherical canopy photograph was taken at the center of each plot. Canopy photographs were converted to greyscale images and the Desktop Mapping System (DMS) (R-Wel 2005) was used to generate greyscale statistics. I estimated percent canopy openness by bifurcating the greyscale values and calculating the proportion of white (open) versus grey (closed) pixels.

Environmental data

From the center of each plot, I recorded location and topographic parameters: Universal Tranverse Mercator (UTM) coordinates, slope position, slope aspect, slope steepness, slope configuration, and elevation. Slope aspect was transformed to a linear scale ranging from 0.00

(SW aspect) to 2.00 (NE aspect) (Beers et al. 1966). A Garmin 76 hand-held Global Positioning System (GPS) was used to record location and elevation (accuracy = 9 to 12 m), while slope aspect and steepness were measured with a Brunton compass. Slope configuration (straight, concave, convex) and position (upper, middle, or lower) were visually assessed from plot center. I used the topographic parameters to calculate a topographic relative moisture index (TRMI: Parker 1982). The TRMI values range from 0 to 60 with higher values indicating more mesic conditions. The presence/absence of microtopographic mounds was recorded in each 7x7 m quadrat and used to calculate the percent occurrence of that substrate within the plots.

A soil sample was taken at 0-10 cm depth from the center of each plot for physical and chemical analyses. I conducted tests for organic matter content, percent sand, and pH within the Geomorphology Laboratory at the University of Georgia, Department of Geography. Tests for percentages of phosphorus, potassium, magnesium, calcium, aluminum, carbon, and nitrogen were performed by the Analytical Chemistry Laboratory at the Institute of Ecology, University of Georgia. Organic matter content was determined by loss-on-ignition from a five gram sample of soil. A sample of soil was suspended in sodium metaphosphate and wet sieved to determine the percentage of sand. Soil acidity was measured with an electronic pH meter in a 1:3 mixture of soil and distilled water. This mixture was necessary because of the high organic matter content of the soils. Flame atomic absorption spectrophotometry was used to determine the percentages of aluminum, calcium, magnesium, and potassium. The percentage of phosphorus was determined by continuous flow colorimetric analysis. Total carbon and nitrogen were determined by micro-Dumas combustion analysis. The percentages of total carbon and nitrogen were used to calculate a carbon/nitrogen ratio for each plot.

Statistical methods

I calculated relative density, relative dominance, and importance value for each tree species inventoried within the study plots. Importance values represent the average of relative density and relative dominance. A matrix of importance values for each tree species by plot was used for all classification and ordination procedures (PC-ORD, version 4.0, McCune and Mefford 1999). No sample plots or species were eliminated prior to analyses.

Ward's method of cluster analysis, also known as minimum variance clustering, was used to classify study sites into forest types. Ward's method is a hierarchical, agglomerative technique that creates clusters of study sites by minimizing the total within-group variance (Tongeren 1995; Legendre and Legendre 1998). I chose this method of cluster analysis because it created the least amount of chaining, thus producing the most ecologically interpretable results. Forest types were delineated by natural breaks in the cluster dendrogram. Analysis of variance (ANOVA) and Bonferroni multiple comparison tests were used to explore significant differences between forest types.

Detrended correspondence analysis (DCA) (Hill and Gauch 1980) was used to arrange study sites according to compositional similarity. DCA was appropriate for this study because the focus was on characteristics of forest composition, and environmental factors were not able to explain compositional variation in constrained ordination adequately. Species importance values and environmental variables were correlated (Spearman's rho) with the DCA axes scores to elucidate compositional and environmental gradients (ter Braak 1995). ANOVA, Bonferroni multiple comparison tests, and Spearman's rho correlations were calculated using Stata release 8 (StataCorp 2003).

Results

Forest classification

Ward's method of cluster analysis yielded four forest types. These forest types were named on the basis of species importance values, and where necessary, moisture status. The four forest types were: *Tsuga canadensis*/*Betula*/*Acer rubrum* (N = 17); *Tsuga canadensis*/*Liriodendron tulipifera*/*Halesia carolina* (N = 6); *Tsuga canadensis*-Mesic (N = 22); and *Tsuga canadensis*-Submesic (N = 5) (Table 2.1).

Tsuga canadensis/*Betula*/*Acer rubrum* forests occurred at the highest elevations (mean = 1037 m, cv = 23.3%) with *Tsuga canadensis*, *Betula* sp., and *Acer rubrum* as canopy dominants (Table 2.2, 2.3). Although *Tsuga canadensis* was among the canopy dominants in this forest type, its importance was less than in the other types. Forest stands of this type were characterized by greater canopy openness and deeper litter layers (mean = 22.6 mm, cv = 31.6%) than the other three types. Tree species richness and diversity was high in this forest type. A relatively dense *Rhododendron maximum* understory was common.

Tsuga canadensis/*Liriodendron tulipifera*/*Halesia carolina* forests were not well represented in this dataset; however, they were distinguished from *Tsuga canadensis*/*Betula*/*Acer rubrum* forests by the presence of *Liriodendron tulipifera* as the leading canopy dominant. Indeed, aside from *Tsuga canadensis*, *Liriodendron tulipifera* in this forest type achieved the highest importance value of any tree species among all forest types. Average stand density, basal area, tree species richness and diversity, and *Rhododendron maximum* cover were highest in this forest type. Soils on these sites were characterized by having high concentrations of aluminum, low pH, and low carbon/nitrogen ratios. The soils of this type also had somewhat higher concentrations of sand in the surface soil layer than the other forest types.

Tsuga canadensis-Mesic forests were dominated by *Tsuga canadensis* with *Betula* sp. and *Halesia carolina* as common associates. Although *Acer saccharum* was uncommon in the *Tsuga canadensis* forests encountered in this study, it did reach its highest density and importance value in this forest type. Similar to the two previously described forest types, a dense *Rhododendron maximum* understory was common. Stands of this type were found on more mesic northeasterly aspects, and the average occurrence of microtopographic mounds was greatest in this forest type. Soils of this type had the highest concentrations of calcium and magnesium among the forest types.

Tsuga canadensis-Submesic forests were not well represented in this dataset, but were dominated by *Tsuga canadensis* to the near exclusion of other species. *Kalmia latifolia*, though uncommon throughout the study sites, exhibited its highest cover in these drier areas; *Rhododendron maximum* cover was substantially lower in this forest type than the others. Stands of this type had the lowest stand densities and tree species richness (mean = 2.2 species per stand, cv = 59.3%) among the forest types. These stands were found at relatively high elevations and on more xeric, steep slopes. The soils were characterized by having the highest pH levels, the most available phosphorus, and the highest carbon/nitrogen ratios. Soils of this association also had the least amount of sand and the highest organic matter percentages in the surface soil layer. The presence of decaying wood was highest in these stands.

Forest-environment relationships

The first DCA axis (DCA 1) was negatively correlated with the importance values of *Tilia americana*, *Liriodendron tulipifera*, *Rhododendron maximum*, *Halesia carolina*, *Acer saccharum*, and *Aesculus flava* (Table 2.4). Positive correlations were observed between DCA 1 and the importance values of *Betula* sp. and *Acer rubrum*. Therefore, DCA 1 separated *Tsuga* *canadensis* forests with northern hardwood affinities from those with cove hardwood affinities; DCA 1 also separated mesic plots from sub-mesic plots. The structure of DCA 1, with an eigenvalue of 0.27, suggests that there are latitudinal and soil gradients linked with the compositional variability among *Tsuga canadensis* forests in GSMNP (Figure 2.2; Table 2.5). DCA 1 arranged plots along soil gradients reflecting carbon/nitrogen ratios, with higher values found at mesic sites, and soil sand content, which was lower at mesic sites. A latitudinal gradient was also present along DCA 1 (r = -0.28), representing changes in species composition across the mountains from Tennessee to North Carolina.

The second DCA axis (DCA 2) was negatively correlated with the importance values of *Betula* sp., *Magnolia fraseri*, *Kalmia latifolia*, *Liriodendron tulipifera*, and *Rhododendron maximum*. The importance values of *Tilia americana*, *Tsuga canadensis*, *Halesia carolina*, *Acer pensylvanicum*, and *Acer saccharum* were positively correlated with DCA 2. Therefore, DCA 2 provided separation between forests with a greater *Tsuga canadensis* component and northern hardwood affinities from those forests with less *Tsuga canadensis* and more cove hardwood affinities. DCA 2 also separated *Tsuga canadensis* forests with a more developed *Rhododendron maximum* or *Kalmia latifolia* understory from those with a less developed evergreen understory. With an eigenvalue of 0.22, DCA 2 suggests gradients of canopy openness and soil characteristics linked with the compositional variability among *Tsuga canadensis* forests of GSMNP. DCA 2 separated more open sites with sandy, nutrient-poor soils from closed canopy sites with more fine-grained, nutrient-rich soils.

Discussion

In the southern Appalachian Mountains, *Tsuga canadensis* forests were found between 500 and 1400 m elevation, and on sites ranging from lower to upper slopes with concave to convex configurations. *Tsuga canadensis* varied in importance within these forests and was commonly associated with *Betula* sp., *Fagus grandifolia*, *Liriodendron tulipifera*, *Acer rubrum*, and *Halesia carolina*. The understory was often dominated by a dense cover of *Rhododendron maximum*.

The *Tsuga canadensis* forest types identified in this study were in general agreement with those of other studies from the area, but some differences were apparent. Miller (1938) and Whittaker (1956) only recognized generic *Tsuga canadensis* forest types, but these were comparable to the types found in other studies within the southern Appalachian Mountains (MacKenzie and White 1998). The present study supported the existence of the *Tsuga canadensis*/*Acer rubrum* and *Tsuga canadensis* types in the southern Appalachian Mountains; a *Tsuga canadensis*/*Halesia carolina* type was not apparent. However, *Halesia carolina* was a minor associate of the *Tsuga canadensis*/*Betula*/*Acer rubrum*, *Tsuga canadensis*-Mesic, and *Tsuga canadensis*-Submesic types identified in this study. This study also supported the existence of a *Tsuga canadensis*/*Liriodendron tulipifera* forest type which was not identified in Golden (1981), but was present in Callaway et al. (1987) and MacKenzie and White (1998). MacKenzie and White (1998) did make comparisons between their *Tsuga canadensis*/*Liriodendron tulipifera* type and the generic *Tsuga canadensis* types of Golden (1981), Miller (1938), and Whittaker (1956). This type has been found in other areas of the southern Appalachian Mountains with some variation in compositional importance between species (Abella et al. 2003; Elliott et al. 1999). Although *Fagus grandifolia* was present across all forest types, excluding the *Tsuga canadensis*-Submesic type, its importance was much less significant than in the previous studies. This may be the result of beech bark disease (*Nectria* sp.), which has killed many individuals throughout the species range. Indeed, *Fagus grandifolia* snags and coarse woody debris were conspicuous in several stands. The discrepancies in these findings may also be the result of differences in sample selection and area: the present study targeted *Tsuga canadensis* stands throughout GSMNP, while the former studies surveyed all forest types within the central (Golden 1981; Whittaker 1956) and western (Callaway et al. 1987) portions of the park. However, MacKenzie and White (1998) did examine data collected across the entire GSMNP landscape, which was part of a vegetation survey during the establishment of the park in the 1930s.

Tsuga canadensis forest types showed overlap in species composition and environment. This was partly explained by the variety of sites on which *Tsuga canadensis* was prominent in the area. The DCA axes did show some compositional distinctness, which can be partially attributed to the varied importance of *Tsuga canadensis* in each of the four types recognized in this study. It also shows the moderate influences of soil characteristics and latitude on *Tsuga canadensis* forest composition. DCA 1 separated *Tsuga canadensis* forests with a northern hardwood component from those with a cove hardwood component, while also distinguishing submesic from mesic forests. DCA 2 separated *Tsuga canadensis* forests with greater canopy openness and lower soil nutrient availability from those with more closed canopies and increased soil fertility. Although the environmental variation encountered within this study was not great enough to explain a significant amount of the compositional differences between plots, slope aspect, litter depth, tree species richness and diversity, were significantly different between forest types.

Some researchers in the region have discussed past land-use histories and stand dynamics as important factors in the explanation of tree distribution (Callaway et al. 1987; Elliott et al. 1999; Runkle 1982). Callaway et al. (1987) concluded that the *Liriodendron tulipifera* forests types of GSMNP would probably become *Tsuga canadensis*/*Liriodendron tulipifera* stands without human influence. The *Tsuga canadensis*/*Liriodendron tulipifera* stands in this study appeared to be the least disturbed and harbored some of the largest trees out of all 50 study sites; however, the presence of *Liriodendron tulipifera* is indicative of past disturbances at these sites. Indeed, Runkle (1998) found that *Liriodendron tulipifera* was associated with larger and older canopy gaps. The *Tsuga canadensis*/*Halesia carolina*/*Fagus grandifolia* forest type of Callaway et al. (1987) may also be a product of human disturbance. This type was most comparable to the *Tsuga canadensis*/*Betula*/*Acer rubrum* forest type of the present study. *Acer rubrum* and *Betula* sp. were clearly more important in this forest type than the others, and it is well known that these species benefit from disturbances. These disturbances could have come from more natural causes such as windthrow, which would create single or multiple tree gaps and provide open regeneration sites for species. Alternatively, the disturbances could have come from the dieback of *Castanea dentata* or *Fagus grandifolia* within the stand. For example, Golden (1981) found that the presence of dead *Castanea dentata* remains in his study sites was the most significant variable in a discriminant analysis of forest types. The evaluation of these types of disturbances and their influences on *Tsuga canadensis* forest dynamics awaits further research.

With mortality induced by the exotic hemlock woolly adelgid, hardwood species such as *Acer* sp., *Betula* sp., *Fagus grandifolia*, *Halesia carolina*, and *Rhododendron maximum* may establish in the resultant canopy gaps. The expansion of *Rhododendron maximum* is especially problematic because it often precludes the regeneration of canopy species (Monk et al. 1985;

Hedman and Van Lear 1995; Van Lear et al. 2002). Shade-intolerant species such as *Liriodendron tulipifera* could be eliminated from the canopy while recruitment of shade-tolerant species such as *Acer* sp. may be significantly reduced. Because *Tsuga canadensis* has been reported to be the only tree species capable of successful regeneration in dense *Rhododendron maximum* cover (Van Lear et al. 2002), it is possible that many of these forests may become monotypic stands of *Rhododendron maximum* in the future, with the loss of *Tsuga canadensis* to the hemlock woolly adelgid.

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Table 2.1. Tree species ≥ 5.0 cm dbh by forest type. Columns refer to density (D; stems/ha), basal area (BA; m^2/ha), and importance value (IV = [relative density + relative basal area]/2).

	Tsuga canadensis/Betula/ Acer rubrum (N = 17)			*Tsuga canadensis/ Liriodendron tulipifera/Halesia carolina* (N = 6)			*Tsuga canadensis*-Mesic (N = 22)			*Tsuga canadensis*-Submesic (N = 5)		
Species	D	BA	IV	D	BA	IV	D	BA	IV	D	BA	IV
Acer pensylvanicum L.	20.0	0.3	1.8	39.7	0.2	3.1	15.5	0.1	1.5	6.8	0.0	0.9
Acer rubrum L.	28.0	7.9	9.7	11.3	0.6	1.2	7.7	1.3	1.6	0.0	0.0	0.0
Acer saccharum Marsh.	8.0	0.0	0.7	11.3	0.9	1.4	20.1	1.5	2.9	0.0	0.0	0.0
Aesculus flava Ait.	10.0	1.6	2.3	0.0	0.0	0.0	1.5	0.0	0.1	0.0	0.0	0.0
Amelachier laevis Wieg.	2.0	0.3	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Betula sp.	62.0	7.1	11.6	11.3	0.2	1.0	37.1	3.6	5.9	6.8	0.4	1.2
Cornus alternifolia L. f.	2.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fagus grandifolia Ehrh.	42.0	0.7	3.9	17.0	0.5	1.6	18.6	2.7	3.6	0.0	0.0	0.0
Halesia carolina L.	42.0	2.0	5.2	56.7	3.2	6.2	41.7	2.9	5.8	6.8	0.2	1.0
Hamamelis virginiana L.	0.0	0.0	0.0	0.0	0.0	0.0	3.1	0.0	0.3	0.0	0.0	0.0
Ilex montana Torr. & Gray.	6.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ilex opaca Ait.	0.0	0.0	0.0	5.7	0.0	0.5	1.5	0.0	0.1	0.0	0.0	0.0
Kalmia latifolia L.	12.0	0.0	1.0	5.7	0.0	0.4	13.9	0.0	1.3	20.4	0.1	2.8
Liriodendron tulipifera L.	8.0	2.5	3.0	62.4	43.9	30.6	4.6	1.5	1.5	6.8	0.0	0.9
Magnolia acuminata (L.) L.	6.0	2.2	2.6	5.7	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0
Magnolia fraseri Walt.	4.0	1.5	1.8	5.7	0.3	0.6	7.7	0.7	1.2	0.0	0.0	0.0

Magnolia tripetala (L.) L.	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.2	0.0	0.0	0.0
Oxydendrum arboretum (L.) DC.	4.0	1.4	1.7	11.3	0.6	1.2	3.1	0.0	0.3	0.0	0.0	0.0
Picea rubens Sarg.	20.0	0.5	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Quercus prinus L.	2.0	0.3	0.5	0.0	0.0	0.0	1.5	1.0	0.8	0.0	0.0	0.0
Quercus rubra L.	4.0	2.2	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhododendron maximum L.	120.0	0.6	9.8	90.7	1.3	7.6	103.6	0.4	9.5	6.8	0.0	0.9
Tilia Americana L.	4.0	1.0	1.3	17.0	0.2	1.4	6.2	0.8	1.1	0.0	0.0	0.0
Tsuga canadensis (L.) Carr.	242.1	19.9	37.8	311.8	32.5	42.7	272.1	52.4	62.2	319.7	72.4	92.2

[a] *Betula* sp. includes *Betula lenta* L. and *Betula alleghaniensis* Britt.

Table 2.2. Mean and coefficient of variation (CV = %) of stand summary characteristics by forest type. Superscript letters denote forest type characteristics that are significantly ($p < 0.05$) different according to a Bonferroni multiple comparison test. The a-d superscripts correspond to the order of the columns.

	Tsuga canadensis/*Betula*/ *Acer rubrum* (N = 17)		*Tsuga canadensis*/ *Liriodendron tulipifera*/ *Halesia carolina* (N = 6)		*Tsuga Canadensis*- Mesic (N = 22)		*Tsuga Canadensis*- Submesic (N = 5)	
Stand Characertistic	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Stand density (stems/ha)	648.3	46.8	663.3	40.9	561.2	32.8	374.1	30.8
Stand basal area (m^2/ha)	1.5	36.9	2.5	45.4	2.0	43.6	2.2	37.6
Number of tree species per stand	5.2^{d}	29.2	5.7^{d}	36.5	4.5^{d}	24.5	2.2^{abc}	59.3
Shannon-Wiener index	1.8^{d}	31.3	1.9^{d}	36.1	1.7^{d}	23.9	0.6^{abc}	108.3
Rhododendron maximum cover (%)	26.7	30.5	31.2	110.2	29.1	92.8	6.7	223.6
Kalmia latifolia cover (%)	0.2	412.3	0.0	0.0	0.1	469.0	3.8	223.6
Canopy openness (%)	3.5	120.8	2.5	88.3	2.8	79.6	2.9	63.2
Decaying wood (%)	74.5	42.7	61.1	53.6	66.7	49.4	83.3	28.3
Litter depth (mm)	22.6^{bc}	31.6	12.4^{a}	36.2	16.8^{a}	38.6	14.6	32.6

Table 2.3. Mean and coefficient of variation (CV = %) of stand environmental characteristics by forest type. Superscript letters denote forest type characteristics that are significantly ($p < 0.05$) different according to a Bonferroni multiple comparison test. The a-d superscripts correspond to the order of the columns.

