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Forest Disturbance History and Stand Dynamics of the Coweeta Basin, Western North Carolina

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DISTURBANCE HISTORY AND STAND DYNAMICS OF THE COWEETA BASIN, WESTERN NORTH CAROLINA

By

Sarah Marie Butler

B.S. Indiana University, 2003

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Forestry)

The Graduate School

The University of Maine

May, 2006

Advisory Committee:

Alan S. White, Professor of Forest Resources, Advisor

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FOREST DISTURBANCE HISTORY AND STAND DYNAMICS OF THE COWEETA BASIN, WESTERN NORTH CAROLINA

By Sarah M. Butler

Thesis Advisor: Dr. Alan S. White

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Master of Science
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Understanding the patterns of past disturbance allows further insight into the composition, structure, and function of today's forests. Disturbance history may also influence how forests will react to future stresses and disturbances. The disturbance histories of the mixed-oak forests at the Coweeta Hydrologic Laboratory (a 2,185 ha long-term research site with some history of harvesting) and the Joyce Kilmer Wilderness (a 6,805 ha old-growth forest with no known harvesting) located in southwestern North Carolina were studied using dendroecology. Dendroecology uses increment cores to determine tree ages and patterns of radial growth. In addition to evaluating the history of these two areas to better understand disturbance dynamic in the southern Appalachians, we compared the radial growth patterns of old-growth trees at Joyce Kilmer to remnant old-growth trees at Coweeta to determine if the trees have similar responses to disturbances throughout time.

We found average decadal disturbance rates (calculated as percent of plot area affected per decade back to the mid-1700s) at Coweeta and Joyce Kilmer (8.7% to 18.3%) were similar to rates common in eastern temperate forests (5% to 20%). The general disturbance history is one of low, but fluctuating, rates, indicating the importance

of small canopy gaps in these forests. Among the typically low rates of disturbance present in all stands are occasional, and noticeably higher, peaks of disturbance.

The dominating peak in disturbance occurred across all stands in the 1920s and 1930s, likely attributable to American chestnut (*Castanea dentata* (Marshall) Borkh.) mortality due to the chestnut blight. Logging created pulses of disturbance in the 1900s, 1910s, and 1920s. Natural disturbances, such as windthrow from hurricanes, drought, insect outbreaks, and ice storms likely contributed to both the peaks in disturbance across the stands (1840s and 1960s) as well as localized pulses unique to single stands.

Disturbance rates and patterns over time were not random with respect to species composition. The more closely related stands were in species composition, the more similar they were in disturbance history. This is likely due to some of the disturbances being specific to one or a few species. However, despite stands similar in species composition also being similar in elevation and slope, disturbance patterns were not influenced by elevation or slope.

The early harvests at Coweeta were most likely selective, favoring some trees over others on the basis of species, size, or form. Thus, the remaining trees from that era were biased, making it unclear as to whether their growth patterns were representative of the pre-harvest disturbance history. Thus, we compared old remnant trees at Coweeta to old-growth trees at Joyce Kilmer, asking if radial growth patterns from old trees surviving harvesting were comparable to those of trees growing in the same time period but free from harvesting. We found similar patterns in radial growth as well as similar disturbance histories, indicating that using remnant trees left behind after harvesting to determine disturbance histories is plausible, at least in these stands.

DEDICATION

To Papa, with love

ACKNOWLEDGEMENTS

I would first and foremost like to thank my advisor, Al White. He is a teacher in the truest sense of the word. His insightful manner, constant support, and patience have made me want to be a better student and scientist. I would also like to thank Kitty Elliott, who was very encouraging and supportive during my field season and studies. She maintained good humor and kindness throughout, even when her life was in my hands, teaching me to drive a standard transmission truck on steep mountain roads. Special thanks are also extended to Bob Seymour who has taught me how to look at a forest in many different lights. Additional thanks go to the U.S. Forest Service, the University of Maine, and the Coweeta LTER for funding throughout this project.

I am grateful to everyone at Coweeta who helped me with field work. Patsy Clinton was immensely helpful, doing preliminary fieldwork for this study and teaching me about the Appalachian forests. Duane Foster's good humor and muscles were critical in the seemingly endless tree coring. I am also eternally thankful to my freakishly strong field assistants Jessie Fly, Jess Riddle, and Grace Livingston, and of all the others who ventured out with me on occasion, including Erin McDonald, Barrett Hoffmann, and Erin Moore, without whom I would still be prying increment borers from huge oak trees.

The supportive circle of graduate students, faculty, and staff at the University has been critical in my success here. In particular, I am extremely grateful to Shawn Fraver for many thorough and thoughtful email exchanges during my analyses, as well as helping me to get started in the lab. Allison Kanoti has helped me enormously with SYSTAT programming, as well as talking to me about dendrochronology or statistics whenever I was confused and other random topics whenever I needed a distraction.

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INTRODUCTION

Past disturbances play an important role in determining the composition, structure, and function of today's forests. They may also influence how forests will react to future stresses and disturbances. Unfortunately, disturbance history often is unknown at the stand level.

The forests now present in the southern Appalachians are the culmination of many factors, including climate, site qualities (slope, aspect, soil), species characteristics (competition, stress tolerance, life history), and disturbances (natural and anthropogenic). The general disturbance history has been one of logging, land clearing for agriculture and homesteads followed by land abandonment, chestnut blight, and various natural disturbances such as wind throw, drought, and ice storms. However, this information is often not site-specific and often does not extend very far back in time, limiting its ecological application.

Various methods can be used to determine the disturbance history of a stand, including paleoecological analysis (Delcourt and Delcourt 1988, Foster et al. 1992, Jacobson et al. 1987), historical land surveys and deeds (Lorimer 1977, Foster 1992, Foster et al. 1992), and dendroecology (Lorimer 1980, Lorimer and Frelich 1989, Nowacki and Abrams 1997). Dendroecology, which uses increment cores to determine tree ages and patterns of radial growth, has high spatial and temporal resolution and can extend back in time to the oldest trees in the stand (Frelich 2002).

Disturbance rates and patterns in various forests types in the Appalachians have been examined, although their focus has been on cove forests (Lorimer 1980), northern hardwood stands (Orwig et al. 2001), or xeric oak-pine forests (Bratton and Meier 1998).

Few studies focus on the disturbance history of the widespread mixed-oak slopes of the southern Appalachian Mountains. Oak species have been prevalent in the southern Appalachians since the climate began to warm after the last glacial maximum and boreal species moved to higher latitudes and elevations (Delcourt and Delcourt 1988, Watts 1975). Mixed-oak forests, once extensive in the Blue Ridge Mountains (Braun 1950), have largely been eliminated in the past century due to changing disturbance regimes (Harrod and White 1999, Abrams et al. 1997, Abrams et al. 1995, Crow 1988). It is unknown if the disturbance history of these forests is similar to other types in the eastern temperate forests, particularly in the southern Appalachians.

The Coweeta Hydrologic Laboratory, located in the southern Appalachian Mountains includes a long-term ecological research forest, referred to hereafter as Coweeta. Coweeta's disturbance history since the early 1900s is fairly well documented, and studies investigating the influence of recent disturbances such as hurricanes, ice storms, and drought on forest structure and composition are abundant (Elliott et al. 2002, Lafon and Speer 2002, Clinton and Baker 2000, Greenberg and McNab 1998, Elliott et al. 1997, Clinton et al. 1993, Douglass and Hoover 1988, Swank and Crossley 1988, Hursh and Haasis 1931). However, the extent to which the disturbance regime prior to 1900 mimics that which has occurred since is unclear.

The early disturbance origins, rates, and patterns occurring at Coweeta before extensive European settlement are not known (Douglass and Hoover 1988). Examining these patterns along temporal scales and environmental and compositional gradients may further elucidate past studies at Coweeta, as well as the current composition and structure.

To construct a disturbance history that extends through centuries in time using dendroecology, old-growth trees are often used. However, due to anthropogenic disturbances in the past century, very few old growth forests remain. Therefore, remnant old-growth trees in second-growth stands are often used (Rentch et al. 2003, Nowacki and Abrams 1997). It is unclear whether these trees contain the same historical information as would have been found in the trees that were cut. One way to address this question is to compare the disturbance histories of second-growth stands with those of comparable stands in old-growth forests. We compared residual old trees left behind after extensive logging occurred at Coweeta in the early 1900s to stands at Joyce Kilmer Wilderness, one of the few remaining old-growth forests in the southern Appalachians (Newell et al. 1997).

The general purpose of this study was to characterize the stand dynamics and disturbance history of Coweeta. The specific objectives were to: a) determine the disturbance history in seven stands at Coweeta, b) determine if stands similar in composition or topography are also similar in disturbance history (e.g. frequency, intensity and origin), and c) determine the disturbance history of two old-growth stands in Joyce Kilmer Wilderness and compare to stands in Coweeta.

METHODS

Study Area Description and History of Coweeta

The Coweeta Hydrologic Laboratory, administered by the U.S. Forest Service, is a 2,185-ha long-term ecological research forest located in Otto, North Carolina (Figure 1). Coweeta is positioned in the Nantahala National Forest in the Blue Ridge Physiographic Province at 35°03'N and 83°25'W (Swank and Crossley 1988). It is composed of two adjacent basins, the Coweeta Basin and Dryman's Fork Basin, with elevation ranging from 675 to 1592 m. Mean annual temperature is 12.6 °C and ranges from an average of 4.9°C in the winter to 21.6°C in the summer. Annual precipitation averages 2000 mm and is evenly distributed throughout the year (Elliott et al. 1999).

The four main forest types at Coweeta are cove forests, oak-chestnut (mixed-oak), oak-pine, and northern hardwood (Swank and Crossley 1988). Mixed-oak forests cover the majority of the slopes and are the focus of this study. Within this forest type, composition varies with topography. Chestnut oak (*Quercus prinus* L.) is most abundant at mid-slope and slopes with mesic aspects, whereas scarlet oak (*Quercus coccinea* Muenchh.) occurs on drier slopes and ridges. Northern red oak (*Quercus rubra* L.) occurs most often at higher elevations (>1070 m), while white oak (*Quercus alba* L.) and black oak (*Quercus velutina* Lam.) are more frequent at lower elevations (< 820 m). Red maple (*Acer rubrum* L.) and hickories (*Carya* spp.) are also common species on the slopes. American chestnut (*Castanea dentata* (Marshall) Borkh.) was previously a dominant species until chestnut blight (*Endothia parasitica* (Murr.) P.) eliminated the species from the canopy (Swank and Crossley 1988).

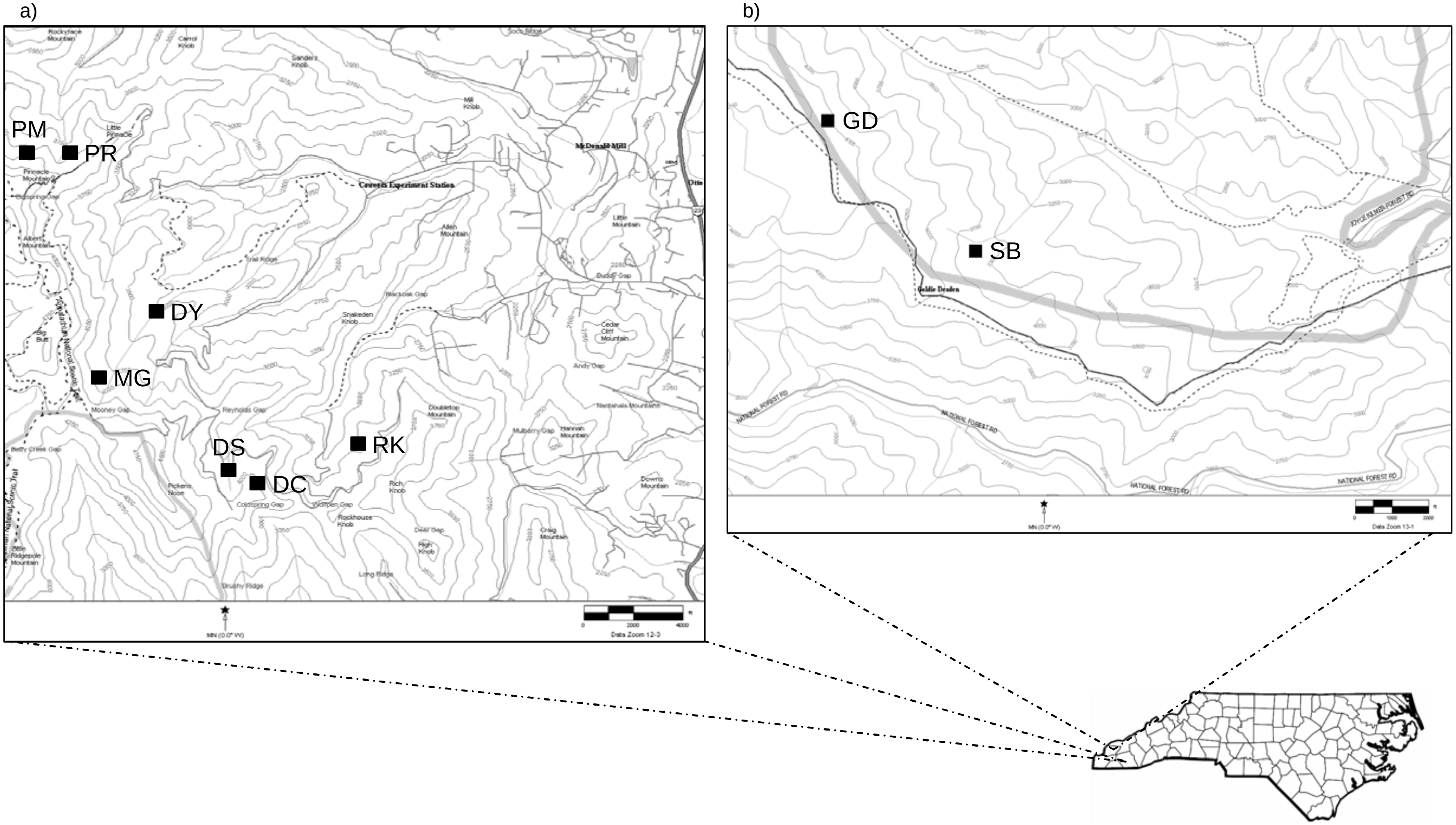


Figure 1. Maps of a) Coweeta and b) Joyce Kilmer in western North Carolina. Black boxes denote approximate stand locations. Stand abbreviations are located in Table A. 1.

The following description of the history of Coweeta is based on Douglass and Hoover (1988). The history of the basin from 1918 (when the land was bought by the U.S. Forest Service) to the present is documented to some extent, with major disturbances known as well as any experimental research conducted in the various watersheds. Prior to 1918, there are only a few natural and anthropogenic disturbances recorded (Table 1).

Table 1. Disturbances documented for the southern Appalachians prior to and after Coweeta was established as a long-term experimental field site (1933).

Date	Disturbance	Sources
1835	Hurricane	Douglass and Hoover 1988
1878-1881	Elm spanworm outbreak	Dodge 1882; Fedde 1964
1915	Glaze storm	Rhoades 1918
1920-1930	Chestnut blight	Nelson 1955
1920s	Logging	Douglass and Hoover 1988
1925	Drought	Hursh and Haasis 1931
1925	Early spring frosts	Beal 1927
1932	Glaze storm	Abell 1934
1950s	Drought	Tainter et al. 1990
1958-1963	Elm spanworm outbreak	Ciesla 1963; Gzenda et al. 1964
1985-1988	Drought	Clinton et al. 1993; Elliott and Swank 1994
1995	Hurricane Opal	Clinton and Baker 2000; Elliott et al. 2002

The Cherokee Indian Nation occupied the land until 1837. They were known to burn the woods to control understory vegetation. In 1837, the Cherokee in the area moved off the land, and Europeans began to settle Coweeta, using the land for agriculture and grazing livestock. Coweeta was divided into holdings ranging from 10 to 256 ha. Thirty-two land grants were issued in Coweeta, but only five families actually lived there. Other families lived elsewhere and cultivated land at Coweeta, and still others just held the land. Many of the slopes were too steep to farm, so cultivation was primarily restricted to flat bottomlands. Because of the steep terrain, livestock grazing was a more important occupation.

Coweeta was surveyed for purchase by the Nantahala Company in 1901, and the land and its uses were described. It is estimated that fewer than 40 ha of land were in cultivation at this time, most of which was located in the lowlands due to rocky mountainous slopes inadequate for farming. Grazing was more prevalent than farming at Coweeta. Annual estimates of grazing activity include 1500 sheep, 3500 hogs, 600 cattle, 30 horses, and 50 mules. Mining also occurred at Coweeta, but the profits were too low to sustain the operations. Boundary lines between properties were poorly drawn, resulting in over 507 ha of unclaimed land.

In 1902, the Nantahala Company bought most of the land for $1.00 an acre ($2.50/ha), and all previous landowners were moved from Coweeta. They then sold it to W.M. Ritter Lumber Company in 1906, which conducted three logging operations. Parts of Coweeta were also owned by individuals who conducted separate logging operations. Trees were harvested using horse and oxen skidding and milled using a sawmill located at the bottom of the Coweeta Basin. The W.M. Ritter Lumber Company began planning extensive logging operations across Coweeta, when the Forest Service offered to buy the land in 1918.

Because of W.M. Ritter's pending logging operations, the Forest Service bought the land with rights to trees smaller than 38.1 cm at the stump. Trees greater than 38.1 cm in diameter were logged from 1919 until 1923. During this time, there were two mills in the Basin and 40 men were logging with horses. Harvesting in Coweeta progressed from the north to the south (Shope Fork followed by Ball Creek) (Figure 1); however, little spatially explicit information about these harvests exists. By 1923, when the Forest Service took over Coweeta, 8 million board feet of timber had been removed. No management (except fire suppression) occurred until 1933, when Coweeta was designated to serve as a long-term research site by the United States Forest Service. Since 1923, only experimental and natural disturbances have affected the basin (except fire suppression).

Study Area Description and History of Joyce Kilmer

Joyce Kilmer Wilderness is a 6805-ha preserve located in the Unicoi Mountains of Graham County, NC and Monroe County, TN (Figure 1). Like Coweeta, the Joyce Kilmer Wilderness is within the Blue Ridge Physiographic Province, spanning the Nantahala and Cherokee National Forests (Newell et al. 1997). There are four watersheds in the Wilderness area (Slickrock Creek, Little Santeetlah Creek, Deep Creek and Horse Cove), all sharing a high-elevation central ridge (>1455 m). Old-growth forests are located in the Little Santeetlah watershed of the wilderness area. The lowest elevation lies in the Slickrock Creek valley (333 m).

Weather stations around the wilderness area are at low elevations and do not provide accurate measurements of Joyce Kilmer's precipitation and temperature. Climate data from similar sites in the Great Smoky Mountains (Shanks 1954) can be used for inference. Average annual precipitation in the high and low elevation sites are 2200 mm and 1760 mm, respectively (Newell et al. 1997). Low elevation sites experience higher summer temperatures (25 to 30º C) than high elevation sites (18° C), with an average decrease of 1.24° C for every 305 m of elevation gain (Newell et al. 1997). The forest communities in the Joyce Kilmer forests include oak-chestnut, cove hardwoods, oak-pine, northern hardwoods, and grassy and heath balds (Newell et al. 1997).

Outside the old-growth forests, past disturbances in the Joyce Kilmer Wilderness area include human settlement, cultivation, logging, fire, storms, and the chestnut blight (Newell et al. 1997). Human settlement occurred mainly in the low and mid-elevation coves, particularly in the Slickrock valley from the mid-1800s to 1935. Spatially specific settlement, cultivation, and grazing information are unknown.

In the 1920s and 1930s, low and mid elevation logging occurred in Slickrock Creek, Deep Creek and Horse Cove valleys; however, Little Santeetlah watershed remained unharvested (Newell et al. 1997). Sites above 1030 m in Slickrock were not logged. Fires also occurred in the Slickrock valley during this time; however, spatial and temporal details are unknown. Little detail is known about historical wind and glaze storms in the Joyce Kilmer Wilderness area. A documented tornado occurred in the early 1900s in Deep Creek watershed, causing windthrow and blowdown. Chestnut blight occurred during this time period as well, with the infestation peaking in 1935, causing changes in species composition and stand dynamics. Currently, anthropogenic disturbances are limited to areas with popular trails, where hiking and camping disturb the understory vegetation (Newell et al. 1997).

Field Sampling and Core Preparation

Seven stands at Coweeta were chosen to represent the moisture gradient from mesic to dry within the mixed-oak type (Figure 1). Stand names were based on nearness to a physical description to Coweeta or Joyce Kilmer, and geographic landmark and stand codes are located in Table A. 1. Stands were selected on the basis of several criteria, including species composition, topographic position, history, and preliminary dating of old trees. Stand history and stand characteristics were evaluated to determine if there had been significant human disturbances in recent history, such as logging, grazing or experimental manipulation, that would make the site unsuitable. Aging of a few dominant trees in each stand ensured that at least some of the trees were old, not just large, and pre-dated logging.

Two additional stands were selected in the Joyce Kilmer Little Santeetlah Creek watershed. They were chosen because of their similarities to the stands in Coweeta. The stands were located in the high elevation mixed hardwood forests or the montane oak forest vegetation classes as described by Newell et al. (1997), with higher slope positions than the rich cove forests of the Little Santeetlah valley (Newell et al. 1997).

Stand composition and structure were sampled with a prism (2.0 BAF, metric) at five to thirteen points in each stand. Points were spaced along transects in each stand at variable distance intervals due to differences in stand shape and size. To avoid counting a tree more than once, the minimum distance between points was at least two times the limiting distance as determined for a typically large tree in each stand.

Species, diameter at breast height (DBH, 1.37 m), and crown class (dominant, codominant, intermediate and overtopped) were recorded for each tree greater than 10 cm DBH in the prism sample. For saplings smaller than 10 cm DBH and greater than 1.37 m high, species and DBH were recorded in a 0.01 ha plots centered on each sample point. In each stand at five randomly chosen points, 5-mm diameter cores were extracted from all trees tallied with the prism. Cores were taken to the pith at one meter from the ground parallel to topographic contours to reduce effects of tension wood. Coring at that height, as compare to breast height, reduces the difficulty of hitting the pith. Approximately 80 trees per stand were cored. Species composition data were examined using all trees sampled (n = 5 – 13 sample points), and in only the sample points (n = 5) where increment cores were taken to ensure that cored plots were representative of the stand. Cores were stored in straws until transported to the lab. Slope, aspect and elevation were recorded for each stand.

Crown dimensions (used later to predict crown projection areas (CPA)) were determined for the five most abundant species sampled: northern red oak, white oak, chestnut oak, red maple, and black birch. Samples were taken in four of the sample stands that spanned the range of topographic gradients. Trees were randomly sampled over a range of diameters (from 10 cm to 120 cm DBH). For each tree sampled, the horizontal distance from the center of the bole to the drip line of the longest radii was measured. Three more radii were subsequently measured at 90 degree intervals from the first, extending from the center of the bole to the drip lines.

In the lab, cores were air dried, mounted, and sanded using progressively finer sandpaper in preparation for analysis (Stokes and Smiley 1996). Once prepared, cores were examined and ring widths were measured to the nearest 0.01 mm using a dissecting microscope, VELMEX sliding stage (VELMEX Inc., Bloomfield, NY), and MeasureJ2X© software (Holderness, NH). Cores were visually cross-dated within species and stands using marker years and then checked with the computer cross-dating program COFECHA (Holmes 1983). For trees where the core did not reach the pith, the center date was estimated using up to 20 concentric rings, beyond which a center date was not identified (Applequist 1958). “Age” refers to age at coring height (1 m), not total age. This was viewed as a relatively minor difference given a) the greater ease and accuracy of cores taken above the swelling at the base of many tree stems, b) that all analyses were done at the decadal level (for example, age distributions were number of stems each decade), and c) that radial growth rates, not age, were the primary source of information about disturbances in this study.

Disturbance Detection

Typically, a disturbance is indicated by an abrupt, large, and sustained increase in radial growth (called a release) or by new stem establishment in a gap (called gap origin) (Lorimer and Frelich 1989). Releases describe a disturbance event in which part of the canopy of the stand is killed, freeing up space or resources for another tree to increase in canopy area and radial growth (Frelich 2002). Various criteria for detecting releases have been used over a variety of forest types and species (see reviews: Fraver and White 2005, Rubino and McCarthy 2004, Chokkalingam 1998). The percent increase method, a commonly used method of release detection, was used in this study. The equation for this method was formalized by Nowacki and Abrams (1997):

$$\%\ GC = [(M_2 - M_1)/M_1] \times 100$$

where %GC is the percent growth change for any given year within a series, M_1 is the average radial growth during the selected window of time prior to a given year including the given year, and M_2 is the average radial growth during the selected window of time after a given year.

The window of time used for this study was ten years. In various silvicultural thinning studies, releases in oaks were shown to last at least ten years and up to 20 years (Cutter et al. 1991, Minckler 1957, Minckler 1967, Shifley 2004). Using a ten-year window of time is sufficient to detect these releases and is appropriate for oak-dominated forests (Nowacki and Abrams 1997) Also, the length of time is long enough to filter out climatic variation in the ring widths, thus reducing the chances that weather patterns would be mistaken for disturbance events. Weather-related variations in growth in eastern forests rarely extend longer than ten years (Lorimer and Gough 1988). A ten-year window of time is probably the most common criteria used in dendroecological studies of disturbance dynamics (Fraver and White 2005).

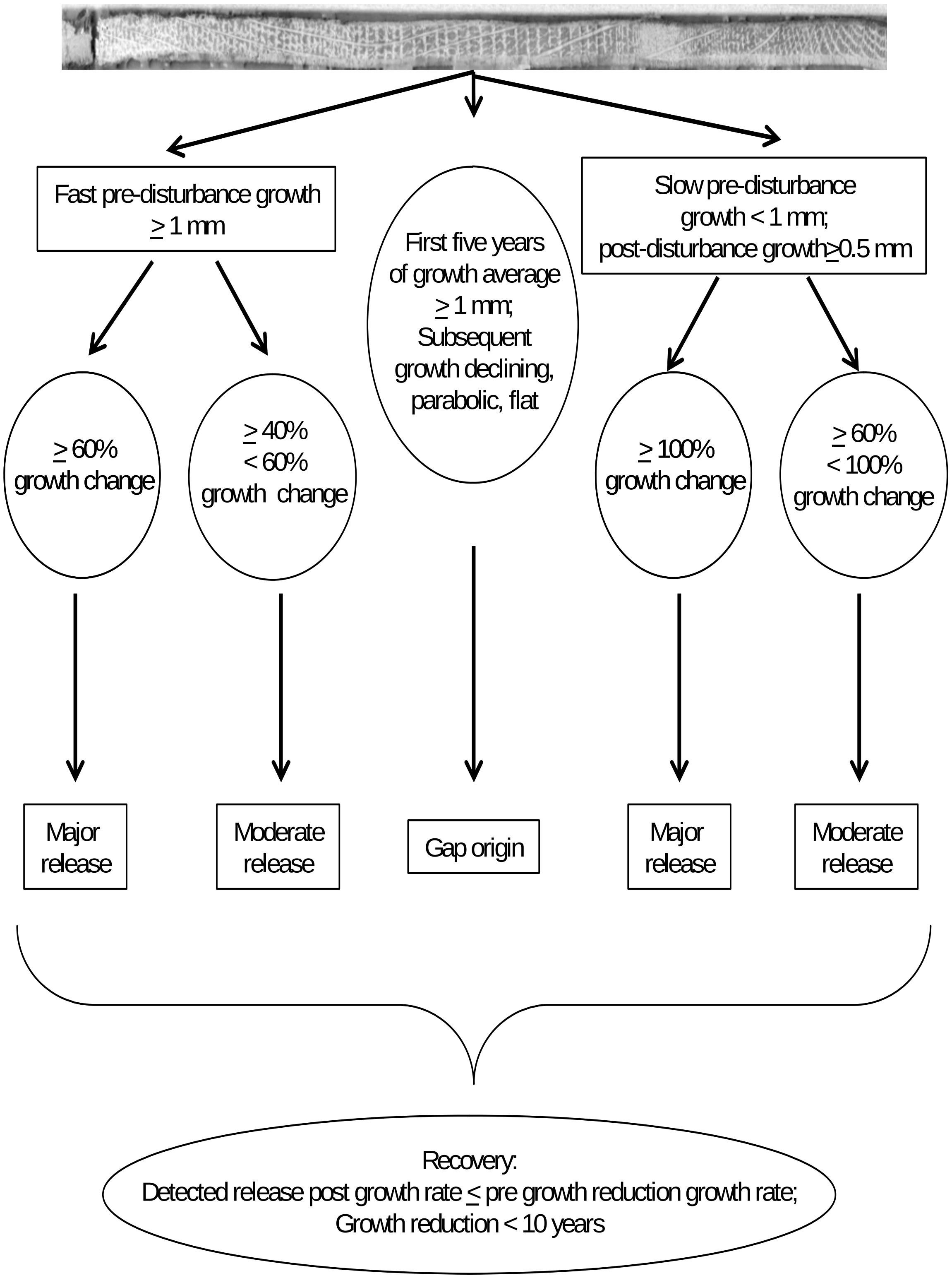
In addition to selecting a window of time in which to analyze growth change, threshold values of increased radial growth must be defined, above which releases are identified. These values range widely in the literature and vary for different species and forest types (see reviews: Fraver and White 2005, Rubino and McCarthy 2004, Chokkalingam 1998). Often, choosing only one threshold value to evaluate the entire length of each series can lead to erroneous conclusions about the occurrence of disturbances, especially at very low or very high, rates of growth (Fraver and White 2005).

To determine the best release criteria for this study, various percent increase values were applied to the trees in one stand at Coweeta. The chosen stand (DC) contains the most abundant species (red maple, black birch (*Betula lenta* L.), hickories, white oak, northern red oak, and chestnut oak) found throughout the sample stands at Coweeta. A graph of ring widths and 10-year running means was created for each tree to examine patterns of radial growth using SYSTAT 11.0 (SYSTAT Software Inc. Richmond, CA). When more liberal criteria were applied, some releases were identified that subjectively seemed like annual variation in growth (false positive releases). When more conservative criteria were applied, some abrupt increases in growth that subjectively seemed like true releases were not detected (false negative releases). Inspection of each release detected by the various thresholds, along with guidance from the literature on the appearance of true releases (Lorimer and Frelich 1989, Frelich 2002, Fraver 2004), helped to determine which criteria limited the false positive and false negative releases the most. This in turn helped us choose threshold values for this study. Although the criteria used to detect releases in this study were subjectively chosen, as all such criteria are, they follow criteria used in other forest types and other species (Groven et al. 2002, Storaunet et al. 2000, Dahir and Lorimer 1996, Lorimer and Frelich 1989, Glitzenstein et al. 1986, Lorimer 1980).

The following criteria for release detection adjusts for slow and fast growing periods in each tree's life, as well as differentiating between major and moderate releases (Figure 2). Major releases result from disturbances large enough to open the canopy, causing a significant increase in the growth of an overstory tree or allowing an understory tree, previously suppressed, to enter into the canopy. A moderate disturbance can occur from a variety of situations. It can be a thinning event, in which some overstory trees are affected, allowing lateral expansion of neighboring trees (Lorimer and Frelich 1989). A moderate release could also be the result of a tree's inability to fully take advantage of a post-disturbance increase in resource availability.

For slow growing trees (< 1 mm), a major release was defined as at least a 100% growth increase, with a post-release growth rate greater than 0.5 mm. Setting the post-release growth rate threshold at 0.5 mm reduces the inclusion of false releases. For

Figure 2. Diagram of release criteria. Pre-disturbance growth rates are based of the ten year window of time prior to the event.



example, a tree growing at 0.15 mm/year would only need to increase its growth to 0.3 mm/year to achieve a 100% increase in growth, yet the 0.3 mm/yr is unlikely to be the rate one would expect of a released tree growing in more open conditions. Thus, combining a percent increase threshold with an absolute minimum post-disturbance growth rate reduces the number of false positive errors (Fraver and White 2005). At the other end of the spectrum, when a tree is growing at moderate to high rates (≥1 mm/yr), a 100% increase in growth can be impossible for the tree to achieve, because the tree is already growing well and thus is less restricted by competition from neighboring trees. Therefore, a major release was counted when the tree had at least a 60% increase in growth and when the pre-disturbance growth rate was ≥ 1 mm/yr, thus reducing the number of false negative errors.

When a tree was growing slowly (<1 mm), a moderate release was recorded when the tree showed a 60%-100% increase in growth, with its post-release growth rate at least 0.5 mm. For a faster growing tree (≥1 mm), a moderate release was recorded when the tree had a 40%-60% increase in growth. In all cases, the previous ten-year window was compared to the subsequent ten-year window for any given year. Using these criteria, the first and last nine years of each chronology can not be analyzed due to the calculation of the growth change for each tree.

In addition to meeting minimum growth thresholds, releases also had to be sustained. To qualify as a sustained release in this research, seven of the ten years following the release must have had a higher growth rate than prior to the release (Fraver 2004). Finally, determining if the release was abrupt or gradual was done by visually inspecting each graphed chronology (Frelich 2002). All release events occurring in a single tree were included in determining disturbance history. Minckler (1967) studied release of suppressed white oak trees in upland forests in Illinois, and found that suppressed trees often did not maintain overstory positions after initial release, lending evidence of the need for multiple releases to achieve a dominant canopy position.

