8-2007

A Multi-scale Analysis of Disturbance Dynamics in Hardwood Forest Communities on the Cumberland Plateau, U.S.A.

Justin L. Hart

University of Tennessee - Knoxville

Recommended Citation

Hart, Justin L., "A Multi-scale Analysis of Disturbance Dynamics in Hardwood Forest Communities on the Cumberland Plateau, U.S.A.. " PhD diss., University of Tennessee, 2007.
https://trace.tennessee.edu/utk_graddiss/183

To the Graduate Council:

I am submitting herewith a dissertation written by Justin L. Hart entitled "A Multi-scale Analysis of Disturbance Dynamics in Hardwood Forest Communities on the Cumberland Plateau, U.S.A.." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Geography.

Henri D. Grissino-Mayer, Major Professor

We have read this dissertation and recommend its acceptance:

Carol P. Harden, Sally P. Horn, Wayne K. Clatterbuck

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

I am submitting herewith a dissertation written by Justin L. Hart entitled "A Multi-scale Analysis of Disturbance Dynamics in Hardwood Forest Communities on the Cumberland Plateau, U.S.A." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Geography.

Henri D. Grissino-Mayer
Major Professor

We have read this dissertation
and recommend its acceptance:

Carol P. Harden

Sally P. Horn

Wayne K. Clatterbuck

Accepted for the council:

Carolyn R. Hodges
Vice Provost and Dean of the
Graduate School

(Original signatures are on file with official student records)

A MULTI-SCALE ANALYSIS OF DISTURBANCE DYNAMICS IN HARDWOOD FOREST COMMUNITIES ON THE CUMBERLAND PLATEAU, U.S.A.

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Justin L. Hart
August 2007

Acknowledgements

I thank my advisor Henri Grissino-Mayer and my committee members Wayne Clatterbuck, Carol Harden, and Sally Horn for guidance. I thank Ryan Foster, Sara Hart, Kevin Horn, Chris Underwood, and Saskia van de Gevel for assistance in the field and Matthew McConnell for assistance in the laboratory. I thank Sara, Joe Henderson, David Mann, Chris, and Saskia for helpful discussion. In addition, Sara, Chris, and Saskia also commented on early drafts of chapters. The map of the Cumberland Plateau physiographic section was created by Alison Miller. I thank The Nature Conservancy, especially Alex Wyss, and the Tennessee Department of Environment and Conservation for sampling permission. Funding was provided by the National Science Foundation under grants BCS-0602445 and DGE-0538420. I also thank the NSF-Arizona AMS Laboratory for providing five radiocarbon dates on charcoal samples.

Abstract

The purpose of this research was to quantify forest disturbance processes and evaluate the influence of these processes on secondary hardwood forest communities on a section of the Cumberland Plateau in Tennessee. The specific objectives of this study were to: (1) reconstruct the disturbance history of a secondary hardwood forest using species composition, stand structure, tree-ring data, and soil charcoal analyses, (2) quantify canopy gap formation mechanisms, (3) document canopy gap characteristics, and (4) determine the forest response to small-scale disturbance events. This information is useful to understand the importance of localized disturbances on stand development and forest successional patterns.

With the exception of one stand-wide disturbance in the early 1980s, the disturbance regime of the forest was characterized by localized, asynchronous events that occurred at variable spatial and temporal scales. Gap-scale disturbance events became frequent after about 40 years of forest development. The presence of soil charcoal indicated that fire had occurred in the Pogue Creek Natural Area in the past, but species composition and a lack of fire-scarred trees indicated that fire had not occurred during the development of the current stand.

The majority of canopy gaps were caused by treefall (either windthrow or basal-shear) and half of all gaps were caused by the death of a *Quercus* individual. Gap ages ranged from 1 to 17 years with a mean of 7 years. Seasonality of death could be accurately determined for 17 gap makers and all but one of these trees died during the growing season. Strong wind associated with convective storms is the most probable disturbance agent in the forest.

The fraction of land area in expanded gaps and true canopy gaps was 15% and 6%, respectively. The amount of land area in canopy gaps was highest for younger gaps and generally decreased with increased gap age. Most expanded and true canopy gaps had elliptical shapes and the majority of gaps were oriented perpendicular to slope contours.

Significant positive relationships were documented between expanded gap size and the density of saplings, trees, and total stems. Only weak relationships existed between stem diversity and expanded gap size. Most of the canopy gaps documented were projected to close by lateral crown expansion rather than height growth of subcanopy individuals, but gaps still provided a means for understory trees to recruit to larger size classes. Over half of all trees located in true canopy gaps with intermediate crown classifications were *Acer saccharum*, *A. rubrum*, or *Liriodendron tulipifera*. Because the gaps documented were relatively small and close by lateral branch growth of perimeter trees, the most shade-tolerant *A. saccharum* has the greatest probability of becoming dominant in the canopy under the current disturbance regime. This study indicated that gap-scale disturbance processes have an influence on stand development and successional patterns of secondary hardwood forests in the absence of large-scale events.

Table of Contents

List of Tables

List of Figures

Chapter 1

Introduction

1.1 Purpose

The purpose of this dissertation research is to investigate the dynamics of natural forest disturbance events in second growth, mixed hardwood forest communities on the Cumberland Plateau. This information will provide insights on the role of natural disturbances in shaping composition, structure, and function at the individual, population, community, and ecosystem level in mixed hardwood forests. Most studies that have analyzed disturbance dynamics in the Eastern Deciduous Forest Region have focused on old growth remnants. Due to anthropogenic influences during the 19th and 20th centuries, the majority of forested land in the eastern United States is composed of secondary (not old growth), mixed hardwood stands and a need exists to better understand disturbance dynamics in developing stands. Knowledge of stand history and disturbance ecology is important for the management of this forest type throughout the eastern United States. Specifically, information on forest resources and processes on the Cumberland Plateau is lacking.

1.2 Forest Disturbance Events

Terrestrial ecosystems are subject to disturbance events such as wildfires, flooding, and mass movements. Forest disturbances are generally defined as events that create more growing space in the forested environment (Oliver and Larson 1996). This is a general definition and it is important to note that, for an event to be classified as a disturbance, it must be relevant to the spatial and temporal scale in question. Disturbances are often classified based on distribution, frequency, return interval, rotation period, predictability, spatial extent, magnitude, severity, and synergism (White and Pickett 1985). More specifically, disturbances may be defined as any relatively discrete event in space and time that disrupts ecosystem, community, or population structure, composition, or function, and changes resource availability or any other aspect of the biotic or abiotic environment (White and Pickett 1985).

The responses of individuals, populations, communities, and ecosystems to large-scale disturbances (such as flooding and large wildfires) have been intensively studied by ecologists. Large-scale disturbances remove most or all overstory vegetation and generally create cohort establishment of trees, with successive changes in species dominance through time. In some ecosystems, stand-devastating disturbances are infrequent and do not significantly influence forest processes. Typical disturbance events in such environments are comparably small and less severe. Events that create canopy gaps, which are openings in the forest canopy, are common types of small-scale disturbances and are important processes in some eastern forests (Figure 1.1). Researchers have used different criteria to define canopy gaps. Currently, no standardized definition is accepted among the scientific community, but the most common definition describes canopy gaps as the ground area under a canopy opening extending to the bases of canopy trees surrounding the canopy void. Thus, differences are seen between a true gap or opening in the canopy and the expanded gap that includes the canopy trees along the perimeter of the opening (Figure 1.2) (Runkle 1981). Canopy gaps occur at sites where partial or total death of one or more canopy individuals has

Figure 1.1 Looking skyward through a small opening in the forest canopy at the Pogue Creek Natural Area, Fentress County, Tennessee (photograph by the author).

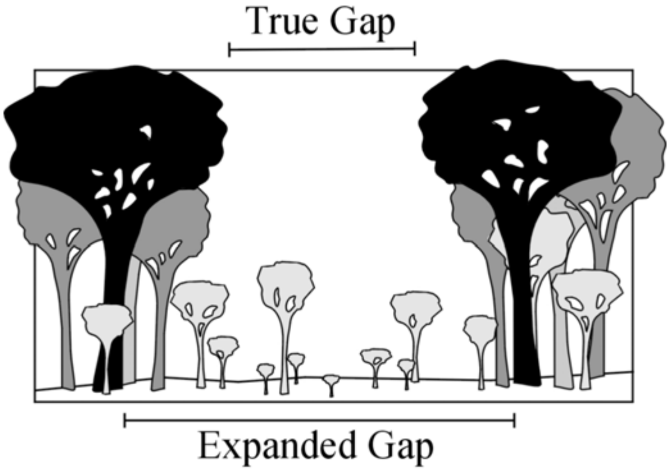


Figure 1.2 The true gap and expanded gap environments. The black trees represent canopy dominants that surround the gap.

occurred and where new individuals are being recruited into the canopy (Watt 1947; Runkle 1981; Runkle 1985a). Canopy gaps are formed by a variety of different mechanisms such as senescence and windthrow. Gaps may be formed by the death of a large branch, an entire tree, or a small cluster of trees (Runkle 1998).

The sizes of canopy gaps vary because of the different mechanisms of gap creation. Disturbances that involve many adjacent individuals create larger gaps at a lower frequency while disturbances that involve many scattered individuals create smaller gaps but with a higher frequency of occurrence (Runkle 1985a). Canopy gaps are characterized by temporary increases in light and potential increases in the availability of water and nutrients (Canham 1988a). In small canopy gaps, greater fluctuations of temperature occur and more available light and soil moisture are found compared to areas underneath the closed forest canopy (Runkle 1985a). As gap size decreases, humidity increases, wind speed decreases, and temperatures fluctuate less (Runkle 1985a). The shape, size, slope, orientation, height of surrounding forest, surviving vegetation, and post-treefall debris of canopy gaps, as well as latitudinal position, are important in determining the microenvironmental conditions of the disturbed area (Brokaw 1985; Runkle 1985a; Poulson and Platt 1989). Because of these many variables, gap-phase dynamics are considered more complicated than stand-initiating disturbance events, which follow the basic tenants of secondary succession (Oliver and Larson 1996).

The scientific study of gap-phase dynamics is important to our understanding of disturbance regimes and successional dynamics in different forest types. Canopy gaps promote uneven-aged forests with patchy canopy dominance (Lorimer 1980; Ross *et al*. 1982; Lewis 1991). Gap events may also cause increases in species density and diversity and modify biomass arrangement within forested environments (Connell 1989; Clinton *et al*. 1994; Reader *et al*. 1995; Runkle 1998; Runkle 2000; Canham *et al*. 2001; Takahashi *et al*. 2001; Frelich 2002; Latham and Tappeiner 2002; Webster and Lorimer 2005). Canopy gaps create heterogeneity in forests and are important for ensuring biological diversity in forest communities (Spies and Turner 1999). Land managers may apply practices based on gap-scale processes to manage for select plant and wildlife species and to better mimic natural forest disturbance regimes.

1.3 Canopy Gaps in Eastern Deciduous Forests

In some eastern deciduous forests, large-scale disturbances occur frequently enough to be dominant influences on forest structure and species composition (Runkle 1991). In regions where large-scale disturbances occur at intervals shorter than the lifespans of dominant taxa, small-scale disturbance events are not major drivers of forest structure or composition change. Regeneration in forests dominated by large-scale disturbances is generally synchronized in pulses that follow the event (Runkle and Yetter 1987). However, research suggests that for much of the forests of the eastern United States, the time between successive stand devastating disturbances is much greater than the lifespans of the dominant taxa (Runkle 1991). Research suggests the average interval between natural stand devastating disturbances in most areas of the eastern United States is approximately 1000 years (Lorimer 1989). In the absence of large-scale disturbance events, most trees die and are replaced individually or in small clusters (Runkle 1982). Thus, small-scale disturbances are important in determining forest structure and species composition. Old growth, hardwood forests throughout the Eastern Deciduous Forest

Region are influenced largely by small-scale disturbances (Runkle 1985a; Runkle 1991; Kupfer *et al*. 1997). In these forests, regeneration is asynchronous and controlled by localized, low-magnitude disturbances that often involve only one or a few canopy individuals (Runkle and Yetter 1987).

Many forests are characterized by a disturbance regime that consists of a combination of large- and small-scale disturbance events, and a relationship between different events does exist. A high frequency of large-scale disturbance events reduces the frequency of small-scale disturbances (Lorimer 1989). Disturbance regimes in hardwood forests of the eastern United States vary greatly. Disturbance mechanisms, spatial extent, severity, and other characteristics vary between and within forests of this region. Several lines of reasoning have been used to document the importance of small-scale disturbance events in eastern hardwood forests. Lorimer (1977) used historical documents from the presettlement period (1793–1827) to estimate the frequency of stand devastating disturbances. Also, permanent plot monitoring in some forests has shown no signs of large disturbance events (Runkle 1991). Lorimer (1980) found age distributions of some eastern deciduous forests to be uneven, indicating tree establishment at many different times. Forest monitoring has also found gaps to be regular occurrences in some eastern forests (Runkle 1982; Runkle 1991). In some stands of the Eastern Deciduous Forest Region, the composition of canopy dominants and gap saplings match, implying that gap-phase processes may have given rise to the current canopy (Runkle 1981; Barden 1989).

1.4 Canopy Gap Creation, Size, and Shape

To create voids in the forest canopy, a portion of a canopy dominant or codominant tree or an entire canopy tree must be removed. A number of different mechanisms can cause the creation of canopy gaps by killing portions of or entire trees. Any event that disrupts a small portion of the contiguous canopy may be considered a mechanism for canopy gap creation. Trees die when they can no longer utilize resources needed to sustain life (Peet and Christensen 1987; Waring 1987). Causes of tree death may be classified as abiotic or biotic (Franklin *et al*. 1987). Biotic mechanisms of gap creation include senescence, mechanical imbalance, starvation, consumption, disease, insect attack, and anthropogenic removal. Abiotic mechanisms include windthrow, ice storms, snow loading, and lightning strike (White and Pickett 1985).

Gap size is largely dependent upon the mechanism of gap creation. For example, a single fallen branch may account for a relatively small gap, while a group of fallen trees will typically result in a much larger gap. Gap size may also vary with forest age. The majority of canopy gaps are formed by the death of a mature individual or the loss of branches from such individuals. Evidence suggests that mature forests have higher rates of canopy gap formation and thus, canopy gaps are a significant type of disturbance in such forests. Lorimer (1989) found that mature forests have a higher frequency of gaps compared to young forests. Also, in mature forests, gaps are less likely to be closed by lateral branch growth. As forests mature, the distance between large individuals increases. Thus, when a large individual dies, the canopy gap that results will be relatively large compared to gaps in younger forests.

The shapes of gaps vary significantly and influence gap microclimate and gap closure. The shapes or holes created by fallen trees are not necessarily easy to determine. Treefalls often result in what may be considered a dumbbell shape (Brokaw 1985). In the idealized dumbbell shape, an upper canopy gap is formed that corresponds to the former tree base, while the majority of the lower forest layers remain intact (Figure 1.3). As the bole falls, neighboring trees are disturbed, resulting in a linear gap away from the tree base. At the end of the idealized dumbbell, the fallen tree crown disturbs the understory while causing little damage to the upper canopy (Figure 1.4) (Brokaw 1985). The fallen crown may kill understory individuals and prevent tree regeneration for that specific site until the debris is removed or decayed from the site (Figure 1.5).

Canopy gaps are not always created by falling trees, however. Dead trees may remain standing, but relatively little forest floor disturbance is associated with trees that die and remain in an upright position (Clinton *et al*. 1994). In gaps created by treefalls, pits and mounds are usually present and act to further disturb the site. For example, treefall debris provides a pulse of nutrients to the immediate environment. Snag (a dead standing tree) gaps result in minimal disturbance to the forest floor and understory individuals (Clinton *et al*. 1994; Cseke 2003). Thus, differences in gap closure may occur between treefall gaps and standing snag gaps. Snags may result from insect infestation or severe drought (Clinton *et al*. 1993) as well as other disturbances and are characteristic of old growth forests (Oliver and Larson 1996).

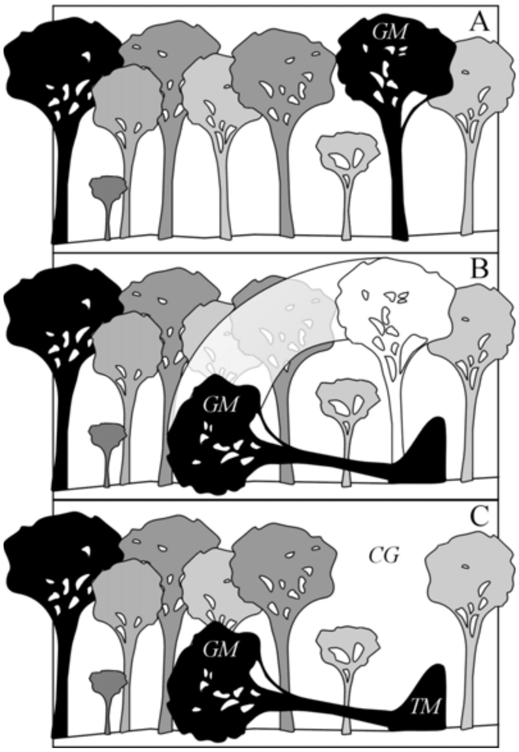


Figure 1.3 Progression of single treefall gap caused by windthrow (A–C). GM: gapmaker; CG: canopy gap; TM: "tip-up" mound.

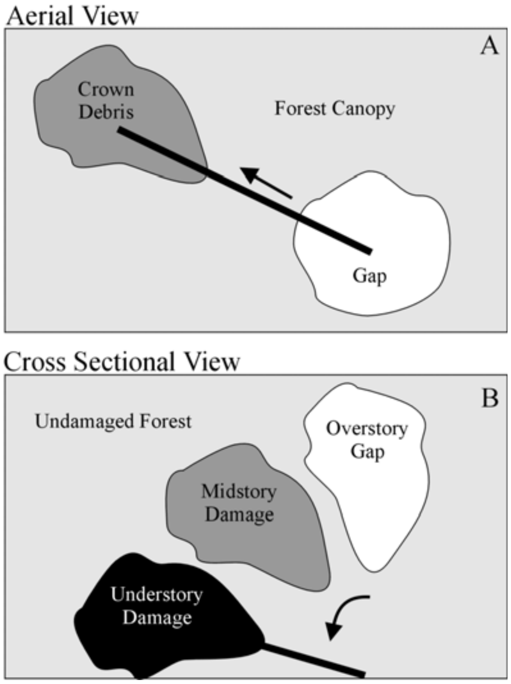


Figure 1.4 Area of damage associated with a single treefall gap shown from aerial (A) and cross sectional (B) views.

Figure 1.5 Post-treefall crown debris from a small canopy gap (photograph by the author).

1.5 Physical Characteristics of Canopy Gaps

The fallout of canopy trees changes ecosystem characteristics and functioning on a small scale. Net primary productivity decreases (Stambaugh 2001), while dead woody debris, light, water, and nutrient availability increase because of the removal of a dominant or codominant canopy individual. Gap-phase studies have primarily focused on changes in available sunlight, water, and nutrients, although other physical modifications do occur.

1.5.1 Light

In eastern hardwood forests, available sunlight is a major factor that limits the establishment and recruitment of plant species. Plants require photosynthetically active radiation (PAR) to perform photosynthesis. Light through the forest canopy may be transmitted as direct or diffuse radiation. Sunflecks play an important role in the photosynthesis of understory plants (Barbour *et al*. 1998; Barnes *et al*. 1998). Sunflecks are small areas of direct light that penetrate through a closed canopy. The position of sunflecks varies throughout the day and year according to the subsolar point. Under a closed canopy, sunflecks are important to ensure adequate light for maintenance and growth of individuals. The creation of canopy gaps allows for increases in PAR to individuals in the understory. Light duration and intensity increase following canopy disturbances (Brokaw 1985; Canham 1988a). Competition for available light increases with time after canopy disturbance as individuals around the gap extend laterally and understory individuals extend vertically into the canopy void (Runkle 1982; Canham 1988b; Stambaugh 2001). The degree of sunlight increases, and subsequent microclimate modification is influenced by gap size and environmental conditions. Sunlight not only has implications for PAR reaching understory individuals, but also for water availability and the overall microclimate of the gap environment.

1.5.2 Water and Nutrients

A lack of quantitative information exists concerning water and nutrient availability after canopy gap events. Vitousek (1985) stated that changes undoubtedly occur in the availability of water and nutrients after the removal of a canopy individual, but few studies have investigated these changes at the gap scale. A limited number of studies that investigated specific species responses to gaps have documented increases in nutrient availability following windfall-created gaps (Cook and Lyons 1983). While working in tropical forests, Anderson and Swift (1983) hypothesized that nutrient availability increases near the zone in which the tree crown falls and is temporarily decreased by microbial immobilization in the zone along the bole. The increase in nutrients is attributed to the concentration of the nutrient-rich leaves of the crown that decompose on site.

1.5.3 Pits and Mounds

Gap-phase disturbances may alter the micro-topography of the gap environment. When trees are uprooted, pits and mounds are often created (Figure 1.6). The overturning of the soil alters soil properties (Runkle 1985a). Pits, which occur in the space previously occupied by the root network, generally contain high levels of litter and standing water. Mounds (often called “tip-up” mounds) usually contain less litter and

Figure 1.6 “Tip-up” mound and pit that resulted from a windblown tree (photograph by the author).

water content than undisturbed soils (Runkle 1985a). These substrates can facilitate the establishment of species within the gap environment. The fallen bole itself may also serve as a nurse log to support vegetation. Seed germination for some species such as *Betula alleghaniensis* (see Appendix A for common name and authority) can benefit or even be dependent on substrates that consist of coarse woody debris. These changes create microhabitats within forest stands, which can significantly influence horizontal structure of the forested environment.

1.6 Tree Response to Canopy Gaps

The ecological response to canopy openings depends upon the mechanism and severity of disturbance, and on the location of the damage (Oliver and Larson 1996). Individuals in the gap environment not injured or killed by the canopy disturbance will respond to potential increases in the availability of light, water, nutrients, and overall growing space. Two primary mechanisms increase these resources to local plants. The first is the reduction in uptake or use of resources by injured or dead individuals. The second is the decomposition and mineralization of nutrients previously contained in living organisms (Canham and Marks 1985).

Increases in resource availability and growing space that result from canopy disturbances cause physiological and morphological changes in residual individuals. Phenotypic plasticity is the ability of an individual to respond to environmental conditions by altering its genotype (Barnes *et al*. 1998). Plants that are plastic can make non-genetic changes to their structure and function to acclimate to their surroundings. Organisms that are more plastic can better respond to changes in environmental conditions, such as increases in light quantity and quality associated with canopy gaps. When additional resources become available, the priority of the individual is first to increase overall leaf area, second to increase height growth, and third to increase radial growth (Oliver and Larson 1996). Tree species with sympodial growth or neoformed shoots are capable of creating more or fewer leaves depending on environmental conditions (Wallace and Dunn 1980). These species support "free growth," where early leaves are created from primordia in the winter bud and late leaves expand from primordia in the winter bud or from new leaf primordia that continue to develop during shoot elongation. When one of these individuals is exposed to increases in available light or increases in other resources, more leaves with the appropriate morphology and anatomy are created (Kozlowski and Pallardy 1997). The number of leaves created by some species with preformed shoots is predetermined. Thus, those individuals are not able to exploit additional resources. This gives an advantage to plastic species and may allow them to outcompete non-plastic species after certain disturbance events. These changes are important in the highly competitive gap environment. Individuals able to create more leaves have more leaf surface area and can create more photosynthate. Some species produce leaves only one time annually and reach maximum leaf area early in the growing season. Other species create leaves throughout the growing season by the production and expansion of new leaf primordia (*i.e.* sympodial growth) or by periodic flushing and formation and opening of buds (Kozlowski and Pallardy 1997).

Leaf area, thickness, specific leaf mass, internal-to-external leaf area ratio, leaf angle, and stomatal size and density can differ between leaves developed in low-light environments and leaves developed in high-light environments (Abrams and Kubiske

1990; Orwig and Abrams 1995). For example, leaves in high-light positions, such as in the top of the canopy, are relatively smaller and thicker than leaves in low-light, lower-canopy positions (Mitchell *et al.* 1999). Leaves created following canopy disturbances may be in high-light environments and may exhibit those characteristics, which makes them better acclimated to exploit additional light in the gap environment.

Following gap-scale disturbance events, uninjured individuals may increase height growth in response to increases in resource availability and growing space. After the tree has increased leaf surface area, more carbon is available for primary and secondary growth. Canopy gaps release suppressed trees in the understory and provide an opportunity for recruitment into larger size classes. The accelerated height growth that follows gap events is important for the release of suppressed individuals of canopy species. For released individuals to reach dominant positions in the canopy, the ability to rapidly increase height is crucial. Lateral growth of shoots is also important following canopy disturbances. Lateral growth can allow the individual to find and exploit favorable microenvironments within the understory and can also serve to cast shade on shorter individuals of less shade-tolerant tree species that become established after gap formation (Canham 1988b).

Additional carbon made available by increased leaf surface area is allocated first for primary or height growth and then for secondary or radial growth. Because radial growth is the last priority, several years may pass between the gap event and an increase in radial growth (Orwig and Abrams 1995). The increase in radial growth is often attributed to increases in the latewood section of the annual xylem ring because the increase in carbon is primarily used for latewood production (production of earlywood is largely influenced by conditions during the previous growing season).

Trees in the gap environment that are not injured do not always show increases in growth after canopy disturbances. Some trees may decrease growth after disturbances while others may show no signs of change. Some individuals may increase growth, but there is a lag to response. At the time of gap formation, some trees may be large enough that they do not increase radial growth. This is true for trees that already have a dominant position in the canopy (Oliver and Larson 1996). Root competition may also prevent trees from being released following canopy disturbances. The death of an individual or small cluster of individuals may increase growing space above ground, but root competition may be high below ground. The failure of a growth rate increase in remnant individuals following partial canopy removal indicates the limiting factor is not light or growing space on the site. In these cases, water or nutrients may be limiting growth.

The seasonality of gaps may also determine plant response. Gaps that form during the growing season expose shade-developed leaves to changes in environmental conditions. When light levels increase, expanding leaves and leaves produced in the new environment may acclimate to high-light conditions. Fully shade-developed leaves are capable of changing the number of chloroplasts, carotenoids, enzymes, and orientation, but are not able to change their anatomy to acclimate to changes in the light regime. Thus, fully shade-developed leaves may undergo a period of photoinhibition after gap events (Kozlowski 1957; Kozlowski and Pallardy 1997; Naidu and DeLucia 1997). Photoinhibition is a decrease in the photosynthetic rate initiated by changes in visible light causing photodamage, repair processes, and down-regulation of photosynthesis because of various protective mechanisms (Naidu and DeLucia 1997). Photoinhibition has a greater influence on trees that will not put on new leaves adapted to high-light conditions during the growing season. For this reason, the seasonality of canopy gap events is important in determining which species will be able to exploit additional resources.

The magnitude of response to gap events by an individual depends not only on the degree of increase in resource availability, but also on the ability of the individual to adapt physiologically and morphologically to additional resources (Canham 1988b). The plant response to the type of canopy opening determines the means (*i.e.* lateral or height growth) and rate of gap closure.

1.7 Canopy Gap Closure

Disturbance characteristics, such as severity and spatial extent, influence the rate at which the impacted community will recover. Vegetative recovery patterns after severe and spatially larger disturbances have been studied by ecologists and follow traditional models of ecological succession. Mild and spatially smaller disturbances are often filled by border trees and individuals in the understory at the time of the disturbance (Runkle 1985a). Small gaps often close by lateral branch growth or branch extension. In such cases, branches of border trees fill void space in the canopy. However, research has shown that crown growth that is too rapid may lead to further gap opening as opposed to gap closure (Young and Perkocha 1994; Runkle 1998). When branches grow at accelerated rates, the probabilities of collapse increase. The subsequent loss of border branches causes gaps to become larger in extent. Thus, individuals whose branches are capable of growing at accelerated rates, while maintaining mechanical balance, possess the best odds of successfully filling gaps. Small gaps have a large ratio of edge to interior (Runkle 1985a) and closure by lateral branch growth is comparatively more likely. Closure by lateral branch extension also depends on the height of individuals in the understory of the disturbed area. Thus, not all small gaps are filled by lateral branch growth. If large saplings are suppressed in the understory when the gap is formed, and if the saplings readily respond to resource availability, gap closure by the suppressed saplings is more probable than closure via lateral branch growth.

Lateral branch growth is not a common means of closure in large canopy gaps. Large gaps are typically filled by individuals present in the understory at the time of the disturbance. In such cases, saplings and seedlings are likely to fill the void space in the canopy. Physiological and morphological characteristics and tree height at the time of disturbance, combined with environmental conditions of the site, determine which individuals will eventually fill the canopy void.

Rates of gap closure depend upon the height of saplings at the time of the disturbance as well as the height growth rate of the understory individuals (Runkle 1985a). Runkle (1982) noted that, after the fifth year following the canopy disturbance, sapling height growth was the primary mechanism of gap closure in old growth mesic forests of the eastern United States. In large gaps where much of the understory vegetation has been destroyed, propagules present in the seedbed at the time of the disturbance or those produced by adjacent individuals may fill void space in the canopy. If a gap is large and severe enough to allow seeds in the seedbed at the time of the disturbance to germinate, establish, and reach the canopy, the disturbance event is best classified at the incomplete-stand initiating scale rather than gap scale.

1.8 Regeneration and Forest Composition Influenced by Canopy Gaps

In the Eastern Deciduous Forest Region, many tree species have the ability to exist in the understory of a closed canopy. These individuals may remain suppressed in the understory until a canopy disturbance creates more growing space and provides the opportunity for understory individuals to be recruited to positions in the canopy. Such species are termed shade-tolerant. Shade-tolerant species can withstand conditions in the understory of a contiguous canopy because their leaves photosynthesize at lower light intensities. Even though many shade-tolerant species can withstand prolonged periods of suppression, most ultimately depend upon canopy gaps or other disturbances to reach a stage of full maturity (Runkle 1990; Oliver and Larson 1996; Schuler and Fajvan 1999; Rentch *et al*. 2003; Rubino and McCarthy 2004).

To survive in the understory of a closed canopy requires a low light compensation point, a low photosynthetic rate, and a slow growth rate (Brokaw 1985). The light compensation point is the light intensity at which photosynthetic gains balance with respirative losses. Late-successional trees are photosynthetically more efficient at lower light intensities compared to early successional, pioneer species (Bazzaz 1979). Though light levels necessary for growth vary among species, research suggests canopy openings accelerate growth of seedlings and saplings in most middle- and upper-story tree species (Brokaw 1985). Because shade-tolerant or primary species can withstand low light conditions in the understory of mature trees, gaps will typically become occupied by such individuals if they are present at the time of formation. Both physiological and morphological traits allow shade-tolerant species to respond to even slight increases in understory light levels (Canham 1990). For example, stomatal opening in response to increases in light intensity is faster for shade-tolerant than intolerant species (Bazzaz 1979). Thus, advanced regeneration is a common means by which gaps are filled.

At the other end of the continuum are species that do not have the ability to withstand substantial periods of suppression. These species are shade-intolerant, and are often termed pioneer or secondary species (Brokaw 1985). Because of their inability to withstand suppression in the understory, most seedlings and saplings will only be present on recently disturbed sites. These species are not likely to be present in seedling or sapling stages in the understory at the time of canopy gap formation. Thus, the majority of pioneer species colonize gaps from seed (Brokaw 1985). Pioneer species produce large seed crops most years. These species typically possess small seeds that are widely distributed and remain viable for long periods. Seed germination is often initiated by a disturbance event such as a canopy gap. For example, changes in light quality, attributed to gaps, may initiate germination of pioneer seeds in the seedbed. Seed germination is a phytochrome response, and is driven by the ratio of red to far-red light. When light passes through the canopy, the green leaves alter the red to far-red ratio of light reaching the forest floor (Barbour *et al*. 1998). Removal of the canopy allows red light to reach the forest floor, converts phytochrome into its active form, and stimulates germination. Seeds of some pioneer species germinate as long as required environmental conditions are met. In such cases, only seedlings in canopy gaps or otherwise disturbed areas will survive. For example, *Liriodendron tulipifera* seeds will germinate under a relatively closed canopy. Because the species is shade-intolerant, mortality will generally occur if a disturbance event does not open the canopy within the first year following germination (Wallace and Dunn 1980).

Gaps provide understory individuals with an opportunity to reach the forest canopy. Growth rates of individuals depend on genetic potential, phenotypic plasticity, and physical conditions within the gap environment (Wilder *et al*. 1999). The establishment of seedlings of woody plants is typically limited, depending on gap size, to the first five years subsequent to gap formation (Canham and Marks 1985; Clinton *et al*. 1994). Early establishment and rapid growth rates are critical for shade-intolerant and moderately intolerant species to remain or become forest components. Shade-intolerant species typically grow faster than shade-tolerant species (Canham 1989), as the rates of photosynthesis are generally higher for sun-adapted species (Bazzaz 1979). Faster rates of growth can provide an advantage in large gaps, or in gaps where much of the understory vegetation has also been injured or killed during or soon after the disturbance event. Following gap events, early-successional species generally use photosynthesis for foliage production, followed by height growth, and then by radial growth (Orwig and Abrams 1995; Oliver and Larson 1996).

The natural maintenance of forest communities depends upon the balance between canopy tree death and replacement (Runkle 1982; Yetter and Runkle 1986). Small-scale disturbances, such as canopy gaps, create patch-work landscapes where dominant species die and are replaced individually. Patches with distinct structure and species composition typically reflect the influence of past disturbances (Veblen 1989). Canopy gaps increase the diversity of the forest environment and promote an uneven-age structure and patchy species composition in the canopy (Lewis 1991). In the absence of large-scale disturbance, many forests maintain high species diversity through canopy gap events. Gaps result in changes in light intensity and quality and soil moisture and nutrient availability, creating microenvironments more suitable to sapling growth than those in the surrounding forest (Yetter and Runkle 1986). Canopy gaps are important for the regeneration of many forest trees (Runkle 1989; Wolf 2005) as gaps promote early and mid-successional tree species that would not otherwise be as abundant in many forests (Runkle 1982; Clinton *et al*. 1994; Wilder *et al*. 1999; Yamamoto and Nishimura 1999; Webster and Lorimer 2005).

Ruderal tree species cannot tolerate prolonged periods of suppression in the understory of a closed canopy. Such shade-intolerant and moderately shade-intolerant species depend upon disturbances for survival (Canham 1989; Canham 1990). Gap events may allow these species to regenerate and become canopy dominants. Shade-intolerant and moderately intolerant species require relatively large gaps or gaps where much of the understory vegetation is removed, because they need gaps that will not likely close via lateral branch growth or by advanced regeneration of shade-tolerant species (Canham 1989; Canham 1990). Without gap events, such individuals would not be present in mature forests where large-scale disturbances are not frequent (Barden 1983). The ability of shade-tolerant species to withstand prolonged periods of suppression in the understory of a contiguous canopy creates a much more complex pattern of canopy dynamics than the simple pattern of gap formation, colonization, and void filling that characterizes communities dominated by shade-intolerant species (Canham 1989).

Species composition also varies within gaps because of differences in gap characteristics, such as size and shape (Whitmore 1989). Canopy gaps typically possess large degrees of variability of both density and diversity of species (Wilder *et al*. 1999; Beckage *et al*. 2000). Differences are attributed to the large number of variables involved in gap formation, allowing a number of species to exploit gap events (Runkle 1989; Wilder *et al*. 1999). Examples include both abiotic features (such as the creation of "tip-up" mounds that may favor certain species), and biotic characteristics such as the crown size and vertical position of the gapmaker may favor individuals in one location over another.

1.9 Justification

During the past two decades, ecologists have increasingly realized the importance of small-scale forest disturbance events in altering ecosystem composition, structure, and function. However, the overwhelming majority of gap-phase and disturbance history research in the Eastern Deciduous Forest Region has been conducted in either protected cove forests or old growth remnants (*e.g*. Lorimer 1977; Lorimer 1980; Runkle 1981; Runkle 1982; Runkle and Yetter 1987; Cho and Boerner 1995; Nowacki and Abrams 1994; McCarthy and Bailey 1996; Nowacki and Abrams 1997; McCarthy *et al*. 2001). These studies have been important for improving our understanding not only of ecological processes in these forest types, but also of gap-scale disturbances and vegetative responses in general. However, these forest types represent a small fraction of forested land in the eastern United States, where the majority of the landscape consists of second growth forests (Cowell 1998; Rebertus and Meier 2001) comprised of mixed

Quercus, *Carya*, and mesophytic species. A need exists to better understand the processes that influence species composition and community structure in these forest ecosystems.

The disturbance events that occur in second growth forest stands influence species diversity and contribute to the future development of the community. Second growth forests are often underappreciated for their diversity and importance in providing necessary habitat for wildlife species. In terms of arboreal species, second growth forests in the eastern United States may support higher species richness than old growth remnants (Clebsch and Busing 1989). Gap-scale disturbances increase this diversity, and a deeper understanding of these processes is essential to the proper management of forest resources, not only on the Cumberland Plateau, but in other regions throughout the eastern United States (Lorimer 1980). This information is not only applicable to forest resource management and conservation, but will also provide the theoretical framework to help improve our understanding of complex dynamics of second growth forest ecosystems throughout the Eastern Deciduous Forest Region. The Cumberland Plateau represents overlapping phytogeographical regions of northern and southern taxa. Although my research focuses on one specific location on the Cumberland Plateau, I believe my research plan can be applied in most eastern deciduous forests. These data will add much needed information on forest disturbance history and climate effects on forest growth and development, such as canopy gap formation and closure rates; fraction of the land they occupy; physical characteristics, such as sizes, shapes, and origins; and how these disturbances influence woody species composition, structure, and tree growth in secondary hardwood forest communities.

To obtain the most comprehensive information possible on canopy gap events in secondary hardwood forests, I am working at multiple hierarchical, spatial, and temporal scales. This research addresses questions spanning from the cellular level to the ecosystem level. I am addressing questions concerning individuals, populations, communities, and ecosystems. I am investigating forest response to individual gaps to the cumulative forest response to gaps throughout a large land tract on the Cumberland Plateau to make generalizations. I am also addressing questions on different time scales from the seasonality of a gap event to the stage of forest development when gaps become important drivers of ecosystem change.