	Tsuga canadensis/Betula/ Acer rubrum (N = 17)		*Tsuga canadensis/ Liriodendron tulipifera/ Halesia carolina* (N = 6)		*Tsuga canadensis-* Mesic (N = 22)		*Tsuga canadensis-* Submesic (N = 5)	
Stand characteristic	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Elevation (m)	1037.0	23.3	932.8	13.9	944.0	19.6	1005.3	8.0
Slope steepness (%)	28.1	61.3	24.2	60.6	27.5	63.9	31.8	54.4
Aspect (0-2)	1.1^{d}	66.0	0.6	122.5	1.2^{d}	53.4	0.2^{ac}	95.4
TRMI (0-60)	29.1	36.1	27.7	43.8	31.9	25.0	29.6	34.1
Microtopographic mounds (%)	2.0	282.3	0.0	0.0	3.8	188.7	0.0	0.0
Organic matter (%)	25.5	60.1	27.2	23.9	30.9	53.0	37.8	62.5
Sand (%)	72.2	11.1	75.5	10.9	71.4	15.3	67.4	20.2
pH	3.86	12.8	3.64	6.7	4.01	10.5	4.34	11.3
Carbon/Nitrogen ratio	19.44	32.9	17.67	12.9	19.35	36.0	20.78	24.2
Potassium (%)	0.001	48.8	0.001	43.4	0.001	64.0	0.001	60.0
Calcium (%)	0.015	314.8	0.005	76.5	0.051	198.4	0.016	176.9
Magnesium (%)	0.007	95.2	0.006	45.8	0.011	93.2	0.009	107.3
Phosphorus (%)	0.001	184.8	0.001	102.1	0.002	171.4	0.004	180.9
Aluminum (%)	0.124	34.4	0.144	22.7	0.115	41.1	0.123	45.2

Table 2.4. Spearman's rank correlations of species importance values with axis scores from DCA ($p < 0.05$, * for $p < 0.01$).

Species	Axis 1	Axis 2
Acer rubrum	0.55*	-
Acer pensylvanicum	-	0.40*
Acer saccharum	-0.48*	0.47*
Aesculus flava	-0.40*	-
Betula sp.	0.46*	-0.34
Halesia carolina	-0.34	0.51*
Kalmia latifolia	-	-0.35*
Liriodendron tulipifera	-0.50*	-0.50*
Magnolia fraseri	-	-0.31
Rhododendron maximum	-0.28	-0.62*
Tilia americana	-0.43*	0.30
Tsuga canadensis	-	0.28

Table 2.5. Spearman's rank correlations of environmental variables with axis scores from DCA ($p< 0.05$).

Variable	Axis 1	Axis 2
C/N ratio	0.34	-0.34
P (%)	-	-0.29
Sand (%)	-0.35	0.29
UTM northing	-0.28	-
Canopy openness (%)	-	0.31

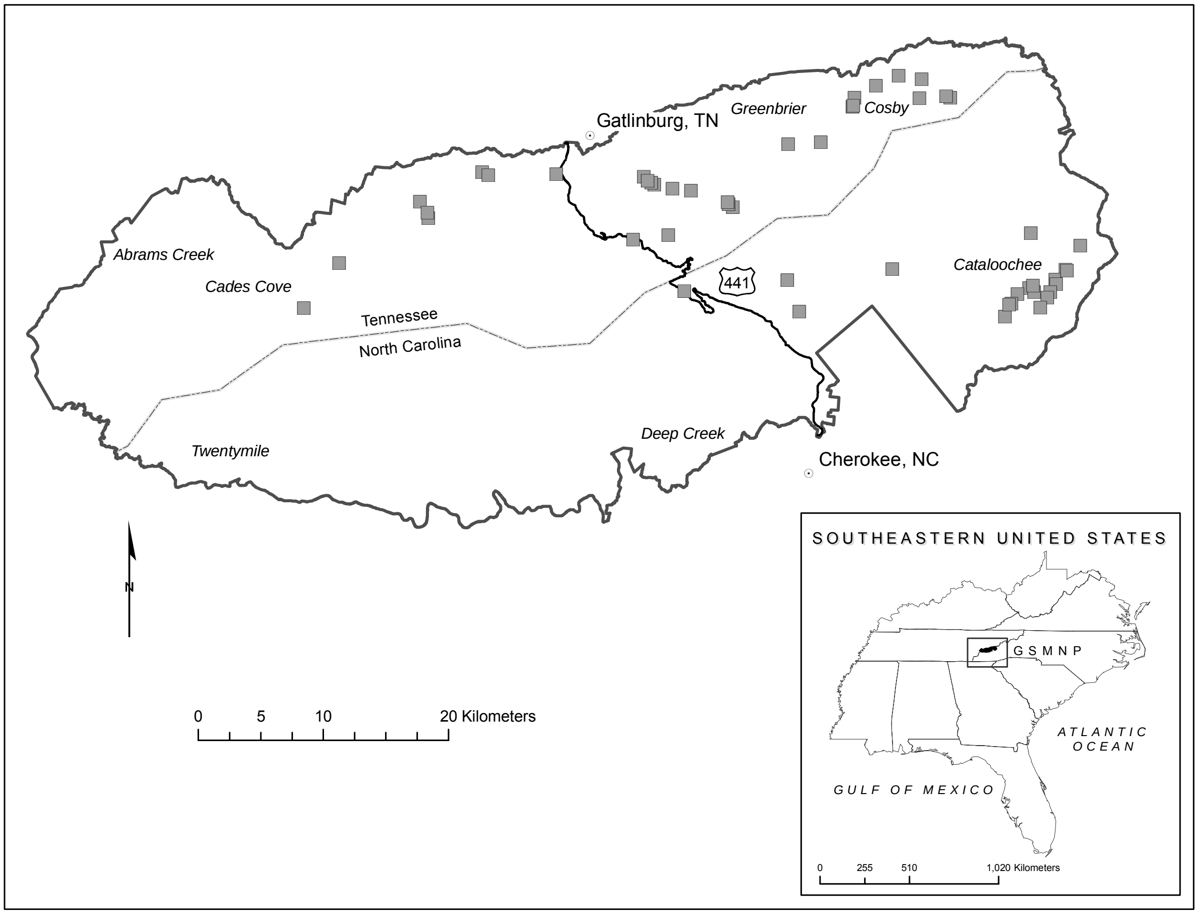

Figure 2.1. Map of Great Smoky Mountains National Park (GSMNP) showing the location of the 50 *Tsuga canadensis* (L.) Carr. forest stands in this study.

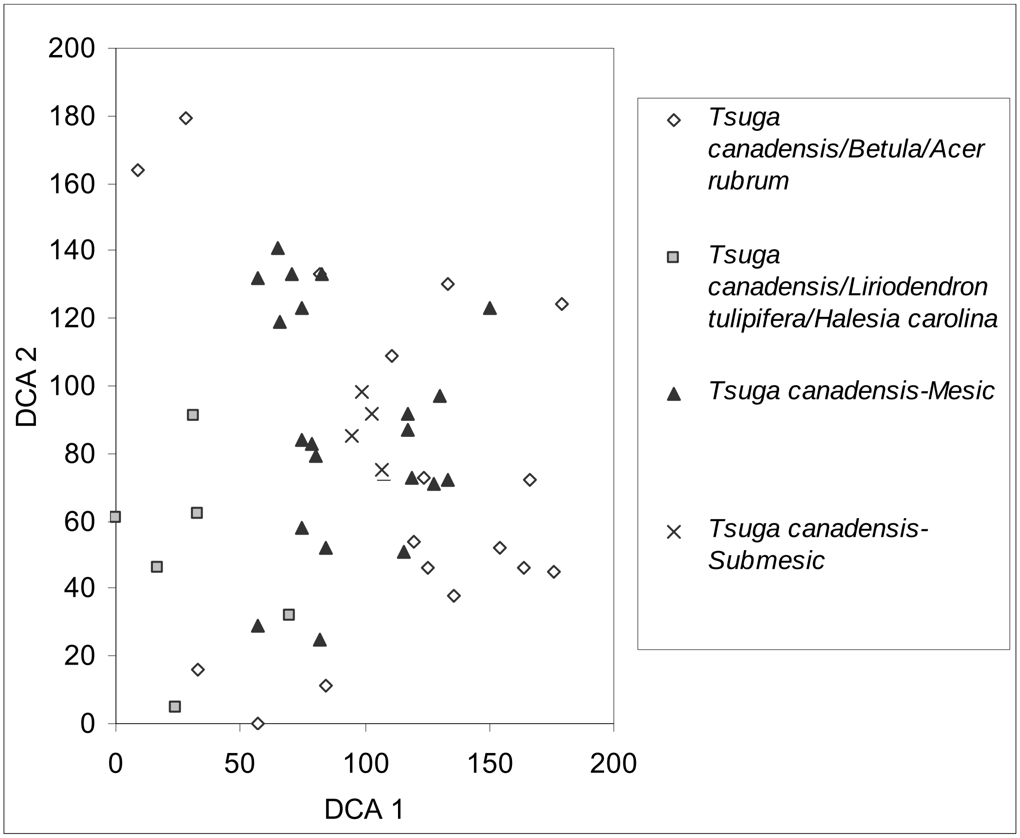

Figure 2.2. Plot of DCA axes one and two. Forest type membership is identified by group symbols.

CHAPTER 3

SPATIAL STRUCTURE AND ENVIRONMENTAL CONTROLS OF *TSUGA CANADENSIS* (L.) CARR. REGENERATION IN THE SOUTHERN APPALACHIAN MOUNTAINS

Introduction

Tree regeneration is a spatiotemporal process by which populations of tree species are maintained across the landscape. Each part of the regeneration process is influenced by the interactions of biotic and abiotic factors such as plant life-history characteristics, disturbances, light and nutrient availability (Barnes et al. 1998). The importance of multiple biotic and abiotic factors interacting either across or within specific spatial and temporal scales is becoming increasingly recognized in the literature on vegetation dynamics (White 1979; Pickett and White 1985; Parker 1993; Mladenoff and Stearns 1993; Spies and Turner 1999; Frelich 2002) This growing body of research shows that results obtained within specific time-space settings should not necessarily be extrapolated across scales or from one place to another. Therefore, it is prudent to obtain as much information as possible on the characteristics of vegetation in specific places.

The study of *Tsuga canadensis* regeneration in southern Appalachian upland forests is crucial for a number of reasons. First, there has been no research which specifically examines the status of *Tsuga canadensis* regeneration in the southern Appalachian Mountains. Therefore, most of our knowledge concerning *Tsuga canadensis* regeneration comes from more northern locales (e.g. Rooney and Waller 1998; Rooney et al. 2000). Because of the importance of *Tsuga canadensis* in southern Appalachian landscapes, it is crucial that we expand our knowledge of the processes operating within these forests. Second, with the invasion of southern *Tsuga canadensis* forests by the exotic hemlock woolly adelgid (*Adelges tsugae* Annand), a species that can cause tree death within four years (McClure 1991; Young et al. 1995), it is necessary to obtain baseline data on these forest ecosystems for future monitoring and management. Research from more northern locales has revealed 50-100% *Tsuga canadensis* mortality in invaded stands (Orwig and Foster 1998; Orwig et al. 2002). Indeed, to manage our protected landscapes effectively, land managers need descriptions of the natural conditions and how these conditions vary spatially and temporally. *Tsuga canadensis* is a dominant component of many southern Appalachian upland forests; the loss of such a species would negatively affect many mammalian and avian species (Allen et al. 1987; Godman and Lancaster 1990; Rogers et al. 1990; Frelich and Lorimer 1991), including several increasingly threatened neotropical migrant birds. This is especially true of *Tsuga canadensis* forests with old growth characteristics (Hooper 1978; Haney 1997; Mitchell 1999). Even fishes such as the brook trout (*Salvelinus fontinalis*) would be negatively affected by the loss of *Tsuga canadensis*. Streams running through *Tsuga canadensis* forests tend to be thermally and hydrologically more stable, and support greater invertebrate and fish populations than those of mixed hardwood forests (Snyder et al. 2002). Finally, several researchers have shown that highly contextual local or regional biotic and abiotic factors (e.g. white-tailed deer browsing, human land-use, disturbance, and climate) can significantly affect *Tsuga canadensis* regeneration in other regions (Anderson and Loucks 1979; Mladenoff and Stearns 1993; Parshall 1995; Rooney and Waller 1998; Rooney et al. 2000; Ziegler 2002).

The overall goal of this research is to provide baseline data on the characteristics of *Tsuga canadensis* regeneration in southern Appalachian upland forests. These data will provide useful baseline information on the regeneration dynamics of *Tsuga canadensis* prior to hemlock woolly adelgid induced mortality. Three questions are posed by this research: 1) What environmental factors are associated with variability in the abundance of *Tsuga canadensis* regeneration?; 2) How is *Tsuga canadensis* regeneration spatially structured, and what factors control this structure in southern Appalachian upland forests?; and 3) How can *Tsuga canadensis* forests be managed to promote the continued regeneration of this species in southern Appalachian landscapes?

Species Background

Tsuga canadensis is a long-lived and shade tolerant coniferous tree species of eastern North America. The species ranges from Nova Scotia to Minnesota and extends south along the Appalachian mountain system to northern Alabama and Georgia, with disjunct populations to the east and west of this range. Within its natural range, *Tsuga canadensis* can be found up to approximately 900 m elevation in the north and between 600 m and 1500 m in the south. In the southern Appalachian Mountains, *Tsuga canadensis* is typically found in mixed-hardwood or pure stands located within moist cool valleys and ravines, but also along rock outcrops and north facing ridges (Little 1998; Kemp, 1998).

Logging practices (i.e. clearcutting) of the late 19th and early 20th century may have eliminated *Tsuga canadensis* seed banks in some areas. *Tsuga canadensis* was logged for the tannin in its bark, used for tanning hides, and for making paper (Kemp 1998). The destruction of *Tsuga canadensis* seed banks by past logging practices has been documented as a possible control on the contemporary dearth of regeneration of the species in northern areas (Mladenoff and Stearns 1993; Rooney and Waller 1998). As a result of this logging and seed bank elimination, there may also have been changes in the nutrient cycling regime in these areas that were once dominated by conifer litter and now have a more purely deciduous litter. The dynamics of nutrient mineralization have been shown to be different between patches of *Tsuga canadensis* and hardwoods (Mladenoff 1987; Frelich et al. 1993). Catovsky and Bazzaz (2000, 2002), using laboratory experiments and empirically based field studies, have shown that unamended soils and low light levels, which are conditions found in *Tsuga canadensis* stands, favor seedlings of that species to the near exclusion of others.

While *Tsuga canadensis* canopy trees produce large seed crops every two to three years (Hough 1960), successful germination and subsequent recruitment into larger size classes requires a consistent source of moisture (Rogers 1978; Mladenoff and Stearns 1993). Exposed mineral soils that are moist, such as north-facing road cuts, trail cuts, and steep slopes, may provide suitable substrates (Mladenoff and Stearns 1993). Proximity to water sources or the presence of substrates that retain moisture (e.g. decaying wood and moss beds) have also been deemed essential factors that promote successful *Tsuga canadensis* regeneration (Rogers 1978; Rooney and Waller 1998). Because *Tsuga canadensis* seedlings grow slowly for the first 10-15 years, interruption of the moisture supply by unfavorable climatic episodes such as prolonged drought may result in mortality by desiccation of the species' shallow roots (Coffman 1978; Mladenoff and Stearns 1993).

Research on the growth-response of *Tsuga canadensis* shows a positive correlation with rainfall on well-drained sites, but a negative association with summer temperatures, a result that is consistent with the expected drought response of trees as temperature increases (Cook and Cole 1991; Tardiff et al. 2001). Parshall (1995) also found a correlation between drought and *Tsuga canadensis* release events, showing a growth lag of 2-3 years following drought in northern Michigan.

Assuming its environmental requirements are met, *Tsuga canadensis* tends to regenerate where gap-phase (local scale) processes are favored; that is, where large or severe disturbances are rare (Frelich 2002). Gap-phase regeneration is typically initiated by tree death or wind disturbance, which removes one or a few trees from the forest canopy, resulting in increased resources and growing space for those individuals growing in the gap. Gap-scale processes have been deemed important for allowing shade-tolerant tree species to persist in an area (Runkle and Yetter 1987). In the southern Appalachian Mountains, *Tsuga canadensis* has shown the highest probability of increase (high ratio of sapling percentage to canopy percentage) in gaps (Runkle 1998). This idea is reinforced by findings from northern Michigan where *Tsuga canadensis* has been found to increase in dominance across size classes independently of major disturbances (Woods 2000a; 2000b). Detailed treatments of *Tsuga canadensis* biology and ecology can be found in Godman and Lancaster (1990); Mladenoff and Stearns (1993); and Rooney et al. (2000).

Study Area

Sampling for this research was conducted within Great Smoky Mountains National Park (GSMNP), which straddles the mountainous border between eastern Tennessee and western North Carolina, USA (Figure 3.1). GSMNP was established in 1934, and was later declared an International Biosphere Reserve (1976) and World Heritage Site (1983). World-renowned for its plant and animal diversity, the park contains as many as 130 different species of trees. At 212,460 ha, GSMNP is one of the largest protected areas in the eastern United States; over 80% of the land area is classified as part of the eastern deciduous forest complex (Houk 1993). General forest patterns within GSMNP range from high elevation (above 1300 m) *Picea-Abies* forests to lower elevation cove hardwoods. At mid-elevations (1000-1500 m), northern hardwoods dominate with *Pinus-Quercus* forests found on more xeric sites. *Tsuga canadensis* is locally important within mid-to-low elevation mesic forests. Johsnon et al. (2000) estimated that there are approximately 1528 ha of *Tsuga canadensis* forests within GSMNP.

Kincaid (2006, submitted) identified four types of *Tsuga canadensis* forests in GSMNP. The four types were: *Tsuga canadensis*/*Betula*/*Acer rubrum*; *Tsuga canadensis*/*Liriodendron tulipifera*/*Halesia carolina*; *Tsuga canadensis*-Mesic; and *Tsuga canadensis*-Submesic. Differentiation among these four types involved *Tsuga canadensis* forests with cove hardwood or northern hardwood affinities, those on mesic or sub-mesic sites, and those with or without a well developed *Rhododendron maximum* understory. Slope aspect, litter depth, tree species richness and diversity were significantly different among forest types; *Tsuga canadensis* regeneration was not consistently different among types.

As part of the Blue Ridge physiographic province, GSMNP is characterized by extreme topographic variation. The core rock group of GSMNP is the Ocoee Supergroup, with most rocks dating to the Precambrian. Ninety percent of the GSMNP land area consists of slopes of greater than 10 degrees (Houk 1993), with elevations ranging from 256 m to 2025 m. Because of this considerable variation in elevation, annual precipitation varies from 1651 mm in the lowlands to 2235 mm at the highest elevations.

Methods

Sampling was restricted to mature *Tsuga canadensis* forests. Sample locations were documented using park maps (Madden et al. 2004), communication with park personnel, and observational field evidence. Plots were accessed using trails and roads.

Vegetation data

I used 14x21 m plots, composed of a 2x3 arrangement of 7x7 m quadrats to sample the vegetation and environment at each site (after Rooney and Waller 1998; Rooney et al. 2000). A total of 50 plots were situated parallel to slope contours and established so as to minimize vegetation-environment heterogeneity. Within the quadrats of each plot, *Tsuga canadensis* seedlings and saplings were inventoried and categorized into four size classes: 4-9 cm; 10-29 cm; 30-99 cm; and ≥ 100 cm but <5cm diameter at breast height (dbh = 1.4 m) (modified from Rooney et al. 2000). Research has shown that sampling seedlings and saplings by size-class, rather than age-class, provides more information on regeneration dynamics.