After releases were tallied for each tree, gap origin trees were identified. Trees where the pith was hit or was estimated to be 10 years or fewer from the last ring of the core, we examined the initial growth rate to determine if the tree was of gap origin. A tree was considered of gap origin when it had an average growth rate of at least 1 mm for the first five years measured. Because species-specific growth rates were not used to determine gap origin, the pattern of each tree ring series was visually inspected. In addition to the growth rate criteria, a tree had to have a typical pattern of growth displayed by gap origin trees, as described in the literature (Frelich 2002, Lorimer and Frelich 1989). These included declining or constant growth patterns, as well as some complex and ambiguous growth patterns. Trees with parabolic growth patterns were considered to be of gap origin if their peak growth rate was reached within 25 years of origin with no subsequent releases (Lorimer and Frelich 1989). Gap origin trees are considered a major disturbance indicator because the canopy was opened enough to allow development of a new cohort of trees.

Once the release criteria were applied to all cores, a graph of each core was examined to validate the releases (Fraver and White 2005). Graphs were also visually inspected to distinguish recovery events from true releases. A recovery event would occur, for example, if the tree's growth rate temporarily decreased due to insect defoliation or ice storm damage, and then returned to its former growth rate. These events are sometimes mathematically counted as releases; however, no growing space is freed up (Fraver and White 2005). Recovery events are still disturbances to the ecosystem and were counted as such. If the growth rate after the release was approximately the same as it was prior to the release, indicating the tree's crown did not expand, the disturbance was counted as a recovery. In some cases, the period of reduction is long enough to make it questionable if the disturbance is a release or a recovery. Recovery from insect defoliations and ice storms take between five and ten years (Lafon and Speer 2002, Oak 2002). If more than ten years lapsed between the onset of the decrease in growth and the subsequent increase in growth, then the disturbance was considered a release. Species-specific growth reduction events were examined separately using standardized growth chronologies (see below methods for growth reduction criteria). Once all disturbances were identified, stand-level temporal descriptions of the events ("disturbance chronologies") were created.

Disturbance Chronologies

Disturbance chronologies describe the percentage of the stand canopy area affected by disturbance in each decade. Area-based disturbance chronologies calculate the portion of the canopy area that dies and regenerates each decade. Each detected release is weighted by its current crown projection area (see below CPA calculation methods) (Lorimer and Frelich 1989).

For each decade, CPA released was summed across trees and divided by the total CPA alive in that decade, assuming that trees alive in any given decade are representative of the population present at that time (Fraver 2004). This proportion was converted to a percentage and is hereafter referred to as the decadal disturbance rate. Further back in time, all chronologies become less reliable as the known amount of crown area alive in that decade decreases. Therefore, the disturbance chronologies were cut off when the sample size became unreliable (<10 trees) (Fraver 2004). Disturbance chronologies were created for each stand using all dominant, co-dominant, and intermediate trees.

Chronologies were divided into three groups: total disturbances (gap origin trees, major releases, moderate releases, and recovery events), major disturbances (gap origin trees and major releases) and minor disturbances (moderate releases and recovery events) for stands at Coweeta and Joyce Kilmer. Peaks in disturbance were identified when the decadal disturbance rate was 5% higher than the average decadal disturbance rate for each stand. This value was arbitrarily chosen; however, many of the decades that qualified as peak decades were well above 5% higher than the average decadal disturbance rates.

Disturbance chronologies were also expressed, by stand, as the percent crown area of white oak, northern red oak, chestnut oak, and 'other' species disturbed in each decade. This was done using the methods described above for each stand. Expressing the chronologies in this way allows the patterns of disturbance in each stand to be examined on the basis of species contributions to the peaks.

Crown Projection Areas

CPA was calculated using the quarter-ellipse method (Lorimer and Frelich 1989). Linear regression models were created to predict the crown projection area (CPA) of the five most abundant species using DBH (northern red oak, white oak, chestnut oak, red maple, and black birch). Since CPA was not collected for all species sampled, published equations developed for predicting the CPA for stand-grown trees were used for the remaining species (Bechtold 2003). Regression equations relating CPA to DBH violated the assumption of constant variance, with the residual variance increasing with increasing diameter. The data were both log and log-log transformed to meet the assumptions of the model (Quinn and Keough 2002). Published CPA equations for these species show both linear and quadratic relationships; therefore, both types of models were developed and compared to determine the best CPA model. Akaike's information criterion (AIC), a statistical model-selection measure, and adjusted R^2 values were used to determine the best fit model (Table 2) (Burnham and Anderson 1998).

Since the sample size for each species was small (<40), second order AIC equations (AIC_c) were used, adjusting for any bias introduced when the sample size is small relative to the number of parameters (Burnham and Anderson 1998). AIC_c compares models based on residual sum of squares values and the number of parameters (K) to determine which one is closest to the true model of the data. Comparisons were made using the AIC_c values, with the smallest value representing the closest approximation of the true model. The AIC_c differences (Δ_i) were used to interpret the AIC_c values, with the largest Δ_i value being the least likely model for the data. In general, if a Δ_i value is ≤ 2, then it is a plausible model for the data. The Δ_i values between 4 and 7 offer little support for a particular model being the best one for the data (Burnham and Anderson 1998).

In cases where AIC_c could not rank the models with certainty, adjusted R^2 values were used to identify the best model. When adjusted R^2 values were not greatly different

Table 2. Crown projection area equations, adjusted R^2 values, and Akaike's information criterion (AIC) (Burnham and Anderson 1998) for five sampled species. Starred equations are significant ($P < 0.05$). Boldface fonts are the equations used to predict CPA for these species. Snowdon's (1990) ratio estimator was used to correct predicted values.

Species	N	Model	Adjusted R^2	AIC_c	ΔAICc	w	Snowdon's log-bias correction
Red maple	13	**ln CPA = 2.612 + 0.032 DBH***	**0.779**	**6.96**	**0.02**	**0.45**	**1.03**
		ln CPA = 2.142 + 0.055 DBH - 0.000 DBH^2	0.772	11.27	4.33	0.05	
		ln CPA = -1.012 + 1.359 ln DBH	0.791	6.94	0.00	0.45	
		ln CPA = 1.533 - 0.045 ln DBH + 0.191 ln DBH^2	0.773	11.27	4.33	0.05	
Black Birch	13	ln CPA = 1.399 + 0.050 DBH*	0.733	7.58	0.23	0.42	
		ln CPA = -0.544 + 0.143 DBH - 0.001 DBH^2	0.836	11.58	4.23	0.06	
		ln CPA = -4.866 + 2.299 ln DBH*	**0.818**	**7.35**	**0.00**	**0.47**	**1.04**
		ln CPA = -5.228 + 2.129 ln DBH + 0.128 ln DBH^2	0.82	11.63	4.28	0.06	
White oak	17	ln CPA = 2.369 + 0.033 DBH*	0.729	6.26	0.18	0.40	
		ln CPA = 0.644 + 0.111 DBH - 0.001 DBH^2*	0.812	9.54	3.45	0.08	
		ln CPA = -2.313 + 1.667 ln DBH*	**0.815**	**6.08**	**0.00**	**0.44**	**1.02**
		ln CPA = -16.207 + 9.124 ln DBH - 0.985 ln DBH^2	0.846	9.47	3.39	0.08	
Chestnut oak	19	**ln CPA = 1.943 + 0.040 DBH***	**0.849**	**5.70**	**0.00**	**0.42**	**1.04**
		ln CPA = 0.011 + 0.033 DBH + 0.000 DBH^2	0.844	8.94	3.25	0.08	
		ln CPA = -3.014 + 1.823 ln DBH*	0.847	5.70	0.01	0.42	
		ln CPA = 3.033 - 1.460 ln DBH + 0.439 ln DBH^2	0.846	8.94	3.24	0.08	
Red oak	23	ln CPA = 2.536 + 0.028 DBH*	0.755	5.42	0.26	0.38	
		ln CPA = 1.263 + 0.074 DBH - 0.000 DBH^2*	0.845	8.15	2.99	0.10	
		ln CPA = -2.402 + 1.660 ln DBH*	**0.863**	**5.16**	**0.00**	**0.43**	**1.03**
		ln CPA = -8.126 + 4.644 DBH - .382 ln DBH^2	0.871	8.08	2.92	0.10	

from each other, the model with fewest transformations and least number of parameters was considered the best model (Burnham and Anderson 1998). Only models with significant variables ($P < 0.05$) were considered.

With all species, the variance added when the DBH^2 term was used in the equation was not worth the decrease in bias when the term was added; therefore all models chosen were linear. The equations for red maple and chestnut oak were log transformed, and the equations for black birch, white oak, and northern red oak were log-log transformed (Table 2). Because the CPA is a log-transformed value, there is an inherent bias when back-transforming the predicted CPA values. To correct for this bias, Snowdon's (1990) ratio estimator of the sample mean to the back-transformed predicted variables was determined for each species and applied to the predicted CPA values (Table 2).

Standardized Growth Chronologies

Once decadal disturbance rates were calculated for each stand, evidence of species-specific disturbances was investigated using standardizations. Different species have, in general, different average growth rates and varying reactions to disturbances (Schweingruber 1996), making it difficult to compare directly patterns of release or growth reduction between species. Standardizing each species' ring widths eliminates species-specific growth trends, making comparisons of growth reduction events more straightforward. Species-wide growth reductions across the stands at Coweeta could therefore be examined. Standardized growth chronologies were created using ARSTAN to compare patterns of growth between common species (Cook and Krusic 2005). From each standardized series, we identified periods of growth reduction and compared them between species.

Standardization divides each ring width by its expected value, creating a relative tree-ring index with a mean of one and a constant variance for each species (Cook et al. 1990). We wanted to choose a standardization method to retain enough variation to detect deviations from mean ring widths associated with releases and growth reductions, in addition to removing age-related growth trends, such as high initial growth rates and low ending growth rates. Depending on the growth pattern of each tree, we fit a negative exponential curve, linear regression line, or horizontal line through the mean of each tree's raw ring widths, using ARSTAN to choose the best fit for each series. This removes the mean level from the raw ring widths, preserving most of the variation. Veblen et al. (1991) found that the standardization technique of fitting a horizontal line through the mean was the most appropriate for detecting releases and growth reductions from insect outbreaks. Our chosen standardization method looked similar to the horizontal lines through the mean, excepting that long-term radial growth trends (high initial growth rates and low final growth rates) were removed.

After each tree ring series was standardized, series of the same species were averaged together using a robust bi-weight mean, which eliminates the effects of outliers and extreme values (Cook et. al. 1990). These standardized growth chronologies were created for the six most common species sampled at Coweeta (red maple, black birch, hickories, white oak, chestnut oak, and northern red oak), and the four most common species at Joyce Kilmer (red maple, white oak, chestnut oak, and northern red oak).

To determine species-wide growth reduction events, standardized growth chronologies were examined to evaluate sustained growth declines (Chokkalingham 1998). Growth reductions in this study identify periods of slow radial growth that might be indicative of a disturbance or stress directly affecting the species, such as insect outbreaks, drought, or damage from ice or wind storms. Growth reductions were identified when at least three years of consecutive tree-ring index values were 0.8 or lower. These growth reductions identify short-term decreases in growth, and they do not address long-term or gradual declines in growth due to canopy closure (Chokkalingham 1998). Instead, the abrupt decreases in growth are likely due to disturbance events.

Disturbance History Along Compositional and Environmental Gradients

Multivariate analyses were used to determine if stands closer together along topographic or compositional gradients would have more similar disturbance histories than stands further apart on those gradients. In addition, analyses were done to determine if stands with similar vegetation composition also had similar environmental characteristics.

Multivariate ordinations were conducted using species composition and decadal disturbance rates separately, and the resulting placements of stands in ordination space were visually compared. Stand-by-composition matrices were created using a variety of combinations of stand characteristics including BA, density, frequency, importance value, relative BA, relative density, and sapling density to examine various relationships between different stand characteristics. We did these exploratory multivariate analyses using different combinations of stand characteristics to better understand what might be important in explaining variation in the stands. Detrended correspondence analysis

(DCA) in PCord was used to ordinate the stands in species space (McCune and Mefford 1999). Analyses were done using all species in each stand, as well as the six most common species in the Coweeta stands (red maple, black birch, hickories, white oak, chestnut oak and northern red oak). Analyses were done examining stands at Coweeta alone, as well as stands at Coweeta and Joyce Kilmer combined.

DCAs were then conducted using stand-by-decade matrices where values were the percent area disturbed during that decade in that plot. Decadal disturbance rates were transformed using an arcsine square root transformation to create a more normal distribution (Quinn and Keough 2002). Decadal rates of total disturbances (gap origin trees, major releases, moderate releases, and recovery events) and major disturbances (gap origin trees and major releases) were used. Because sample size varied between stands, only decades with at least ten trees per stand were used (beginning with 1870). Releases were identified through the 1990s, analyzing 13 decades total (1870-1990). We ordinated stands at Coweeta alone, as well as stands at Coweeta and Joyce Kilmer combined. The placement of stands in ordination space based on species composition and decadal disturbance rates were compared to see if similar groupings of stands occurred.

In addition to visual comparisons of the ordinations, we quantitatively evaluated whether the degree of stand similarity based on species composition was similar to that based on disturbance histories. This was analyzed with a Mantel test, which uses a randomization procedure to detect correlations between distance matrices that are higher than expected by chance (Quinn and Keough 2002). A distance matrix is formed by calculating the correlation between all possible pairs of plots based on any of a variety of similarity indices. We used Sorenson's (Bray-Curtis) distance measure to calculate the similarity of each pair of plots based on species composition, using BA and density of the six most common species (red maple, black birch, hickories, white oak, chestnut oak, and northern red oak). A second distance matrix was formed using stand-level decadal disturbance rates as the basis for calculating the degree of similarity between all possible pairs of plots. The Mantel test then compared the two matrices to determine whether plots with similar vegetation composition also tended to have similar temporal distributions of major disturbances. This matrix was based on decadal rates of major disturbances after transformation by arcsine square root; as above, the distance matrix was created using Sorenson's (Bray-Curtis) measures. Analyses were done examining stands at Coweeta alone, as well as stands at Coweeta and Joyce Kilmer combined.

Mantel tests were also conducted to determine if correlations exist between matrices of decadal disturbance rates and environmental variables (slope and elevation). To determine if slope or elevation were linearly related to decadal disturbance rates, correlation matrices were created. Sample stand scores derived from the DCAs of decadal disturbance rates for axes one and two were compared to environmental variables in SYSTAT. These analyses were repeated using species composition and environmental variables to determine if species composition changes along environmental gradients. Canonical correspondence analyses were also conducted to ordinate species and environmental variables simultaneously (Gauch 1982).

Finally, stands sampled at Coweeta were placed in a graph (modified from Day et al. 1988) describing how forest types were distributed relative to moisture, aspect, and elevation gradients at Coweeta. Once stands were placed in the graph based on their environmental characteristics, the decadal disturbance values were placed by each stand. The graph was visually inspected to determine if the decadal disturbance rates of the sample stands vary with these topographic variables within the scope of forest types found at Coweeta.

Remnant Old Trees

To compare the old-growth trees at Joyce Kilmer to remnant old-growth trees at Coweeta, standardized growth chronologies were created for northern red oak and white oak (see above methods on standardized growth chronologies). Only trees established at breast height in the 1850s or earlier were used. These two species were the only ones common to both sites with more than ten old trees available for analysis. If the estimate of years to pith was ten or fewer and the estimated year of establishment was in the 1850s or earlier, the tree was included in the standardized growth chronologies.

Correlations between standardized growth chronologies of old trees and young trees (trees established at breast height after the 1850s) in Coweeta and Joyce Kilmer were done using the MAT program in the Dendrochronology Program Library (DPL) (Holmes 1999). This program creates correlation matrices comparing time series over various user-designates intervals. Anthropogenic disturbances in the Southern Appalachians commenced on a large scale in the early 1900s. To assess the effect of these disturbances on the trees at Coweeta, correlations between the standardized growth chronologies of old trees at Coweeta and Joyce Kilmer were compared both before and after 1900 using the MAT program in DPL. Coweeta’s young trees were compared to Joyce Kilmer’s young trees as well as old trees between sites, both before and after 1900.

RESULTS

Species Composition and Stand Structure

Stands range in elevation from 1097-1386 m and slope from 5-36 degrees (Table 3). The stand-level BA ranges from 21.7-37.6 m^2/ha, and density ranges from 216-596 stems/ha (Table 3). These values are similar to other BA and density estimates for overstory trees at Coweeta and the southern Appalachians (Day and Monk 1974, Elliott et al. 1999). Crown projection areas range from 8,217 to 15,608 m^2/ha. Density and BA for the six most common species are listed in Table 4. Additional data on the composition and structure of stands are presented in the Appendix (Table A.2- Table A. 8 and Figure A. 1 - Figure A. 2).

Table 3. Slope (degrees), aspect, elevation (meters), basal area (m^2), density, and crown projection area (m^2) for stands at Coweeta and Joyce Kilmer (JK).

Stand	Location	Slope (degrees)	Aspect	Elevation (m)	Basal area (m^2/ha)	Density (stems/ha)	CPA (m^2/ha)
DC	Coweeta	16	N	1234	28.6	426	13016
DS	Coweeta	28	NW	1204	28.3	345	12204
DY	Coweeta	21	E	1097	21.7	223	8789
MG	Coweeta	34	NE	1341	23.2	290	8260
PM	Coweeta	31	NE	1387	37.6	595	12465
PR	Coweeta	36	NW	1265	26.4	292	9541
RK	Coweeta	19	NW	1143	22.6	216	8217
GD	JK	9	SW	1219	27.8	596	15200
SB	JK	5	NE	1183	36.0	467	15608

Species composition ordinations and average decadal disturbance rate ordinations were performed and visually inspected to determine if the stands at Joyce Kilmer were outliers or if they were similar to stands at Coweeta. A DCA ordination of species

Table 4. a) Density (stems/ha) and b) basal area (m^2/ha) for the six most common species across all sample stands at Coweta and Joyce Kilmer.

a)

Stand	Location	Red maple	Black birch	Hickory spp.	White oak	Chestnut oak	Red oak	Other	Total
DC	Coweeta	61	12	68	83	31	39	131	425
DS	Coweeta	53	14	15	19	9	93	142	345
DY	Coweeta	70	0	66	0	26	47	14	223
MG	Coweeta	3	101	0	0	1	61	124	290
PM	Coweeta	0	290	0	1	0	95	209	595
PR	Coweeta	18	40	14	13	88	11	108	292
RK	Coweeta	14	40	14	28	17	42	63	217
GD	Joyce Kilmer	294	0	35	40	78	68	81	596
SB	Joyce Kilmer	91	26	54	10	1	93	191	467

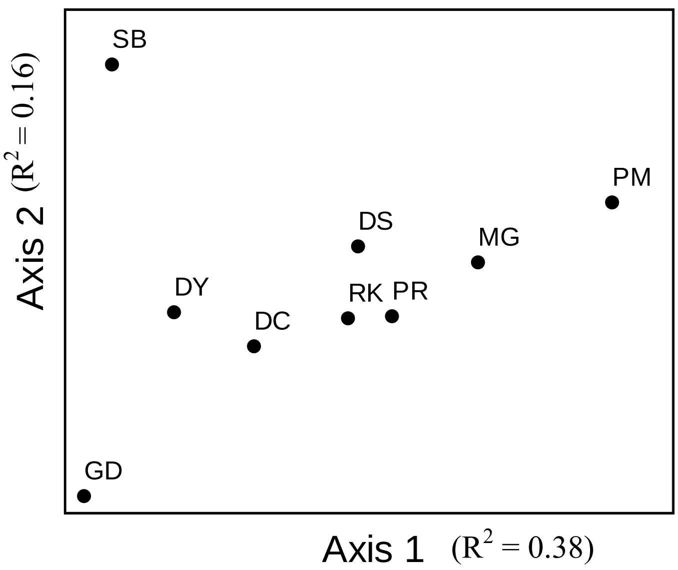
b)

Stand	Location	Red maple	Black birch	Hickory spp.	White oak	Chestnut oak	Red oak	Other	Total
DC	Coweeta	1.8	0.8	2.2	11.6	3.6	5.0	3.6	28.6
DS	Coweeta	2.0	0.6	1.2	4.8	0.8	12.8	6.2	28.3
DY	Coweeta	5.7	0.0	3.7	0.0	3.3	7.3	1.7	21.7
MG	Coweeta	0.8	3.6	0.0	0.0	0.4	15.2	5.2	25.2
PM	Coweeta	0.0	10.0	0.0	0.4	0.0	20.0	7.2	37.6
PR	Coweeta	0.8	1.6	1.2	2.4	4.8	14.4	1.6	26.8
RK	Coweeta	1.2	3.6	0.8	4.0	1.4	6.6	5.0	22.6
GD	Joyce Kilmer	9.0	0.0	0.5	4.8	5.5	6.0	2.0	27.8
SB	Joyce Kilmer	4.7	0.7	2.7	1.0	0.3	20.0	6.7	36.0

composition (relative BA, relative density, and relative sapling density of all species) results in the Joyce Kilmer sites (SB and GD) as outliers (Figure 3). The first axis, which separates the Joyce Kilmer stands from the Coweeta stands, is driven by silverbell (*Halesia tetraptera* L.) on one end, which is only found in the Joyce Kilmer stands. While it is abundant where it is present, it was only found in two stands, making the Joyce Kilmer stands outliers when silverbell is included in the ordinations. The other end of Axis 1 is driven by species such as basswood (*Tilia americana* L.) and eastern hop-hornbeam (*Ostrya virginiana* (Mill.) K. Koch.), which are absent from the Joyce Kilmer stands. When species composition variables are decreased so that only the top six species are analyzed, the Joyce Kilmer stands are not noticeable outliers (Figure 3).

Recruitment age refers to the tree age at one meter (coring height). To examine age structures, we only used cores that hit the pith or whose pith could be estimated. However, cores that were missing the pith were still useful when examining radial growth and were used in constructing the disturbance chronologies (see below section *Disturbance History*). The stands are generally uneven aged (Figure 4 and Figure A. 3). Detectable gap origin and non gap origin trees occur at various densities throughout time, interspersed with peaks in recruitment. The older age classes are generally composed of oak species, with various other species detected throughout time (Figure 5 and Figure A. 4 - Figure A. 11). Comparing age at one meter height and diameter at 1.37 meters height was done because there was typically little taper along the stem between these two heights. The age-diameter relationship shows a slightly negative trend (Figure 5 and Figure A. 4 - Figure A. 11). This decreasing trend is not species specific and includes all trees in the stand.

a)



b)

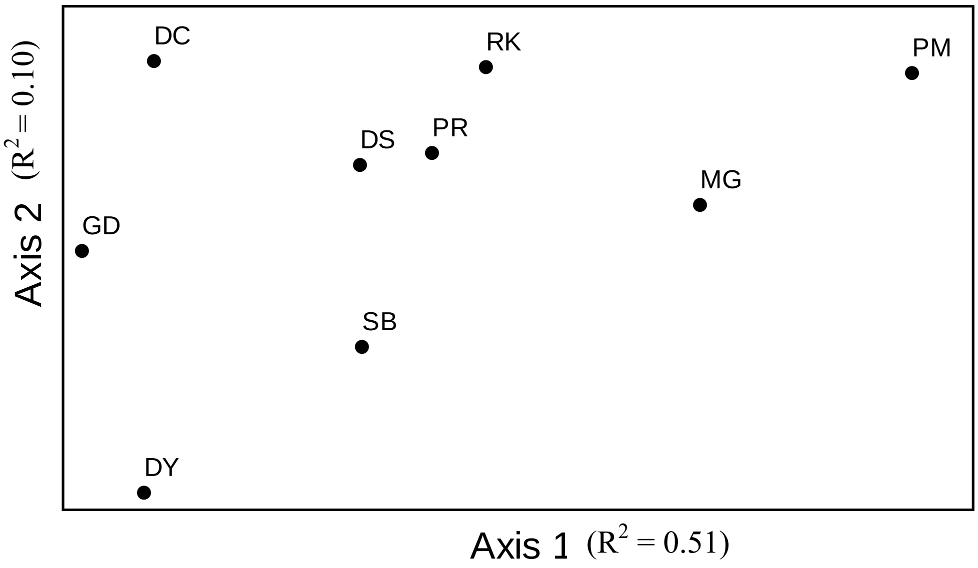


Figure 3. DCA of a) relative basal area, density and sapling density of all species all stands, and b) relative basal area and density of top six species for all stands.

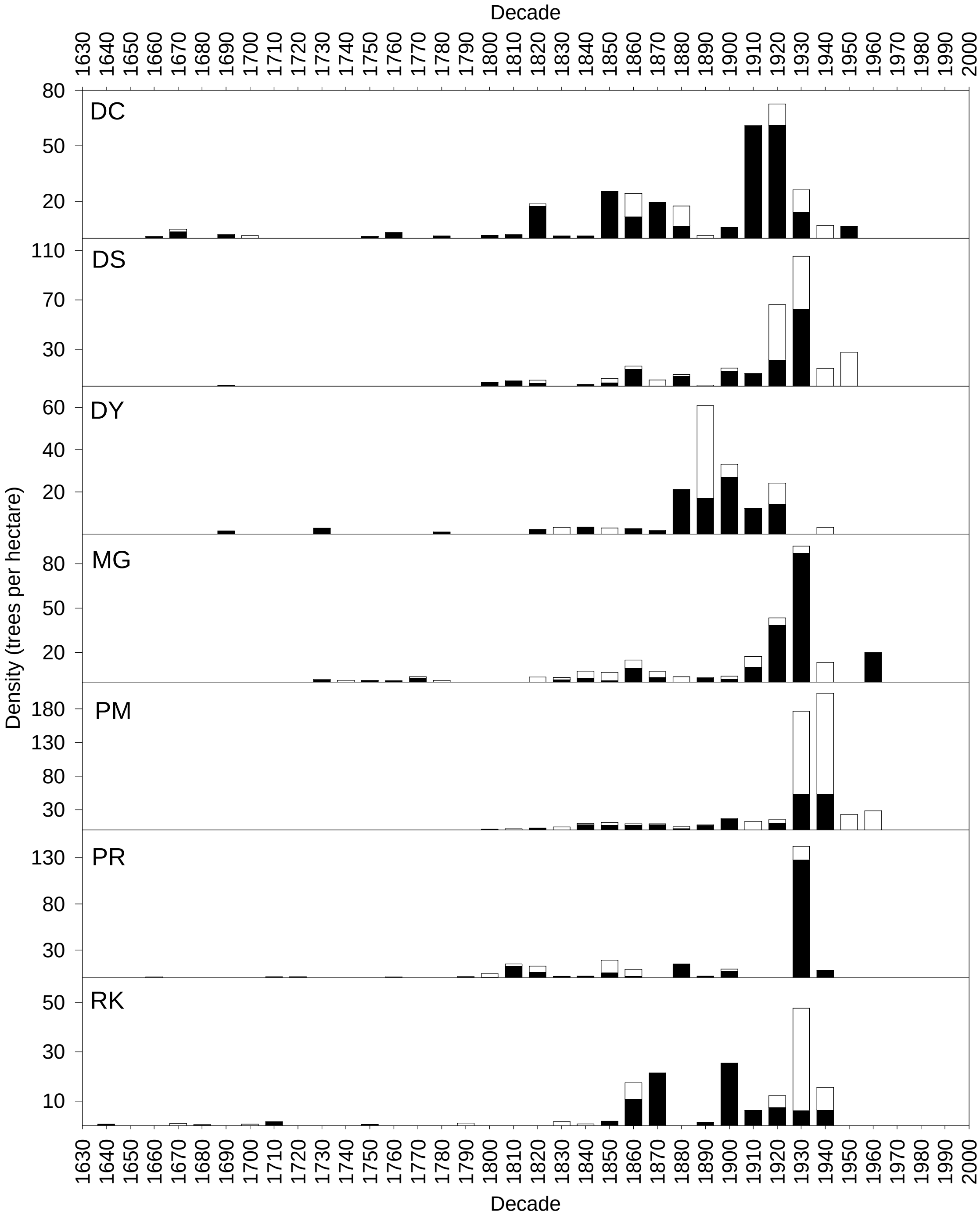


Figure 4. Recruitment age distributions for stands at Coweeta. Open bars indicate gap origin trees and black bars indicate non gap origin trees.

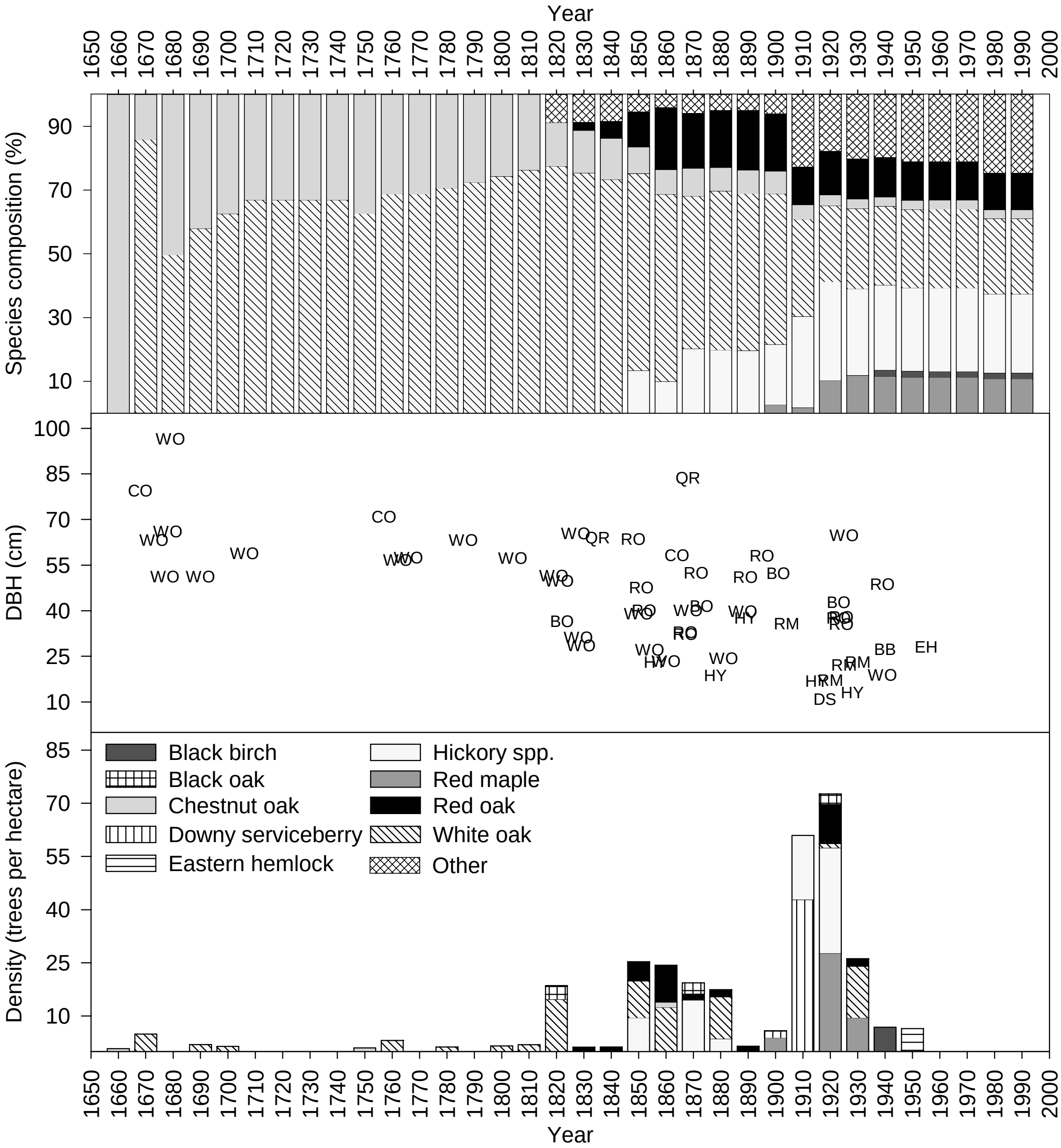


Figure 5. Species composition alive in each decade (%) (top), diameter of each tree by decade of origin (cm) (middle), and age structure by species (bottom) for Coweeta stand DC. The legend applies to both the top and bottom graphs. Species abbreviations are located in Table A. 8. Twenty percent of the cores were rotten or the pith could not be estimated.

When single species are evaluated, the decreasing trend disappears, and a separation can be made between young and old trees. Oak species dominate the older age and size classes, while other species dominate younger and smaller size classes. Several species were recruited into the stand during the peak decades (1920s and 1930s), including shade mid-tolerant (oaks and hickories) and ubiquitous species (red maple and black birch).

In addition to describing stand structure, age distributions can lend evidence to periods of disturbance in a stand. Common peaks in recruitment at Coweeta occur in the 1860s, 1920s and 1930s. In all stands, the highest densities of tree establishment measured at DBH were in the 1920s and 1930s, except for stand DY, which peaked in the 1890s. Peaks in recruitment occur at Joyce Kilmer in the 1920s and 1930s. Peaks of recruitment may occur when disturbances open the canopy enough to allow new trees to enter the overstory.

Disturbance History

For each tree core, all detected releases were included in calculation of the stand - level disturbance history (examples of various releases are shown in Figure A. 12). Percentage of the crown projection area in each stand meeting the various disturbance criteria (major release, moderate release, gap origin, and recovery events) was analyzed to see which type of event occurred most frequently (Table A. 9). At least 44% of the crown area of all the stands has experienced a major release during its lifetime. Moderate releases were less frequent, and recovery events even less. Crown area of trees of gap origin varies greatly with stands ranging from 15% to 49% (Table A. 9).

Average disturbance rate was calculated for each stand and ranges from 8.7% to 18.3% for total disturbances, 4.3% to 13.8% for major disturbances, and 3.0% to 7.0% for minor disturbances (Table 5). Chronology lengths range from 133 to 253 years, beginning with the first decade with at least ten trees until 1993 (Table 5). The decadal disturbance rates across stands vary from 0% to 75.4% (Table A. 10).