Currently, land managers on the Cumberland Plateau are interested in the biological diversity of the region (NRDC 2005) and the processes that influence that diversity. Researchers with and in conjunction with The Nature Conservancy and Oak Ridge National Laboratory have developed an integrated-landscape model for the forest resources of the Cumberland Plateau and Mountains in Tennessee and Kentucky (Druckenbrod and Dale 2004). Desired future conditions of forested environments have been established using historical documents, GIS modeling, and old growth remnants. A need now exists to understand how to direct dynamic forest ecosystems from the current prevailing conditions to the desired successional pathways. For these plans to be successful, the natural disturbance regimes of the mixed hardwood forests of the region must be better understood at both the landscape and gap scales. The lack of information, especially quantitative information, on forest processes in second growth hardwood stands hinders the success of these projects. This study will essentially provide the framework that will help ground proof and test the integrated-landscape model and the results will be incorporated in support of this project. The results of this study will also be beneficial to ongoing efforts to develop a landscape-level habitat conservation plan for a portion of the Cumberland Plateau and Mountains in Tennessee and Kentucky.

1.10 Hypotheses and Objectives

This study addresses a void in our knowledge of disturbance events, especially small-scale disturbances, and of the development of secondary hardwood forests. The goals of the study are to document the physical characteristics, frequency, and timing of disturbance events and the influence of these events on species composition, stand structure, and forest regeneration patterns in second growth stands during the understory reinitiation stage of development. I hypothesize that the disturbance regimes of the hardwood slope forests on the Cumberland Plateau are characterized by localized disturbance events that involve the death of one or a small cluster of trees. I expect canopy gaps to occur at a higher frequency, but with lower magnitudes, during early stages of forest development compared to similar disturbances during the old growth or complex stages. Although I hypothesize that canopy gaps in secondary forests are small relative to gaps in older forests, I expect these localized disturbance events still influence stand structure and species composition. Small canopy gaps likely provide a means for stand structure to shift from a high density of small individuals to a lower density of larger trees. I also hypothesize even small canopy gaps may allow for the recruitment of understory individuals and thus play an important role in the forest development and succession.

I have ten main objectives of this research. I will:

1. Document species composition of a secondary, mixed hardwood forest on a portion of the Cumberland Plateau in Tennessee
2. Quantify stand structural characteristics including forest age, diameter, and canopy class distributions
3. Create a tree-ring chronology using *Quercus* species to determine the relationships between radial tree growth and climate
4. Reconstruct the disturbance history of the forest using composition and structural measures in conjunction with tree-ring data to determine the primary disturbance mechanisms, the spatial extent, magnitude, and frequency of the disturbances, and to determine if events are synchronous or asynchronous in time
5. Project the successional trajectory of the forest under the current disturbance regime
6. Reconstruct a coarse-resolution fire history using macroscopic soil charcoal
7. Document canopy gap formation mechanisms
8. Quantify the land fraction in canopy gaps and gap size and shape characteristics
9. Determine the influence of canopy gap size on stem density and diversity
10. Quantify canopy gap closure and gap capture processes to investigate the role of gap-scale disturbances on forest successional patterns

1.11 Organization of the Dissertation

The remainder of the dissertation consists of five chapters. Chapter 2 provides a regional description of the Cumberland Plateau in the eastern United States with information on the physical setting, vegetation, land-use history, and current conservation status of the region. The composition, structure, and disturbance history of a secondary hardwood forest on a portion of the western Cumberland Plateau in Tennessee are quantified and the results are compared to an old growth forest in Chapter 3 (objectives 1–5). Also in Chapter 3, I explore the frequency and scale of disturbances through the development of the forest and project the successional trajectory of the forest under the current disturbance regime. A coarse-resolution fire history from soil charcoal is constructed in Chapter 4 (objective 6). In Chapter 5, I provide information on the mechanisms of gap formation, the frequency of occurrence, the physical characteristics of canopy gaps, and the response to these disturbance events in a secondary hardwood forest on the Cumberland Plateau in Tennessee (objectives 7–10). Also in this chapter, I compare the findings of my research in second growth forests and with those reported in the literature for old growth remnants. I summarize the major findings of the dissertation in Chapter 6 and make suggestions for future research needs. The Appendices provide scientific names with authorities and common names of plant species listed, descriptive statistics of the *Quercus* tree-ring chronology, and the standardized chronology.

Chapter 2

Regional Description of the Cumberland Plateau

2.1 Overview

The Appalachian Highland realm of the eastern United States is composed of the New England-Maritime, Adirondack Mountains, Piedmont, Blue Ridge, Ridge and Valley, and Appalachian Plateaus physiographic provinces (Fenneman 1938). Tectonic evolution of these provinces differs, making them structurally and lithologically distinct (Shankman and James 2002). The Appalachian Plateaus physiographic province forms the westernmost boundary of the Appalachian Highland realm. The province extends in a linear strip from New York to central Alabama, covering a total distance of approximately 1,600 km. The Appalachian Plateaus are bounded by the Interior Low Plateau physiographic province to the west and the Ridge and Valley physiographic province to the east. The western boundary of the Appalachian Plateaus province is variably indistinct because of the loss of elevation toward the west (Fenneman 1938; de Blij *et al*. 2004). The Allegheny Front and the Cumberland Escarpment separate the Appalachian Plateau from the Ridge and Valley province to the east.

The Appalachian Plateaus physiographic province is subdivided into seven sections: the Unglaciated Allegheny Plateau, Allegheny Mountains, Glaciated Allegheny Plateau, Catskill Mountains, Mohawk Section, Cumberland Plateau, and Cumberland Mountains. Although sections vary in geology, topography, and other characteristics, all sections consist of degrading plateaus (Fenneman 1938). The Cumberland Plateau (Figure 2.1) is the southernmost section of the province. It is named for the Cumberland

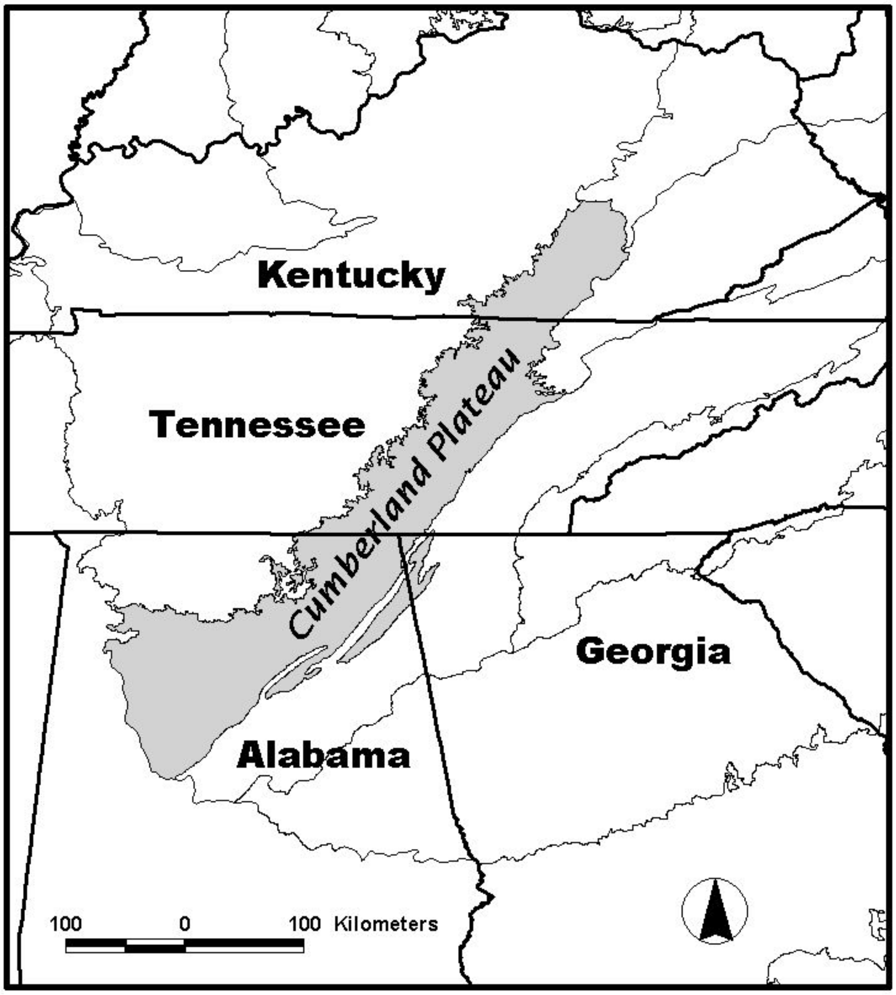


Figure 2.1 Map of the Cumberland Plateau section of the Appalachian Plateaus physiographic province in the southeastern United States (map created by Alison Miller).

River, which was named in honor of the Duke of Cumberland by Thomas Walker in the mid-1700s (Manning 1993). The Cumberland Plateau section extends *ca*. 600 km from southern Kentucky, in the Kentucky River drainage, to the terminus of the province in central Alabama where the Fall Line separates the Appalachian Plateaus province from the northern boundary of the Gulf Coastal Plain. Streams on the plateau drain into the Gulf of Mexico via the Tennessee and Cumberland River systems.

The boundaries of the Cumberland Plateau are in many places vague, and differences in local vernacular often make it difficult to discern which spatial components actually belong to the Cumberland Plateau proper. The names Cumberland Plateau, Cumberland Mountains, or simply Cumberlands are often used synonymously to refer to the section of the Appalachian Plateaus province that occurs in Kentucky, Tennessee, and Alabama. The Cumberland Mountains, however, are a distinct physiographic section of the Appalachian Plateaus province. The Cumberland Mountains section occurs in a linear strip *ca*. 240 km long and 40 km wide through Virginia, Kentucky, and Tennessee and is distinguished from the Cumberland Plateau by altitude and relief (Fenneman 1938). Because the boundaries of distinct sections are not always clear, the greater Cumberland Plateau region is often called the southern Appalachian Plateau in scientific literature.

2.2 Climate

The climate of the Cumberland Plateau varies widely with topography. Generally, precipitation and temperature decrease from south to north. Regionally, the climate is classified as humid mesothermal with adequate precipitation throughout the year (Thornthwaite 1948). The entire region is humid and although precipitation is less in fall, there is no distinct dry season. During summer, the area is dominated by maritime tropical (mT) air as the Bermuda high drives warm, moist air across the region. The mT Gulf/Atlantic air mass is relatively unstable and active in the region from late spring to early fall. During winter, the polar jet stream is displaced southward and cold, dense continental polar (cP) air generally dominates the region. Daily and seasonal weather largely result from the alternating dominance of these two air masses.

The temperature of the region is characterized by long, moderately hot summers and short, mild to moderately cold winters (Smalley 1986). Mean temperature generally decreases from south to north. Near the geographic center of the Cumberland Plateau, the mean temperature is about 13 °C. At Crossville, Tennessee, located near the geographic center of the region, the average January temperature is 1 °C and the July average is 23 °C. Mid-afternoon temperature in summer is on average 2–4 °C cooler on the Cumberland Plateau than in the adjacent Eastern Highland Rim or Ridge and Valley provinces (Smalley 1986). The frost-free period typically lasts from mid-April to mid- to late October. Nighttime temperatures often drop below freezing in December, January, and February (Smalley 1986). The average frost-free period is approximately 180 days. Killing frost can occur as late as the middle of May and as early as late September (Shumann 1984). During winter, soil may freeze to a depth of 5–15 cm and remain frozen for 2–12 days (Smalley 1986).

Precipitation is well distributed throughout the year. Annual precipitation for the region is approximately 120–150 cm (Delcourt 1979; Smalley 1986). Winter is generally the wettest season and fall is generally the driest. During the warm season (March–

August), most precipitation results from convectional thunderstorms. These short storms are characterized by high intensity rain events and may cause flooding at lower elevations. Convectional storms in late spring and summer are often characterized by high winds and may produce hail. High-intensity rainfall that may include hail occurs approximately 50 days each year (Smalley 1986). Throughout the rest of the year, precipitation largely results from cyclonic activity. Mid-latitude cyclones generally cause steady precipitation that may last several days. The Cumberland Plateau also receives some degree of orographic precipitation and is, therefore, slightly wetter than adjacent physiographic provinces (Dickson 1960; Song 1994). Snowfall occurs at the highest elevations, but it is generally minimal (rarely exceeding 7 cm) and melts within a few days (Smalley 1986).

2.3 Geology and Soils

The Appalachian Plateaus physiographic province is underlain by nearly horizontal to deformed clastic sedimentary strata of the Paleozoic era (Shankman and James 2002). The hard rock cap of the plateau consists largely of Pennsylvanian rocks underlain by rocks of Mississippian age (Smalley 1982; Manning 1993). Outcrops of Mississippian rocks occur on lower slopes below the escarpment and where streams are very deeply incised. The age of surface rocks decreases from south to north. Bedrock of the southern Appalachian Plateau surface consists of sandstone, shale, and conglomerate of the Gizzard, Crab Orchard Mountains, and Crooked Fork Groups (Smalley 1982). The sandstones, shales, and conglomerates of the province vary in their resistance to erosion.

In general, the rocks of the Cumberland Plateau are more resistant than those found to the north (Fenneman 1938).

The Appalachian Highland realm has a long and complex history, with some deformation occurring as early as the Precambrian (Miller 1974). The last major deformation episode (the Allegheny orogeny) that influenced the region occurred late in the Paleozoic Era. Sediments that had collected on the eastern margin of the continent for millions of years buckled, fractured, and formed the long, highland chain from Pennsylvania to Alabama (Miller 1974). The Cumberland Plateau marks the westernmost boundary of deformation that occurred during the Allegheny orogeny, with thrust faults and bedding-plane faults that extended well onto the plateau (Luther 1977). Rocks along the eastern edge of the plateau were tightly folded and occasionally stressed to the point of breaking. These forces, however, did not reach the western margin of the province (Luther 1977). Much of the surface of the Cumberland Plateau has been thrust upward and to the northwest along faults. The faults that form the boundary of the displaced section of the plateau are collectively called the Cumberland Plateau overthrust fault (Luther 1977).

In general, the soils of the Cumberland Plateau formed either directly from Pennsylvanian rocks (sandstones, siltstones, and shales) or from materials weathered from them (Springer and Elder 1980). The soils are predominately highly leached Ultisols belonging to siliceous, mesic families, and are mostly Hapludults defined by minimal horizon development in humid settings and Paleudults which are old developments in humid settings (Francis and Loftus 1977; Hinkle 1978; Brady and Weil 2002). Upland soils are generally derived from sandstone and shale parent material.

Ravine soils may be derived from limestone parent material (Hinkle 1978). Soil depth varies, but depth to bedrock is generally 0.5–1.5 m (USDA 1995). Soil properties vary according to changing environmental conditions such as slope aspect and slope position. Regionally, soils are typically well drained, loamy, strongly acidic, and low in natural fertility (Springer and Elder 1980). Nitrogen, phosphorus, and calcium have been shown to limit plant growth in the southern section of the province (Francis and Loftus 1977; Hinkle 1989; Song 1994).

2.4 Topography

The Appalachian Plateaus province is dissected throughout, but the extent and type of dissection varies (Fenneman 1938). The Appalachian Plateau is a tableland that has been deeply incised by streams (Figure 2.2). The tableland surface is especially extensive in Tennessee and some authors consider it a separate section called the Central Uplands (DeSelm and Clark 1975). The entire province has an irregular topography attributed to erosion of the horizontal and slightly dipping strata (Fenneman 1938; de Blij *et al*. 2004). The general elevation of the Cumberland Plateau is approximately 500 to 600 m above mean sea level (Miller 1974). The Cumberland Plateau is 240–610 m above the Ridge and Valley province and 240–300 m above the Eastern Highland Rim section (Fullerton *et al*. 1977). The highest peaks on the Cumberland Plateau are approximately 1,000–1,080 m. In some places, streams have cut valleys over 450 m deep. The Cumberland Plateau was never glaciated and contains well-developed stream networks. The southern portion of the province is less dissected than the more northerly sections (Fenneman 1938). Dissection also increases toward the plateau margins, especially along

Figure 2.2 Incised stream valley on the Cumberland Plateau in Fall Creek Falls State Park, Tennessee (photograph by the author).

the western margin near the Eastern Highland Rim. The Cumberland Plateau has an undulating surface submaturely dissected by young valleys. The steepness of the valleys and degree of stream incision increases toward the edges of the province (Fenneman 1938).

The eastern boundary of the plateau is abruptly marked by the Allegheny Front and the Cumberland Escarpment. The plateau rises almost 300 m above the floor of the Ridge and Valley province to the east. Irregularities in the steep escarpment wall occur where streams flow eastward off the plateau and into the Tennessee River drainage. The extreme irregularity of the western boundary is a result of the dissection of the plateau by numerous streams that flow off the plateau surface (Fullerton *et al*. 1977; Luther 1977). The western boundary contains many deep gorges (known locally as gulfs), waterfalls, and caves (Figure 2.3).

The majority of the Cumberland Plateau surface is considered gently rolling topography. Exceptions do occur, however, especially in the eastern section of the plateau where degradation of complex geologic structures has produced a variety of surface expressions (Fullerton *et al*. 1977). Examples include Cross Mountain (1,077 m elevation) to the north and the Sequatchie Valley or anticline to the south. The Sequatchie Valley is a linear lowland approximately 6–7 km wide that extends about 290 km from southeastern Tennessee to northeastern Alabama. The Sequatchie Valley is underlain by limestone and contains fertile soils. The valley has steep walls rising 245–425 m above the floor (Fullerton *et al*. 1977). The Sequatchie Valley separates the Cumberland Plateau proper to the west from Walden Ridge to the east (Fullerton *et al*. 1977; Luther 1977).

Figure 2.3 Waterfall on the Cumberland Plateau at Fall Creek Falls State Park, Tennessee (photograph by the author).

On a finer scale, the Cumberland Plateau has unique geologic features. Differential weathering of plateau rock has created a number of features including caves, arches, rock shelters, chimneys, and sinks. The higher elevations or tableland of the plateau have been preserved by the resistant sandstone cap that is underlain by softer shales, siltstones, and clays (Figure 2.4). The resistant sandstone cap has prevented the entire region from being lowered by degradational processes (Fullerton *et al*. 1977). The vertical plateau escarpments are also formed from the hard, resistant sandstone that covers the plateau tableland (Luther 1977) (Figure 2.5). Groundwater and streams dissolve the more easily eroded rock strata beneath the sandstone and create caves, arches, and sinks.

2.5 Vegetation

2.5.1 Classification and Description

Braun (1950) and Kuchler (1964) provided the basis of forest classification in the eastern United States. Braun's forest regions closely follow the physiographic provinces established by Fenneman (1938) as a relationship exists between physiographic and floristic regions. This relationship is most pronounced when the boundaries between physiographic provinces are sharp (Shanks 1958). The major forest subdivisions follow latitudinal zones and listed from north to south are the Northern Transitional, Central Hardwood, Southern Transitional, and Southern Evergreen Regions. The Central Hardwood Region encompasses three distinct sections: the *Quercus-Castanea*, mixed mesophytic, and western mesophytic forests. This region occupies the mostly unglaciated central and southern Appalachian Mountains and the Central Lowland

Figure 2.4 Resistant sandstone cap, sheer cliffs, and slope forests of the Cumberland Plateau near Jamestown, Tennessee (photograph by the author).

Figure 2.5 Resistant sandstone caprocks at the Cumberland Plateau surface in Fentress County, Tennessee. This photo was taken from the north side of the ridge (photograph by the author).

physiographic provinces. The Central Hardwood Region contains diverse forests where variability is largely influenced by topographic and edaphic conditions, such that fine-scale community composition and structure are highly complex (Shankman and James 2002).

Mixed mesophytic forests develop on moist, well-drained sites (Runkle 1996) and are considered the dominant forest type on the unglaciated Appalachian Plateaus province in Ohio, West Virginia, Kentucky, Tennessee, and Alabama. Both Braun (1950) and Kuchler (1964) placed the Cumberland Plateau almost wholly within the Mixed Mesophytic Forest Region (with the exception being the extreme southernmost end of the plateau and specific local areas). These forests are noted for their compositional and structural diversity (Muller 1982). Mesophytic forests are characterized by a lack of dominance by any one species, but common canopy species include *Quercus alba*, *Q. rubra*, *Fraxinus americana*, *Fagus grandifolia*, *Acer saccharum*, *Liriodendron tulipifera*, and *Tsuga canadensis*. They also contain specific indicator species (*e.g. Aesculus flava* and *Tilia heterophylla*) in the canopy and possess high species richness in all forest layers. In general, forest communities of this region are characterized by high biodiversity at the community level and contain over 30 canopy species (Hinkle *et al*. 1993). The biodiversity of the region has been attributed in part to the great variety of site conditions (Sampson 1930; Braun 1942; Braun 1950), which results in high beta (different sites) and gamma (regional) diversity (Muller 1982).

2.5.2 Forest Communities

The Cumberland Plateau is an extremely varied landscape that consists of mountains, deeply incised stream valleys, broad floodplains, steep to rolling hills, and a tableland surface with minimal relief. Each of these land types is inhabited by different forest communities. Forest composition is largely a function of slope position, aspect, and form (Hinkle *et al*. 1993). On the Cumberland Plateau, true mixed mesophytic forests are restricted to protected mesic sites such as gorges and coves (Martin 1992). Even Braun (1942) recognized that the entire Cumberland Plateau did not support true mixed mesophytic forests. She hypothesized the forests on the Cumberland Plateau, while still a component of the Mixed Mesophytic Forest Region, supported lower quality forests relative to the Cumberland Mountains because of extreme relief and nutrient-poor soils. Braun speculated the best examples of true mixed mesophytic forests occurred in the Cumberland Mountains.

In general, forests of the Cumberland Plateau proper exhibit greater dominance of *F. grandifolia* and *Q. alba* and reduced dominance of *A. flava*, *T. heterophylla*, *A. saccharum*, *L. tulipifera*, and *Q. rubra* compared to the Cumberland Mountains (Muller 1982). Because of these variations within the Mixed Mesophytic Forest Region, Braun (1950) further subdivided the classifications into sections, subsections, and districts. The majority of the Cumberland Plateau in Tennessee was classified into the Cliff Section subdivision of the Cumberland and Allegheny Plateaus section (the Cliff Section spans from southern Kentucky to northern Alabama). This section was named for the rugged terrain or “bold cliffs” that characterize the plateau through much of Tennessee (Braun

1950). She further subdivided the Cliff Section into Northern and Southern districts, with the Cumberland Plateau of Tennessee being largely within the Southern district.

The complex topography and variations in substrates create a wide range of microclimatic and edaphic conditions on the Cumberland Plateau. However, the vegetation of the region can be classed into one of two broad categories: the flat to rolling plateau uplands and the plateau ravines and gorges (Hinkle 1989). The most spatially comprehensive study on Cumberland Plateau forest communities was conducted by Hinkle (1978) and summarized in Hinkle (1989). Hinkle documented 12 community types through the flat to rolling plateau uplands that ranged from stands dominated by *Acer rubrum*, *Betula nigra*, and *Ilex opaca* on floodplain terraces to stands dominated by *A. rubrum*, *Q. alba*, and *Nyssa sylvatica* on poorly drained swales to stands dominated by *Q. marilandica* and *Pinus virginiana* on xeric ridge tops (Hinkle 1978; Hinkle 1989). Slope forests are generally dominated by mixed *Quercus* species with *Q. alba* being the most abundant followed by *Q. coccinea* and *Q. velutina*. Other common canopy dominants on the plateau tabletop include *Pinus echinata*, *Q. stellata*, *Q. montana,* and mixed *Carya* species (Hinkle 1989). On these upland sites, species composition is controlled by topographic characteristics and factors related to soil water availability such as depth to bedrock and surface stone cover (Hinkle 1978).

Ravines and gorges occur throughout the plateau but become more common near the eastern and western escarpments. In these areas, erosion of the caprock has created steep and often very deep gorges. These gorges were the inspiration for Braun (1950) to name this region the Cliff Section. Hinkle (1978) identified 12 community types in the ravines that ranged from communities dominated by *Q. montana*, *Q. alba*, or *Q. velutina* at upper slope positions to rich *Q. alba*, *Q. rubra*, and *A. saccharum* stands at middle and lower slope positions (Hinkle 1989). Hinkle (1978) noted that the common mixed mesophytic indicator species were present but not important in most of the *A. saccharum-Q. alba*, *Q. rubra-A. saccharum*, and *Q. alba-Q. rubra* communities sampled. He did note, however, that many stands seemed successional to mixed mesophytic types. Stands dominated by *Tsuga canadensis* are restricted to headwaters and along bedrock streams where they occur as ribbon forests. The only other common gymnosperm in ravine communities is *Pinus strobus*, which usually occurs in close proximity to *T. canadensis* stands (Hinkle 1989). Factors related to soil moisture and nutrient availability control community composition in ravine communities (Hinkle 1978).

2.6 Land-Use History

2.6.1 Native American Habitation

Evidence for the earliest human occupation on the Cumberland Plateau is found at Russell Cave in Alabama. Documented artifacts indicate humans began to occupy the plateau about 15,000 BP. The early inhabitants of the Cumberland Plateau were hunters and gatherers. The region supported big game species such as elk (*Cervus canadensis* Erxleben), white-tailed deer (*Odocoileus virginanus* Zimmerman), and American bison (*Bison bison* sp.). Mast, notably acorns, hickory nuts, walnuts, and chestnuts, was collected to supplement the diet of wild game (Delcourt *et al*. 1998; Manning 1993). Ethnobotanical remains of mast shells have been dated to the early Holocene (9,000–8,000 BP) and rind fragments and seeds of gourd/squash have been documented from the past 5,000 years on the Cumberland Plateau in Kentucky (Delcourt *et al*. 1998). Around

3,000 BP, human inhabitants lived along streams and inhabited upland rock shelters. At this time, Native Americans on the Cumberland Plateau began to cultivate food crops. During the late Archaic (*ca*. 3000–1000 BC) and early Woodland (1000 BC–AD 0) periods, new plant cultigens were introduced and new technologies were implemented such as the use of fire to clear forest sites, broadcast planting of seeds within prepared plots, and new processing techniques to collect edible plant parts (Delcourt *et al*. 1988). During the Woodland period, Native American settlement on the Cumberland Plateau increased. Archaeological evidence shows more settled sites and longer durations of occupancy during this period (Wilson and Finch 1980; Kline *et al*. 1982). As horticultural techniques became more refined, people began to move away from the plateau to broad and more fertile stream valleys more suited to agriculture (Manning 1993).

The major organized Native American tribes to inhabit the Cumberland Plateau were the Cherokees and Shawnees (*ca*. AD 1300–mid-1800s), although a number of tribes used the region including the Creek, Chickasaw, Choctaw, and Yuchi. None of these tribes had a concentration of villages on the Cumberland Plateau, but the plateau was considered part of their hunting grounds, especially for the Cherokee and Shawnee. As Europeans began to move west, the Cherokee and Shawnee tribes were forced to rely more heavily on the resources of the plateau (Manning 1993).

2.6.2 European Migration and Settlement

The majority of the early European inhabitants of the Cumberland Plateau were of Scotch-Irish and German ancestry. Many of these early European settlers were veterans who served in the French and Indian Wars as well as the Revolutionary War. Under the Military Reservation Act of 1782, war veterans received land grants as compensation for their service. Millions of hectares of land on the Cumberland Plateau were given to veterans of the Revolutionary War (Manning 1993).

The first European immigrants to the plateau lived in rock shelters. Later, pole cabins with mud floors were constructed and eventually the European inhabitants built cabins made of hewn logs with split-log flooring. With time, second stories and stone chimneys were added (Manning 1993). Small land parcels were cleared for agriculture and livestock grazing, although wild game still supplemented the settlers' diet.

The Cumberland Plateau was a barrier against the westward migration of European settlers (Luther 1977) until a path through the Cumberland Gap was discovered and publicized by Thomas Walker in 1750 (de Blij *et al*. 2004). The western section of the trail, known as Warrior's Path, linked Shawnee and Cherokee villages. The eastern section of the trail, known as the Great Warpath, connected the Iroquois to the north with the Cherokee to the south. The linked paths became known as the Wilderness Road (completed in 1796) and served as the major trans-Appalachian route for European migrants (de Blij *et al*. 2004). The Cumberland Gap was formed by stream erosion and is a relatively low and clear passage near the current intersection of the Virginia, Kentucky, and Tennessee state borders.

Many Europeans viewed the Cumberland Plateau as "wild land" separating the fertile lands of the east (the older settlements) from the fertile lands further to the west (the newer settlements) (Manning 1993). Many European settlers simply traversed the Cumberland Plateau on their migration west. They traveled across the plateau on Native

American trails and harvested game along the way, even though the majority of the Cumberland Plateau in Tennessee still belonged to the Cherokee. In 1787, plans were established to link the European settlements in the Washington district of the east to western settlements. To assist migration, the Tallonteeskee Trail, a Native American trail that was the most used by migrating Europeans to cross the plateau, was widened to 3 m. The road, named the Walton Road, was completed in 1802. Soon after the road was completed, small European settlements were established along its path (Manning 1993). Increasing pressure from European settlers on the Cumberland Plateau eventually forced Native Americans out of the region. By 1819, formal treaties had removed the plateau from Native American ownership. European settlement, however, was rather slow (Fullerton *et al*. 1977; Manning 1993).

European settlement on the Cumberland Plateau occurred later than settlement in the Ridge and Valley or Eastern Highland Rim. Widespread settlement on the plateau did not occur until well into the 1800s (Fullerton *et al*. 1977). Delayed settlement and sparse population density of the region may be partly explained by the land conditions. Historically, the region has been difficult to access. Along with the difficulties presented by the eastern escarpment, travel on much of the plateau surface was hindered by the deeply incised stream valleys that create a highly dissected plateau surface. Also, the soils of the plateau are generally less productive than soils of bordering provinces and more favorable sites for agriculture were sought first. Nonetheless, land parcels on the plateau were cleared for agriculture and the grazing of livestock. Without modern soil amendments and agricultural practices, however, crop farming was only profitable in the Sequatchie Valley and in small isolated valleys with more fertile soil (Manning 1993).

Mining has long been an important activity on the Cumberland Plateau. Saltpeter mining occurred on the plateau from approximately 1812–1865. Saltpeter was used in the making of gunpowder and was an important resource during the War of 1812 and especially during the Civil War (Manning 1993). The discovery of coal on the Cumberland Plateau caused a rapid increase of European settlement in the region. The claiming of mineral rights on the plateau began in the 1880s and actively continued until the 1910s. Strip mining began on the plateau in the 1920s, but drift mines, auger mines, and deep mines were also used.

The forests of the Cumberland Plateau were exploited for a number of products and services, most notably timber for construction and fuel. During the Civil War, large land tracts were cleared, leaving entire slopes devoid of forest vegetation. The arrival of rail lines allowed for further exploitation of forest resources on the plateau (Manning 1993) and it has been reported that enough timber was removed each year from specific areas of the Mixed Mesophytic Forest Region to fill 700 box cars (Baker 1925). Loggers favored the most commercially valuable trees such as *Quercus* spp., *L. tulipifera*, *Juglans nigra*, and *Carya* spp. among others, especially those individuals with straight, knotless boles (Hinkle *et al*. 1993). By 1910, approximately 227 saw mills were active on the Cumberland Plateau (Hall 1910). Near the center of the Cumberland Plateau in Tennessee, logging activity peaked around 1920 (Hinkle *et al*. 1993).

2.6.3 Modern Land Use

Even in modern times, the plateau was difficult to traverse until the construction of highways across and within the region. Settlement on the plateau was hindered by its lack of, and distance from, major transportation networks such as major roadways, railways, and waterways (Fullerton *et al*. 1977). The Cumberland Plateau was the last region to be settled in Tennessee and is still sparsely populated. The largest city on the plateau in Tennessee is Crossville, with a population estimated to be just under 9,000 (US Census Bureau 2006).

The primary natural resources extracted in the region continue to be coal and timber, while grazing is also an important activity. Bituminous coal is the most important and abundant mineral resource on the Cumberland Plateau, although stone and petroleum are also mined (USDA 1995). The development of railways on the plateau in the 1880s allowed for more organized coal extraction. Coal extraction in the region peaked between 1900–1920, although it remains an important resource today. The price of coal has recently increased, making it profitable to re-open abandoned mines. As the cut-off grade, which is the lowest amount of ore in a deposit that will recover mining costs, decreases, the amount of ore in a mineral deposit increases. If this pattern continues, it is expected that the importance of coal mining activities on the Cumberland Plateau will increase. This may be especially true for the Cumberland Mountains sections, where most of the coal occurs.

The Cumberland Plateau is generally considered a region of low agricultural productivity (Fullerton *et al*. 1977; Adams *et al*. 2000), largely because the region has such rugged terrain and poor soils. Because row cropping is not economically viable for much of the region, most cleared land is used for the grazing of livestock, especially cattle. Grazing horses are also common as horseback riding is an important recreational activity in the region.

Over 1.2 million ha of forested land occur on the Cumberland Plateau in Tennessee, as timberland represents 71% of the plateau region within the state (Schweitzer 2000). Of these 1.2 million ha, 1.07 million ha (or 88%) are hardwoods. The dominant forest type is *Quercus-Carya*, which accounts for 85% of all hardwood stands of the Cumberland Plateau in Tennessee (Schweitzer 2000). The vast majority of forested lands on the plateau region of Tennessee are in non-industrial private ownership (72%), while 17% of all forested land in the region is used by the forest industry, and 11% is public land (Schweitzer 2000).

2.7 Current Environmental Issues

Land managers and environmentalists are currently in debate over the status of biological diversity of the Cumberland Plateau and Mountains. The Natural Resources Defense Council has termed the region a “biogem,” claiming the Cumberlands have a higher concentration of endangered species than anywhere else in North America (NRDC 2005). This statement has caused much debate between private and governmental organizations throughout the region. Stakeholders are currently making decisions on limited information. Little quantitative data exist for variables that influence the spatial aspects of biodiversity within the region, such as disturbance events. Stakeholders from a number of different environmental organizations contend the biodiversity of the Cumberland Plateau is being threatened by a number of different mechanisms, including timber practices, residential development, road construction, coal mining, fire suppression, grazing activities, and the introduction of alien species. The three mechanisms most often cited as environmental threats are conversion of native forests to monospecific plantations, residential development and associated impacts, and mining.

McGrath *et al*. (2004) investigated forests on the Cumberland Plateau surface across seven counties (*ca*. 243,000 ha) in southern Tennessee and found all had a net loss of native forests between 1981 and 2000. Conversion of native forests to *Pinus* (especially *Pinus taeda*) plantations was cited as the major cause of native forest decline (McGrath *et al*. 2004). This study found that 25,175 ha (*ca*. 10%) of native hardwood forest were lost to pine conversion during the 9-year study period.

The Cumberland Plateau possesses an aesthetic beauty as well as recreational opportunities that make it an ideal location for leisure communities. Recently, the number of community developments in the region has drastically increased, with others in construction or planning phases. The plateau area has become a desirable location for retirees because of the pleasant climate, attractive landscape, and affordable living expenses. These retirement developments are usually in the form of gated communities that attract homeowners by emphasizing the wilderness and scenic beauty of the Cumberland Plateau. Environmentalists fear these developments will progress in a largely unregulated manner that will compromise ecosystem integrity.

The recent attention given to biodiversity and ecosystem threats of the Cumberland Plateau and Mountains has given rise to several initiatives designed to ensure that the environmental integrity of the region endures as current and future land-use activities proceed. Although a number of conservation programs operate within the region, three initiatives at the landscape level are in the implementation or developmental stages. These initiatives include a habitat conservation plan, a desired future forest conditions program, and a proposed national heritage corridor. The habitat conservation plan is being implemented by private (The Nature Conservancy) and governmental (Tennessee Wildlife Resources Agency) agencies to identify and protect the habitat of 80 target species within the region. These conservation targets include 15 terrestrial animals, 39 aquatic animals, 16 plant species, and 10 plant communities (Mawhorter 2006). The goal of this project is to link landowners with regulatory agencies to develop conservation measures that will result in region-wide benefits for endangered, threatened, or concerned species.

The desired future forests initiative was developed by researchers with and in conjunction with The Nature Conservancy and Oak Ridge National Laboratory using an integrated-landscape model to study the forest resources of the Cumberland Plateau (Druckenbrod and Dale 2004). Desired future conditions of forested environments were established using historic documents, GIS modeling, and old growth remnants. Researchers are now trying to understand how to direct forest communities from the current prevailing conditions to the desired successional pathways. Socio-economic analyses are currently being conducted for the region to investigate landowner decision making and to implement market-based incentives that would foster forest succession toward the desired trajectories (Druckenbrod and Dale 2004). The overall goal of this project is to create forest communities with composition and structural attributes that resemble those of pre-European settlement forests.

The national heritage corridor proposal has been submitted by the Alliance for the Cumberlands to the National Park Service. This proposal emphasizes the physical, biological, cultural, and historical significance of the Cumberland Plateau, which in the proposal is called “a remnant of the old Southwest frontier.” If the proposal is accepted, the Cumberland Plateau National Heritage Area would fall under the direction of the United States Department of the Interior. A number of locations with significant cultural and historical value would be preserved under this designation (Alliance for the Cumberlands 2006).

The Cumberland Plateau has been called one of the “wildest, poorest, prettiest, and most ecologically diverse locales in Tennessee” (Alligood 2005). Although there is much debate and some controversy concerning ecosystem integrity and land-use activities such as timber practices, development, and mining in the region, it is safe to say the Cumberland Plateau is physically, biologically, and culturally unique. Stakeholders on both sides of these issues must find common ground to develop programs to conserve the natural features of the region while realizing the full economic potential of the region. The natural beauty and cultural heritage of the Cumberland Plateau, coupled with the large amount of public land, make the area a very desirable place to live and visit. However, the Cumberland Plateau is a poor region that economically lags behind the rest of the state. Despite limited water availability, it has been proposed that the plateau is the next big region of population and economic growth in Tennessee because of its unique characteristics. Land managers and planners hope to accommodate new people while maintaining many of the environmental qualities that make the area so desirable.

