Disturbance and Long-term Vegetation Change in the High-Elevation Deciduous Forests of Great Smoky Mountains National Park

by
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A dissertation submitted to the faculty of the University of North Carolina at Chapel Hill in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Biology.

Chapel Hill
2005

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ABSTRACT

DAVID B. VANDERMAST: Disturbance and Long-term Vegetation Change in the High-Elevation Deciduous Forests of Great Smoky Mountains National Park.
(Under the direction of Peter S. White)

The high-elevation deciduous forests of Great Smoky Mountains National Park (GRSM) are one of the largest relatively undisturbed forest landscapes in the eastern United States. They are a reference point for late-successional temporal forest dynamics and in this study I use data from them to ask: 1) whether tree densities, basal areas, and biomass in high-elevation forests remain constant over time, 2) what are the drivers of temporal change in these forests, and 3) how the spatial scale of observation influences studies of temporal change in forests?

The dynamics of late-successional forests are far more complex than is commonly assumed. Between 1935-38 and 1976-85, beech density and basal area in high-elevation beech-dominated (>50% beech density) forests increased significantly. In 1993 beech bark disease (BBD) invaded and caused heavy mortality (as much as 90% of beech stems) in infected beech forests, but in disease-free forests beech dominance increased from 1976-85 to 2000-02, with beech basal area increasing nearly 30% on average. The demographic cause of the increase is the accretion of basal area in the largest trees, a pattern that does not fit common perceptions of late-successional forests.

In contrast with trends in beech forests, the mixed species high-elevation deciduous forests exhibited a decline in tree density and basal area by forest type and disturbance history for most species from 1977-78 to 2002. Declines in tree density and basal area were strongly associated with soil chemistry, specifically low soil cation and high aluminum concentrations and were particularly high for northern red oak (*Quercus rubra*).

The relatively high variance in density (nearly 35%) and basal area (> 25%) and the continued decline of basal area variance at grain sizes larger than 0.1 ha suggests that standard vegetation plots of this area do not capture the variance in forest attributes.

Late-successional forests are complex systems whose temporal dynamics are not adequately described by current forest succession models. Temporal changes in the high-elevation deciduous forests of GRSM are influenced by historical and contemporary perturbations, the species composition of the forest, and the spatial scale at which change is observed.

ACKNOWLEDGEMENTS

Ten years ago I left a career in banking and, with an interest in natural resources, returned to school to gain an education in science. My time as a student culminates with the completion of this document and as I reflect on the past decade I realize that I am indeed a fortunate person to have been involved with and influenced by so many good people.

My research committee: Michael Jenkins, Seth Reice, Tom Wentworth, Bob Peet, and Peter White, my advisor, were at all times patient, supportive, and full of good advice. I owe much of my success in completing the academic part of this journey to them. I wish to single out Peter for thanks because he went above and beyond the call in supporting me during my time as his student. I appreciate the logistical support, advice, and some much needed conversation that Mike Jenkins provided during my summers in Great Smoky Mountains National Park. I would also like to especially thank Bob for excellent field trips to unique botanical sites. I will always remember the flora of Big Bend National Park as particularly beautiful and unique.

In the Smokies I was assisted in data collection by Julie Ann Zoleta and Jessica Wall. Logistical and financial support for my research was provided by the National Park Service, the Mr. and Mrs. W.C. Coker Fellowships, the Alma Holland Beers, Smith Graduate Research Fellowship, The Center for Study of the American South, and the Graduate School at the University of North Carolina.

I owe the maintenance of my sanity and a good deal of my education to the friendship and camaraderie of my fellow PEL students and others who befriended me during my time at UNC: Becky Brown, Michelle Cawley, Pat Corry, Andrea Gramling, Joel Gramling, Jason Fridley, Andy Gerschutz, Lee Anne Jacobs, Todd Jobe, Jessica Kaplan, Dane Kuppinger, Chris Liloia, Sarah Marcinko, Megan McKnight, Jeff Ott, Laura Phillips, Amanda Senft, Eileen Vandenburgh, Aläa Wally, Brooke Wheeler, and Wiemin Xie. After the Big Bend trip Andrea, Jessica, Dane, Pat, Michelle, and Andy will forever be remembered by me as Squeak, Scratch, Lizard Crusher, Lizard Healer the Magical Botanist, Homegirl, and Sex Machine, respectively.

The time I spent working with Jean DeSaix as a TA, Head TA, and Supplemental Instruction TA was as helpful and beneficial to me as the time I spent in the field. Jean is a friend and teaching mentor for whom I have great respect and from whom I learned a great deal about being an effective teacher. I also enjoyed my interactions with all of the TAs with whom I worked and are too many to list here.

My last acknowledgment goes to the people most important to me and to whom this dissertation is dedicated: my wife Melanie, daughter Emily, and son Cole. The support and love they give me is the bedrock from which I have worked to build this new career: I truly could not have done it without them. They made all the trials and troubles of being a student, teacher and researcher worthwhile. With them at my side I am complete.

To Melanie, Emily, and Cole

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Chapter 1

Introduction to disturbance and long-term vegetation change in the high-elevation deciduous forests of Great Smoky Mountains National Park

Purpose of dissertation

The purpose of this dissertation is to examine temporal changes in forest attributes such as tree density, basal area and woody understory composition using long-term data sets from deciduous forests at high-elevations (at least 1200 m) in Great Smoky Mountains National Park (GRSM). The chapters contained herein will test, with empirical data, assumptions of the stability of of late-successional temperate deciduous forests in the study area. The approach taken here is to use long-term data covering up to 65 years in a protected landscape (GRSM) to examine whether these forests, often considered "climax" and assumed to represent the endpoint in succession as self-replacing communities, do in fact demonstrate stability when measured over ecologically relevant time periods. Should the attributes of these forests prove not to be stable the suite of factors that constitute potential drivers of change in these forests will be examined.

Background

Ecologists have long debated the relative importance of equilibrium versus non-equilibrium processes in the maintenance of forest attributes. In equilibrium communities, forest attributes are maintained through autogenic processes such as competition and predation; by definition, communities in equilibrium will return to a stable, self-replacing state following perturbation. Evidence for equilibrium in communities comes from studies of organisms with relatively short lifespans, but little evidence for it exists in studies of forest attributes. That forest communities reach an equilibrium is one of the oldest principals in ecology: climax theory is the hypothesis that the endpoint of succession in forest communities is a stable, self-replacing (equilibrium) community whose constituents are late-successional, shade-tolerant species. Although there has been much debate over the mechanisms by which succession proceeds, the idea that forests reach equilibrium is persistent despite little evidence favoring the authenticity of this assertion in forest communities.

In contrast with equilibrium theory, non-equilibrium models invoke external mechanisms such as environmental fluctuations, disturbances, and stochastic processes to explain the maintenance of species coexistence and community diversity. Given the longevity of most forest trees, one or more non-equilibrium processes is likely to occur within the average life span. In recent decades humans have accelerated the rate of climate change and added additional influences on forest communities that no longer meet the classic requirement of disturbances that they be discrete in time. The ongoing nature of perturbations means that at any given time, multiple non-equilibrium processes may be influencing a forest community.

Location of study, forest associations, and available data

Great Smoky Mountains National Park (GRSM) is a unique place in which to address questions regarding the stability of temperate forest communities. As one of the last large (> 200,000 ha) tracts of preserved forestland in the eastern United States, GRSM has been the subject of numerous scientific studies and is renowned as a center of biological diversity. The human history of the area is well documented and the park has been protected since 1935. Because of the remoteness of the park prior to its establishment and the difficulty in accessing of some of the highest elevation areas, it contains large patches of late-successional forest (roughly one-third of the park was never logged), most of which are above 1200 m. The high-elevation forests of GRSM are representative of temperate montane forests in general, and because of the availability of long-term data, an understanding of temporal changes in GRSM forests will have wide applicability. All data used in the completion of this dissertation were collected from 80 permanent plots (≥ 0.1 ha) in high-elevation deciduous forests (> 1200 m) in GRSM.

Because of the species-specific nature of some of the perturbations reported in this study, plots were sorted into two groups of plots based on their composition: beech-dominated plots and mixed-species deciduous forest plots. Of the 80 plots, 39 were American beech (*Fagus grandifolia*) dominated (> 50% relative abundance of beech stems ≥ 10 cm DBH). Beech plot data were collected during the summers 2000-2004 by 1) resampling 19 permanent plots established in the late 1970s and 1980s, and 2) using vegetation maps and interviews of GRSM vegetation monitoring staff to establish 20 new plots in previously un-sampled areas of high-elevation beech forest. Mixed-species deciduous forest data was obtained from Dr. Michael Jenkins at GRSM and consists of 41 plots established in the late 1970s, eighteen of which were resampled in 1995 by Jon Harrod; the remainding plots were resampled 2001-2003 by GRSM vegetation monitoring staff and the author. Soils were collected from 40 of the 41 mixed species deciduous forest plots and all of the beech forest plots. Soil chemical analysis was conducted by A&L Laboratories, Memphis, TN.

American beech is a very shade-tolerant, slow-growing species capable of regenerating from sprouts or seeds under a conspecific canopy (Burns and Honkala 1990). Understory beech stems are capable of responding to small changes in light levels and may undergo several periods of suppression and release before recruitment into the forest canopy (Canham 1990). In high-elevation GRSM beech forests, beech density can exceed 90% (Russell 1953), regeneration is almost exclusively from sprouts (Sain and Blum 1981), and genetic diversity is low (Kitamura and Kowano 2000). Beech-dominated forests in GRSM therefore represent a climax forest community which should, according to the forest succession model, exhibit stability in forest attributes. However, as monodominant forests with low genetic diversity, they are susceptible to disease.

High-elevation mixed species deciduous forests in GRSM are composed of an admixture of northern red oak (*Quercus rubra*), yellow birch (*Betula allegheniensis*), silverbell (*Halesia tetraptera*), buckeye (*Aesculus octandra*), sugar and red maple (*Acer saccharum* and *A. rubrum*), and American beech (Golden 1981, Callaway et al. 1987). These forests have been described as northern hardwood or Appalachian oak depending on the identity of the dominant species (White et al. 1993). Though they are considered late successional, mixed-species deciduous forests in GRSM have large percentages of shade-intolerant gap-phase (yellow birch) and intermediately shade-tolerant species (northern red oak) (Burns and Honkala 1990) and might be expected to exhibit an increase in the importance of shade-tolerant species over the period of this study.

Potential drivers of change in the high-elevation forests of GRSM

The list of potential causes of temporal changes in the attributes of high-elevation forests can be organized as 1) those that occurred prior to the establishment of the park, 2) those that occurred subsequent to its establishment, and 3) those that are ongoing and continuous.

Prior to the establishment of GRSM, Native Americans used high-elevation areas as hunting grounds and their activities may have included intentionally burning forests to improve hunting conditions. Subsequent to European settlement of the area, mountain ridgetops in what eventually became GRSM were used for livestock grazing, with herders felling or girdling trees in some places to improve grazing conditions. The presence of grassy "balds" in GRSM has been attributed to the activities of early herders; however, the plots used in this study are downslope of former balds, in areas known to have remained forested.

Although there is no evidence that herders burned balds or nearby forests to improve grazing, fires set downslope could have burned into high-elevation forests. Forests such as these are commonly thought to have been subject to periodic understory fires, which might have influenced their composition and structure. If this is true, fire suppression following park establishment could be responsible for subsequent temporal changes in these forests.

Industrial logging was widespread at low elevations prior to park establishment. At high-elevations, the most severe logging occurred on the North Carolina side of the central ridgeline. Due to their remoteness and the low economic value of beech wood, most of the beech-dominated stands that are an important source of long-term data for this dissertation avoided heavy cutting. However, some beech and mixed-species stands have been classified as being subject to diffuse disturbance, including selective cutting and grazing.

In forests with "slow dynamics" such as the hemlock-hardwood forests of Michigan (Woods 2000 a,b), the population-level interactions that should result in stable forest attributes occur so slowly that, even with stand-replacing disturbance frequencies on the order of hundreds or thousands of years, the forests will never demonstrate measurable stability before the next stand-replacing event occurs. One reason the attributes of high-elevation forests of GRSM may not be stable is that forest succession is an inherently slow process. Late-successional species, such as American beech (*Fagus grandifolia*) are very shade-tolerant but grow very slowly, even in canopy gaps. Succession in beech forests therefore, may be assumed to be a slow process.

Since 1934 when GRSM achieved protected status, high-elevation forests have been affected by introduced diseases and the European wild boar (*Sus scrofa*). Chestnut blight (*Cryphonectria parasitica*) caused the functional extinction of American chestnut (*Castanea dentata*) throughout its former range. Chestnut was an important species in some high-elevation areas, but a minor component of the forest plots in this study. In 1994 beech bark disease (BBD), a European insect-fungal pathogen complex, was discovered in a high-elevation beech forest near Clingmans Dome in central GRSM. Since then it has spread throughout much of the range of high-elevation beech in GRSM, though the extent of spread and magnitude of damage has not been reported. European wild boar congregate in high-elevation beech forests in the spring where their rooting might cause beech roots to sprout, though their long-term affect on the woody and herbaceous vegetation of these forests is unknown.

On a global scale, increased atmospheric CO_2 levels may enhance tree growth by providing more of a limiting nutrient, and climate warming has been associated with increased growing season length, which might enhance annual tree growth. Locally, high-elevation sites in GRSM receives levels of atmospheric pollutants such as nitrogen high enough to consider them saturated, and on hot summer days, ozone can reach concentrations capable of damaging photosynthetic tissues.

Questions addressed by this study

Chapter 2 examines whether high-elevation beech forests in GRSM have been stable since park establishment over two time scales: prior to and after the invasion of BBD.

Chapter 3 reports on size-specific demographics of structural change in high-elevation beech forests to determine whether they demonstrated stability from 1985 to 2002.

Chapter 4 compares changes in composition and structure in forests of contrasting composition and disturbance histories to determine whether late-successional forests demonstrate similar temporal dynamics.

Chapter 5 reports on the extent and magnitude of beech bark disease in the high-elevation beech forest of GRSM.

Chapter 6 explores the role of spatial scale in observations of temporal change in forest attributes.

Chapter 7 summarizes the results of this dissertation as they apply to forest succession theory and the possible drivers of temporal change in the high-elevation forests of GRSM.

Chapter 2

Long-term compositional change in the high-elevation beech forests of Great Smoky Mountains National Park: 1935-2000.

Abstract

Whether forest composition ever reaches a stable, self-replacing state is a fundamental question in ecology. In this study I examine 65 years of compositional change in a unique, late-successional forest type of Great Smoky Mountains National Park. High-elevation (> 1340 m) beech forests are dominated (> 50% relative density) by American beech (*Fagus grandifolia*), a shade-tolerant, slow-growing tree capable of regenerating by seed or root suckering. My objectives were to determine (1) whether these forests were stable from 1935-38 to 1976-85, (2) whether changes 1935-38 to 1976-85 differed from changes 1976-85 to 2000-02, and (3) whether understory composition is compatible with continued beech dominance. From 1935-38 to 1976-85, the high-elevation beech forests of GRSM were significantly enriched in beech, increasing from 250.8 stems/ha (65.9% relative density) to 496/ha (79.1%), and from 12.4 to 16.8 m^2/ha (43% to 64.8% increase in relative basal area) in basal area and depauperate in less shade-tolerant species. During the period 1976-85 to 2000-02, beech bark disease (BBD) infested some high-elevation beech forests in the park, causing a reversal of the trend towards increased beech density. However, the trend reappears when disease-free plots are examined separately. Composition of woody understory stems suggests that, without the invasion of BBD, these forests would have become more beech-dominated. High-elevation beech forests were not stable during the 65 years covered in this study, and may operate under the "slow-dynamics" successional process described in other forests of the eastern United States.

Introduction

The forest succession model predicts that as forests mature into late-successional stages forest attributes such as density and basal area become stable and shade-tolerant, late-successional species dominate (Huston 1994). From this hypothesis, it follows that late-successional forests dominated by a slow-growing species such as American beech (*Fagus grandifolia*) should be at or near equilibrium in density and basal area (White and Jentsch 2001). Despite the ubiquity of the model, evidence for the development of stability in temperate forests is equivocal: late-successional forests exhibiting "slow dynamics," such as the hemlock-hardwood forests of Michigan, are not in compositional equilibrium over ecologically relevant time frames (i.e. 30 to 100 years; Woods 2000a,b). However, few studies of long-term forest dynamics exist and fewer still cover periods greater than 10 years (Woods 2000a).

The high-elevation, beech-dominated forests of Great Smoky Mountains National Park (GRSM) are an ideal system to address the issue of stability in forest systems. American beech is a slow-growing, long-lived tree species capable of regenerating from seed or root sprouts (Tubbs and Houston 1990), though in the "beech gaps" of GRSM reproduction is almost exclusively from root suckering (Russell 1953, Sain and Blum 1981). Beech is considered very shade-tolerant (Loach 1967) and it is recognized as a climatic climax species throughout much of its range, including the Southern Appalachian Mountains (Tubbs and Houston 1990). Prior to the creation of GRSM, beech was not considered a valuable timber tree, and at high-elevations in GRSM beech trees tend to be stunted (Russell 1953) and therefore less marketable. For these reasons and because of their remoteness, the high-elevation beech forests in GRSM are considered relatively free of human disturbance (Pyle

1988). However, in 1993 beech bark disease (BBD) was discovered in GRSM (Houston 1994) and has progressed through the beech forests in eastern GRSM, causing extensive mortality; western beech stands were free of mortality as of 2000.

The purpose of this study is to establish baseline rates of change in high-elevation beech forests, and to test the hypothesis that these late-successional forests are stable by examining density and basal area changes over 65 years, prior to (1935-38 to 1976-85) and following (1976-85 to 2000-02) the introduction of BBD. Specifically, I sought to determine whether 1) high-elevation beech forest attributes were stable from 1935-38 to 1976-85, 2) changes in the attributes prior to BBD infestation differed from those from those afterward, and 3) the composition of understory stems indicates a shift in overstory composition.

Methods

STUDY LOCATION AND PLOT SELECTION

This study focuses on long-term changes in the density and basal area of monodominant (> 50% beech) high-elevation (< 1340 m) beech stands. In eastern GRSM, high-elevation beech forests occur as deciduous islands within a spruce-fir matrix and are found on south-facing landscape concavities at the tops of coves; canopy beech trees are rare within the spruce-fir matrix. West of the range of spruce-fir, beech occurs in monodominant stands and as a canopy co-dominant in high-elevation northern hardwood and Appalachian oak forest types.

In the 1930s, Frank Miller was hired to conduct a systematic survey of the vegetation of GRSM (MacKenzie and White 1998) resulting in data from nearly 1400 plots distributed throughout the park. Modern analysis of Miller's records indicates that high-elevation, beech-dominated forests have long been a recognizable part of the Smokies' landscape

(MacKenzie and White 1998), and data from more recent studies confirm that beech-dominated forests represent a unique forest type at high-elevations in GRSM (Golden 1981, Callaway et al. 1987).

Environmental and plot characteristics of beech forests: 1935-38 to 2000-02

In order to ensure an accurate comparison between Miller (1935-38) plots and contemporary beech forest plots, I selected only those Miller plots that had beech relative density exceeding 50% and that occurred in areas identified as mature forest using Charlotte Pyle's (1988) disturbance history map of GRSM. In order to compare plots with the same suite of site characteristics, Miller plots occurred at or above 1340 m elevation (the minimum elevation of contemporary plots to which Miller plots are compared), cover the same range of elevation as contemporary plots , and occur on upper slope positions (Table 2.1).

Although the 1935-38 plots were not monumented and therefore could not be relocated, high-elevation beech forests occupy sites defined by a relatively narrow set of environmental conditions. Some 1935-38 plots occur in the same patches of beech forest as contemporary plots (Figure 2.1); therefore, it is assumed that these data represent a snapshot of beech forest composition and structure in 1935-38 that can be compared to equivalent measurements from contemporary plots sampled 1976-85 to establish background changes in these forests prior to the onset of BBD.

Average slope and transformed aspect of 1935-38 plots were not different than that of 2000-02 plots (Table 2.1). Additionally, graphed plot elevations and aspects from 1935-38 and 2002-02 (which includes the 1976-85 plots) occupy the same range and extent of graphical space, indicating overlap in their environmental characteristics (Figure 2.2).

Table 2.1. Summary environmental and plot data for high-elevation beech forest plots.

	1935-38	1976-85	2000-02 all plots	2000-02 no BBD
# Plots	29	19	39	19
Area (ha)	2.3	2.5	4.8	2.1
Elevation range (m)	1341-1768	1473-1715	1342-1759	1406-1715
Mean elevation (sd)	1496^{a} (112.7)	1577^{b} (74.8)	1572.1^{b} (89.4)	1567^{b} (99.0)
Slope range (degrees)	2.9-35	6-30	3-33	3-33
Mean slope (sd)	21.3^{a} (9.6)	21.8^{a} (7.0)	19.7^{a} (7.8)	18.8^{a} (9,4)
Mean aspect (Beers transformed)	1.8^{a} (1.1)	2.2^{a} (1.1)	1.9^{a} (1.0)	1.9^{a} (1.0)

Figure 2.1. Location of 37 high-elevation beech forest plots sampled 1935-38 (yellow circles) and 39 plots established 1976-85 (red circles) and resampled 2000-02 in Great Smoky Mountains National Park.

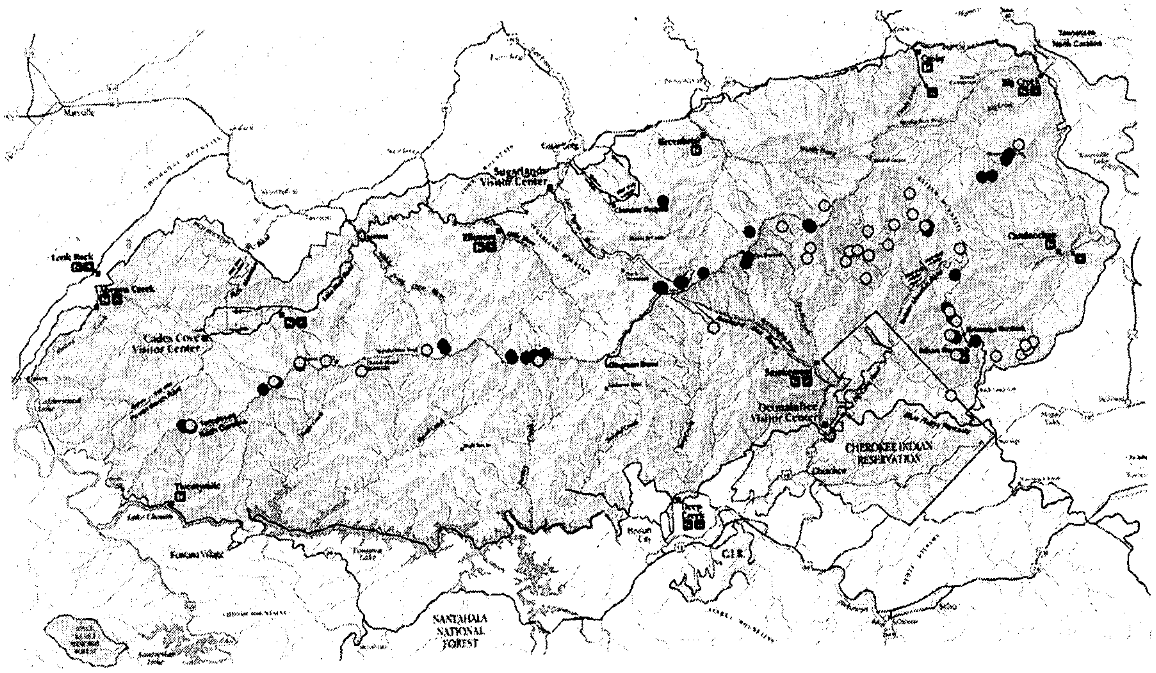
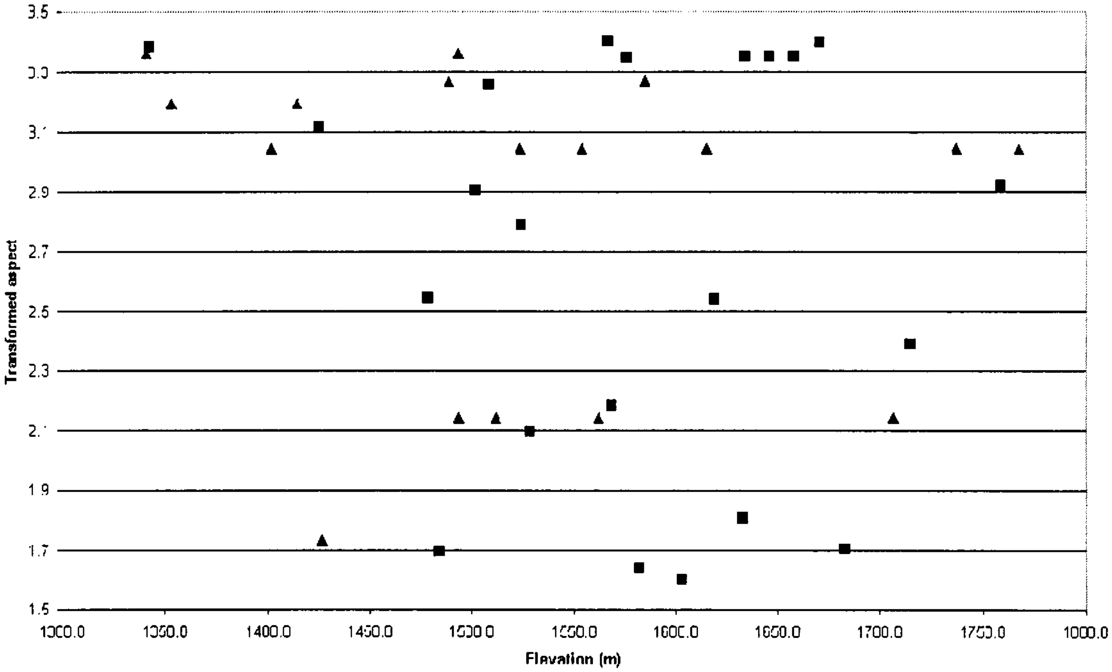

Sugarlands Visitor Center
Cades Cove Visitor Center
Look Rock
Cosby
Big Creek
Cataloochee
Smokemont
Oconaluftee Visitor Center
CHEROKEE INDIAN RESERVATION
Cherokee
Deep Creek
Twentymile
Fontana Village
Fontana Lake
Lake Cheoah
NANTAHALA NATIONAL FOREST
Tennessee
North Carolina
Bryson City

Figure 2.2. The relationship between elevation (m) and Beers transformed aspect for plots from 1935-38 (▲) and 2000-02 (■).


3.5
3.3
3.1
2.9
2.7
2.5
2.3
2.1
1.9
1.7
1.5
Transformed aspect
1300.0
1350.0
1400.0
1450.0
1500.0
1550.0
1600.0
1650.0
1700.0
1750.0
1800.0
Elevation (m)

However, average elevation of 1935-38 plots was significantly lower than that of contemporary plots. In GRSM beech forests stem density increases with elevation. In order to determine whether differences in density and basal area between the periods were due to the greater average elevation of contemporary plots, plots for both time periods were sorted into elevation bands. Differences in overall and beech density and basal area were tested in SAS v 8.2 using the non-parametric Wilcoxon two-sided test.

Contemporary data: 1976-85 to 2000-02

In 1976 two 0.1 ha permanent plots were established in a beech forest near Newfound Gap that Rudolf Becking and Robert Whittaker originally sampled in 1959 (Becking and Olson 1978). From 1976-1978, GRSM personnel established four 0.1 ha permanent vegetation plots in high-elevation beech forests. In 1985, 13 additional plots ranging from 0.12 to 0.25 ha were mapped with the location, identity and DBH of all stems > 10 cm. During the summers 2000-2002 the 19 permanent plots were remeasured and 20 additional plots were established to cover the range of environments occupied by high-elevation beech in GRSM.

All data in this study are relativized to per hectare values. Although the 1935-38 plot sizes are different (0.8 ha vs. 0.1 to 0.24 ha) than contemporary plots, the relevant measures in this study are the plot-level densities and basal areas of all species and of beech, which are not affected by the relatively small differences in plot size. Because the Miller DBH data sorted stems > 10 cm into 30 cm size classes, the geometric mean DBH for each stem was calculated using the methodology of MacKenzie and White (1998). With DBH data, relative basal areas were calculated for each species in all plots.

DATA ANALYSIS

Temporal change in forest composition

Measurements from 1935-38 to 1976-85 were used to compare forest attributes (overall and beech tree species densities and basal areas) of high-elevation beech forest over roughly 45 years before the invasion of beech bark disease (BBD) (Houston 1994). Then, using the 19 permanent plots, changes in the same forest attributes were compared from 1976-85 to 2000-02. Finally, measurements from 1935-38 were compared to all 2000-02 plots (39) and to the 19 plots without BBD mortality. Changes in the density and basal area of all plots and of beech by time period were examined using the Mann-Whitney test. Thus, this study provides a 65-year analysis of change in forest density and basal area prior to and after BBD invasion in the high-elevation beech forests of GRSM.

Temporal trends in community attributes

Community-level differences between 1935-38 and 1975-85 and between 1935-38 and 2000-02 were tested using Multi-response Permutation Procedure (MRPP) in PCORD (McCune and Grace 2002). MRPP is a non-parametric, multivariate statistical program used to test hypotheses of no difference between two groups of data. As a non-parametric procedure, MRPP is useful for ecological data, which often does not meet assumptions of normal distribution. For this analysis, the Sorensen's distance measure and group weighting were used. Groups contained plots sampled in each of the three sampling periods in this study; Group 1 contained 29 Miller plots sampled 1935-38, Group 2 contained 19 permanent plots sampled in the late 1976-85, Group 3 contained the 39 permanent plots sampled in 2000-02. Because they lack spatial independence, the permanent plots established 1975-85 and resampled 2000-02 were tested using Blocked-MRPP (MRBP). Because the question of interest was whether or not beech forest communities sampled at different times were similar, species density and basal area per hectare values were used in the plot X species matrix for MRPP and MRBP analyses.

Understory composition

Stems < 10 cm DBH were tallied by species in the field from 2000-02. These tallies were obtained to project near-term future forest composition in both BBD-free beech and diseased forests. Differences in beech and total woody understory stem densities in BBD-free versus diseased forests were examined using the Mann-Whitney test.

Results

Environmental and plot characteristics of beech forests: 1935-38s to 2000-2

The environmental attributes of the 1935-38 Miller plots and the 1976-85 to 2000-02 permanent plots are similar (Table 1, Figure 2). Plots in all time periods are beech dominated (> 50% beech relative density) and have the similar means and ranges for aspect and slope. Given that stem density increases with elevation, the greater elevation occupied by 2000-02 plots could be responsible for greater average stem density when compared with data from 1935-38. However, the increases in overall (plot) and beech stem density occurred across elevation bands, with significant increases in the lowest elevation plots (Table 2). Basal area decreased with elevation and in general, 2000-02 basal area was lower than in 1935-38.

Table 2.2. Mean plot and beech density (#/ha) and basal area (m^2/ha) in 29 plots sampled in 1935-38 and 39 plots sampled in 2000-02, sorted into 150 m elevation bands. Values in parentheses are standard deviations.