Table 5. Summary of stand level disturbance rates. Total disturbance rate includes major releases, gap origin trees, moderate releases, and recoveries. Major disturbances include major releases and gap origin trees. Minor disturbances include moderate releases and recovery events. All rates are calculated from the earliest decade with at least ten trees to the 1990s. Standard error is displayed in parentheses.

Stand	Total Disturbance Rate (%)	Major Disturbance Rate (%)	Minor Disturbance Rate (%)	Chronology length (years)	Earliest decade with at least 10 trees	Earliest decade with 1 tree
DC	8.7 (1.8)	4.3 (1.2)	4.5 (1.0)	253	1750	1670
DS	14.8 (3.1)	8.8 (2.6)	6.0 (1.5)	183	1820	1680
DY	16.2 (3.5)	8.7 (2.6)	7.6 (0.8)	133	1870	1690
MG	13.6 (2.0)	7.8 (1.4)	5.8 (1.2)	173	1830	1730
PM	17.8 (3.3)	10.8 (3.0)	7.0 (1.0)	163	1840	1800
PR	12.7 (2.2)	6.3 (1.2)	6.4 (1.6)	193	1810	1660
RK	11.3 (3.3)	7.0 (2.6)	4.2 (1.3)	183	1820	1640
GD	15.0 (2.8)	9.8 (2.0)	5.2 (1.3)	213	1790	1680
SB	18.3 (4.5)	13.8 (4.2)	4.5 (0.8)	163	1840	1740

Peak decades of disturbance occurred when the decadal disturbance rate was 5% higher than the average decadal disturbance rate for each stand (Erika Rowland, *personal communication*) (see Figure A. 13 for a graphical display of peak decades). The 1930s was a peak decade of disturbance across all stands at Coweeta and Joyce Kilmer for total and major disturbances (Figure 6 - Figure 9). Peak decades of total disturbance in more then two stands occurred in the 1840s, 1860s, 1920s, 1930s, and 1960s. Peak decades of major disturbance occurring in more than two stands include the 1920s, 1930s, 1940s, and 1910s. Common peaks in minor disturbance rates occurred in the 1840s, 1900s,

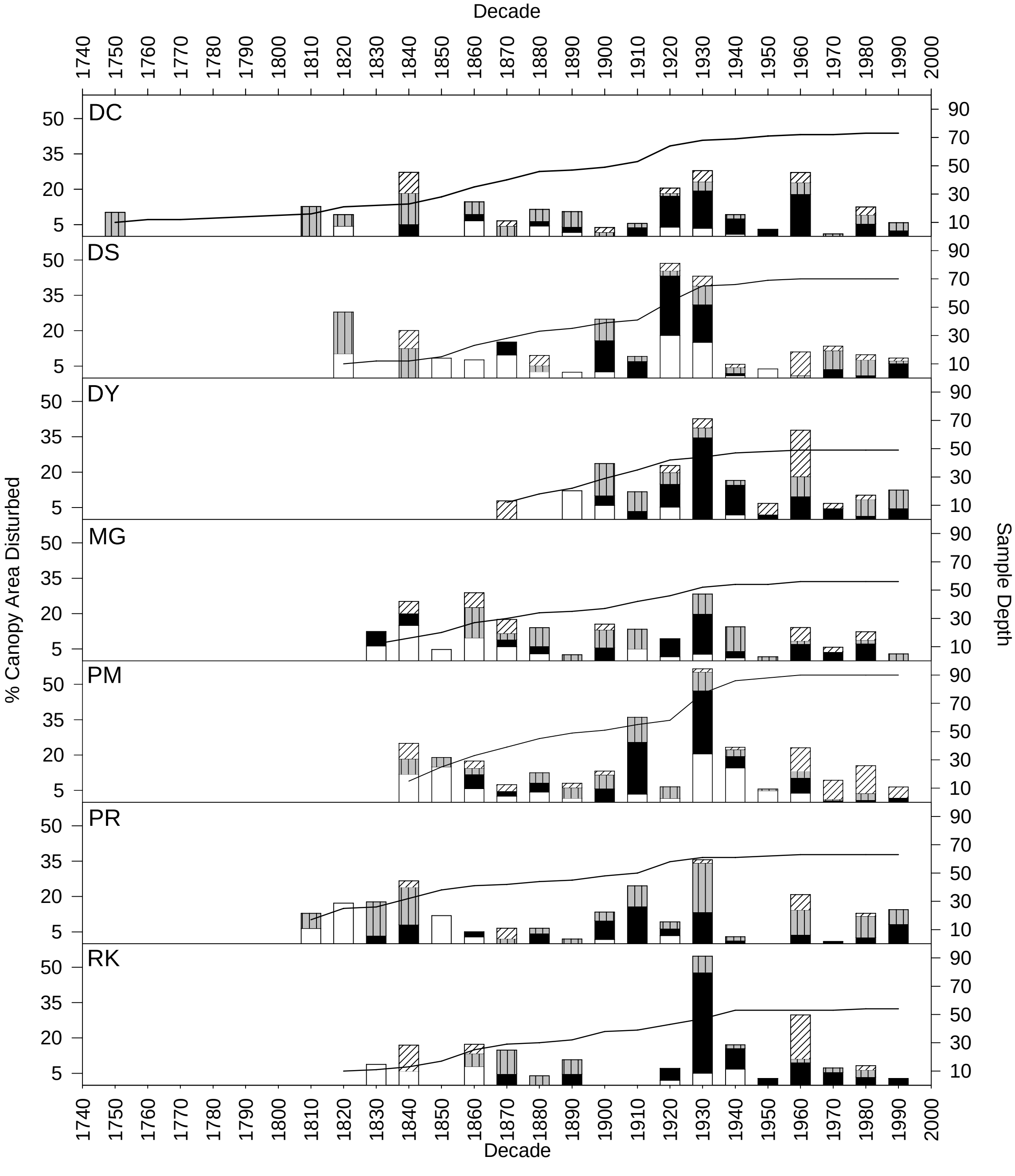


Figure 6. Total disturbance history for Coweeta stands. Open bars indicate gap origin trees; black bars denote major releases; vertical stripes denote moderate releases; diagonal hash indicate recovery events. Chronologies were truncated when the sample size dropped below ten trees.

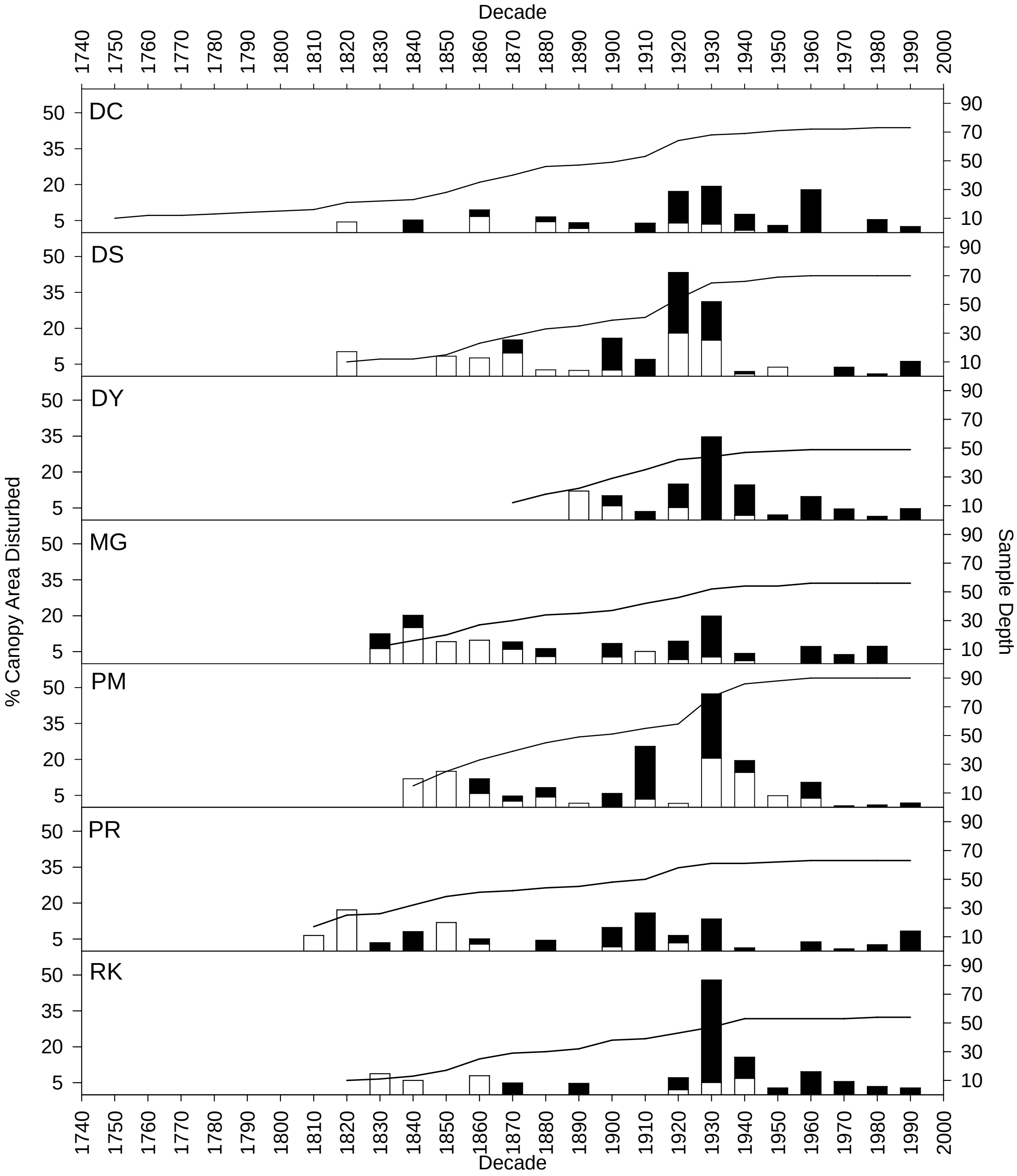


Figure 7. History of major disturbances for Coweeta stands. Open bars indicate gap origin trees and black bars denote major releases. Chronologies were truncated when the sample size dropped below ten trees.

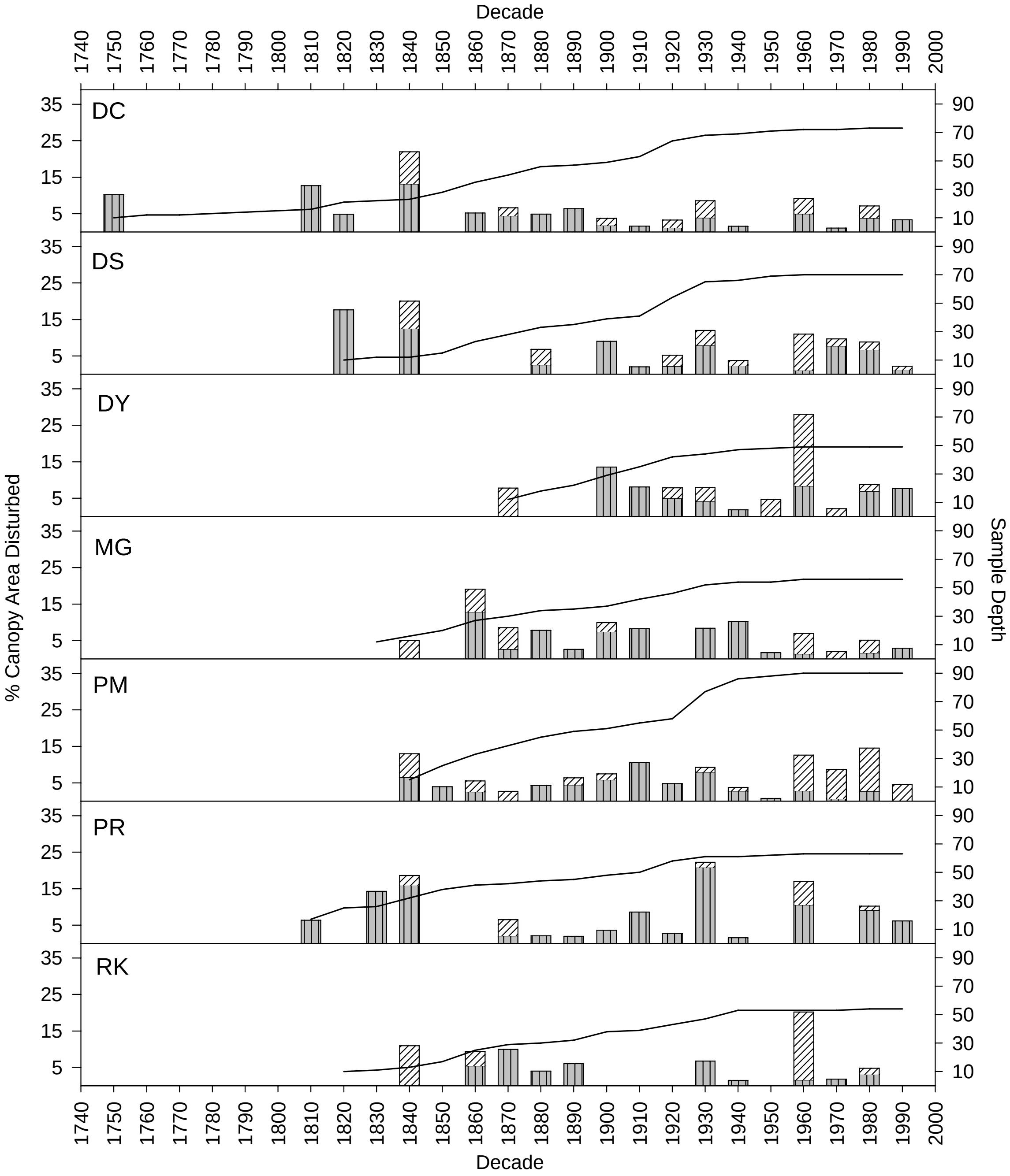


Figure 8. Minor disturbances for Coweeta stands. Gray bars indicate moderate releases and diagonal hashed bars indicate recovery events. Chronologies are truncated when sample size dropped below ten trees.

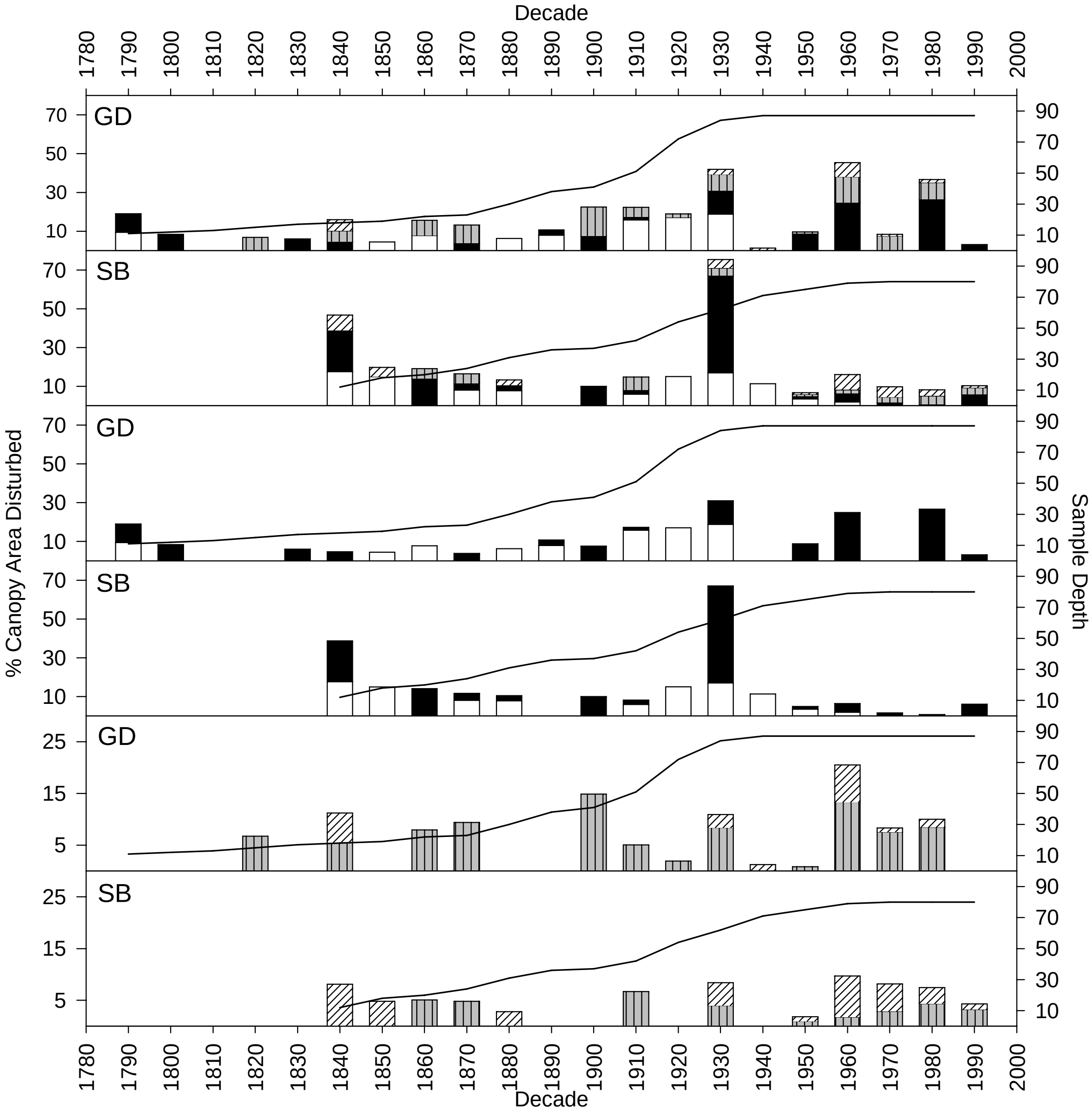


Figure 9. Disturbance chronologies for stands at Joyce Kilmer. Open bars indicate gap origin trees; black bars indicate major releases; gray bars indicate moderate releases; vertical hashed bars indicate recovery events. The top two graphs describe total disturbances; middle two display major disturbances; bottom two graphs display minor disturbances. Chronologies are truncated when sample size drops below ten trees.

1930s, 1960s, and 1980s. Peaks also occur in the 1860s and 1870s for stands DC, DS, MG, and RK. Peaks in disturbance occurring in one stands only include the 1750s (DC), the 1790s (GD), the 1820s (DS), the 1830s and 1850s (PR), and the 1970s (DS). Overall, decades of peaks in disturbance found across stands occur in the 1840s, 1860s and 1870s, 1900s and 1910s, 1920s, 1930s and 1940s, 1960s, and 1980s (Figure 6 - Figure 9).

Characteristics were examined for common species (Table 6). Mean sensitivities describe the difference between successive ring width values, and they are used to evaluate how environmental influences affect the growth rate of a tree (Schweingruber 1988). A low sensitivity value describes a complacent tree, not greatly influenced by external factors, while a high sensitivity value describes a tree responsive to its surroundings. Values range from zero for a complacent series with no change between successive ring widths to two for a tree greatly influenced by its environment (Fritts 1976). Mean sensitivities for the most common species sampled at Coweeta and Joyce Kilmer ranged from 0.185 (northern red oak at Coweeta) to 0.339 (red maple at Joyce Kilmer) (Table 6). Average ring widths were calculated for each core and then averaged

Table 6. Species statistics for stands at Coweeta and Joyce Kilmer. N indicates number of cores. Standard error is displayed in parentheses.

Species	Location	N	Mean sensitivity	Average ring width (mm)
Red maple	Coweeta	27	0.296 (0.065)	1.72 (0.60)
Black birch	Coweeta	45	0.293 (0.054)	1.45 (0.52)
Hickory spp.	Coweeta	26	0.259 (0.053)	0.94 (0.33)
White oak	Coweeta	74	0.202 (0.037)	1.07 (0.34)
Chestnut oak	Coweeta	30	0.211 (0.040)	1.40 (0.48)
Red oak	Coweeta	144	0.185 (0.030)	1.74 (0.66)
Red maple	Joyce Kilmer	44	0.339 (0.079)	1.50 (0.64)
White oak	Joyce Kilmer	22	0.193 (0.037)	1.14 (0.52)
Chestnut oak	Joyce Kilmer	15	0.193 (0.024)	1.14 (0.47)
Red oak	Joyce Kilmer	64	0.196 (0.029)	2.42 (0.78)

within a species. Hickories in Coweeta have the lowest average ring width (0.94 mm), while northern red oak in Joyce Kilmer has the highest average ring width (2.42 mm).

Disturbance chronologies are displayed by species for each stand, highlighting white oak, chestnut oak, and northern red oak to evaluate patterns of disturbance for stands at Coweeta (Figure A. 14 - Figure A. 16) and Joyce Kilmer (Figure A. 17). None of the peak decades show one species dominating the disturbance pattern across all stands. Some individual stands have a single species dominating a peak decade, such as northern red oak in the 1850s in stand MG. To determine if these early decades are dominated by a single species due to a species-specific disturbance versus the stand composition at that time, species composition by decade for each stand was examined (Figure A. 4 - Figure A. 11).

For each decade, the composition was analyzed by taking the ratio of the density of each species to the total density of trees alive in that decade. These graphs show how the species composition changes throughout time, based on the species alive today. The graphs show the top six most important species and others, which are the remaining species in each stand (see Table A.2 for a comprehensive list of species in each stand). In many of the early decades, oak species composed the highest percent of stand density, which corresponds to these early decades where oaks contribute the most to the disturbance peaks. In the later decades with peak disturbances (e.g. 1930s and 1960s), species other than oak contribute more to peaks in disturbance; however, no single species completely makes up any single peak decade.

Standardized Growth Chronologies

Standardized chronologies were created for six species at Coweeta (red maple, black birch, hickory species, white oak, chestnut oak and northern red oak) (Figure 10) and four species at Joyce Kilmer (red maple, white oak, chestnut oak and northern red oak) (Figure 11). Visual inspection of the standardizations show common peaks in the 1930s among species across all stands at Coweeta, except for black birch which shows a recovery from growth reduction during this time and red maple which shows growth hovering around a tree-ring index value of one.

Periods of growth reduction were analyzed to determine if decreases in growth were unique to a single species, lending evidence to a species-specific disturbance (Table 7). Common periods of growth reduction among species occurred in the late 1920s (red maple, hickories, and chestnut oak) and early 2000s (red maple, black birch, hickories, and chestnut oak). Periods of reduction unique to one species occur from 1959-1963 in red maple, 1837-1839 and 1975-1979 in chestnut oak and 1795-1797 in northern red oak (Table 7).

At Joyce Kilmer, common periods of growth reduction occurred from 1925-1927 in red maple and northern red oak and in the 1980s for white oak and northern red oak (Table 7). Species specific reductions at Joyce Kilmer occur in the 1950s for red maple and 1863-1869 for northern red oak. Comparing Joyce Kilmer trees with Coweeta, common periods of reduction occurred in red maple from 1925-1927 and 1959-1962. Chestnut oak showed a similar period of growth reduction from 1837-1839 in both locations; however, during this period, the Joyce Kilmer stands have fewer than ten trees, and thus this result is less reliable.

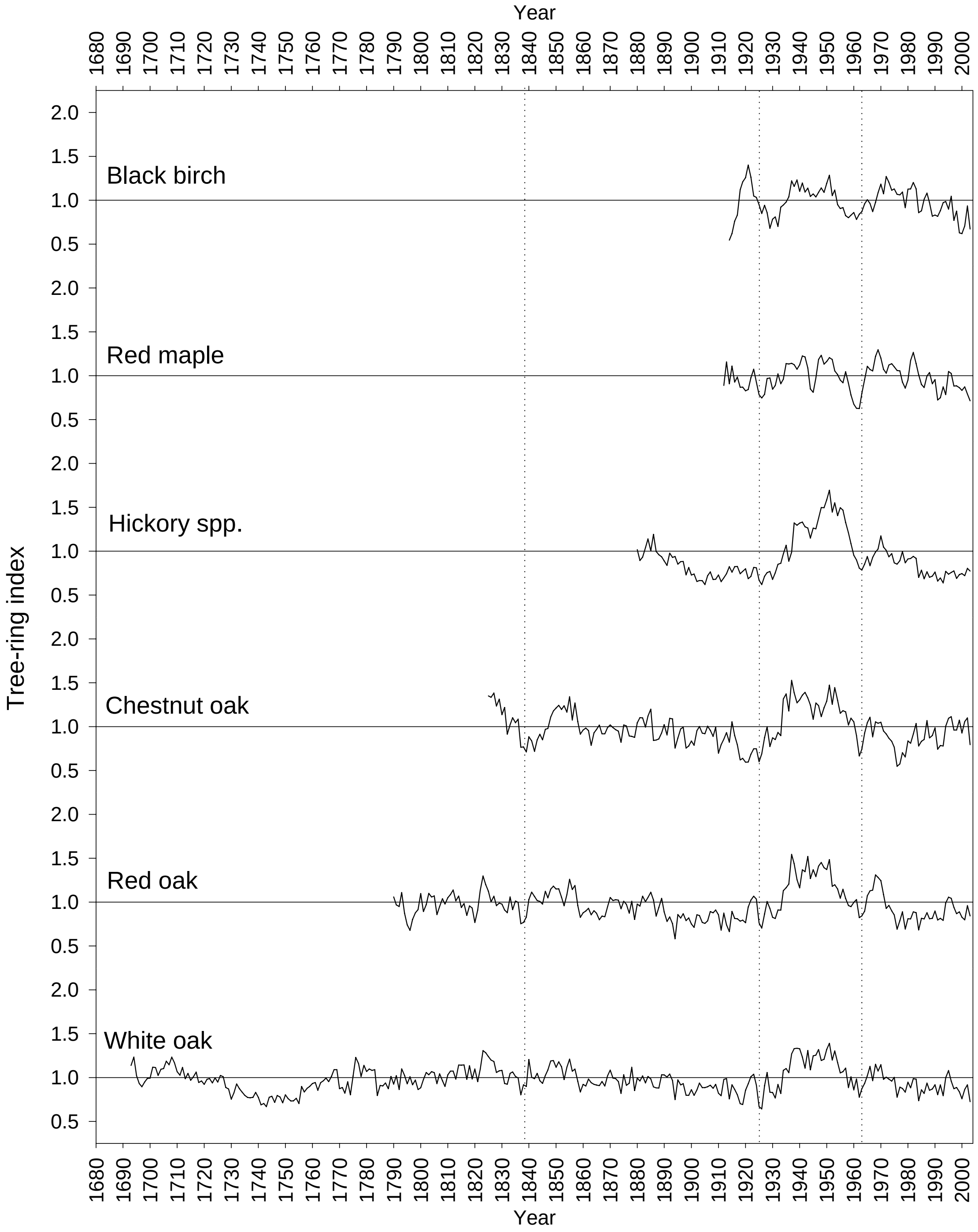


Figure 10. Standardized growth chronologies for the six most common species across all stands at Coweeta. Vertical dotted lines indicate common periods of decreased growth. Chronologies were truncated when sample size dropped below ten trees.

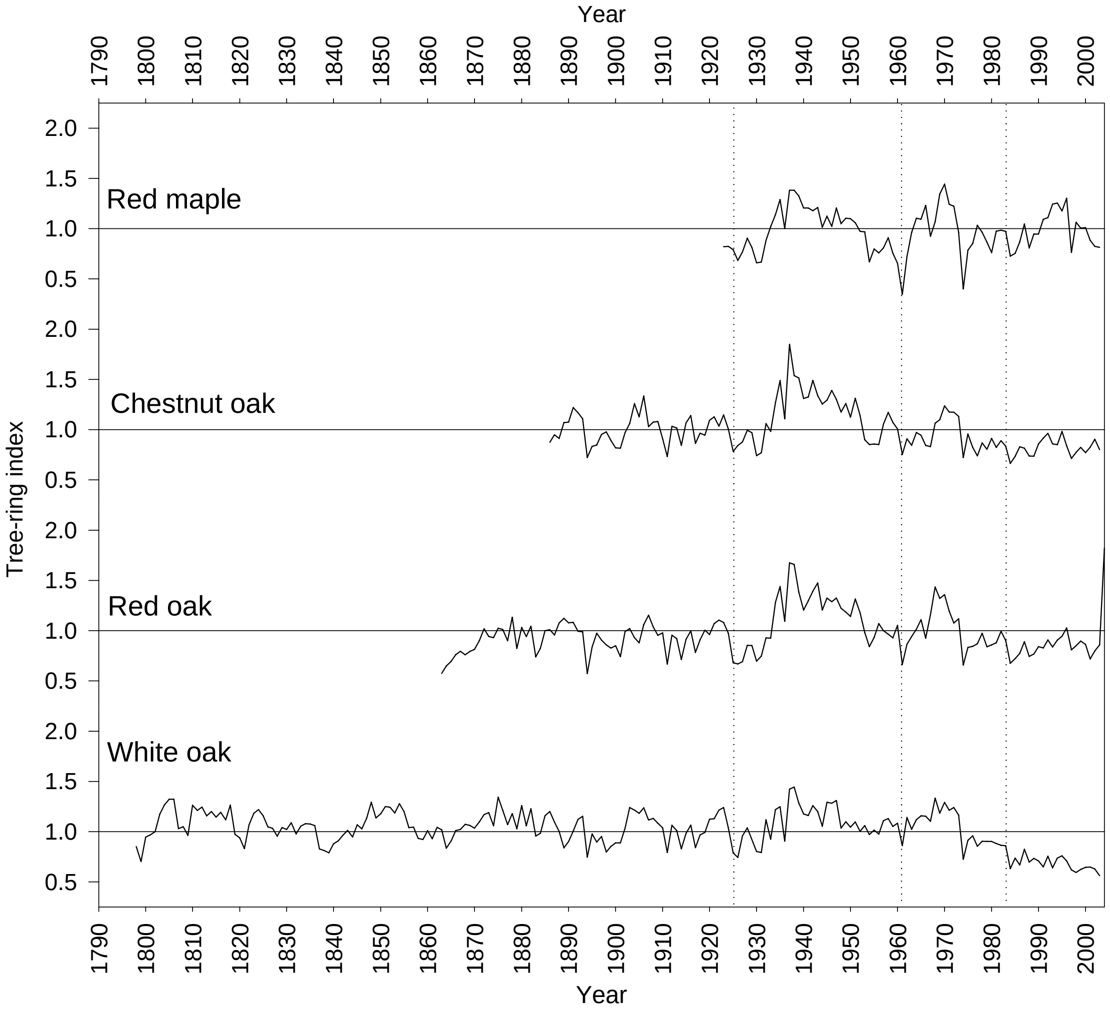


Figure 11. Standardized growth chronologies for the four most common species across all stands at Joyce Kilmer. Vertical dotted lines indicate common periods of decreased growth. Chronologies were truncated when sample size dropped below ten trees

Table 7. Periods of growth reduction for common species at Coweeta and Joyce Kilmer.

Species	Location	Suppressed years
Red maple	Coweeta	1925-1927
		1959-1963
		2002
Black birch	Coweeta	1914-1916
		1999-2003
Hickory spp.	Coweeta	1900-1914
		1918-1922
		1925-1933
		1984-2003
White oak	Coweeta	-----
Chestnut oak	Coweeta	1837-1839
		1917-1926
		1975-1979
		1991-1993
		2003
Red oak	Coweeta	1795-1797
Red maple	Joyce Kilmer	1925-1927
		1954-1956
		1959-1962
White oak	Joyce Kilmer	1984-2003
Chestnut oak	Joyce Kilmer	-----
Red oak	Joyce Kilmer	1863-1869
		1925-1927
		1984-1986

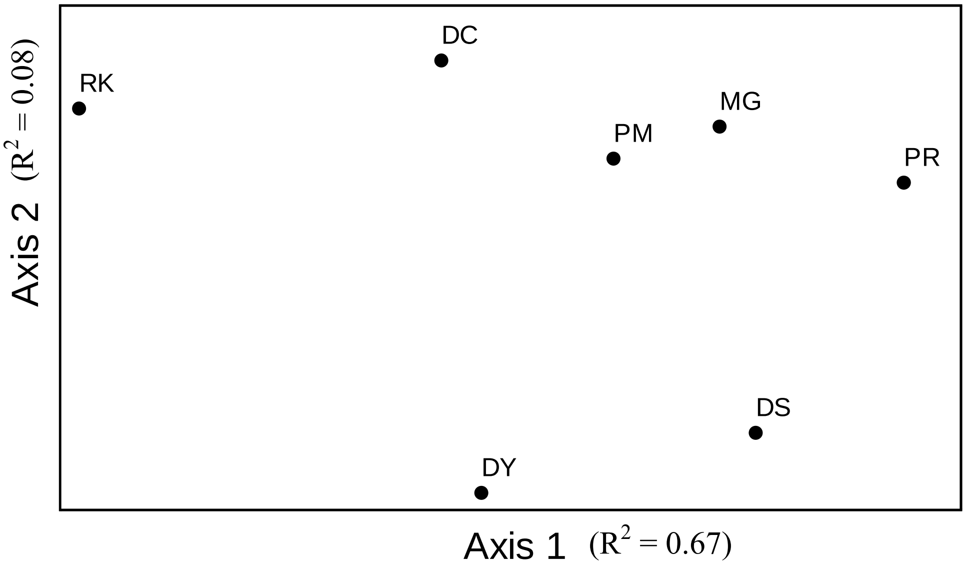
Disturbance History Along Topographic and Compositional Gradients

Ordinations of disturbance history and species composition were compared to see if similar groupings of stands in ordination space exist. Because DCA rescales the axes, percent variation explained by each axis was evaluated using a coefficient of determination (PCord). Coefficient of determination values were higher for the total decadal disturbance rates (including gap origin trees, major releases, moderate releases, and recovery events) than major decadal disturbance rates (including gap origin trees and major releases) when examining Coweeta and Joyce Kilmer stands together (R^2= 0.59 and R^2 = 0.12 for Axis 1 and 2, respectively) (Figure 12). The ordination of Coweeta stands and the decadal disturbance rates for total disturbances results in $R^2 = 0.67$ for Axis 1 and $R^2 = 0.08$ for Axis 2 (Figure 12). Ordinations of matrices of stands by major decadal disturbance rates resulted in slightly lower coefficient of determination values ($R^2 = 0.52$ and 0.41 for Coweeta stands and Coweeta and Joyce Kilmer stands for axes one, respectively) (Figure A. 18 – Figure A. 19). The ordination with the highest variability accounted for (total decadal disturbance rates) for Coweeta stands and Coweeta and Joyce Kilmer stands combined were examined in more detail.