Chapter 3

Composition, Structure, and Dendroecology of the Pogue Creek Natural Area

3.1 Introduction

The forests of the Cumberland Plateau are among the most diverse of the world's temperate-zone forests (Hinkle *et al*. 1993). The Cumberland Plateau is an extremely varied landscape that consists of mountains, deeply incised stream valleys, broad floodplains, steep to rolling hills, and a tableland surface with minimal relief. Each of these land types is inhabited by different forest communities as variability is largely influenced by topographic and edaphic conditions, such that fine-scale community composition and structure are highly complex (Hinkle *et al*. 1993; Shankman and James 2002). A great variety of microenvironmental conditions have resulted in high diversity at the community level and have allowed the region to support taxa that generally dominate forests of higher and lower latitudes (Sampson 1930; Braun 1942; Braun 1950; Muller 1982; Hinkle 1989).

Most forests on the Cumberland Plateau are far from pristine, however, and reflect a long history of anthropogenic land use. Human artifacts on the Cumberland Plateau have been dated to 15,000 BP, indicating that forests of the region have likely been disturbed by anthropogenic activities for millennia (Delcourt and Delcourt 2000). With the arrival of European settlers, the spatial extent and intensity of human impacts on forest communities increased throughout the eastern U.S. (Cronon 1983; Whitney 1994;

Motzkin *et al*. 1999; Foster *et al*. 2003), and the Cumberland Plateau was no exception. Widespread European settlement on the Cumberland Plateau did not occur until the mid-1800s (Fullerton *et al*. 1977) as the eastern escarpment and rugged terrain made travel difficult and the unfertile soils made the region less attractive to settlers (Luther 1977; Manning 1993). During the Civil War, large tracts of forested land on the Cumberland Plateau were cleared largely for wood products and fuel. As a result, forest vegetation was removed from large contiguous areas. The rate of forest exploitation in the region increased with the arrival of the rail lines (Manning 1993). By 1910, approximately 227 saw mills were operating on the Cumberland Plateau (Hall 1910), but logging activity did not peak until 1920 (Hinkle *et al*. 1993). Large land tracts now support forest vegetation, the composition and structure of which is dependent upon a suite of conditions including physical site characteristics, land-use history, and natural and anthropogenic disturbance events during stand development (Raup 1966; Cronon 1983; Christensen 1989; Whitney 1994; Cowell 1998; Foster 2002; Frelich 2002; Foster *et al*. 2003).

Because the majority of the forests in the region consist of secondary stands (*i.e.* not old growth) that developed after widespread timber removal that during the 19th and early 20th centuries, the documentation of successional patterns is important to our understanding of pattern and process in contemporary forest communities. Following a stand initiating disturbance event (such as anthropogenic clearing, a large wildfire, or an insect outbreak), forest development may follow predictable patterns in accordance with biotic and abiotic site characteristics (Bormann and Likens 1979). Oliver and Larson (1996) established a theoretical model of forest growth and development following the removal of overstory vegetation. Forest development is divided into four distinct phases, including stand initiation, stem exclusion, understory reinitiation, and complex stages of development. Each stage is accompanied by changes in species composition and stand structure, as these characteristics are influenced by a number of variables including the accumulation of biomass, the vertical stratification of tree crowns, tree longevity, and growth potential.

Reconstructions of stand development patterns are useful to our understanding of successional processes that influence forest communities (Lorimer 1980; Nowacki and Abrams 1994; Foster *et al*. 1996; Goebel and Hix 1996; McCarthy and Bailey 1996; Oliver and Larson 1996; Goebel and Hix 1997). By analyzing characteristics of live and dead stems and through the interpretation of radial growth patterns of individual trees and composite stand chronologies, we can quantify the processes that have helped shape current forests (Lorimer and Frelich 1989; Fritts and Swetnam 1989; Whitney 1994; Abrams *et al*. 1995; Frelich 2002; Black and Abrams 2005). The specific objectives of this study were to: (1) quantitatively describe species composition and stand structural attributes, (2) reconstruct the disturbance history of the stand using forest inventory measures and dendroecological techniques, and (3) compare the findings of this study with findings for other forests in the region to elucidate patterns of forest growth and development. Data collected and analyzed may also be used as a baseline to which results from future studies can be compared to analyze future changes in forest composition, structure, and disturbance events.

3.2 Study Site

The study was conducted in the Pogue Creek Natural Area (PCNA) located in Fentress County, Tennessee in the north-central portion of the state (Figure 3.1). The 1,505 ha that comprise the PCNA were acquired by The Nature Conservancy in 2004. In 2006, ownership and management of the property were turned over to the State of Tennessee, Department of Environment and Conservation, Division of Natural Areas. The reserve is adjacent to the Big South Fork National River and Recreation Area and the Pickett State Park and Pickett State Forest Complex.

The study site is located within the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman 1938). The underlying geology consists largely of Pennsylvanian sandstone, conglomerate, siltstone, shale, and coal of the Crab Orchard and Crooked Forked Groups (Smalley 1986). The area has irregular topography (Fenneman 1938; de Blij *et al*. 2004) characterized by long, narrow to moderately broad ridges and narrow to moderately broad valleys (Smalley 1986). The stream networks are deeply incised and are capped with sandstone cliffs. The PCNA contains a number of unique geologic features including arches, caves, large boulders, and rock outcrops that are scattered along the slopes. Soils of the region are highly variable but are generally acidic, highly leached, and low in fertility (Francis and Loftus 1977; Smalley 1982). The cobbly loam soils of the PCNA are of the Grimsley-Jefferson-Bouldin association (USDA 1995). They are acidic and relatively low in organic matter (Table 3.1). Depth to bedrock varies from 1–1.8 m and slope gradients range from 15–60%. The elevation of the study plots range from 265–460 m.

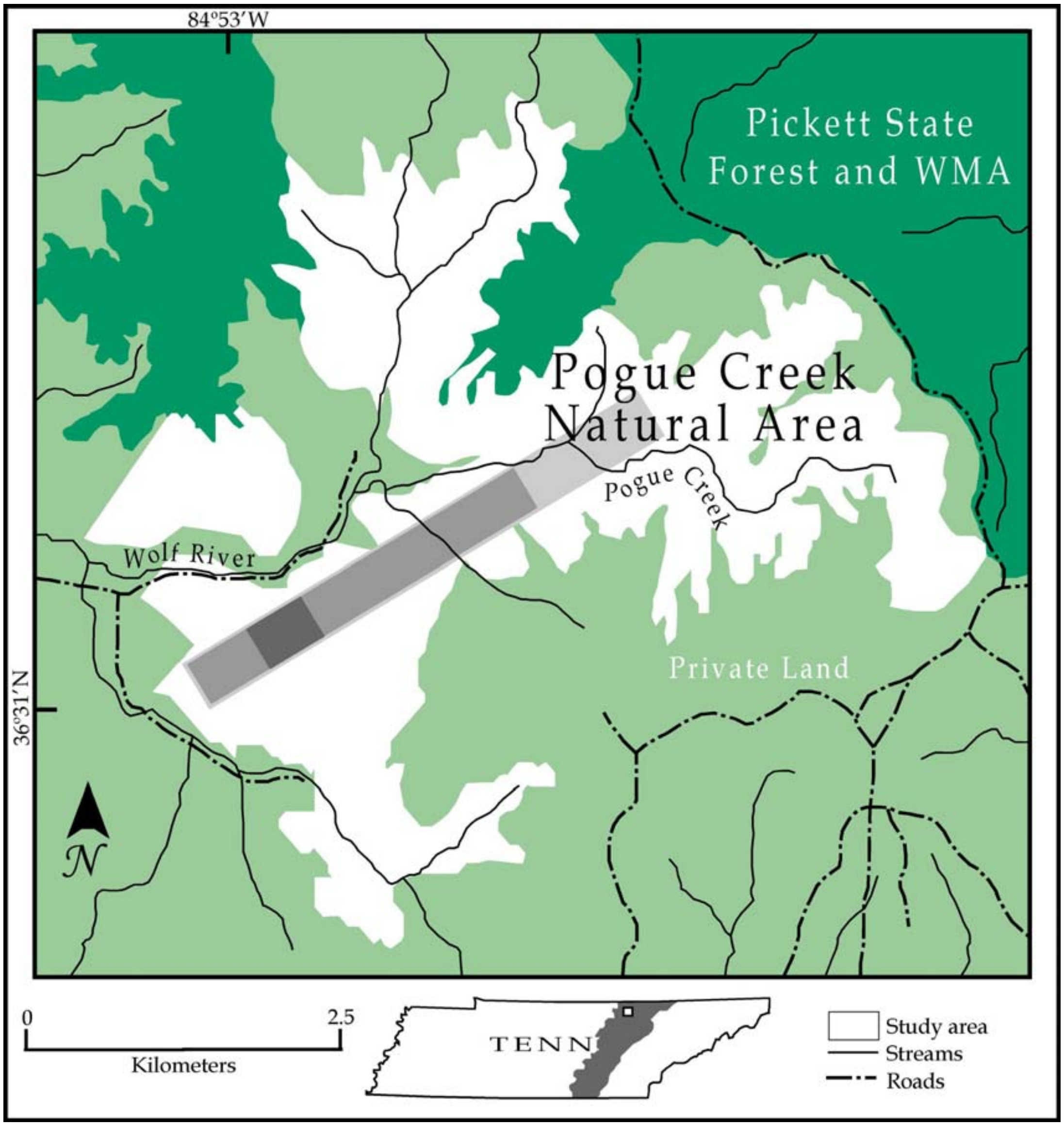


Figure 3.1 Map of the Pogue Creek Natural Area, Fentress County, Tennessee. Dark gray represents area sampled for fire history, medium gray is area sampled for species composition, stand structure, and disturbance history, and light gray is area sampled for canopy gaps. Shaded portion of the Tennessee inset map is the Cumberland Plateau physiographic section (map created by author).

Table 3.1 Soil properties at three depths in the Pogue Creek Natural Area in Fentress County, Tennessee.

	Depth (cm)		
Property	**0–5**	**> 5–15**	**> 15–30**
pH	5.4	4.8	5.3
NO_3 (ppm)	117.0	58.0	26.0
P (ppm)	20.0	14.0	10.0
K (ppm)	151.0	106.0	86.0
Ca (ppm)	1814.0	872.0	695.0
Mg (ppm)	250.0	116.0	154.0
CEC (meq/100 g)	15.1	9.4	9.1
Organic matter (%)	3.6	3.0	1.4

A total of 20 samples were used to create composites for each depth class. Depth classes were selected to follow the natural soil horizons.

The climate is classified as humid mesothermal (Thornthwaite 1948), with moderately hot summers and short-mild to moderately cold winters, although local topography strongly influences microclimatic conditions. The average frost-free period is 160 days (from early-May to late-October) and the mean annual temperature is 13 °C. The July average is 23 °C and the January average is 2 °C (USDA 1995). The area receives steady precipitation during the year with no distinct dry season. Mean annual precipitation is 137 cm and mean annual snowfall is 50 cm (USDA 1995). Late spring and summer are characterized by heavy rains that are often accompanied by moderate to severe thunderstorms (*ca*. 55 days with thunderstorms annually) and strong winds (Smalley 1982).

Braun (1950) classified the area as part of the Cliff Section of the Mixed Mesophytic Forest Region, but local topography influences forest composition and true mesophytic species only dominate on protected sites. Slope forests of the region are generally dominated by mixed *Quercus* species with *Q. alba* being the most abundant followed by *Q. coccinea* and *Q. velutina* (Hinkle 1978; Hinkle 1989). Many forest stands on this section of the Cumberland Plateau are dominated by mixed *Quercus* and *Carya* species. Regionally, the vegetation is intermediate between mixed mesophytic and *Quercus*-*Carya* forest types. On upland sites of the Cumberland Plateau, species composition is largely controlled by topographic characteristics and factors related to soil water availability (Hinkle 1978). The forests of the Cumberland Plateau are characterized by high biodiversity at the community level and contain over 30 canopy species (Hinkle *et al*. 1993). Although small old growth remnants do exist, the vast majority of forest stands in the region are second growth at various stages of succession.

The forests of the PCNA established in the late 1920s after the cessation of local logging operations. From field observations, no signs of large-scale disturbance events were evident since the anthropogenic disturbances of the 1920s. A number of cut stumps exist throughout the forest that indicate selective logging. The property has been owned by several different timber companies during the development of the current stand. Some logging roads have been maintained throughout the reserve, while others have been abandoned. To minimize anthropogenic influences in this study, care was taken to ensure no cut stumps or abandoned logging roads were in close proximity to the study plots.

3.3 Methods

3.3.1 Field Methods

I quantified forest composition and stand structure using 20 0.04 ha fixed-radius (r = 11.29 m) plots established along randomly placed transects throughout the PCNA. All study plots were located at mid-slope positions because the mid-slope forests of the reserve are indicative of slope forests of the greater Cumberland Plateau region. In each plot, I recorded species, crown class, and diameter at breast height (dbh, *ca*. 1.4 m above the surface) of all stems ≥ 5 cm dbh to quantify species composition and the vertical and diameter structure of the stand. Crown class categories (dominant, codominant, intermediate, and overtopped) were based on the amount and direction of intercepted light (Oliver and Larson 1996). I collected core samples from all trees ≥ 5 cm dbh using an increment borer to determine stand age and recruitment pulses, and to evaluate radial growth patterns. The number of snags (dead standing trees) in each plot was also recorded to document structural features, disturbance history, and decay dynamics.

To characterize the understory, each plot contained nested sapling (9 m^2) and seedling (5 m^2) circular plots. All individuals $\geq$ 1 m in height and less than 5.0 cm dbh were considered saplings and all individuals < 1 m in height were considered seedlings. At each plot, I recorded slope gradient, slope position, aspect, and other information useful to infer past disturbance history, such as fire-scarred trees. To document the horizontal structure of the forest, including the locations of live trees, snags, logs, and large boulders, I mapped all stems $\geq$ 5 cm dbh, snags $\geq$ 10 cm dbh, downed logs $\geq$ 25 cm diameter, and boulders in 6 (30%) of the 20 0.04 ha plots. From plot center, an azimuth was shot to all mapped features and distances were measured with a ground tape. Stems were divided into three groups (*Quercus-Carya*, *Acer-Fagus*, and others) and are shown graphically by color and size using 15 cm dbh quartiles (size is to scale of the maximum value). The vegetation measures were analyzed by standard descriptors of stem density, basal area (dominance), species richness, the Shannon diversity index (*H'*), and evenness (*J*) (Cottam and Curtis 1956; Ludwig and Reynolds 1988).

To characterize soil characteristics of the site, I collected soil from two randomly selected locations within each of the 20 plots to quantify soil chemistry characteristics. Soil samples were collected from three depths (0–5, > 5–15, > 15–30 cm) using a tubular soil auger. Depths were approximate as sections were chosen to correspond with natural breaks in the soil horizons. All soil samples were mixed thoroughly in a bag resulting in one composite sample per depth. Soil samples were analyzed for pH, NO_3, P, K, Ca, Mg, percent organic matter, and cation exchange capacity (CEC) by A & L Analytical Laboratories in Memphis, Tennessee to provide information on soil fertility.

3.3.2 Laboratory Methods

In the laboratory, tree core samples were prepared and processed for dating using the methods outlined in Stokes and Smiley (1996). The cores were air-dried, glued to wooden mounts, and sanded to reveal the cellular structure of the wood (Orvis and Grissino-Mayer 2002) before dating the tree rings on all cores with the aid of a stereo zoom microscope. Forest disturbance history was analyzed using *Quercus* individuals because they have clear ring boundaries, do not commonly exhibit locally absent or false rings, are late successional, were dominant canopy species, and have been used successfully in other studies to document disturbance history in the eastern U.S. (McCarthy and Bailey 1996; Nowacki and Abrams 1997; Rubino and McCarthy 2004). Tree rings were measured to the nearest 0.001 mm using a Velmex measuring stage interfaced with Measure J2X software for all *Quercus* series ($n = 66$). The measurement series were visually compared and statistically analyzed to ensure each growth ring was assigned with the exact year of formation using the computer software COFECHA (Holmes 1983; Grissino-Mayer 2001a). The COFECHA program uses segmented time series correlation analyses to determine the strength of association between 50-year segments lagged 25 years from each individual series against a master chronology created from the remaining series. Segments that fell below the predetermined significance threshold ($r = 0.32$, $P > 0.01$) were flagged by the program and all flagged segments were re-inspected for dating errors. The program ARSTAN (Cook 1985) was used to standardize the raw-ring measurements. The raw measurement files were detrended using the default 30-year smoothing spline. The standard chronology was developed by dividing the actual tree-ring measurements by the predicted values generated by the deterministic linear growth models fit to each individual series. The standard chronology was used to document periods of above and below average growth at the stand level and to compare radial growth to climate variables.

Correlation analysis was used to investigate the relationships between climate and radial tree growth. I used divisional climate data available online from the National Climatic Data Center (NCDC 2006) rather than single station data because regionally averaged values generally have stronger relationships to tree growth (Blasing *et al.* 1981; Cook *et al.* 1995). The climatic variables analyzed included monthly average temperature, monthly total precipitation, the Palmer Drought Severity Index (PDSI), and the Palmer Hydrological Drought Index (PHDI). PDSI and PHDI are used by the National Weather Service to monitor drought and wetness conditions and are commonly used in dendroclimatological studies in the eastern U.S. because they are good measures of moisture conditions during the growing season (Cook *et al.* 1988; Cleaveland *et al.* 1992; Grissino-Mayer and Butler 1993; Cook *et al.* 1995; Dai and Trenberth 1998; Stahle *et al.* 1998). I calculated Pearson correlation coefficients between the standardized tree-ring chronology and the climate variables for a 16 month period (previous July–current October). The prior growing season was included in the analysis because previous and current conditions influence the amount of carbon fixed and subsequently used for secondary growth during the subsequent growing season (Kozlowski 1979; Grissino-

Mayer and Butler 1993; Kozlowski and Pallardy 1997; Foster and Brooks 2001; Fritts 2001).

Dendroecological techniques were used to quantify the magnitude and frequency of forest disturbance events. The identification of release episodes in radial growth patterns is one of the fundamental dendroecological techniques used to reconstruct the disturbance history of a forest stand (Fritts and Swetnam 1989; Lorimer and Frelich 1989; Abrams and Nowacki 1992; Nowacki and Abrams 1994; Frelich 2002; Rubino and McCarthy 2004; Black and Abrams 2005). Release episodes are defined as changes in radial growth relative to a predetermined criterion and can be documented using a percent growth change equation (Nowacki and Abrams 1997; Rubino and McCarthy 2004). I analyzed changes in raw-ring widths with respect to the running median of the previous and subsequent 10 years. Release events were identified as periods in which raw-ring width was ≥ 25% (minor) or ≥ 50% (major) of the 10-year preceding and superseding median, sustained for a minimum of three years (Rubino and McCarthy 2004). Release data were analyzed using FHX2 software to graphically display spatial and temporal patterns of release episodes (Grissino-Mayer 1995; Grissino-Mayer 2001b). The FHX2 software displays release events by individual trees and as a composite sample, which allows for the investigation of disturbance events at the stand level.

3.4 Results

3.4.1 Forest Composition

The four most dominant species in the forest based on relative dominance (RDOM) were *Carya ovata* (RDOM = 17.99%), *Quercus rubra* (RDOM = 10.83%), *Q.*

alba (RDOM = 9.94%), and *Q. montana* (RDOM = 8.51%) (Table 3.2). Basal area (m^2/ha) for these species ranged from 5.30 m^2/ha for *C. ovata* to 2.51 m^2/ha for *Q. montana*. There was a distinct second tier of species with high relative dominance values that included *Fagus grandifolia* (RDOM = 7.76%), *Carya tomentosa* (RDOM = 7.11%), *Acer saccharum* (RDOM = 6.8%), *Carya glabra* (RDOM = 6.74%), *Fraxinus americana* (RDOM = 5.81%), and *Acer rubrum* (RDOM = 4.06%). These species had basal area values ranging from 2.28 m^2/ha for *Q. montana* to 1.2 m^2/ha for *A. rubrum* (Table 3.2).

The most abundant species in the tree layer (individuals ≥ 5 cm dbh) based on relative density (RDEN) were *A. saccharum* (RDEN = 28.37%), *C. ovata* (RDEN = 14.29%), and *A. rubrum* (RDEN = 9.72%) (Table 3.2). There was a clear second tier of species with high densities that included *Q. montana*, *F. grandifolia*, and *C. tomentosa* (RDEN = 5.36–5.75%). Total basal area of overstory trees was 29.43 m^2/ha and stem density of trees ≥ 5 cm dbh was 630 stems/ha (Table 3.3). Species richness of stems ≥ 5 cm dbh was 30, diversity (*H'*) was 2.57, and evenness (*J*) was 0.75 (Table 3.3).

Only five species were documented in the sapling layer: *A. saccharum*, *Asimina triloba*, *Q. montana*, *F. grandifolia*, and *Nyssa sylvatica* (Table 3.4). The sapling layer was rather sparse with a sapling density of 2,695 stems/ha. Of these sapling individuals, over 61% were *A. saccharum*. Diversity of the sapling layer was 0.99 and evenness was 0.62 (Table 3.3).

Table 3.2 Density and dominance measures for all stems ≥ 5 cm dbh at the Pogue Creek Natural Area, Fentress County, Tennessee.

Species	**Density (stems/ha)**	**Relative density**	**Dominance (m²/ha)**	**Relative dominance**
Carya ovata	90.00	14.29	5.30	17.99
Quercus rubra	20.00	3.17	3.19	10.83
Quercus alba	21.25	3.37	2.93	9.94
Quercus montana	33.75	5.36	2.51	8.51
Fagus grandifolia	33.75	5.36	2.28	7.76
Carya tomentosa	36.25	5.75	2.09	7.11
Acer saccharum	178.75	28.37	2.00	6.80
Carya glabra	17.50	2.78	1.98	6.74
Fraxinus americana	21.25	3.37	1.71	5.81
Acer rubrum	61.25	9.72	1.20	4.06
Quercus velutina	6.25	0.99	0.84	2.85
Tilia heterophylla	18.75	2.98	0.75	2.56
Liriodendron tulipifera	15.00	2.38	0.69	2.34
Quercus coccinea	2.50	0.40	0.46	1.55
Magnolia acuminata	11.25	1.79	0.41	1.39
Oxydendrum arboreum	7.50	1.19	0.28	0.96
Carya cordiformis	10.00	1.59	0.27	0.92
Nyssa sylvatica	13.75	2.18	0.25	0.84
Ostrya virginiana	3.75	0.60	0.06	0.21
Ulmus rubra	3.75	0.60	0.05	0.18
Prunus serotina	1.25	0.20	0.03	0.12
Diospyros virginiana	2.50	0.40	0.03	0.12
Cornus florida	5.00	0.79	0.03	0.10
Asimina triloba	6.25	0.99	0.03	0.09
Aesculus flava	1.25	0.20	0.02	0.06
Sassafras albidum	1.25	0.20	0.02	0.06
Ailanthus altissima	2.50	0.40	0.02	0.05
Cercis canadensis	1.25	0.20	0.00	0.02
Betula lenta	1.25	0.20	0.00	0.01
Carpinus caroliniana	1.25	0.20	0.00	0.01
Total	**630**	**100**	**29.43**	**100**

Table 3.3 Composition and structural measures for tree, sapling, and seedling layers at the Pogue Creek Natural Area, Fentress County, Tennessee. Trees: ≥ 5 cm dbh; Saplings: < 5 cm dbh, ≥ 1 m ht; Seedlings: < 1 m ht.

	Layer		
Parameter	**Tree**	**Sapling**	**Seedling**
Density (stems/ha)	630	2695	27300
Basal area (m²/ha)	29.43	—	—
Species richness	30	5	12
Diversity (*H*′)	2.57	0.99	1.77
Evenness (*J*)	0.75	0.62	0.71

Table 3.4 Density and relative density for seedlings and saplings at the Pogue Creek Natural Area in Tennessee. Seedlings: < 1 m ht; Saplings: < 5 cm dbh, ≥ 1 m ht.

Species	**Seedlings/ hectare**	**Relative density**	**Saplings/ hectare**	**Relative density**
Acer rubrum	10800	39.56	—	—
Acer saccharum	7400	27.11	1650	61.22
Carya spp.	2400	8.79	—	—
Quercus montana	1500	5.49	110	4.08
Fagus grandifolia	1400	5.13	110	4.08
Quercus rubra	1100	4.03	—	—
Asimina triloba	700	2.56	770	28.57
Cercis canadensis	500	1.83	—	—
Quercus alba	500	1.83	—	—
Fraxinus americana	400	1.47	—	—
Magnolia acuminata	400	1.47	—	—
Sassafras albidum	200	0.73	—	—
Nyssa sylvatica	—	—	55	2.04
Total	**27300**	**100**	**2695**	**100**

The seedling layer contained 27,300 individuals/ha (Table 3.3). Species richness was 12, diversity was 1.77, and evenness was 0.71. The most abundant species were *A. rubrum* and *A. saccharum*, with relative densities of 39.56% and 27.11% respectively. These abundance values far exceeded those of other species in the seedling layer. All *Carya* species were placed into one category because seedlings could not be identified with confidence in the field. The *Carya* species ranked third based on relative density (RDEN = 8.79%). Only one species, *N. sylvatica*, occurred in the sapling layer but not in the seedling layer. Of the 30 tree species that occurred in the study plots, only one alien species was documented (*Ailanthus altissima*).

In the 20 study plots, I documented 68 individuals with dominant positions in the canopy representing 14 species. Of all canopy dominants, 49% were *Quercus* species (Figure 3.2). *Carya ovata* and *Q. montana* were the most common species with dominant positions in the canopy, representing 21% and 19% of canopy dominants respectively. A total of 79 individuals representing 14 species occurred in canopy codominant positions. The most common canopy codominant was *C. ovata* (representing 25% of codominant individuals), followed by *F. americana* (13%), *C. tomentosa* (10%), *Q. alba* (9%), and *Q. rubra* (9%). A total of 231 individuals occurred in overtopped positions with *A. saccharum* (45%) and *A. rubrum* (13%) being the most abundant.

Species were grouped and values were standardized at the hectare level to reveal canopy class distribution patterns. *Quercus* species were most abundant in dominant canopy positions and the number of individuals decreased with decreased height and position (Figure 3.3). In contrast to the *Quercus* distribution, *Acer* species, *F.*

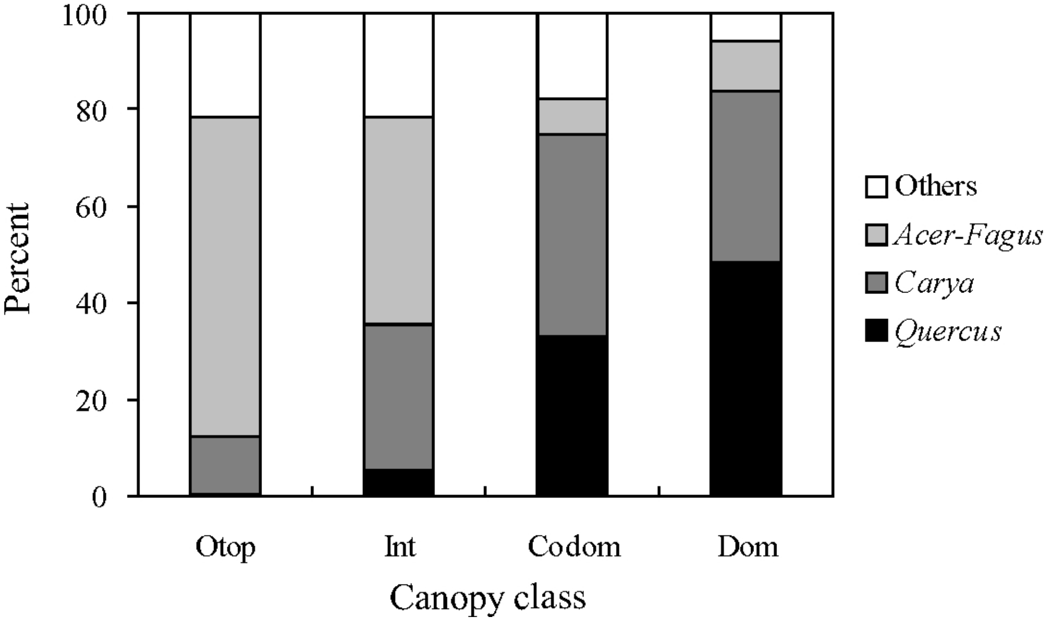


Figure 3.2 Canopy class percentages by group. Canopy class categories are based on the amount and direction of intercepted light (Oliver and Larson 1996). Dom: dominant, Codom: codominant, Int: intermediate, Otop: overtopped.

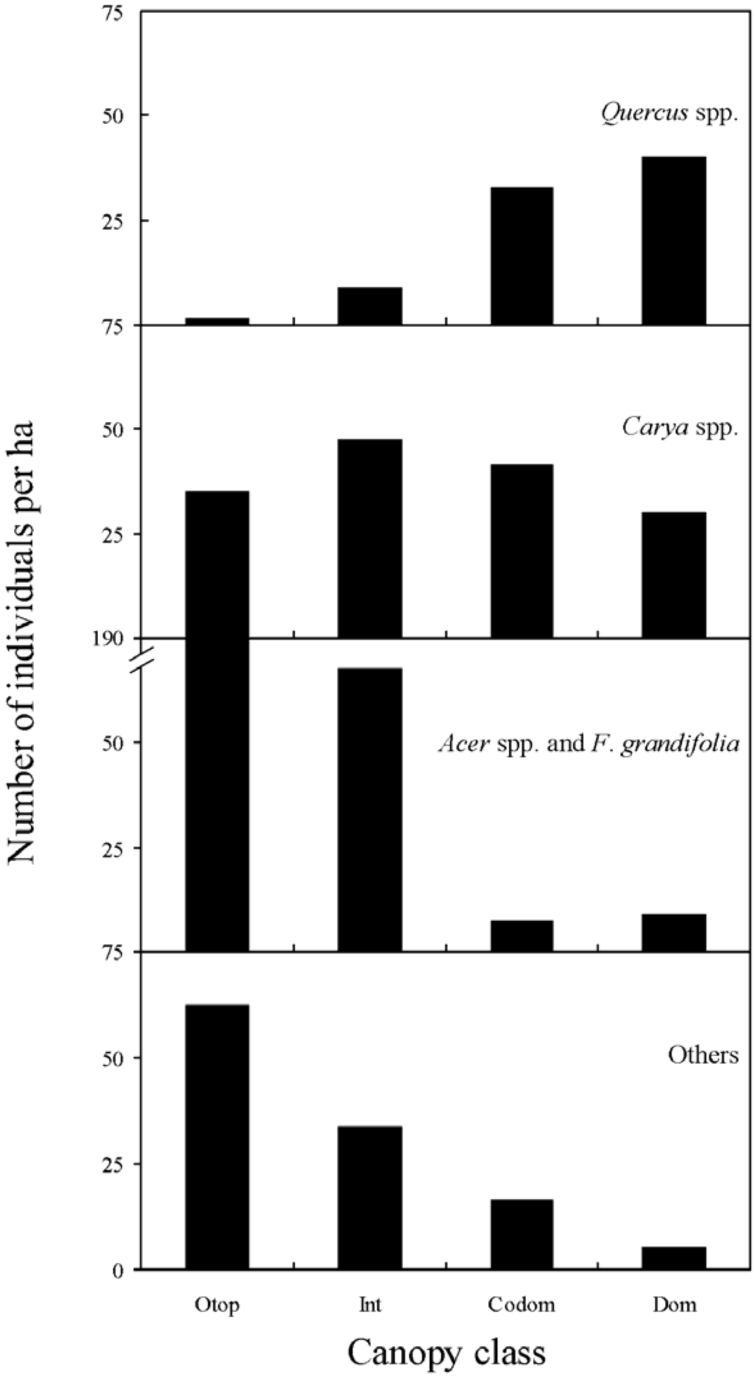


Figure 3.3 Canopy class distributions per hectare by group. Canopy class categories are based on the amount and direction of intercepted light (Oliver and Larson 1996). Dom: dominant, Codom: codominant, Int: intermediate, Otop: overtopped. Note broken scale for *Acer* species and *F. grandifolia* for overtopped individuals.

grandifolia, and species grouped as “other” had the majority of individuals in overtopped positions followed by intermediate positions. The *Carya* species exhibited a bell-shaped canopy class distribution with the majority of individuals in intermediate canopy positions.

3.4.2 Stand Structure

The diameter distribution of all stems was indicative of a mature, regenerating forest as the number of individuals was greatest in the smallest size class and density decreased with increased diameter (Smith *et al*. 1996) (Figure 3.4). Individuals occurred in every size class (*n* = 13 classes). Species were grouped and standardized at the hectare level to reveal patterns of regeneration and recruitment. All groups (*Quercus*, *Carya*, *Acer-Fagus*, and others) contained individuals in the smallest size class. *Quercus* species had a rather uniform diameter distribution and occurred in all but the largest size category. *Carya* species had a bell-shaped curve that peaked in the 15–25 cm dbh range and individuals occurred in all but the 60–65 cm dbh class. *Acer* species and *F. grandifolia* had a reverse J-shaped diameter distribution. These species were by far most abundant in the smallest size class (170 stems 5–10 cm dbh/ha), and individuals were present in all but two categories (37.5 and 47.5 cm dbh classes). Species listed as “other” also showed a reverse J-shaped diameter structure and were only absent from the three largest size classes. Although the size of individual snags was not recorded, I documented 26 snags ≥ 10 cm dbh/ha.

The largest documented individual in the study plots was a *C. glabra* at 69.5 cm dbh followed by an *A. saccharum* at 67.25 cm, a *F. grandifolia* at 65 cm, a *Q. alba* at

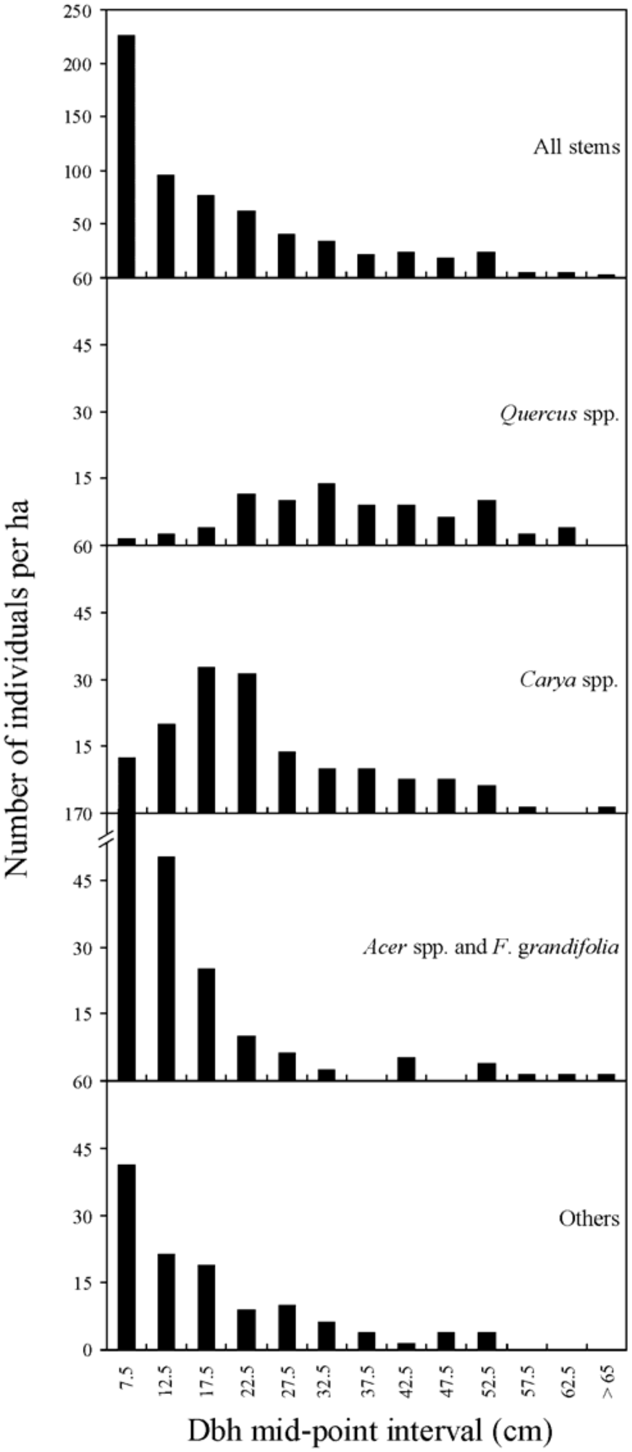


Figure 3.4 Number of trees (≥ 5 cm dbh) per hectare for all species, divided into four groups at the Pogue Creek Natural Area, Fentress County, Tennessee. Each dbh interval includes stems ± 2.5 cm of the stated value with the exception of the > 65 cm class.

64.5 cm, and a *Q. rubra* at 61.5 cm. A total of seven trees ≥ 60 cm in diameter were documented. The largest *C. ovata* was 53.5 cm, the largest *C. tomentosa* was 54 cm, the largest *Q. velutina* was 54 cm and the largest *Q. montana* was 51 cm in diameter. Of note, when walking a transect through the forest, I came across a *F. americana* with a dbh of 125 cm. This large individual was an anomaly relative to other trees in the forest, as the largest *F. americana* documented in a study plot was only 53.25 cm in diameter.

The oldest tree in a study plot was a *C. glabra* with an inner date of 1753. A period of 85 years lapsed before the next tree established, a *C. tomentosa* with an inner date of 1837. The next tree that established was a *Q. alba* with an inner date of 1872 (Figure 3.5). Only 11 trees in the study plots established before 1900 and they were all of the *Quercus* and *Carya* genera with the exception of one *A. saccharum* (inner date 1850) and one *F. americana* (inner date 1898). Two trees established at the turn of the century, a *Q. rubra* with an inner date of 1900 and a *F. grandifolia* with an inner date of 1901. When grouped by species, establishment pulses were evident (Figure 3.5). Although older trees representing several species established before the 1920s, during this decade there was an establishment pulse of *Carya*. Establishment pulses for *Quercus* and *Acer-Fagus* began in the 1930s and 1940s, respectively. There was a lack of *Carya* establishment after 1950 and a lack of *Quercus* establishment after 1960. Establishment of *Acer-Fagus* and species listed as "other" was continuous.