This is primarily the result of mortality being more size-dependent than age-dependent, and the changing importance of vegetation-environment relationships as seedlings and saplings increase in size (Harper 1977; Waller 1996; Rooney and Waller 1998; Rooney et al. 2000). Furthermore, because this study was conducted within a national park threatened with hemlock woolly adelgid induced mortality, destructive sampling to obtain seedling and sapling ages was not justified.

Tree species ≥ 5 cm dbh were also inventoried within the quadrats of each plot. The presence/absence of decaying wood was recorded within each quadrat and used to calculate the percentage occurrence of that substrate for each plot. Litter depth was averaged across all quadrats in a plot. The cover of *Rhododendron maximum* and *Kalmia latifolia* was estimated using the line intercept method along each 21 m section of plot, providing 63 m of line. An estimate of canopy openness was obtained using hemispherical photographs taken from the center of each plot. Canopy photographs were analyzed using a desktop mapping system to ascertain greyscale statistics (R-Wel 2005). Canopy openness, expressed as a percent, was calculated by bifurcating the greyscale values into white (open) versus grey (closed) pixels.

Environmental data

Location and topographic parameters were recorded from the center of each plot: UTM easting and northing, elevation, slope aspect, slope steepness, slope configuration, and slope position. The location and elevation of each plot was estimated using a Garmin 76 hand-held global positioning system (GPS; accuracy = 9 to 12 m). Aspect was transformed to a linear scale ranging from 0.00 (SW aspect) to 2.00 (NE aspect) (Beers et al. 1966). I used the topographic parameters to calculate a topographic relative moisture index (TRMI; Parker 1982).

The TRMI values range from 0 to 60 with higher values indicating more mesic conditions. The presence/absence of microtopographic mounds was recorded within each quadrat and used to calculate the percent occurrence of that substrate for each plot.

A soil sample was taken at 0-10 cm depth from the center of each plot for physical and chemical analyses. Organic matter content was estimated by loss-on-ignition from a five gram sample of soil. The amount of sand in each sample was calculated by suspending a sample of soil in sodium metaphosphate, then wet sieving the sample to remove the fine particles. Soil pH was measured with an electronic meter in a 1:3 mixture of soil and distilled water. This mixture was necessary because of the high organic matter content of the soils. Total carbon and nitrogen content of the soils was determined by micro-Dumas combustion analysis. The percentages of carbon and nitrogen were then used to calculate a carbon/nitrogen ratio. The percentage of phosphorus in each sample was determined by continuous flow colorimetric analysis. Flame atomic absorption spectrophotometry was used to determine the percentages of aluminum, calcium, magnesium, and potassium.

Statistical methods

Tsuga canadensis seedling and sapling data were summarized by quantifying abundance and spatial pattern for each size-class within plots. Spatial pattern was estimated by calculating the index of dispersion, also known as the variance-to-mean ratio, for each seedling and sapling class within plots. The index of dispersion is appropriate for this study because only abundance data were recorded; furthermore, research has shown this index to be robust (Myers 1978; Krebs 1999).

Detrended correspondence analysis (DCA) (Hill and Gauch 1980) was used to arrange study sites according to similarity in *Tsuga canadensis* regeneration abundance. I used untransformed abundance values by study site in this ordination procedure. DCA was appropriate for this study because environmental factors were not able to explain seedling and sapling variation in constrained ordination adequately. Seedling and sapling size-class abundances, species importance values, and environmental variables were correlated (Spearman's rho) with the DCA axes scores to elucidate gradients in environmental factors and regeneration abundance (ter Braak 1995). To aid interpretation of the DCA, flexible beta cluster analysis (beta = -0.25) with the Sorensen (Bray-Curtis) distance measure was used to elucidate clusters of sites with similar seedling and sapling abundances. I used PC-ORD, version 4.0 for the DCA and cluster analysis, and Stata release 8 for the correlation analyses (McCune and Mefford 1999; StataCorp 2003). Six plots were eliminated prior to DCA and cluster analysis because no seedlings or saplings were present at those sites.

To complement the examination of landscape-scale patterns of *Tsuga canadensis* regeneration, I used ordinary least-squares (OLS) regression with diagnostics for spatial effects to relate seedling/sapling abundance and the corresponding index of dispersion directly to vegetation-environment factors. Diagnostics for spatial effects included tests for spatial autocorrelation, heteroskedasticity, and non-normality. If spatial effects were significant, then the appropriate spatial model could be employed. All regression models were estimated using GeoDa, version 0.9.5-I (Anselin 2003). Abundance and spatial pattern variables were square-root transformed [sqrt (n + 0.5)] prior to being used as dependent variables. Independent variables were log transformed [$\log_{10}$ (n+1)] when histograms indicated a skewed distribution in the variable. Transformations were necessary to improve normality and stabilize the error variances. All independent variables were centered on their mean prior to model construction. Correlation and bivariate OLS regression were used to screen independent variables for significant relationships with dependent variables. Only independent variables significant at $P<0.05$ were retained in the final regression models. No plots were eliminated in the regeneration abundance models; however, some were eliminated in each of the spatial pattern models where an index of dispersion could not be calculated because of a lack of seedlings or saplings in a given size-class.

Results

Tsuga canadensis regeneration abundance

Tsuga canadensis regeneration varied widely within and among forests of the southern Appalachian Mountains. While some sites appeared to offer favorable conditions for continuous regeneration and recruitment, many other sites appeared to exhibit episodic regeneration. Only 36% of the plots contained seedlings and saplings in all size-classes, indicating continuous regeneration and recruitment at those sites; 12% of the plots lacked any seedlings or saplings. Seedling and sapling densities varied across sites from a low of 0 stems/ha to a high of 2109 stems/ha.

Only 48% of the study sites contained *Tsuga canadensis* seedlings in the smallest (4-9 cm) size-class (Table 3.1). *Rhododendron maximum* cover, the presence of decaying wood and microtopographic mounds were greatest at sites containing small seedlings (Table 3.2). However, only litter depth, soil sand and calcium content were found to be significantly different between sites with and without small seedlings.

Sixty percent of the sites contained larger *Tsuga canadensis* seedlings in the 10-29 cm size-class. Although *Kalmia latifolia* was uncommon in the study sites, the species exhibited its highest cover at sites containing these larger seedlings**.** Although the soils at these sites were characterized by having the highest average carbon/nitrogen ratios, pH, and aluminum content, only soil sand content was found to be significantly different between sites with and without large seedlings.

Small *Tsuga canadensis* saplings, 30-99 cm in height, were present at 72% of the study sites. Sites containing this size-class had more open canopies and some of the highest values for the index of dispersion, which indicates a strong tendency for small saplings to be spatially aggregated. Soil organic matter and calcium content were also relatively high compared to sites containing the other size-classes; however, no vegetation-environment variables were found to be significantly different between sites with and without small saplings.

Large *Tsuga canadensis* saplings, ≥ 100 cm but <5 cm dbh, were present at 78% of the study sites. Average stem density, the importance value of *Tsuga canadensis*, and litter depth were highest at sites containing larger saplings. In addition, these sites were typically found at higher elevations, on steeper slopes, and on more northern aspects. Average soil sand content was highest at sites containing large saplings. Only the carbon/nitrogen ratios and *Tsuga canadensis* importance values were found to be significantly different between sites with and without large saplings.

The first DCA axis (DCA 1) was negatively correlated with the importance value of *Picea rubens* and the abundance of large *Tsuga canadensis* saplings (Figure 3.2; Table 3.3). Positive correlations were observed between DCA 1 and the importance value of *Rhododendron maximum*, *Rhododendron maximum* cover, and the abundance of small and large *Tsuga* *canadensis* seedlings. DCA 1 segregated *Tsuga canadensis* forests based on regeneration status; sites containing only one or two of the understory size-classes were separated from sites where regeneration and recruitment appear to be continuous. DCA 1 also separated *Tsuga canadensis* forests with relatively open understories and more abundant regeneration from those with well developed evergreen understories dominated by *Rhododendron maximum*. Therefore, the structure of DCA 1, with an eigenvalue of 0.36, suggests gradients in *Tsuga canadensis* regeneration abundance and *Rhododendron maximum* cover within the understories of southern Appalachian *Tsuga canadensis* forests.

The second DCA axis (DCA 2) was negatively correlated with the importance value of *Rhododendron maximum*, the abundance of large *Tsuga canadensis* seedlings and small saplings, and available soil calcium and magnesium (Figure 3.2; Table 3.3). A positive correlation was observed between DCA 2 and the sand content of the soil surface layer. DCA 2, with an eigenvalue of 0.08, reinforces the suggested gradients in *Tsuga canadensis* regeneration and *Rhododendron maximum* cover observed in DCA 1. In addition, DCA 2 arranged regeneration abundance and sites along soil gradients reflecting nutrient availability; sandier sites having less available calcium and magnesium were associated with depressed *Tsuga canadensis* regeneration and recruitment.

Models relating *Tsuga canadensis* regeneration abundance to vegetation-environment factors elucidate the shifting importance of controls on regeneration as seedlings and saplings grow larger (Table 3.4). Model explanatory variance was relatively low, with no model able to explain greater than 20% of the variance in regeneration abundance. The abundance of small seedlings, 4-9 cm tall, was positively related to available soil phosphorus, while negatively related to litter depth. Available soil phosphorus, which had the largest influence, and litter depth, accounted for 20% of the variation in small seedling abundance. The abundance of large seedlings (10-29 cm) and small saplings (30-99 cm) was negatively related to the sand content of the soil surface layer. Sand content accounted for 8% and 14% of the variation in large seedling and small sapling abundance, respectively. The abundance of large saplings, ≥ 100 cm but <5 cm dbh, was negatively related to the amount of *Rhododendron maximum* cover in the understory. *Rhododendron maximum* cover accounted for 14% of the variation in large sapling abundance.

Spatial pattern of Tsuga canadensis regeneration

Tsuga canadensis regeneration abundance and spatial pattern were positively correlated across size-class categories. Small and large seedling abundance showed the strongest positive correlations with spatial pattern (rho = 0.72 and rho = 0.79; $p<0.01$), followed by small and large sapling abundance (rho = 0.65 and rho = 0.62; $p<0.01$). On average, seedlings and saplings were spatially aggregated within plots, and this aggregation increased with increasing abundance (Table 3.1).

Models relating the index of dispersion for *Tsuga canadensis* seedlings and saplings to vegetation-environment factors reinforce the notion that controls on regeneration shift in importance as seedlings and saplings grow larger. These models also emphasize that different sets of vegetation-environment factors may affect the abundance versus spatial pattern of regeneration differently (Table 3.5). However, caution must be used when comparing the abundance and spatial pattern models because an index of dispersion could not be calculated for sites lacking seedlings or saplings in a given size-class. That is, the abundance models are based on all 50 sites, whereas the spatial pattern models are based on those sites were an index of dispersion could be calculated.

The spatial pattern of small seedlings, 4-9 cm tall, was positively related to the importance value of *Acer pensylvanicum*, a light-demanding species, and negatively influenced by litter depth (adjusted $R^2 = 0.27$). *Tsuga canadensis* regeneration is more strongly aggregated at sites with increased *Acer pensylvanicum* importance, but this aggregation is reduced at sites with deeper litter layers.

Spatial pattern in the larger seedlings, 10-29 cm tall, was negatively influenced by slope aspect and UTM northing, but positively influenced by the importance value of light-demanding *Betula* sp. The importance value of *Betula* sp. had the largest standardized coefficient followed by slope aspect and UTM northing, repectively. At 0.49, the adjusted R^2 for the large seedling model was the highest explanatory value of all four spatial pattern models. Sites occurring in the northern portion of the study area, and sites on north-facing aspects, appear to have reduced spatial aggregation of *Tsuga canadensis* regeneration. The spatial aggregation of *Tsuga canadensis* regeneration becomes most pronounced with increases in the importance of *Betula* sp.

Spatial pattern in small saplings, 30-99 cm tall, was, like the larger seedlings, positively related to the importance value of *Betula* sp. and negatively influenced by UTM northing. The importance value of *Betula* sp. had the largest standardized coefficient in this model, followed by UTM northing (adjusted $R^2 = 0.31$). Large seedlings exhibit pronounced spatial aggregation on sites with greater *Betula* sp. importance, but reduced aggregation on north-facing aspects and sites in the northern portion of the study area.

The spatial pattern of larger saplings, ≥ 100 cm but <5 cm dbh, was positively influenced by available soil potassium and canopy openness, but negatively related to litter depth. Litter depth had the largest standardized coefficient followed by potassium and canopy openness, respectively (adjusted $R^2 = 0.30$). Increases in available potassium and canopy openness result in greater spatial aggregation of *Tsuga canadensis* regeneration. However, increased litter depth is associated with less spatial aggregation of regeneration.

Discussion

Seedling abundance was lower than has been reported in other studies assessing *Tsuga canadensis* regeneration. While studies from more northern locales have reported seedling densities exceeding 2500 seedlings/ha (Rooney and Waller 1998), and some has high as 70000 seedlings/ha (Nelson 1997), this study found that seedling densities never exceeded 2041 seedlings/ha. Similarly, sapling densities never exceeded 2109 saplings/ha. Therefore, *Tsuga canadensis* regeneration abundance in the southern Appalachian Mountains can be characterized as generally low, but highly variable.

Landscape scale patterns of regeneration, as revealed by DCA 1, are primarily controlled by understory *Rhododendron maximum* cover. While seedlings are establishing beneath a *Rhododendron maximum* understory, recruitment to the larger sapling classes appears to be limited by the extent of this cover. Other studies conducted in southern Appalachian forests have reported similar findings with reduced tree regeneration or lack of recruitment in understories dominated by *Rhododendron maximum* (Phillips and Murdy 1984; Monk et al. 1985; Hedman and Van Lear 1995; Rivers et al. 2000; Van Lear et al. 2002). Van Lear et al. (2002) did report successful *Tsuga canadensis* seedling establishment in areas of moderately dense *Rhododendron maximum* cover, but even in these locations, regeneration was greatest where *Rhododendron maximum* coverage was lowest.

DCA 2 reinforced the notion that a gradient in *Rhododendron maximum* understory cover exists, but also revealed secondary gradients in soil sand content, and calcium and magnesium availability. Because seedlings are shallowly rooted and grow slowly for the first 10-15 years, they are susceptible to desiccation, making a consistent source of moisture necessary for establishment, growth, and recruitment (Secrest et al. 1940; Olson et al. 1959; Coffman 1978; Godman and Lancaster 1990; Mladenoff and Stearns 1993). The sand content of the soil not only influences moisture status, with sandier soils draining more rapidly, but it also aids in the leaching of nutrients away from the root zone. Other studies have focused on the availability of primary macronutrients (e.g. nitrogen) in *Tsuga canadensis* regeneration (Catovsky and Bazzaz 2000; 2002); however, this study found that secondary macronutrients, namely calcium and magnesium, are influencing landscape scale patterns of regeneration. Calcium has been shown to be important in plant growth, especially root growth, and is essential for proper water uptake and cell formation. Magnesium is necessary for the production of chlorophyll. In sandy soils, these nutrients are easily leached, particularly magnesium, which is more soluble. For *Tsuga canadensis* seedlings, which are slow growing and susceptible to drought, calcium and magnesium would be important for early growth and survival. Although seedling establishment is occurring on sandy soils with less available calcium and magnesium, more regeneration and recruitment is found at sites with less sand and more macronutrient availability. Besides reducing available light to growing seedlings, *Rhododendron maximum* has been shown to decrease available understory moisture, nutrient availability, and mycorrhizal colonization (Walker et al. 1999; Nilsen et al. 2001). Therefore, both above- and belowground resource availability for *Tsuga canadensis* regeneration is reduced in forests with dense *Rhododendron maximum* understories, an influence that is reinforced on sandy substrates.

In the regression framework, small seedling abundance is controlled by available phosphorus and litter depth. The spatial pattern of small seedlings is also related to litter depth, but the importance of *Acer pensylvanicum* is more influential in the model. Litter depth negatively influences regeneration by preventing the penetration of seedling roots, which quickly become desiccated as the leaves dry out (Barnes 1991). At sites comprised of dense *Rhododendron maximum* cover, the thick, schlerophyllous litter may prove especially problematic for seedling establishment and survival. Available phosphorus is necessary for germination and growth of seedlings; it also encourages root growth, rapid development, and stress tolerance. Aside from its influences on litter depth, *Rhododendron maximum* biomass may also be storing large quantities of available nutrients necessary for seedling survival (Monk et al. 1985; Nilsen et al. 2001). While seedlings are establishing in areas of dense *Rhododendron maximum* cover and low nutrient availability, recruitment to the larger size classes appears to be limited under these conditions.

The positive influence of *Acer pensylvanicum*, a species with high gap affinity (Rankin and Tramer 2002), may indicate the importance of canopy disturbances in the regeneration of *Tsuga canadensis*. Indeed, windthrow has been noted as a common component of *Tsuga canadensis* forest dynamics (Lorimer 1980; Brown et al. 1982; Mladenoff and Stearns 1993). Other studies have found significantly more seedlings occurring on decaying wood or microtopographic mounds, and have used this finding to help explain the spatially aggregated distribution of regeneration (Long et al. 1998; Rooney and Waller 1998). Although not statistically significant, this study did find that sites harboring small seedlings also contained greater amounts of decaying wood and microtopographic mounds. The lack of significance may be a result of data collection techniques, because only the presence or absence of decaying wood and microtopographic mounds was recorded. Long et al. (1998) found greater *Tsuga canadensis* regeneration abundance on microtopograhic mounds, which were thought to act as refugia from deer browsing. There was no evidence of deer browsing at sites within this study. Canopy disturbance, abundant moisture, and the high organic matter content of soils at sites within this region may mitigate against the importance of decaying wood and microtopographic mounds by creating favorable regeneration sites in the southern Appalachian Mountains. Rooney and Waller (1998) found that as gap size increased, seedling establishment on leaf litter and soil was not significantly different from establishment on decaying wood.

The abundance of large seedlings and small saplings is being controlled by soil sand content, thus reinforcing the relationships observed in the DCA. Sand content of the soil was a negative influence on both large seedling and small sapling abundance. This relationship is most likely related to decreased moisture and nutrient availability in sandy soils, both of which were deemed important influences on landscape-scale patterns of regeneration.

With the exception of slope aspect, large seedling and small sapling spatial patterns are being governed by the same two vegetation-environment factors: *Betula* importance and geographic location. The shared importance of *Betula* sp. may indicate that canopy disturbances are also influential in the recruitment of *Tsuga canadensis*.

While short-lived *Acer pensylvanicum* is typically associated with relatively recent canopy disturbances and seedling establishment, the larger *Betula* sp. encountered in this study may indicate older canopy gaps and seedling recruitment. Thus, regeneration and subsequent recruitment display a spatially aggregated pattern where disturbances have created favorable sites for regeneration in past decades. Although species such as *Betula* and *Liriodendron tulipifera* have a stronger canopy gap affinity, *Tsuga canadensis* is associated with gaps and experiences more growth releases than the former species (Rankin and Tramer 2002). However, additional research is needed to establish more direct links between canopy dynamics and *Tsuga canadensis* regeneration. Geographic location plays an important role in large seedling and small sapling spatial patterns with less spatial aggregation of regeneration occurring at northern sites. Moreover, large seedlings tend to be less spatially aggregated on north-facing aspects, which may indicate more uniform site conditions with an equitable distribution of moisture and nutrient availability.