Ordinations of decadal disturbance rates in Coweeta alone and with Joyce Kilmer have similar groupings of stands in species space. Axis one in the ordination of Coweeta and Joyce Kilmer stands is driven by the 1890s on one end and the 1900s on the other end ($R^2 = .59$). Axis 2 is driven by the1920s on one end and the 1940s on the other end (R^2=0.12) (Figure 13).

Similarly, Axis 1 in the ordination of Coweeta stands is driven by the1890s on one end and the 1910s on the other end ($R^2 = 0.67$). However, Axis 2 is driven by the 1970s on one end and the 1880s on the other end (R^2=0.08) (Figure 13). Stands close to each other in ordination space include PM, MG, and SB in the ordination of Coweeta and Joyce Kilmer stands combined. Stands are relatively spread out in the ordination of Coweeta stands, with no obvious groupings standing out.

In order to determine if patterns of species composition were present among stands, they were ordinated with DCA using a variety of combinations of stand



b)

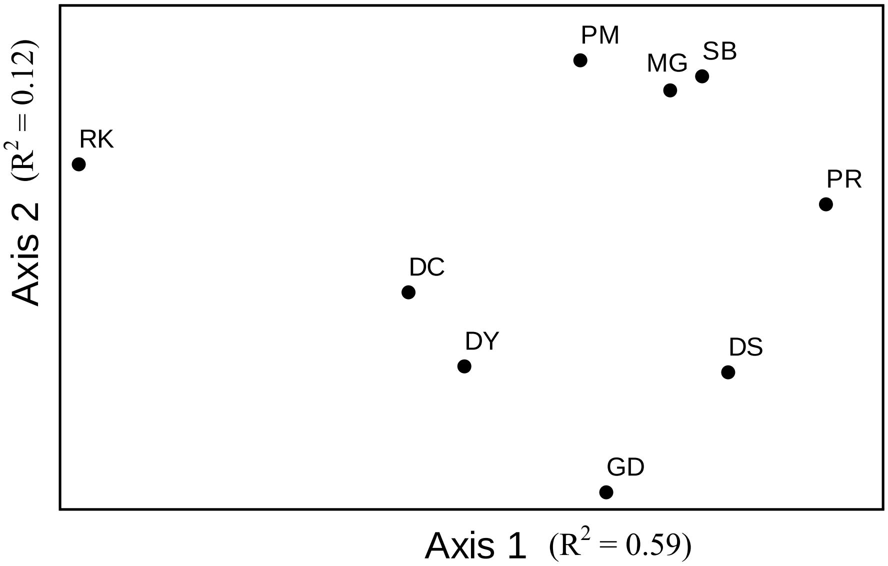


Figure 12. DCA of total decadal disturbance rates for stands at a) Coweeta and b) Coweeta and Joyce Kilmer.

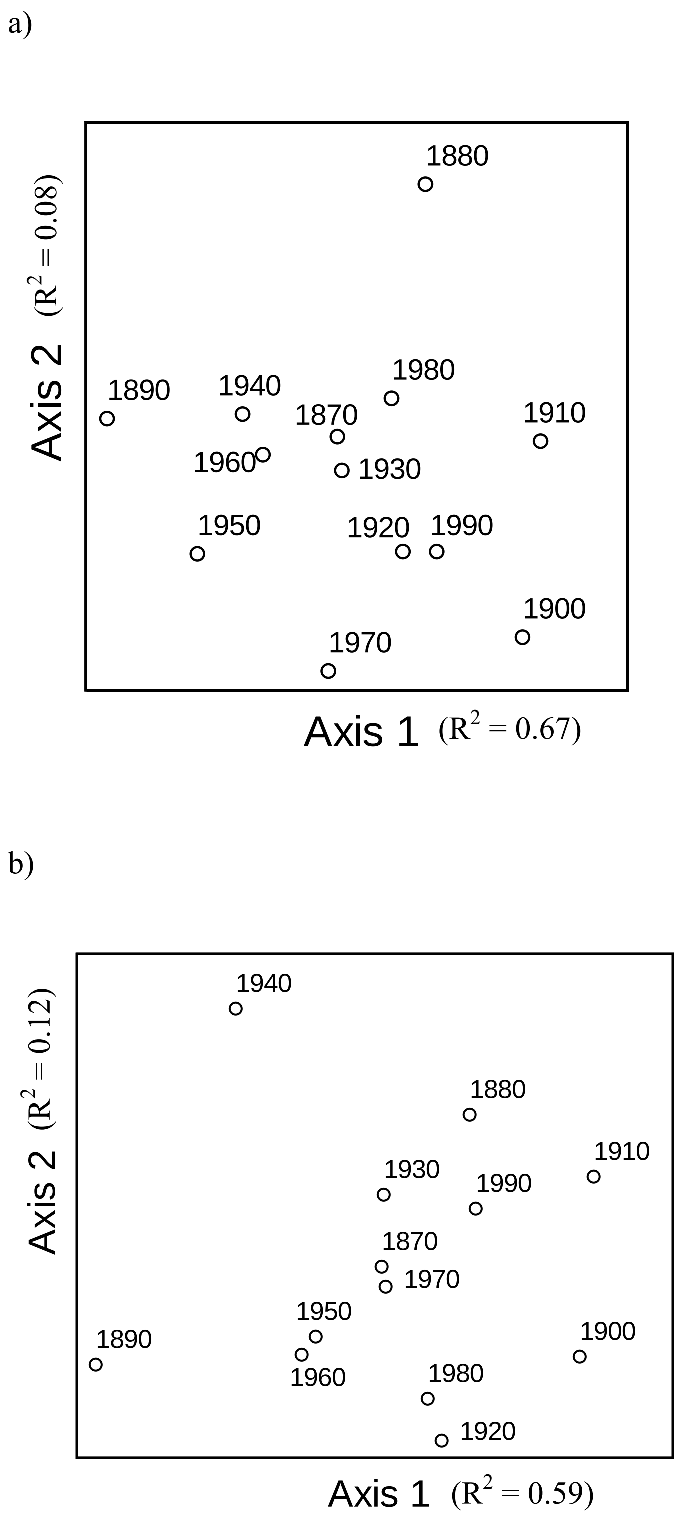
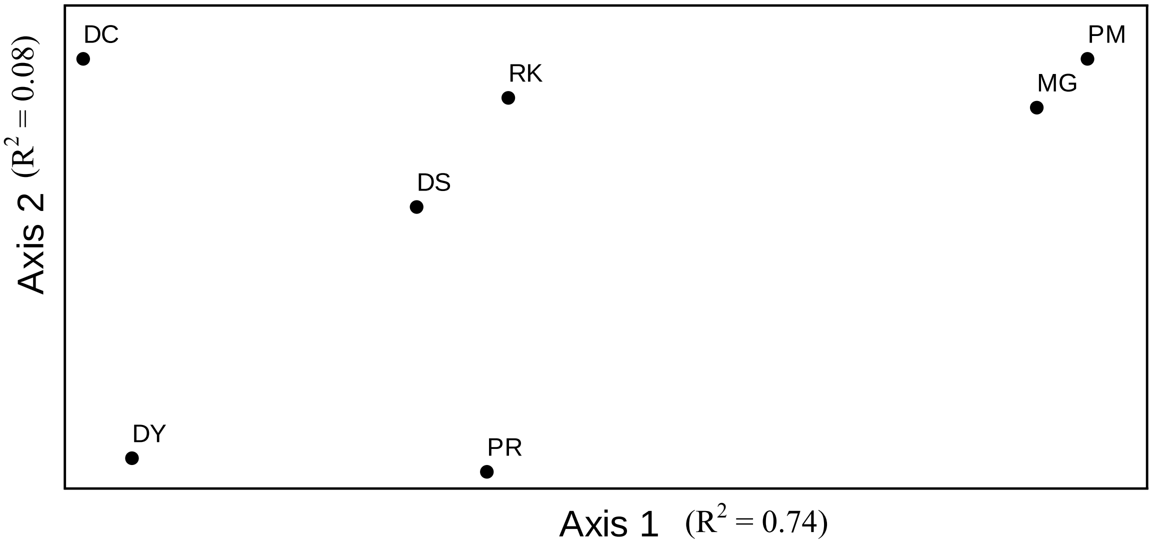


Figure 13. DCA of total decadal disturbance rates at a) Coweeta and b) Coweeta and Joyce Kilmer.

characteristics. BA and density of the six most important species across all stands explained the most variation (Figure 14). When other variables were added to the analysis (e.g. frequency and sapling density), the variation explained by the first two axes did not greatly improve. Relative BA, density, and frequency were also ordinated and showed similar variation along the main axes. In all cases, more of the variation was explained when the analysis was limited to the six most important species.

The ordination of Coweeta stands using BA and density resulted in a coefficient of determination of $R^2 = 0.74$ for Axis 1 and $R^2 = 0.08$ for Axis 2. When the stands at Joyce Kilmer were added to the analysis, the R^2 value did not greatly change ($R^2 = 0.74$ and 0.07 for axes one and two, respectively) (Figure 14). Stands close to each other in ordination space in the ordination of Coweeta and Joyce Kilmer sites include PM and MG at one end of the first axis, and DC, DY, and GD on the other end of Axis 1. A middle group of stands include DS, PR, RK, and SB. On one side of Axis 1, associated with stands PM and MG is black birch (Figure 15). The middle of the ordination is associated with northern red oak. The other side of Axis 1 is closely associated with red maple and chestnut oak. Axis 2, although the coefficient of determination is low, it is associated with white oak at one end and red maple at the other. Stands close together in the ordination of Coweeta sites include PM and MG at one end of Axis 1 associated with black birch and DC and DY at the other end associated with hickory species. Axis 2 is driven by stand PR and red maple on one end and stand DC and white oak on the other end (Figure 15). The ordinations of all sample stands and just stands at Coweeta are similar in groupings and variation explained by each axis.

a)



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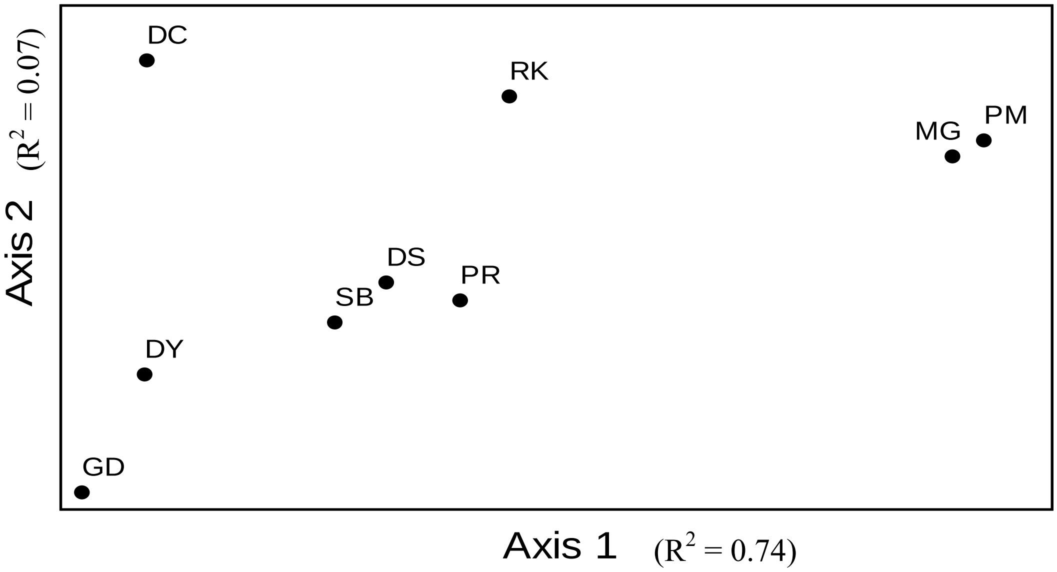

Figure 14. DCA of basal area and density of the top 6 species for a) Coweeta and b) Coweeta and Joyce Kilmer.

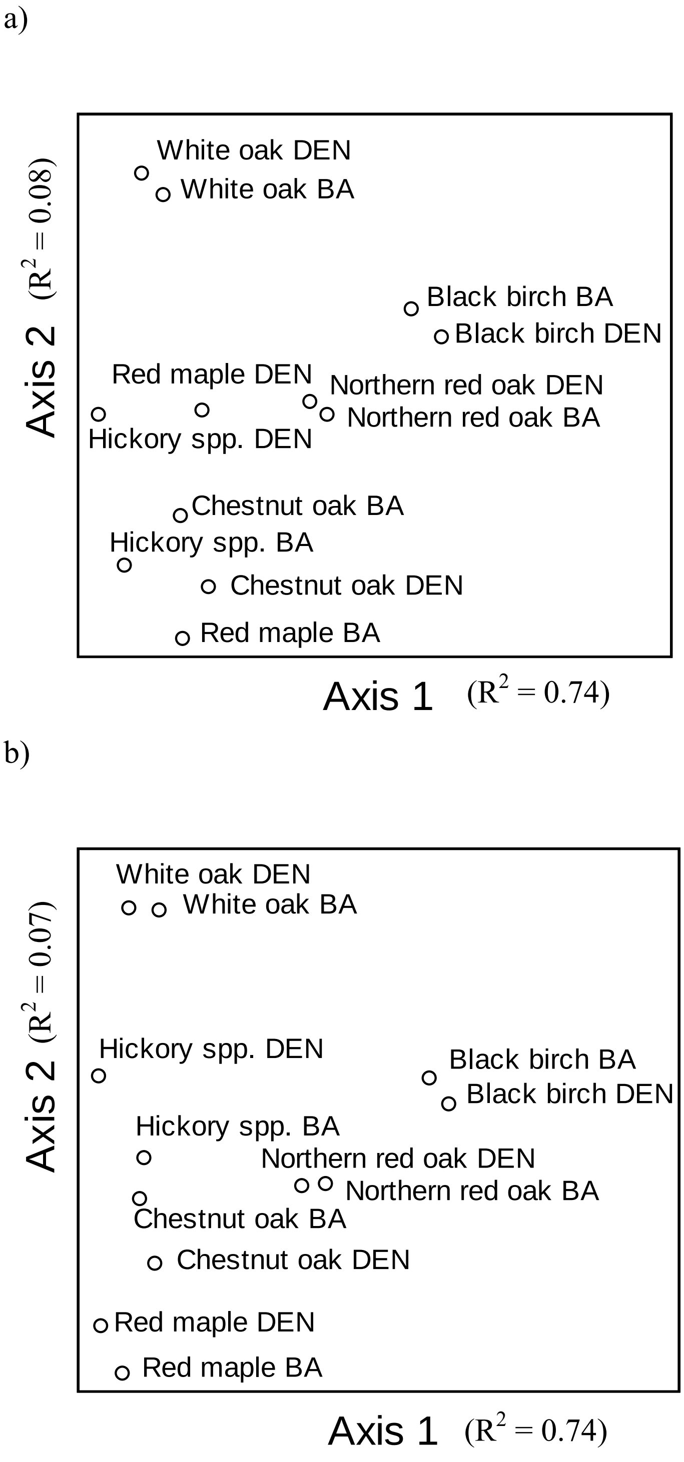

Figure 15. DCA of basal area (BA) and density (DEN) of the top 6 species for a) Coweeta and b) Coweeta and Joyce Kilmer.

When visually comparing the ordinations of species composition and decadal disturbance rates, stands PM and MG are the only ones that group together in both ordination spaces. It seems that stands far apart in ordination space are similar in each ordination. However, strong patterns of stand groupings among these ordinations are not apparent.

To place the sample stands at Coweeta within the matrix of forest types and environmental characteristics present, we modified a chart from Day et al. (1988) which classifies forest types at Coweeta by elevation, terrain shape and aspect (Figure 16). We chose the sample stands partly with the objective of sampling within the mixed-oak forest type across an elevation gradient. When plotted on the modified forest type graph of Coweeta, the stands primarily fall within the oak (-chestnut) forest type.

Two stands (PM and DY) are at high elevations (1387 and 1341, respectively) which places them in the northern hardwood forest type. The graph plots the stands along a moisture gradient based on terrain shape (cove, slope or ridge) and aspect within the landform type. When average decadal disturbance rates are attached to the stands in the forest type graph, no recognizable patterns are detected. No significant relationships were found between DCA sample stand scores for axes one and two of the decadal disturbance rate ordinations and environmental variables (slope and elevation) ($P > 0.05$). Mantel tests were used to further assess the influence of environmental variables and composition on disturbance rates. There was no significant relationship between slope, elevation, or terrain shape and disturbance rates. However, when comparing a matrix of

BA and density of the top six species at Coweeta to average decadal disturbance rates for major disturbances, a significant relationship was determined (standardized Mantel statistic r = 0.39, P = 0.03).

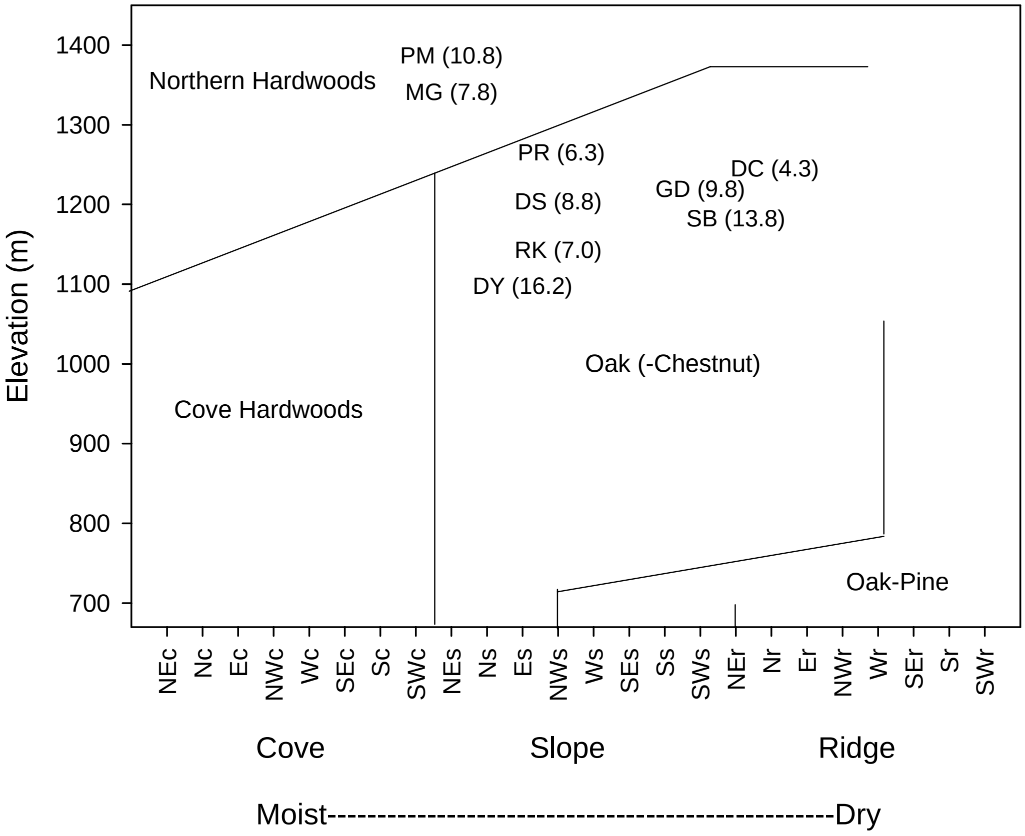

Figure 16. Graph modified from Day et al. (1988) with sample stands placed in the matrix of forest types common at Coweeta. Average major decadal disturbance rates in parentheses.

At Coweeta, elevation and slope were significantly correlated with sample stand scores for Axis 1 of the DCA based on species composition (R = 0.81, P = 0.02 and R = 0.69, P=0.08, respectively). Elevation and slope were also significantly correlated with the stand's scores for Axis 1 at Coweeta and Joyce Kilmer (R = 0.77, P = 0.01 and R = 0.66, P = 0.05, respectively). Little variation is explained by each axis when the species and environmental variables are evaluated concurrently (CCA) (11% and 9.5%, for Axis 1 and 2). The influence of environmental variables on species composition is better explained when the correlations are evaluated after the species are ordinated alone.

Mantel tests were conducted in PCord to further evaluate if species composition and environmental variables are correlated. A distance matrix of BA and density of the Coweeta stands alone, as well as the Coweeta and Joyce Kilmer stands together were compared to a distance matrix of environmental variables (elevation and slope). The Mantel statistic was not significant in either case ($R = -0.27$, $P = 0.1$; $R = -0.31$, $P = 0.06$, respectively).

Remnant Old Trees

Standardized chronologies of white oak and northern red oak trees established in the 1850's or earlier were compared between the stands to detect any effect of anthropogenic disturbance at Coweeta not found at Joyce Kilmer (Figure 17). Visual inspection of the standardized growth chronologies indicates similar peaks and reductions in growth across the species and study sites over time.

Correlation matrices were developed in the MAT program of DPL (Table 8). Old trees (recruitment at one meter occurring in the 1850s or earlier) at Coweeta were significantly correlated to old trees at Joyce Kilmer, for both white oak and northern red oak ($P < 0.01$). Significant correlations occur for the entire length of each chronology, as well as before and after 1900 for white oak ($P < 0.01$) (Table 8).

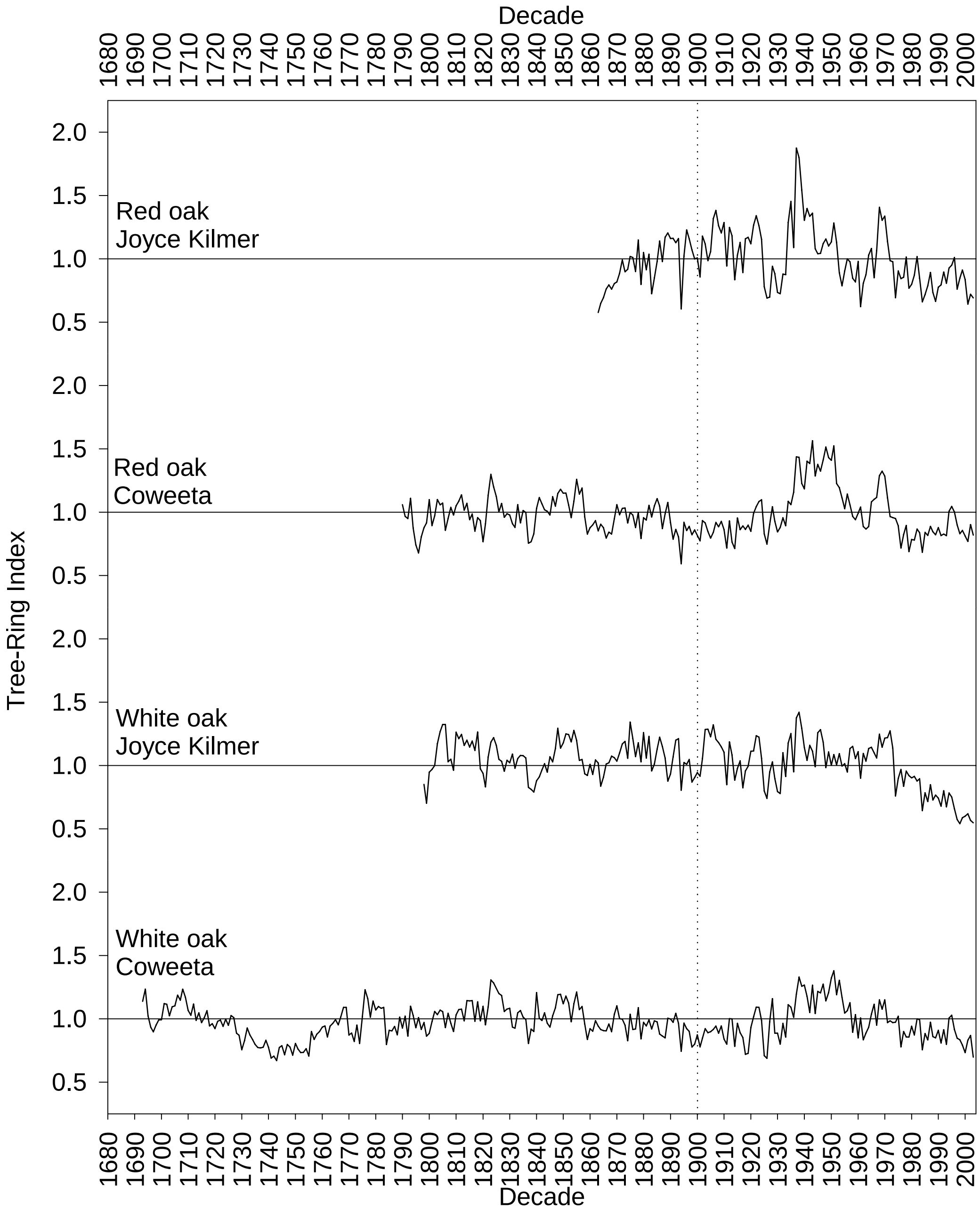

Figure 17. Standardized growth chronologies of the old trees (recruited in the 1850s or earlier) at Coweeta and Joyce Kilmer. Vertical dotted line at 1900 refers to the cut-off date used in the correlation matrices (see Table 8).

Table 8. Correlation values for a) old trees (≥ 1850) and b) young trees (< 1850) at Coweeta and Joyce Kilmer. Significant values ($P < 0.01$) are shown in bold.

a)

			Joyce Kilmer			
			Pre-1900		Post-1900	
			White oak	Red oak	White oak	Red oak
Coweeta	Pre-1900	White oak	**0.55**	-0.06	--	--
		Red oak	**0.48**	0.01	--	--
	Post-1900	White oak	--	--	**0.58**	**0.56**
		Red oak	--	--	**0.51**	**0.61**

b)

			Joyce Kilmer			
			Pre-1900		Post-1900	
			White oak	Red oak	White oak	Red oak
Coweeta	Pre-1900	White oak	**0.64**	**0.56**	--	--
		Red oak	**0.63**	**0.39**	--	--
	Post-1900	White oak	--	--	**0.49**	**0.75**
		Red oak	--	--	**0.69**	**0.88**

Before 1900, northern red oak was not significantly correlated to red or white oak at Coweeta. This may be due to the relatively few number of years analyzed (1835 to 1900). Northern red oak at Joyce Kilmer was significantly correlated to red and white oak at Coweeta after 1900 and when the entire length of the series was considered ($P < 0.01$). All young trees between sites are significantly correlated to each other and the older trees ($P < 0.01$).

DISCUSSION

Species Composition and Stand Structure

Species common in the oak (-chestnut) forest type at Coweeta (Day et al. 1988) were also common to stands in this study. Some of these species, such as black birch, chestnut oak, and red maple, were important in defining gradients based on composition. For example, in one DCA ordination (Figure 14), the first axis (which explains the highest amount of variation within the species by site matrix) represented a compositional gradient varying from black birch on one end of the axis to red maple and chestnut oak on the other. Species common to all stands, such as northern red oak, appeared in the middle of the first axis, indicating that they did not contribute much to the explanation of the variance. Some of the species may be important in defining the second axis, which represents the best way to account for the residual variance not covered in the first axis.

Once established via ordination, these gradients were used for two analyses. First, the stands' positions along each axis indicated how similar or dissimilar the stands were to each other and which species were the best indicators of each stand. For example, stands PM and MG are positioned on the black birch end of Axis 1, indicating that they have a higher abundance of black birch than do the other stands (Figure 15). These stands are located in high elevations slopes with NE aspects, which generally have high precipitation. Black birch trees are often found on mesic sites where precipitation is high (Elliott et al. 1999). Stands grouped near the other end of Axis 1 are associated with greater abundances of red maple and chestnut oak and a smaller component of northern red oak than stands grouped in the middle of the ordination (Figure 15).

Second, these gradients in multivariate space could reflect the degree of similarity in terms of decadal estimates of percent area disturbed. This was approached in two ways in this study. One way was basically the same as above except that species abundances by plot were replaced by percent decadal disturbances by plot. The other way was to overlay the disturbance record on the stand/species ordination to see if disturbance and composition were related. The results from these ways of looking at disturbances and species composition are addressed below in the section entitled *Disturbance History along Topographic and Compositional Gradients).*

Additional analyses were done to determine if the species composition and structure of stands at Coweeta and Joyce Kilmer were similar enough to subsequently compare disturbance histories. DCA of stands at Joyce Kilmer and Coweeta and species composition (based on the six most common species) showed that stands at Joyce Kilmer were close to stands at Coweeta in ordination space. However, when ordinations used all species, Joyce Kilmer stands were separate from the stands at Coweeta along the first axis. The presence of silverbell in the overstory in stands at Joyce Kilmer and its absence in the stands at Coweeta explains the separation. Silverbell is abundant in these stands, but rare across all sample stands, causing Joyce Kilmer to appear as outliers. Usually, the most common species to all stands are adequate enough to characterize common stands in multivariate analyses (Grigal and Ohmann 1975). However, species composition was similar between Coweeta and Joyce Kilmer when the most abundant species were considered, and separation only occurs when rare species were included. Because of this, we determined that Joyce Kilmer stands were similar enough in composition to stands at Coweeta to include in subsequent discussions.

Diameter distributions of the stands generally showed a reverse J curve, typical of a multi-cohort stand (Oliver and Larson 1996) (Figure A.1). This often indicates a balanced age structure; however, these age distributions were not steady. These differences in patterns, along with the age-diameter relationships show that DBH is not a direct indicator of age. Cohorts of various sizes and species composition arise throughout each stand’s history, likely a result of various disturbance patterns and pulses.

The stands are generally uneven-aged, suggesting that they have not been subjected to stand-replacing disturbances that would have created even-aged stands. Old age classes at Coweeta and Joyce Kilmer (maximum age ranged from 200 to 360 years across all plots) tend to be dominated by oak species (and some hickory) (Figure 4, Figure 5, and Figure A. 4 - Figure A. 11). In general, most stands had constant and low recruitment of oak species until the 1920s, 1930s, and 1940s, when red maple, black birch, and hickory increased in abundance. It is not clear if other species are shorter lived and have been in the stands at current densities as long as oak species, or if these species were recruited for the first time in these decades (Johnson et al. 1994). Any given stand may have some or all of the following components: remnant old-growth trees pre-dating European settlement, cohorts associated with various harvests or other anthropogenic disturbances, cohorts arising with the extirpation of American chestnut, and recruitment into natural canopy gaps occurring throughout time. Patterns of recruitment are described in more detail with patterns of disturbance (see below sections *Disturbance Rates and Patterns* and *Disturbance Origins*).

The eastern oak-dominated forests have experienced a decline in regeneration in the past century (Abrams et al. 1997, Abrams et al. 1995, Harrod and White 1999). This has largely been attributed to changes in disturbance regimes through time (Crow 1988), particularly fire suppression (Harrod and White 1999, Abrams et al. 1997, Abrams et al. 1995, Abrams 1992, Mikan et al. 1994, Lorimer 1985, Parker et al. 1985). Regeneration success of oak species in stands sampled at Coweeta and Joyce Kilmer is uncertain. Although not as prevalent as species such as red maple, black birch, and hickory, oaks are present in the smallest diameter size class in each stand. No saplings were aged, and since oaks can remain in the sapling size class for an extended period of time (Nowacki and Abrams 1997), it is impossible to accurately assess recruitment changes over time in our study. All stands in this study except PM and PR have some oak saplings present; however, the densities are very low and not distributed evenly throughout the stands.

Stand PR has complete mid-story canopy closure of rosebay rhododendron (*Rhododendron maximum* L.) and flame azalea (*Rhododendron calendulaceum* L.) and very low densities of any other sapling species. Rosebay rhododendron can have a negative effect on overstory tree recruitment by lowering light levels, varying leaf litter quality, increasing competition for resources, and producing allelopathic chemicals (Clinton and Vose 1996, Monk et al. 1985, Phillips and Murdy 1985). Stems of rosebay rhododendron were aged at Coweeta, and few pre-dated the peak of American chestnut decline; therefore, sapling recruitment since the 1930s was probably limited in these sites due to the expansion of rosebay rhododendron after the blight (Clinton and Vose 1996). Stand MG also has a dense understory of rosebay rhododendron; however, windthrow, likely due to hurricane Opal (1995), created large canopy openings. The increased light and decreased competition (dead rosebay rhododendron were scattered throughout the stand) likely gave northern red oak an opportunity to establish. Stand PM had little rosebay rhododendron, and it is unclear why oak saplings are not present. Black birch increased in the stand in the 1900s and 1910s, which may have created a dense shade layer during the next few decades due to the stem exclusion phase of stand development (Oliver and Larson 1996). Currently, black birch occupies approximately half of the stand density (48%), which may provide too much competition for northern red oak to regenerate.