	# plots		Plot density		Beech density		Plot BA		Beech BA	
Elevation range (m)	1935-38	2000-02	1935-38	2000-02	1935-38	2000-02	1935-38	2000-02	1935-38	2000-02
1340-1500	18	9	346.8^{a} (172.5)	556.7^{b} (155.0)	222.5^{a} (108.6)	367.9^{b} (147.9)	28.8^{a} (12.3)	25.1^{a} (7.7)	12.3^{a} (8.3)	13.0^{a} (8.1)
1500-1650	8	22	384.1^{a} (127.4)	509.5^{a} (301.7)	277.4^{a} (124.1)	308.0^{a} (218.9)	32.1^{a} (12.5)	22.8^{a} (8.6)	13.8^{a} (7.1)	12.8^{a} (7.0)
1650-1800	3	8	571.3^{a} (386.8)	703.9^{a} (319.0)	349.7^{a} (197.6)	521.3^{a} (362.6)	19.7^{a} (6.7)	17.6^{a} (8.7)	9.2^{a} (2.5)	7.9^{a} (8.9)

[a] numbers followed by the same letter in each column pair are not significantly different at $\alpha = .05$.

Temporal trends in forest composition: 1935-38 to 1976-85

Overall stem density of the forests in 1976-85 was significantly greater ($p < 0.05$) than in 1935-38, while basal area exhibited a slight and insignificant decline (Table 2.3). During this period beech density and basal area increased significantly (97.8% and 35.5%, respectively). Beech relative density increased from 65.9% to 78.7% of stems during this period. In 1935-38 there were two relatively common shade-intolerant to medium-tolerant species: yellow-birch (*Betula allegheniensis*) and silverbell (*Halesia tetraptera* var *monticola*). Contrary to expectations of the forest succession model, yellow-birch, a shade-intolerant species, increased in density between 1935-38 and 1976-85 (29.5 vs. 36.4/ha) even while beech density increased. In contrast, silverbell was relatively abundant in 1935-38 but was almost completely absent in 1976-85. Interestingly, even shade-tolerant species such as red spruce (*Picea rubens*), sugar maple (*Acer saccharum*) and eastern hemlock (*Tsuga canadensis*) had reduced densities in 1976-85.

One notable loss was American chestnut (*Castanea dentata*), which disappeared following the invasion of the chestnut blight fungus (*Cryphonectria parasitica*). Because chestnut occurred in only 12.5% of beech forest plots and at a low relative density (2.9%), its loss alone cannot account for the increase in beech density.

Temporal trends in forest composition: 1976-85 to 2000-02

During this period, BBD invaded high-elevation beech forests in eastern GRSM, resulting in a decrease in overall density and a significant decrease in basal area, led by the mortality of beech (Table 2.3). Although beech was still significantly denser in2000-02 than 1935-38 its relative density declined to the 1935-38 level. Most co-occurring tree species (including

Table 2.3. Mean and relative densities (#/ha) and basal areas (m^2/ha) of tree species (≥ 10 cm) (RD) in high-elevation beech forests 1935-2002.

	1935-38				1976-85				2000-02 (all)				2000-02 (No BBD)			
Species	#/ha (sd)	RD	m^2/ha (sd)	RBA	#/ha (sd)	RD	m^2/ha (sd)	RBA	#/ha (sd)	RD	m^2/ha (sd)	RBA	#/ha (sd)	RD	m^2/ha (sd)	RBA
Abies frasieri	0.8 (4.5)	0.2	0.02 (1.0)	0.07					4.1 (9.9)	0.7	0.06 (0.1)	0.3	2.5 (5.5)	0.4	0.03 (<0.01)	0.1
Acer pensylvanicum	0.4 (2.2)	0.1	0.01 (0.1)	0.03	2.9 (12.1)	0.5	0.04 (0.2)	0.2	4.4 (19.3)	0.8	0.08 (0.4)	0.4	8.9 (27.3)	1.3	0.17 (0.5)	0.7
A. rubrum	1.2 (3.7)	0.3	0.41 (1.4)	1.3					0.8 (4.8)	0.1	0.15 (0.1)	0.7				
A. saccharum	18.2 (33.2)	4.8	4.05 (5.9)	14.1	13.4 (25.4)	2.1	1.67 (3.1)	6.5	18.6 (39.1)	3.3	1.17 (2.2)	5.3	22.4 (52.1)	3.2	1.06 (2.0)	4.1
A. spicatum					2.9 (12.1)	0.5	0.03 (0.1)	0.1	6.0 (14.8)	1.1	0.09 (0.2)	0.4	2.8 (9.3)	0.4	0.05 (0.2)	0.2
Aesculus octandra	14.6 (26.5)	3.9	3.28 (7.1)	11.4	53.6 (71.7)	8.5	2.63 (2.5)	10.2	23.0 (40.3)	4.1	1.79 (2.6)	8.1	41.8 (51.3)	6.0	2.68 (2.7)	10.3
Amelanchier arborea	5.9 (14.2)	1.6	0.18 (0.5)	0.6	6.9 (16.9)	1.1	0.21 (0.4)	0.8	15.0 (46.7)	2.8	0.41 (0.9)	1.9	6.3 (14.5)	0.9	0.2 (0.5)	0.8
Betula allegheniensis	28.7 (32.4)	7.5	3.34 (11.1)	11.6	36.4 (42.0)	5.8	3.28 (4.3)	12.7	68.8 (112.3)	12.4	4.03 (5.1)	18.1	40.2 (51.1)	5.8	3.31 (4.5)	12.7
B. lenta	0.8 (3.1)	0.2	0.12 (0.5)	0.4					0.4 (1.8)	0.1	0.02 (0.2)	0.1				
Castanea dentata	9.7 (36.1)	2.6	0.74 (2.5)	2.6												
Fagus grandifolia	250.8^{a} (124.8)	65.9	12.38^{c} (7.5)	43.0	496.0^{b} (172.8)	78.7	16.77^{d} (6.2)	64.8	365.5^{b} (249.7)	65.7	11.85^{c} (7.7)	53.3	539.5^{b} (205.4)	77.9	17.46^{d} (6.0)	67.0
Fraxinus americana									0.5 (3.2)	0.1	0.1 (0.6)	0.4				
Halesia tetraptera	19.4 (33.8)	5.1	1.08 (1.6)	3.8	0.2 (0.7)	<0.1	<0.01 (<0.1)	<0.1	4.4 (21.2)	0.8	0.22 (1.1)	1.0	1.6 (6.9)	0.2	0.11 (0.5)	0.4
Magnolia acuminata	0.4 (2.2)	0.1	0.06 (0.3)	0.2					0.1 (0.6)	<0.1	<0.01 (<0.1)	<0.1	0.2 (0.9)	<0.1	<0.01 (<0.1)	<0.1
Nyssa sylvatica					0.4 (1.5)	0.1	<0.01 (<0.1)	<0.1								
Picea rubens	20.0	5.2	1.02	3.5	9.3	1.5	0.49	1.9	32.1	5.8	1.31	5.9	15.7	2.3	0.51	2.0

	(74.4)		(3.2)		(12.1)		(1.1)		(40.5)		(1.9)		(26.0)		(1.0)	
Prunus pensylvanica									2.6 (11.6)	0.5	0.23 (1.0)	1.0				
P. serotina	1.2 (3.7)	0.3	0.42 (1.4)	1.5	3.7 (7.4)	0.6	0.16 (0.3)	0.6	5.6 (10.3)	1.0	0.6 (1.5)	2.7	4.7 (6.8)	0.7	0.38 (0.7)	1.5
Quercus rubra	1.7 (7.1)	0.4	0.36 (1.6)	1.2	3.9 (11.3)	0.6	0.56 (1.5)	2.2	3.4 (17.0)	0.6	0.9 (0.2)	0.4	5.4 (13.4)	0.8	0.09 (0.2)	0.4
Sorbus americana									0.3 (1.6)	<0.1	<0.01 (<0.1)	<0.1				
Tilia americana	2.1 (6.5)	0.5	0.47 (1.6)	1.6												
Tsuga canadensis	4.2 (11.9)	1.1	0.88 (2.7)	3.1	0.4 (1.5)	1.0	<0.1 (0.1)	0.1	0.4 (1.8)	0.1	0.04 (0.2)	0.2				
Total	380.3^{a} (193.5)		28.8^{c} (12.1)		629.9^{b} (135.4)		25.9^{c} (4.3)		556.7^{b} (83.1)		22.3^{d} (2.6)		692.2^{b} (122.5)		26.1^{c} (3.8)	

[a] Columns with the same letter are not significantly different at $\alpha = .05$.

shade-intolerant species) demonstrated modest gains in density, although yellow buckeye (*Aesculus octandra*), and important co-dominant in beech forests, declined even in disease-free plots. The density of yellow-birch increased nearly 90% (from 36.4 to 68.8 stems/ha), but the gain was smaller in plots without BBD (36.4 to 40.2/ha). Silverbell increased modestly, with a bigger increase in plots affected by BBD.

In plots with no BBD overall density and beech density were significantly greater than in 1935-38. Additionally, beech basal area was significantly greater than in 1935-38 while overall basal area was slightly lower. Between 1976-85 and 2000-02 the trend of increasing density noted prior to BBD infestation continued in disease-free plots.

Remeasurement of the 19 permanent plots (12976-85 to 2000-02) represents a subset of plots that can be used to substantiate patterns from the larger data sets. Data from these plots substantiates trends noted in the larger data set because in disease-free plots tree density increased 1.7% (634.2 to 645 stems/ha), and beech density increased 3.3% (493.9 to 510.1), resulting in an increase in beech relative density from 77.9 to 79.1% and beech basal area increased 13.9% (Table 2.4), although the changes were not significant. Red spruce and sugar maple density also increased (118% and 123% respectively), though these species remain relatively minor components of high-elevation beech forests.

In disease-free plots, the density of less shade-tolerant species such as buckeye, black cherry (*Prunus serotina*), shadbush (*Amelanchier arborea*), and northern red oak (Quercus rubra) declined. Silverbell, which was dramatically lower in density in 1976-85 than 1935-38, was nonexistent in these plots in 2000-02. In a continuation of the trend noted from 1935-38 to 1976-85, yellow-birch density increased slightly in BBD-free plots, as did its relative density.

Table 2.4. Mean and relative tree densities (#/ha) and basal areas (m^2/ha) in 19 permanent plots before and after BBD infestation.

	1976-85 (pre-BBD)				2000-02 (post-BBD)			
	BBD-free (10 plots)		BBD (9 plots)		BBD-free (10 plots)		BBD (9 plots)	
Species	#/ha (sd)/ m^2/ha (sd)	RD/ RBA	#/ha (sd)/ m^2/ha (sd)	RD/ RBA	#/ha (sd)/ m^2/ha (sd)	RD/ RBA	#/ha (sd)/ m^2/ha (sd)	RD/ RBA
Abies frasieri					3.8 (6.8) 0.5 (1.0)	0.6 0.2		
Acer pensylvanicum	5.0 (15.8) 0.8 (0.2)	0.8 0.3			7.0 (22.1) 0.15 (0.4)	1.1 0.5		
A. saccharum	3.4 (6.7) 0.94 (2.0)	4.5 3.0	27.6 (35.4) 2.85 (4.2)	4.4 11.8	7.6 (9.8) 0.83 (1.5)	1.2 2.5	24.4 (26.9) 1.9 (2.2)	6.0 10.3
A. spicatum	5.0 (15.8) 0.05 (1.0)	0.8 2.0			1.4 (3.3) 0.2 (<0.1)	0.2 <0.1		
Aesculus octandra	73.7 (83.1) 3.76 (2.7)	11.6 12.5	25.0 (41.3) 1.56 (1.9)	4.0 6.4	53.4 (62.3) 3.14 (3.0)	8.3 9.6	21.9 (35.3) 1.82 (2.6)	5.3 9.8
Amelanchier arborea	2.5 (7.9) 0.09 (0.3)	0.4 0.3	13.3 (24.3) 0.40 (0.6)	2.1 1.6	1.8 (3.8) 0.10 (0.2)	0.3 0.3	6.9 (15.7) 0.31 (0.7)	1.7 1.7
Betula allegheniensis	33.3 (6.3) 4.31 (5.1)	5.3 14.4	40.7 (38.0) 3.43 (3.0)	6.5 10.0	36.1 (45.8) 4.16 (4.9)	5.6 12.8	37.3 (42.3) 3.05 (5.0)	9.1 16.5
Betula lenta							0.7 (1.9) 0.04 (0.1)	0.2 0.2
Fagus grandifolia	493.9 (171.5) 19.44 (6.1)	77.9 64.8	499.0 (188.4) 15.74 (6.8)	80.0 64.9	510.1 (185.3) 22.14 (5.0)	79.1 67.9	282.1 (199.3) 9.14 (5.1)	68.8 49.4
Halesia tetraptera			0.4 (1.1) <0.01 (<0.1)	0.1 <0.1				
Magnolia acuminata					0.4 (1.3) <0.01 (<0.1)	0.1 <0.1		
Nyssa sylvatica			0.9 (2.3) 0.01 (<0.1)	0.1 <0.1				
Picea rubens	6.5 (9.4) 0.27 (0.6)	1.0 0.9	13.3 (14.9) 0.85 (1.5)	2.1 3.5	14.2 (20.9) 0.62 (1.1)	2.2 1.9	33.0 (24.7) 1.53 (1.9)	8.0 8.3
Prunus serotina	5.3 (9.3) 0.19 (0.3)	0.8 0.7	1.4 (2.4) 0.13 (0.3)	0.2 0.5	4.9 (8.2) 0.44 (1.6)	0.8 0.3	1.4 (2.4) 0.26 (0.6)	0.3 1.4
Quercus rubra	5.6 (14.5) 0.88 (1.9)	0.9 2.9	1.4 (3.8) 0.22 (0.6)	0.2 0.9	4.3 (10.6) 0.95 (2.1)	0.7 2.9	1.4 (3.8) 0.3 (0.8)	0.3 1.6
Tsuga canadensis			0.9 (2.3) 0.(0.2)	0.1 0.2			0.9 (2.3) 0.14 (0.4)	0.2 0.8
Total	634.2 (135.3) 30.0 (5.0)		623.9 (136.2) 24.2 (4.0)		645.0 (134.5) 32.5 (5.5)		410.0 (74.0) 18.5 (2.3)	

In contrast, overall and beech density and basal area decreased in diseased plots. Overall density decreased 34.3% (623.9 to 410 stems/ha) and beech density dropped 43.5% (499 to 282.1/ha), with similar changes in basal area. Yellow-birch, which as a shade-intolerant species should benefit from canopy openings caused by dying beech and the litter-free substrate caused by fallen trees, decreased in density and basal area. Similarly, buckeye, shadbush, and sugar maple (*A. saccharum*) declined in density, and all except buckeye declined in basal area, suggesting that the loss of beech in these forests had a community-level effect. The densities and basal areas of other, less important species, were constant. The exception to this trend was red spruce, whose density increased 148% (13.3 to 33 stems/ha) with a concomitant increase in basal area. Red spruce increased in both BBD-free and diseased plots, suggesting that the increase is not due to the demise of overstory beech.

Temporal trends in community attributes

Results of the multivariate analysis of community composition in MRPP and MRBP are consistent with the changes noted for overall and beech density and basal area (Table 2.5). In general, the within-group agreement value (A) was positive or very close to zero, which means the plots were slightly more homogenous than would be expected by chance, which is predictable in beech-dominated plots. The only period in which beech forests did not differ significantly was between 1975-85 and 2000-02 when the permanent plots were resampled. This result is unexpected in light of the dramatic effect of BBD during this period. However, gains in BBD-free plots probably offset, at least partially, the losses in diseased plots.

From 1935-38 to the late 1970s (prior to the onset of BBD in the park) changes in beech forest community attributes mirror the changes in beech density. During this period

Table 2.5. Results of MRPP and MRBP comparisons of community composition between high-elevation beech forests at time periods 1935-1976, 1935-2002, and 1976-2002.

	Density		Basal Area	
Periods compared	A	p-value	A	p-value
1935-38 to 1976-85	0.128	<0.0001	0.034	0.0028
1976-85 to 2000-02 (permanent plots)	-0.005	0.5164	0.024	0.1331
1935-38 to 2000-02 (all plots)	0.051	0.0090	0.035	0.0003
1935-38 to 2000-02 (no BBD plots)	0.110	<0.0001	0.046	0.0005

community dominance covaried with beech relative density (Table 2.6), which is to be expected in monodominant forest types. Likewise community diversity decreased from 1935-38 to 1976-85 as beech dominance increased, a trend which continued until 2000-02 in plots without BBD. In contrast, plots with BBD-killed beech trees exhibited decreased dominance and increased diversity, though it should be noted that this is due to the decline in beech dominance rather than an increase in the number of tree species.

Understory composition

In BBD-free forest stands there are currently 63% more woody understory stems/ha than in diseased stands (Table 2.7), a significant difference driven by the greater density of beech stems. Beech woody understory stems are significantly denser in BBD-free stands than in diseased stands. Other species found in disease-free stands occur in densities roughly equivalent to those in diseased stands.

The composition of the understory in BBD-free forests suggests that beech dominance of stems > 10 cm DBH will continue as long as the forests remain healthy. Beech is the dominant understory woody species, representing > 92% of all stems < 10 cm DBH in BBD-free stands. In contrast, beech density in diseased forests is diminished relative to that in disease-free stands and it is less dominant (87.5% relative density). Understory species richness in diseased stands is greater than that of healthy stands (9 vs. 8 respectively), and stem densities of all other species are greater in diseased stands. The relatively low understory densities in diseased stands indicates that secondary succession following BBD infestation is somewhat slower than might be expected given the extent of beech mortality and consequent opening of the canopy.

Table 2.6. Summary tree community data for high-elevation beech forest plots.

	1935-38	1976-85 (noBBD)	1976-85 (BBD)	2000-02 (no BBD)	2000-02 (BBD)
Beech relative density (%)	66.4	77.9	80.0	79.1	68.8
Simpson's C (s.d.)	.457 (.107)	.623 (.169)	.648 (.177)	.636 (.167)	.495 (.126)
Shannon's H′ (s.d.)	1.347 (.082)	.854 (.081)	.838 (.070)	.874 (.070)	1.134 (.097)

Table 2.7. Density/ha of woody stems < 10 cm in 19 diseased (9 plots) and BBD-free (10 plots) high-elevation beech forests.

	Stem size (cm)						
Species	Seed	0-1	1-2.5	2.5-5	5-10	Sum	RD (%)
Diseased plots							
Fagus grandifolia	4098[a] (258.8)	921 (75.4)	610 (72.7)	366 (31.7)	250 (27.5)	6245[a] (273.5)	87.5
Acer pensylvanicum	0	55 (14.5)	23 (5.0)	2 (0.6)	10 (2.5)	90 (22.6)	0.6
A. saccharum	334 (68.9)	11 (1.4)	13 (1.4)	26 (2.9)	14 (2.0)	398 (74.0)	5.6
A. spicatum	143 (37.8)	0	4 (0.9)	0	0	147 (38.7)	2.1
Aesculus octandra	60 (10.5)	12 (2.1)	0	5 (1.3)	12 (1.6)	89 (12.0)	1.2
Amelanchier arborea	0	4 (0.9)	0	2 (0.6)	0	6 (1.0)	0.1
Betula allegheniensis	95 (25.2)	12 (2.1)	4 (0.9)	2 (0.6)	2 (0.6)	115 (24.5)	1.6
Picea rubens	0	6 (1.0)	16 (2.9)	33 (6.4)	42 (7.2)	97 (17.2)	1.4
Tsuga canadensis	0	0	0	4 (0.9)	0	4 (0.9)	0.1
Total	**4730[a]**	**971**	**670**	**440**	**330**	**7141[a]**	
No BBD plots							
F. grandifolia	7718[b] (349.8)	1646 (92.3)	697 (55.8)	354 (19.3)	327 (25.6)	10742[b] (426.6)	92.3
Abies fraseri	0	0	1 (0.3)	0	0	1 (0.3)	<0.1
A. pensylvanicum	94 (25.8)	38 (10.6)	16 (4.4)	34 (9.7)	16 (4.4)	198 (55.7)	1.7
A. saccharum	63 (17.7)	141 (38.8)	63 (13.8)	0	41 (8.9)	308 (61.4)	2.6
A. octandra	10 (2.9)	10 (1.5)	18 (2.7)	17 (2.4)	10 (1.5)	65 (6.9)	0.6
B. allegheniensis	219 (31.2)	0	6 (1.8)	13 (2.3)	9 (2.7)	247 (31.6)	2.1
P. rubens	0	0	5 (1.2)	2 (0.6)	3 (0.9)	10 (2.0)	0.1
Q. rubra	63 (17.7)	0	0	0	0	63 (17.7)	0.5
Total	**8167[b]**	**1835**	**806**	**420**	**406**	**11634[b]**	

[a] numbers followed by the same letter in a column are not significantly different at $\alpha = .05$.

Discussion

The high-elevation beech forests of Great Smoky Mountains National Park were not stable during the 65-year period of this study. American beech forests, dominated by an extremely shade-tolerant, late-successional species, were significantly denser, had lower diversity and were more beech-dominated in 1976-85 than in the 1930s. The apparent trend of increasing beech dominance between 1935-38 and 1976-85 continued in BBD-free plots resampled in 2000-02. The relative densities of woody understory species suggests the trend towards increased beech dominance will continue in high-elevation beech stands that remain free of BBD.

Epidemic diseases represent major allogenic disturbances that should disrupt successional processes (Dobson and Crawley 1994), especially in monodominant forest stands where the host tree is the dominant species. The results of this study support this idea: following BBD infestation in 1993, community dominance and diversity measures of diseased beech forests returned to levels near those of the earlier beech forests, while in BBD-free plots the dominance and diversity trends noted from 1935-38 to 1976-85 continued to 2000-02. Beech mortality appears to have community-level consequences: density and basal area of most of the important co-dominant species declined following BBD infestation in diseased stands. Additionally, woody understory stem densities were significantly lower in diseased beech stands.

The eastern United States has already sustained the loss of one forest dominant: in the early 20th century chestnut blight (*Cryphonectria parasitica*), killed as many as 4 billion American chestnut trees (Miller 1987). Results of studies of forest succession following chestnut blight found that the removal of chestnut as a dominant species resulted in forests of greater tree species richness (Castello et al. 1995) composed of species from earlier successional stages (Dobson and Crawley 1994). Results of this study differ in that, at least initially, only red spruce, a very shade-tolerant species (Tubbs and Houston 1990), increased in importance in diseased stands, not the fast-growing, shade-intolerant species expected after the death of as much as 100% of a canopy dominant. Beech replacement by shade-tolerant understory species has been reported in diseased beech forests in New York (Runkle 1990). In this study, forest succession in diseased beech stands might be inhibited by the profuse growth of blackberry (*Rubus canadensis*), which is ubiquitous at high elevations and grows in dense thickets in diseased beech stands. Blackberry seems to have reduced the density even of beech sprouts, which might otherwise be expected to survive competition from blackberry owing to their extreme shade-tolerance and ability to utilize resources from the roots of the mother plant (Chapter 5).

The high relative density of understory beech in BBD-free stands suggests that the high-elevation beech forests of GRSM would be changing even if BBD had not invaded, with beech continuing to increase in dominance. Whether beech would continue to increase in dominance is subject to gap dynamics and storm frequencies which can affect understory/overstory transition probabilities (White et al. 1985) and BBD, which is likely to eventually infect all high-elevation beech stands in GRSM (Chapter 5). With BBD, beech forest composition is likely to be unstable for the foreseeable future. Beech sprouts still dominate the understory, but as genets of susceptible overstory trees, they will eventually become infected themselves, probably without achieving canopy status. The likely outcome of the continual dieback of beech sprouts is the eventual ascension to canopy status of species that were once co-dominant and suppressed species and the loss of this unique forest type.

Because I compared non-permanent plot data collected 1935-38 with data from permanent plots established 1976-85, and resampled 2000-02, it is not possible to rule out the effect spatial variability has on differences in composition. However, the results of this study are validated by 1) the overlap in environmental and plot compositional and structural characteristics between the non-permanent and permanent plots, 2) the continuation from 1976-85 to 2000-02 of trends observed between 1935-38 to 1976-85, and 3) the finding that the greater beech density in contemporary plots is a temporal change and not due to their greater elevation.

Conclusions

The forest succession model proposes that as forests proceed through late-succession, forest attributes such as stem density and basal area will become stabilize and shade-tolerant species will dominate. Empirical data from forests dominated by late-successional species have shown that although the importance of shade-tolerant species increases there is little support for the proposal that they become stable (Woods 2000a,b). The high-elevation beech forests of GRSM demonstrate an analogous "slow-dynamics" successional pattern to that of the forests of the Great Lakes region by exhibited increasing relative density of a shade-tolerant species, greater community dominance, and lower diversity over 65 years. The results of this study, in conjunction with those of Woods (2000a,b), suggest that the "stability" paradigm does not apply to late-successional forests.

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Chapter 3

Temporal trends in tree diameter, basal area, and biomass in the high-elevation beech-dominated forests of Great Smoky Mountains National Park.

Abstract

Temporal trends in size-specific mortality, ingrowth, and accretion of stem diameter, basal area, and aboveground biomass (AGB) are reported for 11 late-successional high-elevation beech forest plots in Great Smoky Mountains National Park. Beech forest demographics indicate that in plots with high beech bark disease (BBD) mortality, beech stem mortality is significantly higher and beech stem ingrowth significantly lower than in plots with little or no mortality, suggesting a compositional shift in BBD-affected plots away from beech dominance. Size-specific trends in mortality indicate that in high-BBD plots, the disease kills beech stems roughly in proportion to their abundance by size class, which is a departure from normal mortality patterns. Beech forests unaffected by BBD increased basal area by as much as 41%, although per capita accretion was greatest in beech forests with high mortality suggesting that the opening of the canopy stimulated growth in co-occurring trees. The temporal pattern of basal area and AGB increase observed in this study is contrary to expectations of late-successional forests and early descriptions of these forests as climax forests growing in extreme conditions. The increases in basal area and biomass in high-elevation beech forests are consistent with the results of other studies in GRSM that suggest that environmental conditions including nitrogen deposition, longer growing seasons, and increased CO_2 concentrations can enhance forest growth.

Introduction

In late-successional forests, system-wide structural attributes such as tree diameter, basal area, and biomass are expected to be stable, albeit with small fluctuations (Woods 2000). Preliminary data covering the period 1985-2002, from putative old-growth beech forest plots in western Great Smoky Mountains National Park (GRSM) suggest that they are accreting basal area at a rate higher than expected in late-successional forests (Chapter 5), which suggests that stand-level growth patterns are inconsistent with the successional paradigm (Smith and Long 2001). Several hypotheses may explain the high growth rates observed in high-elevation beech forests: 1.The forests are not late-successional and are in the aggradation phase of forest succession, in which case the largest stems should account for most of the accretion and stem densities should decrease as a result of self-thinning, 2. The forests are recovering from grazing, reduction in fire, or selective logging, in which case most of the accretion would be in understory stems (ingrowth), 3. The forests are accreting basal area due to environmental changes such as global warming, increased length of the growing season, or nutrient enhancement in the form of atmospheric CO_2 enrichment and/or the deposition of nitrogenous compounds, in which case all stems should accrete basal area with the largest accreting most.

In order to determine which of the above hypotheses applies to accreting beech forests, I examine beech forest size structure and size-related patterns of diameter, basal area, and biomass accretion, stem mortality, and ingrowth, and their correlations with environmental and soil chemical characteristics in 11 permanent, mapped, beech-dominated forest stands in GRSM to answer the following questions: 1. Is the size structure of high-elevation beech consistent with the hypothesis that they are late-successional? 2. What were the size-specific ingrowth, accretion, and mortality patterns for trees > 10 cm in these forests during the study period (more specifically, are all stem sizes contributing equally to accretion in western GRSM beech forests)? 3. Are demographic patterns correlated with environmental or soil characteristics?

Methods

Study location and plot selection and remeasurement

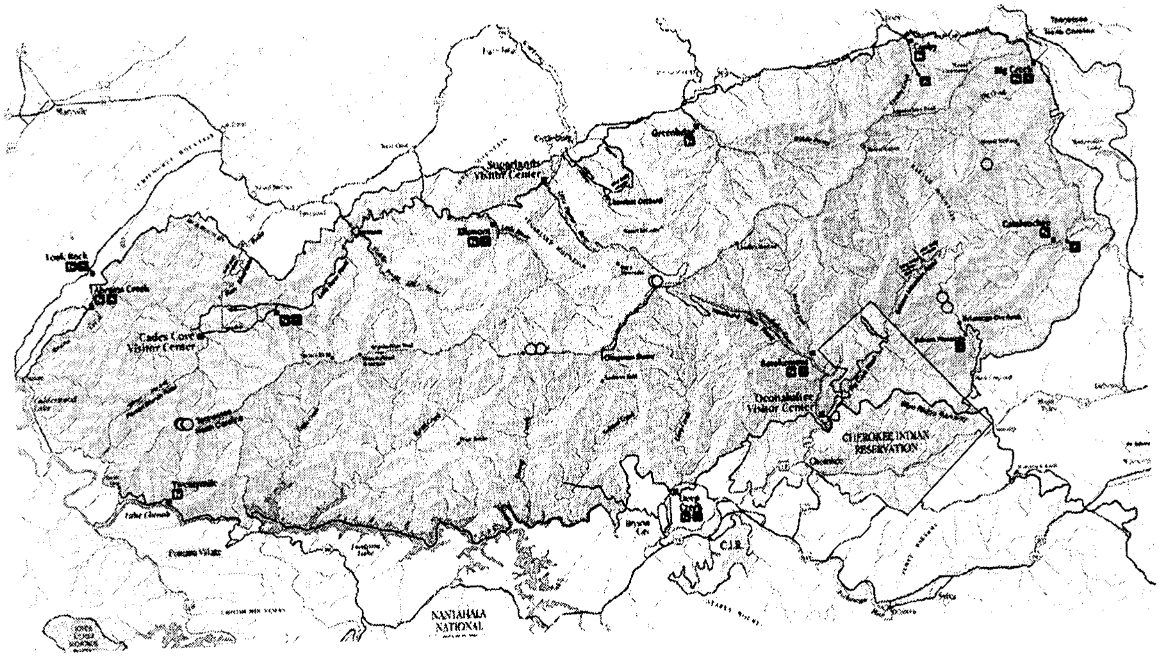
Prior to the establishment of the Great Smoky Mountains National Park in 1934, high-elevation sites were used for livestock grazing; historical records indicate that some of the ridgetop "balds" in the park were created by herders seeking good grazing conditions (Lindsay and Bratton 1979, Brown 2000). Much of the high-elevation forest are in GRSM however, avoided the extensive and heavy logging that occurred at lower elevations (Pyle 1988). High-elevation beech forests in particular were not logged due to their remoteness, the relatively small size and stunted architecture of trees in high-elevation habitat, and the low economic value of beech wood.

In the late 1970s permanent vegetation plots, including fenced exclosures, were established in 11 high-elevation beech forests in GRSM to study the effects of European wild boar (*Sus scrofa*) rooting on herb populations. In 1985, maps of tree species by DBH were created and were used in the summer of 2000 for the remeasurement of all tree stems ≥ 10 cm DBH. The size of the mapped tree plots ranges from 0.12 to 0.25 ha (Table 3.1). The plots occur across the range of high-elevation beech in GRSM (Figure 3.1). In 1993 beech bark disease, an exotic insect-fungal pathogen complex invaded GRSM (Houston 1994), and caused extensive mortality in eastern GRSM (Chapter 5). The disease is slowly migrating

Table 3.1. Plot characteristics for 11 high-elevation beech forest plots in Great Smoky Mountains National Park. Plots are listed from in order from east to west.

