Utah State University
DigitalCommons@USU

All Graduate Theses and Dissertations | Graduate Studies, School of

5-1-2013

Forest Recovery, Nutrient Cycling and Carbon Sequestration in a Southern Appalachian Spruce-Fir Forest

Patrick T. Moore
Utah State University

Recommended Citation
Moore, Patrick T., "Forest Recovery, Nutrient Cycling and Carbon Sequestration in a Southern Appalachian Spruce-Fir Forest" (2013). *All Graduate Theses and Dissertations.* Paper 1519.
http://digitalcommons.usu.edu/etd/1519

This Dissertation is brought to you for free and open access by the Graduate Studies, School of at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact becky.thoms@usu.edu.

FOREST RECOVERY, NUTRIENT CYCLING AND CARBON SEQUESTRATION IN A SOUTHERN APPALACHIAN SPRUCE-FIR FOREST

by

Patrick T. Moore

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

Helga Van Miegroet Major Professor	James Long Committee Member
Fred Baker Committee Member	John Shaw Committee Member
Janis Boettinger Committee Member	Mark R. McLellen Vice President for Research and Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2013

ABSTRACT

Forest Recovery, Nutrient Cycling and Carbon Sequestration in a Southern Appalachian Spruce-Fir Forest

by

Patrick T. Moore, Doctor of Philosophy

Utah State University, 2013

Major Professor: Dr. Helga Van Miegroet
Department: Wildland Resources

In order to fully understand the magnitude of the benefits that forests provide, it is crucial to understand the full suite of ecosystem services that they offer. A southern Appalachian red spruce-Fraser fir forest was intensively analyzed using a variety of methodologies to determine the nature and quantity of some of these services.

Many hypotheses exist regarding the future of these spruce-fir forests, which were heavily disturbed by the non-native balsam wooly adelgid during the 1980s. Direct measurements over the course of a decade assessed these hypotheses and indicate that this forest is recovering structure and function. The forest is accruing overstory biomass, with vegetation composition on a trajectory towards historic conditions.

By using a total forest inventory of all vegetation from overstory trees to understory mosses, rates of productivity and nutrient cycling were determined. Productivity of this forest at low elevations has returned to pre-adelgid levels, while at high elevations

productivity is approaching these levels. In the absence of an intact overstory, forest understory vegetation can compensate by disproportionately cycling and retaining nutrients such as nitrogen that would otherwise leach offsite. The understory of this forest provides an important service in nutrient cycling.

Our ability to actively manage forests in order to manipulate levels and rates of carbon sequestration was assessed using stand data and the Forest Vegetation Simulator Growth and Yield Model. Silvicultural intervention proved effective at sequestering additional carbon over a no action alternative by the end of our simulation period. This forest provides a variety of ecosystem services and has retained its ability to recover their function after catastrophic disturbance.

(141 pages)

PUBLIC ABSTRACT

Forest Recovery, Nutrient Cycling and Carbon Sequestration in a Southern Appalachian Spruce-Fir Forest

by

Patrick T. Moore

Our forests provide us with a variety of services from clean water, forest products and wildlife habitat to the lesser known functions of nutrient cycling and carbon sequestration. This research helps to demonstrate the extent of some of these services in a heavily disturbed southern Appalachian spruce-fir forest within Great Smoky Mountain National Park, the most heavily visited National Park in the United States. Following a catastrophic infestation of the non-native balsam wooly adelgid, the future of this forest was unknown, causing some to speculate about the future of this sensitive forest type. Though predictions about this forest's future varied widely from a full forest recovery to an extinction of tree species, direct measurements of forest conditions demonstrated that this forest is on a trajectory toward full recovery of structure and function of an intact forest. While these forests are recovering it was discovered that the understory is playing a critical role in keeping nutrients, such as nitrogen, on site and out of streamwater where they can contribute to water quality decline. We determined that active management of these forests can sequester more carbon in standing forest biomass and forest products and release less to the atmosphere where it can contribute to global climate change.

ACKNOWLEDGMENTS

For financial support during the course of this project I would like to acknowledge the S. J. and Jessie E. Quinney Foundation, the Ecology Center, USDA National Research Initiative Competitive Grants Program, USGS Biological Research Division, College of Natural Resources, Tennessee Valley Authority's Public Power Institute, and the Utah Agricultural Experiment Station.

Very sincere thanks to my major advisor, Helga Van Miegroet, for her support, patience, and interminable persistence. I would also like to thank my committee members, Fred Baker, Janis Boettinger, Jim Long, and John Shaw, for their encouragement and support in helping me complete this degree. I would also like to recognize Niki Nicholas for her logistical support and co-authorship and Justin DeRose for his co-authorship and true friendship when it was needed most. I am grateful to the team of technicians who assisted me in the lab and in the field, thank you.

Thank you to my friends and family for all their support along the way. Lisa, thank you for all of your love and support and thank you for going on this adventure with me.

Patrick T. Moore

CONTENTS

Page

ABSTRACT ii

PUBLIC ABSTRACT iv

ACKNOWLEDGMENTS v

LIST OF TABLES vii

LIST OF FIGURES viii

CHAPTER

1 INTRODUCTION 1

2 EXAMINATION OF FOREST RECOVERY SCENARIOS IN A SOUTHERN APPALACHIAN *PICEA-ABIES* FOREST 38

3 RELATIVE ROLE OF UNDERSTORY AND OVERSTORY IN CARBON AND NITROGEN CYCLING IN A SOUTHERN APPALACHIAN SPRUCE-FIR FOREST 64

4 USING SILVICULTURE TO INFLUENCE CARBON SEQUESTRATION IN SOUTHERN APPALACHIAN SPRUCE-FIR FORESTS 95

5 SUMMARY AND CONCLUSIONS 123

APPENDIX 127

VITA 133

LIST OF TABLES

Table Page

1.1 Habitat, growth habit, taxon and survey code for species found during our vegetation surveys of the Noland Divide Watershed of Great Smoky Mountain National Park 33

1.2 Rare or regionally rare vascular and nonvascular plant species associated with this community 35

2.1 Standing live biomass (Mg ha^{-1}), number of trees per hectare, and basal area (m^2 ha^{-1}) for four species groups at eight elevation bands at two time periods within the Noland Divide Watershed of Great Smoky Mountain National Park (± standard deviation).....61

2.2 Rates (kg ha^{-1} yr^{-1}) of biomass ingrowth, Increment, mortality and overall balance for three species at eight elevation bands at two time periods within the Noland Divide Watershed of Great Smoky Mountain National Park (± standard deviation) 62

3.1 Aboveground live pools of biomass (Mg ha^{-1}), carbon (Mg ha^{-1}) and nitrogen (kg ha^{-1}) for different forest components at three different elevation ranges within the Noland Divide Watershed of Great Smoky Mountain National Park (± standard deviation) 91

3.2 Predictive biomass equation for herbaceous vegetation in the form y = ax where y = species biomass (g), a = coefficient, and x = estimated percent cover.....92

3.3 Predictive biomass equation information for small woody understory vegetation in the form y = ln(a+bx), where y = biomass, a = intercept, b = coefficient, and x = stem caliper at 15 cm above ground level 93

3.4 Aboveground production of biomass and carbon and uptake of nitrogen (kg ha^{-1} yr^{-1}) for different forest components at three different elevation ranges within the Noland Divide Watershed of Great Smoky Mountain National Park (± standard deviation) 94

LIST OF FIGURES

Figure Page

1.1 Location map of the Noland Divide Watershed and the 4 NAPAP plots in the Great Smoky Mountains National Park 36

1.2 Schematic of a 20 x 20 m permanent plot with 4 x 4 m subplots (gray squares) for shrub and regeneration survey and 1 x 1 m sub subplots (black squares) for herbaceous and moss survey 37

2.1 Map of the Noland Divide Watershed of Great Smoky Mountain National Park and the systematic network of 50 permanent plots 63

4.1 Total aboveground C sequestered (Mg ha^{-1}) for three elevation groups as a result of no-action, even-aged management and uneven-aged management in a southern Appalachian forest 120

4.2 Cumulative aboveground live C, C stored in forest products and C released as emissions (Mg ha^{-1}) for three elevation groups under the even-aged management scenario 121

4.3 Average annual change in aboveground C (AAC; Mg ha^{-1} yr^{-1}) for three elevation groups as a result of no-action, even-aged management and uneven-aged management in a southern Appalachian forest.....122

CHAPTER 1

INTRODUCTION

Red spruce (*Picea rubens* Sarg.) -Fraser fir [*Abies fraseri* (Pursh) Poir.] forests of the southern Appalachian Mountains exist today as a chain of high-elevation vegetation islands located above 1500 meters in elevation and between 34 and 41 degrees north latitude. They represent the remnants of their original range and lower elevation limits of their ecological niche. Historically, the spruce-fir persisted as a contiguous forest type that dominated areas above 41 degrees north latitude under the cooler climates experienced during the last ice age (Cogbill and White, 1991). As the planet has warmed since the Pleistocene glaciation, spruce-fir forests have retreated to the high-elevation peaks and ridges, predominantly within Great Smoky Mountains National Park. Spruce-fir forests cannot retreat higher to cooler sites in the southern Appalachian Mountains because they already occupy the highest sites. The geographic distribution, extreme climatic conditions and a variety of stress factors including land use history, insect infestation and anthropogenic influences such as atmospheric pollution have combined to form a sensitive ecosystem with an uncertain trajectory. Because of the condition of the overstory and the uncertain future of Fraser fir, understanding the biomass and nutrient dynamics of the natural regeneration is vital to ensuring the future of this species as well as the persistence of this ecosystem. By analyzing how this forest type acquires biomass and cycles nutrients we can gain insight the various ecosystem services that it provides and understand how this system will function into the future.

LITERATURE REVIEW

Disturbance

Typical disturbance processes in this ecosystem include gap dynamics from the scale of individual trees, in the case of mortality and windthrow, to entire stands, in the case of the more recent insect infestation. Historically, fire has had little influence on the vegetative characteristics of this ecosystem (Fahey and Reiners, 1981). With lush understory, high rainfall and soil moisture, these forests have even been found to stop the spread of fires started at lower elevations (Korstian, 1937). With a fire return interval of thousands of years (White *et al*., 1985), these systems do not depend on stand replacing fires to reset important soil forming and stand dynamic processes. Furthermore, the present ecosystem could not persist with repeated exposure to fire. Tree species in the spruce-fir forest are not fire tolerant. The organic mat on the forest floor develops slowly and is important to seed viability and slope stability.

In more recent times, the spruce-fir ecosystem has been host to many disturbances that have altered the vegetation composition, stand dynamics and biogeochemistry. Stands are subjected to hurricane winds on a greater than 1000 year cycle making windthrow a significant disturbance factor (White *et al*., 1985). Within the past 15 years, however, three large storms, hurricanes Hugo in 1989, Opal in 1995, and Ivan in 2004, have swept through the area causing large amounts of tree mortality via windthrow. This recent frequency of violent storms would suggest an increased importance of windstorms to stand disturbance dynamics.

Though more common in northern spruce-fir forests, ice storms have caused mortality in southern Appalachian spruce-fir forests. Nicholas and Zedaker (1989) reported that an individual ice storm was responsible for 8.1% and 2.4% mortality in southern Appalachian spruce and fir, respectively, with additional damage to surviving trees.

The logging of eastern forests has changed forest composition for centuries. Though more widespread in the north, logging in the southern Appalachian spruce-fir began in about 1905 and continued until 1927 when the first protection efforts resulted in the creation of the Great Smoky Mountain National Park (GSMNP) (Pyle and Schafale, 1988). In some instances, previously cutover areas were subject to wildfires due to unnatural fuel loads or soil erosion due to lack of sufficient cover. The proportion of lower elevation and hardwood species increased, changing the vegetation composition. Some spruce-fir areas remained treeless for up to six decades after logging events (Eager and Adams, 1992). Due to difficulty in accessing stands in very steep terrain, the majority of the spruce-fir forest in the southern Appalachians has not been logged (Pyle and Schafale, 1988). Virtually all stands within the GSMNP have remained unaffected by logging due to additional protection efforts associated with National Park status.

A more recent, anthropogenic stressor in high-elevation forests in the East is atmospheric deposition and air pollution (Van Miegroet *et al*., 2001; Johnson *et al*., 1991). A low cloud base makes this area susceptible to exposure to increased pollutants because cloud-water generally contains higher concentrations of some ions. Atmospheric sulfur, nitrogen (N) and acid input to these montane forest canopies are significant (Johnson and Lindberg, 1992; Eagar and Adams, 1992). These compounds can have a considerable impact on the soils of an ecosystem, particularly soils with low base

saturation, but their effect on vegetation is uncertain and the source of much debate. The effects of air pollution and acid precipitation were thoroughly evaluated in Eager and Adams (1992). Consensus is that many factors including atmospheric deposition and stand dynamics have contributed to an observed decline in spruce during the 1980s.

Ozone pollution has also been considered detrimental to the vegetation of this ecosystem. A variety of studies have looked at the effects of ozone exposure, at levels found in the Smoky Mountains, on red spruce as a possible explanation for observed red spruce decline. Some effects were decreased foliar biomass (Amundson *et al*., 1991a) or reduced chlorophyll (Amthor and Cumming, 1988). However, other studies found no effects at all (Amundson *et al*., 1991b; Lawrence *et al.*, 1989). No field-based research has made a connection between increased ozone levels and associated decline of red spruce.

As significant as these disturbances have been to this ecosystem, the invasion of the balsam wooly adelgid (BWA) [(*Adelges piceae* (Ratz.)] has caused widespread damage to even the most protected areas of the range of Fraser fir. Imported on nursery stock in the northeastern United States prior to 1900, the BWA was first discovered in the southern Appalachians in 1957 (Speers, 1958) and GSMNP in 1963 (Ceisla *et al*., 1963). Since then the adelgid has invaded the entire range of Fraser fir and has caused extensive mortality of fir trees throughout (Busing *et al*., 1988). A secondary wave of windthrow-related spruce mortality has further reduced the remaining overstory trees (Busing, 2004).

Overstory

Overstory species composition of southern Appalachian spruce-fir forests are primarily driven by elevation. Red spruce can occur at elevations as low as 1,100 meters but only becomes dominant above 1,500 meters. Spruce forests gradually transition to Fraser fir as elevation increases, with fir appearing at about 1,600 meters and becoming dominant at around 1,900 meters, where they can form nearly pure stands. Yellow birch is a significant component of all southern Appalachian spruce-fir forests.

Dramatic changes to the composition of the spruce-fir forest have occurred following the introduction of the BWA. Nicholas *et al*. (1992) compared data collected from the Great Smoky Mountains in 1985 and 1986 to the 1946 measurements made by Oosting and Billings (1951). Basal area and stem densities decreased with increasing elevation. Much of this decrease in live fir basal area from 1946 to 1986 (8-62%) was due to mortality caused by BWA. Smith (1997) found that nearly 70% of standing fir basal area near the peaks of five mountaintops was composed of dead stems. Openings lead to a decrease in small fir seedlings as well as bryophyte cover. Size and age classes were becoming skewed toward younger and smaller Fraser fir individuals. Smith (1997) hypothesized that fir may be eliminated from the lower elevations within its range in the southern Appalachians.

The effects of these disturbances have been profound. In response to the loss of overstory trees, the stem densities of fir and spruce advanced regeneration, mountain ash (*Sorbus Americana* Marsh.), yellow birch (*Betula lutea* Michx. F.), and pin cherry (*Prunus pennsylvanica* L. f.) have all increased (Pauley and Clebsch, 1990; Busing *et al*., 1988; Witter and Ragnovich, 1986; DeSelm and Boner, 1984). A dramatic increase in

density of shrub species has also been observed (Busing *et al*., 1988; DeSelm and Boner, 1984). Forest communities have been extirpated by climate change in the past (Jackson and Wang, 1999). As global climate change continues, the future of this forest type is uncertain.

Historically, spruce-fir forests held considerably more biomass and nutrients in the form of tree stems, branches, and leaves because the overstory was intact (Whittaker, 1966). ince the onset of the adelgid infestation, almost all mature fir trees have been killed (Nicholas *et al*., 1992). This has created large gaps in the overstory allowing many understory plant communities to acquire light and nutrient resources previously unavailable. Physical features such as topographical characteristics as well as light and water resources have been shown to drive understory vegetation composition (Yarie 1980). All of these factors are probably important in understory vegetation composition. The presence of the adelgid in spruce-fir today adds another gap-producing disturbance to an already gap driven forest. As this forest acclimates to this new pest, it is hypothesized that the understory will play an increasingly important role in biomass storage and nutrient sequestration (Barker *et al*., 2002).

Understory

Because of the dramatic changes occurring in the overstory structure of this forest, overstory trees have received the majority of the research focus. Recent research on understory vegetation has focused on the natural regeneration of common overstory species (Smith and Nicholas, 2000; Nicholas *et al*., 1992). Researchers are only beginning to understand the valuable ecosystem service that understory herbaceous plants

provide by storing and cycling nutrients (Gilliam, 2006; Muller, 2003; Van Miegroet *et al*., 2007; Welch *et al*., 2007).

Historically, the scientific focus on understory dynamics in the Smoky Mountains (Smokies) began when Cain (1935) emphasized the importance of including all vegetation strata in any type of forest classification system in his analysis of the entire GSMNP. Crandall (1960) began thorough work on the understory of this system by applying the forest type and site system (Cain, 1935) to the spruce-fir ecosystem specifically. Before the work of Crandall there was little information on site types and ground cover in the spruce-fir. Whittaker (1956) did provide some information on site types; however, they were developed without much scientific rigor.

Oosting and Billings (1951) compared northern spruce-fir forests with southern spruce-fir forests and determined them to be floristically different but both part of the boreal forest complex. Fifty-seven percent of characteristic eastern spruce-fir species, including trees, shrubs and forbs, occur in both northern and southern Appalachian spruce-fir forests. Southern Appalachian forests support eight endemic species (White and Renfro, 1984). Ramseur (1960) provided an extensive flora of southern Appalachian high elevation communities.

Much has happened since the time of Crandall (1960) and Whittaker (1956). Forests have changed as a result of decades of exposure to BWA. Crandall's methods were current at the time; computing power, multivariate statistics, and spatial analyses have improved our ability to differentiate forest and site types quantitatively. Increased computing power can also give us the ability to determine the relation of the understory to the many physical processes at work in this ecosystem.

While overstory biomass (Nicholas, 1992) in this forest type can be significant, other components of the forest cycle significant amounts of biomass and nutrients (Yarie, 1980, Whitaker, 1966). In a system with recent and dramatic ecosystem level disturbance, such as BWA, coupled with a background of natural disturbances, it seems logical that the moss, understory and shrub species may control a greater proportion of biomass and nutrients than has been observed in other systems. This would be especially important shortly after disturbance or during early stages of stand development.

Understory vegetation may be far more responsive to overstory disturbance or nutrient fluxes than the overstory due to high relative light and nutrient demands and nutrient content of understory plants (Yarie, 1980). Different understory plant associations possess distinct nutrient uptake and cycling regimes, even within the same biogeoclimatic zone (Yarie, 1980). However, we are unsure if the understory plays a significant role in cycling nutrients in the spruce-fir. Nitrogen dynamics can vary spatially within small watersheds. Barker *et al*. (2002) showed in the Noland Divide Watershed (NDW) of GSMNP that there is considerable spatial variation of nutrient uptake even within small watersheds.

Soil

In contrast with higher latitudes, landscapes underlying southern Appalachian spruce-fir remained unglaciated during the last ice age. Parent material in the southern Appalachian spruce-fir is generally derived from the Pre-Cambrian Thunderhead sandstone; a thick bedded rock composed of quartz, K-feldspar and some mica (Feldman, 1991). While soil and parent material at higher latitudes were being scraped, churned,

and ground and new parent material was deposited by advancing ice sheets, soils of the high elevation spruce-fir are older, more weathered, and more depleted of important nutrients such as calcium (Ca) and magnesium (Mg), while simultaneously richer in accumulated nitrogen (N). Therefore, these soils are generally acid with low base saturation (Joslin *et al*., 1992; Johnson *et al*., 1991) in contrast to glaciated soils in the northern Appalachians. Differences in surficial geology, mineralogy, slope steepness, elevation, and climate also exist (Fernandez, 1992; Joslin *et al*., 1992).

Many of these soils undergo podzolization, yet the majority (75%) are classified as Inceptisols with spodic characteristics (Feldman *et al*., 1991; Wolfe, 1967; Kelly and Mays, 1989). Histosols (18%) and Spodosols (6%) (Kelly and Mays, 1989) also occur. Though these are three distinct soil orders they represent a continuum of soil-forming process typical of cool coniferous forests.

Spodosols are characterized as highly leached and acidic and may have an accumulation of illuvial humus with aluminum or iron into a spodic horizon due to forest floor leaching of organic acids (Fischer and Binkley, 2000). In the southern Appalachian spruce-fir, Spodosols likely occur in areas of lesser disturbance and on lower gradient slopes (Fernandez, 1992). They maintain similar soil forming processes as in other sites but longer periods of time between disturbances allows for sufficient translocation and the formation of a spodic horizon.

Histosols are described as soils with very high levels of organic matter accumulation (Fisher and Binkley, 2000). In this case the buildup of organic matter is enough to classify the soil as an organic soil, which is capable of containing high levels of carbon (Feldman *et al*., 1991). Like the Spodosols, these soils are quite acidic due to the acids

produced via decomposition of organic matter from the upper soil horizons and leaching of base cations. In this forest, Histosols occur in areas of high rates of organic inputs and low decomposition. This may occur in highly productive sites in areas where organic deposition results from mass movement such as the base of steep slopes.

Inceptisols are the typical soil order of the spruce-fir in the southern Appalachians. They occur on the steep side slopes, prone to soil disturbance that dominates the topography of the spruce-fir. They are generally described as mineral soils with minimum development and little to no subsoil clay accumulation. Because landslides and windthrow are relatively common in these forests, Inceptisols are usually pedogenically younger soils that have had insufficient time to develop subsurface diagnostic horizons such as spodic or argillic horizons. In the absence of disturbance, usually windthrow or mass movement, these soils may develop histic epipedons or spodic horizons. Inceptisols have also been associated with poor site drainage that does not allow normal development of a spodic horizon (Fernandez, 1992). The majority of Inceptisols in the spruce-fir are Umbrepts, because of their high levels of organic matter in near-surface horizons, and many have spodic characteristics but not enough to classify them as Spodosols.

Nitrogen Research

Though N is thought to be a limiting nutrient in many forest systems, this is not true in all cases, especially in the southern Appalachian spruce-fir which is considered N-saturated (Van Miegroet *et al*., 2001). Once thought a rare phenomenon, N-saturated soil conditions and nitrate leaching have been observed in forests across the United States

(Fenn *et al*., 1998; Aber *et al*., 1998). Southern Appalachian spruce-fir forests receive some of the highest rates of N input via atmospheric deposition in North America (Johnson *et al*., 1991; Lovett and Lindberg, 1993) and have limited N uptake ability (Barker *et al*., 2002). They have also been shown to leach significant amounts of nitrate (Johnson *et al*., 1991) and export nitrate into streamwater (Nodvin *et al*., 1995; Van Miegroet *et al*., 2001; Cai *et al*., 2010 and 2011), indicating limited N-retention capacity.

In general, greater net N uptake and retention rates are expected from vigorously aggrading forests while lower N uptake and retention abilities are often seen in older forests (Cole and Rapp, 1981; Emmet *et al*., 1993; Olsson *et al*., 1997). The patchiness of this forest is such that components of the forests are degrading while others are simultaneously aggrading. Individual stands within this forest are in all stages of development.

Overstory and understory generally cycle biomass and nutrients differently. While a forest overstory can immobilize large amounts of C and minerals, understory standing pools are generally smaller (Cole and Rapp, 1981). Forest overstories can also generate higher rates of annual production due to higher leaf areas and lack of shading by superior vegetation.

Carbon Research

Little is known about the C pools and fluxes in mature and unmanaged forest ecosystems (Acker *et al.*, 2000, 2002). The pools of stored C in an ecosystem (the amounts and proportions stored in various components such as soil, litter, foliage and woody tissue) can relate to the total amount of C that an ecosystem can acquire or

sequester, while C fluxes in and out of the ecosystem impact its interaction with atmospheric carbon dioxide (CO_2).

Though unmanaged forests have been hypothesized to be at a relative C balance equilibrium (Odum 1969), expected changing climate conditions (Aber *et al.*, 2001) and current stand dynamics may push these mature forests to be net sources of CO_2. While increment from living trees as well as the ingrowth of new trees into the stand represents a net sink for atmospheric CO_2, the constant decay of standing dead and fallen trees as well as the soil respiration represents a net source of CO_2 into the atmosphere.

One major reason for this potential unbalance is the large input of C into the atmosphere through the decomposition of organic matter. In an ecosystem such as spruce-fir, large amounts of C are held in the organic matter-rich soil (Feldman *et al.*, 1991), litter layer, and in coarse woody debris (Rose and Nicholas, 2008). After the invasion of the BWA and associated mortality these forests now contain large amounts of standing dead and fallen overstory stems. As this large input of newly dead stems decomposes it produces CO_2 at an unusually high rate. A forest that was once at C equilibrium may now be a C source, especially if one takes global climate change scenarios into account as well. Sequestering carbon in the form of biomass is a valuable ecosystem service provided by forests that are net C sinks.

Historically, southern Appalachian spruce-fir forests held considerable C in the form of live standing trees (e.g., 127-147 Mg C ha^{-1} [Johnson and Lindberg, 1992], 96-149 Mg C ha^{-1} [Whittaker, 1966], C taken as 48% of biomass). After the recent wave of mortality due to the BWA and the ongoing waves of windthrow-related spruce mortality, the extent to which the overstory of this forest is accruing C is uncertain. For years after the onset

of the BWA the overstory C lost via decomposition of newly dead trees may have surpassed the ability of increment and ingrowth to compensate, making the living overstory C pool shrink in size (Van Miegroet *et al.*, 2007). Positive C sequestration as an ecosystem service is an important aspect of the recovery of the function of this system. This forest may never approach the historic levels of C contained in the overstory due to the ongoing presence of the BWA.

GOALS

Until recently, it was unknown whether or not this forest was on a path towards the recovery of structure, function and ecosystem services that this forest provided. By analyzing historic and current data sets we determined the trajectory of this ecosystem. By looking at the individual contributions of C, N and biomass within forest strata, we created an integrated image of how the overstory and understory vegetation components in this system held and cycled nutrients and biomass. In a disturbed system such as this the relative roles of the overstory and understory provided new insight into ecosystem function. Prescribing silvicultural manipulation has demonstrated our ability to affect these processes. These concepts have been addressed with the following specific goal statements:

- ***Describe current stand conditions and post-BWA stand trajectory.***

Since the onset of the BWA much has been hypothesized regarding the short-term direction of southern Appalachian spruce-fir forests; such as the coexistence of spruce and fir as dominants, dramatic reduction in the importance of fir, transition to a fir-birch

forest (Busing and Clebsch, 1987) or even complete extirpation of Fraser fir (Smith, 1997).

Because the majority of southern Appalachian spruce-fir forests are within Great Smoky Mountain National Park, the scenic and recreation value of a properly functioning forest is an important ecosystem service. With a set of long-term inventory plots in the southern Appalachians we documented specific trends regarding individual species and size classes since the recent wave of BWA-induced fir mortality. Plot-level ecosystem characteristics such as ingrowth, mortality, growth increment, trees per hectare, and basal area over time gave us a short-term forest trajectory and allowed us to determine whether hypothesized recovery scenarios were supported by our data set.

- ***Quantify ecosystem source or sink strength of all aboveground C, N and biomass pools and fluxes.***

Prior to this work, very little research was done on the role of understory in the cycling and retention of nutrients. Yet this ecosystem component may play an important role in rapid recycling and availability of critical nutrients, especially if annual species are abundant. Also, the entire spruce-fir ecosystem is marked with spatial heterogeneity in forest structure, which can affect understory vegetation composition as well as understory nutrient cycling.

Major C and N pools exist as overstory living trees, standing dead trees and understory vegetation. Though the C and N pools within this stratum were very large, smaller pools were contributing significantly to the cycling of nutrients and biomass. Shifts in the relative size of these pools have strong ramifications on the overall function of this ecosystem as either a C and N source or sink. Ingrowth of new trees into the stand

and positive growth increment of existing trees over time represent a positive flux into aboveground C (i.e., sink). At the same time, trees dying or falling from the overstory represent a removal of C from the active overstory C pool and no longer contribute to C sequestration. If the ecosystem as a whole is sequestering more C as ingrowth and positive increment than it is losing due to decay of dead and windthrown trees from the overstory, then this ecosystem is acting as a sink to trap excess CO_2. This system was profoundly and directly affected by the BWA. This analysis will provide further evidence of the extent and rate at which the forest is recovering from the BWA, and will characterize the ecological and environmental consequences of this disturbance.

The methods outlined below allowed us to also estimate aboveground C, N and biomass pools and fluxes for major forest strata. A complete understanding of how nutrients are cycled within the living components of this ecosystem required the inclusion of the understory, especially when this system is in transition. We hypothesized that the understory is cycling a considerable portion of ecosystem N. The objectives of this section were to determine the role of understory versus overstory in sequestering biomass and cycling N, whether overstory and N dynamics have recently changed from the prior measurement period and whether current biomass, C and N dynamics show elevational patterns.

- ***Determine the effect of active management on C sequestration.***

Though there is some debate over how managed forests sequester carbon (C) relative to their old-growth counterparts (Skog and Nicholson, 1998; Harmon and Marks, 2002; Luyssaert *et al.*, 2008), managed forests have been shown to make valuable contributions to C sequestration efforts (Van Duesen, 2010; Miner, 2006; Hoover and Heath, 2011).

While managed forests were not expected to contain as much standing C as old-growth forests on similar sites, managed forests sequestered more C when both live biomass and harvested biomass are considered, and depending on the fate of harvested biomass [e.g., biofuel *versus* structural wood products, (Van Duesen, 2010; Sorenson *et al.*, 2011)]. Furthermore, as the rate of growth for live biomass is increased by active management for wood products, the potential C sequestration rates in managed forests increase.