Models relating large sapling abundance and spatial pattern to vegetation-environment factors exemplify the problems facing *Tsuga canadensis* in the southern Appalachian Mountains. Abundance within the largest sapling class is being controlled by understory *Rhododendron maximum* cover. While seedling establishment is occurring beneath *Rhododendron maximum*, this understory cover does ultimately reduce canopy recruitment of *Tsuga canadensis*. Similarly, the spatial pattern of large saplings is positively influenced by canopy openness, which further lends support to the idea that canopy disturbances are important in fostering *Tsuga canadensis* regeneration. Large sapling spatial patterns are also influenced by available potassium and litter depth. Litter depth was a negative influence on seedling establishment and the significance of this factor in the larger sapling model reinforces the idea that deeper litter layers reduce both regeneration and subsequent recruitment of *Tsuga canadensis* to larger size-classes within southern Appalachian forests. The availability of potassium, which induces a spatially aggregated pattern of large saplings, is important in tree regeneration and recruitment because it facilitates the transportation of photosynthates, provides winter hardiness, and imparts plant vigor and disease resistance (Foth 1990; Owen and Chiras 1995).

Tsuga canadensis regeneration can be characterized as sparse and highly variable in the southern Appalachian Mountains. Seedling and sapling abundance is even lower in this region than has been reported for more northern locales (e.g. Nelson 1997; Rooney and Waller 1998; Rooney et al. 2000). Rooney and Waller (1998) claim that seedling establishment is predominantly governed by fine-scale and local processes, which may account for the relatively low explanatory power of the regeneration abundance models. Indeed, it is possible that regeneration abundance is responding to vegetation-environment variation at scales below the 14x21 m plot level. Although seedling establishment and recruitment appears to be governed by local processes such as soil conditions and canopy dynamics, broad scale, geographic trends in regeneration are apparent. Rooney et al. (2000) showed that regional differences in ecosystem type and land ownership do have a significant influence on regeneration. Because GSMNP was established in 1934 as a result of the agglomeration of private landholdings in two states, differences in forest legacies could be influencing the landscape scale patterns of *Tsuga canadensis* regeneration that are observed today. However, variables representing different areas within GSMNP were found to be nonsignificant in preliminary regression models. Other researchers have suggested deer browsing and lack of suitable substrates as the causal agents behind the dearth of *Tsuga canadensis* regeneration. In this study, there was no evidence of deer browsing or that substrates such as decaying wood were preferred sites of *Tsuga canadensis* regeneration. This study also shows that understory *Rhododendron maximum* cover, although not precluding regeneration, does reduce recruitment of *Tsuga canadensis* in the southern Appalachian Mountains.

Management considerations

The following management actions can aid land managers in the promotion of successful *Tsuga canadensis* regeneration in areas where hemlock woolly adelgid infestation has been reduced or eliminated. In areas that have not been treated because of financial or logistical problems, these data, along with future research, can aid ecological restoration efforts after the wave of hemlock woolly adelgid induced mortality has passed. First, more forest surveys are necessary to increase our knowledge of the conditions necessary for successful *Tsuga canadensis* regeneration and recruitment in southern Appalachian landscapes. These surveys should cover areas beyond protected landscapes, including private and public ownership units at the local and state levels. During preliminary model construction, variables representing different areas within GSMNP were found to be nonsignificant; however, results did indicate an apparent landscape-scale geographic gradient in regeneration abundance. Although Rooney and Waller (1998) found no regional or habitat-related trends in *Tsuga canadensis* seedling densities, Rooney and others (2000) found that small seedling and sapling abundance did differ significantly among geographically distinct ecological units. Therefore, important contextual influences on *Tsuga canadensis* regeneration and recruitment may exist across land-use or habitat types. Second, land managers may have to utilize silvicultural operations designed to naturally regenerate *Tsuga canadensis*, even in protected landscapes such as GSMNP. Historically, even-aged silivicultural methods such as the shelterwood system have been prescribed to regenerate *Tsuga canadensis* (Eckstein 1980); however, this silivicultural method may be too heavy-handed for certain areas, especially a national park.

A single-tree or group selection method may be necessary to regenerate *Tsuga canadensis* while maintaining important park and forest characteristics such as biodiversity, large trees, and vertical stratification (Rooney and Waller 1998; Webster and Lorimer 2002).

This research has elucidated a link between *Tsuga canadensis* seedling establishment and canopy dynamics. It is also clear that increased canopy openness is positively influencing the recruitment of *Tsuga canadensis* to larger size-classes, and thus perpetuating this species in forests of the southern Appalachian Mountains. Indeed, Runkle (1998) found that *Tsuga canadensis* saplings had the highest probability of increase in canopy gaps when compared to other species. Other research has shown that single-tree selection (i.e. small gaps) may perpetuate *Tsuga canadensis*; whereas, group-selection (i.e. large gaps), may give other species such as *Betula* a competitive advantage (Webster and Lorimer 2002). This finding is reinforced by results from Rankin and Tramer (2002) who found that *Tsuga canadensis* is recruited into the smaller gaps when compared with species such as *Betula* and *Liriodendron tulipifera*. Future research concerning *Tsuga canadensis* forests in the southern Appalachian Mountains will offer more direct links between regeneration and canopy dynamics via the reconstruction of forest histories.

Finally, *Rhododendron maximum* removal operations will be necessary to facilitate the regeneration and sustained recruitment of *Tsuga canadensis*, as well as hardwood species in the southern Appalachian Mountains. This research has shown that while *Tsuga canadensis* seedlings can establish beneath a *Rhododendron maximum* understory, recruitment to the larger size-classes is limited by the extent of this cover. Several other researchers have found that *Rhododendron maximum* often precludes the regeneration of tree species (Monk et al. 1985; Hedman and Van Lear 1995; Van Lear et al. 2002).

Van Lear et al. (2002) reported *Tsuga canadensis* to be the only tree species successfully regenerating under *Rhododendron maximum* cover, and even then, it regenerated best where understory conditions were more open. In the southern Appalachian Mountains, *Rhododendron maximum* appears to be increasing in cover (Dobbs and Parker 2004), and because the species easily expands into canopy gaps (Runkle 1982), future forest composition may be significantly less diverse without prescriptive management of *Rhododendron maximum* densities.

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Table 3.1. Mean and coefficient of variation (CV = %) of vegetative characteristics by seedling/sapling size-class. Superscripts indicate a significantly different mean (t-test; * for p< 0.10; ** for p< 0.05) between sites containing a given size-class and sites lacking that size-class. Student's t-tests were not calculated for density and the index of dispersion.

Vegetative Characteristic	4-9 cm (N = 24)		10-29 cm (N = 30)		30-99 cm (N = 36)		≥ 100 cm < 5 cm dbh (N = 39)	
	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Density (stems/ha)	169.4	224.4	177.0	205.1	218.4	171.4	286.4	130.5
Index of dispersion	3.1	80.0	2.5	112.7	3.5	179.0	2.5	83.4
Tsuga canadensis IV (%)	54.2	38.0	57.2	34.1	56.9	34.5	57.3^{*}	34.0
Rhododendron maximum cover (%)	28.9	81.3	27.1	98.0	23.0	110.3	22.6	114.4
Kalmia latifolia cover (%)	0.6	452.2	0.8	441.8	0.7	484.7	0.6	504.8
Canopy openness (%)	2.8	66.3	2.7	77.6	2.9	73.3	2.8	74.4
Decaying wood (%)	75.0	41.5	73.0	41.0	71.3	40.5	72.7	41.6
Litter depth (mm)	15.9^{**}	36.5	17.1	35.0	17.6	36.6	18.0	36.1

Table 3.2. Mean and coefficient of variation (CV = %) of environmental characteristics by seedling/sapling size-class. Superscripts indicate a significantly different mean (t-test; * for p <0.10; ** for p< 0.05) between sites containing a given size-class and sites lacking that size-class.

Environmental characteristic	4-9 cm (N = 24)		10-29 cm (N = 30)		30-99 cm (N = 36)		≥ 100 cm < 5cm dbh (N = 39)	
	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Elevation (m)	951.3	17.2	955.7	14.7	955.2	14.3	979.6	18.3
Slope steepness (%)	24.7	66.8	27.6	60.1	25.7	58.3	27.9	55.9
Aspect (0-2)	0.9	78.8	0.9	72.5	0.9	76.1	1.0	69.3
TRMI (0-60)	30.3	29.2	30.3	28.8	30.2	28.9	30.0	31.3
Microtopographic mounds (%)	2.8	228.4	1.7	305.1	2.32	252.5	2.1	264.2
Organic matter (%)	30.9	53.8	30.2	51.9	31.2	53.7	30.5	54.7
Sand (%)	68.5^{**}	17.1	69.8^{*}	15.7	70.8	15.7	71.5	15.1
pH	3.85	9.9	3.93	10.7	3.91	10.8	3.89	10.4
Carbon/Nitrogen ratio	19.25	28.8	20.08	27.0	19.97	34.2	20.07^{**}	32.9
Aluminum (%)	0.128	33.0	0.129	31.0	0.122	39.8	0.124	39.0
Calcium (%)	0.011^{*}	184.9	0.017	200.3	0.034	245.5	0.031	256.7
Magnesium (%)	0.008	95.9	0.009	89.4	0.009	96.4	0.009	101.8
Phosphorus (%)	0.002	180.6	0.002	199.8	0.002	178.9	0.002	183.3
Potassium (%)	0.001	54.8	0.001	51.9	0.001	60.6	0.001	60.2

Table 3.3. Forest compositional (IV), structural, and environmental correlations (Spearman's rho) with axis scores from DCA (*p< 0.05, **p< 0.01).

Variable	Axis 1	Axis 2
Acer saccharum	-	-
Aesculus flava	-	-
Magnolia acuminata	-	-
Picea rubens	-0.34*	-
Rhododendron maximum	0.36*	-0.32*
Rhododendron maximum % cover	0.36*	-
Tilia americana	-	-
Small seedlings 4-9 cm	0.76**	-
Large seedlings 10-29 cm	0.50**	-0.36*
Small saplings 30-99 cm	-	-0.51**
Large saplings ≥ 100 cm but <5 cm dbh	-0.35*	-
Ca (%)	-	-0.37*
Mg (%)	-	-0.43**
Sand (%)	-	0.36*

Table 3.4. Regression models of seedling/sapling abundance versus vegetation-environment variables. In all cases, regression coefficients are significantly different from zero (t-test; *p < 0.05, **p< 0.01) and model explanatory variance is significant (F-test; P < 0.01).

Size class and variable	Standardized coefficient	R^2	Adjusted R^2
Small seedlings, 4-9 cm		0.23	0.20
Phosphorus	0.41**		
Litter depth	-0.27*		
Large seedlings, 10-29 cm		0.10	0.08
Sand	-0.31*		
Small saplings, 30-99 cm		0.15	0.14
Sand	-0.39**		
Large saplings, ≥100 cm<5 cm dbh		0.16	0.14
Rhododendron maximum cover	-0.40**		

Table 3.5. Regression models of seedling/sapling index of dispersion versus vegetation-environment variables. In all cases, regression coefficients are significantly different from zero (t-test; *p<0.05, **p<0.01) and model explanatory variance is significant (F-test; p<0.05).

Size class and variable	Standardized coefficient	R^2	Adjusted R^2
Small seedlings, 4-9 cm		0.33	0.27
Acer pensylvanicum IV	0.42*		
Litter depth	-0.38*		
Large seedlings, 10-29 cm		0.54	0.49
Slope aspect	-0.44**		
UTM northing	-0.32*		
Betula sp. IV	0.49**		
Small saplings, 30-99 cm		0.35	0.31
Betula sp. IV	0.43**		
UTM northing	-0.34*		
Large saplings, ≥100 cm but <5 cm dbh		0.35	0.30
Potassium	0.43**		
Canopy openness	0.34*		
Litter depth	-0.48**		

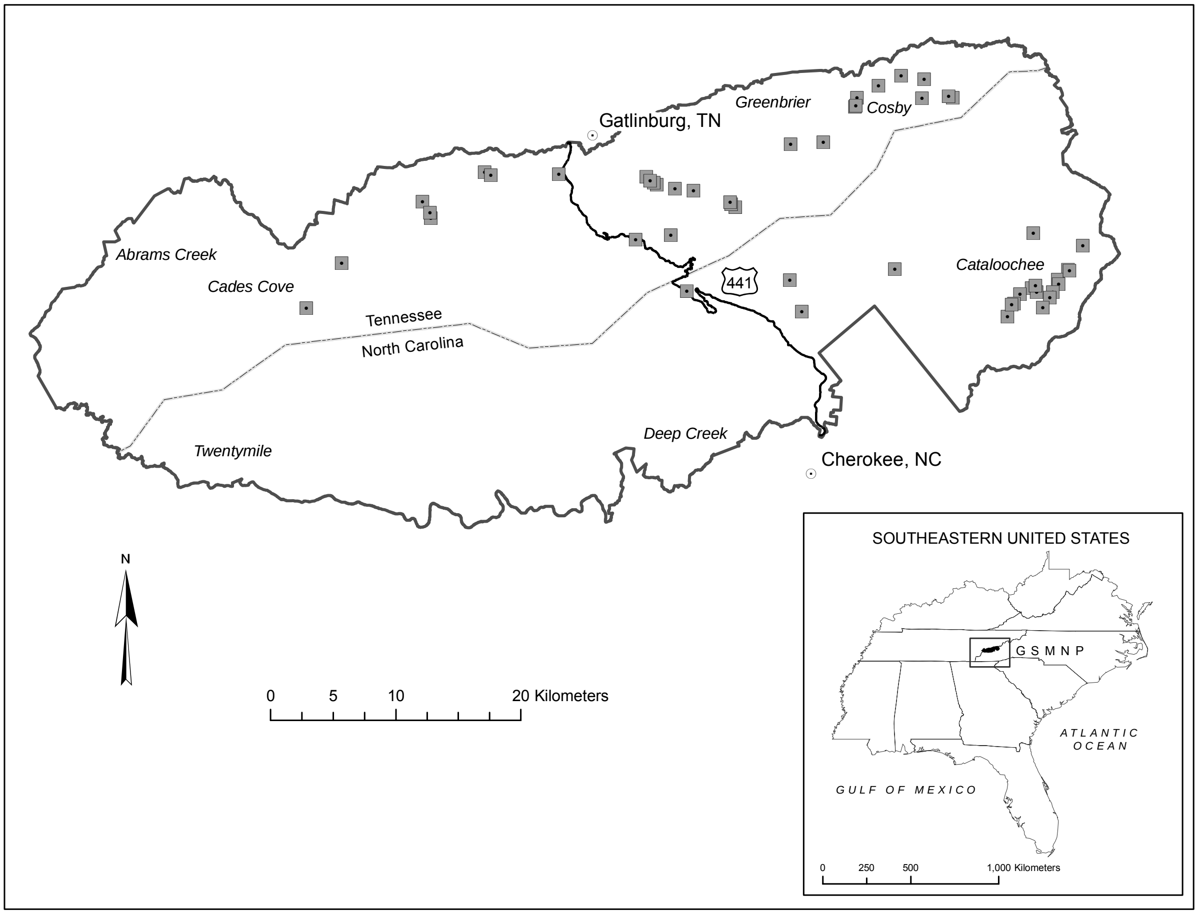

Figure 3.1. Map of Great Smoky Mountains National Park (GSMNP), showing the location of the 50 *Tsuga canadensis* (L.) Carr. forest stands in this study.

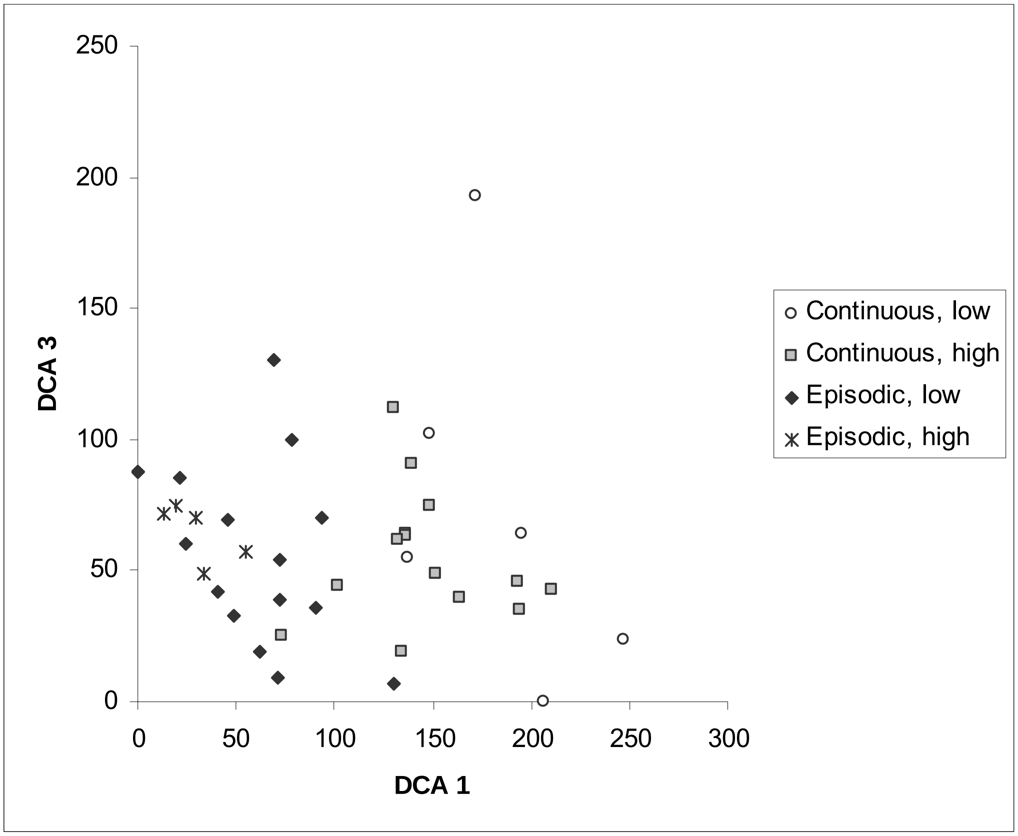

Figure 3.2. Plot of DCA axes one and two. Group symbols indicate sites with continuous or episodic regeneration and high or low levels of establishment.

CHAPTER 4

CANOPY DYNAMICS OF *TSUGA CANADENSIS* (L.) CARR. IN THE SOUTHERN APPALACHIAN MOUNTAINS

Introduction

Forest growth, composition, and structure are determined by the interactions of various biotic and abiotic factors such as species life-history characteristics, climatic factors, soils, and disturbances (White 1979; Harmon et al. 1983; Barnes et al. 1998). While data on forest-environment relationships are important, this information provides only a static view of forest dynamics. For a more complete understanding of the forest system, information on stand disturbance history is necessary. Indeed, disturbances can have profound effects on stand growth, composition, and structure, as well as overall biological diversity (Bormann and Likens 1979; Parker et al. 2001; Frelich 2002). Researchers have become increasingly aware of the effects disturbances can have on vegetation, and as a result, have examined several lines of evidence to characterize the history of forest disturbances in specific places. Evidence and techniques commonly used in disturbance history reconstructions include: pollen and charcoal analyses (e.g. Clark and Royall 1995; McLachlan et al. 2000), historical records (e.g. Lorimer 1977; Whitney 1990), stand structural characteristics (e.g. Johnson and Fryer 1989; Parker 1993), canopy gaps (e.g. Runkle 1981; Rankin and Tramer 2002), and dendroecological (tree-ring) examinations (e.g. Parshall 1995; Ziegler 2002).

The dendroecological approach is especially useful because it provides a history of suppression and release events for individual trees, thus allowing for a characterization of disturbance frequency and magnitude within forest stands.