Age-structure graphs were created for the eight most important species based on relative importance values (Figure 3.6). *Carya ovata* and *C. tomentosa* exhibited bell-shaped curves with peaks in the 1930s and 1940s, respectively, and neither of these species has established since the 1970s. *Quercus rubra* and *Q. alba* had similar age

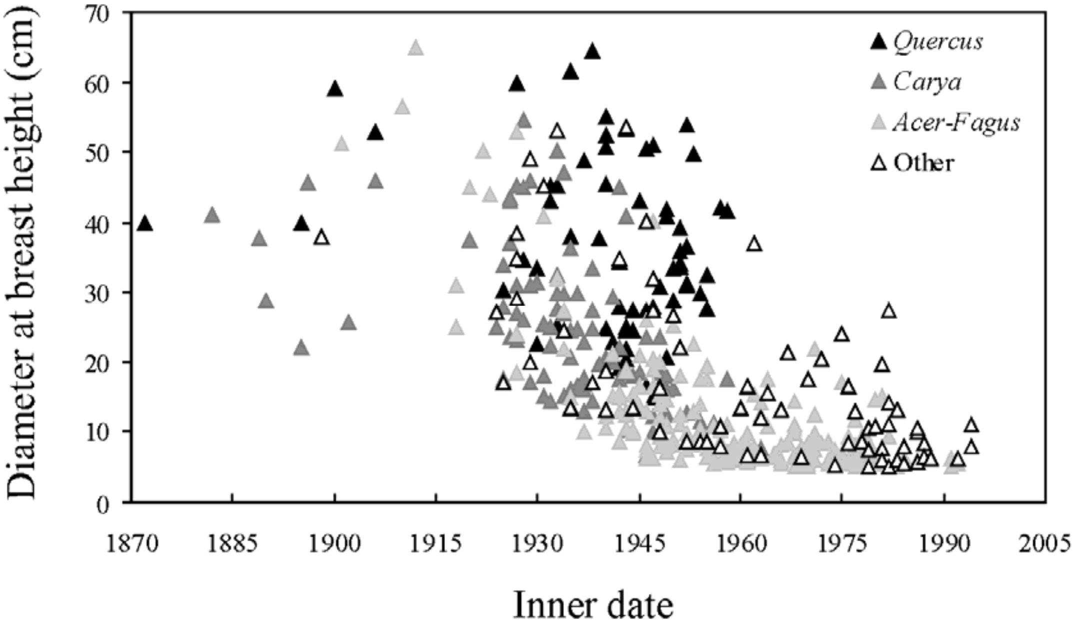


Figure 3.5 Diameter-age relationships for all cored trees that could be accurately dated in the Pogue Creek Natural Area in Tennessee.

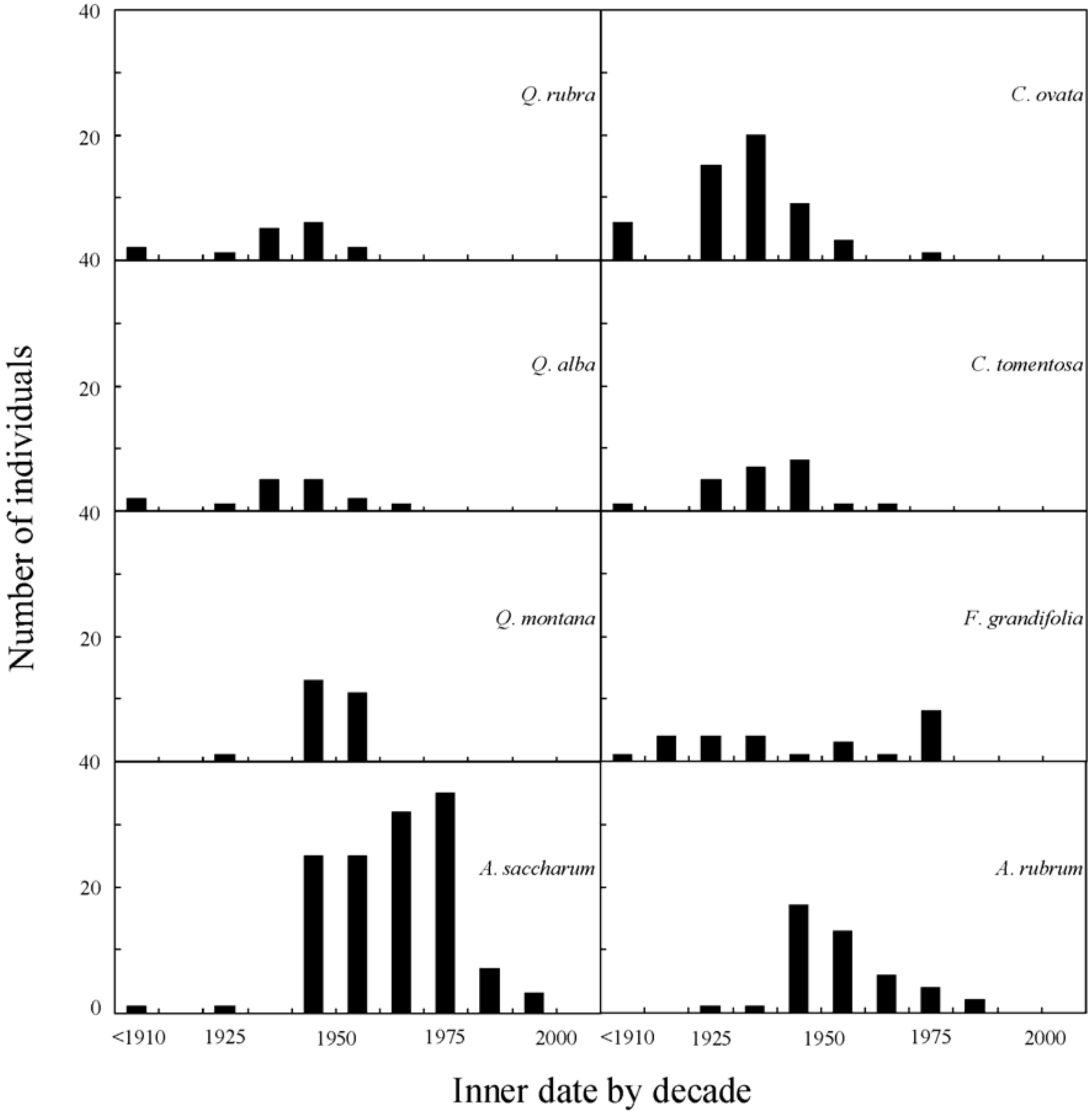


Figure 3.6 Age structure of the eight most important species (based on relative importance values) at the Pogue Creek Natural Area, Fentress County, Tennessee.

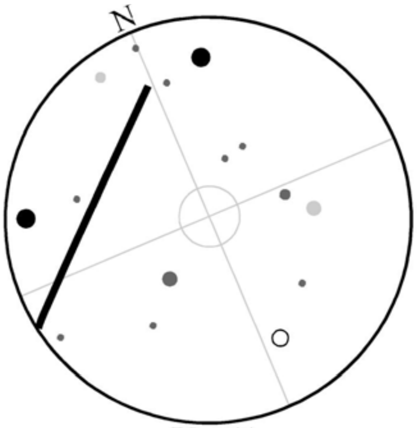
structures with the majority of individuals establishing between 1930 and 1950. *Quercus montana* was offset from the other two *Quercus* species by a decade as establishment was highest between 1940 and 1960. Establishment of *A. rubrum* peaked in the 1940s and gradually declined while *A. saccharum* began in the 1950s and peaked in the 1970s. *Fagus grandifolia* had a rather uniform age distribution as individuals established in all but the three most recent decades. Like *A. saccharum*, *F. grandifolia* establishment peaked in the 1970s.

Stem maps help illustrate the horizontal structure of the forest by showing the distribution of live stems, snags, logs, and boulders (Figure 3.7). The majority of all stems were in the smallest size class (5–15 cm dbh) and all mapped plots contained stems in the largest size class (> 45 cm dbh). All plots contained trees in all four size categories except plots 11 and 18. Downed logs occurred in all plots, four plots contained snags, and three plots contained large boulders. Plot 11 had the steepest slope gradient (55%) and also contained the fewest number of live stems (n = 14). Although tree crowns were not mapped, all plots had closed canopies and lacked light gaps on the forest floor.

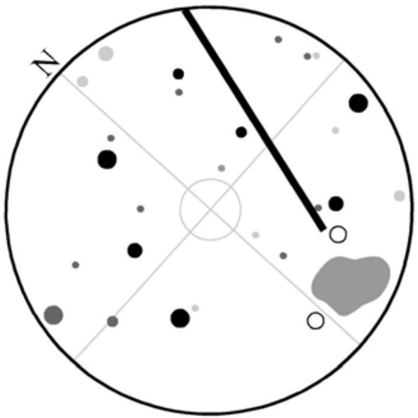
3.4.3 Disturbance History

All *Quercus* individuals were crossdated with confidence. The interseries correlation of the 66 *Quercus* series (from 64 individuals) was significant at 0.44. The interseries correlation is the average of all Pearson correlation coefficients calculated for each series compared to all other series in the tree-ring record and is used as an index of the signal-to-noise ratio in the chronology (Foster and Brooks 2001). A total of 177 50-year segments were analyzed by the COFECHA program. Of these 177 segments, 47

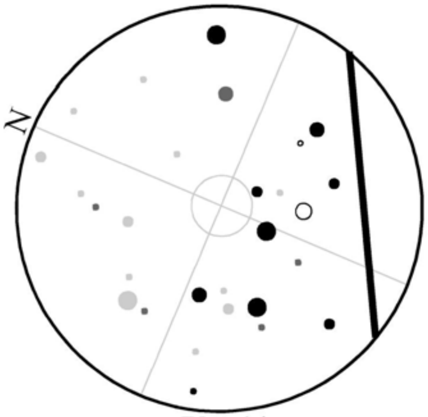
Figure 3.7 Maps of all stems (≥ 5 cm dbh), snags (≥ 10 cm dbh), downed logs, and boulders in six 0.04 ha plots at the Pogue Creek Natural Area. North arrows are oriented to slope aspect. Filled circles indicate live stems (black: *Quercus* and *Carya*; dark grey: *Acer* and *F. grandifolia*; light grey: other) and hollow circles indicate snags. Circle sizes are classed into quartiles at 15 cm dbh intervals. Irregular shapes with medium grey fill represent boulders while dark lines represent downed logs.



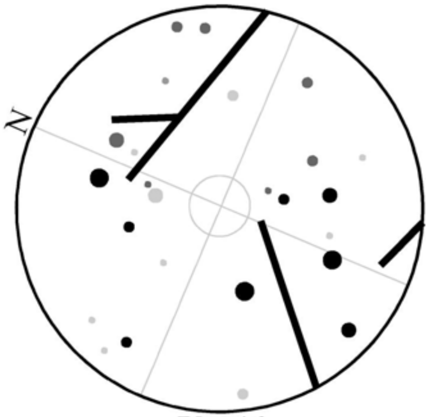
Plot 11
Slope: 55%



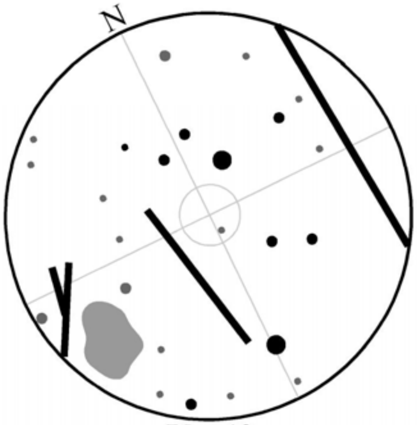
Plot 12
Slope: 32%



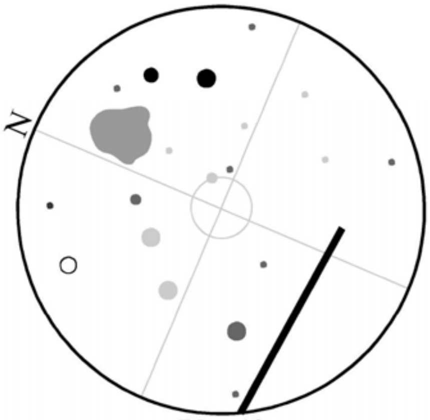
Plot 14
Slope: 22%



Plot 16
Slope: 25%



Plot 18
Slope: 36%



Plot 19
Slope: 23%

(26.5%) were flagged (indicating they were not statistically significant with contemporary segments). Although the percentage of flagged segments was higher than I would like to accept, none of the problems indicated incorrect dating. Average mean sensitivity was 0.22 which is typical for *Quercus* in the southeastern United States (DeWitt and Ames 1978). Mean sensitivity is a measure of the relative difference in ring width of adjacent rings and is an indicator of climate sensitivity in the tree-ring record (Fritts 2001).

The tree-ring record extended 138 years from 1868–2005. A composite radial-growth chronology was created where mean annual growth was standardized to equal 1.0. The composite chronology extends from 1902–2005. The first 35 years of the record were truncated so the start of the chronology (1902) had a sample depth of three series (Figure 3.8). Sample depth increased to four series in 1906. From the standardized chronology, below average radial growth was apparent until the 1920s, followed by a period of above average radial growth from the early 1920s through the late 1930s. There was another notable period of above average growth from the late 1950s through the late 1960s and a period of below average radial growth from 1990 through the end of the chronology.

No significant relationships were found between the standardized chronology and monthly mean temperature, PDSI, or PHDI for the previous and current years (Figure 3.9). Significant positive relationships occurred between total monthly precipitation of the previous August ($r = 0.30$, $P < 0.05$) and previous October ($r = 0.27$, $P < 0.05$) and the standardized chronology. I found no clear patterns for monthly mean temperature. Patterns were evident for PDSI and PHDI. PDSI and PHDI had the strongest negative

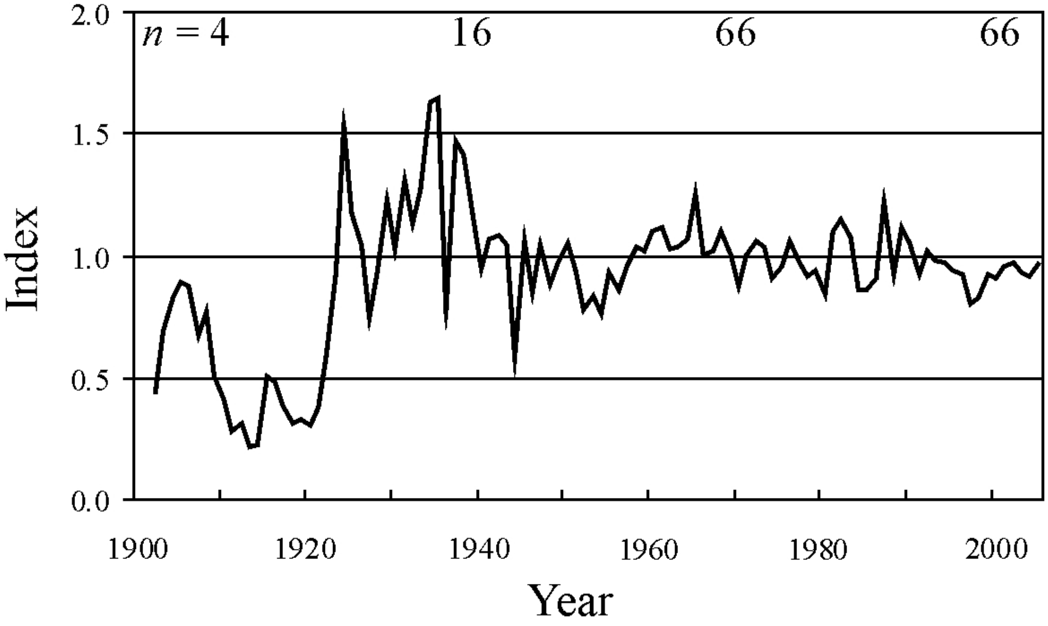


Figure 3.8 Composite ring-width index generated from all *Quercus* series sampled at the Pogue Creek Natural Area with mean growth standardized to 1.0 (*n* = number of series in that year).

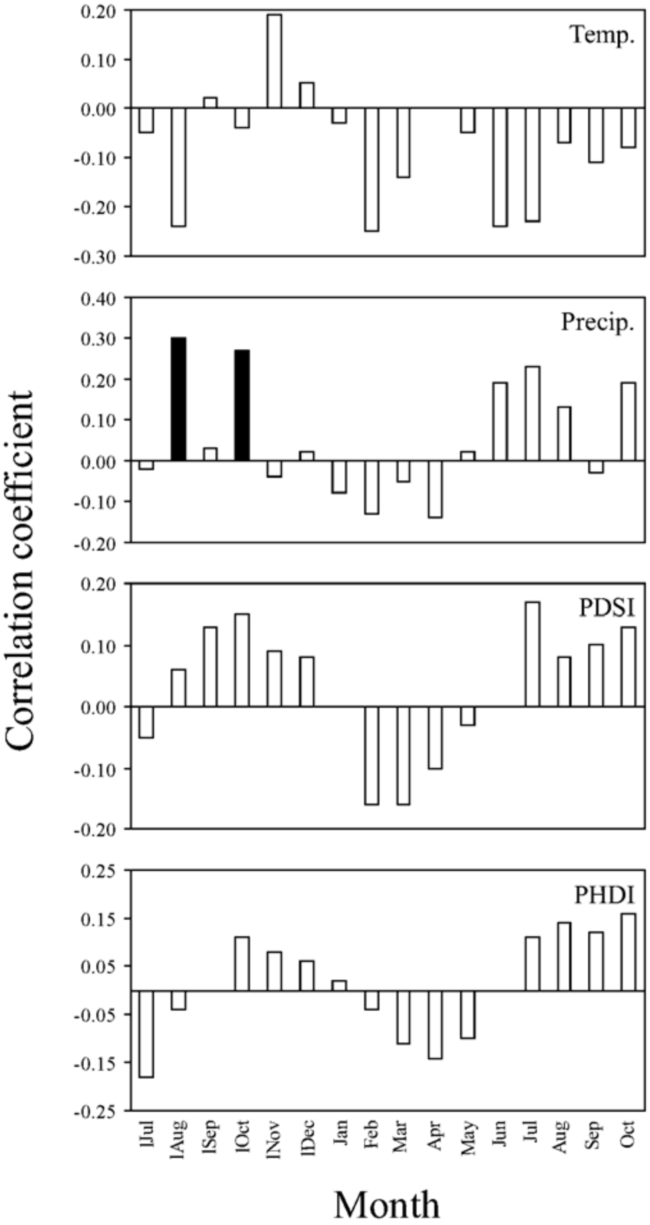


Figure 3.9 Correlation analysis between the standardized tree-ring chronology and regional climate variables. Temp: monthly mean; Precip: monthly total; PDSI: Palmer Drought Severity Index; PHDI: Palmer Hydrological Drought Index. Month abbreviations preceded with an "l" indicate the previous year. Solid bars indicate significant values (*P* < 0.05). Note that the y-scale varies.

relationships to the chronology in spring and both relationships were weak in January and June.

Of the 64 *Quercus* individuals analyzed using the 10-year running median method, 54 (84%) exhibited release events. A total of 90 release events were detected from the 64 individuals with some trees experiencing multiple releases during their life (Figure 3.10). All detected release episodes were visually checked to ensure accurate dating. Of the 90 detected release events, 55 (61%) were minor and 35 (39%) were major. One individual (a *Q. rubra*) experienced five separate release episodes during its life (1900–2005, Figure 3.11a), while two individuals (a *Q. alba* and a *Q. velutina*) experienced four separate release events during their lives (1868–2005 and 1929–2005, respectively). A *Q. rubra* experienced the greatest percent growth change of 380% over the 10-year running median (Figure 3.11b). Seven individuals sustained increased radial growth of over 100% for three years, the longest of which was exhibited by a *Q. alba* that sustained increased radial growth of over 100% for six years. The longest sustained release was nine years observed in a *Q. montana* from 1982–1990 (Figure 3.11c). The mean release duration was 4.2 years ± 1.42 (SD). The longest period between release events (after the 1920s) was 11 years (occurring from 1947–1958) and the shortest was 1 year. Releases occurred in consecutive years in many instances (*e.g.* 1978, 1979, 1980, 1981, 1982) (Figure 3.10 composite). The mean release return interval was 2.37 years ± 3.2 (SD).

I analyzed the temporal and spatial patterns of release episodes to determine if disturbance events were stand-wide or local in spatial scale. Stand-wide disturbances are typically defined as release episodes where a minimum of 25% of individuals release

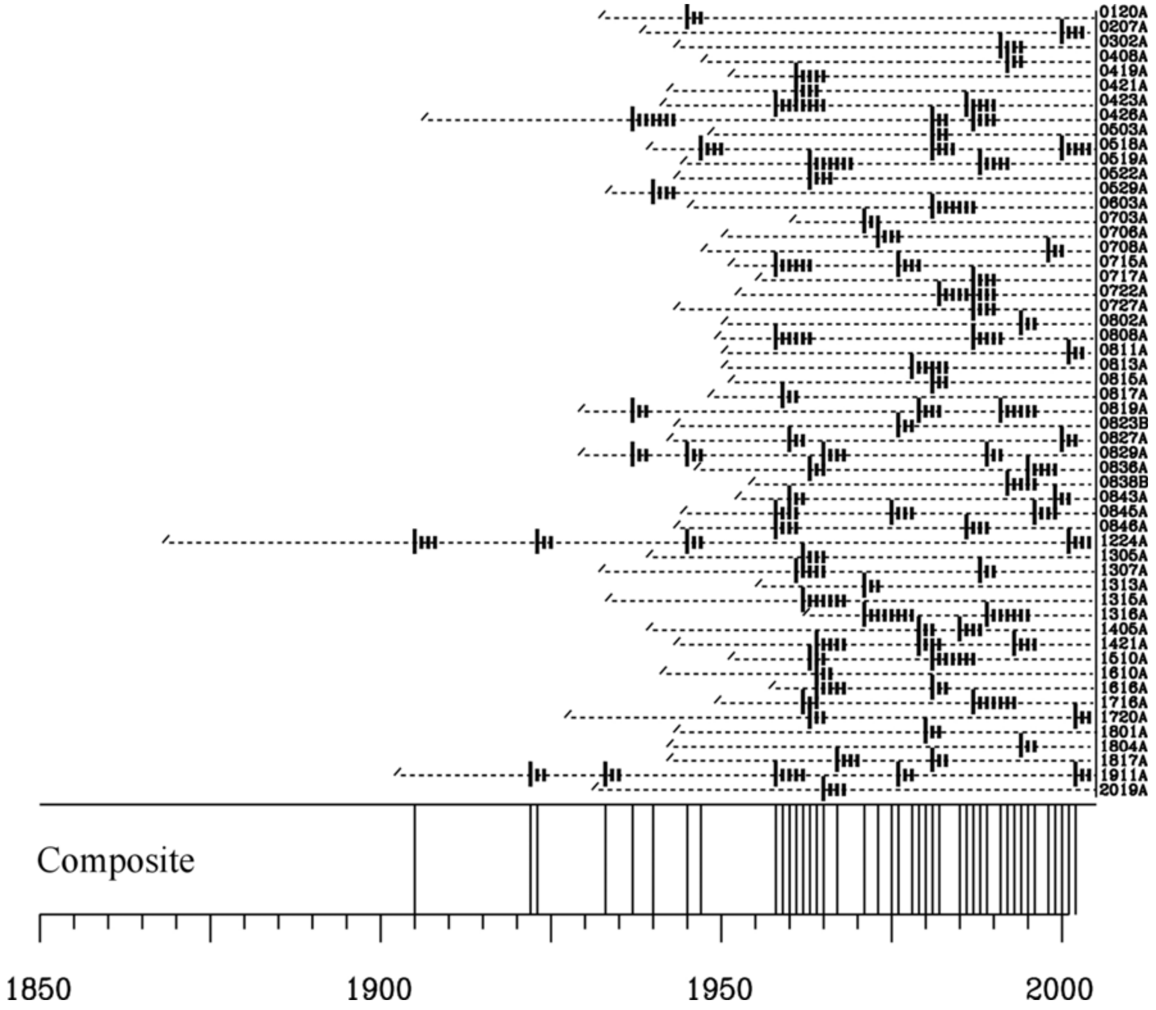


Figure 3.10 Detected release events using the 10-year running median method for 64 *Quercus* individuals sampled at the Pogue Creek Natural Area, Fentress County, Tennessee. Each horizontal line represents the record from one individual tree, long vertical bars indicate release events, and short vertical bars indicate release duration. A composite of release events for the study site is shown across the bottom.

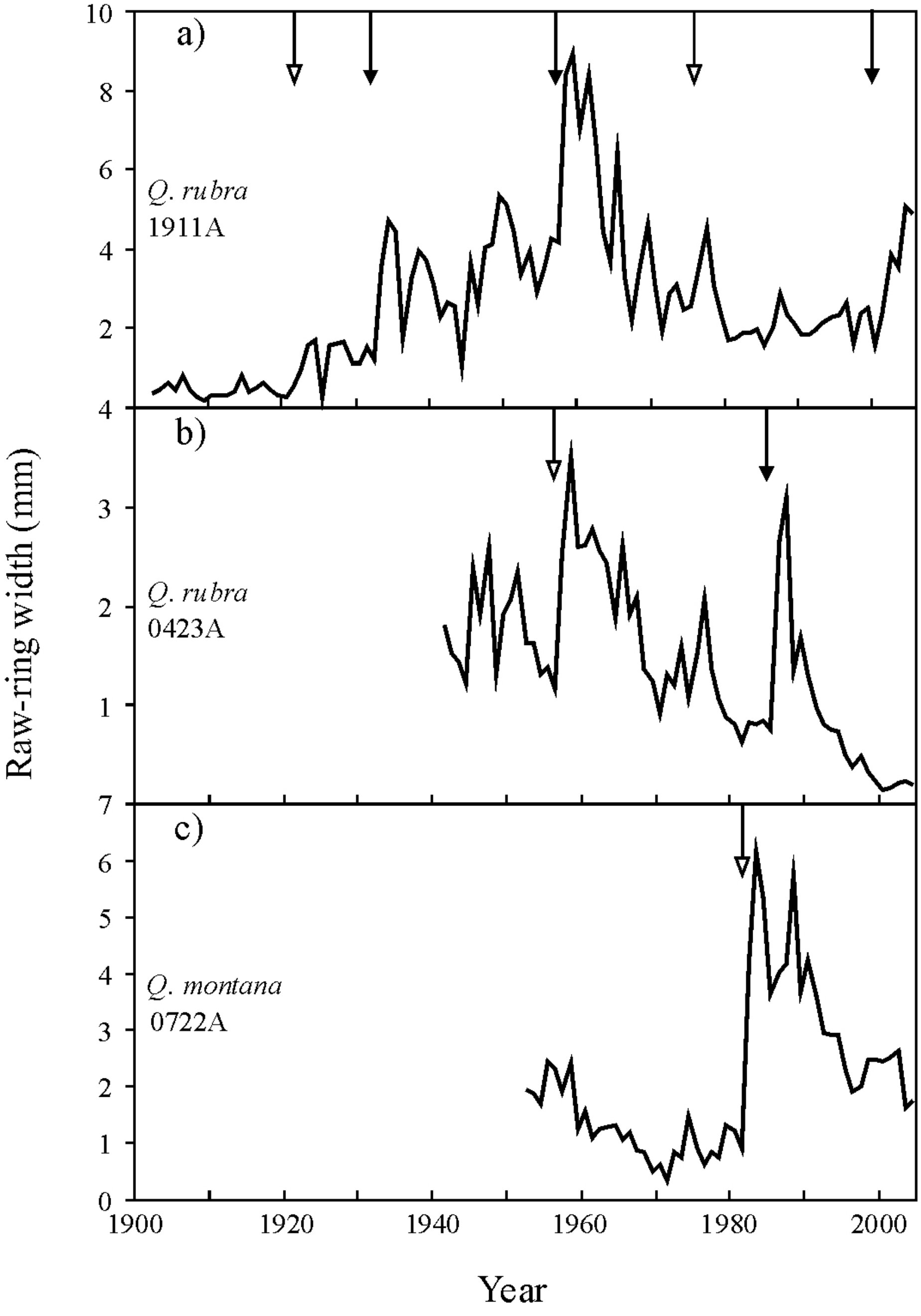


Figure 3.11 Raw-ring width measurements for individuals sampled at the Pogue Creek Natural Area. Open arrows indicate minor release and filled arrows indicate major release episodes. a) *Q. rubra* with five release events, b) *Q. rubra* with a growth change of 380%, c) *Q. montana* with a minor release sustained for nine years.

simultaneously (Nowacki and Abrams 1997; Rubino and McCarthy 2004). In this study, I consider a stand-wide disturbance event an episode where there was a simultaneous release experienced by a minimum of one tree in 25% (*n* = 5) of the study plots. By evaluating release events across plots, I eliminate the possibility of labeling a local event that causes all individuals in one plot to release a stand-wide phenomenon. At this level, stand-wide release events indicate exogenous disturbances that removed overstory vegetation at a larger spatial scale than local events. Possible disturbance agents include insect attacks, tornado events, and ice storms. Only one stand-wide release was documented and it was initiated in 1981. During this stand-wide event, individuals in seven (35%) of the 20 plots experienced a release in radial growth. In two of these individuals, the radial growth release lasted until 1987 with releases in other trees ending in 1983 and 1984. Archives of *Monthly Weather Review* from 1980–1982 were studied to determine if a notable extreme weather event may have caused the stand-wide release. No extreme events were recorded in the journal, but this does not mean a local storm that may have killed trees throughout the reserve did not occur.

With the exception of this one stand-wide episode, release events were asynchronous throughout the forest. Release events occurred over variable temporal and spatial scales. The spatio-temporal patterns of release events indicated a disturbance regime characterized by localized disturbance events that influence only neighboring trees such as small canopy gaps (Lorimer 1980; Orwig and Abrams 1994a; Black 2003). The majority of the forest trees established in the 1920s and there was a pulse of release events in the 1960s (Figure 3.12), indicating that small-scale canopy disturbance events became important mechanisms of forest change after *ca*. 40 years of development.

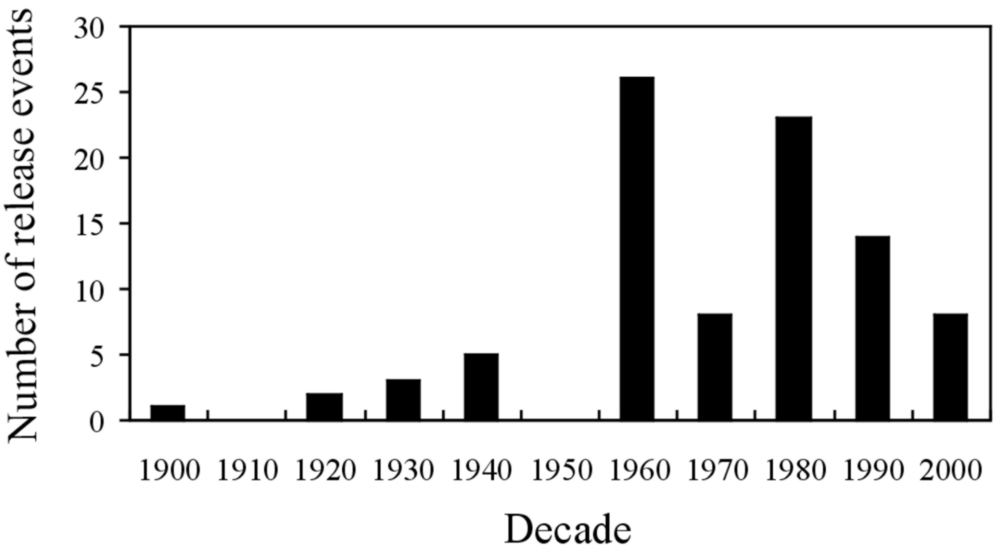


Figure 3.12 Number of release events per decade at the Pogue Creek Natural Area, Fentress County, Tennessee. Release events were detected using the 10-year running median method.

3.5 Discussion

3.5.1 Composition, Structure, and Disturbance History

Species diversity was highest for the tree layer and lowest in the sapling layer. A similar pattern was evident for species evenness. Individuals were more evenly distributed among the represented species in the tree layer. The relatively low evenness value for the sapling layer was the result of the majority of saplings (61%) being of one species (*A. saccharum*). Although species abundance in the seedling layer was more evenly distributed, *Acer* species represented 67% of all seedlings. Species richness was lowest in the sapling layer. Species richness could not be directly compared between forest layers because true richness was used rather than a richness index. However, the seedling plots which represented a smaller area compared to sapling plots contained more species. The sapling layer was sparse and only five species were represented (note *Carya* species were grouped for seedling and sapling layers).

Only the tree layer contained a woody alien species. *Ailanthus altissima* is shade-intolerant (Miller 2003) and its clustered distribution (both spatially and temporally) indicated it established in a small canopy gap. It is believed that gaps serve as sites for the diffusion of alien plants into forest interiors (Goldblum and Beatty 1999). The likely establishment of *A. altissima* in a small gap indicates that canopy gaps have enabled this species to extend into the forest interior. *Ailanthus altissima* has been shown to successfully invade old growth forests by colonizing canopy gaps (Knapp and Canham 2000). The species has a rapid growth rate and the potential to outcompete native trees in large gaps.

The stand exhibited a reverse J-shaped diameter distribution. The number of individuals was greatest in the smallest size class and density declined with increased size. This diameter structure indicates a regenerating forest (Smith *et al*. 1996). In the absence of a large-scale disturbance event, composition of the forest is projected to shift. The forest canopy was dominated by *Quercus* and *Carya* species. However, the most abundant individuals in the understory were *Acer* species and *F. grandifolia*. *Acer rubrum* and *A. saccharum* were also the most abundant species in seedling plots. In the absence of a large-scale disturbance event, *Acer* species will likely increase in dominance as understory individuals are recruited to larger size classes and to codominant and dominant positions in the forest canopy. Both *A. saccharum* and *A. rubrum* are shade-tolerant species that may remain suppressed in the understory until the occurrence of small-scale disturbance events allows them to recruit. *Acer saccharum* has been shown to respond quickly and substantially to canopy disturbances (Tryon *et al*. 1992). As *Acer* individuals in understory and intermediate canopy positions reach dominant and codominant positions in the canopy, the forest will change from a *Quercus-Carya* dominated system to one with a much more important *Acer* component. This pattern of *Acer* regeneration (coupled with a lack of regeneration of other species, especially *Quercus*) has been documented throughout the eastern U.S. (Lorimer 1984; Crow 1988; Fralish *et al*. 1991; Abrams 1992; Loftis and McGee 1993; Mikan *et al*. 1994; Goebel and Hix 1997; Signell *et al*. 2005; Albrecht and McCarthy 2006; Pierce *et al*. 2006).

The interseries correlation for the 66 *Quercus* series was significant, but low by dendrochronological standards. The interseries correlation was lowered by 12 segments that fell below the significance threshold of 0.33. I sampled relatively young trees from a closed canopy forest at mid-slope positions from a number of different aspects. The sampling scheme was not designed to analyze regional-scale patterns, but rather local microsite conditions within the forested environment. The sampling resulted in an average mean sensitivity of 0.22 which is low (meaning the tree-ring series were rather complacent as opposed to sensitive), but typical for forest interior trees in the eastern U.S. Also, the *Quercus* series measured and statistically analyzed represented five different species and species specific responses to environmental conditions may have contributed to the rather low interseries correlation.

The standardized chronology showed below average radial growth from the start of the chronology in 1902 until the 1920s. This increase is radial growth is likely related to the disturbance history of the site. The forest was last cleared in the 1920s and all economically mature *Quercus* individuals would have been removed. The *Quercus* individuals that were spared likely exhibited poor form or were of a small size. I speculate the clearing of the forest reduced competition and the remnant individuals were allowed to increase growth and become dominant trees in the next stand.

Although significant relationships were found between the standardized tree-ring chronology and late summer and early fall precipitation of the previous year, both relationships were weak, indicating that the forest was not responsive to broad-scale climate conditions. The tree-ring chronology was developed to ensure accurate dating of release events and thus no series (even those that fell below the significance threshold) were removed from the chronology, which is a common practice in dendroclimatological studies. Variations in radial growth patterns have likely been influenced by forest stand dynamics. The sampled trees were growing in a closed-canopy forest, where the effects of climate were likely overshadowed by competition (Fritts 2001). In mesic closed-canopy forests, such as the PCNA, light is generally the factor limiting tree growth. Thus, variations in radial growth likely result from increased light caused by canopy disturbances rather than broad-scale climatic conditions. The weak relationship between the chronology and the climate variables emphasizes the influence of canopy disturbance events on forest productivity.

Only one stand-wide release event was detected in the tree-ring record from the PCNA. This stand-wide release episode occurred in the early 1980s. A stand-wide release indicates overstory vegetation was removed from the forest at a large spatial scale, as trees experienced simultaneous releases in 25% of the study plots. A stand-wide release would be the result of an exogenous disturbance event that influenced large areas of the reserve. At the PCNA, such exogenous disturbance events may have included strong winds associated with tornadic storms, ice storms, or snow loading, among other factors.