The goal of this part of the research was to simulate the possible effect of silvicultural activities on long-term C storage potential of managed forests compared to their unmanaged counterparts using the large comprehensive re-measurement data set described below from the Great Smoky Mountains. By pairing this data set with the readily available and easily used Forest Vegetation Simulator (FVS), we attempted to provide a straightforward demonstration that active management may well be a better strategy for C sequestration than passive management. This may help to demonstrate whether and to what extent managed forests can to provide greater ecosystem services then their unmanaged (protected) counterparts.

MATERIALS AND METHODS

In order to address the specific goals stated above we needed a complete forest inventory (Wharton and Griffith, 1993) to estimate biomass of all growth forms present in this ecosystem including overstory and understory trees, shrubs and forbs. To understand change in this system over time, the remeasurement of existing long-term monitoring plots was necessary. This research built upon the long-term data set constructed and first measured in 1993. While many equations existed in published

literature (Nicholas, 1992; Weaver, 1972; Whittaker, 1962) to estimate biomass for many forest components, biomass equations for some small trees, shrubs and forbs needed to be developed. These relationships were derived using a double sampling approach with a combination of destructive and non-destructive vegetation surveys.

Study Area

As the majority of southern Appalachian spruce-fir forests are located within GSMNP, the park is the ideal location to study this forest type. Due to the heterogeneity in stand structure, strong elevation gradient affecting species composition (Nicholas, 1992) and the effects of these on nutrient cycling processes (Pauley and Clebsch, 1990), the Noland Divide Watershed (NDW) within the GSMNP was selected as an appropriate site for our study. The NDW is a 17.4 hectare high-elevation catchment entirely within the spruce-fir zone of the GSMNP and lies on the North Carolina and Tennessee border. Clingman's Dome road, built in 1938, divides the catchment roughly in half at 1800 m. The catchment has not been impacted by logging or fire (Pyle and Schafale, 1988) and is considered typical of the southern Appalachian spruce-fir ecosystem.

The NDW is a well-researched watershed. Experiments on forest dynamics (Nicholas *et al.*, 1992), nutrient cycling (Johnson *et al.*, 1991; Johnson and Lindberg, 1992; Van Miegroet *et al*., 1993; Barker *et al.*, 2002), soil processes (Garten and Van Miegroet, 1994; Van Miegroet, 1995), and watershed dynamics (Nodvin *et al.*, 1995; Van Miegroet *et al.*, 2001) have all been performed on this high-elevation catchment.

In 1993, 50 permanent plots were established systematically along nine elevation bands ranging from approximately 1700 m to 1900 m in elevation (Figure 1.1). Each of

the permanent plots (Figure 1.2) measures 20 x 20 m with 4 distinct corner posts and a center post as recommended by Zedaker and Nicholas (1990). Plot edges were oriented in the four cardinal directions, north, east, south, and west and with plot corners pointing northeast, southeast, southwest and northwest. The use of these existing long-term monitoring plots capitalized on an abundance of historic data sets collected within this watershed.

This network of 50 plots formed the basis for this research. The size of this catchment minimized variation due to differing parent material while being able to detect the fine scale nutrient uptake processes that have been shown in the NDW (Barker *et al*., 2002). Also, because slopes and aspects are relatively homogenous across the watershed, these factors were controlled for while we are trying to assess nutrient dynamics. The entire spruce-fir ecosystem is marked with spatial heterogeneity in forest structure, which can affect understory vegetation composition as well as understory nutrient cycling. In addition, this watershed provided a range of elevations, which has been shown to dramatically influence vegetation composition as well. This variety of overstory conditions and other physical site factors reflected the diversity of understory plant associations.

Field Measurements

Overstory

An overstory inventory of all trees >5cm was completed in 1993 and 1998 for the 50 NDW plots. The 1993 and 1998 data sets were made available to us by the Tennessee Valley Authority (TVA) and the Environmental Protection Agency (EPA) and allowed us to measure changes in the forest such as tree increment growth, forest ingrowth, biomass acquisition, and mortality between measurement periods as well as standing biomass, nutrient pools and fluxes over time.

The plots were remeasured in 2003. Diameter at breast height (dbh, tree diameter at 1.37m above ground level), species, unique identification number, and crown position (dominant, co-dominant, intermediate, or suppressed) of each live and dead overstory (≥ 5 cm dbh) tree was recorded, using inventory protocol described in Zedaker and Nicholas (1990). All overstory trees not included in the last inventory (ingrowth) were tagged with a uniquely numbered 1 ½" aluminum tag and a 2 ¼" aluminum siding shank nail. Care was taken to ensure that the shank nails were not fully driven in to give overstory trees room for 10 cm of radial growth.

Using the predictive equations of Nicholas (1992) biomass of foliage, live branches, dead branches, bole bark and bole wood were determined using dbh as the independent variable. Individual tree component masses were summed to equal total tree biomass. These equations were used for red spruce, Fraser fir and yellow birch to estimate biomass of tree species within our plots. Biomass of other species was estimated similarly with the predictive equations of Weaver (1972). C content of individual tree components were determined by multiplying component biomass values times the component C

percentages of Barker *et al.* (2002). Data collected during stand inventories in 1993 and 1998 as well as the overstory inventory performed in 2003 was used to calculate standing biomass and nutrient pools as well as fluxes over time. The Nicholas (1992) equations were shown to be reliable for some spruce-fir populations but may need a correction factor for use in the GSMNP (Barker *et al.*, 2002) due to the fact that spruce and fir in the GSMNP are generally shorter than spruce and fir in the rest of the Southern Appalachians.

Understory Trees and Shrubs

Within each of the permanent plots, four 4 x 4 m subplots were established in the manner shown in figure 1.2 (gray boxes). The diagonals of these 4 x 4 m square plots were measured to ensure that each plot was plumb and square. All shrub and tree stems less than 5 cm dbh but greater than 2 cm were included in this survey. Species was recorded and caliper measurement was taken 15 cm above ground level. Using the predictive equations of Nicholas (1992) and Weaver (1972) biomass of foliage, live branches, dead branches, bole bark and bole wood was determined using caliper at 15 cm above ground level as the independent variable.

Herbaceous Vegetation and Seedlings

There are no published equations relating herbaceous vegetation and seedling biomass to a nondestructive vegetation parameter. These equations were generated for the most common species listed in table 1.1. A two-part double sampling approach was used to estimate herbaceous vegetation and seedling biomass (Forman, 1969). Such an

approach will created a valuable set of allometric equations for future use while protecting the permanent plot system.

The method consisted of a nondestructive survey coupled with destructive sampling outside the permanent plots. For the non-destructive survey of the permanent plot system, sixteen 1 x 1 m sub subplots were delineated with a 1 x 1 m PVC square within each of the permanent plots. The sub subplots (four in each 4 x 4 m sapling and shrub plot) were arranged in the manner shown in figure 1.2 (black boxes). Percent cover of all herbaceous plants present within each sub subplot was estimated ocularly and recorded. Herbaceous vegetation was defined as all herbs, grasses and mosses. Because of the relatively short growing season (May through September) only one sampling was made in 2003 (Yarie, 1980). Aboveground herbaceous biomass was assumed to be the peak standing biomass at the end of the growing season and our estimate of net primary production (NPP).

Concurrent with the non-destructive sampling in the permanent plots was a destructive sampling of herbaceous plants in temporary 1 x 1 m plots established in the fall of 2003 outside of the permanent plots. Each of these temporary plots was centered 10 m west of the northwest corner of the permanent NDW plots. Plots were located in this manner in order to represent the entire watershed, also to ensure that temporary plots did not interfere with the permanent plot system.

At each of these temporary plots, percent cover by species was assessed by ocular estimation to the nearest percent. After cover of each individual plant species was measured, it was clipped at ground level and placed in a uniquely numbered plastic bag until adequate samples (n=12) of all species present were measured and collected. If

additional samples were needed, they were selectively sampled in order to obtain adequate observations of all species. Rare or protected species were not sampled (Table 1.2).

Once removed from the field in individually labeled and sealed Ziploc bags, plant specimens were dried in a 65-degree C° oven for 24 hours and then weighed. Recorded dry weights were used to develop a set of species-specific predictive equations to estimate dry plant biomass from recorded plant parameters. This set of equations was derived by regressing percent cover against individual dry weight, using the PROC REG procedure in SAS. Dried plant specimens were then ground through a 40-mesh screen in a Wiley mill. The ground and dried plant samples were sent to the analytical laboratory at Colorado State University (CSU) for C and N analysis.

Although mosses contribute little in terms of ecosystem biomass, their high turnover rates and high nutrient content make them important in biogeochemical cycling (Tamm, 1953; Binkley, 1981). Moss was destructively and non-destructively surveyed similar to forbs and estimated by percent cover. Net primary productivity (NPP) will be estimated as 1/3 of the estimated biomass following Tamm (1953).

Predictive biomass equations were produced for seedlings as well in a manner similar to that for herbaceous cover above. Seedlings were defined as woody plants that have stem diameters <2cm at 15 cm above ground level. All destructive seedling sampling was performed in the nearby Pisgah National Forest, NC. 12 individuals of each of four woody species, red spruce, Fraser fir, yellow birch and viburnum were measured at 15 cm above ground level, clipped at ground level, dried and weighed. Allometric relationships between stem diameter and aboveground mass were developed using the

PROC REG procedure in SAS. Within the plots, seedlings were measured within the 1 x 1 m sub-sub plots along with herbaceous vegetation. Seedling biomass was determined using derived predictive equations described above.

Site Characterization

As the 50 NDW plots are part of a permanent plot system that dates back to the early 1990's, site classification and characterization variables were previously collected. Included in these data are elevation, aspect, slope, landform, slope position and microrelief of each plot (Zedaker and Nicholas, 1990). Site data for individual plots were remeasured only upon evidence of an event that may have changed the site classification such as a landslide or other severe disturbance.

Instrument and Personnel Calibration

Research protocol including site classification and characterization as well as quality assurance / quality control procedures were based on Zedaker and Nicholas (1990) except where noted. Tools and instruments used in the inventory such as compasses, diameter tapes and fiberglass distance tapes and all other field gear was regularly cleaned and maintained following Zedaker and Nicholas (1990). Field technicians responsible for individual mensurative procedures were trained before entering the field. Technicians were required to be comfortable with all instruments and tools and meet measurement accuracy tolerances (Zedaker and Nicholas, 1990) before measuring plots.

Data Manipulation

We compared hypothesized scenarios of overstory forest conditions and trajectories to our 1993-2003 data set. In order to understand current stand conditions we determined biomass allocation by species across elevation bands by applying existing and developed allometric equations. This gave us a picture of forest conditions across the forest in 2003. From this we developed an understanding of the current forest trajectory by tracking individual trees through a ten-year time step by monitoring growth of trees into the stand, growth increment of existing trees, and mortality of existing trees (a negative value). Summing these three values at the stand level gave us a picture of how species acquired or lost biomass across the elevation gradient and allowed us to compare our observations with published hypothesized forest trajectories.

We described the relative contribution of understory and overstory in terms of the cycling of C, N and biomass by determining nutrient content of all growth forms and their uptake by applying existing and developed allometric equations. This gave us an understanding of the distribution of biomass, C and N throughout the system and allowed us to calculate fluxes in these growth forms. Comparing the understory contribution to nutrient and biomass cycling to the overstory gave us a clearer picture of the value of the understory to this important ecosystem service.

We demonstrated the effects of active management on the sequestration of C by producing a long-term predictive model that compared the C dynamics of applying a management action against a no action alternative using the Forest Vegetation Simulator (FVS, Dixon 2002). The FVS is an individual-tree distance independent growth and

yield model that is widely used by managers and researchers to model forest change and stand dynamics over time in response to management activities. This tool predicted whether the active management of forests sequestered more C than their undisturbed counterparts when standing forest carbon as well as the fate of forest products were considered.

PRODUCTS GENERATED

The following products were designed to meet the objectives outlined above:

- Synthesis paper co-authored with Dr. Helga Van Miegroet and Chloe Tewksbury on the overall ecosystem C balance of the southern Appalachian spruce-fir forest, including overstory, understory, litter and soil components, published in 2007.
- Manuscript comparing hypothesized scenarios of forest conditions and trajectories to our 1993-2003 data set, published in 2008 (Chapter 2).
- Manuscript describing the relative contribution of understory and overstory in terms of the cycling of C, N and biomass 1993-2003, published in 2007 (Chapter 3).
- Manuscript describing application of FVS to produce long-term predictive model of the effects of active management on the sequestration of C, published in 2012 (Chapter 4).

LITERATURE CITED

Aber, J.D., McDowell, W.H., Nadelhoffer, K.J., Magill, A., Bernston, G., Kamakea, M., McNulty, S.G., Currie, W., Rustad, L. and Fernandez, I. 1998 Nitrogen saturation in temperate forest ecosystems: hypothesis revisited. *BioScience*. **48**:921-934.

Aber, J.D., Nelson, R.P., McNulty, S., Lenihan, J.T., Bachelet, D. and Drapek, R. J. 2001 Forest process and global environmental change: Predicting the effects of individual and multiple stressors. *BioScience*. **51(9)**:735-751.

Acker, S.A., Harcombe, P.A., Greene, S.E. and Harmon, M.E. 2000 Biomass accumulation over the first 150 years in coastal Oregon spruce hemlock forest. *J. Veg. Sci*. **11**:725-738.

Acker, S.A., Halpern, C.B., Harmon, M.E. and Dyrness, C.T. 2002 Trends in bole biomass accumulation, net primary production, and tree mortality in Pseudotsuga menziesii forests of contrasting age. *Tree Physiology*. **22**:213-217.

Amundson, R.G., Alscher, R.G., Fellows, S., Rubin, G., Fincher J., Van Leuken, P. and Weinstein L.H. 1991a Seasonal changes in the pigments, carbohydrates, and growth of red spruce as affected by exposure to ozone for two growing seasons. *New Phytology*. **118**:127-138.

Amundson, R.G., Kohut, R.J. and Laurence, J.A. 1991b Mineral nutrition, carbohydrate content, and cold tolerance of foliage of potted red spruce saplings exposed to ozone and simulated acidic precipitation treatments. *Water, Air, Soil Pollution*. **54**:175-182.

Amthor, J.S. and Cumming, J.R. 1988 Low levels of ozone increase bean leaf maintenance respiration. *Can. J. of Botany* **66(4)**:724-726.

Barker, M., Van Miegroet, H., Nicholas, N.S. and Creed, I.F. 2002 Variation in overstory uptake in a small, high-elevation southern Appalachian spruce-fir watershed. *Can. J. For. Res*. **32**:1-12.

Binkley, D. and Graham, R.L. 1981. Biomass, production, and nutrient cycling of mosses in an old-growth Douglas-fir forest. *Ecology*. **62**:1387-1389.

Busing, R.T., Clebsch E.E.C., Eager, C.C. and Pauley, E.F. 1988 Two decades of change in a Great Smoky Mountain spruce-fir forest. *Bull. Torr. Bot. Club*. **115**:25-31.

Busing, R.T. and Clebsch, E.E.C. 1987 Application of a spruce-fir canopy model. *For. Ecol. Manage*. **20:**151-169.

Busing, R.T. 2004 Red spruce dynamics in an old southern appalachian forest. *Bull. Torr. Bot. Club*. **131**:337-342.

Cai, M., Schwartz, J.S., Robinson, R.B., Moore, S.E. and Kulp, M.A. 2010 Long-term effects of acidic deposition on water quality in a high-elevation Great Smoky Mountains National Park Watershed: Use of an ion input-output budget. *Water, Air, Soil Pollution*. **209**: 143-156.

Cai, M., Schwartz, J.S., Robinson, R.B., Moore, S.E. and Kulp, M.A. 2011 Long-term annual and seasonal patterns of acidic deposition and stream quality in a Great Smoky Mountains high-elevation watershed. *Water, Air, Soil Pollution*. **219**:547-562.

Cain S.A. 1935 Ecological studies of the vegetation of the Great Smoky Mountains. *American Midland Naturalist*. 566-584.

Ceisla, W.M., Lambert, H.L. and Franklin R.T. 1963 The status of the balsam wooly adelgid in North Carolina and Tennessee. USDA Forest Service, Div. S. & P. F., Zone 1, F. I. &D. C. Office, Asheville, NC. Report 65-1-1.

Cole, D.W. and Rapp, M. 1981 Elemental cycling in forest ecosystems. In *Dynamic Properties of Forest Ecosystems*. Ed. D.E. Reichle. Cambridge University Press, London, pp 341–409.

Cogbill, C.V. and White, P.S. 1991 The latitude elevation relationship for Appalachian spruce-fir. *Vegetatio*. **94**:153-175.

Crandall D. L. 1960 Ground vegetation patterns of the spruce-fir area of the Great Smoky Mountains National Park. *Ecol. Mono*. **28**:337-360.

DeSelm, H.R. and Boner, R.R. 1984 Understory changes in spruce-fir during the first 16-20 years following the death of fir. In White, P.S. (ed) *The Southern Appalachian Spruce-fir Ecosystem: Its Biology and Threats*. USDI, National Park Service, Southeastern Regional Office. Research/Resource Management Report SER-71, Atlanta, GA, pp. 51-59.

Dixon, Gary E. 2002 Essential FVS: A user's guide to the Forest Vegetation Simulator. Internal Rep. Fort Collins, CO: U. S. Department of Agriculture, Forest Service, Forest Management Service Center. 226p. (Revised: January 17, 2013)

Eagar, C. and Adams, M. B. eds. 1992 *Ecology and decline of red spruce in the Eastern United States*. Springer-Verlag, New York.

Emmett, B.A., Reynolds, B., Stevens, P.A., Norris, D.A., Hughes, S., Gorres, J. and Lubrecht, I. 1993 Nitrate leaching from afforested Welsh catchments-interactions between stand age and nitrogen deposition. *Ambio*. **22**:386-394.

Fahey, T.J. and Reiners, W.A. 1981 Fire in the forests of Maine and New Hampshire. *Bull. Torr. Bot. Club*. **108**:362-373.

Feldman S.B., Zelazny L.W. and Baker, J.C. 1991 High elevation forest soils of the southern Appalachians: I. Distribution of parent materials and soil landscape relationships. *Journal of the Soil Science Society of America*. **55**:1629-1637.

Fenn, M.E., Poth, M.A., Aber, J.D., Baron, J.S., Bormann, B.T., Johnson, D.W., Lemly, A.D., McNultry, S.G., Ryan, D.F. and Stottlemyer, R. 1998 Nitrogen excess in North American ecosystems: predisposing factors, ecosystem responses and management strategies. *Ecol. App*. **8**:706-733.

Fischer, R.F. and Binkley, D. 2000 *Ecology and Management of Forest Soils*. Wiley Publishing 3rd edition. 512 pp.

Fernandez, J. 1992 Characterization of eastern U.S. spruce-fir soils. Pages 40-63 in Eager, C. and Adams, M.B., eds. *Ecology and decline of red spruce in the eastern United States*. Springer-Verlag, New York, NY.

Forman, R.T.T. 1969 Comparison of coverage, biomass, and energy as measures of standing crop of bryophytes in various ecosystems. *Bull. Torr. Bot. Club*. **96**:582-591.

Garten C.T. and Van Miegroet, H. 1994 Relationship between site nitrogen dynamics and natural ^{15}N abundance in plant foliage from the Great Smoky Mountains National Park. *Can. J. For. Res*. **24**:1636-1645.

Gilliam, F.S. 2006 Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Ecology*. **94**:1176-1191.

Harmon, M.E. and Marks, B. 2002 Effects of silvicultural practices on carbon stores in Douglas-fir-western hemlock forests in the Pacific Northwest, USA: Results from a simulation model. *Can. J. For. Res.* **32**:863-877.

Hoover, C.M. and Heath, L.S. 2011 Potential gains in C storage on productive forestlands in the northeastern United States through stocking management. *Ecol. Appl*. **21**:1154-1161.

Jackson, S.T. and Wang C. 1999 Late Quarternary extinction of a tree species in eastern North America. *Ecology*. **96**:13847-13852.

Johnson, D.W., Van Miegroet, H., Lindberg, S.E. and Todd, D.E. 1991 Nutrient cycling in red spruce forests of the Great Smoky Mountains. *Can. J. For. Res*. **21**:769-787.

Johnson, D.W. and Lindberg, S.E., eds. 1992 *Atmospheric Deposition and Nutrient Cycling in Forest Ecosystems-A Synthesis of the Integrated Forest Study*. Springer-Verlag, New York.

Joslin, J.D., Kelly, J.M. and Van Miegroet, H. 1992 Soil chemistry and nutrition of North American spruce–fir stands: evidence for recent change. *J. Env. Qual*. **21**:12–30.

Kelly, J.M. and Mays, P.A. 1989 Root zone physical and chemical characteristics in southeastern spruce-fir stands. *Journal of the Soil Science Society of America*. **53**:1248-1255.

Korstian, C.F. 1937 Perpetuation of spruce on cutover and burned lands in the higher Appalachian mountains. *Ecol. Mono*. **7**:125-167.

Lawrence, J.A, Kohut, R.J. and Amundson, R.G. 1989 Response of red spruce seedlings exposed to ozone and simulated acidic precipitation in the field. *Arch. Env. Cont. Tox.* **18**:285-290.

Lovett, G.M. and Lindberg, S.E. 1993 Atmospheric deposition and canopy interactions of nitrogen in forests. *Can. J. For. Res.* **23**:1603-1616.

Luyssaert, S., Schulze, E.D., Borner, A., Knohl, A., Hessenmoller, D., Law, B.E., Philippe, C. and Grace, J. 2008 Old-growth forests as global carbon sinks. *Nature*. 455:213-215.

Miner, R. 2006 The 100-year method for forecasting carbon sequestration in forest products in use. Mitigation and Adaptation Strategies for Global Change.

Muller, R.N. 2003 Nutrient relations of the herbaceous layer in deciduous forest ecosystems. In *The herbaceous layer in forests of eastern North America*. F.S. Gilliam and Roberts, M.R. eds. Oxford University Press, New York, pp. 15-37.

Nicholas, N.S. and Zedaker, S.M. 1989 Ice damage in Spruce-fir forests of the Black Mountains, North Carolina. *Can. J. For. Res*. **19**:1487-1491.

Nicholas, N.S., Zedaker S.M. and Eagar C. 1992 A comparison of overstory community structure in three southern Appalachian spruce-fir forests. *Bull. Torr. Bot. Club*. **119(3)**:316-332.

Nicholas, N.S. 1992 *Stand structure, growth and mortality in southern Appalachian spruce-fir*. Ph.D. dissertation, Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Nodvin, S.C., Van Miegroet, H., Lindberg, S.E., Nicholas, N.S. and Johnson, D.W. 1995 Acidic deposition, ecosystem processes and nitrogen deposition in a high elevation southern Appalachian watershed. *Water, Air, Soil Pollution*. **85**:1647-1652.

Olsson, U., Binkley, D. and Smith, F.W. 1997 Nitrogen supply, nitrogen use and production in and age sequence of lodgepole pine. *Forest Science*. **44**:454-457.

Oosting, H.J. and Billings, W.D. 1951 A comparison of virgin spruce-fir in the northern and southern Appalachian systems. *Ecology*. **32**:84-103.

Odum, E. 1969. The strategy of ecosystem development. *Science.* **164**:262-270.

Pauley, E.F. and Clebsch E.C.C. 1990 Patterns of *Abies fraseri* in a Great Smoky Mountains spruce-fir forest. *Bull. Torr. Bot. Club*. **117**:375-381.

Pyle, C. and Schafale, M.P. 1988 Land use history of three spruce-fir forest sites in southern Appalachia. *J. For. Hist*. **32**:4-21.

Ramseur G.S. 1960 The vascular flora of high mountain communities of the southern Appalachians. *Journal of the Mitchell Society*. 82-112.

Rose, A.K. and Nicholas, N.S. 2008 Coarse woody debris in a southern Appalachian spruce-fir forest of the Great Smoky Mountains National Park. *Natural Areas Journal*. **28(4)**: 342-355.

Skog, K. and Nicholson, G. 1998 Carbon cycling through wood products: The role of wood and paper products in carbon sequestration. *Forest Products Journal*. **48**:75-83.

Sorenson, C.D. Finkral, A.J. Kolb, T.E. and Huang, C.H. 2011.Short- and long-term effects of thinning and prescribed fire on carbon stocks in ponderosa pine stands in northern Arizona. *For. Ecol. Manage*. **261**:460-472.

Speers, C.F. 1958 The balsam wooly aphid in the southeast. *J. For*.

Smith G.F. and Nicholas, N.S. 2000 Size and age class distributions of Fraser fir following balsam wooly adelgid infestation. *Can. J. For. Res*. **30**:948-957.

Smith, G.F. 1997 *Southern Appalachian Fir and Fir-Spruce Forest Community Changes Following Balsam Wooly Adelgid Infestation*. M.S. Thesis, Department of Forestry, University of Tennessee, Knoxville Tennessee.

Tamm, C.O. 1953 Growth, yield and nutrition in carpets of a forest moss (*Hylocomium splendens*). *Meddelanden fran Statens Skogsforskningsinstitut*. **43**:1-140.

White, P.S., MacKenzie, M.D. and Busing, R.T. 1985 Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests. *Can. J. For. Res.* **15**:233-240.

Van Deusen, P. 2010 Carbon sequestration potential of forest land: Management for products and bioenergy *versus* preservation. *Biomass Bioenergy*. **34**:1687-1694.

Van Miegroet, H., Creed, I.F., Nicholas, N.S., Tarboton, D.G., Webster, K.L., Shubzda, J., Robinson, B., Smoot, J., Johnson, D.W., Lindberg, S.E., Lovett, G., Nodvin, S. and Moore, S. 2001 Is there synchronicity in N input and out fluxes at the Noland Divide Watershed, a small N-saturated forested catchment in the Great Smoky Mountains National Park. *The Scientific World*. 1(S2):480-492. (E-Journal).

Van Miegroet, H., Johnson, D.W. and Todd, D.E. 1993 Foliar response of red spruce saplings to fertilization with Ca and Mg in the Great Smoky Mountains National Park. *Can. J. For. Res*. **23**:89-95.

Van Miegroet, H., Moore, P.T., Tewksbury, C., and Nicholas, N.S. 2007 Carbon sources and sinks in high-elevation spruce-fir forests in the Southeastern US. *For. Ecol. Manage.* **238**:249-260.

Van Miegroet, H. 1995 Inorganic nitrogen determined by laboratory and field extractions of two forest soils. *Journal of the Soil Science Society of America*. **59**:549-553.
Weaver, G.T. 1972 *Dry matter and nutrient dynamics in red spruce-Fraser fir and yellow birch ecosystems in the balsam mountains, western North Carolina*. Ph.D. Dissertation. University of Tennessee, Knoxville TN.

Welch, N.T., Belmont J.M. and Randolph, J.C. 2007 Summer ground layer biomass and nutrient contribution to above ground litter in an Indiana temperate deciduous forest. *American Midland Naturalist*. **157**:11-26.

Wharton, E.H. and Griffith, D.M. 1993 Methods to estimate total forest biomass for extensive forest surveys in the northeastern U.S. Res. Pap. NE-681. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 52 pp.

White, P.S. MacKenzie, M.D. and Busing, R.T. 1985 Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests. *Can. J. For. Res*. **15**:233-240.

White, P.S. and Renfro, J. 1984 Vascular plants of southern Appalachian spruce-fir: annotated checklists arranged by geography, habitat, and growth form, pp. 235-246. In P.S. White (editor), *The southern Appalachian spruce-fir ecosystem: its biology and threats*. Research/Resources Management Report SER-71. Atlanta, GA: United States Department of the Interior, National Park Service, Southeast Region. 268 pp.

Whittaker, R.H. 1956 Vegetation of the Great Smoky Mountains. *Ecology*. **26**:1-80.

Whittaker, R.H. 1962 Net production relations of shrubs in the Great Smoky Mountains. *Ecology*. **43**:357-377.

Whittaker, R.H. 1966 Forest dimensions and production in the Great Smoky Mountains. *Ecology*. **47**:103-121.

Whitter, J.A. and Ragenovich, I.R. 1986 Regeneration of Fraser fir at Mt. Mitchell after depredations by the balsam woolly adelgid. *For. Sci.* **32**:585-594.

Wolfe, J.A. 1967 *Forest soil characteristics as influenced by vegetation and bedrock in the spruce-fir zone of the Great Smoky Mountains*. Ph.D. Dissertation, University of Tennessee, Knoxville, TN.

Yarie, J. 1980 The role of understory vegetation in the nutrient cycle of forested ecosystems in the mountain hemlock biogeoclimatic zone. *Ecology*. **61**:1498-1514.

Zedaker, S.M. and N.S. Nicholas. 1990 Quality Assurance and Methods Manual for Forest Site Classification and Field Measurements. EPA/600/3-90/082. U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, OR.