Disturbance Rates and Patterns

Many types of disturbance can cause the changes in a tree's radial growth rates that we used to identify disturbances. These various agents may act independently or in various combinations. Although we tried to identify the cause(s) of disturbances, we chose not to categorize the agents as to whether they were included or excluded in the calculation of disturbance rates. For example, human-caused disturbances were included as were those of non-human origin. However, by identifying the causes whenever possible, readers are free to divide or lump these causes as they wish.

Mean decadal disturbance rates at Coweeta and Joyce Kilmer ranged from 8.7 to 18.3%, which are comparable to rates found in eastern temperate forests (Bratton and Meier 1998, Runkle 1982) (Table 5). Disturbance patterns over time consist of constantly varying but relatively low decadal rates of disturbance combined with occasional peaks. Disturbances in the southern Appalachian Mountains are largely shaped by frequent small gaps associated with single tree deaths interspersed with less frequent multiple tree gaps resulting from larger disturbances, such as windstorms (Bratton and Meier 1998, Clinton et al. 1993, Runkle 1982). The percent of total land per year converted to gaps in an eastern cove forest is 1% (ranging from 0.5 to 2% per year) (Runkle 1982). A similar study in the Chattooga Watershed (spanning the Georgia, South Carolina, and North Carolina borders) found a comparable gap formation rate that averaged 10.6% per decade (Bratton and Meier 1998). It is important to remember that these rates are averages and can be derived from many different spatial and temporal patterns. For example, a 1% annual average could be due to 1% disturbed each year for 100 years or 100% in one year and nothing for 99 years. Similarly, the 1% in one year could be spatially arranged as many small and widely dispersed gaps or as a singe large gap.

Decades of disturbance common to most of our stands include the 1840s, 1930s, and 1960s (Figure 6 - Figure 9). These disturbances occurred in stands across Coweeta and Joyce Kilmer, and their origins were likely region-wide events. Decades of disturbance common to several stands, but not as widespread as those listed above, include the 1900s-1920s, 1940s, and 1980s. Speculation on the origin of these peaks, based on historical documentation, common disturbances in eastern temperate forests, patterns of release, and peaks in recruitment are described below (see *Disturbance Origins*).

Coupling age structure and recruitment with peaks in disturbance as determined by radial growth patterns is often used to describe a forest's disturbance history (Fraver 2004, Orwig et al. 2001, Abrams et al. 1998, Abrams et al. 1997, Lorimer 1980). Detecting disturbances from age structure works especially well with shade intolerant species, which require a canopy-opening disturbance for establishment (Lorimer and Frelich 1989). In such cases, date of cohort establishment would be highly, but not perfectly, correlated with date of disturbance.

Detecting disturbance from increases in radial growth works well with shade tolerant species, which can remain in the understory until the canopy opens, increasing light and inducing increases in radial growth (Lorimer and Frelich 1989). In these cases, recruitment into a height class (for example, breast height) should be associated with the disturbance date because of the sudden availability of more light and other resources. However, total age would not necessarily be correlated with the date of disturbance because the advance regeneration could have established over many years. In general, the common oaks in this study are classified as shade mid-tolerant, red maple is shade tolerant, the hickories range in tolerance from mid-tolerant to intolerant, and black birch is generally shade mid-tolerant.

Disturbance Origins

The following section describes peak decades of disturbance, both watershed and region wide and localized at the stand level (Figure A. 13). In addition, we speculate on the disturbance origins based on historical documentation, common disturbances in eastern temperate forests, and radial growth patterns.

1920s, 1930s, and 1940s

The dominating peak in disturbance across all stands in the study was in the 1920s, 1930s, and 1940s (Figure 6 - Figure 9). Every stand in Coweeta and Joyce Kilmer had a peak in disturbance in the 1930s (ranging from 75.4% in stand SB to 19.4% in stand DC). Coweeta stands DC, DY, MG, PM, and RK also show disturbance peaks in the 1940s (ranging from 23.3% in PM to 16.5% in RK). Stands showing a peak in disturbance in the 1920s include Coweeta stands DC, DS, DY, and Joyce Kilmer stand GD (ranging from 46.8% in DS to 18.9% in GD). The peak in the 1920s is likely a result of a combination of factors (see below sections *1900s, 1910s, and 1920s* and *1920s*). Because these peaks were found throughout Coweeta, they were likely watershed wide, and their occurrence at Joyce Kilmer lends evidence to them being region-wide events.

The peaks in recruitment in the 1920s, 1930s, and 1940s correspond to the peaks in decadal disturbance rates (Figure 4 and Figure A. 3). Across all stands, these are the only decades where peaks in age structure and disturbance history consistently coincide. Most of the species recruited into the stands in these decades were not oak, but rather a suite of species that generally have higher growth rates in gaps and are more competitive than oaks in the absence of drought and fire.

In the early 1920s, chestnut blight was found infecting American chestnut trees in the Coweeta Basin (Elliott and Swank, *unpublished manuscript*). These peaks in disturbance are likely due to American chestnut mortality. Chestnut was an important species in the southern Appalachians. At Coweeta in 1934, American chestnut still comprised 41% of the basal area of a single watershed; however, by 1953, American chestnut was reduced to less than 1% (Nelson 1955). Analysis of species composition across all permanent plots found that American chestnut was the most important species in the Coweeta Basin in 1934. It was found in 98% of the plots, comprised 22% of the density, and 36% of the total BA (Elliott and Swank, *unpublished manuscript*). Today in the southern Appalachians, American chestnut primarily occurs as sprouts from trees established before the blight. Sprouts were found in all sample stands, lending evidence of its presence in each stand in the pre-blight era. In addition, several stands still had remnant American chestnut logs.

A pattern of growth was determined for trees surrounding canopy gaps created by American chestnut death in the Great Smoky Mountains (approximately 60 km northwestern of Coweeta) (Woods and Shanks 1959). This pattern showed stages of gradual and rapid increases in growth of surrounding trees following the initial infection of chestnut. Once a tree was infested, the blight gradually killed it in two to four years (Day et al. 1988). However, rapid increases in growth of trees surrounding American chestnut gaps did occur in the five to eight year period following infestation. The varying rates of decline of individual trees make determining a definite signal in the tree rings difficult.

In our study, American chestnut decline likely contributed to peaks in disturbance in the 1930s and 1940s, while the 1920s peak was likely a combination of American chestnut decline, harvesting, and various other stresses (see below section *1920s*). The elimination of American chestnut (a fast-growing shade-intolerant tree, which likely out-competed many other species for dominance) may have allowed other species, particularly red maple, to increase in abundance in these stands since the 1930s. The decrease in competition from American chestnut likely spurred species compositional changes in the stands, such as increases in red maple, while its elimination in the overstory likely caused lateral expansion of codominant trees present at the time of mortality as well as the establishment of new cohorts. Oaks in these stands were likely codominants at the time of the chestnut decline, causing lateral expansion and recruitment into the overstory.

A short term drought was also recorded for the southern Appalachians in 1934 (Biocca et al. 1993). Narrow rings were detected in our study in many trees in 1934, and they were subsequently used as markers years when cross-dating. Sustained decreases in radial growth following 1934 were not typically detected. This stress factor, although not sustained, likely contributed to peaks of disturbance in the 1930s.

Historical documentations of ice storms in western North Carolina also indicate a damaging storm in 1932 (Abell 1934). Standardized growth chronologies detect a year of growth reduction for hickories at Coweeta in 1933 (Table 7), and narrow rings were detected in many of the cores in this year. Reductions could occur after an ice storm if damage was incurred on the tree from the ice itself, or falling branches from other affected trees (Whitney and Johnson 1984). The historical ice storm may have contributed to growth reductions and releases in the 1930s.

The dominating peak in disturbance and recruitment in the 1930s was likely a combination of gaps created from American chestnut mortality and damage and mortality from the ice storm and drought. However, the documented widespread nature and extensive change in the southern Appalachians resulting from chestnut mortality leads us to believe that the blight is the overriding contributor to the peak in this decade.

1900s, 1910, and 1920s

High rates of disturbance occurred in decades preceding the blight in many stands. Peaks in major or total disturbance in the early 1900s included the 1900s (Coweeta stands DS, DY, and Joyce Kilmer stand GD), 1910s (Coweeta stands PM and PR (adjacent stands) and Joyce Kilmer stand GD), and 1920s (DC, DS, DY, and GD). These peaks ranged from 22.3% to 46.8% of canopy area disturbed (Figure 6 - Figure 9). Peaks in recruitment occurred in stand DY and RK in the 1900s, which corresponded to peaks in disturbance. Coweeta stands DC, DS, DY, MG, and Joyce Kilmer stands GD and SB showed peaks in recruitment in the 1920s, coinciding with peaks of disturbance in this decade (Figure 4 and Figure A.3).

Spatial and temporal documentation of harvesting patterns and intensity at Coweeta are lacking; however, the timing of these peaks in disturbance and recruitment coincide with the estimated dates of harvesting at Coweeta. Documentation indicates logging occurred at Coweeta in the early 1900s. The W. M. Ritter Company harvested from 1906 to 1918, and J.A. Porter logged from 1919 to 1923 (Douglass and Hoover 1988). Although exact percentages could not be found, Hale (1883) estimated 20% of the land in Macon and Graham counties were cleared either for agriculture or timber in the late 1800s. By the time logging ceased at Coweeta in 1923, approximately 20% of the basal area of the Basin was harvested (Elliott and Swank, *unpublished manuscript*).

The stands at Joyce Kilmer have no documented harvests. Stand SB has no peaks of disturbance coinciding with decades of high harvest intensity in the region. However, stand GD has similar peak decades of disturbance as the stands likely harvested at Coweeta (1900s, 1910s, and 1920s). Gap origin trees compose the majority of the disturbances detected in the 1910s and 1920s, and recoveries constitute most of the disturbance events in the 1900s. In the 1880s, red maple is present in the stand, and its detected abundance increases from 1910s until the present (40%). However, this apparent increase in red maple may also be an artifact of cohort mortality, with trees alive further back in time undetectable by our study. Red maple readily sprouts and captures canopy gaps, and it is a competitive species, contributing to the evidence supporting disturbance in these decades; however, the reason for its increased abundance is unknown. The only documented disturbance in the early 1900s is a tornado, which may be linked to the detected disturbances (Newell et al. 1997). The stand is located on the border of the wilderness area, where harvesting might not have been restricted, and it is possible that logging might have occurred here and not been documented.

Historical documentations of ice storms in western North Carolina indicate a damaging storm in 1915 (Rhoades 1918). This storm may contribute to peaks in disturbance in the 1910s in Coweeta stands DY, PM, PR, and Joyce Kilmer stand GD. Standardized growth chronologies detect a year of growth reduction for black birch in 1916 (Table 7). Species resistance to ice storm damage varies throughout the literature, with susceptibility extent based on forest type, topographic position, aspect, stand age, and species size classes (Warrillow and Mou 1999, Boerner et al. 1988, Whitney and Johnson 1984). Black birch contributed a large percentage of the stand density in the 1910s in stand PM. Warrillow and Mou (1999) found that intermediate size classes often experienced the most damage during ice storms due to falling branches of larger trees. Most of the black birch in stand PM was young (and likely small) in the 1910s, making it more susceptible to damage from falling branches. The documented ice storm may have contributed to the growth reduction detected in 1916, as well as the peak in disturbance in this decade.

1920s

The occurrence of harvesting and chestnut blight in the 1920s makes separation of these disturbances difficult. Both disturbances show similar patterns of release, with increases in radial growth occurring soon after crown release (Rentch et al. 2002, Woods and Shanks 1959). Based on surveys of cut stumps in permanent plots established in 1934, Elliott and Swank (*unpublished manuscript*) estimated 20% of the total basal area of the stand was removed. However, even after logging subsided, American chestnut was the most important species at Coweeta. Therefore, harvested stands may still have had enough American chestnut present to show further release of surrounding trees following its death.

Because the effects of logging are generally seen within three years of the harvest (Rentch et al. 2002), and harvesting ended at Coweeta in 1923, releases seen in the 1930s and 1940s are likely due to death of American chestnut and not logging. However, harvesting and death of American chestnut likely occurred simultaneously in the 1920s, and our study could not identify patterns of release unique to either disturbance.

In addition to logging and blight in the 1920s, a severe drought and a late freeze were recorded in the southern Appalachians in 1925 (Hursh and Haasis 1931, Beal 1926). The severe drought occurred in July and August, killing and injuring many upper elevation oak species in the southern Appalachians (Hursh and Haasis 1931). The freeze of 1925 occurred in late May and affected only mature trees at high elevations (Beal 1926). Narrow rings were detected in many trees in 1925, and they were subsequently used as markers years when cross-dating. Sustained decreases in radial growth following this dip in 1925 were not typically detected. These stress factors, although not sustained, likely contributed to peaks of disturbance in the 1920s.

1830s and 1840s

Peaks in total and major disturbance in the 1840s occur in Coweeta stands DC, DS, MG, PM, PR and Joyce Kilmer stands GD and SB, and stand RK showed a peak in minor disturbance during this decade. Stands at Coweeta with peaks of disturbance in the 1840s varied from 16.9 to 27.2% canopy area disturbed (Figure 6). A combination of recovery events, releases, and gap origin trees contribute to peaks in disturbance in the 1840s. In addition, stand PR has a peak of disturbance in the 1830s.

In 1835, a hurricane struck Jones Creek (north of Coweeta), causing major blowdown at Coweeta (Douglass and Hoover 1988). The peaks in the 1830s and 1840s may partially be due to damage or mortality from this hurricane. Hurricanes affect the southern Appalachian Mountains every one to 24 years (Greenberg and McNab 1998). These windthrow events occur at varying scales, influencing forest species composition and structure (Canham and Loucks 1984). They can cause considerable gaps in the canopy in addition to single tree falls, which may explain the peaks occurring during these decades. Winds from hurricane Opal (1995) caused gaps at Coweeta ranging in size from 181 to 4043 m^2 (Clinton and Baker 2000).

Stand DC, located on a ridge, had the highest percent canopy area disturbed in the 1840s (27.2%), while stand RK, occupying a lower elevation (1143 m) experienced the lowest canopy area disturbed (16.9%). Most damage from hurricane Opal (1995) occurred on ridges and upper slopes, where shallow soils, large crowns, and saturated soils made trees more susceptible to windthrow (Clinton and Baker 2000). Joyce Kilmer stands experienced peaks in disturbance in the 1840s, as well, with 46.8% canopy area of stand SB disturbed and 15.9% of stand GD affected (Figure 9). Stand SB is a northeast-facing ridge, while GD is a southwest-facing slope. Although wind direction of the hurricane can not be predicted, varying exposures of the two stands to prevailing winds may explain discrepancies between disturbance intensity. Exposure is a combination of slope, aspect, topographic position, and landscape placement relative to other landforms that might provide some barrier to the wind (Foster and Boose 1992). Although prevailing wind direction from hurricanes can often be predicted, the common occurrence of downbursts during hurricanes in the southern Appalachians makes exposure to storms difficult to estimate. Damage from hurricane Opal at Bent Creek Experimental Forest, located in the southern Appalachian Mountains, was concentrated at low elevations, primarily due to greater exposure (Greenburg and McNab 1998).

Species most frequently damaged (uprooted, snapped off, or injured by other falling trees) following hurricane Opal include red maple, scarlet oak, and chestnut oak (Greenburg and McNab 1998). Although species-specific mortality could not be analyzed for the 1835 hurricane, species-specific growth reductions and recoveries around this time were determined. Standardized growth chronologies for chestnut oak at Coweeta (as well as Joyce Kilmer, although sample size is too low to be reliable) show a period of growth reduction from 1837-1839 (Table 7). This may be a result of damage incurred by the high winds from the hurricane.

Standardized growth chronologies for species at Coweeta and Joyce Kilmer show synchronous dips in tree-ring index in 1836 (chestnut oak, white oak) and 1837 (northern red oak, hickory species). These dips in growth, although not defined as growth reductions (except chestnut oak), are likely due to damage from the hurricane as well. Species showing recoveries in the 1840s include white oak, chestnut oak, and northern red oak. It is unclear if other species would show similar trends if more abundant in the stands in the 1840s. Red maple, the most frequently damaged species after hurricane Opal, did not extend far enough back in time to be analyzed for the 1835 hurricane, and scarlet oak was not abundant enough in the stands to be examined.

1960s

Coweeta stands DC, DY, PM, PR, RK, and Joyce Kilmer stand GD showed peaks in total disturbance in the 1960s, consisting mostly of recovery events and moderate releases (Figure 6 - Figure 9). Peaks ranged from 20.8 to 45.3% canopy area disturbed. In addition, standardized growth chronologies at Coweeta show dips in growth in the early 1960s for white oak, northern red oak, hickories, chestnut oak, and black birch; however, red maple was the only species to meet the growth reduction criteria for this time period (1959-1963) (Table 7). Species showing releases in the 1960s in stands where a peak decade of disturbance was detected include red maple, northern red oak, black oak, black birch, chestnut oak, black cherry (*Prunus serotina* Ehrh.), white ash (*Fraxinus americana* L.), hickory species, sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), yellow poplar (*Liridendron tulipifera* L.), downy serviceberry (*Amalanchier arborea* (Michx. f.) Fern.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.). Red maple in stands at Joyce Kilmer showed a similar period of growth reduction from 1959-1962. Only Coweeta stands MG and PM and Joyce Kilmer stand SB show any recruitment in the 1960s. This may be because we only cored trees 10 cm DBH or greater, and no saplings were aged.

Declining radial growth of oak species across the southern Appalachians has been reported for the 1950s and 1960s (Tainter et al. 1990, Phipps and Whiton 1987, Tainter et al. 1984, Tryon and True 1958), including the Wayah Bald district of the Nantahala Mountains in western North Carolina (Biocca et al. 1993). These decreases in growth have been attributed to oak decline, an interaction between climatic conditions (drought, late freeze), insect infestations, and fungal pathogens (shoestring fungus) causing reduced growth (Oak et al. 2004, Biocca et al. 1993, Tainter et al. 1990, Phipps and Whiton 1988). Interactions between drought and insect defoliation may account for the peaks of disturbance in the 1960s.

Climate data for Coweeta show below average precipitation values for the early 1950s (Figure A. 20). In general, trees recovery quickly from short term droughts; however, if the low precipitation initiates an onset of further stresses (e.g. insect infestations, wind stress, fungal pathogens), prolonged decreases in radial growth may occur (Tainter et al. 1990). The short term droughts of the early 1950s, along with insect infestations may have caused growth reduction and release of trees in this study.

In the southern Appalachians, elm spanworm (*Ennomos subsignarius* Hubner) defoliated 1.6 million acres of forest from 1954-1964s (peaking in 1960) (Drooz et al. 1976). Elm spanworm primarily defoliates oaks, hickories, black walnut (*Juglans nigra* L.), white ash , black gum (*Nyssa sylvatica* Marsh.), and red maple (Drooz 1980, Fedde 1964). In 1960, the insect's egg masses were found throughout Coweeta (Grzenda et al. 1964). The entire Basin was sprayed with DDT in 1961, and the upper ridges and slopes were subsequently sprayed in 1962. The effect of the DDT sprayings on controlling the outbreak was not reported (Grzenda et al. 1964). The outbreak ended in 1964, largely due to elm spanworm egg parasitism by *Telenomus* species (Ciesla 1963).

Red maple at Joyce Kilmer also shows the highest percent canopy area disturbed in the 1960s (34.2% canopy area disturbed in GD and 8.2% in stand SB). Lack of growth reduction of oak species may be a result of mortality of affected trees. Trees released in the 1960s are generally younger, and much recruitment generally occurred in the 1930s. Mortality of overstory trees as a result of drought and elm spanworm may have caused canopy gaps, allowing for release of younger (and perhaps smaller) trees. Younger trees may have been more vigorous and able to recovery from drought and elm spanworm infestations. The outbreaks caused symptoms of decline as well as mortality in affected trees (Ciesla 1963), explaining the presence of recoveries and releases in sample stands.

An extensive elm spanworm infestation was recorded on Rich Mountain (southwest of Coweeta) in 1878, peaking in 1881 (Dodge 1882). The infestation was reported in counties south and west of Coweeta, but no documentation of the outbreak was found for North Carolina. Coweeta stands DS and RK showed a peak in disturbance in the 1870s, but no stands showed a peak of disturbance in the 1880s. Elm spanworm infestations may have contributed to the peak, but because it is not seen across the stands, the outbreak was likely not as severe as it was in the 1960s.

1980s

Coweeta stands DC, PM, and Joyce Kilmer stand GD in this study show a peak in disturbance in the 1980s, and stand PR shows a peak in the early 1990s (Figure 6 - Figure 9). A major drought was recorded at Coweeta from 1985-1988 (peaking in 1986), which may contribute to peaks of disturbance in these stands (Clinton et al. 1993). During the peak year, precipitation was 31% below average. Gaps were surveyed following the drought, and Clinton et al. (1993) found 74% of the gaps were standing dead trees, and 67% were on ridges and mid-slopes. Oak species were the source of 84% of the gap makers, primarily scarlet oak.

Although Clinton et al. (1993) found high mortality rates in mature oak species following the 1980s drought, oak species in the stands at Coweeta (DC, PM, and PR) show a release in the 1980s. Kloeppel et al. (2003) found that growth rates of oak species remain relatively constant through drought periods due to their deep root systems allowing them to pull water from deeper soil in times of low precipitation. Oak species likely took advantage of their ability to draw on deep water in the 1980s, when mortality was high due to low precipitation or secondary causes (e.g. shoestring fungus). The only species analyzed showing growth reduction in the 1980s was hickory.

At Joyce Kilmer, stand GD shows a peak in disturbance in the 1980s; however, the primary species released was red maple. White oak experienced a growth reduction from 1984-2003 (Table 7). The factors causing white oak growth reduction likely prevented the species from taking advantage of freed resources and growing space in the 1980s, thus allowing red maple to be released.

Disturbances of Unknown Origin

Although not watershed wide, peaks in disturbance also occurred in more than one stand in the 1860s and 1870s. Historical documentation of forest disturbance in these decades could not be found. The disturbances detected in the 1860s and 1870s are characterized by trees of gap origin, major releases, moderate releases, and recovery events (detected in Coweeta stands RK, MG, DC, and DS) (Figure 6). Standardized growth chronologies detected periods of growth reduction in the 1860s in northern red oak trees at Joyce Kilmer (Table 7). Oak species dominated the known species composition in most stands at this time, making the determination of species-specific disturbances difficult. Peaks in recruitment occurred in stands DC and RK in these decades. Peaks in decadal disturbance rates further back in time in the other stands may correspond to peaks in recruitments that are not detectable anymore because of cohorts of shorter-lived species dying out (Johnson et al. 1994).

Peaks in disturbance occurring in decades unique to only one stand include the 1820s and 1970s in DS, 1750s and 1810s in stand DC, 1850s in stand PR, and the1790s in stand GD (Figure 6 - Figure 9). These disturbances were likely more localized instead of basin or region wide. The peaks may be a result of disturbances similar to those discussed above, such as hurricanes or wind damage, insect defoliations, or extreme drought. They could alternatively be due to other disturbances common to the southern Appalachians, including ice storm, lightning caused fire, or interactions of these events. However, some of these disturbances may be more likely to occur in isolation than others. For example, extreme drought would not be localized at the stand level whereas wind might be relatively local. Our data do not allow us to separate these possibilities.

Ice Storms

A signal identifying ice storms in the southern Appalachians has been developed; however, climatic variation must first be subtracted out so droughts will not be interpreted as glaze events (Lafon and Speer 2002). Climatic data extending past 1895 were not attainable for this study; therefore the signal was not utilized to detect ice storms. However, ice storms occur locally in the southern Appalachian Mountains frequently (Abell 1934) and are likely contributors to peaks of disturbance at Coweeta. The damage incurred by the storms created canopy gaps, allowing release of trees less affected by the glaze (Lemon 1961).

Ice storms in southwest Virginia were detected in 1911, 1918, 1920, 1925, and 1934 from tree rings (Lafon and Speer 2002). Decreases in ring width were detected in 1911, 1925, and 1934 in our study; however, there were also documented severe short-term droughts associated with these years, making separation from ice damage difficult. The disturbances may have occurred in the same year, both contributing to the decrease in ring widths.

Fire

Historically, fire was been an important disturbance in the southern Appalachian Mountains, reducing competition and maintaining xeric oak-pine and mixed-oak forest types (Harrod et al. 2000, Harrod et al. 1998, Abrams and Nowacki 1992). However, we found no evidence of fire in the tree rings at Coweeta. This may be due to our inability to detect evidence of fire in the cores or their infrequency at Coweeta. Fire scars are rapidly compartmentalized in oaks, leaving no evidence of fire on the bark and not leaving scars at all unless fire intensity is great enough to kill the cambium (Smith and Sutherland 1999, Harmon 1982). In addition, all scars resulting from low-intensity fires in Ohio were below one meter in height, which was coring height for this study (Smith and Sutherland 1999). Therefore, if our cores did not by chance encounter a scar, we would likely not detect fire.

Fires were probably infrequent in sample stands at Coweeta due to the upper elevations forests averaging 2000 mm/year of precipitation and experiencing cooler temperatures. In addition, stands were located primarily on north and east slopes, where lightning fire ignitions are generally lower than on south and west aspects (Bratton and

Meier 1998, Harmon 1982). In the Great Smoky Mountains (northwest of Coweeta) and the Chattooga River Watershed (just south of Coweeta), lightning strikes primarily occur on south and west aspects and ridges, varying in elevation with topography (Bratton and Meier 1998, Barden and Woods 1974). In general, lightning strikes were found to be less frequent at higher elevations with cooler moister climate (Bratton and Meier 1998, Barden and Woods 1974).

A return fire interval of 12.7 years was calculated for xeric oak-pine forests in Great Smoky Mountain National Park from 1856 to 1940 (Harmon 1982). Estimates were not made for more mesic mixed-oak forests; however, return intervals were predicted to be longer than for xeric forests (Harmon 1982). Historical records of the Chattooga River Watershed estimate 4 lightning ignitions 100,000 ha^{-1} yr^{-1} (Bratton and Meier 1998). In addition, the portion of this watershed closest in location to Coweeta displayed the lowest frequency of fire.

Disturbance History Along Topographic and Compositional Gradients

Significant relationships were detected between decadal disturbance rates and species composition. Elliott et al. (1999) found that environmental variables explained only 50% of the variation in species composition across Coweeta. They hypothesized that disturbance might account for additional variation not explained by site factors. Correlations between disturbance matrices and species composition lends support to this hypothesis.

Species recruitment and survival characteristics might be more related to disturbance intensity than environmental characteristics (Ruffner and Abrams 2003).

Species capable of recruiting across environmental gradients (e.g. red maple, black birch) may be better competitors and more likely to recruit after intense disturbances that affect the canopy enough to increase the amount of light that reaches the forest floor. Similarly, shade mid-tolerant species (e.g. oak species) may prefer different disturbance regimes where competition is reduced, preventing competing species from establishing (Crow 1988). The disturbance characteristics may dictate if species composition changes with varying disturbances (Frelich et al. 1993, Clebsch and Busing 1993, Harmon et al. 1982). If disturbance type maintains the gap characteristics needed for current species recruitment (such as wind disturbances in the upper Great Lakes region), the species composition may not correlate with disturbance regimes (Frelich et al. 1993).

Species composition and disturbance patterns may also be correlated because of species-specific disturbances, such as insect outbreaks (Fraver 2004). In this study, the distribution of American chestnut likely influenced the percent canopy area disturbed in the 1920s, 1930s, and 1940s. The response of the forest vegetation to American chestnut decline has been found to be correlated with chestnut density. New recruitment and establishment occurred where chestnut density was high; while lateral expansion of trees surrounding canopy gaps occurred on sites where chestnut density was lower (Woods and Shanks 1959). Therefore, where chestnut was more abundant, the resulting species composition is composed of shade intolerant species and opportunistic competitors during chestnut decline; where chestnut was less abundant, the species composition may remain constant, with canopy gaps filling in with lateral expansion instead of new recruitment (Harmon et al. 1982).

No significant relationships were found between decadal disturbance rates and environmental variables (elevation and slope). Often, disturbance intensity and frequency increase with elevation and exposure (Ruffner and Abrams 2003, Clinton and Baker 2000). These relationships were not found between disturbances and elevation in our study. This may be due to the relatively similar environmental characteristics of the stands. Studies determining relationships between increasing disturbance intensity and frequency with elevation and exposure often compare a greater range of forest types, such as riparian, side slopes, and upland terrains (Ruffner and Abrams 2003, Whitney 1984). Stand sampled at Coweeta generally fell into a more narrow classification of mixed-oak stands along a slope. Exposure was not quantified for the stands, which may have better explained variation in decadal disturbance rates.

To determine patterns within the matrix of all forest types at Coweeta, stands were placed in a graph modified from Day et al. (1988) (Figure 16). There were not any obvious patterns when average decadal disturbance rates were attached to the placement of the stands in this graph.

Environmental variables, such as elevation, slope, aspect, and topography influence species composition patterns in southern Appalachian forests (Elliott et al. 1999, Bolstad et. al. 1998, Day et al. 1988, Day and Monk 1974, Whittaker 1956). Elliott et al. (1999) and Bolstad et al. (1998) describe changes in species composition, density, and basal area with changes in environmental variables, such as elevation, slope, and terrain shape (a value derived from digital calculations of elevation, slope, aspect, and landform). The analyses spanned the entire Coweeta Basin, from low elevation cove forests, to mid elevation slopes and ridges, to high elevation terrain. Community types, such as xeric oak-pine and mesic cove hardwoods could be distinguished by elevation and terrain shape. However, much of Coweeta is composed of transitional forests, classified as mixed-deciduous and composed of ubiquitous species such as red maple, which can not easily be separated into unique groups (Elliott et al. 1999).

No significant relationships were found between patterns of species composition and patterns of slope and elevation among stands. The sample stands may be within the “transitional” forest types at Coweeta, with many species common across a variety of elevations and slopes. Patterns of species composition may not be correlated to patterns in elevation and slope in the sample stands they fall within a narrow range of forest type with many ubiquitous species.

Significant linear relationships between the ordination scores based of species composition and environmental variables occurred in the stands. Elevation and slope both increase along Axis 1, with black birch found at the highest elevations and steepest slopes. As elevation and slope increase within the mixed oak forest type, stands begin to include species also found in northern hardwood forests. This pattern was also seen when stands were placed in the Day et al. (1988) graph, with the two high elevation stands with high abundances of species associated with northern hardwood forest types (e.g. yellow birch, black birch, basswood, eastern hop-hornbeam). Stands MG and PM may be transitional between oak (-chestnut) and northern hardwood types. At lower elevations and slopes, species more common across all mixed deciduous forests (e.g. red maple and chestnut oak) are more abundant. Expansion of environmental variables tested (e.g. soil moisture, soil aeration, exposure, solar radiation) might further explain species distribution (Ruffner and Abrams 2003, Day et al. 1988, Mowbray and Oosting 1968).

CCA were also used to assess the relationships between the various gradients. While DCA is most often used to evaluate the relationships of the stands to each other based on species composition alone, CCA relates vegetation variation directly to environmental variables (Gauch 1992). In a CCA, all of the variation due to environmental variables not examined is not taken into account (Okland 1996). Because the number of environmental variables analyzed was limited in our study, indirectly relating slope and elevation to the species composition to evaluate gradients may be more appropriate. DCA and subsequent correlations with environmental variables revealed that elevation and slope are significantly correlated with species composition in the stands; however, they are likely not the only explanatory variables (Okland 1996).

Remnant Old Trees

Old growth forests are rare in the southern Appalachian Mountains as a result of anthropogenic disturbances in the past 150 years (e.g. logging, chestnut blight). Many studies use remnant old-growth trees located in second-growth forests to determine presettlement disturbance regimes (Rentch et al. 2003, Nowacki and Abrams 1997). Old trees at Joyce Kilmer, an old-growth forest with no documented harvests, were compared to old trees at Coweeta, with the intensity and spatial variation of the harvests unknown.

At Coweeta, selective harvesting of trees over 31 cm at the stump occurred until 1923. Stands containing remnant old-growth trees were used in this study. Remnant old-growth trees could remain in the stands for several reasons, including small diameter, poor form, or some other reason such as inaccessibility. It is unclear if these old-growth trees are an adequate representation of the presettlement forests. If they were left because of poor form, it is unclear if their tree rings would record disturbance events in the same manner as old-growth trees in an intact undisturbed forest.

Standardized growth chronologies of old trees at Joyce Kilmer were significantly correlated to old trees at Coweeta. Various conclusions could be drawn from these results. Joyce Kilmer stand GD has similar peaks in disturbance in the decades logging was widespread at Coweeta. These peaks may be from various other disturbances occurring in the same decades, causing trees to experience similar growth trends as those with harvests releasing them. It is also possible that logging occurred in this stand during these decades and was not recorded. The intensity of harvesting is unknown at Coweeta. However, Elliott and Swank (*unpublished manuscript*) estimate that approximately 20% of the basal area of the Basin was harvested between 1906 and 1918. However, typically low elevation mesic coves were harvested first and most intensively. Stands sampled for this study are located primarily on higher elevations slopes and ridges. These stands may have been harvested less intensively, causing the growth patterns of old trees to correlate to old trees at Joyce Kilmer.