With the exception of this one stand-wide release episode, forest disturbance events were asynchronous. They occurred at variable spatial and temporal scales. Interestingly, other studies in mixed *Quercus* forests of the eastern U.S., using similar release detection methods, have documented the return interval of stand-wide release events to be 20 to 30 years (Nowacki and Abrams 1997; Rubino and McCarthy 2004). For the PCNA, only one stand-wide release event was detected in the 130+ years of record indicating the return interval for stand-wide disturbances is longer at the PCNA than has been reported elsewhere in the eastern U.S. The return interval of these events may be related to biotic or abiotic site characteristics, atmospheric events, or the stage of forest development as other studies were conducted in different physiographic sections, at higher latitudes, and in older forests. Based on the occurrence of only one stand-wide release episode and the high number (*n* = 90) of release events detected in the 64 individuals sampled, I conclude that gap-phase dynamics are the primary forest disturbance events at the PCNA. The majority of release episodes were detected in only one or a few individuals, indicating increased radial growth during release episodes likely resulted from small, localized canopy disturbances that involved the partial or total death of one or a small group of canopy individuals (Runkle 1982; Nowacki and Abrams 1997; Rubino and McCarthy 2004; Black and Abrams 2005). These small-scale events would have only influenced neighboring individuals, and that is the pattern revealed from the disturbance reconstruction.

The magnitude of the disturbance may be inferred from the release duration. The duration of increased radial growth varied by event, but in general was four years. Because the 10-year running median method takes into account the 10-years preceding and superseding each growth ring, release events indicate a period of above average growth relative to the previous and subsequent decades. Thus, release events indicate periods when trees were responding to increased available resources (largely light) due to the removal of an adjacent individual. I interpret the mean release duration to indicate that the voids from canopy disturbance events closed in approximately four years. This is not enough time to allow individuals in the understory to recruit to the canopy. These gaps closed by lateral branch growth and release events coincide with lateral crown expansion (Rubino and McCarthy 2004). In these small gaps, it is possible for understory trees to be released and then become suppressed again as the gap closes (Oliver and

Larson 1996). For example, multiple gap events may be required for understory *Quercus* individuals to reach canopy positions (Rentch *et al*. 2003). Some canopy disturbances lasted longer than the four year average and may have allowed individuals in the understory to reach canopy positions before becoming suppressed.

3.5.2 Forest Growth and Development

The forest is currently in a stage of understory reinitiation (Oliver and Larson 1996). As individuals die and are removed from the canopy, canopy individuals are expanding their crowns and understory trees are being recruited to larger size classes. Although some trees pre-date the 1900s, the majority of canopy individuals established in the 1920s. To investigate forest development patterns, I compared composition and structural attributes of the secondary forest of the PCNA to those of an old growth remnant on the Cumberland Plateau (Table 3.5). Martin (1975, 1992) summarized forest composition and structural measures of Lilley Cornett Woods (LCW), an old growth forest in Kentucky approximately 130 km northeast of the PCNA. Both forests are located on the Cumberland Plateau, but the PCNA is near the western boundary and LCW is near the eastern boundary of the province. A moisture gradient across the plateau does exist and may influences species composition of the region. Old growth remnants are often used to predict the development of maturing stands. Although this technique is not without problems (Sprugel 1991; Drury and Runkle 2006) it does provide a model of forest development and a baseline for which to compare developing stands.

Table 3.5 Comparisons of composition and structural measures of second growth stands at the Pogue Creek Natural Area (PCNA) with old growth stands at Lilley Cornett Woods (LCW).

Parameter	**PCNA**	**LCW**[a]
Species richness	25	26[b]
Diversity (*H*′)	2.57	3[c]
Canopy species	16	20[c]
Basal area (m²/ha)	28.6	25–35[c]
Trees ≥ 75 cm dbh/ha	0	7[c]
Trees ≥ 10 cm dbh/ha	413	250[c]
Snags ≥ 10 cm dbh/ha	26	10[c]

[a] Data from Martin (1992)
[b] Data from mixed *Quercus* stands at LCW
[c] Data from mixed mesophytic stands at LCW

Species richness was similar for the PCNA and old growth mixed *Quercus* stands at LCW as the old growth remnant contained only one species more than the secondary forest. However, tree species diversity was lower for the secondary forest relative to old growth mixed mesophytic stands at LCW. Mixed mesophytic forests are known for their high diversity (Muller 1982; Martin 1992; Hinkle *et al*. 1993; Runkle 1996) and the PCNA, while within the Mixed Mesophytic Forest Region (Braun 1950), is dominated by *Quercus* and *Carya* species. Perhaps the difference in species diversity is more a function of forest type over forest age. Old growth mixed mesophytic stands at LCW contained 20 canopy species while the PCNA had only 16 species with dominant or codominant positions in the canopy. As the secondary forest matures, it is possible the number of canopy species will increase because some species that existed only in the understory have the potential to reach canopy positions, such as *Nyssa sylvatica*.

Basal areas between the PCNA and LCW were similar, or at least the basal area of the PCNA is within the range expected for old growth mixed mesophytic forests (Held and Winstead 1975; Muller 1982). However, the arrangement of the biomass was very different. LCW contained about 250 trees ≥ 10 cm dbh/ha while the PCNA contained over 400 trees of this size (60% increase). Further, while LCW contained at least seven trees ≥ 75 cm dbh/ha, no tree of this size occurred in any of the study plots at the PCNA (although one *F. americana* in this size category was documented while walking a transect). Tree biomass between the sites was similar, but the arrangement of that biomass was represented in vastly different ways. LCW contained large trees at a relatively low density, while the PCNA contained small trees at a much higher density. Based on the abundance of snags and the high number of release events at the PCNA, I propose that the frequency of canopy gap events is higher in secondary forests relative to old growth remnants, but the magnitude of the disturbances is less (*i.e.* a higher frequency of small gaps in secondary forests compared to old growth stands).

Based on these comparisons, I hypothesize the biomass of the PCNA will remain at a dynamic equilibrium, but the spatial arrangement of the biomass will change as the forest matures. At the PCNA, it is apparent that trees are dying and being removed from the canopy. In fact, the number of snags ≥ 10 cm dbh/ha was higher for the PCNA than at LCW. This finding supports other studies that have found second growth stands to have higher snag densities than old growth remnants (Muller 1982; McComb and Muller 1983). Localized small-scale canopy gaps are occurring at the PCNA based on the disturbance history of the stand. The duration of radial growth release events was much shorter than what has been reported in older forests, indicating that canopy disturbances at the PCNA are relatively small compared to similar disturbances in other forests. These small canopy gaps are likely being filled via lateral branch growth. Thus, as individuals are removed from the canopy (the losers), neighboring trees (the winners) increase radial growth and overall diameter. The lost basal area from the dead tree is recovered by the increased growth of residual individuals. Over time, this process will cause the diameter structure of the PCNA to more closely resemble that of an old growth stand. The biomass will be distributed among a lower number of larger individuals as opposed to a high number of small individuals.

The last stand-initiating disturbance that occurred at the PCNA was in the 1920s. That event was anthropogenic, caused by timber removal. The return interval of natural stand initiating disturbances is not known for the region. Stand initiating events in the region are likely highly variable depending on a suite of biotic and abiotic characteristics including species composition, slope aspect, and elevation and are thus unpredictable. Possible stand initiating events at the PCNA include high winds associated with tornadoes, severe ice or snow loading from polar outbreaks, and large wildfires. In the absence of a stand initiating disturbance, species composition is predicted to change as *Acer* and *Fagus* individuals in sub-canopy positions are recruited to larger size classes. The structure of the stand will also shift to larger, but fewer trees at wider spacings. I predict the number of canopy disturbances will decrease, but that the magnitude of each individual disturbance will increase. If a stand initiating event does occur, the development of the next stand would likely follow the successional pattern documented in this study. However, some variables that will exist during the development of the next stand will be inherently different. Biotic and abiotic characteristics of the site have changed during the growth of the current stand and disturbance events themselves often have lost lasting influences. It is also possible new factors, such as *Lymantria dispar* L. (gypsy moth), may alter development of future stands.

Chapter 4

Soil Charcoal Evidence of Fire History

4.1 Introduction

Recently, the role of fire in hardwood forests throughout the eastern U.S. has received increased attention because of successional changes believed to be associated with fire suppression that began in the early 1900s (Lorimer 1985; McCarthy *et al*. 1987; Crow 1988; Abrams and Downs 1990; Cho and Boerner 1991; Lorimer 1993; Goebel and Hix 1997). Fire as an ecosystem process in mixed hardwood stands of the Appalachian Highland region is not well understood. Although *Quercus* species dominate forest overstories throughout the eastern U.S., a lack of *Quercus* advanced regeneration has been reported (Lorimer 1984; Abrams and Downs 1990; Loftis and McGee 1993; McCarthy and Bailey 1996; Abrams 2003; Pierce *et al*. 2006). Fire suppression has allowed more shade-tolerant species, such as *Acer saccharum*, *Acer rubrum*, and *Fagus grandifolia*, among others, to establish and become abundant in the understory of *Quercus*-dominated forests. Also, it is believed fire suppression has allowed forest canopy gaps to be filled by *Liriodendron tulipifera* and other early successional, gap-phase species rather than by *Quercus* (Loftis 1990; Loftis 2004). It is hypothesized that *Quercus* stands were historically maintained by frequent, low-intensity fires that removed more mesic and fire-intolerant species from the understory and effectively reduced competition for the more fire-tolerant *Quercus* species (Crow 1988; Abrams 1992; Brose *et al*. 2001; Lorimer 2001). An understory densely populated with shade-tolerant species inhibits the establishment of *Quercus* individuals (Lorimer 1993; Lorimer *et al*. 1994).

Although *Quercus* individuals are often abundant in seedling layers of closed canopy forests, they are generally unable to recruit to larger size classes and may be considered ephemeral in the absence of fire or other large-scale disturbances (Cho and Boerner 1991; Goebel and Hix 1997; Hutchinson *et al*. 2003).

Undoubtedly, fire by natural or anthropogenic ignitions has occurred in mixed hardwood stands of the southern Appalachian Highlands, but characteristics of the fire regime (such as frequency, magnitude, and spatial extent) are poorly understood. This information is needed to manage forests according to historic disturbance regimes, for the regeneration and maintenance of *Quercus* species, and for the proper classification of forests based on assumed species composition at equilibrium. The mixed hardwood slope forests of the Cumberland Plateau, however, do not consist of any taxa, such as *Pinus*, that scar easily during fires and the vast majority of forests throughout the region are young (< 100 years) and the time since the last fire exceeds the ages of trees. In this study, I used macroscopic charcoal recovered from soil cores as an indicator of past fire events. I focused on macroscopic charcoal sufficiently large to be retained on a 2 mm mesh screen because charcoal of this size is not readily transported by wind during or after fires or by overland flow on hillslopes. Such charcoal is generally considered primary charcoal (*i.e.* introduced during or shortly after a fire event), and its presence in soils is evidence of local fire (Patterson *et al*. 1987; Clark 1988; Gavin 2003; Gavin *et al*. 2003).

One previous study (Welch 1999) documented the presence or absence of macroscopic charcoal in *Pinus*-dominated stands on the Cumberland Plateau. However, the present study is the first to document the occurrence and amount of macroscopic charcoal in soil of mixed hardwood forests on the Cumberland Plateau. The specific objectives of the study were to: (1) document the presence of charcoal in soil samples as evidence of fire occurrence, (2) quantify charcoal mass in each sample as possible evidence of fire magnitude, and (3) compare charcoal quantities at different depths and at different locations to infer temporal and spatial patterns of past fire events in mixed hardwood forests. The development of a coarse-resolution fire history is useful to elucidate forest successional patterns and to determine the importance of fire in *Quercus*-dominated ecosystems of the Cumberland Plateau.

4.2 Methods

Soil charcoal was quantified from 10 soil cores collected from the Pogue Creek Natural Area (PCNA). All cores were collected from mid-slope positions at points located along transects spread randomly throughout the reserve and the location of each point was recorded. The cores were collected using a tubiform root corer following methods described by Horn *et al*. (1994). The core diameter was 10 cm and the samples were collected in contiguous 10 cm depth intervals to unconsolidated bedrock or an impenetrable clay layer (which was less than 50 cm depth for all cores). Each 10 cm increment was considered a separate soil sample, which resulted in a total of 30 samples. Each sample was stored in a labeled bag and transported to the laboratory for analyses.

Following the methods outlined by Horn *et al*. (1994), each sample was soaked in approximately 1.5 L of water overnight to disaggregate soil particles. I then wet sieved each sample through 2 mm mesh brass screens. All charcoal particles remaining on the screens from each of the 30 samples were identified with the aid of a stereozoom scope and placed in labeled glass vials. The vials were dried in an oven at 100 °C for approximately 24 hours. I then measured the dry weight of charcoal in each sample to the nearest 0.0001 g.

The presence or absence of macroscopic charcoal was determined for each sample to document past fire occurrence. Charcoal masses were compared within each core by depth and across all cores at the same depth interval to analyze temporal and spatial patterns. I calculated the total mass of macroscopic charcoal for each core as a possible indicator of the magnitude of past fire events at each site. I also classified tree-ring structure as either diffuse porous or ring porous for larger charcoal fragments that contained a minimum of one complete growth ring. Ring-structure was classified to determine possible taxa that were present at the time of past fires and that were killed or injured by them. Five samples were submitted to the NSF-Arizona AMS Laboratory for radiocarbon dating using accelerator mass spectrometry (AMS). All five samples consisted of multiple pieces of charcoal from the same depth interval of a single soil core. The five samples submitted for dating were selected because they were from the lowermost soil samples that contained charcoal and were judged likely to provide the best estimate of the maximum age of collected charcoal. The maximum age of the charcoal at the site will in turn provide an estimate of the timing of the earliest recorded fires, although charcoal ages could predate fire ages by a century or more, depending on the age of the wood at the time it was burned.

4.3 Results

Soil depth was rather shallow. Average maximum sampling depth was 24.9 ± 11.1 (SD) cm and ranged from 14 to 47 cm. Macroscopic charcoal was present in all 10 soil cores (Figure 4.1). Charcoal occurred in 19 of the 30 soil samples (63%). The deepest soil core was core 1, which extended to a depth of 47 cm before hitting bedrock. Core 1 did contain charcoal in the deepest layer (40–47 cm). Charcoal was present in all depth intervals of cores 2, 4, 5, and 9. Only two cores (cores 3 and 7) did not contain macroscopic charcoal in the 0–10 cm depth interval. Half of the cores contained charcoal in the two uppermost depth intervals. Macroscopic charcoal in core 1 occurred in alternating layers. No depth layer contained macroscopic charcoal across all cores and no clear pattern of charcoal presence or absence was evident.

The total amount of macroscopic charcoal recovered was 4.06 g. Core 2 contained the largest amount of charcoal (2.76 g) followed by core 4 (0.78 g) (Figure 4.1). The least amount of charcoal recovered was from core 6 (0.002 g), but cores 3 and 7 also had relatively small amounts. When charcoal from all cores was totaled by depth layer, a pattern of charcoal accumulation was revealed. The amount of charcoal was greatest near the surface and the amount of charcoal decreased with increased depth (Figure 4.2). This pattern occurred in individual cores 2, 4, and 10 and emerged across all cores driven by the relatively large amount of charcoal in the uppermost layers of cores 2 and 4. In cores 3, 5, 7, and 9, however, charcoal mass was greatest in the deepest layer sampled. The largest piece of charcoal occurred in the 10–15 cm depth sample of core 5.

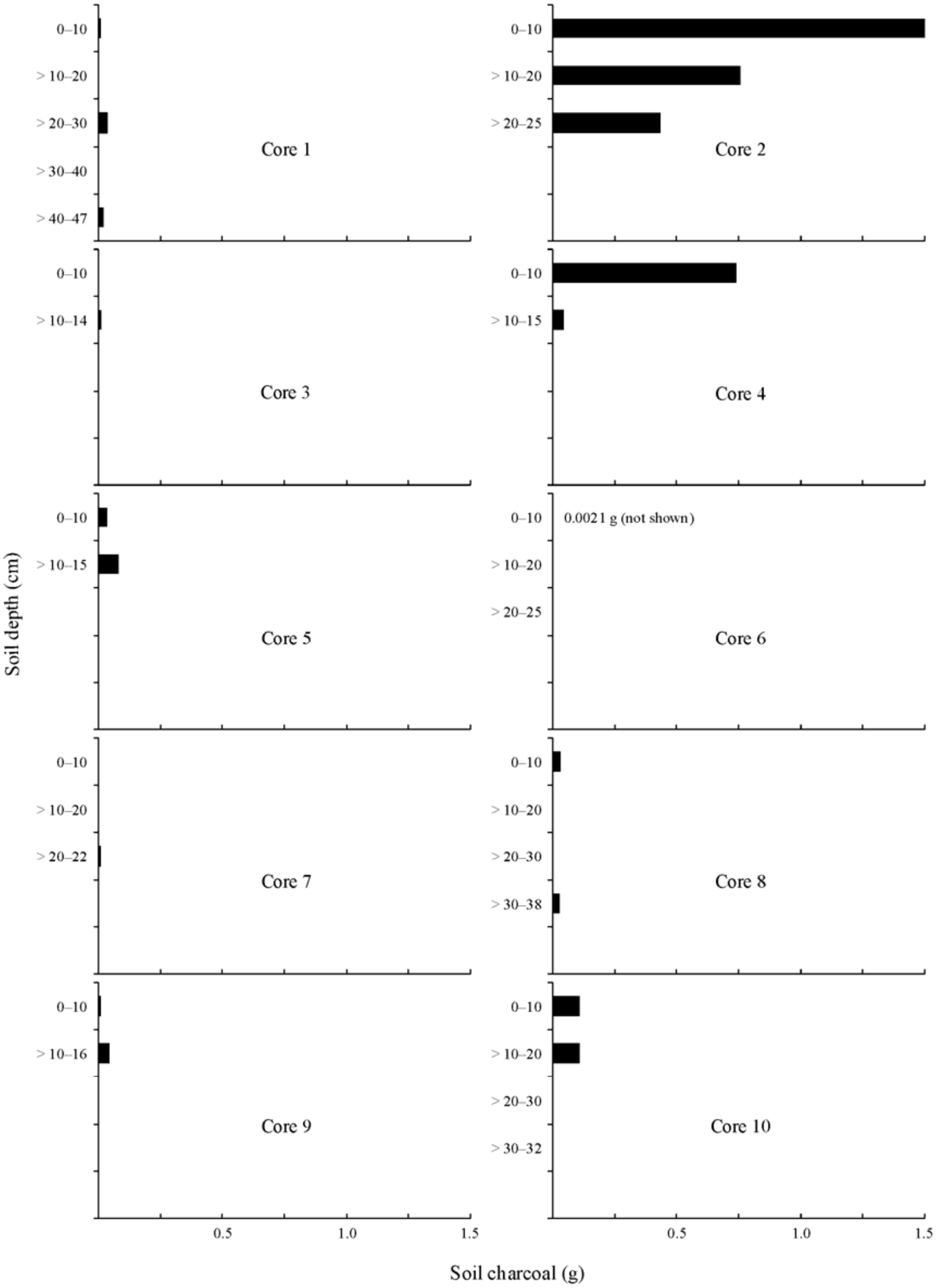


Figure 4.1 Amount of macroscopic charcoal captured on a 2 mm sieve from 10 soil cores from a mixed hardwood forest on the Cumberland Plateau.

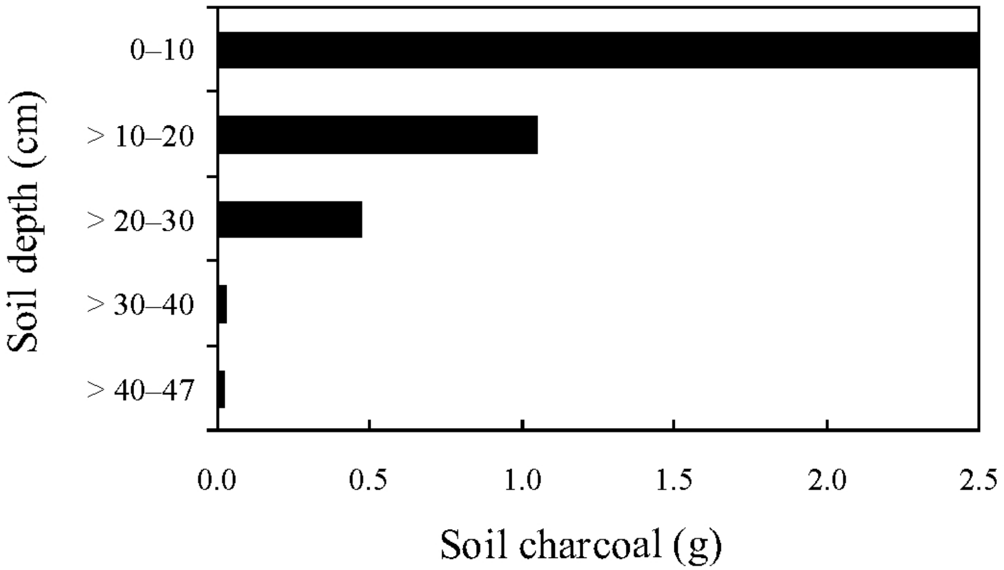


Figure 4.2 Total macroscopic charcoal captured on a 2 mm sieve by depth from 10 soil cores from a mixed hardwood forest on the Cumberland Plateau.

The total mass of macroscopic charcoal was plotted by core to analyze spatial patterns of fire occurrence (Figure 4.3). Core 2 contained the most charcoal. However, relatively small amounts of charcoal were recovered from cores 1 (which was in a similar slope position) and 3 (which were nearest to core 2). Core 4 had the second most amount of charcoal and relatively small amounts were recovered from the nearest cores.

Although many charcoal fragments could not be taxonomically classified with confidence, visual examination of larger fragments revealed the wood was from individuals with diffuse porous growth-ring structures. Common diffuse porous species that inhabit the study site include *A. saccharum*, *A. rubrum*, *F. grandifolia*, and *L. tulipifera*.

4.4 Discussion

Without radiocarbon dates, it cannot be determined if charcoal at the same depth in separate cores originated from the same event. In general, the deeper layers are thought to be older than layers nearer the surface. However, macroscopic charcoal in soil does not form distinct bands of accumulation that may be linked to one fire event (Patterson *et al*. 1987). The preservation of distinct charcoal layers is not possible in forest soils because of overland flow, bioturbation, and physical processes such as tree blowdown. If the five AMS dates I receive are close in age, it will suggest that the charcoal may have been produced during the same fire event. To test for this, I will calibrate the dates using the latest version of the CALIB radiocarbon calibration program (Stuiver and Reimer 1993) and will examine the calibrated age ranges to see the extent to which the two-sigma age ranges overlap. If dates do not overlap, I would take this to

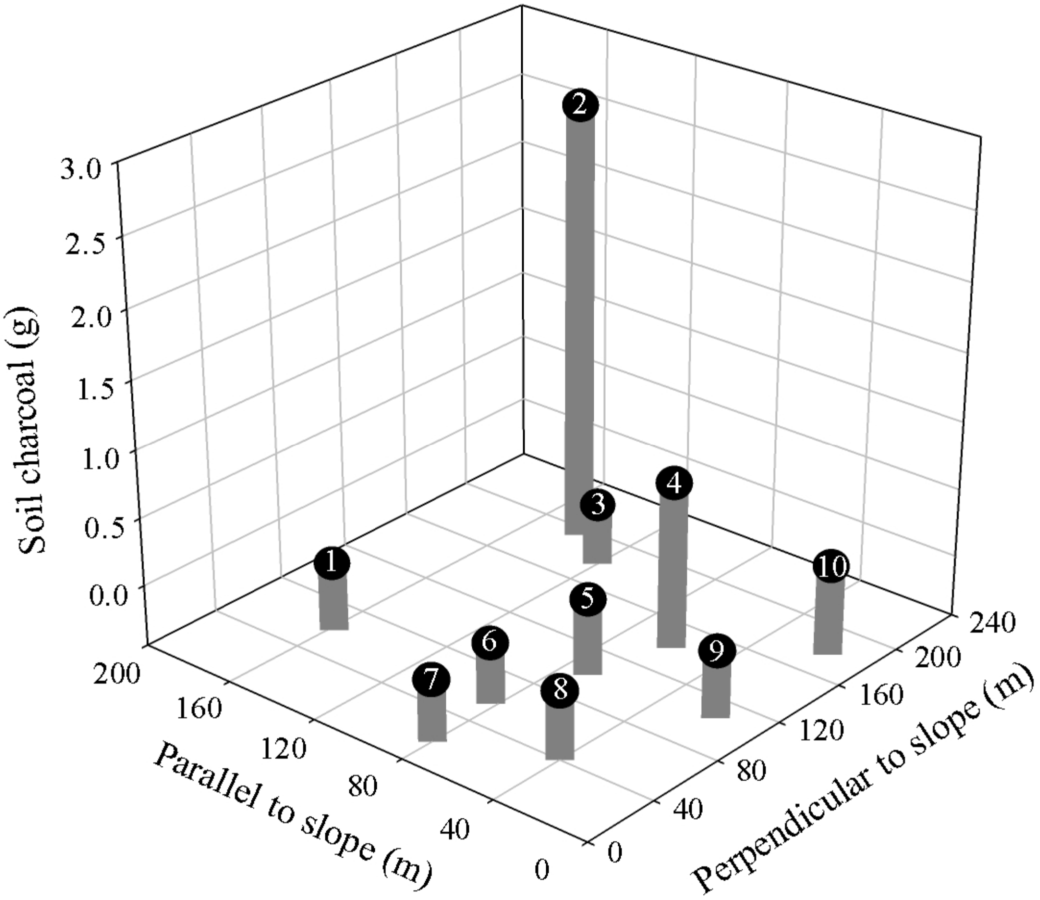


Figure 4.3 Total macroscopic charcoal captured on a 2 mm sieve from 10 soil cores from a mixed hardwood forest on the Cumberland Plateau.

indicate distinct fires at those times, although the variable age of the wood burned to produce the charcoal needs to be taken into account. The calibrated age ranges for two pieces of charcoal produced in the same fire could be separated by a century or more if one piece was from old wood and the other from young.

Most macroscopic charcoal mass occurred in the upper 0–10 cm. This suggests that fire has occurred fairly recently at the site and was not common historically, although, charcoal did occur in the deepest sample (40–47 cm). Results showed fire has occurred in the reserve in the past. Charcoal presence or absence and dry mass information alone is useful because the presence of charcoal indicates fire is a disturbance mechanism that has occurred in the reserve. In the absence of fire, more mesophytic and fire intolerant taxa (such as *Acer*) will likely increase in dominance.

Charcoal accumulation patterns were similar for cores 2 and 4. This was interesting because these two cores were not collected near one another and they also contained the largest amounts of charcoal. Core 3 was located between cores 2 and 4, but contained a relatively small amount of macroscopic charcoal. The spatial pattern of charcoal accumulation indicated that fires in the stand were small events that only influenced local areas. Macroscopic charcoal has been recovered from multiple topographic forms and slope positions on the Cumberland Plateau (Welch 1999). In this study, all soil cores were collected from mid-slope positions, but microtopography may influence charcoal accumulation.

The presence or absence as well as dry mass of macroscopic charcoal is useful to reconstruct a coarse-resolution fire history, but it does not give precise information on fire frequency, magnitude, or ignition source. The high amount of charcoal in the upper samples of cores 2 and 4 may be the result of the last logging episode at the site, which occurred in the 1920s. It is possible the slash was burned after logging or the site was burned for grazing purposes immediately following timber removal. Radiocarbon dating of near-surface charcoal would provide a test for this hypothesis. The pending AMS dates on the deepest charcoal from the site could reveal that the charcoal is also from fires associated with logging at the site in the 1920s. Alternatively, the deep charcoal might return dates of several hundred to several thousand years indicating that these fires occurred during the early European period or the prehistoric period. Fires may have been set by Native peoples prior to European settlement (Delcourt and Delcourt 1997; Delcourt and Delcourt 1998) or by lightning, although lightning fires are believed to be relatively rare in the southern Appalachian Highlands (Van Lear and Waldrop 1989; Meier and Bratton 1995; Mitchener and Parker 2005). Fires during the early historic or prehistoric period could also be responsible for some of the charcoal in the 0–10 cm depth interval, owing to a slow rate of soil accretion on these mid-slope positions or to soil mixing from anthropogenic activities, treefall, and burrowing animals.

This study showed the site has burned in the past and that macroscopic charcoal produced by those fires may be recovered from forest soil. Likely, fires at the site influenced only small spatial areas. The site is presently mesic and would not facilitate fire movement under normal (*i.e.* non-drought) conditions (Mitchener and Parker 2005). The identified charcoal was from species with diffuse porous ring structures. The most abundant species presently at the site with this ring structure are *A. saccharum*, *A. rubrum*, *F. grandifolia*, and *L. tulipifera*. Based on this observation, I suggest these mesic species were likely present when past fires occurred at the site. Thus, I propose that fires burned stands composed of species not considered fire-tolerant. High amounts of charcoal in soil layers may be from one fire or multiple events, as it is possible charcoal from one fire could be mixed vertically into the soil profile (Patterson *et al*. 1987). The pending AMS dates will provide a first estimate for the timing of the earliest fires recorded at the site. The extent to which dates overlap will reveal if the charcoal records a single early fire or multiple early and later fires. When combined with the AMS results, the patterns of charcoal occurrence within and across cores will provide an initial, coarse-resolution fire history for a mixed hardwood forest on the Cumberland Plateau in Tennessee. This study documents local fire history at a site lacking other fire records, and provides a basis for assessing the utility of more detailed study of soil charcoal mass and taxonomy to reconstruct fire history and understand the influence of fire on mixed hardwood communities of the southeastern U.S.

Chapter 5

Gap-Scale Disturbances in a Secondary Hardwood Forest on the Cumberland Plateau

5.1 Introduction

All forest ecosystems are subject to natural disturbance events that shape species composition and stand structure. Gap-scale disturbance processes are the dominant disturbance mechanisms in many forest types. Thus, canopy gap characteristics and forest response have been studied in forests throughout the eastern U.S. to elucidate patterns of gap-scale processes and forest vegetation dynamics. However, the overwhelming majority of canopy gap studies have been conducted in old growth remnants that have reached compositional equilibrium and structural stability (*e.g.* Lorimer 1980; Barden 1981; Runkle 1982; Cho and Boerner 1991; Runkle 2000). Throughout the Eastern Deciduous Forest Region, most forested land supports secondary stands composed of mixed hardwood species (Cowell 1998; Rebertus and Meier 2001). Few studies have analyzed gap-scale disturbances and forest response in secondary forests (but see Clebsch and Busing 1989; Dahir and Lorimer 1996; Wilder *et al*. 1999; Yamamoto and Nishimura 1999), and no such research has been conducted in mixed hardwood stands on the Cumberland Plateau.

Undoubtedly, forest disturbance dynamics differ between old growth remnants and mature secondary stands. Differences in disturbance characteristics are attributed to variations in species composition, biomass arrangement, and tree-age distribution. As forests mature, the distance between large individuals increases. Tree crowns separate into distinct categories, creating a more complex vertical structure, and species composition shifts to favor later successional species (Goebel and Hix 1996; Oliver and Larson 1996; Goebel and Hix 1997). Forest response to disturbance events likely differs between old growth and secondary stands because of differences in stand structure and species composition, and also because of the ages of the oldest trees, as older trees are less able to respond to increases in available resources resulting from disturbance events (Fritts 2001).

In old growth forests, the spacing between large individuals is greater than in secondary forests. Thus, when a canopy tree is removed from an old growth stand, the size of the canopy gap created should be larger than a comparable disturbance during earlier stages of forest development (Clebsch and Busing 1989; Spies *et al.* 1990; Tyrell and Crow 1994; Runkle 1998; Yamamoto and Nishimura 1999). Because canopy gaps are generally larger in old growth remnants, the majority of gaps in these forests close by the height growth of subcanopy individuals rather than lateral crown expansion of perimeter trees (Runkle 1982). This gap-replacement process creates forests with complex age and size structures and patchy species composition in the canopy (Lorimer 1980; Runkle 1982; Yetter and Runkle 1986; Runkle and Yetter 1987; Lewis 1991). Although canopy gaps in secondary forests are hypothesized to be smaller in size, they may still act as a mechanism for canopy tree replacement and stand structural changes associated with older forests (Clebsch and Busing 1989; Wilder *et al.* 1999; Taylor and Lorimer 2003; Cole and Lorimer 2005).

In this study, gap-scale disturbance processes were investigated in a secondary mixed hardwood forest on the Cumberland Plateau in Tennessee. The specific objectives of this study were to: (1) examine patterns of gap formation including gap origins, gap maker species, gap maker size, and rate of gap occurrence), (2) quantify the physical characteristics of canopy gaps such as land fraction in gaps, gap size distribution, gap shape, and orientation, and (3) document the forest response to localized disturbance events focusing on density and diversity within gaps, gap closure mechanisms, and gap-phase replacement and recruitment in a mature hardwood forest. The results of the study were viewed in the context of other gap-scale disturbance studies conducted in the Eastern Deciduous Forest Region, especially in the southern Appalachian Highlands.

5.2 Methods

5.2.1 Field Sampling

Canopy gaps (*n* = 40) were located along transects throughout the reserve using the line intersect method (Runkle 1982; Runkle 1985b; Veblen 1985; Runkle 1992). Transects were established parallel to slope contour beginning at randomly selected points throughout the forest. Transects were randomly located at mid-slope positions. I sampled at mid-slope positions because the mid-slope forests of the reserve are indicative of slope forests of the greater Cumberland Plateau region. Total transect length and transect length in expanded (boundary defined by the base of surrounding canopy trees (Runkle 1981)) and true (area unrestricted from above) canopy gaps were documented by recording the number of paces across each. The fraction of land area in canopy gaps was calculated by dividing transect distance in gaps by total transect length (Runkle 1985b;

Runkle 1992). At each gap, physical site characteristics were recorded including percent slope, aspect, and elevation.

Gap area was determined for expanded and true gaps by measuring length (largest distance from gap edge to gap edge) and width (largest distance perpendicular to the length). These measurements were fitted to the formula of an ellipse (Runkle 1985b; Runkle 1992). Although gap shapes can be highly variable (Ferreira de Lima 2005) most gaps at the PCNA had elliptical shapes, which is common for forests of the southern Appalachian Highlands (Runkle 1982; Runkle 1992; Clinton *et al*. 1994). Thus, fitting the measurements to the formula of an ellipse was appropriate for this study.

Canopy gaps can be created by several different mechanisms that remove overstory trees. Biotic and abiotic forest conditions can be modified differently by canopy disturbances that are caused by different gap formation mechanisms. Differences between gap origins may also influence forest response. To analyze these patterns, gap formation mechanisms were classified into one of three categories (snag, windthrow, or basal-shear) according to gap origin (Clinton *et al*. 1993). The number of trees involved in gap formation was also recorded to document the abundance of single tree versus multi-tree events.

Gap maker trees were taxonomically classified to quantify any species-specific mortality patterns and possible composition changes associated with small canopy disturbances. I measured gap maker diameter at breast height (dbh, *ca*. 1.4 m above the surface or root collar for downed individuals) and length. Basal area (m^2) was calculated for all gap makers that could be accurately measured and totaled by gap to determine the amount of basal area lost per disturbance event. This information may be used to document the amount of biomass naturally removed from a stand through gap-scale processes. Direction of gap maker fall relative to slope was also recorded and all gap makers were placed into one of four decay classes (1–4, with 4 being the most decayed) following criteria adapted from McCarthy and Bailey (1994).

In each gap, I recorded species, crown class, and diameter of all trees ≥ 5 cm dbh to characterize forest gap vegetation. Crown class categories (dominant, codominant, intermediate, and overtopped) were visually assessed based on the amount and direction of intercepted light (Oliver and Larson 1996). The location of each of these individuals was also recorded as being in either an expanded or true canopy gap. All saplings (woody stems ≥ 1 m height, < 5 cm dbh) in the expanded gap area were tallied by species to characterize gap regeneration patterns. The number of perimeter trees with dominant or codominant positions in the canopy was documented for each gap to analyze the number of trees required to complete the canopy surrounding gaps and the number of canopy individuals with the potential to close the void space through lateral crown expansion.

Tree core samples were collected to aid in the documentation of gap age. A minimum of nine trees were cored (mean = 18.6) per gap resulting in the collection of 742 cores. Tree core samples or cross sections were also collected from all gap makers that were not in an advanced state of decay to aid with gap age determination and to document the seasonal timing of gap events based on the amount of xylem produced during the last year of growth.

5.2.2 Data Analyses

Tree core and cross section samples were prepared and processed for dating using the methods outlined in Stokes and Smiley (1996). The samples were air-dried, glued to wooden mounts, and sanded to reveal the cellular structure of the wood (Orvis and Grissino-Mayer 2002) before tree rings were dated with the aid of a stereo zoom microscope. All tree cores were visually analyzed for radial growth releases to document gap age. To document gap maker death dates, tree rings were measured to the nearest 0.001 mm using a Velmex measuring stage interfaced with Measure J2X software for all sampled gap makers (Cseke 2003). The measurement series were visually compared to a reference *Quercus* chronology developed for the site. I confirmed the graphical crossdating of all gap maker tree-ring series using the computer software COFECHA, a quality-control program that uses segmented time series correlation analyses to confirm the placements of all tree rings (Holmes 1983; Grissino-Mayer 2001a). In COFECHA, I tested consecutive 50-year segments (with 25-year overlaps) on each undated gap maker series to the reference *Quercus* chronology. Once statistically confirmed, I assigned calendar years to all tree rings in each individual undated measurement series. All gap ages were confirmed using gap maker decay classifications.

Canopy gaps can be caused by the removal of a single tree or a small cluster of trees. Because single tree gaps may result from the death of a large canopy tree and multi-tree gaps may result from the deaths of relatively small trees, the amount of basal area lost between single and multi-tree gaps was statistically analyzed using a two-tailed t-test. This information may be useful to analyze the quantity of basal area lost by small canopy disturbance events and applied to harvesting techniques that may mimic natural disturbance processes.

The rate of gap formation and closure may be balanced or vary through time. Non-parametric correlation techniques were used to analyze the relationship between land fraction in gaps and gap age. Gaps may be caused by a variety of formation mechanisms that differ in the way overstory vegetation is removed, and the mechanism of canopy tree removal may influence gap size. To determine if a relationship existed between gap size and gap origin, data were analyzed using a one-way ANOVA. A Tukey HSD (honestly significant difference) test was used to compare mean expanded and true gap sizes across origin categories to determine if gap size varied by gap formation mechanism.