Table 1.1: Habitat, growth habit, taxon and survey code for species found during our vegetation surveys of the Noland Divide Watershed of Great Smoky Mountain National Park

Habitat	Growth habit	Taxon	Code
Forest	Woody	*Abies fraseri*	ABSFRA
Forest	Woody	*Acer spicatum*	ACRSPC
Forest	Woody	*Amalanchier laevis*	AMLLVS
Forest	Woody	*Betula alleghaniensis*	BTLALL
Forest	Woody	*Cornus alternifolia*	CRNALT
Forest	Woody	*Hydrangea arborescens*	HYDARB
Forest	Woody	*Picea rubens*	PICRBN
Forest	Woody	*Prunus pensylvanica*	PRNPNS
Forest	Woody	*Rhododendron catawbiense*	RHDCTW
Forest	Woody	*Rhododendron maximum*	RHDMXM
Forest	Woody	*Ribes rotundifolia*	RBSRTN
Forest	Woody	*Rubus canadensis*	RBSCND
Forest	Woody	*Rubus idaeus*	RBSIDS
Forest	Woody	*Sambucus pubens*	SMBPBN
Forest	Woody	*Sorbus americana*	SRBAMR
Forest	Woody	*Vaccinium corymbosum*	VCCCRY
Forest	Woody	*Vaccinium erythrocarpum*	VCCERY
Forest	Woody	*Viburnum alnifolium*	VBRALN
Forest	Herbaceous	*Aconitum uncinatum*	ACNUNC
Forest	Herbaceous	*Arisaema triphyllum*	ARSTRP
Forest	Herbaceous	*Aster acuminatus*	ASTACM
Forest	Herbaceous	*Aster divaricatus*	ASTDVR
Forest	Herbaceous	*Chelone lyoni*	CHLLYN
Forest	Herbaceous	*Cimicifuga americana*	CMCAMR
Forest	Herbaceous	*Clintonia borealis*	CLNBRL
Forest	Herbaceous	*Dryopteris campyloptera*	DRYCMP
Forest	Herbaceous	*Eupatorium rugosum*	EUPRGS
Forest	Herbaceous	*Galium triflorum*	GALTRF
Forest	Herbaceous	*Houstonia serpyllifolia*	HSTSRP
Forest	Herbaceous	*Impatiens pallida*	IMPPLL
Forest	Herbaceous	*Laportea canadensis*	LPRCND
Forest	Herbaceous	*Lycopodium lucidulum*	LYCLCD

Table 1.1 continued. Habitat, growth habit, taxon and survey code for species found during our vegetation surveys of the Noland Divide Watershed of Great Smoky Mountain National Park

Habitat	Growth habit	Taxon	Code
Forest	Herbaceous	*Lycopodium selago*	LYCSLG
Forest	Herbaceous	*Monarda didyma*	MNRDDY
Forest	Herbaceous	*Oxalis acetosella*	OXLACT
Forest	Herbaceous	*Rudbeckia laciniata*	RDBLCN
Forest	Herbaceous	*Solidago glomerata*	SLDGLO
Forest	Herbaceous	*Tiarella cordifolia*	TRLCRD
Forest	Herbaceous	*Trillium erectum*	TRLERC
Forest	Herbaceous	*Trillium undulatum*	TRLUND
Forest	Herbaceous	*Viola blanda*	VIOBLN
Roadside	Herbaceous	*Prunella vulgaris*	PRNVLG
Roadside	Herbaceous	*Senecio smallii*	SNCSML

Table 1.2: Rare or regionally rare vascular and nonvascular plant species associated with this community

Taxon
Betula papyrifera var. *cordifolia*
Cardamine clematitis
Glyceria nubigena
Phegopteris connectilis
Poa palustris
Rhododendron vaseyi
Stachys clingmanii
Streptopus amplexifolius
Botrychium oneidense
Calamagrostis canadensis
Carex projecta
Carex ruthii
Geum geniculatum
Prenanthes roanensis
Rhododendron carolinianum
Rugelia nudicaulis
Stellaria coreii
Bazzania nudicaulis
Brachydontium trichodes
Leptodontium excelsum
Metzgeria temperate
Nardia scalaris
Plagiochila corniculata
Sphenolobopsis pearsonii
Gymnoderma lineare

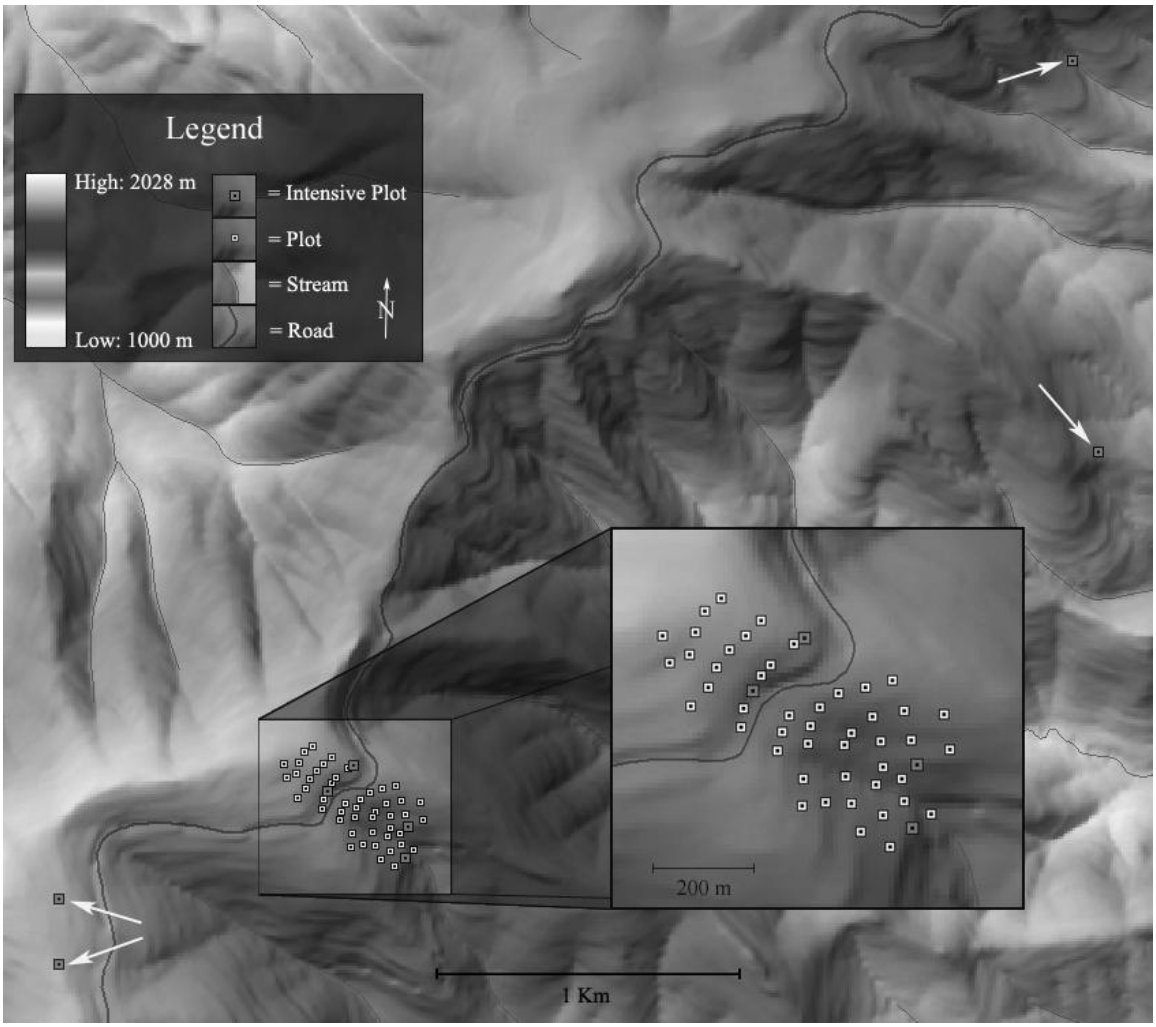

Figure 1.1. Location map of the Noland Divide Watershed and the 4 NAPAP plots in the Great Smoky Mountains National Park

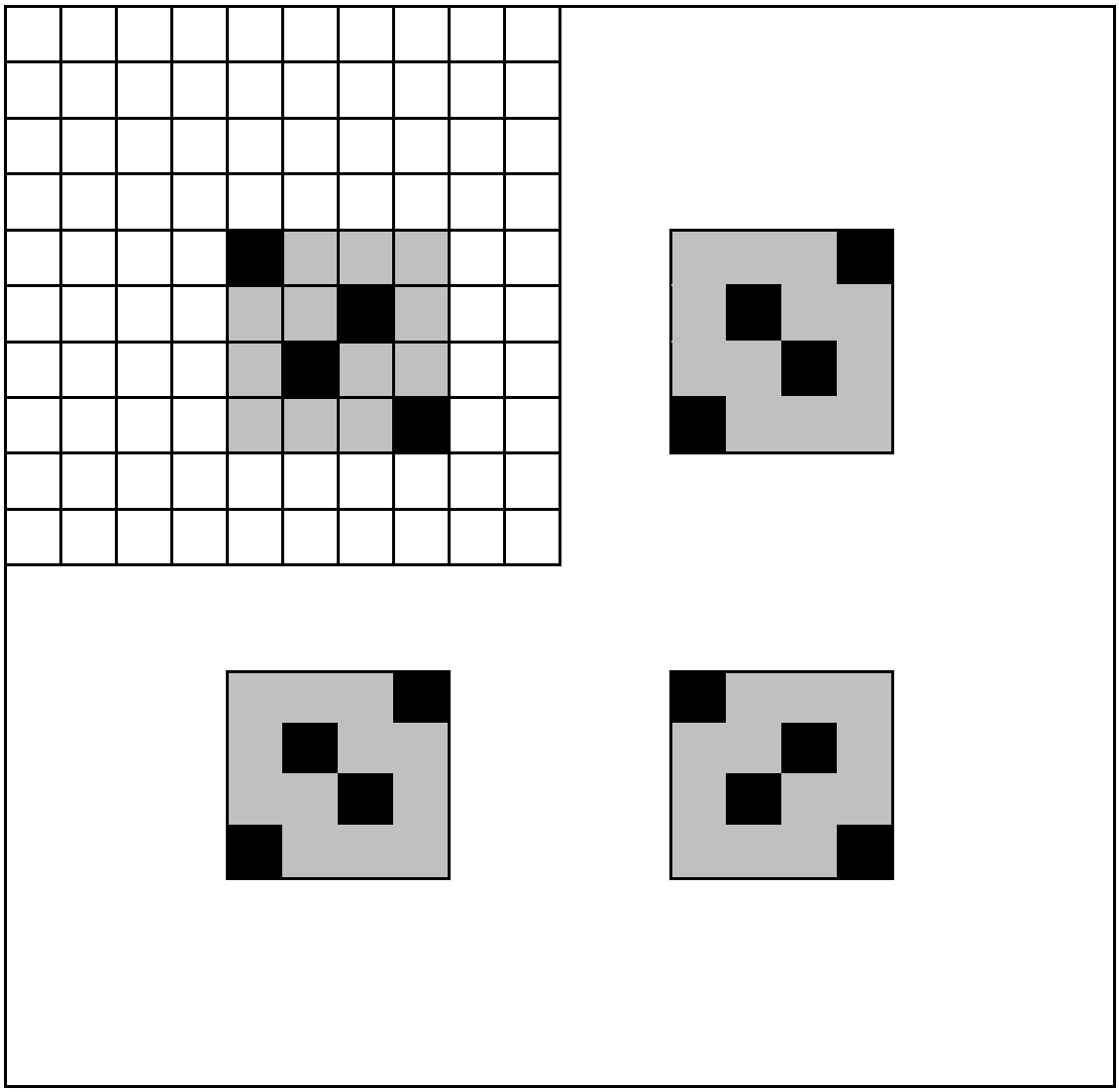

Figure 1.2. Schematic of a 20 x 20 m permanent plot with 4 x 4 m subplots (gray squares) for shrub and regeneration survey and 1 x 1 m sub subplots (black squares) for herbaceous and moss survey.

CHAPTER 2

EXAMINATION OF FOREST RECOVERY SCENARIOS IN A SOUTHERN APPALACHIAN *PICEA-ABIES* FOREST [1,2]

ABSTRACT

This study contrasts various forest recovery scenarios in a *Picea rubens* Sarg. *Abies fraseri* (Pursh.) Poir. forest 20 years after the onset of *Adelges picea* Ratz. and tests them against a 10-year data set from an intensive catchment study in the Great Smoky Mountains National Park. Standing live biomass, increment, ingrowth, mortality and net change in live biomass are analyzed by species and elevation based on inventory data gathered in 1993, 1998 and 2003 at a network of 50 permanent plots stratified along nine elevation bands (1700-1900 m). Total standing live biomass at the study site remained stable between inventories (~260 Mg ha^{-1}). *Betula* showed little, if any, response to the recent set of catastrophic overstory disturbances. Biomass and increment of *Picea* increased somewhat; but overall, there is limited evidence that *Picea* is expanding. *Abies* showed significant increases in standing live biomass (from 3.3 to 12.7 Mg ha^{-1}), increment (380 to 850 kg ha^{-1} yr^{-1}) and ingrowth (320 to 610 kg ha^{-1} yr^{-1}) over time. While some scenarios have not fully played out yet, at this time, total elimination of *Abies* is not indicated and there is considerable evidence to support the stable *Picea* and *Abies* scenario.

---

[1] This chapter appeared in the journal Forestry as: Moore, P.T., H. Van Miegroet and N.S. Nicholas. 2008. Examination of forest recovery scenarios in a southern Appalachian Picea-Abies forest. Forestry 81(2): 183-194

[2] Coauthored by Patrick T. Moore, Helga Van Miegroet and Niki S. Nicholas

INTRODUCTION

Red spruce (*Picea rubens* Sarg.) Fraser fir [*Abies fraseri* (Pursh) Poir.] forests of the central and southern Appalachian Mountains exist today as a series of high-elevation vegetation "islands" located above 1500 meters in elevation between 34 and 41 degrees north latitude (White and Cogbill, 1992), 74% of which are within the boundaries of Great Smoky Mountain National Park (GSMNP, Dull *et al.*, 1988). They are remnants of the original post-glacial range, representing the lower elevation limits of their high-elevation ecological niche (Delcourt and Delcourt, 1988) and are highly disturbed due to anthropogenic stressors as well as recent widespread infestations by the balsam woolly adelgid (BWA, *Adelges piceae* Ratz.). These recent disturbances have combined to form a sensitive ecosystem with an unknown future. Many researchers have suggested that forest dynamics may permanently change due to these recent disturbances (Witter and Ragenovich, 1986; Busing and Clebsch, 1987; McLaughlin *et al.*, 1987; Witter, 1988; Dale *et al.*, 1991; Nicholas *et al*., 1992).

Many disturbance agents are acting on this forest. Windthrow has been responsible for significant mortality of overstory trees and the creation of larger overstory gaps in southern Appalachian *Picea-Abies* forests during strong windstorms (White and Cogbill, 1992). Within the past 25 years, for example, three extremely large storms, hurricanes Hugo in 1989, Opal in 1995 (Smith, 1997), and Ivan in 2004 have swept through the area causing significant tree mortality via windthrow. Ice storms (Nicholas and Zedaker, 1989) have also caused significant mortality of overstory trees. As a consequence of these disturbances and in concert with steep slopes and abundant precipitation, the landscape is susceptible to landslides (White and Cogbill, 1992). While such disturbance is rare, it is

nevertheless highly destructive. Logging has not been significant due to the historic inaccessibility (steep, high-elevation slopes) and current land management status (National Park, Pyle and Schafale, 1988). Fires are rare in these forests due to year-round moisture and wet climate and lush understory vegetation (White and Cogbill, 1992).

More recently, additional anthropogenic stressors are impacting these forests including infestations of exotic pests (Johnson *et al.*, 1991; Nicholas, 1992) and air pollution (Johnson and Lindberg, 1992). The invasion of the BWA has caused widespread mortality in even the most protected areas of the range of *Abies*. BWA feeds at the base of needles and at fissures in *Abies* bark, where its saliva alters growth patterns within stems, killing trees 3-9 years after infestation (Amman and Speers, 1965). This exotic pest was first discovered in the southern Appalachians in 1957 (Speers, 1958), GSMNP in 1963 (Ciesla *et al*., 1963). Since then, BWA has invaded the entire range of *Abies* and has caused extensive mortality of this species (Johnson *et al*., 1991), killing over 90% of stems and virtually every individual fir tree >10cm DBH (Smith and Nicholas, 2000). Though regeneration of *Abies* is occurring, it is patchy across the landscape (Smith and Nicholas, 2000). The responses of the other woody species in this forest overstory as well as the role of BWA on the future of this forest are still unknown.

The southern Appalachian *Picea-Abies* forest consists of three main overstory species as well as several minor hardwood species. Elevation is the major driver of ecosystem composition in this forest (Whittaker, 1956). Prior to the outbreak of the BWA infestation, *Picea* dominated slopes from 1500-1800 m, transitioning to an *Abies*-dominated system at the higher ridges and peaks above 1800 m. Yellow birch (*Betula alleghaniensis* Britt.) is a smaller component of the overstory at lower elevations along

with the shallow rooted (Burns and Honkala, 1990a) and windthrow-prone *Picea*. Other hardwoods, including mountain maple (*Acer spicatum* Lam.), striped maple (*Acer pensylvanicum* L.), serviceberry [*Amelanchier laevis* (Weigand) Ahles.], pin cherry (*Prunus pensylvanica* L. f.) and mountain-ash (*Sorbus americana* Marshall) are minor components of the overstory and understory across elevations, with *Sorbus* extending into the highest elevations while the others are minor components at lower and mid elevations.

Prior to the BWA, southern Appalachian *Picea-Abies* forests held considerable biomass in the form of live standing trees (200-310 Mg ha^{-1}, Whittaker, 1966). For years after the onset of the BWA, the mortality of insect-killed *Abies* trees, as well as the subsequent windfall of many large *Picea* trees due to exposure in a newly opened canopy (Busing, 2004), overwhelmed the ability of the existing trees (increment) and new trees (ingrowth) to compensate, causing the overstory biomass pool to shrink. The ability of this forest to once again hold large amounts of biomass in the overstory is a critical step in the post-BWA recovery of this system.

The future of this ecosystem is uncertain and many scenarios have been suggested ranging from a full forest recovery of *Abies* to the extinction of the species. Witter (1988) predicted that *Abies* would persist to some degree in the overstory based solely on the fact that trees currently survive to cone-bearing age, but said little regarding the stand structure of the *Abies* component of future *Picea-Abies* forests. McLaughlin and coworkers (McLaughlin *et al.*, 1987; McLaughlin and Tjoelker, 1992) predicted that the effects of acidic precipitation on soil processes and nutrient availability would lead to slower growth rates of overstory tree species. Subsequent increased susceptibility of

Picea and *Abies* to pathogens and mortality is possibly the cause of regional *Picea* decline observed in the 1980s (McLaughlin *et al.*, 1987). It has also been suggested that *Abies* may evolve resistance to the effects of the BWA (Witter and Ragenovich, 1986) and that the forest may return to pre-BWA conditions.

Dale *et al.* (1991) used Leslie matrices to forecast four possible scenarios of *Abies* response to the BWA including the complete extinction of *Abies* under repeated attacks of the BWA, complete recovery of *Abies* after the BWA dies off, stable coexistence of BWA and *Abies*, and finally persistent oscillations in space and time between the populations of BWA and *Abies*. The predictions of Dale *et al.* (1991) did not incorporate information regarding the indirect response of other important forest species, *Picea*, *Betula*, and other hardwoods, to the BWA-induced *Abies* mortality. Nicholas *et al.* (1992) stressed that not enough is known to adequately predict the future of *Abies* in the overstory and that researchers will learn much by the second, imminent wave of BWA-induced mortality.

Busing and Clebsch (1987) used a FORET gap model to predict several possible outcomes based on the combined impacts of BWA and acid deposition. If BWA negatively affected *Abies* while acid deposition negatively affected *Picea* (McLaughlin *et al.*, 1987), a decline in both species as well as the potential for the release of *Betula* may occur. This scenario may also be supported by the release of other minor understory hardwood species into the overstory. However, if BWA causes significant damage to *Abies* populations without the negative effect of acid deposition on *Picea*, then *Picea* may increase its dominance at higher elevations.

Based on the above literature, future *Picea-Abies* forests may comply with one of several forest change scenarios:

1) Expansion of *Betula*
2) Introduction of other hardwoods as overstory species
3) Increased dominance of *Picea* at higher elevations
4) Elimination of *Abies*
5) Stabilizing populations of *Picea* and *Abies* over time

To date, reliable data on forest dynamics of southern Appalachian *Picea-Abies* forests has been largely lacking (Peart *et al.*, 1992) for a variety of reasons, i.e. unrepresentative sampling design, small sample sizes, lack of permanently marked plots and trees, too brief a monitoring period and the use of subjective measurements. Reliable data are difficult to collect because vegetation characteristics and composition can vary greatly from peak to peak and even between stands on the same peak.

While many scenarios have been advanced in recent years regarding the future of this forest (Witter and Ragenovich, 1986; Busing and Clebsch, 1987; McLaughlin *et al.*, 1987; Witter, 1988; Dale *et al*., 1991; Nicholas *et al.*, 1992), an analysis of the viability of these scenarios has not been performed. The objective of this study is to analyze these individual forest change scenarios (expansion of birch and other hardwoods, increased dominance of *Picea*, elimination of *Abies*, and the stabilization of *Picea* and *Abies*) proposed by others and determine whether current forest dynamics in a forested watershed within the GSMNP support any of these projections.

This research examined current biomass pools of a southern Appalachian *Picea-Abies* forest, as well as changes over a 10-year period in order to determine the present status of

these forests. We then examined the nature of recent biomass changes in terms of increment, ingrowth, mortality, and overall mass balance and assess if there is evidence to support any of the scenarios relative to the major overstory species. Biomass dynamics (pool size, changes in increment, ingrowth, mortality and overall balance) over a 10-year period were used to examine significant shifts in each species over that time period. We used changes in standing live biomass pools and as well as changes in increment, ingrowth, mortality and overall mass balance as indicators of overstory change because this method is able to differentiate between the individual components of forest growth. We used dynamics in one watershed to understand some of the processes that may be occurring at larger scales.

MATERIAL AND METHODS

Because 74% of existing *Picea-Abies* forest land area in the southern US exists within GSMNP, conducting this research within the park is appropriate. This study was performed at the Noland Divide Watershed (NDW, 35°34'N, 83°29'W) a 17.4 ha, high-elevation catchment within GSMNP, because of the broad elevation gradient (1700-1910m) and resulting variability in overstory species composition, thought to represent much of the range of forest conditions occurring within the park. Pre-existing plot infrastructure, as well as access to previously collected data, and similar parent material allowed analysis of forest dynamics over a 10-year period while controlling for some confounding factors (parent material, aspect, and climate). The study area has not been impacted by logging or fire (Pyle *et al.*, 1988), but has been severely impacted by the BWA (Barker *et al.*, 2002; Pauley and Clebsch, 1990). The soils are mainly Inceptisols,

occasionally with spodic characteristics (McCracken *et al.,* 1962; Van Miegroet *et al.,* 1993), and are underlain by Thunderhead Sandstone (King *et al.,* 1968). They are generally shallow, (<50 cm depth to bedrock) and have a silt loam to sandy loam texture (Van Miegroet *et al.,* 2007). Precipitation is >200 cm annually and is distributed evenly throughout the year (Johnson and Lindberg, 1992). Ten percent of annual precipitation falls as snow and covers the ground for an average of 50 days per year (Johnson *et al.,* 1991). Mean air temperatures range from -2°C in February to 17°C in August with a frost-free period from May through September (Johnson *et al.,* 1991; Shanks, 1954).

In this study, we used a repeated overstory inventory of 50 20 x 20 m permanent plots in and around this high elevation catchment placed systematically along nine elevation bands (1700, 1725, 1755, 1785, 1800, 1835, 1865, 1890 m, Figure 2.1). Overstory tree inventories were conducted at the NDW in 1993, 1998, and 2003, using protocols described by Zedaker and Nicholas (1990). In 1993, all trees ≥ 5 cm diameter at breast height (DBH, 1.37m) were measured and tagged with a permanent and unique ID tag. Species and DBH of each live and dead overstory tree were recorded. In 1998 and 2003, ingrowth was tagged as they entered the stand. Live trees that had fallen over since the last inventory were considered windthrow.

Biomass of foliage, live branches, dead branches, bole bark, and bole wood of each tree were calculated from DBH using allometric equations developed for *Picea*, *Abies* and *Betula* by Nicholas (1992). Biomass of other overstory species and shrubs were estimated with the predictive equations of Weaver (1972).

Standing live biomass at each time period was estimated by summing individual tree biomass values across individual plots. In order to investigate dynamics between time

periods, we divided annualized change in live overstory biomass into three components; live increment, ingrowth, and mortality. Increment was defined as the positive difference in individual tree biomass between inventory periods, ingrowth was defined as the mass of a tree that grew to >5cm DBH since the previous inventory, and mortality was defined as the whole tree biomass of a tree that died since the previous inventory. Summing plot-level increment, ingrowth, and mortality provided a mass balance for each plot and a picture of the biomass dynamics across the entire watershed. A positive mass balance corresponded with a biomass gain for the period, while a negative mass balance indicated that the site had lost biomass during the period.

Differences in standing live biomass between 1993 and 2003 were determined for each of the three main species, *Abies*, *Betula* and *Picea* as well as the group of other hardwoods, using a series of repeated measures ANOVAs (SAS Institute, 2002). Analyses were performed across the watershed as well as by elevation band to determine changes at each elevation. Due to the fact that there was only one plot in the highest elevation band (1910 m), making analysis of this band impossible, data from that band were pooled with the data from the next highest band (1890 m), for a total of eight elevation bands. We were interested in how biomass dynamics for the entire overstory and individual overstory species changed over time, rather than how species composition changed across the elevation gradient. Temporal trends were tested with simple one-way repeated ANOVAs, using 1993 and 2003 biomass values, with no test for interactions because they were not germane to our study question and the effect of elevation on species composition and standing biomass has already been documented (Whittaker, 1956). With eight elevation bands, and four species groups, the analysis of standing live

biomass required more than thirty separate analyses. Statistical analysis and model construction was adapted from Cody and Smith (1997). Change in increment, ingrowth, mortality, and overall mass balance was determined by species during the 1993-1998 and 1998-2003 time periods using a repeated measures ANOVA (SAS Institute, 2002), similar to the method used for standing live biomass. Significant change in ingrowth, increment, mortality and overall balance from the first time period to the second time period was determined for each species group at each elevation band. Differences between the means were tested for significance by Duncan's mean comparison test. Significant changes over time will be used to determine whether evidence exists to support the postulated scenarios about declines and/or increases in the major overstory species.

RESULTS

Overall, average standing live biomass for the NDW did not significantly change over the 10-year period from 267 Mg ha^{-1} in 1993, to 260 Mg ha^{-1} in 2003 (Table 2.1). When analyzed individually, however, all three main species changed significantly over this time period; *Abies* ($P<0.0001$) from 3.3 Mg ha^{-1} to 12.7 Mg ha^{-1}, *Betula* ($P<0.0013$) from 56 Mg ha^{-1} to 61 Mg ha^{-1}, and *Picea* ($P<0.0344$) from 206 Mg ha^{-1} to 184 Mg ha^{-1}.

Standing live biomass across a 10-year period increased for *Abies* across four of the eight elevation bands (Table 2.1), not only at the high elevations but at middle and low elevations as well. Significant increases ranged from 156% to 631%. No significant changes in *Picea* and *Betula* standing live biomass occurred at any elevation over a 10-year period. Standing live biomass of "other hardwood species" did not increase from

1993 to 2003 at any elevation band. Density and basal area information are presented in Table 2.1.

Across the watershed and across species, increment, the growth of existing trees, increased significantly ($P<0.0001$) from 4,100 to 5,500 kg ha^{-1} yr^{-1} from the 1993-1998 to the 1998-2003 time periods (Table 2.2). Across all elevations, increase of *Abies* ($P<0.0001$, 380 to 850 kg ha^{-1} yr^{-1}) and *Picea* ($P<0.0022$, 2,800 to 3,700 kg ha^{-1} yr^{-1}) increased significantly, while *Betula* remained unchanged. The combined increment of the three main species increased significantly at one low and two high elevation bands. When analyzed by elevation band, overstory species responded differently, but no specific elevation trend consistently stood out. Increment of *Abies* increased by 75%-190% over the 10-year period at three elevation bands in the middle and upper watershed. Increment of *Picea* significantly increased at one lower elevation band by 36%. Increment of *Betula* showed no significant change in increment from the first to the second inventory period at any elevation band.

Ingrowth, the growth of new trees, also increased significantly ($p>0.0001$) across the watershed and across species, from 450 to 840 kg ha^{-1} yr^{-1} between the two inventory periods (Table 2.2). Across elevations, ingrowth of *Abies* increased significantly ($P<0.0001$) from 320 to 610 kg ha^{-1} yr^{-1}. Ingrowth of *Picea* also increased significantly ($P<0.0005$) from 100 to 180 kg ha^{-1} yr^{-1}, while ingrowth rates of *Betula* (28 to 44 kg ha^{-1} yr^{-1}) remained unchanged. The combined ingrowth of the three main species increased significantly at two middle and two high elevation bands. When analyzed by elevation band, the rate of *Abies* ingrowth increased significantly between the two time periods at four elevation bands in the lower, middle and upper watershed. Significant increases

ranged from 92% to 347%. *Betula* ingrowth rates significantly increased at one middle elevation band by 743%. *Picea* ingrowth increased significantly at two elevation bands in the middle and upper watershed by 80% and 144%, respectively.

Overall, mortality was similar for the 1993-1998 time period (5,900 kg ha^{-1} yr^{-1}) and the 1998-2003 time period (5,700 kg ha^{-1} yr^{-1}). Across elevations, mortality of *Abies* increased significantly ($P<0.0285$) from 60 kg ha^{-1} yr^{-1} to 220 kg ha^{-1} yr^{-1} while *Betula* and *Picea* mortality remained constant. Inventory data and field observations of downed wood indicated that windthrow was responsible for the virtually all *Picea* mortality.

The overall stand biomass balance for the overstory, consisting of increment, ingrowth and mortality for each species, reversed from a negative value in the 1993-1998 time period (-1,350 kg ha^{-1} yr^{-1}) to a positive value in the 1998-2003 time period (610 kg ha^{-1} yr^{-1}) across the range of elevations and species, though this change was not statistically significant. *Abies* showed a significant increase in mass balance ($P<0.0001$) from 640 to 1,240 kg ha^{-1} yr^{-1} across all elevations, as well as a significant positive change in mass balance in four middle and lower elevation bands (121% to 262%). *Betula* had small rates of ingrowth, moderate rates of increment, and low rates of mortality of existing trees, and these rates showed no significant increase between the two time periods. In *Picea*, higher elevation bands showed a decline in biomass during the first time period while the lower elevation bands showed a net increase. The opposite was true during the second time period where high elevations corresponded with positive mass balances and low elevations corresponded with negative mass balances.

Variability was very large in these analyses, and coefficients of variation were often over 100%. Thus, while trends can be observed, it is obvious that results are not uniform

across this watershed. Nevertheless, significant differences between time periods for biomass pools and fluxes existed, despite the large degree of variability. These differences can be interpreted as general temporal trends within this watershed.

DISCUSSION

The methods and data presented here provide a framework for testing specific scenarios against a current 10-year data set. In general, there is no evidence that this forest is declining. In fact, many components of this forest are aggrading in terms of standing live biomass and growth, especially *Abies* and at low, middle and high elevation bands. Overstory standing biomass estimates were similar to other post-adelgid research in the southern Appalachians (260 Mg ha^{-1} in this study compared to 258 Mg ha^{-1} measured in the mid-1980s at the nearby Spruce "Becking" Site and 265 and 308 Mg ha^{-1} at the two nearby Smokies "Tower" sites, Johnson and Lindberg, 1992).

