FOREST DYNAMICS OF TWO MULTI-AGED HEMLOCK-MIXED MESOPHYTIC FORESTS IN THE NORTHERN CUMBERLAND PLATEAU, KENTUCKY

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DEDICATION

This thesis is dedicated to my family,
Greg, Susan, Jim, Irene, and Alan.
Your love and support means the world
to me. I would also like to dedicate my
thesis to Dottie. You will always be
in my thoughts and in my heart.

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ABSTRACT

Tsuga canadensis (eastern hemlock) is a foundation species that performs a unique ecological role within the Appalachian mixed mesophytic forest of the eastern United States. However, the non-native hemlock woolly adelgid (HWA; *Adelges tsugae* Annand), a novel invasive colonizer, is significantly altering the natural processes within *T. canadensis* ecosystems. Few studies have documented *T. canadensis* forests before, during, and after HWA infestation. This study documented the pre-HWA conditions of two old hemlock-mixed mesophytic forests in eastern Kentucky by examining the composition, *T. canadensis* crown health, stand structure, age structure, and disturbance history. Rock Creek Research Natural Area (RCRNA) is a multi-aged primary forest while the Cold Hill Area (CHA) is a multi-aged mature secondary forest. Age structure and recruitment patterns at the RCRNA gorge imply limited, selective cutting at one end with old-growth forest conditions throughout the majority of the study area. In contrast, CHA appears to have experienced more intense selective cutting throughout a greater proportion of the study area. Larger synchronous disturbance peaks occurred in the decades of 1900 and 1980 and appear to be the result of logging in the early 1900s and, potentially, a combination of drought and windstorms in the 1980s. The most dominant canopy species at both study sites was *T. canadensis*, followed by *Liriodendron tulipifera* (tulip poplar). Like many forests across the eastern United States, *Acer rubrum* (red maple) had the greatest seedling density at both study sites. Nearly all *T. canadensis* trees were healthy with no visible signs of HWA. The disturbance history, tree recruitment, and pre-HWA data from this study provides important baseline information for comparing the future dynamics of Kentucky’s Appalachian mixed mesophytic forest and other hemlock-dominated forests as HWA continues to significantly disrupt ecosystem processes.

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1. INTRODUCTION

Forest structure and composition are determined by stand dynamics at differing spatial and temporal scales. Depending on severity, frequency, and type (i.e., fire, logging, wind throw, insects, and disease), disturbances in the forest canopy can cause long-term successional change and alter biodiversity (Nelson 1955, Oliver and Larson 1996, Ellison *et al.* 2005). Climate change can affect the natality and mortality of trees, influence recruitment patterns, and weaken trees when combined with additional disturbance such as herbivory, insects, or pathogens (Manion 1981, Villalba and Veblen 1998, Brown and Wu 2005, Pedersen 1998, Allen *et al.* 2010). Understanding a forest's past disturbance regime is essential to conserving or restoring forest health and can aid forest managers and scientists in constructing management strategies and plans (Bergeron *et al.* 1999, Schuler and Favjan 1999, Rentch *et al.* 2002).

Tsuga canadensis (eastern hemlock), a foundation species, performs a unique ecological role within the Appalachian mixed mesophytic forest of the eastern United States (Braun 1950, Hart and Shankman 2005, Ellison *et al.* 2005). *Tsuga canadensis* is a long-lived, late-successional tree that is extremely shade tolerant and slow growing (Godman and Lancaster 1990). As a foundation species, *T. canadensis* modifies its environment by influencing ecosystem processes such as nitrogen cycling, decomposition rates, stream flow, and soil moisture (Jenkins *et al.* 1999, Ellison *et. al* 2005). A distinct microclimate is created beneath the canopy and is characterized by acid litter, deep shade, and cooler air, soil, and water temperatures (Daubenmire 1930, Godman and Lancaster 1990, Snyder *et al.* 2002). As one of the few native conifers within the mixed mesophytic forest, *T. canadensis* provides valuable habitat for several species of plants and animals (Godman and Lancaster 1990, Lapin 1994, SAMAB 2002, Snyder *et al.* 2002, Ross *et al.* 2003).

The non-native hemlock woolly adelgid (HWA; *Adelges tsugae* Annand; (Homoptera: Adelgidae), a small aphid-like insect, will significantly alter the natural processes within *Tsuga canadensis* ecosystems (Ellison *et al.* 2005, Eschtruth *et al.* 2006). HWA feeds on *T. canadensis* in all stages of development and causes mortality within three to ten years of the initial infestation (Bonneau *et al.* 1999, USDA Forest Service 2005). According to the criteria outlined by Davis and Thompson (2000), HWA would be classified as a novel, long distance, invasive colonizer that has spread to a new geographical region and is causing widespread ecological change. Native to Japan, HWA was first reported in Virginia in 1951 and became widespread in the mid-Atlantic and New England region during the late 1980s (USDA Forest Service 2011). In 2001, HWA moved into the southern range of *T. canadensis* and has been advancing westward; reaching Kentucky in 2006. HWA is currently found in eighteen states (USDA Forest Service 2011). *Tsuga canadensis* has shown little resistance to HWA (Orwig *et al.* 2002, Eschtruth *et al.* 2006, Caswell *et al.* 2008) and long-term monitoring is needed to determine the effectiveness of biological control agents (McClure 2001, Mausel *et al.* 2010, Hakeem *et al.* 2010).

The decline of *Tsuga canadensis* has prompted biologists to document pre-HWA infestation conditions (Mahan *et al.* 2004, Blozan and Riddle 2005, Eschtruth *et al.* 2006). In the northeastern United States, Eschtruth *et al.* (2006) conducted the first, and one of the very few, long-term studies to provide pre-HWA disturbance data, annual infestation severity monitoring, and annual records of *T. canadensis* health. The results showed positive correlations between HWA severity and *T. canadensis* decline, increased species richness of seedlings and groundcover, and the presence of previously absent invasive species (Eschtruth *et al*. 2006). Similar to the functional extinction of *Castanea dentata* (American chestnut) by the invasive pathogen *Cryphonectria parasitica* (chestnut blight; Nelson 1955), HWA will likely cause the functional extinction of *T. canadensis*, further underscoring the need for long-term studies (Ellison *et al.* 2005). The loss of *T. canadensis* will have significant repercussions in the developmental processes and ecology of southern Appalachian mixed mesophytic ecosystems. Therefore, it is important now to document the forest dynamics of *T. canadensis* in the mixed mesophytic forests of the greater southern Appalachian region.

Forest dynamics within the hemlock-mixed mesophytic forest can be reconstructed through tree-ring analysis, pre-HWA infestation structure, and composition. Primary forests are preferred locations for these kinds of reconstructions because of the information embedded in old trees (Shepperd and Cook 1988). Unfortunately, only isolated stands remain of Kentucky's original primary mixed mesophytic forest (Muller 1982) and past investigations lack disturbance history analysis (e.g., Martin 1975, Winstead and Nicely 1976, Cameron and Winstead 1978, Muller 1982, Romme and Martin 1982, Muller 2003, Galbraith and Martin 2005, McEwan *et al.* 2005, McEwan and Muller 2006). Gap dynamics are the principal disturbance regime influencing stand development in mixed mesophytic forests (Runkle 1982, Muller 2003). These disturbances create a patchwork of small canopy gaps and promote the diversification of canopy structure and composition (Runkle 1982). Studies of mixed mesophytic forests have shown that increases in the importance of more mesic, shade tolerant species correspond with the decline of shade intolerant species (Zaczek *et al.* 2002, Galbraith and Martin 2005). However, hemlock woolly adelgid will likely alter this century-scale trajectory. Unlike studies focused solely on structure and composition or maximum tree ages, a reconstructed disturbance history can garner information from the past to document disturbance processes, long-term changes in forest structure and composition, and give insight to the effects of future disturbances.

The objectives of this study were to: 1) document forest structure and composition in the canopy and understory, 2) assess current *Tsuga canadensis* health, 3) document stand age, and 4) reconstruct past disturbance history to determine frequency and intensity of disturbance events within two hemlock-mixed mesophytic forests in eastern Kentucky. The results of this study will be used to address these questions: *Are these primary forests? What type and scale of past disturbance has occurred in these forests? What is species composition in the overstory and understory? Did T. canadensis regenerate in the last century and what is the current state of T. canadensis health?* The disturbance history, tree recruitment, and pre-HWA data from this study will provide important baseline information for comparing the future dynamics of Kentucky’s Appalachian mixed mesophytic forest and other hemlock-mixed mesophytic forests impacted by HWA. The urgency and need for investigating the dynamics of known and still undiscovered primary forests cannot be understated due to the threat of invasive species, climate change, and future unforeseen disturbances. In addition, this study could provide insights into how other novel and episodic disturbances affect succession and composition in eastern North American ecosystems.

2. METHODS

2.1 Study Areas

This study took place at the Rock Creek Research Natural Area (RCRNA) and Cold Hill Area (CHA; Figure 1). Both areas are located in Laurel County, Kentucky within the London Ranger District of the Daniel Boone National Forest. According to Braun (1950), the study areas are within the Mixed Mesophytic Forest Region and lie on the western edge of the Cliff Section of the Northern Cumberland Plateau. Ross *et al.* (1981) described Laurel County as a dissected plateau with elevations ranging from 305 to 427 m above sea level. The ridge tops are predominately sloping and narrow with steep side slopes, and the alluvial valleys are very narrow and level. The soils of the RCRNA and CHA are underlain by siltstone, sandstone, and shale of the Pennsylvanian system. The soils of the RCRNA and CHA are described as Shelocta-Rigley-Latham (Ross *et al.* 1981).

The climate of Laurel County is temperate with warm, humid summers, moderately cold winters, and a fairly even annual precipitation distribution. Climatic data were obtained from the London-Corbin Airport (LCAP) weather observation station (KY154898; 37°05”14’N, 84°04”37’W) in London, Kentucky. The LCAP weather observation station is located 24.2 km northeast of the RCRNA and 19.4 km east of the CHA. For the 1971-2000 period, mean annual temperature within the study region was 13.3° C, the coldest mean monthly temperature occurred in January (1.3° C) and the warmest occurred in July (24.3° C; NOAA 2000). Due to the sloping and steep topography of the RCRNA and CHA, the microclimates created within these areas may vary considerably from recorded temperature data (Clark 1966). Mean annual precipitation within the study region was 120.4 cm. Highest mean monthly precipitation occurred in May (11.9 cm) and the lowest occurred in October (7.1 cm). Mean annual snowfall within the study region was 34 cm. Highest mean monthly snowfall occurred in January (13.7 cm). The mean annual growing season is approximately 184 days (NOAA 2000).

2.2 Study Sites

2.2.1 Rock Creek Research Natural Area

The Rock Creek Research Natural Area (RCRNA) is a 430 ha mixed mesophytic forest and is the sole Research Natural Area (RNA) in Kentucky (Figure 1). The RCRNA was designated as a RNA by the USDA Forest Service in 1939 to protect a gorge containing a 77-ha stand of old-growth hemlock-mixed mesophytic forest (Thompson *et al*. 2000, Thompson and Jones 2001). In 1975, the RCRNA was declared a National Natural Landmark (Thompson *et al*. 2000, Thompson and Jones 2001). Thompson *et al*. (2000) documented 350 species from 93 families within the RCRNA gorge. An annotated catalogue consisted of 117 species of woody vines, shrubs, and trees from 43 families (Thompson and Jones 2001).

The study site at the RCRNA was confined to the aforementioned 77-ha gorge (Figure 1). The gorge is northwest-southeast trending and approximately 0.4 km wide and 1.9 km long. Elevations range from 215 m at the mouth of the gorge to 366 m in the upper portions (Thompson *et al.* 2000). The sandstone cliffs surrounding the gorge are nearly unbroken, with only six gaps allowing access into the study site. Large fallen boulders, some having a volume of over 142 m^3, are found throughout the gorge (Hemingway 1938). Although the gorge is mostly inaccessible to logging, historically some harvesting did occur at the intersection of the Rockcastle River and the mouth of the gorge (Hemingway 1938). By 1939, logging was prohibited in the RCRNA gorge (Winstead and Cameron 1978), but large, scattered trees such as *Quercus alba* (white oak), *Liriodendron tulipifera* (tulip poplar), *Tsuga canadensis* (eastern hemlock), and other *Quercus* spp. (oaks) were harvested during 1915-1917 (Hemingway 1938). Excluding the gorge study area, the remaining 353 ha of the RCRNA watershed is composed of second growth pine-oak and oak-hickory-pine forest which has been logged in the past, with some tracts clear-cut within the last 44 years (Thompson and Jones 2001).

2.2.2 Previous Investigations at RCRNA

Braun (1950) reported that *Tsuga canadensis*, *Liriodendron tulipifera*, and *Acer rubrum* (red maple) comprised 75% of the canopy in the RCRNA gorge. In the upper portions of the gorge, Winstead and Nicely (1976) found that *T. canadensis*, *L. tulipifera*, *Betula lenta* (black birch*)*, and *Acer saccharum* (sugar maple) made up 82% of the basal area and 64% of the total species within the upper one-third of the gorge. Unlike Braun (1950), Winstead and Nicely (1976) did not record the presence of *Quercus montana* (chestnut oak), *Oxydendrum arboreum* (sourwood), and *Castanea dentata* (American chestnut). It has been suggested the elimination of *C. dentata* due to chestnut blight during the 1930s may have led to an increase in *B. lenta* (Winstead and Nicely 1976). In the upper three-fourths of the RCRNA gorge, Cameron and Winstead (1978) found the four most dominant species were *T. canadensis*, *O. arboreum*, *B. lenta*, and *L. tulipifera*. Thompson *et al.* 2000 conducted a study on the mesic northeast and subxeric southwest trending slopes at the mouth of the gorge near the Rockcastle River. Belt transect data revealed that *T. canadensis*, *Fagus grandifolia* (American beech), *A. saccharum*, *L. tulipifera*, and *A*. *rubrum* were the five most abundant species present in the lower portion of the gorge and documented the presence of *Q. montana* near the mouth of the gorge. Braun (1950) described the RCRNA as an extreme type of hemlock-mixed mesophytic forest due to the precipitous cliffs, and the orientation and narrowness of the gorge. The RCRNA is suggested to be representative of the original vegetation of the physiographic region (Winstead and Nicely 1976). One increment core collected from a *T. canadensis* measured 57.1 cm DBH and had 255 annual rings (Winstead and Nicely 1976).

2.2.3 Cold Hill Area

The Cold Hill Area (CHA) is composed of upland mixed hardwood and ravine mixed mesophytic forests. The study site was confined to the northeastern section of the central Cane Creek ravine (Figure 1). This section of the Cane Creek ravine lies north of Kentucky Highway 192, southwest of Line Creek Road and southeast of Forest Service

Road 121. The ravine has steep side slopes and sandstone cliffs with elevations ranging from 225 to 384 m above sea level. The mouth of the Cane Creek ravine intersects with the Rockcastle River at the Pulaski-Laurel County line. It has been suggested (David Taylor, Botanist, Daniel Boone National Forest; personal communication) that the trees in the ravine date to 1878, trees along the western ridge to 1913, and trees on the upper slopes to 1994. However in August 2006, a survey of the canopy species and forest structure suggested the trees in the ravine may be significantly older than 130 years (Neil Pederson, Research Forest Ecologist, Columbia University, personal communication).

2.3 Plot Selection

Plots at each study site were selected using targeted sampling. Plots were targeted in the ravine areas of the RCRNA and CHA in order to collect data in hemlock-dominated forests. Plot locations were obtained by viewing a digital satellite image of each ravine and selecting points approximately equal distance apart along the ravine stream bottom. Equal distances were chosen to maximize sampling coverage and disturbance history of the study sites while minimizing bias towards any particular section of each ravine. The coordinate for each selected point was entered into a handheld global positioning system (GPS). When each coordinate was located in the field, the center of the sampling plot was established 25 m from the coordinate in a pre-determined, randomly selected, cardinal direction.