Plot	**Size (ha)**	**Elev (m)**	**Slope %**	**Aspect (^{0} azimuth)**	**BBD severity**
PHG	0.16	1576	24	123	High
BM1	0.1925	1568	24	230	High
BM2	0.1925	1593	28	189	High
SPAC	0.3	1621	27	183	High
SPA1	0.1	1659	25	167	Low
SPA2	0.1	1646	28	167	Low
SPA3	0.1	1634	30	167	Low
DS1	0.12	1715	6	345	None
DS2	0.12	1629	30	166	Low
GB1	0.2375	1784	20	347	None
GB2	0.25	1494	11	31	None

Figure 3.1. Location of 11 high-elevation beech forest plots in Great Smoky Mountains National Park mapped in 1985 and resampled in 2000.


Sugarlands Visitor Center
Cades Cove Visitor Center
Oconaluftee Visitor Center
CHEROKEE INDIAN RESERVATION
NANTAHALA NATIONAL
Look Rock
Greenbrier
Elkmont
Cosby
Big Creek
Cataloochee
Smokemont
Deep Creek
Bryson City
Cherokee
Fontana Village
Tennessee
North Carolina

westward, but as of 2000 no BBD-caused beech mortality had been recorded in western GRSM forests.

During remeasurement of the mapped plots, diameter breast height (DBH), tree condition (1: no canopy dieback, 2: 1-25% dieback, 3: 25-50% dieback, 4: 50-75% dieback, 5: 75-99% dieback), and XY coordinates of all surviving stems were recorded, as were the DBH and coordinates of dead stems (tree condition 6). Trees present on the original maps, but missing during remeasurement, were assumed to have died. The identity, DBH, tree condition, and coordinates of any new stems ≥ 10 cm (ingrowth) were also recorded and the maps updated to note their location.

Beech forest size structure and age relationships

In order to examine the size structure of beech forests, stems of all species were sorted into 5 cm DBH classes. Negative exponential or power function size structure curves (Hett and Loucks 1971, 1976) describe uneven-aged forests (Leak 1965) and are considered to be representative of late-successional forests. Size structure may not be predictive of age structure in some forests however. This criticism may be particularly true in forests dominated by extremely shade-tolerant and clonally reproducing trees such as high-elevation beech in GRSM (Blozan 1995). To determine whether the beech forests deviate from the expected size-age relationships, data from 215 cored and aged beech stems collected from forests spanning the range of beech in GRSM (Blozan 1995) were analyzed using regression analysis (PROC REG in SAS 8.2).

Size-specific demographic trends in forest attributes

Size-specific accretion, mortality, and ingrowth were calculated to examine plot and species-level changes in forest attributes such as diameter growth (cm), basal area (BA in m^2/ha), and aboveground biomass (ABG in Mg/ha) during the study period. Size-specific diameter by size class are reported change in accretion, mortality and ingrowth are reported because it is the only measure that increases linearly for all stem sizes and therefore is the best measure for depicting growth by size class. Because stem diameter estimates of ingrowth represent the total diameter of trees growing into the 10 cm diameter class between 1985 and 2000 they do not adequately represent the change in diameter of these stems during the study period. In order to more accurately estimate the diameter increase of ingrowing stems so that it is more directly comparable to the diameter increase of accreting stems, it was assumed that their per capita rate of diameter accumulation of ingrowth was equivalent to that of trees in the 10-15 cm size class during the study period. In order to compare demographic patterns of temporal change in these attributes, stems were allocated to 5 cm diameter classes.

Biomass regressions obtained from measurements of local trees are recommended for biomass estimation in relatively small-scale studies such as this one (Jenkins et al. 2004). However, local biomass estimates based on DBH were available for only some of the species found in high-elevation beech forests in GRSM (Busing et al. 1993). Because the biomass estimates differed only slightly by species and across DBH classes, the equations provided by Jenkins et al. (2003) were used to because they offer a standard, consistent method of estimating aboveground biomass of forest trees from DBH alone. Although DBH and tree height are recommended for regional and larger scale applications, adding tree height to biomass regressions results in a minimal increase in R^2 (Ter-Mikaelian and Korzukhin 1997), and DBH is adequate for local biomass estimation (Jenkins et al. 2003). Aboveground annual net primary production (ANPP in Mg/ha/yr) was estimated by adding the increase in ABG due to accretion to the ABG increase of ingrowth and dividing by the number of years in the study.

Because it has a stronger relationship to stand volume and biomass (Avery and Burkhart 1994), quadratic mean diameter (the diameter of the tree of mean basal area) [QMD = $\sqrt{\sum(D^2/N)}$], where D = the diameter of each tree in each size class, and N is the number of stems in each size class, was computed for trees in each DBH class in each time period in order to characterize groups of trees by size class and as another method of gauging the relative change in forest structure through time.

Relationship between forest attributes, BBD, and environmental and soil characteristics

To assess the effect of BBD on the forest attributes measured in this study, plots with extensive mortality were separated from those with little or no mortality in 2000. Differences in stem ingrowth, accretion, and mortality between beech forests with BBD and without BBD were analyzed using the Wilcoxon two-way test, a non-parametric two-sided test of no difference between two population means (SAS 8.2). Because they contain a greater number of trees that survived during the study period, total accretion should be greater in plots with less mortality from BBD. To assess whether BBD affected patterns of accretion of tree diameter, basal area, and biomass increment values were calculated for all trees in forests with and without BBD. The Wilcoxon two-way test was used to evaluate accretion between trees in diseased plots versus those in disease-free plots, all beech trees versus all non-beech trees, and all pair-wise comparisons of beech trees and non-beech trees in forests with and without BBD. Environmental factors including elevation, slope, aspect (Beers transformed), landform index (LFI) and terrain shape index (TSI) were recorded in each plot. Soils were collected from each plot during the summer of 2003. They were dried as soon as possible after collection, and stored in a cool, dry, stable environment in paper bags until they were analyzed by Brookside Labs, New Knoxville, OH.

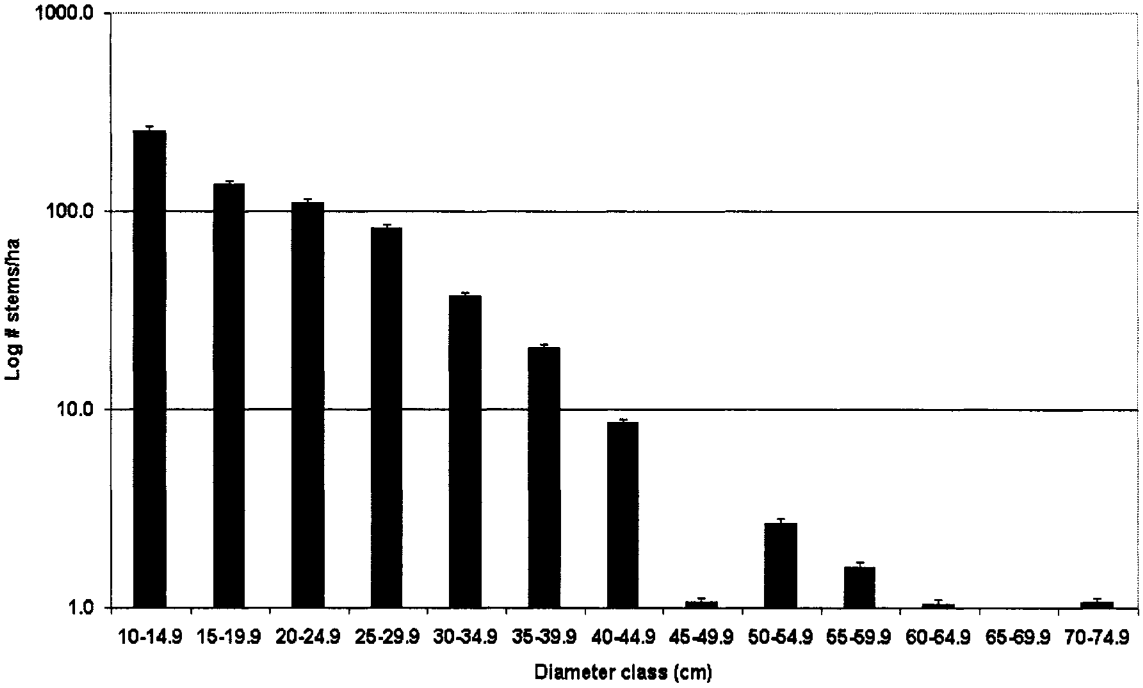
In order to determine whether plots demonstrated consistency in the direction of change relative to BBD severity and environmental and soil chemical characteristics, plots were ordinated using Non-metric Multidimensional scaling (NMS) with varimax rotation in PC-ORD (McCune and Grace 2002) on 10 of the 11 plots in this study (soils data for PHG were not available). The plot by species data matrix used raw basal areas standardized to per hectare values. Because the raw data ranged over several orders of magnitude the matrix was log-transformed before ordination. Environmental and soil chemical characteristics that demonstrated a strong correlation ($R^2 > .250$) with NMS axes were further analyzed using PROC CORR in SAS v. 8.2 to determine whether they were correlated with temporal changes in diameter, basal area, and biomass in these forests.

Results

Beech forest size structure and age relationships

The size structure of the stems > 10 cm in sites in this study is linear on a log-normal scale (Figure 3.2), which is consistent with the hypothesis that they are late-successional forests. The size structure of stems in all plots individually was the same as in Figure 3.2, except on plot in which stems in the 10-14.9 cm class had a small deficiency (nor reported here).

Figure 3.2. Size structure (# stems per ha by 5 cm diameter class) of high-elevation beech trees in 11 beech dominated forest plots in 1985, prior to BBD. The relationship is negative exponential with an r^2 of 0.9113.


1000.0
100.0
10.0
1.0
Log # stems/ha
10-14.9
15-19.9
20-24.9
25-29.9
30-34.9
35-39.9
40-44.9
45-49.9
50-54.9
55-59.9
60-64.9
65-69.9
70-74.9
Diameter class (cm)

Plot-level demographic trends in high-elevation beech forests

Across all plots and for all species mortality averaged 241 stems/ha from 1985 to 2000. Of this, beech mortality was 216 stems/ha, or 89.6% of total mortality. By comparison, beech mortality in plots with high BBD was 387 stems/ha, while in plots with low or no mortality it averaged 91 stems/ha. In plots with high-BBD mortality losses of diameter, BA, and AGB exceeded gains from ingrowth and accretion (Table 2). This pattern was apparent even in some low-BBD plots. However, in plots with no BBD-mortality, gains in diameter, BA, and AGB from ingrowth and accretion greatly exceeded losses in these attributes from mortality. The pattern of ingrowth, accretion, and mortality in plots with no BBD-mortality probably represent background patterns of these attributes in high-elevation beech forests.

From 1985 to 2000, ingrowth of all species across all plots averaged 122 stems/ha, of which 91% occurred in the smallest measured diameter class (10-15 cm). Beech ingrowth averaged 89 stems/ha, or 73% of all ingrowth. In plots with low or no BBD mortality, ingrowth of beech stems was 140 stems/ha versus 30 stems/ha in high-mortality plots, whereas ingrowth of non-beech stems across all plots was 33/ha. Because beech ingrowth as a percent of total ingrowth was less than beech mortality as a percent of total mortality, and because ingrowth of non-beech species exceeds beech ingrowth in high mortality plots, there exists in these stands the potential for a future shift in the composition of high BBD-mortality plots away from beech dominance. Beech ingrowth in high-mortality plots was significantly ($p < .05$) lower than in low or no BBD-mortality plots.

Diameter accretion exceeded mortality in only two plots, neither of which contained trees that died from BBD (Table 3.2). The data reveal that, except in the stands with the heaviest BBD mortality, there was a trend towards an increase in basal area, becoming more

Table 3.2. Changes in tree diameter, basal area, and biomass per hectare for 11 high-elevation beech forest plots in Great Smoky Mountains National Park (1985-2000).

Plot/BBD severity	**1985**	**Ingrowth**	**Accretion**	**Mortality**	**2000**
PHG/High					
Diameter (cm)	6778.8	830.0	1315.0	4618.8	4305.0
BA (m2/ha)	21.1	1.0	5.3	10.8	16.6
AGB (Mg/ha)	180.3	3.7	39.9	74.2	149.7
BM1/High					
Diameter (cm)	10738.7	445.0	1213.4	3396.9	9000.2
BA (m2/ha)	17.3	0.5	5.8	5.2	18.4
AGB (Mg/ha)	156.3	1.7	44.2	34.3	167.9
BM2/High					
Diameter (cm)	11738.7	668.5	1263.2	5387.2	8283.2
BA (m2/ha)	18.2	0.6	5.5	7.7	16.6
AGB (Mg/ha)	171.8	2.9	46.8	49.6	171.9
SPAC/High					
Diameter (cm)	17764.0	727.6	693.0	14118.0	5066.6
BA (m2/ha)	25.7	0.9	2.7	21.1	8.2
AGB (Mg/ha)	242.8	4.1	21.8	179.3	89.3
SPA1/Low					
Diameter (cm)	15448.0	2459.0	1391.0	3520.0	15778.0
BA (m2/ha)	26.0	2.8	5.2	6.8	27.2
AGB (Mg/ha)	209.8	12.3	40.0	45.2	216.9
SPA2/Low					
Diameter (cm)	17286.0	1443.0	1836.0	3850.0	16715.0
BA (m2/ha)	27.8	1.6	6.4	7.1	28.7
AGB (Mg/ha)	237.9	8.1	51.7	47.9	249.8
SPA3/Low					
Diameter (cm)	15887.0	1802.0	1450.0	3230.0	15909.0
BA (m2/ha)	25.9	1.7	5.2	5.5	27.3
AGB (Mg/ha)	211.0	8.1	40.5	36.7	222.9
DS1/None					
Diameter (cm)	16022.8	3986.0	2323.4	2566.5	19765.7
BA (m2/ha)	18.9	3.9	6.9	4.3	25.4
AGB (Mg/ha)	146.0	18.5	37.3	28.2	173.6
DS2/Low					
Diameter (cm)	17081.8	3477.0	3190.7	2499.9	21249.6
BA (m2/ha)	18.7	3.4	8.4	4.1	26.5
AGB (Mg/ha)	158.0	16.5	55.8	25.0	205.3
GB1/None					
Diameter (cm)	9429.1	1326.0	1263.7	1980.0	10038.8
BA (m2/ha)	29.3	1.1	9.4	3.7	36.1
AGB (Mg/ha)	302.4	7.2	82.5	32.2	359.9
GB2/None					
Diameter (cm)	14391.6	1818.0	2201.6	2076.0	16335.2
BA (m2/ha)	22.4	1.7	8.2	4.1	28.2
AGB (Mg/ha)	204.7	8.0	64.3	27.0	250.0

pronounced in the most westerly plots (DS1, DS2, GB1, and GB2) which increased between 23 and 42% between 1985 and 2000. Plot BM1, which had significant beech mortality from BBD, increased in basal area during this period. Basal area accretion in all diseased plots except SPAC was equivalent to between 20-34% of 1985 basal area, suggesting that these plots, in the absence of BBD, would have increased in basal area (Table 3.2). Furthermore, since the surviving beech trees on these plots are heavily diseased and therefore are no longer growing rapidly, the majority of the basal area increase must have occurred prior to BBD infesting the stand.

Stem diameter ingrowth exceeded losses from mortality in only two of the 11 plots but it exceeded accretion in all but three plots (Table 3.2). Although the majority of the increase in plot-level diameter can be attributed to ingrowth in most plots, on a per-capita basis ingrowing stems were not more productive than extant trees during the period of this study. Because the lower DBH limit in this study was 10 cm, any stem exceeding this limit in 2000 would have its entire diameter counted in the ingrowth estimate though it did not actually accrete its entire diameter during the study period. If ingrowing trees accumulated diameter at the same rate as trees in the 10-14 cm size class (Table 3.3), ingrowth was less than accretion or mortality in all plots.

Size-specific demographic trends in high-elevation beech forests

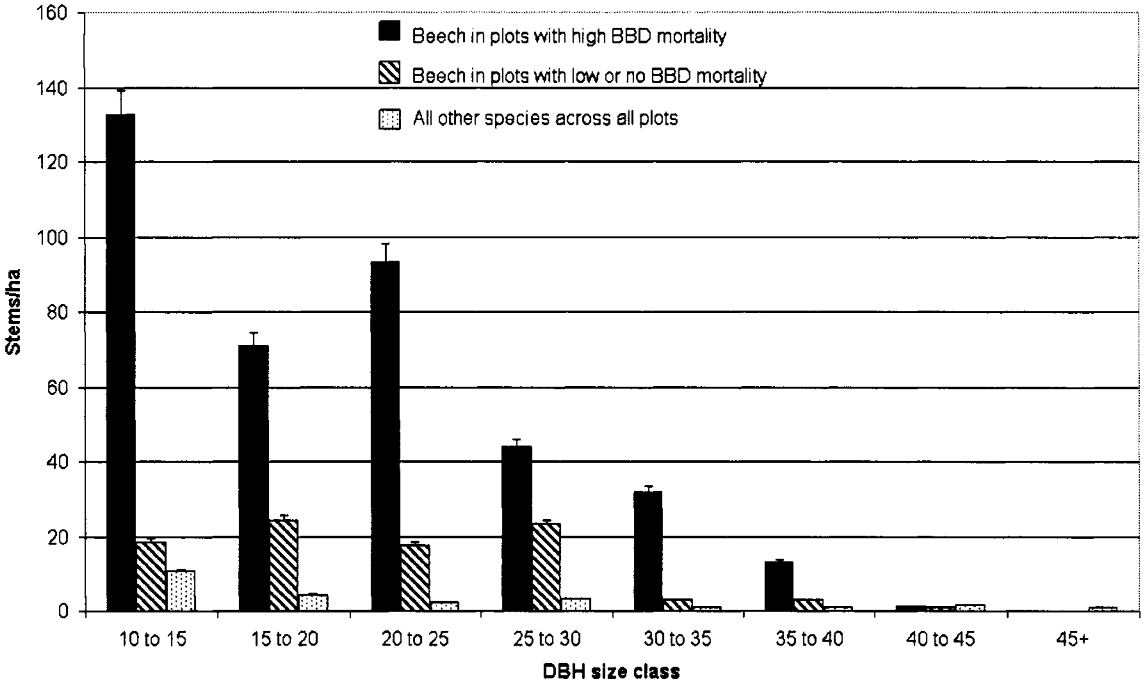
Size-specific mortality patterns between plots with high BBD-mortality versus those with low or no BBD-mortality indicate that losses of beech stems per hectare were significantly higher in high-mortality plots for all size classes except those 40 cm or greater (Figure 3.3). Additionally, the pattern of mortality by size class in high-mortality plots mirrors the beech

Table 3.3. Changes in diameter (DBH), basal area (BA), biomass (AGB), and quadratic mean diameter (QMD) by size class for accreting tree species (1985-2000) in 7 high-elevation beech forests plots with low or no BBD mortality in Great Smoky Mountains National Park (1985-2000).

1985 DBH class (cm)	**# stems**	**Cumulative Change**			**Per Capita Change**		
		DBH (cm/ha)	**BA (m^2/ha)**	**AGB (Mg/ha)**	**QMD (cm)**	**BA (m^2)**	**AGB (Mg)**
10 to 14	252	889.6	2.00	12.2	3.6^{a}	0.01^{a}	0.05^{a}
15 to 19	120	433.8	1.34	9.2	3.7^{a}	0.01^{b}	0.08^{b}
20 to 24	93	329.7	1.30	10.0	3.7^{a}	0.01^{c}	0.11^{c}
25 to 29	65	291.5	1.37	11.6	4.6^{b}	0.02^{d}	0.18^{d}
30 to 34	27	113.6	0.62	5.5	4.3^{b}	0.02^{d}	0.20^{d}
35 to 39	18	79.6	0.50	4.4	4.5^{b}	0.03^{d}	0.25^{d}
40 to 44	9	53	0.39	3.4	6.0^{b}	0.04^{d}	0.38^{d}
45+	6	29.2	0.29	3.0	4.9^{b}	0.05^{d}	0.49^{d}

[a] numbers followed by the same letter in a column group are not significantly different at ($\alpha < 0.05$).

Figure 3.3. Size specific mortality of stems in high-elevation beech forests (# stems/ha) from 1985-2000. Beech plots separated by degree of BBD mortality. Columns for all other species represents size specific mortality across all plots.


Beech in plots with high BBD mortality
Beech in plots with low or no BBD mortality
All other species across all plots
Stems/ha
160
140
120
100
80
60
40
20
0
10 to 15
15 to 20
20 to 25
25 to 30
30 to 35
35 to 40
40 to 45
45+
DBH size class

size class distribution, suggesting that BBD kills the same proportion of beech in each size class. The pattern of mortality after BBD infestation appears to be a deviation from pre-BBD patterns, as evidenced by the pattern of mortality in plots with low or no BBD-mortality, which show roughly the same number of stems dying in each size class up to 30 cm DBH. The drop in mortality after 30 cm can be attributed to the relatively small number of beech stems that exceed that diameter in high-elevation forests. No beech stems on the plots in this study exceeded 45 cm DBH.

Analysis of size-specific temporal trends in diameter, basal area and aboveground biomass indicate that the largest stems in beech forests account for the majority of growth for each of these attributes (Table 3.3). These results indicate that the greatest cumulative increase in each of these attributes was in size classes > 30 cm. However on a per capita basis, larger stems (> 25 cm) accumulated more diameter and consequently more basal area and biomass, indicating that the increase from smaller stems was due to greater density, not greater individual growth rates. Per capita accumulation of diameter and basal area were significantly greater in the 40-44 cm size class though biomass accumulation was greatest in trees > 45 cm.

Per capita increase in diameter increment, BA, and AGB was significantly greater for trees in plots with high BBD mortality than those in plots unaffected by BBD, suggesting that one of the affects of the disease has been to increase the growth rate of the surviving trees. However, the growth rate of surviving beech trees in plots with high BBD severity was not different than that of beech trees in undiseased plots (Table 3.4). Across all plots, and in plots without BBD, per capita growth of beech was significantly less rapid than that of non-beech trees. Additionally, non-beech trees in high-BBD plots grew more rapidly than non-

Table 3.4. Per capita increases in diameter, basal area, and biomass 1985-2000 for beech trees and co-occurring species in 11 high-elevation beech forest plots in Great Smoky Mountains National Park.

Pair-wise comparison	Per capita increase in surviving stems		
	Diameter (cm)	**BA (m^2/ha)**	**AGB (kg/ha)**
All stems BBD plots	4.74^a	$.0197^a$	161.4^a
All stems no BBD plots	3.76^b	$.0132^b$	103.0^b
All Beech in all plots	3.53^a	$.0118^a$	96.3^a
All non-beech in all plots	5.36^b	$.0234^b$	177.2^b
Beech in BBD plots	3.55^a	$.0134^a$	115.4^a
Beech no BBD plots	3.52^a	$.0113^a$	90.4^a
Non-beech BBD plots	7.72^b	$.0354^b$	275.0^b
Non-beech no BBD plots	4.49^c	$.0189^c$	140.9^a

[a] numbers followed by the same letter in a column group are not significantly different at $(\alpha < 0.05)$.

beech trees in plots without BBD. In plots with high BBD mortality, ANPP averaged 2.7 Mg/ha and ranged from 1.6 to 3.2 Mg/ha. In plots with little or no BBD, ANPP averaged 3.9 Mg/ha and ranged from 3.0 to 5.7.

Relationship between forest attributes, BBD, and environmental and soil characteristics

There was no consistency in the direction of change for the plots in this study from 1985 to 2000 (Figure 3.4). In general, plots with high BBD-mortality appear to have moved farther in ordination space than those with low or no BBD-mortality and in general they appear to be moving relative to the second axis away from beech and other species representative of high-elevation beech forests. The plot with the most severe mortality from BBD (SPAC) moved farthest, and in a direction opposite to the movement of diseased plots with less severe mortality (BM1 and BM2). The coefficients of determination (r^2) for the plot x species matrix in ordination space were 0.620 for axis 1 and 0.312 for axis 2. Plot elevation and 11 soil characteristics were correlated with the arrangement of beech forests in ordination space. The varimax rotation aligned elevation and several of the soil characteristics (Mn, P, and Z) and along axis 1 of the NMS ordination, while other characteristics (bulk density, Cu, and pH) aligned along axis 2. The remaining variables were not aligned parallel to either axis (Figure 3.5).

The environmental variables identified as influencing beech forests in ordination space were correlated with changes in BA and AGB for ingrowth, accretion, and mortality across all plots (Table 3.5). These results indicate that increases in BA and AGB from ingrowth and accretion were strongly associated soil chemistry, particularly with relation to soil elements affected by acidity. In particular, declines in BA and AGB from mortality were associated

Figure 3.4. Results of NMS ordination and paired plot vectors based on log transformed basal area for high-elevation beech forests with three severities of BBD 1985 and 2000 (cumulative r^2 = .933). Symbols are plots coded for year □= no BBD 1985, ■= no BBD 2000, Δ= low BBD mortality 1985, ▲ low BBD mortality 2000, ○ = high BBD mortality 1985, ● = high BBD mortality 2000.

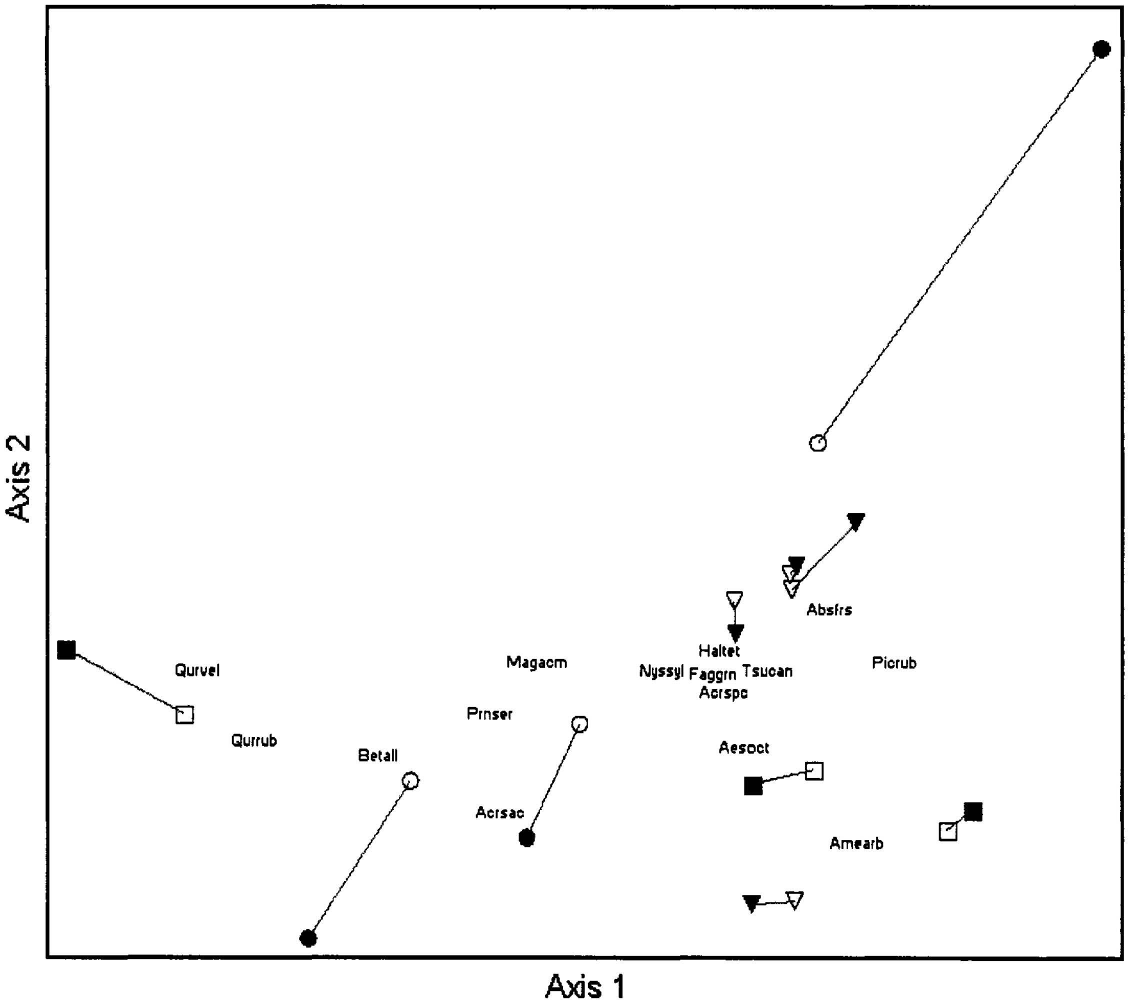

Axis 2
Absfrs
Haltet
Qurvel
Magacm
Nyssyl
Faggrn
Tsucan
Picrub
Acrspc
Prnser
Qurrub
Betall
Aesoct
Acrsac
Amearb
Axis 1

Figure 3.5. Results of NMS ordination biplot based on log transformed basal area for high-elevation beech forests with three severities of BBD 1985 and 2000 using the same plot configuration as Figure 5 (correlation vectors based on a minimum r^2 = .25). Symbols are plots coded for year □= no BBD 1985, ■= no BBD 2000, Δ= low BBD mortality 1985, ▲ low BBD mortality 2000, ○ = high BBD mortality 1985, ● = high BBD mortality 2000. Elements are identified by their symbol, except soluble sulfur (Sol S) and easily extractable P (EEP,) and were measured in parts per million (ppm). Other characteristics include estimated nitrogen release (ENR in kg/ha)), percent base saturation (Bsat), and percent organic matter (% OM).

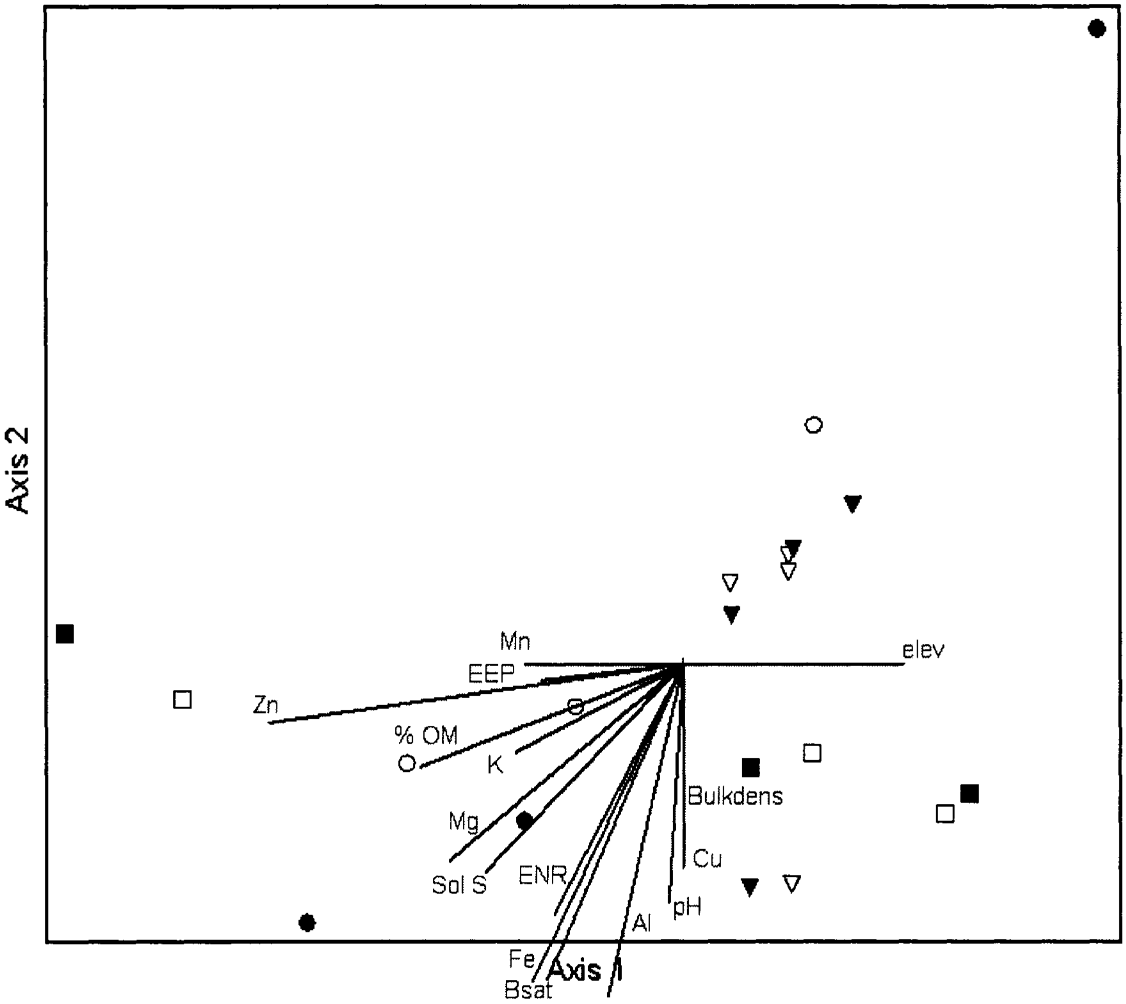

Axis 2
Mn
EEP
Zn
% OM
K
Mg
Sol S
ENR
Fe
Bsat
Axis 1
Al
pH
Cu
Bulkdens
elev

Table 3.5. Pearson correlation coefficients for environmental and soil chemical characteristics significantly associated $p < 0.05$ (*$p < 0.01$) with the basal area (BA in m^2/ha) and aboveground biomass (AGB in Mg/ha) of ingrowth, accretion, and mortality in high-elevation beech forests between 1985 and 2000.