Betula Expansion

There is no evidence that *Betula* is becoming more dominant or expanding into higher elevations. There is considerable standing live biomass, especially at the lower elevations, however, higher elevations continue to carry little standing live biomass of *Betula*. Also, there has been no increase of standing live *Betula* at any particular high elevation band. While standing live biomass increased significantly across the entire watershed, this accounted for only a 10% increase. While there is considerable increment of existing trees, this does not result in an increase in net biomass balance over the measurement period. Ingrowth of *Betula* was generally quite small, and did not significantly increase over time. The magnitude of *Betula* ingrowth does not seem

sufficient to dramatically alter future stand composition, because *Betula* ingrowth is dwarfed by the magnitude of *Abies* ingrowth across elevations. The capture of new spaces in the overstory would be a critical step in the expansion of this species, but that is not occurring in this watershed.

Though more shade tolerant than other *Betula* species in North America, *Betula allegheniensis* is reported to be a fast growing tree species and capable of capturing moderately sized gaps in the overstory (Burns and Honkala, 1990b). Relative to the shallow-rooted *Picea* and slightly deeper-rooted *Abies*, *Betula* has a more extensive and deeper root system (White and Cogbill, 1992). This would decrease the likelihood of this species succumbing to windthrow unlike the other major overstory species. We are suggesting that while *Betula* may acquire limited additional spaces in the overstory at mid elevations (as exemplified by the 1785-m elevation band, Table 2.2), we find no evidence for the expansion of *Betula*, especially at the higher elevations.

Other Hardwoods

A set of other hardwood species including *Acer spicatum*, *Acer pensylvanicum*, *Amelanchier laevis*, *Prunus pensylvanica*, and *Sorbus americana* may, under some conditions, be able to compete for overstory positions (Burns and Honkala, 1990b; Eyre, 1980). Growth characteristics of these species suggest that they may become more important in terms of overstory live biomass. Over our 10-year study period, these hardwood species did not significantly change standing biomass at any elevation band. None of these species captured canopy openings created by BWA. In addition, though these species may be more competitive under other edaphic conditions, in the *Picea*-

Abies system they likely do not have the growth form necessary to successfully compete with *Picea* and *Abies* trees that have faster growth rates and are taller. A shift in canopy species composition might have resulted if both *Picea* and *Abies* were experiencing significant and repeated disturbance (Busing and Clebsch, 1987). However, there is little evidence to suggest that the disturbances acting on *Picea* and *Abies* will be repeated and significant enough to cause long-term forest change. Due to the complete lack of change in standing live biomass of "other" tree species, robust presence of *Abies* in the understory, apparent resiliency of and strong increment of the major overstory species, there is no evidence to support the *Other Hardwoods* scenario.

Picea Dominance

The *Picea* dominance scenario suggested the possibility of *Picea* responding to an open canopy by becoming more dominant, especially at high elevations where *Abies* was more prevalent pre-BWA. In our analysis, this scenario would manifest itself by large amounts and increasing standing live biomass, a positive change in increment and ingrowth from the first to the second inventory period, as well as an overall positive mass balance for the overstory. *Picea* did not meet all of these criteria, but met some. *Picea* accounted for the majority of standing live biomass; however, unlike *Abies*, this standing stock did not significantly increase over the 10-year period from 1993-2003. The majority of increment was also dominated by *Picea*, but increment significantly increased at only one low elevation band between the two time periods. Ingrowth of *Picea* increased at two elevation bands but was considerably less than that of *Abies*, even at lower elevations.

Large amounts of *Picea* died during our survey period. *Picea* accounted for 95% and 89% of all mortality in the two time periods; however, due to the large between-plot variability in mortality, likely driven by the heterogeneity in forest structure, no statistically significant differences in mortality between time periods emerged for any of the species at any elevation. It appears that extensive mortality of *Picea* followed that of BWA-induced *Abies* mortality by 15-20 years. Though some degree of windthrow mortality was anticipated and observed in several studies (Hollingsworth and Hain, 1991; Peart *et al.*, 1992; Busing and Pauley, 1994; Busing, 2004), the magnitude of this mortality in our study area was unexpected. Scenarios of increased *Picea* dominance were based partially on the expectation that the *Picea* overstory would sustain little mortality via windthrow after the initial catastrophic *Abies* mortality. This did not occur, however, and the biomass and growth dynamics of both *Picea* and *Abies* have been considerably reduced.

Windthrow-induced *Picea* mortality appears to have moved from higher elevations to lower elevations. This mortality started first in the higher elevations with lower *Picea* dominance (fewer, more spread out *Picea* trees) during the 1993-1998 time period and was observed later at the lower elevations with high *Picea* dominance (stands of more dense *Picea* trees) during the 1998-2003 time period. In contrast, the wave of BWA-induced *Abies* mortality began at the lower elevations of the *Abies* population and moved up to the mountaintops (White and Cogbill, 1992). Because the *Picea* windthrow mortality did not follow the same spatio-temporal pattern as the adelgid mortality, we are suggesting that the large amount of *Picea* mortality is a function of canopy openness and exposure to winds and elements, rather than a function of time since BWA disturbance.

Mortality and the overall mass balance at the lowest elevation band seemed to emulate processes occurring at the highest elevations with higher levels of mortality from 1993-1998 and lower levels of mortality from 1998-2003. However, the four plots in this band showed some of the highest data variability. One particular low elevation plot (C1700) lost over 70 % of its standing live biomass between the 1993-1998 surveys due to a very large multi-tree windthrow event. The timing of this event coincided with the large amount of individual *Picea* stem windthrow occurring in higher elevations. It is hypothesized that C1700's location along a ridge position made it more vulnerable to a large windthrow event and may explain its temporal resemblance to the higher elevation bands. Others have found that *Picea* on exposed ridges are more susceptible to mortality (Busing and Pauley, 1994). The lowest band displayed the type of heterogeneity in forest structure that is very typical of this forest type.

Despite considerable windthrow, *Picea* is still holding considerable biomass in the overstory and is contributing the majority of increment. *Picea* shows some significant increases in increment and ingrowth. However, it is not apparent that *Picea* is taking over many overstory positions previously held by *Abies*. *Picea* will remain a considerable component of this forest overstory, but there is only limited evidence to support the *Picea* dominance scenario from above.

Abies Elimination

There is no evidence to support the elimination of *Abies* as suggested by Smith (1997). While some aspects of the future of *Abies* are unknown, such as future interactions of *Abies* and the BWA, all evidence suggests that, in general, *Abies* is

currently making a rapid recovery. *Abies* is again becoming a substantial part of the forest overstory in terms of standing live biomass. This species is making significant gains in biomass acquisition over time and *Abies* seedlings are dominating ingrowth at all elevations, even surpassing those by *Picea* at the lower elevations. Relatively large (several over 25 cm DBH) *Abies* trees are currently producing cones, though viability rates of those seeds may be significantly less than normal (Nicholas *et al.*, 1992). With the adequate regeneration we have observed, we have no direct evidence to support the *Abies* elimination scenario from above.

Stable Picea-Abies

Two important factors influencing the future of *Abies* are the nature and timing of the next, imminent wave of BWA-induced mortality. The more time passes before the BWA returns, the more time this recovering forest has to return to pre-BWA conditions. The nature of the next wave of BWA-induced mortality (i.e. number and size of trees killed) will tell us much about the long-term prognosis of this host-parasite relationship. Frequent and severe *Abies* mortality events will signal a dramatic departure of this forest type from pre-BWA conditions, while infrequent and mild mortality events may yield a forest that is quite similar to pre-BWA forests with stable populations of *Picea* and *Abies*.

Across the watershed, standing live biomass of overstory trees is no longer in decline. Between 1993 and 2003, the forest has evolved from losing biomass each year in the 1993-1998 time period to a forest that is positively accruing biomass in the 1998-2003 time period. Standing live biomass values are similar to measurements taken pre-BWA (200-310 Mg ha^{-1}, Whittaker, 1966), though there is likely a difference in the diameters

of the trees where this biomass is stored. The recovery of *Abies* is mainly responsible for this turnaround. Many large *Picea* on the edges of overstory gaps, the most susceptible to windthrow, have fallen and the overall mass balance is expected to become increasingly positive in coming years due to the lack of additional *Picea* mortality. Both *Picea* and *Abies* have asserted themselves in the mid-story by producing abundant ingrowth that is appearing in the smaller size classes, also indicated by higher tree density in the 1998-2003 time period. Our biomass and growth trends support a recovery of *Abies* while *Picea* remains a solid component of the overstory. These data indicate a stabilizing relationship between the two overstory species and support the stable *Picea*-*Abies* scenario.

Observations over 10 years from 50 plots in and around a catchment of the GSMNP do not support many of the scenarios that have been suggested in the literature about the future of this forest. Though this high-elevation forest has possibly not seen the last of the exotic BWA; there is little, if any, direct evidence that the initial wave of adelgid-induced mortality will have recurring catastrophic impact on this forest type. Under current conditions, neither *Betula* nor any of the other hardwood species seem poised to take a more dominant role in the overstory of this forested watershed. *Picea* will remain the dominant species at lower elevations, but will maintain a relatively low density in the higher elevations due to the prolific ingrowth of the next generation of *Abies* trees. A wave of windthrow mortality has swept through the standing *Picea* trees here, but is unlikely to cause further large-scale damage in the near future due to the fact that the largest and most wind-prone stems have already fallen. There is no evidence to support the possible extinction of *Abies*, only reason to suspect a slightly modified role in the

forest overstory. *Abies* is now doing quite well across all elevations and can be expected to make a consistent recovery until the next wave of BWA induced mortality. In spite of its limited inference space, valuable insights can be gleaned from the study of this Southern Appalachian forest.

LITERATURE CITED

Amman, G.D. and Speers, C.F. 1965 Balsam woolly aphid in the southern Appalachians. *Journal of Forestry*. **63**:18-20.

Barker, M., Van Miegroet, H., Nicholas, N.S. and Creed, I.F. 2002 Variation in overstory nitrogen uptake in a small, high-elevation southern Appalachian spruce-fir watershed. *Can. J. For. Res.* **32**:1741-1752.

Burns, R.M. and Honkala, B.H., tech. coords. 1990a *Silvics of North America: vol. 1, conifers*. Agricultural Handbook 654 Washington, DC: U.S. Department of Agriculture, Forest Service. 675 p.

Burns, R.M. and Honkala, B.H., tech. coords. 1990b *Silvics of North America: vol. 2, hardwoods*. Agricultural Handbook 654 Washington, DC: U.S. Department of Agriculture, Forest Service. 877 p.

Busing, R.T. and Clebsch, E.E.C. 1987 Application of a spruce-fir canopy model. *For. Ecol. Manage*. **20**:151-169.

Busing, R.T. and Pauley, E.F. 1994 Mortality trends in a southern Appalachian red spruce population. *For. Ecol. Manage*. **64**: 41-45.

Busing, R.T. 2004 Red spruce dynamics in an old southern Appalachian forest. *J. Torr. Bot. Soc*. **131**: 337-342.

Ciesla, W.M., Lambert, H.L. and Franklin, R.T. 1963 The status of the balsam woolly adelgid in North Carolina and Tennessee. USFS, S & PF, Div, FPM, Asheville, NC. Report 1-1-63.

Cody, R.P. and Smith, J.K. 1997 *Applied statistics and the SAS programming language 4th edition.* Prentice Hall, New Jersey. Pp. 181-188.

Dale, V.H., Gardner, R.H, DeAngelis, D.L., Eagar, C.C. and Webb, J.W. 1991 Elevation mediated effects of balsam woolly adelgid on southern Appalachian spruce-fir forests. *Can. J. For. Res*. **21**:1639-1648.

Delcourt, H.R. and Delcourt, P.A. 1988 Quaternary landscape ecology: relevant scales in space and time. *Landsc. Ecol*. **2**:23-44.

Dull C.W., Ward J.E., Brown H.D., Ryan G.W., Clerke W.H. and Uhler, R.J. 1988 Evaluation of spruce and fir mortality in the southern Appalachian mountains. USDA, Forest Service, Protection Report R8-PR 13, Atlanta, GA. pg 92.

Eyre, F.H. (ed.). 1980 *Forest cover types of the Unites States and Canada.* Society of American Foresters. Washington D.C.

Hollingsworth, R.G. and Hain, F.P. 1991 Balsam woolly adelgid (homoptera: adelgidae) and spruce-fir decline in the southern Appalachians: assessing pest relevance in a damaged ecosystem. *Fla. Entomol*. **74**:179-187.

Johnson, D.W. and Lindberg, S.E. (eds.). 1992 *Atmospheric Deposition and Nutrient Cycling in Forest Ecosystems -- A Synthesis of the Integrated Forest Study*. Springer-Verlag, New York.

Johnson D.W., Van Miegroet, H., Lindberg, S.E. and Todd, D.E. 1991 Nutrient cycling in red spruce forests of the Great Smoky Mountains. *Can. J. For. Res.* **21**:769-787.

King, P.B., Neuman, R.B. and Hadley, J.B. 1968 Geology of the Great Smoky Mountains National Park, Tennessee and North Carolina. U.S Geological Survey Professional Paper 587.

McCracken, R.J., Shanks, R.E. and Clebsch, E.E.C. 1962 Soil morphology and genesis at higher elevation of the Great Smoky Mountains. Soil Science Society of America Proceedings. **26**:384-388.

McLaughlin, S.B., Downing, D.J., Blasing, T.J., Cook, E.R. and Adams, H.S. 1987 An analysis of climate and competition as contributors to decline of red spruce in high elevation Appalachian forests of the Eastern United States. *Oecologia*. **72**:487-501.

McLaughlin, S.B. and Tjoelker, M.G. 1992 Growth and Physiological changes in red spruce sapling associated with acid deposition levels in high elevation sites in the southern Appalachians USA. *For. Ecol.Manage.* **51**:43-51.

Nicholas, N.S., Zedaker, S.M. and Eagar, C. 1992 A comparison of overstory community structure in three southern Appalachian spruce-fir forests. *Bull. Torr. Bot. Club*. **119**: 316-332.

Nicholas, N.S. 1992 *Stand structure, growth and mortality in southern Appalachian spruce-fir*. Ph.D. dissertation, Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Nicholas, N.S. and Zedaker, S.M. 1989 Ice damage in Spruce fir forests of the Black Mountains, North Carolina. *Can. J. For. Res.* **19**:1487-1491.

Pauley, E.F. and Clebsch E.E.C. 1990 Patterns of *Abies fraseri* in a Great Smoky Mountains spruce fir forest. *Bull. Torr. Bot. Club*. **117**:375-381.

Peart, D.R., Cogbill, C.V. and Palmiotto P.A. 1992 Effects of logging history, and hurricane damage on canopy structure at the Hubbard Brook Experimental Forest, NH. *Bull. Torr. Bot. Club*. **119**:29-38.

Pyle, C. and Schafale, M.P. 1988 Land use history of three spruce-fir forest sites in southern Appalachia. *J. For. Hist*. **32**:4-21.

SAS Institute Inc. 2002 *SAS User's Guide: Statistics*, Version 9.0 Edition. SAS Institute Inc., Cary, North Carolina.

Shanks, R.E. 1954 Climates of the Great Smoky Mountains. *Ecology*. **35**:354-361.

Smith, G.F. 1997 *Southern Appalachian fir and fir-spruce forest community changes following balsam woolly adelgid infestation*. M.S. Thesis, Department of Forestry, University of Tennessee, Knoxville Tennessee.

Smith, G.F. and Nicholas, N.S. 2000 Size and age class distributions of Fraser fir following balsam woolly adelgid infestation. *Can. J. For. Res*. **30**:948-957.

Speers, C.F. 1958 The balsam woolly aphid in the southeast. *J. For.* **56**:515-516.

Van Miegroet, H., Johnson, D.W. and Todd, D.E. 1993 Foliar response of red spruce saplings to fertilization with Ca and Mg in the Great Smoky Mountains National Park. *Can. J. For. Res.* **23**:89-95.

Van Miegroet, H., Moore, P.T., Tewksbury, C. and Nicholas, N.S. 2007 Carbon sources and sinks in high-elevation spruce-fir forests in the Southeastern US. *For. Ecol. Manage.* **238**:249-260.

Weaver, G.T. 1972 *Dry matter and nutrient dynamics in red spruce-Fraser fir and yellow birch ecosystems in the balsam mountains, western North Carolina*. Ph.D. Dissertation. University of Tennessee, Knoxville TN.

White, P.S. and Cogbill, C.V. 1992 Spruce fir forests of eastern North America. Pp. 3-39 In: Eagar, C. and Adams, M.B. (eds.) *Ecology and decline of red spruce in the Eastern United States*. Springer-Verlag, New York.

Whittaker, R.H. 1956 Vegetation of the Great Smoky Mountains. *Ecology*. **26**:1-80.

Whittaker, R.H. 1966 Forest dimensions and production in the Great Smoky Mountains. *Ecology*. **47**:103-121.

Witter, J.A. 1988 Balsam woolly adelgid and spruce-fir interactions in the southern Appalachian mountains. In: Proceedings of the Society of American Foresters national convention. Oct 16-19, 1988, Rochester, New York.

Witter, J.A. and Ragenovich, I.R. 1986 Regeneration of Fraser fir at Mt. Mitchell after depredations by the balsam woolly adelgid. *For. Sci*. **32**:585-594.

Zedaker, S.M. and Nicholas, N.S. 1990 Quality assurance and methods manual for forest site classification and field measurements. U.S. Environmental Protection Agency, nvironmental Research Laboratory, Corvallis, OR, EPA/600/3-90/082.

Table 2.1. Standing live biomass (Mg ha^{-1}), number of trees per hectare, and basal area (m^2 ha^{-1}) for four species groups at eight elevation bands at two time periods within the Noland Divide Watershed of Great Smoky Mountain National Park (± standard deviation)

				1993					2003		
	Elevation (m)	*Abies*	*Betula*	*Picea*	Other	Combined	*Abies*	*Betula*	*Picea*	Other	Combined
Standing Live Biomass (Mg ha^{-1})	1700	0.4 ± 0.3	109 ± 131	229 ± 131	3.4 ± 5.8	341 ± 152	2.9 ± 1.8	121 ± 143	194 ± 109	2.0 ± 1.4	319 ± 153
	1725	1.1 ± 1.8	113 ± 116	183 ± 125	1.8 ± 2.1	299 ± 81	6.5 ± 10	130 ± 134	163 ± 81	2.0 ± 2.1	302 ± 97
	1755	**0.5 ± 0.6#****	76 ± 79	215 ± 108	1.3 ± 1.6	292 ± 109	**3.9 ± 2.7****	76 ± 74	214 ± 95	1.7 ± 2.7	296 ± 94
	1785	**0.9 ± 1.9****	43 ± 59	197 ± 111	3.0 ± 4.2	244 ± 73	**5.7 ± 5.2****	47 ± 56	150 ± 88	3.1 ± 3.9	206 ± 64
	1800	0.9 ± 1.8	64 ± 27	244 ± 66	0.4 ± 0.6	309 ± 77	5.3 ± 6.4	67 ± 25	275 ± 68	0.8 ± 0.9	349 ± 70
	1835	**1.6 ± 1.6****	39 ± 66	221 ± 75	0.5 ± 0.9	262 ± 64	**12 ± 6.1****	45 ± 72	210 ± 136	0.5 ± 0.8	267 ± 119
	1865	4.1 ± 7.1	10 ± 18	218 ± 106	1.9 ± 2.8	234 ± 107	21 ± 19	12 ± 21	182 ± 106	2.5 ± 3.8	216 ± 99
	1890	**18 ± 10***	1.4 ± 2.1	165 ± 56	1.3 ± 1.9	185 ± 60	**46 ± 27***	2.6 ± 3.1	122 ± 70	1.9 ± 2.4	172 ± 71
	overall	**3.3 ± 6.8****	**56 ± 78****	**206 ± 97***	1.7 ± 2.8	267 ± 95	**12.7 ± 18.2****	**61 ± 85****	***184 ± 99**	1.9 ± 2.6	260 ± 105
Trees ha^{-1}	1700	38 ± 25	131 ± 90	550 ± 134	100 ± 91	819 ± 247	250 ± 157	144 ± 99	706 ± 134	144 ± 107	1,244 ± 178
	1725	82 ± 140	82 ± 55	314 ± 171	121 ± 134	600 ± 171	396 ± 620	89 ± 52	350 ± 164	100 ± 95	936 ± 521
	1755	50 ± 60	281 ± 176	463 ± 144	75 ± 76	869 ± 222	294 ± 184	263 ± 156	556 ± 174	63 ± 81	1,175 ± 305
	1785	75 ± 132	200 ± 210	397 ± 189	81 ± 72	753 ± 381	353 ± 278	209 ± 145	566 ± 377	125 ± 149	1,253 ± 463
	1800	81 ± 146	163 ± 139	406 ± 83	44 ± 52	694 ± 234	319 ± 267	188 ± 153	650 ± 219	56 ± 66	1,213 ± 512
	1835	125 ± 118	89 ± 64	307 ± 120	18 ± 37	539 ± 243	636 ± 379	129 ± 85	496 ± 136	39 ± 43	1,300 ± 455
	1865	242 ± 336	46 ± 89	271 ± 81	33 ± 49	592 ± 287	1,175 ± 1,117	54 ± 75	388 ± 151	25 ± 27	1,642 ± 1,012
	1890	925 ± 503	42 ± 79	233 ± 83	42 ± 49	1,242 ± 466	1613 ± 853	58 ± 85	308 ± 177	54 ± 53	2,033 ± 839
	overall	199 ± 350	135 ± 147	362 ± 158	65 ± 79	760 ± 348	628 ± 708	146 ± 128	490 ± 236	75 ± 91	1,339 ± 631
Basal Area (m^2 ha^{-1})	1700	0.1 ± 0.1	14 ± 15	34 ± 18	1.7 ± 2.0	49 ± 18	0.9 ± 0.6	15 ± 16	30 ± 16	0.9 ± 0.8	47 ± 17
	1725	0.3 ± 0.6	13 ± 13	28 ± 18	0.8 ± 0.9	42 ± 11	2.0 ± 3.2	15 ± 14	25 ± 12	0.7 ± 0.8	43 ± 9.1
	1755	0.2 ± 0.2	11 ± 10	31 ± 13	0.9 ± 1.0	43 ± 13	1.2 ± 0.8	11 ± 8.6	31 ± 10	0.7 ± 0.9	44 ± 11
	1785	0.3 ± 0.6	6.5 ± 8.5	30 ± 15	0.8 ± 0.9	37 ± 10	1.8 ± 1.6	7.0 ± 8.0	23 ± 11	1.1 ± 1.5	33 ± 8.0
	1800	0.3 ± 0.6	8.9 ± 2.2	35 ± 8.3	0.2 ± 0.3	44 ± 9.0	1.6 ± 1.9	9.4 ± 2.6	39 ± 8.5	0.3 ± 0.4	50 ± 9.0
	1835	0.5 ± 0.5	5.1 ± 7.9	32 ± 12	0.1 ± 0.2	38 ± 10	3.6 ± 1.9	5.8 ± 8.5	31 ± 19	0.2 ± 0.2	41 ± 18
	1865	1.2 ± 2.1	1.7 ± 3.1	33 ± 14	0.5 ± 0.8	36 ± 14	6.3 ± 6.0	2.0 ± 3.5	27 ± 14	0.6 ± 0.9	36 ± 12
	1890	5.2 ± 2.7	0.3 ± 0.4	25 ± 7.0	0.5 ± 0.7	31 ± 8.6	13 ± 7.6	0.5 ± 0.6	18 ± 10	0.5 ± 0.7	32 ± 11
	overall	1.0 ± 2.0	7.4 ± 9.4	31 ± 13	0.7 ± 1.0	40 ± 12	3.8 ± 5.2	8.0 ± 9.8	28 ± 13	0.7 ± 0.9	40 ± 12

bold indicates significant differences in standing live biomass for a given elevation range and species combination between 1993 and 2003 at the *0.05 and **0.01 levels

Table 2.2. Rates (kg ha^{-1} yr^{-1}) of biomass ingrowth, Increment, mortality and overall balance for three species at eight elevation bands at two time periods within the Noland Divide Watershed of Great Smoky Mountain National Park (± standard deviation)

		1993-1998				1998-2003			
	Elevation (m)	*Abies*	*Betula*	*Picea*	Combined	*Abies*	*Betula*	*Picea*	Combined
Ingrowth	1700	125 ± 155	10 ± 20	101 ± 99	236 ± 244	279 ± 109	27 ± 32	243 ± 117	549 ± 176
	1725	181 ± 374	6.1 ± 16	38 ± 37	225 ± 370	441 ± 675	36 ± 37	83 ± 92	560 ± 654
	1755	**83 ± 80#***	34 ± 67	128 ± 134	246 ± 184	**373 ± 271***	19 ± 26	96 ± 66	488 ± 307
	1785	175 ± 161	**15 ± 30****	**128 ± 197***	**319 ± 344***	458 ± 419	**130 ± 93****	**231 ± 259***	**819 ± 574***
	1800	**100 ± 90****	20 ± 23	164 ± 141	**284 ± 227***	**307 ± 151****	57 ± 89	196 ± 143	**560 ± 311***
	1835	**356 ± 283***	77 ± 76	81 ± 96	**514 ± 369***	**684 ± 364***	22 ± 41	301 ± 345	**1,007 ± 531***
	1865	**684 ± 911***	8.6 ± 21	**80 ± 68***	**773 ± 923***	**1,371 ± 1,236***	19 ± 30	**196 ± 142***	**1,586 ± 1,217***
	1890	888 ± 642	39 ± 69	99 ± 113	1,026 ± 659	904 ± 458	26 ± 42	148 ± 155	1,079 ± 596
	overall	**323 ± 488****	28 ± 51	**100 ± 119****	**451 ± 520****	**611 ± 635****	44 ± 64	**182 ± 195****	**837 ± 683****
Increment	1700	22 ± 17	876 ± 910	3,827 ± 2,864	4,724 ± 2,819	141 ± 122	1,996 ± 1,987	3,721 ± 2,013	5,858 ± 1,826
	1725	152 ± 257	1,564 ± 1,788	2,971 ± 1,282	**4,687 ± 1,424***	358 ± 637	2,468 ± 2,464	3,281 ± 1,400	**6,107 ± 1,340***
	1755	67 ± 74	1,385 ± 1,010	**3,193 ± 1,117***	4,645 ± 808	193 ± 234	1,137 ± 1,064	**4,350 ± 1,631***	5,680 ± 1,668
	1785	**119 ± 197***	1,006 ± 1,275	3,247 ± 1,913	4,372 ± 1,689	**314 ± 344***	775 ± 850	3,200 ± 1,376	4,290 ± 1,209
	1800	135 ± 249	605 ± 404	3,152 ± 1,798	3,891 ± 1,977	352 ± 508	841 ± 1,180	5,572 ± 1,879	6,766 ± 2,328
	1835	**274 ± 212***	659 ± 776	2,500 ± 1,572	3,433 ± 1,549	**794 ± 447***	396 ± 357	4,073 ± 3,613	5,264 ± 3,712
	1865	423 ± 610	228 ± 520	2,509 ± 1,477	**3,160 ± 1,620***	1,449 ± 1,550	302 ± 553	3,331 ± 1,579	**5,081 ± 972***
	1890	**1,887 ± 1,167***	109 ± 145	1,552 ± 759	**3,548 ± 1,266****	**3,292 ± 1,981***	134 ± 165	2,318 ± 1,675	**5,745 ± 2,037****
	overall	**379 ± 728****	853 ± 1,087	**2,842 ± 1,599****	**4,074 ± 1,598****	**851 ± 1,323***	986 ± 1,411	**3,659 ± 2,045****	**5,496 ± 2,011****
Mortality	1700	-32 ± 64	0 ± 0	-13,242 ± 25,650	-13,274 ± 25,628	-34 ± 49	-37 ± 74	-698 ± 1,288	-769 ± 1,241
	1725	-8.1 ± 22	-26 ± 68	-2,338 ± 6,186	-2,372 ± 6,171	-46 ± 121	-348 ± 920	-7,787 ± 12,292	-8,180 ± 12,174
	1755	-5.6 ± 16	-364 ± 754	-1,362 ± 3,496	-1,732 ± 4,250	-43 ± 64	-1,750 ± 3,296	-6,440 ± 10,957	-8,232 ± 10,251
	1785	-9.3 ± 26	-743 ± 2,026	-4,278 ± 6,605	-5,031 ± 6,375	-83 ± 224	-297 ± 699	-11,311 ± 13,100	-11,691 ± 13,001
	1800	0 ± 0	-384 ± 767	-1,045 ± 2,089	-1,428 ± 1,971	-26 ± 53	-10 ± 20	-1,265 ± 2,487	-1,301 ± 2,463
	1835	0 ± 0	-22 ± 58	-7673 ± 12,741	-7,696 ± 12,725	-85 ± 127	0 ± 0	-1,412 ± 3,476	-1497 ± 3443
	1865	-59 ± 99	-169 ± 415	-9,696 ± 9,628	-9,925 ± 9,645	-531 ± 911	0 ± 0	-2,421 ± 5,894	-2,952 ± 6,790
	1890	-379 ± 536	-37 ± 91	-8,068 ± 8,264	-8,484 ± 8,214	-929 ± 1,033	-34 ± 84	-4,560 ± 9,308	-5,523 ± 9,428
	overall	**-59 ± 213***	-239 ± 890	-5,579 ± 10,204	-5,877 ± 10,187	**-219 ± 547***	-384 ± 1,452	5,123 ± 9,369	-5,725 ± 9,370
Balance	1700	**115 ± 175***	886 ± 909	-9,314 ± 27,180	-8,313 ± 27,448	**386 ± 182***	1,986 ± 2,030	3,267 ± 2,682	5,639 ± 2,664
	1725	326 ± 615	1,544 ± 1,815	670 ± 6,014	2,540 ± 6,831	753 ± 1165	2,157 ± 2,223	-4,422 ± 11,803	-1,513 ± 12,109
	1755	**145 ± 133****	1,056 ± 1,529	1,959 ± 3,384	3,159 ± 4,405	**523 ± 364****	-594 ± 2,285	-1,994 ± 10,804	-2,065 ± 10,634
	1785	**284 ± 292***	279 ± 1,283	-903 ± 7,245	-340 ± 7,198	**689 ± 502***	608 ± 1,117	-7,880 ± 12,824	-6,582 ± 12,665
	1800	235 ± 332	241 ± 732	2,271 ± 3,396	2,747 ± 3,786	633 ± 599	888 ± 1,145	4,504 ± 3,006	6,025 ± 3,907
	1835	**630 ± 393***	714 ± 798	-5,092 ± 13,923	-3,748 ± 13,944	**1393 ± 767***	418 ± 360	2,963 ± 5,648	4,774 ± 5,800
	1865	1048 ± 1,239	68 ± 106	-7,107 ± 10,470	-5,992 ± 9,735	2,289 ± 2,809	321 ± 548	1,106 ± 5,214	3,716 ± 6,637
	1890	2,396 ± 2,060	111 ± 119	-6,416 ± 8,721	-3,910 ± 8,252	3,268 ± 2,559	126 ± 111	-2,094 ± 9,246	1,300 ± 8,861
	overall	**644 ± 1,090****	641 ± 1,181	-2,636 ± 10,879	-1,352 ± 10,888	**1,243 ± 1,640****	646 ± 1,640	-1,281 ± 9,487	608 ± 9,667

bold indicates significant differences in growth characteristics (ingrowth, increment, mortality and overall balance) for a given elevation range and species combination between the 1993-1998 time period and the 1998-2003 time period at the *0.05 and **0.01 levels