Length and width of gaps were measured in the field. Ratios were calculated for length to width (L:W) of expanded and true gaps to document gap shape characteristics. This information is useful to understand the variation in shape of gaps created by the disturbance and has implications for forest response and microenvironmental changes within the gap environment.

For each gap, density and diversity (*H'*) measures were calculated for saplings, trees, and total stems (all woody stems ≥ 1 m height) to document forest response to canopy disturbances. Gap size is believed to strongly influence stem density and diversity. Correlation coefficients were calculated to determine if a relationship existed between gap size and density of individuals in gaps. Regression techniques were then used to model gap size and density relationships. To analyze the relationship between expanded gap area and diversity patterns, correlation coefficients were calculated for sapling, tree, and total stem diversity. I hypothesized that larger gaps would support higher levels of diversity because they should contain more microsite heterogeneity and the likelihood of documenting rare species increases by sampling a larger spatial area.

Canopy gaps can close by crown expansion of perimeter trees at canopy level or by the height growth of understory individuals. The likely closure mechanism, either by height growth or lateral crown expansion, of each gap was recorded in the field to document changes in forest structure following the removal of canopy trees. Probable gap successors, which are the individuals that will likely fill the canopy void, can often be determined in the field (Barden 1979; Barden 1980; White *et al*. 1985; Yamamoto and Nishimura 1999). The documentation of replacement trees is useful to project the future composition of the stand and to analyze the influence of canopy gaps on forest succession. To quantify recruitment following overstory removal, crown class distributions were constructed for all trees located in true gap environments for the 15 most dominant species with canopy potential. These measures may be used to document future canopy trees and recruitment patterns associated with gap-scale disturbance processes.

5.2.3 Summary of Methods and Data Analyses

1. I quantified land fraction in canopy gaps, expanded and true gap area, gap shape (L:W), and the number of canopy trees that border the gap to document the abundance of canopy gaps, the amount of land area they occupy, and gap physical characteristics,

2. To quantify gap origin, I documented the mechanism of formation and number of gap maker trees for all canopy gaps.

3. I recorded species, diameter, direction of fall relative to slope, and decay class for all gap makers to investigate gap maker characteristics and species and size patterns of removed trees.

4. To analyze gap formation and closure patterns and to document the timing of gap formation, I determined gap age and the seasonality of gap maker death.

5. I documented species, crown class, diameter, and relative position within the gap for all trees and I tallied all saplings by species to quantify vegetation characteristics and response to canopy disturbances.

7. I used a two-tailed t-test to analyze the relationship between the amount of biomass lost and the type of canopy disturbance (single v. multi-tree).

8. To quantify gap formation and closure patterns, I used non-parametric correlation techniques to analyze transect distance in gaps by gap age.

9. To determine if a relationship existed between gap size and gap origin, I used a one-way ANOVA and post-hoc test to compare mean expanded and true gap sizes across origin categories.

10. Shape characteristics of true and expanded gaps were analyzed by calculating length to width ratios.

11. Density and diversity values were calculated for all saplings, trees, and total stems to document forest response to canopy disturbances. Correlation techniques were used to analyze the relationship between gap size and these

measures. Regression techniques were used to model gap size and stem density relationships.

12. The probable closure mechanism of each gap was recorded in the field to document changes in forest structure following the removal of canopy trees.

13. Replacement tree species was documented for gaps that were projected to close by understory height growth to project the future composition of the stand and to analyze the influence of canopy gaps on forest succession.

14. To document future canopy trees and recruitment patterns associated with gap-scale disturbances, I analyzed crown class distributions for all trees located in true gap environments for the 15 most dominant species with canopy potential.

5.3 Results

5.3.1 Mechanisms of Formation

Of the 40 gaps sampled, 8 (20%) were created by snags, 16 (40%) were created by windthrow, and 16 (40%) were created by basal-shear. Windthrow and basal-shear gaps likely resulted from high wind events that either uprooted trees or caused boles to snap. Snags may have been the result of pathogens, lightning strikes, mortality because of competition, or a number of other factors. Eventually snag trees will fall, generally during mild to severe wind events, possibly causing further disturbance to the forest. It is possible that a gap created by a snag, but since blown down, was classified incorrectly. However, measures were taken to avoid this issue, such as documenting the decay class of gap makers and noting the position of the gap maker relative to other downed logs.

The number of gap maker trees involved with opening the canopy ranged from one to four. The majority (78%) of the canopy gaps involved the death of only one individual. Of the nine multi-tree gaps, six (66%) resulted from windthrow including the gap that consisted of the removal of four canopy individuals while the three other multi-tree gaps resulted from snapped boles.

5.3.2 Gap Maker Characteristics

I identified 50 gap maker trees in the 40 canopy gaps studied. Most gap makers (n = 36, 72%) could be identified to the species level, however four (8%) could only be identified to genus and 10 (20%) were too decayed to be taxonomically classified. Of the 36 gap makers that could be identified to species, 12 different species were represented. The most common species that caused canopy gap formation was *Quercus montana* (n = 8). At the genus level, 50% of all gap makers were *Quercus*.

Diameter was measured at *ca*. 1.4 m above the surface or root collar for 46 gap makers. Diameter measurements could not be collected for 4 gap makers that were in a state of advanced decay. Average gap maker diameter at breast height was 38.38 cm ± 11.6 (SD). The minimum diameter of a tree involved in a gap was 19.5 cm and the maximum was 70 cm. The gap maker with a diameter of 19.5 cm was involved in a multi-tree windthrow event that also included the death of an individual with a diameter of 28 cm. Average basal area lost per gap was 0.16 m^2 ± 0.10 (SD). The minimum removed was 0.05 m^2 and the maximum was 0.52 m^2. Multi-tree gaps (mean = 0.24 m^2 ± 0.13 (SD)) resulted in a higher amount ($P < 0.01$) of basal area lost compared to single tree events (mean = 0.14 m^2 ± 0.08 (SD)).

5.3.3 Gap Age and Seasonality

Age was determined for all canopy gaps by the identification of radial growth releases, crossdating the gap makers to document death dates, field observation, and gap maker decay classification. Gap ages ranged from 1 to 17 years with a mean of 7 years. Multiple gaps occurred during 13 years. The highest frequency of gap events during any one year was five, which occurred during 3 years (1999, 2002, and 2003).

Gap seasonality was determined for 17 gaps by examining the amount of xylem produced during the last year of growth. Of these 17 events, only one occurred during the dormant season. For the dormant season gap, the latewood portion of the last ring was complete and buds were still present on the tree. All other gap makers had partial rings, indicating the gap events occurred during the growing season. Because the majority of these individuals had already completed the production of earlywood prior to death (Figure 5.1), I surmise these events occurred in the middle or later part of the growing season.

5.3.4. Land Area in Canopy Gaps

Total transect length was 4.47 km, with 15% of the total length in expanded gaps and 6% in true light gaps. When percentage values were standardized at the hectare level, 1,500 m^2/ha were in expanded gaps and 600 m^2/ha were in true gap environments. When walking transects through a forest, large gaps are more likely to be encountered than relatively small gaps and sampling estimators have been created to correct for sampling bias (see De Vries 1974; Pickford and Hazard 1978). However, values

Figure 5.1 Formation of complete earlywood cells in a *Carya tomentosa* prior to death during the growing season (photograph by author).

obtained with the use of estimator equations and those obtained by simply dividing transect distance in gaps by total transect length are similar (Runkle 1985b).

Total transect length in true light gaps was plotted by gap age to analyze patterns of gap formation and closure (Figure 5.2). The largest amount of land area in true canopy gaps occurred in gaps that were 2 years of age and no gap area occurred in gaps aged 5, 6, 14, 15, or 16 years. Spearman's rank correlation was used to analyze the relationship between land fraction in gaps and gap age. A significant negative relationship existed, where older gaps occupied a smaller amount of land area relative to younger gaps.

5.3.5 Gap Size and Shape Patterns

Average expanded gap area was 213.34 m^2 ± 108.44 (SD). The maximum expanded gap area was 587.91 m^2 and the minimum was 47.10 m^2. Average true gap area when sampled was 42.78 m^2 ± 40.16 (SD), with a maximum of 157.84 m^2 and a minimum of 1.14 m^2. The expanded gap area does not change as the canopy void is filled. However, the true area in a light gap changes as the forest responds to the disturbance by lateral crown expansion of border trees and height growth of both perimeter trees and residuals in the gap. Expanded size of gaps created by windthrow was significantly higher than that of gaps created by snags (Figure 5.3). No other sizes differences between gap origins were significant.

The average L:W ratio of expanded gaps was 1.58:1 with a maximum of 3.60:1 and a minimum of 1.01:1 (Figure 5.4). Thus, the average expanded gap was 58% longer than it was wide. Similar patterns were observed for true gap areas, for which the mean ratio was 2.58:1. The maximum length of true gaps was 475% the width. The minimum

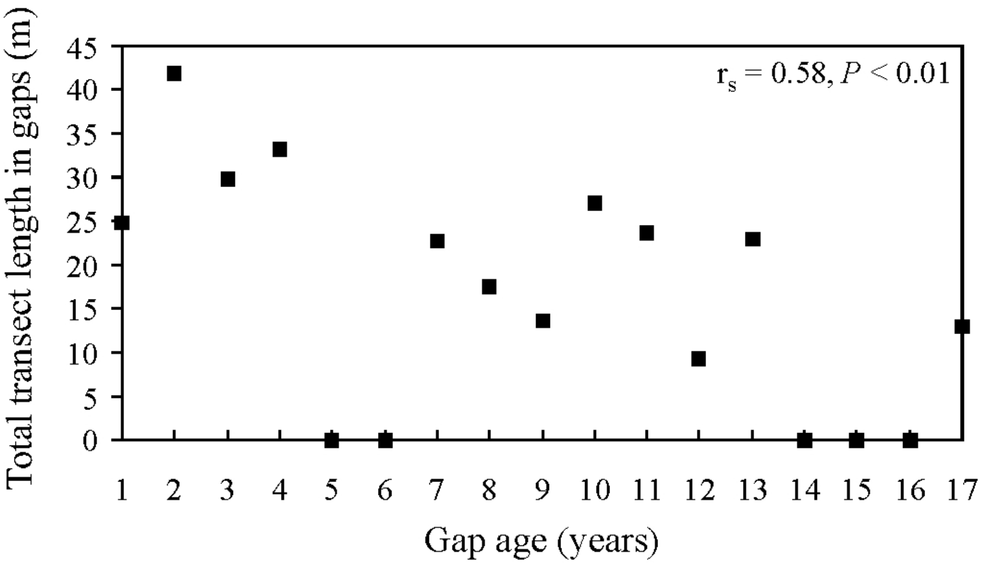


Figure 5.2 Relationship between land fraction in true canopy gaps and gap age in the Pogue Creek Natural Area in Tennessee.

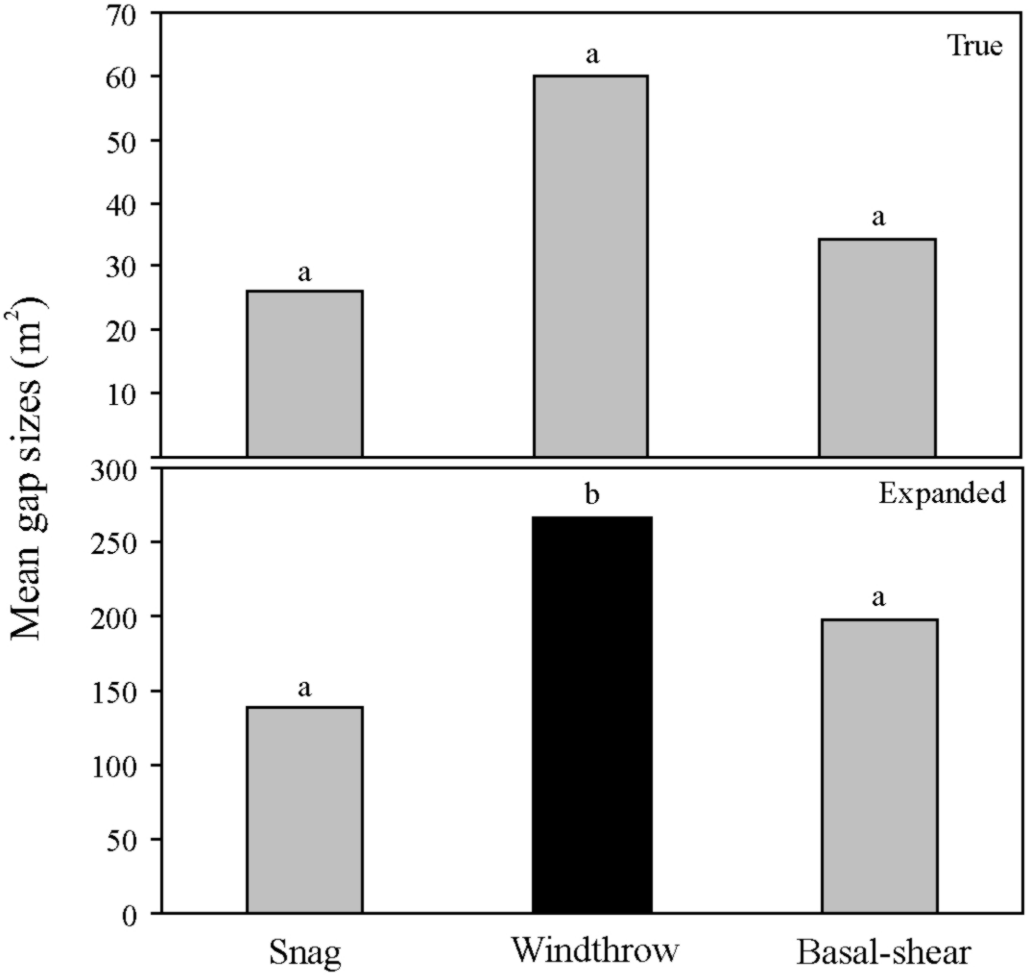


Figure 5.3 Mean sizes of expanded and true canopy gaps by gap origin. Solid bar and different letters denote a significant difference between gap origins ($P < 0.05$).

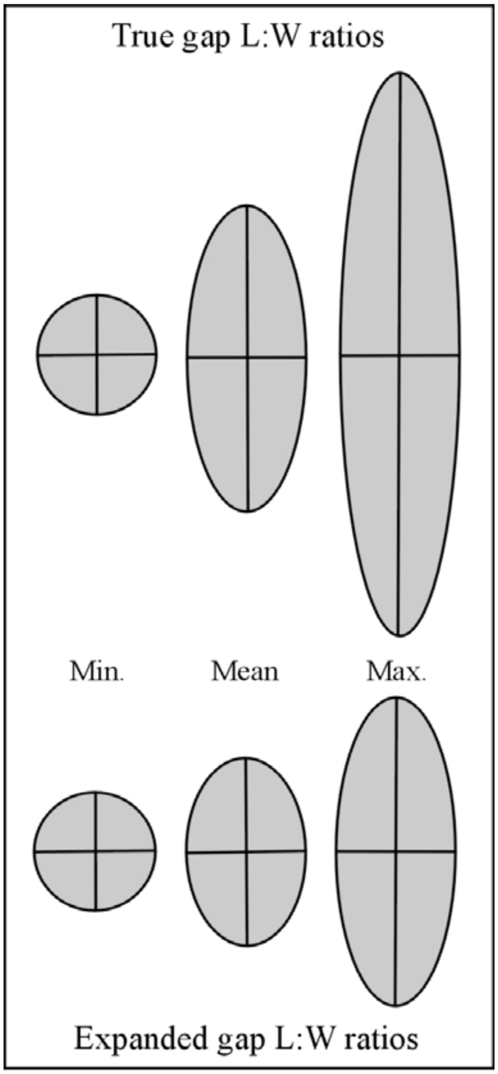


Figure 5.4 Mean, minimum, and maximum length to width (L:W) ratios for expanded and true canopy gaps in the Pogue Creek Natural Area in Tennessee. Note this figure represents shape not size characteristics and all width values are equal.

L:W patterns of expanded and true gaps revealed circular over ellipsoidal shapes. The shape of the disturbed canopy area is largely a function of the mechanism of tree death and architecture of the gap maker. Circular gap shapes resulted from canopy disturbances related to snags rather than windthrow or basal-shear origins. Mean gap shape for expanded and true gap areas was ellipsoidal. This pattern was attributed to the higher frequency of treefall gaps rather than canopy disturbances that were created by standing dead trees.

5.3.6 Density and Diversity within Gaps

The mean number of canopy trees that bordered gaps was 6.38 ± 1.79 (SD). The maximum number of perimeter trees was 12 and minimum number of trees required to complete the canopy around a gap was 4. In general, larger canopy gaps were bordered by a higher number of canopy trees relative to smaller gaps.

The number of saplings and trees were documented for each expanded gap area to investigate disturbance related changes in density within the gap microenvironment. Average sapling density in expanded gaps was 54.48 ± 28.47 (SD) with a maximum density of 144 and a minimum density of 13 (Figure 5.5). The average number of trees in expanded gaps was 22.73 ± 7.99 (SD) with a maximum of 44 and minimum of 11. The average number of all stems $\geq$ 1 m height in expanded gaps was 74.20 ± 34.14 (SD). The highest stem density in an expanded gap was 188 and the lowest was 28 individuals. The highest density values for saplings and trees occurred in the same gap that was 10 years old and originated from a windthrow event.

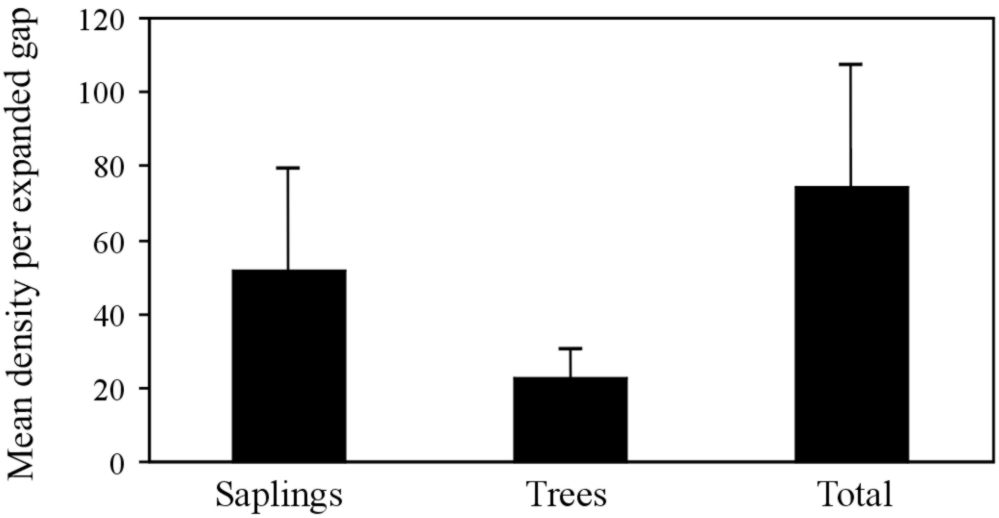


Figure 5.5 Mean number of saplings (≥ 1 m height, < 5 cm dbh), trees (≥ 5 cm dbh), and total stems (all stems ≥ 1 m height) with standard deviations in expanded canopy gaps in the Pogue Creek Natural Area in Tennessee.

The sum of all saplings in all expanded gaps was calculated by species and standardized at the hectare level to document sapling establishment and possible species recruitment in gap environments. The most abundant species in the sapling layer of expanded gaps was *Acer saccharum* (relative density (RDEN) = 35.70%) followed by *Fagus grandifolia* (RDEN = 19.62%) and0 *Acer rubrum* (RDEN = 13.55%) (Table 5.1). Together these three species comprised almost 69% of all saplings in expanded gaps.

Density and dominance measures were calculated for all trees located in true gap environments (standardized to 0.2 ha) to analyze recruitment patterns and possible replacement tree species. *Acer saccharum* represented 29.18% of all trees in true canopy gaps followed by *A. rubrum* (RDEN = 14.16%) and *Liriodendron tulipifera* (RDEN = 9.09%) (Table 5.2). Collectively these three species represent over half of all trees in true canopy gaps. Dominance (based on basal area) was also calculated for all canopy gap trees. The most dominant species were *A. saccharum* (relative dominance (RDOM) = 24.34%) and *A. rubrum* (RDOM = 13.15%) (Table 5.2). The *Acer* species were followed by a second tier of species that included *L. tulipifera* (RDOM = 9.37%) and *Carya ovata* (RDOM = 8.68%). No other species represented more than 6% of the basal area. Species and diameter of all snags in true light gaps was also recorded. A total of 40 snags were documented and mean snag diameter at breast height was 10.89 cm ± 6.21 (SD). Of the 40 snags within true gaps, 12 different species were represented with *A. rubrum*, *A. saccharum*, and *Q. montana* being the most common (*n* = 8 for all species).

Diversity measures were calculated for all saplings, trees, and total woody stems $\geq$ 1 m height in expanded gaps to document biodiversity patterns associated with gap sites. Expanded canopy gaps contained 34 different species in the sapling layer. Mean

Table 5.1 Density of saplings (≥ 1 m height, < 5 cm dbh) in expanded canopy gaps in the Pogue Creek Natural Area in Tennessee.

Species	**Density/ ha**	**Relative density**
Acer saccharum	863.63	35.70
Fagus grandifolia	474.70	19.62
Acer rubrum	327.83	13.55
Asimina triloba	168.03	6.95
Magnolia acuminata	158.63	6.56
Fraxinus americana	88.13	3.64
Liriodendron tulipifera	49.35	2.04
Oxydendrum arboreum	48.18	1.99
Cornus florida	37.60	1.55
Ulmus rubra	31.73	1.31
Nyssa sylvatica	30.55	1.26
Cercis canadensis	29.38	1.21
Tilia heterophylla	12.93	0.53
Aesculus flava	11.75	0.49
Carpinus caroliniana	8.23	0.34
Ilex opaca	8.23	0.34
Magnolia tripetala	8.23	0.34
Quercus montana	8.23	0.34
Carya ovata	5.88	0.24
Ostrya virginiana	5.88	0.24
Sassafras albidum	5.88	0.24
Ailanthus altissima	4.70	0.19
Betula lenta	4.70	0.19
Diospyros virginiana	4.70	0.19
Quercus alba	4.70	0.19
Ulmus alata	3.53	0.15
Amelanchier laevis	2.35	0.10
Carya tomentosa	2.35	0.10
Quercus rubra	2.35	0.10
Ulmus americana	2.35	0.10
Hamamelis virginiana	1.18	0.05
Magnolia macrophylla	1.18	0.05
Morus rubra	1.18	0.05
Quercus velutina	1.18	0.05
Total	**2419.33**	**100.00**

Table 5.2 Density and dominance measures for all trees (stems ≥ 5 cm dbh) in true canopy gaps in the Pogue Creek Natural Area in Tennessee.

Species	**Density/ 0.2 ha**	**Relative density**	**Dominance (m^2/0.2 ha)**	**Relative dominance**
Acer saccharum	161.46	29.18	0.12	24.34
Acer rubrum	78.39	14.16	0.06	13.15
Liriodendron tulipifera	50.31	9.09	0.05	9.37
Carya ovata	29.25	5.29	0.04	8.68
Oxydendrum arboreum	29.25	5.29	0.03	5.91
Fagus grandifolia	35.10	6.34	0.03	5.48
Tilia heterophylla	24.57	4.44	0.02	4.15
Carya tomentosa	16.38	2.96	0.02	3.58
Carya glabra	12.87	2.33	0.02	3.38
Nyssa sylvatica	19.89	3.59	0.02	3.25
Fraxinus americana	14.04	2.54	0.01	2.95
Quercus alba	1.17	0.21	0.01	2.85
Cornus florida	22.23	4.02	0.01	2.59
Quercus montana	8.19	1.48	0.01	1.94
Magnolia acuminata	10.53	1.90	0.01	1.44
Quercus rubra	4.68	0.85	0.01	1.40
Ulmus rubra	8.19	1.48	0.01	1.16
Cercis canadensis	7.02	1.27	0.00	0.89
Carya cordiformis	3.51	0.63	0.00	0.67
Ostrya virginiana	4.68	0.85	0.00	0.66
Diospyros virginiana	2.34	0.42	0.00	0.51
Sassafras albidum	2.34	0.42	0.00	0.49
Prunus serotina	1.17	0.21	0.00	0.31
Aesculus flava	1.17	0.21	0.00	0.25
Ulmus alata	1.17	0.21	0.00	0.21
Betula lenta	1.17	0.21	0.00	0.17
Magnolia tripetala	1.17	0.21	0.00	0.13
Ulmus americana	1.17	0.21	0.00	0.10
Total	**553.41**	**100.00**	**0.48**	**100.00**

sapling diversity (*H'*) was 1.43 ± 0.42 (SD) (Figure 5.6). Maximum sapling layer diversity was 2.22 and the minimum was 0.78. Total species richness of the tree layer was 28. Average diversity of all trees in expanded gaps was 1.90 ± 0.35 (SD) with maximum and minimum values of 2.44 and 1.20 respectively. Mean total diversity of all stems $\geq$ 1 m height was 1.95 ± 0.36 (SD). The highest total diversity value was 2.46 and the lowest was 1.17. Interestingly, diversity patterns differed by category (*i.e.* sapling, tree, and total). For example, the gap with the lowest sapling diversity was not the same gap with the lowest tree diversity. However, the gap with the highest sapling and highest total woody stem diversity values, provided an exception to this pattern.

Significant positive relationships were found for the density of saplings ($r = 0.54$, $P = 0.0003$), trees ($r = 0.73$, $P < 0.0001$), and total stems ($r = 0.62$, $P < 0.0001$) (Figure 5.7). This result is not surprising because a larger sample area should result in the documentation of a higher number of individuals. However, the largest gap did not contain the highest stem density, which occurred in a gap of an intermediate size class (188 individuals/231.97 m^2).

A weak negative relationship existed between sapling diversity and gap size ($r = -0.33$, $P = 0.04$) (Figure 5.8). A similar pattern was also observed for total stem diversity ($r = -0.39$, $P = 0.01$). Tree diversity showed no relationship to expanded gap size. Shannon diversity (*H'*) is a dimensionless index such that gap size would not bias the diversity measure.

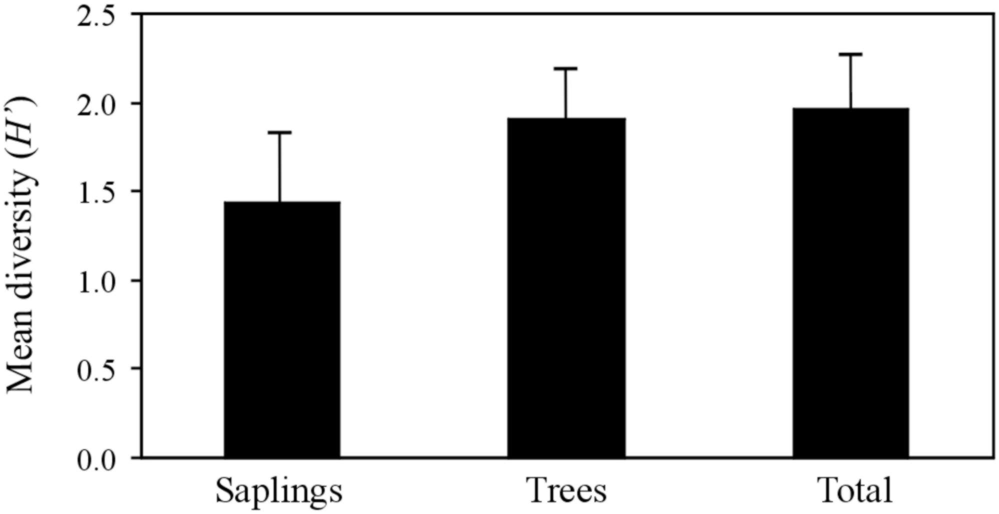


Figure 5.6 Mean diversity for saplings (≥ 1 m height, < 5 cm dbh), trees (≥ 5 cm dbh), and total stems (all stems ≥ 1 m height) with standard deviation in expanded canopy gaps in the Pogue Creek Natural Area in Tennessee.

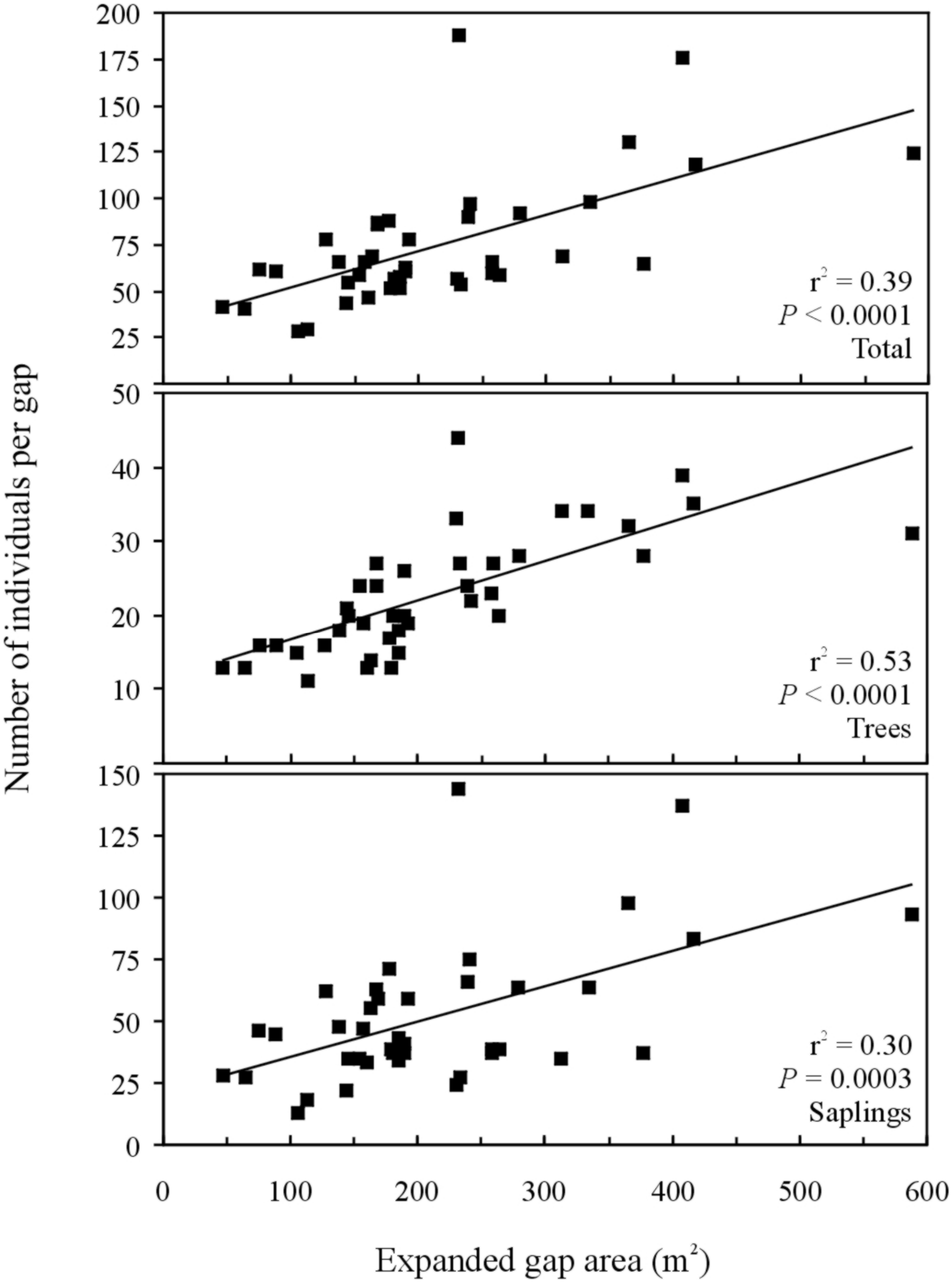


Figure 5.7 Relationships between the number of saplings (≥ 1 m height, < 5 cm dbh), trees (≥ 5 cm dbh), and total stems (all stems ≥ 1 m height) and expanded gap area in the Pogue Creek Natural Area in Tennessee.

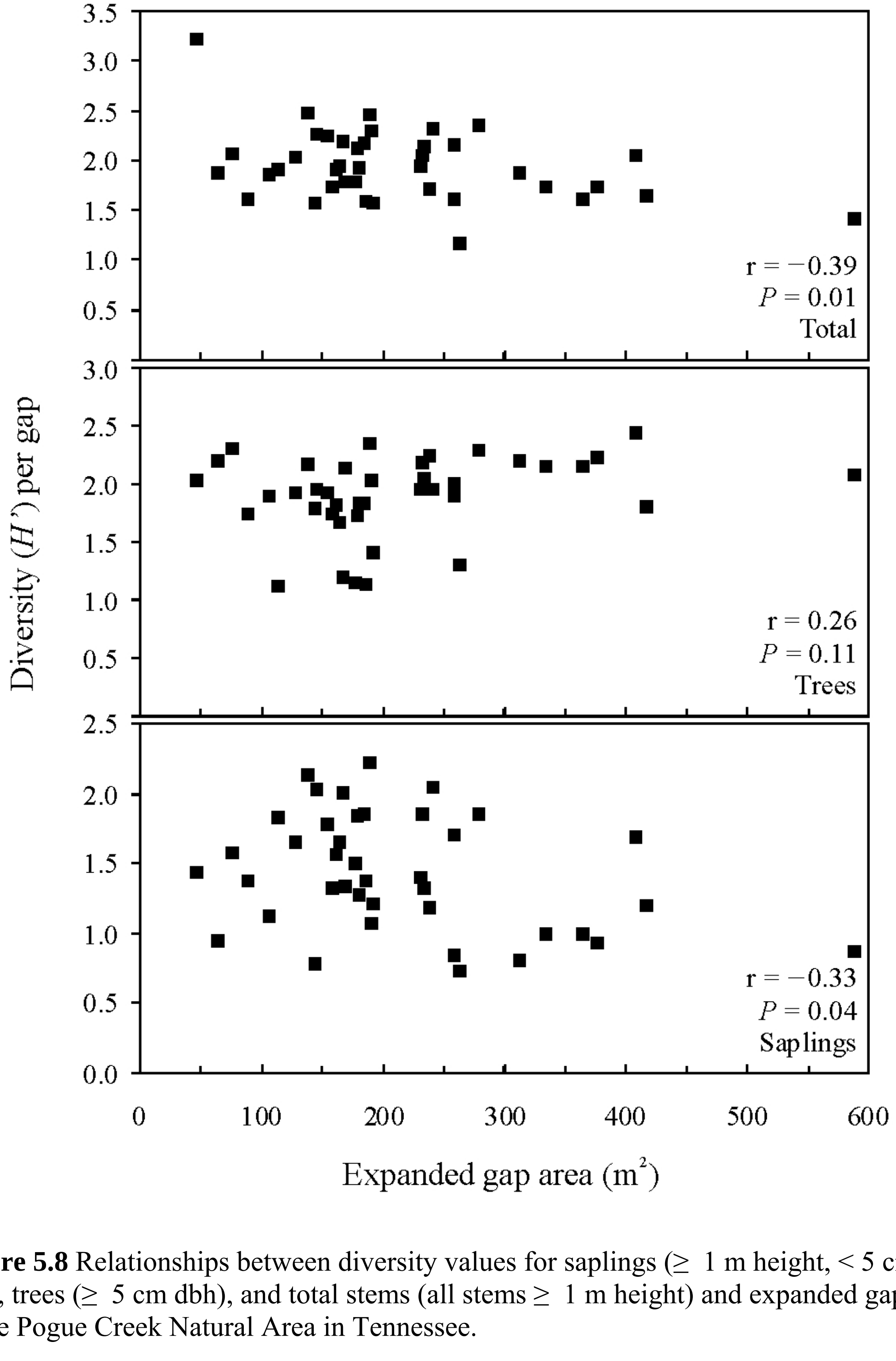


Figure 5.8 Relationships between diversity values for saplings (≥ 1 m height, < 5 cm dbh), trees (≥ 5 cm dbh), and total stems (all stems ≥ 1 m height) and expanded gap area in the Pogue Creek Natural Area in Tennessee.

5.3.7 Gap Closure and Recruitment

The probable closure mechanism, either by height growth or lateral crown expansion, of each gap was recorded in the field. Of the 40 gaps studied, 10 would likely close by height growth of understory individuals and the remaining 30 gaps would likely close by lateral branch growth of canopy trees surrounding the voids. Mean expanded area of gaps likely to close via the height growth of understory trees was 285.13 m^2 ± 137.58 (SD), which was *ca*. 34% greater than mean expanded area for all 40 gaps (213.34 m^2). The gap with the largest expanded area (587.91 m^2) was projected to close by understory height growth. However, a relatively small gap (153.59 m^2) was also projected to close by height growth of a subcanopy individual.

Probable gap successors (individuals that will likely fill the canopy void) can often be determined in the field (Barden 1979; Barden 1980; White *et al*. 1985; Yamamoto and Nishimura 1999). Of the 10 successor trees documented, five species were represented (*A. saccharum*, *A. rubrum*, *C. ovata*, *Q. montana*, and *Quercus alba*). *Acer rubrum* was the most common gap successor (*n* = 3) followed by *A. saccharum* (*n* = 2), *C. ovata* (*n* = 2), *Q. montana* (*n* = 2), and *Q. alba* (*n* = 1). No clear species-specific patterns were observed with gap successors, indicating that the location of an individual within the gap and its vertical crown position prior to the disturbance may be the most important factors that determine how the gap is closed and by what species. As further evidence of this point, radial growth response of understory individuals has been shown to be related to position within a canopy gap (Tryon *et al*. 1992).

Crown class distributions were constructed for all trees located in true gap environments for the 15 most dominant species with canopy potential to investigate recruitment in gaps. Species that are well represented in intermediate crown positions are more likely to fill canopy gaps when they occur. *Acer saccharum* represented 28.7% of trees with intermediate positions of all 15 selected species within true gap environments (Table 5.3). *Acer saccharum* was followed by *A. rubrum* (13.45%) and *L. tulipifera* (13.45%), a noted gap-phase species (Buckner and McCracken 1978; Orwig and Abrams 1994b). Collectively, these three species represented 55.6% of the intermediate trees from the 15 selected species. A similar pattern was observed for overtopped positions with *A. saccharum* being the most abundant (36.36%) followed by *A. rubrum* (18.69%) and *F. grandifolia* (10.61%).