Characteristic	**Ingrowth**		**Accretion**		**Mortality**	
	BA	**AGB**	**BA**	**AGB**	**BA**	**AGB**
Elevation (m)		.62		-.62		
pH	.82*	.86*				
% organic matter	-.72	-.68				
Est. nitrogen release (kg/ha)	-.73	-.72				
Soluble sulfur (ppm)		.69				
Extractable phosphorous (ppm)			-.67	-.85*	.86*	
Potassium (ppm)						
Base saturation (%)	-.82*	-.86*				
Manganese (ppm)		-.72	-.73		.81*	.84*
Zinc (ppm)	-.73	-.74				
Aluminum (ppm)			.9*			

with high P and Mn concentrations, while ingrowth and accretion were negatively associated with the concentration of those elements.

Discussion

In the high-elevation beech forests of GRSM, the period from 1985 – 2000 was characterized by heavy losses of beech and consequent plot-level declines in diameter, basal area, and biomass in the BBD-affected beech forests of eastern GRSM. In contrast, beech forests in western GRSM with little or no BBD demonstrated increases in the same forest attributes; increases that are surprisingly large given that these are late-successional forests. The increases in BA and AGB come from accretion rather than ingrowth, and are driven by growth of the largest stems. Although beech is responsible for the majority of the increase because of its density in these forests, it grew less rapidly on a per capita basis than co-occurring species.

Aboveground biomass estimates for the forests in this study range from 89.1 to 171.9 Mg/ha in BBD-affected forest and 173.6 to 359.9 Mg/ha in beech forests with little or no BBD. The AGB values for disease-free high-elevation beech forests overlap slightly but are generally lower than AGB values reported for deciduous old-growth cove forests in GRSM (Busing et al.1993), which is consistent with the high-elevation forests being cooler and having a shorter growing season. Average ANPP (Mg/ha/yr) estimates for high-elevation forests are less than half those of old-growth deciduous cove forests in GRSM (Busing et al. 1993) and southern Appalachian forests generally (Bolstad et al. 2001).

American beech is a slow-growing, highly shade-tolerant species (Baker 1949) whose slower growth rate compared to co-occurring species in this study is consistent with other observations of beech growth in the forests of the eastern United States (Canham 1988, 1990, Poage and Peart 1993, Poulson and Platt 1995). What appears to be unusual, however, is the finding that these forests are accreting diameter, basal area, and biomass at a rate higher than would be expected given their successional status (Binkley et al. 2002). Possible reasons for this include: 1.The forests are not late-successional and are in the aggradation phase of forest succession, in which case the largest stems should account for most of the accretion and stem densities should decrease as a result of self-thinning, 2. The forests are recovering from grazing, reduction in fire, or selective logging, in which case most of the accretion would be in understory stems (ingrowth), 3. The forests are gaining basal area due to environmental changes such as global warming, increased length of the growing season, or nutrient enhancement in the form of atmospheric CO_2 enrichment and/or the deposition of nitrogenous compounds, in which case all stems should accrete basal area with the largest accreting most. The evidence in favor of each hypothesis is discussed in the following paragraphs.

High-elevation beech forests in GRSM are not late-successional

The size-structure relationships in high-elevation beech forests in GRSM are consistent with them being late-successional (Leak 1965, Hett and Loucks 1971, 1976). As suggested by Blozan (1995), shade-tolerant species such as beech may not fit traditional size-frequency relationships but Blozan's data for high-elevation beech forests suggests that in GRSM, beech size is a good predictor of age.

High-elevation beech forests have long been a distinctive, mature forest association in GRSM (Cain 1931, Russell 1953, Whittaker 1956, Schofield 1960, Golden 1981, Callaway et al. 1987, MacKenzie and White 1998), and have been considered climax forests (Cain 1931, Russell 1953). Because of the distinctive stunted architecture of individual trees and stand physiognomy characterized by a sedge or herbaceous understory with little woody undergrowth, which Whittaker (1956) considered a characteristic of forests growing in extreme conditions. Several of the beech forests in this study, specifically those described by plots SPAC, SPA1, SPA2, SPA3, and DS1 were also studied by Cain (1931) and Russell (1953), who considered them late-successional. Furthermore some high-elevation beech trees exceed 200 years of age (Blozan 1995), and the forests in GRSM have been protected from direct human influence (logging and grazing) since 1935 (Pyle 1988). It is reasonable to conclude that these forests are late-successional and that from 1985 to 2000 they demonstrated a rate of basal area increase that is inconsistent with the forest succession model.

Beech forests are recovering from reduction in fire, grazing, logging or another disturbance

Burning to improve grazing conditions was a common practice prior to the creation of GRSM and might have been used to maintain grassy balds but little evidence of burning exists on the balds near the forests in this study (Lindsay and Bratton 1979). Additionally, due to their thin bark even adult beech trees are susceptible to fire (Swan 1970, Tubbs and Houston 1990).

Feral hogs (*Sus scrofa*), an introduced species from Europe, have been in GRSM since the 1950s and spend their summers feeding at high-elevations, particularly in beech forests (Bratton 1975). Hog rooting is known to increase beech sprout densities through mechanical disturbance of the forest floor and injury to beech roots (Huff 1977). Hogs, and other herbivores such as the animals early settlers grazed on grassy balds, find beech foliage unpalatable so densities increase following rooting. However, tree size structure is not with beech sprout density increases accounting for the increase in basal area.

According to Pyle (1988), prior to park establishment some beech forests were potentially subject to heavy cutting, such as would occur in industrially logged areas and some were classified as having diffuse disturbance, which includes random cutting and livestock grazing. Due to the relative inaccessibility of high-elevation beech forests, the stunted architecture of beech trees, and the low economic value of beech wood, it seems unlikely that high-elevation beech forests would have been worthy of economic exploitation and therefore would probably have been free of heavy logging.

Whittaker (1956) considered undisturbed vegetation in GRSM to be representative of climax, or self-replacing forests except those forests recovering from the death of American chestnut (*Castanea dentata*) by chestnut blight (*Cryphonectria parasitica*). The beech forests in this study are unlikely to be responding to the blight as chestnut was a minor component of high-elevation beech forests (Russell 1953, Whittaker 1956), and no chestnut sprouts or downed woody debris was noted in any plots in this study.

It is not possible, from the data collected in this study, to conclusively reject recovery from disturbance as a cause of beech forest basal area growth. However, if this were the case, ingrowth and smaller stems should account for most of the increase. Because the results of this study indicate that they do not, recovery from disturbance unlikely to be the reason for the basal area gain.

High-elevation beech forests are gaining basal area because of environmental changes

In this study it was assumed that environmental conditions did not change between 1985 and 2000. Due to the ubiquity of atmospheric deposition of anthropogenic pollutants, globally increasing CO_2 concentrations, and increased growing season length from global warming, that assumption may not be realistic. High-elevation forests, including beech forests, throughout GRSM are subject to levels of atmospheric deposition of nitrogenous compounds and acid rain as high as anywhere in the eastern United States (Nodvin et al. 1995). In the eastern United States, atmospheric nitrogen deposition is thought to disrupt ecosystem function (Aber 1992), and possibly cause declines in eastern forests (Fenn et al. 1998). Nitrogen addition often stimulates forest growth initially, followed by decline as deposition continues, acidity increases, aluminum mobilizes, and cation concentrations fall (Aber et al. 2003). Some European forests may respond to nitrogen deposition by increasing growth, including forests dominated by European beech (*Fagus sylvatica*), although high-elevation beech forests are apparently not part of this trend (Dittmar et al 2001).

In this study the forests demonstrating the greatest proportional increase in basal area and biomass are in western GRSM. This may be due to variations in N mineralization in forests of different composition (Lovett and Rueth 1999); beech forest soils had lower N mineralization levels than maple forest soils under equivalent levels of N deposition, possibly because of the poor litter quality in beech forests. If this is the case, beech forest soils might become N saturated less quickly than the soils of other forest types, and the harmful effects of nitrogen deposition may be delayed.

Nitrogen deposition in GRSM forests could have a synergistic interaction with increasing CO_2 concentrations and longer growing seasons to enhance beech forest growth. Forest growth models predict increases in temperate forest productivity from increasing concentrations of long-lived greenhouse gases (Mellilo et al 1993). The increase in basal area and biomass in high-elevation beech forests documented in this study is consistent with the hypothesis that their growth rate is being enhanced by changes in environmental conditions.

Soil chemistry, as it is affected by soil acidity, has been associated with compositional and structural changes in other high-elevation forest types in GRSM (Chapter 4). In this study, increases in BA and AGB are correlated with low cation concentrations, and high Al and S, whereas in the other study, soil Al was correlated with a decline in basal area, especially in oak-dominated forests. Why beech forests might respond differently than other forest types to acidity-related changes in soil elements is not clear. Some evidence suggests that soils under different forest types react differently to the deposition of atmospheric nitrogen (Lovett and Rueth 1999). The forests in this study share many species with other high-elevation forests in GRSM, but differ in their overwhelming dominance by American beech. Because beech leaves are unpalatable to most herbivores they might harbor lower microbial detritivore loads than the litter of other forests, lowering the rate of nutrient cycling in beech forest soils (Lovett and Rueth 1999).

Conclusions

From 1985 to 2000 some high-elevation beech forests in GRSM exhibited rates of increase in basal area that are inconsistent with the forest succession paradigm. The results suggest that at the plot-level the increase is due to accretion, and not ingrowth. Size-specific analysis of accretion patterns indicate that the largest trees in these forests are growing fastest.

Although the reason for the increase cannot be determined from data collected in this study, the size structure of the forests, and the patterns of basal area gain are consistent with the idea that their growth is being enhanced by changing environmental conditions.

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Chapter 4

Temporal dynamics in the late-successional, high-elevation deciduous forests of Great Smoky Mountains National Park.

Abstract

Basal area and stem density were measured in 1977-78 and 2002 in 43 high-elevation deciduous forest plots in Great Smoky Mountains National Park to test the hypothesis that these late-successional forests are stable. Across all plots, basal area and stem density declined 2.6 and 10.9%, respectively. Indicator species analysis identified three forest types, BEECH, COVE, and HERO (high-elevation red oak), each of which contained plots with three disturbance histories (undisturbed, diffuse disturbance, and heavy-cut). All forest types and disturbance histories declined in stem density, and all but COVE and diffuse disturbance forests declined in basal area. Multivariate analyses of compositional differences in each forest type and disturbance history showed that all were significantly changed except BEECH and diffuse disturbance forests. Comparing basal area and stem density values in 1977-78 with those in 2002 by forest type and disturbance history yielded no significant changes, but northern red oak (*Quercus rubra*) basal area declined as much as 53% and density declined as much as 43% in all forest types regardless of disturbance history. Other species had less consistent and severe changes. Across all plots changes in basal area and stem density were correlated with steep slopes, low soil cations, and high soil Al, suggesting that soil acidification might be responsible for the forest-wide pattern of decline observed in this study.

Introduction

The high-elevation forest area of Great Smoky Mountains National Park (GRSM) is one of the largest landscapes of protected forests remaining in the eastern United States. Because they have been protected since the mid-1930s and because significant areas have no record of human influence, it has been proposed that the processes in these forests are representative of climax (late-successional) forest communities (Whittaker 1956). The forest succession model proposes that, in late-successional forests, attributes such as species composition and basal area accumulation should reach a stable state, described by some researchers as a bounded equilibrium (Bormann and Likens 1979, Woods 2000a, White and Jentsch 2001). Additionally, these forests are expected to become increasingly dominated by shade-tolerant, late-successional species (Rees et al. 2001). Ecologists most often assess stability in primary old-growth forests (White et al. 1993, Woods 2000a, b) but stability should be evident in any late-successional forest, regardless of its primary or secondary status. Few studies however, have used empirical data to test these hypotheses by comparing temporal changes in the attributes of both primary and secondary forest types.

In high-elevation (> 1150 m) areas of GRSM, steep slopes and complex topography create a mosaic of habitat types harboring different forest associations with varying proportions of shade-tolerant to shade-intolerant trees. Because these associations are contiguous with one another over a relatively small area, they offer an opportunity to compare temporal forest dynamics among forest associations without having to control for regional differences in climate. Although much high-elevation forest area in GRSM is considered primary old-growth (Pyle 1988), in some areas pre-park industrial logging has created second-growth forests. In 1977-78, 43 permanent vegetation plots were established in high-elevation deciduous forest areas in western GRSM (White and Busing 1993), and are located in both primary and secondary forest types.

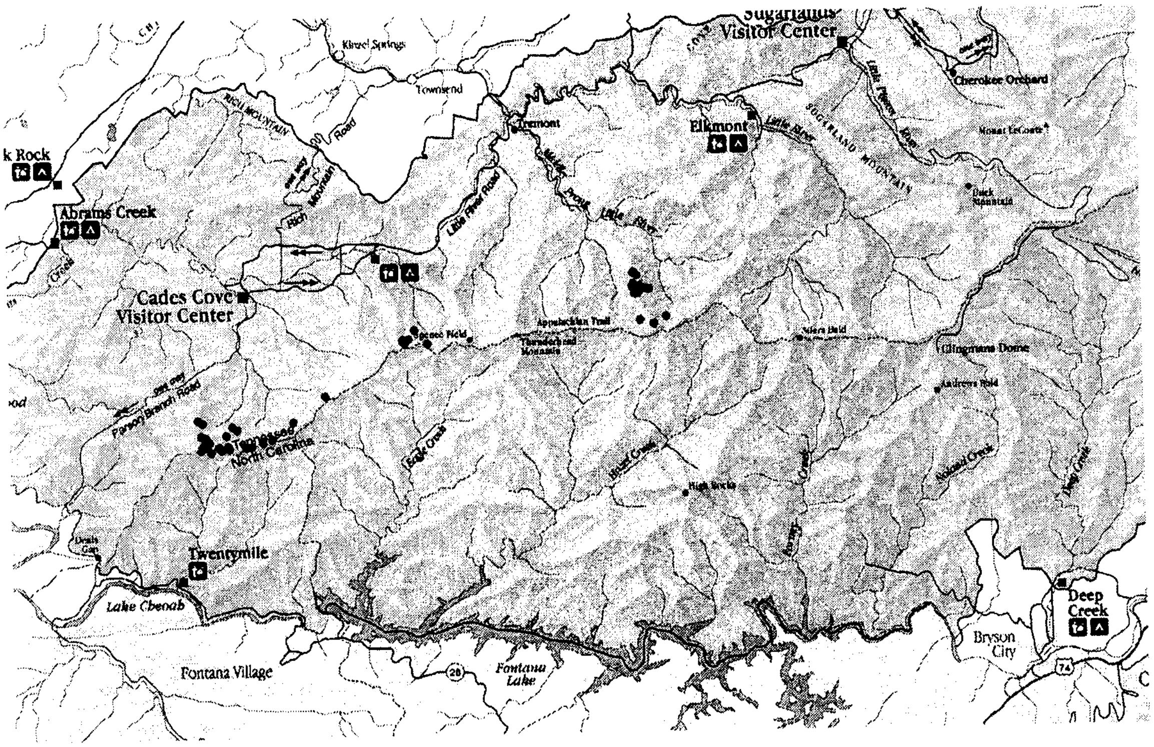
The purpose of this study is to compare the temporal (1977-78 to 2002) tree ($\geq$ 10 cm) dynamics in 43 permanent plots in high-elevation deciduous forests of mixed composition and successional history to determine whether they are stable and if not, whether the changes in forest attributes are correlated with environmental and soil chemical characteristics. In this study I ask: 1. Are the forests in this study stable or are they changing (in density and basal area)? 2. In forests of contrasting composition, are those with greater proportions of shade-tolerant species more stable than other forest associations? 3. Are undisturbed forests more stable than forests with a known history of human influence? And, 4. Are the changes in these forests correlated with environmental or soil chemical characteristics?

Methods

Study location

The plots in this study are located north and east of Gregory Bald (N = 23), and north of Russell Field (N = 6) and north of Mt. Davis (N = 14) (Figure 4.1). All plots are on the north side of the main ridgeline that bisects GRSM west to east. GRSM was created in 1935 therefore the forests in the park have been protected from logging for almost 70 years. Disturbance history of the plots was determined using data from Pyle (1988), digitized on maps to 90 m resolution. Permanent plots near Gregory Bald and Russell Field have been described as undisturbed (N=11), or diffuse disturbance (N=18), which might include livestock grazing and light burning. Near Mt. Davis forests were industrially logged (heavy-

Figure 4.1. Location of 43 high-elevation deciduous forest plots in western Great Smoky Mountains National Park.


Kinzel Springs
Townsend
Sugarlands Visitor Center
Cherokee Orchard
Tremont
Elkmont
Little River
SUGARLAND MOUNTAIN
Little Pigeon River
Mount LeConte
Duck Mountain
k Rock
Abrams Creek
RICH MOUNTAIN
Road
one way
Rich Mountain
Little River Road
Middle Prong Little River
Cades Cove Visitor Center
Spence Field
Appalachian Trail
Thunderhead Mountain
Silers Bald
Clingmans Dome
Andrews Bald
one way
Parson Branch Road
Tennessee
North Carolina
Eagle Creek
Hazel Creek
High Rocks
Forney Creek
Noland Creek
Deep Creek
Deals Gap
Twentymile
Lake Cheoah
Fontana Village
28
Fontana Lake
Bryson City
74
Deep Creek

cut, N=14) prior to the creation of GRSM. Although it is not known when logging occurred in the heavy-cut plots in this study, it was generally confined to the period 1890-1920 in GRSM (Brown 2000). In the Abrams Creek watershed, where the Gregory Bald and Russell field plots are located, there was no industrial logging and small logging operations were restricted to coves and lower slope positions (Pyle 1988); hence, it is unlikely that these plots were ever logged. Because they were forested at the time GRSM was established, because they contain relatively large and old trees, and because they are dominated by late-successional tree species all plots in this study are considered late-successional regardless of their primary or secondary status.

Dimensions of all plots in this study are 20 x 50 m (0.1 ha), with the long axis arranged parallel to the slope. The plots were established in 1977 and 1978 by GRSM science staff, and were resampled in 2002 by GRSM vegetation monitoring staff and the author. Species and DBH were recorded for all stems, though only those ≥ 10 cm (trees) are used in this study. In order to ensure as much homogeneity among plots as possible for the purposes of comparing temporal dynamics, the plots in this study are located above 1150 m (ranging from 1159-1509 m); they are also generally north-facing.

Forest associations

The plots in this study contain a mixture of deciduous trees, the most important of which are northern red oak (*Quercus rubra*), yellow birch (*Betula alleghenienss*), American beech (*Fagus grandifolia*), silverbell (*Halesia tetraptera* var *monticola*), eastern hemlock (*Tsuga canadensis*) and sugar and red maples (*Acer saccharum* and *A. rubrum*). Based on their location and the identity of the dominant species, the plots in this study fall within the

Southern Appalachian Northern Hardwood (NatureServe Ecological System ID CES 202.029), and Southern and Central Appalachian Cove ecosystems (CES 202.373) (NatureServe 2005).

In order to determine which high-elevation forest associations were represented by the plots in this study, cluster analysis was performed in PC-ORD (McCune and Grace 2002) on a plot by species matrix of raw abundance values from 1977-78 data using relative Euclidean distance and Ward's group linkage method. Indicator species analysis identified trees species most strongly associated ($p < 0.01$) with each group by comparing observed indicator values with a Monte Carlo randomization test using 1000 permutations. Indicator values for the most important species in each group were used to determine which community associations were represented in the forests in this study.

Changes in forest composition and structure by forest association and disturbance history

In order to determine whether there were statistically significant compositional (species densities per ha) and basal area (m^2/ha) differences in plot groups for all plots, and by year for different forest associations and disturbance histories, blocked Multi-response Permutation Procedure (MRBP), a non-parametric, multivariate procedure in PCORD (McCune and Grace 2002) using matrices of raw species abundance. MRBP was used to test the hypothesis of no changes in forest composition over time because it negates the lack of sample independence inherent in studies using repeated measures. In this analysis, forest plots were blocking variables and sample years 1977-78 vs. 2002 were grouping variables. MRBP was used to determine the significance of compositional change across all plots, within each forest association identified with cluster analysis, and by disturbance history.

Consistency in the direction of change by forest association and disturbance history was determined by ordinating plots using Nonmetric Multidimensional Scaling (NMS) with varimax rotation (Mather 1976) in PC-ORD (McCune and Grace 2002). The Bray-Curtis dissimilarity measure and species abundances were used to determine compositional dissimilarity. The appropriate dimensionality was determined using a Monte Carlo test. The direction of compositional change was evaluated by connecting the observations of each plot in two time periods with vectors.

As a measure of the magnitude of change, percent similarity (PS) was calculated for each plot pair using species abundances in 1977-8 and 2002-3. The formula used was ($PS = 1-[\Sigma|p_i-q_i|/2]$), where p_i is the number of species i in 1977-8, and q_i is the number of species i in 2002-3. Percent similarity was chosen because it has the advantage of measuring changes in abundance, unlike Jaccard's and Sorensen's coefficients (Brower et al. 1998).

Correlations with environmental and soil chemical characteristics

Biplots were constructed on the ordinations described above to analyze the strength of plot environmental factors (elevation, slope %, and Beers transformed aspect), and soil chemical characteristics (soil pH, CEC, % organic matter, exchangeable Al (mg/kg), and % saturation and concentration (ppm) of K, Ca, Mg, and P) on 38 of the 43 plots for which soils were collected (Table 4.1). The environmental variables with the strongest patterns were then analyzed using correlation analysis (PROC CORR in SAS 8.2) to determine whether they were correlated with plot forest attributes such as: stem density, basal area and species richness and with the change in these measures over the period of the study.

Table 4.1. Environmental and soil chemical variables collected in 38 high-elevation deciduous forest plots in Great Smoky Mountains National Park.

Variable	Description	Mean	SD	Min	Max
Elevation	Plot elevation (m)	1302.1	101.7	1100	1509
Aspect	Beers transformed	1.9	0.995	0.589	3.38
Slope	Plot slope (%)	15.9	10.9	0	36
pH	A horizon soil pH	4.2	0.371	3.7	5.3
CEC	Cation exchange capacity (meq/100g)	8.1	0.925	6.4	10.3
K	Potassium (ppm)	49.6	16.299	4	73
Ca	Calcium (ppm)	130.7	59.572	43	384
Mg	Magnesium (ppm)	26.725	9.384	15	58
P	Phosphorous (ppm)	24.7	16.299	7	68
OM	A horizon % organic matter	4.062	2.353	.9	8.5
Al	Exchangeable aluminum (mg/kg)	321.208	109.528	37	692

Results

Forest associations

Cluster analysis separated the plots in this study into three groups by composition (Figure 4.2). The species identified as indicators for each group were the most abundant species and occupied the greatest basal area in their group in 1977-78 (Table 4.2). Indicator species analysis identified Group 1 as forests dominated by American beech (*Fagus grandifolia*) with yellow buckeye (*Aesculus octandra*) as an important codominant (Table 4.2), corresponding with NatureServe forest associations CEGL006130 and CEGL006246, high-elevation beech dominated forests. These plots are henceforth called beech forest plots (BEECH). Group 2 is dominated by species associated with cove forest associations (COVE) and represents a high-elevation subset of association CEGL007693. Group 3 defines high-elevation red oak (HERO) forests (CEGL007299, CEGL07300, and CEGL008527) (NatureServe 2005).

The ordination clustered by composition in a manner consistent with the results of cluster analysis (Figure 4.3a). The paired-plot vectors show HERO forest plots exhibiting consistency in the direction of change along the second axis. NMS ordination of plots in species space with correlation vectors with environmental and soil characteristics indicate that percent slope and soil pH were important characteristics (Figure 4.3b). Ordination of paired-plot vectors for basal area data indicates consistency in the direction of both BEECH and HERO plots (Figure 4.5). BEECH plots appear to move parallel to axis 1 but they move in either direction. HERO plots consistently move from right to left along axis 1. However, in the basal area ordination no environmental or soil characteristics met the minimum r^2 criteria (0.25) for inclusion (ordination not shown). Because of low correlations between

Figure 4.2. Cluster analysis of 43 high-elevation deciduous forest plots in Great Smoky Mountains National Park (□ = beech dominated plots, Δ = cove forest plots, + = high-elevation red oak forest plots).

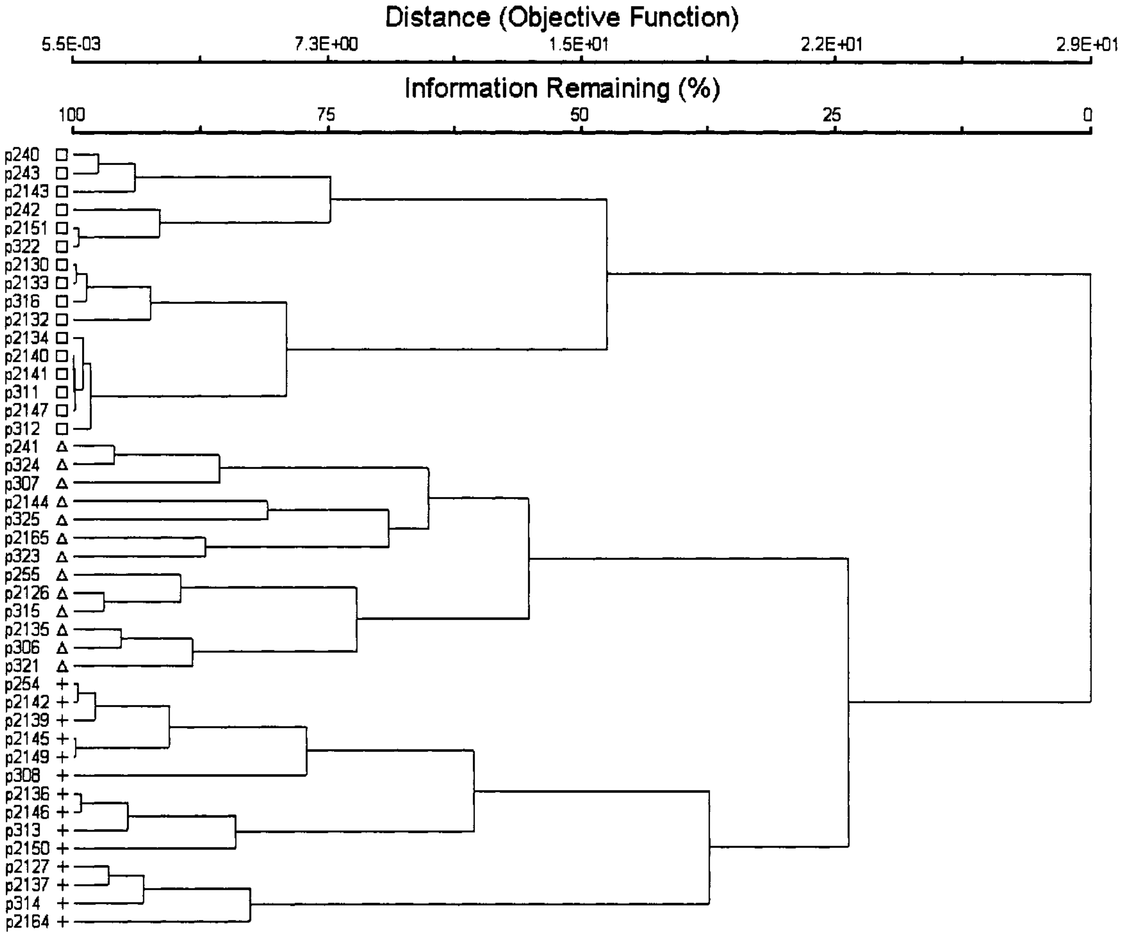
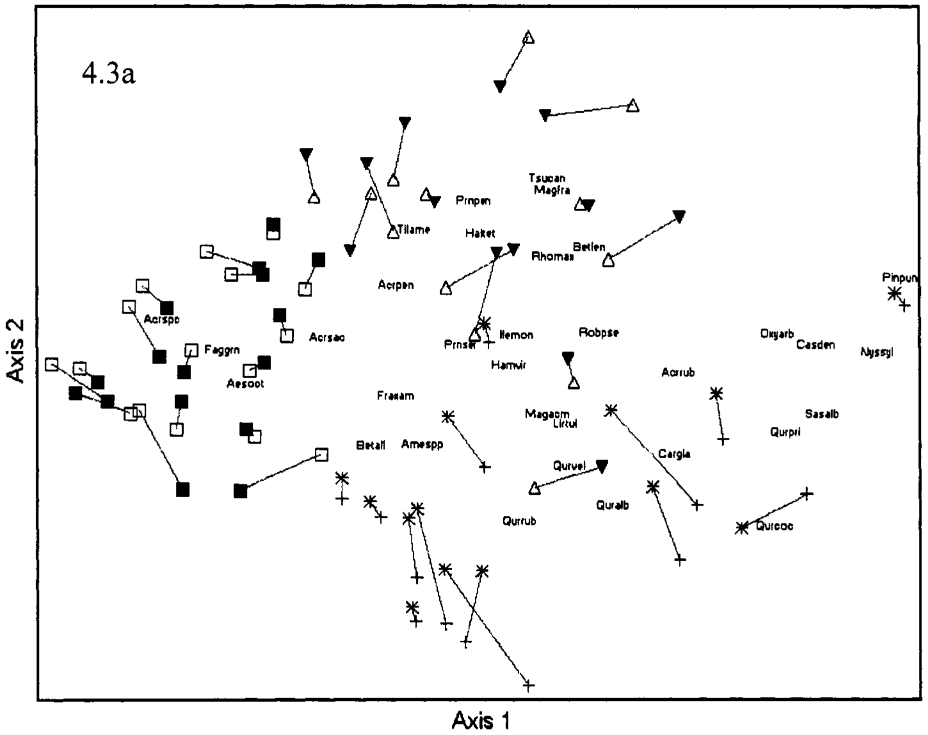

Distance (Objective Function)
5.5E-03
7.3E+00
1.5E+01
2.2E+01
2.9E+01
Information Remaining (%)
100
75
50
25
0
p240 □
p243 □
p2143 □
p242 □
p2151 □
p322 □
p2130 □
p2133 □
p316 □
p2132 □
p2134 □
p2140 □
p2141 □
p311 □
p2147 □
p312 □
p241 Δ
p324 Δ
p307 Δ
p2144 Δ
p325 Δ
p2165 Δ
p323 Δ
p255 Δ
p2126 Δ
p315 Δ
p2135 Δ
p306 Δ
p321 Δ
p254 +
p2142 +
p2139 +
p2145 +
p2149 +
p308 +
p2136 +
p2146 +
p313 +
p2150 +
p2127 +
p2137 +
p314 +
p2164 +

Table 4.2. Indicator species for the three forest associations identified using cluster analysis on 1977-78 density data. Species are listed in order of descending indicator value in the group in which their maximum indicator value occurred. Relative density (RD) and relative basal area (RBA) values are specific to the group for which the species is an indicator. Only species with p-value < 0.01 are listed.