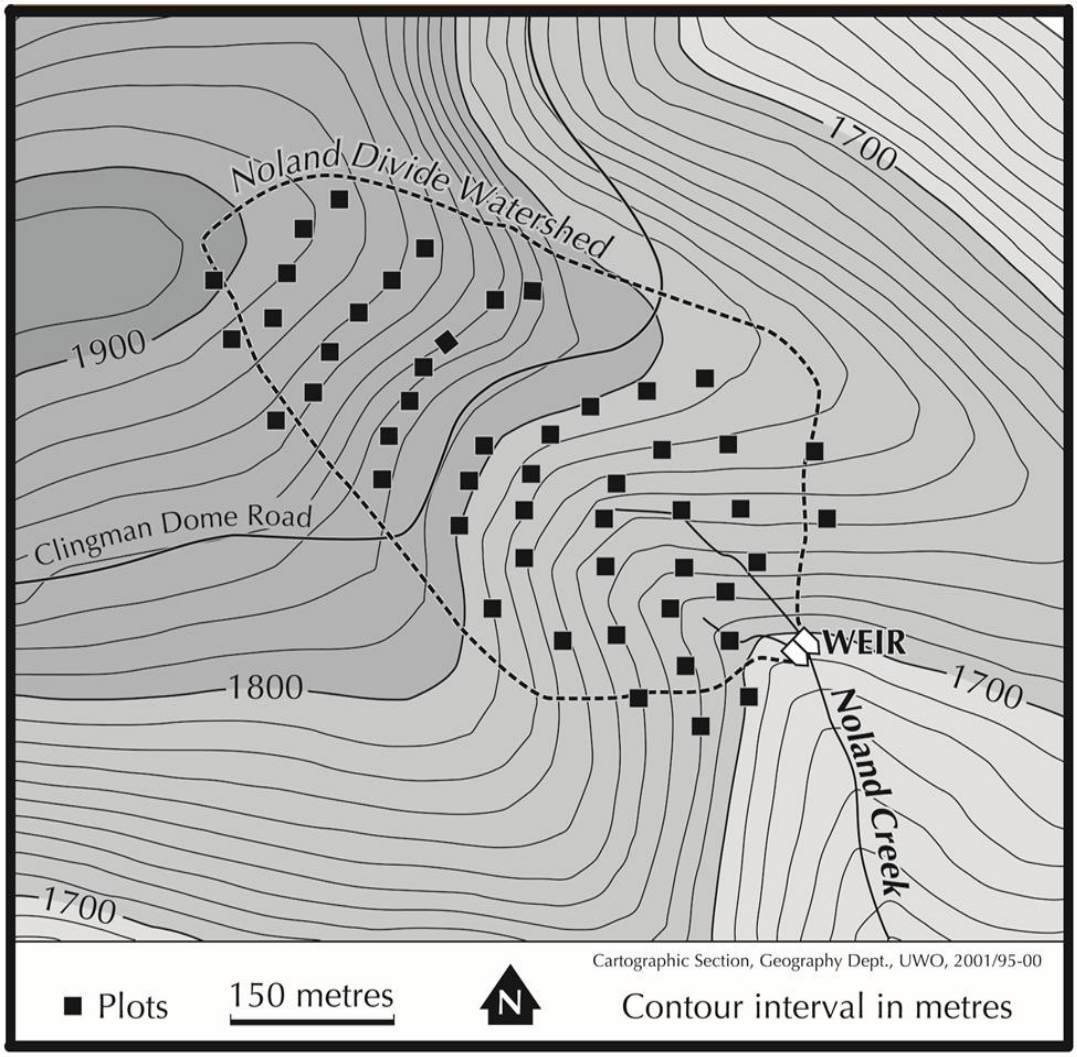

Figure 2.1. Map of the Noland Divide Watershed of Great Smoky Mountain National Park and the systematic network of 50 permanent plots.

CHAPTER 3

RELATIVE ROLE OF UNDERSTORY AND OVERSTORY IN CARBON AND NITROGEN CYCLING IN A SOUTHERN APPALACHIAN SPRUCE-FIR FOREST [3,4]

ABSTRACT

This study investigated post-disturbance aboveground pools and fluxes of biomass, carbon (C) and nitrogen (N) in overstory and understory vegetation in a southern Appalachian red spruce (*Picea rubens* Sarg.) Fraser fir [*Abies fraseri* (Pursh.) Poir.] forest in a small catchment of Great Smoky Mountains National Park. Using 50 20 x 20 m plots, stratified by elevation (1700-1900 m), we estimated standing biomass pools and fluxes of all growth forms from periodic stand inventories (1998-2003) and plot vegetation surveys and existing or derived allometric equations. Total C and N pools and fluxes were calculated from plant- and tissue-specific C and N concentrations.

Total aboveground biomass ranged from 313 Mg ha^{-1} at the lower elevations to 204 Mg ha^{-1} at the upper elevations; 96% contained in live overstory trees (>5cm DBH). Understory woody and herbaceous vegetation comprised 7.8 Mg ha^{-1} (3%) and 1.7 Mg ha^{-1} (1%) of biomass, respectively. Despite recent disturbance-induced mortality, forest productivity was high, averaging 7.7 Mg ha^{-1} yr^{-1}, with overstory accounting for 73%; understory woody vegetation, 10%; and herbaceous plants, 27% of total productivity and C sequestration. Aboveground N uptake in the catchment was estimated at 37 kg ha^{-1} yr^{-1}, with > 50% of N uptake (18-21 kg ha^{-1} yr^{-1}) by the herbaceous understory and ~7 kg

---

[3] This chapter appeared in the Canadian Journal of Forest Research as: Moore, P.T., H. Van Miegroet and N.S. Nicholas. 2007. Relative role of understory and overstory in carbon and nitrogen cycling in a southern Appalachian spruce-fir forest. Canadian Journal of Forest Research 37:2689-2700.
[4] Coauthored by Patrick T. Moore, H. Van Miegroet and Niki S. Nicholas

ha^{-1} yr^{-1} by woody understory. Overstory biomass increment and N uptake (11-15 kg ha^{-1} yr^{-1}) had increased over earlier reported values and was highest at the upper elevations where mortality had been most severe.

INTRODUCTION

Southern Appalachian red spruce (*Picea rubens* Sarg.) Fraser fir [*Abies fraseri* (Pursh.) Poir] forests, 74% of which are located in Great Smoky Mountain National Park (GSMNP), receive some of the highest amounts of atmospheric N deposition (~30 kg ha^{-1} yr^{-1}) and are considered N-saturated (Nodvin et al. 1995). The N retention capacity of these systems is limited and significant amounts (~15 kg ha^{-1} yr^{-1}) of inorganic N leave the system via streamwater (Nodvin et al. 1995; Van Miegroet et al. 2001). In the Noland Divide Watershed (NDW) of GSMNP, Barker et al. (2002) found that the overstory of this system had an uptake rate of approximately 8 kg ha^{-1} yr^{-1}, though rates were spatially variable. Since that time, productivity in this forest has significantly recovered and the uptake rate of the overstory may be considerably higher.

Increased N deposition in forested ecosystems can cause increased nitrate leaching and streamwater export (Aber et al. 2003), decreased mycorrhizal community diversity (Egerton-Warburton and Allen 2000; Lilleskov et al. 2002), changes in lichen communities (Nash and Gries 2002), and decreases in net primary productivity and foliar biomass (Aber et al. 1998). In the western U.S., low background levels of atmospheric N deposition coupled with ‘hotspots’ of elevated N deposition have caused significant impacts on ecosystem function (Fenn et al. 2003). In northeastern forests, N deposition is altering N status, expressed by increased N in surface water, increased nitrification, and

decreased C:N ratios in soil (Aber et al. 2003). The role of vegetation and soil in the uptake and storage of N has been the subject of some debate (Aber et al. 1989; Fenn et al. 1998). Nutrient uptake and sequestration by vegetation can retain large amounts of increased N deposition inputs within forest ecosystems (Aber et al. 1989, 1998; Fenn et al. 2003). However few, if any studies have considered the role of understory in N uptake and retention.

Recent disturbances in high-elevation spruce-fir forests of the southern Appalachians have reduced the ability of this forest to take up N (Barker et al. 2002). These disturbances include the infestation of the balsam wooly adelgid (BWA, *Adelges picea* Ratz., Nicholas et al. 1992), atmospheric pollution (Johnson et al. 1991), ice storms (Nicholas and Zedaker 1989), and gap dynamics (White et al. 1985; Busing and Clebsch 1987). The disturbance that has caused the most widespread and catastrophic damage to these forests is the infestation by the BWA. Prior to the onset of the BWA, these forests contained large amounts of biomass in the overstory (Whittaker 1966). After the BWA, which killed most mature fir, only 12% of fir stems remained alive, and these remaining individuals were exclusively in the smaller size categories (Smith and Nicholas 2000). In the years following the BWA-induced thinning of fir stands, many remaining dominant and co-dominant spruce were subject to windthrow as a result of exposure to the more open canopy conditions (Hollingsworth and Hain 1991; Busing 2004). Since that time, the forest has shown signs of recovery, as indicated by increased standing live biomass, increased growth, and conifer regeneration.

Overstory vegetation characteristics and nutrient dynamics have been documented for spruce-fir (Johnson and Lindberg 1992; Nicholas et al. 1992; Busing 2004), with the

most intensive determination of nutrient storage and uptake in southern Appalachians as part of the Integrated Forest Study (IFS) in the mid-1980s (Johnson et al. 1991; Johnson and Lindberg 1992). In that study, the standing live biomass of two post-adelgid red spruce plots was estimated at 273 Mg ha^{-1} and 314 Mg ha^{-1} for the Smokies Tower site (ST), located just outside of the NDW at 1740 m, and at 264 Mg ha^{-1} for the nearby Becking site (SS). Corresponding biomass production ranged from 1,360 to 4,530 kg ha^{-1} yr^{-1} and uptake of N from 7 to13 kg ha^{-1} yr^{-1} (Johnson and Lindberg 1992). Pauley et al. (1996) provided an estimate of post-BWA biomass and N pools within the NDW of GSMNP. They found that spruce contained over 70% of overstory N, while fir contained less than 2%. Spruce needles accounted for over 35% of overstory N but represented only 6% of overstory biomass, showing that biomass and nutrient dynamics are not necessarily congruent.

Compared to the overstory, the understory of this forest has received little attention and is not well understood (Barker et al. 2002). Several authors have characterized the pre-BWA understory of this forest (Oosting and Billings 1951; Crandall 1960; Ramseur 1960; Whitaker 1962), but this was done in a taxonomical or botanical manner and without much regard to nutrient cycling or ecosystem function. Smith and Nicholas (2000) analyzed regeneration of spruce and fir, but only focused on woody seedlings, saplings and trees in the highest elevations. Johnson and Lindberg (1992) provided an estimate of understory pools but did not attempt to estimate understory C and N fluxes. Since the IFS analysis, the structure and function of the understory trees, shrubs and herbs may have changed. With many young spruce and fir entering the stand since the BWA onset, and with those small trees containing higher foliage to stem mass ratio

(Waring and Schlesinger 1985), understory nutrient dynamics may have changed considerably.

We hypothesize that this disturbed forest may be recovering its ability to sequester and store excess N. The majority of research on this system so far has dealt with overstory response to these disturbances (Nicholas et al. 1992; Pauley et al. 1996; Smith and Nicholas 2000; Busing 2004) and not much is known about the role of understory nutrient cycling. A complete understanding of how nutrients are cycled within the living components of this ecosystem requires the inclusion of the understory, especially when this ecosystem is in transition. We hypothesize that the understory is cycling a considerable portion of total ecosystem N. The objectives of this paper are to determine (1) the role of understory versus overstory in sequestering biomass and cycling N; (2) whether overstory N and biomass dynamics have recently changed from prior measurements; and (3) whether current biomass, and C and N dynamics show elevational patterns.

METHODS

Study Area

This research was conducted at the NDW (35°34'N, 83°29'W, 1700-1910m), a 17.4 ha catchment within GSMNP. The broad elevation gradient, resulting variability in overstory species composition, similar parent material, and pre-existing plot infrastructure give us the ability to study watershed-level dynamics. Because of prior research at this site by others (Pauley et al. 1996; Barker et al. 2002), as well as access to data previously collected by collaborators (repeated 1993 and 1998 overstory

measurements), we are able to evaluate changes in nutrient dynamics over time. While our analysis was done within only one watershed and thus has a somewhat limited inference space, the intensive sampling scheme and plot layout captured much of the variability existing at the larger landscape, and may thus reveal some general patterns and lead to conclusions that may also apply to spruce-fir forests within the GSMNP and the southern Appalachians.

Average annual precipitation is >200 cm and is distributed evenly throughout the year (Johnson and Lindberg 1992). Ten percent of annual precipitation falls as snow and covers the ground for an average of 50 days per year (Johnson et al. 1991). Mean air temperatures range from -2°C in February to 17°C in August with a frost-free period from May through September (Shanks 1954; Johnson et al. 1991). The soils are mainly Inceptisols, occasionally with spodic characteristics (McCracken 1962; Van Miegroet et al. 1993), and are underlain by Thunderhead Sandstone (King et al. 1968). They are generally shallow and have a silt loam to sandy loam texture, and are rich in N and C but low in exchangeable bases (Johnson and Lindberg 1992). This catchment has not been impacted by logging or fire (Pyle and Schafale 1988), but has been severely impacted by the BWA beginning as early as 1977 (Pauley et al. 1996; Barker et al. 2002). A full description of current forest composition can be found in Van Miegroet et al. (2007).

In this study, we used a repeated overstory inventory of 50 20 x 20 m permanent plots, placed systematically within this high elevation catchment, along nine elevation bands (1700, 1725, 1755, 1785, 1800, 1835, 1865, 1890 and 1910 m, Figure 1). We determined watershed biomass and N dynamics of all vegetation strata, including overstory trees, understory woody trees and shrubs, herbs and mosses. In analyzing the

data for elevational patterns, the nine elevation bands of the NDW were split into three elevation ranges; low, the lowest three bands (1700, 1725 and 1755 m), totaling 19 plots; middle, the middle three elevation bands (1785, 1800 and 1835 m), totaling 19 plots; and high, the highest three elevation bands (1865, 1890 and 1910 m), totaling 12 plots. One-way analysis of variance (PROC ANOVA) was be used to determine significant differences in biomass, N pool, and uptake values across the three elevation ranges (SAS Institute 2002).

Overstory measurements

Barker et al. (2002) estimated overstory N uptake using repeated measurements (1993 and 1998) of individual tree diameter at 1.37 m above ground level (DBH) at each of the 50 permanent NDW plots. A similar methodology was used to determine overstory N uptake and production for the 1998-2003 period for each of the 50 NDW plots. DBH, species, and unique identification number of each live overstory (≥ 5 cm DBH) tree were recorded, using inventory protocol described in Zedaker and Nicholas (1990). As the NDW plots are part of a permanent plot system where individual trees are tagged and cataloged, and since an inventory had not been performed since 1998, new ingrowth was measured and tagged for future measurements.

Biomass of foliage, live branches, dead branches, bole bark and bole wood were determined from DBH using the predictive equations of Nicholas (1992). Individual tree component masses were summed to equal total aboveground tree biomass. These equations were applied to red spruce, Fraser fir and yellow birch (*Betula lutea* F. Michx.) to estimate biomass of tree species within each plot. Aboveground biomass of other

species was estimated similarly with the predictive equations of Weaver (1972). The C and N content of individual tree components was determined using the nutrient concentration values in Barker (2000). Current standing live biomass and N pools were determined using 2003 inventory data. Uptake fluxes were determined by mass difference of individual trees from the 1998 to the 2003 inventory (Clark et al. 2001). This allowed us to quantify how much N dynamics within those five years had changed relative to earlier studies (Johnson et al. 1991; Barker et al. 2002)

Nutrient uptake can vary considerably from one forest type to another and spatially within the same forest type and watershed (Barker et al. 2002). Also, various uptake calculation methods can produce dramatically different results (Bockheim and Leide 1990; Barker et al. 2002). Because we were interested in change over time, and consistency in methodology is essential, the simpler of the eight N uptake determination methods (U_2, net aboveground increment) was used to compare our current uptake values with those of Barker et al. (2002). Belowground biomass and N content are not addressed in this study. Van Miegroet et al. (2007) provided an analysis of belowground biomass and C for this area.

Understory Woody Vegetation

Within each of the 50 permanent plots of the NDW, four 4 x 4 m subplots were established as shown in Figure 2 (gray boxes). In 2003, large understory woody vegetation (<5 cm but >2 cm DBH) was measured at 15 cm above ground level, and species-specific predictive equations of Nicholas (1992) and Weaver (1972) were used to calculate biomass of individual tree components based on this stem diameter as the

independent variable. The C and N content of individual tree components of aboveground biomass were determined from values in Barker (2000). Production of other woody understory vegetation was determined using biomass accumulation ratios (BAR) of woody understory plants, *i.e.*, empirical relationships between standing biomass and productivity (Whittaker 1962). They generally range from 1-3 in grasslands, 2-10 in deserts, 3-12 in shrublands, 10-30 in woodlands, and 20-50 in mature forests (Whittaker 1975). We used a conservative value of 10 based on Whittaker's reported findings from understory shrubs in the southern Appalachians (7.0, Whittaker 1966), and general shrub communities (3-12, Whittaker 1975), and Alaback's values for forest understory of disturbed Sitka spruce sites in eastern Alaska (8, Alaback 1984).

Due to the lack of existing allometric equations for biomass and nutrient content of small understory woody vegetation (stems <2 cm DBH), a two-part, destructive/non-destructive double sampling approach was used to derive these equations. All destructive sampling was performed in the nearby Pisgah National Forest, NC. Twelve individuals of each of four woody species [red spruce, Fraser fir, yellow birch and hobblebush (*Viburnum alnifolium* Michx.)] were measured with a caliper at 15 cm above ground level, clipped at ground level, dried and weighed. These four species were chosen because they were, by far, the most common understory woody vegetation. Allometric relationships between stem diameter and aboveground biomass were developed using the PROC REG procedure in SAS (SAS Institute 2002). Diameters of all small woody understory plants were measured in 16 1 x 1 m subplots within each of the 50 permanent plots (Figure 1.2; black boxes) and converted to biomass values using the calculated allometric equations. For species other than the four most common, the equation with the

species most similar in growth form was applied. Seedling biomass increment was determined using a BAR of 10, similar to larger understory vegetation.

Herbaceous Vegetation

Predictive biomass equations were produced for herbaceous vegetation in a manner similar to that for understory woody vegetation above, i.e., nondestructive survey within the NDW plots was coupled with destructive sampling outside the permanent plots to protect plot integrity (Forman 1969). In the non-destructive herbaceous survey of the permanent plot system, the 16 1 x 1 m subplots used for the small woody vegetation survey were used. Percent cover of all herbaceous plant species present within each subplot was estimated via ocular estimation to the nearest percent. Herbaceous vegetation was defined as all non-woody herbs, grasses and mosses. Concurrent with the non-destructive sampling in the permanent plots was a destructive sampling of herbaceous plants in temporary 1 x 1 m plots established in the Fall of 2003 outside the permanent NDW plots but still within the NDW. Each of these temporary plots was centered 10 m west of the northwest corner of the permanent NDW plots in order to capture the entire watershed yet not interfere with the permanent plot system. Percent cover by species was assessed by ocular estimation to the nearest percent. Then each species was clipped at ground level and placed in a uniquely numbered plastic bag until adequate samples (n=12) of each species present in our surveys were measured and collected. If additional samples were needed, they were selectively sampled randomly from populations throughout the watershed in order to obtain adequate observations and ranges of all species.

Once removed from the field in individually labeled and sealed Ziploc bags, plant specimens were individually oven dried at 65 C^o for 24 hours and weighed. Dry weights were then used to develop species-specific predictive equations to estimate dry plant biomass from percent cover estimate using the PROC REG procedure in SAS (SAS Institute 2002). Dried plant specimens were then ground through a 40-mesh screen in a Wiley mill, and analyzed for C and N using a LECO CHN analyzer (LECO Corp. St. Joseph, MI).

Because of the relatively short growing season (May through September) only one sampling period was necessary during the year (Yarie 1980). Therefore, aboveground herbaceous biomass was assumed to be the peak standing biomass at the end of the growing season. It was assumed that herbaceous biomass and N are cycled annually; therefore, pool estimates were used as N uptake values as well, with two exceptions: *Rubus* and moss species. Since the aboveground portion of *Rubus* is semelparous and each stem usually survives for two seasons, flux of biomass and N into the herbaceous pool was estimated to be one-half of the live biomass pool. Although mosses contribute little in terms of ecosystem biomass, their high turnover rates and high nutrient content make them important in biogeochemical cycling (Tamm 1953; Binkley and Graham 1981). Mosses were destructively and non-destructively surveyed similar to forbs and estimated by percent cover. Production was estimated as one-third of the estimated biomass following Tamm (1953).

RESULTS

Distribution of Biomass, Carbon and Nitrogen in Live Vegetation

These forests contained large amounts of biomass in the live aboveground vegetation components (Table 3.1). Biomass values averaged from 313 Mg ha^{-1} in the lower watershed to 204 Mg ha^{-1} in the upper watershed. The vast majority (96-97%) of aboveground live biomass was in trees larger than 5 cm DBH. Woody vegetation <5 cm DBH contained 7.8 Mg ha^{-1}, a considerably smaller proportion of aboveground biomass (2.7-3.9%), with smaller understory woody vegetation (<2 cm DBH) concentrated in the lower watershed and larger understory woody vegetation (2-5 cm DBH) concentrated in the upper watershed. Understory herbaceous vegetation, on average 1.7 Mg ha^{-1}, represented only a small proportion (0.6-1.0%) of total aboveground live biomass.

Allometric equations for the relationship between herbaceous plant percent cover and standing herbaceous biomass are shown in Table 3.2, with nomenclature following Radford et al. (1968). Linear relationships were most effective in describing this relationship, with R^2 ranging from 0.76 to 0.98. Allometric equations for understory woody vegetation <2 cm DBH are shown in Table 3.3 and required a correction factor for logarithmic bias (Spruegel 1983). Log-linear relationships were most effective in describing this relationship, with R^2 ranging from 0.78 to 0.93. Aboveground C pools were on average 48.2% of biomass values and the distribution of C in the ecosystem was very similar to that of biomass. Therefore, for the remainder of this paper, biomass and C dynamics will be discussed simultaneously.

Aboveground N pools were on average 0.22% of biomass values, but the N distribution did not follow that of biomass and C. Overstory trees contained on average 489 kg N ha^{-1}, a smaller proportion of aboveground N (78-84%) compared to biomass and C; however, the overstory still contained the majority of N in this system. Understory woody vegetation contained a considerably smaller amount (70 kg ha^{-1}) and proportion of aboveground N (10.8-14.4%), but this was four times higher than the small woody vegetation proportion of biomass and C pools. Herbaceous vegetation represented the smallest absolute (34 kg ha^{-1}) and relative N pool (4.7-7.7%) of any of the vegetation strata. However, total live aboveground N in the herbaceous layer was disproportionately higher (eight times) than biomass and C pools.

The amount of biomass and nutrients contained in the forest differed among elevations bands. Total live ecosystem biomass, C and N content were highest at lower elevations compared to mid and high elevations. Overstory biomass, C and N pools also tended to be higher at the lower elevations but the differences were statistically significant for N pools only. Elevation patterns, however, varied by overstory species. There was significantly more overstory fir biomass, C and N in higher elevations while biomass, C and N of pools in birch were significantly greater in lower elevations than higher elevations. There were no distinct patterns for spruce overstory; however, more biomass, C and N was stored in small understory spruce at lower elevations. No other differences could be detected, possibly due to the high degree of variability that is common in these forests. Coefficients of variation (CV) for pool size of individual forest components across species were often high (37-95%) and by species even higher (routinely >100%).

Carbon and Nitrogen Fluxes

Over the last five years this system has produced large amounts of new biomass, ~7,370 kg biomass ha^{-1} yr^{-1}, with the highest levels of net production, 7,730 kg ha^{-1} yr^{-1} in the lower elevation range (Table 3.4). Most biomass production occurred in the overstory, 5,650 kg ha^{-1} yr^{-1}, accounting for 75-78% of the total. Woody vegetation <5 cm DBH produced 824 kg ha^{-1} biomass annually, 11% of aboveground live production, with small woody understory vegetation (<2 cm DBH) production concentrated in the lower elevations and larger woody understory vegetation (2-5 cm DBH) production, mostly fir, concentrated in the higher elevations. Herbaceous vegetation produced 933 kg ha^{-1} yr^{-1} live aboveground biomass, 11-14% of total, concentrated in the upper elevations.

Total aboveground N uptake was 37 kg ha^{-1} yr^{-1} across the watershed with the highest uptake values, 43 kg ha^{-1} yr^{-1}, in the higher elevations. The distribution of N uptake across overstory components did not follow biomass and C increment patterns. Overstory took up 11-15 kg ha^{-1} yr^{-1}, or about 31% of total aboveground N uptake. Understory woody vegetation took up an additional 7 kg ha^{-1} yr^{-1} or about 19% of total N uptake, with generally higher N uptake values for smaller understory woody vegetation (<2 cm DBH) in the lower watershed and larger understory woody vegetation (2-5 cm DBH) in the upper watershed. Herbaceous vegetation, despite the modest biomass pools and fluxes, took up 18-21 kg N ha^{-1} yr^{-1}, exceeding that of overstory. The herbaceous vegetation was responsible for 51% of total aboveground N uptake by vegetation annually, disproportionately high for its relative pool size. There were some patterns in N uptake with elevation, although many were not statistically significant. Total

ecosystem N and overstory N uptake rates were highest in the high elevation band. Patterns by overstory species were consistent with those of biomass and C increments: highest for fir at highest elevations and for birch at the lower elevations, with no discernible pattern for spruce. For the other overstory components, N uptake also generally followed spatial patterns in biomass increment.

DISCUSSION

Distribution of Biomass, Carbon and Nitrogen in Vegetation

The majority of biomass and C was contained in the overstory of this system. Biomass values in the lower elevations have attained pre-BWA levels (>300 Mg ha^{-1}), but aboveground biomass and C pools decreased sharply with increasing elevation where the BWA had a greater effect (Smith and Nicholas 1999). Recent forest recovery is also indicated by the higher overstory biomass than those reported around 20 years ago for nearby lower elevation (ST, 252-261 Mg ha^{-1}) and middle elevation (SS, 223 Mg ha^{-1}) (Johnson and Lindberg 1992). Higher elevation spruce-fir stands contained less biomass than the lower elevations, even before the onset of the BWA, but present biomass levels at upper elevations are still at the very lowest of pre-BWA historic observations (200-310 Mg ha^{-1} Oosting and Billings 1951; Whittaker 1966). This elevational pattern is likely a result of the initial wave of fir mortality, heaviest at the higher elevations, and one would expect the loss of overstory biomass and C with elevation to be a response to the greater amounts of disturbance at higher elevations as well as the naturally lower historic levels of aboveground biomass and C in the higher elevations. Prevalence of fir increased with

elevation while prevalence of birch decreased with elevation, a trend that is typical of southern Appalachian spruce-fir forests (Whittaker 1966).

In general, understory spruce biomass was concentrated in the lower elevations and fir seedlings and saplings in the higher elevations, reflecting pre-adelgid composition. However, biomass of fir trees 2-5 cm DBH was greater than that of spruce even at the lower elevations. Fraser fir is a prolific sprouter and responds well to release under a spruce mid-story. It is possible that fir claimed understory positions before understory spruce responded to the recent canopy openings, especially at the higher elevations where disturbances were most severe. These stands are currently well stocked with small fir trees, i.e., advanced regeneration is present, ensuring that fir will be an important component of future spruce-fir forests, at least until the next wave of BWA-induced mortality.

The shifts in composition and distribution of the small woody understory (<2 cm DBH) with elevation closely resemble the pre-BWA overstory distribution of spruce and fir, where spruce is more abundant at lower elevations, while fir dominates higher elevations (Oosting and Billings 1951; Whittaker 1956). This supports the hypothesis that this forest may be returning to pre-BWA conditions, at least in the immediate future, in absence of further BWA-induced mortality. The large amount of "other" species in the small woody understory size class represents the abundance of shrubs and other small diameter woody plants across elevations.

The herbaceous biomass in NDW was substantially higher than values reported for various conifer systems (30-200 kg ha^{-1}). Among the ecosystems cited only woody understory biomass in Douglas-fir forests in Oregon (8,700 kg ha^{-1}) approximated values

our values for herbaceous biomass (Muller 2003). Though the herbaceous vegetation represented a rather insignificant amount of biomass, this stratum contained a far greater proportion of N-rich foliage and green stems, similar to an observation made by Welch et al. (2007) for the herbaceous layers in eastern deciduous forests. As a result, the herbaceous layer in this system contained a disproportionately high amount of N (4.7-7.7% of total N pool).