2.4 Establishment and Sampling of Permanent Plots

Sixteen 0.04-ha permanent circular plots were established for this study (Figures 1 and 2). As HWA moves into this region, the establishment of permanent plots provides the opportunity for continued long-term studies of forest response during and post-HWA infestation. In 2007, eight plots were established in the northeastern portion of the CHA ravine (Figure 1). In 2007 and 2008, a total of eight plots were established within the 77-ha gorge at the RCRNA (Figure 1). Plot locations were recorded using a handheld GPS and marked by placing a steel dowel at each plot center. All steel dowels were inscribed with the year of plot establishment and a three-letter abbreviation of the plot name. For further identification of plot centers, the three trees closest to each plot center were designated as witness trees. Witness trees were marked with a bark scribe twice in a diagonal direction at breast height and were visible from each plot center. The distance and azimuth from each witness tree to a plot center was recorded to facilitate plot relocation should steel dowels become absent. The three witness trees were selected based on the following criteria: a) having diameter at breast height (DBH) ≥ 10 cm and b) excluding *T. canadensis* due to the likelihood of HWA eradicating existing trees within the plots.

To document understory composition, four nested subplots were established within each of the 16 permanent plots (Figure 2). During the summer of 2008, a total of 64 subplots were established, 32 at the RCRNA and 32 at the CHA. The nested subplot centers were established at 90° intervals in each cardinal direction from the permanent plot center and marked with an orange wire stake flag. At each subplot center, concentric circular plots were established for sampling the ground/seedling layer and sapling/shrub layer. Within each permanent plot, the total area of the four ground/seedling layer subplots was equal to 1/100 the area of an individual permanent plot (0.0004-ha/plot) and the total area of the 4 shrub/sapling layer subplots was equal to 1/10 the area of an individual permanent plot (0.004-ha/plot; Figure 2; McEwan *et al.* 2000).

Within each 0.04 ha permanent plot, species, diameter, and crown class were documented for all trees (DBH ≥10 cm). Distance and azimuth from each tree (DBH ≥10cm) to the center of each plot were recorded. All trees (DBH ≥10 cm) were bark scribed with a horizontal mark at breast height. All horizontal marks were visible from the center of each plot. Crown classes were defined as dominant, co-dominant, intermediate, and suppressed (Smith 1986). For each tree species, relative density (number of trees), relative dominance (basal area), and relative frequency (presence or absence in plots) were calculated and an importance value determined for each study area (Curtis and McIntosh 1950).

The visual crown rating was used to determine *Tsuga canadensis* crown health (USDA Forest Service 2007). Uncompacted live crown ratio (ULCR; % of live crown length compared to actual tree length), crown density ("fullness" and density of branches and foliage), crown dieback (loss of needles at branch tips), and crown transparency (relative amount of light that passes through the tree crown) were assessed for each *T. canadensis* (DBH ≥10-cm) in all permanent plots. Based on these measurements, each tree was assigned to a vigor class: a) Vigor Class 1 (≥ 35 % ULCR, ≤ 5% dieback, and ≥ 80% normal foliage), b) Vigor Class 2 (any ULCR, any amount of dieback, and ≥ 21% normal foliage, and c) Vigor Class 3 (any ULCR, and 1-20% normal foliage; USDA Forest Service 2007).

All trees (DBH ≥ 10 cm) were cored at breast height with a Haglöf Increment Borer® (Haglof Company Group, Långsele, Sweden). In each plot, three increment cores per tree were collected to determine age and detect radial growth patterns. To maximize the probability of intercepting pith, coring location was determined individually for each tree based on tree size and shape. An additional 20 out-of-plot trees were cored at the CHA and RCRNA to target older looking trees and gain further information on disturbance history. Two increment cores per tree were taken from out-of-plot individuals. Six indicators used to target older looking trees were: 1) patchy, balding, or smooth bark on the lower bole, 2) low stem taper, 3) high stem sinuosity or having a "serpentine" shape, 4) having only a few, large and thick branches, 5) low crown volume resembling a celery stalk, and 6) a low leaf area to trunk volume ratio (Pederson 2010).

Within nested ground/seedling layer subplots, all seedlings (DBH < 1cm), herbs, vines, ferns, and subshrubs were counted, identified to species if possible, and percent cover estimated. Within nested shrub/sapling layer subplots, all saplings (DBH ≥ 1cm <

10cm) were counted and identified to species. All shrubs were identified to species and percent cover was visually estimated.

2.5 Tree-Ring Analysis

Increment cores were collected and processed using standard tree-ring analysis techniques (Stokes and Smiley 1968, Fritts 1976, Cook and Kairiukstis 1990). Cores were dried, glued to wooden core mounts, and sanded using up to 1200-grit 3M® sandpaper (3M, St. Paul, MN) to reveal cellular ring structure. Cores were visually cross-dated with a dissecting microscope. Cross-dating is a technique used to assign each tree ring to the correct year of formation. This is accomplished by matching patterns of wide and narrow rings among cores from the same tree and of the same species (Stokes and Smiley 1968, Fritts 1976, Cook and Kairiukstis 1990). At least two out of three in-plot increment cores and both out-of-plot increment cores were cross-dated. Ring widths were measured to the nearest 0.001 mm using a Velmex® (Velmex, Inc., East Bloomfield, NY) measuring system. The cross-dated measurements were checked with the quality control program COFECHA (Holmes 1983). Out-of-plot cores were not used in age structure analysis.

For increment cores missing pith, a combination of ocular estimation and a tracing technique were adapted from Clark and Hallgren (2004) and Villalba and Veblen (1997). The tracing technique was performed by placing transparent tape on the two oldest cores from each tree and tracing the 20 innermost rings. The tape from these two cores were transferred to a sheet of paper and fixed to replicate their respective positions in each tree. Annual rings were matched and curved lines were drawn to connect all rings. When the arcs of the innermost rings were joined, a circular or elliptical pattern was revealed. To estimate the missing radius to pith, the innermost circle was measured or the lengths of the longest and shortest diameters for each innermost ellipse were determined and averaged. The distance of the estimated missing radius to pith was divided by the mean of the innermost 10 rings to estimate number of years to pith. The innermost 10 rings were used instead of total mean ring width to exclude growth patterns such as release from suppression and declining growth occurring in the later part of the core. The cumulative radial growth curves used to estimate number of missing rings to pith applied in Villalba and Veblen (1997) were not used in this study because: a) cross sections and cores were not collected from seedlings (<100 cm tall) and b) cores reaching pith were not adequately distributed across all species. Using the above criteria, cores were placed in one of the following categories: a) very close to pith, missing 1 to 2 rings, b) close to pith, missing 3-10 rings with circular ring curvature, c) near pith, missing 11 to 25 rings with elliptical ring curvature, d) far from pith, missing at least 26 rings, no ring curvature or weakly elliptical, and e) very far from pith, missing at least 50 rings from pith, no ring curvature or weakly elliptical. For each tree species, the ability to withstand suppression was considered when assigning pith categories (e.g., some *T. canadensis* were strongly elliptical but were missing an estimated 26 or more rings).

Disturbance history was constructed by examining the radial growth patterns of 335 in-plot trees (670 increment cores) and 40 out-of-plot trees (80 cores). Cores were screened for: 1) rapid initial growth rates and 2) abrupt increases in radial growth. Trees with initial average growth rates of ≥ 1.2 mm/year were assumed to be gap-recruited and the innermost ring on the core was recorded as the canopy accession date (Lorimer *et al.* 1988). A radial growth averaging technique developed by Lorimer and Frelich (1989) was used to identify canopy disturbance by using yearly increments and comparing the mean preceding and subsequent 15 years of radial growth. A “major sustained release” is defined as a mean increase in radial growth ≥ 100% lasting 15 years or more relative to the preceding 15 years and a “moderate temporary release” is defined as a mean increase in radial growth ≥ 50% lasting 10-15 years relative to the preceding 10-15 years (Lorimer and Frelich 1989). The maximum percent growth increase for each release was identified and assigned as the year of probable disturbance (Nowacki and Abrams 1997). The 10-15 year period was chosen to filter out short-term climate effects (Leak 1987, Lorimer and Frelich 1989, Nowacki and Abrams 1997). Additional criteria were used to identify gap-recruited trees not detected by initial growth rates using the aforementioned release criteria. Trees not qualifying as gap-recruited or showing a release were plotted and screened for radial increment patterns suggesting gap origin (declining, constant, or parabolic) or release from suppression (ambiguous or irregular; Lorimer and Frelich 1989, D'Amato and Orwig 2008).

3. RESULTS

3.1 Species Composition

Tsuga canadensis (eastern hemlock) was the most important tree at the RCRNA and CHA, ranking highest in importance value (IV) and comprising 46% and 49% of the relative basal area, respectively (Tables 1 and 2).[1] *Liriodendron tulipifera* (tulip poplar) was the second most important tree at each study site, followed by *Acer rubrum* (red maple), *Betula lenta* (black birch), and *Fagus grandifolia* (American beech; Tables 1 and 2).

The sapling density was 1188 stems/ha at the RCRNA and 3156 stems/ha at the CHA (Tables 3 and 4). *Asimina triloba* (pawpaw), a small understory deciduous tree, was absent at the RCRNA, but was the most abundant sapling at the CHA. Excluding *A. triloba*, the species with the greatest sapling density at both sites was *Magnolia macrophylla* (bigleaf magnolia), followed by *B. lenta* (Tables 3 and 4). *Tsuga canadensis* saplings comprised 21% of the sapling density at the RCRNA and only 6% at the CHA. Notably, *Stewartia ovata* (mountain stewartia), a small rare deciduous tree, was found at both sites (Tables 3 and 4). *Stewartia ovata* density at the CHA (approx. 344 stems/ha) was higher than at the RCRNA (approx. 63 stems/ha; Tables 3 and 4).

The shrub layer covered approximately 44% of all the RCRNA and CHA plots. *Rhododendron maximum* (great laurel) was the most dominant shrub, comprising 99% of the shrub cover at the RCRNA and 95% at CHA (Table 5).

Understory tree seedling regeneration was sparse. Seeding density was 2813 stems/ha at the RCRNA and 5625 stems/ha at the CHA. *Acer rubrum* was the most abundant seedling at both sites followed by *Ilex opaca* (American holly) and *Magnolia tripetala* (umbrella magnolia) at the CHA and *M. macrophylla* and *Quercus* spp. at the

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[1] See appendix for all tables and figures.

RCRNA (Tables 3 and 4). *Tsuga canadensis* seedlings were absent at the RCRNA and comprised only 11% of seedling density at the CHA (Tables 3 and 4).

Total ground cover was 3.0% at the RCRNA and 10.9% at the CHA (Table 8). *Dryopteris intermedia* (intermediate wood fern) was the dominant species at both sites, in terms of importance value, followed by *Mitchella repens* (partridgeberry; Tables 6 and 7). Although no invasive species were documented within nested subplots, *Microstegium vimineum* (Nepalese browntop), an exotic invasive, and *Phytolacca americana* (American pokeweed), a native weed, were found growing near the widest portion of the CHA ravine bottom.

3.2 Eastern Hemlock Crown Health

Tsuga canadensis trees were evaluated for crown health and assigned to a vigor class (Table 9). No visible signs of HWA infestation were apparent at either site. Eighty-one percent of the RCRNA *T. canadensis* trees were in Vigor Class 1, while the remaining 19% belonged to Vigor Class 2 (Table 9). With the exception of one tree, all *T. canadensis* in Vigor Class 2 were found in the same plot, had 100% normal foliage, and <35% uncompacted live crown ratio (ULCR). The singular cause of the low ULCR appears to be the result of shading due to competition. One codominant *T. canadensis* at the RCRNA had 10 % dieback and brown foliage found exclusively on one side of the crown top. At the CHA, 95% of the *T. canadensis* were in Vigor Class 1. The remaining 5% were in Vigor Class 2 and had <35% ULCR (Table 9). Shading and broken lower branches contributed to the low ULCR. At the CHA, *Tsuga canadensis* trees in Vigor Class 2 belonged to the codominant crown class and had 100% normal foliage. The most common *T. canadensis* crown shape at both study sites was conical (Table 10).

3.3 Age and Stand Structure

A total of 340 in-plot trees were cored (RCRNA, n=186; CHA, n=154). Due to excessive rot (> ½ of the core missing or rotten), two trees from the RCRNA and three trees from the CHA were not used in the data analysis. Trees cored reaching pith or near-pith curvature comprised 85% and 84% of all in-plot trees at the RCRNA and CHA, respectively.

Tree age structure at the RCRNA ranged from 35 to 376 years old (Figure 4). Thirteen percent of the RCRNA trees were 200 years or older. Notable in-plot trees at the RCRNA included three *L. tulipifera* (317 to 376 years old), three *M. macrophylla* (77 to 96 years old) and an *O. arboreum* (sourwood; 197 years old; Figure 4). Notable out-of-plot trees included four *L. tulipifera* (309 to 333 years old) and an *I. opaca* (ca. 240 years old). Tree age-structure at the CHA ranged from 30 to 318 years old (Figure 5). Approximately seven percent of the CHA trees were 200 years or older. Notable in-plot trees at the CHA included a *B. lenta* (314 years old), *Carya glabra* (pignut hickory; 318 years old), and five *M. macrophylla* (75 to 99 years old; Figure 5). Notable out-of-plot trees included a *L. tulipifera* (322 years old), four *Quercus alba* (white oak; 289 to 318 years old) and three *Quercus montana* (chestnut oak; 289 to 308 years old).

Tsuga canadensis comprised the highest percentage of trees in each crown class (dominant, codominant, intermediate, and suppressed) at the RCRNA and CHA, excluding the dominant crown class at the CHA (Figure 3). The following species occurred almost exclusively in the dominant or codominant crown classes: *L. tulipifera*, *C. glabra*, *Juglans nigra* (black walnut), *Nyssa sylvatica* (blackgum), *Q. alba*, and *Sassafras albidum* (sassafras). The majority of *B. lenta* were codominant (Figure 3). *Oxydendrum arboreum* and *M. macrophylla* occurred exclusively in codominant and intermediate classes. Species present in all crown classes were *B. lenta*, *F. grandifolia*, and *T. canadensis* at the RCRNA and *A. rubrum* and *T. canadensis* at the CHA. *Acer rubrum* was absent from the RCRNA in the suppressed class (Figure 3).

3.4 Disturbance Dynamics

3.4.1 Tree Recruitment

Both the RCRNA and CHA are multi-aged stands. Continuous stem recruitment occurred at the RCRNA from the 1840s to 1979 and at the CHA from the 1820s to 1979

(Figures 4 and 5). Recruitment patterns are defined as “continuous” if they are uninterrupted in time, sequence, or extent and “episodic” if they occur at irregular intervals (Merriam Webster 2012). Continuous *Tsuga canadensis* recruitment occurred at the RCRNA from the 1890s to 1969 and at the CHA from the 1820s to 1969 with a rise in recruitment at both study sites occurring in the early-to-mid 1900s (Figures 4 and 5).

Similarities among the RCRNA and CHA study sites include: 1) three synchronous recruitment peaks (1850s-1879, 1900s-1929, and 1940s-1959), 2) nearly continuous recruitment of species such as *Acer rubrum* (RCRNA, 1900s-1949; CHA, 1880s-1969) and *Magnolia macrophylla* (RCRNA, 1910s-1969; CHA, 1900s-1969) and 3) episodic recruitment of *Oxydendrum arboreum* (RCRNA, 1810s-1929; CHA, 1850s-1939; Figures 4 and 5). Differences among sites include: 1) *Ilex opaca* absence at the CHA, but mostly continuous recruitment at the RCRNA from the 1870s to 1939, 2) episodic *Liriodendron tulipifera* recruitment at the RCRNA throughout the sample record compared to continuous recruitment at the CHA from the 1880s to 1969, and 3) predominantly episodic *Betula lenta* and *Fagus grandifolia* recruitment at the CHA (1690s-1949; 1750s-1909) compared to continuous *B. lenta* and *F. grandifolia* recruitment at the RCRNA (1850s-1969; 1860s-1899; Figures 4 and 5).

Two large recruitment events occurred within an individual plot at each study site (Figures 6 and 7). Fifty-eight percent (n=26) of trees recruited during the 1920s at the RCRNA originated in study plot 6 (Figure 6) and 58% (n=14) of trees recruited during the 1940s at the CHA originated in study plot 8 (Figure 7).