Indicator species	Indicator Value	p-value	RD (%)	RBA (%)
Group 1(BEECH)				
Fagus grandifolia	79.5	0.001	41.6	28.0
Aesculus octandra	70.8	0.001	17.9	21.4
Group 2 (COVE)				
Tsuga candensis	78.4	0.001	16.0	21.4
Halesia tetraptera	73.4	0.001	20.9	15.2
Betula lenta	50.5	0.001	5.0	2.3
Acer pensylvanicum	48.7	0.001	3.0	1.0
Magnolia fraseri	46.6	0.001	7.1	5.9
Group 3 (HERO)				
Quercus rubra	77.7	0.001	38.2	56.1

Figure 4.3a,b. Results of NMS ordination and paired plot vectors (3a - cumulative r^2 = .721) and ordination biplot (3b) based on abundance data for three forest types between 1977-78 and 2002. Symbols are plots coded for year □= beech plots 1977-78, ■= beech plots 2002, Δ= cove plots 1977-78, ▲ cove plots 2002, + = HERO plots 1977-78, * = HERO plots 2002. Correlation vectors in Fig 3.b are based on minimum r^2 =.25.


4.3a
Tsucan
Magfra
Prnpen
Tilame
Haket
Betlen
Rhomas
Acrpen
Pinpun
Acrspc
Faggrn
Acrsac
Ilemon
Robpse
Oxyarb
Casden
Nyssyl
Prnser
Hamvir
Acrrub
Aesoct
Fraxam
Sasalb
Magacm
Lirtul
Qurpri
Betall
Amespp
Cargla
Qurvel
Quralb
Qurrub
Qurcoc
Axis 2
Axis 1

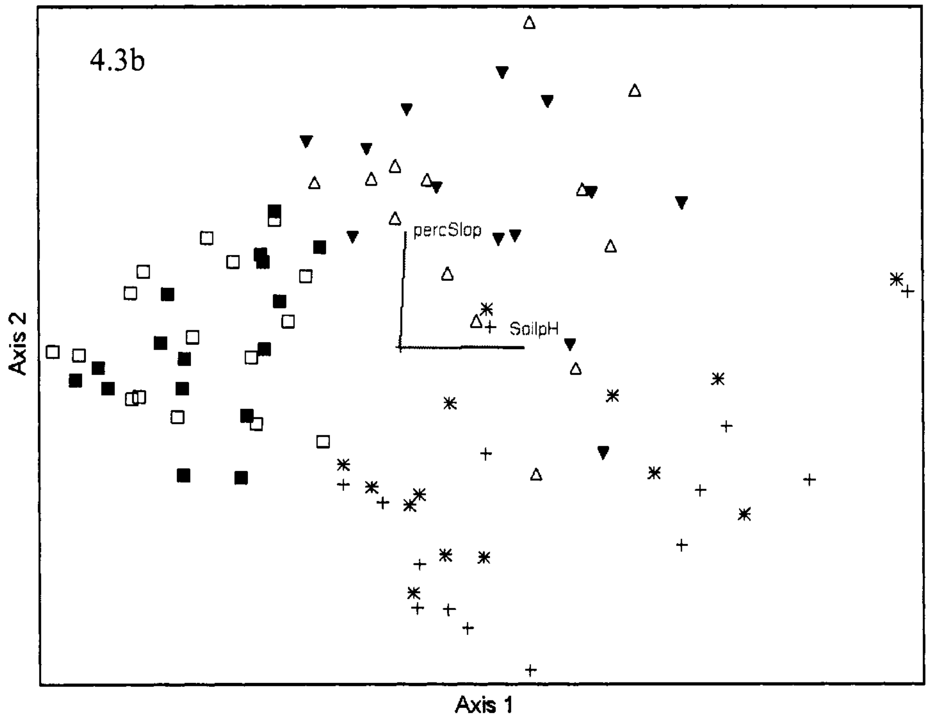
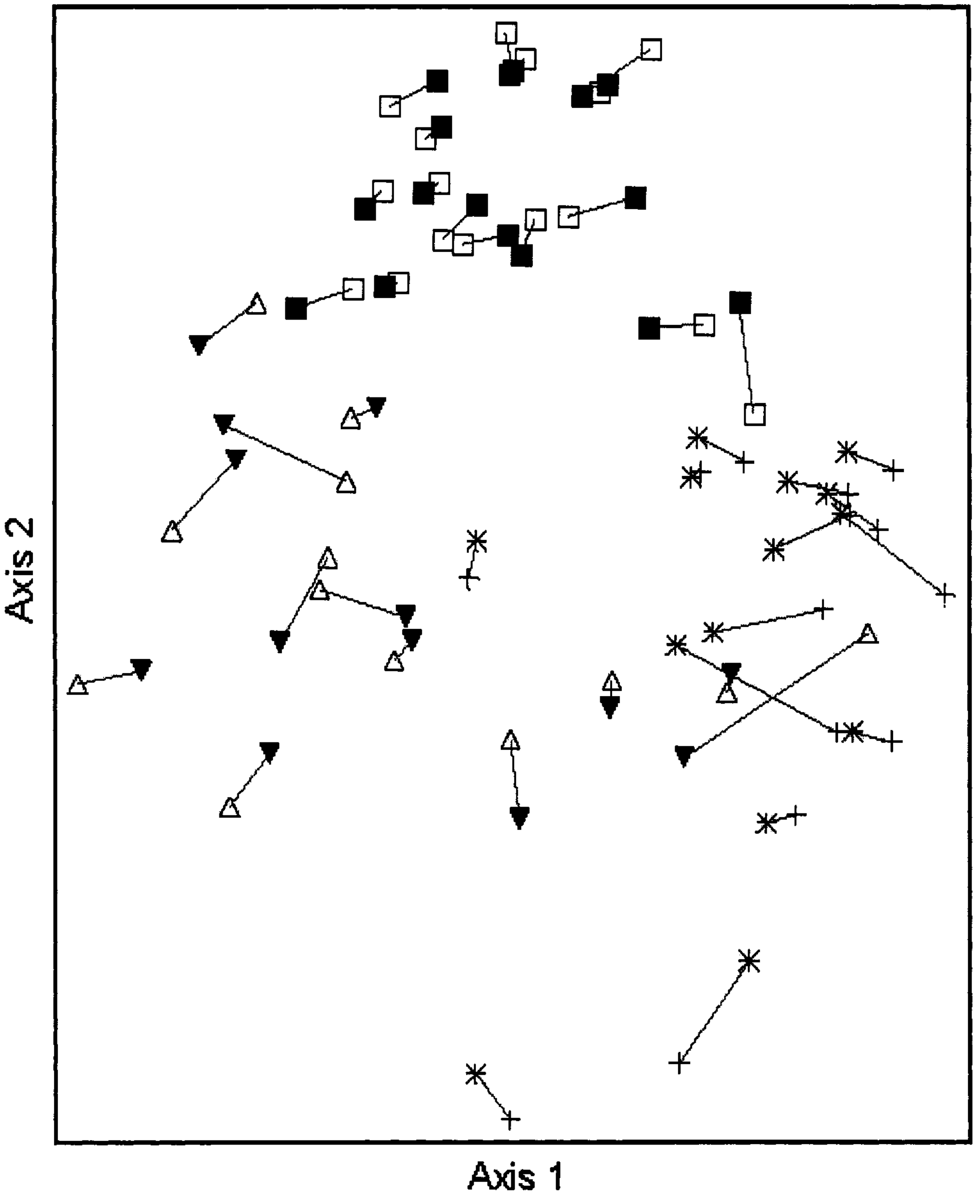

4.3b
percSlop
SoilpH
Axis 2
Axis 1

Figure 4.4. Results of NMS ordination and paired plot vectors based on basal area data for three forest types between 1977-78 and 2002 (cumulative r^2 = .756). Symbols are plots coded for year □= beech plots 1977-78, ■= beech plots 2002, Δ= cove plots 1977-78, ▲ cove plots 2002, + = HERO plots 1977-78, * = HERO plots 2002.


Axis 2
Axis 1

environmental characteristics and axis 3, only axes 1 and 2 are shown. Ordinations did not cluster plots by disturbance history nor was there consistency in the direction of change.

Changes in forest composition and structure by forest association and disturbance history

From 1977-78 to 2002 the forests in this study were not structurally or compositionally stable. Overall, the plots in this study declined in stem density from 593.3 to 528.4 stems/ha (10.9%) and basal area from 31.9 to 31.1 m^2/ha (2.6%). MRBP analysis indicates that the changes in composition ($p < 0.0001$, $A = .0352$) and basal area ($p = 0.0129$, $A = 0.0129$) were significant between time periods. Overall, 32 of 43 plots (74.4%) lost stems, basal area declined in 22 of the 43 plots (51.1%).

For all forest associations and by disturbance history, tree stem density declined (Table 4.3). Basal area declined in two of the three forest associations (COVE forest basal area increased 0.8%), and in all plots by disturbance history. MRBP indicated that in 2002 COVE and HERO forest types, but not BEECH were significantly different ($p < 0.05$) than in 1977-78. By disturbance history, undisturbed and heavy-cut forests differed significantly in 2002, but not selectively cut forests. Forest types were from 79.3-82.8% similar between 1977-78 and 2002. BEECH plots were most similar despite changing significantly in composition during the period. Plots by disturbance history were from 78 to 85.5% similar with diffuse disturbance plots maintaining the greatest similarity.

Examining forest types by disturbance history for all species and for indicator species within each type reveals a mosaic pattern of change (Table 4.4), although none of the comparisons were significant. Undisturbed BEECH (N=4) and COVE (N=3) forests declined in basal area and stem density as did their indicator species. Undisturbed HERO

Table 4.3. Summary of community attributes by disturbance history and forest type and MRBP results for trees $\geq$ 10 cm DBH in 43 plots in western Great Smoky Mountains National Park. Disturbance histories are: UN (undisturbed), DD (diffuse disturbance), HC (heavy cut). Forest types are: COVE (*Tsuga canadensis – Halesia tetraptera* upper cove forest types), BEECH (*Fagus grandifolia* dominated forests) and HERO (high-elevation red oak forests). Attributes are: mean stem density (D # stems/ha), mean basal area (BA in m^2/ha), and PS (percent similarity). MRBP results p-value of comparison of forests between time periods, A (within-group agreement).

	UN (N=11)		DD (N=18)		HC (N=14)		COVE (N=13)		BEECH (N=16)		HERO (N=14)	
Attribute	1977-8	2002	1977-8	2002	1977-8	2002	1977-8	2002	1977-8	2002	1977-78	2002
Density	576	504	568	529	639	546	650	542	467	428	683	631
BA	32.8	28.8	28.9	31.0	35.2	33.1	36.6	36.9	29.9	27.5	30.0	29.8
PS	78.0		85.5		78.0		82.8		81.4		79.3	
p-value	0.0025		0.1099		0.0032		0.008		0.0605		0.0008	
A	0.0799		0.0184		0.0437		0.0509		0.0453		0.1260	

Table 4.4. Summary of mean basal area (BA in m^2/ha) and mean stem density (D in #/ha) by forest type and disturbance for all trees ≥ 10 cm DBH within a forest type and for indicator species in 43 plots in western Great Smoky Mountains National Park. Disturbance histories are: UN (undisturbed), DD (diffuse disturbance), HC (heavy cut). Forest types are: COVE (*Tsuga Canadensis – Halesia tetraptera* upper cove forest types), BEECH (*Fagus grandifolia* dominated forests) and HERO (high-elevation red oak forests). Top number in each 1977-78 cell is number of plots represented by the 1977-78 BA and D values in each forest type by disturbance history comparison; numbers in parentheses are standard deviation.

	Undisturbed				Diffuse disturbance				Heavy cut			
	BA		D		BA		D		BA		D	
Forest Type	1977-8	2002	1977-8	2002	1977-8	2002	1977-8	2002	1977-8	2002	1977-78	2002
BEECH	4 34.8 (4.9)	25.5 (5.7)	44.0 (167.5)	35.8 (122.5)	8 26.8 (9.2)	29.1 (4.6)	455 (178.1)	470 (167.9)	4 31.2 (3.2)	26.4 (5.6)	518 (90.0)	415 (102.5)
F. grandifolia	1.55 (0.13)	0.37 (0.05)	40 (4.8)	20 (2.2)	9.11 (0.54)	9.25 (0.81)	228 (13.5)	216 (17.2)	13.81 (0.58)	11.90 (0.72)	283 (14.7)	213 (16.0)
A. octandra	13.53 (1.15)	9.82 (0.47)	170 (14.1)	128 (6.2)	4.92 (0.36)	4.46 (0.48)	59 (18.8)	53 (3.2)	2.33 (0.26)	2.17 (0.26)	48 (5.5)	38 (4.5)
COVE	3 33.4 (12.9)	30.3 (3.3)	550 (10.0)	490 (191.6)	3 33.6 (2.2)	39.0 (6.4)	590 (291.4)	510 (225.4)	7 39.3 (7.7)	39.1 (12.0)	719 (189.8)	577 (162.7)
T. canadensis	8.20 (1.39)	2.75 (0.40)	97 (14.2)	57 (7.2)	1.20 (0.21)	1.97 (0.30)	63 (11.0)	83 (11.2)	10.46 (1.17)	11.89 (1.27)	124 (15.1)	164 (14.1)
H. tetraptera	1.90 (0.17)	1.78 (0.20)	50 (4.6)	33 (3.1)	8.87 (0.53)	10.42 (0.79)	217 (8.0)	163 (2.5)	5.66 (0.37)	4.86 (0.36)	139 (7.0)	107 (8.1)
B. lenta	0.60 (0.07)	0.65 (0.06)	33 (3.1)	20 (2.0)		0.13 (0.02)		3 (0.6)	1.29 (0.19)	1.24 (0.22)	46 (7.2)	31 (6.2)
M. fraseri	0.23 (0.04)	0.21 (0.04)	7 (0.6)	10 (1.7)					3.87 (0.41)	4.07 (0.47)	81 (10.4)	63 (7.3)
HERO	4 30.4 (5.2)	31.3 (11.2)	733 (217.9)	660 (88.3)	7 29.3 (2.0)	29.7 (4.2)	689 (117.3)	606 (89.2)	3 30.9 (18.1)	28.0 (11.0)	613 (92.4)	650 (177.8)
Q. rubra	19.08 (0.81)	14.73 (0.73)	313 (17.1)	210 (14.1)	17.55 (0.99)	16.15 (0.75)	309 (25.5)	226 (15.1)	11.12 (1.49)	5.17 (0.50)	83 (13.6)	47 (7.2)

(N=4) forests increased slightly in basal area but the increase was not due to northern red oak (*Q. rubra*), the HERO indicator species, which declined almost 23%.

The basal area of all diffuse disturbance forest types increased and stem density decreased, except BEECH (N=8) forests. This overall pattern is characteristic of forests in the self-thinning phase of succession. However, only in COVE (N=3) and BEECH forests did the changes in the basal area of the indicator species mirror the forest type pattern. As in undisturbed forests, northern red oak declined in basal area despite a slight increase in HERO (N=7) plots. Although BEECH forest stem density increased, it was not driven by increases in the indicator species, American beech (*Fagus grandifolia*) and yellow buckeye (*Aesculus octandra*).

Because of their more recent history of disturbance, forests on heavy-cut plots might be expected to follow a pattern similar to that of diffuse disturbance plots. However, the period from 1977-78 to 2002 in these forests was characterized by a decline in basal area for all forest types and, in stem density for BEECH (N=4) and COVE (N=7). BEECH forest indicator species followed the forest type pattern, but in COVE forests eastern hemlock (*Tsuga canadensis*) basal area and stem density increasd and Fraser magnolia (Magnolia fraseri) basal area increased, despite overall forest type declines in both attributes. Heavy-cut HERO (N=3) forests declined slightly in basal area but gained stems while northern red oak declined over 53% in basal area and 43% in stem density.

Correlations with environmental and soil chemical characteristics

Some environmental and soil chemical characteristics were strongly correlated with basal area and stem density in each period (1977-78 and 2002) (Table 4.5), and with the change in

Table 4.5. Pearson correlation coefficients for environmental and soil chemical characteristics significantly associated $p < 0.05$ (*$p < 0.01$) with plot basal area and stem density 1977-78, and 2002 and the % change in these measures during the study period.

	Basal Area			Density		
Variable	1977-8	2002	% change	1977-8	2002	% change
% slope					-.37	-.34
CEC				.51*	.40	
% K	-.35		.45*			
P (ppm)						.31
K (ppm)			.43*		.37	
% OM					.39	
Exch Al		-.31	-.42*			

these attributes during the period of study. The results indicate that the forest attributes were associated with different characteristics 1977-78 than in 2002, and that declines in density and basal area during the study period were associated with high soil cation levels (P and K) and high soil aluminum (Table 5). These correlations contrast with changes in basal area and stem density in high-elevation beech-dominated forests which had gains in basal area associated with low soil cations and high aluminum (Chapter 3).

Discussion

The period from 1977-78 to 2002 is marked by declining stem densities and basal areas which, because they occur across forest associations and disturbance histories, appear to be a system-wide problem in which tree-sized stems are dying, but are not being replaced by smaller stems.

Declining stem densities are to be expected during some stages of secondary succession: if all the plots in these forests were of secondary origin and were in the transition phase of succession, a net loss of stems might be explained as self-thinning as a consequence of size-dependent asymmetric competition (Peet 1981, Coomes et al. 2003). However, several lines of evidence suggest that this is not what is happening in the forests in this study. First, the structure and history of the forests suggests that they were late-successional at the time the plots were established in the late 1970s. Second, during self-thinning basal area should increase because the dying stems are small and winning stems continue to accrete biomass but in this study there was an overall decline in basal area. The third and perhaps most telling reason self-thinning is not an explanation for the pattern of decline seen in these forests is the observation that the proportional decline in stem density in undisturbed forests was larger than in selectively cut forests, and almost as large as heavily cut forests. Additionally, the proportional basal area decline in undisturbed forests was larger than in any other disturbance category, suggesting that the decline is independent of disturbance history.

Of the forest associations identified in this study, HERO and COVE forests changed significantly, and BEECH forests did not. Because beech is an extremely shade-tolerant species (Canham 1990, Poage and Peart 1993), it is considered characteristic of successional endpoint forest associations in the eastern United States. The observation that BEECH forest composition remained statistically unchanged while HERO and COVE forest associations did change (though they contained greater proportions of less shade-tolerant species), is consistent with predictions about the relative stability forests dominated by shade-tolerant species. However, BEECH forests were not entirely stable: they declined in basal area and stem density, and considering their marginal MRBP p-value, it is likely that these forests would have changed significantly given more time, suggesting that BEECH forests are not unchanging but that their rate of change is slower than that of HERO and COVE forests. The comparatively slow temporal dynamics in western GRSM beech forests will be altered because beech bark disease in eastern GRSM is slowly spreading westward (Chapter 5). When BBD reaches the plots in this study, beech trees are likely to suffer the same high rates of mortality as eastern GRSM beech forests.

Disturbance histories do not appear to be the reason for changes in forest attributes in this study, and changes in forest attributes by disturbance history do not follow the predictions of the forest succession model. The model predicts that undisturbed forests should be stable, or demonstrate less change than diffuse disturbance and heavy-cut forests. But in this study, undisturbed forests changed significantly and the changes in basal area and stem density were similar to those of heavy-cut forests. The change in attributes by disturbance history within each forest type reinforces the idea that forest landscapes at large spatial scales are mosaic. No single pattern emerged from the analysis: the attributes of plots by forest type or disturbance history did not behave in a consistent manner.

The pattern of decline in attributes in forests of different associations and disturbance histories suggests that something other than population based successional processes are operating here. There are several possibilities: feral hogs (*Sus scrofa*) spend their summers in high-elevation deciduous forests. They can directly consume seedlings and their rooting disturbs the soil A horizon, potentially inhibiting the germination of tree seeds (Bratton 1974, Huff 1977). However, sapling densities in these plots appear to be more than adequate to replace dying overstory trees (unpublished data, Chapter 2), which suggests that the decline in tree-sized individuals is not due to regeneration failure and therefore must be due to a failure of sapling-sized individuals to recruit into tree size classes. For the same reason, white-tailed deer (*Odocoileus virgninanus*) browsing is unlikely to be the cause of the observed recruitment failure.

The loss of American chestnut (*Castanea dentata*), particularly in HERO forests, could be associated with changes in forest composition and structure. Prior to the invasion of chestnut blight (Cryphonectria parasitica), American chestnut was an important species in GRSM forests (Woods and Shanks 1959), and was locally abundant at elevations exceeding 1200 m and formed associations with various oak species, including northern red oak (Whittaker 1956), though northern red oak also formed high-elevation stands containing little or no chestnut. At high-elevations, silverbell and shade-tolerant understory species were predicted to replace chestnut following its death from the blight (Whittaker 1956). However, the death of chestnut more than 50 year ago cannot explain the decline in northern red oak during the past 25 years. In this study, oak decline has two components: the death of canopy trees, and the failure of advance regeneration to replace them. It is possible that the high rate of death of canopy oak trees is due to a natural pattern of senescence of an age cohort and the growth of shade-tolerant canopy trees has suppressed oak advance regeneration. However, the oak size-structure distribution does not reveal a size cohort, and it indicates that there is ample advance regeneration (unpublished data).

The demography of tree populations in this study and the published history of fire in this area suggest that fire suppression is unlikely to be a cause of the observed decline of canopy trees. Fire suppression, particularly in oak-dominated stands, has been associated with oak forest decline in mesic sites in the eastern United States (Abrams 1992, Goebel and Hix 1996), but while oaks decline there is a commensurate increase in the stem densities of fire-intolerant species, a pattern which is not documented in this study. In this study, even fire-intolerant species, such as *F. grandifolia* and *A. octandra* are declining. Since the creation of GRSM, fire suppression has greatly decreased fire frequency in the park (Lindsay and Bratton 1979, Harmon 1983), particularly on dry sites. In GRSM, fires at the highest elevations are rare (Harmon 1981), and though high-elevation red oak forests in the southern Appalachians are commonly thought to have been subject to fire (DeLapp 1978, NatureServe 2005), including the ones in GRSM (Albert Meier, personal communication), the sites in this study receive abundant rainfall, distributed relatively evenly throughout the year (White et al. 1993), and therefore would be unlikely to burn frequently. Additionally, the plots in this study are close to Gregory Bald and Russell Field, historic balds in GRSM for which Lindsay and Bratton (1979) reported no evidence of burning by herders.

During the summer ozone levels at high-elevations in GRSM can be high enough to damage leaf tissues (Shaver et al. 1994). However, the species known to be most susceptible to leaf tissue damage from high ozone levels are not the ones in decline in this study (Neufeld et al. 1992). Furthermore, ozone damage has never been associated with large-scale forest decline.

A final possibility is that high deposition rates of atmospheric compounds of nitrogen and sulfur are causing changes in tree species composition. The results of this study are consistent with studies of forest decline in the eastern United States that report that soil acidity, low soil cation concentrations and the mobilization of Al at low pH contributes to the mortality of forest trees (Decker and Boerner 1997, Driscoll et al. 2001, Drohan et al. 2002, Bailey et al. 2004). It was assumed that soil chemical characteristics had not changed between 1977-78 and 2002, but correlation analysis indicates that the soil characteristics to which plot basal area, stem density and species richness were correlated in 1977-78 were different than the characteristics to which they were correlated in 2002. Moreover, soil chemistry was strongly correlated with the change in these forest attributes between 1977-78 and 2002. Although soils data from 1977-78 do not exist, there is circumstantial evidence supporting the possibility that high-elevation forest soils in GRSM became more acid during the period of this study. Golden (1981) and Callaway et al. (1987) studied high-elevation deciduous forests in GRSM forest of the same composition and from the same region of the park and reported soil pH values ranging from 4.6 to 5.3. In contrast, soil pH in this study ranged from 3.7 to 5.3, with a median value of 4.1. Soil Al mobilizes and becomes toxic to plant roots at soil pH values below 4.5 (Brady 1990); only three of the 43 plots in this study had soil pH exceeding 4.5.

Conclusions

Overall, the high-elevation forests of GRSM changed in composition and structure during the time period covered in this study. Contrary to the expectation of the forest succession model, these forests, though late-successional, do not represent an endpoint in succession. As demonstrated in this study, stability in forest attributes is not common. Therefore, the paradigm that temperate forest communities progress towards a stable climatic climax is impractical and should be replaced with the understanding that forest continually change, even over relatively short time scales. Additionally, the results of this study suggest that forest conservation strategies aimed at preserving particular species assemblages are short-sighted. The rate at which forest attributes change might slow down, but stability is an unlikely and unrealistic expectation.

In this study forest decline is attributed to tree responses to soil chemistry, specifically low soil cations and mobilized Al. If soils are indeed becoming more acidic due to inputs of atmospheric nitrogen and sulfur, acid deposition represents a ubiquitous and persistent exogenous disturbance. The results of this study suggest that in addition to adjustments in the ranges of forest trees due to climate change, local declines may be associated with acid deposition, further complicating land management, and conservation efforts.

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Chapter 5

The distribution and severity of Beech Bark Disease in high-elevation beech (*Fagus grandifolia* Ehrh.) forests of Great Smoky Mountains National Park, Tennessee and North Carolina.

Abstract

In this study in the effect of beech bark disease (BBD) on the high-elevation (> 1200 m) beech forests in Great Smoky Mountains National Park (GRSM) is reported. BBD was first identified in 1993 near Clingmans Dome in central GRSM and has since spread eastward causing average losses in beech stems and basal area in excess of 46%. In contrast, western GRSM beech forests lost less than 15% of stems and basal area. The longitudinal gradient of high disease severity in the east and low in the west is counterintuitive given the mobility of the disease and the greater continuity of the beech population in western GRSM. Possible reasons for this paradox are discussed. In contrast with the findings of studies conducted elsewhere, BBD severity was not greater for dominant beech trees, stands with denser beech populations or those with greater beech basal area. BBD severity was strongly associated with landform index (LFI), soil sodium, sulfur, and aluminum, and % clay. Woody understory stem densities are significantly reduced in areas with high blackberry (*Rubus Canadensis*) cover such as those in eastern forests. Woody understory stem densities are significantly lower in eastern beech forests but short-term succession is likely to be influenced by a greater number of species than western forests, which will continue to be beech dominated in the absence of BBD.

Introduction

Beech-bark disease (BBD) is an introduced, insect-fungal pathogen complex of American beech (Houston 1994). In the late 19th century it was discovered in Nova Scotia (Ehrlich 1934) and has since spread southward; a spot infection was discovered in Great Smoky Mountains National Park (GRSM) in 1993 near Clingmans Dome (Houston 1994) in a patch of high-elevation beech forest. BBD establishment requires infestation by beech scale (*Cryptococcus fagisuga*), a parthenogenic insect that alters the bark of the tree facilitating fungal infection by one of two *Nectria* species (*N. coccinea*, an exotic fungus, or *N. galligena*, a native species) in meristematic tissue (Mahoney et al. 1999). As the insect spreads across the range of American beech, *N. galligena* is often first to infect beech stems; if *N. coccinea* subsequently invades a stand, it will eventually dominate (Houston 1994). Fungal growth eventually girdles the tree and the bark characteristically dissociates from the sapwood making for easy forensic identification of BBD as the causal agent of beech mortality (Erhlich 1934). Because the fungi cannot infect beech stems unless the scale insect first wounds the tree (Houston et al. 1979a), the spread of BBD is dependent on the dispersal of the insect. Larvae of the insect are motile for only a short period in the summer (Wainhouse 1980) and are dependent on wind for travel off the host tree (Dajoz 2000).

The extent and severity of BBD, genetic aspects of host resistance to it, and its effect on forest composition and structure have been studied in the deciduous forests of northeastern North America (Ehrlich 1934, Houston 1975, Houston et al. 1979a, Houston et al. 1979b, Twery and Patterson 1984, Houston 1988, Houston 1994, Houston and Houston 2000, Runkle 1990, Peart and Gavin 1993, Griffin et al. 2003, Latty et al. 2003). In diseased forests of northeastern North America high beech mortality has been linked to dominant beech trees, high stem density (Mize and Lea 1979, Houston 1983, Runkle 1990, Gavin and Peart 1993, Griffin et al. 2003, Latty et al. 2003), bark amino nitrogen content (Wargo 1988, Latty et al. 2003), forest basal area (Griffin et al. 2003), and the lack of genetic resistance (Houston and Houston 2000). Environmental factors that have been associated with increased disease spread and severity include elevation (Griffin et al. 2003), and minimum winter temperature (Ehrlich 1934). However, in GRSM, no comprehensive study of the distribution of BBD and its effect on the forests of GRSM has been published. In GRSM, high-elevation beech populations represent the southernmost range extension of gray beech, which is most common in the northeastern United States, and has been most affected by BBD.

The purpose of this study is to describe the distribution and severity of BBD as they relate to beech forest structural characteristics, environmental and soil characteristics, and pre-park disturbance history and to use stem densities of woody understory species to speculate of future forest composition. Specifically, I ask whether: 1) beech mortality from BBD is higher for dominant beech trees, in plots with greater beech densities, or in plots with greater beech basal areas, 2) beech mortality patterns are correlated with environmental and soil chemical characteristics, or pre-park disturbance history, and 3) blackberry (*Rubus canadensis*) cover in diseased plots decreases woody understory stem densities and alters the future composition of high-elevation beech forests.