Further evidence that remnant old trees respond similarly to trees in old-growth stands is the similar decadal disturbance rates of stands in Coweeta and Joyce Kilmer. Average decadal disturbance rates at Joyce Kilmer are also comparable to rates in eastern temperate forests (15% for stand GD and 18% for stand SB) (Runkle 1982). In fact, these rates are slightly higher than rates found at Coweeta, which is unexpected since there is no documentation of logging at Joyce Kilmer. The high average decadal disturbance rate in stand SB may be due to the peak in the 1930s (75.4%). The stand was likely greatly affected by the chestnut blight in the 1930s. Stand GD has average rates and patterns more comparable to stands at Coweeta. The decadal disturbance rates may be high in these old-growth stands when compared to stands at Coweeta because of their ridge-top location. Although disturbance rates are not correlated with elevation and aspect, exposure was not examined. Other studies have shown an increase in disturbance rates associated with exposure, with the highest rates on exposed ridges (Ruffner and Abrams 2003, Whitney 1984).

Another possible explanation of the slightly higher disturbance rates in the Joyce Kilmer stands when compared to the stands at Coweeta is the abundance of large canopy trees at times of large disturbances, such as the chestnut blight. In the Coweeta stands, large trees (especially American chestnut) may have been harvested in the early 1900s, resulting in fewer present at the peak of the blight. At Joyce Kilmer, the presence of more American chestnut trees at the time of the blight would have caused more canopy gaps and higher decadal disturbance rates in this decade.

CONCLUSIONS

The decadal disturbance rates at Coweeta and Joyce Kilmer since the mid-1700s (8.7%-18.3%) fall within the range typically found in eastern temperate forests (5%-20%) (Runkle 1982). Similar patterns of disturbance appear across all stands, with decades of constant low rates of disturbance intermixed with peaks of more intense events. The large pulses of disturbance were widespread, affecting stands across Coweeta and Joyce Kilmer. However, there were also scattered pulses of disturbance unique to single stands, suggesting that localized canopy gaps also play a role in the disturbance dynamics. Constant low rates of disturbance present in all stands indicate the importance of small canopy gaps in these forests as well. Age structure patterns coincided with peaks in disturbances in certain decades; however, consistent pulses in recruitment following disturbance events were not detected. This may be due in part to the intermediate shade tolerance (oaks, black birch, and hickories) and high shade tolerance (red maple) of common species, able to remain in the understory for extended periods of time.

Combining peaks in disturbance, age-structures, growth reductions, and historical documentation, the origin of peak disturbance decades can be speculated upon. American chestnut mortality, combined with a severe drought and ice storm, likely caused the dominating peak in disturbance in the 1930s. Harvesting at Coweeta contributed to peaks in disturbance in the 1900s, 1910s, and 1920s. Logging and American chestnut mortality occurred simultaneously in the 1920s, making the distinction of these events difficult. Peaks of disturbance across stands also occurred in the 1840s and 1960s, likely attributable to windthrow from a hurricane and drought and insect damage. The 1860s and 1870s were peak decades for many stands; however, the disturbance origin is unknown. Localized pulses of disturbance were likely caused by disturbances common to the southern Appalachians, such as windthrow, drought, ice storms, or insect outbreaks. As seen in many decades (1910s, 1920s, 1930s, 1960s), combinations of disturbance events and stresses contribute to pulses in canopy area disturbed.

We found that stands similar in disturbance regimes were also similar in species composition. This may be due to species-specific disturbances or disturbance events causing similar changes in species composition across stands. We did not, however, find that species with similar disturbance patterns also had similar topographic characteristics, which may be due to the relatively similar environmental characteristics of the stands or the widespread nature of the disturbances pulses. Species composition was correlated with elevation and slope, with species such as black birch more common at higher elevations and steeper slopes and species such as red maple and chestnut oak more common at lower elevations and lesser slopes. Additional environmental variables (such as exposure or soil moisture) may further explain these trends.

Comparing remnant old trees in second-growth stands at Coweeta with old-growth trees at Joyce Kilmer, we found similar disturbance histories, both before and after European settlement in the 1900s. Using remnant old trees in previously disturbed stands to discern disturbance regimes back in time seems plausible.

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APPENDIX

Table A. 1. Physical landmark near the sample stands, location, and stand abbreviation.

Physical landmark	Location	Stand abbreviation
Devils Ball Alley Cliff	Coweeta	DC
Devils Ball Alley Slopes	Coweeta	DS
Dyke Gap Road	Coweeta	DY
Mooney Gap	Coweeta	MG
Pinnacle Mountain	Coweeta	PM
Pinnacle Mountain rhododendron	Coweeta	PR
Rich Knob	Coweeta	RK
Goldie Deaden	Joyce Kilmer	GD
Stratton Bald	Joyce Kilmer	SB

Table A. 2. Density (stems/ha) of all species at Coweeta and Joyce Kilmer.

	Coweeta							Joyce Kilmer	
Species	DC	DS	DY	MG	PM	PR	RK	GD	SB
Black birch	12	14	0	101	290	40	40	0	26
Black cherry	0	3	0	0	4	0	20	0	0
Black gum	0	23	1	0	0	0	2	1	0
Black locust	1	8	0	48	4	26	13	54	7
Black oak	6	0	1	0	0	0	2	0	1
Basswood	0	0	0	0	8	0	4	0	0
Cucumber magnolia	13	0	0	0	0	0	3	0	0
Chestnut oak	31	9	26	1	0	88	17	78	1
Downy serviceberry	105	41	0	28	3	0	0	6	0
Eastern hemlock	3	2	0	0	0	0	0	0	12
Eastern hop-hornbeam	0	0	0	0	60	0	0	0	0
Hickory	68	15	66	0	0	14	14	35	54
Red maple	61	53	70	3	26	18	14	294	91
Red oak	39	93	47	61	95	91	42	68	93
Silverbell	0	0	0	0	0	0	0	19	156
Sugar maple	0	8	0	0	33	0	0	0	0
Scarlet oak	0	0	1	13	0	0	0	0	0
Sourwood	3	0	8	0	0	0	0	0	0
Striped maple	0	0	0	0	26	0	0	0	0
White ash	0	20	0	0	21	0	9	0	0
White oak	83	19	0	0	1	13	28	40	10
Yellow birch	0	23	0	35	22	3	0	0	0
Yellow poplar	0	13	3	0	2	0	10	0	14
Total	425	345	223	290	595	292	217	596	467

Table A. 3. Basal area (m^2/ha) for all species at Coweeta and Joyce Kilmer.

	Coweeta							Joyce Kilmer	
Species	DC	DS	DY	MG	PM	PR	RK	GD	SB
Black birch	0.8	0.6	0.0	3.6	10.0	1.6	3.6	0.0	0.7
Black cherry	0.0	0.6	0.0	0.0	0.8	0.0	2.0	0.0	0.0
Black gum	0.0	0.5	0.3	0.0	0.0	0.0	0.2	0.3	0.0
Black locust	0.2	0.8	0.0	1.2	0.4	0.8	0.8	1.3	0.7
Black oak	0.8	0.0	0.3	0.0	0.0	0.0	0.4	0.0	0.3
Basswood	0.0	0.0	0.0	0.0	0.8	0.0	0.2	0.0	0.0
Cucumber magnolia	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Chestnut oak	3.6	0.8	3.3	0.4	0.0	4.8	1.4	5.5	0.3
Downy serviceberry	1.8	0.9	0.0	0.8	0.4	0.0	0.0	0.3	0.0
Eastern hemlock	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.7
Eastern hop-hornbeam	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0
Hickory	2.2	1.2	3.7	0.0	0.0	1.2	0.8	0.5	2.7
Red maple	1.8	2.0	5.7	0.8	0.0	0.8	1.2	9.0	4.7
Red oak	5.0	12.8	7.3	13.2	20.0	14.4	6.6	6.0	20.0
Silverbell	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	4.0
Sugar maple	0.0	0.5	0.0	0.0	0.8	0.0	0.0	0.0	0.0
Scarlet oak	0.0	0.0	0.3	2.0	0.0	0.0	0.0	0.0	0.0
Sourwood	0.4	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Striped maple	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
White ash	0.0	0.5	0.0	0.0	0.8	0.0	0.8	0.0	0.0
White oak	11.6	4.8	0.0	0.0	0.4	2.4	4.0	4.8	1.0
Yellow birch	0.0	1.1	0.0	1.2	1.6	0.4	0.0	0.0	0.0
Yellow poplar	0.0	1.2	0.3	0.0	0.4	0.0	0.4	0.0	1.0
Total	28.6	28.3	21.7	23.2	37.6	26.4	22.6	27.8	36.0

Table A. 4. a) Relative density (stems/ha) and b) relative basal area (m^2/ha) of all species at Coweeta and Joyce Kilmer.

a)

	Coweeta							Joyce Kilmer	
Species	DC	DS	DY	MG	PM	PR	RK	GD	SB
Black birch	3	4	0	35	51	14	18	0	6
Black cherry	0	1	0	0	1	0	9	0	0
Black gum	0	7	0	0	0	0	1	0	0
Black locust	0	2	0	16	1	9	6	9	2
Black oak	1	0	0	0	0	0	1	0	0
Basswood	0	0	0	0	1	0	2	0	0
Cucumber magnolia	3	0	0	0	0	0	1	0	0
Chestnut oak	7	3	12	0	0	30	8	13	0
Downy serviceberry	25	12	0	10	0	0	0	1	0
Eastern hemlock	1	1	0	0	0	0	0	0	3
Eastern hop-hornbeam	0	0	0	0	11	0	0	0	0
Hickory	16	4	30	0	0	5	6	6	11
Red maple	14	15	31	1	0	6	6	49	20
Red oak	9	27	21	21	17	31	20	11	20
Silverbell	0	0	0	0	0	0	0	3	33
Sugar maple	0	2	0	0	6	0	0	0	0
Scarlet oak	0	0	0	4	0	0	0	0	0
Sourwood	1	0	4	0	0	0	0	0	0
Striped maple		0	0	0	5	0	0	0	0
White ash	0	6	0	0	4	0	4	0	0
White oak	19	6	0	0	0	4	13	7	2
Yellow birch	0	7	0	12	4	1	0	0	0
Yellow poplar	0	4	1	0	0	0	5	0	3

b)

	Coweeta							Joyce Kilmer	
Species	DC	DS	DY	MG	PM	PR	RK	GD	SB
Black birch	2.8	2.2	0.0	15.5	26.6	6.0	15.9	0.0	1.9
Black cherry	0.0	2.2	0.0	0.0	2.1	0.0	8.8	0.0	0.0
Black gum	0.0	1.6	1.5	0.0	0.0	0.0	0.9	0.9	0.0
Black locust	0.7	2.7	0.0	5.2	1.1	3.0	3.5	4.5	1.9
Black oak	2.8	0.0	1.5	0.0	0.0	0.0	1.8	0.0	0.9
Basswood	0.0	0.0	0.0	0.0	2.1	0.0	0.9	0.0	0.0
Cucumber magnolia	0.7	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0
Chestnut oak	12.6	2.7	15.4	1.7	0.0	17.9	6.2	19.8	0.9
Downy serviceberry	6.3	3.3	0.0	3.4	1.1	0.0	0.0	0.9	0.0
Eastern hemlock	0.7	0.5	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Eastern hop-hornbeam	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0
Hickory	7.7	4.3	16.9	0.0	0.0	4.5	3.5	1.8	7.4
Red maple	6.3	7.1	26.2	3.4	0.0	3.0	5.3	32.4	13.0
Red oak	17.5	45.1	33.8	56.9	53.2	53.7	29.2	21.6	55.6
Silverbell	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	11.1
Sugar maple	0.0	1.6	0.0	0.0	2.1	0.0	0.0	0.0	0.0
Scarlet oak	0.0	0.0	1.5	8.6	0.0	0.0	0.0	0.0	0.0
Sourwood	1.4	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0
Striped maple	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0
White ash	0.0	1.6	0.0	0.0	2.1	0.0	3.5	0.0	0.0
White oak	40.6	16.8	0.0	0.0	1.1	9.0	17.7	17.1	2.8
Yellow birch	0.0	3.8	0.0	5.2	4.3	1.5	0.0	0.0	0.0
Yellow poplar	0.0	4.3	1.5	0.0	1.1	0.0	1.8	0.0	2.8

Table A. 5. a) Importance values ((relative BA + relative density)/2) and b) frequency (%) of all species at Coweeta and Joyce Kilmer.

a)

	Coweeta							Joyce Kilmer	
Species	DC	DS	DY	MG	PM	PR	RK	GD	SB
Black birch	2.8	3.0	0.0	25.2	38.8	9.2	17.1	0.0	3.7
Black cherry	0.0	1.5	0.0	0.0	1.4	0.0	9.0	0.0	0.0
Black gum	0.0	4.1	0.9	0.0	0.0	0.0	0.9	0.5	0.0
Black locust	0.5	2.5	0.0	10.8	0.9	5.5	4.8	6.8	1.7
Black oak	2.1	0.0	1.0	0.0	0.0	0.0	1.3	0.0	0.6
Basswood	0.0	0.0	0.0	0.0	1.8	0.0	1.4	0.0	0.0
Cucumber magnolia	1.9	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0
Chestnut oak	9.9	2.7	13.5	1.1	0.0	22.8	6.9	16.4	0.6
Downy serviceberry	15.5	7.5	0.0	6.6	0.8	0.0	0.0	1.0	0.0
Eastern hemlock	0.7	0.5	0.0	0.0	0.0	0.0	0.0	0.0	2.3
Eastern hop-hornbeam	0.0	0.0	0.0	0.0	6.4	0.0	0.0	0.0	0.0
Hickory	11.9	4.4	23.2	0.0	0.0	4.4	5.0	3.9	9.4
Red maple	10.4	11.3	28.7	2.2	0.0	4.3	5.8	40.9	16.3
Red oak	13.3	36.0	27.5	39.0	34.9	41.1	24.4	16.6	37.8
Silverbell	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	22.3
Sugar maple	0.0	2.0	0.0	0.0	4.0	0.0	0.0	0.0	0.0
Scarlet oak	0.0	0.0	1.0	6.5	0.0	0.0	0.0	0.0	0.0
Sourwood	1.1	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0
Striped maple	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.0
White ash	0.0	3.7	0.0	0.0	2.9	0.0	3.9	0.0	0.0
White oak	30.0	11.2	0.0	0.0	0.6	6.5	15.3	11.9	2.5
Yellow birch	0.0	5.3	0.0	8.6	4.1	1.2	0.0	0.0	0.0
Yellow poplar	0.0	4.1	1.4	0.0	0.7	0.0	3.2	0.0	2.9

b)

	Coweeta							Joyce Kilmer	
Species	DC	DS	DY	MG	PM	PR	RK	GD	SB
Black birch	40	23	0	100	100	20	50	0	33
Black cherry	0	23	0	0	20	0	40	0	0
Black gum	0	15	17	0	0	0	10	13	0
Black locust	10	31	0	20	20	40	20	13	33
Black oak	20	0	17	0	0	0	20	0	17
Basswood	0	0	0	0	40	0	10	0	0
Cucumber magnolia	10	0	0	0	0	0	10	0	0
Chestnut oak	70	15	83	20	0	100	30	88	17
Downy serviceberry	50	38	0	40	20	0	0	13	50
Eastern hemlock	10	7.7	0	0	0	0	0	0	33
Eastern hop-hornbeam	0	0	0	0	40	0	0	0	0
Hickory	70	46	67	0	0	20	40	25	83
Red maple	50	62	100	20	0	40	50	100	0
Red oak	90	100	100	100	100	100	100	100	100
Silverbell	0	0	0	0	0	0	0	13	100
Sugar maple	0	15	0	0	40	0	0	0	0
Scarlet oak	0	0	17	0	0	0	0	0	0
Sourwood	20	0	17	0	0	0	0	0	0
Striped maple	0	0	0	0	20	0	0	0	0
White ash	0	15	0	0	40	0	30	0	0
White oak	90	69	0	0	20	20	70	100	33
Yellow birch	0	31	0	40	60	20	0	0	0
Yellow poplar	0	46	17	0	40	0	20	0	50

Table A. 6. Sapling density (stems/ha) for Coweeta and Joyce Kilmer. See Table A. 7. for sapling abbreviations.

Stand	Location	AC	AD	BB	BC	BG	BL	BN	BW	CH	CM	CO	DS	DW	EH	FA	FM	HB	HY	ML	MV	RM
DC	Coweeta	680	0	210	20	0	40	110	0	10	0	30	160	0	0	2010	20	12	90	480	0	670
DS	Coweeta	323	0	31	15	0	0	15	15	0	0	8	92	0	0	769	23	0	108	8	0	638
DY	Coweeta	683	0	67	0	0	0	250	0	0	0	0	0	33	33	317	200	0	0	0	67	483
MG	Coweeta	420	0	0	0	0	120	0	0	0	0	0	360	0	0	3220	0	0	20	0	0	240
PM	Coweeta	180	0	20	0	0	60	0	220	0	0	0	0	0	20	0	0	0	0	0	0	20
PR	Coweeta	80	0	20	0	0	0	0	0	0	0	0	40	0	0	580	0	0	0	0	0	40
RK	Coweeta	430	20	290	50	70	40	210	40	0	10	0	0	10	0	70	0	0	30	0	60	680
GD	JK	1038	0	0	25	38	175	6113	0	0	0	0	38	0	0	500	0	0	0	63	13	488
SB	JK	300	0	0	200	33	167	0	0	117	17	0	67	0	0	0	0	0	0	0	0	367

(continued)

Stand	Location	RO	RR	SB	SF	SM	SS	ST	SW	VC	WA	WH	WO	YB	YE	YP
DC	Coweeta	90	270	0	110	0	0	420	0	210	0	0	10	0	0	0
DS	Coweeta	46	69	0	23	300	8	362	0	92	100	46	0	62	15	46
DY	Coweeta	33	67	0	17	0	33	117	0	0	0	0	0	0	0	100
MG	Coweeta	100	1640	0	0	0	0	80	0	0	60	0	0	60	0	0
PM	Coweeta	0	0	0	0	260	0	1180	0	20	80	0	0	60	0	320
PR	Coweeta	0	2800	0	0	0	0	40	0	140	0	40	0	0	0	0
RK	Coweeta	120	150	0	40	0	480	320	10	10	100	0	0	0	0	0
GD	JK	25	0	188	38	0	0	13	0	13	0	0	0	0	0	0
SB	JK	17	0	1783	67	100	0	67	0	0	17	0	0	0	0	167

Table A. 7. Common names, Latin names, and species abbreviations for saplings and shrubs at Coweeta and Joyce Kilmer.

Common name	Latin name	Abbreviation
Alternate-leaf dogwood	*Cornus alternifolia* L. f.	AD
American chestnut	*Castanea dentata* (Marsh.) Borkh.	AC
Basswood	*Tilia americana* L.	BW
Black birch	*Betula lenta* L.	BB
Black cherry	*Prunus serotina* Ehrh.	BC
Black gum	*Nyssa sylvatica* Marsh.	BG
Black locust	*Robinea pseudoacacia* L.	BL
Buffalo nut	*Pyrularia pubera* Michx.	BN
Carolina holly	*Ilex montana* L.	CH
Chestnut oak	*Quercus prinus* L.	CO
Cucumber magnolia	*Magnolia acuminata* L.	CM
Dogwood	*Cornus florida* L.	DW
Downy serviceberry	*Amalanchier arborea* (Michx. f.) Fern.	DS
Eastern hemlock	*Tsuga canadensis* (L.) Carr.	EH
Eastern hop-hornbeam	*Ostrya virginiana* (Mill.) K. Koch.	HH
Flame azalea	*Rhododendron calendulaceum* L.	FA
Fraser magnolia	*Magnolia fraseri* L.	FM
Hickory spp.	*Carya* spp.	HY
Huckleberry	*Gaylussacia ursine* (Curtis.) Torr. & Gray.	HB
Maple-leaved viburnum	*Viburnum acerifolium* L.	MV
Mountain laurel	*Kalmia latifolia* L.	ML
Red maple	*Acer rubrum* L.	RM
Red oak	*Quercus rubra* L.	RO
Rosebay rhododendron	*Rhododendron maximum* L.	RR
Sassafras	*Sassafras albidum* (Nutt.) Nees.	SF
Silverbell	*Halesia tetraptera* L.	SB
Sourwood	*Oxydendrum arboreum* (L.) DC.	SW
Striped maple	*Acer pensylvatica* L.	ST
Sugar maple	*Acer saccharum* Marsh.	SM
Sweet shrub	*Calycanthus floridus* L.	SS
White ash	*Fraxinus americana* L.	WA
White oak	*Quercus alba* L.	WO
Witch hazel	*Hamamelis virginiana* L.	WH
Yellow birch	*Betula alleghaniensis* Britton	YB
Yellow buckeye	*Aesculus octandra* (Marshall.)	YE
Yellow poplar	*Liridendron tulipifera* L.	YP
Blueberry species	*Vaccinium* spp.	VC

Table A. 8. Common names, Latin names, and species abbreviations for overstory tree species at Coweeta and Joyce Kilmer.

Common name	Latin name	Species abbreviation
Black birch	*Betula lenta* L.	BB
Black cherry	*Prunus serotina* Ehrh.	BC
Black gum	*Nyssa sylvatica* Marsh.	BG
Black locust	*Robinia pseudoacacia* L.	BL
Black oak	*Quercus velutina* Lam.	BO
Basswood	*Tilia americana* L.	BW
Cucumber magnolia	*Magnolia acuminata* L.	CM
Chestnut oak	*Quercus prinus* L.	CO
Hickory	*Carya* spp.	HY
Downy serviceberry	*Amalanchier arborea* (Michx. f.) Fern.	DS
Eastern hemlock	*Tsuga canadensis* (L.) Carr.	EH
Eastern hop-hornbeam	*Ostrya virginiana* (Mill.) K. Koch.	HH
Red maple	*Acer rubrum* L.	RM
Red oak	*Quercus rubra* L.	RO
Silverbell	*Halesia tetraptera* L.	SB
Sugar maple	*Acer saccharum* Marsh.	SM
Scarlet oak	*Quercus coccinea* Muenchh.	SO
Sourwood	*Oxydendrum arboreum* (L.) DC.	SW
Striped maple	*Acer pensylvatica* L.	ST
White ash	*Fraxinus americana* L.	WA
White oak	*Quercus alba* L.	WO
Yellow birch	*Betula alleghaniensis* Britton	YB
Yellow poplar	*Liridendron tulipifera* L.	YP

Table A. 9. Percentage of crown projection area in each stand meeting the various disturbance criteria for Coweeta and Joyce Kilmer.

	Coweeta							Joyce Kilmer	
Disturbance criteria	DC	DS	DY	MG	PM	PR	RK	GD	SB
At least one major release	57	50	67	41	44	45	63	65	61
More than one major release	10	4	13	10	6	12	16	14	11
Gap origin	15	39	16	24	49	20	19	41	49
At least one major release and gap origin	10	13	10	5	11	5	8	23	18
At least one moderate release	33	30	41	40	24	58	26	42	20
More than one moderate release	4	6	3	7	6	16	2	6	1
At least one recovery event	18	22	36	18	37	12	22	14	22
More than one recovery event	1	3	0	1	4	1	2	0	1

Table A. 10. a) Total (gap origin trees, major releases, moderate releases, and recovery events), b) major (gap origin trees and major releases), and c) minor (moderate releases and recovery events) decadal disturbance rates (%) for all stands. Rates are shown for decades with at least ten trees alive.

a)

Decade	DC	DS	DY	MG	PM	PR	RK	GD	SB
1750	10.3								
1760	0.0								
1770	0.0								
1780	0.0								
1790	0.0							19.0	
1800	0.0							8.4	
1810	12.7					12.9		0.0	
1820	9.3	27.9				17.2	0.0	6.7	
1830	0.0	0.0		12.4		17.7	8.8	6.0	
1840	27.2	20.1		25.2	24.9	26.7	16.9	15.9	46.8
1850	0.0	8.4		9.2	19.0	11.9	0.0	4.5	19.7
1860	14.7	7.7		28.8	17.5	5.1	17.3	15.7	19.1
1870	6.7	15.2	7.8	17.6	7.4	6.5	14.8	13.2	16.4
1880	11.5	9.5	0.0	14.1	12.5	6.6	4.0	6.2	13.2
1890	10.5	2.4	12.1	2.6	8.1	2.0	10.8	10.7	0.0
1900	3.7	24.9	23.7	18.4	13.2	13.4	0.0	22.4	10.0
1910	5.6	9.1	11.7	13.4	36.0	24.5	0.0	22.3	14.8
1920	20.5	46.8	22.9	9.3	6.5	9.3	7.1	18.9	15.0
1930	27.9	41.6	42.7	28.3	56.6	35.6	54.7	41.9	75.4
1940	9.2	5.8	16.5	14.5	23.3	2.9	17.1	1.2	11.3
1950	3.0	3.8	6.7	1.7	5.6	0.0	2.9	9.6	6.7
1960	27.1	11.0	37.7	14.1	23.1	20.8	29.8	45.3	16.0
1970	1.1	13.5	6.8	5.7	9.3	0.9	7.3	8.3	9.7
1980	12.5	9.8	10.2	12.3	15.5	12.9	8.2	36.6	8.1
1990	5.8	8.4	12.4	2.9	6.4	14.5	2.8	3.1	10.3

b)

Decade	DC	DS	DY	MG	PM	PR	RK	GD	SB
1750	0.0								
1760	0.0								
1770	0.0								
1780	0.0								
1790	0.0							19.0	
1800	0.0							8.4	
1810	0.0					6.5		0.0	
1820	4.4	10.3				17.2	0.0	0.0	
1830	0.0	0.0		12.4		3.4	8.8	6.0	
1840	5.2	0.0		20.2	11.9	8.0	6.0	4.7	38.7
1850	0.0	8.4		9.2	15.0	11.9	0.0	4.5	14.9
1860	9.4	7.7		9.7	11.9	5.1	8.0	7.7	14.0
1870	0.0	15.2	0.0	9.0	4.7	0.0	4.9	3.8	11.7
1880	6.6	2.7	0.0	6.2	8.2	4.5	0.0	6.2	10.5
1890	4.1	2.4	12.1	0.0	1.7	0.0	4.7	10.7	0.0
1900	0.0	15.9	10.1	8.4	5.8	9.8	0.0	7.6	10.0
1910	4.0	7.0	3.5	5.1	25.5	15.9	0.0	17.3	8.1
1920	17.2	41.5	14.9	9.3	1.7	6.5	7.1	17.0	15.0
1930	19.4	29.6	34.7	19.9	47.4	13.4	47.9	30.9	67.0
1940	7.7	2.0	14.6	4.3	19.5	1.3	15.6	0.0	11.3
1950	3.0	3.8	2.1	0.0	4.9	0.0	2.9	8.8	4.9
1960	17.9	0.0	9.7	7.2	10.4	3.8	9.6	24.8	6.3
1970	0.0	3.8	4.6	3.7	0.6	0.9	5.5	0.0	1.6
1980	5.4	1.0	1.5	7.2	1.0	2.6	3.4	26.6	0.7
1990	2.5	6.2	4.7	0.0	1.8	8.3	2.8	3.1	6.0

c)

Decade	DC	DS	DY	MG	PM	PR	RK	GD	SB
1750	10.3								
1760	0.0								
1770	0.0								
1780	0.0								
1790	0.0							0.0	
1800	0.0							0.0	
1810	12.7					6.4		0.0	
1820	4.9	17.6				0.0	0.0	6.7	
1830	0.0	0.0		0.0		14.3	0.0	0.0	
1840	22.0	20.1		5.0	13.0	18.6	11.0	11.2	8.1
1850	0.0	0.0		0.0	3.9	0.0	0.0	0.0	4.8
1860	5.2	0.0		19.1	5.5	0.0	9.4	7.9	5.1
1870	6.7	0.0	7.8	8.6	2.7	6.5	9.9	9.4	4.8
1880	4.9	6.8	0.0	7.8	4.3	2.1	4.0	0.0	2.8
1890	6.4	0.0	0.0	2.6	6.4	2.0	6.1	0.0	0.0
1900	3.7	9.0	13.5	9.9	7.5	3.6	0.0	14.9	0.0
1910	1.6	2.0	8.1	8.3	10.5	8.6	0.0	5.0	6.7
1920	3.3	5.2	7.9	0.0	4.8	2.7	0.0	1.9	0.0
1930	8.6	12.0	8.0	8.4	9.3	22.2	6.7	10.9	8.4
1940	1.6	3.8	1.9	10.2	3.8	1.6	1.5	1.2	0.0
1950	0.0	0.0	4.7	1.7	0.8	0.0	0.0	0.8	1.8
1960	9.2	11.0	28.0	7.0	12.6	17.0	20.2	20.5	9.7
1970	1.1	9.7	2.2	2.0	8.7	0.0	1.8	8.3	8.1
1980	7.1	8.8	8.8	5.1	14.5	10.2	4.8	10.0	7.5
1990	3.3	2.2	7.7	2.9	4.6	6.2	0.0	0.0	4.3

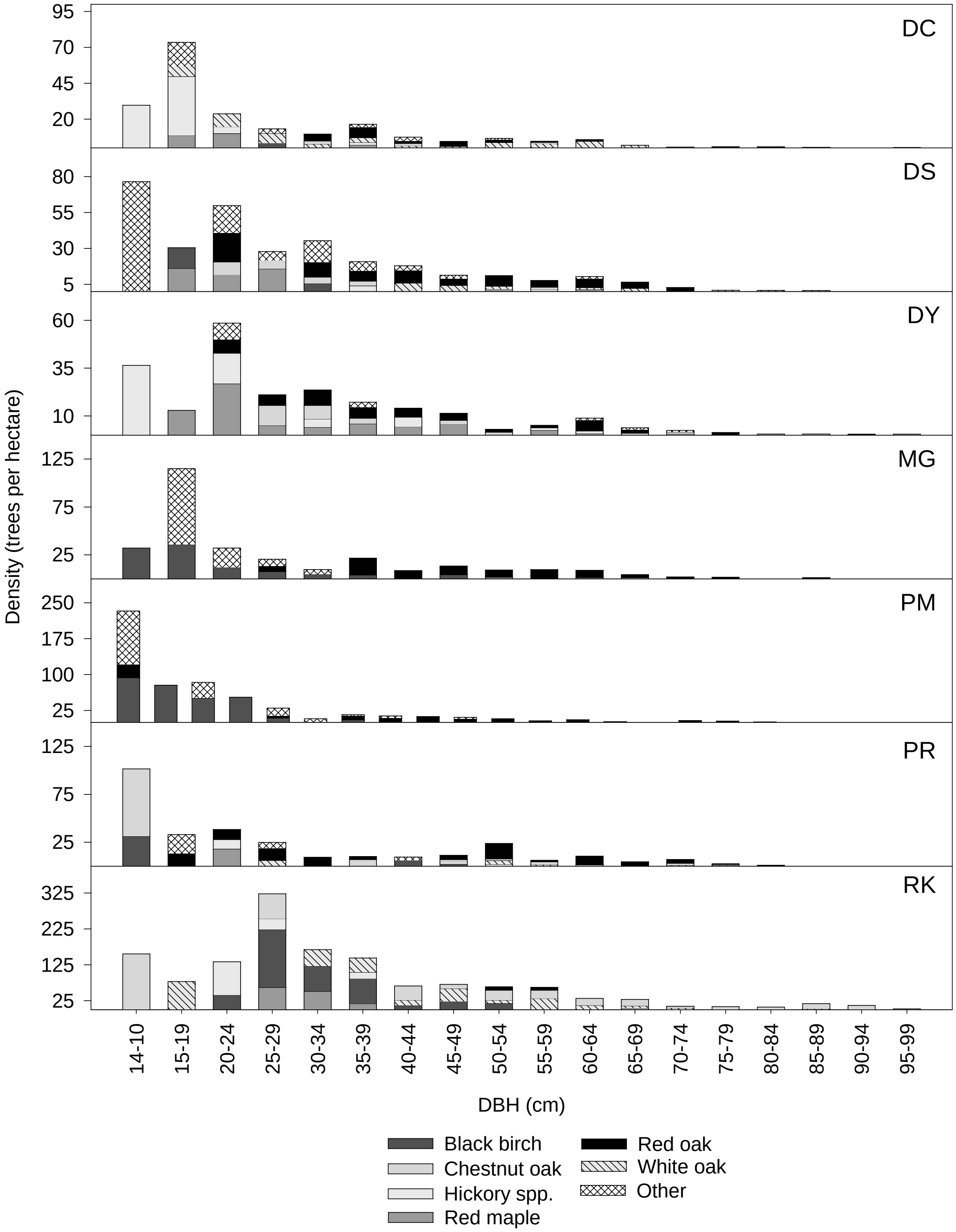


Figure A. 1. Diameter distributions for stands at Coweeta by species.

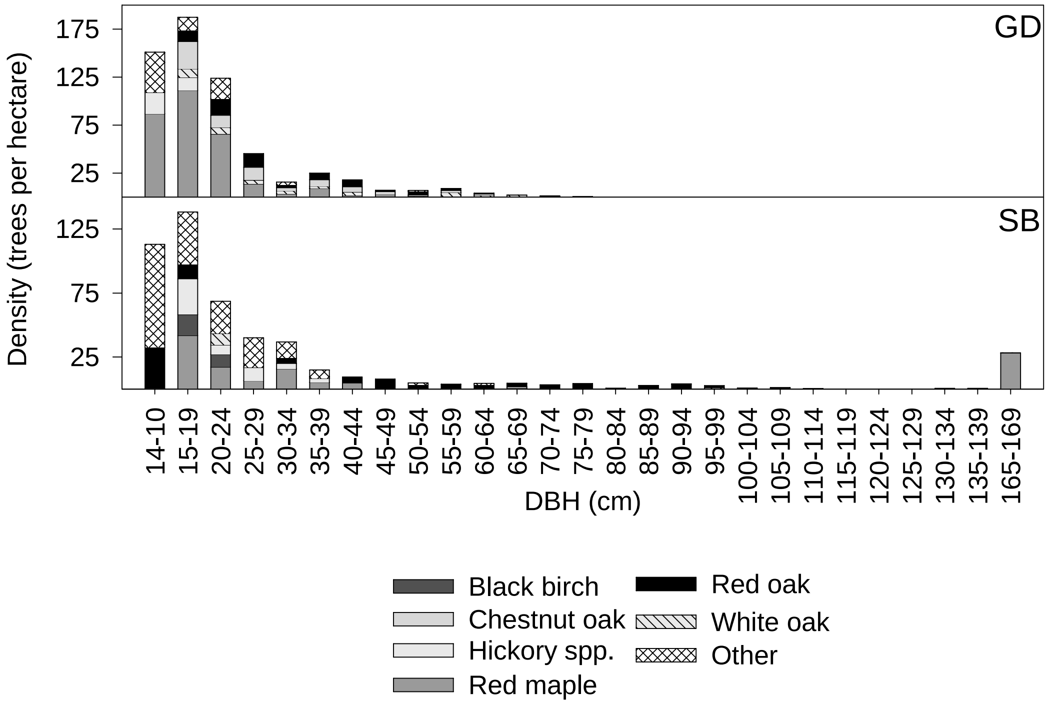


Figure A. 2. Diameter distribution of Joyce Kilmer stands by species.