Sixty-one percent of the RCRNA trees (n=113) and 61% of the CHA trees (n=92) were used to determine gap recruitment status (Figures 8 and 9). Only trees with cores that either reached pith or missed pith by 10 years or less were used in this analysis. The majority of RCRNA trees before 1720 and after 1910 were gap-recruited (Figure 8). The exception to this pattern is the 1930s, which is characterized by non-gap recruited trees and generally low recruitment. At the RCRNA, the 1910s, 1920s, and 1950s had the highest number of gap-recruited trees per decade, with the top species recruited being

B. lenta in the 1910s and *T. canadensis* in the 1920s and 1950s (Figure 8). Seventy percent of all trees at the RCRNA in the 1860s to 1909 were non-gap recruited with the most common species being *A. rubrum* and *B. lenta* followed by *F. grandifolia* and *I. opaca* (Figure 8). Prior to 1850, all CHA trees were non-gap recruited with the most common species being *T. canadensis* and *F. grandifolia* (Figure 9). From the 1870s-1959, the majority of CHA trees were gap recruited, with the 1900s-1910s having the highest number of gap-recruited trees per decade (Figure 9). The top species recruited in the latter two decades was *L. tulipifera* and the majority of trees were shade intolerant (*L. tulipifera*) or mid-shade tolerant (*A. rubrum*, *B. lenta*, *M. macrophylla*, and *O. arboreum*). From the 1960s-1979, all trees recruited at the CHA were gap-recruited while 55% of all trees at the RCRNA were gap-recruited during these same decades (Figures 8 and 9).

At the RCRNA and CHA study sites, all *Juglans nigra*, *L. tulipifera*, and *O. arboreum* were gap-recruited species and all *Quercus alba*, *Carya glabra*, and most *F. grandifolia* were non-gap recruited (Figures 8 and 9). *Acer rubrum*, *B. lenta*, *I. opaca*, *M. macrophylla*, *M. tripetala*, and *T. canadensis* recruited in both gap and non-gap conditions at both study sites (Figures 8 and 9).

3.4.2 Canopy Disturbance History

Of all release events identified in this investigation, 222 and 164 events were recorded by trees at the RCRNA and the CHA, respectively (Figures 8 and 9). Release events from 13 RCRNA and 14 CHA older out-of-plot trees were included to obtain more information regarding disturbance history across each study area. The median major growth release was 170% at the RCRNA and 206% at the CHA. Major release events accounted for 57% of all the RCRNA releases and 73% of all the CHA releases (Figures 8 and 9). Large synchronous disturbance peaks occurred at both study sites in the 1900s, 1950-60s, and 1980s. Other synchronous disturbance peaks with fewer release events occurred in the decades of 1800 and 1870. Overall, the decades with the most release events were the 1900s and 1980s at both sites (Figures 8 and 9). Notably, 39% of all releases recorded during the 1920s at the RCRNA occurred in study plot 6 where the large recruitment event took place (Figures 6 and 8). The single major growth release (502%) recorded during the 1940s at the CHA occurred in study plot 8 where the other large recruitment event took place (Figures 7 and 9).

4. DISCUSSION

4.1 Species Composition

The species composition documented at the RCRNA and CHA are characteristic of the mesic ravine-slopes of the hemlock-mixed mesophytic forest described in Braun (1950) because *Tsuga canadensis* (eastern hemlock) was the dominant canopy species and *Liriodendron tulipifera* (tulip poplar), *Acer rubrum* (red maple) and *Fagus grandifolia* (American beech) were among the higher-ranked canopy species in terms of importance value (Tables 1 and 2). Additionally, several other southern tree and shrub species common to hemlock-mixed mesophytic forests were found in this investigation, i.e., *Quercus alba* (white oak), *Magnolia macrophylla* (bigleaf magnolia), *Magnolia tripetala* (umbrella magnolia), *Oxydendrum arboreum* (sourwood), *Ilex opaca* (American holly), *Stewartia ovata* (mountain stewartia), and *Clethra acuminata* (mountain sweet pepperbush; Braun 1950; Tables 1,2,3,4 and 5). Over the past 70 years, several studies have been conducted at the RCRNA (Braun 1950, Winstead and Nicely 1976, Cameron and Winstead 1978, Thompson *et al.* 2000, and Thompson and Jones 2001). The overall canopy species composition identified in each investigation, including the current investigation, varied and likely reflects different sampling techniques and location sites within the RCRNA gorge (Braun 1950, Winstead and Nicely 1976, Cameron and Winstead 1978, Thompson *et al.* 2000, Thompson and Jones 2001; Table 11). The floristic surveys conducted by Thompson *et al*. (2000) and Thompson and Jones (2001) found all the canopy species described in the current and other previous investigations at the RCRNA. Eight canopy species were common among the current and previous investigations at the RCRNA (Braun 1950, Winstead and Nicely 1976, Cameron and Winstead 1978, Thompson *et al.* 2000, and Thompson and Jones 2001; Table 11).

The most abundant shrub, *Rhododendron maximum* (great laurel), and most abundant ground cover species, *Mitchella repens* (partridgeberry), found at the RCRNA and CHA are typical understory species of hemlock-mixed mesophytic forests (Braun

1950, Tables 5, 6, and 7). The dominance of *R. maximum* in the canopy gaps of these forests can limit seedling density and species richness (Rivers *et al.* 1999) In the Appalachian Mountains, *R. maximum* (great laurel) has exhibited increased abundance and growth rates in response to HWA-induced *T. canadensis* decline (Spaulding and Rieske 2010, Ford *et al.* 2011). This suggests that *R. maximum* could limit regeneration in the understory of southern Appalachian forests (Spaulding and Rieske 2010, Ford *et al.* 2011); however, where *R. maximum* is less dominant, *T. canadensis* could be replaced by species such as *Acer rubrum* (red maple), *B. lenta*, and *Liriodendron tulipifera* (tulip poplar; Ford *et al.* 2011).When the RCRNA and CHA become infested by the HWA, it is expected that *R. maximum* will become more dominant in response to increased light conditions in the understory. This response would influence the post-HWA regeneration processes, especially since *R. maximum* is reported to exceed 100 years of age (Plocher and Carvel 1987).

Since the RCRNA and CHA are hemlock-dominated forests, it is surprising to document relatively low numbers of *T. canadensis* saplings and seedlings (Tables 3 and 4). Most notably, there is an absence of *T. canadensis* seedlings at the RCRNA (Table 3). Generally, *T. canadensis* has low seed viability but is a frequent cone producer with seed crops occurring every two to three years (Godman and Lancaster 1990). Contributing factors which can exert a strong-influence on *T. canadensis* seedling survival are herbivory and weather. In the Upper Great Lakes Region of the United States, herbivory resulting from high densities of *Odocoileus virginianus* (white-tailed deer) have caused substantial damage to, and the complete removal of *T. canadensis* seedlings (Anderson and Loucks 1979, Frelich and Lorimer 1985, Anderson and Katz 1993). Although *O. virginianus* populations are not reported to be high in Laurel County, Kentucky (KDFWR 2011), the hypothesis that high densities of *O. virginianus* are limiting *T. canadensis* regeneration could be tested by establishing fenced plots within the RCRNA and CHA.

Since *T. canadensis* is extremely sensitive to desiccation during the germination and seedling stage, the drought of 2007 (NOAA 2011) likely restricted germination and caused seedling mortality at the RCRNA (Table 3); and limited the number of seedlings at the CHA (Table 4). If increased disturbance occurred at both study sites, this would cause increased light and temperatures on the forest floor, possibly initiating germination failure; especially if these conditions were coupled with drought (Godman and Lancaster 1990). It is also likely that the *T. canadensis* did not produce a seed crop at the RCRNA during the sampling year. This would explain the absence of *T. canadensis* seedlings at RCRNA and the presence at the CHA. Since *T. canadensis* is present in the sapling layer and all canopy crown classes, it shows that regeneration has occurred in the past at both study sites. Regardless, future investigations are needed to give insight to the understory regeneration processes occurring at the RCRNA and CHA.

Fagus grandifolia seedlings and saplings were absent at the RCRNA (Table 3). The lack of seedlings and saplings may be due to low seed viability (Ward 1961, Keever 1973) and the variable number of years (2 to 8) between seed crop production (Tubbs and Houston 1990). For example, Keever (1973) documented the absence of *F. grandifolia* seedlings in several mixed mesophytic stands with overstory densities ranging from 20 to 90 *F. grandifolia* trees/ha in southeastern Pennsylvania. Additionally, Keever (1973) reported only 1 out of 200 seeds contained a plump embryo. While *F. grandifolia* nuts are a preferred food of *Odocoileus virginianus* (Barnes 1993), studies have found an increase in *F. grandifolia* seedlings and saplings in forests associated with high densities of *O. virginianus* (Marquis 1974, Tilghman 1989). Generally, *O. virginianus* browse leaves of *F. grandifolia* only as a starvation food (Hough 1965). The absence of *F. grandifolia* seedlings and saplings at the RCRNA could reflect low population densities of *O. virginianus* and further support the idea that herbivory may not be the cause of *T. canadensis* seedling absence at the RCRNA. *Fagus grandifolia* trees were present in all crown classes (Figure 3) and recruitment occurred from 1860s-1899 (Figure 4); suggesting continuous but sporadic recruitment of this species at the RCRNA. Takahashi *et al*. (2010) found that *F. grandifolia* (stems< 2 m tall) regeneration occurred mainly by root suckering on upper and mid slopes and by seedlings on lower slopes in an old-growth *Acer-Fagus* forest in southern Quebec, Canada. Other research suggests root suckering populations of *F. grandifolia* are better adapted to northern and high elevation areas of the species geographic range (Held 1983, Kitamura *et al*. 2000). Therefore, *F. grandifolia* regeneration on the lower ravine slopes at the RCRNA and CHA may be primarily dependent upon seed crop production which would explain the absence of this species at the RCRNA and low abundance at the CHA.

It is interesting that a very shade tolerant angiosperm (*F. grandifolia*) and gymnosperm (*T. canadensis*) are not recruiting into the understory of the RCRNA, a forest with fairly-frequent canopy disturbance. Kincaid and Parker (2008) found that *T. canadensis* regeneration was more successful in stands that experienced frequent, moderate intensity disturbance; however, in stands with higher *R. maximum* cover, *T. canadensis* regeneration was limited. Since *R. maximum* is the most dominant shrub at both the RCRNA and CHA, *R. maximum* cover could be limiting *T. canadensis* regeneration at both sites. However, the lack of recruitment noted in this study should not be interpreted as a potential loss of each species. *Fagus grandifolia* and *T. canadensis* have experienced what seems to be periodic recruitment since the 1600s (Figures 4 and 5); and, HWA notwithstanding, the presence of both species in the canopy gives “storage” for the potential future recruitment of each species into the seedling and sapling layers (Chesson and Warner 1981, Chesson 1985).Despite the exact cause, the absence of these shade tolerant species (*T. canadensis* and *F. grandifolia*) in the understory at the RCRNA is unexpected since the RCRNA is a forest in a greater state of development and appears to have less anthropogenic disturbance than the CHA. Admittedly, the data collected during a single sampling season is not sufficient to draw accurate conclusions. Future monitoring of these permanent plots at the RCRNA and CHA is needed to accurately describe the species recruitment patterns occurring in the understory. Given the speed at which the HWA is invading Kentucky, it is not likely that another generation of *T. canadensis* will survive in these forests until a successful treatment and restoration plan is accomplished. The HWA will likely play a large role in altering the regeneration processes in the near future.

Acer rubrum was the most abundant seedling documented at both study sites (Tables 3 and 4). An increase of *A. rubrum* in the understory of many forests across the eastern United States is a widely documented trend (Larsen 1953, Lorimer 1984, Abrams and Downs 1990, Abrams 1998, McEwan *et al.* 2005). The practice of fire suppression since the 1930s is thought to be the cause of increased densities of *A. rubrum* in these forests (Abrams 1998). It is thought that *A. rubrum* expansion will continue due to its ability to survive in a variety of edaphic conditions and to persist in early and late successional forests in the absence of fire (Abrams 1998). However, there has also been a reduction of aridity since the late-1800s (Cook *et al*. 1988, McEwan *et al*. 2011, Pederson *et al*. 2012), which suggests a more favorable climate for a mesophytic species like *A. rubrum*. Reduced aridity, rather than fire, may be a more relevant factor influencing increased densities of *A. rubrum* in mesic, stream-filled, hemlock-dominated ravines because these ecosystems are less likely to burn compared to drier uplands (Harmon *et al.* 1984, Clebsch and Busing 1989).

Importantly, I did not find an increase in *A. rubrum* trees after the 1930s (Figures 4 and 5). Seventy-five percent of *A. rubrum* trees at the RCRNA established during the 1860s to 1929 (Figure 4) and 50% of the *A. rubrum* trees at the CHA established during the 1880s to 1929 (Figure 5). At the RCRNA, *A. rubrum* seedlings have increased in density while the importance value of *A. rubrum* canopy trees (≥ 10 cm dbh) has remained relatively consistent for more than three decades (Cameron and Winstead 1978). Cameron and Winstead (1978) reported approximately 138 seedlings/ha while I calculate 2187.5 seedlings/ha in the current investigation. Cameron and Winstead (1978) reported that at the RCRNA, *A. rubrum* was 6th in importance value for all canopy trees and 3rd in importance value for all canopy trees on east-facing slopes. Since 75% of my study plots were located on north or east-facing slopes, my results showing *A. rubrum* as 3rd in canopy importance value is consistent with Cameron and Winstead (1978). Additionally, the abundance of *A. rubrum* in the canopy at the RCRNA has remained relatively consistent for more than seven decades, ranking 3rd in abundance in the current investigation and in Braun (1950) and 4th in abundance in

Cameron and Winstead (1978). Typically, *A. rubrum* seedling survival rate is low despite the species' ability to respond quickly to canopy disturbance (Orwig 2002). Despite the increase in *A. rubrum* seedling density, this increase has not translated into a change in the importance of *A. rubrum* in the canopy at the RCRNA over the last 30 years. Further, fewer *A. rubrum*, as a percentage, have recruited into the lower canopy layers (intermediate and suppressed) at the RCRNA compared to the CHA. Due to more inferred evidence of disturbance via logging at the CHA, it seems that the more-regular opening of the forest canopy has promoted more *A. rubrum* succession into the lower canopy layers of the CHA forest. The current succession of *A. rubrum* into these forests shows that decadal-scale movement into the canopy may be potentially aided through timber harvesting. However, the functional extinction of *T. canadensis* through HWA invasion could facilitate significant changes to the current structure and function of these forests. HWA infestations alter the seedling and sapling composition by allowing more light to reach the canopy floor and can facilitate the regeneration and potential canopy recruitment of less shade tolerant species such as *A. rubrum*, *B. lenta*, *L. tulipifera*, *Quercus* spp. and *Sassafras albidum* (sassafras; Orwig and Foster 1998, Orwig 2002, Small *et al.* 2005, Eschtruth *et al.* 2006, Ford *et al*. 2011).

No non-native invasive species were documented within study plots at the RCRNA and the CHA (Tables 6 and 7). Similarly, previous studies of hemlock-dominated forests have shown that little to no non-native invasive species were present in plots prior to HWA infestation (Small *et al*. 2005, Eschtruth *et al*. 2006). However, these same studies found that non-native invasive species were present after HWA infestation and included *Berberis thunbergii* (Japanese barberry), *Celastrus orbiculatus* (Oriental bittersweet), *Lonicera japonica* (Japanese honeysuckle), *Rosa multiflora* (multiflora rose), *Ailanthus altissima* (tree-of-heaven), *Alliaria petiolata* (garlic mustard), and *Microstegium vimineum* (Nepalese browntop; Small *et al*. 2005, Eschtruth *et al*. 2006). While non-native invasive species were not found within the study plots at either site, the non-native invasive, *Microstegium vimineum*, and native weed, *Phytolacca americana* (American pokeweed)*,* were observed in the CHA adjacent to an old logging road. This suggests that the increased logging and opening of the canopy at the CHA allowed for the introduction of invasive species. Unfortunately, a HWA infestation was documented approximately 8 km from the CHA and RCRNA study sites in 2010 (Songlin Fei, Assistant Professor, University of Kentucky, personal communication). Therefore, when the RCRNA and CHA become infested with HWA, an increase of non-native invasive species is expected at both study sites.