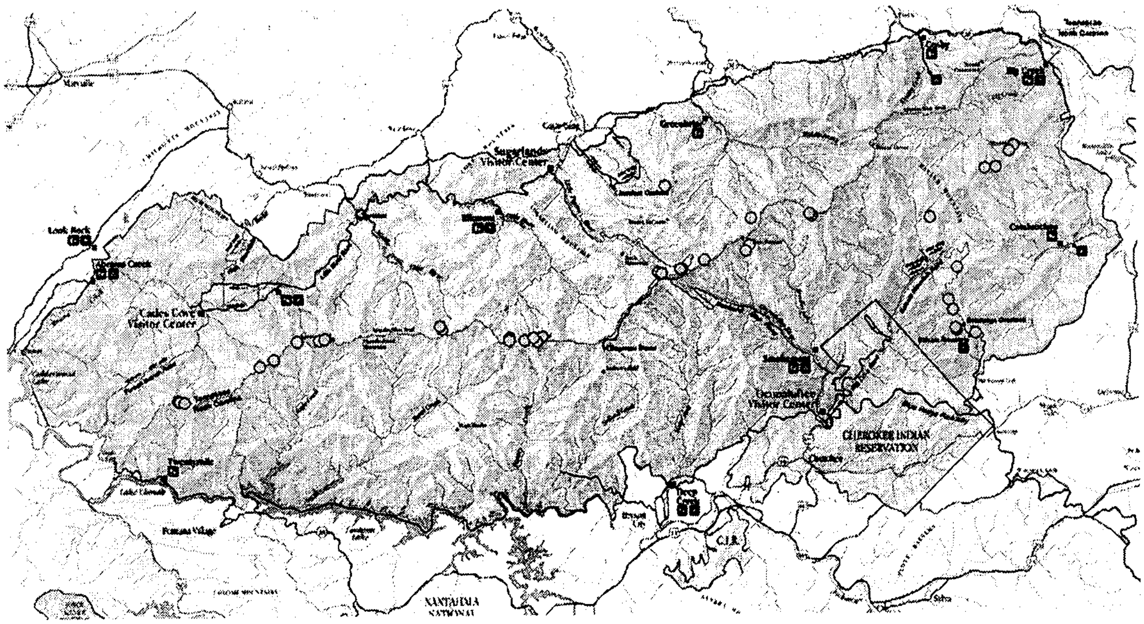
Methods

Study location and plot characteristics

This study was conducted in the high-elevation beech-dominated forests of Great Smoky Mountains National Park (Figure 5.1). High-elevation beech forests are found throughout the park above 1200 m, and are noticeable as distinct compositional and structural patches, having canopy beech stem relative densities > 50%, and an orchard-like physiognomy (Russell 1953). In eastern GRSM, within the range of spruce-fir (*Picea abies-Abies fraseri*) forests, beech forests are generally south-facing and form deciduous islands in landscape concavities at the uppermost cove positions (gaps). Because canopy beech trees are rare in the spruce-fir matrix the beech forests are like islands that are effectively isolated from one another. West of the range spruce-fir, near Silers Bald (35^0 34'N 83^0 33'W), beech forms distinct pockets of monodominant forest surrounded by a northern hardwood and high-elevation red oak forest matrix (White et al. 1993). In contrast with its habitat restrictions in the spruce-fir zone, beech occurs on all aspects and is an important canopy co-dominant throughout the deciduous forest matrix in western GRSM.

Of the 39 plots in this study, 18 were permanent plots established in the late 1970s through mid-1980s and resampled in the summers 2000-02. In 1977-78, park personnel established five 0.1 ha permanent plots in high-elevation beech-dominanted forests in western GRSM. In 1985 beech forests surrounding hog exclosures (N=11) were mapped in plots ranging in size from 0.12 to 0.25 ha. The maps give the XY coordinates, DBH, and species identity of each stem ≥ 10 cm. The 17 plots described above were resampled in the summer of 2000. In 1976, two 0.1 ha permanent plots were established and stems ≥ 10 cm were mapped and

Figure 5.1. Location of 40 high-elevation beech plots in Great Smoky Mountains National Park.


Sugarlands Visitor Center
Cades Cove Visitor Center
Oconaluftee Visitor Center
CHEROKEE INDIAN RESERVATION
NANTAHALA NATIONAL
Cataloochee
Look Rock
Abrams Creek
Elkmont
Smokemont
Deep Creek
Fontana Village
Gatlinburg
Cosby
Big Creek
Bryson City
Cherokee
Maryville

tagged near Newfound Gap to replicate non- permanent plots sampled by Rudolf Becking and Robert Whittaker in 1959 (Becking and Olson 1976). These were located and resampled in the summer of 2002. The permanent plots give direct observation of the composition and structure of high-elevation beech forests prior to BBD infestation and were used to report temporal forest population dynamics in diseased (N=7) versus BBD-free (N=11) forests.

In order to cover the entire geographic and environmental range of high-elevation beech-dominated forests in GRSM, 21 additional permanent plots were established in 2002. The new plots were placed in high-elevation beech-dominated (> 50% relative density) forests in areas of the park not already represented by permanent plots.

Distribution and severity of BBD in GRSM

Each stem $\geq$ 10 cm in each plot was measured for DBH and assigned a tree condition (1 = no canopy dieback, 2 = 1-25%, 3 = 25-50%, 4 = 50-75%, 5 = 75-99%, 6 = dead), and canopy position class (1 = dominant, 2 = subdominant, 3 = intermediate, 4 = suppressed). Using data from all 39 plots, pre-blight forest stem density and basal area were estimated by assuming that the sum of all living and all dead stems on plots in 2000-2002 could be used to characterize their pre-blight condition (i.e. before 1993). This approach is reasonable because BBD has been in GRSM since only 1993, because it leaves a characteristic "calling card" for easy forensic identification of BBD-killed beech trees, and because most dead beech stems > 10 cm were still standing as of 2000-02. Data from BBD-free plots indicate that natural background mortality of stems $\geq$ 10 cm DBH is low (< 1 stem per decade per 0.1 ha plot) so BBD could safely be assumed to be the cause of death of the beech stems on each plot. Ingrowth from saplings (stems < 10 cm) into tree size classes following BBD infestation represents a small fraction of total stems and their diameter is small so basal area changes from these individuals are negligible. The spatial distribution and severity of BBD in GRSM, was assessed by organizing plots along an east-west axis and summing the proportion of beech basal area represented by dead stems using reconstructed plot data. Near-term (1-3 years) mortality was estimated by assuming that beech with tree condition classes 4 and 5 would die in the near future. Pre-blight versus post-blight densities of plots with high BBD-mortality versus those with low mortality were compared using Wilcoxon's signed-rank test for matched pairs in SAS v 8.2. Pre- and post-blight densities/ha and basal areas/ha of high and low mortality plots were compared using the Wilcoxon two-sample test.

Data from the 18 permanent plots established 1976-85 were used to establish temporal changes in densities/ha and basal areas/ha of beech and co-occurring species. Because the fates of individual trees could be followed using mapped plots (N=13), data from them were used to determine annual mortality rates and canopy residence times for all species $\geq$ 20 cm DBH because in these stems exceeding this diameter are canopy co-dominants. Annual mortality (AMR) was calculated using the formula $\mathrm{AMR} = [\ln N(t_2) - \ln N(t_1)]/(t_2 - t_1)$, where $N(t_2)$ and $N(t_1)$ are the stem numbers at the beginning and end of the time interval. Canopy residence time (CRT) was calculated as the reciprocal of AMR: CRT = 1/AMR.

The relationship between beech mortality and dominant stems, plot density, and basal area

To determine whether dominant beech trees were more affected by BBD than subdominant trees, beech stems were sorted into 5 cm diameter classes (for stems $\geq$ 10 cm). The mean tree conditions of beech stems $\geq$ 30 cm was compared to stems < 30 cm. Additionally, logistic regression tested whether beech mortality in each size class differed from a pre-blight reconstruction of beech stems by size class. The relationship between beech mortality and beech stem density and basal area was tested by regressing pre-blight beech densities (#/ha) and basal areas (m^2/ha) with dead beech density in each plot. All statistics were performed in SAS v 8.2.

Beech mortality and environmental and soil characteristics and prepark disturbance

For all plots elevation, slope, aspect (which was later Beers transformed), landform index (LFI) and terrain shape index (TSI) (McNab 1992) were recorded. Soils were collected from the A horizon in 25 of the 39 high-elevation beech plots and were analyzed by Brookside Labs, New Knoxville, OH. Beech mortality (density/ha) was tested for correlation with percent clay, sand and silt, and bulk density, total exchange capacity (M.E./100 g), pH, estimated nitrogen release (lb/acre), soluble sulfur, phosphorous, Ca, Mg, K, Na, B, Fe, Mn, Cu, Zn, and Al (all measured in ppm), and percent base saturation of Ca, Mg, K, and Na.

Maps of disturbance history in GRSM (Pyle 1988) were used to assign a pre-park disturbance level to each plot. These levels were then correlated with beech mortality. Environmental and soil characteristics that were significantly correlated with beech mortality were further tested for significance by comparing their mean values in diseased versus BBD-free forests using the Wilcoxon two-way test in SAS.

Woody understory composition and regeneration patterns

The stem density of woody understory species (< 10 cm DBH) was recorded by size class: < 1.4 m tall, 1.4 m tall to 2.4 cm DBH, 2.5-4.9 cm, 5.0-7.4 cm, and 7.5-9.9 cm in all 39 plots. Because blackberry is ubiquitous in high-elevation disturbed areas in GRSM, stem density, and cover were recorded for this species.

Short-term successional patterns were examined by comparing abundances of woody understory stems in BBD-affected beech forests with those in BBD-free beech forests. To determine whether blackberry cover affects woody understory densites the sum of woody understory densities was correlated with average % blackberry (*Rubus canadensis*) cover in BBD-free and diseased plots using PROC CORR in SAS v. 8.2. Population means of woody understory densities by size class in BBD-free versus diseased forests were compared using the nonparametric Wilcoxon two-sample test in SAS.

Results

General mortality patterns: distribution and severity of disease in GRSM

For reconstructed plots, stem density of all species averaged 750/ha pre-blight (prior to 1993) and 556/ha post-blight (Table 5.1). For beech, average density dropped from 534/ha to 366/ha. Average plot basal area decreased from 30.1 to 23.1 m^2/ha, while beech BA fell from 17.1 to 12.1 m^2/ha. Beech became less important in these forests as its relative density dropped from 70.8% to 62.1%, and relative basal area from 58.6 to 51.9%. All temporal changes in stem density and basal area were significant ($p < 0.05$). BBD created a significant disparity in average plot-level (all species) and beech stem densities and basal areas in western GRSM versus those the east. Prior to BBD, there was no difference in the average values of these measures between western and eastern plots. Following BBD, plot-level and beech stem densities and basal areas were significantly higher in western GRSM.

The longitudinal pattern in stem density and basal area caused by BBD is apparent when

Table 5.1. Mean pre-blight and post-blight stem densities (#/ha) and basal areas (m^2/ha) in 39 plots using reconstructed plot data. Average plot ([a] and [b]) density and basal area and the average density and basal area of beech ([c] and [d]) stems in western GRSM plots were compared with those in eastern beech forests.

	Pre-blight (1993)		Post blight	
	Density	Basal area	Density	Basal area
All plots (n=39)	750 (239.7)	30.2 (7.5)	556 (271.6)	23.1 (8.7)
Beech	534 (243.2)	17.1 (7.1)	366 (249.7)	12.1 (8.3)
% beech	70.8	58.6	62.1	59.1
Western plots (N=15)	789[a] (250.5)	31.6[a] (4.1)	697.5[a] (198.9)	27.5[a] (4.3)
Beech	595[c] (270.7)	19.3[c] (7.1)	522[c] (226.1)	16.6[c] (6.5)
% beech	75.4	61.1	74.8	59.9
Eastern plots (N=24)	725[a] (320.5)	29.3[a] (9.0)	467[b] (276.6)	20.4[b] (9.7)
Beech	496[c] (221.8)	15.8[c] (6.9)	268[d] (213.9)	9.3[d] (8.1)
% beech	68.3	57.0	57.3	46.8

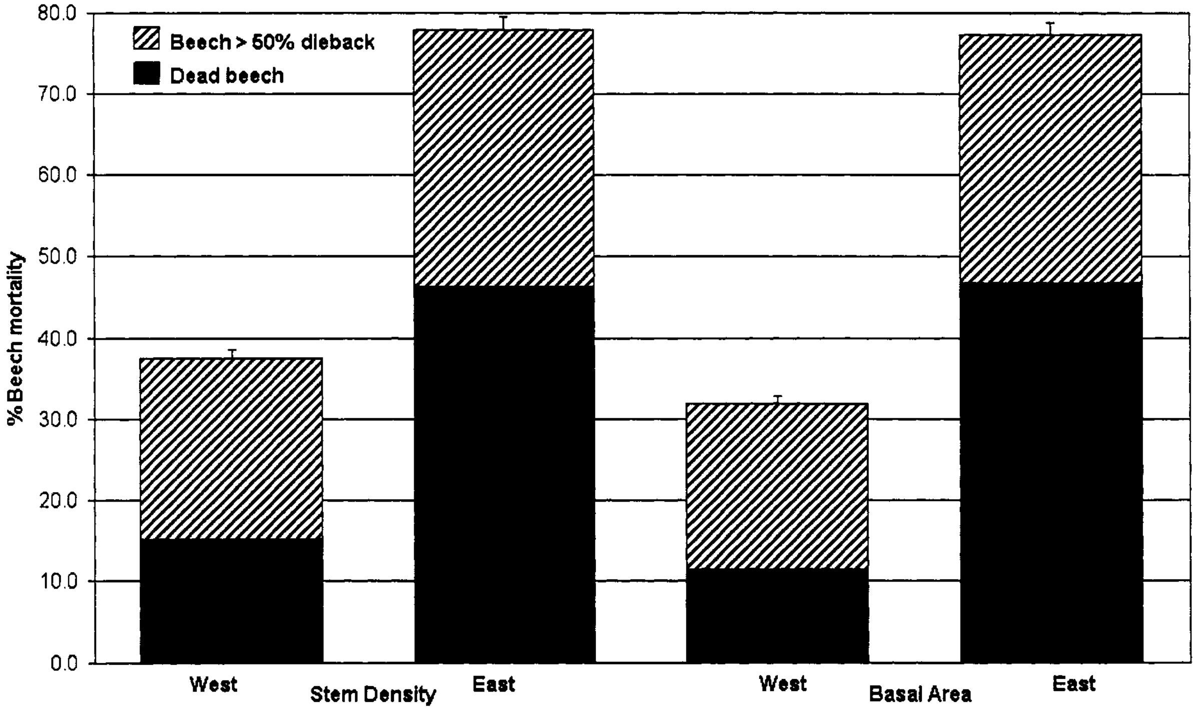
[a] Numbers in a column with the same letter are not significantly different at ($\alpha < 0.05$)

examining beech mortality as well (Figure 5.2). The relative density of dead beach averaged 46.1% and relative basal area averaged 46.7% in eastern plots but only 14.9% and 11.3%, respectively, in western GRSM. If all stems living as of 2002, but with > 50% dieback eventually die, relative beech stem and basal area losses will approach 80% in eastern GRSM. As of 2002, the projected declines in beech relative density and basal area in western GRSM were less than 40%. Although BBD was first discovered in the central part of the park near Clingmans Dome, it appears to have migrated eastward, through the relatively isolated patches of beech forest in spruce-fir, faster than westward, where patches of beech-dominated forest are connected by beech trees in the deciduous forest matrix.

Because the above estimation of pre-blight stem densities and basal areas requires that dead stems be added to living ones at the time the plots were sampled, this method does not take into account ingrowth (stems growing into the smallest tree size class) or accretion (growth of living stems) in the time since BBD infestation, either of which could more than exceed losses from mortality. Data from the resampled permanent plots (N=18) shows that from 1985-2000 western GRSM beech forests gained stems and basal area, while eastern forests declined in both measures (Figure 5.3). In western GRSM plots, beech stem density increased an average of 13.1% and basal area increased 28.3%, during the same period those measures in eastern GRSM forests declined 31.7% and 26.1%, respectively. The increase in beech density and particularly basal area in western GRSM is remarkable given the late-successional status of these forests and the purported slow growth rate of American beech (Canham 1988). The demographics of the basal area increase are examined in Chapter 3.

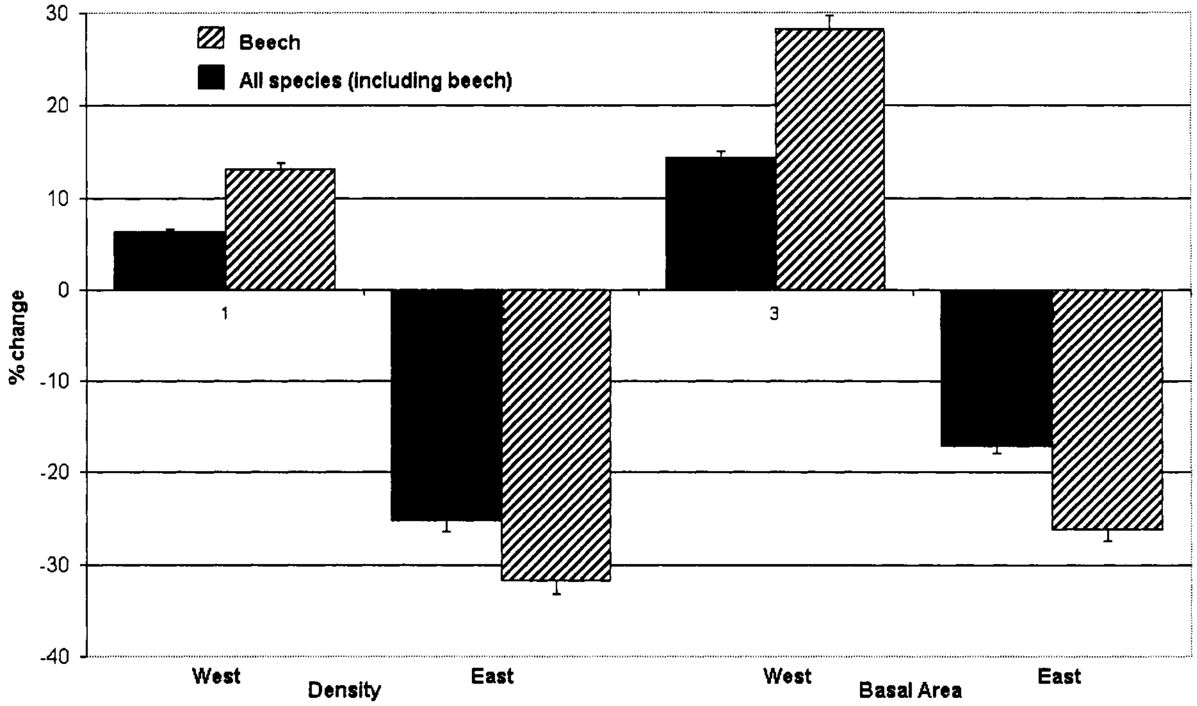
From 1985-2002 beech had the highest annual mortality rate and shortest canopy residence

Figure 5.2. Current mortality (black columns) and estimated future mortality (diagonal pattern) of average stem density (#/ha) and basal area (m^2/ha) for reconstructed high-elevation beech populations west (N=15) and east (N=24) of Clingmans Dome in Great Smoky Mountains National Park.



80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
% Beech mortality
Beech > 50% dieback
Dead beech
West
Stem Density
East
West
Basal Area
East

Figure 5.3. Comparison of average percent change in stem density (#/ha) and basal area (m^2/ha) from 1985 to 2002 in eastern (N=9) and western (N=9) high-elevation beech forest plots in Great Smoky Mountains National Park.



▨ Beech
■ All species (including beech)
% change
30
20
10
0
-10
-20
-30
-40
1
3
West
Density
East
West
Basal Area
East

time of all canopy codominants ($\geq$ 20 cm DBH) except shadbush (*Amelancher arborea*) and silverbell (*Halesia tetraptera* var *monticola*), which were relatively minor canopy species in these forests (Table 5.2). Across all plots, beech annual mortality ranged from less than 1% on Gregory Bald in far western GRSM to over 13% at Double Springs Gap (Table 3). Annual mortality rates were significantly higher and canopy residence times lower in eastern plots than western plots. No BBD-caused mortality was recorded in the plots on Gregory Bald; the low mortality rates and canopy residence times there probably represent pre-blight patterns.

The relationship between beech mortality and dominant stems, plot density, and basal area

Dominant beech trees were no more likely to suffer BBD infection in GRSM beech forests than subdominant trees. The average tree condition of canopy dominant beech trees (CP=1) was not significantly different (p=0.2919) than that of subdominant, intermediate, and suppressed trees. Furthermore there was no correlation between canopy position and tree condition (p=0.6871). Results of logistic regression indicate that in GRSM the disease kills all stem size classes in proportion to their density (p<0.0001) . In eastern GRSM plots, where mortality is greatest, from 40-45% of all stems in 5 cm size classes > 10 cm have been killed by BBD. However, appears to be a DBH below which beech stems in GRSM do not become infected. Though data was not collected that could confirm this hypothesis, personal observation indicates that it is 7-8 cm DBH.

In GRSM, BBD severity is not correlated with beech stem density or basal area. The relationships between pre-blight beech density and basal area and beech mortality were both negative and neither was significant.

Table 5.2. Annual mortality rate and canopy residence time for codominant trees (≥ 20 cm) in 13 mapped high-elevation beech forest plots in Great Smoky Mountains National Park

Species	**Pre-BBD**	**Post-BBD**	**Annual mortality (%/yr)**	**Canopy residence (yrs)**
Acer saccharum	16	12	1.9	52.1
Aesculus octandra	51	43	1.1	87.9
Amelanchier arborea	5	2	6.1	16.4
Betula alleghениensis	35	32	0.6	167.4
Fagus grandifolia	502	247	4.7	21.2
Halesia tetraptera	1	0	100	
Picea rubens	8	6	1.9	52.1
Prunus serotina	4	4	0	
Quercus rubra	12	10	1.2	82.3
Tsuga canadensis	1	1	0	

Table 5.3. Annual mortality rate and canopy residence time for beech trees (≥ 20 cm) in 13 mapped high-elevation beech forest plots in Great Smoky Mountains National Park. Annual mortality was calculated based with t=26 years for Newfound L3 and L5, and t=15 years for the rest of the plots.

Site	**Pre-BBD**	**Post-BBD**	**Annual mortality (%/yr)**	**Canopy residence (yrs)**
Pretty Hollow Gap	50	19	6.5	15.5
Balsam Mountain 1	35	18	4.4	22.6
Balsam Mountain 2	31	7	9.9	10.1
Newfound Gap L3	30	21	1.4	72.9
Newfound Gap L5	10	7	1.4	72.9
Indian Gap 1	46	30	2.8	35.1
Indian Gap 2	44	25	3.8	26.5
Indian Gap 3	36	23	0.3	33.5
Indian Gap 4-6	102	22	10.2	9.8
Double Springs 1	12	4	7.3	13.7
Double Springs 2	15	2	13.4	7.4
Gregory Bald 1	45	35	1.7	59.7
Gregory Bald 2	46	34	0.2	49.6
BBD plots	384	172	5.4[a]	18.7
Non-BBD plots	118	75	3.0[b]	33.1

Table 5.4. Correlation coefficients between % dead beech basal area and density and environmental and soil characteristics in 25 high-elevation beech forests.

	% clay	**LFI**	**Soluble S (ppm)**	**Na (ppm)**	**Na (% saturation)**	**Al (ppm)**
Dead beech (% BA)	** -.51449	*** .42645	** -.46980	*** .41658	** .45493	** -.40696
Dead beech (% density)	* -.40437	** .42798	** -.49609	** .42856	** .42856	** -.43378
Longitude (UTM-E)	[a].37237	*** -.62296	*** .68552	*** -.69739	* -.38383	** .43097

Beech mortality and environmental and soil characteristics and prepark disturbance

Beech mortality was significantly and positively correlated with LFI, Na (ppm), and % Na and negatively correlated with % clay, soluble S, and Al (Table 5.5). However, all of the above soil characteristics except % clay were also significantly correlated with the east-west orientation of plots in GRSM, therefore % clay is the only soil characteristic that cannot be explained by the change in soil factors along the longtudinal range of plots.

Comparison of the mean values for LFI, % clay, soluble S (ppm), and Na (ppm) were significantly different between western and eastern beech forests. However, despite their significant correlation with beech mortality, diseased forests and BBD-free forests did not differ significantly in Al (ppm) or Na % saturation (Table 5.6).

Plots in this study had pre-park disturbance categories of undisturbed, low-cut, selective cut and heavy cut. Analysis of the correlation between disturbance level and % beech mortality indicated no relationship (p=0.6682).

Woody understory composition and regeneration patterns

Woody understory stems ≤ 1.4 m tall, those 1.4 m tall to < 10 cm and the sum of both were strongly correlated with blackberry cover. Average densities of stems 1.4 m tall to < 10 cm DBH and the sum of all woody understory stems were significantly lower and blackberry cover and frequency were significantly greater in plots in eastern GRSM. The mean density of stems ≤ 1.4 m tall was not significantly different between diseased and BBD-free plots.

The relative density of woody understory species in western GRSM suggests that for the near-future forests will be dominated by beech, which represents 90.6% of stems (Table 5.7). No other species represented more than 3% of woody understory stems. In eastern plots

Table 5.5. Comparison of mean values of environmental and soil characteristics between BBD-free and diseased high-elevation beech forests in GRSM. Numbers in parentheses are standard deviations.

Characteristic	**Mean Value**	
	Eastern	**Western**
LFI	0.1519[a] (0.05)	0.0689[b] (.030)
% clay	5.5[a] (4.9)	12.6[b] (5.0)
Soluble S (ppm)	31.5[a] (9.5)	46.2[b] (12.1)
Na (ppm)	16.5[a] (5.8)	11.9[b] (4.0)
Na (% saturation)	0.8[a] (0.7)	0.6[a] (0.4)
Al (ppm)	640.1[a] (287.7)	922.0[a] (177.0)

Table 5.6. Results of Wilcoxon two-way test for significant differences in mean values of tree seedlings, saplings, the sum of understory tree stems (seedlings = saplings) and blackberry cover and within-plot frequency. Numbers in parentheses are standard deviations.

Characteristic	**Mean Value**	
	Eastern	**Western**
Stems $\leq$ 1.4 m tall (#/ha)	647^{a} (391.0)	972^{a} (482.1)
Stems 1.4 m tall to < 10 cm DBH (#/ha)	242^{a} (131.2)	379^{b} (109.5)
All woody understory (#/ha)	889^{a} (380.4)	1351^{b} (543.2)
Blackberry cover (%)	15.0^{a} (19.9)	3.0^{b} (3.7)
Blackberry frequency (%)	72.4^{a} (28.5)	58.2^{b} (39.8)

[a] numbers in a row followed by the same letter are not significantly different at ($p < 0.05$).

Table 5.7. Shade tolerance (t = tolerant, m = intermediate, I = intolerant), stem density (#/ha), and relative density (%) of woody understory species (< 10 cm DBH) in western (N=15) and eastern (N=24) high-elevation beech forest plots in Great Smoky Mountains National Park (2002).

Species	Eastern plots		Western plots	
	Density/ha	%	Density/ha	%
Abies fraseri (t)	495 (134.6)	5.6	17 (6.5)	0.1
Acer pensylvanicum (t)	134 (24.6)	1.5	215 (48.6)	1.6
Acer rubrum (t)	92 (25.0)	1.0	0	
Acer saccharum (t)	688 (108.3)	7.8	402 (95.3)	3.0
Acer spicatum (t)	663 (103.4)	7.5	0	
Aesculus octandra (m)	74 (13.7)	0.8	133 (132.8)	1.0
Amelanchier arborea (m)	411 (135.0)	4.6	15 (3.6)	0.1
Betula allegheniensis (i)	599 (105.9)	6.8	306 (53.6)	2.3
Fagus grandifolia (t)	4998 (218.0)	56.5	12246 (515.6)	90.6
Picea rubens (t)	121 (25.6)	1.4	7 (4.4)	<0.1
Quercus rubra (m)	11 (5.3)	0.1	100 (22.8)	0.7
Tolerant (values do not include beech)	2193[a] (421.6)	24.8	497[b] (151.5)	3.7
Intermediate	496[a] (154.0)	6.8	248[a] (57.8)	1.8
Intolerant	599[a] (105.9)	6.8	306[a] (53.6)	2.3

beech represents only 56.5% of the woody understory and several species have relative densities > 5%. In eastern plots, sugar maple (*Acer saccharum*), yellow birch (*Betula allegheniensis*) and shadbush are potential canopy trees with beech. However, whether beech will reoccupy the canopy in plots with heavy BBD mortality is unclear; most beech understory stems are sprout clones of dead canopy trees and as such will be as susceptible to BBD as their parents.

In eastern plots the densities of species in all shade-tolerance categories is greater than their densities in western plots but the only significant difference is for shade-tolerant species (Table 5.7). This pattern suggests that, all else equal, the short-term replacement of beech in eastern GRSM plots will be dominated by shade-tolerant species.

Some of the differences in understory composition between western and eastern plots are surely due to BBD, though how much is unclear. Some species, such as Fraser fir (*Abies picea*) and red spruce (*Picea rubens*) are naturally more abundant in eastern GRSM. The elevated densities of sugar maple and yellow birch could be a response to the opening of the canopy because of BBD.

Discussion

General mortality patterns: distribution and severity of disease in GRSM

As of 2000-2002, BBD had caused the greatest mortality in high-elevation plots in eastern GRSM resulting in losses of roughly 46% of beech stems and basal area. If stems with > 50% canopy dieback also succumb to BBD, the losses in eastern GRSM will approach 80%. Because infestation by the scale insect is required for fungal infection, and because the insect has a short motile period and is passively dispersed (Wainhouse 1980) the disease would be expected to spread relatively easily through forests in which beech is codominant, such as those in western GRSM. Alternatively, BBD should spread more slowly among the beech gaps in eastern GRSM, which are from 0.5 to 8 km apart, and which are surrounded by a spruce-fir matrix in which beech is essentially non-existent. However, BBD has apparently moved rapidly eastward from Clingmans Dome as far as Mt. Sterling (approximately 65 km, a rate of > 8 km/year) and westward only about 8 km during the same period.

There are several possible explanations for the counterintuitive eastward spread of BBD. First, it is possible that although BBD was first identified near Clingmans Dome in 1993, it invaded eastern GRSM beech forests earlier than this. This scenario is unlikely because Clingmans Dome is a plausible location for BBD invasion because it is a popular destination and the road to it is well-traveled and passes through several beech gaps. A tourist could have inadvertently transported the disease from the northeast. Second, prevailing winds in GRSM are generally from the west. Given the high density of insects and their motile nymphs in an infected stand, some of them would be expected to disperse relatively long distances to land in another beech forest. The scale insect was identified in some western GRSM forests as early as 1994 (Blozan 1995), but as of 2002 their population densities were not large enough to be obvious, and had not begun to cause beech mortality. Third, western GRSM beech forests may be more genetically diverse and less susceptible to BBD. Regeneration in high-elevation beech forests has long been thought to be clonal (Russell 1953), because seedlings are rarely observed (Sain and Blum 1981). Studies of the genetic diversity of high-elevation beech forests in GRSM have focused on eastern beech gaps, with contradictory results (Kitamura et al. 2001, Morris et al. 2002). However, in western GRSM where beech occurs throughout the range of forest types, sexual reproduction might be more common resulting in greater genetic diversity and resistance, and slowing the westward spread of BBD.

Beech annual mortality rates in this study are consistent with those reported in studies conducted in other forests infected with BBD (Gavin and Peart 1993). Runkle (1990) found the highest beech AMR in forests with the greatest beech density; beech AMR in plots with relatively few beeches were only slightly greater than the overall mortality rates of other species. Overall mortality in this study is greater than that reported by Twery and Patterson (1984) (34% vs. 21%) even though the current study covers a shorter period of time and mortality is expected to continue to increase.

The relationship between beech mortality and dominant stems, plot density, and basal area

In the BBD-infected forest of northeastern North America, stems > 25 cm DBH are thought to be most susceptible to BBD because they show higher rates of mortality (Houston 1979b, Runkle 1990). In GRSM, Morris et al. (2002) found that stems > 3 cm were susceptible. It appears that 7-8 cm is the minimum DBH at which beech becomes susceptible, in this study BBD did not discriminate against dominant beech trees or those in the largest diameter classes.

Contrary to results reported from New York (Runkle 1990, Griffin et al. 2003) and Massachusetts (Twery and Patterson 1984) beech forests beech stem density and basal area did not increase BBD severity in this study. High-elevation GRSM beech forests may have more consistent beech densities than elsewhere. In this study, beech densities were high enough that most beeches were not more than a few meters from a conspecific stem and the branches of canopy beech trees intertwined. It is possible that even in the least dense high-elevation beech forests in GRSM, densities are still high enough that when BBD invades it can spread easily between host trees.