5.4 Discussion

5.4.1 Gap Formation Patterns

Of the 40 gaps sampled, 32 (80%) originated from windthrow or basal-shear mechanisms. Other studies have also found treefall gaps to be the most common means of gap formation in the southern Appalachians (Barden 1979; Barden 1981; Romme and Martin 1982; Runkle 1982). Because windthrow and basal-shear were the most common means by which canopy trees were removed, I speculate that high wind events are the dominant disturbance agents in the forest as strong winds have the potential to uproot trees and snap boles. Wind also has the potential to alter forest composition and structure by blowing down snag trees. Standing dead trees are often felled by mild to severe wind events, but the potential for snags to be felled varies by site conditions (Jans *et al.* 1993). Further, snags that eventually fall likely alter the forest differently than gaps that are caused rapidly (Franklin *et al.* 1987; Krasny and Whitmore 1992; Clinton *et al.* 1994).

Table 5.3 Crown class distributions for all trees (stems ≥ 5 cm dbh) in 40 true canopy gaps in the Pogue Creek Natural Area in Tennessee.

	Overtopped		**Intermediate**	
Species	**Density**	**Relative density**	**Density**	**Relative density**
Acer saccharum	72	36.36	64	28.70
Acer rubrum	37	18.69	30	13.45
Liriodendron tulipifera	13	6.57	30	13.45
Carya ovata	4	2.02	21	9.42
Tilia heterophylla	11	5.56	10	4.48
Oxydendrum arboreum	16	8.08	9	4.04
Fraxinus americana	3	1.52	9	4.04
Carya glabra	1	0.51	9	4.04
Fagus grandifolia	21	10.61	8	3.59
Carya tomentosa	5	2.53	8	3.59
Quercus alba	1	0.51	8	3.59
Quercus montana	1	0.51	6	2.69
Nyssa sylvatica	12	6.06	5	2.24
Quercus rubra	0	0.00	4	1.79
Carya cordiformis	1	0.51	2	0.90
Total	**198**	**100.00**	**223**	**100.00**

Most (78%) of all documented canopy gaps were caused by single tree events. The percentage of single tree gaps is within the range of what has been reported from old growth forests of the eastern U.S. (Romme and Martin 1982; Yamamoto 1989; Runkle 1990). Of the multi-tree disturbance events, windthrow was the most common origin. Windthrow gaps have the potential to cause more site modification than gaps caused by other mechanisms because as the root network is lifted, microtopography (pits and mounds) and soil characteristics are also modified (Clinton *et al*. 1994; Beckage *et al*. 2000).

Although *Q. montana* was the most common species involved in gap formation, no species-specific patterns of mortality were observed in the forest. However, at the genus level, half of all canopy gaps in the reserve resulted from the death of a *Quercus* individual. The next most common genus involved in gap formation was *Acer* representing 12.5% of all gap makers.

Average diameter of gap maker trees was 38.38 cm at breast height. The average diameter of canopy trees (dominant and codominant crown classes) that surrounded gaps was 38.83 cm ± 6.04 (SD). Thus, the average sizes of gap maker trees and canopy trees were almost exactly the same. This result is contrary to what has been reported for old growth forests of the southern Appalachians where gap makers were significantly larger than border trees (Runkle 1998). This pattern may be related to the age of the forest. In second growth forests, canopy trees are within a narrower diameter range as their age (and diameter) structure is not complex. Thus, in mature second growth forests, size does not indicate that one individual is more likely to be removed from the canopy than another. Also, the smallest gap maker was just 19.5 cm dbh, but was a component of a multi-tree gap with another individual of 28 cm. Although both of these individuals were below the average size for gap makers, the removal was enough to open the canopy and modify the forest. This indicates that the death of a small cluster of relatively small trees can still influence forest composition and structural patterns.

Average basal area lost per gap event was 0.16 m^2. If the amount of biomass the forest can support has reached a state of dynamic equilibrium, this amount of basal area must be recovered from residual individuals and new germinants. Although gaps can be formed by the removal of a cluster of relatively small trees, multi-tree gaps did result in a significantly higher amount of basal area lost compared to single tree events.

Gap ages ranged from 1 to 17 years with an average of 7 years. However, only one gap was older than 13 years of age. No gaps of 5 or 6 years were documented. This two-year gap-free period may have been a result of chance with the random sampling design or it may be an indication of a period with a lower number of disturbance events. Gap seasonality was determined for 17 events. Of these 17 disturbances, all but one occurred during the growing season. Most growing season deaths occurred after the formation of earlywood cells but before the completion of latewood cells. I interpret the amount of xylem produced during the last year of growth to indicate that the majority of the canopy disturbance events occurred during the middle or later part of the growing season. The timing of death combined with the primary origins of formation (windthrow and basal-shear) indicated high wind events associated with convection storms may be the major agents that disrupt the forest. Severe wind events in the region are associated with thunderstorms that occur *ca*. 50 days per year, usually during late-spring and summer (Smalley 1982).

5.4.2 Physical Gap Characteristics

The fraction of land area in expanded gaps and true gaps was 15% and 6% respectively. These values are both within the range of what has been reported elsewhere in the Eastern Deciduous Forest Region (Runkle 1982; Beckage *et al*. 2000). The fraction of land area in gaps was highest for younger gaps and generally decreased with increased gap age. This pattern was expected because older gaps have had a longer time to be filled. No gaps were documented over 17 years of age. From this, I propose that most gaps in the forest are filled within 20 years of formation, but many are likely filled within shorter periods.

Average expanded gap area was 213.34 m^2 and average true gap area was 47.10 m^2. Expanded area of gaps caused by windthrow events was significantly larger than expanded area of gaps caused by snags. No significant differences in gap area were documented for true canopy gaps among the different origins.

Although L:W ratios do not provide detailed information about gap perimeters, they do provide information on the general shape of the gap. This information combined with gap orientation is useful to understand microenvironments within canopy gaps. In general, L:W patterns were similar for expanded and true gaps. The minimum values for expanded and true gaps were circular rather than ellipsoidal. Circular gap shapes resulted from gaps caused by standing dead trees. Trees that remained standing after their death did not fall and cause the removal of vegetation in a linear pattern starting at the base of the tree as is normal for treefall disturbances. Mean and maximum length relative to width was greater for true gaps compared to expanded gaps. Ellipsoidal shapes were evident for both gap classifications. The majority (55%) of the gaps were oriented downslope from the base of the tree, while 40% were oriented across slope and 5% of the trees fell up slope. Thus, most canopy disturbances resulted in ellipsoidal shaped gaps that were oriented perpendicular to slope contours.

5.4.3 Forest Response to Gaps

The mean number of canopy trees bordering gaps was six. Larger gaps were generally bordered by a higher number of perimeter trees. Trees that border the opening in the canopy have the greatest potential to fill the void space by crown expansion. Perimeter individuals are at a competitive advantage in smaller gaps that are more likely to close via lateral branch growth rather than understory height growth.

Significant positive relationships were documented between expanded gap size and the density of saplings, trees, and total stems. This result was expected because larger areas should contain more individuals. Interestingly, the largest gap did not support the highest number of stems, which occurred in an intermediate sized gap. The density measures analyzed were for expanded gap areas. Individuals in the entire area of an expanded gap do not benefit from increased resources such as light. Because the true gap area gets smaller with time since the disturbance, gap age may play an important role in the number of individuals that inhabit a gap site (Runkle 1982; Clinton *et al*. 1994).

In expanded gaps, species richness of the sapling layer was 34 and mean sapling layer diversity was 1.43. The tree layer of expanded gaps had slightly lower species richness, with 28 species, but had higher mean diversity at 1.95. I hypothesized that larger gaps would support higher diversity values. By containing more surface area, larger gaps have the potential to contain more site heterogeneity and microsites that may favor certain species over others. However, only weak relationships existed between diversity and gap size and two of the relationships (saplings and total stems) were negative. Perhaps gap size is not as important to diversity as the physical site characteristics of the gap or the biotic assemblage of the gap prior to formation. Although canopy gaps should increase biological diversity, this pattern does not necessarily occur at the gap-level but at the stand level where a collection of different sized and aged canopy gaps across a variety of sites may support species that are otherwise absent or sparse under the closed forest canopy.

Species composition of gaps is a good predictor of future forest composition (Runkle and Yetter 1987). Three species (*A. saccharum*, *F. grandifolia*, and *A. rubrum*) represented almost 70% of all saplings in expanded gaps. Because saplings represent the pool of individuals that may be recruited to larger size classes following disturbance events, I hypothesize *Acer* species and *F. grandifolia* will become more abundant in intermediate and eventually canopy positions under the current disturbance regime. There is a greater likelihood that individuals of these species will be able to exploit current and future gap events because they are so abundant in the sapling layer.

Although saplings in expanded gaps have the potential to recruit to larger size classes, trees located in true gap environments have the potential to reach canopy positions after overstory removal (Cole and Lorimer 2005; Webster and Lorimer 2005). *Acer saccharum* and *A. rubrum* represented 43% of all trees in true gap environments. *Liriodendron tulipifera* followed the *Acer* species and represented 9% of gap trees. Collectively, these species represented over half of all trees in gaps. These three species were also the most dominant in true gaps based on relative dominance values.

I projected that the majority of the canopy gaps would close by lateral crown expansion rather than height growth of understory individuals. However, even gaps that close by lateral branch growth still provide a means for understory trees to recruit to larger size classes. This process may allow overtopped trees to reach intermediate positions and eventually the canopy following future disturbance events. Trees already in intermediate positions may expand their crowns to become dominant or codominant in the canopy. Over half of all trees located in true gaps with intermediate crown classifications were *A. saccharum*, *A. rubrum*, or *L. tulipifera*.

Acer species and *L. tulipifera* have the greatest potential to recruit in gaps based on density, dominance, and crown class measures. It is interesting that species with such different life history characteristics were well represented in canopy gaps and employ different strategies to reach canopy level. *Acer saccharum* is very shade-tolerant and has the ability to persist in the understory of a closed canopy while maintaining the ability to rapidly respond to increased light (Canham 1988b; Tryon *et al*. 1992). *Acer rubrum* is classed as moderately shade-tolerant and can exist in the understory of a relatively closed canopy until the formation of gaps when the species has also been shown to quickly respond to increased resources (Wallace and Dunn 1980). In general, the life history characteristics of the *Acer* species may be classed as conservative. Both *A. saccharum* and *A. rubrum* can establish in at least relatively shaded conditions and wait for the formation of small canopy gaps to recruit to larger size classes and higher canopy positions. In contrast to the *Acer* species, *L. tulipifera* is disturbance obligate. The species is shade-intolerant and cannot exist under a closed forest canopy. However, *L. tulipifera* is capable of quickly responding to increased resources when they become available and is a common component in forests with disturbance regimes that consist of small localized events (Buckner and McCracken 1978; Wallace and Dunn 1980; Orwig and Abrams 1994b; Busing 1995; Lafon 2004).

Shade-intolerant species, such as *L. tulipifera*, must reach the canopy in one gap event because once the gap closes they will not be able to survive under the canopy (Hibbs 1982; Runkle and Yetter 1987; Cole and Lorimer 2005; Webster and Lorimer 2005). Thus, in forests with a disturbance regime characterized by small localized events, there are few opportunities for shade-intolerant species to exist (Runkle 1998). Shade-tolerant species are more likely to be present in a gap when they form, thus, they are generally more likely to recruit or reach the canopy in small gaps (Henry and Swan 1974; Dahir and Lorimer 1996; McClure *et al*. 2000; Taylor and Lorimer 2003). Gaps of a larger size, however, may allow time for germinants to establish and recruit. Because of its rapid growth, *L. tulipifera* can reach the canopy in gaps of 400 m^2 and larger. Although gaps of that size were documented in this study, I do not think *L. tulipifera* will reach the canopy at any of the gap sites before closure. The majority of the gaps documented will close by lateral branch growth before allowing understory individuals to reach the canopy. Although individuals are recruited to larger size classes and higher vertical positions in these gaps, it will take multiple disturbance events for most subcanopy individuals to reach canopy level. Because it will generally take multiple events for individuals to be recruited to the canopy, shade-tolerant *A. saccharum* and moderately-tolerant *A. rubrum* are the species most likely to attain canopy dominance under the current disturbance regime. Interestingly, half of the canopy gaps were caused by the removal of a *Quercus* individual, but *Acer* species represented a large proportion of trees likely to either reach the canopy or recruit to larger size classes. These data indicate a likely shift in composition if gap processes continue to remove *Quercus* from the canopy and provide the means for *Acer* recruitment.

Canopy gaps obviously have an important influence on forest composition and structure. However, little information is available on natural gap-scale disturbances in secondary hardwood forests. By analyzing gap formation mechanisms, physical gap characteristics, and forest response to canopy gaps, we can gain a better understanding of the role of gap-scale disturbance processes in the development of hardwood forests. This study showed that disturbances that involved the death of a single tree or a small cluster of trees were common events throughout the secondary forest on the Cumberland Plateau. These localized disturbances modified biomass arrangement and tree-age distribution patterns as they allowed for crown expansion of canopy trees, recruitment of understory individuals, and in some instances establishment of new germinants. Thus, canopy gaps provide the mechanism for forests to develop a complex size and age structure indicative of older stands. Gap-scale processes may also be used to help explain shifting species composition that has been widely reported throughout the Eastern Deciduous Forest Region. Half of the canopy gaps documented in this study were caused by the removal of a *Quercus* individual, but *A. saccharum*, *A. rubrum*, and *L. tulipifera* were the most likely species to capture canopy gaps. The gaps documented favored the very shade-tolerant *A. saccharum* because most gaps were small and multiple overstory removal events would be required for trees to reach the main canopy level. In conclusion, this study demonstrated that natural disturbance processes have significant influences on forest development and successional patterns. Thus, disturbance events must be considered when developing long-term forest management plans.

Chapter 6

Conclusions and Future Research

The overall purpose of this study was to quantify forest disturbance processes and evaluate the influence of these processes on secondary hardwood forest communities on the Cumberland Plateau. Little research has been conducted to investigate the role of natural disturbance events on species composition and stand structure in forests that have not reached a compositional equilibrium and complex structure. Also, there is a lack of quantitative information on forest communities of the Cumberland Plateau. Thus, this research fills a void in our knowledge of disturbance processes and successional patterns and provides information for a region that has been relatively understudied. This chapter summarizes the major findings and makes recommendations for future research.

6.1 Forest Composition, Stand Structure, and Dendroecology

1. The mid-slope forests of the Pogue Creek Natural Area supported high species richness and were dominated by mixed Quercus *and* Carya *species.*

Total woody species richness in the reserve was 30 and diversity (*H'*) was 2.57 for the tree layer, 0.99 for the sapling layer, and 1.77 for the seedling layer. The forest was dominated by *Carya ovata*, *Quercus rubra*, *Quercus alba*, and *Quercus montana*. *Acer saccharum*, *C. ovata*, and *Acer rubrum* had the highest density values. The sapling layer was rather sparse and only contained five species: *A. saccharum*, *Asimina triloba*, *Q. montana*, *Fagus grandifolia*, and *Nyssa sylvatica*. Species richness in the seedling layer was 12 and the most abundant species were *A. rubrum* and *A. saccharum*. These two species represented almost 70% of all seedlings.

2. The forest established in the 1920s and had a diameter structure indicative of regenerating stands.

The majority of the canopy trees established in the 1920s after the last anthropogenic clearing of the forest. The diameter structure of the stand revealed a reverse J-shaped distribution, typical of regenerating forest. Age structure analyses showed that *C. ovata* and *Carya tomentosa* exhibited bell-shaped curves with peaks in the 1930s and 1940s respectively and neither has established since the 1970s. *Quercus rubra* and *Q. alba* had similar age structures with the majority of individuals establishing between 1930 and 1950. Establishment of *Q. montana* was highest between 1940 and 1960. In the 1940s, *A. rubrum* establishment peaked and then gradually declined while *A. saccharum* establishment began in the 1950s and peaked during the 1970s. The age structure of *Fagus grandifolia* was uniform with establishment in all but the three most recent decades.

3. Correlations between radial growth of **Quercus** *species and climate variables indicated forest productivity was driven by disturbance processes rather than large-scale climate patterns.*

Statistically significant relationships were documented between the standardized *Quercus* tree-ring chronology and precipitation of the previous late summer and early fall. However, both relationships were weak, indicating the forest was not responsive to regional-scale climate conditions. Variations in radial growth patterns have likely been influenced more by forest disturbance events. In closed canopy forests, the effects of competition for resources (mainly light) outweigh climatic variation. Thus, radial growth patterns of trees in the PCNA likely resulted from increased light caused by canopy disturbances rather than broad-scale climatic conditions.

4. The disturbance regime was characterized by localized, asynchronous events that occurred at variable temporal and spatial scales.

A total of 64 *Quercus* tree-ring series were analyzed for release episodes. In these series, 90 release events were detected from 54 individuals. The majority of the release events were classified as minor releases. The longest sustained release was 9 years and the average release duration was 4.2 years. With the exception of one stand-wide release episode in the early 1980s, the disturbance regime was characterized by asynchronous events that occurred at variable spatial and temporal scales. Small-scale disturbances became abundant after *ca*. 40 years of forest development.

5. As the forest continues to develop, species composition and stand structure are projected to change.

The forest canopy was dominated by mixed *Quercus* and *Carya* species, while *A. saccharum*, *A. rubrum*, and *F. grandifolia* had high densities in the understory. Under the current disturbance regime, the successional trajectory of the forest is projected to shift from a *Quercus–Carya* dominated system to one with a much stronger *Acer–Fagus* component. Stand structure is also projected to shift from a high density of small trees to a lower density of larger trees at wider spacings.

6.2 Fire History from Soil Charcoal

1. Soil charcoal evidence indicates that fires have occurred in the reserve.

This study was the first to quantify the dry mass of macroscopic charcoal from soil in mixed hardwood forests on the Cumberland Plateau. Charcoal was recovered from all 10 soil cores and was documented at all depths sampled, but not all depths in each core. The presence of macroscopic charcoal indicated the forest has burned in the past. No fire-scarred trees or logs were documented and the species composition of the reserve indicated that fires have not occurred during the development of the current stand.

2. Fire events varied through space and time, but charcoal mass was greatest nearer the surface, indicating that fires were more frequent in the recent past.

Charcoal accumulation was examined across cores and by depth to analyze spatio-temporal patterns of historic fires. When analyzed by depth, charcoal mass was greatest near the surface. This pattern indicated that fires have occurred in the recent past, but before the development of the current stand. Total charcoal mass was spatially variable. The core with the largest amount of charcoal was nearest to cores with relatively small amounts. This pattern indicated that the influence of fires may have been localized as fires were not widespread events throughout the forest. The mesic site conditions would not facilitate the movement of fire in the area. Lightning is generally associated with convection storms and rainfall that may also hinder the spread of fire.

6.3 Gap-Scale Disturbance Processes

1. The majority of canopy gaps were caused by the removal of a single tree of average canopy tree size.

Treefall gaps (caused by windthrow and basal-shear) represented 80% of the canopy gaps sampled. The majority (78%) of gaps were caused by the death of a single tree. *Quercus* species represented 50% of all gap makers. The average diameter of gap maker trees was 38.38 cm at breast height which is the approximate average diameter of canopy trees (38.83 cm). Gap ages ranged from 1 to 17 years with a mean of 7 years. Of the gaps with known seasonality (n = 17), all but one occurred during the growing season after the completion of earlywood cells. Strong wind associated with convection storms is the most probable disturbance agent in the forest.

2. Canopy gaps represented 15% (expanded gaps) and 6% (true gaps) of the study area, average canopy gap size was relatively small, and most gaps had elliptical shapes.

The fraction of land area in expanded gaps and true canopy gaps was 15% and 6%, respectively. The amount of land area in canopy gaps was highest for younger gaps and generally decreased with increased gap age. Average expanded gap area was 213.34 m^2 and average true gap area was 47.10 m^2. Windthrow events resulted in significantly more expanded gap area than gaps caused by snags. No other significant differences were documented between gap origin and gap size. Most expanded and true canopy gaps had elliptical shapes. However, the minimum length to width values for expanded and true gaps were circular rather than ellipsoidal. Circular shapes resulted from gaps caused by standing dead trees rather than treefall. Most (60%) of the canopy gaps were oriented perpendicular to slope contours.

3. Significant positive relationships were documented between stem density and gap size, but no relationships existed between gap size and stem diversity.

Significant positive relationships were documented between expanded gap size and the density of saplings, trees, and total stems. Only weak relationships existed between stem diversity and expanded gap size. I suggest physical site characteristics of the gap and biotic assemblages prior to gap formation are more important to diversity than gap area. Although canopy gaps are known to increase biological diversity, this pattern does not necessarily occur at the gap-level but at the stand level, where a collection of different sized and aged canopy gaps across a variety of sites may support a variety of species adapted to different niches.

4. The majority of the canopy gaps will close by lateral crown expansion, but gaps still allow for the recruitment of individuals to larger size classes.

Most of the canopy gaps documented were projected to close by lateral crown expansion rather than height growth of subcanopy individuals. However, the canopy gaps still provided a means for understory trees to recruit to larger size classes. This process may allow overtopped trees to reach intermediate positions, and eventually the canopy, after future disturbance events. Over half of all trees located in true canopy gaps with intermediate crown classifications were *A. saccharum*, *A. rubrum*, or *Liriodendron tulipifera*. These three species have different life history characteristics, but their abundance in canopy gaps indicated they may all be represented in the future canopy. Because the gaps documented were relatively small and close by lateral branch growth of perimeter trees, the most shade-tolerant *A. saccharum* has the greatest probability of becoming dominant in the canopy under the current disturbance regime. Half of all gap maker trees removed from the canopy were *Quercus*; however, *Acer* species are the most probable replacement trees. These data indicated that gap-scale disturbance processes have an influence on the successional pattern of the forest.

6.4 Recommendations for Future Research

This study demonstrated the importance of localized disturbance processes in the development of a secondary hardwood forest. This work can be used as a base from which to address broader questions concerning gap-scale processes, forest development patterns, and successional pathways. Major areas for future studies include: (1) further analyses on the role of canopy gaps in the development of a complex age and size structure, (2) quantification of gap-scale processes as successional pathways in hardwood forests, and (3) additional fire history information from macroscopic soil charcoal.

Patterns of forest development may be elucidated by comparing forest composition and structural measures of secondary forests to those of old growth remnants. The biomass of the reserve was within the range expected for old growth stands. This indicated that the biomass of the secondary forest had reached a dynamic equilibrium. As trees are removed by disturbance processes, the lost basal area must be recovered by residual trees or new germinants. The small canopy gaps in the secondary forest are mostly filled by lateral crown expansion. This process allows canopy trees along the perimeter of gaps to increase their size. As gaps continue to form and close through time, the spacing between large individuals will increase creating a structure more indicative of forests in a complex stage of development. This study showed that gap processes provide the mechanism for forests to move from a high density of small trees to a lower density of large trees. As the distance between large individuals increases, the size of the canopy gaps formed by their removal should also increase. At some point, the size of the gap will likely cross a threshold (varying by site) where gaps can no longer close by lateral branch growth, thus providing an opportunity for the establishment of new germinants and recruitment of saplings in the understory at the time of the disturbance. This process will create an uneven-aged and complex forest structure. Future research could quantify these processes in forests of various ages. A chrono-sequence study would reveal more detailed information on the role of localized disturbance events through the development of a stand.

Most successional theories state that in the absence of major disturbance, community composition will reach a dynamic steady-state based on regional climate and edaphic conditions. Changing resource availability during succession influences the successional trajectory or pathway of the community as species are adapted to a variety of site conditions that change after disturbance events. Localized disturbances may preferentially favor one species over another providing a competitive advantage. The canopy gaps documented in this study were relatively small and favored shade-tolerant species, such as *A. saccharum*, that have the ability to exist in shaded conditions because multiple gap events will be required for most individuals to reach the canopy.

The replacement of *Quercus* by *Acer* species has been widely reported throughout the Eastern Deciduous Forest Region. This study indicated that canopy gaps remove *Quercus* from the canopy (half of all gap makers were *Quercus*) and provide a mechanism for *Acer* recruitment. Thus, gap-scale processes may be used to explain the pattern of shifting species composition. To further analyze this pattern, researchers could quantify species-specific responses to small canopy disturbances by studying bud scars and node lengths or radial growth patterns across a number of species. Repeat sampling of canopy gaps or experiments in permanent plots could be used to investigate rates of gap formation and closure in developing hardwood stands. The seasonal timing of canopy gap events may also influence the forest response. To analyze species responses to gaps formed during different seasons, artificial gaps could be created by the mechanical removal of canopy trees at different times of the year. This information may help relate disturbance processes to successional patterns.

Additional work needs to be conducted to document the historic fire regime of hardwood stands in the southern Appalachian Highlands. Quantitative information on the fire history of mesic hardwood stands is needed for the proper classification of many forests and to manage forests according to their historic conditions. Because disturbance histories are site dependent, future studies should be conducted in areas of interest. Soil charcoal documented in this study indicated that fire has occurred in the reserve. However, the timing of the fire events has not been documented. Samples recovered from this study have been sent for radiocarbon dates and this information will provide a more detailed fire history of the site. The documentation of macroscopic soil charcoal is currently one of the only reliable techniques to document the fire history of hardwood stands that have developed since the last fire event. Prescribed fire programs are being implemented in many eastern hardwood forests to in efforts to maintain *Quercus* dominance; however, if fire is not a common component to these ecosystems, a transition to more mesic and fire-intolerant species is likely a “natural” and inevitable process. To understand these patterns on a larger spatial scale, studies could use similar techniques to document macroscopic charcoal in soils from hardwood forests throughout the eastern U.S.

In conclusion, this study showed that canopy gaps became important drivers of forest change after *ca*. 40 years of stand development. The forest canopy was dominated by mixed *Quercus* and *Carya* species, while *Acer* species had especially high densities in the understory. Half of the canopy gaps were formed by the death of a *Quercus* individual, but *A. saccharum*, *A. rubrum*, and *L. tulipifera* were in the best positions to capture canopy gaps. Because most gaps were small, multiple overstory removal events would be required for most understory trees to reach the main canopy stratum. This process favors the very shade-tolerant *A. saccharum*. The pattern of increased *Acer* importance and lack of *Quercus* regeneration has been reported throughout the Eastern Deciduous Forest Region. For this reason, prescribed fire has been proposed and is being used, with varying degrees of success, to maintain *Quercus* dominance and decrease competition from more mesic species. Soil charcoal indicated that the forest had burned in the past, but species composition and a lack of fire-scarred trees indicated fire has not occurred during the development of the current stand. If fire is proven to be an important historic disturbance event in the reserve, then it may provide the justification for prescribed fire to mimic the historic disturbance regime. Additional studies are needed to further investigate these disturbance processes and their influence on forest vegetation patterns in the region.

REFERENCES

Abrams, M.D. and J.A. Downs. 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. *Canadian Journal of Forest Research* 20: 1864–1870.

Abrams, M.D. and M.E. Kubiske. 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade-tolerance rank. *Forest Ecology and Management* 31: 245–253.

Abrams, M.D. and G.J. Nowacki. 1992. Historical variation in fire, oak recruitment, and post-logging accelerates succession in central Pennsylvania. *Journal of the Torrey Botanical Society* 119: 19–28.

Abrams, M.D. 1992. Fire and the development of oak forests. *BioScience* 42: 346–353.

Abrams, M.D., D.A. Orwig, and T.E. Demeo. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white-pine-mixed-oak forest in the southern Appalachians, USA. *Journal of Ecology* 83: 123–133.

Abrams, M.D. 2003. Where has all the white oak gone? *BioScience* 53: 927–393.

Adams, M.B., J.A. Burger, A.B. Jenkins, and L. Zelany. 2000. Impact of harvesting and atmospheric pollution on nutrient depletion of eastern U.S. hardwood forests. *Forest Ecology and Management* 138: 301–319.

Albrecht, M.A. and B.C. McCarthy. 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. *Forest Ecology and Management* 226: 88–103.

Alliance for the Cumberlands. 2006. The Cumberland Plateau Heritage Corridor: feasibility study and assessment of impacts for National Heritage Corridor designation. http://www.tdec.net/recreation/cumberlandplateau.pdf

Alligood, L. 2005. If Cumberland Plateau is state's next "big thing," region wants to be ready. *The Tennesseean*. 29 October 2005.

Anderson, J.M. and M.J. Swift. 1983. Decomposition in tropical forests, pp. 287–309. *In* S.L. Sutton, T.C. Whitmore, and A.C. Chadwick (Eds), *The Tropical Rain Forest: Ecology and Management*. Blackwell Scientific: U.K.

Baker, H.L. 1925. The forests of Lee County, Virginia, pp. 179–207. *In* A.W. Giles (Ed.), *The geology and coal resources of the coal bearing portion of Lee County, Virginia*. Virginia Geological Survey Bulletin Number 26.

Barbour, M.G., J.H. Burk, W.D. Pitts, F.S. Gilliam, and M.W. Schwartz. 1998. *Terrestrial Plant Ecology*, Third Edition. Benjamin/Cummings Publishing Company: Menlo Park, California.

Barden, L.S. 1979. Tree replacement in small canopy gaps of a *Tsuga canadensis* forest in the southern Appalachians, Tennessee. *Oecologia* 44: 141–142.

Barden, L.S. 1980. Tree replacement in a cove hardwood forest of the southern Appalachians. *Oikos* 35: 16–19.

Barden, L.S. 1981. Forest development in canopy gaps of a diverse hardwood forest of the southern Appalachian Mountains. *Oikos* 37: 205–209.

Barden, L.S. 1983. Size, age, and growth rate of trees in canopy gaps of a cove hardwood forest in the southern Appalachians. *Castanea* 48: 19–23.

Barden, L.S. 1989. Repeatability in forest gap research: studies in the Great Smoky Mountains. *Ecology* 70: 558–559.

Barnes, B.V., D.R. Zak, S.R. Denton, and S.H. Spurr. 1998. *Forest Ecology*, Fourth Edition. John Wiley and Sons: New York.

Bazzaz, F.A. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* 10: 351–371.

Beckage, B., J.S. Clark, B.D. Clinton, and B.L. Haines. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. *Canadian Journal of Forest Research* 30: 1617–1631.

Black, B.A. 2003. A boundary-line approach to establishing dendroecological release criteria. Ph.D. Dissertation, Pennsylvania State University, College Park.

Black, B.A. and M.D. Abrams. 2005. Disturbance history and climate response in an old-growth hemlock-white pine forest, central Pennsylvania. *Journal of the Torrey Botanical Society* 132: 103–114.

Blasing, T.J., D.N. Duvick, and D.C. West. 1981. Dendroclimatic calibration and verification using regionally averaged and single station data. *Tree-Ring Bulletin* 41: 37–43.

Bormann, F.H. and G.E. Likens. 1979. *Pattern and Process in a Forested Ecosystem*. Spring-Verlag Publishing: New York.

Brady, N.C. and R.R Weil. 2002. *The Nature and Properties of Soils*, Thirteenth Edition. Prentice Hall: Upper Saddle River, New Jersey.

Braun, E.L. 1942. Forests of the Cumberland Mountains. *Ecological Monographs* 12: 413–437.

Braun, E.L. 1950. *Eastern Deciduous Forests of North America*. Blakiston: Philadelphia, Pennsylvania.

Brokaw, N.V.L. 1985. Treefalls, regrowth, and community structure in tropical forests, pp. 53–69. *In* S.T.A. Pickett and P.S. White (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press: San Diego, California.

Brose, P.H., D.H. Van Lear, and R. Cooper. 2001. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. *Forest Ecology and Management* 113: 125–141.

Buckner, E. and W. McCracken. 1978. Yellow-poplar: a component of climax forests? *Journal of Forestry* 76: 421–423.

Busing, R.T. 1995. Disturbance and the population dynamics of Liriodendron tulipifera: simulations with a spatial model of forest succession. *Journal of Ecology* 83: 45–53.

Canham, C.D. and P.L. Marks. 1985. The response of woody plants to disturbance: patterns of establishment and growth, pp. 197–216. *In* S.T.A. Pickett and P.S. White (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press: San Diego, California.

Canham, C.D. 1988a. An index for understory light levels in and around canopy gaps. *Ecology* 69: 1634–1638.

Canham, C.D. 1988b. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69: 786–795.

Canham, C.D. 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70: 548–550.

Canham, C.D. 1990. Suppression and release during canopy recruitment of *Fagus grandifolia*. *Bulletin of the Torrey Botanical Club* 117: 1–7.

Canham, C.D. M.J. Papaik, and E.F. Latty. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. *Canadian Journal of Forest Research* 31: 1–10.

Cho, D. and R.E.J. Boerner. 1991. Canopy disturbance patterns and regeneration of *Quercus* species in two old-growth forests. *Vegetatio* 93: 9–18.

Cho, D. and R.E.J. Boerner. 1995. Dendrochronological analysis of the canopy history of two Ohio old-growth forests. *Vegetatio* 120: 173–183.

Christensen, N.L. 1989. Landscape history and ecological change. *Journal of Forest History* 86: 116–124.

Clark J.S. 1988. Particle motion and the theory of charcoal analysis: source area, transport, deposition, and sampling. *Quaternary Research* 30: 67–80.

Clebsch, E.E.C. and R.T. Busing. 1989. Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. *Ecology* 70: 728–735.

Cleaveland, M.K., E.R. Cook, and D.W. Stahle. 1992. Secular variability of the Southern Oscillation detected in tree-ring data from Mexico and the southern United States, pp. 271–291. *In* H.F. Diaz and V. Markgraf (Eds.), *El Nino: Historical and Paleoclimatic Aspects of the Southern Oscillation*. Cambridge University Press: Cambridge, U.K.

Clinton, B.D., L.R. Boring, and W.T. Swank. 1993. Canopy gap characteristics and drought influence in oak forests of the Coweeta Basin. *Ecology* 74: 1551–1558.

Clinton, B.D., L.R. Boring, and W.T. Swank. 1994. Regeneration patterns in canopy gaps of mixed-oak forests of the southern Appalachians: influence of topographic position and evergreen understory. *American Midland Naturalist* 132: 308–319.

Cole, W.G. and C.G. Lorimer. 2005. Probabilities of small-gap capture by sugar maple saplings based on height and crown growth data from felled trees. *Canadian Journal of Forest Research* 35: 643–655.

Connell, J.H. 1989. Some processes affecting the species composition in forest gaps. *Ecology* 70: 560–562.

Cook, R.E. and E.E. Lyons. 1983. The biology of *Viola fimbriatula* in a natural disturbance. *Ecology* 64: 654–660.

Cook, E.R. 1985. A time-series analysis approach to tree-ring standardization. Ph.D. Dissertation, University of Arizona, Tucson.

Cook, E.R., M.A. Kablack, and G.C. Jacoby. 1988. The 1986 drought in the southeastern United States: how rare an event was it? *Journal of Geophysical Research* 93: 14257–14260.

Cook, E.R., D.W. Stahle, and M.K. Cleaveland. 1995. Dendroclimatic evidence of the North Atlantic Oscillation using tree-ring chronologies from North American and Europe. *The Holocene* 8: 9–17.

Cottam, G. and J.T. Curtis. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37: 451–460.

Cowell, C.M. 1998. Historical change in vegetation and disturbance on the Georgia Piedmont. *American Midland Naturalist* 140: 78–89.

Cronon, W. 1983. *Changes in the Land: Indians, Colonists, and the Ecology of New England*. Hill and Wang Publishing: New York.

Crow, T.R. 1988. Reproductive mode and mechanism for self-replacement of northern red oak (*Quercus rubra*): a review. *Forest Science* 34: 19–40.

Cseke, J.J. 2003. A dendroecological approach for dating individual small-scale canopy disturbance events, Great Smoky Mountains National Park, Tennessee, U.S.A. M.S. Thesis, University of Tennessee, Knoxville.

Dahir, S.E. and C.G. Lorimer. 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. *Canadian Journal of Forest Research* 26: 1875–1892.

Dai, A. and K.E. Trenberth. 1998. Global variations in droughts and wet spells: 1900–1995. *Geophysical Research Letters* 25: 3367–3370.

de Blij, H.J., P.O. Muller and R.S. Williams, Jr. 2004. *Physical Geography: The Global Environment*, Third Edition. Oxford University Press: New York.

Delcourt, H.R. 1979. Late Quaternary vegetation history of the Eastern Highland Rim and adjacent Cumberland Plateau of Tennessee. *Ecological Monographs* 49: 255–280.

Delcourt, H.R. and P.A. Delcourt. 1997. Pre-Columbian Native American use of fire on southern Appalachian landscapes. *Conservation Biology* 11: 1010–1014.

Delcourt, P.A., H.R. Delcourt, C.R. Ison, W.E. Sharp, and K.J. Gremillion. 1998. Prehistoric human use of fire, the eastern agricultural complex, and Appalachian oak-chestnut forests: Paleoecology of Cliff Palace Pond, Kentucky. *American Antiquity* 63: 263–278.

Delcourt, P.A. and H.R. Delcourt. 1998. The influence of prehistoric human-set fires on oak-chestnut forests in the southern Appalachians. *Castanea* 64: 337–345.

Delcourt, H.R. and P.A. Delcourt. 2000. Eastern Deciduous Forests, pp. 357–395. *In* M.G. Barbour and W.D. Billings (Eds.), *North American Terrestrial Vegetation*. Cambridge University Press: Cambridge, U.K.

DeSelm, H.R. and G.M. Clark. 1975. Potential national natural landmarks of the Appalachian Plateaus province of Alabama, Georgia, southern Kentucky, and Tennessee, Final Report. Prepared for the Appalachian Potential National Natural Landmark Program of West Virginia University, Morgantown.

De Vries, P.G. 1974. Multi-stage line intersect sampling. *Forest Science* 20: 129–133.

DeWitt, E. and M. Ames. 1978. Tree-ring chronologies of eastern North America. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona. Chronology Series IV, Volume 1.

Dickson, R.R. 1960. Climates of the states: Tennessee. U.S. Department of Commerce, Weather Bureau. Government Printing Office: Washington, D.C.