The overall goal of this research is to characterize the structure and canopy dynamics of selected *Tsuga canadensis* forest stands within the southern Appalachian Mountains. These data will provide useful baseline information on *Tsuga canadensis* forest dynamics in the southern Appalachian Mountains prior to hemlock woolly adelgid (*Adelges tsugae* Annand) induced changes in stand structure and disturbance regime. The hemlock woolly adelgid was first detected in Great Smoky Mountains National Park (GSMNP) in 2002, and although broad-scale mortality has yet to be observed, many areas are experiencing stress and decline. Two main questions are posed by this research: 1) What is the frequency and magnitude of disturbances within *Tsuga canadensis* forests of the southern Appalachian Mountains?; and 2) Is there a connection between *Tsuga canadensis* regeneration, stand structure and disturbance history in forests of the southern Appalachian Mountains?

Although *Tsuga canadensis* forests are found from Nova Scotia and Minnesota to northern Alabama and Georgia, most of our knowledge concerning their dynamics comes from northern locations, such as the Great Lakes region and New England (Frelich and Lorimer 1991; Parshall 1995; Abrams et al. 2000; Ziegler 2002). Because of possible differences in climatic influences, vegetation assemblages, and disturbance regimes, research from more northern locations may not apply to the southern Appalachian Mountains (Yost et al. 1994). Some researchers have examined canopy gap characteristics within selected southern Appalachian *Tsuga canadensis* forest stands (Runkle 1982; Runkle and Yetter 1987). Runkle (1982) found that gap creation rates in old-growth mesic forests of the southern Appalachian Mountains ranged from ~0.3 to 3.6%/year with a natural rotation period varying from ~50 to 200 years. In old-growth cove forests of the southern Appalachian Mountains, Busing (2005) estimated gap disturbance frequencies to be 0.001 to 0.025/year with return intervals ranging from 40 to 1000 years. Lorimer (1980) provided the first detailed dendroecological analysis of an old-growth *Tsuga canadensis* -hardwood forest in the southern Appalachian Mountains. He found that the diameter and age structures of nearly all species had well-defined peaks and attributed this to decades with gap formation and unusually high survival or recruitment. Lorimer (1980) found no consistent relationship between growth release events and climatic factors. This is in agreement with Ziegler (2002) who found no evidence of a relationship between drought and growth releases in *Tsuga canadensis* forests of New York. By contrast, Parshall (1995) did find an association between drought and growth release events in *Tsuga canadensis* forests of Michigan. Despite the lack of a climate-growth release relationship, Lorimer (1980) did find the percentage of trees released during the decade (1928-1938) of chestnut (*Castenea dentata* (Marsh.) Borkh.) mortality to be greater than that of other decades. Chestnut blight, the result of an introduced fungus (*Cryphonectria parasitica* (Murrill) Barr.), has decimated chestnut throughout its native range. This wave of mortality created openings in the forests, which have been filled by other species, such as *Tsuga canadensis* (L.) Carr., *Halesia carolina* L., *Liriodendron tulipifera* L., *Acer* sp., *Carya* sp., and *Quercus* sp.

Study Area

This study was conducted within the Cataloochee watershed in the far eastern part of GSMNP (Figure 4.1). GSMNP straddles the border of Tennessee and North Carolina, U.S.A., and is world renowned for its biological diversity, including over 1,500 species of flowering plants (White 1996), and as many as 130 native tree species (Houk 1993; Kemp 1998).

Despite the logging boom from approximately 1885-1939, many scientists assert that 90% of the old-growth forests remaining in the eastern United States are located within GSMNP (Kemp 1998).

Many of the minimally-disturbed or old-growth forest stands in GSMNP lie within the Cataloochee watershed (Yost et al. 1994). Pyle (1988) estimated that 32% of the Cataloochee watershed remained undisturbed during settlement; 21% of the watershed was affected by concentrated settlement around the time of park establishment in 1934. Although large areas of minimally-disturbed or old-growth forest exist within the watershed, it is possible that some forest stands were affected by diffuse human disturbances such as scattered fires, early selective logging, and grazing. Although the National Park Service is currently working to protect many of the *Tsuga canadensis* forest stands of GSMNP, including those in the Cataloochee watershed, personal observations do suggest some stress and decline as a result of hemlock woolly adelgid infestation within the area.

According to a National Weather Service Cooperative Station in Cataloochee, North Carolina (808 m elevation), mean annual temperature within the Cataloochee watershed ranges from 4°C to18°C. Total annual precipitation averages 1318 mm (North Carolina State Climate Office 2006). The rugged and highly variable terrain within the watershed causes temperature and precipitation to vary substantially with changes in topography (Shanks 1954) typical of the Blue Ridge physiographic province (Whittaker 1956).

Methods

Forest-environmental and structural data

A total of four *Tsuga canadensis* forest stands were selected from those examined in Kincaid (2006, submitted): two stands possessed substantial *Tsuga canadensis* regeneration and two stands contained a dearth of *Tsuga canadensis* regeneration. In each forest stand, a 14x21 m plot composed of a 2x3 arrangement of 7x7 m quadrats was established parallel to slope contours (Rooney and Waller 1998; Rooney et al. 2000). At the center of each plot, we recorded location and topographic parameters: UTM easting and northing, elevation, slope aspect, slope steepness, slope configuration, and slope position. Location and elevation were estimated using a Garmin 76 hand-held global positioning system (GPS; accuracy = 9 to 12 m). We used the topographic parameters to calculate a topographic relative moisture index (TRMI; Parker 1982); TRMI values range from 0 (xeric) to 60 (mesic).

Within the quadrats of each plot, we categorized *Tsuga canadensis* stems into four vertical forest layer categories: seedlings were stems 4-99 cm tall; saplings were stems > 100 cm but < 5 cm diameter at breast height (dbh = 1.4 m); subcanopy trees were stems ≥ 5 cm dbh, but not occurring in the canopy; and canopy trees were all stems ≥ 5 cm dbh at canopy level, regardless of the degree of light restriction. Other tree species ≥ 5 cm dbh were also recorded in each plot. We calculated density, dominance, and importance value for each tree species inventoried within the plots. Importance values represent the average of relative density and relative dominance. The presence/absence of decaying wood was recorded in each quadrat and expressed a percentage of the quadrats per plot. Understory cover of *Rhododendron maximum* was estimated using the line-intercept method along each 21 m section of plot, providing 63 m of line. Canopy openness was estimated using hemispherical photographs taken at the center of each plot. We converted each photograph to a greyscale image (DMS, R-Wel 2005) and canopy openness, expressed as a percentage of pixels, was estimated by examining the proportion of white (open) versus grey (closed) pixels.

Dendroecological data

At each stand, either within or adjacent to individual plots, *Tsuga canadensis* individuals ≥ 10 cm dbh were cored at breast height (1.4 m). Sampling within and adjacent to each plot allowed for the inclusion of several age and size-classes. In the laboratory, all cores were air-dried, glued to wooden mounts, and sanded with progressively finer-grit sand paper (Phipps 1985; Stokes and Smiley 1996). Fragmented cores are common when working with *Tsuga candensis* and often require extensive reconstruction (Phipps 1985; Rankin and Tramer 2002). Visual crossdating of cores was accomplished using list method techniques (Phipps 1985; Yamaguchi 1991). Crossdated cores were measured to the nearest 0.01 mm using a binocular microscope and stage micrometer. Precision of crossdating was verified statistically by analyzing each measurement series with the program COFECHA (Holmes 1983; Grissino-Mayer 2001). A total of 56 increment cores across four stands were used in this research. Despite the relatively small sample size, Frelich (2002) found that increment cores from as few as five trees per stand could reduce your chances of missing a cohort to less than 5.0%, so long as the stand structure was not characterized by a series of spatially restricted cohorts.

Individual measurement series were examined for growth-release events to assess tree-level and stand-wide canopy disturbances. We analyzed growth-release events using radial growth averaging methods (i.e. running means) modified from Lorimer and Frelich (1989) and Nowacki and Abrams (1997). Major growth releases were defined as mean growth increases of ≥ 100.0 %, while growth increases between 50.0 and 99.9% were considered moderate releases.

Minor release events were defined as mean growth increases between 25.0 and 49.9%. The radial growth averaging approach to disturbance history reconstruction is widely considered to be an effective alternative to regression techniques, which detrend age-size relationships in tree-ring data (Lorimer and Frelich 1989; Nowacki and Abrams 1997; Parshall 1995; Ziegler 2002). In all cases, criteria dictated that growth-release events had to be sustained for ≥ 10 years and were preceded by ≥ 10 years of suppressed growth. These criteria are typically employed to screen out the effects of short-term climatic fluctuations on tree-growth (Lorimer and Frelich 1989; Frelich 2002). The growth-release data were used to construct decadal disturbance chronologies detailing the history of canopy disturbance within each stand. Stand-wide disturbance events were identified when ≥ 25.0% of the sample trees exhibited a growth-release during a given decade (Nowacki and Abrams 1997). Stata release 8 was used to calculate unequal variance-adjusted Student's t-tests to explore significant differences in the number of release events per tree by intensity class between forest stands with and without successful *Tsuga canadensis* regeneration (StataCorp 2003).

Results

Forest stand environmental and structural characteristics

The four forest stands contained a total of eight tree species with *Tsuga canadensis* as the leading canopy dominant (Table 4.1). Importance values (IV) for *Tsuga canadensis* ranged from 60.6% to 87.0%. The stem density of *Tsuga canadensis* was high across all forest stands, and was second only to the density of *Rhododendron maximum* at two stands. Other species with IVs >10.0% in one or more forest stands included *Acer rubrum*, *Rhododendron maximum*, and *Betula* sp. (includes *Betula lenta* L. and *Betula alleghaniensis* Britt.).

Distinct environmental and structural differences were apparent between forest stands with and without successful *Tsuga canadensis* regeneration. CFK and BFR-II, both of which had successful *Tsuga canadensis* regeneration, were located above 1000 m in elevation on well-drained, moderately steep slopes, and had the greatest canopy openness (Figure 4.2a-d; Table 4.2). BGM and BFR-I, sites characterized by a dearth of *Tsuga canadensis* regeneration, were found at elevations below 1000 m on more mesic sites with relatively closed canopies. In stands with little *Tsuga canadensis* regeneration, diameter structures revealed missing cohorts of *Tsuga canadensis*, and exhibited a distinctly bimodal distribution of stems (Figure 4.3a-d). By contrast, the forest stands where *Tsuga canadensis* was successfully regenerating approximated a negative exponential or even distribution of diameter classes. *Tsuga canadensis* age-structures, estimated from a diameter-age regression model (Lorimer 1980), indicated a tendency for *Tsuga canadensis* regeneration to be episodic, especially at those sites lacking successful regeneration (Figure 4.4a-d). At sites where *Tsuga canadensis* was regenerating, recruitment appeared to be more or less continuous for longer periods such as from approximately 1700 to 1900 at BFR-II, and from about 1800 to the 1900s at CFK.

Canopy dynamics

Only 27% of the 56 increment cores revealed pith or near-pith ring curvature because of internal rot, fragmentation, or the large size of individual *Tsuga canadensis* stems. Despite these problems, disturbance events were easily identified, with many trees showing multiple releases (Table 4.3). A total of 188 release events were recorded across stands for disturbances eliciting $\geq 25.0\%$ mean growth increases. During the common period 1796-1994, 186 release events were observed, which translates to a mean canopy turnover rate of 9.4%/decade (0.94/year) and a mean canopy residence time of 105 years. Ninety-five release events were identified if disturbances eliciting ≥ 50.0% mean growth increases were examined. This resulted in an estimated mean canopy turnover rate of 4.8%/decade (0.48/year), corresponding to a mean canopy residence time of approximately 208 years. It must be emphasized that the aforementioned estimates of canopy turnover rate and residence time were calculated using total release events across all forest stands; therefore, they are dependent upon sample size.

At the forest stand level, the mean return interval per tree indicated that minor canopy disturbances were much more frequent than moderate and major disturbance events (Table 4.4). Indeed, individual tree release rates ranged from ~0.2/decade (0.02/year) for minor disturbance events to ~0.03/decade (0.003/year) for major disturbances. Student's t-tests examining the number of release events per tree by intensity class between forest stands with and without successful *Tsuga canadensis* regeneration yielded significant results. Releases per tree for all events resulting in minor (≥ 25.0%) and major (≥ 100.0%) growth increases were significantly different ($t = -2.05$; $t = -2.01$, $p<0.05$) between forest stands with and without successful *Tsuga canadensis* regeneration. Moderate release events (≥ 50.0%) elicited an even greater contrast ($t = -3.11$, $p<0.003$) between forest stands with and without successful *Tsuga canadensis* regeneration. Therefore, forest stands where *Tsuga canadensis* was successfully regenerating experienced more frequent canopy disturbances, especially events of moderate intensity.

Disturbance chronologies for the two sites where *Tsuga canadensis* was currently regenerating, CFK and BFR-II, show 5 to 7 decades, respectively, when disturbances affected ≥ 25.0% of the canopy (Figure 4.5). At CFK, these disturbances occurred during the 1850s and1860s, 1900s, 1960s, and 1990s. The disturbances at BFR-II occurred in the 1830s, 1870s, 1900s, 1920s and 1930s, and 1980s and 1990s. Larger disturbances affecting ≥ 40.0% of the canopy occurred during the 1870s and 1930s at BFR-II, and during the 1850s, 1860s, 1900s, and

1930s at CFK. While many of these disturbances appeared to be unique to individual stands, the disturbances of the 1900s, 1930s, and 1990s may have been more widespread as they affected both stands. Growth release data showed that these two sites experienced minor to major standwide releases during the 1990s, which resulted in canopy openings that facilitated much of the *Tsuga canadensis* regeneration observed in Kincaid (2006, submitted). When all disturbance events were included, mean percentage of canopy disturbed per decade at CFK and BFR-II was 17.3% (cv = 7.0%). If only events at the ≥ 50.0% growth threshold are examined, mean percentage of canopy disturbed per decade was 9.9% (cv = 4.8%).

The incidence of disturbance events affecting ≥ 40.0% of the canopy was substantially reduced at the two sites where *Tsuga canadensis* was not regenerating very well. Disturbances affecting ≥ 40.0% of the canopy occurred only during the 1980s at BGM. By contrast, incidences of disturbance events affecting ≥ 25.0% of the canopy were similar across all four forest stands. At BFR-I, these more moderate disturbance events were recorded in four decades: the 1890s, 1930s and 1940s, and 1990s. At BGM, such disturbance events occurred during the 1880s, 1910s and 1920s, 1950s, and 1980s and 1990s. The detection of minor and moderate release events during the 1990s within these stands supports the idea that these events were not localized, but widespread in the Cataloochee watershed. Mean percentage of canopy disturbed per decade at BFR-I and BGM was 12.0% (cv = 18.3%). If those events meeting the ≥ 50.0% growth release threshold were examined, mean percentage of canopy disturbed per decade was 5.2% (cv = 10.6%). Therefore, sites where *Tsuga canadensis* was experiencing a current dearth of regeneration were less frequently disturbed by standwide disturbance events.

Discussion

Forest-environmental characteristics

Forest stands experiencing a current dearth of *Tsuga canadensis* regeneration were found to have relatively closed canopies and the highest mean stand basal area (mean = 98.4 m^2/ha, cv = 5.8% versus mean = 74.9 m^2/ha, cv = 68.9%), which indicates the presence of large trees with broad crowns. In addition, these forest stands occurred at the lowest elevations (mean = 892.9 m, cv = 14.8%) and on more mesic sites. Previous researchers have found a positive association between canopy openness and *Tsuga canadensis* regeneration (Rooney at al. 2000; Kincaid 2006, submitted). Others have mentioned that the shade cast by a well-stocked overstory and associated root competition may preclude *Tsuga canadensis* regeneration (Hett and Loucks 1976; Lorimer 1995; Orwig et al. 2001). *Rhododendron maximum* L., has been reported to be expanding along streamsides and in cooler, more mesic areas in the southern Appalachian Mountains (Dobbs and Parker 2004). This species easily expands in response to disturbance, including individual tree-fall gaps (Plocher and Carvell 1987; Dobbs and Parker 2004); therefore, canopy gap formation that could facilitate *Tsuga canadensis* regeneration may lead to understory *Rhododendron maximum* expansion instead. While this may be the case at BFR-I with a *Rhododendron maximum* understory cover of 66.7%, it is not the case at BGM. BGM has very little understory *Rhododendron maximum* cover (1.6%), but does have a dense ground cover of *Leucothoe fontanesiana* (Steud.) Sleumer occurring throughout much of the stand. Like *Rhododendron maximum*, *Leucothoe fontanesiana* is an ericad found primarily near streams and in mesic settings. Despite having the highest presence of decaying wood (100% versus 16.7% to 50.0%), indicative of canopy gap formation, and providing elevated sites for seedling germination, BGM is still characterized by a dearth of *Tsuga canadensis* regeneration. Decaying wood has been reported in other settings to provide favorable sites for *Tsuga canadensis* regeneration, and the elevated nature of this substrate type has been said to alleviate ground competition (Waller et al. 1996; Rooney and Waller 1998), but this is not the case at BGM. Kincaid (2006, submitted) found that decaying wood was not a significant predictor of *Tsuga canadensis* regeneration abundance or the spatial pattern of seedlings and saplings across a suite of 50 sites in the southern Appalachian Mountains. He suggested that increased canopy light penetration from disturbance may reduce dependence on decaying wood as a regeneration substrate in many of these sites.

Tsuga canadensis regeneration appears to be hindered somewhat by the forest dynamics and environmental characteristics of the mesic settings found at BFR-I and BGM, while conditions at the more xeric sites of BFR-II and CFK seem to be more favorable for regeneration of the species. In fact, Nienstaedt and Olson (1955) found that *Tsuga canadensis* may grow better than hardwoods on dry, sandy sites if individuals became established during relatively moist years. Kavanagh and Kellman (1986) also found *Tsuga canadensis* to be most successful on what they considered to be drier sites, and suggested that the species may become displaced by deciduous trees at more mesic sites. This observation agrees with that of Parshall (1995) who concluded that *Acer saccharum* Marsh. appears to be replacing *Tsuga canadensis* in areas where they are both present. Despite having the least amount of decaying wood (mean = 33.4%, cv = 70.6%), *Tsuga canadensis* is regenerating successfully within these two forest stands. In addition, these two forest stands currently have the lowest percentage of understory *Rhododendron maximum* cover (mean = 0.8%, cv = 141.4%). The cover of *Rhododendron maximum* or *Kalmia latifolia* L., particularly at BFR-II, can be expected to expand as a result of future canopy disturbance events. However, the xeric conditions at these sites, and their distances from streams, will slow the future expansion of *Rhododendron maximum*. The lack of a well-developed *Rhododendron maximum* understory occurring concomitantly with open overstory conditions driven by disturbances allows *Tsuga canadensis* to persist at these sites.

Forest stand structural attributes

The diameter distribution of stems at sites with successful regeneration are flat and relatively even at CFK, or because of abundant small stems, approach a negative exponential form at BFR-II. While these forest stands have some gaps in their diameter structures, *Tsuga canadensis* stems are present in all vertical layers, which approximates a negative exponential form at CFK and bell-shaped distribution at BFR-II. Diameter structures at sites currently lacking successful regeneration, BGM and BFR-I, are bimodal and flat, while the distribution of vertical layers show gaps in the seedling or sapling classes, respectively. Researchers have found a variety of diameter distributions when working in older growth *Tsuga canadensis* forests, including the negative exponential (Abrams and Orwig 1996; Hart and Shankman 2005), bell-shaped (Tyrell and Crow 1994), and unimodal types (Lorimer and Krug 1983; Knebel 1999; Ziegler 2000; Orwig et al. 2001). A bimodal distribution typically indicates episodic regeneration.