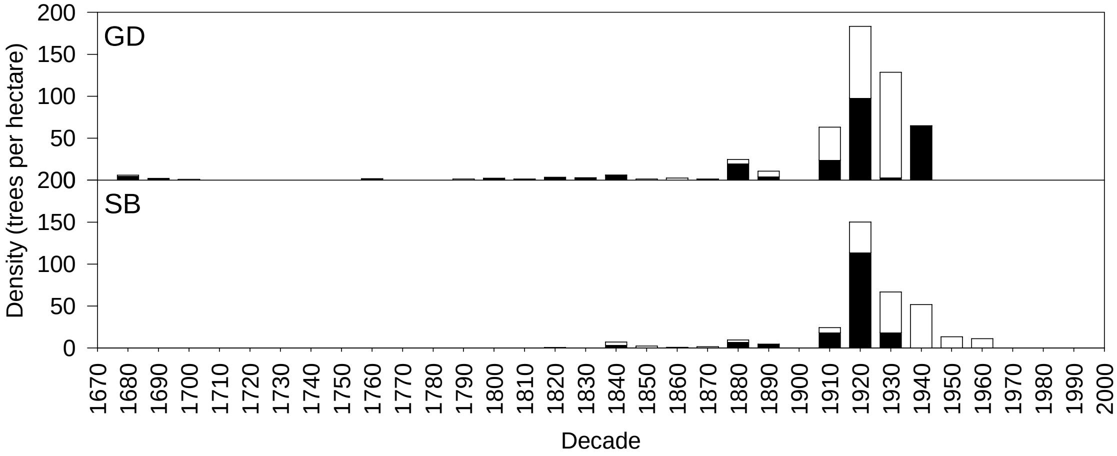


Figure A. 3. Recruitment age distributions for Joyce Kilmer stands. Open bars indicate gap origin trees and black bars indicate non-gap-origin trees.

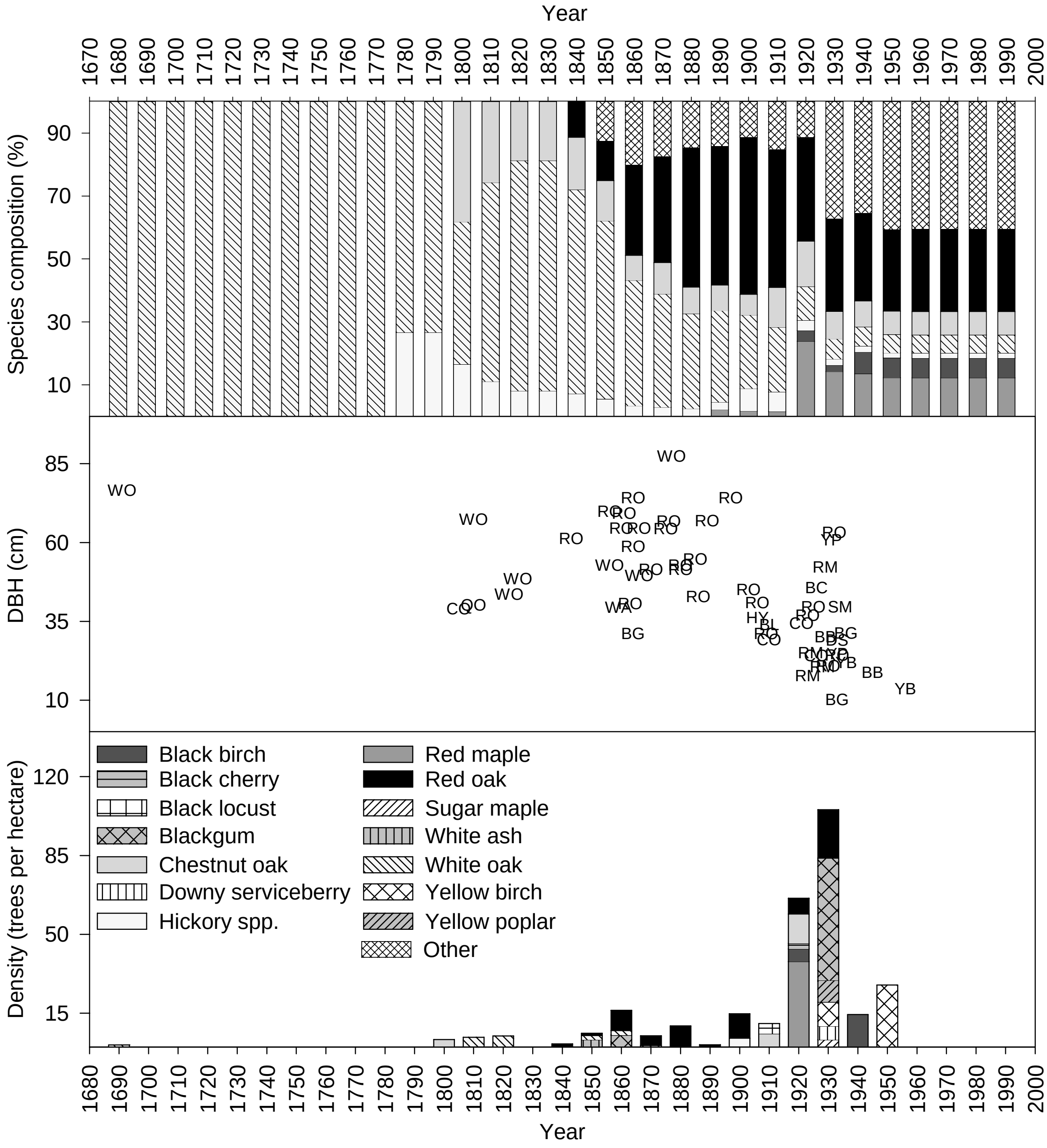


Figure A. 4. Percent of total species composition for each decade (top), diameter by decade of origin (middle), and age structure (bottom) for stand DS. The legend applies to both the top and bottom graphs. Species abbreviations are located in Table A. 8. Nine percent of the cores were rotten or the pith could not be estimated.

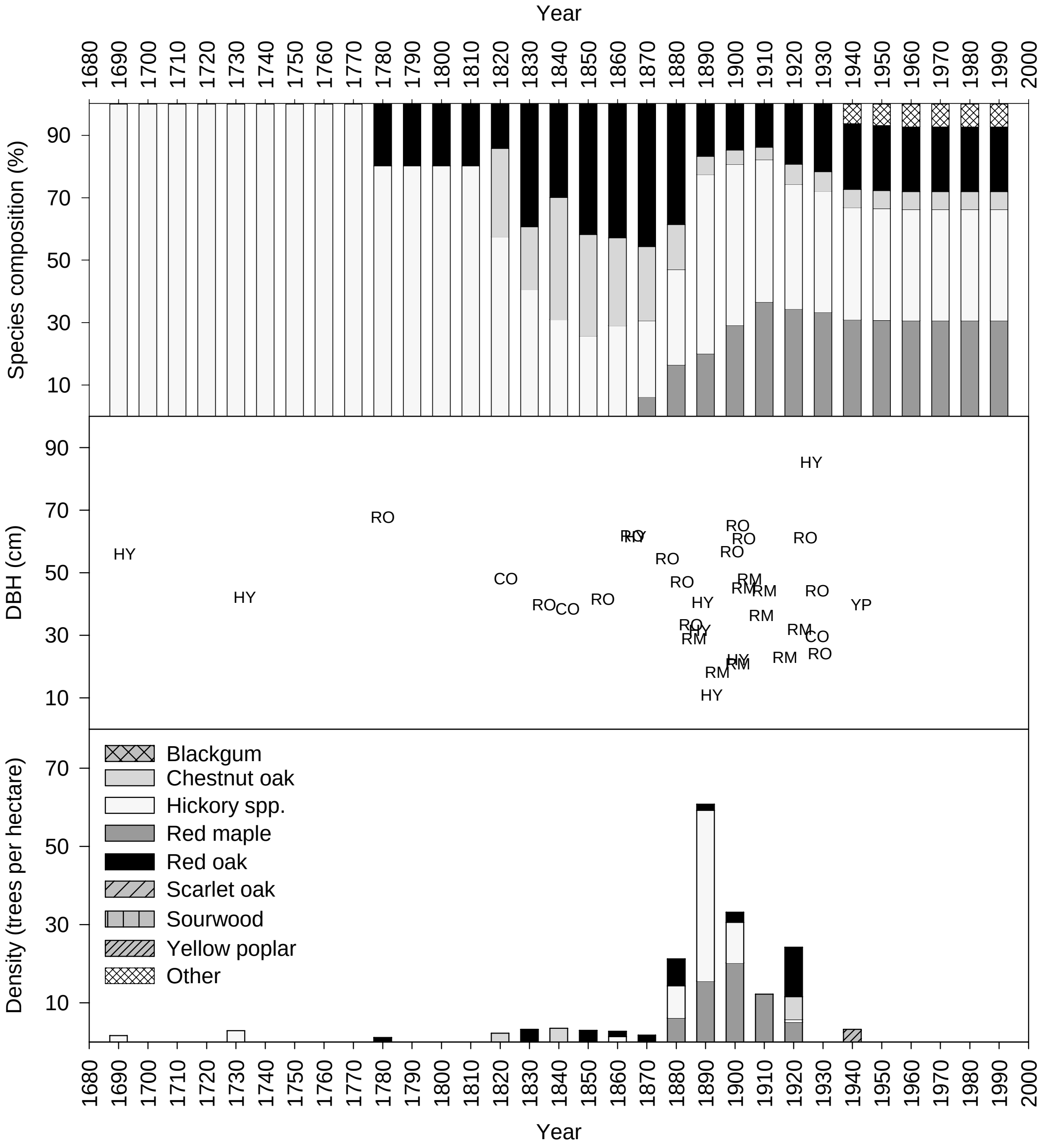


Figure A. 5. Percent of total species composition for each decade (top), diameter by decade of origin (middle), and age structure (bottom) for stand DY. The legend applies to both the top and bottom graphs. Species abbreviations are located in Table A. 8. Nineteen percent of the cores were rotten or the pith could not be estimated.

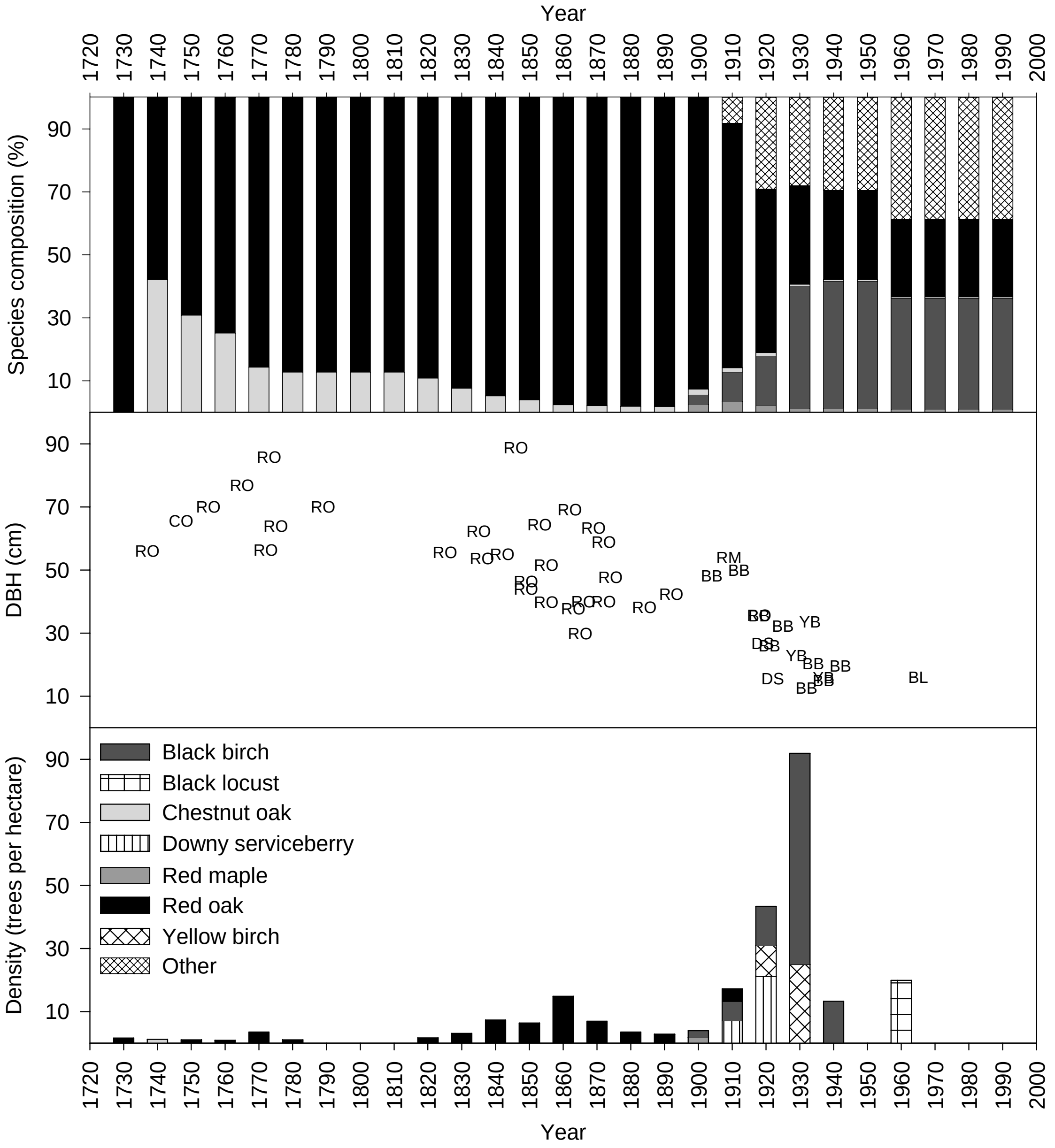


Figure A. 6. Percent of total species composition for each decade (top), diameter by decade of origin (middle), and age structure (bottom) for stand MG. The legend applies to both the top and bottom graphs. Species abbreviations are located in Table A. 8. Fourteen percent of the cores were rotten or the pith could not be estimated.

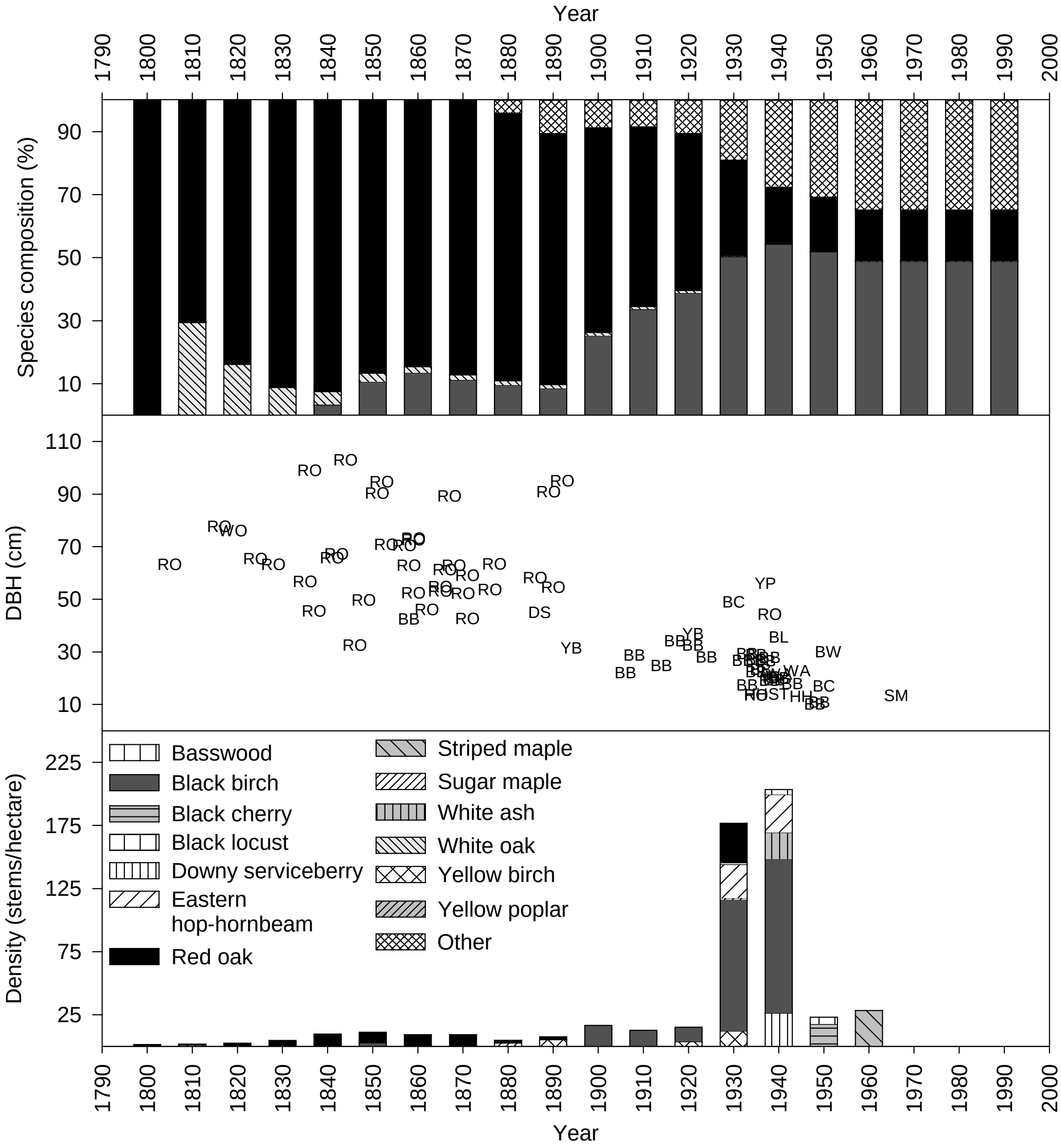


Figure A. 7. Percent of total species composition for each decade (top), diameter by decade of origin (middle), and age structure (bottom) for stand PM. The legend applies to both the top and bottom graphs. Species abbreviations are located in Table A. 8. Four percent of the cores were rotten or the pith could not be estimated.

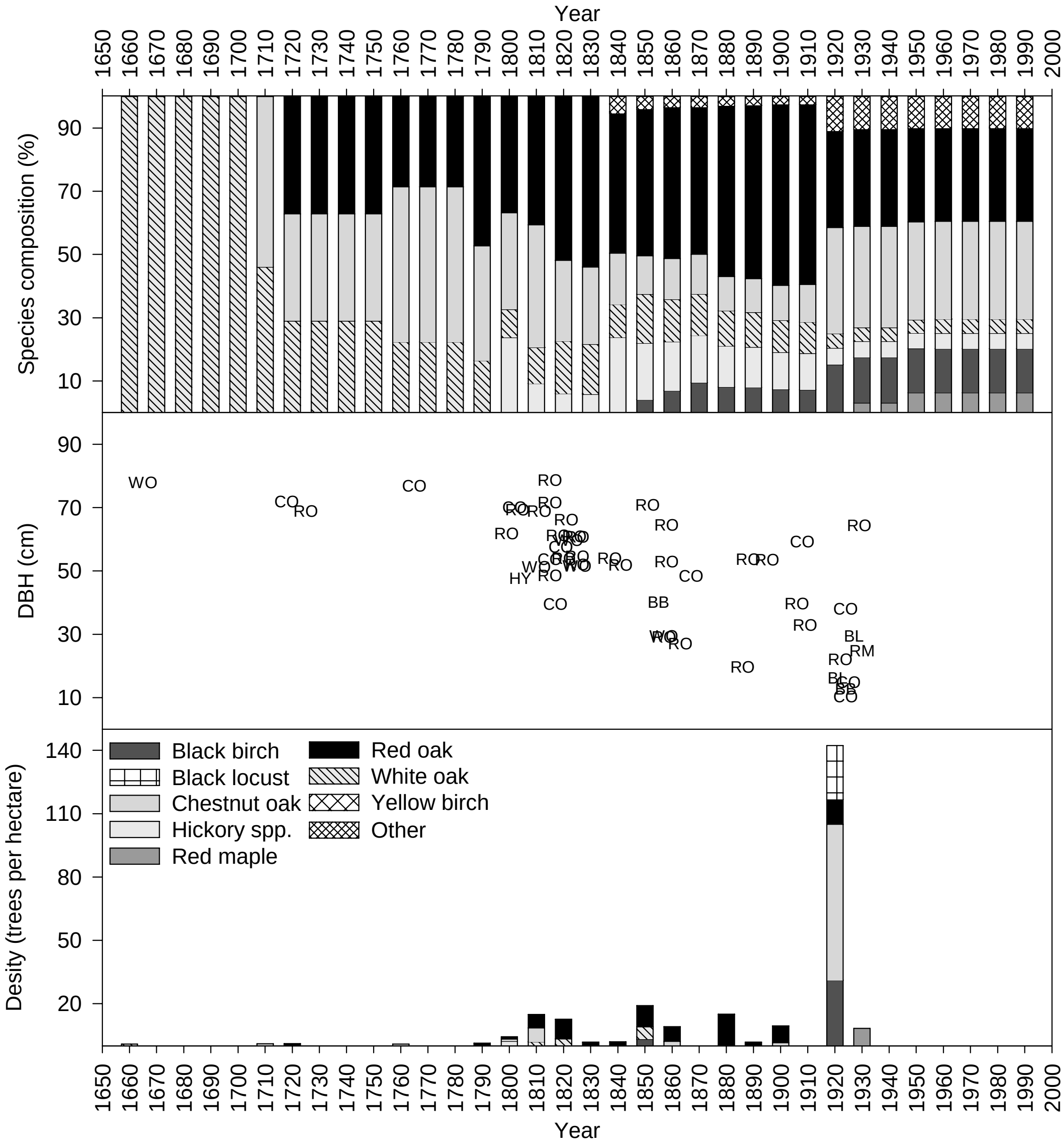


Figure A. 8. Percent of total species composition for each decade (top), diameter by decade of origin (middle), and age structure (bottom) for stand PR. The legend applies to both the top and bottom graphs. Species abbreviations are located in Table A. 8. Fourteen percent of the cores were rotten or the pith could not be estimated.

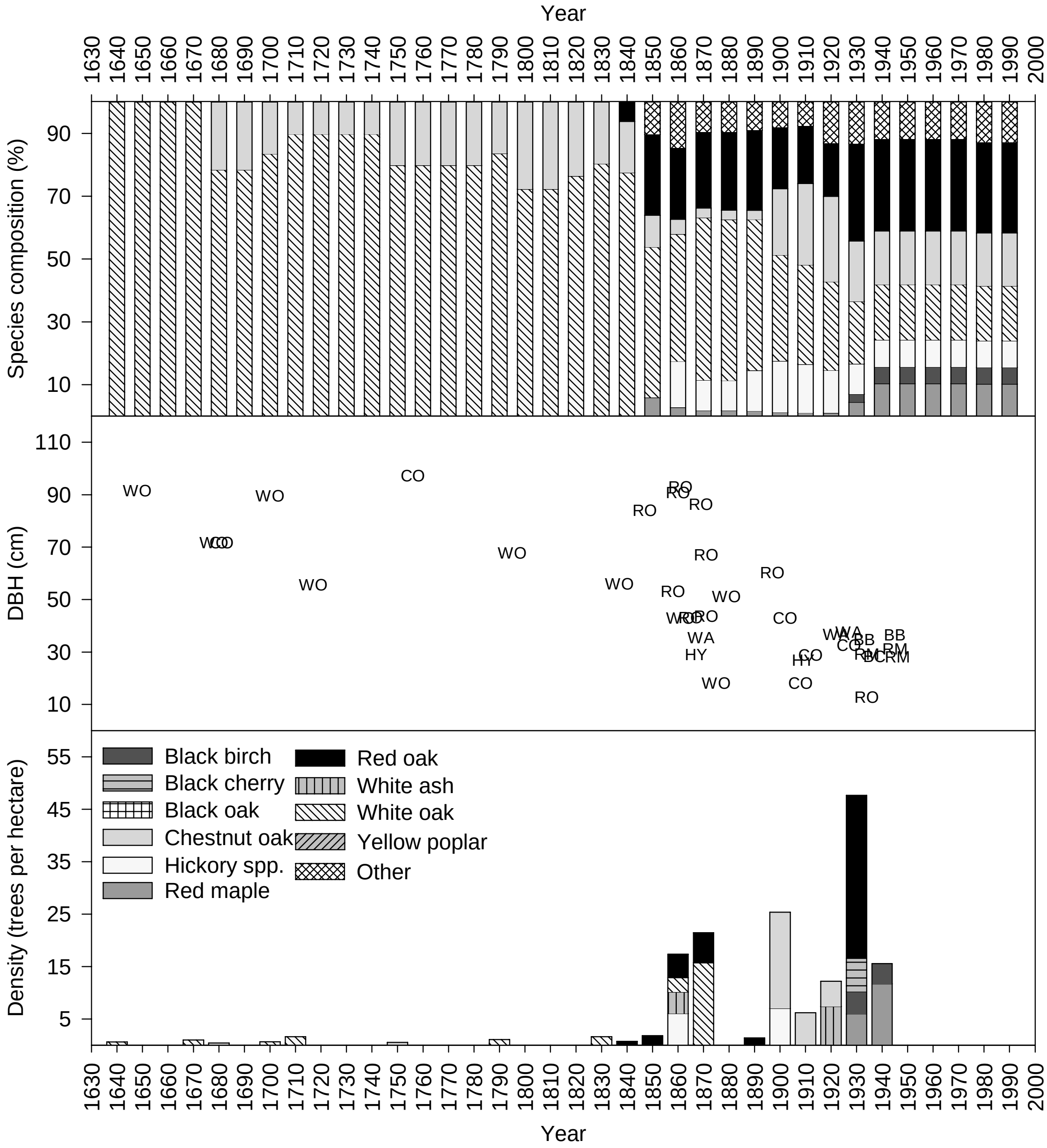


Figure A. 9. Percent of total species composition for each decade (top), diameter by decade of origin (middle), and age structure (bottom) for stand RK. The legend applies to both the top and bottom graphs. Species abbreviations are located in Table A. 8. Fifteen percent of the cores were rotten or the pith could not be estimated.

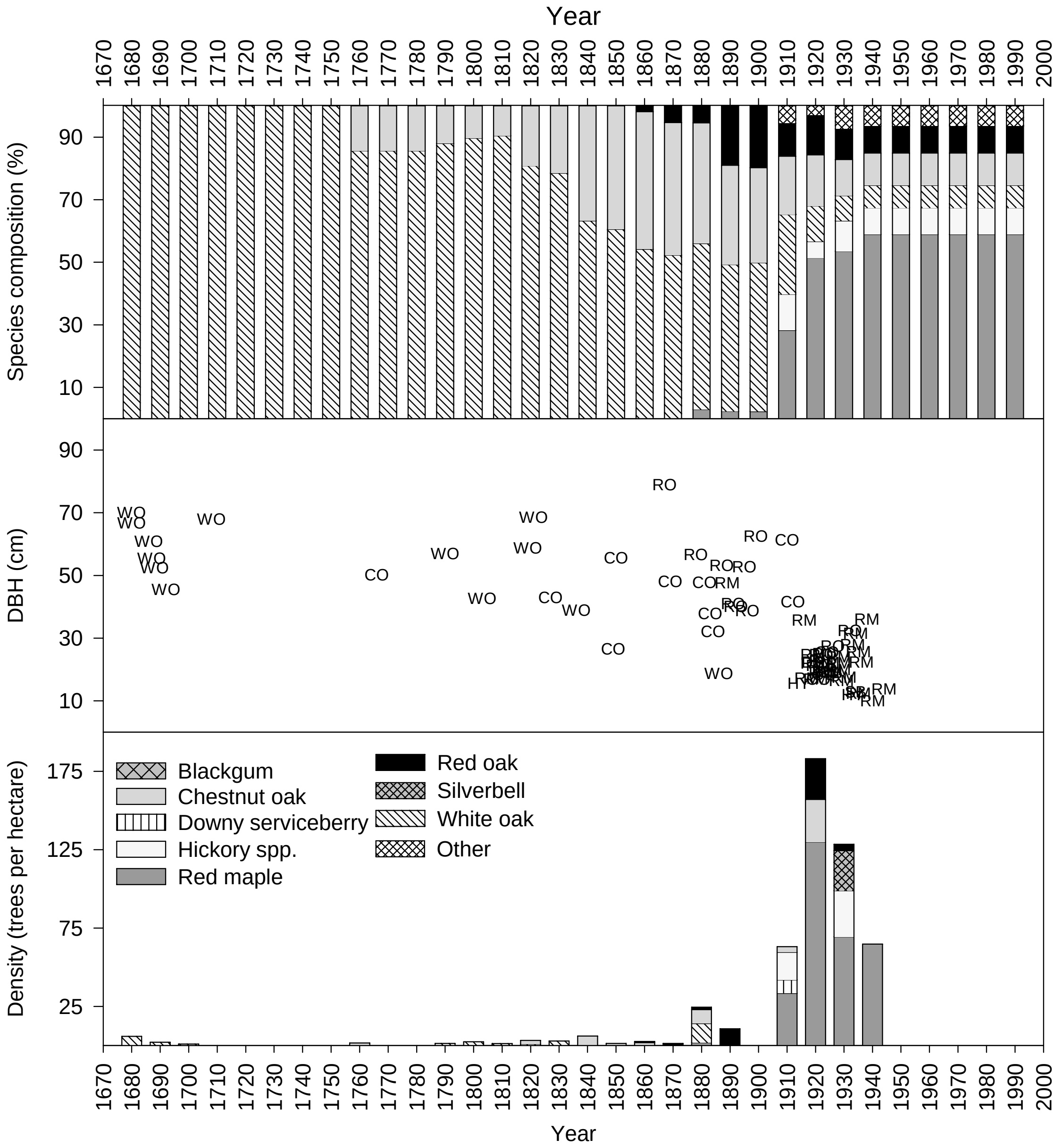


Figure A. 10. Percent of total species composition for each decade (top), diameter by decade of origin (middle), and age structure (bottom) for stand GD. The legend applies to both the top and bottom graphs. Species abbreviations are located in Table A. 8. Eight percent of the cores were rotten or the pith could not be estimated.

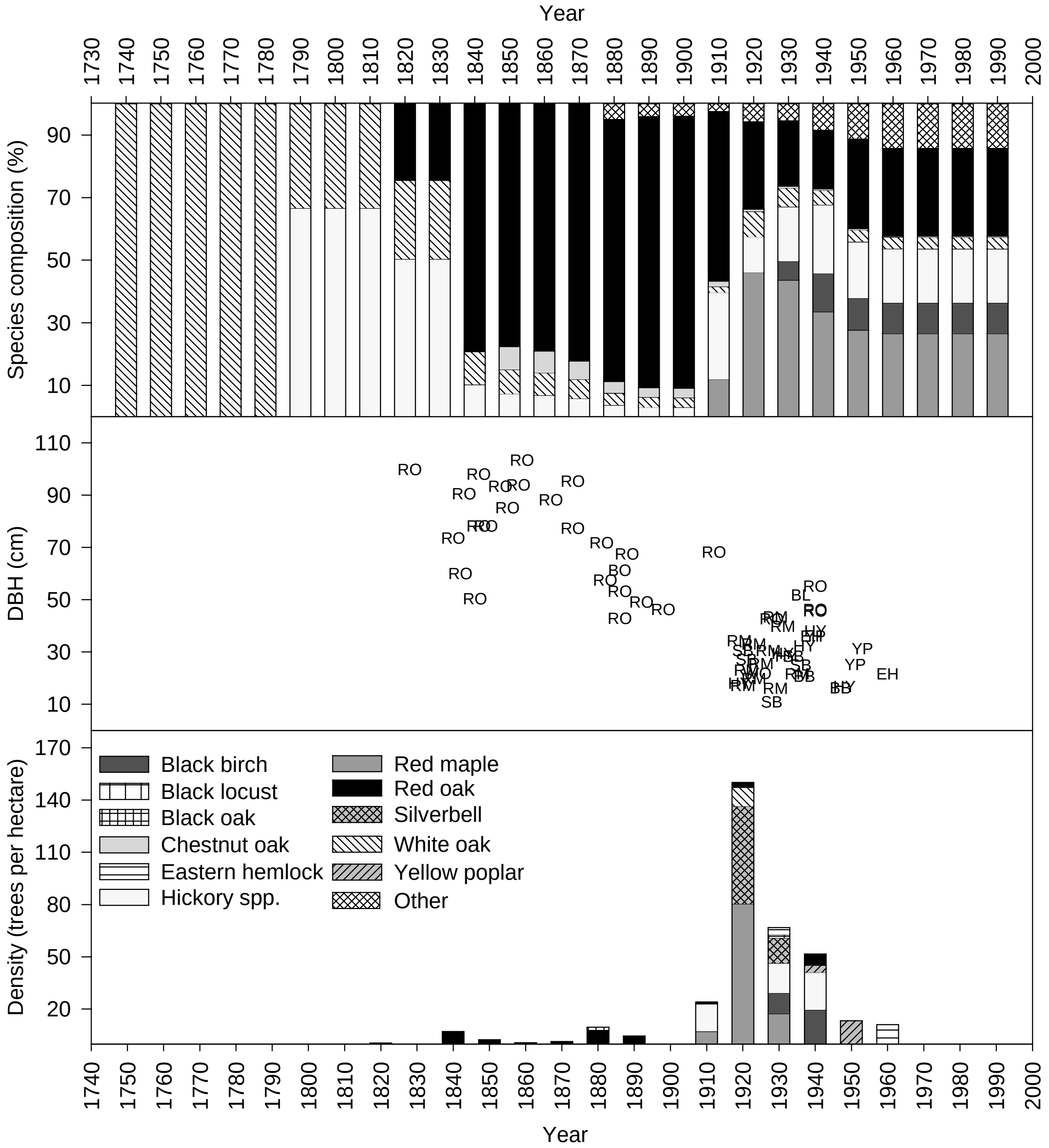


Figure A. 11. Percent of total species composition for each decade (top), diameter by decade of origin (middle), and age structure (bottom) for stand SB. The legend applies to both the top and bottom graphs. Species abbreviations are located in Table A. 8. Twenty percent of the cores were rotten or the pith could not be estimated.