4.2 Eastern Hemlock Crown Health

In 2008, the current investigation determined that nearly all *Tsuga canadensis* trees at the RCRNA and CHA were healthy with normal foliage (Table 9). At the RCRNA, one *T. canadensis* exhibited brown foliage at the top of the crown but this is an unlikely indicator of early HWA infestation. HWA infestations typically cause the crown health to decline from bottom to top and the needles turn from a dark green to a gray-green before falling from the tree (McClure 2001). The current proximity of HWA to the RCRNA and CHA emphasizes the need for long-term monitoring in these forests. The permanent plots established and information gathered during the current investigation will be a resource that can be utilized by forest managers. In 2011, the hemlock woolly adelgid was officially declared a public nuisance in Kentucky's forests and the U.S. Forest Service implemented a project titled "Suppression of Hemlock Woolly Adelgid on the Daniel Boone National Forest"(Agpaoa 2011). Under this project, 74 areas were designated as Hemlock Conservation Areas (HCA). The project's objectives were to maintain a genetic representation of *T. canadensis* across the DBNF, support the survival of ecologically and culturally important *T. canadensis* stands, and reduce *T. canadensis* mortality (Agpaoa 2011). The RCRNA gorge was designated as a HCA. Hopefully the data collected during the current investigation and the project implemented by the U.S. Forest Service will help to preserve at least some representative *T. canadensis* trees within the RCRNA gorge, especially since the gorge is considered an extreme type of hemlock-mixed mesophytic forest (Braun 1950).

4.3 Age and Stand Structure

From my results, the RCRNA study site would be classified as a multi-aged primary forest and the CHA study site a multi-aged mature secondary forest (Figures 4 and 5). Following Frelich (2002), I define a multi-aged forest as a forest containing the following: 1) an uneven age class, 2) old growth characteristics, and 3) a dbh distribution characterized by many small trees, with a decline in the middle size class that levels off, followed by a another sharp decline of trees in the largest size class. Following Duffy and Meier (1992), I define a primary forest as a forest that has never been clear cut and has experienced minimal or no anthropogenic disturbance. Under this definition, anthropogenic disturbances such as removal of individual trees or grazing are allowed but must have been limited in duration and extent (Duffy and Meier 1992). A mature secondary forest is defined as a forest that has been extensively logged or clear cut in the past but is approaching the conditions (i.e. species composition, successional status, forest structure, and age structure) found in primary forests of the same type in the same region (Duffy and Meier 1992, CBD 1999). The RCRNA and CHA lack evidence of past stand replacing disturbance (Figures 4 and 5). However, some degree of anthropogenic disturbance was detected at both study sites.

Within the RCRNA gorge, the only historically documented logging involved the removal of individual scattered trees from the most accessible portions of the ravine during the years of 1915-1917 (Hemingway 1938). In 1939, the RCRNA was designated as a natural area to permanently preserve the gorge in unmodified condition (Hemingway 1938). In the current investigation, one old skid trail was discovered approximately 600 meters from the gorge mouth. One would expect to find evidence of cutting within study plots 8, 7, and 6 because these plots are located approximately 800, 1000, and 1,240 meters, respectively, from the mouth of the gorge (Figure 1). For study plots 8 and 6, the highest number of trees recruited per decade occurred during the 1920s, nearly all of these trees were *T. canadensis* (Figure 6); and the majority of *T. canadensis* were gap-recruited trees (Figure 8). If cutting occurred in these study plots, the age structure and species composition of existing trees implies only select trees were removed (Figure 6). If a large-scale logging operation had occurred, large canopy gaps would have been created and shade intolerant, faster growing tree species such as *L. tulipifera* would have outcompeted *T. canadensis* (Rankin and Tramer 2002). Several of the oldest trees, including all *Q. alba,* were located within study plots 8 and 6 at the RCRNA (Figure 6) suggesting if cutting occurred in these plots, these trees were left behind due to poor growth form (Abrams 2007, Pederson 2010). The eastern portion of the RCRNA (study plots 1-5; Figure 6) is likely uncut old growth due to its inaccessibility, uneven age structure, and lack of large synchronous recruitment events. Interestingly, study plot 4 also showed a peak in recruitment during the 1920s, but nearly all trees were non-gap recruited (Figure 6). Approximately 22% of all in-plot trees at the RCRNA gorge were more than 130 years old (Figure 4) and predate the peak logging era for Kentucky (Collins 1975). The spatial and temporal age structure data combined with the species composition provides insight into the intensity of logging and suggests minimal anthropogenic disturbance at the RCRNA.

At the CHA, no historic documentation of logging was found (Robert Sitzlar, Daniel Boone National Forest, Forester, personal communication) but two old logging roads were discovered near the middle section of the ravine. Several coppiced trees were found within the southernmost study plot and stumps were observed on the upper slopes outside of this plot (Figure 1b, study plot 8). While coppicing naturally occurs in many hardwood species, the presence of many coppiced trees in a forest can be indicative of past logging (Wessels 1997). Logging most likely occurred in study plot 8 during the 1940s based on the large peak in recruitment and lack of older trees (Figure 7). However, the majority of logging throughout the CHA probably took place during the decade of 1910 and possibly 1900 because larger recruitment peaks occurred in these decades and most trees recruited were shade intolerant or mid-shade tolerant species (Figures 5 and 7). It was suggested that the trees in the CHA ravine date to 1878 (D. Taylor, Daniel Boone National Forest Botanist, personal communication). However, approximately 17% of all in-plot trees were more than 130 years old (Figure 5) and eight out-of-plot commercially important trees (*L. tulipifera*, *Q. alba*, and *Q. montana*) were greater than 200 years old. The age structure of the CHA implies that selective cutting or high grading may have occurred in the more accessible portions of the ravine and many old trees were left behind, making CHA a very mature, second-growth forest today.

Despite evidence of past anthropogenic disturbance, both the RCRNA and CHA study sites exhibit eight of the twelve potential old-growth characteristics for mixed mesophytic forests (Martin 1992). These eight characteristics are: (1) at least 7 trees/ha must be ≥ 75 cm DBH; (2) the oldest trees must be ≥ 200 years; (3) one or more commercially valuable tree species in the canopy; (4) an average overstory basal area of > 25 m^2/ha; (5) uneven-aged with canopy species in several size classes (Figures 3, 4, 5, 10, and 11); (6) the presence of logs and snags; (7) tree fall gaps by windthrow; and (8) evidence suggesting undisturbed soils (Martin 1992). At the RCRNA and CHA, the number of trees/ha ≥ 75 cm DBH (RCRNA = 34 trees/ha and CHA = 25 trees/ha; out-of-plot trees included) and average overstory basal area (RCRNA= 57.14 m^2/ha, CHA=54.3 m^2/ha; Tables 1 and 2) far exceed the minimum suggested by Martin (1992). The oldest trees are ≥ 200 years and comprise 13.0% of all in-plot trees at the RCRNA and 7.3% of all in-plot trees at the CHA (Figures 4 and 5). The RCRNA had two and the CHA had three commercially valuable canopy species ≥ 200 years old (Figures 4 and 5; out-of-plot trees included). At the RCRNA, ten in-plot and ten out-of-plot commercially valuable trees ≥ 200 years old were found and include *Q. alba* and *L. tulipifera.* While no commercially important trees ≥ 200 years were found in the CHA study plots, eight were found outside of the study plots and include *L. tulipifera*, *Q. alba*, and *Q. montana*. Both study sites had snags (RCRNA = 6 snags/ha; CHA = 16 snags/ha; Tables 1 and 2). Although the presence of downed logs, canopy gaps due to windthrow, and pit and mound topography were observed within and outside sample plots, their presence was not quantified. Although the RCRNA has less evidence of past anthropogenic disturbance than the CHA, the current age and stand structure of both of these study sites are approaching old-growth status.

The region surrounding the study sites was not settled until the 1790s and Laurel County was not formed until 1825 (Clark 1989). The aforementioned old growth characteristics, uneven age structure, and presence of trees ≥ 200 years old suggests the two study sites are mature forests. However, it is apparent that the RCRNA is in a later state of forest development than the CHA. While shade tolerant species such as *T. canadensis* and *F. grandifolia* are present in the upper canopy classes at the CHA, evidence suggesting the second growth status of CHA include the lack of shade tolerant species such as *F. grandifolia* and *I. opaca* in the lower canopy classes and the nearly continuous recruitment of *L. tulipifera* from the 1880s to 1969 (Figures 3 and 5). Additionally, major release events accounted for 73% of all the CHA releases compared to 57% in the RCRNA (Figures 8 and 9). The majority of trees at the CHA from the 1870s to 1959 were gap recruited (Figure 9). In general, the age structure and species composition suggests that the RCRNA is a multi-aged primary forest because it is mostly an old growth forest with limited historic cutting (Figures 4 and 6) and the CHA is a multi-aged mature secondary forest because historic cutting appears to have occurred in various portions of the ravine; but many old trees were left behind and the forest possesses old growth characteristics (Figures 5 and 7).

4.4 Disturbance Dynamics: Tree Recruitment and Canopy Disturbance History

The discussion of the disturbance history for the RCRNA and CHA is divided into four time periods based upon the historic settlement and environmental history of Kentucky: 1) 1670-1769 (pre-European settlement), 2) 1770-1869 (European settlement), 3) 1870-1939 (Logging era), and 4) 1940-2009 (Establishment of the Daniel Boone National Forest, formerly the Cumberland National Forest). When possible, known historical events and weather are provided for context. However, the inclusion of these events does not imply direct causation of decadal disturbance. It should be noted as a reminder to the reader that conclusions based upon gap recruitment status are limited because only trees reaching pith or close to pith were used.

1670-1769: Pre-European settlement

While no release events were recorded before 1670 at the RCRNA, the recruitment of several *L. tulipifera* during the 1630s to 1660s suggests the creation of large canopy gaps or a series of canopy disturbance events (Figure 4). During the 1670s to 1720s, several *L. tulipifera* and *Q. alba* recruited at the RCRNA further supporting the idea that this was a time of increased disturbance (Figure 4). Major release events were recorded in the decades of 1670 and 1710 (Figure 8). The disturbance and recruitment during the 1670s to 1720s may suggest the dieback of *T. canadensis* in the canopy at the RCRNA because *L. tulipifera* is a documented successor in canopy gaps formed primarily by the fall of *T. canadensis* (Barden 1981). From the 1720s to 1760s, shade tolerant species such as *T. canadensis* and *Nyssa sylvatica* (blackgum) recruited at the RCRNA (Figure 4). Overall, prior to the 1720s, the RCRNA seems to be characterized by larger canopy disturbance and the subsequent recruitment of the shade intolerant, *L. tulipifera* (Figure 4). After the 1720s, the RCRNA seems to be characterized by smaller canopy disturbance due to the low tree recruitment, recruitment of only shade tolerant species, and a majority of minor release events (Figures 4 and 8).

Haasis (1923) documented the age structure of a forest in southeastern Kentucky and found that most trees established after 1660. Haasis (1923) suggested this establishment may have been a result of a dry period occurring between 1640 and 1660 followed by a pronounced drought in 1662. Drought is associated with increased tree mortality and can create larger multi-tree gaps depending upon drought severity (Olano and Palmer 2003, Klos *et al.* 2009, Allen *et al.* 2010). Further, tree mortality can intensify if coupled with other stresses such as pest and disease outbreaks (Balch 1927, Allen *et al.* 2010). Additional studies suggest the 17th and 18th centuries were dry periods (McEwan *et al*. 2011, Pederson *et al.* 2012). McEwan *et al.* 2011 reported the occurrence of intense and frequent droughts across the eastern United States from 1500 to 1900. During this time, a megadrought occurred around 1630 and a multi-year drought occurred around 1700 (McEwan *et al*. 2011). Pederson *et al.* 2012 revealed that the 18th century was a dry period and a substantial drought affected the southern Appalachian Mountains from 1696 to 1709. It is possible that the late 17th and early 18th century recruitment of *L. tulipifera* at the RCRNA was a result of increased canopy openings due to tree mortality caused by the aforementioned dry period and associated multi-year droughts. Although drought sensitive, *L. tulipifera* produces high seed fall when conditions are dry with high temperatures (Beck 1990). However post-drought, *L. tulipifera* would have required a suitable seed bed, sufficient moisture, and sunlight to germinate and survive (Beck 1990). If a combination of these factors discussed above occurred, it would offer another alternative to explain the recruitment of *L. tulipifera* and *Q. alba* during the 1630s to 1720s at the RCRNA.

At the CHA during the 1670s to 1720s, tree recruitment was lower, most release events were minor, and the majority of trees recruited were shade tolerant species such as *T. canadensis* and *F. grandifolia* (Figures 5 and 9). It appears that the 1670s to 1720s at the CHA was characterized by fewer, less intense disturbances than the RCRNA. Since CHA is a mature secondary forest, most trees recruited during this time period could have been harvested. Additional tree-ring data from older trees are needed to characterize the disturbance regime at CHA during the 1670s to 1720s.

It appears unlikely that European settlers influenced the disturbance and recruitment patterns documented at the RCRNA and CHA during the 1670s to 1769. European settlement in the area did not begin until the 1790s and Laurel County was not officially established until 1825 (Clark 1989). Several factors contributed to why Laurel County had not formed before 1825 and include the ruggedness of the terrain, the density of the forest, and the Cherokee Indian “menace” (Clark 1989). One could hypothesize that forest dynamics at the RCRNA during this time were influenced by Native Americans. It is thought that Kentucky was used by the Cherokees, Shawnees, Iroquois, Creeks, and Chickasaws exclusively for hunting grounds (Davis 2000). In the 16th and 17th centuries, the Mississippian Indians were believed to use incendiary fires for the purpose of clearing underbrush within forests to create more favorable habitat for desired birds, mammals, and plants (Davis 2000). However by the 1700s, Native American populations were greatly diminished due to European diseases such as smallpox and influenza (Davis 2000). No further documentation was found describing the extent of Cherokee presence within Laurel County. Additionally, no fire scars were evident on extant trees or among core samples to suggest the occurrence of historic fire events at either study site.

The most noteworthy finding for the 1670s-1769, a period prior to European settlement (Clark 1989) and a century after the decline of most native American populations (Davis 2000), is that a majority of the trees recruited at the RCRNA were relatively shade intolerant and recruited into gaps (Figure 8); suggesting either frequent disturbance or large mortality events, especially between the 1690s to 1729.

1770-1869: European settlement

A small disturbance peak is discernible at both the RCRNA and CHA during the decade of 1800 (Figures 8 and 9). Although tree replication was low prior to 1800, the disturbance peak during the decade of 1800 could indicate a potential landscape level disturbance event. The low tree recruitment at both study sites suggests the creation of smaller canopy gaps (Figures 4 and 5). Haasis (1923) reported increased tree growth just prior to the year 1800 in an age structure analysis study of an old forest in southeastern Kentucky. Although settlers arrived in Laurel County the 1790s, they were mainly concentrated toward the northern and eastern borders of the county and these settlements are estimated to be 56 km and 48 km, respectively, from the study sites. By 1825 when Laurel County was formed, the natural resources of the area had been narrowly exploited. Even in 1835, only 15 people lived in London, a community located approximately 30 km from the RCRNA and 18 km from the CHA; and just 2,206 resided in the entire county (Clark 1989). The results from the current investigation and Haasis (1923) provide limited evidence of a landscape level disturbance event occurring during or just prior to the decade of 1800. Despite inconclusive results, the location of both study sites and settlement history of Laurel County during the early 1800s implies this disturbance event was of non-anthropogenic origin.

At the RCRNA and CHA, disturbance was relatively low throughout the 1810s-1860s (Figures 8 and 9). For the 1770-1869 period, tree recruitment was the highest during the 1860s at both study sites (Figures 4 and 5), but release events during the 1860s were among the lowest at the RCRNA (Figure 8) and highest at the CHA (Figure 9). By 1860, the population in Laurel County was 5,488 people, but more than half of the population was under 10 years of age (Clark 1989). The early settlement of Laurel County (1820s to 1860s) was considered gradual compared to the rapid population growth experienced in other parts of Kentucky at the time (Clark 1989). If the disturbances and recruitment events in the 1860s noted at the RCRNA and CHA study sites are of anthropogenic origin, it suggests low-intensity logging that likely resulted from fuel wood cutting or the harvesting of a few trees for structures like log cabins. Wood fuel was the primary method of heating homes in Laurel County until the latter quarter of the 19th century (Clark 1989). The process~~es~~ impacting forest composition at the RCRNA and CHA study sites during this time period was likely gap-scale dynamics, the principal disturbance regime influencing stand development in mixed mesophytic forests (Runkle 1982, Muller 2003); but impacts on forest integrity at each study site arising from individual cutting of trees is certainly possible.