In this study, the age-structures of the four forest stands were estimated using the diameter-age regression model of Lorimer (1980). Although actual tree-ages are preferable, the equation of Lorimer (1980) was based on *Tsuga canadensis* forest stands from the study region. Other researchers have found the regression method of age estimation to provide the lowest absolute error when compared to methods that use mean ring widths to extrapolate tree age (Clark and Hallgren 2004). Although diameter has been shown to be poorly correlated with age in northern forests (Rogers 1978; Ziegler 2000), Lorimer (1980) and Hart and Shankman (2005) found strong positive correlations between diameter and age in southern populations of *Tsuga canadensis*. Moreover, Tyrell and Crow (1994) found that older-growth *Tsuga canadensis* (>300 years old) stands were more likely than younger old growth to show positive relationships between age and diameter. Estimated age-structures show a history of somewhat episodic *Tsuga canadensis* regeneration at all sites. BFR-II appears to have the most continuous regeneration although it lacks stems estimated at <100 years old. CFK, the other site where *Tsuga canadensis* is currently regenerating, had an age structure similar to BGM, a site lacking regeneration. Regeneration appears to be arrested at BFR-I, which had a distinctly bimodal distribution of ages with no stems estimated at <180 years old, and most at least 280 years old. The arrested regeneration at BFR-I may be linked to human settlement because this forest stand is close to a former homestead, and thus may have been affected by early selective logging or grazing. The existence of a link between *Tsuga canadensis* regeneration failures and past land-use activities has been mentioned by other researchers (Mladenoff and Stearns 1993). With the exception of BFR-I with its distinctly bimodal distribution of age-classes, the age-structures of the other three forest stands are representative of reproduction through noncatastrophic disturbances, such as single or multiple-tree canopy gaps (Tyrell and Crow 1994).

Disturbance regimes

Despite the small number of forest stands and increment cores examined in this study, reasonably good estimates of disturbance frequency and magnitude were obtained for *Tsuga canadensis* forests of the southern Appalachain Mountains. The mean canopy turnover rate of 9.4%/decade (0.94%/year) and associated mean canopy residence time of 105 years meshes well with the estimated mortality rates (~1.0%/year) and rotation periods (~100 years) of Runkle (1982, 2000). Our canopy turnover rates are, however, slightly higher than those from more northern forests, which for *Tsuga canadensis* generally range from about 0.52%/year to 0.74%/year (Frelich and Lorimer 1991; Frelich and Graumlich 1994; Parshall 1995; Ziegler 2002). However, this estimate is based on the more liberal criteria of including all releases eliciting a ≥ 25.0% mean growth increase. If we include only those releases resulting in ≥ 50.0% growth increases, then the mean canopy turnover rate becomes 4.8%/decade (0.48/year), which is more comparable to those studies from the Great Lakes region and New York. In fact, Frelich and Lorimer (1991) estimated disturbance rates in the 4.6 to 4.9% range in two of their study areas in Michigan. This figure is also close to the mortality estimates of Busing (2005) (0.3%/year) and Lorimer (1980) (5.6%/decade) for *Tsuga canadensis* in the southern Appalachian Mountains. Annual tree-level releases and return intervals by forest stand generally agree with the results of Busing (2005) who found gap disturbance frequencies of 0.001 to 0.025/year, and return intervals of 40 to 1000 years across canopy gap sizes in old growth cove forests of the southern Appalachian Mountains.

The overall mean frequency of minor to major canopy disturbances is significantly different between forest stands with and without successful *Tsuga canadensis* regeneration. It appears that minor canopy disturbances, although occurring more frequently, are not meaningful events in terms of *Tsuga canadensis* regeneration. Major canopy disturbances may be of greater importance than indicated in this study, but these events occurred too infrequently in the forest stands to obtain an adequate sample. Canopy disturbances of moderate intensity appear to be the most important in terms of facilitating *Tsuga canadensis* regeneration. Forest stands lacking successful *Tsuga canadensis* regeneration experience less frequent canopy disturbance events, especially those of moderate intensity. The occurrence of these disturbance events may explain the tendency for *Tsuga canadensis* regeneration to be spatially aggregated at the stand scale.

Kincaid (2006, submitted) thought this spatial aggregation to be the result of canopy gap formation, especially considering the positive association between the spatial pattern of seedlings and saplings and the importance of *Acer pensylvanicum* L. and *Betula* sp., both of which tend to proliferate in canopy gaps. He also observed a positive association between the spatial pattern of saplings and canopy openness, which further supports the canopy gap-*Tsuga canadensis* regeneration link. Many of these events appear to be localized and random, but it is clear that the two *Tsuga canadensis* forest stands with successful regeneration experience more frequent canopy disturbances. The notion that *Tsuga canadensis* regeneration is associated with relatively frequent, localized canopy gap creation, rather than larger, more severe disturbances, is strongly supported by the existing literature (Runkle and Yetter 1987; Woods 2000a, 2000b; Frelich 2002).

Age-class peaks at 120.0 to139.9 years and 160.0 to 179.9 years indicate a series of canopy disturbance events during the periods of 1824 to 1844 and 1864 to 1884 at BFR-II and CFK. These age-class peaks coincide with evidence of stand-wide disturbances affecting as much as 55.0% of the canopy. The same age-class peaks are also present at BGM, which may indicate disturbance events that affected a large part of the Cataloochee watershed. At BFR-I and BGM, age-class peaks at 280.0 to 299.9 years and 220.0 to 239.9 years are probably related to disturbances that occurred in these forest stands during the periods of 1704 to 1724 and 1764 to 1784. However, lack of sample depth during these periods prevents any conclusive interpretations. Lorimer (1980) found that release events and age-class peaks suggested possible area-wide disturbances in the 1720s, 1750s, 1780s and 1820s at his sites in the southern Appalachian Mountains. These findings suggest that some of the canopy disturbances evident in our data may be the result of historical weather events affecting large areas of the southern

Appalachian Mountains. The age-class peaks and associated disturbances during the periods of 1824 to 1844 and 1864 to 1884 may be linked to diffuse events initiated by human settlement in the Cataloochee watershed. Land clearing associated with permanent residency occurred in the 1830s and a wave of settlers arrived during the 1850s (Davis 1999). Pyle (1988) stated that some 1200 people once lived a subsistence lifestyle in the Cataloochee watershed. CFK and BFR-II also appear to have been affected by *Castanea dentata* dieback, although to different degrees. *Castanea dentata* is currently sprouting within the two forest stands and both areas were altered by canopy disturbances affecting ~10.0 to 40.0% of the canopy during the 1920s and 1930s when mortality was observed in the region (Woods and Shanks 1959; Lorimer 1980). Disturbances during the 1920s and 1930s were also evident in the two forest stands lacking successful *Tsuga canadensis* regeneration, BGM and BFR-I, but evidence of the presence of *Castanea dentata* was lacking at these lower elevation, more mesic sites. Evidence of direct human impacts was also absent from these two forest stands. The more recent disturbances of the 1990s were widespread as they occurred across all four forest stands. Because the chronology ends at 1994 instead of 2004, an artifact of using a 10-year running mean, this must be interpreted with caution. That is, the actual peak growth release may have occurred after 1994, but the precise year of disturbance is not discernable with the methods employed. These growth releases are likely the result of hurricanes Andrew (1992) or Opal (1995), both of which caused localized blowdowns throughout the southern Appalachain Mountains.

Parshall (1995) found a positive association between drought events and canopy mortality in the Great Lakes region. He showed that drought events coincided with peaks in tree growth releases. Parshall (1995) concluded that in addition to periodic windstorms, drought events should be considered when examining canopy mortality in a region. This research found no correlation between the number of release events within or across sites and mean annual or seasonal Palmer Drought Severity Index (PDSI) values from 1895 to 1994 (NOAA 2006) (results not presented). However, peaks in release events were found to exist during the drought years of 1902, 1930, 1960, and 1988. These finding agree with Lorimer (1980) who found no consistent relationship between the frequency of abrupt growth increases and temperature or precipitation variables in *Tsuga canadensis* forests of the southern Appalachian Mountains, and Ziegler (2002) who found no relationship between canopy disturbance and PDSI values in New York. Ziegler (2002) did, however, find above-mean disturbance rates at some of her sites in the 1930s (a dry period), but below-mean disturbance rates in the 1960s (a dry period), further indicating an inconsistent relationship between drought and disturbance.

More research is clearly needed to document the structural attributes and disturbance regimes of *Tsuga canadensis* forests in the region. Most of our knowledge concerning the dynamics of these forest systems comes from more northern locations such as the Great Lakes region and New England (e.g. Frelich and Lorimer 1991; Parshall 1995; Ziegler 2002). This call for more research takes on added urgency as many of the *Tsuga canadensis* forest stands within the study region are currently experiencing stress and decline as a result of hemlock woolly adelgid infestation; this is also true of those in the Cataloochee watershed of GSMNP. The present study is based on only four forest stands within the Cataloochee watershed of GSMNP; future research should examine *Tsuga canadensis* forest stands throughout the park, as well as other populations in the southern United States. Several researchers have recommended silvicultural operations such as single or group selection methods to facilitate successful *Tsuga canadensis* regeneration (Rooney and Waller 1998; Webster and Lorimer 2002), which if conducted at the average rate for the region (Singer and Lorimer 1997), would closely mimic the canopy dynamics of many *Tsuga canadensis* forest stands. Indeed, the results of this research in conjunction with others (Rooney et al. 2000; Kincaid 2006, submitted), has elucidated a link between canopy openness or gap creation and *Tsuga canadensis* regeneration. Because *Rhododendron maximum* has been shown to easily invade canopy gaps (Plocher and Carvell 1987; Dobbs and Parker 2004), and it is well known that this species often precludes the regeneration of *Tsuga canadensis*, as well as other tree species (Monk et al. 1985; Hedman and Van Lear 1995; Van Lear et al. 2002), any silvicultural treatment resulting in canopy gap creation may also have to include *Rhododendron maximum* removal to further promote tree regeneration. The baseline information provided by this research and future studies can aid land managers in the promotion of *Tsuga canadensis* regeneration in areas where treatment against hemlock woolly adelgid infestation is successful. In areas that cannot be treated, or where treatment is unsuccessful, this information can aid future restoration efforts after the wave of hemlock woolly adelgid induced mortality has passed.

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Table 4.1. Compositional characteristics by forest stand. Columns refer to density (D; stems/ha), basal area (BA; m^2/ha), and importance value (IV = [relative density + relative basal area]/2).

Species	BGM			BFR-I			CFK			BFR-II		
	D	BA	IV	D	BA	IV	D	BA	IV	D	BA	IV
Acer pensylvanicum L.	0.0	0.0	0.0	0.0	0.0	0.0	34.0	0.2	4.0	0.0	0.0	0.0
Acer rubrum L.	34.0	8.3	8.2	0.0	0.0	0.0	0.0	0.0	0.0	136.1	22.8	37.4
Betula sp.	102.0	0.9	12.0	0.0	0.0	0.0	34.0	2.3	4.9	0.0	0.0	0.0
Fagus grandifolia Ehrh.	0.0	0.0	0.0	68.0	0.2	4.9	0.0	0.0	0.0	0.0	0.0	0.0
Halesia carolina L.	0.0	0.0	0.0	34.0	0.1	2.4	34.0	0.9	4.2	0.0	0.0	0.0
Kalmia latifolia L.	68.0	0.2	7.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhododendron maximum L.	0.0	0.0	0.0	374.2	1.4	26.9	0.0	0.0	0.0	34.0	0.1	2.0
Tsuga canadensis (L.) Carr.	238.1	85.0	72.0	238.1	100.6	65.8	340.1	108.0	87.0	714.3	15.5	60.6

[a] *Betula* sp. includes *Betula lenta* L. and *Betula alleghaniensis* Britt.

Table 4.2. Vegetation and environmental characteristics by forest stand.

Stand characteristic	BGM	BFR-I	CFK	BFR-II
Stand density (stems/ha)	442.2	714.3	442.2	884.4
Stand basal area (m^2/ha)	94.3	102.3	111.4	38.4
Rhododendron maximum cover (%)	1.6	66.7	0.0	1.6
Kalmia latifolia cover (%)	0.0	0.0	0.0	3.2
Canopy openness (%)	0.9	0.3	4.2	7.2
Decaying wood (%)	100.0	33.3	50.0	16.7
Elevation (m)	799.8	986.0	1111.3	1058.9
Slope aspect (^{o})	335.0	347.0	356.0	260.0
Slope steepness (%)	10.0	49.0	30.0	32.0
TRMI (0-60)	49.0	33.0	27.0	16.0

Table 4.3. Summary of *Tsuga canadensis* release events by forest stand and disturbance intensity class.

Forest Stand	Period	Number of cores	25.0-49.9%	50.0-99.9%	≥ 100.0%	Total events
BGM	1743-1994	16	33	16	6	55
BFR-I	1796-1994	11	14	5	6	25
CFK	1763-1994	9	17	10	12	39
BFR-II	1796-1994	20	29	29	11	69
Total	_____	56	93	60	35	188

Table 4.4. Tree-level release rates and mean return intervals (MRI; years) by intensity class and forest stand.

All events ≥ 25.0%

Stand	Trees	Releases	Years	Releases/Tree	Releases/Century	MRI
BGM	16	53	252	3.3	1.3	76.1
BFR-I	11	25	199	2.3	1.1	87.6
CFK	9	39	232	4.3	1.9	53.5
BFR-II	20	69	199	3.5	1.7	57.7
All stands	56	186	199	3.3	1.7	59.9

All events ≥ 50.0%

Stand	Trees	Releases	Years	Releases/Tree	Releases/Century	MRI
BGM	16	22	252	1.4	0.6	183.3
BFR-I	11	11	199	1.0	0.5	199.0
CFK	9	22	232	2.4	1.1	94.9
BFR-II	20	40	199	2.0	1.0	99.5
All stands	56	95	199	1.7	0.9	117.3

All events
≥ 100.0%

Stand	Trees	Releases	Years	Releases/Tree	Releases/Century	MRI
BGM	16	6	252	0.4	0.2	672.0
BFR-I	11	6	199	0.6	0.3	364.8
CFK	9	12	232	1.3	0.6	174.0
BFR-II	20	11	199	0.6	0.3	361.8
All stands	56	35	199	0.6	0.3	318.4

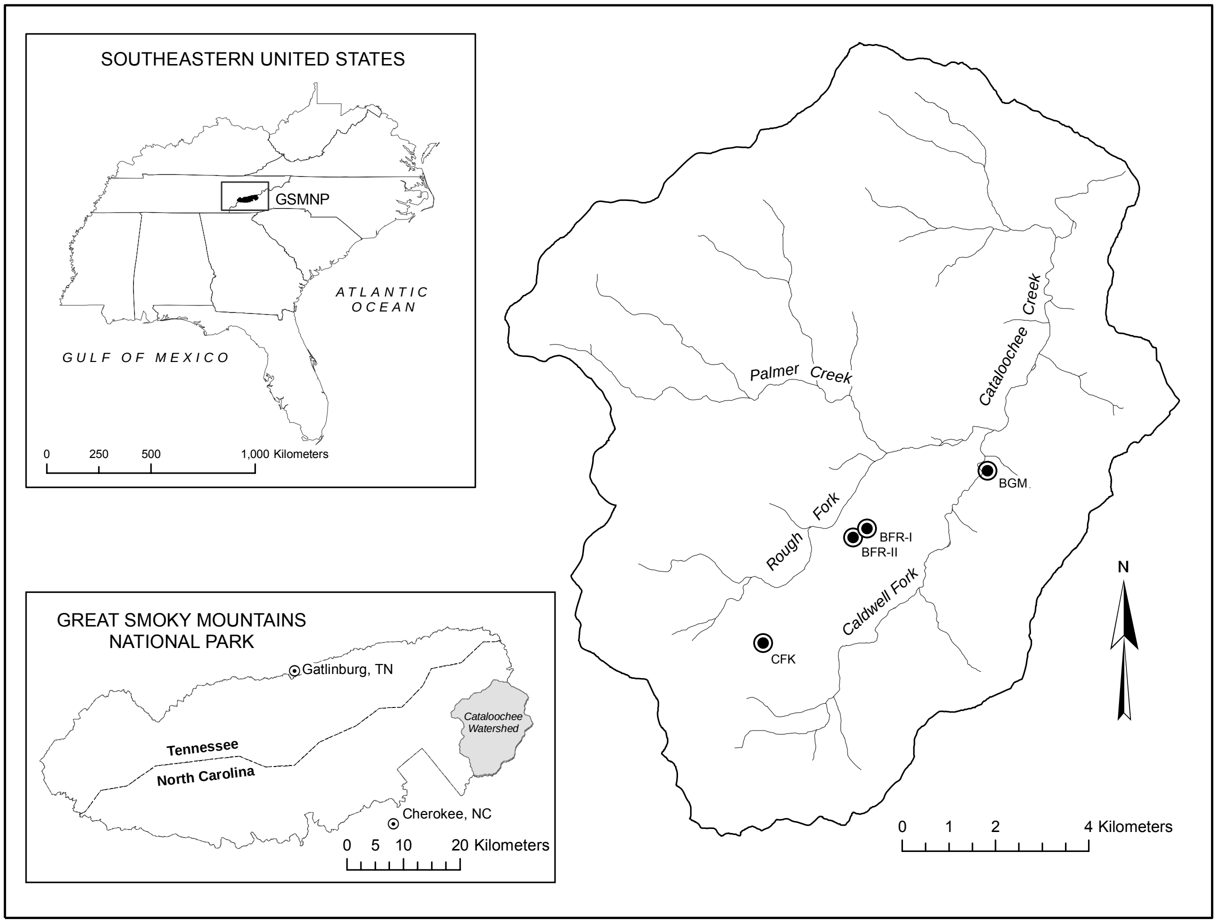
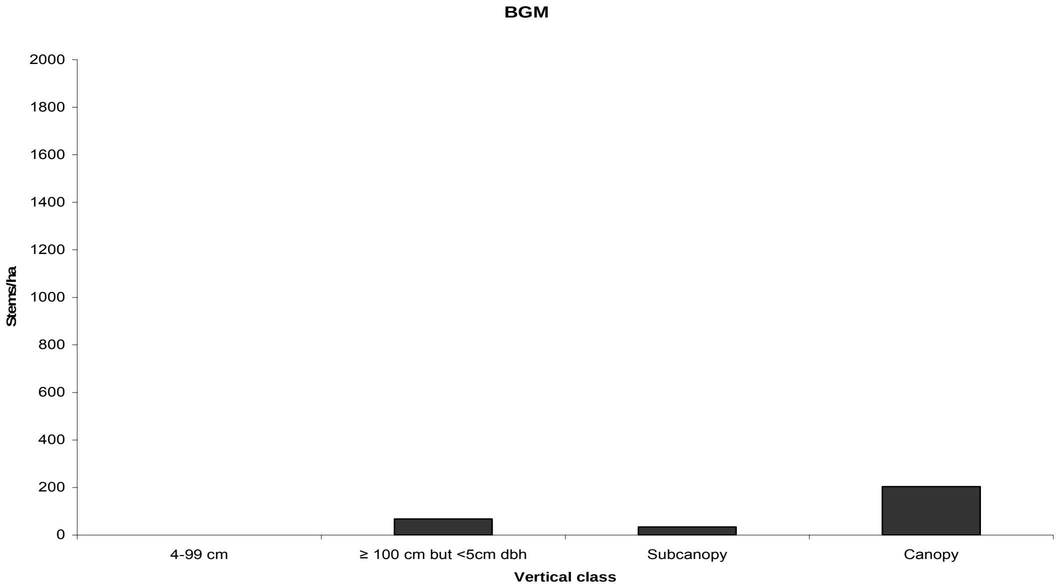
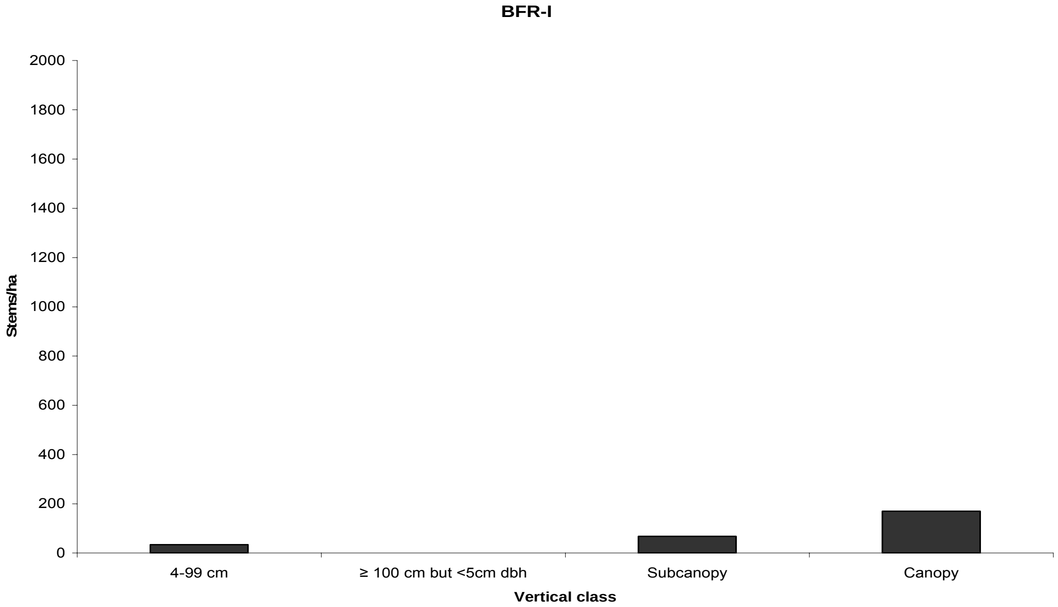


Figure 4.1. Map of Great Smoky Mountains National Park (GSMNP), showing the location of the four *Tsuga canadensis* forest stands within the Cataloochee watershed. Forest stand labels refer to the Boogerman Trail (BGM), Big Fork Ridge (BFR-I, II), and Caldwell Fork (CFK).