Our understory biomass and N pools exceeded values recorded during IFS in the spruce-fir forest (5.8 –8.7 Mg ha^{-1} for biomass, 48–85 kg ha^{-1} for aboveground N pool) (Johnson and Lindberg 1992), indicating a denser understory and possibly signaling dynamic changes in ecosystem structure over the last two decades. Huber (2005) observed a similar temporal trend in understory biomass and N accumulation in the wake of massive Norway Spruce [Picea abies (L.) Karst.] dieback caused by bark beetle attacks in Bavaria, Germany. As in this study, understory N pools in the German chronosequence study were substantially higher 15-20 years after the disturbance (100-126 kg N ha^{-1}), compared to intact (65 kg N ha^{-1}) or more recently disturbed spruce stands (44-66 kg N ha^{-1}) (Huber 2005).

Despite large variations among individual ecosystem components, overall biomass, and C and N content were remarkably similar among elevation bands. The coefficient of variation (CV) for overall biomass, 37%, was lower than the CV of individual forest components; overstory, 38%; small woody understory, 74%; large woody understory, 95%; herbaceous vegetation, 46%; and total understory, 56%. The CVs for N pools were lower, 27% for total N pools, and followed a trend similar to that of biomass.

Carbon and Nitrogen Fluxes

Current net biomass production rates of this system (7.3-8.0 Mg ha^{-1} yr^{-1}) were considerably higher than post-adelgid measurements at the Tower site (1.4-4.5 Mg ha^{-1} yr^{-1}, Johnson and Lindberg 1992), and reached the high end of pre-BWA measurements (4.5-8.5 Mg ha^{-1} yr^{-1}, Whittaker 1962, 1966). This would indicate that the overstory in this forest has recovered, or even increased its productivity since the mid-1980s.

Though the overstory contained the vast majority (97%) of living ecosystem biomass and C, it was responsible for only 77% of the biomass production, the majority as nonphotosynthetic tissues (bole, bark and branches) with relatively long turnover time (i.e., C sequestration). Overstory uptake of N also increased since the Barker et al. (2002) estimates (from 7.8 kg ha^{-1} in 1998 to 11.5 kg ha^{-1} in 2003). Productivity increases in aggrading forests or after disturbance due to the rapid expansion of foliage to capture critical light resources (Waring and Schlesinger 1985). The increased ability to take up N, an increase of 47% in 5 years, was another important sign that this system is recovering not only standing biomass and N, but also ecosystem processes.

Understory played an important role in N cycling, accounting for two-thirds of annual aboveground N uptake, especially by the herbaceous layer. There is only limited published understory N uptake data against which to compare our estimates, but the 18-21 kg N ha^{-1} yr^{-1} for the herbaceous uptake and 25-30 kg N ha^{-1} yr^{-1} for total annual understory N uptake were within the range of values (8-106 kg N ha^{-1} yr^{-1}) reported for these forests (Johnson and Lindberg 1992). Compared to mature trees, the woody understory had a higher proportion of their mass as photosynthetic needles and leaves

and were therefore more important to the N pools and fluxes in this system than to biomass. Herbaceous vegetation contained only a small proportion of total aboveground biomass (0.7%) and N (5.8%), but accounted for a disproportionately large amount of N uptake (51%) and was actually responsible for much of the annual N cycling in this forest. This was due to the fact that herbaceous vegetation must produce new aboveground tissue each year and this tissue contains a higher proportion of N-rich foliage compared to the other forest components. Through this seasonal biomass accumulation and turnover pulses, understory may stimulate internal N cycling (Welch et al. 2007) and curtail N leaching losses (Muller 2003) . In Bavarian spruce forests subject to similar stressors and disturbances as the high-elevation spruce-fir in the Appalachians (high atmospheric N inputs, insect-induced dieback), Huber (2005) had similarly noted while the net N uptake by understory vegetation was generally limited, this stratum nevertheless had a significant role in curtailing NO_3-N leaching losses. Lower NO_3-leaching in beech gaps at the Solling site in Germany, was similarly associated more abundant ground vegetation (Bauhus and Bartsch 1995). However, the small amount of biomass held in the understory makes this vegetation stratum less important in terms of long term sequestration of C or retention of N.

It appears that different elevation bands cycled biomass and nutrients differently. Similar to the pools, fir was more important to the sequestration of biomass and N at higher elevations, while birch showed the opposite trend. Overall, the overstory and the total live ecosystem uptake of N was significantly higher at the higher elevations, while biomass and C increments showed no trend with elevation.

The CV for ecosystem biomass production, 24%, is considerably lower than the CV of individual forest components; overstory, 35%; small woody understory, 95%; large woody understory, 79%; herbaceous vegetation, 46%; and total understory, 37%. Thus, the overall plot productivity appeared spatially more uniform than the productivities of the individual forest components or the distribution of standing biomass.

Estimates of productivity required several assumptions in the calculations. Error in overstory productivity (>5 cm DBH) is likely relatively small because we had discrete measurements at two time periods. The mass difference approach of determining production and uptake (Clark et al. 2001) was previously used in this watershed by Barker et al. (2002) in their analysis of variability in N pools and fluxes within the NDW, and it was necessary to use the same approach to compare our results to prior research. Production values for understory woody plants (<5 cm DBH) were determined using a BAR of 10, *i.e.* production was calculated as 10% of current biomass. This value was a conservative estimate based on the BAR of woody forest understory plants (Whittaker 1966, 1975; Alaback 1984). Actual production may have been somewhat higher depending on light and nutrient resources due to canopy openings. When estimating understory production, we assumed moss production to be one third of live biomass following Tamm (1953). We further assumed that because *Rubus* is semelparous, it generally produces total plant biomass over the course of two seasons; annual production was one half of total standing biomass. Realistically, individual *Rubus* stems may sprout, flower, set seed and die within one year or it may take three to five years depending on the individual. Hence, assuming production as 50% of standing stock may be an underestimate, but it seems to be the best available data.

Another source of potential error in our N uptake estimates is the resorption of nutrients between the aboveground and belowground portion of perennial herbaceous plants. Understory N uptake values may be overestimated because uptake rates calculated here are actually estimates of N requirement and assumed that N requirement was met entirely by N uptake. In reality, N requirement could have been met by N stored in their root systems as well as N assimilation from the soil and atmosphere. We need to account for N resorption to more accurately assess uptake by perennial forbs. Resorption rates of N during drought periods have reached 31-41% for grasses in a tallgrass prairie (Heckathorn and DeLucia 1994) and 58% for foliage of dry tropical tree species (Lal et al. 2001). Aerts (1996) performed a meta-analysis of nutrient resorption in forbs (n=33) and determined a N resorption efficiency of 41%. Based on these studies, as well as the fact that not all understory species in the southern Appalachian spruce fir are perennials, a broad assumption of 50% N resorption across all herbaceous species (annual and perennial) is probably a conservative estimate, as it is unlikely that herbaceous resorption would exceed that value. Even these conservative estimates of herbaceous N uptake (9.3 kg ha^{-1} yr^{-1} at 50% resorption) still approach our estimates of overstory N uptake (11.5 kg ha^{-1} yr^{-1}), and when other woody understory components are included, understory N uptake (16.3 kg ha^{-1} yr^{-1}) exceeds the overstory estimates. Though the ability of the understory component of this system to permanently sequester N may be limited, its ability to take up and recycle large amounts of N may keep these nutrients on site and represents a dynamic mechanisms of N retention. What is not known at this time is to what extent the high N deposition regime may alter the composition and the biogeochemical functioning of the understory in the future (see Gilliam 2006).

CONCLUSIONS

Nutrient cycling in this forest has changed, with 2003 overstory N uptake rates considerably greater than the 1998 rates reported by Barker et al. (2002). Neither the BWA nor other disturbances have significantly suppressed productivity of this site; production values are as high as or higher than pre-adelgid values. Forests in lower elevations appear to have completely recovered from the catastrophic effects of the BWA in terms of biomass and productivity. Upper elevation stands still have much recovery ahead of them, but the destructive effects of the BWA as well as subsequent windthrow mortality of exposed overstory spruce stems have decreased for now. It is hypothesized that the overstory will not decline below present biomass and C levels in the near future, and that this stratum has indeed begun to rapidly sequester more biomass and C.

Though conducted in a small catchment, this research provides important insight into the C and nutrient dynamics of post-BWA southern Appalachian spruce-fir forests. The understory of this system, especially the herbaceous layer, is very important to the overall productivity of this system. It serves a vital role in cycling nutrients as well as keeping nutrients on site. Though this understory offers little long-term storage of C, biomass and nutrients, the continual uptake and cycling of N are preventing additional N from being leached to streamwater. As this forest returns to pre-disturbance stand dynamics, the relationships between overstory and understory communities may shift. Future work should address the relationships between overstory, understory and site variables to determine how nutrient cycling in this forest may change in the future.

REFERENCES

Aber, J.D., Nadelhoffer, K.J., Steudler, P., and Melillo, J.M. 1989. Nitrogen Saturation in Northern Forest Ecosystems. BioScience, 39: 378-386.

Aber, J.D., McDowell, W.H., Nadelhoffer, K.J., Magill, A., Bernston, G., Kamakea, M., McNulty, S.G., Currie, W., Rustad, L., and Fernandez, I. 1998. Nitrogen saturation in temperate forest ecosystems: hypothesis revisited. BioScience, 48:921-934.

Aber, J.D., Goodale, C.L., Ollinger, S.V., Smith, M. L., Magill, A.H., Martin, M.E., and Stoddard, J.L. 2003. Is nitrogen altering the nitrogen status of northeastern forests? BioScience, 53:375-390.

Aerts, R. 1996. Nutrient Resorption from Senescing Leaves of Perennials: Are there General Patterns? Ecology, 84:597-608.

Alaback, P.B. 1984. Secondary succession following logging in the Sitka spruce-western hemlock forests of southeast Alaska: implications for wildlife management. Gen. Tech. Rep. PNW-173. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. Portland, OR.

Barker, M. 2000. The role of overstory nitrogen uptake as a sink of atmospheric deposition in southern Appalachian spruce-fir forests. M.S. thesis, Utah State University, Logan, Utah.

Barker, M., Van Miegroet, H., Nicholas, N. S., and Creed, I. F. 2002. Variation in overstory uptake in a small, high-elevation southern Appalachian spruce-fir watershed. Can. J. For. Res. 32:1-12.

Bauhus, J., and Bartsch, N. 1995. Mechanisms of carbon and nutrient release and retention in beech forest gaps. I. Microclimate, water balance and seepage water chemistry. Plant and Soil, 168-169:579-584.

Binkley, D., and Graham, R.L. 1981. Biomass, production, and nutrient cycling of mosses in an old-growth Douglas-fir forest. Ecology, 62:1387-1389.

Bockheim, J.G., and Leide, J.E. 1990. Estimating nutrient uptake in forest ecosystems. *In* Sustained Productivity of Forest Soils, Proceedings of the 7th North American Forest Soils Conference. *Edited by* S.P Gessel, Faculty of Forestry, Univ. of British Columbia, Vancouver. pp. 155-177.

Busing, R.T., and Clebsch, E.E.C. 1987. Application of a spruce-fir canopy model. For. Ecol. Manage. 20:151-169.

Busing, R.T. 2004. Red spruce dynamics in an old southern Appalachian forest. J. Torrey Bot. Soc. 131:337–342.

Clark, D.A., Brown, S.D., Kicklighter, W., Chambers, J.Q., Thomlinson, J.R., and Ni, J. 2001. Measuring net primary production in forests: concepts and field methods. Ecol. Appl. 11:356–370.

Crandall, D.L. 1960. Ground vegetation patterns of the spruce fir area of the Great Smoky Mountains National Park. Ecol. Monogr. 28:337-360.

Egerton-Warburton, L.M., and Allen, E.B. 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. Ecol. Appl. 10:484-496.

Fenn, M.E., Poth, M.A., Aber, J.D., Baron, J.S., Bormann, B.T., Johnson, D.W., Lemly, A.D., McNulty, S.G., Ryan, D.F., and Stottlemyer, R. 1998. Nitrogen excess in North American ecosystems: Predisposing factors, ecosystem responses, and management strategies. Ecol. Appl. 8:706-733.

Fenn, M.E., Baron, J.S., Allen, E.B., Rueth, H.M., Nydick, K.R., Geiser, L., Bowman, W.D., Sickman, J.O., Meixner, T., Johnson, D.W., and Neitlich, P. 2003 Ecological effects of nitrogen deposition in the western United States. BioScience, 53:391-403.

Forman, R.T. 1969. Comparison of coverage, biomass, and energy as measures of standing crop of bryophytes in various ecosystems. Bull Torrey Bot. Club, 96:582-591.

Gilliam, F.S. 2006. Responese of the herbaceous layer of forest ecosystems to excess nitrogen deposition. Ecology, 94:1176-1191.

Heckathorn S.A., and DeLucia, E.H. 1994. Drought-induced nitrogen retranslocation in perennial C4 grasses of tallgrass prairie. Ecology, 75:1877–1886.

Hollingsworth, R.G., and Hain, F.P. 1991. Balsam woolly adelgid (Homoptera: Adelgidae) and spruce-fir decline in the Southern Appalachians: assessing pest relevance in a damaged ecosystem. Florida Entomologist, 74:179-187.

Huber, C. 2005. Long lasting nitrate leaching after bark beetle attack in the highlands of the Bavarian Forest National Park. J. Environ. Qual. 34:1772-1779.

Johnson, D.W., and Lindberg, S.E. (*Editors*) 1992. Atmospheric deposition and nutrient cycling in forest ecosystems -- A synthesis of the integrated forest study. Springer-Verlag, New York.

Johnson, D.W., Van Miegroet, H., Lindberg, S.E., and Todd, D.E. 1991. Nutrient cycling in red spruce forests of the Great Smoky Mountains. Can. J. For. Res. 21:769-787.

King, P.B., Neuman, R.B., and Hadley, J.B. 1968. Geology of the Great Smoky Mountains National Park, Tennessee and North Carolina. U.S. Geol. Surv. Prof. Pap. 587.

Lal, C.B., Annapurna, C., Raghubanshi, A.S., and Singh, J.S. 2001. Effect of leaf habit and soil type on nutrient resorption and conservation in woody species of a dry tropical environment. Can. J. Bot. 79:1066–1075.

Lilleskov, E.A., Fahey, T.J., Horton, T.R., and Lovett, G.M. 2002. Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. Ecology, 83:104-115.

McCracken, R.J., Shanks, R.E., and Clebsch, E.E.C. 1962. Soil morphology and genesis at higher elevations of the Great Smoky Mountains. Soil Sci. Soc. Am. Proc. 26:384-388.

Muller, R.N. 2003. Nutrient relations of the herbaceous layer in deciduous forest ecosystems. *In* The herbaceous layer in forests of eastern North America. *Edited by* F.S. Gilliam and M.R. Roberts. Oxford University Press. New York. pp.15-37.

Nash, T.H., and Gries, C. 2002 Lichens as bioindicators of sulfur dioxide. *Symbiosis*. 33:1-22.

Nicholas, N.S. 1992. Stand structure, growth and mortality in southern Appalachian spruce-fir. Ph.D. dissertation, Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Nicholas, N.S., and Zedaker, S.M. 1989. Ice damage in Spruce fir forests of the Black Mountains, North Carolina. Can. J. For. Res.19:1487-1491.

Nicholas, N.S., Zedaker, S.M., and Eagar, C. 1992. A comparison of overstory community structure in three southern Appalachian spruce-fir forests. Bull. Torrey Bot. Club, 119:316-332.

Nodvin, S.C., Van Miegroet, H., Lindberg, S.E., Nicholas, N.S., and Johnson, D.W. 1995. Acidic deposition, ecosystem processes and nitrogen deposition in a high elevation southern Appalachian watershed. Water Air Soil Pollut. 85:1647-1652.

Oosting, H.J., and Billings, W.D. 1951. A comparison of virgin spruce-fir in the northern and southern Appalachian systems. Ecology, 32:84-103.

Pauley, E.F., Nodvin, S.C., Nicholas, N.S., Rose, A.K., and Coffey, T.B. 1996. Vegetation, biomass and nitrogen pools in a spruce-fir forest of the Great Smoky Mountains National Park. Bull. Torrey Bot. Club, 123: 318-329.

Pyle, C., and Schafale, M.P. 1988. Land use history of three spruce-fir forest sites in southern Appalachia. J For. Hist. 32:4-21.

Radford, A.E., Ahles, H.F., and Bell, C.R. 1968. Manual of the Vascular Flora of the Carolinas. University of North Carolina Press, Chapel Hill, NC.

Ramseur, G.S. 1960. The vascular flora of high mountain communities of the southern Appalachians. J. Mitchell Soc. pp. 82-112.

SAS Institute Inc. 2002. SAS User's Guide: Statistics, Version 9.0 Edition. SAS Institute Inc., Cary, NC.

Shanks, R.E. 1954. Climates of the Great Smoky Mountains. Ecology, 35:353-361.

Spruegel, D.G. 1983. Correcting for bias in log-transformed allometric equations. Ecology, 64:209-210.

Smith, G.F., and Nicholas, N.S. 1999. Post-disturbance spruce-fir stand dynamics at seven disjunct stands. Castanea, 64:175-186.

Smith, G.F., and Nicholas, N.S. 2000. Size and age class distributions of Fraser fir following balsam wooly adelgid infestation. Can. J. For. Res. 30:948-957.

Tamm, C.O. 1953. Growth, yield and nutrition in carpets of a forest moss (Hylocomium splendends). Meddelanden Statens Skogsforskningsinst. 43:1-140.

Van Miegroet H., Johnson, D.W., and Todd, D.E. 1993. Foliar response of red spruce saplings to fertilization with Ca and Mg in the Great Smoky Mountains National Park. Can. J. For. Res. 23:89-95.

Van Miegroet, H., Moore, P., Tewksbury C., and N.S. Nicholas. 2007. Carbon sources and sinks in high-elevation spruce-fir forests in the Southeastern US. Forest Ecol. Manage. 238:249-260.

Van Miegroet, H., Creed, I F., Nicholas, N.S., Tarboton, D.G., Webster, K.L., Shubzda, J., Robinson, B., Smoot, J., Johnson, D.W., Lindberg, S.E., Lovett, G., Nodvin, S., and Moore, S. 2001. Is there synchronicity in N input and out fluxes at the Noland Divide Watershed, a small N-saturated forested catchment in the Great Smoky Mountains National Park. The Scientific World, 1(S2):480-492.

Waring, R.H., and Schlesinger, W.H. 1985. Forest ecosystems: concepts and management. Academic Press, Orlando, FL.

Weaver, G.T. 1972. Dry matter and nutrient dynamics in red spruce-Fraser fir and yellow birch ecosystems in the balsam mountains, western North Carolina. Ph.D. Dissertation. University of Tennessee, Knoxville, TN.

Welch, N.T., Belmont, J.M., and Randolph, J.C. 2007. Summer ground layer biomass and nutrient contribution to above-ground litter in and Indiana temperate deciduous forest. Amer. Midl. Nat. 157:11-26.

White, P.S., MacKenzie, M.D., and Busing, R.T. 1985. Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests. Can. J. For. Res. 15: 233-240.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecology, 26:1-80.

Whittaker, R.H. 1962. Net production relations of shrubs in the Great Smoky Mountains. Ecology, 43:357-377.

Whittaker, R.H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology, 47:103-121.

Whittaker, R.H. 1975. Communities and ecosystems. MacMillan Publishers, New York. 385 pp.

Yarie, J. 1980. The role of understory vegetation in the nutrient cycle of forested ecosystems in the mountain hemlock biogeoclimatic zone. Ecology, 61:1498-1514.

Zedaker, S.M., and Nicholas, N.S. 1990. Quality assurance and methods manual for forest site classification and field measurements. U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, OR, EPA/600/3-90/082.

Table 3.1. Aboveground live pools of biomass (Mg ha^{-1}), carbon (Mg ha^{-1}) and nitrogen (kg ha^{-1}) for different forest components at three different elevation ranges within the Noland Divide Watershed of Great Smoky Mountain National Park (± standard deviation)

			Biomass			Carbon			Nitrogen		
			Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper
Overstory	*Abies*		4.63 ± 6.46b*	7.80 ± 6.24b	33.3 ± 26.0a	2.27 ± 3.17b	3.83 ± 3.06b	16.3 ± 12.7a	18 ± 25b	30 ± 24b	127 ± 100a
Vegetation	*Betula*		105 ± 111a	50.6 ± 56.1ab	7.26 ± 14.9b	51.6 ± 54.3a	24.8 ± 27.5ab	3.54 ± 7.28b	240 ± 246a	118 ± 128ab	18 ± 36b
>5 cm DBH	*Picea*		191 ± 90.6†	198 ± 111	152 ± 91.4	91.3 ± 43.3	94.9 ± 53.2	72.6 ± 43.7	307 ± 132	317 ± 166	243 ± 138
	Other		1.88 ± 2.15	1.70 ± 2.79	2.20 ± 3.02	0.901 ± 1.03	0.815 ± 1.34	1.05 ± 1.45	5 ± 5.6	4.6 ± 7.4	5.8 ± 8
Overstory Total			303 ± 103a	259 ± 102ab	195 ± 84.5b	146 ± 50.2a	124 ± 48.8ab	93.5 ± 40.3b	570 ± 206a	469 ± 160ab	394 ± 128b
Understory	*Abies*		1.73 ± 1.40	2.08 ± 2.93	3.35 ± 4.95	868 ± 702	1.050 ± 1.470	1.68 ± 2.49	17 ± 14	21 ± 29	33 ± 49
Vegetation	*Betula*		0.106 ± 0.463	0.294 ± 0.491	0.201 ± 0.431	55 ± 238	151 ± 253	0.103 ± 0.221	1 ± 4.3	2.8 ± 4.6	1.9 ± 4
2-5 cm DBH	*Picea*		1.01 ± 1.16	1.24 ± 2.28	1.07 ± 1.28	517 ± 593	637 ± 1.170	0.550 ± 0.654	8.4 ± 10	10.3 ± 19	8.9 ± 11
	Other		.928 ± 1.16	.930 ± 1.89	0.481 ± 0.613	463 ± 578	465 ± 940	0.242 ± 0.312	7.6 ± 9.4	7.7 ± 15	4.1 ± 5.5
	Total		3.77 ± 1.53	4.55 ± 4.45	5.10 ± 5.71	1.900 ± 776	2.300 ± 2.250	2.58 ± 2.88	34 ± 14	41 ± 41	48 ± 56
Understory	*Abies*		0.479 ± 0.779	0.795 ± 1.05	1.05 ± 1.41	0.241 ± 0.392	0.400 ± 0.527	0.525 ± 0.711	4.8 ± 7.7	7.9 ± 10	10 ± 14
Vegetation	*Betula*		0.031 ± 0.063	0.013 ± 0.040	0.013 ± 0.039	0.016 ± 0.032	0.006.8 ± 0.021	0.0067 ± 0.020	0.3 ± 0.6	0.1 ± 0.4	0.1 ± 0.4
<2 cm DBH	*Picea*		1.71 ± 2.09a	0.752 ± 1.10ab	0.196 ± 0.139b	0.875 ± 1.07a	0.386 ± 0.563ab	0.100 ± 0.071b	14 ± 17a	6.2 ± 9.1ab	1.6 ± 1.2b
	Other		2.46 ± 3.21	1.06 ± 1.18	1.57 ± 2.67	1.23 ± 1.61	0.527 ± 0.586	0.779 ± 1.32	20 ± 27	8.6 ± 10	12 ± 21
	Total		4.68 ± 4.44	2.62 ± 1.73	2.83 ± 3.96	2.36 ± 2.24	1.32 ± 0.873	1.41 ± 1.97	39 ± 37	23 ± 15	25 ± 34
Herbaceous			1.64 ± 0.518	1.74 ± 1.04	1.98 ± 0.897	0.745 ± 0.239	0.815 ± 0.503	0.946 ± 0.438	32 ± 10	34 ± 20	39 ± 17
Understory Total			10.0 ± 4.90	8.91 ± 4.95	9.90 ± 6.84	5.00 ± 2.49	4.43 ± 2.50	4.94 ± 3.44	105 ± 41	99 ± 48	112 ± 64
Ecosystem Total			313 ± 102a	267 ± 101ab	204 ± 83.3b	151 ± 49.7a	129 ± 48.5ab	98.4 ± 39.8b	675 ± 198a	567 ± 153ab	506 ± 128b

* Different letters indicate statistical differences ($p<0.05$) among elevation bands for each species or forest component

† When there were no statistical differences, no letters were used

Table 3.2. Predictive biomass equation for herbaceous vegetation in the form y = ax where y = species biomass (g), a = coefficient, and x = estimated percent cover

Species	Number of observations	a	r^2	Standard error of Estimate (g)
Aconitum uncinatum	7	1.293	0.980	0.076
Arisaema triphyllum	12	0.504	0.760	0.085
Aster sp.	15	0.919	0.907	0.079
Chelone lyoni	13	1.439	0.794	0.211
Clintonia borealis	15	0.699	0.950	0.043
Cimicifuga americana	12	0.590	0.932	0.048
Dryopteris campyloptera	16	1.257	0.883	0.118
Eupatorium rugosum	14	1.294	0.856	0.148
Galium triflorum	12	0.583	0.912	0.055
Grass	16	2.012	0.891	0.182
Houstonia serpyllifolia	12	1.246	0.973	0.063
Impatiens pallida	13	0.865	0.872	0.096
Laportea canadensis	12	0.723	0.865	0.086
Lycopodium sp.	12	4.793	0.946	0.346
Monarda didyma	12	1.466	0.941	0.111
Moss	16	4.636	0.942	0.298
Oxalis acetosella	14	0.309	0.968	0.016
Prunella vulgaris	13	0.910	0.886	0.094
Rubus canadensis	15	9.108	0.900	0.811
Rudbeckia laciniata	12	2.395	0.965	0.138
Solidago glomerata	13	0.939	0.833	0.121
Sambucus pubens	12	1.410	0.863	0.169
Senecio rugelia	21	0.979	0.960	0.045
Tiarella cordifolia	11	0.666	0.930	0.058
Trillium sp.	8	0.634	0.927	0.067
Viola sp.	12	0.403	0.972	0.021

Table 3.3. Predictive biomass equation information for small woody understory vegetation in the form y = ln(a+bx), where y = biomass, a = intercept, b = coefficient, and x = stem caliper at 15 cm above ground level

Species	Number of observations	a	b	r^2	Standard error of Estimate (g)	cf
Abies fraseri	10	3.199	1.144	0.780	0.215	1.02
Betula lutea	8	1.148	2.435	0.879	0.368	1.07
Picea rubens	10	2.269	1.755	0.876	0.234	1.03
Viburnum alnifolium	10	1.512	2.143	0.930	0.207	1.02

Table 3.4. Aboveground production of biomass and carbon and uptake of nitrogen (kg ha^{-1} yr^{-1}) for different forest components at three different elevation ranges within the Noland Divide Watershed of Great Smoky Mountain National Park (± standard deviation)

			Biomass			Carbon			Nitrogen		
			Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper
Overstory		*Abies*	280 ± 800b*	550 ± 754b	2,480 ± 2,410a	137 ± 393b	270 ± 370b	1,220 ± 1,180a	1.1 ± 3b	2.1 ± 2.9b	9.7 ± 9.3a
Vegetation		*Betula*	1,810 ± 1,870a	656 ± 774b	220 ± 395b	889 ± 922a	321 ± 380b	108 ± 193b	4.1 ± 4.1a	1.5 ± 1.8b	0.5 ± 0.9b
>5 cm DBH		*Picea*	3,840 ± 1,610†	4,050 ± 2,440	2,840 ± 1,640	1,830 ± 769	1,930 ± 1,160	1,360 ± 785	5.9 ± 2.2	6 ± 3	4.3 ± 2.3
		Other	80 ± 114	71 ± 152	57 ± 106	38 ± 54	34 ± 73	28 ± 51	0.2 ± 0.3	0.2 ± 0.4	0.2 ± 0.3
Overstory Total			6,010 ± 1,530	5,320 ± 2,660	5,600 ± 1,670	2,900 ± 748	2,560 ± 1,280	2,710 ± 820	11.2 ± 3.5b	9.8 ± 4.6b	14.6 ± 7.5a
Understory		*Abies*	173 ± 140	208 ± 293	335 ± 495	87 ± 70	105 ± 147	168 ± 249	1.7 ± 1.4	2.1 ± 2.9	3.3 ± 4.9
Vegetation		*Betula*	11 ± 46	29 ± 49	20 ± 43	5 ± 24	15 ± 25	10 ± 22	0.1 ± 0.4	0.3 ± 0.5	0.2 ± 0.4
2-5 cm DBH		*Picea*	101 ± 116	124 ± 228	107 ± 128	52 ± 59	64 ± 117	55 ± 65	0.8 ± 1	1 ± 1.9	0.9 ± 1.1
		Other	93 ± 116	93 ± 189	48 ± 61	46 ± 58	47 ± 94	24 ± 31	0.8 ± 0.9	0.8 ± 1.5	0.4 ± 0.6
		Total	377 ± 153	455 ± 445	510 ± 571	190 ± 78	230 ± 225	258 ± 288	3.4 ± 1.4	4.1 ± 4.1	4.8 ± 5.6
Understory		*Abies*	48 ± 78	79 ± 105	104 ± 141	24 ± 39	40 ± 53	53 ± 71	0.5 ± 0.8	0.8 ± 1	1 ± 1.4
Vegetation		*Betula*	3.1 ± 6	1.3 ± 4	1.3 ± 4	1.6 ± 3	0.7 ± 2	0.7 ± 2	0 ± 0.1	0 ± 0	0 ± 0
<2 cm DBH		*Picea*	171 ± 209a	75 ± 110ab	20 ± 14b	88 ± 107a	39 ± 56ab	10 ± 7b	1.4 ± 1.7a	0.6 ± 0.9ab	0.2 ± 0.1b
		Other	246 ± 321	106 ± 118	157 ± 266	123 ± 161	53 ± 59	78 ± 132	2 ± 2.7	0.9 ± 1	1.2 ± 2.1
		Total	468 ± 444	262 ± 173	283 ± 396	236 ± 224	132 ± 87	141 ± 197	3.9 ± 3.7	2.3 ± 1.5	2.5 ± 3.4
Herbaceous			880 ± 303	925 ± 538	1,030 ± 479	396 ± 134	436 ± 258	491 ± 232	17.7 ± 6.3‡	18.7 ± 10.4‡	20.9 ± 9.5‡
Understory Total			1,730 ± 496	1,640 ± 706	1,830 ± 778	823 ± 245	798 ± 346	890 ± 388	25.0 ± 6.2	25.1 ± 11.2	28.2 ± 10.4
Ecosystem Total			7,730 ± 1,310	6,970 ± 2,500	7,430 ± 1,070	3,720 ± 638	3,360 ± 1,210	3,600 ± 522	36.2 ± 5.8b	34.9 ± 10.4b	42.8 ± 7.6a

* Different letters indicate statistical differences ($p<0.05$) among elevation bands for each species or forest component

† When there were no statistical differences, no letters were used

‡ Values include potential resorption

CHAPTER 4

USING SILVICULTURE TO INFLUENCE CARBON SEQUESTRATION IN SOUTHERN APPALACHIAN SPRUCE-FIR FORESTS [5,6]

ABSTRACT

Enhancement of forest growth through silvicultural modification of stand density is one strategy for increasing carbon (C) sequestration. Using the Fire and Fuels Extension of the Forest Vegetation Simulator, the effects of even-aged, uneven-aged and no-action management scenarios on C sequestration in a southern Appalachian red spruce-Fraser fir forest were modeled. We explicitly considered C stored in standing forest stocks and the fate of forest products derived from harvesting. Over a 100-year simulation period the even-aged scenario (250 Mg C ha^{-1}) outperformed the no-action scenario (241 Mg C ha^{-1}) in total carbon (TC) sequestered. The uneven-aged scenario approached 220 Mg C ha^{-1}, but did not outperform the no-action scenario within the simulation period. While the average annual change in C (AAC) of the no-action scenario approached zero, or carbon neutral, during the simulation, both the even-aged and uneven-aged scenarios surpassed the no-action by year 30 and maintained positive AAC throughout the 100-year simulation. This study demonstrates that silvicultural treatment of forest stands can increase potential C storage, but that careful consideration of: (1) accounting method (*i.e.*, TC *versus* AAC); (2) fate of harvested products and; (3)

---

[5] This chapter appeared in the journal Forests as: Moore, P.T., R.J. DeRose, J. Long and H. Van Miegroet. 2012. Using silviculture to influence carbon sequestration in southern Appalachian spruce-fir forests. Forests 3:300-316. doi:10.3390/f3020300

[6] Coauthored by Patrick T. Moore, R. Justin DeRose, James N. Long and Helga Van Miegroet.

length of the planning horizon (e.g., 100 years) will strongly influence the evaluation of C sequestration.