1870-1939: Logging Era

Synchronous disturbance peaks with relatively few release events were documented at the RCRNA and CHA during the 1870s (Figures 8 and 9), a time period that marks the beginning of the logging era in Kentucky (Collins 1975). These release events may be the result of selective cutting or gap-scale dynamics. A large proportion of Laurel County still remained undeveloped in 1870 and prior to 1882 transportation was a serious handicap to profitable timber harvesting in Laurel County (Clark 1989). Since wood was still the main method of heating homes during the 1870s (Clark 1989), disturbance caused by individual cutting of trees for home use is feasible. In a study investigating the role of climate on oak forests in the eastern United States, McEwan *et al.* 2011 reported the occurrence of a many severe multi-year droughts with one centered on 1872. Many studies of forests across the eastern United States have attributed tree mortality to more recent, less severe droughts than those reported by McEwan *et al.*2011 (Stringer *et al*. 1989, Clinton *et al*. 1993, Olano and Palmer 2003). Despite the low recruitment and low number of gap recruited trees at the RCRNA and CHA, the multi-year drought of 1872 certainly could have caused tree mortality and contributed to the disturbance peak recoded at both study sites in the 1870s (Figures 4,5,8,and 9)

Disturbance peaks documented for the RCRNA and CHA from 1900 to 1909 (Figures 8 and 9) coincide with the peak logging period in Kentucky (Collins 1975). Tree establishment (n=5) from 1900 to 1909 at the RCRNA (Figure 4) was 67% lower compared to the CHA (n=15; Figure 5). Lower tree establishment at the RCRNA may have resulted from the lower number of major release events (n=13; Figure 8) compared to CHA (n=24; Figure 9). At the RCRNA, only 40% of trees established in gaps (Figure 8) compared to 80% at the CHA (Figure 9). These results suggest a landscape level disturbance, such as logging, that resulted in larger canopy gaps at both the RCRNA and CHA study sites; however the CHA was apparently more heavily impacted by this disturbance event.

If one had travelled through Laurel County in 1900, one would not notice any improvements in the roads since 1840 (Clark 1989). By 1903, three-fourths of the county’s virgin timber had been harvested or destroyed by wildfires and most of the timber sold to market had been floated down the lower portions of the Rockcastle and Cumberland Rivers (Clark 1989). The low tree establishment and low number of gap recruited trees originating at the RCRNA from 1900 to 1909 may reflect the difference in topographic accessibility between study sites. Individual cutting of trees may have occurred at the less accessible RCRNA study site and more intense logging, such as high grading or selective cutting, likely occurred at the CHA.

The great blizzard of 1899 could have contributed to the peak in disturbance noted at the RCRNA and CHA study sites during the decade of 1900. This blizzard affected the southeastern United States; causing below zero temperatures in Florida's panhandle and the flow of ice down the Mississippi River past New Orleans into the Gulf of Mexico (NOAA 2009). Although weather records from 1899 were not available for Laurel County, the temperatures in two cities located approximately 160 kilometers north and south of the study sites reached - 33°F (Sandy Hook, Kentucky) and -30°F (Erasmus, Tennessee). Snow, ice, and glaze storms can cause widespread canopy damage and create gaps of different sizes (Boerner *et al.* 1988, Rhoades 1999, Lafon 2006). However, the dramatic peak in recruitment (Figure 5), gap-recruited trees, and disturbance (Figure 9) combined with the increased number of shade intolerant and mid-shade tolerant tree species (Figure 5) suggests that more extensive logging or high-grading occurred in the more accessible portions of the CHA ravine from 1900 to 1909. While the RCRNA also experienced a dramatic peak in disturbance from 1900 to 1909 (Figure 8), it is difficult to infer from the species composition (mostly mid shade tolerant and shade tolerant) and lower tree recruitment (Figure 4) what processes were responsible. However, it appears that smaller canopy gaps likely occurred. The cutting of individual trees, a natural process such as the aforementioned blizzard, or more likely a combination of both or several processes, may have resulted in the disturbance noted from 1900 to 1909 for the RCRNA.

A sharp increase in tree recruitment during the 1920s at the RCRNA suggests the occurrence of a significant canopy disturbance (Figure 6, study plot 6,). Fifty-eight percent (n=26) of trees recruited in the 1920s occurred in study plot 6 and resulted in almost exclusive recruitment of gap-origin *T. canadensis* (Figure 8). This study plot also had the highest tree density compared to all other plots at the RCRNA (Figure 6). Other small recruitment events occurred during the 1920s at the RCRNA within study plot 8 (n = 5) and study plot 4 (n = 7; Figure 6). Within these two study plots, most trees recruited in the 1920s were *T. canadensis.* However, trees in study plot 8 were all gap-recruited and trees in study plot 4 were mostly non-gap recruited. The recruitment peak at study plot 8 during the 1920s at the RCRNA may have resulted from the same disturbance affecting study plot 6, but the extent appears considerably smaller. Study plot 8 was located approximately 0.5 kilometers from study plot 6 (Figure 1).

Webster and Lorimer (2002) studied the effects of canopy gap area on species composition and stem density and found that as canopy gaps increased to >400 m^2, *Betula alleghaniensis* (yellow birch), a mid-shade tolerant species, outcompeted *T. canadensis* in all but the younger gaps. Overall, *T. canadensis* stem density significantly declined with increasing gap area. As recruitment during the 1920s within study plots 6 and 8 at the RCRNA was dominated by the shade-tolerant, *T. canadensis,* and not mid-shade tolerant species, it seems the disturbance that allowed for the recruitment of *T. canadensis* was <400 m^2.

Selective cutting is known to have occurred in the RCRNA from 1915-1917; hence, the peak in recruitment in the 1920s at study plot 6 may have been the result of logging. Furthermore, automobiles in Laurel County were commonplace by 1915 and the Federal-Aid Road Act of 1916 was passed to offer grants to any state and county agreeing to pay 50% of road construction costs (Clark 1989). By 1918, organized surfaced roads had been established in Laurel County. The passage of the Federal Highway Act of 1921 initiated the construction of the U.S. national highway system (Clark 1989). This increase in infrastructure and mechanization in the U.S. would make timber harvesting more accessible and suggests that cutting in my study areas in the 1920s was possible since individual trees were harvested in the more accessible portions of the RCRNA gorge in the preceding decade. The old logging road and mouth of the gorge was located approximately 640 meters and 1.2 kilometers northwest of this plot (Figure 1). Selective cutting is suspected at study plot 6 due to the propensity of *T. canadensis* to dominate in smaller canopy gaps.

Historic *Castor canadensis* beaver (North American beaver) activity could have occurred at the RCRNA during the 1920s; recent *C. canadensis* activity was apparent approximately 150 meters from study plot 6. Although feeding preferences vary throughout the United States, *C. canadensis* have utilized the following tree species in the eastern United States: *L. tulipifera*, *A. rubrum*, *F. grandifolia*, *P. serotina* (black cherry), *N. sylvatica*, *S. albidum*, and *Q. alba* (Brenner 1962, Nixon and Ely 1969, Svendsen 1980, Lacki *et al.* 2001). The dominance of *T. canadensis* in the 1920s recruitment event (Figure 6) could indicate that *C. canadensis* played a role in selectively utilizing shade intolerant and mid-shade tolerant tree species. However, the most plausible explanation is anthropogenic disturbance because this time period coincides with peak logging in Kentucky and improved road conditions throughout Laurel County (Collins 1975, Clark 1989).

1940-2009: Establishment of the Daniel Boone National Forest

A large recruitment peak occurred at the CHA during the 1940s (Figure 5), but only one major release event was recorded for the decade (Figure 9). This major release event occurred in the southernmost study plot (Figure 1, Study Plot 8) and was a 502% growth increase, which suggests the creation of a very large gap (Rentch *et al*. 2002). Fifty eight percent (n=14) of all trees recruited during the 1940s at the CHA were found in study plot 8 (Figure 7). Several factors could have caused the large recruitment peak; the loss of the *Castanea dentata* (American chestnut), logging, or a combination of both. Due to the accessibility of the terrain, existence of coppiced trees within and near study plot 8, and the lack of synchronous disturbance within other study plots at the CHA, logging is probably the primary factor contributing to the 1940s recruitment peak. Old stumps were observed on the upper slopes outside of study plot 8. If *C. dentata* was a major component of the CHA forest and *Cryphonectria parasitica* (chestnut blight) had occurred in this part of *C. dentata*'s range during the 1940s, synchronous disturbance peaks would be expected throughout the CHA ravine. However, no synchronous disturbance peaks were observed in other CHA study plots and no similar recruitment or disturbance peaks were evident at the RCRNA (Figure 6); nothing to suggest a widespread disturbance event such as *C. parasitica*. Braun (1950) reported *C. dentata* comprised 3.4% of the species composition at the RCRNA during the 1920s and 1930s, but Hemingway (1938) did not mentioned *C. dentata* in a timber survey report. This suggests that *C. dentata* most likely was a small component of the RCRNA gorge forest as well as the CHA. The most feasible explanation for the large recruitment peak occurring during the 1940s at study plot 8 in the CHA is logging due to the accessible terrain and existence of coppiced trees and nearby stumps.

Disturbance peaks documented for the RCRNA and CHA during the 1950s and especially the 1960s suggest a landscape level disturbance event (Figures 8 and 9). During the 1960s at both study sites, the majority of release events were major releases and the majority of tree species recruited were either mid-shade tolerant or shade intolerant suggesting the creation of larger gaps. While all the trees were gap recruited at the RCRNA in the 1960s, the majority of trees at the CHA were non-gap recruited. Despite the fact that the 1960s disturbance peak was larger than the 1950s disturbance peak, tree recruitment at both study sites was higher in the 1950s. While the majority of release events during the 1950s at both sites were major, the majority of trees recruited at the RCRNA were the shade tolerant, *T. canadensis*, and the majority of trees recruited at the CHA were mid-shade tolerant or shade intolerant. Despite this, the majority of trees at both study sites were gap recruited in the 1950s, but at the CHA most gap recruited trees were the shade intolerant, *L. tulipifera*. This suggests that large gaps were created at the CHA. Further, tree recruitment at the RCRNA occurred in 75% of all study plots during the 1950s (Figure 6), and three study plots (Plots 1, 7 and 8; Figure 1) accounted for approximately 70% of all tree recruitment. Because 92% of these trees at the RCRNA were *T. canadensis* (Figure 6), it suggests they were recruited through the creation of small gaps.

No documentation of logging was found for the RCRNA and CHA study sites during the 1950s to 1969 (Robert Sitzlar, Daniel Boone National Forest, Forester, personal communication). While logging may be suspected as the primary disturbance affecting recruitment at the RCRNA gorge during the 1950-1960s period, the designation of the RCRNA gorge as a natural area in 1939 suggests at least two things; illegal logging or an intense natural disturbance. The uplands outside of the RCRNA gorge study site were heavily logged and clear-cut in 1965 (Winstead 1989, Thompson and Jones 2001). During this time, other disturbance events were recorded for Laurel County, e.g., an ice storm in 1951, a severe drought from 1952-1954, tornados in 1954 (F2) and 1956 (F0), and thunderstorm winds reaching 65 mph in 1964 (NOAA 2011). At the CHA, 73 % of trees recruited during the 1950s and 40% of the trees recruited during the 1960s (Figure 7) occurred in the southernmost study plot (Figure 1, study plot 8). Similar to the 1940s recruitment event in this plot, the accessibility of the terrain, existence of coppiced trees within and near the plot, and the lack of synchronous disturbance within other plots at the CHA suggests logging may have been the primary disturbance in this plot during the 1950s-1960s. It may also be possible that if logging occurred within the southernmost plot at the CHA during the 1940s, the trees left behind would be more exposed and therefore more susceptible to mortality by ice and wind. In addition, the aforementioned storms and severe drought might partly explain the synchronous disturbance found at the RCRNA and CHA during the 1950s-1960s (NOAA 2011; Figures 8 and 9).

The highest number of release events per decade occurred during the 1980s at both the RCRNA and CHA study sites (Figures 8 and 9). However, the disturbance in the 1980s is likely exaggerated due to increased tree replication during the latter part of the record. Nevertheless, these release events most likely resulted from a combination of local windstorms, tornados, and drought. Increased tree mortality associated with drought is well documented across North America, especially when coupled with other stresses such as pest and pathogen outbreaks, ice and wind storms, or fire (Clinton *et al*. 1993, Fahey 1998, Olano and Palmer 2003, Allen *et al.* 2010). Drought occurred across the state of Kentucky in 1986 and 1988. During the 1980s in Laurel County, tornados occurred in 1980 (F1), 1982 (F1), and 1984 (F2) and thunderstorm winds were recorded in 7 of the years during this decade (NOAA 2011). Other studies have suggested that the droughts occurring in eastern United States during the mid-to-late 1980s contributed to decreased tree growth and increased tree mortality (Stringer *et al*. 1989, Clinton *et al*.

1993, and Olano and Palmer 2003). Kincaid and Parker (2008) did not find any correlation between disturbances and mean annual or seasonal Palmer drought severity index values for forests in the southern Appalachian Mountains, but disturbance peaks did coincide with known drought years, including 1988. Romme and Martin (1982) documented tree fall gaps during 1973-1982 at Lilley Cornett Woods, an old growth forest in southeastern Kentucky, and found that tree fall gaps increased substantially during 1981-1982. Romme and Martin (1982) suggest tree falls were strongly related to local windstorms. While logging may be suspected due to the large increase in disturbance events, no record of logging was found for the RCRNA or CHA (Robert Sitzlar, Daniel Boone National Forest, Forester, personal communication).

5. CONCLUSIONS

While the RCRNA and CHA study sites have experienced anthropogenic disturbance, both forests are multi-aged, mature forests. The RCRNA is mostly a primary forest with old-growth characteristics and minimal human disturbance. Evidence indicates that the CHA is a secondary forest that possesses old-growth characteristics despite more extensive logging. Disturbances have occurred in the RCRNA and CHA at the stand and landscape levels and likely includes disturbance types such as drought and windstorms, as well as logging. The species composition of the RCRNA and CHA study sites are typical of hemlock-mixed mesophytic forests. *Tsuga canadensis* (eastern hemlock) was present in all canopy classes and regeneration occurred throughout the past century at both the RCRNA and CHA. While nearly all *T. canadensis* trees were healthy with normal foliage, the imminent threat of HWA infestation will alter the natural processes occurring at both the RCRNA and CHA study sites.

Limited information exists involving the dynamics of *T. canadensis* forests impacted by HWA in the southern Appalachian Mountains (Ford and Vose 2007, Spaulding and Rieske 2010, Krapfl *et al.* 2011, Ford *et al.* 2011) and more studies documenting pre-HWA conditions and using tree-ring analysis are needed (e.g., Kincaid and Parker 2008). In the northeastern United States, HWA has initiated the prolific establishment of *Betula lenta* (black birch) and has led to reductions in the compositional diversity and structural complexity of the understory (Orwig *et al.* 2002, Stadler *et al.* 2005). In southern Appalachian forests, it is predicted that *T. canadensis* could be replaced by species such as *Acer rubrum, B. lenta*, and *L. tulipifera* (Ford *et al.* 2011) The gradual decline of this foundation species will allow changes in ecosystem processes to begin before HWA-induced mortality is complete (Ellison *et al.* 2005, Eschtruth *et al.* 2006). In addition, HWA is co-occurring with many other disturbances such as invasive pathogens and plants, nitrogen deposition, and increased populations of *Odocoileus virginianus* (white-tailed deer; Frelich and Lorimer 1985, McClure 1990**,** Waller and Alverson 1997, Bauer *et al.* 2001). As we face these and other ecological challenges, researchers need to incorporate the use of tree-ring data from all canopy species to more fully understand and describe the stand dynamics of hemlock-mixed mesophytic forests and other forest types within the southern Appalachian region and across eastern North America.

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APPENDIX A:

Tables and Figures

Table 1. Ecological importance of tree species at Rock Creek Research Natural Area, Laurel County, KY.