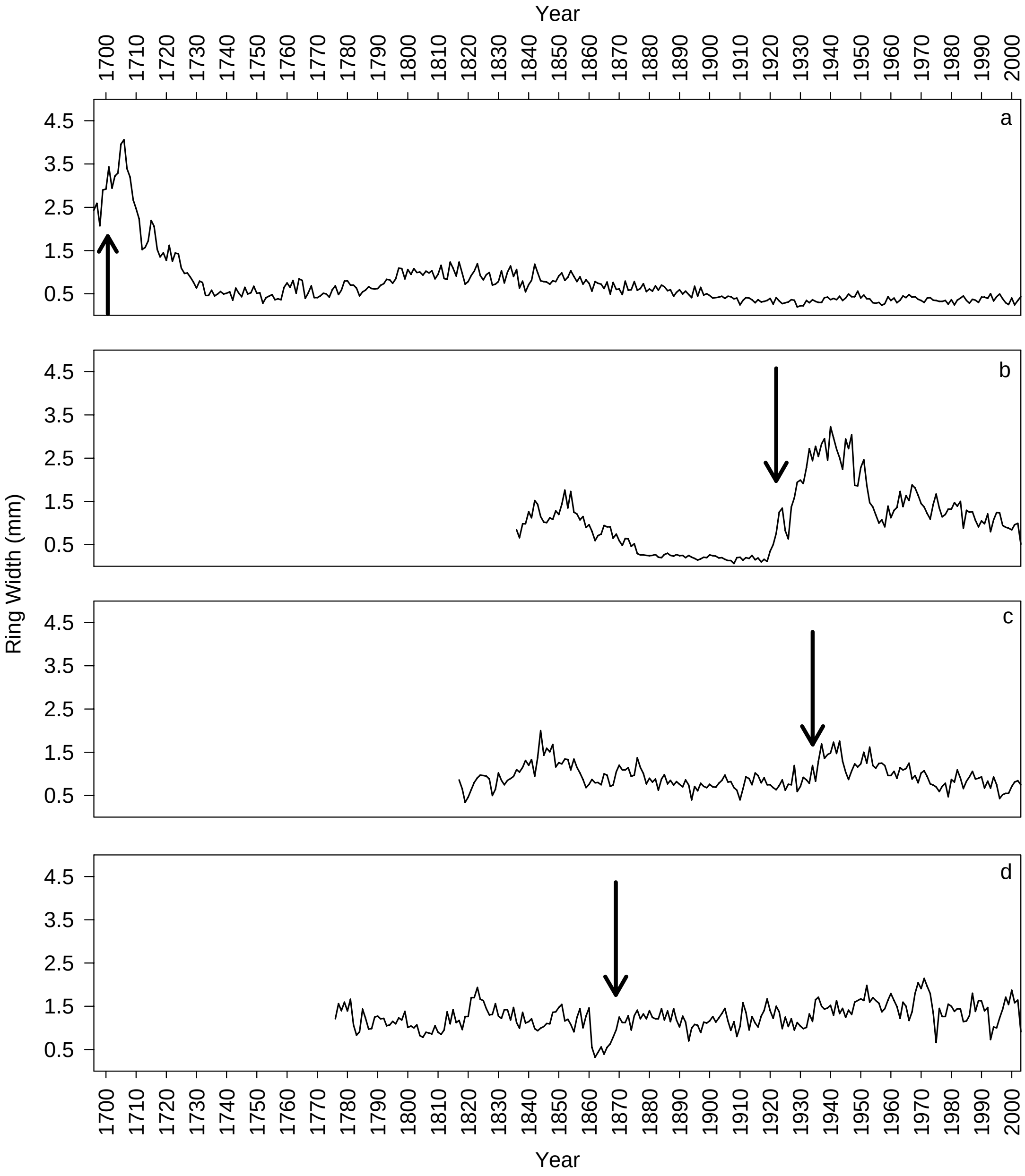


Figure A. 12. Examples of disturbance responses: a) gap origin tree b) major release c) moderate release d) recovery event. Arrows denote the beginning of the response.

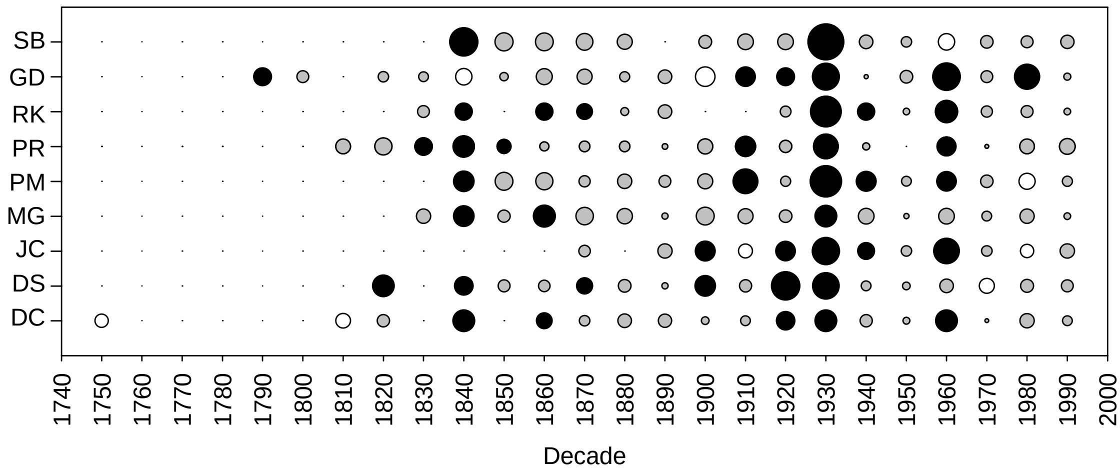


Figure A. 13. Disturbance chronologies for each stand showing peak decades. Stand names are along the y-axis. The size of the circle is proportional to the percent canopy area disturbed in each decade. Black circles indicate peaks in total (gap origin trees, major releases, moderate releases, and recovery events) or major disturbance (gap origin trees and major releases). White circles denote peaks in minor disturbance (moderate releases and recovery events). Gray circles indicate a non-peak decade. Chronologies were truncated when the sample size dropped below ten trees.

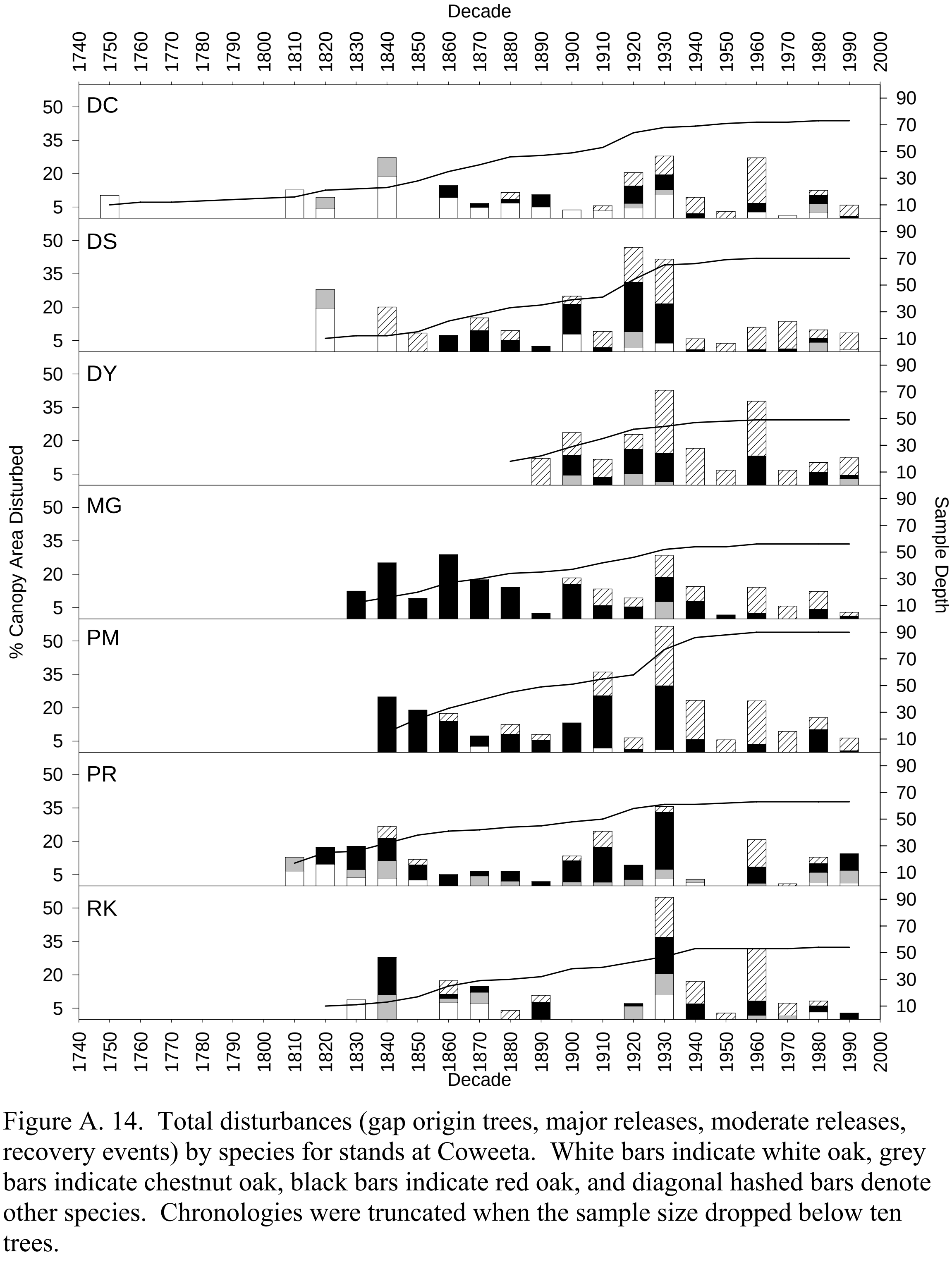


Figure A. 14. Total disturbances (gap origin trees, major releases, moderate releases, recovery events) by species for stands at Coweeta. White bars indicate white oak, grey bars indicate chestnut oak, black bars indicate red oak, and diagonal hashed bars denote other species. Chronologies were truncated when the sample size dropped below ten trees.

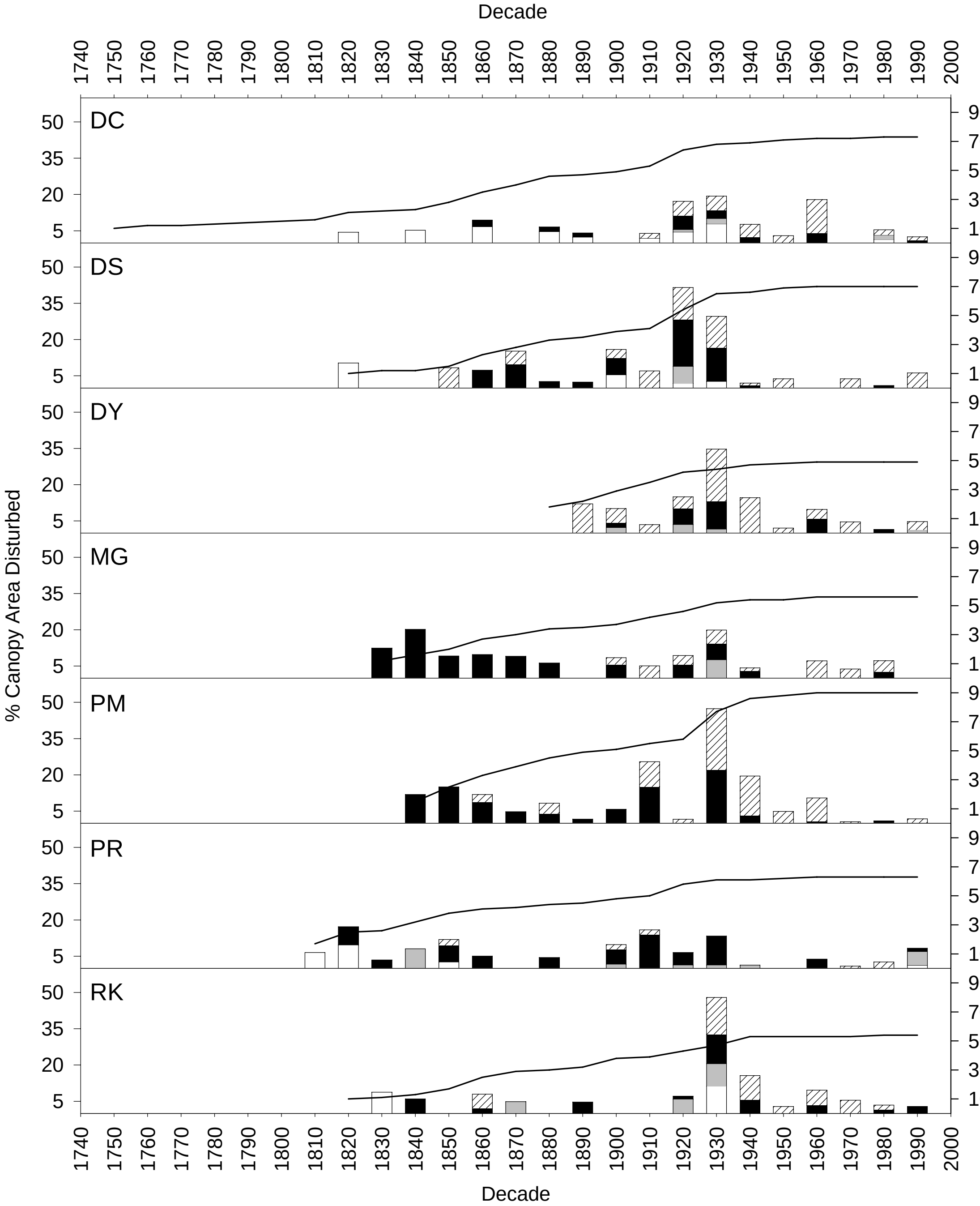


Figure A. 15. Major disturbances (gap origin trees and major releases) by species for stands at Coweeta. White bars indicate white oak, grey bars indicate chestnut oak, black bars denote red oak, and diagonal hashed bars indicate other species. Chronologies were truncated when the sample size dropped below ten trees.

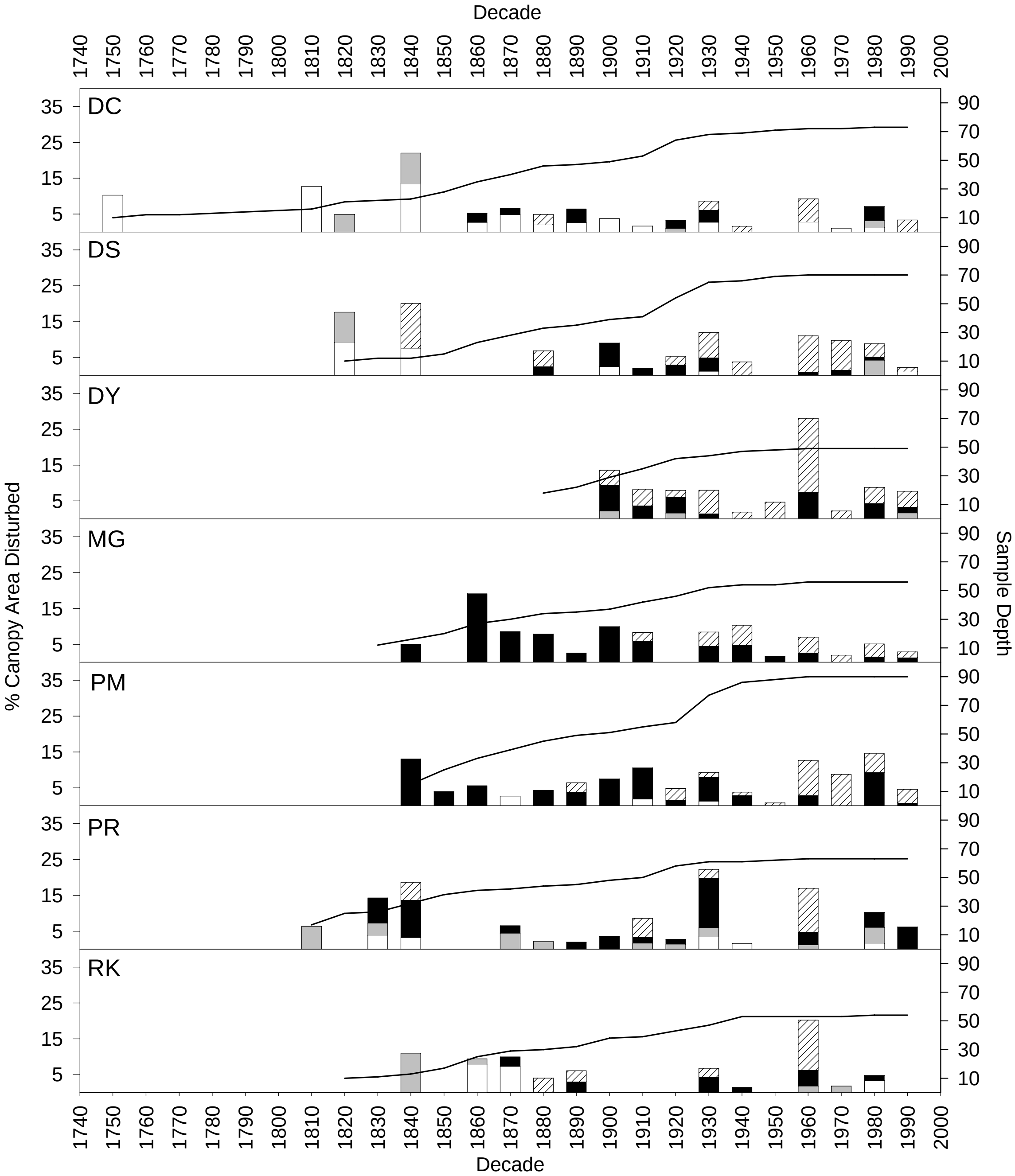


Figure A. 16. Minor disturbances (moderate releases and recovery events) by species for stands at Coweeta. White bars indicate white oak, grey bars indicate chestnut oak, black bars denote red oak, and diagonal hashed bars indicate other species. Chronologies were truncated when the sample size dropped below ten trees.

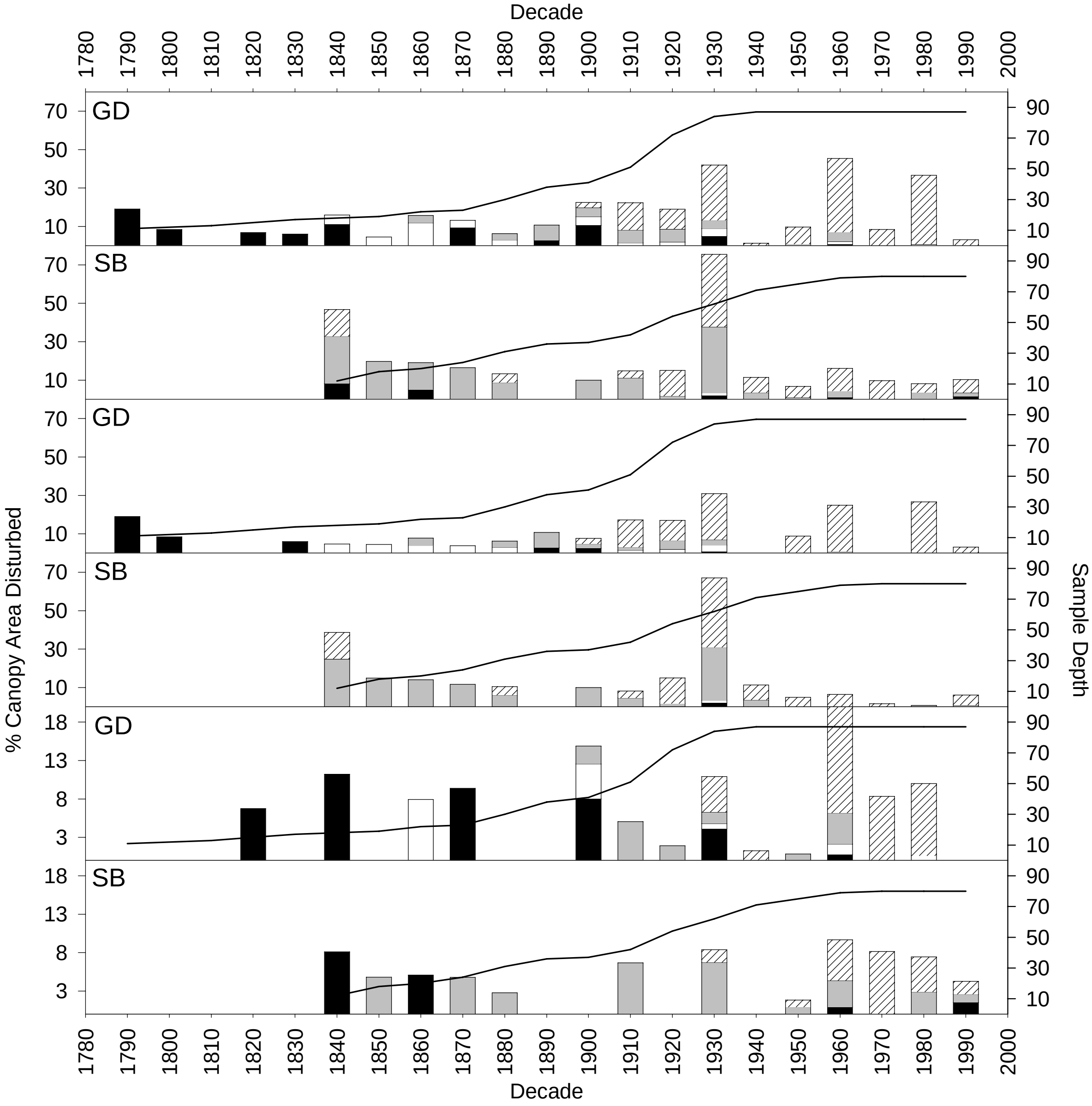


Figure A. 17. Total disturbances (gap origin trees, major releases, moderate releases, and recovery events), major disturbances (gap origin trees and major releases), and minor disturbances (moderate releases and recovery events) by species for stands in Joyce Kilmer. White bars indicate white oak, grey bars indicate chestnut oak, black bars denote red oak, and diagonal hashed bars indicate other species. Chronologies were truncated when the sample size dropped below ten trees. Note the Y-axes scales for the minor disturbances are different.

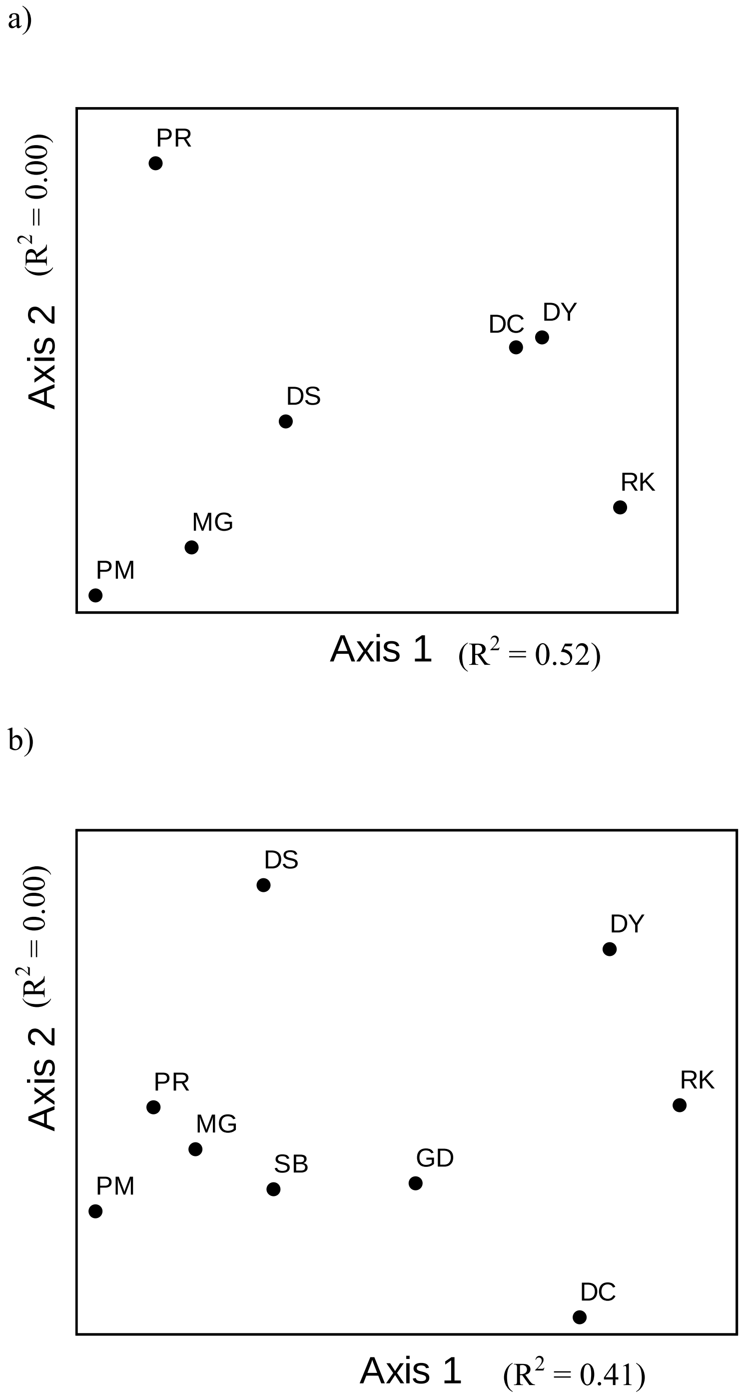
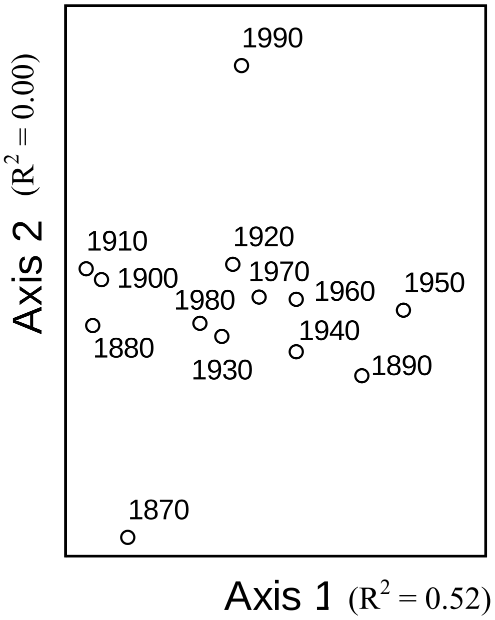


Figure A. 18. DCA of major decadal disturbance rates (%) by plot for stands at a) Coweeta and b) Coweeta and Joyce Kilmer

a)



b)

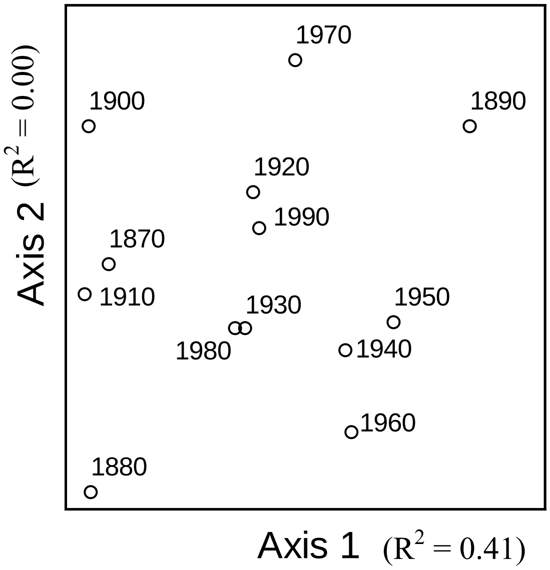


Figure A. 19. DCA of major decadal disturbance rates for stands at a) Coweeta and b) Coweeta and Joyce Kilmer

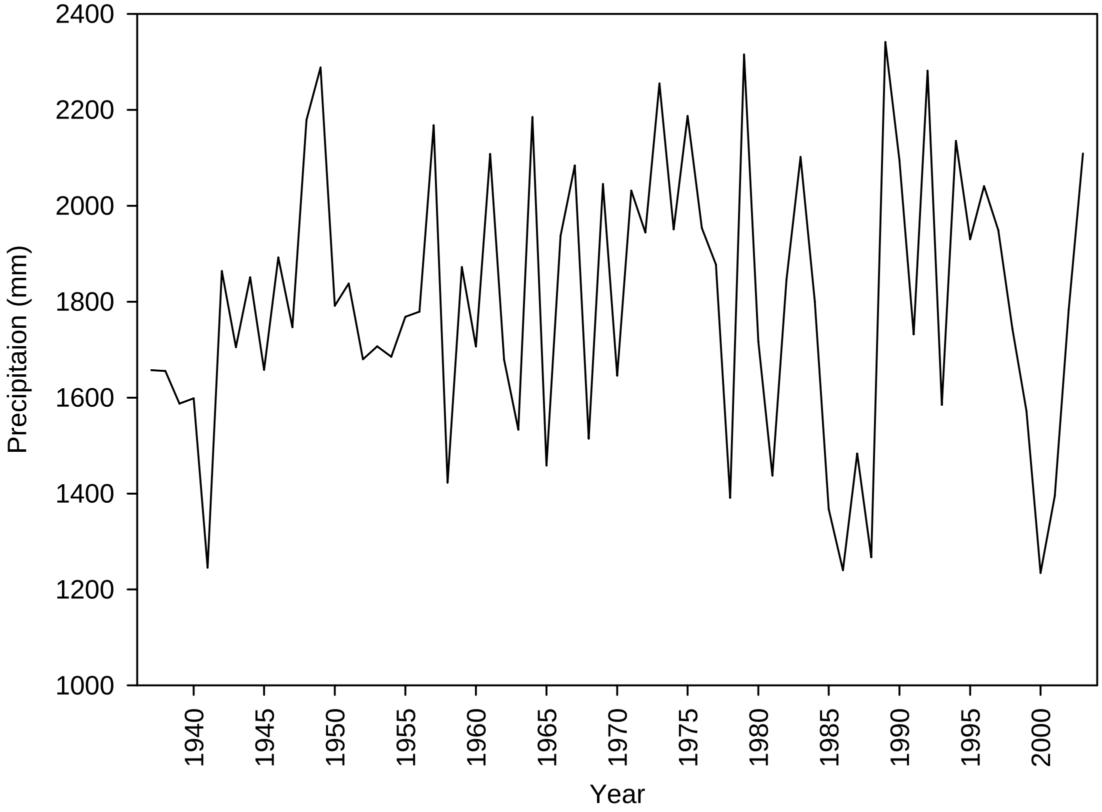


Figure A. 20. Yearly precipitation averages (mm) for Coweeta from 1937 to 2003.

BIOGRAPHY OF THE AUTHOR

Sarah Marie Butler was born in Laport, Indiana on February 27, 1981. She grew up outside of Indianapolis with her two sisters Laura and Jennifer. She graduated from Carmel High School in May, 1999. Throughout her childhood, Sarah developed a respect and love for the natural world from her parents and grandparents, which then inspired her to focus her education and career on natural science.

Sarah attended Indiana University in Bloomington, Indiana and graduated in 2003 with a Bachelor of Science degree in Environmental Science. In the spring of 2003, Sarah got accepted to the University of Maine's Department of Forest Ecosystem Science program. In the fall of 2003, she packed up her cat Banyan and a warm coat and was on her way. Although she never quite took to lobster rolls or Moxie, she did take to Maine and has truly enjoyed her time there.

Sarah is next on her way to New York to work for the Lamont Doherty Earth Observatory Tree Ring Lab. She hopes to apply all she has learned in Maine to the next phase of her life. She is a candidate for the Masters of Science degree in Forestry from The University of Maine in May 2006.