BGM
Stems/ha
0
200
400
600
800
1000
1200
1400
1600
1800
2000
4-99 cm
≥ 100 cm but <5cm dbh
Subcanopy
Canopy
Vertical class

(A)


BFR-I
Stems/ha
0
200
400
600
800
1000
1200
1400
1600
1800
2000
4-99 cm
≥ 100 cm but <5cm dbh
Subcanopy
Canopy
Vertical class

(B)

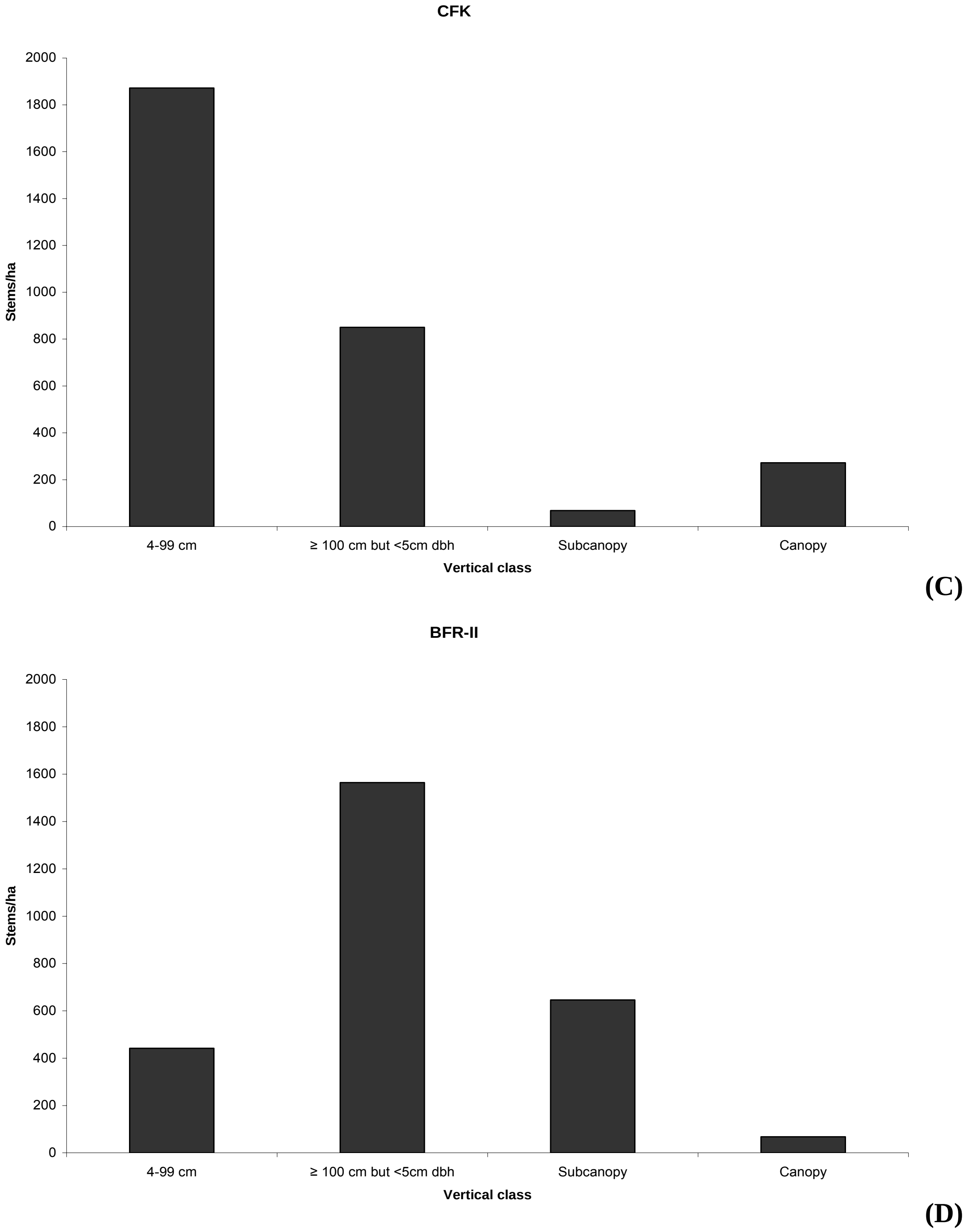
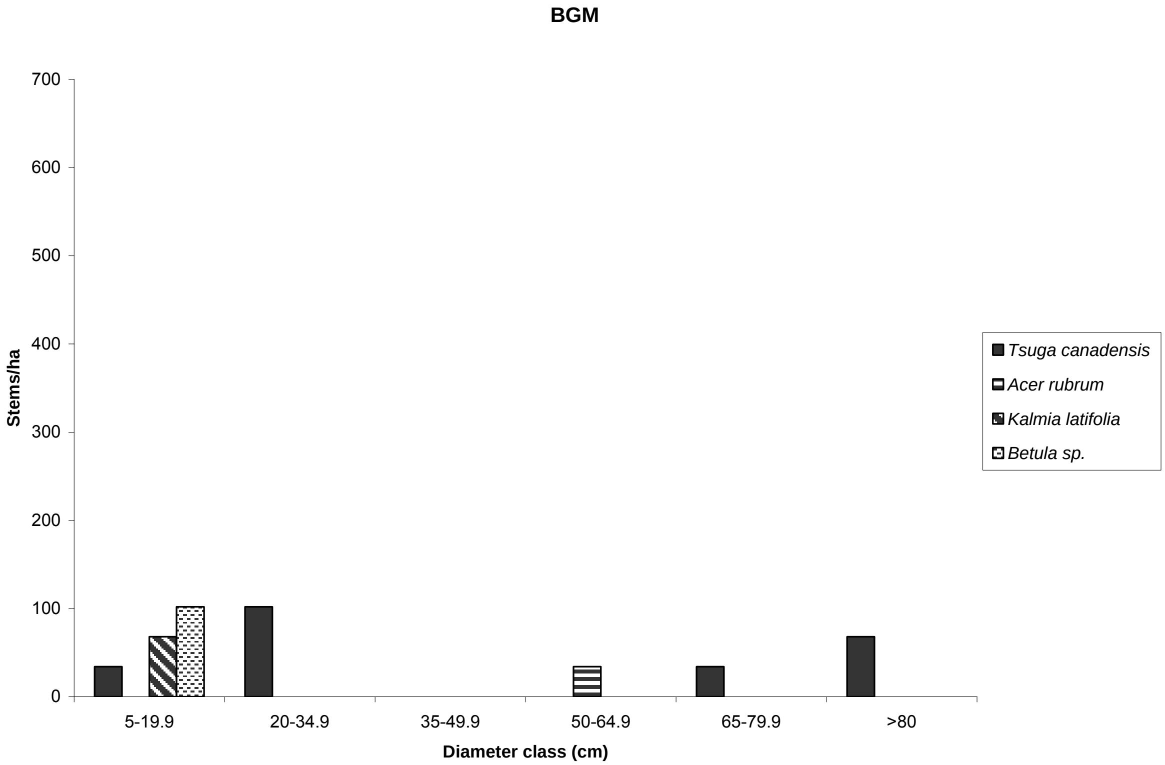
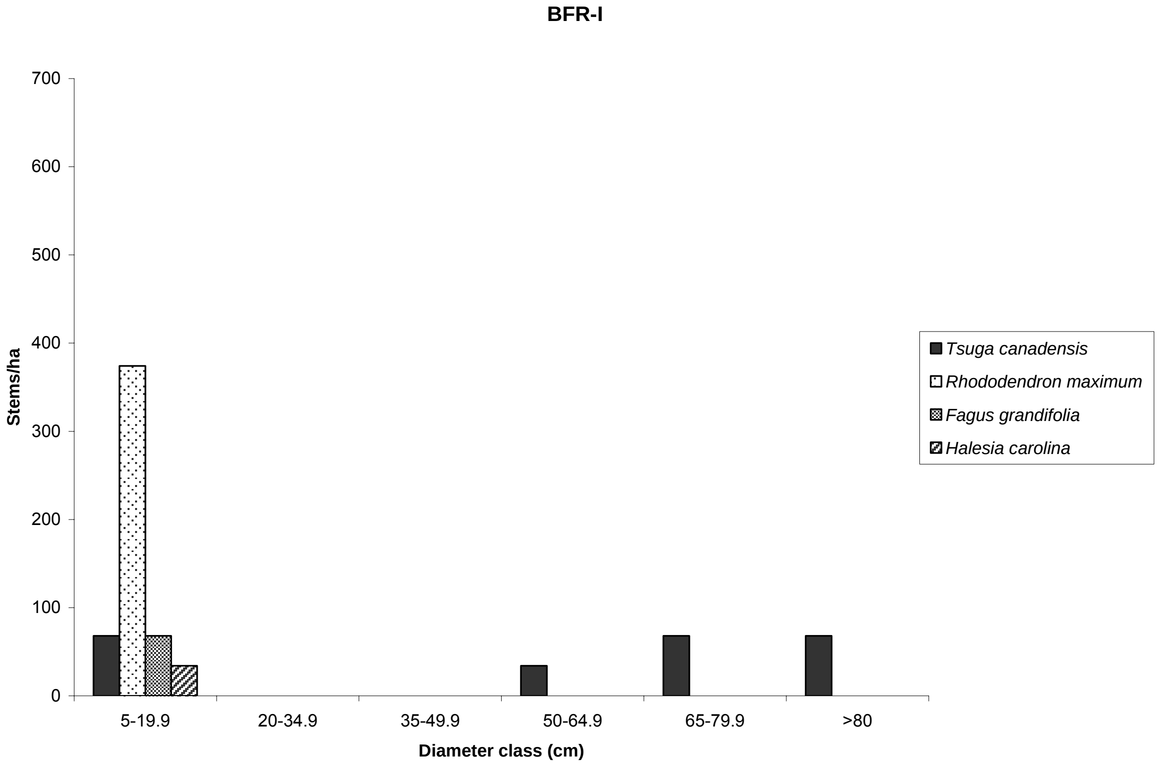


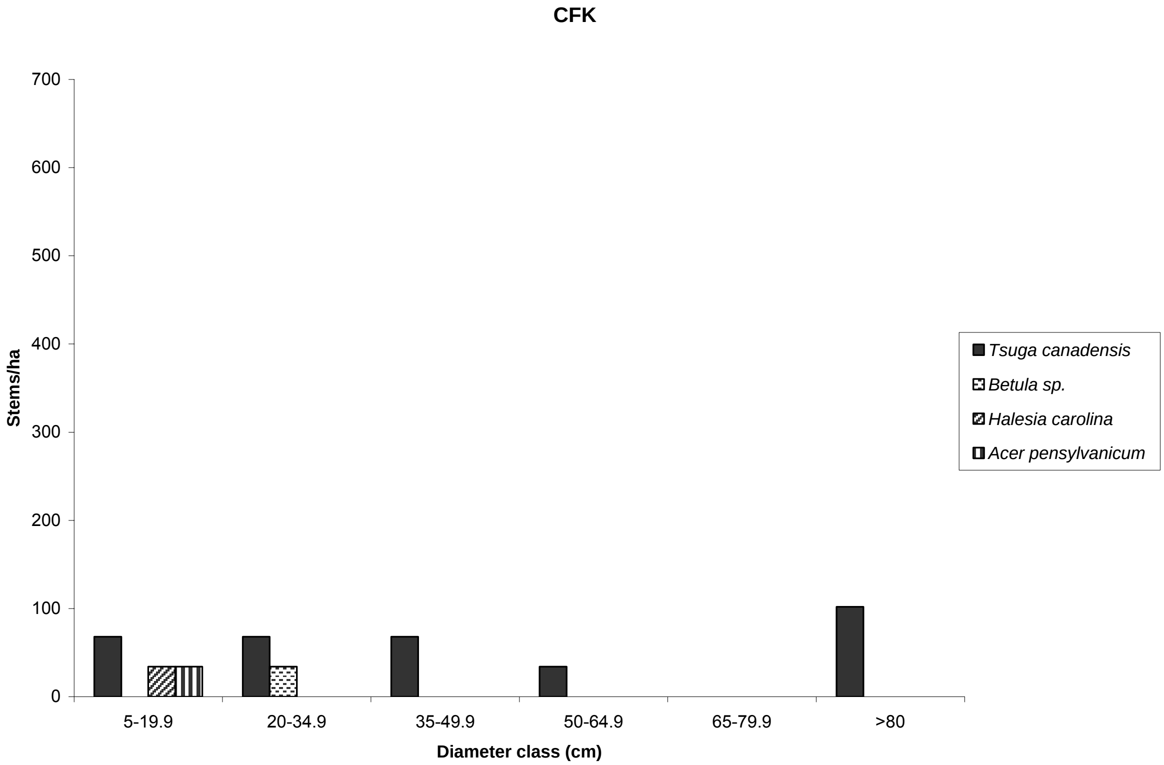
Figure 4.2. Vertical class distributions for *Tsuga canadensis* in each forest stand.


BGM
Stems/ha
700
600
500
400
300
200
100
0
5-19.9
20-34.9
35-49.9
50-64.9
65-79.9
>80
Diameter class (cm)
Tsuga canadensis
Acer rubrum
Kalmia latifolia
Betula sp.

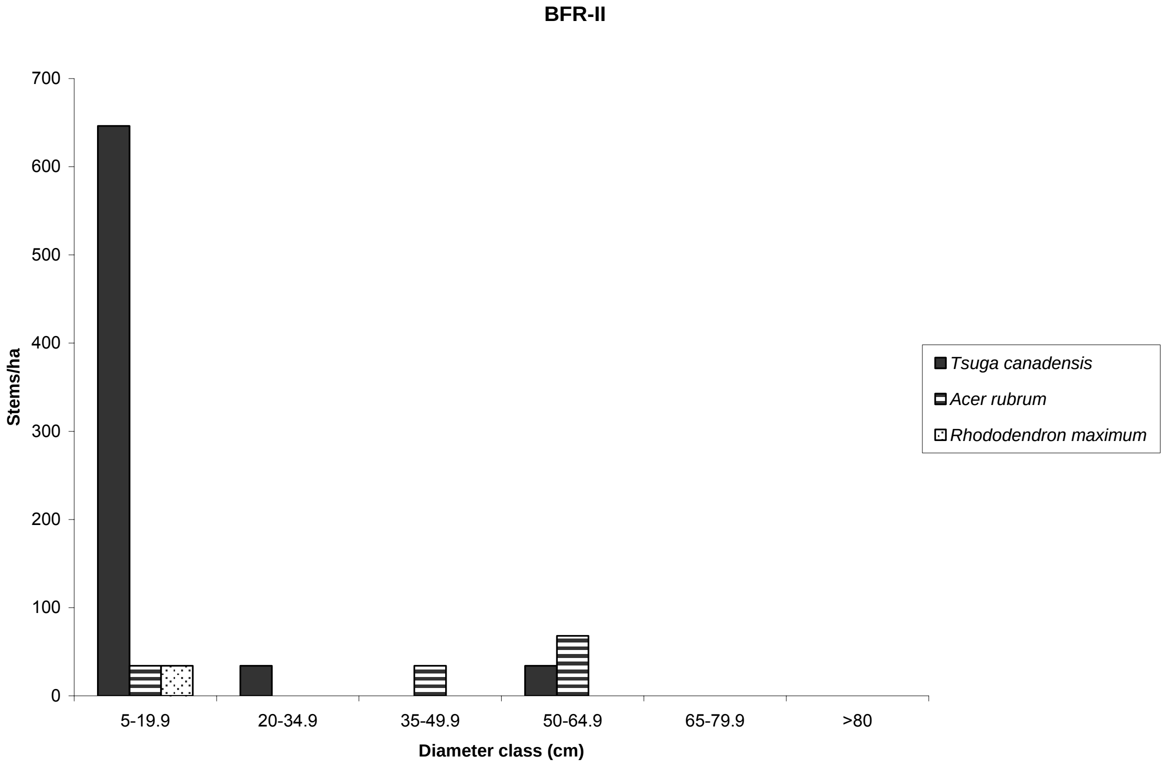
(A)


BFR-I
Stems/ha
700
600
500
400
300
200
100
0
5-19.9
20-34.9
35-49.9
50-64.9
65-79.9
>80
Diameter class (cm)
Tsuga canadensis
Rhododendron maximum
Fagus grandifolia
Halesia carolina

(B)

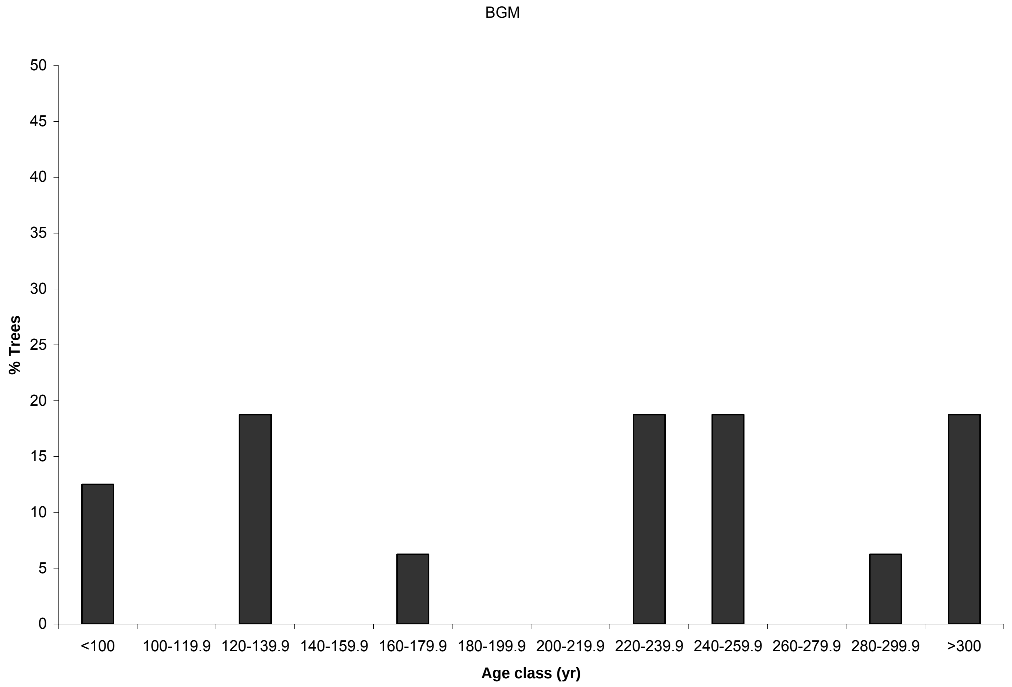


(C)