RCRNA Species	Density (trees/ha)	Frequency (%/plots)	Dominance (Basal Area) (m^2/ha)	Relative Density	Relative Frequency	Relative Dominance	Relative Importance
Tsuga canadensis	269	100.0	26.25	45.74	15.09	45.94	106.77
Liriodendron tulipifera	38	87.5	9.98	6.38	13.21	17.46	37.05
Acer rubrum	53	50.0	3.12	9.04	7.55	5.46	22.05
Betula lenta	63	100.0	4.55	10.64	15.09	7.96	33.69
Fagus grandifolia	28	50.0	2.78	4.79	7.55	4.87	17.21
Magnolia macrophylla	19	50.0	0.39	3.19	7.55	0.69	11.43
Magnolia tripetala	22	37.5	0.30	3.72	5.66	0.52	9.90
Oxydendrum arboreum	22	25.0	1.88	3.72	3.77	3.29	10.78
Quercus alba	12	25.0	4.57	2.13	3.77	8.00	13.90
Ilex opaca	43	62.5	1.11	7.45	9.43	1.94	18.82
Carya glabra	3	12.5	0.26	0.53	1.89	0.45	2.87
Sassafras albidum	3	12.5	0.53	0.53	1.89	0.93	3.35
Nyssa sylvatica	6	25.0	0.44	1.06	3.77	0.77	5.60
Snags	6	25.0	0.98	1.06	3.77	1.72	6.55
Total	587	662.5	57.14	100.00	100.00	100.00	300.00

Table 2. Ecological importance of tree species at Cold Hill Area, Laurel County, KY.

CHA Species	Density (trees/ha)	Frequency (%/plots)	Dominance (basal area) (m^2/ha)	Relative Density	Relative Frequency	Relative Dominance	Relative Importance
Tsuga canadensis	209	100.0	26.67	42.41	16.67	49.12	108.20
Liriodendron tulipifera	84	87.5	10.11	17.09	14.58	18.61	50.28
Acer rubrum	53	75.0	3.59	10.76	12.50	6.62	29.88
Betula lenta	34	50.0	3.29	6.96	8.33	6.06	21.35
Fagus grandifolia	25	62.5	6.16	5.06	10.42	11.34	26.82
Magnolia macrophylla	47	87.5	1.16	9.49	14.58	2.15	26.22
Magnolia tripetala	6	25.0	0.07	1.27	4.17	0.13	5.57
Oxydendrum arboreum	13	37.5	0.57	2.53	6.25	1.04	9.82
Carya glabra	3	12.5	0.89	0.63	2.08	1.65	4.36
Juglans nigra	3	12.5	0.22	0.63	2.08	0.40	3.11
Snags	16	50.0	1.57	3.16	8.33	2.90	14.39
Total	493	600.0	54.30	100.00	100.00	100.00	300.00

Table 3. Seedling and sapling layer composition at Rock Creek Research Natural Area, Laurel County, KY.

RCRNA Species	Sapling Layer Density (stems/ha)	Seedling Layer Density (stems/ha)	Seedling Cover (%/ha)	Relative Seedling Cover
Magnolia macrophylla	312.50	312.50	0.06	31.25
Betula lenta	281.25	0.00	0.00	0.00
Tsuga canadensis	250.00	0.00	0.00	0.00
Ilex opaca	218.75	0.00	0.00	0.00
Acer rubrum	62.50	2187.50	0.11	53.13
Stewartia ovata	62.50	0.00	0.00	0.00
Quercus spp.	0.00	312.50	0.03	15.63
Total	1187.50	2812.50	0.20	100.00

Table 4. Seedling and sapling layer composition of Cold Hill Area, Laurel County, KY.

CHA Species	Sapling Layer Density (stems/ha)	Seedling Layer Density (stems/ha)	Seedling Cover (%/ha)	Relative Seedling Cover
Asimina triloba	750.00	625.00	0.19	24.20
Magnolia macrophylla	656.25	0.00	0.00	0.00
Stewartia ovata	343.75	0.00	0.00	0.00
Betula lenta	281.25	0.00	0.00	0.00
Acer rubrum	250.00	1562.50	0.05	6.90
Tsuga canadensis	187.50	625.00	0.02	2.00
Ilex opaca	187.50	937.50	0.23	29.50
Fagus grandifolia	93.75	0.00	0.00	0.00
Magnolia acuminata	93.75	0.00	0.00	0.00
Magnolia tripetala	93.75	937.50	0.07	9.10
Acer saccharum	62.50	0.00	0.00	0.00
Nyssa sylvatica	62.50	0.00	0.00	0.00
Fraxinus pennsylvanica	31.25	0.00	0.00	0.00
Prunus serotina	31.25	0.00	0.00	0.00
Quercus rubra	31.25	625.00	0.13	16.20
Quercus spp.	0.00	312.50	0.09	12.10
Total	3156.25	5625.00	0.77	100.00

Table 5. Shrub layer composition at Rock Creek Research Natural Area and Cold Hill Area, Laurel County, KY.

Shrub Layer	RCRNA Cover (%/ha)	CHA Cover (%/ha)
Rhododendron maximum	43.98	41.56
Clethra acuminata	0.078	0.32
Lindera benzoin	0.00	1.48
Viburnum acerifolium	0.00	0.23
Hamamelis virginiana	0.00	0.08
Total	44.06	43.67

Table 6. Ground layer composition at Rock Creek Research Natural Area, Laurel County, KY.

RCRNA Ground Layer	Cover (%/ha)	Density (stems/ha)	Frequency (# of plots)	Relative Cover	Relative Density	Relative Frequency	IV
Dryopteris intermedia	2.44	10312.50	18.75	80.62	30.00	33.33	143.95
Mitchella repens	0.41	19687.50	18.75	13.69	57.27	33.33	104.29
Medeola virginiana	0.02	312.50	3.13	0.52	0.91	5.56	7.00
Viola sp.	0.04	2187.50	3.13	1.29	6.36	5.56	13.21
Parthenocissus quinquefolia	0.03	312.50	3.13	1.03	0.91	5.56	7.50
Smilax rotundifolia	0.03	312.50	3.13	1.03	0.91	5.56	7.50
Smilax glauca	0.05	1250.00	6.25	1.81	3.64	11.11	16.56
Total	3.02	34375.00	56.25	100.00	100.00	100.00	300.00

Table 7. Ground layer composition at Cold Hill Area, Laurel County, KY.

CHA Ground Layer	Cover (%/ha)	Density (stems/ha)	Frequency (# of plots)	Relative Cover	Relative Density	Relative Frequency	IV
Dryopteris intermedia	5.89	11562.50	18.75	54.12	12.54	12	78.66
Thelypteris noveboracensis	1.00	12500.00	9.38	9.19	13.56	6	28.75
Polystichum acrostichoides	0.88	6250.00	12.50	8.04	6.78	8	22.82
Mitchella repens	0.79	28750.00	21.88	7.25	31.19	14	52.44
Medeola virginiana	0.53	5937.50	18.75	4.88	6.44	12	23.32
Huperzia lucidula	0.31	3437.50	3.13	2.87	3.73	2	8.60
Tiarella cordifolia	0.25	3125.00	3.13	2.30	3.39	2	7.69
Viola sp.	0.23	8437.50	18.75	2.09	9.15	12	23.24
Vitis sp.	0.19	312.50	3.13	1.72	0.34	2	4.06
Maianthemum racemosum	0.20	1875.00	12.50	1.87	2.03	8	11.90
Epifagus virginiana	0.16	3437.50	6.25	1.44	3.73	4	9.17
Chimaphila maculata	0.09	1250.00	3.13	0.86	1.36	2	4.22
Dioscorea quaternata	0.09	625.00	3.13	0.86	0.68	2	3.54
Smilax rotundifolia	0.07	625.00	6.25	0.65	0.68	4	5.33
Smilax glauca	0.06	937.5.00	3.13	0.57	1.02	2	3.59
Parthenocissus quinquefolia	0.06	1875.00	3.13	0.57	2.03	2	4.60
Goodyera pubescens	0.05	937.50	6.25	0.43	1.02	4	5.45
Uvularia sp.	0.03	312.50	3.13	0.29	0.34	2	2.63
Total	10.88	92187.50	156.30	100.00	100.00	100	300.00

Table 8. Comparison of site characteristics at Cold Hill Area and Rock Creek Research Natural Area, Laurel County, KY.

SITE	Ground cover (%)	Total shrub cover (%)	Total seedling density (stems/ha)	Total sapling density (stems/ha)	Total tree density (stems/ha)	Basal area (m^2/ha)
CHA	10.88	33.13	5625.00	3156.25	493.75	54.30
RCRNA	3.02	44.06	2812.50	1187.50	587.50	57.14

Table 9. Summary of eastern hemlock (*Tsuga canadensis*) crown health based on "Visual crown rating" methods developed by the U.S. Forest Service (USDA Forest Service 2007).

SITE	VC 1 (%)	VC 2 (%)	Mean ULCR (%)	Mean FD (%)	Mean FT (%)	# trees with Dieback
CHA (n=65)	95	5	64	53	42	1
RCRNA (n=84)	81	19	50	47	45	1

Note: VC1 = Vigor class 1, VC2 = Vigor class 2, ULCR = Uncompacted live crown ratio, FD = Foliar density, FT = Foliar transparency.

Table 10. Summary of eastern hemlock (*Tsuga canadensis*) crown shapes based on "Visual crown rating" methods developed by the U.S. Forest Service (USDA Forest Service 2007).

SITE	Crown Shape (%)						
	Conical	Columnar	Oval	V-shaped	Irregular	Pyramidal	Parabolic
CHA (n=65)	43	18	23	3	2	8	3
RCRNA (n=84)	52	7	14	0	4	13	10

Table 11. List of tree species documented from the current and previous studies at Rock Creek Research Natural Area, Laurel County, KY.

RCRNA Tree Species	**Current Study (n=186)**	**Thompson *et al.* 2000 (n=492)**	**Cameron and Winstead 1978 (n=412)**	**Winstead and Nicely 1976 (n=100)**	**Braun 1950 (n=117)**
Tsuga Canadensis	x	x	x	x	x
Liriodendron tulipifera	x	x	x	x	x
Acer rubrum	x	x	x	x	x
Betula lenta	x	x	x	x	x
Fagus grandifolia	x	x	x	x	x
Magnolia macrophylla	x	x	x	x	x
Magnolia tripetala	x				
Oxydendrum arboreum	x	x	x		x
Carya glabra	x	x			
Quercus alba	x	x	x	x	
Ilex opaca	x	x	x	x	x
Sassafras albidum	x	x			
Nyssa sylvatica	x	x	x	x	x
Acer saccharum		x			
Quercus montana		x	x		x
Pinus rigida		x			
Magnolia acuminata		x	x		
Quercus rubra		x	x	x	x
Tilia americana		x			
Pinus virginiana		x	x		
Quercus coccinea		x			
Carya cordiformis		x			
Aesculus flava		x	x		
Cornus florida			x	x	
Prunus serotina				x	
Carpinus caroliniana				x	
Castanea dentata					x
Pinus taeda			x		
Carya ovata			x		

Source: Data from 1) Thompson *et al*. 2000. Botanical survey of Rock Creek Research Natural Area, Kentucky. Gen. Tech. Rep. NE-272. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 23 p., 2) Cameron, III, M., and J. Winstead. 1978. Structure and composition of a climax mixed mesophytic forest system in Laurel County, Kentucky. Transactions of the Kentucky Academy of Science 39: 1-11., 3) Winstead, J. and K. Nicely. 1976. A preliminary study of a virgin forest tract of the Cumberland Plateau in Laurel County, Kentucky. Transactions of the Kentucky Academy of Science 37: 29-32., and 4) Braun, L. 1950. Deciduous forests of eastern North America. Hafner Press, New York, New York.

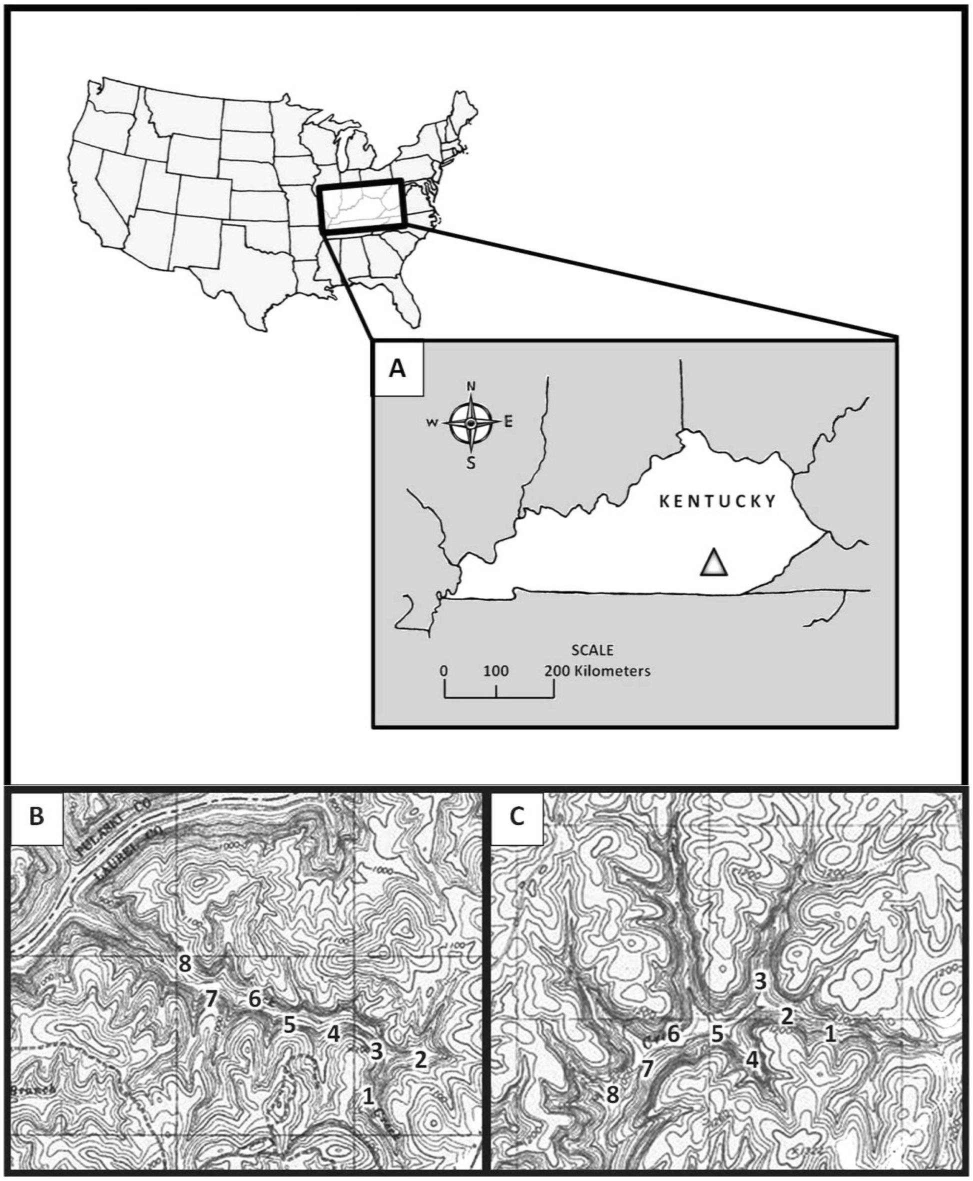

Figure 1. A) General location of study areas within the United States. The triangle represents the approximate location of both study sites in Kentucky.
B & C) Topographical maps of study sites within the Daniel Boone National Forest, Laurel County, KY: B) Rock Creek Research Natural Area (RCRNA) 36°59”30’N and 84°19”00’W and C) Cold Hill Area (CHA) 37°03”14’N and 84°28”06’W.

Note: In Figures 1B and 1C, numbers represent each individual 0.04 ha permanent plot. Maps are adapted from the Sawyer Quadrangle (RCRNA) and London Southwest Quadrangle (CHA) Daniel Boone National Forest maps. Scale = 1/14,000.