Beech mortality and environmental and soil characteristics and prepark disturbance

Beech mortality was significantly correlated with LFI and several soil characteristics. All of the soil characteristics, except % clay, were also significantly correlated with longitude, suggesting that soil changes across the range of beech in GRSM might explain the correlation between these characteristics and beech mortality. The results of this analysis suggest that soil chemistry and structure, might influence BBD severity. Higher soil S and Al levels in disease-free beech stands might confer resistance if beech trees can take up these elements in their meristematic tissue, impeding the population growth and/or pathogenicity of the insect and fungus, though I know of no evidence to support this hypothesis.

It is also possible that the correlations between beech mortality and environmental factors are coincidental and that mortality in high-elevation beech forests is a function of the dispersal of the disease insect. Evidence supporting this alternative hypothesis is that BBD has dispersed eastward with the wind since its discovery near Clingmans Dome in central GRSM. Additionally, some western beech stands are diseased, suggesting that the longitudinal gradient in soil chemistry might not convey resistance to BBD.

Differences in topography and vegetation between eastern and western GRSM might explain the difference in LFI. The mountains in eastern GRSM are higher, and because beech co-occurs with spruce/fir (*Picea rubens/Abies fraseri*) in eastern GRSM, it is found only in sheltered gaps between mountain peaks, In contrast, western GRSM beech forests occupy the tops of mountains and span ridge tops, resulting in a lower LFI than eastern beech forest plots.

Latty et al. (2003) found that old-growth beech forests were more severely affected by BBD, though apparently because old-growth forests had higher bark amino nitrogen concentrations. In this study, disturbance history did not influence beech mortality.

Woody understory composition and regeneration patterns

Stem densities of woody understory species are significantly lower in eastern forests than in western forests. This disparity occurs for all understory size classes, and appears to be driven by blackberry cover, which increases rapidly following the death of canopy beech trees in diseased forests. Beech, a shade-tolerant species whose regeneration is predominantly from root sprouts, might be expected to be able to withstand competition from blackberry. However, beech was significantly lower in density in eastern forests.

Rapid blackberry growth in southern Appalachian clearcuts has been associated with slow growth of shade-intolerant species during secondary succession (Wilson and Shure 1993). Blackberry has always been an important colonizer of high-elevation forest gaps in GRSM (Crandell 1958), but its rate of colonization, density, persistence and consequent capacity to inhibit forest reorganization on these sites may be enhanced by atmospheric N deposition (Tilman 1987). Atmospheric N deposition is highest at high elevations in GRSM (Fowler et al. 1988), and N mineralization rates are highest in high-elevation hardwood forests when compared among different plant communities along an elevational gradient (Knoepp and Swank 1998).

During the course of this study it was noted that blackberry density was reduced near the transition zone between diseased beech forest and adjacent healthy forest, presumably because of the shading effect of the healthy trees. In these transitional areas it was common to find sapling-sized individuals of species that were absent near the center of the opening. This pattern suggests that tree establishment in areas of low blackberry density at the edge of diseased patches will enhance the replacement of beech by advance regeneration of shade-tolerant species. Encroachment on forest openings by tree establishment at forest-field interfaces has been noted in other studies in the southern Appalachians (Copenheaver et al. 2004).

Short-term successional development in western beech forests is likely to continue to be dominated by beech, which was 90.6% of stems in these forests. The relative density of understory beech is higher than the relative density of beech stems ≥ 10 cm, suggesting that western beech forests will become more beech dominated, as was found in Chapter 2. In eastern forests short-term succession is also likely to remain dominated by beech despite the influence of blackberry. Eastern forests differ in that beech relative density (56.5%) is lower and other species are more important. Many of the potential canopy codominant understory species in eastern forests are shade-tolerant, suggesting that shade-intolerant, early-successional species will play a relatively minor role. Replacement of beech by shade-tolerant species in forests affected by BBD has been noted elsewhere (Runkle 1990, LaGuerrier et al. 2003). Species' understory densities are suggestive of longer-term successional patterns but are dependent on the gap dynamics of the forest and storm frequencies of the region (White et al. 1985), which can alter understory/overstory transition probabilities.

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Chapter 6

The influence of spatial scale on temporal changes in forest structural attributes in Great Smoky Mountains National Park.

Abstract

To investigate whether temporal changes in forest attributes follow predictions of the forest succession model, the effect of grain size (sampling area) on tree density and basal area was determined in late-successional deciduous forests in western Great Smoky Mountains National Park. Forty-one 0.1 ha (20 x 50 m) plots established in 1977-78, and located in three forest types (BEECH, COVE, and high-elevation red oak "HERO") with three pre-park disturbance histories (undisturbed, diffuse disturbance, heavy-cut), were resampled in 2002. Tree density and basal area for each plot were calculated in each of five 0.02 ha (20 x 10 m) modules, then values from all possible combinations of adjacent modules were summed to obtain 0.04, 0.06, 0.08 ha and plot-level (0.1 ha) grain sizes for which attribute means and variances were obtained for 1977-78 and 2002 for the sum of all plots and for each forest type and disturbance history. It was predicted that the variance in forest attributes would decrease through time at grain sizes larger than the area of the average disturbance patch ($\leq$ 0.02 ha) and that variances calculated for each forest type and disturbance history would exhibit patterns similar to the sum of all plots, given the late-successional nature of the forests. Tree density variance in 2002 was lower than in 1977-78 at all grain sizes, but 2002 basal area variance was only lower at the smallest (0.02 and 0.04) grain sizes. Basal area variance declined with increasing grain sized faster than tree density variance. Variances of attributes for plots organized by forest type and disturbance history did not exhibit patterns similar to the overall pattern, or to each other. Attributes of BEECH and COVE forests generally had higher variances than HERO forests and the stem density variance of undisturbed and heavy-cut forests was higher in 2002 than in 1977-78. From

these results it is concluded that these forests do not conform to ideas of temporal change in late-successional forests.

Introduction

Conclusions about whether an ecosystem is at equilibrium and driven by processes such as competition and predation, or non-equilibrium and driven by disturbances and exogenic processes are due, in part, to the scale at which observations about the system are made. In general, the variance of ecosystem attributes (for example, tree density and basal area) should be lower at larger areas of observation (the area encompassed by a vegetation plot, also called "grain" size) than smaller areas. As grain size increases, the observed average attribute variances should approach that of the ecosystem as a whole. In equlibrial ecosystems, the variance should stay the same from year to year.

Although ecologists have long known that the spatio-temporal scale at which forest attributes are measured can influence conclusions drawn about forest dynamics, studies that examine the adequacy of commonly used plot sizes in capturing the variability of forest attributes such as tree density and basal area are rare. One rule of thumb, Shugart's (1984) 1:50 hypothesis, predicts that an equilibrating landscape for biomass will be at least 50 times as large as the size of its typical disturbance patch. Busing and White (1993) tested Shugart's quasi-equilibrium hypothesis using measures of forest attributes collected at a variety of spatial scales and found that variance from mean attribute values declines with increasing scale, but that conclusions about forest equilibrium depend on the attribute being measured; structural attributes approached equilibrium at smaller scales than did compositional attributes. On a landscape scale, high variance in forest attributes among plots suggests high spatial heterogeneity, which would be expected to stabilize at scales equal to or smaller than the average size of a disturbance patch, and decrease through time at scales larger than the average patch size. Whether the variance in forest attributes decreases through time is unknown.

The purpose of this chapter is to describe the influence of scale on temporal changes in tree density and stand basal area in 0.1 ha permanent plots in late-successional, high-elevation forest plots resampled approximately 25 years apart (1977-78 to 2002). In particular, I seek to determine whether: 1) the variance in tree density and basal area decreased at spatial scales larger than the average patch size, 2) temporal changes in mean stem density and basal area become smaller at larger grain sizes, and 3) forests of different compositions and disturbance histories demonstrate similar patterns of spatial heterogeneity.

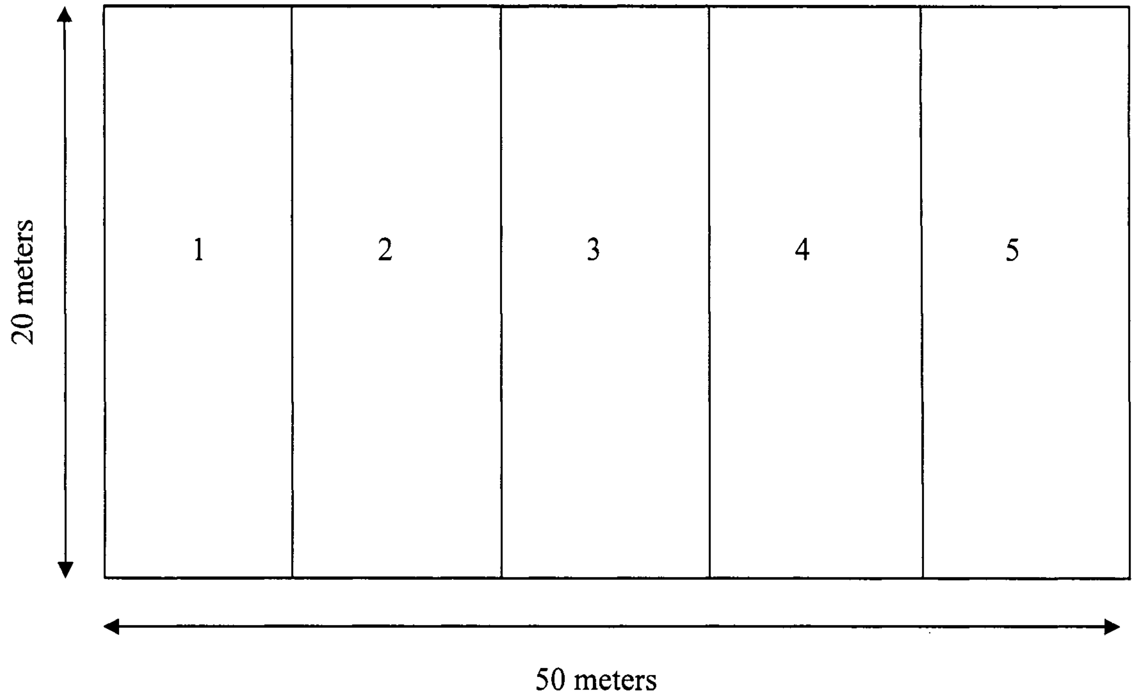
Methods

Study location and plot scale

Data used in this study comes from 41 late-successional high-elevation deciduous forest plots established 1977-78 and resampled in 2002. The plots are located north and northeast of Gregory Bald (35^0 31′N, 83^0 52′W) in western Great Smoky Mountains National Park (GRSM) on north-facing slopes between 1159-1509 m elevation.

Plot dimensions are 20 x 50 m (0.1 ha). Within each plot woody stems $\geq$ 10 cm were identified by species and measured for DBH in 5 nested 20 x 10 m (0.02 ha) subplots (Figure 6.1). The arrangement of subplots allows for comparison of the variance and paired-plot mean population values of forest attributes of physical structure (tree density and basal area) between plot-pairs at 0.02, 0.04, 0.06, 0.08 and 0.1 ha scales or "grain sizes" (Wiens 1989). Tree densities and basal areas obtained from each plot at each scale were standardized to 1-ha values. Because the average size of a disturbance patch in high mountain GRSM forests

Figure 6.1. Plot dimension and nested modules from which tree density (#.ha) and basal area (m^2/ha) were collected in 41 high-elevation deciduous forest plots in western Great Smoky Mountains National Park in 1977-78 and 2002.


20 meters
1
2
3
4
5
50 meters

is though to be ≤ 0.02 ha (personal observation, Runkle 1982, Busing and White 1993), the range of grain sizes can be used to determine whether the variance in attributes above the average patch size decreases over time in late-successional forests.

Influence of scale on year-pair variances and forest attribute means

Spatial heterogeneity was determined by calculating the variance of tree density and basal area/ha at each grain size from the mean across plots (Levin 1989). Here, the variance in attribute values is the sum of the squares of the deviation divided by the degrees of freedom. The attributes measured at each scale were tested for normality using PROC UNIVARIATE NORMAL in SAS v. 8.2. Because the data were non-normal, non-parametric tests were used in the examination of significant differences in the variability and mean values of plot attributes at different scales. The average variances and mean attribute values were compared in all possible year-pair combinations at each scale for contiguous modules. For example at the 200 m^2 scale, the average variances and means of attributes in module 1 in 1977-78 were compared to the averages for module 1 in 2002. The year-pair average values in modules 2-5 were also tested. At scales above 200 m^2, all possible combinations of contiguous plots were added together to obtain variances and mean attribute values.

Mean values for stem density and basal area of year-pairs were compared using Wilcoxon's signed-rank test in PROC UNIVARIATE because the samples being compared lack independence. Changes in paired variances were tested using a procedure developed by Sandvik and Olson (1982) in which a statistic, G_i,is calculated, where $G_i = |X_i - \text{median}(X)| - |(Y_i - \text{median}(Y)|$, where X_i and Y_i represent the data from paired-plots at each scale. The test of the null hypothesis $H_0 : \sigma^2_x = \sigma^2_y$ was conducted by performing Wilcoxon's signed-rank test on the statistic, G_i.

In order to compare variation among forest attributes with different mean values, coefficients of variation (standard deviation as a percentage of the mean of each attribute at each scale) were calculated. This provides a common value with which to compare the variation in stem density and basal area in 1977-78 and 2002 (Busing and White 1993).

Influence of scale by forest type and disturbance history

The plots in this study occupy beech dominated (BEECH, N = 12), upper cove (COVE, N = 14), and high-elevation red oak (HERO, N = 15) forest types (Chapter 4) and are part of the Southern Appalachian Northern Hardwood (NatureServe Ecological System ID CES 202.029), and Southern and Central Appalachian Cove ecosystems (CES 202.373) (NatureServe 2005). American beech (*Fagus grandifolia*), and yellow buckeye (*Aesculus octandra*) are indicators of BEECH forest, northern red oak (*Quercus rubra*) of HERO forests, and eastern hemlock (*Tsuga canadensis*), black birch (*Betula lenta*), silverbell (*Halesia tetraptera* var *monticola*), and Fraser magnolia (*Magnolia fraseri*) of COVE forests. Because the plots are in protected late-successional forests they are representative of typical forest sampling plots that would be used to measure forest attributes (stem density and basal area), and which would be resampled periodically to assess temporal change. Forest types contain an unequal number of disturbance history plots which could confound their interpretation. However, an earlier study found that disturbance history was not responsible for forest attribute changes by forest type (Chapter 4).

Disturbance history of the plots was determined using data from Pyle (1988), digitized on maps to 90 m resolution. Plots for which there is not record of grazing or logging are considered undisturbed (N=11). Plots with diffuse disturbance (N=18) might have had livestock grazing and/or light burning. Some of the forests occupied by plots in this study were industrially logged (heavy cut, N=12) prior to the creation of GRSM. Although it is not known when logging occurred in the heavy-cut plots in this study, it was generally confined to the period 1890-1920 in GRSM (Brown 2000).

Results

Influence of scale on year-pair variances and forest attribute means

Stem density variances in 2002 were always lower than in 1977-78. Changes in the variances of stem density (1977-78 to 2002) were significant ($p < 0.05$) for one of the year-pair comparisons at 0.06 ha, two of the four year-pair comparisons at 0.04 ha, and one of the five at 0.02 ha (Table 6.1). In contrast, changes in variance of basal area in plots paired by year were not significant and there was no consistent pattern of decline in variances.

Average stem densities declined across all spatial scales and year-pair comparisons (Table 6.2). Twelve of the 15 year-pair declines were significant, including the comparison of mean stem densities at 0.1 ha, where stem density declined from 583 to 519 stems/ha. In contrast, basal area was unchanged at 32.6 m^2/ha at the 0.1 ha grain size. Changes in mean basal area exhibited no consistent pattern of change, most decreased slightly, three increased and two were unchanged. None of the changes in mean basal area were significant.

Coefficients of variation for stem density and basal area in 1977-78 and 2002 all declined with increasing grain size (Figure 6.2). The coefficients for stem density in both periods

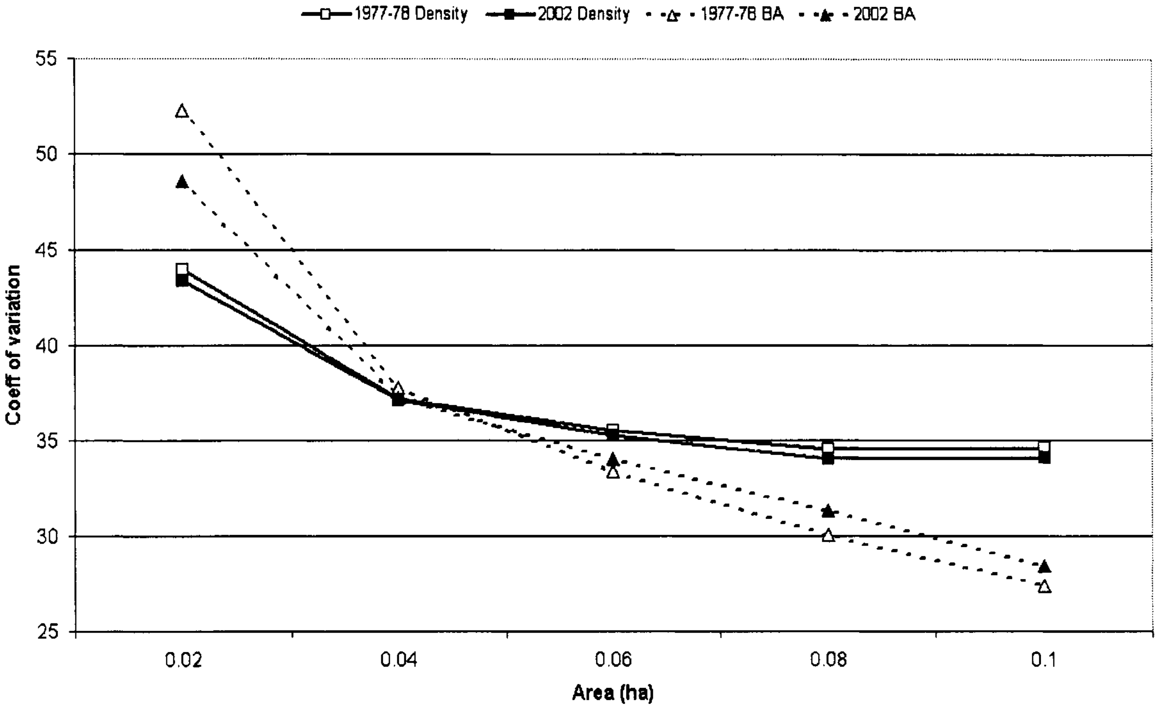
Table 6.1. Changes in the variance of stem density (#/ha) and stand basal area (m^2/ha) for 15 year-pair comparisons at 5 grain sizes in 41 high-elevation deciduous forest plots in Great Smoky Mountains National Park.

		Variance			
		Stem density (#/ha)		Basal area (m^2/ha)	
Grain size (ha)	Modules	1977-78	2002	1977-78	2002
0.1	1,2,3,4,5	40770	31327	79.6	79.6
0.08	1,2,3,4	40199	31874	104.3	93.9
	2,3,4,5	42352	31219	90.4	98.4
0.06	1,2,3	44479	33278	171.6	114.9
	2,3,4	39998	32086	130.0	126.9
	3,4,5	47452[a]	36557[b]	76.7	101.3
0.04	1,2	49592[a]	37379[b]	211.8	135.9
	2,3	45319	32545	270.2	145.9
	3,4	45168	39612	95.3	139.3
	4,5	50788[a]	40881[b]	89.0	124.6
0.02	1	79128	71095	304.5	237.8
	2	50305	33774	489.6	242.2
	3	63524	47006	316.2	224.1
	4	51369[a]	48314[b]	195.8	229.5
	5	85598	56475	205.6	222.2

Table 6.2. Changes in the mean values of stem density (#/ha) and stand basal area (m^2/ha) for 15 year-pair comparisons at 5 grain sizes in 41 high-elevation deciduous forest plots in Great Smoky Mountains National Park. Numbers in parentheses are standard deviations.

		Mean			
		Stem density (#/ha)		Basal area (m^2/ha)	
Grain (ha)	Modules	1977-78	2002	1977-78	2002
0.1	1,2,3,4,5	583 (201.9)^{a}	519 (177.0)^{b}	32.6 (8.9)	32.6 (8.9)
0.08	1,2,3,4	588 (200.5)^{a}	523 (178.5)^{b}	33.4 (10.2)	32.0 (9.7)
	2,3,4,5	588 (205.8)^{a}	520 (176.7)^{b}	32.3 (9.5)	30.6 (9.9)
0.06	1,2,3	585 (210.9)	518 (182.4)	34.8 (13.1)	32.2 (10.7)
	2,3,4	596 (200.0)^{a}	524 (179.1)^{b}	33.3 (11.4)	31.2 (11.3)
	3,4,5	589 (217.8)^{a}	524 (191.2)^{b}	30.9 (8.8)	30.8 (10.1)
0.04	1,2	574 (222.7)^{a}	512 (193.3)^{b}	35.0 (14.6)	32.2 (11.7)
	2,3	595 (212.9)^{a}	517 (180.4)^{b}	35.3 (16.4)	31.1 (12.1)
	3,4	602 (212.5)^{a}	534 (199.0)	31.7 (9.8)	31.7 (11.8)
	4,5	580 (225.4)^{a}	522 (202.2)^{b}	29.3 (9.4)	30.2 (11.2)
0.02	1	563 (281.3)	518 (266.6)	33.7 (17.4)	34.3 (15.4)
	2	584 (224.3)^{a}	506 (183.8)^{b}	36.3 (22.1)	30.2 (15.6)
	3	606 (252.0)^{a}	528 (216.8)^{b}	34.2 (17.8)	32.0 (15.0)
	4	598 (226.6)^{a}	539 (219.8)^{b}	29.3 (14.0)	31.5 (15.1)
	5	562 (292.6)	505 (237.6)	29.2 (14.3)	28.9 (14.9)

Figure 6.2. Coefficients of variation as a function of grain size for stem density and basal area in 1977-78 and 2002.

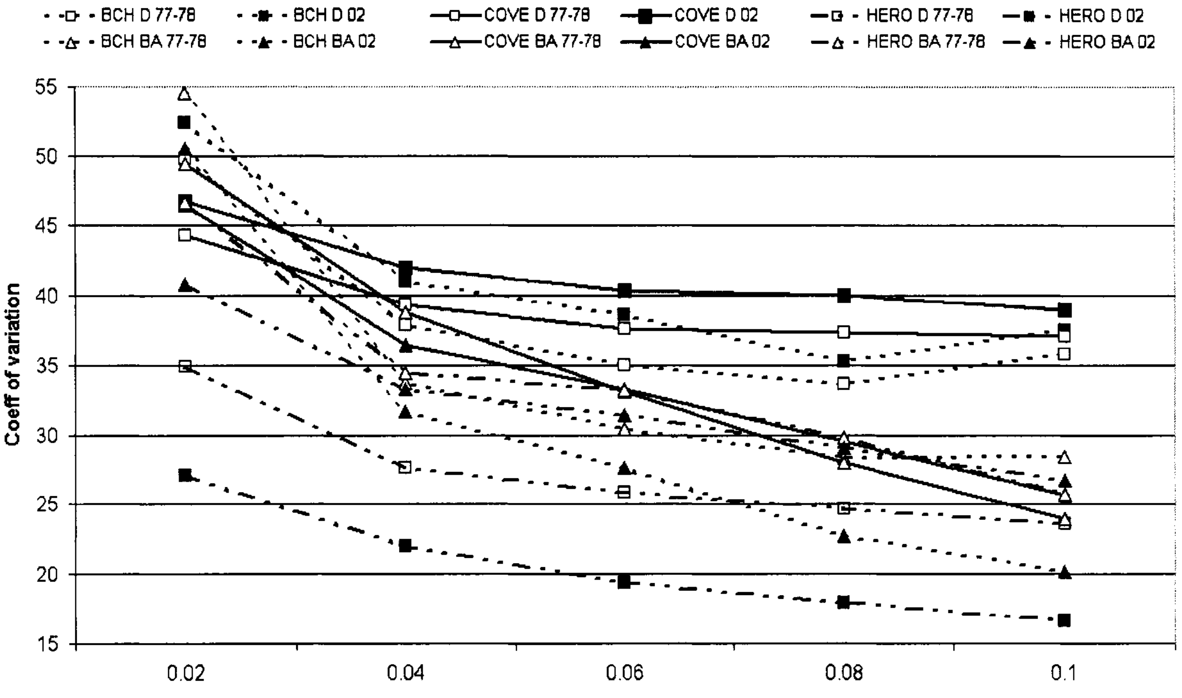

1977-78 Density
2002 Density
1977-78 BA
2002 BA
55
50
45
40
35
30
25
Coeff of variation
0.02
0.04
0.06
0.08
0.1
Area (ha)

tracked one another closely, with 1977-78 always slightly higher. The coefficient for 1977-78 basal area is higher than the 2002 coefficient at the smallest grain size but crosses and falls below it at grain sizes above 0.04 ha and the separation between paired coefficients is narrower at 0.1 ha. The coefficients for basal area are higher than those for stem density at the 0.02 ha grain size but decline more rapidly and fall below the density coefficients at grain sizes > 0.04 ha. All coefficients decline most steeply between 0.02 and 0.04 grain sizes. At 0.1 ha all attributes in both periods still exhibited a high degree of variability (< 25% for basal area and almost 35% for stem density). The variance in stem density became level at grain sizes above 0.08 ha but the trend in variance in basal area suggests it would continue to decrease at scales > 0.1 ha.

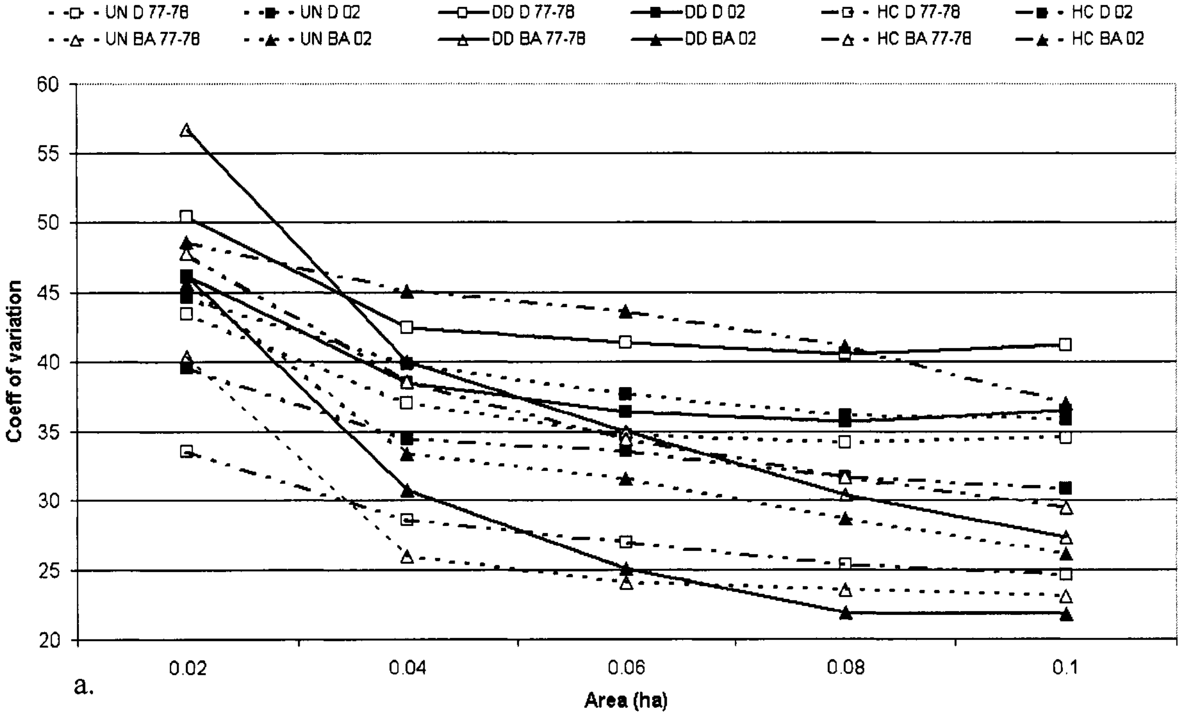
Influence of scale by forest type and disturbance history

The overall relationship between variation and scale in plots sorted by forest type was similar to the pattern described for all plots combined: variation was high at the smallest scale (0.02 ha) and decreased with increasing grain size (Figures 6.3 a and b). The 1977-78 density and basal area coefficients are always higher than their paired 2002 coefficient at the 0.02 ha grain size although many of them had switched by the largest grain size. The declines in basal area coefficients in each forest type are steeper than those for density and all coefficients decline most steeply between 0.02 and 0.04 ha. The coefficients for HERO density in both periods are consistently low at all grain sizes, while those for BEECH and COVE forests are consistently high. In 2002 the variance in HERO density was lower than 1977-78 but in BEECH and COVE forests the 2002 variance was higher than 1977-78 at all scales. Additionally, the variance in BEECH and COVE densities is consistently more than

Figure 6.3a,b. Change in coefficients of variation with increasing grain size for stem density (squares) and basal area (triangles) in 1977-78 (open symbols) and 2002 (closed symbols) for 41 high-elevation deciduous plots sorted by forest type (3a) and disturbance history (3b).


BCH D 77-78
BCH D 02
COVE D 77-78
COVE D 02
HERO D 77-78
HERO D 02
BCH BA 77-78
BCH BA 02
COVE BA 77-78
COVE BA 02
HERO BA 77-78
HERO BA 02
Coeff of variation
55
50
45
40
35
30
25
20
15
0.02
0.04
0.06
0.08
0.1
Area (ha)

6.3a.


UN D 77-78
UN D 02
DD D 77-78
DD D 02
HC D 77-78
HC D 02
UN BA 77-78
UN BA 02
DD BA 77-78
DD BA 02
HC BA 77-78
HC BA 02
Coeff of variation
60
55
50
45
40
35
30
25
20
0.02
0.04
0.06
0.08
0.1
Area (ha)

a.

6.3b

50% higher than the variance in HERO density. With increasing scale, the trend for most attributes in each forest type suggested a continued decline at scales > 0.1 ha, but BEECH density coefficients in both 1977-78 and 2002 increased from 0.08 to 0.1 ha.

The overall patterns between variation and scale by disturbance history are the same as those by forest type. Variances for undisturbed and diffuse disturbance forest basal areas are roughly equivalent to those of heavy-cut forests at 0.02 ha, but they decline more steeply between 0.02 and 0.04 ha and are lower than those of heavy-cut forests at 0.1ha. However, in diffuse disturbance forests the 2002 variance is lower than the 1977-78 variance at all scales, but in undisturbed and heavy-cut forests the 2002 variance is higher than 1977-78. Density coefficients exhibit a different pattern. The variation in heavy-cut density in both periods is lower than that of undisturbed or diffuse disturbance density at all scales. Between 0.08 and 0.1 ha density coefficients for undisturbed and diffuse disturbance forests are level or increase slightly, while in heavy-cut forests there is a mild decline.

Discussion

Spatial heterogeneity (as measured by variance) in tree stem density decreased from 1977-78 to 2002 at all spatial scales. This result supports the hypothesis that processes in late-successional forests decrease spatial heterogeneity at scales larger than the average disturbance patch size. However, the observed decrease in variance could be due either to greater forest stability or as a consequence of a system-wide decline (Chapter 4). Mean density values also decreased across all scales and year-pair comparisons. Decreases in stem density in these forests have been correlated with low soil P, which might be due to soil acidification from deposition of atmospheric N and S (Nodvin et al. 1995).

In contrast with the consistent scale-wide decreases in density, spatial heterogeneity in tree basal area at grain sizes > 0.04 ha was higher in 2002 than in 1977-78, though it was lower at the 0.02 and 0.04 ha scales. The rapid decline between 0.02 and 0.04 ha in all attributes gives credence to the observation that the size of the average disturbance patch in these forests is ≤ 0.02 ha.