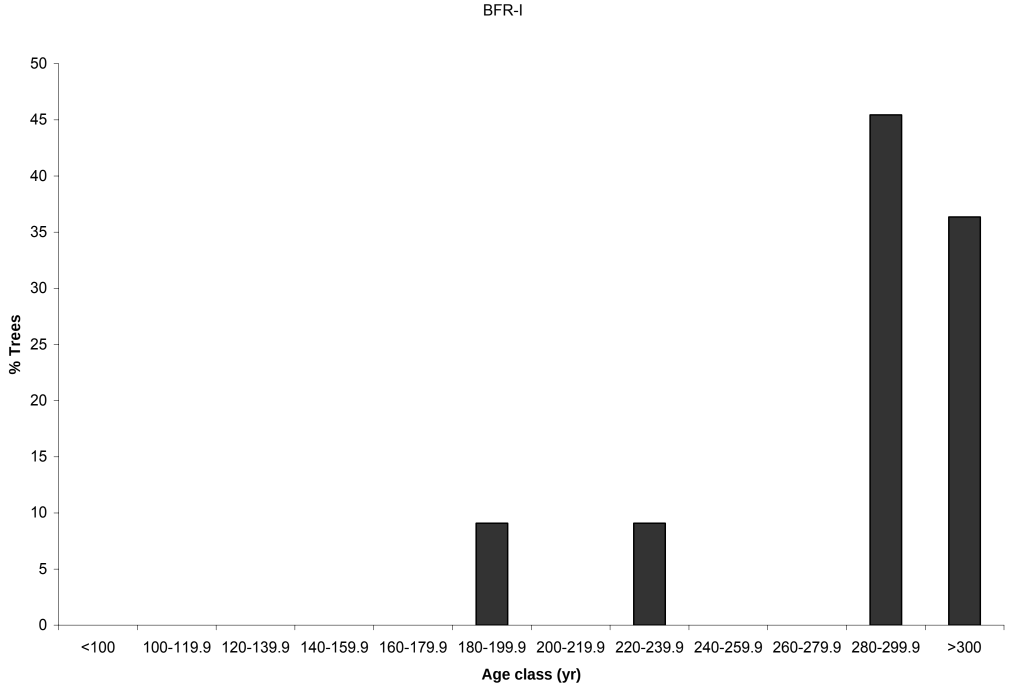


(D)

Figure 4.3. Diameter class distributions for all tree species in each forest stand.


BGM
% Trees
0
5
10
15
20
25
30
35
40
45
50
<100
100-119.9
120-139.9
140-159.9
160-179.9
180-199.9
200-219.9
220-239.9
240-259.9
260-279.9
280-299.9
>300
Age class (yr)

(A)


BFR-I
% Trees
0
5
10
15
20
25
30
35
40
45
50
<100
100-119.9
120-139.9
140-159.9
160-179.9
180-199.9
200-219.9
220-239.9
240-259.9
260-279.9
280-299.9
>300
Age class (yr)

(B)

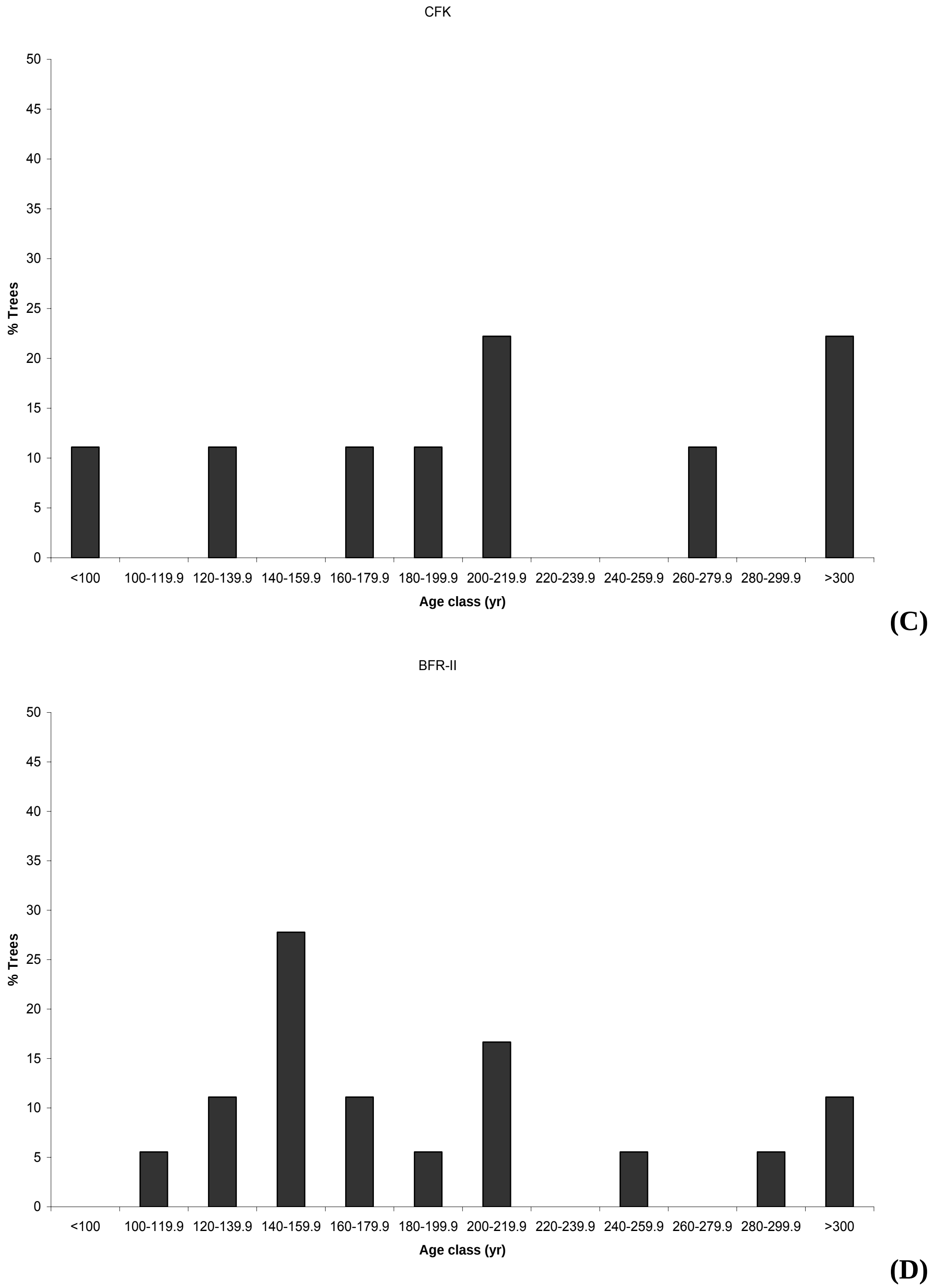


Figure 4.4. Age class distributions for *Tsuga canadensis* in each forest stand.

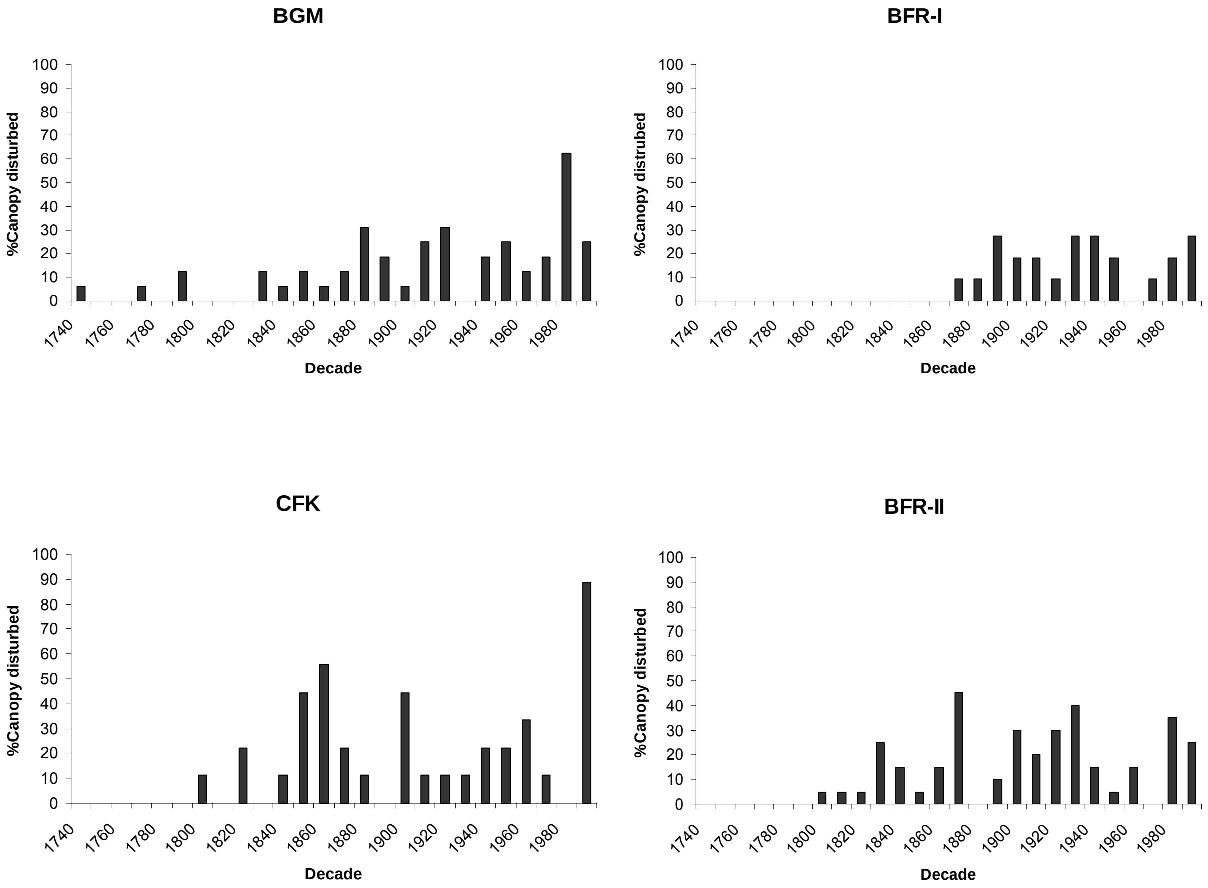


Figure 4.5. Disturbance chronologies for *Tsuga canadensis* in each forest stand. The chronologies include all events eliciting a ≥ 25.0% mean growth increase.

CHAPTER 5

CONCLUSION

The forest stands examined in this research are dominated by *Tsuga canadensis* (L.) Carr., in some cases to the near exclusion of other tree species. Other tree species commonly encountered within the forest stands include *Acer rubrum* L., *Halesia carolina* L., *Liriodendron tulipifera* L., and *Betula* sp (includes *Betula lenta* L. and *Betula alleghaniensis* Britt.). *Rhododendron maximum* L. dominates the understory of many of these forest stands. *Tsuga canadensis* forest stands are found between 500 and 1400 m elevation, and are present at sites with lower to upper slope positions and concave to convex configurations. Despite the environmental and compositional variability observed among these forest stands, only slope aspect, litter depth, tree species richness and diversity are statistically different among *Tsuga canadensis* forest types sampled. In terms of landscape-scale patterns of *Tsuga canadensis* forest composition, there is clear separation among forest stands by geographic location and soil physical and chemical properties, such as the carbon-to-nitrogen ratio, phosphorus, and sand content.

Landscape-scale patterns of *Tsuga canadensis* regeneration also appear to be linked to variation in soil physical and chemical properties, as well as the understory cover of *Rhododendron maximum*. Regeneration abundance is lower in the southern Appalachian Mountains than has been reported in the Great Lakes region (Nelson 1997; Rooney and Waller 1998); only 36% of the 50 sample sites contained seedlings and saplings in all size-classes. Although *Tsuga canadensis* is regenerating across a variety of forest-environmental settings, it is most successful in forest stands having more soil nutrients, primarily calcium and magnesium, lower sand content, and less understory *Rhododendron maximum* cover. However, the importance of forest-environmental factors in *Tsuga canadensis* regeneration varies by the size-class of individual stems. Size-class, rather than age-class, has been found to provide improved information on regeneration dynamics because mortality is more size-dependent than age-dependent, and the forest-environmental requirements of seedlings and saplings change as they grow larger (Rooney et al. 2000). Successful regeneration and recruitment to larger size-classes is associated with higher soil phosphorus levels, shallower litter layers, lower soil sand content and *Rhododendron maximum* understory cover. *Rhododendron maximum* is especially problematic because it easily expands into canopy gaps (Plocher and Carvell 1987; Dobbs and Parker 2004) and reduces understory moisture, mycorrhizal colonization, light, and nutrient availability, all of which are important for successful *Tsuga canadensis* regeneration (Walker et al. 1999; Nilsen et al. 2001).

Spatial pattern in *Tsuga canadensis* regeneration is also controlled by forest-environmental factors that vary in importance as seedlings and saplings grow larger. Increased spatial aggregation of seedlings and saplings is associated with increases in the importance of *Acer pensylvanicum* L. and *Betula* sp., soil potassium content, and canopy openness. Decreases in the spatial aggregation of seedlings and saplings is associated with deeper litter layers, northern aspects, and geographic location. Previous researchers have often cited decaying wood and tip-up mounds as important *Tsuga canadensis* regeneration substrates, which often induce a spatially aggregated pattern of regeneration (Long et al. 1998; Rooney and Waller 1998). Although forests stands with more seedlings also contain greater amounts of decaying wood and microtopographic mounds, these substrates lack statistical significance in predicting regeneration abundance. However, this finding may be the result of data collection techniques because only the presence or absence of decaying wood and microtopographic mounds was recorded within the quadrats of each plot by forest stand. This research suggests that canopy gap creation may mitigate against the importance of decaying wood and microtopographic mounds as important *Tsuga canadensis* regeneration substrates in forest stands of the southern Appalachian Mountains.

Forest stands where *Tsuga canadensis* is currently regenerating are more frequently disturbed by stand-wide canopy disturbance events. In fact, growth-release rates per tree between forest stands with and without successful *Tsuga canadensis* regeneration are statistically different. Therefore, forest stands with successful *Tsuga canadensis* regeneration experience more frequent canopy disturbance events, especially those of moderate intensity. Although disturbance events of minor intensity occur more frequently, they do not seem to be important in terms of successful *Tsuga canadensis* regeneration. Major canopy disturbances may be of greater importance to *Tsuga canadensis* regeneration than indicated in this research, but these events occur too infrequently to obtain an adequate sample. Forest structural data support these findings by suggesting that forest stands currently supporting successful *Tsuga canadensis* regeneration have histories of more or less continuous regeneration and recruitment. Mean canopy turnover rates, release-events per tree, and residence times, are comparable to other studies from the region, as well as those from the Great Lakes and New England regions (Lorimer 1980; Frelich and Lorimer 1991; Frelich and Graumlich 1994; Parshall 1995; Ziegler 2002; Busing 2005).

More research is clearly needed to detail the forest-environmental characteristics, regeneration dynamics, and disturbance regimes of *Tsuga canadensis* forests in the southern Appalachian Mountains. This call for more research takes on added urgency because many *Tsuga canadensis* forest stands in the southern Appalachian Mountains are beginning to experience stress and decline as a result of hemlock woolly adelgid (*Adelges tsugae* Annand) infestation, which has caused 50-100% *Tsuga canadensis* mortality in more northern forest stands (Orwig and Foster 1998; Orwig et al. 2002). First, permanent plots should be established so any changes in the compositional and environmental characteristics of these forests can be monitored over the long term. Second, there is a dearth of research concerning the regeneration of *Tsuga canadensis* in the southern Appalachian Mountains. This study was conducted within Great Smoky Mountains National Park, a protected landscape. Previous researchers have found differences in *Tsuga canadensis* regeneration across ecological and land ownership units (Rooney et al. 2000); therefore, future studies should be conducted across land-use or habitat types to adequately detect contextual influences on regeneration, if present. Finally, aside from canopy gap studies (e.g. Runkle 1982; Runkle and Yetter 1987; Busing 2005), and the disturbance history reconstruction of Lorimer (1980), there is very little data concerning the dendroecological characteristics of *Tsuga canadensis* in the southern Appalachian Mountains. Future research should seek to document the structure and dynamics of these forest systems prior to, and following, large-scale *Tsuga canadensis* mortality events.

The results of this research will prove useful to land managers trying to maintain the ecological integrity of forests in the southern Appalachian Mountains. Specifically, this research will aid land managers in maintaining the compositional and structural characteristics of *Tsuga canadensis* forest stands where treatment for hemlock woolly adelgid infestation is successful.

In forest stands where treatment is unsuccessful or impractical, these data will be useful in ecological restoration efforts after the wave of hemlock woolly adelgid-induced *Tsuga canadensis* mortality has passed.

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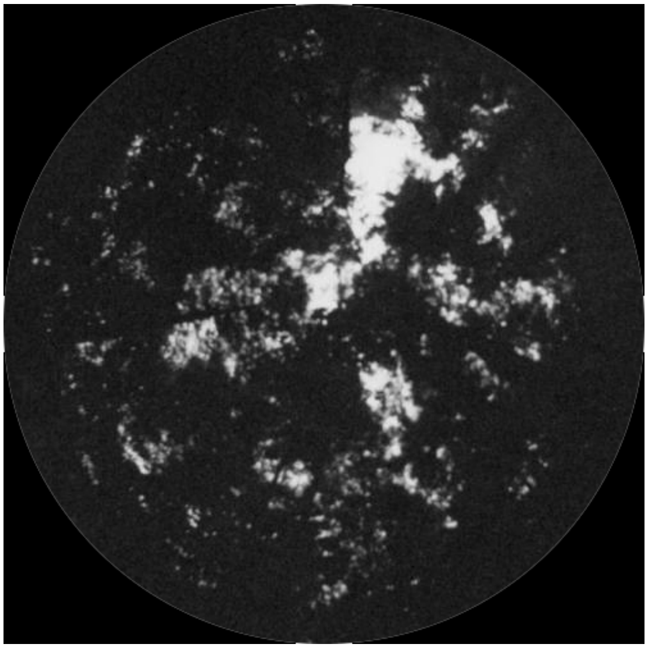
APPENDIX

Appendix A.1. *Tsuga canadensis* (L.) Carr. forest stand.

Appendix A.2. *Tsuga canadensis* (L.) Carr. forest stand with an understory of *Rhododendron maximum* L.

Appendix A.3. *Rhododendron maximum* L. understory cover.



Appendix A.4. Example of a hemispherical canopy photograph taken at plot center.

Appendix A.5. Hemlock woolly adelgid (*Adelges tsugae* Annand) infestation. The white masses are eggsacs at the bases of *Tsuga canadensis* (L.) Carr. needles. Photograph available at: http://www.upenn.edu/PaFLORA/plantClinic/woollyadelgid.html.

Appendix A.6. Hemlock woolly adelgid induced mortality of *Tsuga canadensis* (L.) Carr. in Shenandoah National Park, Virginia. Photograph available at: http://www2.nature.nps.gov/YearinReview/yir/2003/04_E.html.