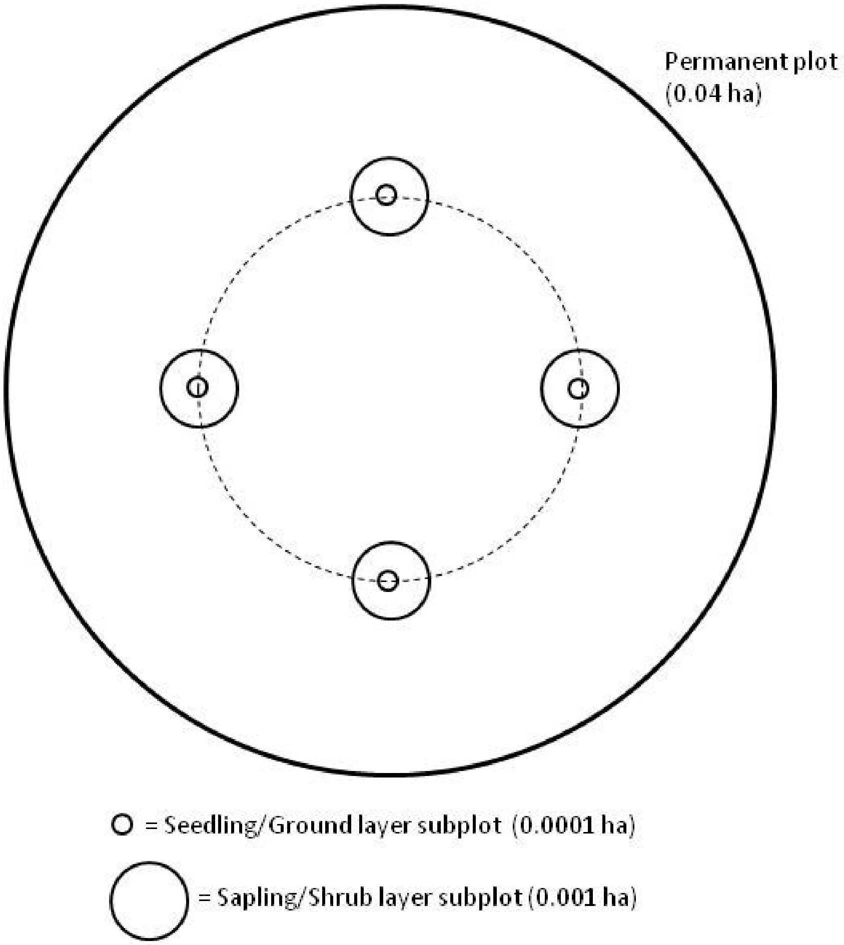

Figure 2. Layout of sample plots for Rock Creek Research Natural Area and Cold Hill Area, Laurel County, KY.

Note: Total area of 4 seedling/ground cover subplots is equal to 1/100 (0.0004 ha) of permanent plot. Total area of 4 sapling/shrub subplots is equal to 1/10 (0.004 ha) of total permanent plot.

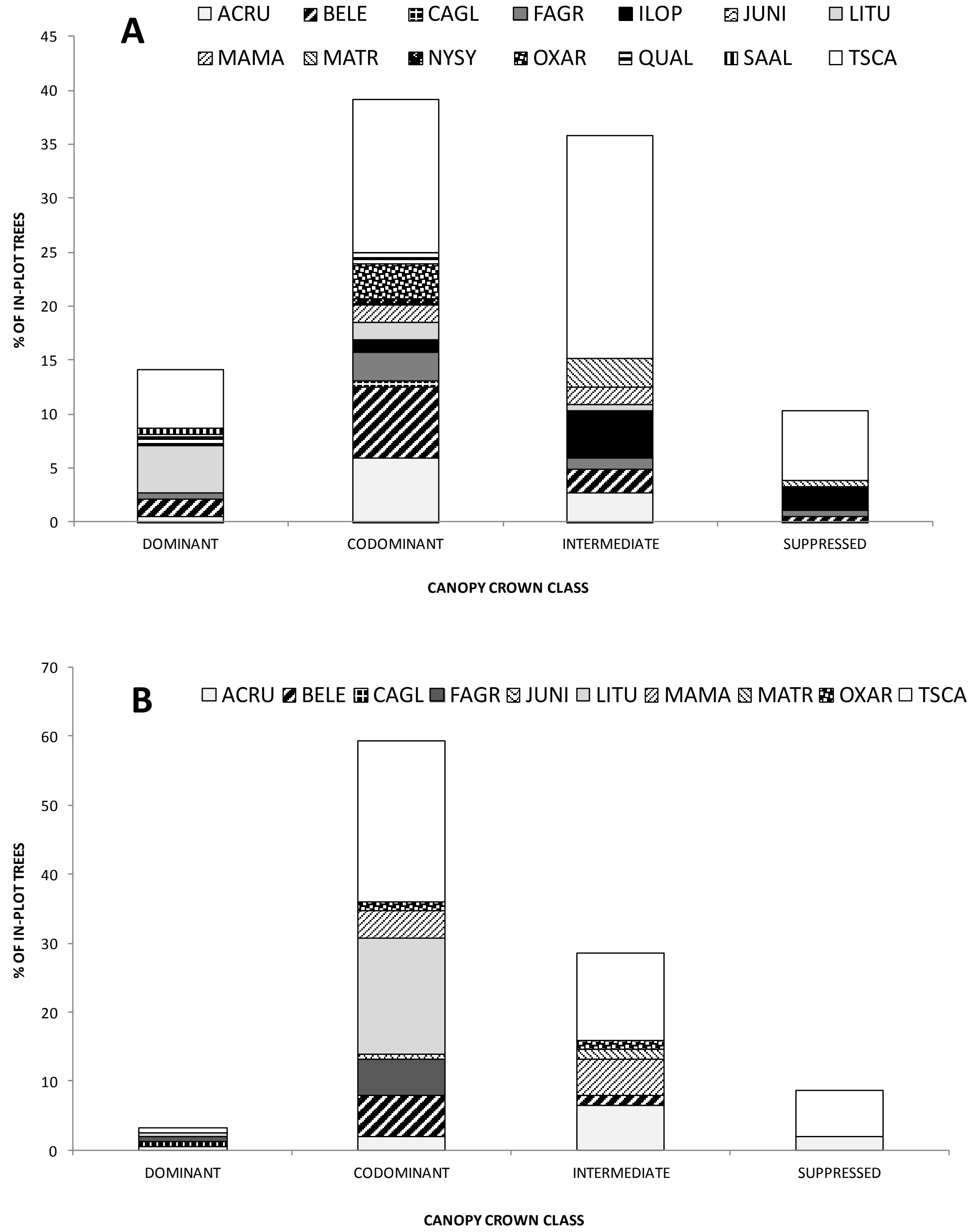

Figure 3. Canopy crown classes A) Rock Creek Research Natural Area and B) Cold Hill Area, Laurel County, KY.

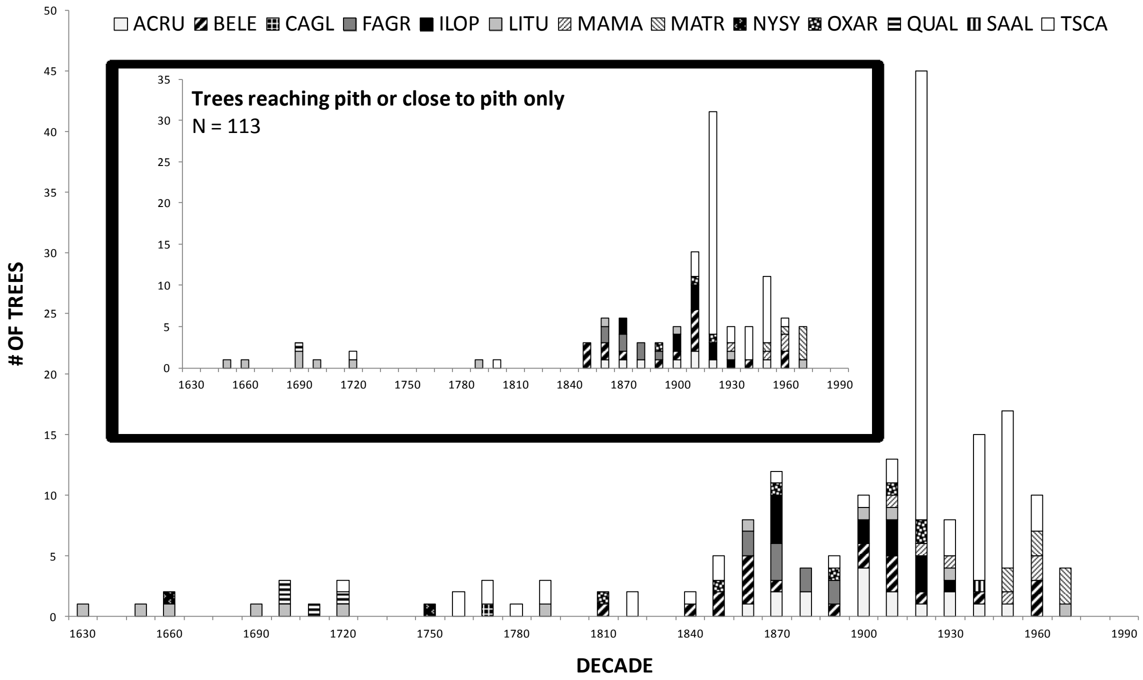

Figure 4. Age class distribution for in-plot trees at Rock Creek Research Natural Area, Laurel County, KY

Note: Large graph includes trees (N = 184) in all pith categories.

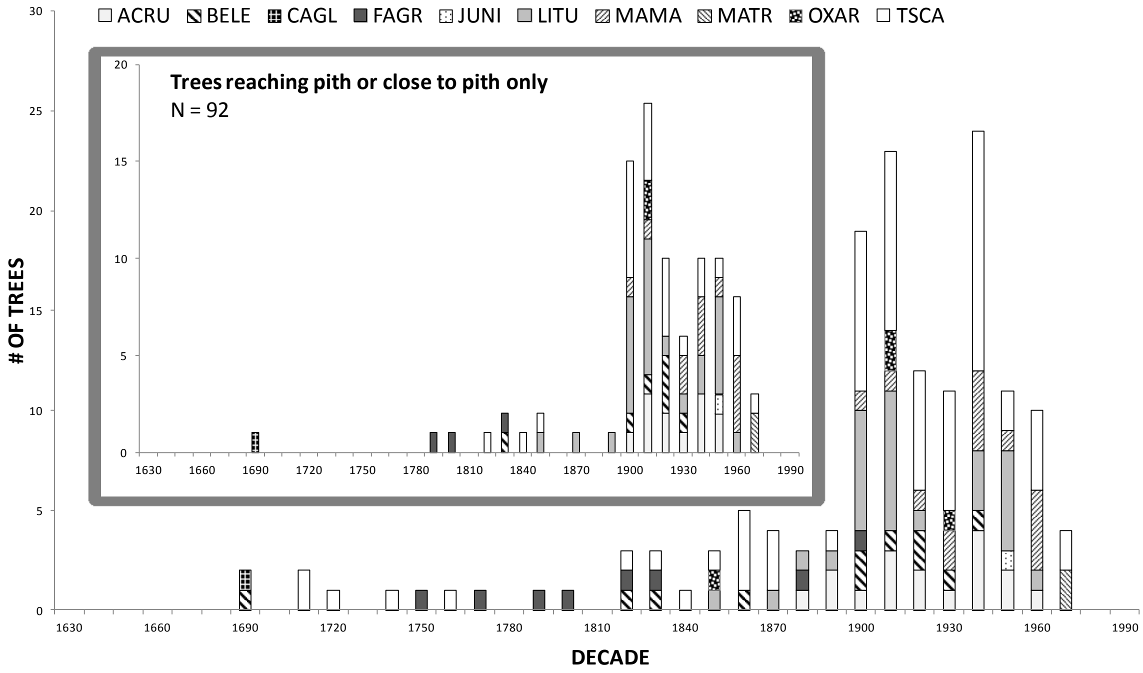

Figure 5. Age class distribution for in-plot trees at Cold Hill Area, Laurel County, KY.

Note: Large graph includes trees (N = 151) in all pith categories.

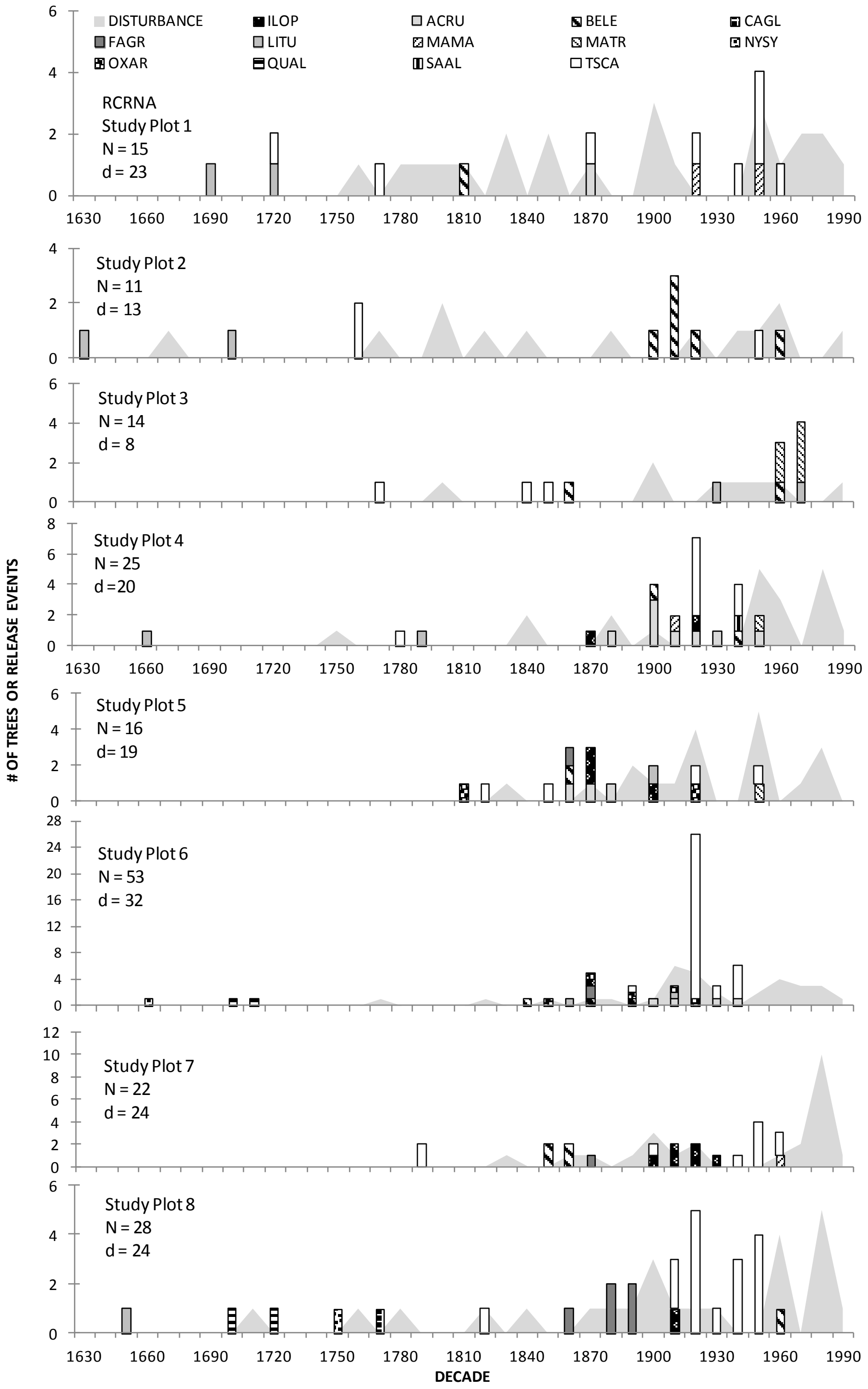

Figure 6. Age class distribution by plot at Rock Creek Research Natural Area, Laurel County, KY.

Note: Includes trees in all pith categories.