The forest succession model proposes greater stability in forest attributes over time (Huston 1994). The model, however, does not distinguish amongst the various spatial scales at which stability can be measured, or the rate at which various forest attributes reach stability, despite research indicating that compositional attributes reach equilibrium at larger scales than structural ones (Kershaw 1957, Busing and White 1993) the forest succession model remains simplistic relative to our advancing understanding of forest dynamics. The inconsistent pattern of temporal change in basal area variance, together with the uncertainty of the reason for the temporal decrease in stem density variance, suggests that the temporal changes in the high-elevation deciduous forests of western GRSM, when measured at a maximum grain size of 0.1 ha, do not support the hypothesis that the variance in attributes decreases through time at spatial scales larger than the sized of the average disturbance patch.

For vegetation ecologists studying natural systems one of the goals of field research is to establish plots that adequately characterize the range of variation present in a particular vegetative community. In the field, plots 0.1 ha in size are common (Peet et al 1998). The efficacy of this plot size in capturing the variation of such commonly measured forest attributes as tree density and basal area within a forest type is an important question. The results of this study suggest that the variation in stem density might stabilize at grain sizes less than 0.1 ha, while the variation in basal area would continue to decline at larger grain sizes. The results of this study support those of Busing and White (1993), who suggested minimum sampling areas of 0.5 ha for structural attributes, such as those measured here, and 1 ha for compositional attributes, which were not measured in this study.

Results of this study indicate that the spatial scale at which the variance in attributes declines is different in forests by compositional type and disturbance history. As measures of the physical structure of a forest, tree density and basal area should reflect the size and dispersion of canopy gaps. Their variation should be greatest at scales equal to or less than normal gap sizes ($\leq$ 0.02 ha in these forests) (Busing and White 1993). Variances in tree density and basal area were greatest at the smallest grain size measured in this study (0.02 ha), but BEECH and COVE forest stem density and basal area variances were considerably higher than those for HERO forests at the smallest scale and density remained higher at all scales, suggesting that the processes influencing these attributes occur at different scales in forests of different composition.

The changes in variance of tree density and basal area by disturbance history contradict expectations of late-successional forests. In GRSM, undisturbed and diffuse disturbance forests differ relatively little in the magnitude of human influence prior to the creation of the park (Pyle 1988) when compared to heavy-cut forests. In this study, it was expected that the temporal changes in variance in undisturbed and diffuse disturbance would exhibit similar patterns. However, undisturbed forests were more similar to heavy-cut forests than those subject to diffuse disturbance. This finding confirms results that showed significant changes in the attributes of both undisturbed and heavy cut forests (Chapter 4) but not diffuse disturbance forests. That the means and variances of undisturbed and heavy cut high-elevation deciduous forests in GRSM changed significantly from 1977-78 to 2002 indicates that the dynamics of these late-successional forests do not meet the expectations of the forest succession model.

Conclusions

In this study the relationship between variance and scale for trees does not follow predicted patterns of temporal change, given current thoughts on forest succession and the relationship between stability in forest attributes and disturbance patch size. Additionally, this study demonstrates that questions of temporal forest change are influenced by composition and disturbance history. Future work should focus on additional attributes, including descriptors of composition, and on the spatio-temporal variability in herbs and woody understory stems.

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Chapter 7

Disturbances, perturbations, and vegetation changes in the high-elevation deciduous forests of Great Smoky Mountains National Park

Abstract

The high-elevation forests of Great Smoky Mountains National Park (GRSM) have often been considered late-successional climax forests because much of the high-elevation area was never logged and because they have been protected since 1935. Thus, these forests are an ideal place to empirically test the following hypothesis of temporal change in late-successional forests: that in the absence of stand-replacing disturbance, late-successional forest attributes such as tree density, basal area, and biomass are stable because, with increasing time since stand establishment, forest dynamics become increasingly dominated by internal, population level processes whose influence on forest attributes occurs over small spatial scales. Although studies of temporal change in forest communities over periods greater than 10 years are rare, they are increasing in number, and they rarely provide evidence of stability in forest attributes. The purpose of this paper is to review some concepts relevant to the study of temporal changes in vegetation and more specifically to compile a list of the potential drivers of changes in the composition and structure of the high-elevation deciduous forests of GRSM Of the drivers, soil cation concentrations and aluminum are associated with temporal changes in the tree density and basal area of high-elevation forests in GRSM. From this review and from the results of studies of temporal vegetation change in the high-elevation deciduous forests of GRSM, conclusions will be drawn as to the existence of climax forests in GRSM and the legitimacy of the forest succession model.

Historical basis and concepts of long-term vegetation change

The work of early botanists and plant ecologists was focused on identifying individual species and describing patterns of coexistence, which at large scales were coined "ecosystems" (Tansley 1935). Although early botanists wrote about the dynamics of plant communities (Cowles 1899), the idea that ecological process deserved recognition in its own right was not formalized until the early 20th century with Clements' (1916) and Gleason's (1926) competing views on the mechanisms of plant succession. Subsequent work (Watt 1947, Whittaker 1953) addressed emerging and often conflicting theories of succession. By the time Whittaker (1953) published his synthetic paper on the nature of vegetation climax, studies of patterns of vegetation succession on newly denuded ground or abandoned agricultural land (Oosting 1942) were becoming increasingly common. Evidence for the development and persistence of a climax vegetation type however, met with much disagreement (Whittaker 1953). In the more than 50 years since Whittaker's paper there is still disagreement as to whether late-successional or old-growth forests are "climax" or self-replicating forest types, or whether they continually change in composition and structure.

Climax forests are those in which the influence of factors external to the forest, such as extreme weather events, are relatively unimportant and factors internal to the forest, such as those related to species life histories, are dominant. Climax forests are, by definition, self-replicating; the constituent species are adapted to the intrinsic climatic conditions and ecosystem processes of the community in which they exist. As a concept, stability requires definition. It would be unwise to suggest that climax vegetative communities are stable in an absolute sense; plants die, and may be replaced by conspecifics or other species. For this reason ecologists have termed stability a “qualitative equilibrium” (White and Jentsch 2001), or “persistence within stochastically defined bounds” (Connell and Sousa 1983), in recognition that some degree of variation is expected in any forest system. The amount of variation that is acceptable before a community is considered unstable has generally been left up to the researcher.

An understanding of the impact of disturbances on natural systems is central to the study of succession towards a compositional climax in plant communities (White and Jentsch 2001). Mechanisms of succession in plant communities can be defined as originating from outside the community (allogenic), or caused by the organisms within the community (autogenic). Plant successional theory holds that as succession proceeds, community properties will be less of a reflection of allogenic disturbances and become more stable and more influenced by autogenic mechanisms (Huston 1994).

Historically, ecologists have recognized disturbances as being “natural” versus those that are of human origin “anthropogenic”, a distinction that is of increasing relevance, but for which many exceptions exist. An important implication here is that “natural” disturbances are “normal” and fall within the suite historical events for which the impacted organisms have adaptive traits. Calling a disturbance “natural” implies an evolutionary relationship where the organisms in the ecosystem, through natural selection, become capable of resisting or rebounding from the disturbance. Populations subject to natural disturbances may lose individuals but will not go extinct. Ecosystems subject to natural disturbances are capable of eventually regaining their function. However, resistance to or resilience following a disturbance may be less likely when the event falls outside of the adaptive history of the organisms in the ecosystem.

Anthropogenic disturbances may be intentional, accidental, or incidental. Often the introduction of novel organisms is of no consequence, and may sometimes be beneficial, but occasionally the results are dire (Mooney and Hobbs 2000). Plant communities have been altered by introduced organisms that create novel disturbances to which the native plants were not adapted (White and Jentsch 2001). Novel disturbances have been termed "perturbations" to distinguish them from natural disturbances to which organisms are adapted (White and Pickett 1985) though the term also refers to events that represent a departure from normal ecosystem dynamics, such as the cessation of fire in a fire-adapted ecosystem.

Disturbances are often defined as events that are relatively discrete in time and space (White and Jentsch 2001) but the introduction and establishment of exotic pests, and other anthropogenic disturbances such as climate change (Honnay et al. 2002), and air-pollution (Aber et al. 2003), are chronic perturbations that can harm native plants and alter ecosystem processes. Additionally, the persistent nature of these perturbations suggests that some ecosystems may be simultaneously subjected to more than one novel disturbance.

Chronic perturbations may force ecologists to reconsider the predictions of some common forest ecology models. Models of biomass accumulation propose distinct stages during succession: reorganization, aggradation, transition or stagnation, and steady-state phases (Bormann and Likens 1979; Peet 1981), with increasing stability in the structure and composition of late-successional forests. These models suggest that after forests reach a late successional steady-state phase, aboveground biomass and composition should become relatively stable. Deposition of atmospheric nitrogen is an example of a chronic resource influx that may change this balance, prolonging or altering each phase and changing the nature of the forest (Aber et al. 2003). Comprehensive demographic analysis of forest trees can provide insight into the alteration of forest growth processes and the potential impact on forests of chronic resource additions.

The effect of chronic perturbations on native plant populations can best be appreciated when compared with the long-term rates of vegetation change prior to the perturbation. Forest successional theory proposes that in the late stages of succession communities become ecologically saturated, autogenic processes become more important, and late-successional species competitively exclude early successional ones because of their ability to withstand lower levels of limiting resources (Huston 1994, Weins 1994, Rees et al. 2001). An important question in ecology is whether, in the absence of a major exogenous (i.e. stand-replacing) disturbance, late-successional forests ever reach equilibrium (Woods 2000a). The answer to this question may depend on the spatio-temporal scale of the study: over short distances or periods of time forest attributes may seem to be at equilibrium, while over long distances, or interglacial time scales, compositional equilibrium is unlikely (Davis 1981). Studies that examine temporal changes in temperate forest dynamics over time scales relevant to conservation decisions or the life span of the dominant species are rare (Woods 2000a), though data from studies of long-term changes of late-successional temperate forests indicate that their composition is not stable (Peet 1984, Woods 2000a,b); additional data from other habitats would strengthen this conclusion.

In relatively stable, or "quasi-equilibrium" communities, Shugart (1984) suggested the landscape area necessary to measure constancy in biomass was about 50 times the size of the average disturbance patch size. In a spatially explicit test of this hypothesis, Busing and White (1993) found that different classifications of community properties demonstrated constancy at different patch sizes; equilibrium of structural properties such as biomass and basal area at smaller spatial scales than did equilibrium of compositional properties such as relative basal area.

As the studies discussed above illustrate, the results of temporal and spatial studies of equilibrium in forests raise questions about the validity of equilibrium models of forest dynamics. Furthermore, these studies highlight the importance of research using permanent plots, which can be used to collect empirical long-term data with which to test forest succession models. Still, the question of "how long is long-term?" is an open one (Bakker et al. 2002); ecologists recognize that over thousands of years forest composition inevitably changes as species respond individualistically to environmental change (Webb 1986). Many studies of long-term forest change cover periods of less than 10 years (Woods 2000a); by comparison, studies covering multiple decades are uncommon.

Overview of GRSM and high-elevation deciduous forests

High-elevation forests in GRSM have been described as climax forests that, in the absence of allogenic disturbance, are self-replacing (Russell 1953, Whittaker 1956). Because they have been protected for 70 years, the forests of GRSM represent a standard for late-successional forests by which processes in other forests can be compared. Due to the foresight of park personnel, data sets covering the periods from 1935-38 to the late 1970s and 2000-03 are available to address questions regarding the stability of forest attributes, the effect of novel perturbations, and the importance of scale in long-term forest dynamics.

Whittaker (1956) documented four high-elevation deciduous forest types: two American beech (which were distinguished by differences in herb composition influenced by changes in soil moisture) and two oak dominated forest types, which he differentiated by the greater importance of northern red oak (*Quercus rubra*) on moister sites, and white oak (*Q. alba*) on dryer sites. Subsequent studies confirmed the importance of northern red oak at higher elevations in GRSM and identified additional community types (Golden 1981, Callaway et al. 1987) but interestingly failed to identify white oak forests as a unique compositional forest type above 1200 m (Golden 1981).

American beech is a very shade-tolerant, slow-growing species capable of regenerating from sprouts or seeds under a conspecific canopy (Burns and Honkala 1990). Understory beech stems are capable of responding to small changes in light levels and may undergo several periods of suppression and release before recruitment into the forest canopy (Canham 1990). In high-elevation GRSM beech forests, beech density may exceed 90% (Russell 1953); regeneration is almost exclusively from sprouts (Sain and Blum 1981), which is probably the reason for reports of low genetic diversity in these forests (Kitamura and Kowano 2000). Beech-dominated forests in GRSM should represent a climax forest community and therefore exhibit stability in compositional and structural attributes in the absence of allogenic disturbance. However, as monospecific forests with low genetic diversity, they are susceptible to disease.

High-elevation mixed species deciduous forests in GRSM are an admixture of northern red oak (*Quercus rubra*), yellow birch (*Betula allegheniensis*), silverbell (*Halesia tetraptera*), buckeye (*Aesculus octandra*), sugar and red maple (*Acer saccharum* and *A. rubrum*), and American beech (Golden 1981, Callaway et al. 1987, White et al. 1993). These forests have been described as northern hardwood or Appalachian oak depending on the identity of the dominant species (White et al. 1993). Although they are considered late successional, mixed-species deciduous forests in GRSM have large percentages of shade-intolerant gap-phase (yellow birch) and intermediately shade-tolerant species (northern red oak) (Burns and Honkala 1990) and might be expected to exhibit an increase in the importance of shade-tolerant species over the period of this study.

Potential causes of change in the high-elevation forests of GRSM

Recovery from historic disturbances

It is likely that all forests on earth are in some stage of recovery from past disturbance; depending on the length of time since the disturbance, the reestablishment of ecosystem processes, and the inherent rate of recovery of a particular forest, even late-successional forests may not be compositionally or structurally stable. Evidence of continual change in the attributes of late-successional forests would contradict traditional theories of forest succession that state that stability in the form of a "qualitative equilibrium" is an obligatory outcome of succession. For example, late-successional forests with "slow dynamics" such as the hemlock and hemlock-hardwood forests of Michigan have exhibited measurable changes in composition during the past three-quarters of a century (Woods 2000a,b) as they continue to lose shade-intolerant species such as yellow-birch (Betula allegheniensis) hundreds of years removed from stand-replacing disturbance events.

Nevertheless, forests dominated by extremely shade-tolerant tree species whose offspring are capable of growing under the shade of canopy conspecifics, such as American beech, should be at or near equilibrium and therefore exhibit little compositional change. In a pattern consistent with that found by Woods (2000a,b), high-elevation beech dominated forests in GRSM have been changing in composition since at least 1935 as beech relative density has increased from 62% to almost 81% (Chapter 2). The increase in beech density has come at the cost of less shade-tolerant species, such as yellow-birch but even shade-tolerants like red spruce (Picea rubens) decreased in density. The superior competitive ability of beech in the habitats it occupies at high-elevations may be most evident in the absence of stand-replacing disturbances and is probably the cause of its observed increase in dominance.

In the deciduous forests of eastern North America, a commonly reported change in forest composition is the replacement of oaks by more shade-tolerant species on mesic sites (Abrams 1992, Goebel and Hix 1996). Oaks have good seed crops every 3 to 7 years (Burns and Honkala 1990, Smith 1993), which may extend to once per decade in some species (Lorimer 1993). Nevertheless, oak canopy recruitment failure is not associated with regeneration failure, and is recognized as a widespread problem on mesic and quality sites throughout the range of oaks in the eastern United States (Smith 1993).

Recovery from recent disturbances: selective logging

Though most of the plots used to collect data for this study are in undisturbed or old-growth forests, roughly 20% occur in forests with varying degrees of human disturbance, including logging. The decline of oak dominance in high-elevation forests may be due to successional processes following some prior disturbance that enhanced oak importance.

Diffuse disturbances such as selective logging occurred in some high-elevation forests prior to the creation of the park (Pyle 1988). However, many of the plots in this study are in forests considered unlogged because they are on the Tennessee side of the main ridgeline that bisects the park longitudinally, where logging was less severe due to the multitude of ownership claims there compared with the North Carolina side (Brown 2000). In this study, plots on the North Carolina side are also considered unlogged as they are just below the ridgeline and are dominated by American beech (*Fagus grandifolia*), a species with little commercial value given its relatively small diameter and stunted form at high elevations (Russell 1953). If selective logging had significantly altered the composition of high-elevation forests prior to park establishment, and promoted the establishment of the dominant species in each forest association, a diameter frequency distribution of the 1977-78 survey should indicate size cohorts that coincide with the cessation of those activities.

However, for the high-elevation beech and red oak forest types, no size cohorts are evident (Chapters 3 and 4) and size-frequency relationships are consistent with the hypothesis that these forests uneven aged. Despite reproducing by sprouts and being highly shade tolerant and therefore capable of remaining indefinitely in the understory, high-elevation beech populations conform to expected age-size relationships (Chapter 3). Because the size is a good predictor of age in beech forests, and because of the lack of a size cohort in high-elevation beech and red oak forests, the evidence for recovery from logging as the cause of the observed temporal changes in the high-elevation forests of GRSM is tenuous.

Recovery from recent disturbances: livestock grazing

High-elevation areas in GRSM were used for livestock grazing by early European colonists (Lindsay 1976, Lindsay and Bratton 1979); livestock grazing was widespread throughout almost all forests in GRSM, except spruce-fir, so even unlogged forests may have been grazed. Mountaintops and high ridges were sometimes cleared to improve grazing conditions although the plots in this study are located in areas that remained forested. Livestock almost certainly descended from the cleared areas into the forests below (where some of the plots in this study are located) but the degree to which their grazing altered forest composition is not known. If livestock grazing reduced seedling densities then the removal of livestock should have resulted in a tree size cohort. This cohort should be apparent in a size-class distribution, but it is not and therefore, recovery from livestock grazing is not an important cause of change in these forests.

Recovery from recent disturbances: chestnut blight

In his study of the forests of GRSM, Whittaker (1956) recognized red oak-chestnut as a distinct vegetation type, and noted that the two species constituted as much as 80% of the overstory. At elevations above 1400 m Whittaker reported few other species reaching canopy status in this forest association. Silverbell (*Halesia tetraptera*) was the most abundant submesic understory species; therefore, northern red oak and silverbell may have increased in importance following the demise of American chestnut (*Castanea dentata*) (Whittaker 1956, Woods and Shanks 1959). Historically, chestnut forests have been described as relatively xeric and open (Woods and Shanks 1959), possibly due to purported allelopathic qualities of chestnut leaves (Vandermast et al. 2002). Reports of the invasion of formerly chestnut-dominated stands by mesophytic species are common (Vandermast and Van Lear 2002), causing the stands to become shadier and more densely populated. Oaks in general, are relatively intolerant of shade (Larsen and Johnson 1998); oak advance regeneration has slow growth but high survival in moderate shade (Johnson 1993) and in the more open forests dominated by chestnut, may have been able to regenerate adequately. After the demise of chestnut in the southern Appalachians and in GRSM, shade-tolerant understory stem densities reportedly increased (Keever 1953, Woods and Shanks 1959), either from the cessation of additions of allelopathic chestnut leaf litter or the removal of chestnut as a competitive dominant, and oak regeneration was suppressed.

In GRSM, the demise of chestnut may have caused a surge in recruitment of canopy oak and other species, followed by oak regeneration failure as forest understories became shadier due to increased stem densities. However, the oak regeneration problem exists outside the former range of American chestnut (Lorimer 1993) and thus does not explain regeneration failure across the geographic range of oak species. Also, given the relatively long life of red oak it would not explain a decline in abundance of larger oak stems in GRSM (Chapter 4).

Ongoing disturbances: beech bark disease

In GRSM, long-term forest dynamics are being affected by beech bark disease (BBD) an insect-fungal pathogen complex introduced from Europe. Beech bark disease has caused severe beech mortality in eastern GRSM since 1993, when it was discovered near Clingmans Dome (Houston 1994, Chapter 5). The insect has been observed on beech trees in western GRSM beech forests, but as of the summer of this study, the characteristic effects of BBD had not been recorded in these stands. Mortality in western GRSM beech forests is not due to BBD, therefore it represents normal background patterns of mortality to which mortality in affected stands can be compared (Chapter 5). Additionally, it is unlikely that BBD has caused significant beech mortality in the mixed species stands in that area and therefore cannot be the cause of temporal changes documented in them (Chapter 4).

BBD can cause structural changes in beech populations by killing canopy beech trees and causing them to sprout prolifically. In beech populations in the northeastern United States, BBD causes diseased beech to sprout (Houston 1975), though sprout densities in the severely infected beech forests of eastern GRSM appear to be low in comparison (Chapter 5).

Ongoing disturbances: feral hogs

Feral hogs (European wild boar) have been a factor in GRSM, particularly in western high-elevation deciduous forests since the 1950s (Bratton 1976). The hogs are generalist foragers, who spend summers in high-elevation forests, particularly in beech-dominated forests. Hogs could alter forest dynamics through the direct consumption of mast, such as acorns, changes in the litter layer following rooting, or the increase in beech stem densities resulting from hog rooting (Huff 1977). However, seedling densities appear adequate for most species in the mixed deciduous forests of GRSM (unpublished data), which indicates that the populations are stable and that neither hogs, nor any other disturbance, have significantly affected seedling numbers. Also, hogs probably don't consume stems > 1 cm DBH, thus hog rooting can't explain changes in sapling and canopy tree density. Additionally, evidence from the effects of insect and deer herbivory on oak seedlings in other areas of the eastern US suggests that although they may be able to consume large proportions of acorns locally, their activities are highly spatially variable. Oak decline is a regional problem and not explainable from herbivory alone (Lorimer 1993).

Ongoing disturbances: fire suppression

Certain processes may have been more common prior to the establishment of the park than in subsequent years. In particular, fire suppression a may have caused an increase in the density of fire-intolerant understory stems and decrease in less shade-tolerant species as has been reported in other eastern US forests (Abrams 1992). In GRSM, fire suppression has dramatically decreased fire frequencies (Harmon et al. 1983), essentially eliminating it as a disturbance. However, high-elevation forests in GRSM, such as the ones in this study, get more rainfall than the lower elevation xeric ridges in western GRSM that burn more frequently (Harmon 1982). According to Harmon (1982) for the period 1940-1979, both man and lightning-caused fires on mesic sites above 1500 m were < 1% of all fires. In GRSM lightning-caused fires are more frequent below 610 m than above (Barden and Woods 1973) as precipitation increases with elevation; temperature, lightning strikes and anthropogenic ignitions decrease with elevation (Harmon 1982).

In the high-elevation mixed species deciduous forest, northern red oak is the most abundant species and has the greatest basal area (Chapter 3). As a canopy dominant, northern red oak is not considered an indicator of frequent historical fire, though it does expand into cutover and burned areas (Crow 1988, Abrams 1992). In comparison with most other oaks, northern red oak is intolerant of fire and even large individuals are known to sustain cambial damage during wildfire events. Wounds from fires provide entry points for wood decay fungi, consequently prescribed fires have been avoided in hardwood forest stands (Van Lear and Waldrop 1998). Evidence for the maintenance by fire of red oak forests on mesic sites is equivocal.

Northern red oak is considered intermediate in shade-tolerance but is less shade-tolerant and less drought-tolerant (Burns and Honkala 1990) than other canopy co-dominants such as sugar and red maple, silverbell, and other oak species, such as white oak, with which it co-occurs in GRSM. It widely believed that high-elevation red oak forests in the southern Appalachians and GRSM were subject to understory burning (NatureServe 2005) in the past;

if fire was indeed historically frequent enough to promote northern red oak in the sites in this study, fire suppression may have favored an increase in shade-tolerant understory stems, which in turn could have suppressed northern red oak regeneration. However, as noted in the discussion on hog rooting, oak seedling numbers appear to be adequate in number to replace dying canopy conspecifics and size structure of northern red oak indicates that there is ample density of smaller stems. Moreover, there is no evidence that in the forests of GRSM red oak canopy trees are being replaced by fire-intolerant species, in fact the decline in red oak forests appears to be part of a larger pattern of decline; therefore, the decline in oak overstory abundance (Chapter 4) is unlikely to be due to fire suppression.

Ongoing disturbances: atmospheric pollutant deposition and soil N, cations, and Al

Soil chemical changes from atmospheric deposition of nitrogen have been reported to alter northern hardwood forests in northeastern United States and Europe (Aber et al. 2003, Vacek et al. 1999). In GRSM, data collected in 1990 at a relatively low elevation (860 m) site near Elkmont registered levels of nitrate concentrations in rainfall that were surpassed only by areas in the Ohio Valley and Pennsylvania. Results of another study of dry and wet deposition at 15 sites within the park found the highest levels of acid deposition at the highest elevation site (Noland Divide; 1740 m). Furthermore, streams originating within GRSM have the highest nitrate loadings of any streams draining undisturbed watersheds in the United States (Stoddard 1994). Stream water nitrate concentration is the recommended measure of nitrogen status in terrestrial systems (Aber et al. 2003).

In GRSM, stream nitrogen (N) and sulfur (S) can originate from natural sources: nitrate leaches from old-growth forest litter and sulfur from bedrock formations such as Anakeesta, which forms much of the ridgeline in eastern GRSM. Atmospheric deposition from anthropogenic sources has also been cited for the high levels of nitrate and sulfur in GRSM streams (Cook et al. 1994). The initial effects of nitrogen deposition may be to enhance growth (Aber et al. 2003), and it may enhance the shade tolerance of some species (Catovsky and Bazzaz 2002). Continued deposition has been reported to benefit European beech (*Fagus sylvatica*) (Dittmar et al. 2003), but long-term exposure to nitrogen deposition is expected to negatively affect forest health. Acid deposition in the form of nitrogen and sulfur can damage trees directly through the affects of acids on plant tissues, or it can cause the loss of important soil cations such as calcium (Ca), magnesium (Mg), and potassium (K) and mobilize soil aluminum (Al), which is toxic to plant roots (Brady 1990). Additionally, a low Ca:Al ratio has been implicated as a limiting factor in the growth of northern red oak (Decker and Boerner 1997, Fisher and Binkley 2000). High levels of soil aluminum have been reported in some GRSM forests (Johnson et al. 1991).

Additions of both atmospheric S and N may affect forest growth by increasing the concentration of anions, including Al, which increases faster than other cations. Sulfate leaching can further compound the problem of Al availability by removing base cations, lowering their supply in forest soils. Nitrates can cause nutritional imbalances in forest trees by altering foliar N:Mg ratios (Fisher and Binkley 2000). Though there is some disagreement among researchers, it has never been conclusively shown that atmospheric N additions lead to forest decline, and in Europe atmospheric additions of N have been correlated with enhanced tree growth of 20-40%.

In the high-elevation forests of GRSM soil chemicals are strongly associated with changes in forest structure (Chapters 3 and 4), but not with BBD severity (Chapter 5). In the high-elevation beech dominated forests found throughout GRSM, soils typically have low pH, but biomass accumulation is associated with low soil cation and high Al concentrations (Chapter 3). Given the toxicity of soil Al at low soil pH, this pattern is contrary to what would be expected, but might be explained by either the ability of beech to thrive in low pH soils, or the nature of soils under beech dominated forest canopies. High-elevation beech forests have long been known to have some of the most acid soils of any deciduous forest (Cain 1931), which gives evidence that high-elevation beech are well-adapted to such conditions. Furthermore, beech litter, which would be the dominant litter in high-elevation beech forests because they contain more than 80% beech, may harbor smaller microbial populations which would decrease nitrogen mineralization rates (Lovett and Rueth 1999). If either or both of these circumstances is true, beech forests could continue to thrive with continual inputs of atmospheric acids.

In the mixed species forests of western GRSM, patterns of forest decline are associated with low concentrations of certain soil cations and high soil Al (Chapter 4), which is consistent with predictions that changes in soil acidity can cause forest-wide patterns of decline. In contrast with the results of Chapter 3, beech populations in this study declined modestly in basal area and abundance. However, the beech forest plots that were part of this analysis were almost entirely different than the plots used in Chapter 3 and beech relative abundance was only about half that of the high-elevation beech forest study. Given the likelihood that the abundance of beech leaf litter can influence the cycling of soil nutrients, the contrasting results in Chapters 3 and 4 is a reasonable hypothesis but needs further work.

Ongoing disturbances: ozone damage

At high elevations in the park ozone reaches levels high enough to damage leaf tissues (Shaver et al. 1994). Studies of the affect ozone has on individual tree species indicate that black cherry (*Prunus serotina*), ash (*Fraxinus americana*), sassafras (*Sassafras albidum*), tulip poplar (*Liriodendron tulipifera*) and table mountain pine (*Pinus serotina*) are susceptible to foliar injury from ozone (Shaver et al. 1994) but only about 2% of leaf area was affected. Ozone concentrations can be twice as high at high-elevations as at low. In a study of the ozone susceptibility of trees found in GRSM, Neufeld et al. (1992) listed several susceptible species found at high-elevations, but northern red oak was not one of them; northern red oak showed no decline in growth when subjected to various levels of ozone (Simini et al. 1992, Samuelson et al. 1996). It does not appear that ozone, by itself, is a likely driver of changes in forest dynamics in GRSM. It is important to note however, that in GRSM, areas with the highest ozone concentrations also had the highest levels of atmospheric nitrogen and sulfur deposition. Both ozone and acid deposition have been linked to reduced cold hardiness in some trees (Barnes and Davison 1988, Barnard and Lucier 1990).

Scale of observation

Although scale itself is not a driver of forest change, the scale at which observers measure forest attributes can influence their conclusions about the stability of the system. It is easy to imagine very small spatial and temporal scales of observation at which equilibrium could be observed, but those scales are often not relevant to the study of plant communities. Possibly because of the dearth of usable old data sets, studies of temporal forest change rarely exceed

10 years. Whether data from studies covering periods less than a decade adequately predicts longer-term forest dynamics is an open question (Bakker et al. 1996), but studies covering longer periods are needed.

In an attempt to identify the scale at which quasi-equilibrium could be reached, Shugart (1984) proposed that at a minimum, an area of at least 50 times the sized of the average disturbance patch was necessary. Biomass is an attribute commonly used by ecologists to measure forest stability (Bormann and Likens 1979), but as Busing and White (1993) demonstrated, compositional attributes require greater area to reach equilibrium than structural ones. In GRSM variances of tree density and basal area at grain sizes ranging from 0.02 to 0.1 ha did not conform to the forest succession model (Chapter 6).

Conclusions

The late-successional high-elevation forests of GRSM are not examples of climax, self-replacing, or steady-state forest associations. Because of their frequency and ubiquity disturbances and perturbations keep these forests in a continual state of transition, recovering from the last event, or in some cases, evolving in response to an ongoing event. High-elevation beech dominated forests have long been considered a climax forest type but data from this dissertation indicates that successional changes there have been continuous for 65 years and are ongoing. Similar those documented in other eastern forests, changes in the attributes of the high-elevation forests of GRSM may be slow enough that a disturbance event will inevitably set back succession before any semblance of stability is reached.

One of the patterns that emerges from a holistic view of the results of this dissertation is that the high-elevation forests of GRSM are all changing, but not in the same direction, nor to the same degree. Even in forests dominated by beech, some have gained basal area and biomass in recent decades, while others appear to be in decline. Because the decline cannot be attributed to BBD, and the main difference between them is the greater relative abundance of beech in the overstory of biomass accreting forests, the contrasting successional trajectories could be due to mass of beech leaf litter on the forest floor and its influence on nutrient cycling.

This dissertation provides empirical evidence that even protected, late-successional forests do not demonstrate stability in attributes. The concept of climax or stable forests that represent an endpoint in succession has only heuristic value in forest ecology, it is perhaps best to refer to them as late-successional.

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