Druckenbrod, D.L. and V.H. Dale. 2004. Sustaining the landscape: a method for comparing current and desired future conditions of forest ecosystems in the north Cumberland Plateau and Mountains. Oak Ridge National Laboratory, TM-2004/314.

Drury, S.A. and J.R. Runkle. 2006. Forest vegetation change in southeast Ohio: do older forests serve as useful models for predicting the successional trajectory of future forests? *Forest Ecology and Management* 223: 200–210.

Fenneman, N.M. 1938. *Physiography of Eastern United States*. McGraw-Hill Book Company: New York.

Ferreira de Lima, R.A. 2005. Gap size measurement: the proposal of a new field method. *Forest Ecology and Management* 214: 413–419.

Foster, D.R., D.A. Orwig, and J.S. McLachlan. 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Trends in Ecology and Evolution* 11: 419–424.

Foster, T.E. and J.R. Brooks. 2001. Long-term trends in growth of *Pinus palustris* and *Pinus elliottii* along a hydrological gradient in central Florida. *Canadian Journal of Forest Research* 31: 1661–1670.

Foster, D.R. 2002. Insights from historical geography to ecology and conservation: lessons from the New England landscape. *Journal of Biogeography* 29: 1269–1275.

Foster, D.R., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, and A. Knapp. 2003. The importance of land-use legacies to ecology and conservation. *BioScience* 53: 77–88.

Fralish, J.S., F.B. Crooks, J.L. Chambers, and F.M. Harty. 1991. Comparison of presettlement, second-growth and old-growth forests on six site types in the Illinois Shawnee Hills. *American Midland Naturalist* 125: 294–309.

Francis, J.K, and J.S. Loftus. 1977. Chemical and physical properties of the Cumberland Plateau and Highland Rim forest soils. U.S.D.A., Forest Service, *Research Paper* SO-138.

Franklin, J.F., H.H. Shugart, and M.E. Harmon. 1987. Tree death as an ecosystem process. *Bioscience* 37: 550–556.

Frelich, L.E. 2002. *Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergree-Deciduous Forests*. Cambridge University Press: Cambridge, U.K.

Fritts, H.C. and T.W. Swetnam. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Advances in Ecological Research* 19: 111–188.

Fritts, H.C. 2001. *Tree Rings and Climate*. Blackburn Press: Caldwell, New Jersey.

Fullerton, R.O., H.G. McDowell, O.M. McMillion, J. Phelps, J.B. Ray, and R.P. Terrell. 1977. *Tennessee*: *Geographical Patterns and Regions*. Kendall/Hunt Publishing: Dubuque, Iowa.

Gavin, D.G. 2003. Forest soil disturbance intervals inferred from soil charcoal radiocarbon dates. *Canadian Journal of Forest Research* 33: 2514–2518.

Gavin, D.G., L.B. Brubaker, and K.P. Lertzman. 2003. Holocene fire history of a coastal temperate rain forest based on soil charcoal radiocarbon dates. *Ecology* 84: 186–201.

Goebel, P.C. and D.M. Hix. 1996. Development of mixed-oak forests in southeastern Ohio: a comparison of second and old-growth forests. *Forest Ecology and Management* 84: 1–21.

Goebel, P.C. and D.M. Hix. 1997. Changes in the composition and structure of mixed-oak, second-growth forest ecosystems during the understory reinitiation stage of stand development. *Ecoscience* 4: 327–339.

Goldblum, D. and S.W. Beatty. 1999. Influence of an old field/forest edge on a northeastern United States deciduous forest understory community. *Journal of the Torrey Botanical Society* 126: 335–343.

Grissino-Mayer, H.D. and D.R. Butler. 1993. Effects of climate on growth of shortleaf pine (*Pinus echinata* Mill.) in northern Georgia: a dendroclimatic study. *Southeastern Geographer* 33: 65–81.

Grissino-Mayer, H.D. 1995. Tree-ring reconstructions of climate and fire history at El Malpais National Monument, New Mexico. Ph.D. Dissertation, University of Arizona, Tucson.

Grissino-Mayer, H.D. 2001a. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57: 205–221.

Grissino-Mayer, H.D. 2001b. FHX2 – Software for analyzing temporal and spatial patterns of fire regimes from tree rings. *Tree-Ring Research* 57: 115–124.

Hall, R.C. 1910. Preliminary study of the forest conditions of Tennessee. Tennessee Geological Survey Series 10A: 1–56.

Held, M.E. and J.E. Winstead. 1975. Basal area and climax status in mesic forest ecosystems. *Annals of Botany* 39: 1147–1148.

Henry, J.D. and J.M.A. Swan. 1974. Reconstructing forest history from live and dead plant material – an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55: 772–783.

Hibbs, D.E. 1982. Gap dynamics in a hemlock-hardwood forest. *Canadian Journal of Forest Research* 12: 522–527.

Hinkle, C.R. 1978. The relationship of forest communities and selected species to edaphic and topographic factors on the Cumberland Plateau of Tennessee. Ph.D. Dissertation, University of Tennessee, Knoxville.

Hinkle, C.R. 1989. Forest communities of the Cumberland Plateau of Tennessee. *Journal of the Tennessee Academy of Science* 64: 123–129.

Hinkle, C.R., W.C. McComb, J.M. Safely, Jr., and P.A. Schmalzer. 1993. Mixed mesophytic forests, pp. 203–253. *In* W.H. Martin, S.G. Boyce, and A.C. Echternacht (Eds.), *Biodiversity of the Southeastern United States: Upland Terrestrial Communities*. John Wiley and Sons: New York.

Holmes, R.L. 1983. Computer assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43: 69–78.

Horn, S.P., T.R. Wallin, and L.A. Northrop. 1994. Nested sampling of soil pollen, charcoal, and other soil components using a root corer. *Palynology* 18: 87–89.

Hutchinson, T.F., E.K. Sutherland, and C.T. Scott. 2003. Composition and abundance of tree regeneration, pp 85–98. *In* E.K. Sutherland and T.F. Hutchinson (Eds.), Characteristics of mixed-oak forest ecosystems in southern Ohio prior to the reintroduction of fire. U.S.D.A, Forest Service, Northeastern Research Station, GTR-NE-299. Newton Square, Pennsylvania.

Jans, L., L. Porter, R.S.A.R. van Rompaey, and F. Bongers. 1993. Gaps and forest zones in tropical moist forest in Ivory Coast. *Biotropica* 25: 258–269.

Kline, G.W., G.D. Crites, and C.H. Faulkner. 1982. The McFarland project: early Middle Woodland settlement and subsistence in the upper Duck River valley in Tennessee. Tennessee Anthropology Association Miscellaneous Paper 8.

Knapp, L.B. and C.D. Canham. 2000. Invasion of old-growth forests by Ailanthus altissima: sapling growth and recruitment in canopy gaps. *Journal of the Torrey Botanical Society* 127: 307–315.

Kozlowski, T.T. 1957. Effect of continuous high light intensity on photosynthesis of forest tree seedlings. *Forest Science* 3: 220–224.

Kozlowski, T.T. 1979. *Tree Growth and Environmental Stresses*. University of Washington Press: Seattle, Washington.

Kozlowski, T.T. and S.G. Pallardy 1997. *Physiology of Woody Plants*, Second Edition. Academic Press: San Diego, California.

Krasny, M.E. and M.C. Whitmore. 1992. Gradual and sudden forest canopy gaps in Allegheny northern hardwood forests. *Canadian Journal of Forest Research* 22: 139–143.

Kuchler, A.W. 1964. *Potential Natural Vegetation of the Conterminous United States*. American Geographical Society, Special Publication, No. 36. New York.

Kupfer, J.A., J.R. Runkle, and G.P. Malanson. 1997. Factors influencing species composition in canopy gaps: the importance of edge proximity in Hueston Woods, Ohio. *Professional Geographer* 49: 165–178.

Lafon, C.W. 2004. Stand dynamics of a yellow-poplar (*Liriodendron tulipifera* L.) forest in the Appalachian Mountains, Virginia, USA. *Dendrochronologia* 22: 43–52.

Latham, P. and J. Tappeiner. 2002. Response of old-growth conifers to reduction in stand density in western Oregon forests. *Tree Physiology* 22: 137–146.

Lewis, M.E. 1991. Windfall disturbance in a Piedmont uplands forest. *Southeastern Geographer* 31: 1–14.

Loftis, D.L. 1990. A shelterwood method for regenerating red oak in the southern Appalachians. *Forest Science* 36: 917–929.

Loftis, D.L. and C.E. McGee. 1993. Oak regeneration: serious problems, practical recommendations. U.S.D.A., Forest Service, *General Technical Report* SE-84. Asheville, North Carolina.

Loftis, D.L. 2004. Upland oak regeneration and management, pp. 163–167. U.S.D.A., Forest Service, Southern Research Station, *General Technical Report* SRS-73. Asheville, North Carolina.

Lorimer, C.G. 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. *Ecology* 58: 139–148.

Lorimer, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* 61: 1169–1184.

Lorimer, C.G. 1984. Development of the red maple understory in Northeastern oak forests. *Forest Science* 30: 3–22.

Lorimer, C.G. 1985. Methodological considerations in the analysis of forest disturbance history. *Canadian Journal of Forest Research* 15: 200–213.

Lorimer, C.G. and L.E. Frelich. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research* 19: 651–663.

Lorimer, C.G. 1989. Relative effects of small and large disturbances on temperate hardwood forest structure. *Ecology* 70: 565–567.

Lorimer, C.G. 1993. Causes of oak regeneration problems, pp. 14–39. *In* D.L. Loftis and C.E. McGee (Eds.), Oak regeneration: serious problems, practical recommendations. U.S.D.A., Forest Service, Southeastern Forest Experiment Station, *General Technical Report* SE-84. Asheville, North Carolina.

Lorimer, C.G., J.W. Chapman, and W.D. Lambert. 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. *Journal of Ecology* 82: 227–237.

Lorimer, C.G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. *Wildlife Society Bulletin* 29: 425–439.

Ludwig, J.A. and J.F. Reynolds. 1988. *Statistical Ecology*. John Wiley and Sons: New York.

Luther, E.T. 1977. *Our Restless Earth: The Geologic Regions of Tennessee*. University of Tennessee Press: Knoxville.

Manning, R. 1993. *The Historic Cumberland Plateau*: *An Explorer's Guide*. University of Tennessee Press: Knoxville.

Martin, W.H. 1975. The Lilley Cornett Woods: a stable mixed mesophytic forest in Kentucky. *Botanical Gazette* 136: 171–183.

Martin, W.H. 1992. Characteristics of old-growth mixed mesophytic forests. *Natural Areas Journal* 12: 127–135.

Mawhorter, J. 2006. A review of Tennessee's regulatory framework for habitat conservation planning efforts in the Cumberland region. Cumberlands habitat onservation plan, White Paper, http://www.cumberlandhcp.org/files/Cumberland_hcp_water_mawhorter.pdf

McCarthy, B.C., C.A. Hammer, G.L. Kauffman, and P.D. Cantino. 1987. Vegetation patterns and structure of an old-growth forest in southeastern Ohio. *Bulletin of the Torrey Botanical Club* 114: 33–45.

McCarthy, B.C. and D.R. Bailey. 1994. Distribution and abundance of coarse woody debris in a managed forest landscape. *Canadian Journal of Forest Research* 24: 1317–1329.

McCarthy, B.C. and D.R. Bailey. 1996. Composition, structure, and disturbance history of Crabtree Woods: an old-growth forest of western Maryland. *Bulletin of the Torrey Botanical Club* 123: 350–365.

McCarthy, B.C., C.J. Small, and D.L. Rubino. 2001. Composition, structure, and dynamics of Dysart Woods, an old-growth mixed mesophytic forest of southeastern Ohio. *Forest Ecology and Management* 140: 193–213.

McClure, J.W., T.D. Lee, and W.B. Leak. 2000. Gap capture in northern hardwoods: patterns of establishment and height growth in four species. *Forest Ecology and Management* 127: 181–189.

McComb, W.C. and R.N. Muller. 1983. Snag densities in old-growth and second-growth Appalachian forests. *Journal of Wildlife Management* 47: 376–382.

McGrath, D., J.P. Evans, K. Smith, N. Pelkey, D. Haskell, R. Gottfried, C. Brocket, M. Lane, and E.D. Williams. 2004. Mapping land-use change and monitoring the impacts of hardwood-to-pine conversion on the southern Cumberland Plateau in Tennessee. *Earth Interactions* 8: 1–24.

Meier, A.J. and S.P. Bratton. 1995. Disturbance dynamics in the Chattooga watershed. U.S.D.A., Forest Service, Chattooga River Demonstration Project. Clemson, South Carolina.

Mikan, C.J., D.A. Orwig, and M.D. Abrams. 1994. Age structure and successional dynamics of a presettlement-origin chestnut oak forest in the Pennsylvania Piedmont. *Bulletin of the Torrey Botanical Club* 121: 13–23.

Miller, R.A. 1974. The geologic history of Tennessee. Tennessee Division of Geology Bulletin, 74.

Miller, J.H. 2003. Nonnative invasive plants of Southern forests: a field guide for identification and control. U.S.D.A., Forest Service, Southern Research Station GTR SRS-62. Asheville, North Carolina.

Mitchell, K.A., P.V. Bolstad, J.M. Vose. 1999. Interspecific and environmentally induced variation in foliar dark respiration among eighteen southeastern deciduous tree species. *Tree Physiology* 19: 861–870.

Mitchener, L.J. and A.J. Parker. 2005. Climate, lightning, and wildfire in the national forests of the southeastern United States: 1989–1998. *Physical Geography* 26: 147–162.

Motzkin, G., P. Wilson, D.R. Foster, and A. Allen. 1999. Vegetation patterns in heterogeneous landscapes: the importance of history and environment. *Journal of Vegetation Science* 10: 903–920.

Muller, R.N. 1982. Vegetation patterns in the mixed mesophytic forest of eastern Kentucky. *Ecology* 63: 1901–1917.

Naidu, S.L. and E.H. DeLucia. 1997. Acclimation of shade-developed leaves on saplings exposed to late-season canopy gaps. *Tree Physiology* 17: 367–376.

National Climatic Data Center (NCDC). 2006. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Asheville, North Carolina. http://www.ncdc.noaa.gov

Natural Resources Defense Council (NRDC). 2005. NRDC’s 2005 Biogems: Twelve most threatened wildlands in the Americas. Press Release, http://www.nrdc.org/media/pressreleases/050308.asp

Nowacki, G.J. and M.D. Abrams. 1994. Forest composition, structure, and disturbance history of the Alan Seegers Natual Area, Huntington County, Pennsylvania. *Bulletin of the Torrey Botanical Club* 121: 277–291.

Nowacki, G.J. and M.D. Abrams. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs* 67: 225–249.

Oliver, C.D., and B.C. Larson. 1996. *Forest Stand Dynamics*, Update Edition. John Wiley and Sons: New York.

Orvis, K.H. and H.D. Grissino-Mayer. 2002. Standardizing the reporting of abrasive papers used to surface tree-ring samples. *Tree-Ring Research* 58: 47–50.

Orwig, D.A. and M.D. Abrams. 1994a. Land-use history (1720–1992), composition, and dynamics of oak-pine forests within the Piedmont and Coastal Plain of northern Virginia. *Canadian Journal of Forest Research* 24: 1216–1225.

Orwig, D.A. and M.D. Abrams. 1994b. Contrasting radial growth and canopy recruitment patterns in *Liriodendron tulipifera* and *Nyssa sylvatica*: a gap-obligate versus gap-facultative tree species. *Canadian Journal of Forest Research* 24: 2141–2149.

Orwig, D.A. and M.D. Abrams. 1995. Dendroecological and ecophysiological analysis of gap environments in mixed-oak understoreys of northern Viginia. *Functional Ecology* 9: 799–806.

Patterson, W.A., K.J. Edwards, and D.J. Maguire. 1987. Microscopic charcoal as an indicator of fire. *Quaternary Science Reviews* 6: 3–23.

Peet, R.K. and N.L. Christensen. 1987. Competition and tree death. *BioScience* 37: 586–595.

Pickford, S.G. and J.W. Hazard. 1978. Simulation studies on line intersect sampling of forest residue. *Forest Science* 24: 469–483.

Pierce, A.R., G.R. Parker, and K. Rabenold. 2006. Forest succession in an oak-hickory dominated stand during a 40-year period at the Ross Biological Reserve, Indiana. *Natural Areas Journal* 26: 351–359.

Poulson, T.L., and W.J. Platt. 1989. Gap light regimes influence canopy tree diversity. *Ecology* 70: 553–555.

Raup, H.M. 1966. The view from John Sanderson’s farm: a perspective for the use of land. *Journal of Forest History* 10: 1–11.

Reader, R.J., S.P. Bonser, T.E. Duralia, and B.D. Bricker. 1995. Interspecific variation in tree seedling establishment in canopy gaps in relation to tree density. *Journal of Vegetation Science* 6: 609–614.

Rebertus, A.J. and A.J. Meier. 2001. Blowdown dynamics in oak-hickory forests of the Missouri Ozarks. *Journal of the Torrey Botanical Society* 128: 362–369.

Rentch, J.S., M.A. Fajvan, and R.R. Hicks, Jr. 2003. Oak establishment and canopy accession strategies in five old-growth stands in the central hardwood forest region. *Forest Ecology and Management* 184: 285–297.

Romme, W.H. and W.H. Martin. 1982. Natural disturbance by tree-falls in old-growth mixed mesophytic forest: Lilley Cornett Woods, Kentucky, pp. 367–383. *In* R.N. Muller (Ed.), Proceedings of the Central Hardwood Forest Conference. University of Kentucky, Lexington.

Ross, M.S., T.L. Sharik, and D.W. Smith. 1982. Age-structure relationships of tree species in an Appalachian oak forest in southwestern Virginia. *Bulletin of the Torrey Botanical Club* 109: 287–298.

Rubino, D.L. and B.C. McCarthy. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia* 21: 97–115.

Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62: 1041–1051.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of the eastern United States. *Ecology* 63: 1533–1546.

Runkle, J.R. 1985a. Disturbance regimes in temperate forests, pp. 17–33. *In* S.T.A. Pickett and P.S. White (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press: San Diego, California.

Runkle, J.R. 1985b. Comparison of methods for determining fraction of land area in treefall gaps. *Forest Science* 31: 15–19.

Runkle, J.R. and T.C. Yetter. 1987. Treefalls revisited: gap dynamics in the southern Appalachians. *Ecology* 68: 417–424.

Runkle, J.R. 1989. Synchrony of regeneration, gaps, and latitudinal differences in tree species diversity. *Ecology* 70: 546–547.

Runkle, J.R. 1990. Gap dynamics in an Ohio Acer-Fagus forest and speculations on the geography of disturbance. *Canadian Journal of Forest Research* 20: 632–641.

Runkle, J.R. 1991. Gap dynamics of old-growth eastern forests: management implications. *Natural Areas Journal* 11: 19–25.

Runkle, J.R. 1992. Guidelines and sample protocol for sampling forest gaps. U.S.D.A., Forest Service, Pacific Northwest Research Station, *General Technical Report* 283.

Runkle, J.R. 1996. Central Mesophytic Forests, pp. 161–177. *In* M.B. Davis (Ed.), *Eastern Old-Growth Forests*. Island Press: Washington, D.C.

Runkle, J.R. 1998. Changes in southern Appalachian canopy tree gaps sampled thrice. *Ecology* 79: 1768–1780.

Runkle, J.R. 2000. Canopy tree turnover in old-growth mesic forests of eastern North America. *Ecology* 81: 554–576.

Sampson, H.C. 1930. The mixed mesophytic forest community of northeastern Ohio. *Ohio Journal of Science* 30: 340–356.

Schuler, T.M. and M.A. Fajvan. 1999. Understory tree characteristics and disturbance history of a central Appalachian forest prior to old-growth harvesting. U.S.D.A., Forest Service, Northeastern Research Station, *Research Paper* NE-710.

Schweitzer, C.J. 2000. Forest statistics for Tennessee's plateau counties. U.S.D.A., Forest Service, Southern Research Station, *Resource Bulletin* SRS-49.

Shankman, D. and L.A. James. 2002. Appalachian and the eastern cordillera, pp. 291–306. *In* Antony R. Orne (Ed.), *The Physical Geography of North America*. Oxford University Press: New York.

Shanks. R.E. 1958. Floristic regions of Tennessee. *Journal of the Tennessee Academy of Science* 33: 195–210.

Shumann, H.W. 1984. Potential for moisture stress on vegetation on the Cumberland Plateau of Tennessee. M.S. Thesis, University of Tennessee, Knoxville.

Signell, S.A., M.D. Abrams, J.C. Hovis, and S.W. Henry. 2005. Impact of multiple fires on stand structure and tree regeneration in central Appalachian oak forests. *Forest Ecology and Management* 218: 146–158.

Smalley, G.W. 1982. Classification and evaluation of forest sites on the mid-Cumberland Plateau. U.S.D.A., Forest Service, Southern Research Experiment Station, *General Technical Report* SO-38. New Orleans, Lousiana.

Smalley, G.W. 1986. Classification and evaluation of forest sites on the northern Cumberland Plateau. U.S.D.A., Forest Service, Southern Research Experiment Station, *General Technical Report* SO-60. New Orleans, Louisiana.

Smith, D.M., B.C. Larson, M.J. Kelty, and P.M.S. Ashton. 1996. *The Practice of Silviculture: Applied Forest Ecology*, Ninth Edition. John Wiley and Sons: New York.

Song, U. 1994. Use of a land classification system in growth and yield prediction on the Cumberland Plateau of Tennessee. M.S. Thesis, University of Tennessee, Knoxville.

Spies, T.A., J.F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Canadian Journal of Forest Research* 20: 649–658.

Spies, T.A. and M.G. Turner. 1999. Dynamic forest mosaics, pp. 95–160. *In* M.L. Hunter (Ed.), *Maintaining Biodiversity in Forest Ecosystems*. Cambridge University Press: Cambridge, U.K.

Springer, M.E. and J.A. Elder. 1980. Soils of Tennessee. University of Tennessee Agriculture Experiment Station Bulletin 596, Knoxville, Tennessee.

Sprugel, D.G. 1991. Disturbance, equilibrium, and environmental variability: what is "natural" vegetation in a changing environment? *Biological Conservation* 58: 1–18.

Stahle, D.W., R.D. D'Arrigo, P.J. Krusic, M.K. Cleaveland, E.R. Cook, R.J. Allan, J.E. Cole, R.B. Dunbar, M.D. Therrell, D.A. Gay, M.D. Moore, M.A. Stokes, B.T. Burns, J. Villanueva-Diaz, and L.G. Thompson. 1998. Experimental dendroclimatic reconstructions of the Southern Oscillation. *Bulletin of the American Meteorological Society* 79: 2137–2152.

Stambaugh, M.C. 2001. Forest canopy gap dynamics in shortleaf pine forests of the Ozark Highlands. M.S. Thesis, University of Missouri, Columbia.

Stokes, M.A. and T.L. Smiley 1996. *An introduction to tree-ring dating*. University of Arizona Press: Tucson.

Stuiver, M. and P.J. Reimer. 1993. Extended C-14 database and revised CALIB 3.0 C-14 age calibration program. *Radiocarbon* 35: 215–230.

Takahashi, K., S. Tatsuyuki, and T. Kohyama. 2001. Responses to canopy openings in architectural development of saplings in eight deciduous broad-leaved tree species. *Canadian Journal of Forest Research* 31: 1336–1347.

Taylor, S.O. and C.G. Lorimer. 2003. Loss of oak dominance in dry-mesic deciduous forests predicted by gap capture methods. *Plant Ecology* 167: 71–88.

Thornthwaite, C.W. 1948. An approach toward rational classification of climate. *Geographical Review* 38: 55–94.

Tryon, E.H., M. Lanasa, and E.C. Townsend. 1992. Radial growth response of understory sugar maple (*Acer saccharum*) surrounding openings. *Forest Ecology and Management* 55: 249–257.

Tyrell, L.E. and T.R. Crow. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. *Ecology* 75 370–386.

US Census Bureau. 2006. Crossville, Tennessee.

USDA. 1995. Soil survey of Fentress and Pickett Counties, Tennessee, U.S.D.A., Soil Conservation Service.

Van Lear, D.H. and T.A. Waldrop. 1989. History, uses, and effects of fire in the Appalachians. U.S.D.A., Forest Service, Southeastern Forest Experiment Station, *General Technical Report* SE-54. Asheville, North Carolina.

Veblen, T.T. 1985. Forest development in tree-fall gaps in the temperate rain forest of Chile. *National Geographic Research* 1: 162–183.

Veblen, T.T. 1989. Tree regeneration responses to gaps along a trans-Andean gradient. *Ecology* 70: 541–543.

Vitousek, P.M. 1985. Community turnover and ecosystem nutrient dynamics, pp. 325–333. *In* S.T.A. Pickett and P.S. White (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, San Diego, California.

Wallace, L.L. and E.L. Dunn. 1980. Comparative photosynthesis of three gap phase successional tree species. *Oecologia* 45: 331–340.

Waring, R.H. 1987. Characteristics of trees disposed to die. *Bioscience* 37: 569–574.

Watt, A.S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35: 1–22.

Webster, C.R. and C.G. Lorimer. 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: a retrospective approach. *Ecological Applications* 15: 1245–1262.

Welch, N.T. 1999. Occurrence of fire in southern Appalachian yellow pine forests as indicated by macroscopic charcoal in soil. *Castanea* 64: 310–317.

Whitmore, T.C. 1989. Canopy gaps and the two major groups of forest trees. *Ecology* 70: 536–538.

White, P.S., M.D. MacKenzie, and R.T. Busing. 1985. Natural disturbance and gap-phase dynamics in southern Appalachian spruce-fir forests. *Canadian Journal of Forest Research* 15: 233–240.

White, P.S., and S.T.A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction, pp. 3–13. *In* S.T.A. Pickett and P.S. White (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press: San Diego, California.

Whitney, G.G. 1994. *From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America from 1500 to the Present*. Cambridge University Press: Cambridge, U.K.

Wilder, C.M., F.W. Holtzclaw, Jr., and E.E.C. Clebsch. 1999. Succession, sapling density and growth in canopy gaps along a topographic gradient in a second growth east Tennessee forest. *American Midland Naturalist* 142: 201–212.

Wilson, R.C. and D.W. Finch. 1980. The Big South Fork National River and Recreation Area: phase I archeological reconnaissance survey in McCreary County, Kentucky, Pickett, Fentress, Scott, and Morgan Counties, Tennessee. Draft submitted to the U.S. Army Corps of Engineers, Nashville District, Nashville, Tennessee.

Wolf, A. 2005. Fifty year record of change in tree spatial patterns within a mixed deciduous forest. *Forest Ecology and Management* 215: 212–223.

Yamamoto, S. and N. Nishimura. 1999. Canopy gap formation and replacement pattern of major tree species among development stages of beech (*Fagus crenata*) stands, Japan. *Plant Ecology* 140: 167–176.

Yetter, T.C., and J.R. Runkle. 1986. Height growth rates of canopy gap tree species in southern Appalachian gaps. *Castanea* 51: 157–167.

Young, T.P., and V. Perkocha. 1994. Treefalls, crown asymmetry, and buttresses. *Journal of Ecology* 82: 319–324.

APPENDICES

APPENDIX A Scientific names with authorities and common names for listed plant species.

Scientific name and authority	Common name
Acer rubrum L.	red maple
Acer saccharum Marsh.	sugar maple
Aesculus flava Ait.	yellow buckeye
Ailanthus altissima (Mill.) Swingle	tree-of-heaven
Amelanchier laevis Weig.	Alleghany serviceberry
Asimina triloba (L.) Dunal	pawpaw
Betula alleghaniensis Britt.	yellow birch
Betula lenta L.	sweet birch
Betula nigra L.	river birch
Carpinus caroliniana Walt.	American hornbeam
Carya cordiformis (Wangenh.) K. Koch	bitternut hickory
Carya glabra (P. Mill.) Sweet	pignut hickory
Carya ovata (P. Mill.) K. Koch	shagbark hickory
Carya tomentosa (Poiret) Nutt.	mockernut hickory
Cercis canadensis L.	eastern redbud
Cornus florida L.	flowering dogwood
Diospyros virginiana L.	common persimmon
Fagus grandifolia Ehrh.	American beech
Fraxinus americana L.	white ash
Hamamelis virginiana L.	witch-hazel
Ilex opaca Ait.	American holly
Liriodendron tulipifera L.	tulip-poplar
Magnolia acuminata (L.) L.	cucumbertree
Magnolia macrophylla Michx.	bigleaf magnolia
Magnolia tripetala L.	umbrella magnolia
Morus rubra (L.)	red mulberry
Nyssa sylvatica Marsh.	black gum
Ostrya virginiana (P. Mill.) K. Koch	hophornbeam
Oxydendrum arboreum (L.) DC.	sourwood
Pinus echinata P. Mill.	shortleaf pine
Pinus strobus L.	eastern white pine
Pinus virginiana P. Mill.	Virginia pine
Prunus serotina Ehrh.	black cherry
Quercus alba L.	white oak
Quercus coccinea Muenchh.	scarlet oak
Quercus marilandica Muenchh.	blackjack oak

APPENDIX A *continued*

Scientific name and authority	**Common name**
Quercus montana Willd.	chestnut oak
Quercus rubra L.	northern red oak
Quercus stellata Wangenh.	post oak
Quercus velutina Lam.	black oak
Sassafras albidum (Nutt.) Nees	sassafras
Tilia heterophylla Vent.	white basswood
Tsuga canadensis (L.) Carr.	eastern hemlock
Ulmus alata Michx.	winged elm
Ulmus americana L.	American elm
Ulmus rubra Muhl.	slippery elm

APPENDIX B Statistical descriptions for the 66 *Quercus* series in the tree-ring chronology.

Seq	Series ID	Interval		No. years	Corr. w/ master	Mean sens	Std dev	Auto corr	AR ( )
1	PCT0120A	1932	2004	73	0.334	0.190	0.390	-0.045	1
2	PCT0207A	1938	2004	67	0.402	0.203	0.381	0.024	2
3	PCT0211A	1953	2004	52	0.477	0.195	0.426	-0.083	1
4	PCT0302A	1943	2004	62	0.653	0.215	0.463	-0.137	1
5	PCT0408A	1947	2004	58	0.393	0.203	0.483	-0.022	1
6	PCT0419A	1951	2004	54	0.334	0.169	0.408	0.028	1
7	PCT0421A	1942	2004	63	0.513	0.180	0.383	-0.091	1
8	PCT0423A	1941	2004	64	0.535	0.256	0.377	-0.089	1
9	PCT0426A	1906	2004	99	0.598	0.259	0.306	-0.068	1
10	PCT0503A	1948	2004	57	0.436	0.259	0.412	0.037	1
11	PCT0518A	1939	2004	66	0.547	0.206	0.425	-0.047	2
12	PCT0519A	1944	2004	61	0.250	0.358	0.485	0.045	1
13	PCT0522A	1943	2004	62	0.213	0.190	0.419	0.038	2
14	PCT0529A	1933	2004	72	0.636	0.221	0.429	-0.026	1
15	PCT0603A	1945	2004	60	0.333	0.171	0.392	0.017	3
16	PCT0610A	1944	2004	61	0.453	0.179	0.393	0.059	1
17	PCT0703A	1960	2004	45	0.389	0.197	0.523	0.001	1
18	PCT0706A	1950	2004	55	0.415	0.176	0.384	-0.023	1
19	PCT0708A	1947	2004	58	0.297	0.243	0.507	-0.013	2
20	PCT0709A	1955	2004	50	0.638	0.162	0.409	0.074	1
21	PCT0712A	1957	2004	48	0.579	0.171	0.309	-0.019	1
22	PCT0715A	1951	2004	54	0.462	0.162	0.342	-0.092	1
23	PCT0716A	1958	2004	47	0.298	0.147	0.363	0.005	2
24	PCT0717A	1955	2004	50	0.376	0.185	0.367	-0.077	1
25	PCT0722A	1952	2004	53	0.045	0.249	0.306	-0.127	1
26	PCT0727A	1943	2004	62	0.333	0.174	0.429	-0.072	1
27	PCT0802A	1950	2004	55	0.270	0.183	0.512	0.038	1
28	PCT0808A	1949	2004	56	0.383	0.187	0.444	-0.029	1
29	PCT0811A	1950	2004	55	0.414	0.216	0.462	-0.034	1
30	PCT0813A	1950	2004	55	0.528	0.247	0.471	-0.025	1
31	PCT0815A	1951	2004	54	0.556	0.157	0.447	-0.039	1
32	PCT0817A	1948	2004	57	0.481	0.221	0.328	-0.048	1
33	PCT0819A	1929	2004	76	0.393	0.205	0.397	-0.090	1
34	PCT0823B	1943	2004	62	0.310	0.247	0.497	0.016	1
35	PCT0827A	1942	2004	63	0.303	0.236	0.336	-0.081	2

APPENDIX B *continued*

36	PCT0829A	1929	2004	76	0.488	0.282	0.406	-0.105	1
37	PCT0831A	1945	2004	60	0.416	0.190	0.536	0.013	1
38	PCT0836A	1946	2004	59	0.385	0.232	0.475	0.063	1
39	PCT0838B	1954	2004	51	0.510	0.146	0.412	-0.026	1
40	PCT0843A	1952	2004	53	0.501	0.163	0.502	0.081	1
41	PCT0844A	1943	2004	62	0.288	0.210	0.292	-0.093	1
42	PCT0845A	1944	2004	61	0.418	0.213	0.510	0.042	1
43	PCT0846A	1943	2004	62	0.628	0.193	0.396	-0.015	1
44	PCT0846B	1943	2004	62	0.631	0.187	0.488	0.015	1
45	PCT1014A	1944	2004	61	0.612	0.168	0.449	-0.016	1
46	PCT1224A	1868	2005	138	0.477	0.256	0.357	-0.019	1
47	PCT1224B	1892	2005	114	0.513	0.274	0.430	-0.051	1
48	PCT1305A	1939	2005	67	0.554	0.199	0.406	-0.073	1
49	PCT1307A	1932	2005	74	0.453	0.331	0.383	-0.088	1
50	PCT1313A	1955	2005	51	0.406	0.247	0.497	-0.042	1
51	PCT1315A	1933	2005	73	0.512	0.233	0.388	-0.138	1
52	PCT1316A	1962	2005	44	0.035	0.406	0.493	0.028	1
53	PCT1405A	1939	2005	67	0.331	0.227	0.448	0.089	3
54	PCT1421A	1943	2005	63	0.416	0.286	0.435	-0.031	1
55	PCT1510A	1951	2005	55	0.408	0.209	0.435	-0.044	3
56	PCT1610A	1941	2005	65	0.392	0.178	0.513	0.011	1
57	PCT1616A	1957	2005	49	0.452	0.193	0.427	-0.099	1
58	PCT1716A	1949	2005	57	0.325	0.199	0.380	-0.003	1
59	PCT1720A	1927	2005	79	0.497	0.274	0.373	-0.080	1
60	PCT1801A	1943	2005	63	0.165	0.301	0.394	-0.019	1
61	PCT1804A	1942	2005	64	0.525	0.223	0.379	0.003	1
62	PCT1817A	1942	2005	64	0.449	0.273	0.352	-0.047	1
63	PCT1821A	1943	2005	63	0.574	0.155	0.317	-0.023	1
64	PCT1822A	1935	2005	71	0.552	0.230	0.443	0.017	1
65	PCT1911A	1902	2005	104	0.432	0.309	0.375	-0.067	2
66	PCT2019A	1931	2005	75	0.355	0.287	0.492	-0.014	1
Total or mean:				**4193**	**0.435**	**0.224**	**0.415**	**-0.290**	

Correlation with master (Corr. w/ master) is the Pearson correlation coefficient of each individual series to the master chronology created with the remaining series. Mean sensitivity (Mean sens) is the relative difference in width from one ring to the next and is calculated by averaging the percent change from ring to adjacent ring. Standard deviation (Std dev.) is the variability about the mean which has been standardized to 0.0 for all series. AR ( ) represents the order of the autoregressive model used in the detrending. Higher values are indicative of persistence over several years and the normal range for AR coefficients is between 1 and 4 (Grissino-Mayer 2001a).

APPENDIX C Standard tree-ring chronology for the Pogue Creek Natural Area in Fentress County, Tennessee.

Year	0	1	2	3	4	5	6	7	8	9
1902			43	69	83	89	87	68	77	51
1910	41	28	31	22	23	51	48	39	32	33
1920	30	38	58	93	153	117	105	75	94	123
1930	103	131	113	127	163	164	77	147	141	115
1940	95	106	109	104	58	106	85	104	88	97
1950	105	94	77	84	76	93	86	96	104	102
1960	110	112	103	103	107	126	101	102	110	100
1970	88	100	106	104	91	96	106	97	92	94
1980	84	110	115	108	86	86	91	122	92	115
1990	105	93	102	98	97	94	92	80	82	92
2000	90	95	97	93	92	98				

These values are the tree-ring indices for each year in the chronology. The indices are displayed without the decimal points, but the actual value can be obtained by dividing the numbers by 100. The mean value for all indices is 1.0. Each line represents one decade of indices and the decades are shown in the lefthand column. The numbers across the top of the table are the last numbers of the year for each decade. This is called the "Tucson format" and is the internationally accepted format of the World Data Center for Paleoclimatology.

Vita

Justin L. Hart earned a Bachelor of Science degree from the Department of Earth Sciences at the University of Memphis with a concentration in environmental and earth science and a minor in geological sciences in 2002. He received the Master of Science degree from the Department of Geography at the University of Alabama in 2004. While at the University of Alabama, he served as the Environmental Education Coordinator for the University Arboretum and taught lecture and laboratory classes in introductory physical geography. In 2007, he was awarded the Doctorate of Philosophy degree from the Department of Geography at the University of Tennessee. While working towards the doctorate, he worked as a Graduate Teaching Assistant in the Departments of Geography and Earth and Planetary Sciences and he served as a Graduate Fellow for the University of Tennessee Earth Project funded by the National Science Foundation. After graduation, Justin accepted a position as Assistant Professor of Geography at the University of North Alabama.