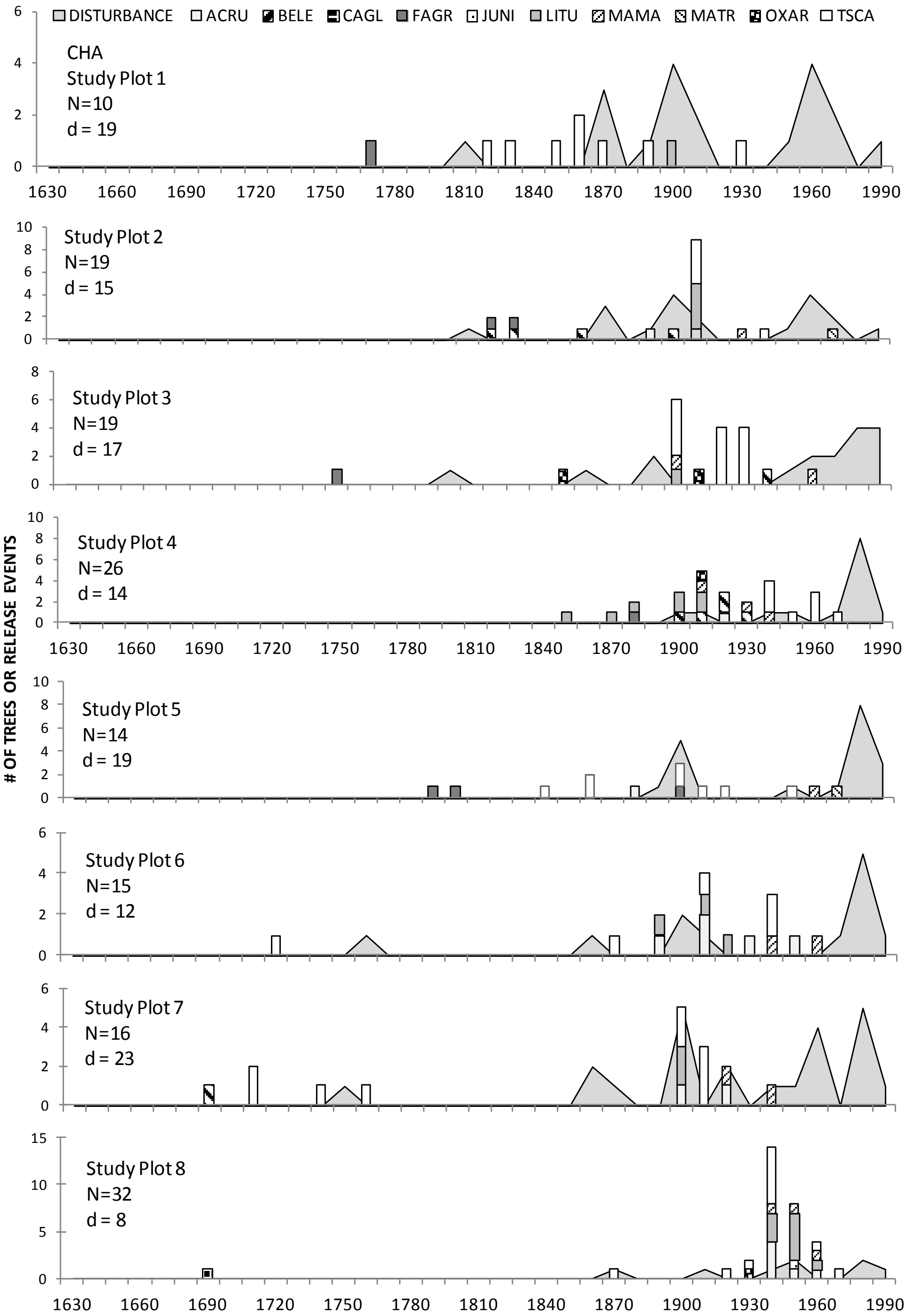

Figure 7. Age class distribution by plot at Cold Hill Area, Laurel County, KY.

Note: Includes trees in all pith categories.

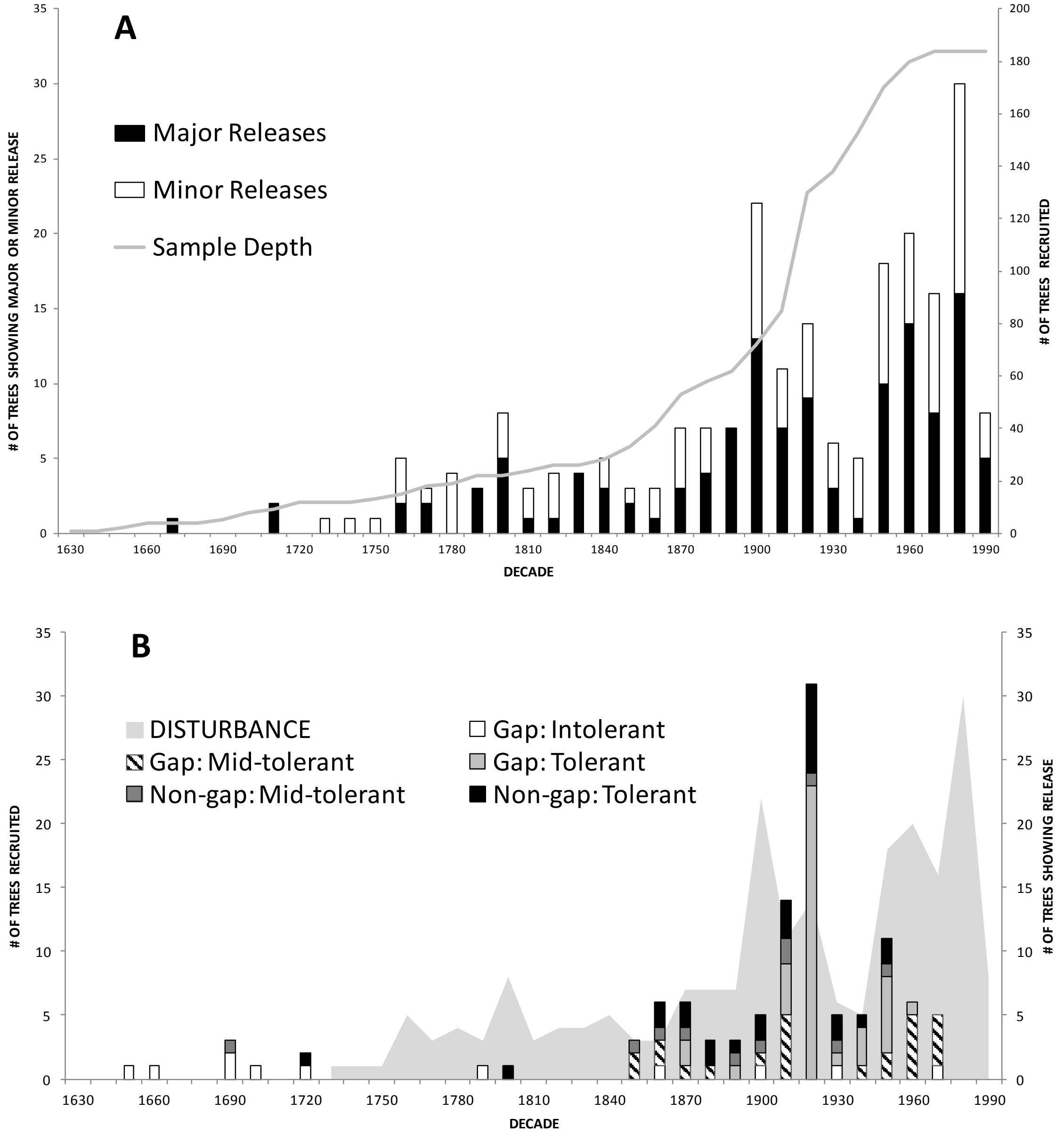

Figure 8. (A) Summary of major (≥ 100%; N = 127) and moderate (≥ 50%; N = 95) growth releases and (B) summary of gap and non-gap recruited trees (N = 113) at Rock Creek Research Natural Area, Laurel County, KY.

Note: (A) Includes # of releases from in-plot and out-of-plot trees (B) Includes only trees reaching pith or close to pith. Species grouped based on canopy gap recruitment and shade tolerance. (Gap: Shade intolerant) = LITU, (Gap: Mid-shade tolerant) = ACRU, BELE, MAMA, MATR, (Gap: Shade tolerant) = FAGR, ILOP, OXAR, TSCA, (Non-gap: Mid-shade tolerant) = ACRU, BELE, MAMA, MATR, QUAL and (Non-gap: Shade tolerant) = FAGR, ILOP, TSCA. Total number of release events (N = 222).

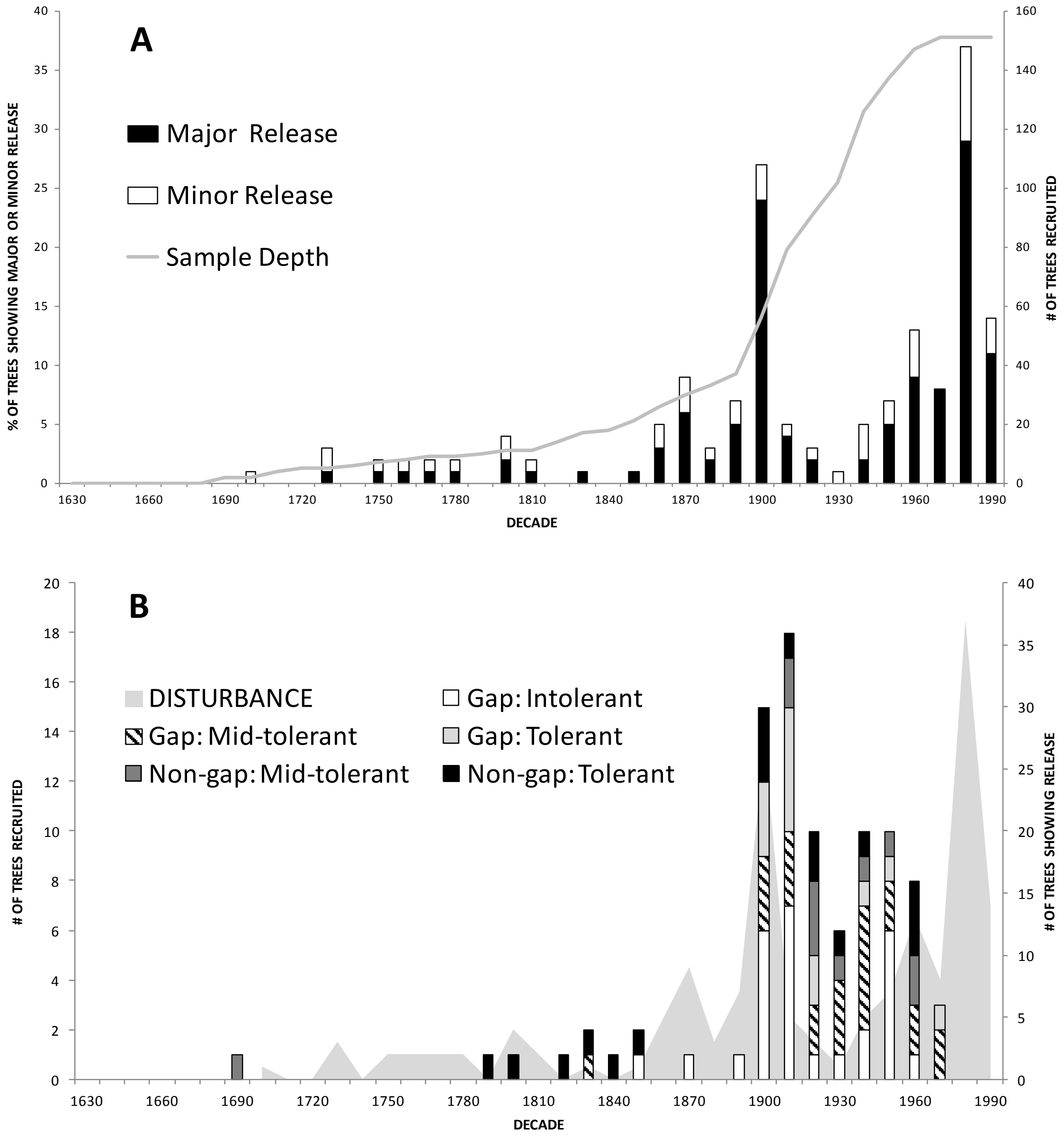

Figure 9. (A) Summary of major (≥ 100%; N = 120) and moderate (≥ 50%; N = 44) growth releases and (B) summary of gap and non-gap recruited trees (N = 92) at Cold Hill Area, Laurel County, KY.

Note: (A) Includes number of releases from in-plot and out-of-plot trees (B) Includes only trees reaching pith or close to pith .Species grouped based on canopy gap recruitment and shade tolerance. (Gap: Shade intolerant) = JUNI, LITU, (Gap: Mid-shade tolerant) = ACRU, BELE, MAMA, MATR, (Gap: Shade tolerant = OXAR, TSCA, (Non-gap: Mid-shade tolerant) = ACRU, BELE, CAGL, MAMA, MATR, and (Non-gap: Shade tolerant) = FAGR, TSCA. Total number of release events (N = 164).

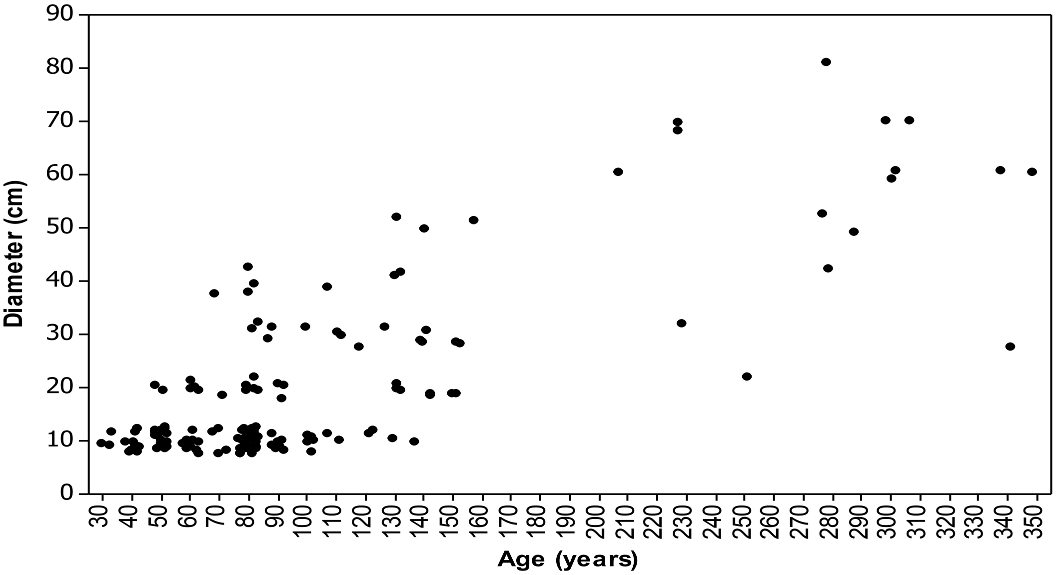

Figure 10. Age-diameter relationship for in-plot trees at Rock Creek Research Natural Area, Laurel County, KY.

Note: Only cores reaching pith, close to pith, or near pith were used.

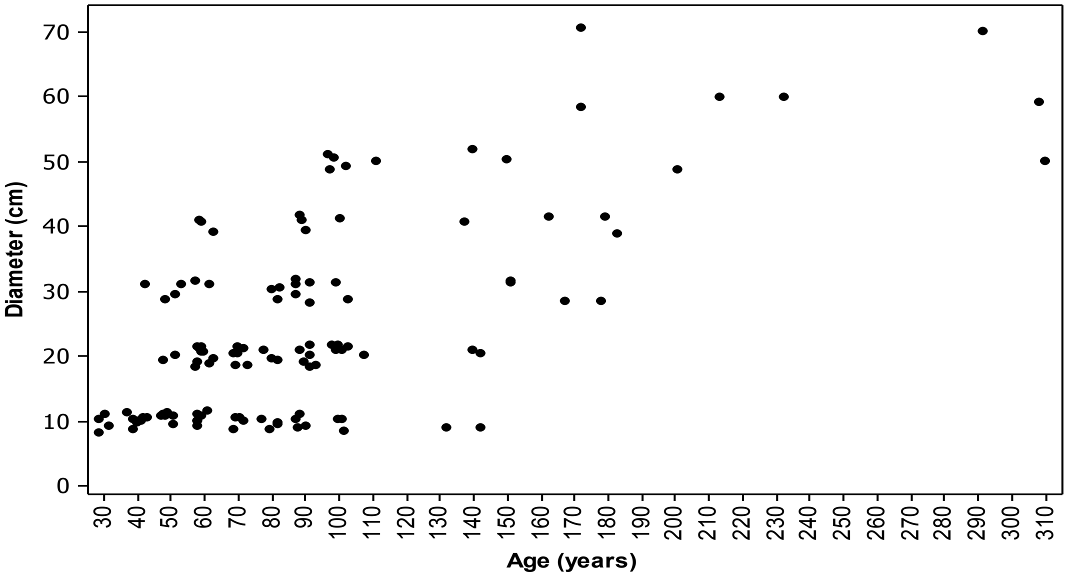

Figure 11. Age-diameter relationship for in-plot trees at Cold Hill Area, Laurel County, KY.

Note: Only cores reaching pith, close to pith, or near pith were used.