INTRODUCTION

As global awareness of the effects of climate change increases (Metz *et al.*, 2007), so will the importance of management strategies for terrestrial ecosystems that maximize atmospheric/global CO_2 mitigation (Ryan *et al.*, 2010). Though there is some debate over how managed forests sequester carbon (C) relative to their old-growth counterparts (Skog and Nicholson, 1998; Harmon and Marks, 2002; Luyssaert *et al.*, 2008), managed forests have been shown to make valuable contributions to C sequestration efforts (Van Deusen, 2010; Miner, 2006; Hoover and Heath, 2011). While managed forests are not expected to contain as much standing C as old-growth forests on similar sites, managed forests could potentially sequester more C when both live biomass and harvested biomass are considered, and depending on the fate of harvested biomass (e.g., biofuel *versus* structural wood products; Van Deusen, 2010; Sorenson *et al.*, 2011). Furthermore, if the rate of growth for live biomass is increased by active management for wood products, the potential C sequestration rates in managed forests might be increased. This begs the question, what role can silviculture play in the long-term C sequestration potential of forests?

Numerous factors influence growth and biomass accumulation as well as potential standing C pools in forested systems. These factors include site quality (Keyser, 2010), stage of stand development (Long and Smith, 1984) and stand composition (Long and Shaw, 2010), forest type and disturbance regime (Ryan *et al.*, 2010). Realistically, one

cannot control site quality; however, silviculturists can modify stand structure, species composition, and stand density. This allows the direct control of stand developmental stage and growing stock potential, and therefore rates of C sequestration. By maintaining stand stocking within a desired range of relative stand density associated with various levels of growth potential (*i.e.*, maximum tree growth *versus* maximum stand growth; Long, 1985), silviculturists can potentially influence the rate of C sequestration.

In the southeastern United States, southern Appalachian red spruce (*Picea rubens* Sarg.)–Fraser fir (*Abies fraseri* Pursh.) forests were historically heavily cut over (Korstian, 1937) and, although productive (7.7 Mg biomass ha^{-1} yr^{-1}, see Chapter 2), these spruce-fir forests can either be C sinks or C sources depending on the management regime, the dynamics of snags or coarse woody debris (see Chapters 2 and 3; Fahey, 2010) or natural disturbance regimes. Historically, hurricane-induced windthrow and ice storm damage were responsible for gap-phase dynamics in these forests (Nicholas, 1992). In the last two decades southern Appalachian spruce-fir forests have been heavily influenced by a catastrophic insect outbreak of the non-native balsam wooly adelgid (BWA; *Adelges piceae* (Ratzeburg)). As a result of the BWA the high elevation spruce-fir forests of the southern Appalachians have experienced higher disturbance-related mortality and have been set back to an earlier stage of stand development. In recent years the aboveground components of this system have shown a substantial increase in standing biomass (see Chapter 2).

The vast majority (74%; Dull *et al.*,1988) of southern Appalachian spruce-fir forests are within the boundaries of Great Smoky Mountains National Park, where active forest management has been precluded since National Park designation in 1943. It is therefore

impossible to directly determine the effect of various management scenarios on C sequestration. However, modeling approaches provide an excellent vehicle to estimate the effects of hypothetical management treatments on C sequestration (*sensu* Harmon and Marks, 2002; Sorenson *et al.,* 2011). There are several C accounting tools available to land managers and researchers and guidelines have been established to assist with field data collection and C accounting methods (Pearson *et al.,* 2007; Hoover, 2008). Smith *et al.,* (2006) provided estimates of standing C stocks for several forest types as a function of stand age and included a methodology for assessing the effects of harvesting on C sequestration. Although these estimates cannot incorporate stand-specific data, they are readily available and easy to use. The Carbon Online Estimator relies on USFS Forest Inventory and Analysis (FIA) data and can produce standing C pool as well as growth and yield estimates at the county scale and larger (Van Deusen and Heath, 2012). The US Forest Carbon Calculation Tool also relies on FIA data and can provide state and national estimates of stored C (Smith *et al.,* 2006). The most recent version of the US Forest Carbon Budget Model also relies mainly on FIA data. This model generates easily interpretable and useful outputs but the data input process can be complicated and may require a user with advanced programming skills.

The Forest Vegetation Simulator (FVS) is an individual-tree distance independent growth and yield model that is widely used by managers and researchers to model forest change and stand dynamics over time in response to management activities (Crookston and Dixon, 2005). FVS allows the input and analysis of user-collected stand data and produces easily interpretable output through the Suppose graphical user interface. In addition, FVS can track the simulation of various management scenarios at the tree- or

stand-level for a user-specified time interval. Recently, C accounting has been incorporated into FVS through the Fire and Fuels Extension (FFE; Reinhardt *et al.,* 2007; Hoover and Rebain, 2011). Although publicly available and easily implemented, relatively few studies have utilized FVS-FFE to assess the long-term temporal dynamics of C sequestration at the stand-level (but see Hurteau *et al.,* 2008; Hurteau and North, 2009).

The goal of this research is to simulate the possible effect of silvicultural activities on long-term C storage potential of managed forests compared to their unmanaged counterparts using a large comprehensive re-measurement data set from the Great Smoky Mountains. By pairing this data set with FVS, we attempt to provide a straightforward demonstration that active management may well be a better strategy for C sequestration than passive management. Current greenhouse gas accounting protocols require any management action intended to offset CO_2 emission to exhibit "additionality", *i.e.,* to be additional to the "business-as-usual" scenario (Malmshimer *et al.,* 2011). Carbon accounting protocols further require management-caused changes in carbon stocks to be assessed over a 100-year planning horizon (Broekhoff *et al.,* 2009). The potential influence of silvicultural activities on the C sequestration potential of southern Appalachian spruce-fir forests was examined using FVS-FFE to simulate forest growth and associated C dynamics for 100 years under three scenarios: (1) a no-action scenario (*i.e.*, business-as-usual); (2) an even-aged silvicultural system; and (3) an uneven-aged silvicultural system. Total C sequestration (TC) and the average annual changes in C sequestration (AAC; Hoover and Rebain, 2011) are calculated to compare the three scenarios. While TC demonstrates the overall difference in C sequestration between

management practices over the life of a project or rotation, AAC can be used to demonstrate the additional C sequestered on an annual basis and has application in C accounting protocols such as the Regional Greenhouse Gas Initiative (RGGI, 2012). We hypothesize the no-action scenario will exhibit the highest TC, but that the even-aged management scenario will exhibit the highest positive AAC.

METHODS

Study Area

Data for the study were collected in the Noland Divide Watershed (NDW, 35°34'N, 83°29'W) a 17.4 ha, high elevation catchment within Great Smoky Mountain National Park. This catchment was chosen because of the broad elevation gradient (1700–1910 m) and resulting variability in overstory species composition thought to represent much of the range of forest conditions occurring within southern Appalachian spruce-fir forests. Access to previously collected data as well as a pre-existing plot infrastructure allowed improved modeling and interpretation of model results through control of some potentially confounding factors (parent material, aspect, and climate). The NDW is dominated by red spruce at lower elevations transitioning into Fraser fir at higher elevations with a component of yellow birch (*Betula alleghaniensis* Britton) and various other hardwoods distributed across the range of elevations. The NDW has not been impacted by logging or fire (Pyle, 1988), but has been severely impacted by the BWA (Barker *et al.*, 2002; Pauley and Clebsch, 1990) and wind related events (see Chapter 3; Nicholas, 1992). The soils are mainly Inceptisols, occasionally with spodic characteristics (McCracken *et al.*,1962; Van Miegroet *et al.*,1993), are generally shallow, (<50 cm depth

to bedrock) and have a silt loam to sandy loam texture (Van Miegroet *et al.,* 2007). Precipitation is >200 cm annually and is distributed evenly throughout the year (Johnson *et al.,* 1991). Mean air temperatures range from −2 °C in February to 17 °C in August with a frost-free period from May through September (Johnson *et al.,*1991, Shanks, 1954).

Data Collection

Overstory forest inventories were performed in the NDW in 1993, 1998 and 2003 on a system of 50–400 m^2 plots stratified along a series of nine elevation bands (1700, 1725, 1755, 1785, 1800, 1835, 1865, 1890 and 1910 m, Figure 2.1). For the analysis, these are divided into three elevation groups; low (1700, 1725 and 1755 m, 19 plots), medium (1785, 1800 and 1835 m, 19 plots) and high (1865, 1890, and 1910 m, 12 plots). All trees ≥5 cm diameter at breast height (DBH, 1.37 m) were measured using protocols described by Zedaker and Nicholas (1990), and tagged with a permanent and unique ID tag. Species, DBH, and status (live or dead) of each overstory tree were recorded. In 1998 and 2003, ingrowth was tagged as trees entering the 5-cm diameter class. Live trees that had fallen since the last inventory were considered windthrow. On each plot in 2003, all trees >2 cm and <5 cm DBH were sampled on a system of 4–16 m^2 subplots in order to estimate saplings. Trees <2 cm DBH were sampled on a system of 16–1 m^2 nested plots within each 16 m^2 sapling subplot and averaged across elevation bands in order to estimate natural regeneration (see Chapter 2).

Data Preparation

Although the southern variant of FVS (SN-FVS) is capable of running simulations with very limited data (e.g., DBH, species; Keyser, 2008), additional tree and stand information can improve model estimates (e.g., height, diameter increment, site index; Dixon, 2002). Also, while included in the western variants, the eastern variants of FVS have not yet been modified to take into account forest dynamics under climate change (*i.e.*, Climate-FVS). SN-FVS has not been explicitly evaluated for spruce, fir or yellow birch; however, it has been validated and analyzed for other species (DeRose *et al.*, 2008; Vacchiano *et al.*, 2008; Herring, 2007) that displayed its ability to effectively simulate stand dynamics. Trees in the NDW watershed are generally shorter than in other southern Appalachian (or nearby) spruce-fir forests (Barker *et al.*, 2002). To estimate tree height for red spruce, Fraser fir and yellow birch, we used site-specific allometric equations fit from the height-diameter data from Barker *et al.* (2002). This resulted in at least three modeled individual tree heights for each species, on any given plot, the minimum necessary for SN-FVS to modify height growth to reflect local conditions. In addition, SN-FVS will modify the large-tree (>7.6 cm DBH) growth model to reflect local conditions if the user specifies the diameter increment for 3 or more individuals of a given species on a particular plot in the input data (Dixon, 2002). We calculated 1998–2003 diameter increment for all live sampled trees measured during both the 1998 and 2003 inventories, assuming bark thickness was constant, and included them in our FVS input tree list. While assuming constant bark thickness potentially introduces bias, this will not affect comparisons between scenarios. In addition, 5-year changes in bark are

likely to be marginal. To incorporate natural regeneration into each management scenario, when appropriate, we calculated average understory stocking (stems/ha) for each of the dominant tree species in each of the three elevation groups from the 1 m^2 subplots. SN-FVS uses site index (height in feet at base age 50, SI) to model the site productivity potential of individual stands. Because site index was not measured in the field, we incorporated the influence of site quality into the model simulations by identifying a range of SIs consistent with Nicholas and Zedaker (1992). Simulations for each elevation band (low, medium, high) were run for each of three SIs. The SI range for each elevation group was: low elevation (60, 65 and 70); medium elevation (55, 60 and 65); and high elevation (55, 60 and 65).

Silvicultural Scenarios

We used the 2003 data as the starting point for each of the silvicultural scenarios and ran 100-year simulations (2003–2103). For each scenario the CarbCalc keyword was used to set C accounting parameters. Parameters selected included the base FVS biomass equations, default decay rates, and model output in Mg ha^{-1}. The CarbRept keyword was used to generate a C report every 5 years for 100 years while the CarbCut keyword was used to generate a harvested C report every 5 years, and finally the SiteCode keyword was used to vary the SI above for each elevation group.

In the no-action scenario, stands were able to develop without the effect of management activities. Stand density index (SDI) maximum was constrained at 460. All calculations of SDI were done within FVS, which uses a summation method (Dixon, 2002). Standing dead trees fell and decayed according to default model parameters.

Although in this scenario the measured understory data from the 2003 inventory were included during the 2003 time step, no additional understory trees were added during the simulation period. Theoretically, fully stocked stands would not promote the establishment of understory trees, or allow their ascension to the canopy (Smith *et al.*, 1997). While in actuality some regeneration is likely to occur over a 100-yr scenario, we made the simplifying assumption that no disturbance or gaps promoting establishment would occur over the scenario in lieu of arbitrarily adding regeneration.

Under the even-aged scenario we sought to control stand density so as to maintain "full-site occupancy" and avoid substantial density-related mortality (Long, 1985). Plot level SDI was maintained between 45% (207) and 60% (276) of maximum SDI through simulated harvesting using a conditional statement in the ThinSDI keyword. Although in this scenario we included the measured understory data from the 2003 inventory during the 2003 time step, we did not add any additional understory during the simulation period. This scenario simulates a series of commercial thinning, which should not typically result in establishment of understory trees, or allow their ascension to the canopy (Smith *et al.*, 1997).

For the uneven-aged scenario, we relaxed the constraint to maximize stand growth, while simultaneously seeking to build the structural attributes of an uneven-aged or late successional spruce-fir forest exhibiting gap-phase dynamics. In this scenario, the Uneven-aged Management Action option in FVS was used to implement an individual tree selection system that constrained SDI between 45% and 60% of maximum SDI (207–276). Residual stocking was distributed, expressed as SDI, relatively evenly across the DBH classes. Simply thinning within each DBH class to the desired SDI may

excessively reduce stocking over time because some DBH classes may be initially deficit. The Uneven-aged Management Action adjusts for this by detecting deficit size classes and allowing additional trees to remain in the adjacent lower DBH classes in order to achieve the target SDI for the plot. A Liocourt or diminution coefficient (q) of 1.3 between each of the 8-12.7 cm DBH classes was used to push the stand DBH distribution toward a negative exponential or reverse J-shape over time. Our initial estimates of understory stocking were input into FVS on a 5-year cycle.

Carbon Accounting

Carbon pools were estimated from the Stand Carbon Report and the Harvested Carbon Report generated by FFE. These two reports include C pools consistent with the Intergovernmental Panel on Climate Change Good Practice Guidance (Penman *et al.*, 2000) for national greenhouse gas inventories (Hoover and Rebain, 2011). FFE C estimates are produced by multiplying standard FVS dry weight biomass estimates for all pools by 0.5 (assumed 50% C) except for the forest floor pool which is converted using 0.37 (Smith *et al.*, 2006; Hoover and Rebain, 2011). Soil C is not accounted for in FFE. TC was calculated as the sum of all reported forest carbon from the Stand Carbon Report. This includes dynamic predictions for the following C pools: total aboveground live, merchantable aboveground, standing dead, belowground live, belowground dead, down dead, duff, litter herbs and shrubs using methods described in Reinhardt *et al.* (2007). Calculation methods for C pools were held constant across all scenarios in order to more fairly test the effects of silvicultural manipulation on C sequestration. Any C removed during thinning is reported in the Harvested Carbon Report including the following C

pools: forest products in use, products in landfills, and C emitted from combustion with and without energy capture. These pools were accounted for following the decay fates for harvested products in Smith *et al.* (2006). Although protocols exist to explicitly monitor the products and their inefficiencies (e.g., the CO_2Fix model; Perez-Cruzado *et al.*, 2012) the FFE accounting system is built-in to the FVS framework, follows international C sequestration protocols (Reinhart *et al.*, 2007) and is most likely to be used by forest managers.

To compare TC between silvicultural scenarios we added total standing carbon to harvested carbon in wood products for each plot and each 5-year time step before averaging over plots in each elevation and SI group. By only including the harvested carbon in wood products we effectively remove C that is only stored short-term or is released as emissions due to the decay of forest products and energy required to transport the C out of the forest. Average annual change in C sequestration (AAC) was calculated as the 5-year difference in total C (calculated above) for the 100-year simulation (Hoover and Rebain, 2011). Results for TC and AAC were plotted over time to compare potential C sequestration by management scenario. To account for additionality (Huang and Sorenson, 2011), we compared the AAC for the two management scenarios relative to the no-action scenario. This gives an indication of the patterns of relative increases (positive) or decreases (negative) in potential C sequestration when deviating from the no-action, or “business-as-usual” scenario.

RESULTS

Total Carbon Sequestration

Although we modeled a range of SIs within each elevation group to test the influence of site quality on C sequestration, the effect was minimal (coefficient of variation = 12.9–17% by the end of the 100-year simulation) and the variation occurred in an expected manner. That is, between elevation bands productivity increased with decreasing elevation, and within each elevation band, productivity increased with increasing SI, as expected. Therefore, results are only presented for the middle SI value in each elevation group. TC in the no-action scenario increased rapidly during the first part of the simulation period for each elevation group before leveling off towards the end of the simulation (Figure 4.1). This value increased from 174, 152 and 132 Mg ha^{-1} in the low, medium and high elevation band, respectively, and approached a maximum in 2103 of 242, 227 and 198 Mg ha^{-1} in the low, medium and high elevation band, respectively.

In the even-aged scenario, initial TC (total C sequestered in biomass and forest products) was slightly lower than the no-action scenario due to the effects of harvesting at the beginning of the simulation. This value increased from 161, 141 and 123 Mg ha^{-1} in the low, medium and high elevation bands, respectively, and continued with a positive slope throughout the simulation period, reaching a value of 250, 231 and 211 Mg ha^{-1} in the low, medium and high elevation bands, respectively, by the end of the simulation period (2103).

In the uneven-aged scenario, TC similarly began slightly lower than the no-action scenario due to the effects of harvesting at the beginning of the simulation. Sequestration

increased from 163, 143 and 124 Mg ha^{-1} in the low, medium and high elevation band, respectively, through the simulation period with 220, 204 and 193 Mg C ha^{-1} sequestered by the end of the simulation period in 2103. These values were well below those obtained in the even-aged scenario, which resulted in highest TC values by the end of the simulation period.

Results from the even-aged scenario were further broken down into 3 major categories in order to demonstrate the fate of various C components in our accounting (Figure 4.2). The standing C category represented the C stored in the forest. The forest products category represented additional C stored in forest products produced from material removed from the forest over time. These two components together comprised the TC sequestration of the scenario. In addition, a cumulative emissions category represented C lost as emissions from the decomposition of the forest products category. Across the three elevation bands, standing C, products, and emissions accounted for approximately 51%, 34% and 15%, respectively, of the C accounted for over the simulation period.

Average Annual Change in Carbon

The AAC (average annual change in C sequestered in biomass and forest products) during the no-action scenario immediately decreased from 3.4, 3.5 and 3.7 Mg ha^{-1} yr^{-1}, approaching zero in all elevation bands (Figure 4.3). In the even-aged scenario, AAC began low (0–1 Mg ha^{-1} yr^{-1}) due to the effect of reduced stocking, and reached a maximum at 1.6, 1.6, and 1.2 Mg ha^{-1} yr^{-1} in the 2053–2058 time period, before they stabilized towards the end of the simulation at 0.8, 0.7 and 0.6 Mg ha^{-1} yr^{-1} at the low,

medium and high elevation bands, respectively. In the uneven-aged scenario, AAC also began low (−0.1 to 0.3 Mg ha^{-1} yr^{-1}) due to the effect of reduced stocking, reached a plateau at 0.9, 0.9 and 1.3 Mg ha^{-1} yr^{-1} in the 2018–2033 time period, and stabilized at 0.4, 0.5 and 0.4 Mg ha^{-1} yr^{-1} at the low, medium and high elevation band, respectively.

DISCUSSION

Using a forest growth and yield model (FVS) we have demonstrated that silvicultural manipulation can yield improvement in C sequestration over the no-action (*i.e.*, business-as-usual) scenario. By controlling stand density and stand development, it should be possible to increase C sequestration. The amount of predicted C sequestered varied by silvicultural scenario (*i.e.*, even-aged or uneven-aged). It is especially noteworthy that whether a silvicultural scenario actually was predicted to have met the additionality objective (*i.e.*, an improvement over no-action) over the mandatory 100-year planning horizon depended primarily on how additional C sequestration was assessed. For example, if just considering TC, *i.e.*, C pool size, dense, older stands would likely be considered the largest C pools. On the other hand, if the focus was on AAC, *i.e.*, the rate of C accumulation, young, rapidly growing stands are likely to accumulate C faster, even if their TC is lower (Kolari *et al.*, 2004). Furthermore, accounting for the fate of harvested material (*i.e.*, percent in long-term storage) will influence the assessment of managed and no-action scenarios with respect to long-term C sequestration.

In this study the even-aged scenario marginally outperformed the no-action scenario in TC sequestration over the 100-year time period for all three elevation bands. This demonstrated that silvicultural manipulation including commercial harvest can be an

effective tool for sequestering C over time when wood harvested for long-term products is included in the analysis. Although the increased TC of this scenario over the no-action was manifest after nearly 100 years, it emphasizes the importance of timely implementation in order to achieve future results. The uneven-aged scenario did not outperform the no-action scenario during the simulation period in terms of TC sequestration. It did, however, come close, and would likely surpass the no-action scenario over a longer time period.

In terms of AAC, both the even-aged and uneven-aged scenarios outperformed the no-action scenario within 20–30 years and continued to outperform the no-action scenario for most of the simulation period. While decay fates of forest products will likely determine how long AAC will remain positive, the end-of-rotation harvest in the even-aged scenario would temporarily create a carbon source (Kolari *et al.*, 2004). Unlike comparisons of TC, calculating AAC takes into account the fact that the silviculture scenarios include periodic reductions in stand stocking due to thinning schedules. In contrast with TC, comparisons of AAC between the no-action and the silvicultural scenarios highlight the potential benefits of management. The somewhat modest gains in TC, which did not occur until well into the 100-year simulation, mask what were actually important management-induced changes in sequestration (wood products) and growth rate (increased subsequent growth due to density regulation) that translated into much higher AAC for the managed stands. In other words, by calculating AAC, we accounted for the fact that the no-action scenario, although starting with higher TC, had a relatively slow rate of C increase over time in comparison to managed stands.

That we found potential increases in C sequestration as a result of silvicultural intervention is especially noteworthy, as the spruce-fir forest type is likely not the ideal candidate for C sequestration. For example, the large amounts of decaying organic matter created as a result of the BWA has been documented for this spruce-fir forest (Van Miegroet *et al.*, 2007) and could lead to the release of CO_2 into the atmosphere. Therefore, if incorporated into the analysis, forest response to a disturbance like BWA could potentially affect C sequestration trajectories when compared to an undisturbed spruce-fir ecosystem. Therefore, other forest types with lower amounts of decaying organic matter might exhibit a stronger C sequestration effect in response to silvicultural activities. In general, decadent forests with high levels of standing C but little net C accumulation may provide the greatest potential for C sequestration through silvicultural intervention (Malmshimer *et al.*, 2011; Odum, 1969); however, implementing management in older forests of all types may be difficult given their potential old-growth status. Converting decadent stands to younger and more vigorous stands (*i.e.*, below the zone of imminent density-dependent mortality; Drew and Flewelling, 1977), could potentially increase sequestered C, in the form of both forest products and increased growth, from many currently unmanaged forests. In addition, Keyser (2010) determined that higher quality sites (high SIs) may sequester more C over time, which is consistent with our results. Therefore, potential C sequestration could be further maximized by focusing on higher quality sites; in this case high SIs and lower elevation sites (Figure 4.3).

In southern Appalachian spruce-fir forests, management which aims to reduce the occurrence or severity of disturbance can help moderate the fluctuation of C losses over

time. For example, the probability for recurrence of the non-native BWA might be minimized by maintaining lower stocking levels of suitable host (Fraser fir) thereby lowering insect hazard. Although the no-action scenario appears desirable in terms of TC, this comes with the increased probability of future BWA mortality and the associated C release that would ultimately threaten the long-term effectiveness of the no-action strategy for sequestering C. The same reasoning has been applied to southwestern forests threatened by wildfire. Hurteau *et al.,* (2008) suggested maintaining low ponderosa pine (*Pinus ponderosa* Dougl.) stand densities via thinning and prescribed fire to reduce the risk of wildfire and subsequent release of large amounts of C into the atmosphere. Indeed, large-scale disturbances, although they occur at longer intervals, have the potential to drastically change C dynamics in forested systems. In particular, the effect of climate change-induced shifts in forest stand dynamics or disturbance processes on Appalachian spruce-fir C dynamics is a topic for future study.

Historically, spruce-fir forests may have been C neutral or near-neutral as forest growth, mortality, and soil respiration fluctuated over time. Using *in situ* C estimates, Van Miegroet *et al.,* (2007) found the NDW spruce-fir forest exhibited near-neutral ecosystem C over a 10-year period (1993–2003). The discrepancy between C neutrality observed by Van Miegroet *et al.,* (2007) and these results, which suggest C is accumulating, is likely a result of precluding soil C dynamics in our modeling. Changes in soil C are very difficult to estimate and there are few studies that document soil C dynamics even though it is a large forest C pool (Van Miegroet *et al.,* 2007; Birdsey, 1992), which might explain why soil C models such as Yasso (Liski *et al.,* 2005) are not yet supported in FVS. Van Miegroet *et al.* (2007) found soil C comprised >50% of

ecosystem C in our study area. Changes in soil C dynamics due to management actions (e.g., thinning) might alter interpretations of C sequestration potential, especially considering possible differences between active harvesting and no-action scenarios (Jandl *et al.*, 2007). However, based on reviews of various disturbance regimes, including forest management strategies, soils were found to be generally less responsive to disturbance compared to the forest floor (Jandl *et al.*, 2007; Van Miegroet and Olsson, 2011). In general, soil C changes tend to be large near the surface and diminish with depth depending on management-related disturbances to the soil (Jandl *et al.*, 2007). With minimal soil disturbance both the no-action and uneven-aged scenario would reduce soil C loss over time compared to the even-aged scenario, which necessitates a regeneration harvest at the end-of-rotation. However, labile soil C after regeneration harvest under the even-aged scenario is likely to return to pre-harvest conditions in a relatively short time period (Jandl *et al.*, 2007).

Management Implications

To mitigate the effects of climate change a diverse set of strategies will have to be implemented. One very important and effective strategy is silvicultural intervention that enhances the rate of forest C sequestration by actively managing forest stands. We have shown that silviculture can increase C sequestration rates in a southern Appalachian spruce-fir forest, and suggest similar outcomes could be achieved in other forest types, particularly more productive types. In general, results from our simulations are consistent with Hoover and Heath (2011), who proposed that stocking management could considerably increase C sequestration on a regional basis (northeast US). Our analysis

further demonstrated the tools and carbon accounting protocol that any silviculturist could use to model the effect of silvicultural activities on aboveground C sequestration. FVS is easily accessible, readily available to land managers and is part of a nationally supported framework. We suggest that FVS-FFE could be used in a variety of applications to evaluate whether active management may be a better strategy than passive management for aboveground C sequestration. Finally, we have demonstrated that whether the objective of additionality can be met is potentially influenced by: (1) the C accounting method (*i.e.*, TC *versus* AAC); (2) the carbon-community dictated planning horizon of 100 years; (3) whether or not long-term storage (*i.e.*, solid wood products) is considered. Therefore, silviculturists wishing to evaluate C sequestration potential would do well to consider these factors before evaluating the efficacy of their treatments.

LITERATURE CITED

Barker, M., Van Miegroet, H., Nicholas, N.S. and Creed, I.F. 2002 Variation in overstory nitrogen uptake in a small, high-elevation southern Appalachian spruce-fir watershed. *Can. J. For. Res.* **32**:1741–1752.

Birdsey, R.A. 1992 *Carbon Storage and Accumulation in United States Forest Ecosystems*; USDA Forest Service, Washington Office (GTR-WO-59): Washington, DC, USA, p. 51.

Broekhoff, D., Nickerson, J. and Raven, H. 2009 *Forest Project Protocol*, Version 3.1; Climate Action Reserve: Los Angeles, CA, USA.

Crookston, N.L. and Dixon, G.E. 2005 The forest vegetation simulator: A review of its structure, content, and applications. *Comput. Electron. Agric.* **49**:60–80.

Dixon, G.E. 2002 Essential FVS: A user's guide to the Forest Vegetation Simulator. US Forest Service, Forest Management Service Center: Fort Collins, CO, USA, p. 208. Available online: www.fs.fed.us/fmsc/fvs/documents/userguides.shtml (accessed on 21/2/2012).

DeRose, R.J., Shaw, J.D., Vacchiano, G. and Long, J.N. 2008 Improving longleaf pine mortality predictions in the Southern Variant of the Forest Vegetation Simulator. In *Third Forest Vegetation Simulator Conference*; USDA Forest Service, Rocky Mountain Research Station (RMRS-P-54): Fort Collins, CO, USA.

Drew, T.J. and Flewelling, J.W. 1977 Some recent Japanese theories of yield-density relationships and their application to Monterey pine plantations. *For. Sci.* **23**:517–534.

Dull, C.W., Ward, J.E., Brown, H.D., Ryan, G.W., Clerke, W.H. and Uhler, R.J. 1988 *Evaluation of Spruce and Fir Mortality in the Southern Appalachian Mountains*; USDA Forest Service Southern Region(R8): Atlanta, GA, USA.

Fahey, T.J., Woodbury, P.B., Battles, J.J., Goodale, C.L., Hamburg, S.P., Ollinger, S.V. and Woodall, C.W. 2010 Forest carbon storage: Ecology, management, and policy. *Front. Ecol. Environ*. **8**:245–252.

Harmon, M.E. and Marks, B. 2002 Effects of silvicultural practices on carbon stores in Douglas-fir-western hemlock forests in the Pacific Northwest, USA: Results from a simulation model. *Can. J. For. Res.* **32**:863–877.

Herring, N.D. 2007 Sensitivity Analysis of the Forest Vegetation Simulator Southern Variant (FVS-SN) for Southern Appalachian Hardwoods. M.S. Thesis, Virginia Polytechnic Institute, Blacksburg, VA, USA.

Hoover, C.M. 2008 *Field Measurements for Forest Carbon Monitoring: A Landscape-Scale Approach*; Springer: New York, NY, USA.

Hoover, C.M. and Heath, L.S. 2011 Potential gains in C storage on productive forestlands in the northeastern United States through stocking management. *Ecol. Appl*. **21**:1154–1161.

Hoover, C.M. and Rebain, S.A. 2011 Forest carbon estimation using the Forest Vegetation Simulator: Seven things you need to know. USDA Forest Service, Northern Research Station (GTR-NRS-77): Newtown Square, PA, USA.p. 20. Available online: htpp://www.treesearch.fs.fed.us/pubs/37449 (accessed on 21/2/2012).

Huang, C.H. and Sorenson, C. 2011 The economic value of selling carbon credits from restored forests: A case study from the Navajo Nation's tribal forests. *West. J. Appl. For*. **26**:37–45.

Hurteau, M.D., Koch, G.W. and Hungate, B.A. 2008 Carbon protection and fire risk reduction: Toward a full accounting of forest carbon offsets. *Front. Ecol. Environ*. **6**:493–498.

Hurteau, M. and North, M. 2009 Fuel treatment effects on tree-based forest carbon storage and emission under modeled wildfire scenarios. *Front. Ecol. Environ*. **7**:409–414.

Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkkinen, K. and Byrne, K.A. 2007 How strongly can forest management influence soil carbon sequestration? *Geoderma*. **137**:253–268.
Johnson, D.W., Van Miegroet, H., Lindberg, S.E. and Todd, D.E. 1991 Nutrient cycling in red spruce forests of the Great Smokey Mountains. *Can. J. For. Res*. **21**:769–787.

Keyser, C.E. 2008 Southern (SN) Variant Overview Forest Vegetation Simulator. US Forest Service, Forest Management Service Center: Fort Collins, CO, USA. p. 68. Available online: www.fs.fed.us/fmsc/fvs/documents/userguides.shtml (accessed on 21/2/2012).

Keyser, T.L. 2010 Thinning and site quality influence aboveground tree carbon stocks in yellow-poplar forests of the southern Appalachians. *Can. J. For. Res*. **40**:659–667.

Kolari, P., Pumpanen, J., Rannik, U., Hanni, I., Hari, P. and Berninger, F. 2004 Carbon balance of different aged Scots pine forests in southern Finland. *Glob. Change Biol.* **10**:1106–1119.

Korstian, C.F. 1937 Perpetuation of spruce on cut-over and burned lands in the higher southern Appalachian. *Ecol. Monogr*. **7**:125–167.

Liski, J., Palosuo, T., Peltoniemi, M. and Sievanen, R. 2005 Carbon and decomposition model Yasso for forest soils. *Ecol. Mod*. **189**:168–182.

Long, J.N. 1985 A practical approach to density management. *For. Chron*. 61:23–27.

Long, J.N. and Shaw, J.D. 2010 The influence of compositional and structural diversity on forest productivity. *Forestry*. **83**:121–128.

Long, J.N. and Smith, F.W. 1984 Relation between size and density in developing stands: A description and possible mechanisms. *For. Ecol. Manag*. **7**:191–206.

Luyssaert, S., Schulze, E.D., Borner, A., Knohl, A., Hessenmoller, D., Law, B.E., Philippe, C. and Grace, J. 2008 Old-growth forests as global carbon sinks. *Nature*. **455**:213–215.

Malmshimer, R.W., Bowyer, J.L., Fried, J.S., Gee, E., Izlar, R.L., Reid, R.A., Munn, I.A., Oneil, E. and Stewart, W.C. 2011 Managing forests because carbon matters: Integrating energy, products, and land management policy. *J. For*. **109**:S7–S50.

McCracken, R.J., Shanks, R.E. and Clebsch, E.E.C. 1962 Soil morphology and genesis at higher elevations of the Great Smoky Mountains. *Soil Sci. Soc. Am. Proc*. **26**:384–388.

Metz, B., Davidson, O.R., Bosch, P.R., Dave, R. and Meyer, L.A. 2007 *Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*; Cambridge University Press: New York, NY, USA.

Miner, R. 2006 The 100-year method for forecasting carbon sequestration in forest products in use. *Mitig. Adapt. Strateg. Glob. Change*. doi: 10.1007/s11027-006-4496-3.

Nicholas, N.S. 1992 Stand Structure, Growth and Mortality in Southern Appalachian Spruce-Fir. Ph.D. Thesis, Department of Forestry, Virginia Polytechnic Institute and State University: Blacksburg, VA, USA.

Nicholas, N.S. and Zedaker, S.M. 1992 Expected stand behavior: Site quality estimation for southern Appalachian red spruce. *For. Ecol. Manag*. **47**:39–50.

Odum, E.P. 1969 The strategy of ecosystem development. *Science*. 164:262–270.

Pauley, E.F. and Clebsch, E.E.C. 1990 Patterns of *Abies fraseri* in a Great Smoky Mountains spruce fir forest. *Bull. Torr. Bot. Club*. **117**:375–381.

Pearson, T.R.H., Brown, S.L. and Birdsey, R.A. 2007 *Measurement Guidelines for the Sequestration of Forest Carbon*; USDA Forest Service (GTR-NRS-18): Newtown Square, PA, USA. Available online: http://www.treesearch.fs.fed.us/pubs/13292 (accessed on 21/2/2012).

Penman, D., Kruger, I., Galbally, T., Hiraishi, B., Nyenzi, S., Emmanul, L., Buendia, R., Hoppaus, T., Martinsen, J., Meijer, T., Miwa, T. and Tanabe, K. editors. 2000 *Intergovernmental Panel on Climate Change, Good Practice Guidance*; J. IPCC national greenhouse gas inventories programme. Institute for Global Environmental Strategies, Hayama, Kanagawa, Japan. Available online: http://www.ipcc-nggip.iges.or.jp/public/gp/english/index.html (accessed on 21/2/2012).

Perez-Cruzado, C., Mohren, G.M.J., Merino, A. and Rodriguez-Soalleiro, R. 2012 Carbon balance for different management practices for fast growing tree species planted on former pastureland in southern Europe: A case study using the CO_2Fix model. *Eur. J. For. Res.* **131**:1695-1716.

Pyle, C. 1988 The type and extent of anthropogenic vegetation disturbance in the Great Smoky Mountains before National Park Service acquisition. *Castanea*. 53:183–196. Regional Greenhouse Gas Initiative. Available online: http://www.rggi.org (accessed on 21/2/2012).

Reinhardt, E.D., Crookston, N.L. and Rebain, S.A. 2007 The fire and fuels extension to the forest vegetation simulator. USDA Forest Service, Rocky Mountain Research Station (RMRS-GTR-116): Ogden, UT, USA. p. 220. Available online: http://www.fs.fed.us/rm/pubs/rmrs_gtr116.html (accessed on 21/2/2012).

Ryan, M.G., Harmon, M.E., Bridsey, R.A., Giargina, C.P., Heath, L.S., Houghton, R.A., Jackson, R.B., McKinley, D.C., Morrison, J.F. and Murray, B.C. 2010 A synthesis of the science on forests and carbon for U.S. forests. *Ecol. Soc. Am. Issue Ecol*. **13**:1–16.
Shanks, R.E. 1954 Climates of the Great Smoky Mountains. *Ecology*. **35**:353–361.

Skog, K. and Nicholson, G. 1998 Carbon cycling through wood products: The role of wood and paper products in carbon sequestration. *For. Prod. J*. **48**:75–83.

Smith, D.M., Larson, B.C., Kelty, M.J. and Ashton, P.M.S. 1997. *The Practice of Silviculture: Applied Forest Ecology*, 9th ed. John Wiley & Sons: New York, NY, USA.

Smith, J.E., Heath, L.S., Skog, K.E. and Birdsey, R.A. 2006 Methods for calculating forest ecosystem and harvested carbon with standard estimates for forest types of the United States. USDA Forest Service Northeastern Research Station (GTR-NE-343): Newtown Square, PA, USA. p. 216. Available online: http://www.treesearch.fs.fed.us/pubs/22954 (accessed on 21/2/2012).

Sorenson, C.D., Finkral, A.J., Kolb, T.E. and Huang, C.H. 2011 Short- and long-term effects of thinning and prescribed fire on carbon stocks in ponderosa pine stands in northern Arizona. *For. Ecol. Manag*. **261**:460–472.

Vacchiano, G., Shaw, J.D., DeRose, R.J. and Long, J.N. 2008 Inventory-based sensitivity analysis of the large tree diameter growth submodel of the Southern Variant of FVS. In *Third Forest Vegetation Simulator Conference*; USDA Forest Service, Rocky Mountain Research Station (RMRS-P-54): Fort Collins, CO, USA.

Van Deusen, P. 2010 Carbon sequestration potential of forest land: Management for products and bioenergy *versus* preservation. *Biomass Bioenergy*. **34**:1687–1694.

Van Deusen, P. and Heath, L.S. 2012 *COLE Web Applications Suite*; NCASI and USDA Forest Service, Northern Research Station, USA. Available only on the internet: http://www.ncasi2.org/COLE/ (accessed on 21/2/2012).

Van Miegroet, H., Johnson, D.W. and Todd, D.E. 1993 Foliar response of red spruce saplings to fertilization with Ca and Mg in the Great Smoky Mountains National Park. *Can. J. For. Res*. **23**:89–95.

Van Miegroet, H., Moore, P.T., Tewksbury, C.E. and Nicholas, N.S. 2007 Carbon sources and sinks in high-elevation spruce-fir forests of the southeastern US. *For. Ecol. Manage.* **238**:249–260.

Van Miegroet, H. and Olsson, M. 2011 Ecosystem disturbance and soil organic carbon—A review. In *Soil Carbon in Sensitive European Ecosystems: From Science to Land Management*; Jandl, R., Rodeghiero, M., Olsson, M., Eds. John Wiley & Sons Ltd.: West Sussex, UK.

Zedaker, S.M. and Nicholas, N.S. 1990 *Quality Assurance and Methods Manual for Forest Site Classification and Field Measurements*; EPA/600/3-90/082; U.S. Environmental Protection Agency: Corvallis, OR, USA. pp. 44–45.

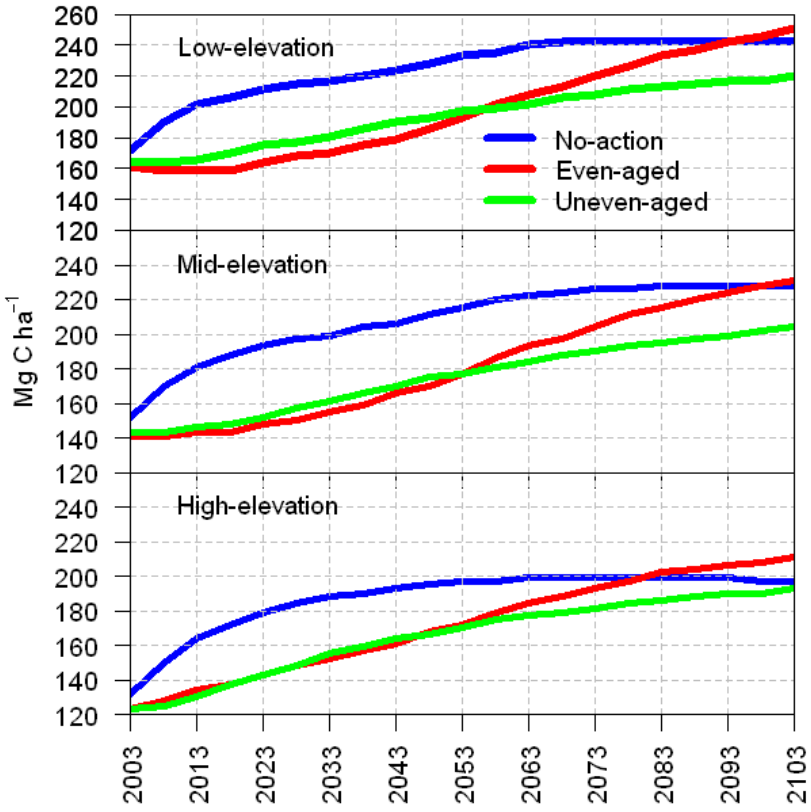

Figure 4.1. Total aboveground C sequestered (Mg ha^{-1}) for three elevation groups as a result of no-action, even-aged management and uneven-aged management in a southern Appalachian forest.

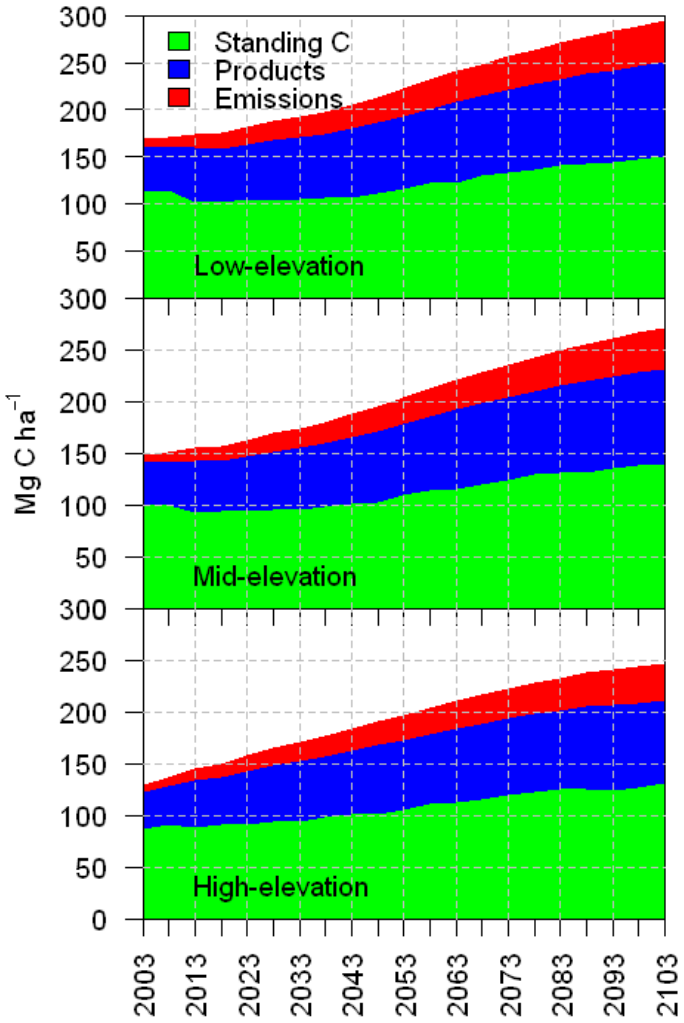

Figure 4.2. Cumulative aboveground live C, C stored in forest products and C released as emissions (Mg ha^{-1}) for three elevation groups under the even-aged management scenario.

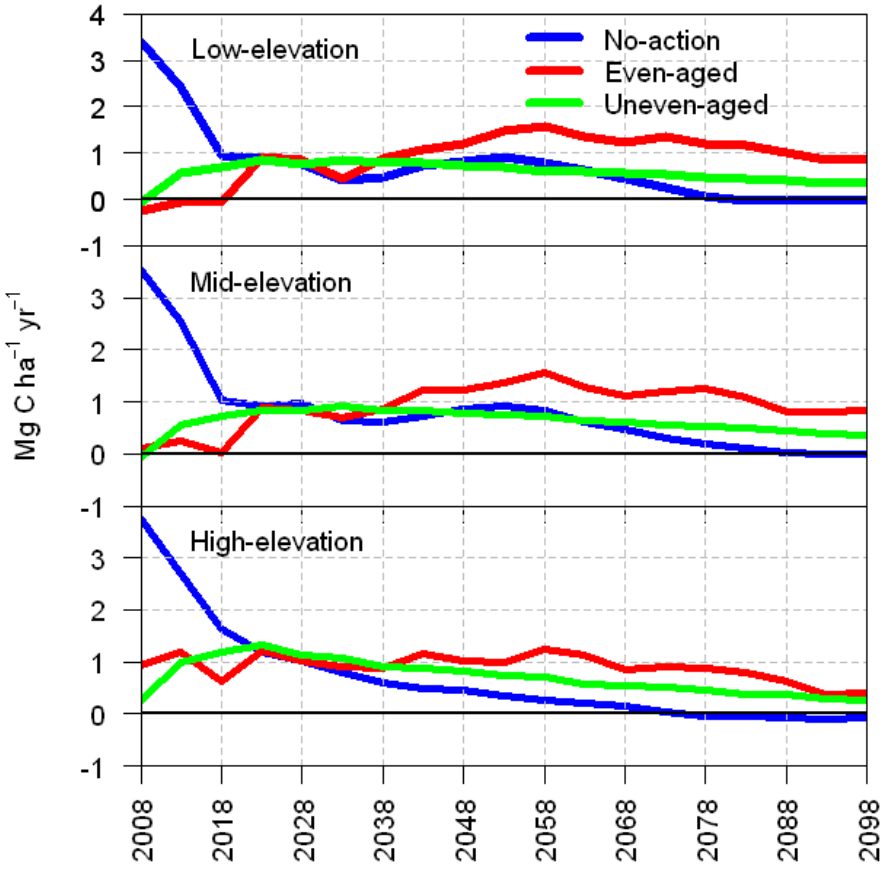

Figure 4.3. Average annual change in aboveground C (AAC; Mg ha^{-1} yr^{-1}) for three elevation groups as a result of no-action, even-aged management and uneven-aged management in a southern Appalachian forest.

CHAPTER 5

SUMMARY AND CONCLUSIONS

Using multiple approaches, a variety of ecosystem services were explored in this heavily disturbed southern Appalachian spruce fir forest. Specifically, forest structure, function, nitrogen cycling and carbon sequestration were assessed. Though the future interaction between the BWA and Fraser fir remains to be seen, this forest is on a trajectory towards recovery of forest structure and the reallocation of biomass into standing live trees of the historically predominant species. A total forest inventory and the development of site specific allometric equations demonstrated that this forest has recovered productivity and that the forest understory is responsible for the uptake of a disproportionately large amount of nitrogen. The active management of these forests was shown to be a tool for sequestering carbon in the long term as well as reducing risk of disturbance from insects in the shorter term. Though the effects of the BWA on this forest were catastrophic, southern Appalachian spruce-fir forests have retained the ability to recover.

FOREST TRAJECTORY

Our measurements of stand structure and changes in forest biomass suggest that this forest in on a trajectory towards recovery of historic stand structure and function. We found little evidence to support hypotheses of either an expansion of *Betula* or other hardwoods across our elevation gradient, an increase in dominance of *Picea* at higher elevations, nor the elimination of *Abies* from this forest. Though this forest was heavily disturbed by the BWA, current stand structure suggests that this forest is recovering with

a significant and stable composition of both spruce and fir. The potential effects of the BWA on current populations of Fraser fir will tell us much about the future of this sensitive forest type.

Nitrogen Cycling

A total forest inventory of this southern Appalachian spruce fir forest has indicated that forest processes such as productivity have recovered. Our estimates of productivity are similar to pre-adelgid levels. The contribution of the forest understory to processes such as nitrogen cycling and retention was surprisingly high, suggesting that forest understory vegetation may be more important to these processes than was previously thought. We detected a unique mechanism where in the absence of an intact overstory, forest understory vegetation can compensate by cycling and retaining nitrogen that would otherwise leach offsite and contribute to water quality degradation downstream. Indeed the understory of this forest provides an important service in nitrogen cycling.

Carbon Sequestration

An application of the Forest Vegetation Simulator has demonstrated that silvicultural manipulation can provide increased carbon sequestration when compared to a no action alternative. This suggests that active management of our forest resources may prove to be an effective tool in mitigating the effects of atmospheric carbon dioxide on global climate change. Though it took nearly the entire 100 year simulation period to show the effects of management on levels of total aboveground carbon, the annualized rate of carbon sequestration (AAC) demonstrated the benefits of active management within 20

years. Decadent forests with stable levels of total carbon would more likely show a more dramatic effect of management on total carbon as well annualized rate of carbon sequestration. This research demonstrates the potential contribution of forests to addressing climate change and quantifies their carbon sequestration services.

LOOKING FORWARD

Land management agencies (primarily the National Park Service and United States Forest Service) charged with the stewardship of these forests have challenging decisions ahead of them. Agencies can choose to do little to accelerate the recovery of these forests from the non-native BWA or they can decide to take steps to return these forests to their historic structure and function. By neglecting to make a decision, agencies are choosing the former alternative and allowing a sensitive forest to remain in an unnatural condition.

With the lack of active management these forests will slowly approach historic structure and function, though this may take hundreds of years. Nitrogen retention will stabilize at a maximum and the role of the understory may diminish as productivity shifts to the overstory. This forest will become carbon neutral within 50 years. Without action, another possibility includes the potentially significant effects of the BWA. With a high proportion of fir in the understory, these forests are at high risk for future and chronic BWA infestations that will make a return to historic conditions unlikely.

Active management, similar to the uneven-aged silvicultural activities described in Chapter 4, would accelerate the recovery of forest structure and function dramatically. The 10 million visitors annually to GSMNP would experience a forest more similar to historic conditions than without action. Continued thinnings would maintain understory

productivity and would contribute to net C sequestration far into the future due to the contribution of harvested products. Treatments focused on minimizing stand level BWA hazard while maintaining individual tree vigor would create conditions less susceptible to future BWA infestations. Regardless of their decision, it is recommended that agencies take a deliberate course of action.

APPENDIX

March 19, 2013

Patrick T. Moore
Dixie National Forest
1789 North Wedgewood
Cedar City, Utah 84720

Dear R. Justin DeRose,

I am preparing my dissertation to obtain a Ph.D. in the Department of Wildland Resources at Utah State University. I hope to complete my degree in May 2013. I am requesting your permission to include the articles co-authored by you as shown. You will be cited as a co-author on the title page of the chapter for which you are a co-author. Please indicate your approval of this request by signing in the space provided below. If you have any questions, please contact me.

Thank you for your cooperation,
Patrick T. Moore

I, R. Justin DeRose, hereby give permission to Patrick T. Moore to reprint the following material in his dissertation:

Moore, P.T., R.J. DeRose, J. Long and H. Van Miegroet. 2012. Using silviculture to influence carbon sequestration in southern Appalachian spruce-fir forests. Forests 3:300-316. doi:10.3390/f3020300

Signed _____

Date 3/19/2013

March 19, 2013

Patrick T. Moore
Dixie National Forest
1789 North Wedgewood
Cedar City, Utah 84720

Dear Niki Nicholas,

I am preparing my dissertation to obtain a Ph.D. in the Department of Wildland Resources at Utah State University. I hope to complete my degree in May 2013. I am requesting your permission to include the articles co-authored by you as shown. You will be cited as a co-author on the title page of the chapter for which you are a co-author. Please indicate your approval of this request by signing in the space provided below. If you have any questions, please contact me.

Thank you for your cooperation,
Patrick T. Moore

I, Niki Stephanie Nicholas, hereby give permission to Patrick T. Moore to reprint the following material in his dissertation:

Moore, P.T., H. Van Miegroet and N.S. Nicholas. 2008. Examination of forest recovery scenarios in a southern Appalachian Picea-Abies forest. Forestry 81(2): 183-194

Moore, P.T., H. Van Miegroet and N.S. Nicholas. 2007. Relative role of understory and overstory in carbon and nitrogen cycling in a southern Appalachian spruce-fir forest. Canadian Journal of Forest Research 37:2689-2700.

Signed Niki Stephanie Nicholas

Date March 27 2013

Marsha Bailey

From: Moore, Patrick T -FS [ptmoore@fs.fed.us]
Sent: Monday, April 01, 2013 2:59 PM
To: Marsha Bailey
Subject: permission chapter 2

The journal that published chapter 2 has this on their website:

Rights retained by ALL Oxford Journal Authors

- The right, after publication by Oxford Journals, to use all or part of the Article and abstract, for their own personal use, including their own classroom teaching purposes;
- The right, after publication by Oxford Journals, to use all or part of the Article and abstract, in the preparation of derivative works, extension of the article into book-length or in other works, provided that a full acknowledgement is made to the original publication in the journal;
- **The right to include the article in full or in part in a thesis or dissertation, provided that this not published commercially**;

For the uses specified here, please note that there is no need for you to apply for written permission from Oxford University Press in advance. Please go ahead with the use ensuring that a full acknowledgment is made to the original source of the material including the journal name, volume, issue, page numbers, year of publication, title of article and to Oxford University Press and/or the learned society.

I am assuming that I do not need permission for that one either...

Marsha Bailey

From:	Moore, Patrick T -FS [ptmoore@fs.fed.us]
Sent:	Monday, April 01, 2013 4:20 PM
To:	Marsha Bailey
Subject:	permission chapter 3,
Attachments:	Format and Style Form PTMoore.pdf

The permission page for the chapter 3 journal states that I have retained the right to reuse my chapter 4 by my interpretation of #4 below...

Authors' rights

As of 2009, copyright in all articles in NRC Research Press journals remains with the authors. All articles published previously are copyright Canadian Science Publishing (which operates as NRC Research Press) or its licensors (also see our Copyright information).

Under the terms of the license granted to NRC Research Press, authors retain the following rights:

1. To post a copy of their submitted manuscript (pre-print) on their own Web site, an institutional repository, or their funding body's designated archive (no embargo period).
2. To post a copy of their accepted manuscript (post-print) on their own Web site, an institutional repository, or their funding body's designated archive (no embargo period). Authors who archive or self-archive accepted articles are asked to provide a hyperlink from the manuscript to the Journal's Web site.
3. Authors, and any academic institution where they work at the time, may reproduce their manuscript for the purpose of course teaching.
4. **Authors may reuse all or part of their manuscript in other works created by them for noncommercial purposes, provided the original publication in an NRC Research Press journal is acknowledged through a note or citation**.

Creative Commons

Creative Commons License Deed

Attribution 3.0 Unported (CC BY 3.0)

This is a human-readable summary of the Legal Code (the full license).
Disclaimer

You are free:

to Share — to copy, distribute and transmit the work

to Remix — to adapt the work

to make commercial use of the work

Under the following conditions:

Attribution — You must attribute the work in the manner specified by the author or licensor (but not in any way that suggests that they endorse you or your use of the work).

With the understanding that:

Waiver — Any of the above conditions can be waived if you get permission from the copyright holder.

Public Domain — Where the work or any of its elements is in the public domain under applicable law, that status is in no way affected by the license.

Other Rights — In no way are any of the following rights affected by the license:

- Your fair dealing or fair use rights, or other applicable copyright exceptions and limitations;
- The author's moral rights;
- Rights other persons may have either in the work itself or in how the work is used, such as publicity or privacy rights.

- **Notice** — For any reuse or distribution, you must make clear to others the license terms of this work. The best way to do this is with a link to this web page.

VITA

Patrick Terrence Moore

EDUCATION

Ph.D.	2013	Ecology	Utah State University
M.S.	2006	Forestry	Southern Illinois University
B.S.	1998	Biology	Maryville University

PUBLICATIONS

Moore, P.T., R.J. DeRose, J. Long and H. Van Miegroet. 2012. Using silviculture to influence carbon sequestration in southern Appalachian spruce-fir forests. Forests, 3:300-316, doi:10.3390/f3020300

Moore, P.T., H. Van Miegroet, and N.S. Nicholas. 2008. Examination of forest recovery scenarios in a southern Appalachian *Picea-Abies* forest. Forestry 81(2):183-194.

Moore, P.T., H. Van Miegroet, and N.S. Nicholas. 2007. Relative role of understory and overstory in carbon and nitrogen cycling in a southern Appalachian spruce-fir forest. Canadian Journal of Forest Research. 37:2689-2700.

Van Miegroet, H., **P.T. Moore**, C. Tewksbury, and N.S. Nicholas. 2007. Carbon sources and sinks in high-elevation spruce-fir forests in the Southeastern US. Forest Ecology and Management 238: 249-260.

PROFESSIONAL EXPERIENCE

Supervisory Forester, Dixie National Forest. 1/2011-present

Area Forester, Utah Division of Forestry, Fire and State Lands. 9/2006-1/2011